Systematic Review of the Rhesus Macaque, *Macaca mulatta* (Zimmermann, 1780)

Jack Fooden
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Systematic Review of the Rhesus Macaque, *Macaca mulatta* (Zimmermann, 1780)

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Systematic Review of the Rhesus Macaque, *Macaca mulatta* (Zimmermann, 1780)

Jack Fooden

**Abstract**

The rhesus macaque, *Macaca mulatta* (Zimmermann, 1780), is systematically reviewed, based on examination of 638 museum specimens, observation of natural populations, and survey of relevant literature. The natural distribution of *M. mulatta* extends from eastern Afghanistan and western India to eastern China and northern Vietnam. This review includes analyses of geographic variation in pelage characters, external measurements and proportions, cranial characters, molecular biology and genetics, and physiology and disease. Information also is presented concerning natural history, reproduction, and paleontology. Taxonomically, local and regional populations are regarded as inadequately differentiated to warrant recognition of subspecies in *M. mulatta*. A hypothesis is proposed to explain the evolution and dispersal of this species. In an appendix, an annotated gazetteer lists 1,239 localities where *M. mulatta* has been collected or observed.

**Introduction**

The rhesus macaque, *Macaca mulatta* (Zimmermann, 1780), probably is the most intensively studied species of non-human primate (see, e.g., Primate Information Center, 1998, p. 27). The present systematic review of *M. mulatta* is based on examination of 638 museum specimens (Appendix 1); observation of natural populations in India, Thailand, and China; and survey of relevant literature. The principal subjects covered in this review are geographic variation in characters; natural history, reproduction, and paleontology; taxonomy; and evolution and dispersal. Specimens examined are preserved in the following institutions (number of specimens in parentheses), which hereafter are cited by means of the indicated abbreviations:

<table>
<thead>
<tr>
<th>Institution</th>
<th>Location</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>American Museum of Natural History, New York</td>
<td>53</td>
</tr>
<tr>
<td>ANSP</td>
<td>Academy of Natural Sciences, Philadelphia</td>
<td>8</td>
</tr>
<tr>
<td>BMNH</td>
<td>Beijing Museum of Natural History, Beijing</td>
<td>7</td>
</tr>
<tr>
<td>BM(NH)</td>
<td>British Museum (Natural History), London</td>
<td>122</td>
</tr>
<tr>
<td>BNHS</td>
<td>Bombay Natural History Society, Mumbai</td>
<td>39</td>
</tr>
<tr>
<td>CTNRC</td>
<td>Centre for Thai National Reference Collections, Thailand Institute of Scientific and Technological Research, Bangkok</td>
<td>1</td>
</tr>
<tr>
<td>FCXM</td>
<td>Forestry College of Vietnam, Xuan Mai</td>
<td>5</td>
</tr>
<tr>
<td>FDCG</td>
<td>Forestry Designing Centre of Guangxi, Nanning</td>
<td>8</td>
</tr>
<tr>
<td>FMNH</td>
<td>Field Museum of Natural History, Chicago</td>
<td>23</td>
</tr>
<tr>
<td>FUBD</td>
<td>Fudan University, Biology Department, Shanghai</td>
<td>2</td>
</tr>
<tr>
<td>HUBD</td>
<td>Hangzhou University, Biology Department, Hangzhou</td>
<td>1</td>
</tr>
<tr>
<td>IEWR</td>
<td>Institute of Ecology and Biological Resources, Hanoi</td>
<td>38</td>
</tr>
<tr>
<td>IRSN</td>
<td>Institut Royal des Sciences Naturelles de Belgique, Brussels</td>
<td>3</td>
</tr>
<tr>
<td>IZCAS</td>
<td>Institute of Zoology, Chinese Academy of Sciences, Beijing</td>
<td>47</td>
</tr>
<tr>
<td>KIZ</td>
<td>Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming</td>
<td>28</td>
</tr>
<tr>
<td>MCZ</td>
<td>Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts</td>
<td>8</td>
</tr>
</tbody>
</table>

FIELDIANA: ZOOLOGY, N.S., NO. 96, JUNE 30, 2000, PP. 1–180
Fig. 1. Known locality records of *Macaca mulatta*; specimens examined include living monkeys personally observed in the field. For details, see Figures 2A–C.

MZB  Museum Zoologicum Bogoriense, Bogor (1)
MNHN  Muséum National d’Histoire Naturelle (Mammifères), Paris (15)
NHMB  Naturhistorisches Museum, Basel (2)
NWPIB  Northwest Plateau Institute of Biology, Chinese Academy of Sciences, Xining (6)
P-CM  Powell-Cotton Museum, Birchington, Kent (2)
RMNH  National Museum of Natural History, Leiden (2)
SCIEA  South China Institute of Endangered Animals, Guangzhou (23)
SIZ  Shaanxi Institute of Zoology, Xi’an (4)
SMNH  Shanghai Museum of Natural History, Shanghai (54)
UPS  University of Puget Sound, Tacoma (1)
USNM  National Museum of Natural History, Washington, D.C. (39)
ZMB  Zoologisches Museum des Humboldt-Universität, Berlin (6)

ZMNH  Zhejiang Museum of Natural History, Hangzhou (2)
ZMVNU  Zoological Museum, Vietnam National University, Hanoi (47)
ZRC  Zoological Reference Collection, Department of Zoology, National University of Singapore (6)
ZSBS  Zoologisches Sammlung des Bayerischen Staates, Munich (1)
ZSI  Zoological Survey of India, National Zoological Collection, Calcutta (25)
—  Private collections (9)

**Geographic Distribution and Current Population Estimates**

*Macaca mulatta* inhabits parts of 11 countries in southern and southeastern Asia (Figs. 1, 2, 21), from ca. 15°N (in India, Thailand, Laos, and Vietnam) to ca. 36°N (in Afghanistan, Pakistan, India,
Table 1. Estimated population of *Macaca mulatta* in five countries for which data are available.1

<table>
<thead>
<tr>
<th>Country</th>
<th>Population estimate (× 1,000)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Afghanistan</td>
<td>&gt;4</td>
<td>Puget, 1971, p. 199</td>
</tr>
<tr>
<td>Bangladesh</td>
<td>190–276</td>
<td>Gittins &amp; Akonda, 1982, p. 277; Feeroz et al., 1995, p. 75</td>
</tr>
<tr>
<td>India</td>
<td>&gt;500</td>
<td>Southwick &amp; Siddiqi, 1995, p. 19</td>
</tr>
<tr>
<td>Vietnam</td>
<td>20</td>
<td>Dang, 1983, p. 1284</td>
</tr>
<tr>
<td>Total</td>
<td>&gt;919</td>
<td></td>
</tr>
</tbody>
</table>


and China) and from ca. 70°E (in Afghanistan and India) to ca. 120°E (in China). An isolated population that formerly occurred at 40°24′N in northeastern China apparently was extirpated in 1987 (Zhang et al., 1989, p. 380). The natural range of *M. mulatta* is known to include 12 shallow-water islands—one off the coast of southeastern Bangladesh (Maishkhali), four off the coast of northeastern Vietnam (Cat Ba, Quan Lan, Van Canh, and Van Hai), and seven off the coast of southeastern China (Hainan, Dahao, Dangan, Erzhou, Xianggang [= Hong Kong], Neilingding, and Shangchuan; the last six of these islands are near the mouth of the Zhujiang [= Pearl River]). Archaeological evidence suggests that ca. 4000 B.P. the range of *M. mulatta* may have extended as far west as Moenjo Daro, Pakistan (27°19′N, 68°07′E) (Mackay, 1931, p. 349; Iyer, 1977, p. 15).

Although the northern limit of natural distribution of *M. mulatta* apparently is determined primarily by physiographic or climatological factors, the southern limit apparently is determined primarily by interspecific competition. The northern limit of distribution is defined by the Great Indian Desert, the north-central limit by the Himalayas and Xizang-Qinghai (Tibetan) Plateau, and the northeastern limit in China by the transition from mesothermal to microthermal climate (Trewartha, 1978, p. 9). Contrastingly, the southwestern limit probably is related to competition with neighboring *M. radiata* (Foodeen et al., 1981, p. 464), and the southeastern limit probably is related to competition with neighboring *M. fascicularis* (Foodeen, 1997, p. 226). The actual distribution of *M. mulatta* is of course much more restricted than indicated above, primarily as a result of human activity (cf. McNeely, 1992, p. 374).

Two rejected locality records—one in Rajasthan, India, and the other in Xizang (= Tibet), China—are outside the limits of distribution of *M. mulatta*, indicated in Figures 1 and 21. In western Rajasthan, Bhargava (1982, p. 7) cited a postal survey report of *M. mulatta* at Babuwali, Jaisalmer District (26°47′N, 69°44′E); subsequently this report was found to be spurious (Bhargava, 1984, p. 43).

In north-central Xizang, south of a pass through the “Dupleix” mountain chain (ca. 33°38′N, 89°43′E), Bonvalot (1891, vol. 1, p. 210; cf. 1892, p. 218) reported a sighting of “monkeys” with external characters suggestive of *M. mulatta*:

Today [18 January 1890] we have seen monkeys crossing the frozen river and playing on the rocks which form its banks. But we cannot kill one of these animals, which are very short with red hair, small head, and an almost imperceptible tail.

According to Professor Feng Zuojian, IZCAS (pers. comm., 27 September 1985), who is an authority on Tibetan mammals, the occurrence of monkeys in this part of the Tibetan Plateau is highly improbable. Professor Feng suspects that Bonvalot actually observed a small group of marmots, presumably *Marmota himalayana* (Zhang et al., 1997, p. 170), which he misidentified as monkeys.

Although populations of *M. mulatta* now inhabit the Mumbai (= Bombay) region of India, this region is outside the natural range of the species; the existing populations in this region (Raj Bhavan compound, ca. 18°56′N, 72°55′E; Borivli National Park, ca. 19°10′N, 72°55′E) are the result of artificial introductions that occurred during World War II (Serra & Amladi, 1979, p. 30). The populations that now inhabit the vicinity of Kouloon, China (ca. 22°20′N, 114°10′E), probably are the result of an artificial introduction that occurred during World War I (Herklotz, 1951, p. 83); how-
Fig. 2A. Detail map of Macaca mulatta localities, western section; for documentation, see Gazetteer, Appendix 2. Abbreviations in parentheses are those used in gazetteer locality codes; specimens examined include living monkeys personally observed in the field.
Afghanistan (A)
1. Asmar, east of; Asmar, northeast of; Barikowt, southeast of; Kamu Valley; Kouelchals, south of; Landay Sind, left bank, near confluence with Kunar R.; Landay Sind, left bank, near Pule Saret; Landay Sind, near Chascoup; Landay Sind, near Merdech; Landay Sind, right bank, between Mandagal and Ormul; Landay Sind, right bank, near Sang e Safed; Landay Sind Valley, near Kamu Valley; Landay Sind Valley, southern slope; Mandagal, northwest of; Nurestan, eastern.
2. Wama, north of.
5. Alicheng River, east of.
6. Ailingar, east of.
7. Outapour, south of.
8. Chigha Sarai, north of.
10. Kotgay (= Cotgai), east of.
11. Chamkani, northeast of.
12. Chamkani, southeast of.

China (C)
1. Gyirong Subcounty.

India (I)
1. Lolab; Lolab Valley.
2. Ovra Sanctuary, proposed.
3. Kotihar India.
4. Ramban Township vicinity.
5. Akknoor; Chowkichora; Jammu; Nandini Wildlife Sanctuary; Narota-Bun, highway between.
7. Surinsar.
8. Kathua vicinity.
9. Ramnagar.
10. Dumel; Jhajjarkotli; Udhampur.
11. Dunwein.
12. Dharmsala; Kangra; Kangra Fort; Samayala.
15. Kasol; Kulu District; Kulu valley; Pulga.
16. Sainj; Sarahan; Tirthan.
17. Narkanda, ca. 1 km north of; Narkanda, ca. 4 km south of; Narkanda, ca. 5 km north of; Rampur, northwest of; Sungri, ca. 2 km south of; Sungri, ca. 4 km north of; Sungri, ca. 6 km northwest of; Sungri, ca. 10 km northwest of; Sungri, ca. 10 km southwest of; Sungri, ca. 15 km southwest of; Sungri, ca. 20 km south-southwest of; Sungri, north of.
18. Boileauganj; Cecil; Chail Sanctuary; Jakko Hill; Kasauli; Kufri, ca. 0.5 km southeast of; Kufri, ca. 1.5 km southeast of; Kufri, ca. 3 km southeast of; Nhera/Tara Devi; Simla, western suburb; Simla vicinity; Simla Water Catchment Reserve; Solon District; View, Simla vicinity.
20. Ambala District.
22. Saraswati Forests.
23. Karnal District.
24. Kurukshetra District; Veer Sontri forests.
25. Saharanpur vicinity.
26. West Timli.
27. Aglar River; Asarori Forest; Dehra Dun; Dehra Dun vicinity; Dehra Dun vicinity, 600 m; Dhaulkot Forest; Hardwar; Kansrao; Mohan; Mussoorie vicinity; Rajaji Wildlife Sanctuary.
28. Tehri-Garhwal District.
29. Kedarnath Sanctuary.
30. Motla.
31. Bageshwar.
32. Haldwani; Hanumangarhi Hill; Kumaun Hills; Naini Tal; Ratighat.
33. Deja; Jhima; Ramganga River; Ramnagar.
34. Bijnor; Sita Bani.
35. Meerut District.
36. Sonarpur District.
37. Kheri Sahi; Panipat-Rhotak, highway between: Rhohtak District.
38. Jind District.
39. Hisar District.
40. Bhiwani District.
41. Delhi; Delhi vicinity; Delhi-Mathura Road; Ghaziaabad District; Lal Kuan; Meetha Pur; Tughlaqabad.
42. Rewari-Putudi-Gurgaon, highway between.
43. Delhi-Agra.
44. Khair.
45. Delhi-Hathras.
46. Bulandshahr District; Delhi-Aligarh.
47. Rampur-Ghaziabad.
49. Makhena.
50. Moradabad vicinity.
51. Pilibhit-Tanakpur.
52. Bareilly; Kurei, west of; Karghena, west of; Ramganga South Station.
53. Shahjahanpur Bareilly, highway between.
54. Sitapur-Bareilly.
55. Haripur.
56. Nishangara; Nishangara vicinity.
57. Shahjahanpur-Lucknow.
58. Lucknow-Sitapur.
59. Gonda vicinity.
60. Ayodhya; Faizabad-Ajodhya; Faizabad vicinity.
61. Balrampur forest.
62. Ayodhya-Gorakhpur.
63. Azamgarh vicinity.
64. Sultanpur vicinity.
65. Lucknow-Faizabad.
66. Halwupura; Kakori; Lucknow vicinity.
67. Sitapur-Shahjahanpur, highway between.
68. Delhi-Kanpur, highway between.
69. Achal Tank; Aliagar; Aliagar vicinity; Bag Garhi Bridge; Barauli Bridge; Barota; Chautara; Chhatari-do-Raha; Harduaiganj; Hathras; Jawan; Nanau; Qasimpur Canal; Sasan; Satha; Sindholi; Sumera; Sumera Fall Jungle.
70. Agra.
71. Mathura; Vrindavan.
73. Alwar District.
74. Bandipul; Sariska Tiger Reserve.
75. Ambagarh Reserve Forest; Amer; Barri Chapal; Gatta; Jaipur.
76. Umri Devi.

(continued on following page)
1. Chaur.
2. Barmedo Mandi; Sukla Phanta.
3. Bilauri.
4. Dhangarhi.
5. Aurn River, ca. 20 km above mouth; Babai River vicinity; Karnali River, ca. 30 km above mouth; Karnali River/Aurn River, ca. 10 km above confluence.
6. Hutu Forest; Pina, forests above.
7. Bheri River.
8. Dudurhani; Simri, Narayani River.
11. Trisuli Bazar, 4 mi (= 6.5 km) southeast of.
12. Bouzini; Gaushalla; Gokarna; Katmandu; Nagarkot; Pashupati; Swayambunath.
13. Chandikholo; Hazaria Patherghatta; Russian Camp; Simri, Birganj Forest District; Singaul.
14. Supplemental Nepalese localities (received too late for inclusion in map; listed in Gazetteer): Balthali, Kavre; Ghodaghodi Tal; Pokhara; Ramnagar; Shanku-Bajrajogini; Tripureswor, Thapathali.

Pakistan (P)
1. Kanti vicinity; Kootai; Kunar River; Mirkhani; Sheshi Koh vicinity; Utzun vicinity.
2. Dokdusra; Gwaldri Valley; Landrai Valley.
3. Swat Kohistan region.
5. Swat River.
6. Bar Chanrai Hill.
7. Pajja Hill.
8. Hazara District, southern.
10. Paia; Paras vicinity; Shogran vicinity.
12. Dunga Gali vicinity; Ghora Dhaka, 1 mi (= 1.6 km) east of; Kazing; Machayara Game Reserve; Murree, outskirts; Nathia Gali; Patriata; Phala/Kutbor Game Reserve.

Nepal (N)
1. Chaur.
2. Barmedo Mandi; Sukla Phanta.
3. Bilauri.
4. Dhangarhi.
5. Aurn River, ca. 20 km above mouth; Babai River vicinity; Karnali River, ca. 30 km above mouth; Karnali River/Aurn River, ca. 10 km above confluence.
6. Hutu Forest; Pina, forests above.
7. Bheri River.
8. Dudurhani; Simri, Narayani River.
11. Trisuli Bazar, 4 mi (= 6.5 km) southeast of.
12. Bouzini; Gaushalla; Gokarna; Katmandu; Nagarkot; Pashupati; Swayambunath.
13. Chandikholo; Hazaria Patherghatta; Russian Camp; Simri, Birganj Forest District; Singaul.
14. Supplemental Nepalese localities (received too late for inclusion in map; listed in Gazetteer): Balthali, Kavre; Ghodaghodi Tal; Pokhara; Ramnagar; Shanku-Bajrajogini; Tripureswor, Thapathali.
ever, this area probably had previously been inhabited by a natural population of *M. mulatta*.

Population estimates are available for *M. mulatta* in Afghanistan, Bangladesh, China, India, and Vietnam—five of the 11 countries inhabited by this species (Table 1). In these countries, the total estimated population is >919,000. Although comparable estimates are not available for Bhutan, Laos, Myanmar, Nepal, Pakistan, and Thailand, the combined area of *M. mulatta* habitat in these six countries is less than in the preceding five (Fig. 1), which probably indicates that the total living population of *M. mulatta* is less than two million. According to reports published in 1995, the population of *M. mulatta* recently has been increasing in India (Southwick & M. F. Siddiqi, 1995, p. 18) and has been decreasing in China (Jiang Haisheng et al., 1995, p. 178).

**Pelage**

**General Characterization**

Dorsal pelage coloration is a key character for species identification of *M. mulatta*. In *M. mulatta*, the fur of the lower back is conspicuously more erythristic than that of the upper back (Fig. 3). In specimens in prime pelage (see “Seasonal Variation,” below), the color of the upper back varies from yellowish gray to golden brown to burnt orange, and the color of the lower back varies correspondingly from golden brown to burnt orange to intense burnt orange (“almost fiery red”; Pocock, 1932, p. 531; cf. Sikorska-Pirowska, 1959, p. 272). On the upper back, the proximal two-thirds of individual dorsal hairs is gray, and the distal one-third is annulated with alternating pale and dark bands, yellowish to golden and blackish (cf. Koppikar & Sabnis, 1976, p. 7); on the lower back, the grayish color of the proximal two-thirds of individual hairs is paler, the pale distal annulations are more erythristic, and the dark distal annulations are more dilute. The crown, nape, and sides of the head are approximately the same color as the adjacent upper back; the anterior edge of the crown is marked by a blackish superciliary streak, and the cheeks often are also fringed with blackish hairs. Crown hairs usually are smoothly directed posteriorly. Hairs on the side of the head usually form a small crest or whorl near the angle of the jaw (infrazygomatic crest; Fooden, 1995, p. 19); occasionally, this crest is elongated and extends upward between the eye and the ear as far as the side of the crown (transzygomatic crest; 44 of 240 specimens examined). The thinly haired facial skin is buffy to reddish, except for the upper eyelids, which are whitish (unpigmented). On the proximal part of the limbs, dorsal pelage is similar in color to that on the adjacent trunk; more distally, the pelage color of the limbs becomes less erythristic and more dilute. The basal one-fourth of the tail is approximately the same color as the adjacent lower back; the distal three-fourths is bicolor, dark brown dorsally and buffy ventrally. The ventral surface of the trunk and limbs is thinly haired, pale buffy to whitish. Broadly distributed areas of sexual skin undergo cyclical changes in color and swelling (see “Reproduction,” below); in adult males, the glans is blue-black (Wilson & Vessey, 1968, p. 5).

The pelage in *M. mulatta* populations at upper elevations (ca. 2400 m) in India apparently is longer and sleeker than in nearby populations at lower elevations (Dodsworth, 1914, p. 730). In captivity, the pelage of dominant individuals, particularly high-ranking males, reportedly is sleeker than that of subordinate individuals (Chance, 1956, p. 5; Waterhouse & Waterhouse, 1971, p. 19). The large amount of grooming received by dominant individuals may contribute to their sleekness.

Abnormally pale “golden” *M. mulatta* individuals reportedly occur in various parts of India and Pakistan at an estimated frequency of 1/10,000 (Pickering & van Wagenen, 1969, p. 161; cf. Anonymous, 1978, p. 12; Kessler et al., 1986, p. 264). Dorsal pelage color in these aberrant individuals is pale yellowish anteriorly and pale reddish-golden posteriorly; the skin is virtually unpigmented, and retinal pigmentation also is reduced. Experimental breeding indicates that the “golden” condition probably is inherited as an autosomal recessive trait. Among specimens examined, a fluid-preserved late fetus or neonate with umbilical cord still attached (BM(NH) 1972.836), collected at Pyaungammaung, Myanmar, 14 May 1915, appears to be of the “golden” phenotype.

**Early Development**

Pelage color in *M. mulatta* neonates is pale brown to dark brown, generally somewhat darker than in adults (Tinklepaugh & Hartman, 1932, p.
Fig. 2B. Detail map of *Macaca mulatta* localities, central section; for documentation, see Gazetteer, Appendix 2. Abbreviations in parentheses are those used in gazetteer locality codes; specimens examined include living monkeys personally observed in the field.
Bangladesh (Ba)
1. Dinajpur District.
2. Rangpur District.
3. Nawabganj vicinity.
5. Madhupur, ca. 100 km west of.
7. Madhupur National Park; Rasulpur vicinity.
8. Madhupur National Park, southern portion.
11. Patharia.
12. Fechugang.
13. Harargaj; Rajkandi; Rema-Kalenga; Srimangal Tea Estate; Srimangal vicinity; Sylhet Forest Division; Tarap; West Bhanagach.
15. Barmi; Borne.
17. Meherpur.
18. Chuadanga.
20. Satkhira.
21. Sundarbans, ca. 50 mi (= 80 km) east of Calcutta.
22. Satkhira, southern.
24. Wazipur.
25. Char mugoria; Madaripur Township.
26. Faridpur District.
27. Bondor; Dhaka; Narayanganj; Sonargaon.
28. Matlab Bazar; Chandpur Bazar, Old; Puran Bazar.
29. Comilla District.
30. Matlab, southeast of.
32. Sitakunda.
33. Chittagong, northern.
34. Chittagong Hill Tracts, northern; Pabakkhal.
35. Chittagong, eastern; Hazarikhil; Kaptai; Kaptai Lake; Satghar; Sitapahar/Rampahar.
36. Chittagong Hill Tracts, eastern.
37. Cox’s Bazar, northern; Sangu/Matamuhari.
38. Chittagong, southern; Chokoria Sunderbans; Chunar Wildlife Sanctuary; Cox’s Bazar; Himchari; Kaptai, south of; Maiskhal Island; Padua.
39. Ukhiya.
40. Teknaf Peninsula.

Bhutan (Bh)
1. Royal Manas National Park.

China (C)
1. Yadong Xian.
2. Maizhokungar Xian.
3. Qusum Xian.
4. Lhünze Xian.
5. Tsari Chu.
7. Gyaca Xian.
8. Gongbo’ gyamda Xian.
11. Yigong; Yigong Forest Reserve.
17. Yushu Xian.
18. Jegu Xian; Maluling.
19. Dainkog.
20. Routoumdo.
21. Qamdo.
22. Dēgē vicinity.
23. Baima.
27. Kangding; Moshemien.
28. Olongché.
29. Yajiang.
30. Xi Golog.
31. Litang-Batang.
32. Batang vicinity; Kiang-ka.
33. Dzo La, southeast of.
34. Zayü Xian.
35. Yanjing vicinity.
36. Dēqên.
37. Xiangcheng.
38. Zhongdian.
40. Yanyuan.
41. Wéixi.
42. Fugong.
43. Bifoxue Shan.
44. Ashi.
45. Lijiang.
46. Yongsheng [Xian].
47. Huaping [Xian].
48. Miyi.
49. Yuanmou.
50. Luquan.
51. Shuangbai.
52. Chuxiong.
53. Nanhua.
54. Nanjian.
55. Yunlong [Xian].
56. Baoshan.
57. Datang.
58. Hui-yao.
59. Tengchong (= Momien); Tengchong Xian.
60. Yingjiang.
61. Hotha Valley.
62. Sanyaishan.
63. Cala Shan.
64. Changning [Xian].
65. Nu Jiang, above Changlung.
66. Minglang; Yongde vicinity.
67. Gengma.
68. Nanding He.
69. Lincang Prefecture.
70. Lincang Jiang.
71. Jingdong Xian.
72. Ailaoshan (= Mountain) Reserve.
73. Wuliang Shan (= Mountain) Reserve; Zhényuan Xian.
74. Jinggu Xian.
75. Mojiang Xian.
76. Lüchun.
77. Pu’er Xian.
78. Simao Xian.
79. Lancang Xian.
80. Meng-ban.

(continued on following page)
81. Menghai; Menghun; Shanman.
82. Menglong.
83. Mengyang.
84. Menglun.
85. Manpa.
86. Nonglin.

India (I)

1. Harinbhanga.
2. Jhilla.
3. Calcutta, Hastings Road; Calcutta, Indian Museum Compound; Calcutta, northern.
4. Basirhat Reserve Forest.
5. Bhagalpur District.
6. Mangpu; Narbong; Panighatta; Siliguri; Simulbari-Pankhabari; Sivok; Sivok, ca. 3 km east of; Sivok, ca. 5 km east of; Sivok, ca. 6 km east of; Sukna; Sukna-Kurs cong.
7. Sikkim; Tarkhola.
8. Gorubathan forest.
10. Jamduar vicinity; Maure, near; Raimona vicinity.
11. West Garo Hills District.
13. Garo Hills; Rongrenggiri vicinity.
15. Kulsi [River]; Rajapara.
17. Nongpoh.
20. Lamsakhang.
22. Golaghat.
23. Neghereting.
25. Adpuria; Akhoiphutia; Bahgara; Bezoaugon; Cherekapar, near; Chetia; Dichialgaon; Dihajan habi; Hattiguli; Japisoja; Jayrapar; Jhanji; Judi-Jatakia; Kathpar; Khanamukh; Luprini gaon; Mesogarh; Meteka; Misajan; Moduri; Nanglamora; Nima jan-Bahdhora; Rajma tea garden, east of National Highway No. 37; Rajma tea garden, west of National Highway No. 37; Sala Reserve Forest; Saraguri; Tipomia.
26. Dangori Nadi, near; Tinsukia District (Bherjan, Bor rajan, Podumoni R. E.).
27. Yongyap Chu.
29. Margherita.
30. Dhuniopathar; Dillighat; Diroi (Rangoli) Reserve Forest; Sapekhati Reserve Forest.
31. Changchang Pani.
32. Chungtia.
33. Mikir Hills.
34. Samaguting.
35. Cachar District.
37. Imphal, ca. 4 mi (= 6.5 km) north of; Imphal, Mahabali temple.
38. Bishenpur.
39. Ghammer, ca. 1 km south of; Nagorhgena; North District, northeastern; Paach pior mukam.
40. Ampi Bazar, ca. 3 km southeast of resthouse; Charilam resthouse; Gumi ti Sanctuary; North District, north-central; North District, northwestern; North District, western; South District, north-central; South District, south-central; South District, southeastern; South District, southwestern; South District, west-central; West District, east-central; West District, south-central; West District, southern; West District, southwestern; West District, western.
41. North District, eastern.
42. North District, southeastern; North District, southwestern; North District, northeastern.
43. Phawngpui Wildlife Sanctuary.

Supplementary Indian locality (received too late for inclusion in map; listed in Gazetteer): Manas National Park.

Laos (L)

1. Ou, Nam, between Muang Khoua and Muang Noy.
2. Ou, Nam (= Nam hou).
3. Louangphrabang.
4. Xaignabouli.
5. MeKong River, 90 km above Viangchan.
6. Ban Kuai, several km south of; Ban Napo vicinity; Ban So vicinity; Ban Wangma vicinity.
7. Viangchan.

Myanmar (M)

1. Bawmwang; Htingnan Triangle.
2. Hkandau.
3. N’Changyung.
4. Tanga-Shingaw, road between.
5. Karen Chaung; Myitkyina; Tang Hpre.
7. Taga Hka; Tar o.
8. Singkaling Hkami, northern Chindwin River; Singkaling Hkami, right (west) bank; Singkaling Hkamit, upper Chindwin River, east bank.
10. Moklo.
11. Tamanthi Wildlife Sanctuary.
15. Bham o.
17. Ali Cha.
18. Kindat; Tatkon, near Kindat, east bank of Chindwin River; Tatkon, near Kindat, west bank of Chindwin River.
19. Mansam Falls; Se-eng.
20. Pyuangoaung.
21. Lethan Hka; Maymyo.
22. Madaya.
23. Mingun.
24. Kin; Yin, east bank of lower Chindwin River; Yin, lower Chindwin River.
26. Irrawaddy River, left bank, below Yenangyaung.
27. Popa Hill.
29. Toungoo, 30 mi (= 48 km) northwest of.
30. Toungoo, 15 mi (= 24 km) north of.

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259; Hill, 1974, p. 565; Roonwal & Mohnot, 1977, p. 147; Kessler et al., 1986, p. 264; Higley et al., 1987, p. 9); the crown hair of neonates is parted by a midline bare area. At birth, the bare skin of the face, hands, and feet is dull purple, but within about 5 minutes it gradually becomes pale pink (Rawlins, 1979, p. 432). Skin color changes from pinkish to buffy by age ca. 2 months, and the dark neonatal pelage is gradually replaced by paler pelage, similar in color to that in adults and without a coronal part, by age ca. 6 months (Hinde et al., 1964, p. 611; Roonwal & Mohnot, 1977, p. 147; Higley et al., 1987, p. 9).

In two young infant specimens examined (FMNH 82806, 82807, Yin, Myanmar, 18 June 1915), with deciduous first incisors emerging (age <7 weeks; cf. Fig. 16), the dorsal pelage is relatively thin and fine-textured—brown on the crown, pale yellowish-brown on the upper back, pale burnt orange on the lumbosacral region, and pale ochraceous on the tail and limbs; the face is nearly naked, and the underparts are thinly covered with short pale ochraceous hairs. In two older infants (AMNH 57108, Eastern Tombs, China, winter 1929; FMNH 99671, Huai Kwang Pah, Thailand, 29 March 1967), with deciduous second upper molars erupting (age ca. 5 months), the pelage is essentially similar in color and texture to that in adults. However, fine-textured pelage may be retained by some young juveniles, even after the permanent first molars have begun to erupt (USNM 20122, Lolab, India, 9 September 1891, age >1 year).

The reaction of captive adult females to 6-month-old infants with either naturally colored buffy faces or artificially colored pink faces (similar in color to the faces of neonates) has been investigated experimentally (Higley et al., 1987, p. 16). In this study, the adult females paid more attention to pink-faced (neonate-like) infants than to buffy-faced infants.

Seasonal Variation

Macaca mulatta undergoes seasonal molting, both in natural populations (Pocock, 1932, p. 531; Pearl et al., 1987, p. 38) and in captivity (Hartman, 1931, p. 141; Stewart, 1933, p. 30; Rowell, 1963, p. 195; Vessey & Morrison, 1970, p. 90; Morrison & Menzel, 1972, p. 63; MacArthur et al., 1978, p. 155; Wolfe, 1985, p. 243; O'Neill-Wagner, 1997, p. 138). In natural populations, most postinfantile specimens collected during the period September–February are in prime pelage (Fig. 4; cf. Pocock, 1932, p. 531; Pearl et al., 1987, p. 38). In this condition, the fur on the dorsal surface is richly colored, lustrous, long, soft, and smooth; the pale distal annulations on individual dorsal hairs are bright, crisp, and conspicuous (e.g., FMNH 35448, adult male, Mangpu, West Bengal, India, 5 December 1930). A slight fading of the pelage may become evident as early as October, but this early-stage fading is most commonly seen in March; compared with prime pelage, the dorsal fur is more grayish, less lustrous, and somewhat disheveled, and the contrast between the pale distal annulations and adjacent darker regions of individual hairs is reduced (FMNH 99668, adult female, Ban Mae Lamao, Thailand, 21 March 1967). In subsequent months fading continues, with the result that dorsal fur in most specimens collected from April through June is dull colored, weakly annulated, streaky, harsh textured, and scraggily (late-stage fading); at this
Fig. 2C. Detail map of *Macaca mulatta* localities, eastern section; for documentation, see Gazetteer, Appendix 2. Abbreviations in parentheses are those used in gazetteer locality codes; specimens examined include living monkeys personally observed in the field.
China (C)
1. Huashi, north of; Liulipenshan; Xianglong Xian, southern.
2. Yicheng.
4. Jiyuan, ca. 30 km northwest of; Manghe Nature Reserve; Taihang Shan.
5. Yangcheng.
6. Jincheng; Shanxi, southeastern.
7. Lingchuan, southeast of.
8. Huixian.
9. Xinhua Xian.
10. Xiwu Xian.
11. Boai; Qinyang.
12. Jiyuan, ca. 20 km northeast of.
13. Jiyuan, ca. 80 km west-northwest of.
14. Yuanqu; Zhongtiao Shan.
15. Ruicheng.
16. Liangdang.
17. Huixian.
18. Baishuijiang Natural Reserve.
20. Chengxian.
22. Nanping.
23. Qingchuan.
24. Shennongjia Forestry Region.
25. Huangliangping.
27. Yichang; Yichang (= Ichang), Chang Jiang (= Yangtze) gorges above.
29. Qiangxian.
30. Guanzhong.
31. Tongjiang Xian.
32. Dashuping.
33. Nanjiang.
34. Chengjia.
35. Dahe; Longchi.
36. Zhengba Xian.
37. Wanyuan.
38. Wanxian.
40. Wushan.
41. Zhenping.
42. Zhushan.
43. Shennongjia Forestry Region.
44. Huangliangping.
45. Zigui.
46. Yichang; Yichang (= Ichang), Chang Jiang (= Yangtze) gorges above.
47. Zhaotan.
48. Gunjiujiang; Liukou, Qimen Xian.
49. Gecong.
50. Jiuhua Shan; Tangxi.
51. Jiuhua Shan, ca. 30 km east of.
52. Jiuhua Shan, ca. 30 km northeast of.
53. Biyan, ca. 30 km north of.
54. Yanyiupu.
55. Duoshan; Hule; Qingliangfeng.
56. Anji Xian.
57. Laodian.
58. Xindeng.
59. Changhua vicinity.
60. Jixi.
122. Sandu.
123. Dushan.
124. Huishui.
125. Guliang.
126. Weng’an.
127. Kaiyang.
128. Meitan, near.
129. Zunyi.
130. Suiyang.
131. Guin.
133. Nanchuan.
134. Xishui.
135. Tongzi.
136. Hejiang.
137. Yibin.
138. Tse-o-Jia-Geo; Yunnan border; Yunnan border, south of Yibin.
139. Emei Shan; Leshan (= Kai-ting), mountains 30 mi southwest of; Shihshahshu Temple.
140. Gin Keo Ho, cliff above; Wa Shan.
141. Meiigu.
142. Leibo; Yongshan.
143. Yiliang.
144. Shuicheng Xian vicinity.
145. Qingzhen.
146. Changshun.
147. Fuyuan.
148. Mile.
149. Gejiu.
150. Jinping.
151. Pingbian.
152. Hekou.
153. Guangnan.
154. Maojie Bird Reserve.
155. Fameng; Jinzhong Shan Bird Reserve.
156. Xingyi.
157. Anlong.
158. Wangmo.
159. Chenhong.
161. Huagong Water Regulation Forest Reserve.
162. Nazuo Water Regulation Forest Reserve.
163. Funing.
164. Defu Water Regulation Forest Reserve; Longhua Water Regulation Forest Reserve.
165. Nongxin Water Regulation Forest Reserve.
166. Dizhou Water Regulation Forest Reserve.
167. Ditin; Gulong Shan Water Regulation Forest Reserve; Motianling.
169. Baidonghe Water Regulation Forest Reserve; Chengbihe Water Regulation Forest Reserve.
170. Batu.
171. Cenwanglaoshan Nature Reserve; Yuhun.
172. Gao Lo Shan.
173. Bamo village, near; Buliuhe Water Regulation Forest Reserve; Chuan Dong; Chuandonghe Water Regulation Forest Reserve; Guangli, 50 m above; Hongshui He, between Tian’e and Hai Zhou; Hongshui He, left bank, 9 km and 10 km below Heke: Hongshui He, right bank, 500 m below Heke; Koditan; Sanpihu Water Regulation Forest Reserve; Tian’e.
174. Liuzhai vicinity; Lungli vicinity.
175. Libo.
176. Xunle vicinity; Xunle Water Regulation Forest Reserve.
177. Dongmen; Dongshan; Jenli, 2–3 km north of; Mulun Nature Reserve; Pochuan, 6–7 km west of; Xianan; Xianan-Mulun.
178. Cioupu Shan; Hechi Prefecture; Jinchengjiang.
179. Luocheng.
180. Sijian Shan Water Regulation Forest Reserve.
183. Shoucheng (= Shocheng) Water Regulation Forest Reserve.
185. Longsheng.
186. Chengbu.
187. Xinning Xian, Southern.
188. Quanzhou.
191. Qianjiandong Water Regulation Forest Reserve.
194. Jiualqolin Water Regulation Forest Reserve; Lagou Bird Reserve; Xilin Shan Water Regulation Forest Reserve.
195. Dayao Shan Nature Reserve; Laoshan; Piangzu; Puquan Road Maintenance Station.
197. Wuzhou; Xi Jiang.
198. Nan Ling.
200. Wangqianshan.
201. Liangzhou.
203. Shanzhong.
204. Yingde.
205. Boluo.
206. Qionglong.
207. Huaaji.
208. Luofu Shan.
209. Huidong.
210. Dazhao Dao; Eagle’s Nest Trail; Kam Shan Entrance; Sam Shui Wan Valley; Shing Mun Country Park; Tai Po Kau Nature Reserve; Tai Tam Reservoir; [Victoria] Peak.
211. Dagan Dao; Erzhou Dao.
212. Nelingding Dao.
213. Beiichuanshan; Miwan.
214. Tiantang Shan Water Regulation Forest Reserve.
216. Guixi.
217. Shiwan Dashan Water Regulation Forest Reserve.
218. Shangsi.
219. Bapong.
220. Nanning.
221. Daming Shan Nature Reserve.
222. Longjun (= Lingjun) Hsienmu Reserve.
223. Daxin Rare Animal Reserve; Zhongzhou.
224. Chunxiu Water Regulation Forest Reserve; Qinglong Shan Water Regulation Forest Reserve; Xialei Water Regulation Forest Reserve.
stage, the tips of individual hairs frequently are abraded (FMNH 99669, adult male, Huai Ap Nang, Thailand, 29 March 1967). From June to October, but most commonly in July and August—which is the peak of the rainy season in most parts of the range of *M. mulatta*—molting occurs, and the faded old fur is replaced by short bright new fur, first on the crown and tail, next on the arms and legs, and finally on the back and flanks (BMNH 1915.5.5.3, adult male, Homalin, Myanmar, 14 July 1914). Although the process of fading, molting, and hair replacement is gradual, and the assignment of marginal specimens to particular stages in the process is therefore somewhat arbitrary, the general pattern is reasonably clear.

Captive populations in England and in Maryland and Florida, U.S.A., reportedly molt in the spring or summer (Hartman, 1931, p. 141; Rowell, 1963, p. 195; MacArthur et al., 1978, p. 155; Wolfe, 1985, p. 243; O’Neill-Wagner, 1997, p. 138); this is similar to the timing of molting in natural populations (Fig. 4). In individual members of a captive free-ranging population (n = 156–186), the duration of the molting stage varied from 4 weeks to 16 weeks and generally was longest in adult males (Vessey & Morrison, 1970, p. 90).

Pocock (1932, p. 532; 1939, p. 47) suggested that the molting season in *M. mulatta* may vary geographically, depending on local environmental conditions. This suggestion is supported by evidence from two free-ranging colonies studied by Vessey and Morrison (1970, p. 92) and evidence from one translocated free-ranging group studied by Morrison and Menzel (1972, p. 63). Vessey and Morrison found that the molting period in a colony at Cayo Santiago, Puerto Rico (January–May), is about 3 months earlier than in a colony at La Parguera, Puerto Rico (April–August). The La Parguera colony inhabits a pair of relatively dry islands ca. 160 km southwest of Cayo Santiago, which is relatively wet; the timing of molting in the La Parguera colony is fairly close to that in natural populations of *M. mulatta* (Fig. 4). The group studied by Morrison and Menzel was translocated in July 1966 from Cayo Santiago to Descheo I., a relatively dry island ca. 60 km north-
west of La Parguera; after a transitional molting season in 1967, the onset of the molting season in the Descecho group apparently shifted to May (1968–1971), close to the onset at La Parguera, instead of January, when the molting season begins at Cayo Santiago.

In natural populations, the peak of the molting season usually coincides with the end of the birth season, and most individuals are in prime pelage during the mating season (cf. Fig. 4, Table 22). A similar relationship between molting and birth seasons also prevails in the free-ranging Cayo Santiago and La Parguera populations (Vessey & Morrison, 1970, p. 92); in the Descecho group, the molting peak apparently occurs after the birth season (Morrison & Menzel, 1972, p. 75). In the La Parguera colony, molting tended to occur earlier in mature males and mature nonpregnant females than in immatures and pregnant females, which usually molted after parturition (cf. O’Neill-Wagner, 1997, p. 138); this suggests that molting may be controlled, at least in part, by sex hormones (cf. Dietz et al., 1995, p. 282). Anomalously, one 4-year-old pregnant female in the La Parguera colony molted twice in the same year, once after the mating season and once after the birth season.

Other species of macaques in which seasonal molting has been reported are *M. fuscata, M. radiata, M. assamensis*, and *M. thibetana* (Pocock, 1931. p. 276; 1939, p. 52; Hill, 1974, p. 765; Fooden, 1981, p. 9; 1982a, p. 52; 1983, p. 8; Inagaki & Nigi, 1988, p. 82). Molting in *M. fuscata, M. radiata,* and *M. assamensis* apparently occurs in May or June, which probably is slightly earlier than usual in natural populations of *M. mulatta*. Molting in *M. thibetana* apparently occurs in late summer (ca. August), which is about the same as in natural populations of *M. mulatta*.

**Geographic Variation**

Pelage characters have served as the primary basis for recognition of subspecies in *M. mulatta*. For this reason, detailed analysis of geographic variation of these characters is required. As indicated by Pocock (1932, p. 533), the preferred standard of comparison for such an analysis would be the type specimen, which unfortunately has not been preserved. Lacking the type specimen, specimens collected at or near the type locality will be used as standards of comparison.

**Nepalese Standards**—The type locality of *M. mulatta*, originally given as “India,” subsequently was restricted by Pocock (1932, p. 533) to “Nepal Tarai” (now spelled “Terai”), which is the narrow plain that extends along the southern border of Nepal (Karan, 1960, p. 1). One specimen from the Nepal Terai is now available; this toptype is BM(NH) 1922.5.16.2, an adult male in prime pelage, collected 17 February 1921 at Hazaria Patherghatta (ca. 27°00’N, 85°15’E), 180 m (Fig. 3A). Dorsal pelage in this specimen is bright golden brown anteriorly, becoming intensely burnt orange on the lumbosacral region (cf. Pocock, 1932, p. 534). Interscapular hair length (ISHL) is ca. 50 mm. The tail is not particularly bushy; midstail hair length (MTHL) is ca. 25 mm.

Two near toptypes, also in prime pelage, are available from higher elevations in Nepal—BM(NH) 1921.5.1.1, adult female, 15 October 1920, Nagarkot (ca. 85 km northeast of Hazaria Patherghatta), 2400 m, and BM(NH) 1931.1.11.11, late juvenile male, 7 December 1922, Chengli (ca. 130 km northwest of Hazaria Patherghatta), altitude unspecified. Dorsal pelage color in these two skins is slightly more erythristic than in the toptype. Hair length (female, ISHL = 40 mm, MTHL = 10 mm; male, ISHL = 60 mm, MTHL = 30 mm) is similar to that in the toptype.

Ten additional Nepalese specimens examined are less useful for pelage comparisons. These are BM(NH) 1921.5.1.2, infant female; FMNH 104164, young juvenile male (M1, II), early-stage faded pelage; BM(NH) 1931.1.11.10, juvenile female collected in June, beginning to molt; four badly deteriorated skins collected before 1846 (BM(NH) 1845.1.8.222⎯1845.1.8.224, 1972.1015); and three juveniles preserved in fluid (FMNH 135427–135429).

**Survey of Sample Areas**—In subsequent paragraphs, postinfantile *M. mulatta* specimens collected in 30 sample areas within the specific range (Fig. 5) are compared with the three Nepalese skins that are in prime pelage (BM(NH) 1921.5.1.1, 1922.5.16.2, 1931.1.11.11). Museum catalog numbers are indicated where the number of specimens in a cited sample subset is less than five.

1. India: northern Uttar Pradesh, ca. 600 km west-northwest of Hazaria Patherghatta; 12 skins, seven localities. Eleven specimens, collected October–March, are in prime pelage, and one (BM(NH) 1931.1.11.3), collected in January, is early-stage faded. In seven of the specimens in prime pelage, collected October–March, dorsal pelage color is essentially similar to that in the three Nepalese standards; in the remaining four (BM(NH)
Fig. 3. Dorsal pelage color in *Macaca mulatta*. A. Topotype—bm(nh) 1922.5.16.2, adult male, collected 17 Feb. 1921 at Hazaria Pathergatta, 600 ft (= 180 m), Nepal. B. Contrasting pelage color in two adult males collected 4 days apart at Rajapara, 600 ft (= 180 m), Assam, India—bm(nh) 1931.1.11.7, 21 Nov. 1920 (left), and bm(nh) 1921.7.9.3, 25 Nov. 1920 (right). Scale bar = 15 cm.

1914.7.10.3–5; BNHS 5108), collected October–January, the color is distinctly less erythristic—pale yellowish brown anteriorly becoming washed with burnt orange on the lumbosacral region. Bright and dull specimens have been collected in the same month at each of two localities (Bageshwar and Ratighat). ISHL is $51.4 \pm 2.9$ mm (mean ± SD) in three adult females and $61.0 \pm 6.5$ mm in five adult males. MTHL is 20 mm and 30 mm in two adult females and $27.5 \pm 5.0$ mm in four adult males; in two of these males (BM(NH) 1914.7.10.1 and 1914.7.10.2, both collected at Bageshwar), the tail is somewhat bushy.

2. India: northwestern Himachal Pradesh, ca. 1,000 km northwest of Hazaria Pathergatta; six skins, three localities. Of three specimens in prime pelage, two (BM(NH) 1933.12.1.2; BNHS 5112), collected in February and March, are brightly colored—similar to the Nepalese standards, and one (BNHS 5114), collected in March, is slightly less erythristic. Three specimens (BM(NH) 1923.9.1.118, 1931.1.11.34–35), collected in March and May, are late-stage faded—pale yellowish gray anteriorly, faintly washed with burnt orange posteriorly. ISHL is 65 mm in one adult female and 60 and 80 mm in two adult males; MTHL is 20 and 35 mm in two adult males.

3. India: southwestern Jammu and Kashmir, ca. 1,300 km northwest of Hazaria Pathergatta; 11 skins, four localities (including type locality of *Macacus rhesus villosus* True, 1894). Ten specimens are in prime pelage, and one (USNM 173814), collected in February, is early-stage faded. Five of the specimens in prime pelage, collected in September and month unspecified (one specimen), are brightly colored—similar to the Nepalese
Fig. 4. Monthly incidence of prime, faded, and molting pelage stages in wild-collected specimens of *Macaca mulatta*.

Standards; the remaining five, collected in October, November, and month unspecified (one specimen), are slightly less erythristic. The holotype of *Macaca rhesus villosus* (USNM 20120; September) is one of the brightly colored specimens in prime pelage—golden brown anteriorly, becoming burnt orange on the lumbosacral region. In all these specimens, the pelage is notably dense. ISHL is 65 and 70 mm in two adult females and 75 and 85 mm in two adult males (cf. Pocock, 1932, p. 359); MTHL is 40 and 45 mm in two adult females and 40 mm in two adult males. Tails are bushy in all 11.

4. Northeastern Pakistan, ca. 1,400 km northwest of Hazaria Patherghatta; five skins, four localities. One skin (USNM 353186), collected in September, is in prime pelage and is slightly less erythristic than the Nepalese standards. Two skins (BM(NH) 1923.11.4.1; BNHS 5113), collected in June, are late-stage faded. One skin (USNM 353187), collected in August, is in the process of molting; most of the pelage consists of short (30 mm) bright new hairs, but scattered among these are a few long (90 mm) faded old hairs. In the fifth skin (USNM 326332), collected in September, the molt apparently had just been completed; the fur is short (35 mm) and bright, similar in color to that in the Nepalese standards. ISHL is 65 mm in one adult female and 50 and 70 mm in two adult males; MTHL is 30 and 40 in two adult males. In the male in prime pelage, the tail is bushy.

5. Northwestern Pakistan and eastern Afghanistan, ca. 1,600 km northwest of Hazaria Patherghatta; three skins, three localities (including type locality of *Macaca mulatta mcmahoni* Pocock,
1932). These three specimens—one wild-collected and two captives—are the only preserved skins known to have originated at the northwestern limit of distribution of *M. mulatta*. The wild-collected specimen (BM(NH) 1920.6.11.1), an adult male, was taken in early February 1914 in Pakistan near the border with Afghanistan. One of the captives (BM(NH) 1931.1.9.1, skin only) apparently originated in eastern Afghanistan (Pocock, 1932, p. 543); it was received at the Regent’s Park Zoological Gardens, London, on 3 April 1906, died there on 19 January 1910, and was cataloged at BM(NH) in 1931. Available information concerning the sex of this specimen is contradictory. Although zoo records and the zoo tag on the skin indicate that the specimen was a male (P. Jenkins, BM(NH), letter, 21 June 1995), BM(NH) records and the museum tag on the skin indicate that it was a female (Pocock, 1932, p. 543); the skull has not been preserved, and my examination of the skin for evidence of sexual characters was inconclusive. Pending further information, the zoo records are regarded as more reliable, and the specimen is considered to be a male; it probably was an adult (cf. Pocock, 1932, p. 543). The other captive (FMNH 102839), a juvenile female that reportedly also originated in eastern Afghanistan, was purchased on 2 November 1965 near Gandahar, Afghanistan, ca. 600 km southwest of the reported place of original capture (Hassinger, 1968, p. 72).

Pelage color is diverse in these three skins. The captive male, which died in January, is in prime pelage—dark golden brown on the dorsal thoracic region and bright burnt orange on the lumbosacral region; the color of the lumbosacral region is similar to that in the Nepalese standards, but the color of the dorsal thoracic region is much darker than in most specimens of *M. mulatta*. The wild-collected male (BM(NH) 1920.6.11.1, holotype of *Macaca mulatta memahoni*), taken in February, is yellowish gray anteriorly, becoming washed with burnt orange posteriorly. The shaggy, dull-colored, weakly annulated fur probably indicates that this specimen is early-stage faded; this interpretation differs from that of Pocock (1932, p. 545), who noted that the pelage of this male is similar to that of a late-stage faded specimen (BM(NH) 1923.11.4.1) collected at Patriata, Murree, Pakistan, but concluded that, because BM(NH) 1920.6.11.1 was collected in February, it should be in prime pelage (cf. late-stage faded BM(NH) 1923.9.1.118, India: Kangra Fort, Himachal Pradesh, collected 18 March). The captive juvenile female, obtained in November, is relatively dull-colored—yellowish brown anteriorly, becoming golden brown on the sacral region. This skin is more uniformly brown than most specimens of *M. mulatta*; the texture of the pelage does not suggest that the specimen is seasonally faded. In the adult males, ISHL is 50 and 90 mm, and MTHL is 30 and 50 mm. The tails of the adult males are bushy.

6. India: central Madhya Pradesh and southern Gujarat, ca. 600 to 1,400 km southwest of Hazaribagh; six skins, four localities. One skin from Gujarat (BM(NH) 1931.1.11.3), collected in 1922–1923, is in prime pelage and is brightly colored but is slightly paler than the Nepalese standards. Another skin from Gujarat (BM(NH) 1931.1.11.2), also collected in 1922–1923 and brightly colored, appears from its disheveled pelage to be early-stage faded. Two skins from Madhya Pradesh (BM(NH) 1931.1.11.4–5), collected in April and May, are late-stage faded. The remaining two skins (BM(NH) 1931.1.11.1; BNHS 5107), collected in 1922–1923 and date unknown, are pale juveniles. ISHL is 46.7 ± 2.9 mm in three adult females and 50 mm in one adult male; MTHL is 20.0 ± 0.0 mm in the females and 20 mm in the male.

7. India: southwestern Bihar, western and southern Orissa, and eastern Andhra Pradesh, ca. 600 to 1,300 km south-southwest of Hazaribagh; seven skins, five localities. One skin (BM(NH) 1928.3.7.4), collected in Orissa in September, is in prime pelage and is similar to the Nepalese standards. Two skins (ZSI Coll. No. OM/DD/30; ZSI, Siddeldar Hill, unnumbered), collected in Orissa and Andhra Pradesh in November and December, are in prime pelage but are distinctly less erythristic than the Nepalese standards. The remaining four skins were collected in Bihar and Orissa in August; of these, three (BM(NH) 1915.4.3.2, 1928.3.7.3; BNHS 5089) were in the process of molting, and one (BM(NH) 1915.4.3.1) is newly molted. The bright new fur in all four is similar in color to that in the Nepalese standards. ISHL is 15 mm in one adult female (molting, new fur), 30 mm in a subadult or adult female (skin only), 50 mm in a subadult or adult male (skin only), and 65 mm in an adult male; MTHL is 20 mm in the subadult or adult female and 30 mm in the subadult or adult male.

8. Bangladesh: Sundarbans and India: Tripura, ca. 700 km southeast of Hazaribagh; nine skins, three localities. The two specimens from Tripura, an adult male (ZSI Coll. No. TM18) collected in November and a subadult male (ZSI Coll. No. TM4) collected in January, are in prime
Fig. 5. Sample areas cited in Macaca mulatta pelage color. Key to included localities (for details, see Gazetteer, Appendix 2): Nepalese standards—Hazaria Pathergatta; Nagarkot; Chengli. 1. Northern Uttar Pradesh, India—Bageshwar; Dela; Haripur; Jhirna; Ramnagar; Ratighat; Sita Bani. 2. Northwestern Himachal Pradesh, India—Dharmsala; Kangra; Samayalas. 3. Southwestern Jammu and Kashmir, India—Dunwei; Kashmir; Kotihar; Lolab. 4. Northeastern Pakistan—Dunga Gali vicinity, 2470 m; Ghorakhel; Paia; Patrista. 5. Northwestern Pakistan and eastern Afghanistan—Chigha Sarai; Koatai; Nuristan, eastern. 6. Central Madhya Pradesh and southern Gujarat, India—Dangs; Kakara; Malwa; Sohagpur. 7. Southwestern Bihar, western and southern Orissa, and eastern Andhra Pradesh, India—Deoghar; Gudari; Luia; Malkangiri; Siddeldar Hill. 8. Sundarbans, Bangladesh, and Tripura, India—Ampi Bazar; Charilam; Sundarbans, ca. 50 mi east of Calcutta. 9. Sikkim and northern West Bengal, India—Bharanbhiri; Hasimara; Mangpu; Narbong; Sikkim; Sivok. 10. Assam, Meghalaya, Manipur, and Nagaland, India—Bishenpur; Bogra Nadi; Changchang Pani; Golaghan; Hot Springs; Impthal, ca. 4 mi north of; Kushi; Lamsakhang; Nagphoh; Samaguting. 11. Arunachal Pradesh, India—Dening; Margherita. 12. Eastern Xizang, China—Yigong, 2250 m. 13. South-central Qinghai, China—Jegu Xiang. 14. Northern Myanmar—Bawmwing; Bhamo; Heinsun; Hisweht; Hkandau; Homalin; Htingnna Triangle; Karen Chaung; Maungkan; Moklok; Nanyeik; N’Changyang; Singkaling Hkamti (24 July, 5 Aug., and June–Aug. 1914); Taga Hka; Tanga-Shingaw; Tang Hpre; Taro. 15. Western Yunnan, China—Ashi; Biloxue Shan; Datang; Hotha Valley; Hui-yao; Sattaishan; Tengchong. 16. West-central Sichuan, China—Gin Keo Ho; Kangding; Leshan; Olongche; Wa Shan. 17. Southeastern Sichuan, China—Tseo-Jia-Geo; Yibin; Yunnan border, south of Yibin. 18. Guizhou, China—Getou; Zunyi. 19. Northeastern Sichuan, China—Tongjiang Xian. 20. Northeastern Hebei, China—Xinglong Xian. 21. Northern Fujian, China—Chong’an Xian; Kuatun. 22. Dawanshan Islands, China—Dangan Dao; Neilingding Dao; Shangchuan Dao (Miwan). 23. Hainan Dao, China—Bawangling; Changtian; Dongfang; Hainan; Henan; Jianfengling; Miouling; Nada; Nanfeng; Shi; Nanwan; Xingcun-gang; Nychow; Pisu; Wuzhi Shan; Xinlong; Yiajia; Zhayun. 24. Northeastern Vietnam and southern Guangxi, China—Bac Can; Ban Thi; Chiem Hoa; Linh Thong; Ly Bon; Nanning; Nghia Dan; Nghia Dung; Thanh Tuong; Van Hai; Yen Bai. 25. Northern Laos, northwestern Vietnam, and southern Yunnan, China—Lai Chau; Mengla Xian; Menglan; Muong Boun; Muong Muon; Muong Pon; Ou, Nam; Shanman; Xishuangbanna. 26. Central Myanmar—Ali Cha; Kin; Kindat. 20 mi northwest of; Kokkosaiing; Lethan Hka; Madaya; Mansam Falls; Maymyo; Mingun; Popa Hill (1000 m; 1512 m); Pyuanguang; Se-eng; Tatkon, east bank of Chindwin River; Tatkon, west bank of Chindwin River. 27. Southwestern Myanmar—Py, 30 mi southeast of; Pye 35 mi southeast of; Toungoo, 13 mi east of; Toungoo, 15 mi north of; Toungoo, 20 mi west of; Toungoo, 30 mi northwest of; Toungoo, east side of Sittang River. 28. Northwestern Thailand—Ban Mae Lamo;
pelage but are darker and less erythristic than the Nepalese standards. The adult is dark golden brown anteriorly, becoming strongly washed with burnt orange posteriorly; the subadult is grayish tipped with yellowish anteriorly, becoming faintly washed with burnt orange posteriorly. ISHL is 55 mm in the subadult and 65 mm in the adult.

The seven Sundarbans skins, collected in April 1870, are difficult to interpret. The pelage, which is harsh in texture, is grayish brown to golden brown anteriorly, becoming variably washed with burnt orange posteriorly. The unusual pelage condition may be a result of seasonal fading, deterioration in storage, or both.

Feeroz et al. (1995, p. 75) report that pigmentation of the face and ventral surface in living *M. mulatta* observed at Sitakunda, southeastern Bangladesh, appeared to differ from that in *M. mulatta* observed elsewhere in Bangladesh. No further details concerning this color difference are specified.

9. India: Sikkim and northern West Bengal, ca. 400 km east of Hazaria Pathergatta; 10 skins, seven localities. Eight specimens are in prime pelage. Four of these (BM(NH) 1916.7.29.2, 1931.11.119; FMNH 35447, 35448), collected in November–January, are brightly colored—similar to the Nepalese standards; one (FMNH 35449), collected in December, is slightly less erythristic; two (BM(NH) 1891.10.7.4, 1916.7.29.1), collected in January and month unknown, are slightly darker; and one (BM(NH) 1931.1.118), collected in February but apparently in prime pelage, is much darker and less erythristic—grayish brown anteriorly, becoming faintly washed with burnt orange on the sacral region. In the remaining two specimens, seasonal fading may have begun. One of these (BM(NH) 1915.9.1.1), collected in March, is paler and has weaker agouti hair banding than the preceding eight specimens; the other (ZSI 7294), collected in April, is drab yellowish brown anteriorly and bright burnt orange posteriorly. ISHL is 45.0 ± 8.7 mm in three adult females and 55.0 ± 5.0 mm in five adult males; MTHL is 20.0 ± 0.0 mm in three adult females and 28.8 ± 6.3 mm in four adult males. The tail is bushy in one adult male (BM(NH) 1891.10.7.4, the only postinfant specimen available from Sikkim).

10. India: Assam, Meghalaya, Manipur, and Nagaland, ca. 600 to 1,000 km east-southeast of Hazaria Pathergatta; 15 skins, 12 localities. Nine specimens in prime pelage, collected August–February, are brightly colored—similar to the Nepalese standards. Two others in prime pelage, a male (ZSI 11187) collected in November and another male (BM(NH) 1943.60) collected in February, are somewhat darker and less erythristic—dark golden brown anteriorly, faintly washed with burnt orange posteriorly; although both of these relatively dull specimens were collected in Manipur, one of the bright specimens (BM(NH) 1943.61) also was collected in that state. One skin (BM(NH) 1931.1.11.15), collected in May, is late-stage faded. Two specimens (BM(NH) 1921.7.9.4; BNHS 5087), collected in July and September, were in the process of molting; the short bright new fur is sparsely covered by long faded old hairs.

The most aberrant specimen in this group is a very dark and dull-colored adult male (BM(NH) 1921.7.9.3) collected on 25 November 1920 at Rajapara, Assam (Fig. 3B). This specimen, which is in prime pelage, is dark yellowish gray anteriorly, becoming faintly washed with burnt orange on the lumbosacral region. Pocock (1932, p. 530) has drawn attention to the striking contrast between this adult male and a brightly colored adult male (BM(NH) 1931.1.117; included among nine bright specimens cited above) that was collected 4 days earlier at the same place (Fig. 3B); Pocock cited these two specimens as an illustration of the broad range of individual variation to which pelage color is subject in *M. mulatta*. ISHL is 45 and 60 mm in two adult females and 50.0 ± 8.7 mm in three adult males; MTHL is 20 and 25 mm in two adult females and 20 and 25 mm in two adult males.

11. India: Arunachal Pradesh, ca. 1,100 km east of Hazaria Pathergatta; four skins, two localities. These four skins (BM(NH) 1931.1.11.13–14; BNHS 5086; ZSI 12090), collected in November–April, are similar to the Nepalese standards. In two adult

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Ban Umphang; Chiang Mai; Huai Ap Nang; Huai Kwang Pah; Kaeng Mae Hat. 29. Northeastern Thailand and west-central Laos—Ban Mak Nao; Dan Sai District; Mekong River; Nong Khai; Pang Nam Un. 30. Southern Laos and Central Vietnam—Dak Sut; Ky Son; Song-Ta-Voy; Son Tra Mt., 3.9 km west and 0.3 km south of: Thateng, Muang: Xuan Ninh,

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females. ISHL is 50 and 60 mm and MTHL is 20 and 30 mm.

12. China: eastern Xizang, ca. 1,000 km north-east of Hazaria Patherghatta; one skin, one locality. This skin (NWPHB Coll. No. 73066, juvenile female), collected in June, is late-stage faded; the dorsal pelage is gray tipped with golden anteriorly, becoming washed with pale burnt orange posteriorly. The specimen’s faded condition hinders comparison with the Nepalese standards. ISHL is 55 mm (juvenile).

13. China: south-central Qinghai, ca. 1,300 km northeast of Hazaria Patherghatta; two skins, one locality. One skin (NWPHB Coll. No. 63167), collected in June, is early-stage faded—gray tipped with golden anteriorly, becoming reddish brown posteriorly; the other (NWPHB 00033), collected in May, is late-stage faded—pale gray tipped with gold anteriorly, becoming weakly washed with burnt orange posteriorly. Seasonal fading in these skins hinders comparison with the Nepalese standards. Both specimens are juvenile males with long hair and bushy tails; ISHL is 65 and 70 mm, and MTHL is 40 and 50 mm.

14. Northern Myanmar, ca. 1,000 to 1,300 km east-southeast of Hazaria Patherghatta; 27 skins, 17 localities. Ten specimens collected in October—March are in prime pelage; four collected in January—May are early-stage faded; five collected in January—April are late-stage faded; and eight collected in July—August were in the process of molting. Of the 10 specimens in prime pelage, seven are brightly colored and generally similar to the Nepalese standards. The remaining three in prime pelage are somewhat deviant: one (BM(NH) 1950.373) is brightly colored but has unusually dark gray hair bases, one (AMNH 112734) is notably paler than the other nine, and one (USNM 279191) has the burnt orange coloration narrowly restricted to an area near the ischial calllosities. Of the four early-stage faded specimens, two (BM(NH) 1937.12.3.75, 1937.12.3.77), collected in May, are slightly more erythristic than the Nepalese standards; one (BM(NH) 1950.372), collected in January, is brightly colored but has unusually dark gray hair bases; and one (AMNH 112739), collected in March, is less erythristic. Of the five late-stage faded specimens, three (AMNH 112740, 112741, 114547) were collected in March or April, which is unremarkable; the other two (AMNH 112722, 112723), somewhat incongruously, were collected in January. ISHL is 50.0 ± 6.0 mm in eight adult females and 50 and 65 mm in two adult males (excludes molting specimens); MTHL is 19.3 ± 6.7 mm in seven adult females and 30 and 35 mm in two adult males.

15. China: western Yunnan, ca. 1,500 east-southeast of Hazaria Patherghatta; 13 skins, seven localities. Of nine specimens in prime pelage, eight collected in December (five skins), April (one skin), and month unknown (two skins) are brightly colored—similar to the Nepalese standards; the other specimen (ZSI 11986), collected in July, is somewhat less erythristic. Two skins (AMNH 43084, 43086), collected in April, are late-stage faded, and a hunter’s flat skin (KIZ Coll. No. 780417), reportedly taken in October, is molting. One skin (ZSI 619), collected in March—July 1868, has become severely deteriorated in storage. In one adult female, ISHL is 60 mm, and MTHL is 15 mm.

16. China: west-central Sichuan, ca. 1,600 to 1,800 km east-northeast of Hazaria Patherghatta; six skins, five localities (including type locality of Macacus vestitus Milne-Edwards, 1892). Four skins collected in February, March, and June are in prime pelage; one (MNHN 1891/388, holotype of Macacus vestitus), collected in June or July, is early-stage faded; and one (USNM 241160), collected in July, is late-stage faded. Two of the specimens in prime pelage (RMNH 4585/V67, 4585/W50, March) are similar in color to the Nepalese standards, one (MNHN 1891/387; June) is slightly less erythristic, and one (BM(NH) 1911.9.8.1; February) is darker and more erythristic—rich golden brown anteriorly, becoming dark burnt orange on the lumbosacral region; the last of these is very slightly paler than BM(NH) 1950.373, collected at Bawmawng, northern Myanmar. In the early-stage faded holotype of Macacus vestitus, dorsal pelage is pale grayish tipped with golden anteriorly, becoming pale burnt orange on the lumbosacral region. In two adult females, ISHL is 60 and 80 mm, and MTHL is 40 and 50 mm; in one of these (BM(NH) 1911.9.8.1), the tail is bushy, particularly distally.

Three additional specimens, with vague locality information, may also have been collected in or near west-central Sichuan. One of these is BM(NH) 1871.4.21.4, the holotype of Macacus lasiotus Gray, 1868. This tailless adult male was a captive that reportedly originated in “Szechuen”; it reached London, via Shanghai, shortly before 15 January 1868 and died on 25 May 1870. It is in prime pelage, dark and strongly erythristic; the dorsal pelage is dark burnt orange anteriorly, becoming intensely burnt orange on the sacral region; ISHL is 65 mm. The nearest match is
BM(NH) 1927.12.1.18 (Bac Can, northeastern Vietnam), which is slightly paler and less erythristic.

The other two specimens possibly collected in west-central Sichuan (MNH 1892/315, 1894/1432) are of limited value for pelage comparison. The former is late-stage faded, and the latter has suffered severe postmortem deterioration and discoloration. These two specimens were taken in May–July 1890 by the collectors of MNHN 1891/387 and 1891/388 cited above; the only locality information available is “Tibet,” which, for the collectors, included part of what is now Sichuan.

17. China: southeastern Sichuan, ca. 1,900 km east of Hazaria Patherghatta; four skins, three localities. Two specimens collected in October and January are in prime pelage, and two (USNM 258183, 258184), collected in February and March, are late-stage faded. Dorsal pelage coloration in the two in prime pelage, both juveniles, is dissimilar and unusual. The younger specimen (USNM 239133; M1), collected in October, is pale but erythristic—pale golden brown anteriorly, becoming intensely burnt orange on the lumbosacral region; the older juvenile (USNM 256669; 11-2, M2), collected in January, is much darker and less erythristic—yellowish brown anteriorly, becoming golden brown on the lumbosacral region. In one adult female, ISHL is 55 mm, and MTHL is 40 mm.

18. China: Guizhou, ca. 2,100 to 2,300 km east of Hazaria Patherghatta; six skins, two localities. Four specimens (BM(NH) 5.66.150–153), collected in May, are late-stage faded, and two (KIZ 03179, 03181), collected in early September, were in the process of molting. Because of fading or molting, these specimens cannot be compared with the Nepalese standards. MTHL is 40 and 45 mm in two adult females; in the latter specimen, the tail is bushy.

19. China: northeastern Sichuan, ca. 2,200 km northeast of Hazaria Patherghatta; two skins, one locality. These two adult females, collected in July, had just begun to molt on their crowns and tails; the dorsal pelage is late-stage faded. In one specimen (SIZ 00001), the upper back is grayish, and the lower back is pale golden brown; in the other (SIZ 00002), the upper back is pale golden brown, and the lower back is golden brown. No comparison can be made with the Nepalese standards. ISHL is 45 and 50 mm.

20. China: northeastern Hebei, ca. 3,200 km northeast of Hazaria Patherghatta; 10 skins, one locality (type locality of Macacus tchelienis Milne-Edwards, [1872]). Five specimens are in prime pelage, four (FMNH 39376, 39377; MNHN 335/381A/1867.557; USNM 240705) appear to be early-stage faded, and one (AMNH 57039) is late-stage faded; the month of collection or death is reliably known for only one of these 10 specimens (BM(NH) 1931.1.7.2, male in prime pelage, received at Regent’s Park Zoo 17 August 1880, died 6 March 1881). Of the specimens in prime pelage, BM(NH) 1931.1.7.2 is long-haired and very brightly colored—pale burnt orange anteriorly, becoming intensely burnt orange on the lumbosacral region; this skin is similar in color to BM(NH) 1937.12.3.7.7 (Karen Chaung, northern Myanmar) and is somewhat more erythristic than the Nepalese standards. Another specimen in prime pelage (AMNH 57040) also is strongly erythristic but is much darker—dark golden brown anteriorly, becoming burnt orange posteriorly. The remaining three specimens in prime pelage (AMNH 57042; FMNH 39378; USNM 240704) are darker and less erythristic than the Nepalese standards. The holotype of Macacus tchelienis (MNHN 335/381A/1867.557), which apparently is early-stage faded, is less erythristic than the Nepalese standards—pale golden brown anteriorly, becoming washed with burnt orange on the lumbosacral region. In two adult males, ISHL is 70 mm (both specimens), and MTHL is 30 and 35 mm.

21. China: northern Fujian, ca. 3,300 km east of Hazaria Patherghatta; six skins, two localities (including type locality of Pithecus littoralis Elliot, 1909). Three specimens collected in November and May are in prime pelage; one (AMNH 84476), collected in August, was in the process of molting, and two (MNHN 1874/480, 1874/481, Kuantun), collected in November 1873, are severely faded as a result of extended postmortem exposure to light. Of the three specimens in prime pelage, the holotype of Pithecus littoralis (BM(NH) 1900.5.8.1; November) is the brightest—pale golden brown anteriorly, becoming washed with burnt orange on the sacral region; the coloration of this specimen, which almost perfectly matches that of BM(NH) 1931.11.7 (India: Rajapara, Assam State; Fig. 3B), is similar to that of the Nepalese standards. Another of the specimens in prime pelage (AMNH 84474; May) is slightly less erythristic, and the third (BM(NH) 1898.11.1.29; May) is somewhat darker and less erythristic. ISHL is 40 mm in one adult female (holotype of Pithecus littoralis) and 80 mm in one adult male; MTHL is 25 mm in the female and 40 mm in the male; the tail of the female is relatively bushy.

22. China: Dawanshan Islands, South China Sea.
ca. 3,000 km east-southeast of Hazaria Patherghatta; five skins, three localities (including type locality of *Inuus sanctijohannis* Swinhoe, [1867]). One skin (SCiEA Coll. No. 2155), collected in October, is in prime pelage; three (SCiEA Coll. Nos. 2150, 2151, 2153), collected in March and April, are late-stage faded; and one (BM(NH) 1868.12.29.10, holotype of *Inuus sanctijohannis*), collected in month unknown, was in the process of molting. The specimens in prime pelage is brightly colored, similar to the Nepalese standards. Hair length measurements of adults are not available.

23. China: Hainan Dao, ca. 2,700 km southeast of Hazaria Patherghatta; 30 skins, 16 localities (including type locality of *Pithecos breviceadus* Elliot, 1913). Twenty-one specimens, collected in October–April, are in prime pelage; four (AMNH 27569, 27575, 60038; ZMB A1904.09), collected in October and March, are early-stage faded; and five, collected in March, May, and July, are late-stage faded. Eleven of the 21 specimens in prime pelage (collected October–February) are brightly colored—similar to the Nepalese standards; these bright specimens include AMNH 27577, the holotype of *Pithecos breviceadus*, which closely matches AMNH 112733 (northern Myanmar: Taro). Seven of the specimens in prime pelage, collected in October–April, are slightly less erythristic than the Nepalese standards. The remaining three (AMNH 27570, October; BM(NH) 1909.7.11.11, October; SCiEA Coll. No. 0089, December) are notably less erythristic than the Nepalese standards. ISHL is 46.2 ± 4.8 mm in four adult females and 45 and 70 mm in two adult males; MTHL is 27.5 ± 2.9 mm in four adult females and 20 and 30 mm in two adult males.

24. Northeastern Vietnam, and China: southern Guangxi, ca. 2,200 to 2,400 km southeast of Hazaria Patherghatta; 20 skins, 11 localities. Six specimens collected in November–January are in prime pelage, eight collected in December–June (7) and month unknown (1) are early-stage faded, one collected in June is late-stage faded, and four collected in October–January have short bright fur and apparently had just completed the molt; a captive (KIZ Coll. No. 631425), obtained in Nanning, China, and kept alive for an unknown period at KIZ, is long-haired and appears somewhat faded. All six specimens in prime pelage were collected in Vietnam; of these, two closely match the Nepalese standards (BM(NH) 1927.12.1.19, Bac Can; ZMVNU 063/16.4, Van Hai), two are slightly darker (BM(NH) 1927.12.1.18, Bac Can; IEBR 733 (833)/560/175, Nghia Dung), one is slightly less erythristic (IEBR 33, Ly Bon), and one is notably less erythristic (ZMVNU 167/3.18.14, Chiem Hoa). In adult females, ISHL is 45.0 ± 8.9 mm (n = 8), and MTHL is 24.3 ± 7.9 mm (n = 7); in one adult male, ISHL is 45 mm, and MTHL is 25 mm. The tail is moderately bushy to bushy in four of the females.

25. China: southern Yunnan, northern Laos, and northwestern Vietnam, ca. 1,600 to 1,900 km southeast of Hazaria Patherghatta; 12 skins, nine localities. Three skins (AMNH 87264; FMIN H3176; KIZ Coll. No. 75840), collected in November–May, and two skins (KIZ 03172, 03180), collected in month unknown, are in prime pelage and are brightly colored—similar to the Nepalese standards; one skin (IEBR D3/M37), collected in month unknown, is early-stage faded; one skin (FMINH 31763), collected in May, and two (KIZ 03173, 03174), collected in month unknown, are late-stage faded; and a captive (AMNH 87278), obtained in November 1931, was in the process of molting when it died on 15 June 1932. The remaining two specimens are somewhat aberrant in their dorsal pelage coloration: a juvenile male (KIZ 000150), collected in October, is much less erythristic than the Nepalese standards—grayish tipped with golden anteriorly, becoming pale golden brown posteriorly; and a ?subadult female (KIZ 000153, skin only), collected in November, is more brownish and less erythristic than usual in *M. mulatta*. Hair length measurements of adults are not available.

26. Central Myanmar, ca. 1,000 to 1,300 km southeast of Hazaria Patherghatta; 33 skins, 16 localities. Fifteen specimens collected in September–May are in prime pelage, 15 collected in May–August are late-stage faded, and three (BM(NH) 1914.7.19.1, 1931.1.11.23, 1931.1.11.27), collected in June–July, were in the process of molting. Of the specimens in prime pelage, seven were collected at various localities, and eight were collected at Papa Hill. The seven collected at various localities average slightly paler and less erythristic than the Nepalese standards; one of these (BM(NH) 1931.1.11.26; January) is similar to the Nepalese standards, five are slightly paler and/or less erythristic, and one (BM(NH) 1931.1.11.22; January) is much darker and less erythristic—yellowish gray anteriorly, washed with burnt orange posteriorly. The eight collected at Papa Hill average notably less erythristic than the Nepalese standards; one (BNHS 5106; September) is similar to the Nepalese standards, two (AMNH 163611, 163613; September–October) are slightly paler and less erythristic,
three (AMNH 163612, 163614, BM(NH) 1914.7.19.2; September–October) are more grayish, and two (AMNH 16310, 16315; October–November) are unusual in their strongly mottled (coarsely agouti) pelage. ISHL is 44.6 ± 5.6 mm in 13 adult females and 46.2 ± 5.5 mm in four adult males; MTHL is 21.9 ± 5.9 mm in eight adult females and 23.3 ± 2.9 mm in three adult males.

27. Southwestern Myanmar, ca. 1,400 km southeast of Hazaria Pathergatta; 10 skins, seven localities. Of seven skins in prime pelage, two (BM(NH) 1931.1.11.20-21), collected in September and October, are similar to the Nepalese standards, and five, collected in November–February, are somewhat less erythritic. One of two skins collected at Toungoo in May (BM(NH) 1931.1.11.18) is early-stage faded—somewhat paler than the Nepalese standards, and the other (BM(NH) 1931.1.11.19) is late-stage faded. Unaccountably, the skin of an early juvenile (BM(NH) 1931.1.11.17), collected near Toungoo in December, also is faded—pale yellowish brown anteriorly, becoming faintly washed with burnt orange on the sacral region (cf. Pocock, 1932, p. 533). ISHL is 43.0 ± 5.7 mm in five adult females; MTHL is 18.3 ± 2.9 mm in three adult females.

28. Northwestern Thailand, ca. 1,700 to 2,000 km southeast of Hazaria Pathergatta; six skins, six localities (including type locality of Macaca sianica Kloss, 1917). Only one of these skins (ZRC 4–154), month of collection unknown, is in prime pelage; this bright skin is similar to the Nepalese standards. Three skins (CTNRC, catalog number unknown; FMNH 99668; ZRC 4–188, holotype of Macaca sianica), collected in March–April, are early-stage faded, and one (FMNH 99669), collected in March, is late-stage faded. One skin (AMNH 54816, subadult male), collected in early February, appears to have been in the process of molting; this does not accord with the late summer molting schedule that generally applies in M. mulatta. ISHL is 50 mm in one adult female and 50 and 70 mm in two adult males; MTHL is 25 mm in one adult female and 35 mm in one adult male.

29. Northeastern Thailand and west-central Laos, ca. 1,800 to 2,100 km southeast of Hazaria Pathergatta; eight skins, five localities. Five skins, collected in January–March and month unknown (one specimen), are in prime pelage; of these, three (USNM 300017; ZRC 4–150, 4–151), collected in February–March, are brightly colored—similar to the Nepalese standards, and two (USNM 296917, 307716), collected in January and month unknown, are somewhat less erythritic. One skin (ZRC 4–152), collected in February, is early-stage faded; one (USNM 307715), collected in month unknown, is late-stage faded; and one (USNM 240488), collected in July, was molting. ISHL is 45 mm in two adult females and 45.0 ± 5.0 mm in three adult males; MTHL is 20 mm in one adult female and 25 mm in one adult male.

30. Southern Laos (one locality) and central Vietnam, ca. 2,800 km southeast of Hazaria Pathergatta; nine skins, six localities. Dorsal pelage color is highly variable in these specimens, all of which appear to be in prime pelage. One skin (IEBR 560/3, adult male, Xuan Ninh) is golden brown anteriorly and burnt orange posteriorly, similar to the Nepalese standards. Two others (USNM 356968, subadult female, Mt. Sontra; USNM 320780, adult female, Dak Sut) are almost uniformly golden brown anteriorly and posteriorly, approximately as in M. fascicularis (cf. Fooden, 1995, p. 25; 1997, p. 227); these two specimens are now allocated to M. mulatta solely on the basis of their relative tail length (USNM 356968, 59.7%; USNM 320780, 64.5%). In the remaining six skins, dorsal pelage color is slightly brighter posteriorly than anteriorly, variably intermediate between that in typical M. mulatta and M. fascicularis (IEBR 40, adult male, Ky Son; MNHN 1899/54, adult female, Song Ta-Voy; ANSP 15135, juvenile female, and ANSP 15138, juvenile, Muang Thateng, Laos; USNM 320781, adult female, and USNM 320782, juvenile male, Dak Sut). In two adult females, ISHL is 65 mm, and MTHL is 10 and 15 mm; in two adult males, ISHL is 50 mm, and MTHL is 30 and 40 mm.

Summary—Judging from specimens examined, there is no general pattern of geographic variation in dorsal pelage color in M. mulatta. Of 166 postinfantile specimens in prime pelage from 30 sample areas, 78 are similar in color to the Nepalese standards, 55 are variably less erythritic, and 33 from scattered sample areas are either more erythritic, darker, paler, browner, or more mottled. Individual variation is great among specimens from the same sample area and even from the same locality; this is vividly demonstrated by the two contrastingly colored adult males collected 4 days apart at Rajapura, Assam, India (Fig. 3B). Conversely, specimens from widely separated parts of the specific range may be nearly identical in color, as illustrated by the following examples of matching pairs: USNM 326332, Gora Dhaka, Pakistan, and USNM 240175, Ashi, Yunnan, China; FMNH 35448, Mangpu, Sikkim, India, and FMNH 31766, Muong Boum, Viet-
nam; BM(NH) 1931.1.11.7. Rajapara, Assam, India, and BM(NH) 1900.5.8.1, Kuantun, Fujian, China; AMNH 112733, Taru, Myanmar, and AMNH 27577, Wuzhi Shan, Hainan, China; AMNH 112732, Taru, Myanmar, and AMNH 57043, Xinglong Xian (= Eastern Tombs), Hebei, China; and BM(NH) 1931.1.11.17, Toungoo, 30 mi northwest, Myanmar, and BM(NH) 1870.7.18.19, Nyochow, Hainan, China.

Limited available evidence suggests that specimens from northwestern Pakistan and eastern Afghanistan (Sample Area No. 5), Tripura, India (No. 8), and China, northeastern Hebei (No. 20) may tend to average somewhat darker than usual in M. mulatta and that specimens from central Myanmar (No. 26) and southwestern Myanmar (No. 27) may tend to average somewhat less erithrrystic. Dorsal pelage color in southern Laos and central Vietnam (No. 30) is transitional between that in typical M. mulatta and neighboring M. fascicularis.

ISHL averages greater in the northern part of the geographic range of M. mulatta, north of ca. 28°N latitude, than in the southern part of the range (Fig. 6). MTHL, which presumably is correlated with perceived bushiness of the tail, also averages greater in the northern part of the range (Fig. 7; cf. Roonalw & Tak, 1981, p. 96; Tak & Kumar, 1984, p. 203).

In the original description of Macacus lasiotus Gray, 1868 (p. 61), hairiness of the ears is casually cited as a diagnostic character of rhesus macaques in Sichuan, China (cf. Jiang Xuelong et al., 1991, p. 244). This appears to be invalid, as indicated by the following list of BM(NH) specimens of M. mulatta in which hairiness of the ears equals or exceeds that in the holotype of Macacus lasiotus (BM(NH) 1871.4.21.4): Afghanistan—1931.1.9.1; Myanmar—1931.1.11.21, 1931.1.11.24; China, Fujian—1900.5.8.1; China, Hubei—1931.1.7.2; India, Assam—1921.7.9.4; India, Jammu and Kashmir—1871.3.3.5; India, Sikkim—1891.10.7.4; India, Uttar Pradesh—1914.7.10.2, 1914.7.10.4; India, West Bengal—1916.7.29.1; Nepal—1921.5.1.2; Pakistan—1920.6.11.1, 1923.11.4.1; and Vietnam—1927.12.1.19, 1927.12.1.20, 1928.7.1.11.

External Measurements and Proportions

Sex and Age Variation

In wild-collected adult M. mulatta specimens examined, mean head and body length in 48 males (531.8 mm) is 13% greater than in 72 females (468.8 mm), and mean body weight in 25 males (7.70 kg) is 44% greater than in 33 females (5.34 kg) (Table 2). Relative length of the tail, hindfoot, and ear in adult females is similar to relative length of these appendages in adult males. From infancy to adulthood, relative length of these appendages declines, indicating that the postnatal growth rate of the appendages is less than that of the head and body (cf. Schultz, 1933, p. 12; Lumer & Schultz, 1941, p. 284). The 33% decline in relative ear length from infancy to adulthood is particularly striking.


Smith (1994c, p. 282) reports that, in captivity, weight gain from age 1 year to age 4 years is more rapid in hybrid Chinese-Indian M. mulatta than in nonhybrid Indian M. mulatta.

Geographic Variation

HEAD AND BODY LENGTH—Collectors’ measurements of head and body length in M. mulatta are
Fig. 6. Latitudinal variation in interscapular hair length in Macaca mulatta adults. In this graph, the measurement for one Afghan male (50 mm) is included with Pakistani data, and the measurement for one Laotian female (45 mm) is included with Thai data; measurements of interscapular hair length are not available for Bangladeshi adults.
available for 120 adult specimens—72 females and 48 males—collected at 93 localities (Table 3). Although these data are invaluable, some inter-collector variation in measurement techniques is inevitable and must be borne in mind.

Head and body length in both sexes tends to increase with latitude (Fig. 8, Table 3), in accord with Bergmann’s rule (cf. Mayr, 1963, p. 319). However, the relationship between head and body length and latitude is not as close as that between

**Fig. 7.** Latitudinal variation in midtail hair length in *Macaca mulatta* adults. In this graph, the measurement for one Afghan male (30 mm) is included with Pakistani data; measurements of midtail hair length are not available for Bangladeshi adults.
greatest length of skull and latitude (Fig. 17, Table 9). In particular, head and body length is aberrantly large, relative to latitude, in one male collected in peninsular India (15°-20°N, 75°-80°E), near the southwestern limit of the specific range, and in 12 females and 6 males collected in southeastern China and northern Vietnam (15°-25°N, 105°-110°E), near the southeastern limit of the specific range; the aberrant group of northern Vietnamese specimens includes one large female and two large males collected on Dao Cat Ba, an island in the Gulf of Tonkin, South China Sea (Fig. 8). Head and body length is small, relative to latitude, in one female collected on Neilingding Dao and one male collected on Dangan Dao, two Chinese islands in the South China Sea (Fig. 8).

Jiang Haisheng et al. (1991, p. 210) compared “body length” in samples of Chinese *M. mulatta* from Hainan Dao (ca. 18°30’N, island) and Guangxi (ca. 23°N, mainland). Although body length in the Hainan Dao sample is less than in the Guangxi sample, the significance of this finding is acknowledged by the authors to be questionable because no information is available concerning whether measured specimens were immatures or adults. In one adult female collected on Hainan Dao that is included in the present study, the relationship between head and body length and latitude does not appear unusual (Fig. 8). Krishnan (1972, p. 541) indicates, without documentation, that body size is reduced in a population of *N. mulatta* at Jaldapara Wildlife Sanctuary, northeastern India.

Crown-rump length in *M. mulatta* captives imported from China has been compared with crown-rump length in *M. mulatta* captives descended from monkeys imported from India (Clarke & O’Neil, 1999, pp. 340, 341). In males, crown-rump length in Chinese-origin adults equalled that in Indian-derived adults; in females, crown-rump length in Chinese-origin adults was less than that in Indian-derived adults. No information is available concerning the region of origin of these monkeys within India or China.

**Tail Length**—Collectors’ measurements of tail length are available for 120 adult specimens of *M. mulatta* (Table 4; see “Head and Body Length,” p. 26). Mean tail length (±SD) is 207.6 ± 32.72 mm in 72 adult females and 228.9 ± 35.78 mm in 48 adult males.

Tail length is aberrantly large (289 mm, 298 mm) in two adult females collected in central Vietnam (10°-15°N, 105°-110°E; Dak Sut), at the southeastern border of the species geographic range. These two outlier specimens have previously been interpreted as evidence of hybridization between *M. mulatta* and *M. fascicularis* (Fooden, 1996, p. 859; 1997, p. 228).

Excluding the two aberrant Dak Sut females, tail length apparently tends to increase slightly with latitude (Fig. 9; cf. Roonwal & Tak, 1981, p. 98). More conspicuously, tail length tends to decrease with longitude, particularly east of ca. 95°E (Fig. 10); marking the eastern end of this west-east cline are six short-tailed specimens collected on four shallow-water islands—Cat Ba, Dangan Dao, Hainan Dao, Neilingding Dao—in the South China Sea (105°-115°E) and two short-tailed specimens collected in Fujian Province on the Chinese mainland (115°-120°E). The shortness of the tail in specimens collected on Hainan Dao and in Fujian was previously noted by Elliot (1909, p. 250) and Jiang Haisheng et al. (1991, p. 210).

Although the tail in *M. mulatta* is shorter than in most other monkeys, it retains an important function in intraspecific communication. Tail carriage serves as a signal of dominance status both in natural populations (Neville, 1968c, p. 15; Lindburg, 1971, p. 60; Ojha, 1974, p. 164; Roonwal & Tak, 1981, p. 96; Wada, 1984, p. 492) and in captive colonies (Altmann, 1962, p. 378; Sade, 1967, p. 101; 1971, p. 294; Waterhouse & Waterhouse, 1976, p. 87; cf. Rodriguez, 1998, abstract no. 307). In captivity, the tail may also function as a rudimentary prehensile organ (Erwin, 1974, p. 130). Preliminary observations in northern India suggest that tail carriage may vary geographically (Roonwal & Tak, 1981, p. 96; Tak & Kumar, 1984, p. 203).

**Relative Tail Length**—Relative tail length, the ratio of tail length to head and body length (T/HB), is a measure of the functional and perceived length of the tail. Geographic variation in this ratio is given separate treatment here because variation in tail length in *M. mulatta* is not entirely congruent with variation in head and body length (see above). This ratio is available for 120 wild-collected adult specimens (see “Head and Body Length,” p. 26). Because relative tail length is similar in females and males (Table 2; Fooden, 1997, p. 223), mixed-sex samples are used in the present analysis.

Latitudinal variation in relative tail length in *M. mulatta* is relatively minor (Fig. 11, Table 5; Fooden, 1997, p. 225), excluding two aberrant specimens collected in central Vietnam (ca. 15°N; see “Tail Length,” above). Longitudinal variation

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Table 2. External measurements and proportions in age/sex classes of wild-collected *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Age/sex class</th>
<th>Head and body length (mm)</th>
<th>Relative tail length (T/HB × 100)</th>
<th>Relative hindfoot length (HF/HB × 100)</th>
<th>Relative ear length (E/HB × 100)</th>
<th>Weight (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infants</td>
<td>284.2 ± 58.6</td>
<td>46.8 ± 9.9</td>
<td>34.2 ± 5.0</td>
<td>12.1 ± 2.1</td>
<td>1.24 ± 0.75</td>
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<tr>
<td></td>
<td>170–387</td>
<td>28.7–62.3</td>
<td>25.5–45.3</td>
<td>9.4–17.6</td>
<td>0.43–2.30</td>
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<tr>
<td></td>
<td>(25)</td>
<td>(24)</td>
<td>(24)</td>
<td>(19)</td>
<td>(8)</td>
</tr>
<tr>
<td>Juveniles</td>
<td>406.2 ± 67.3</td>
<td>46.4 ± 8.9</td>
<td>32.7 ± 5.3</td>
<td>9.1 ± 1.9</td>
<td>3.19 ± 1.51</td>
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<tr>
<td></td>
<td>265–620</td>
<td>27.8–74.0</td>
<td>23.1–65.0</td>
<td>4.9–14.7</td>
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<td>(88)</td>
<td>(86)</td>
<td>(80)</td>
<td>(77)</td>
<td>(47)</td>
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<tr>
<td>Subadults</td>
<td>—</td>
<td>45.4 ± 7.1</td>
<td>30.1 ± 3.4</td>
<td>7.9 ± 1.3</td>
<td>—</td>
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<td></td>
<td></td>
<td>32.1–59.7</td>
<td>21.2–36.9</td>
<td>5.4–10.3</td>
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</tr>
<tr>
<td>Subadult females</td>
<td>453.5 ± 50.6</td>
<td>48.0 ± 8.9</td>
<td>30.9 ± 3.5</td>
<td>8.6 ± 1.2</td>
<td>4.66 ± 0.28</td>
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<tr>
<td></td>
<td>385–530</td>
<td>32.8–59.7</td>
<td>26.3–36.9</td>
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<td>4.50–4.99</td>
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<td>(10)</td>
<td>(10)</td>
<td>(9)</td>
<td>(8)</td>
<td>(3)</td>
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<tr>
<td>Subadult males</td>
<td>525.6 ± 43.2</td>
<td>44.3 ± 6.1</td>
<td>29.7 ± 3.3</td>
<td>7.7 ± 1.4</td>
<td>7.69 ± 2.75</td>
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<td>440–597</td>
<td>32.1–56.0</td>
<td>21.2–34.3</td>
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<td>(24)</td>
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<td>(17)</td>
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<tr>
<td>Adults</td>
<td>—</td>
<td>44.4 ± 8.9</td>
<td>30.0 ± 3.1</td>
<td>8.0 ± 1.2</td>
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<td>19.3–35.7</td>
<td>4.8–11.9</td>
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<td>Adult females</td>
<td>468.8 ± 49.1</td>
<td>45.0 ± 9.64</td>
<td>30.0 ± 3.2</td>
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<td>19.3–35.5</td>
<td>5.2–10.3</td>
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<td>(72)</td>
<td>(72)</td>
<td>(65)</td>
<td>(61)</td>
<td>(33)</td>
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<tr>
<td>Adult males</td>
<td>531.8 ± 55.2</td>
<td>43.5 ± 7.94</td>
<td>29.9 ± 3.1</td>
<td>7.9 ± 1.3</td>
<td>7.70 ± 2.33</td>
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<tr>
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<td>410–660</td>
<td>20.0–62.0</td>
<td>21.6–35.7</td>
<td>4.8–11.9</td>
<td>4.01–14.06</td>
</tr>
</tbody>
</table>

1 Mean ± SD, extremes, and sample size (italicized figures in parentheses).
2 Dental specifications: infants, deciduous teeth only; juveniles, some permanent teeth erupted; subadults, M3 in females or C in males incompletely erupted; adults, all permanent teeth completely erupted.
3 These data are uncontrolled for seasonal weight variation, which has been reported both in females and in males in natural populations (Lindburg, 1977b, p. 247; Pearl et al., 1987, p. 36; cf. Small, 1981, p. 93; Zeng, 1992, p. 22).
4 These values differ slightly from those published previously (Foodeen, 1997, p. 224) because of inclusion here of data for specimens with intermediate relative tail length (60%–75%) and exclusion here of data for specimens that had been held in captivity prior to collection.

in relative tail length in the western half of the geographic range also is relatively minor (Fig. 12, Table 5); from Pakistan (ca. 73°E) to Myanmar (ca. 95°E), mean relative tail length is 46.7 ± 7.0% (SD; extremes, 31.9%–62.0%; n = 68). East of Myanmar, in the northeastern part of the range (northern Vietnam, China), relative tail length tends to decline from west to east, reaching ca. 30% at 120°E; six specimens collected on four islands in the South China Sea are included in this cline. Conversely, relative tail length increases in the extreme southeastern part of the range; in Thailand and Laos (ca. 100°E), mean relative tail length is 53.0 ± 4.9% (extremes, 47.5%–60.8%; n = 8), and in the two aberrant specimens collected in central Vietnam, relative tail length is 64.5% and 72.1%. High relative tail length in these southeastern specimens may be interpreted as further evidence of hybridization between *M. mulatta* and *M. fascicularis* (see "Tail Length," p. 29).

Judging from dry-skin measurements and a published illustration (Table 6; Milne-Edwards, [1870], pl. 32; Pocock, 1932, p. 550), relative tail length apparently was low (730% in adults) in the now-extinct population that formerly inhabited Xinglong Xian (= Eastern Tombs; ca. 40°24′N, 117°30′E), northeastern China (cf. Zhang Yongzu et al., 1989, p. 380). This would be in accord with the pattern of longitudinal variation in relative tail length indicated above (cf. Fig. 11).

**Body Weight**—Body weight data are available for 33 wild-collected adult females and 25 wild-collected adult males (Table 7). Weight, like head and body length, tends to increase with latitude (Fig. 13); at 30° to 35°N, mean weight (females, 7.45 kg, n = 5; males, 12.48 kg, n = 2) is approximately twice that at 15° to 20°N (females,
Table 3. Geographic variation in head and body length (mm) in adult *Macaca mulatta*. First line in each cell (5-degree latitude–longitude block) indicates mean and standard deviation (where sample size is greater than two), second line indicates extremes, and third line indicates sample size (italicized, in parentheses).

| Latitude (°N) | Longitude (°E) | Adult females: 469 ± 49, 370–580, (72) | | |
|---------------|---------------|-----------------------------------------|---|---|---|---|---|---|---|---|
| 30–35         | 70–75         | 510 (1)                                 | 580 (1)                     | 75–80         | 495–525 (2)  | 550 (1)                     | 510 (1)                     | 80–85         | 90–95         | 95–100         | 100–105        | 105–110        | 110–115        | 115–120        |
|                | 85–90         | 450 (1)                                 | 451 ± 37 (1)                | 510 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 510 (1)                     | 580 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     |
| 25–30         | 70–75         | 460–475 (2)  | 470 ± 60 (1)                | 450 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
|                | 80–85         | 400–533 (4) | 450 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
| 20–25         | 85–90         | 430 (1)                                 | 450 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
| 15–20         | 90–95         | 462 ± 39 (1)                | 450 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
| 10–15         | 95–100        | 478 ± 28 (1)                | 480 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
|                | 100–105       | 485 ± 54 (2)  | 490 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
|                | 105–110       | 519 ± 37 (4) | 495 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
|                | 110–115       | 440 (2)                                 | 450 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |
|                | 115–120       | 440 (2)                                 | 450 (1)                                 | 451 ± 37 (1)                | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 | 451 (1)                     | 480 (1)                                 |

Adult males: 532 ± 55, 410–660, (48)

| Latitude (°N) | Longitude (°E) | | |
|---------------|---------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 30–35         | 70–75         | 583 ± 41 (3) | 559–630 (3) | 559 ± 74 (3) | 500–660 (3) | 559 ± 74 (3) | 500–660 (3) | 80–85         | 90–95         | 95–100         | 100–105        | 105–110        | 110–115        | 115–120        |
|                | 100–105       | 514 (2)                                 | 514 (2)                                 | 514 (2)                                 | 514 (2)                                 | 514 (2)                                 | 514 (2)                                 | 105–110       | 110–115       | 115–120        |
|                | 105–110       | 600 (1)                                 | 600 (1)                                 | 600 (1)                                 | 600 (1)                                 | 600 (1)                                 | 600 (1)                                 | 110–115       | 115–120       |
|                | 110–115       | 561 (2)                                 | 561 (2)                                 | 561 (2)                                 | 561 (2)                                 | 561 (2)                                 | 561 (2)                                 | 115–120       |                |
|                | 115–120       | 522–600 (2) | 522–600 (2) | 522–600 (2) | 522–600 (2) | 522–600 (2) | 522–600 (2) | 522–600 (2) |                |

Adult females: 469 ± 49, 370–580, (72)

Adult males: 532 ± 55, 410–660, (48)
Fig. 8. Latitudinal variation in head and body length in *Macaca mulatta* adult non-captives; data points for insular specimens are indicated by two-letter abbreviations (CB = Cat Ba; DD = Dangan Dao; HD = Hainan Dao; ND = Neilingding Dao). In this graph, the measurement for one Laotian female (395 mm) is included with Thai data; measurements of head and body length are not available for Bangladeshi adults.
Table 4. Geographic variation in tail length (mm) in adult *Macaca mulatta*. First line in each cell (5-degree latitude-longitude block) indicates mean and standard deviation (where sample size is greater than two), second line indicates extremes, and third line indicates sample size (italicized, in parentheses).

<table>
<thead>
<tr>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
<th>Adult females: 208 ± 33, 125-298, (72)</th>
<th>Adult males: 229 ± 36, 125-310, (48)</th>
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<tr>
<td></td>
<td>70–75</td>
<td>75–80</td>
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<td>30–35</td>
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<td>185</td>
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<td>225–237 (2)</td>
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<td>25–30</td>
<td>232</td>
<td>222 ± 8</td>
<td>205</td>
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<td>215</td>
<td>233 ± 10</td>
<td>199 ± 18</td>
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<td></td>
<td>228–258 (5)</td>
<td>218–245 (6)</td>
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<tr>
<td>10–15</td>
<td>269 ± 36</td>
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<td>229–300 (3)</td>
<td>228–310 (4)</td>
<td>220–225</td>
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<tr>
<td>25–30</td>
<td>253 ± 26</td>
<td>227 ± 25</td>
<td>222</td>
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<tr>
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<td>220–286 (5)</td>
<td>200–260 (4)</td>
<td>(2)</td>
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<tr>
<td>20–25</td>
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<td>200–229</td>
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<tr>
<td>15–20</td>
<td>260</td>
<td>234</td>
<td>222 ± 18</td>
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<tr>
<td></td>
<td>(I)</td>
<td>234–235 (2)</td>
<td>205–240</td>
</tr>
</tbody>
</table>
Fig. 9. Latitudinal variation in tail length in *Macaca mulatta* adult noncaptive; data points for insular specimens are indicated by two-letter abbreviations (CB = Cat Ba; DD = Dangan Dao; HD = Hainan Dao; ND = Neilingding Dao). In this graph, the measurement for one Laoian female (240 mm) is included with Thai data; measurements of tail length are not available for Bangladeshi adults.
Fig. 10. Longitudinal variation in tail length in *Macaca mulatta* adult noncaptives. For detailed comments, see Figure 9.
Fig. 11. Latitudinal variation in relative tail length (tail length/head and body length) in Macaca mulatta adult noncaptives; data points for insular specimens are indicated by two-letter abbreviations (CB = Cat Ba; DD = Dangan Dao; HD = Hainan Dao; ND = Neilingding Dao). In this graph, the value for one Laotian female (0.61) is included with Thai data; values are not available for Bangladeshi adults.

Data points for specimens collected on four shallow-water islands (Cat Ba, Dangan, Hainan, Neilingding) in the South China Sea fit well within the latitudinal body weight cline.

Weights previously reported for M. mulatta in Hainan Dao (18°23'N, 110°00'E) and northern Pakistan (34°03'N, 73°22'E) are similar to those of specimens examined from the same latitudes (Fig. 13). For Hainan Dao specimens of unknown maturity, Jiang Haisheng et al. (1991, p. 210) reported that mean weight was 3.88 ± 0.20 kg in 33 females and 5.08 ± 0.72 kg in 16 males. In northern Pakistan, Pearl et al. (1987, p. 36) reported that mean weight of adult females was 7.3 kg and that the weight of a large male was 11.9 kg.

Body weight in M. mulatta captives imported from China has been compared with body weight in M. mulatta captives descended from monkeys imported from India (Clarke & O'Neil, 1999, pp. 340, 341; see "Head and Body Length," p. 26). In males, body weight in Chinese-origin adults exceeded that in Indian-derived adults; in females, body weight in Chinese-origin adults was less than that in Indian-derived adults. As previously indicated, no information is available concerning the region of origin of these monkeys within India or China.
Table 5. Geographic variation in relative tail length (tail length/head and body length; %) in adult *Macaca mulatta*, females and males (cf. Table 2). First line in each cell (5-degree latitude-longitude block) indicates mean and standard deviation (where sample size is greater than two), second line indicates extremes, and third line indicates sample size (italicized, in parentheses).

<table>
<thead>
<tr>
<th>Latitude (°N)</th>
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<th>110–115</th>
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<tr>
<td>30–35</td>
<td>46 ± 3.8</td>
<td>44 ± 11.2</td>
<td>47 ± 5.9</td>
<td>47 ± 8.3</td>
<td>49</td>
<td>36 ± 4.4</td>
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<td>45–53</td>
<td>32–41</td>
<td>28–32 (2)</td>
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<tr>
<td>25–30</td>
<td>49 ± 4.2</td>
<td>38–56  (3)</td>
<td>41–46</td>
<td>40 ± 6.6</td>
<td>36 ± 6.7</td>
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<td>(7)</td>
<td>43–53  (15)</td>
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<td>41 ± 3.8</td>
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<td>36–57</td>
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<td>(2)</td>
<td>42–46  (11)</td>
<td>(I)</td>
<td>41 ± 3.8</td>
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<td>28–36 (2)</td>
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<tr>
<td>15–20</td>
<td>44</td>
<td>55 ± 5.1</td>
<td>54 ± 4.7</td>
<td>50</td>
<td>37 ± 6.3</td>
<td>28–44</td>
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<td>(I)</td>
<td>48–60 (8)</td>
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<td>10–15</td>
<td>68</td>
<td>64–72 (2)</td>
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</table>
Cranial Characters

Sex and Age Variation

In wild-collected adult specimens of *M. mulatta* (Figs. 14, 15, Table 8), greatest length of skull (excluding incisors) in 80 males (121.8 ± 8.3 mm) averages about 13% greater than in 120 females (107.8 ± 7.1), and rostral-postrostral ratio in 69 males (50.5 ± 3.0%) averages about 15% greater than in 111 females (44.1 ± 3.7%) (cf. Cochard, 1985, p. 237; Cheverud & Richtsmeier, 1986, p. 392; Mouri, 1995, p. 189). Relative zygomatic breadth (ZB/GL) in 79 males (70.7 ± 2.6%) averages only 2% greater than in 118 females (69.0 ± 2.2%).

From infancy to adulthood, rostral length increases much faster than postrostral length, whereas zygomatic breadth increases only slightly faster than greatest skull length (Table 8). In males, rostral-postrostral ratio in adults is more than 100% greater than in infants (cf. Bhatia, 1978, p. 66), and relative zygomatic breadth in adults is about 10% greater than in infants. Fluctuating asymmetry of the skull and teeth in *M. mulatta* tends to increase ontogenetically to age 6 years (Halgrímsson, 1999, p. 139). An intensive study of maxillomandibular growth in captive *M. mulatta* has been published by Schneiderman (1993, p. 75), and craniofacial growth in laboratory-colony captives has been compared with that in free-ranging captives by King and Schneiderman (1991, p. 105).

Dental emergence norms have been carefully studied in the Yale University laboratory colony...
of *Macaca mulatta* (Fig. 16); in this study, emergence was defined as initial penetration of the gingiva by each tooth. In the Yale colony, deciduous teeth apparently emerged in four major waves. Teeth in the first wave (*i*1, *i*2, *i*3) emerged at median age ca. 0.05 year (18 days), those in the second wave (*i*4) at age ca. 0.1 year (36 days), those in the third wave (*c*1, *c*2, *m*1, *m*2) at age ca. 0.2 year (73 days), and those in the fourth wave (*m*3, *m*4) at age ca. 0.4 year (156 days). Following a diapause of approximately 1 year, permanent teeth also apparently emerged in four major waves. Teeth in the first wave of permanent teeth (*M*1, *M*3) emerged at median age ca. 1.4 years, those in the second wave (*M*2, *P*3, *C*1, *C*2, *P*4) at age ca. 2.5 years, those in the third wave (*M*3, *M*4) at age ca. 3.5 years, and those in the fourth wave (*M*5, *M*6) at age ca. 5.7 years. Mandibular teeth, particularly those in the permanent set, usually emerged slightly earlier than their maxillary counterparts. Ages of dental emergence in females were generally similar to those in males, except for *C*1 and *C*2, which emerged ca. 0.6 year earlier in females (3.13 years, 3.46 years) than in males (3.84 years, 4.04 years), and *M*1 and *M*2, which emerged ca. 0.6 year earlier in males (5.30 years, 5.40 years) than in females (5.74 years, 6.23 years). The elapsed time between initial emergence of a tooth and its complete eruption to full height apparently is a few months for most teeth but probably is ca. 2 years for the permanent canines of males (Cheverud, 1981, pp. 158, 163). In

the free-ranging colony of *M. mulatta* introduced in Cayo Santiago, the second and third molars reportedly emerged as much as 1 year later than in some laboratory colonies (Turnquist & Kessler, 1990, p. 309); this suggests that dental emergence in natural populations of *M. mulatta* may also be retarded relative to that in laboratory colonies.

**Geographic Variation**

**SKULL LENGTH**—Greatest length of skull provides the most comprehensive and reliable indication of geographic size variation in *M. mulatta* (Table 9). This measurement is available for 170 well-localized adult specimens—104 females and 66 males—collected at 126 localities.

Greatest length of skull in both sexes generally increases with increasing latitude (Fig. 17, Table 9). South of 20°N, mean greatest length is 101.1 ± 3.32 mm in 18 adult females and 113.7 ± 3.50 mm in 10 adult males; north of 30°N, mean greatest length is 119.0 ± 4.42 mm in nine adult females and 131.2 ± 6.02 mm in 12 adult males (cf. Albrecht, 1978, p. 129; Gelvin & Albrecht, 1996, p. 111). In 13 adult specimens collected on five islands in the South China Sea, greatest length is similar to that in continental specimens collected at the same latitude (Fig. 17). In the single adult skull (AMNH 57039, male) available from northeastern China, at the northeastern limit of the specific range, greatest length is surprisingly small
Table 7. Geographic variation in body weight (kg) in adult *Macaca mulatta*. First line in each cell (5-degree latitude-longitude block) indicates mean and standard deviation (where sample size is greater than two), second line indicates extremes, and third line indicates sample size (italicized, in parentheses).

<table>
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<th>90–95</th>
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<tr>
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<td>4.5 ± 0.3</td>
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<td>5.1 ± 0.6</td>
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<tr>
<td>Adult females: 5.3 ± 1.3 kg, 3.0–10.0 kg, (33)</td>
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<tr>
<td>Adult males: 7.7 ± 2.3 kg, 4.0–14.1 kg, (25)</td>
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Note: Weight is not controlled for seasonal variation (see Table 2, footnote 3).
Fig. 13. Latitudinal variation in body weight in *Macaca mulatta* adult noncaptive; data points for insular specimens are indicated by two-letter abbreviations (CB = Cat Ba; DD = Dangan Dao; HD = Hainan Dao; ND = Neilingding Dao). Weight data are not available for Bangladeshi and Nepalese adults.
Skull of adult female *Macaca mulatta*—FMNH 99668, Thailand: Ban Mae Lamao. (Photographs by John Weinstein, the Field Museum, negative Nos. Z 94270.1–4.)

(123.8 mm), considering the latitude (40°24'N) of collection of this specimen (Fig. 17); in a subadult female (USNM 240704) collected in the same area, greatest length also is small (100.6 mm).

Longitudinal variation in greatest length of skull is relatively minor (Fig. 18). For example, mean greatest length in a sample of adults collected between 30°N and 35°N in Pakistan and India (females, 120.9 ± 3.26 mm, n = 5; males, 129.3 ± 3.23 mm, n = 8) is similar to that in a sample collected 2,500 km to the east, across the Xizang-Qinghai (Tibetan) Plateau, at the same latitude in China (females, 116.7 ± 4.98 mm, n = 4; males, 136.8 mm [132.6–141.0 mm], n = 2).

Cranial and Dental Morphology—Variation in suites of cranial and dental measurements in >150 specimens that were collected in various sample areas in China and in six specimens that originated in India (localities unspecified) has been studied by two groups of Chinese investi-
Fig. 15. Skull of adult male *Macaca mulatta*—FMNH 99669, Thailand: Huai Ap Nang. (Photographs by John Weinstein, the Field Museum, negative Nos. Z 94271.1-4.)
Table 8. Cranial measurements and proportions in age/sex classes of wild-collected Macaca mulatta.

<table>
<thead>
<tr>
<th>Age/sex class</th>
<th>Greatest length (mm)</th>
<th>Relative zygomatic breadth (ZB/GL × 100)</th>
<th>Postrostral length (mm)</th>
<th>Rostral–postrostral ratio (R/PR × 100)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infants</td>
<td>78.6 ± 6.8</td>
<td>64.3 ± 2.6</td>
<td>67.3 ± 4.6</td>
<td>24.2 ± 3.1</td>
</tr>
<tr>
<td></td>
<td>65.8–93.6</td>
<td>59.1–69.9</td>
<td>59.7–79.2</td>
<td>19.8–34.3</td>
</tr>
<tr>
<td></td>
<td>(37)</td>
<td>(37)</td>
<td>(33)</td>
<td>(33)</td>
</tr>
<tr>
<td>Juveniles</td>
<td>97.8 ± 10.0</td>
<td>67.3 ± 2.2</td>
<td>76.4 ± 5.4</td>
<td>36.1 ± 6.0</td>
</tr>
<tr>
<td></td>
<td>79.1–126.7</td>
<td>61.8–73.5</td>
<td>60.9–91.5</td>
<td>26.8–53.6</td>
</tr>
<tr>
<td></td>
<td>(148)</td>
<td>(146)</td>
<td>(133)</td>
<td>(132)</td>
</tr>
<tr>
<td>Subadult females</td>
<td>101.0 ± 4.3</td>
<td>68.1 ± 1.8</td>
<td>77.8 ± 3.0</td>
<td>39.6 ± 2.8</td>
</tr>
<tr>
<td></td>
<td>95.0–112.0</td>
<td>64.7–71.6</td>
<td>72.1–85.0</td>
<td>34.6–46.8</td>
</tr>
<tr>
<td></td>
<td>(20)</td>
<td>(19)</td>
<td>(19)</td>
<td>(19)</td>
</tr>
<tr>
<td>Subadult males</td>
<td>118.4 ± 7.5</td>
<td>68.9 ± 2.6</td>
<td>85.8 ± 4.7</td>
<td>49.7 ± 3.0</td>
</tr>
<tr>
<td></td>
<td>105.9–136.8</td>
<td>64.1–73.7</td>
<td>78.8–96.3</td>
<td>43.6–56.4</td>
</tr>
<tr>
<td></td>
<td>(36)</td>
<td>(36)</td>
<td>(32)</td>
<td>(32)</td>
</tr>
<tr>
<td>Adult females</td>
<td>107.8 ± 7.1</td>
<td>69.0 ± 2.2</td>
<td>80.7 ± 4.5</td>
<td>44.1 ± 3.7</td>
</tr>
<tr>
<td></td>
<td>92.9–126.5</td>
<td>60.1–73.9</td>
<td>71.3–92.6</td>
<td>37.6–59.4</td>
</tr>
<tr>
<td></td>
<td>(120)</td>
<td>(118)</td>
<td>(111)</td>
<td>(111)</td>
</tr>
<tr>
<td>Adult males</td>
<td>121.8 ± 8.3</td>
<td>70.7 ± 2.6</td>
<td>86.4 ± 4.2</td>
<td>50.5 ± 3.0</td>
</tr>
<tr>
<td></td>
<td>107.1–143.1</td>
<td>65.0–76.1</td>
<td>77.8–96.9</td>
<td>41.3–58.2</td>
</tr>
</tbody>
</table>

Note: Mean ± SD, extremes, and sample size (italicized figures in parentheses). For definition of cranial measurements, see Foeden (1969, p. 40).

1 Dental specifications: infants, deciduous teeth only; juveniles, some permanent teeth erupted; subadults, third molars in females or canines in males incompletely erupted; adults, all permanent teeth completely erupted.

Gators (Jiang Xuelong et al., 1991, p. 242; 1995, p. 44; Pan et al., 1992, p. 40; Peng et al., 1993, p. 2; Yao et al., 1995, p. 113; Yu et al., 1996, p. 152; cf. Sikorska-Piwowska, 1970, p. 9). Although distributions of cranial and dental measurements overlap in these samples, statistically significant differences were discovered among the Chinese samples and between the Chinese and the Indian samples. The two groups of investigators disagree concerning the morphological relationships of samples of M. mulatta collected in south-central China; one group found its south-central Chinese sample to be most similar to a southeastern Chinese sample (Jiang Xuelong et al., 1995, p. 46), whereas the other group found its south-central Chinese sample to be most similar to a southwestern Chinese sample (Yu et al., 1996, p. 153).

Mandibular measurements in specimens of M. mulatta collected in three regions of China have been analyzed by Zhao et al. (1999, p. 63).

Comparison with Macaca fascicularis

Skull length in both sexes averages greater in M. mulatta than in its southern relative, M. fascicularis (cf. Foeden, 1995, p. 38). Conversely, the rostrum in M. mulatta protrudes less than in M. fascicularis (cf. Mouri, 1996, p. 296; Pan et al., 1998, p. 525). Width of the braincase and rostrum appear to be greater in M. mulatta than in M. fascicularis. A median sagittal crest, formed by ontogenetic convergence of the temporal lines, is rare in M. mulatta adult males (well-defined crest in three of 71 specimens examined, incipient crest in one specimen), whereas a sagittal crest is common in M. fascicularis adult males.

Molecular Biology and Genetics

Mitochondrial DNA

Data concerning the geographic variation in mitochondrial DNA (mtDNA) in M. mulatta have been published by three research groups: Hayasaka et al. (1988, p. 271; 1996, p. 1044), Melnick et al. (1993, p. 284; cf. Morales & Melnick, 1998, p. 7), and Zhang and Shi (1989, p. 334; 1993a, p. 8; 1993b, p. 591). In addition, Disotell et al. (1992, p. 6) have published the nucleotide se-
Fig. 16. Dental emergence chronology in *Macaca mulatta*, laboratory colony sample (Hurme & van Wagenen, 1953, pp. 297, 299; 1961, pp. 111-112, 128; Hurme, 1960, pp. 796-797; cf. Maity & Rathore, 1998, p. 250); median, 2nd percentile, and 98th percentile values are indicated for age at initial penetration of gingiva by deciduous and permanent teeth in females and males. Abbreviations: i/I = incisor, c/C = canine, P = premolar, m/M = molar; lowercase letters indicate deciduous teeth, uppercase letters indicate permanent teeth; subscripts indicate mandibular teeth, superscripts indicate maxillary teeth. Arrowheads (lower left in graph) indicate six off-scale 2nd percentile values; i₁, females and males, 0 years (i.e., tooth already erupted at birth); i₂ and i₃, males, 0 years; i₂ and i₃, females, 0.0082 years. Sample sizes: i₁, i₂, i₃—females (n = 53), males (44); c₁, c'—females (51), males (41-42); m₁, m'—females (50), males (41); mₑ, m₂—females (43-44), males (32-33); M₁, M'—females (42), males (30); i₁, i', i₂, i₃—females (41-42), males (22-25); M₁, M'—females (39-40), males (18-19); P₃, P', C₁, C', P₄—females (35-39), males (13-17); M₄, M₅—females (30-31), males (10-12). For additional dental emergence age data collected by various procedures, see Schultz, 1935, p. 499; Eckstein, 1949, p. 367; Gavan, 1967, p. 985; McNamara et al., 1977, p. 701; Trotter et al., 1977, p. 111; Cheverud, 1981, p. 163; Zeng et al., 1984, p. 83; Sharma & Lal, 1986, p. 145; Turnquist & Kessler, 1990a, p. 309; 1990b, p. 239; Zeng, 1992, pp. 20, 22; Smith et al., 1994, pp. 215, 226.

The sequence of the mitochondrial COI gene in one *M. mulatta* individual from an unspecified locality.

Hayasaka et al. (1988, p. 271) used 17 endonucleases to study mtDNA restriction sites in one *M. mulatta* specimen of Indian origin (no further locality information available) and subsequently (1996, p. 1046) determined the nucleotide sequence of an 896-bp region of mtDNA in this.
TABLE 9. Geographic variation in greatest length of skull (mm) in adult *Macaca mulatta*. First line in each cell (5-degree latitude-longitude block) indicates mean and standard deviation (where sample size is greater than two), second line indicates extremes, and third line indicates sample size (italicized, in parentheses).

<table>
<thead>
<tr>
<th>Latitude (°N)</th>
<th>70-75</th>
<th>75-80</th>
<th>80-85</th>
<th>85-90</th>
<th>90-95</th>
<th>95-100</th>
<th>100-105</th>
<th>105-110</th>
<th>110-115</th>
<th>115-120</th>
</tr>
</thead>
<tbody>
<tr>
<td>30-35</td>
<td>120 ± 0.9</td>
<td>118</td>
<td>118-126</td>
<td>(3)</td>
<td>120</td>
<td>114</td>
<td>119-120</td>
<td>109-118</td>
<td>116 ± 1.8</td>
<td></td>
</tr>
<tr>
<td>20-25</td>
<td>104</td>
<td>104 ± 4.9</td>
<td>108 ± 3.6</td>
<td>102</td>
<td>106-113</td>
<td>96-107</td>
<td>98-111</td>
<td>104-117</td>
<td>101</td>
<td></td>
</tr>
<tr>
<td>10-15</td>
<td>104-105</td>
<td>(2)</td>
<td>105</td>
<td>105</td>
<td>105</td>
<td>105</td>
<td>105</td>
<td>105</td>
<td>105</td>
<td></td>
</tr>
</tbody>
</table>

**Adult females: 108 ± 7.0, 93-126, (104)**

**Adult males: 121 ± 8.0, 107-143, (66)**

---

1 Includes 16 imprecisely localized specimens that are included in Table 8.
2 Includes one aberrantly large skull (GL = 124.8 mm) purchased at Zuyu Xian, Xizang Province, China. Excluding this skull, this entry would be 105 ± 2.9, 100-111, (18).
3 Excludes 14 imprecisely localized specimens that are included in Table 8.
4 Includes one aberrantly large skull (GL = 134.0 mm) purchased at Zuyu Xian, Xizang Province, China. Excluding this skull, this entry would be 117 ± 6.8, 109-124, (4).
5 Includes one aberrantly large skull (GL = 131.8 mm) collected at Calcutta, West Bengal State, India.
Indian specimen and in two *M. mulatta* specimens of unknown country of origin; the mtDNA data of these three *M. mulatta* specimens were compared with data derived from *M. cyclopi* (Taiwan; n = 1), *M. fuscata* (Japan; n = 3), and other macaque species. Although the nucleotide sequences of the two *M. mulatta* specimens of unknown country of origin differ from each other at only
0.2% of the sites, their sequences differ from that of the Indian specimen at ca. 6.2% of the sites; this intraspecific sequence divergence greatly exceeds the interspecific divergence between the Indian *M. mulatta* specimen and *M. cyclops* (3.2%) and between the Indian *M. mulatta* specimen and *M. fuscata* (ca. 3.6%). Sequence divergence between the two *M. mulatta* specimens of unknown
country of origin and *M. cyclops* and *M. fuscata* is ca. 5.1% and 5.8%, respectively. Hayasaka et al. (1996, p. 1052) suggest that the taxonomically incongruous intraspecific and interspecific divergences in their *M. mulatta*, *M. cyclops*, and *M. fuscata* sequence data may be the result of either retention of ancestral polymorphism or interspecific hybridization.

Melnick et al. (1993, p. 284) used 15 endonucleases to study mtDNA restriction sites in 18 individuals representing five *M. mulatta* populations—one each from Pakistan (n = 3), northern India (n = 4), and Myanmar (n = 4) and two from southern China (n = 5, n = 2); the exact provenance of these five samples and the number of localities represented by each are unspecified (cf. Melnick et al., 1984, p. 342; Morin et al., 1997, p. 201). Of the 10 haplotypes that were identified in this study, one is unique to the smaller Chinese sample, and three sets of three haplotypes each are unique to the Indian, Myanmar, and larger Chinese samples, respectively; the single haplotype common to the three individuals in the Pakistani sample is the same as that of one individual in the Indian sample. Distance-based and character-based trees reveal similar patterns of relationships among the *M. mulatta* samples studied. In both kinds of trees, the primary divergence is between the Pakistani/Indian (western) samples and the Myanmar/Chinese (eastern) samples (divergence = 3.9% ± 0.45%); on the basis of the magnitude of this divergence, Melnick et al. (1993, p. 287) suggest that western and eastern populations of *M. mulatta* formerly were separated by a major barrier. Divergences among the seven individuals in the Pakistani/Indian samples are very small (d = 0.4% ± 0.31%). The divergence between the Myanmar sample and the two Chinese samples (d = 2.3% ± 0.58%) is approximately twice as great as that between the two Chinese samples (d = 1.2% ± 0.15%).

As a supplement to their investigation, Melnick et al. (1993, pp. 283, 286) compared their data with Hayasaka et al.’s (1988, p. 271) data for one Indian specimen of *M. mulatta*, one specimen of *M. cyclops*, and three specimens of *M. fuscata* (see above). The haplotype of Hayasaka et al.’s Indian *M. mulatta* specimen is most divergent from haplotypes of Melnick et al.’s Chinese samples (d = 3.3% ± 0.16%), next most divergent from the Pakistani/Indian samples (d = 3.0% ± 0.25%), and least divergent from the Myanmar sample (d = 2.1% ± 0.12%); this suggests that Hayasaka et al.’s Indian *M. mulatta* specimen may have originated in eastern India, nearer to Myanmar than to Pakistan. Distance- and character-based trees indicate that haplotype similarity among eastern *M. mulatta*, *M. cyclops*, and *M. fuscata* is greater than haplotype similarity between eastern and western *M. mulatta*; this discrepancy between the gene tree revealed by mtDNA and the species tree revealed by morphology and allozymes (see “Blood Proteins,” p. 52) parallels the taxonomically incongruous findings reported by Hayasaka et al. (see above). Melnick et al. (1993, p. 290; cf. Hoelzer, 1997, p. 624) interpret the pattern of mtDNA haplotype relationships as a retention of ancestral mtDNA similarity by eastern *M. mulatta*, *M. cyclops*, and *M. fuscata*.

In a geographically detailed study, Zhang and Shi (1993b, p. 591) used 20 endonucleases to study mtDNA haplotypes in 36 *M. mulatta* individuals collected at 23 localities in China, Myanmar, and Vietnam (Fig. 19); their analysis also includes Hayasaka et al.’s haplotype data for the Indian *M. mulatta* specimen cited above. Restriction fragment length analysis revealed that each of the 24 localities sampled by Zhang and Shi is characterized by a distinctive mtDNA haplotype; at each of the nine localities represented by more than one individual, haplotypes were uniform in all individuals sampled (n = 2-4). Two trees—one based on the unweighted pair group (UPG) method and the other based on the neighbor-joining (NJ) method (cf. Melnick et al., 1992, p. 196)—were constructed by Zhang and Shi to investigate the pattern of resemblance among the 24 local haplotypes. Although Zhang and Shi favored the UPG tree because of its general congruence with one of several previously proposed subspecific classifications of *M. mulatta* (Jiang Xuelong et al., 1991, p. 242; cf. 1995, p. 44), a consensus tree of stable clusters common to both the UPG tree and the NJ tree provides an independent estimate of geographic variation in mtDNA haplotypes that is not biased by taxonomic preconceptions (Fig. 20).

As indicated by the consensus tree, the largest mtDNA haplotype divergence is between Zhang and Shi’s insular Hainan *M. mulatta* sample (20, n = 2) and 20 mainland locality samples (d = 3.5% ± 0.49%); the positions of three mainland locality samples (E Guangxi, 6; Henan, 12; Fujian, 15) are unresolved relative to this dichotomy. The second-largest mtDNA haplotype divergence is between Hayasaka et al.’s Indian sample (24, n = 1) and the remaining 19 locality samples (d =
2.8% ± 0.35%). The third-largest divergence is between the northwestern Sichuan sample (1, n = 3) and 17 locality samples from Myanmar, China, and Vietnam (d = 1.6% ± 0.29%; the position of one Chinese locality sample (northwestern Yunnan, 19) is unresolved relative to this dichotomy. The fourth-largest divergence is between the eastern Myanmar sample (23, n = 2) and the remaining 16 locality samples (d = 1.3% ± 0.23%). Although the branching pattern of the residual 16 locality samples is not completely resolved, 15 of these samples are positioned within three stable clusters (Fig. 18) as follows:

1. Southwestern Yunnan (22, n = 2); west-central Yunnan (4, n = 1); southeastern Hubei (17, n = 1). Within this cluster, the close resemblance between the west-central Yunnan sample and the southeastern Hubei sample is particularly noteworthy; although these two localities are separated by ca. 1,100 km, the haplotype divergence between the samples is only 0.17%.

2. Central Yunnan (21, n = 1); northeastern Yunnan; Yongshan (8, n = 1); northeastern Yunnan; Yillang (9, n = 1); southern Sichuan (14, n = 2); Hunan (5, n = 1). This and the preceding cluster overlap geographically (Fig. 17).

3. West-central Sichuan (7, n = 1); eastern Sichuan (2, n = 2); Anhui (13, n = 1); Guizhou (3, n = 3); northern Guangxi (16, n = 1); northern Vietnam (10, n = 1); northern Vietnam (11, n = 1).

On the basis of available information (see above), the following hypotheses may be proposed concerning geographic variation in mtDNA in *M. mulatta*:

1. Haplotypes usually are uniform in each local population of *M. mulatta.*

2. Haplotypes in each local population of *M. mulatta* usually differ from those in other local populations.

3. Intraspecific haplotype variation may exceed interspecific haplotype variation.
4. Haplotypes in eastern populations of *M. mulatta* (Myanmar, China, Vietnam) are more divergent from those in western populations of *M. mulatta* (Pakistan, northern India) than they are from those in *M. cyclopis* (Taiwan) and *M. fuscata* (Japan). To determine whether haplotype variation between eastern and western populations of *M. mulatta* is gradual or abrupt, data from geographically intermediate populations would be required.

5. The known haplotype in the insular Hainan population of *M. mulatta* diverges strongly from haplotypes in eastern mainland populations of *M. mulatta*.

6. The known haplotype in the northwestern Sichuan population of *M. mulatta* diverges strongly from haplotypes in other mainland Chinese populations, Vietnamese populations, and eastern Myanmar populations.

7. Haplotypes in Myanmar populations of *M. mulatta* are divergent from those in Chinese and Vietnamese populations.

Authors cited above differ in their interpretation of the chronological significance of mtDNA haplotype variation. Hayasaka et al. (1996, p. 1052) and Zhang and Shi (1993b, p. 594) assume a constant rate of mtDNA nucleotide substitution.
in *Macaca*, whereas Melnick et al. (1993, p. 290; cf. Melnick and Hoelzer, 1993, p. 6; Hoelzer et al., 1998, p. 29) present evidence that this rate may be variable.

**Nuclear DNA**

Using nine enzymes (*Alu1, BamH1, EcoRI, HindIII, Hinfl, HpaI, PstI, PvuII, and XmnI*), Crovella et al. (1994, p. 66) studied highly repeated nuclear DNA restriction patterns in two *M. mulatta* captives. One captive, identified as *M. m. mulatta*, presumably originated in India, and the other, identified as *M. m. lasiotus*, presumably originated in China. The restriction patterns of these two captives were indistinguishable.

*M. mulatta* is polymorphic for the chemokine receptor CXCR4 (a coreceptor for human immunodeficiency virus), but this polymorphism is not known to vary geographically (Chen et al., 1997, p. 2707; Prétet et al., 1998, p. 639). Of 17 rhesus monkeys tested for CXCR4 alleles, allele 1 (adenine at nucleotide 641) was detected in two Indian samples, and allele 2 (thymidine at nucleotide 641) was detected in six Indian samples, seven Chinese samples, and two samples of unknown geographic origin.

Twenty *M. mulatta* captives—10 of Chinese origin and 10 of Indian origin—were included in two studies of restriction fragment length polymorphism at four loci in the β-globin gene cluster (Shimizu & Takenaka, 1991a, p. 178; 1991b, p. 191). Although *M. mulatta* is reported to be polymorphic at all four loci, no data are available concerning the possibility of a relationship between polymorphism and country of origin in this species.

Morin et al. (1997, p. 206; cf. Smith, 1994a, p. 205; Kanthaswamy & Smith, 1998, p. 141) report that mean gene diversity for 15 simple sequence repeat loci is greater in a Chinese *M. mulatta* sample (0.78) than in Indian (0.66) and Thai (0.61) *M. mulatta* samples. Watanabe et al. (1997, p. 351) have compared the nucleotide sequence at the HPRT locus in one *M. mulatta* specimen of unspecified geographic origin with that of other macaque species and nonmacaque catarrhines.

**Blood Proteins**

Judging from available information, geographic variation in blood-protein allele frequencies in *M. mulatta* is relatively minor (Table 10; $F_{ST} = 0.0253$); the most variable locus is Tf (transferrin). Melnick (1988, p. 207; cf. Su et al., 1997, p. 112) studied 25 to 37 loci in samples of this species from Pakistan, India, China, and Thailand; the geographic span of these samples exceeds 3,000 km. For the loci studied, Melnick estimates that the total blood-protein gene diversity in *M. mulatta* is 0.0814; he allocates ca. 86.5% of this diversity to individual differences among members of the same troop, ca. 3.8% to differences among neighboring troops, and 1.0% to differences among local populations within the same country, and ca. 8.7% to differences among populations in different countries. In another study, Melnick et al. (1986, p. 136) found that intercountry variation is weakly clinal. In this cline, the Pakistani and Indian samples form one cluster and the Chinese and Thai samples form another; when a Bangladeshi sample was included in the analysis, it clustered with the Pakistani and Indian samples. Smith et al. (1987, p. 204), in a brief summary comment, indicate that Indian and Chinese samples from unspecified localities approach fixation for opposite alleles at genetic loci for carbonic anhydrase II, properdin factor B, and albumin.

Ding et al. (1998, p. 172) studied blood-protein variation in *M. mulatta* samples collected at six localities in western Yunnan, China. Samples from three localities north of 25°30'N tended to differ from those from three localities south of 25°30'N. Within the northern and southern groups of samples, blood-protein divergence was not related to the distance between localities.

Schmitt and Tomiuk (1995, p. 126) have shown that the distribution of blood-protein allele frequencies per locus in *M. mulatta* closely approximates that predicted by the neutral mutation hypothesis. Three recent studies have investigated the use of blood-protein data in monitoring and maintaining genetic variability in captive research colonies of this species (Gill et al., 1992, p. 89; Smith, 1994a, p. 204; Ely et al., 1994, p. 212).

**Karyology**

Although chromosomal polymorphism has been reported in *M. mulatta* (Sharma & Seth, 1984, p. 380; Small et al., 1985, p. 66), no information is available concerning possible geographic variation in karyotype. The diploid chromosome number in this species is 42.
Table 10. Frequencies (%) of major alleles at polymorphic blood-protein loci in samples of *Macaca mulatta* from six countries (sample sizes indicated by italicized figures in parentheses). Because variability at the Tf locus is exceptionally large, frequency data are provided for six alleles at this locus. For key to locus abbreviations, additional frequency details, and references, see Fooden and Lanyon (1989, p. 214).

<table>
<thead>
<tr>
<th>Locus</th>
<th>Allele</th>
<th>Pakistan</th>
<th>India</th>
<th>Bangladesh</th>
<th>China</th>
<th>Thailand</th>
<th>Vietnam</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acp</td>
<td>A</td>
<td>100 (219)</td>
<td>100 (214)</td>
<td>— (0)</td>
<td>98 (76)</td>
<td>100 (31)</td>
<td>— (0)</td>
</tr>
<tr>
<td>ADA</td>
<td>2</td>
<td>97 (216)</td>
<td>99 (214)</td>
<td>— (0)</td>
<td>92 (76)</td>
<td>94 (31)</td>
<td>— (0)</td>
</tr>
<tr>
<td>Alb</td>
<td>A</td>
<td>98 (32)</td>
<td>40 (214)</td>
<td>— (0)</td>
<td>98 (76)</td>
<td>95 (31)</td>
<td>— (0)</td>
</tr>
<tr>
<td>CA-I</td>
<td>A</td>
<td>100 (219)</td>
<td>100 (238)</td>
<td>100 (26)</td>
<td>96 (76)</td>
<td>85 (46)</td>
<td>— (0)</td>
</tr>
<tr>
<td>CA-II</td>
<td>B</td>
<td>71 (186)</td>
<td>— (0)</td>
<td>— (0)</td>
<td>81 (76)</td>
<td>46 (31)</td>
<td>— (0)</td>
</tr>
<tr>
<td>Dia</td>
<td>C</td>
<td>67 (32)</td>
<td>77 (214)</td>
<td>— (0)</td>
<td>83 (76)</td>
<td>75 (31)</td>
<td>— (0)</td>
</tr>
<tr>
<td>IDH</td>
<td>2</td>
<td>100 (219)</td>
<td>99 (214)</td>
<td>— (0)</td>
<td>97 (76)</td>
<td>99 (46)</td>
<td>— (0)</td>
</tr>
<tr>
<td>PGD</td>
<td>A</td>
<td>99 (219)</td>
<td>84 (238)</td>
<td>84 (25)</td>
<td>97 (76)</td>
<td>96 (31)</td>
<td>— (0)</td>
</tr>
<tr>
<td>PGM-I</td>
<td>1</td>
<td>100 (219)</td>
<td>100 (214)</td>
<td>— (0)</td>
<td>97 (76)</td>
<td>100 (31)</td>
<td>— (0)</td>
</tr>
<tr>
<td>PGM-II</td>
<td>1</td>
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<td>100 (214)</td>
<td>— (0)</td>
<td>96 (76)</td>
<td>96 (31)</td>
<td>— (0)</td>
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<td>1</td>
<td>92 (216)</td>
<td>93 (214)</td>
<td>— (0)</td>
<td>99 (76)</td>
<td>99 (46)</td>
<td>— (0)</td>
</tr>
<tr>
<td>Pi</td>
<td>C</td>
<td>100 (32)</td>
<td>100 (314)</td>
<td>94 (25)</td>
<td>100 (76)</td>
<td>83 (44)</td>
<td>— (0)</td>
</tr>
<tr>
<td>TBPA</td>
<td>F</td>
<td>83 (32)</td>
<td>88 (342)</td>
<td>88 (39)</td>
<td>80 (76)</td>
<td>28 (59)</td>
<td>30 (67)</td>
</tr>
<tr>
<td>Tf</td>
<td>C</td>
<td>26 (219)</td>
<td>45 (688)</td>
<td>35 (55)</td>
<td>23 (106)</td>
<td>28 (59)</td>
<td>30 (67)</td>
</tr>
<tr>
<td>D</td>
<td>7</td>
<td>22</td>
<td>12</td>
<td>20</td>
<td>7</td>
<td>13</td>
<td></td>
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<td>E</td>
<td>1</td>
<td>2</td>
<td>10</td>
<td>9</td>
<td>14</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>14</td>
<td>4</td>
<td>9</td>
<td>9</td>
<td>19</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>F'</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>26</td>
<td>16</td>
<td>11</td>
<td>28</td>
<td>24</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>26</td>
<td>8</td>
<td>23</td>
<td>8</td>
<td>9</td>
<td>9</td>
<td></td>
</tr>
</tbody>
</table>

Physiology and Disease

Blood, Cerebrospinal Fluid, and Temperament

Champoux et al. (1994, p. 352; 1996, p. 81; 1997, p. 56) compared *M. mulatta* infants of Indian ancestry (n = 29) and *M. mulatta* infants of mixed Indian-Chinese ancestry (n = 13) with respect to hematology, serum biochemistry, cerebrospinal 5-HIAA values, and temperament; all infants were nursery reared, and no infants of pure Chinese ancestry were available for this study. The two groups of infants differed significantly (P < 0.05) in hematocrit, hemoglobin, mean corpuscular hemoglobin concentration, mean corpuscular hemoglobin, erythrocyte count, gamma-glutamyltransferase, phosphorus, and total protein. The authors were uncertain whether the same differences would be found in mother-reared infants, and they also were uncertain whether to attribute the hematological and serum biochemical differences to environmental adaptation or random genetic drift.

Compared with the purebred Indian infants, the Chinese-Indian hybrids exhibited lower orientation ability and higher irritability. In separation-reunion experiments, the Chinese-Indian hybrids tended to exhibit greater locomotor stereotypy, less vocalization, and less social play.

Lead Content of Molars

Gląb and Szostek (1996, p. 216) compared the lead content of the lower first molar in 16 *M. mulatta* immatures collected in western India with that in 29 immatures collected in Thailand. The mean lead content in the Indian sample (7.12 ± 2.18 μg/g) was nearly five times that in the Thai sample (1.51 ± 0.48 μg/g; P < 0.001). The authors indicate that the difference probably was the result of exposure to different levels of lead in the environment.

Malaria

The geographic range of *M. mulatta* is mainly north of the geographic range of the Leucospirur group of *Anopheles* mosquitoes, which is the group that includes all known natural vectors of macaque malaria (Fooden, 1994, p. 575). Reported natural malaria infections in *M. mulatta* are restricted to Bangladesh, Thailand, and Vietnam, all in the area where the range of *M. mulatta* over-
lapses that of the Leucosphyrus group. In this area, the known incidence of natural infection is 9.3% (n = 290); contrastingly, in northern India, outside of this area, the incidence of infection is 0% (n > 24,000).

The two species of malarial parasites that are known to naturally infect *M. mulatta* are *Plasmodium cynomolgi* and *P. inui*, the most widely distributed of the seven species of *Plasmodium* that infect macaques (Fooden, 1994, p. 578). Natural and experimental infections with *P. cynomolgi* and *P. inui* are relatively benign in *M. mulatta*. However, experimental infections of *M. mulatta* with *P. knowlesi*, a macaque parasite that does not occur within the geographic range of *M. mulatta*, usually are fatal (n > 90). This suggests that *M. mulatta* has evolved partial resistance to the malarial parasites with which it is sympatric.

**Viral Infections**

In a field study, 24 *M. mulatta* individuals in Bangladesh and six *M. mulatta* individuals in Thailand were tested for antibodies to reveal infections with simian T-lymphotropic retrovirus, type 1 (Ishida et al., 1985, p. 841; Ishida & Varavudhi, 1992, p. 163). Of these 30 individuals, only one from Thailand was seropositive. In other species of macaques studied in Thailand, four of 367 *M. fascicularis* individuals and two of 137 *M. arctoides* individuals were seropositive for this virus; no species of macaque other than *M. mulatta* was tested in Bangladesh.

In a laboratory study, five *M. mulatta* individuals imported from India and six imported from China were compared with respect to susceptibility to experimental infection with simian immunodeficiency virus of macaques (SIV<sub>mac</sub>-239) (Joag et al., 1994, p. 439). Plasma virus titer, infectious cell frequency, and virus burden in spleen and lymph nodes all indicated that the rhesus monkeys imported from India were significantly less resistant to infection with SIV<sub>mac</sub>-239 than were those imported from China.

**Natural History**

**Habitats**

Judging from the geographic distribution of *M. mulatta*, which is centered at ca. 25°N (Fig. 1), the primary adaptation of this species probably is to the seasonal climate of the subtropical zone (cf. Darlington, 1957, p. 413); captives kept in warm climates apparently are highly susceptible to heat-stroke (Vickers, 1986, p. 522). However, the natural range of *M. mulatta* does extend to temperate or subalpine habitats in the north (Table 11). The range of humidity extremes tolerated by *M. mulatta* includes arid areas in western India and tidal swamps in eastern India and Bangladesh. Although most elevational records of *M. mulatta* are below 2000 m (Table 12), this species has been observed or collected as high as ca. 3200 m in Nepal (Hutu Forest) and ca. 4000 m in Qinghai Province, China (Baizha Plantation, Yushu Xian). Among vegetation types, broadleaf forest is the most common habitat of *M. mulatta*, but this species also occurs in mixed broadleaf-needleleaf forests and, least frequently, in needleleaf forests. *M. mulatta* often inhabits disturbed areas (Blanford, 1888b, p. 14; Mills, 1923, p. 222; McCann, 1933b, p. 810; Fooden, 1982b, p. 574; Richard et al., 1989, p. 569; Chalise, 1997, p. 31; Ruggeri & Timmins, 1997, p. 2), where it raids adjacent cultivated fields, and in India it frequently lives in populated areas as a commensal with humans (Southwick et al., 1961, p. 705; Prakash, 1962, p. 83). Habitat variables apparently are related to geographic variation in the scream call of *M. mulatta* (Feng et al., 1997, p. 27).

**Arboreality/Terrestriality**

Judging from the few samples of *M. mulatta* for which daily arboreality/terrestriality activity patterns have been estimated, this species spends, on average, about 72% of its daylight hours on the ground and about 28% in trees (Table 13; cf. Blanford, 1888b, p. 14; McCann, 1933b, p. 810). Unsurprisingly, forest groups may tend to be somewhat more arboreal than nonforest groups, and in the Sundarbans tidal swamp forests, *M. mulatta* reportedly rarely descends from the trees (Mandal, 1964, p. 154; Mukherjee & Gupta, 1965, p. 145). In response to sudden danger, *M. mulatta* flies either on the ground (K. G. Gairdner, 14 April 1916, ZRC 4-188, field tag: Hingston, [1920], p. 244; Green, 1978, p. 154; Mukherjee, 1978b, p. 741; Dang, 1983, p. 1283; Poirier, 1985, p. 298) or into the trees (Mandal, 1964, p. 154; Mukherjee, 1969, p. 53; Fooden, 1971, p. 32; Lindburg, 1971, p. 45; Pirta & Singh, 1978, p. 277; Wada,
<table>
<thead>
<tr>
<th>Sample area</th>
<th>Climate</th>
<th>Forest type</th>
<th>Cultivated field</th>
<th>Village, temple, etc.</th>
<th>Misc. other habitat types</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Afghanistan</td>
<td>Tropical +</td>
<td>Broadleaf +</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td>Pakistan</td>
<td>Subtropical +</td>
<td>Mixed +</td>
<td>+</td>
<td>+</td>
<td>Arid</td>
<td>2</td>
</tr>
<tr>
<td>India, northern²</td>
<td>Temperate +</td>
<td>Needleleaf +</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>3</td>
</tr>
<tr>
<td>India, western³</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Swamp</td>
<td>4</td>
</tr>
<tr>
<td>India, central⁴</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>India, eastern⁴</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>Nepal</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>Bhutan</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>Bangladesh</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Swamp</td>
<td>9</td>
</tr>
<tr>
<td>Myanmar</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>Thailand</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>11</td>
</tr>
<tr>
<td>Vietnam</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>12</td>
</tr>
<tr>
<td>China, southern⁶</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Subalpine</td>
<td>13</td>
</tr>
<tr>
<td>China, western⁷</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>China, central⁸</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>15</td>
</tr>
<tr>
<td>China, northern⁹</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>16</td>
</tr>
<tr>
<td>China: Xianggang (= Hong Kong)¹⁰</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>17</td>
</tr>
</tbody>
</table>

Table 12. Frequency distribution of elevation records of *Macaca mulatta* (see Gazetteer, Appendix 2).

<table>
<thead>
<tr>
<th>Elevation (m)</th>
<th>Number of records</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–500</td>
<td>155</td>
</tr>
<tr>
<td>500–1000</td>
<td>92</td>
</tr>
<tr>
<td>1000–1500</td>
<td>34</td>
</tr>
<tr>
<td>1500–2000</td>
<td>13</td>
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<tr>
<td>2000–2500</td>
<td>20</td>
</tr>
<tr>
<td>2500–3000</td>
<td>7</td>
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<tr>
<td>3000–3500</td>
<td>3</td>
</tr>
<tr>
<td>3500–4000</td>
<td>1</td>
</tr>
<tr>
<td>4000–4500</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>327</td>
</tr>
</tbody>
</table>

1984, p. 494; Choudhury, 1991b, p. 123; Chopra et al., 1992, p. 81). Nighttime sleeping sites generally are in trees (Hingston, 1920, p. 244; Koford, 1963, p. 143; Mandal, 1964, p. 154; Shou et al., 1964, p. 60; Lindburg, 1971, p. 29; Vessey, 1973, p. 614; Makwana, 1978, p. 486; 1979b, p. 919), but groups in Afghanistan and northern China have been reported to sleep on the ground (Puget, 1971, p. 200; Qu et al., 1993, p. 616), and urban groups often sleep on the roofs of buildings (Ojha, 1977, p. 519; Mukherjee, 1969, p. 49; 1978a, p. 278). Two parturitions that have been observed in wild populations apparently occurred on the ground (Lindburg, 1971, p. 77; Mathur, 1994, p. 132).

Geographic variation in the relative frequency of terrestrial locomotion in *M. mulatta* reportedly is correlated with variation in morphology of the scapula, clavicle, and humerus (Yu et al., 1993, p. 87; Xue et al., 1998a, p. 147; 1998b, p. 29; 1999, p. 140).

Swimming

*M. mulatta* is capable of swimming across a water gap ca. 1 km wide (Drickamer & Vessey, 1974, p. 362; Varley & Vessey, 1977, p. 54; Sade, 1985, p. 28; Rawlins & Kessler, 1986b, p. 26). This species reportedly swims to search for food (Mukherjee & Gupta, 1965, p. 145; Dang, 1983, p. 1283), to escape from danger (Muir, 1916, p. 353; Southwick et al., 1974, p. 198; Berman, 1977, p. 763), and apparently also for pleasure and/or thermoregulation (McCann, 1933b, p. 810; Pillari & Pilleri, 1982, p. 158; Malik & Menon, 1992, p. 39). In captivity, 2-day-old infants are capable of swimming (Riopelle, 1980, p. 262), and juveniles have been trained to swim underwater and to open a food box underwater (Anderson et al., 1992, p. 2; 1994, p. 356).

Group Size and Composition

The mean size of ca. 1,182 nonprovisioned or minimally provisioned groups for which data are available is ca. 32.2 individuals (Table 14); reported extremes are two and ca. 250 individuals. The size of nonprovisioned groups apparently tends to average largest (86.1–ca. 105.0 individ-

Table 13. Arboreal/terrestrial behavior recorded during daylight hours in samples of *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>% Arboreality</th>
<th>Extremes</th>
<th>Sample size</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SD</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>34</td>
<td></td>
<td>1 group</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td></td>
<td>1 locality</td>
<td>2</td>
</tr>
<tr>
<td>Ancient fort area</td>
<td>27.8 ± 2.3</td>
<td>25.2–29.5</td>
<td>3 localities</td>
<td>3</td>
</tr>
<tr>
<td>Temple</td>
<td>17.1 ± 3.4</td>
<td>13.2–19.4</td>
<td>3 groups (2 localities)</td>
<td>3</td>
</tr>
<tr>
<td>Urban</td>
<td>34.1 ± 13.9</td>
<td>10.2–46.5</td>
<td>5 localities</td>
<td>3</td>
</tr>
<tr>
<td>Pond area</td>
<td>21.0</td>
<td></td>
<td>1 locality</td>
<td>3</td>
</tr>
<tr>
<td>Roadside</td>
<td>21.8</td>
<td>20.1–23.6</td>
<td>2 localities</td>
<td>3</td>
</tr>
<tr>
<td>Canal bank</td>
<td>40.2 ± 11.7</td>
<td>29.3–52.6</td>
<td>3 localities</td>
<td>3</td>
</tr>
<tr>
<td>Forest</td>
<td>22.5 ± 5.6</td>
<td>16.5–27.7</td>
<td>3 individuals</td>
<td>4</td>
</tr>
<tr>
<td>Island colony</td>
<td>28.4 ± 11.1</td>
<td>10.2–52.6</td>
<td>20 groups or localities</td>
<td>4</td>
</tr>
</tbody>
</table>

uals) at the northern extremes of the species’ geographic range—in Afghanistan and in the Chinese provinces of Qinghai and Henan (cf. Southwick et al., 1996, p. 102). Solitary males, living independently of nearby troops, have been observed in all parts of the species range (references cited in Table 14). Provisioned groups—one of which reportedly included 1,045 members—tend to average larger than nonprovisioned groups.

Nonprovisioned and provisioned groups of various sizes have been observed to split permanently into two autonomous daughter groups (Southwick & Beg, 1961, p. 390; Koford, 1966, p. 2; Missakian, 1973b, p. 622; Malik et al., 1984, p. 315; 1985, p. 417; Seth et al., 1986, p. 115; Malik, 1992, p. 8; Wang et al., 1996, p. 265). The smallest group known to have undergone fission included 28 individuals (daughter groups, 10 and 18 individuals) (Melnick & Kidd, 1983, p. 230). Fission probably usually occurs between matri-lines (Chepko-Sade & Sade, 1979, p. 70).

In nonprovisioned and provisioned groups, the average sex ratio is approximately one sexually mature male to three sexually mature females (Table 15). The reported minimum ratio is approximately one male to 12 females, and the reported maximum ratio is approximately three males to two females.

Home Range, Day Range

Home range averages approximately 65 ha in 323 nonforest groups of *M. mulatta* and 196 ha in 129 forest groups (Table 16). Overlap of home ranges of adjacent troops is extensive (Lindburg, 1971, p. 32; Southwick et al., 1982, p. 623; Jiang Haisheng et al., 1991, p. 212) and may reach 100% (Makwana, 1979b, p. 919). Depending on local food and water sources and snow cover, different parts of a group’s home range may be used in different seasons (Kurup, 1965, p. 193; Neville, 1968b, p. 113; Lindburg, 1977b, p. 241; Wada, 1984, p. 487; cf. Pearl et al., 1987, p. 36).

Day ranges average 1.15 km in nine nonforest groups and 1.91 km in ≥16 forest groups (Table 17).

Population Density

In areas inhabited by *M. mulatta*, the mean reported population density is 37.2 individuals/km² in forest habitats and 201.1 individuals/km² in nonforest habitats (Table 18). Among the nine forest habitat areas surveyed, mean population density was unusually high—120.0 individuals/km²—on Hainan Dao, a tropical island off the southeastern coast of China. In the provisioned free-ranging population of *M. mulatta* that was introduced in 1938 on Cayo Santiago (area 0.152 km²), Puerto Rico, the mean population density in 1983 had reached 7638.2 individuals/km².

Diet

The natural diet of *M. mulatta* is primarily vegetarian and includes fruits, seeds, flowers, leaves, buds, shoots, twigs, stems, roots, bark, pith, and resin of hundreds of species of angiosperms, gymnosperms, and fungi (Table 19). Angiosperm plants consumed include trees, shrubs, climbers, grasses, and other herbs. In six carefully surveyed geographic areas, the following minimum numbers of species of wild plants were discovered to be exploited for food by *M. mulatta*: northern Pakistan, 35 species (Goldstein & Richard, 1989, p. 552); Himachal Pradesh, northern India, 121 species (Pirta et al., 1997, p. 103); Uttar Pradesh, northern India, 150 species (Lindburg, 1977a, pp. 263–268; Makwana, 1979a, p. 244); central Nepal, 61 species (Marriott, 1978a, p. 759); Bangladesh, 41 species (Ahsan, 1994, p. 82); and Henan, east-central China, 73 species (Qu et al., 1993, p. 612). On Cayo Santiago, Puerto Rico, the provisioned introduced population of *M. mulatta* supplements its diet of monkey chow by feeding on 73 of the 163 plant species that grow on the island (Marriott et al., 1993, p. 332). In addition to exploiting wild plants, natural populations of *M. mulatta* opportunistically raid numerous species of cultivated crop plants (Makwana, 1979a, p. 247; Siddiqi & Southwick, 1980, p. 55; Poirier & Hu, 1983, p. 387; Malik & Southwick, 1988a, p. 339; Lal, 1990, pp. 113, 123; Gupta & Kumar, 1992, p. 227; Datta, 1996, p. 941). Seasonal variation has been noted in the species and parts of plants that are consumed (Lindburg, 1977a, p. 263; Wada, 1984, p. 480; Goldstein & Richard, 1989, p. 554; Fellows, 1992, p. 132; Gupta & Kumar, 1992, p. 227; Qu et al., 1993, p. 611).

Plant consumption by *M. mulatta* apparently also varies geographically (Table 19). Judging from available data, grasses and other herbs provide most of the natural food for this species in

**FOODEN: SYSTEMATIC REVIEW OF THE RHESUS MACAQUE, MACACA MULATTA**
### Table 14. Group size reported for *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Mean</th>
<th>Minimum</th>
<th>Maximum</th>
<th>No. of groups</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nonprovisioned or minimally provisioned groups</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Afghanistan</td>
<td>ca. 105.0</td>
<td>ca. 30</td>
<td>ca. 250</td>
<td>≥12</td>
<td>1</td>
</tr>
<tr>
<td>Pakistan</td>
<td>ca. 40.0</td>
<td>ca. 12</td>
<td>ca. 78</td>
<td>≥9</td>
<td>2</td>
</tr>
<tr>
<td>India, northern</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jammu and Kashmir, Himachal Pradesh</td>
<td>ca. 30.8</td>
<td>4</td>
<td>50</td>
<td>78</td>
<td>3</td>
</tr>
<tr>
<td>Punjab, Haryana, Rajasthan</td>
<td>24.0</td>
<td>≤11</td>
<td>≥73</td>
<td>35</td>
<td>4</td>
</tr>
<tr>
<td>Uttar Pradesh</td>
<td>ca. 28.9</td>
<td>5</td>
<td>127</td>
<td>ca. 77</td>
<td>5</td>
</tr>
<tr>
<td>Various states(^2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urban</td>
<td>33.5</td>
<td>4</td>
<td>116</td>
<td>134</td>
<td>6</td>
</tr>
<tr>
<td>Rural</td>
<td>29.4</td>
<td>3</td>
<td>165</td>
<td>318</td>
<td>6</td>
</tr>
<tr>
<td>Forest</td>
<td>33.3</td>
<td>4</td>
<td>ca. 100</td>
<td>111</td>
<td>6</td>
</tr>
<tr>
<td>India, peninsular</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>—</td>
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<td>—</td>
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<td></td>
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<td>26</td>
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<td>128</td>
<td>14</td>
<td>27</td>
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<tr>
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<td></td>
<td></td>
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<td>—</td>
<td>—</td>
<td>1</td>
<td>30</td>
</tr>
<tr>
<td>Nepal(^3)</td>
<td>54.6</td>
<td>≤29</td>
<td>138</td>
<td>12</td>
<td>31</td>
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<td>China</td>
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<td>Hainan Dao</td>
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<td>83</td>
<td>123</td>
<td>3</td>
<td>33</td>
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<tr>
<td>Mean</td>
<td>ca. 76.9</td>
<td>8</td>
<td>1,045</td>
<td>64</td>
<td></td>
</tr>
</tbody>
</table>

Provisioned introduced population (Puerto Rico)

| Cayo Santiago                      | 191.7 | 100 | 306 | 6 | 34 |

northern Pakistan, whereas fruits and leaves of trees, shrubs, and climbers provide most of the food in Bangladesh and in the Indian states of Uttar Pradesh and Rajasthan. Similarly, gymnosperm seeds and needles are frequently consumed in northern parts of the geographic range (Afghanistan, Pakistan, Himachal Pradesh, Punjab, Henan, Hubei) but apparently are less frequently eaten elsewhere; this obviously is correlated with the geographic distribution of gymnosperms (Küchler, 1978, p. 17).

Larval and adult insects (Orthoptera, Isoptera, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera) apparently are the most common animal food of *M. mulatta* (Lindburg, 1971, pp. 23, 33; Makwana, 1979a, pp. 243–247). Other known animal food includes spiders, crayfish, crabs, shellfish (?bivalves), fish, birds’ eggs, and honeycombs (Table 19). In Vietnam, animal food is estimated to constitute 5–7% of the diet of *M. mulatta* (Dang, 1983, p. 1283). In parts of India, however, consumption of animal foods may be less frequent; at three Indian localities, feeding on insects was never observed (Siddiqi & Southwick, 1980, p. 55; Malik & Southwick, 1988a, p. 340; Gupta & Kumar, 1992, p. 227), and at another locality, *M. mulatta* individuals appeared reluctant to eat hen’s eggs that were provided for them (Lindburg, 1971, p. 33).

Ingestion of soil (geophagy) by *M. mulatta* has been observed at three localities in India (Delhi, Rajasthan, Asarori), one locality in Nepal, and one locality in China (Table 19). At one of the Indian localities (Asarori), the soil was specifically identified as termite mound soil; monkeys at this locality also occasionally licked whitewash off painted walls. Geophagy also has been reported in the provisioned introduced population of *M. mulatta* on Cayo Santiago, Puerto Rico (Sultana & Marriott, 1982, p. 338); in these monkeys, selective ingestion of clay may function to prevent or ameliorate gastrointestinal disorders, including endoparasitism (Mahaney et al., 1995, p. 331; Knezevich, 1997, p. 73; cf. Bolton et al., 1998, p. 204).

For captive, relatively sedentary adult female *M. mulatta* (mean weight = 7.7 kg), the daily maintenance energy requirement is estimated to be 430 kcal (Henderson et al., 1993, p. 10; cf. Bourne, 1975, p. 99). This can be supplied by 150 g of monkey chow (10 large biscuits), supplemented by small amounts of fresh fruit and multivitamin tablets; such a diet has been shown to maintain body weight in singly housed monkeys for at least 11 weeks. In the free-ranging provisioned group on Key Lois, Florida, adults consume a daily average of ca. 225 g of chow in addition to naturally available food (Pucak et al., 1982, p. 207). Preliminary experimental evidence suggests that calorie-restricted diets may retard age-related pathology in captive *M. mulatta* (Couzin, 1998, p. 1018).

During the rainy season, water requirements of *M. mulatta* are met primarily by consumption of succulent plant food (Mukherjee & Gupta, 1965, p. 146; Lindburg, 1971, p. 35; Malik & South-
<table>
<thead>
<tr>
<th>Sample area</th>
<th>Pooled sex ratio</th>
<th>Group sex ratios</th>
<th>Number of sexually mature individuals</th>
<th>No. of groups</th>
<th>References¹</th>
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<td>Non-provisioned or minimally provisioned groups²</td>
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<td>?</td>
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<td>7</td>
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<tr>
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<tr>
<td>Jammu and Kashmir, Himachal</td>
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<td>0.29</td>
<td>1.43</td>
<td>1,029</td>
<td>68</td>
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<td></td>
<td></td>
<td></td>
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<td>0.50</td>
<td>103</td>
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<td>1.00</td>
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<td>43</td>
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<td>Various states³</td>
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<td></td>
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<td></td>
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<td>0.34</td>
<td>≤0.16</td>
<td>≥1.17</td>
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<td>111</td>
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<td>0.64</td>
<td>129</td>
<td>11</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>6</td>
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<tr>
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<td>1.00</td>
<td>629</td>
<td>44</td>
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<td>≥0.67</td>
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<td>0.18</td>
<td>0.50</td>
<td>131</td>
<td>6</td>
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<td>1.00</td>
<td>208</td>
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<td>?</td>
<td>46</td>
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<tr>
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<td>0.08</td>
<td>1.43</td>
<td>12,343</td>
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<td></td>
<td></td>
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<td>0.29</td>
<td>0.85</td>
<td>375</td>
<td>14</td>
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<td>≤0.21</td>
<td>≥0.47</td>
<td>961</td>
<td>16</td>
</tr>
<tr>
<td>Various states³</td>
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<td></td>
<td>56</td>
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<td>0.48</td>
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<td>≤0.21</td>
<td>0.85</td>
<td>1,967</td>
<td>54</td>
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</tbody>
</table>


² Cf. Wang et al., 1996, pp. 267, 268.
³ Pooled data reported for groups observed in several northern Indian states; some of these groups probably also are included in reports cited in preceding entries for northern Indian states.

wick, 1988a, p. 345). During the dry season, these monkeys move as a group to drink at streams or other open water sources, often in the morning and evening (N. A. Baptista in Hinton & Fry, 1923, p. 403; Lindburg, 1971, p. 36; Puget, 1971, p. 200; Naumann & Nogge, 1973, p. 92; Makanwa, 1979b, p. 919). Drinking apparently is usually by oral suction, but monkeys also sometimes
### Table 16. Home range area reported for groups of *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Habitat</th>
<th>Home range area (ha)</th>
<th>Mean group size</th>
<th>No. of groups</th>
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<td>Minimum</td>
<td>Maximum</td>
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<td>ca. 10</td>
<td>ca. 10</td>
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<td>—</td>
<td>69</td>
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<tr>
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<td>Forest</td>
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<td>—</td>
<td>84</td>
</tr>
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<td>?</td>
<td>?</td>
<td>37.0</td>
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<tr>
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<td>Forest</td>
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<td>100</td>
<td>400</td>
<td>?</td>
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<td>China</td>
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<tr>
<td>Hainan Dao</td>
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<td>16</td>
<td>72</td>
<td>ca. 60</td>
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<td>Forest</td>
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<td>1,100</td>
<td>1,500</td>
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<td>35.4</td>
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<td>16</td>
<td>≥2,020</td>
<td>ca. 41.3</td>
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<tr>
<td>India, northern</td>
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<td></td>
</tr>
<tr>
<td>Rajasthan</td>
<td>Forest⁴</td>
<td>400</td>
<td>—</td>
<td>—</td>
<td>68</td>
</tr>
<tr>
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<td>Temple</td>
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<td>1.5</td>
<td>2</td>
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<td>76</td>
<td>≤70</td>
<td>≥230</td>
<td>135.2</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Manipur</td>
<td>Temple</td>
<td>8</td>
<td>—</td>
<td>—</td>
<td>128</td>
</tr>
<tr>
<td>Nepal</td>
<td>Temple</td>
<td>?</td>
<td>2.5</td>
<td>24</td>
<td>54.6</td>
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<tr>
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<td>1,800</td>
<td>2,200</td>
<td>103.0</td>
</tr>
<tr>
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<td>Temple</td>
<td>64.6</td>
<td>1.5</td>
<td>≥230</td>
<td>131.0</td>
</tr>
<tr>
<td>Mean</td>
<td>Forest</td>
<td>1466.7</td>
<td>400</td>
<td>2,200</td>
<td>91.3</td>
</tr>
</tbody>
</table>


dip their hands into a water source and lick the water from their hands (Lindburg, 1971, p. 36; Morrison & Menzel, 1972, p. 54; Makwana, 1979a, p. 251; Malik & Menon, 1992, p. 39). Adults in the provisioned group on Key Lois, Florida, drink ca. 500 ml of water per day (Pucak et al., 1982, p. 207).

In indigenous *M. mulatta* populations studied, the average proportion of waking hours that are spent in feeding varies from 15.8% to 45.0% (Table 20). Feeding activity generally peaks twice a day—in the morning, shortly after waking, and in the afternoon, before roosting for the night (Siddiqi & Southwick, 1980, p. 60; Jiang et al., 1988b, p. 295; Malik & Southwick, 1988b, p. 101; Gupta & Kumar, 1992, p. 229). In winter, the length of the midday feeding pause tends to be reduced (Lindburg, 1977b, p. 231; Pearl et al., 1987, p. 38).

### Predators

Observers have recorded attacks on *M. mulatta* by raptorial birds, dogs, weasels, leopards, and ti-
### Table 17. Day range reported for groups of *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Habitat</th>
<th>Day range (km)</th>
<th>Number of groups observed</th>
<th>References¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Minimum</td>
<td>Maximum</td>
</tr>
<tr>
<td><strong>India</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Himachal Pradesh</td>
<td>Urban</td>
<td>1.11</td>
<td>0</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>1.22</td>
<td>0</td>
<td>4.6</td>
</tr>
<tr>
<td>Rajasthan</td>
<td>Urban</td>
<td>1.75</td>
<td>?</td>
<td>≥2.0</td>
</tr>
<tr>
<td></td>
<td>Rural</td>
<td>0.90</td>
<td>?</td>
<td>≥1.0</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>4.00</td>
<td>?</td>
<td>≥4.0</td>
</tr>
<tr>
<td>Uttar Pradesh</td>
<td>Urban</td>
<td>0.93</td>
<td>?</td>
<td>≥1.0</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>2.04</td>
<td>≤0.4</td>
<td>≥3.5</td>
</tr>
<tr>
<td>Bangladesh</td>
<td>?</td>
<td>2.00</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>China: Hainan Dao</td>
<td>Forest</td>
<td>?</td>
<td>≤1.0</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>1.15</td>
<td>0</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>1.91</td>
<td>0</td>
<td>4.6</td>
</tr>
</tbody>
</table>


...gers (see below); additional reported predators are sharks and crocodiles (in the Sundarbans tidal swamps) and snakes (Mukherjee & Gupta, 1965, p. 145; Seth et al., 1983, p. 42). In Uttar Pradesh, India, hawks were observed to kill young rhesus monkeys (Pirta & Singh, 1978, p. 275; cf. Lindburg, 1971, p. 43), and in Henan, China, an eagle was observed to injure two juveniles (Qu et al., 1993, p. 610). The sight of raptorial birds is known to provoke alarm responses in *M. mulatta*, both in India (Roonwal & Mohnot, 1977, p. 134; Singh & Pirta, 1983, p. 85) and in the introduced population on Cayo Santiago, Puerto Rico (Chapais & Schulman, 1980, p. 740). At a temple in India, rhesus monkeys attacked and killed two hawks (Pirta, 1984, pp. 271, 276).

Attacks by dogs that resulted in injury or death to *M. mulatta* have been documented in Uttar Pradesh and Delhi, India (Lindburg, 1971, p. 73; Makwana, 1978, p. 485; Johnson & Southwick, 1984, p. 211; Malik et al., 1985, p. 418); Champion (1929, p. 424) noted that *M. mulatta* individuals invariably called in the direction of his dog when he and the dog walked together in the forest. Fatal attacks by weasels on *M. mulatta* infants have been reported by Pirta and Singh (1978, p. 275; cf. Singh & Pirta, 1983, p. 85), who also report an alarm response to a weasel by these monkeys. Leopards are a major predator of *M. mulatta* (Champion, 1934, p. 120; Roberts, 1977, p. 88; Roonwal & Mohnot, 1977, p. 134). Predation by tigers, alarm responses, and the apparent mobbing of a tiger by *M. mulatta* have been reported in India and Bangladesh (Mandal, 1964, p. 157; Hendrichs, 1975, p. 184; Lindburg, 1977b, p. 242).

Experimental study of captive *M. mulatta* indicates that fearful avoidance of snakes is much stronger in wild-reared individuals than in laboratory-reared individuals (Joshi et al., 1964, p. 349; Mineka et al., 1980, p. 655). Naive, fearless laboratory-reared monkeys may become fearful of snakes as a result of exposure to the fearful behavior of other monkeys (Mineka et al., 1984, p. 363; Cook et al., 1985, p. 595). In captive *M. mulatta*, fear of snakes seems to be greater in dominant individuals than in subordinate individuals (Brennan & Anderson, 1988, p. 357; Peugeot et al., 1994, p. 88).

### Intergroup Behavior

The behavioral interactions of adjacent groups of *M. mulatta* appear to be highly variable (Table 21). Some observers report frequent intergroup contacts, whereas others report that intergroup contacts are rare and apparently avoided (Malik et al., 1984, p. 315; Makwana, 1979b, p. 920). Although harmonious intergroup encounters, including intergroup matings, have been observed, most contacts seem to arouse antagonism, which may range from tense behavior or relatively mild branch shaking to violent physical combat (Southwick et al., 1965, p. 143; Neville, 1968c, p. 15; Lindburg, 1971, p. 37). At some localities, both peaceful and hostile contacts have been observed between the same groups. During contacts, larger
### Table 18. Population density reported for *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Habitat</th>
<th>Population density (individuals/km²)</th>
<th>Number of groups surveyed</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Minimum</td>
<td>Maximum</td>
</tr>
<tr>
<td>India, northern</td>
<td>Mixed²</td>
<td>109.0</td>
<td>21.2</td>
<td>217.0</td>
</tr>
<tr>
<td>Himachal Pradesh</td>
<td>Ancient fort area³</td>
<td>51.0</td>
<td>32.0</td>
<td>70.2</td>
</tr>
<tr>
<td>Delhi</td>
<td>Urban</td>
<td>385.4</td>
<td>3.1</td>
<td>418.4</td>
</tr>
<tr>
<td>Rajasthan</td>
<td>Temple¹</td>
<td>947.6</td>
<td>882.7</td>
<td>1,012.6</td>
</tr>
<tr>
<td>Uttar Pradesh</td>
<td>Urban</td>
<td>752.0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Rural</td>
<td>44.8</td>
<td>—</td>
<td>—</td>
<td>5</td>
</tr>
<tr>
<td>Forest</td>
<td>27.0</td>
<td>—</td>
<td>—</td>
<td>57.1</td>
</tr>
<tr>
<td>Various states⁴</td>
<td>Urban</td>
<td>154.2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Rural</td>
<td>192.5</td>
<td>85.9</td>
<td>356.4</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>34.2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Temple¹</td>
<td>243.6</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>India, eastern</td>
<td>Assam</td>
<td>Forest</td>
<td>28</td>
<td>—</td>
</tr>
<tr>
<td>Nepal</td>
<td>Forest</td>
<td>9.3</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Bangladesh</td>
<td>Forest</td>
<td>21.1</td>
<td>5.0</td>
<td>52.0</td>
</tr>
<tr>
<td>China</td>
<td>Hainan Dao</td>
<td>Forest⁵</td>
<td>120.0</td>
<td>≥50.0</td>
</tr>
<tr>
<td></td>
<td>Guangdong</td>
<td>Forest</td>
<td>48.0</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Guangxi</td>
<td>Forest</td>
<td>55.6</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Hunan</td>
<td>Forest</td>
<td>12.0</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Henan</td>
<td>Forest⁵</td>
<td>7.2</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>Nonforest</td>
<td>201.1</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>Forest</td>
<td>36.2</td>
<td>≤5.0</td>
</tr>
</tbody>
</table>

**Introduced provisioned populations (U.S.A.)**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th>Mean</th>
<th>Minimum</th>
<th>Maximum</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>South Carolina</td>
<td>Morgan Island</td>
<td>2.320</td>
<td>—</td>
<td>—</td>
<td>—³</td>
<td>5</td>
</tr>
<tr>
<td>Florida</td>
<td>Key Lois</td>
<td>1.270</td>
<td>—</td>
<td>—</td>
<td>—²</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Raccoon Key</td>
<td>1.790</td>
<td>—</td>
<td>—</td>
<td>—³</td>
<td>16</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Cayo Santiago</td>
<td>7.638</td>
<td>—</td>
<td>—</td>
<td>—³</td>
<td>17</td>
</tr>
</tbody>
</table>

¹ Key to references: I. Camperio Ciani, 1984, p. 373; Ross et al., 1993, p. 161; cf. Pirta et al., 1997, p. 100. 2

² Includes nonforest and forest groups; some of the nonforest groups are provisioned.
³ Provisioned.
⁴ Pooled data for groups observed in several northern Indian states; some of these groups may be included in reports cited in preceding entries for northern Indian states.
⁵ Includes two provisioned groups.
⁶ 3.758 individuals.
⁷ Ca. 699 individuals.
⁸ Ca. 1,030 individuals.

Groups almost invariably displace smaller groups. In crowded introduced provisioned free-ranging populations, intergroup contacts are more frequent than in indigenous populations, but these contacts are otherwise generally similar (Tables 18,21).

In *M. mulatta*, as in other species of macaques, males nearly always leave their natal group before reaching sexual maturity and join a nearby group (Neville, 1968a, p. 772; Lindburg, 1969, p. 1177; Melnick et al., 1984, p. 238; Teas, 1984, p. 241; Singh, 1986, p. 607); subsequently, these males apparently transfer to other nearby groups at intervals ranging from a few months to a few years. Most intergroup transfers apparently coincide ei-
Table 19. Foods reported eaten by *Macaca mulatta*. Dietary proportions are indicated where data are available.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Fruits, seeds</th>
<th>Flowers</th>
<th>Leaves</th>
<th>Other</th>
<th>Grasses</th>
<th>Other herbs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Afghanistan</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Pakistan</td>
<td>1.7%</td>
<td>5.5%</td>
<td>7.4%</td>
<td>1.0%</td>
<td>12.7%</td>
<td>48.5%</td>
</tr>
<tr>
<td>India</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Himachal Pradesh</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Punjab</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>Haryana</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Delhi</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Rajasthan</td>
<td>59%</td>
<td>10%</td>
<td>30.6%</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Uttar Pradesh</td>
<td>ca. 70%</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Asarori/Dhulokot</td>
<td>36.3%</td>
<td>9.2%</td>
<td>33.7%</td>
<td>+</td>
<td>+</td>
<td>18.8%</td>
</tr>
<tr>
<td>Chhatari-do-Raha</td>
<td>+16</td>
<td>+16</td>
<td>+16</td>
<td>+16</td>
<td>1.0%</td>
<td>6.4%</td>
</tr>
<tr>
<td>Sumera Fall</td>
<td>+18</td>
<td>+18</td>
<td>+18</td>
<td>+18</td>
<td>+18</td>
<td>+18</td>
</tr>
<tr>
<td>Orissa</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>West Bengal</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Assam</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Manipur</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Tripura</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Nepal</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Bangladesh</td>
<td>53%</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Thailand</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Vietnam</td>
<td>+9,23</td>
<td>+9,23</td>
<td>+9,23</td>
<td>+9,23</td>
<td>+9,23</td>
<td>+9,23</td>
</tr>
<tr>
<td>China</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Hainan</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Xianggang (= Hong Kong)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Sichuan</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hubei</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Henan</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hebei</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

1 Pine, fit, cedar, yew.
2 Includes roots, bark, shoots, reeds, stems, twigs, buds, pith, and resin.
3 Includes bark, cones, shoots, and exudate.
5 Residual 12.6% of diet not specified.
6 Composite grass/clover percentage here arbitrarily split equally between grass and clover.
7 Hen’s eggs, provided by humans.
8 Residual 0.4% of diet not specified.
9 May include herbs.
10 Birds’ eggs.
11 Includes termites, grasshoppers, ants, beetles, and honeycomb from nest of wild bees.
12 Experimentally provisioned hen’s eggs were eaten by some monkeys after initial hesitation.
### Table 19. Extended.

<table>
<thead>
<tr>
<th>Gymnosperms&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Fungi</th>
<th>Cultivated plants</th>
<th>Provisioned food</th>
<th>Insects, spiders, crustaceans</th>
<th>Other animal food</th>
<th>Soil</th>
<th>References&lt;sup&gt;1&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seeds</td>
<td>Leaves</td>
<td>Other&lt;sup&gt;2&lt;/sup&gt;</td>
<td></td>
<td></td>
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<tr>
<td>10.4%</td>
<td>0.2%</td>
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<td>7</td>
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<td>2.0</td>
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<td>10</td>
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<tr>
<td>+</td>
<td>17.5%</td>
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<td>+</td>
<td>14</td>
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<td>+</td>
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<td>+</td>
<td>&gt;50%</td>
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<td>+</td>
<td>+</td>
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<td>+</td>
<td>67%</td>
<td>+</td>
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</tr>
<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>20</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>21</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>5%–7%&lt;sup&gt;24&lt;/sup&gt;</td>
<td>+</td>
<td>+</td>
<td>22</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>23</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>24</td>
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<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>25</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>26</td>
</tr>
<tr>
<td>+</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>27</td>
</tr>
<tr>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>28</td>
</tr>
</tbody>
</table>

---

<sup>1</sup> Termite mound soil with high iron content.

<sup>2</sup> Includes grass.

<sup>3</sup> Termite mound soil; whitewash licked off wall.

<sup>4</sup> Total angiosperm nonherb dietary proportion, 5.9%.

<sup>5</sup> Crow killed by monkeys at Chhatari-do-Raha or Sumera Fall, not eaten; unsuccessful attempt to catch another bird also observed.

<sup>6</sup> Total angiosperm nonherb dietary proportion, 47.0%.

<sup>7</sup> Plant parts eaten by monkeys are not specified.

<sup>8</sup> Fish.

<sup>9</sup> Brood nest section was removed from wild bec nest by monkeys.

<sup>10</sup> Bird’s egg.

<sup>11</sup> Fruits constitute 80% of diet in winter; leaves constitute most of diet in summer.

<sup>12</sup> Includes insects, crayfish, shellfish, and fish.

<sup>13</sup> Population probably introduced (Herklots, 1951, p. 83).

<sup>14</sup> Unspecified invertebrates, presumably arthropods.

<sup>15</sup> Population now extinct.

---

In provisioned introduced populations, male transfer is approximately four times more frequent during the peak mating season than during other seasons (Vandenbergh, 1967, p. 189; Boelkins & Wilson, 1972, p. 132). A recent study indicates that the age at which a male transfers to another
group is positively correlated with the level of central nervous system serotonin activity (Mehlman et al., 1995, p. 909).

**Interspecific Behavior**

**INTRAGENERIC—** *M. mulatta* is broadly sympatric with *M. assamensis*, *M. thibetana*, and *M. arctoides*; it is more narrowly sympatric with *M. nemestrina*; and it is marginally sympatric or parapatric with *M. radiata* and *M. fascicularis* (Fooden, 1980, p. 4). Ecologically, *M. assamensis*, *M. thibetana*, *M. arctoides*, and *M. nemestrina* generally prefer primary broadleaf evergreen forest, whereas *M. mulatta*, *M. radiata*, and *M. fascicularis* generally prefer secondary or deciduous forest and disturbed habitats (Fooden, 1982b, p. 574).

Groups of *M. mulatta* and *M. assamensis* have been observed in close proximity in eastern Nepal (one locality; J. A. McNeely in Fooden, 1982a, p. 26). West Bengal, India (two localities; Khajuria, 1966, p. 284; Mukherjee et al., 1995, p. 30), and western Thailand (one locality; Eudy, 1979, pp. 92, 97, 199). However, these apparently were casual contacts, and no mixing of *M. mulatta* and *M. assamensis* groups was observed at any of these localities. *M. mulatta* and *M. assamensis* also reportedly coexist at one locality in Bangladesh (Feeroz et al., 1995, p. 76); no further information is available concerning this interspecific association.

In China, the local distribution of *M. mulatta* tends to be negatively correlated with that of *M. thibetana*, which generally inhabits higher elevations (Wada et al., 1986, p. 93). However, three mixed groups have been reported in Zhejiang Province (Kang Ximin, ZMNH, pers. comm., 24 October 1985), and another possibly mixed group has been reported in Jiangxi province (David, 1875, vol. 2, p. 256). In the Zhejiang groups (Zhoucong, January 1985, two groups; Zhidaikou, August 1985, one group), most members were *M. mulatta*. In the possibly mixed group in Jiangxi (Kuatun, ca. 20 km northwest, 8 October 1873), 10 individuals were *M. thibetana*, and one may have been *M. mulatta*.

In Tripura, eastern India, a group of *M. mulatta* and a group of *M. arctoides* have been observed

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### Table 20. Daily waking-hour time budget estimates (%) for *Mucaca mulatta.*

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Feeding</th>
<th>Locomotion</th>
<th>Resting</th>
<th>Social behavior</th>
<th>Other</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pakistan: forest</td>
<td>45</td>
<td>10</td>
<td>35</td>
<td>10</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>India, northern</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delhi: fort site</td>
<td>22.8</td>
<td>18.6</td>
<td>33.7</td>
<td>20.8</td>
<td>4.1</td>
<td>2</td>
</tr>
<tr>
<td>Uttarakhand: forest</td>
<td>32.3</td>
<td>44.8</td>
<td>22.9</td>
<td>—</td>
<td>—</td>
<td>3</td>
</tr>
<tr>
<td>Various states</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temple</td>
<td>26.7</td>
<td>15.8</td>
<td>36.7</td>
<td>18.6</td>
<td>2.2</td>
<td>4</td>
</tr>
<tr>
<td>Urban</td>
<td>21.9</td>
<td>19.3</td>
<td>36.7</td>
<td>19.7</td>
<td>2.4</td>
<td>4</td>
</tr>
<tr>
<td>Pond</td>
<td>28.0</td>
<td>11.2</td>
<td>39.3</td>
<td>20.5</td>
<td>1.0</td>
<td>4</td>
</tr>
<tr>
<td>Roadside</td>
<td>31.3</td>
<td>14.3</td>
<td>34.7</td>
<td>19.3</td>
<td>0.4</td>
<td>4</td>
</tr>
<tr>
<td>Canal bank</td>
<td>25.0</td>
<td>19.9</td>
<td>40.0</td>
<td>13.0</td>
<td>2.1</td>
<td>4</td>
</tr>
<tr>
<td>Forest</td>
<td>33.6</td>
<td>24.2</td>
<td>35.1</td>
<td>5.6</td>
<td>1.5</td>
<td>4</td>
</tr>
<tr>
<td>Nepal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temple*</td>
<td>27</td>
<td>25</td>
<td>28</td>
<td>21</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Forest</td>
<td>15.8</td>
<td>39.4</td>
<td>27.0</td>
<td>15.1</td>
<td>2.7</td>
<td>6</td>
</tr>
</tbody>
</table>

**Introduced provisioned population (U.S.A.)**

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Feeding</th>
<th>Locomotion</th>
<th>Resting</th>
<th>Social behavior</th>
<th>Other</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cayo Santiago</td>
<td>13.3</td>
<td>23.1</td>
<td>36.3</td>
<td>25.0</td>
<td>2.3</td>
<td>7</td>
</tr>
</tbody>
</table>

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1 Ca. 13 hr/day (Marriott, 1978b, p. [27]; Malik & Southwick, 1988b, p. 101).
3 Includes foraging and drinking.
4 Includes self-grooming and category “Look.”
5 Includes allogrooming and playing.
8 Means for five groups (extremes: feeding, 10.6%-47.8%; locomotion, 32.8%-71.2%; resting, 15.6%-36.5%).
9 Percentages reported as rounded whole numbers (sum 102%).
Table 21. Intergroup contact behavior reported in *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Habitat</th>
<th>Frequency of contacts</th>
<th>Mood of contacts</th>
<th>Larger group displaces smaller group</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Common</td>
<td>Rare</td>
<td>Peaceful</td>
<td>Hostile</td>
</tr>
<tr>
<td>Pakistan India</td>
<td>Forest</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Himachal Pradesh</td>
<td>Temple</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Delhi</td>
<td>Rural</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uttar Pradesh</td>
<td>Fort site</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aligarh</td>
<td>Temple</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Asarori Forest</td>
<td>Forest</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Bareilly</td>
<td>Roadside</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Dehra Dun</td>
<td>Rural</td>
<td>+</td>
<td></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Haldwani area</td>
<td>Forest</td>
<td>+</td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Kaukori</td>
<td>Rural</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>West Bengal</td>
<td>Swamp</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>China: Henan</td>
<td>Forest</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Provisioned introduced populations (U.S.A.)**

| Puerto Rico     |               |          |      |          | +        | +                              | 13         |
|                 | Cayo Santiago | Island   | +    |          | +        | +                              |            |
|                 | La Cueva I.   | Island   | +    |          | +        | +                              | 14         |
| South Carolina  | Morgan I.     | Island   | +    |          | +        | +                              | 15         |


2 Includes one mixed rhesus-langur group.

10 to 150 m from one another, peacefully feeding on the ground (Mukherjee, 1977, p. 111; 1982, p. 75). In Bangladesh, *M. mulatta* and *nenestrina* are listed as sympatric at five localities (Feeroz et al., 1995, p. 76).

*M. mulatta* and *M. radiata* have been reported in mixed-species groups in peninsular India at three close-lying localities near the 1,000-km-long boundary between the geographic ranges of these two species (Fooden et al., 1981, p. 465; Koyama & Shekar, 1981, p. 248). One of these mixed-species groups included one *M. mulatta* female and three *M. radiata* males; these four monkeys were ca. 50 m from a larger group of *M. mulatta*. Another mixed group included at least 22 *M. mulatta* individuals and one *M. radiata* male; two additional unseen *M. radiata* individuals reportedly were also associated with this group. The third mixed group included 18 *M. mulatta* individuals and one *M. radiata* male. At another nearby locality, a group of 20 *M. mulatta* individuals remained within 10 to 50 m of a group of 22 *M. radiata* individuals for ca. 45 min (Fooden et al., 1981, p. 472); neither mixing nor overt interaction occurred between these two groups.

The boundary between the geographic ranges of *M. mulatta* and *M. fascicularis* extends approximately 2,000 km across the Indochinese peninsula. Although direct contact between these two species has not been reported, a few morphologically intermediate specimens have been collected near the interspecific boundary (Fooden, 1997, fig. 3). This probably indicates that limited hybridization has occurred between *M. mulatta* and *M. fascicularis*. Hybridization between *M. mulatta* and *M. fascicularis* has been reported in mixed-species groups in Xianggang (= Hong Kong) that are the result of human introduction (Southwick & Southwick, 1983, p. 19; Southwick & Manry, 1987, p. 48; Burton & Chan, 1996, p. 395).
In summary, divergent habitat preferences apparently limit contact between *M. mulatta* and *M. assamensis*, *M. thibetana*, *M. arcoides*, and *M. nemestrina*. In marginal habitats, *M. mulatta* may encounter these four species; such contacts apparently are not hostile, and they may result in the formation of mixed groups. The habitat preferences of *M. mulatta* are similar to those of *M. radiata* and *M. fascicularis*. Along the boundary between the geographic ranges of *M. mulatta* and *M. radiata*, nonhostile interspecific contact and mixed-species groups have been observed; along the boundary between the ranges of *M. mulatta* and *M. fascicularis*, morphological evidence indicates the occurrence of occasional hybridization.

**INTERGENERIC**—In northern and peninsular India, the geographic range of *M. mulatta* broadly overlaps that of the Hanuman langur, *Semnopithecus entellus*, and frequent contacts between these two species have been observed. In antagonistic encounters, *M. mulatta* usually is more aggressive and displaces *S. entellus* (Makwana, 1979b, p. 920; Pirta, 1984, pp. 274–279; Lindburg, 1971, p. 43; Ross et al., 1993, p. 162; Mathur, 1996, p. 360); however, at one locality groups of each species defended territories against incursion by the other species (Mathur, 1982, p. 12), and at another locality a male *S. entellus* successfully drove off a male *M. mulatta* (Neville, 1968c, p. 16). Peaceful encounters that have been reported include groups of *M. mulatta* and *S. entellus* feeding together in the same tree and in the same cultivated field (Oboussier & von Maydell, 1960, p. 144; Jay, 1965, p. 212; Lindburg, 1971, p. 43; Prater, 1980, p. 37; Mathur, 1982, p. 12) and interspecific play by infants and juveniles (Manohar & Mathur, 1992, p. 114). Mixed-species groups also have been reported; these usually are composed of one or two *M. mulatta* individuals in a group of *S. entellus* (Jay, 1963, p. 274; 1965, pp. 200, 212, 249; Roonwal & Mohnot, 1977, p. 264; Singh & Sen, 1977–78, p. 136; Mathur & Lobo, 1990, p. 308); in at least two of these groups, the *M. mulatta* individuals were dominant to the *S. entellus* individuals (Jay, 1963, p. 274; Roonwal & Mohnot, 1977, p. 264). In a mixed-species group that included 40 *S. entellus* individuals and eight *M. mulatta* individuals, an adult female *S. entellus* nursed an infant *M. mulatta*, and a young male *S. entellus* carried an infant *M. mulatta* on his back (Das & Sharma, 1981, p. 496).

In northeastern India, *M. mulatta* is sympatric with the golden langur, *Trachypithecus geei*. Interspecific behavior between these monkeys apparently is variable, as they have been reported to maintain distance from one another (Khajuria, 1962b, p. 128); to casually encounter one another peacefully (Mukherjee & Saha, 1974, p. 337); to feed in close proximity, but with *M. mulatta* on the ground and *T. geei* in the branches overhead (Mukherjee, 1978b, p. 741); to feed together harmoniously in favored food trees (Oboussier & von Maydell, 1959, p. 106); and, in two instances, to contest for possession of a feeding site, with *M. mulatta* prevailing on both occasions (Mukherjee, 1978b, p. 742).


In northern India, *M. mulatta* individuals were observed to chase a jackal, *Canis aureus*, and frequently to chase away crows, *Corvus* sp., that were competing for provisioned food (Lindburg, 1971, p. 43).

**Reproduction**

**Seasonality**

Matings and births are strongly seasonal in natural populations of *M. mulatta* (Table 22). At localities widely dispersed across the geographic range of this species, reported matings consistently peak in the fall and winter, and births peak in the spring and summer. At four sample areas in India, a second, minor birth peak in the fall
Table 22. Mating and birth periods reported for natural populations of *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Approximate latitude (N)</th>
<th>Mating period</th>
<th>References</th>
<th>Birth period</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Afghanistan</td>
<td>35°</td>
<td>(No data)</td>
<td></td>
<td>Apr.–Nov.</td>
<td>1</td>
</tr>
<tr>
<td>Pakistan</td>
<td>34°</td>
<td>Aug.–Nov.</td>
<td>2, 3</td>
<td>Mar.–May</td>
<td>2, 4</td>
</tr>
<tr>
<td>India</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Himachal Pradesh</td>
<td>31°</td>
<td>Aug.–Nov.</td>
<td>5, 6</td>
<td>Mar.–May²</td>
<td>5</td>
</tr>
<tr>
<td>Delhi</td>
<td>28°</td>
<td>Sept.–Feb.</td>
<td>7</td>
<td>Mar.–July (major)</td>
<td>8</td>
</tr>
<tr>
<td>Rajasthan</td>
<td>27°</td>
<td>Oct.</td>
<td>9</td>
<td>Mar.–July (major)</td>
<td>9, 10</td>
</tr>
<tr>
<td>Uttar Pradesh</td>
<td>29°</td>
<td>Sept.–Feb.³</td>
<td>11, 12</td>
<td>Mar.–July (major)</td>
<td>11, 13</td>
</tr>
<tr>
<td>Calcutta</td>
<td>23°</td>
<td>Dec.</td>
<td>14</td>
<td>Apr.–May (major)</td>
<td>15</td>
</tr>
<tr>
<td>Sundarbans</td>
<td>22°</td>
<td>(No data)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nepal</td>
<td>28°</td>
<td>Oct.–Feb.</td>
<td>16</td>
<td>Apr.–Aug.</td>
<td>16, 17</td>
</tr>
<tr>
<td>Vietnam</td>
<td>20°</td>
<td>(No data)</td>
<td></td>
<td>Summer, primarily⁴</td>
<td>18</td>
</tr>
<tr>
<td>China</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hainan</td>
<td>18°</td>
<td>Nov.–Mar.</td>
<td>19</td>
<td>Apr.–Aug.</td>
<td>19</td>
</tr>
<tr>
<td>Xianggang (= Hong Kong)⁵</td>
<td>22°</td>
<td>(No data)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Guangxi</td>
<td>23°</td>
<td>Nov.–Jan.</td>
<td>21</td>
<td>Apr.–Aug.</td>
<td>21</td>
</tr>
<tr>
<td>Yunnan⁷</td>
<td>22°</td>
<td>Sept.–Jan.</td>
<td>22</td>
<td>Mar.–June</td>
<td>22</td>
</tr>
<tr>
<td>Hubei</td>
<td>31°</td>
<td>Jan.–Mar.⁴</td>
<td>23</td>
<td>July–Aug., peak⁶</td>
<td>23, 24</td>
</tr>
<tr>
<td>Henan</td>
<td>35°</td>
<td>Sept.–Nov.</td>
<td>25</td>
<td>Mar.–May</td>
<td>25</td>
</tr>
</tbody>
</table>


Also has been reported; this presumably implies an unreported minor mating peak in the spring. The occurrence of a minor birth peak in the fall may account for the somewhat protracted birth seasons that have been reported in Afghanistan and Vietnam. There is no evidence that births in natural populations living at higher latitudes occur later than in those living at lower latitudes (Table 22), as previously suggested by data derived primarily from translocated captive populations (Van Horn, 1980, p. 192; cf. Lindburg, 1987, p. 197). In captive groups of *M. mulatta* housed outdoors in the northern hemisphere, reproductive seasonality is generally similar to that in natural populations (Harrison, 1980, p. 271; Van Horn, 1980, p. 183; Curie-Cohen et al., 1983, p. 129; Goo & Fugate, 1984, p. 67; Small & Smith, 1986, p. 293; Taub & Mehman, 1989, p. 164; Bercovitch, 1992, p. 275; Ouyang & Ma, 1992, p. 14; Lehman et al., 1994, p. 120; Johnson & Kapsalis, 1995b, p. 272); captives in the southern hemisphere exhibit reversed cycles, generally mating in March–August and giving birth in September–February, in accord with southern hemisphere seasons (Hartman, 1931, p. 135; Strahan et al., 1973, p. 385; Coimbra-Filho & Maia, 1977, p. 75; Bielert & Vandenbergh, 1981, p. 231; de Faaria & Guerra, 1985, p. 187). Captives housed indoors tend to

lose reproductive seasonality (Valerio et al., 1969a, p. 66; Michael & Zumpe, 1976, p. 308; Herndon et al., 1985, p. 735).

Sexual Maturation

In natural populations, females may become sexually mature (i.e., capable of engaging in fertile copulations) as early as age 2.5 years (Table 23); more commonly, however, female sexual maturity is not achieved until age 3.5 to 5.5 years. Males in natural populations apparently become sexually mature later than females, perhaps usually at age 6.5 years. In captive colonies, most females become sexually mature at age 3.5 years (Vandenbergh, 1973, p. 7; Rawlins & Kessler, 1986c, p. 52; Ouyang & Ma, 1992, p. 14; Bercovitch & Berard, 1993, p. 105); reproductive capability in captive females probably requires a minimum body weight of ca. 4 kg (Bercovitch et al., 1998, p. 137). Although captive males are capable of fertilizing females at age 3.5 years (Catchpole & van Wagenen, 1975, p. 133; Stern & Smith, 1984, p. 24; Bernstein et al., 1991, p. 33), males in the free-ranging Cayo Santiago colony usually do not participate in breeding activity before age 4.5 or 5.5 years (Conaway & Koford, 1964, p. 586; Sade, 1968, p. 25; cf. Ouyang & Ma, 1992, p. 14). In captivity, sexual maturation is influenced by diet, housing, group density, and social rank (Zimmermann et al., 1975, p. 298; Wilen & Naftolin, 1976, p. 358; Schwartz et al., 1988, p. 240; Wilson et al., 1988, p. 2655; Bercovitch & Berard, 1993, p. 105; Mann et al., 1998, p. 497).

In 59 captive females, the first menstrual bleeding (menarche) preceded sexual maturity by ca. 1 year (Bercovitch & Goy, 1990, p. 64). The mean age at menarche in this group was 29.8 ± 0.6 months (SEM; extremes, 20.1–42.4 months); in another colony, the mean age at menarche was 9 months less (20.6 months, n = 25; extremes, 13.9–25.3 months) (van Wagenen, 1972, p. 25).

In males, the testes usually are scrotal at birth (Wislocki, 1933a, p. 134; 1933b, p. 234). Within a few months they ascend to the inguinal region and remain there until age 3 to 4 years, when they return to the scrotum (Schultz, 1933, p. 26; Sade, 1964, p. 175; Goy et al., 1982, p. 288). During the next year or two, the testes may temporarily reascend to the inguinal region, but after about age 5.5 years they become permanently scrotal. At or before the age of permanent testis descent, males generally emigrate from their natal group, usually near the beginning of a mating season (Koford, 1966, p. 5; Sade, 1968, p. 26; Missakian, 1973a, p. 228; Drickamer & Vessey, 1974, p. 361; Sade et al., 1977, p. 256; Colvin, 1983, p. 161; Jiang et al., 1988a, p. 110; Kaplan et al., 1995, p. 231). Subsequently, males also generally emigrate again as adults (Lindburg, 1969, p. 1177); in one captive free-ranging colony, the average group tenure of postjuvenile males was ca. 2 years (Vessey & Meikle, 1987, p. 289). Females apparently rarely emigrate from their natal group; in one captive free-ranging colony, fewer than 3% of females

### Table 23. Age of sexual maturity reported for natural populations of *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Approximate latitude (N)</th>
<th>Provisioned</th>
<th>Adolescent sample size</th>
<th>Estimated age (yr) at first fertile copulation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Females</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Youngest age</td>
</tr>
<tr>
<td>Pakistan, N</td>
<td>34°</td>
<td>No</td>
<td>6</td>
<td>4.5</td>
</tr>
<tr>
<td>India: Delhi</td>
<td>28°</td>
<td>Yes</td>
<td>13</td>
<td>2.5</td>
</tr>
<tr>
<td>Vietnam</td>
<td>20°</td>
<td>?</td>
<td>? (1.5, puberty)</td>
<td>3.5</td>
</tr>
<tr>
<td>China: Hainan</td>
<td>18°</td>
<td>Yes</td>
<td>&lt;24</td>
<td>4.5 1</td>
</tr>
<tr>
<td>China: Henan</td>
<td>35°</td>
<td>Yes</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Males</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Youngest age</td>
</tr>
<tr>
<td>Pakistan, N</td>
<td>34°</td>
<td>No</td>
<td>?</td>
<td>—</td>
</tr>
<tr>
<td>Vietnam</td>
<td>20°</td>
<td>?</td>
<td>?</td>
<td>—</td>
</tr>
<tr>
<td>China: Henan</td>
<td>35°</td>
<td>Yes</td>
<td>&lt;24</td>
<td>4.5 4</td>
</tr>
</tbody>
</table>

1. During the mating season, all individuals are approximately midway between their birth anniversaries.
3. Reported as 4 to 5 years.
4. Reported as 4.5 to 6 years.
emigrated during a 3-year observation period (Koford, 1966, p. 6).

Sexual Skin

In postjuvenile females and males, regions of the skin undergo intermittent swelling and/or reddening (Darwin, 1871, p. 279; 1876, p. 19; Anderson, 1879, p. 58; Langley & Sherrington, 1891, p. 284; Heape, 1896, p. 202; 1897, p. 139; Corner, 1923, p. 82; Allen, 1926, p. 226; 1927, p. 9; Collings, 1926, p. 272; Zuckerman, 1930, p. 702; Stewart, 1933, p. 29). In captive females, the earliest manifestation of this “sexual skin” (Langley & Sherrington, 1891, p. 290) is the development during the second or third year of life of a pair of pinkish pubic swellings (Hartman, 1928c, p. 182; 1932, p. 20; Zuckerman et al., 1938, p. 385; van Wagenen, 1950, p. 26; Eckstein & Zuckerman, 1956, p. 139; Hadidian & Bernstein, 1979, p. 436); the location of these swellings is similar to that of the scrotum in a male. After approximately 2 weeks, these pubic swellings subside and the first menstrual bleeding occurs. Within the next few months, the fully developed sexual skin of puberty appears; this consists of a large bilobed blister-like pubic swelling, from which a less prominent edematous midline swelling extends posteriorly as far as the sides of the vulva. During the subsequent menstrual cycles of adolescence, a period that may extend up to 2 years, the sexual skin of puberty is gradually transformed, becoming less acutely swollen, redder, and more extensive; the cyclically edematous area of sexual skin often extends beyond the vulva and anus to the root of the tail, over the buttock area and posterior surface of the thighs, and over the iliac region. In sexually mature females (beginning at age ca. 3.5–5.5 years), the primary cyclical manifestation of sexual skin is reddening rather than swelling; in addition to the buttocks and adjacent regions, the areas of redness frequently include the face and nipples. During the menstrual cycle, the red color of the sexual skin generally reaches maximum intensity near the day of ovulation (Anonymous, 1973, p. 9; Czaja & Bi-elert, 1975, p. 587; Czaja et al., 1975, p. 1681; cf. Zuckerman, 1930, p. 728; Zuckerman et al., 1938, p. 389; Carpenter, 1942a, p. 131); this cyclic variation apparently may be diminished in older females (Hartman, 1932, p. 21; Stewart, 1933, p. 29; Valerio et al., 1969b, p. 284). Sexual skin color reportedly is brighter during the mating season than during the nonmating season (Gordon & Bernstein, 1973, p. 223; Baulu, 1976, p. 487; Rab et al., 1991, p. 221; cf. McCann, 1933b, p. 810). The bright red color of the sexual skin is retained during pregnancy and frequently during lactation (Heape, 1894, p. 456; 1897, p. 140; Hartman, 1928b, p. 539; 1928c, p. 187; 1932, p. 21; Tinklepaugh & Hartman, 1930, p. 66; Bielet al., 1976, p. 182).

In pubertal and adolescent males, red sexual skin develops in approximately the same posterior and facial regions as in females, but there is no pubertal swelling of the sexual skin in males (Zuckerman, 1937, p. 327). As in females, the red color in males is brighter during the mating season than during the nonmating season (Sade, 1964, p. 179; Koford, 1965, p. 165; Lindburg, 1971, p. 91; 1983, p. 47; Gordon & Bernstein, 1973, p. 223; Baulu, 1976, p. 485; Bielet al., 1981, p. 231; Rab et al., 1991, p. 221). Subcutaneous fat deposits also vary seasonally in sexually mature males, increasing prior to the mating season and decreasing during the mating season (Lindburg, 1977b, p. 247; Bernstein et al., 1989, p. 253; Bercovitch, 1992, p. 277; Zeng, 1992, p. 22; Bercovitch & Nürnberg, 1996, p. 63).

Menstrual Cycle

In three studies of 4.626 menstrual cycles (ca. 600 females), modal cycle lengths were 27, 28, and 28/30 (bimodal) days (Valerio et al., 1969b, p. 286; Anand Kumar et al., 1980, p. 38; Dailey & Neill, 1981, p. 562); extreme cycle lengths were 6 and 237 days, but few cycles were longer than 50 days, and longer cycles (?anovulatory periods) generally occurred during the summer season of infrequent matings. The modal durations of menstrual flow reported in two of these studies were 3 and 4 days (3.370 cycles, 490 females); extreme durations in both studies were 1 and 11 days, and mean durations were 3.5 and 3.9 days.

Estrus

During the mating season, female sexual activity (estrus) is cyclical in nature and seminatal groups of *M. mulatta* (Carpenter, 1942a, p. 117; Conaway & Koford, 1964, p. 584; Kaufmann, 1965, p. 501; Loy, 1971, p. 2; Lindburg, 1971, p. 94). Within groups, the estrous periods of individual females are asynchronous, and male sexual activity apparently is not cyclical. In five studies
of ca. 160 females, length of the estrous period averaged 8 to 12 days (Wilson & Gordon, 1980, p. 639; Lindburg, 1983, p. 50; Berman et al., 1993, p. 393; cf. Loy, 1970, p. 287), and length of the intervening period of sexual inactivity averaged 19 to 22 days (not reported in two studies). The midpoint of a female's estrous period approximately coincides with her day of ovulation (ca. 11–14 days after onset of previous menstruation), which is the day on which she generally participates in the maximum number of ejaculatory copulations (Ball & Hartman, 1935, p. 118; Michael, 1965, p. 596; Valerio et al., 1969b, p. 292; Wallen, 1990, p. 236; Michael & Zumpe, 1993, p. 226). During three years of observation, 34 to 40 females in a seminatural group averaged 2.2 estrous periods per mating season (extremes, 0–5 periods per season) (Kaufmann, 1965, p. 504), and a similar frequency of estrous periods per season was observed during a 10-month study of 35 females in a natural population (Lindburg, 1971, p. 95). In two groups, 63% and 77% of the females apparently were impregnated during their first estrous periods of the mating season (Conaway & Koford, 1964, p. 585; Lindburg, 1971, p. 95); most of these females apparently also had subsequent postconception estrous periods during the same mating season (cf. Altmann, 1962, p. 389; Lindburg, 1983, p. 50). In captive females, estrous cycles may be attenuated (Tinklepaugh, 1933, p. 336; Rowell, 1963, p. 198; Kuehn & Young, 1965, p. 688; Johnson & Phoenix, 1978, p. 167; Keverne, 1981, p. 119).

**Consortship**

In natural and seminatural groups, temporary copulatory associations (consortships) are formed between estrous females and their male partners (Carpenter, 1942a, p. 118; Altmann, 1962, p. 393; Kaufmann, 1965, p. 502; Southwick et al., 1965, p. 151; Vandenbergh & Vessey, 1968, p. 73; Lindburg, 1971, p. 91; Brereton, 1981, p. 419; Hill, 1987, p. 443; Rab et al., 1991, p. 222; Berard et al., 1993, p. 483; cf. Manson, 1996b, p. 156; 1997, p. 353). The duration of these consortships reportedly varies from ≤25 minutes to 11 days; a duration of 1 to 2 days probably is typical (Southwick et al., 1965, p. 152; Hill, 1987, p. 446). A female usually consorts with more than one male during each of her estrous periods; in a natural group, females changed consort partners in 24 of 38 estrous periods observed (Lindburg, 1971, p. 94; cf. Carpenter, 1942a, p. 138). Over the course of one mating season, one female was observed to consort with 11 of 12 group males, and one male was observed to consort with 18 of 34 group females (Conaway & Koford, 1964, p. 582); during a single day, a female may consort with more than one male, and a male may consort with more than one female (Southwick et al., 1965, p. 152; Vandenbergh & Vessey, 1968, p. 73). Although either sex may initiate a consort relationship (Kaufmann, 1965, p. 502; Lindburg, 1971, p. 92; 1983, p. 54; Rab et al., 1991, p. 222), in one study of 53 consortships, male partners were responsible for maintaining proximity approximately twice as frequently as females (Hill, 1987, p. 446). The consortships of high-ranking individuals usually are conducted near the center of their group; those of low-ranking individuals may be conducted several hundred meters from other group members (Lindburg, 1971, p. 92; Rab et al., 1991, p. 222). In a seminatural population, females occasionally have been observed to move temporarily into another group and to form a consortship there (Carpenter, 1942b, p. 154; Brereton, 1981, p. 419).

**Copulatory Behavior**

Copulations, like consortships, may be initiated by either sex (Hinde & Rowell, 1962, p. 16; Harlow, 1965, p. 235); in laboratory pair tests with multiple copulations, the frequency of female initiations in second copulations (ca. 35%) tends to exceed that in first copulations (ca. 15%) (Michael & Zumpe, 1970, p. 176; Dixon et al., 1973, p. 42). Near the beginning of a copulation, the female typically presents by turning her perineal region toward the male, and the male mounts dorsoventrally by grasping the female's waist and shanks with his hands and feet, respectively (Carpenter, 1942a, p. 132; Altmann, 1962, p. 374; Southwick et al., 1965, p. 152). Although ejaculation in *M. mulatta* occasionally is accomplished in a single mount (Kaufmann, 1965, p. 502; Michael et al., 1973, p. 249; Shively et al., 1982, p. 376; Curie-Cohen et al., 1983, p. 129; Manson 1996a, p. 1225), usually a series of mounts, separated by dismounts, is required to complete a copulation. Each mount includes one to 15 introgressive thrusts and usually lasts less than 1 min (Prakash, 1962, p. 84; Southwick et al., 1965, p. 152; Michael & Saayman, 1967b, p. 462; Shively et al., 1982, p. 376; Lindburg, 1983, p. 51).
copulation may include as many as ca. 100 mounts and dismounts (Carpenter, 1942a, p. 133) and may last up to 30 min or, rarely, 1 hr (Prakash, 1962, p. 84; Kaufmann, 1965, p. 502; Southwick et al., 1965, p. 152; Lindburg, 1971, p. 94; Manson, 1996a, p. 1223); in laboratory pair tests with multiple copulations, the number of mounts per copulation and the duration of copulations tend to increase in successive copulations (Kuehn & Young, 1965, p. 688; Michael & Saayman, 1967b, p. 463; Missakian et al., 1969, p. 234). The copulation rate of estrous females in a seminatural group has been estimated to be ca. 0.4/hr (Manson, 1992, p. 412). In caged animals, the rate of copulatory behaviors apparently is greater at 0900 than at 2100 (Chambers et al., 1982, p. 38), and copulation rarely occurs late at night (Erffmeyer, 1982, p. 246). Following copulation, coagulated semen often is visible on the perineum of the female ("vaginal plug.") Hartman, 1932, p. 39; cf. Carpenter, 1942a, p. 119; Altmann, 1962, p. 375; Mastroianni & Manson, 1963, p. 1026; Vandenberg & Vessey, 1968, p. 73; Blandau, 1973, p. 295; Lindburg, 1983, p. 47).

Dominance Rank and Reproductive Success

The relationship between male copulation frequency, fertilization success, and dominance rank in M. mulatta has been studied in natural groups, free-ranging seminatural groups, and compound-housed groups (cf. Bercovitch, 1997, p. 248). Evidence from natural groups suggests that male copulation frequency and fertilization success are positively correlated with dominance rank, and evidence from seminatural and compound-housed groups equivocally tends in the same direction (cf. Paul, 1997, p. 345; Bercovitch & Nürnberg, 1997, p. 1703; Rifkin et al., 1999, p. 93). Field studies at two localities in India and one locality in Pakistan indicate that a male’s copulation frequency and number of female partners are correlated with his dominance rank (Southwick et al., 1965, p. 152; Iqbal & Rub, 1980, p. 214; Lindburg, 1983, p. 52; Rab et al., 1991, p. 222); preliminary analysis of blood protein data from two groups at the Pakistan locality suggests that most of the infants born during three years were fathered by the alpha male of each group (Melnick & Hoelzer, 1996, p. 430). Although most studies of the seminatural Cayo Santiago population similarly indicate that male copulation frequency is positively correlated with dominance rank (Carpenter, 1942b, p. 156; Koford, 1963, p. 150; Conaway & Koford, 1964, p. 582; Kaufmann, 1965, p. 507; Sade, 1980, p. 182; McMillan, 1982b, p. 312; Chappais, 1983, p. 219; Hill, 1987, p. 445; Manson, 1992, p. 412; 1996a, p. 1223; Berard et al., 1993, p. 485), a few studies of this population have failed to find such a correlation (Loy, 1971, p. 8; McMillan, 1982a, p. 207; Berard, 1993, p. 298; 1999, p. 163); factors that may tend to bias these observations are the relatively low visibility of low-ranking males (Drickamer, 1974a, p. 119) and the relatively low mating success of low-ranking subadult males (McMillan, 1982a, p. 207). Available results of genetic paternity tests in the Cayo Santiago population are inconclusive concerning a correlation between fertilization success and dominance rank (Sade, 1980, p. 182; Berard et al., 1993, p. 484; 1994, p. 184; Berard & Schmidtke, 1996, abstract no. 459). Male reproductive success in the Cayo Santiago population may be affected by the abnormally large group size in this provisioned population and the high ratio of sexually mature males to sexually mature females (Tables 14.15; Manson, 1992, pp. 407, 414). Most, but not all, evidence from studies of compound-housed groups suggests that copulation frequency may be correlated with dominance rank (Gordon et al., 1976, p. 239; Ruiz de Elvira et al., 1982, p. 829; Shively, 1982, p. 377; Wilson et al., 1982, p. 24; Curie-Cohen et al., 1983, p. 130; Stern & Smith, 1984, p. 29; Jebavý et al., 1994, p. 202; Bercovitch & Nürnberg, 1996, p. 61) and that fertilization success also may be correlated with dominance rank (Duvall et al., 1976, p. 29; Smith, 1980, p. 248; 1981, p. 87; 1993, p. 474; 1994b, p. 234; Berenstein et al., 1981, p. 1058; Curie-Cohen et al., 1983, p. 133; Stern & Smith, 1984, p. 27; Smith & Smith, 1988, p. 557; Bercovitch & Nürnberg, 1996, p. 61; Bercovitch, 1997, p. 248). In seminatural and compound-housed groups, dominant males and females often harass and disrupt the copulations of subordinate group members (Herndon et al., 1986, p. 95; Manson, 1994, p. 136; 1996a, p. 1224).

Inbreeding

Blood-protein evidence from five groups in Pakistan indicates that close inbreeding is rare in natural populations of M. mulatta (Melnick et al., 1984, p. 235); the opportunity for such inbreeding is obviously limited by the tendency for pubertal males to emigrate from their natal groups (see
above). In the Cayo Santiago free-ranging population, relatively few mother-son and brother-sister copulations have been observed (Kaufmann, 1965, p. 508; Sade, 1968, pp. 18, 33, 36; 1972, p. 392; Loy, 1971, p. 12; Missakian, 1973a, p. 230; Sade et al., 1984, p. 213; Manson & Perry, 1993, p. 340; Berard & Schmidtke, 1996, abstract no. 459), and the same is true of the Yerkes compound-housed population (Wilson, 1981, p. 475). Genetic paternity tests of compound-housed groups at Davis, California, indicate that matrilineal inbreeding is rare (two of 132 infants) but that patrilineal inbreeding, except for father-daughter mating, is common (Smith, 1982, p. 448; 1986a, p. 219; 1986b, p. 864; 1995, p. 34).

Nonreproductive Sexual Behavior


Gestation Length

In a large laboratory colony of *M. mulatta*, the mean (±SD) gestation length was 165.4 ± 6.1 days for 1,067 viable female births and 166.2 ± 6.7 days for 1,115 viable male births (Shaughnessy et al., 1978, p. 132; cf. Hartman, 1928a, p. 15); in two other large colonies, mean gestation length was 166.5 days (n = 709; Silk et al., 1993, p. 97) and 168.4 days (n = 311; van Wagenen, 1972, p. 9). Reported minimum and maximum lengths of viable pregnancies are 133 days and 200 days (Silk et al., 1993, p. 97). Gestation length averages greater in young primiparous mothers (ca. 169 days) than in old multiparous mothers (ca. 162 days) (Hartman, 1932, p. 53; Silk et al., 1993, p. 98). In an experimental study of nutritional effects, gestation length was ca. 8.5 days less in pregnant females fed a high-protein diet than in those fed a low-protein diet (Riopelle & Hale, 1975, p. 1173); this suggests that gestation length in unprovisioned natural populations may be greater than gestation length in provisioned captive populations.

Parturition

Parturition is rarely observed in natural populations of *M. mulatta*, even in those that have been closely studied (Southwick et al., 1965, p. 155; Lindburg, 1971, p. 77; Teas et al., 1981b, p. 580; Mathur, 1994, p. 132). Most newborn infants in closely studied natural populations are first seen early in the morning, which presumably implies that births usually occur at night. Of the five births and one stillbirth that have been partially or completely observed during daylight hours (early morning to late afternoon), all apparently occurred while the mother was on the ground—in undergrowth in at least three cases (Lindburg, 1971, p. 77; Teas et al., 1981b, p. 581; Mathur, 1994, p. 132). From the first observed contraction to delivery of the afterbirth, the approximate duration of three of the live births was 15 min, 1 hr, and 0.5 to 2.5 hr. The placenta was eaten by at least two of the five mothers. Observed births in captive populations apparently are generally similar to those in natural populations with respect to timing, duration, and consumption of the placenta (Pocock, 1906, p. 562; Hartman, 1932, p. 52; Hinde et al., 1964, p. 613; Valerio et al., 1969a, p. 72; Brandt & Mitchell, 1971, p. 199; Shaughnessy et al., 1978, p. 130; Rawlins, 1979, p. 432; Adachi et al., 1982, p. 585; Gibber, 1986, p. 121).

The frequency of stillbirths was 5.5% (259 stillbirths/4,711 births) in four large captive colonies (Shaughnessy et al., 1978, p. 130; Scanlan et al., 1985, p. 363; Rawlins & Kessler, 1986c, p. 52; Small & Smith, 1986, p. 293). The frequency of twinning was 0.23% (13 twin pairs/5,561 live births) in three large captive colonies (Geissmann, 1990, p. 392; cf. Chalise & Ghimire, 1998, p. 11).
Birth Weight, Infant Sex Ratio

Birth weight in one large laboratory colony averaged 476.0 g in 1.067 female infants and 502.8 g in 1.115 male infants (Table 24); in five other large colonies, birth weight averaged somewhat less. The birth weight of inbred infants averages less than that of non-inbred infants (Smith, 1986b, p. 869). Judging from the relatively low weight of infants born to females that were pregnant when imported (Table 24), birth weight in natural populations may be less than in laboratory colonies.

The male/female infant sex ratio was 1.16 in three natural populations of M. mulatta (n = 212 sexed infants) and 1.03 in 10 captive populations (n = 7,445 sexed infants) (Table 25; cf. Debyser, 1995, p. 955); neither of these ratios differs significantly from 1.00 (P > 0.10). The possibility that infant sex ratio in this species may be influenced by maternal dominance rank has been investigated with equivocal results in four captive colonies. In two compound-housed colonies, high-ranking females tended to have female-biased infant sex ratios (Simpson & Simpson, 1982, p. 440; 1985, p. 85; Small & Smith, 1985, p. 356; Small & Hrdy, 1986, p. 362; Comendio, 1990, p. 369; Nevison et al., 1996, p. 127; Nevison, 1997, p. 287); the skew was statistically significant in one colony—at least in smaller matrilines—but not significant in the other colony. Conversely, in one large seminatural colony, high-ranking females had significantly male-biased infant sex ratios (Meikle et al., 1984, p. 179), and in another large seminatural colony, maternal rank and infant sex ratio were not significantly correlated (Berman & Rawlins, 1985, p. 332; Rawlins & Kesseler, 1986a, p. 12; Berman, 1988, p. 313). Paternal dominance rank had no apparent effect on infant sex ratio in a compound-housed colony (Small & Smith, 1985, p. 359).

Birth Rate, Infant Mortality Rate

The mean annual birth rate (births/sexually mature females) in natural populations of M. mulatta varies from 42.9% to 90.8% (Table 26); only three of 17 reported means are less than 63%. One of the three low outlier values is based on observations of 14 Indian temple groups; the other two are based on observations of the two northernmost populations for which birth rate data are available (Pakistan, 34°03’N; China, 35°10’–35°17’N). At both northern localities, females usually produce infants only in alternate years (Qu et al., 1993, p. 619). In captivity, the mean annual birth rate varies from 65.0% to 76.7% in four free-ranging colonies (Vandenbergh, 1973, p. 7; Rawlins & Kesseler, 1986c, p. 52, live births to females age ≥4 years; Johnson & Kapsalis, 1995b, p. 273), and is 65.8% and 71.8% in two compound-housed colonies (Casebolt et al., 1985, p. 291; Goo, 1986, p. 75; cf. Litton & Izard, 1999, p. 74).

The reported mean annual infant mortality rate, during the first year of life, was 7.0% in southern...
Table 25. Infant sex ratio in *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Locality or colony¹</th>
<th>N</th>
<th>Females</th>
<th>Males</th>
<th>Sex unknown</th>
<th>Male:female ratio</th>
<th>References²</th>
</tr>
</thead>
<tbody>
<tr>
<td>India: Dehra Dun</td>
<td>23</td>
<td>10</td>
<td>10</td>
<td>3</td>
<td>1.00</td>
<td>1</td>
</tr>
<tr>
<td>China: Longhu Shan</td>
<td>56</td>
<td>23</td>
<td>33</td>
<td>0</td>
<td>1.43</td>
<td>2</td>
</tr>
<tr>
<td>China: Nan Wan</td>
<td>136</td>
<td>65</td>
<td>71</td>
<td>0</td>
<td>1.09</td>
<td>3</td>
</tr>
<tr>
<td>Totals</td>
<td>215</td>
<td>98</td>
<td>114</td>
<td>3</td>
<td>1.16</td>
<td></td>
</tr>
</tbody>
</table>

**Natural populations**

**Captive populations³**

<table>
<thead>
<tr>
<th>Location</th>
<th>N</th>
<th>Females</th>
<th>Males</th>
<th>Sex unknown</th>
<th>Male:female ratio</th>
<th>References²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cayo Santiago, PR</td>
<td>1,407</td>
<td>665</td>
<td>720</td>
<td>22</td>
<td>1.08</td>
<td>4</td>
</tr>
<tr>
<td>PR</td>
<td>815</td>
<td>399</td>
<td>398</td>
<td>18</td>
<td>1.00</td>
<td>5</td>
</tr>
<tr>
<td>DOGYU</td>
<td>301</td>
<td>161</td>
<td>150</td>
<td>0</td>
<td>0.93</td>
<td>6</td>
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<tr>
<td>La Parguera, PR</td>
<td>362</td>
<td>183</td>
<td>179</td>
<td>0</td>
<td>0.98</td>
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<tr>
<td>LBI</td>
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<td>1,115</td>
<td>0</td>
<td>1.04</td>
<td>8</td>
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<td>LPP</td>
<td>235</td>
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<td>119</td>
<td>0</td>
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<td>UCM</td>
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<td>148</td>
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<td>0.98</td>
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<td>UMCG</td>
<td>169</td>
<td>83</td>
<td>83</td>
<td>3</td>
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<td>10</td>
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<tr>
<td>WRPRC</td>
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<td>808</td>
<td>808</td>
<td>0</td>
<td>1.00</td>
<td>11</td>
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<tr>
<td>YPRPCFS</td>
<td>97</td>
<td>37</td>
<td>55</td>
<td>5</td>
<td>1.49</td>
<td>12</td>
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<tr>
<td>Totals</td>
<td>7,493</td>
<td>3,670</td>
<td>3,775</td>
<td>48</td>
<td>1.03</td>
<td></td>
</tr>
</tbody>
</table>

¹ CRPRC = California Regional Primate Research Center, Davis, CA; DOGYU = Department of Obstetrics and Gynecology, Yale University School of Medicine, New Haven, CT; LBI = Litton Bionetics, Inc., Kensington, MD; LPP = Laboratory of Perinatal Physiology, National Institute of Neurological Diseases and Stroke, San Juan, PR; UCM = University of Cambridge, Madingley, Cambridge, England; UMCG = University of Miami, Coral Gables, FL; WRPRC = Wisconsin Regional Primate Research Center, Madison, WI; YPRPCFS = Yerkes Regional Primate Research Center Field Station, Lawrenceville, GA.


China. 15.5% to 18.0% in northern India, 16.0% to 29.0% in Nepal, and 28.5% to 31.5% in northeastern China (Table 27). In a group of 19 primaparous captive females, the mortality rate (to age 6 months) of male infants (5/11) exceeded that of female infants (1/8) (Bercovitch et al., 1998, p. 138; cf. Dai et al., 1998, p. 30). When an infant dies, its mother often carries the corpse for several days, even after it has decayed; this has been observed in natural populations (Dodsworth, 1914, p. 730; Prakash, 1962, p. 85; Neville, 1968c, p. 18; Mukherjee, 1969, p. 55; Lindburg, 1971, p. 17; Taylor et al., 1978, p. 346; Shukla et al., 1984, p. 20) and in captive populations (Yerkes, 1915, p. 404; Carpenter, 1942c, p. 199; Koford, 1965, p. 169; Sade, 1968, p. 21; Rawlins & Kessler, 1983, p. 170).

**Nursing, Weaning**

In two captive groups, 41 infants (age 0–6 weeks) nursed from the left nipple approximately 50% more than from the right nipple (Tomaszycki et al., 1998, p. 308). In natural populations, infants sometimes begin to take small amounts of solid food at age 2 weeks, and mothers begin to resist nursing attempts about 3 months later (Lindburg, 1971, p. 84). The weaning process gradually intensifies over the next several months, but it may extend through the subsequent mating season and not be completed until the birth of the next infant, when the first infant is ca. 1 year old (Prakash, 1962, p. 85; Southwick et al., 1965, p. 156; Lindburg, 1971, pp. 63, 84). The weaning process in captive populations is generally similar to that in natural populations (Pocock, 1906, p. 569; Hartman, 1932, p. 22; Hinde et al., 1964, p. 637; Sade, 1968, p. 24; Vandenberg & Vessey, 1968, p. 75; Comendio, 1989, p. 452; Simpson & Tarbini, 1992, p. 31). An experimental study indicates that prolongation of the nursing period delays subsequent conception (Goo & Fugate, 1984, p. 67); the mean (±SD) interbirth interval of mothers of infants artificially weaned at age 6
Table 26. Annual birth rate (births/sexually mature females × 100) in natural populations of *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>Study period</th>
<th>No. of groups</th>
<th>Annual birth rate (%)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pakistan Dungia Gali</td>
<td>1978–80</td>
<td>1</td>
<td>~50</td>
<td>I</td>
</tr>
<tr>
<td>India Delhi: Tughlaqabad</td>
<td>1980–87</td>
<td>2–5</td>
<td>78.8</td>
<td>2</td>
</tr>
<tr>
<td>Uttar Pradesh Aligarh District</td>
<td>1961–85</td>
<td>8–21</td>
<td>83.7</td>
<td>3</td>
</tr>
<tr>
<td>Chhatari-do-Raha</td>
<td>1959–79</td>
<td>2</td>
<td>90.3</td>
<td>5</td>
</tr>
<tr>
<td>Dehra Dun</td>
<td>1965–66</td>
<td>5</td>
<td>90.8</td>
<td>4</td>
</tr>
<tr>
<td>Northern India Temple</td>
<td>1981–91</td>
<td>14</td>
<td>42.9</td>
<td>7</td>
</tr>
<tr>
<td>Urban</td>
<td>1981–91</td>
<td>103</td>
<td>64.7</td>
<td>7</td>
</tr>
<tr>
<td>Village</td>
<td>1981–91</td>
<td>42</td>
<td>68.8</td>
<td>7</td>
</tr>
<tr>
<td>Village/pond</td>
<td>1981–91</td>
<td>60</td>
<td>64.2</td>
<td>7</td>
</tr>
<tr>
<td>Pond</td>
<td>1981–91</td>
<td>28</td>
<td>66.2</td>
<td>7</td>
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<tr>
<td>Roadside</td>
<td>1981–91</td>
<td>33</td>
<td>71.1</td>
<td>7</td>
</tr>
<tr>
<td>Canal side</td>
<td>1981–91</td>
<td>22</td>
<td>64.8</td>
<td>7</td>
</tr>
<tr>
<td>Forest</td>
<td>1981–91</td>
<td>70</td>
<td>64.1</td>
<td>7</td>
</tr>
<tr>
<td>Nepal Kathmandu Valley</td>
<td>1975–78</td>
<td>12</td>
<td>63.0</td>
<td>8</td>
</tr>
<tr>
<td>China Hainan: Nanwan</td>
<td>1978–90</td>
<td>2</td>
<td>~75</td>
<td>9</td>
</tr>
<tr>
<td>Guangxi: Longbushan</td>
<td>1988–95</td>
<td>6</td>
<td>75.4</td>
<td>10</td>
</tr>
<tr>
<td>Xianggang (= Hong Kong)</td>
<td>1981</td>
<td>3</td>
<td>75.0</td>
<td>11</td>
</tr>
<tr>
<td>Henan: Juyuan</td>
<td>1987–88</td>
<td>2</td>
<td>46.9</td>
<td>12</td>
</tr>
</tbody>
</table>


months was 382 ± 34 days (n = 153), whereas that of mothers of infants artificially weaned at age 12 months was 403 ± 63 days (n = 147). If a mother fails to produce a second infant during the following birth season, she may suckle the first infant for 2 years (Hartman, 1929, p. 157; Fleischman, 1963, p. 706).

Menopause

In a natural population in India, one female apparently became menopausal and ceased mating activity at an estimated age of >20 years (Malik & Johnson, 1992, p. 28); subsequent to menopause, this female survived for 4 years. In three closely observed captive colonies, menopause occurred at ages 26.9, 27.6, and 29.0 years (van Wagenen, 1972, p. 26; van Wagenen & Simpson, 1973, p. 24; cf. Hodgson et al., 1977, p. 582; Davis, 1985, p. 79; Ouyang & Ma, 1992, p. 14). One female in each of two other colonies apparently became menopausal as early as age ca. 17 years (Tilford, 1981, p. 638; Vančatová et al., 1986, p. 263). The frequency of menopause in old females reported in three studies of captive colonies is as follows: 49 females, ages 25 to 27 years, 43% menopausal (Johnson & Kapsalis, 1998, p. 757); seven females, ages 26 to 34 years, 71% menopausal (Walker, 1995, p. 61); 10 females, ages 28 to 34.6 years, 100% menopausal (Champ et al., 1996, p. 486). Based on hormone profiles of 26 captive females aged 21–29 years, 11 were determined to be premenopausal (mean age 22.5 years), 13 were determined to be perimenopausal (mean age 24.0 years), and 2 were determined to be postmenopausal (mean age 29.5 years) (Gilardi et al., 1997, p. 337). The greatest age at which a captive fe-
Table 27. Infant mortality rate in natural populations of *Macaca mulatta*.

<table>
<thead>
<tr>
<th>Sample area</th>
<th>No. of groups</th>
<th>Study period</th>
<th>No. of years of data</th>
<th>Infant mortality rate(^1) (%)</th>
<th>References(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>India</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uttarakhand Valley</td>
<td>8–21</td>
<td>1961–76(^3)</td>
<td>15</td>
<td>18.0 ± 10.0</td>
<td>1</td>
</tr>
<tr>
<td>Aligarh District</td>
<td>8</td>
<td>1990–91</td>
<td>1</td>
<td>2.3</td>
<td>2</td>
</tr>
<tr>
<td>Chhatari-do-Raha</td>
<td>2</td>
<td>1961–76</td>
<td>16</td>
<td>15.5 ± 14.5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1990–91</td>
<td>1</td>
<td>2.2</td>
<td>2</td>
</tr>
<tr>
<td>Nepal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kathmandu Valley</td>
<td>5–6</td>
<td>1975–78</td>
<td>3</td>
<td>29.0 ± 2.6</td>
<td>3</td>
</tr>
<tr>
<td>Pashupati</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Swayambhu</td>
<td>7–10</td>
<td>1975–78</td>
<td>3</td>
<td>16.0 ± 7.0</td>
<td>3</td>
</tr>
<tr>
<td>China</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Guangxi</td>
<td>1–2</td>
<td>1988–95(^4)</td>
<td>3</td>
<td>7.0 ± 3.8</td>
<td>4</td>
</tr>
<tr>
<td>Longhu Shan</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Henan: Jiayuan</td>
<td>1</td>
<td>1987</td>
<td>1</td>
<td>31.5</td>
<td>5</td>
</tr>
<tr>
<td>Doudin</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shagon</td>
<td>1</td>
<td>1987</td>
<td>1</td>
<td>28.5</td>
<td>5</td>
</tr>
</tbody>
</table>

\(^1\) Annual infant deaths during first year of life/annual births.
\(^3\) Data for 1975 missing.

The annual mortality rate was 6.8% (7-year average; Rawlins & Kessler, 1986c, p. 51).

Observed causes of death in natural populations include infanticide, intraspecific fighting, predation (dog, tiger), and an accidental fall from a cliff (Lindburg, 1971, p. 17; Campero Ciani, 1984, p. 373; Singh, 1986, p. 607). In a provisioned Nepalese population, ca. 40 monkeys were accidentally electrocuted in 1996 (Shrestha, 1997, p. 31; Chalise & Ghimire, 1998, p. 11). During winter, members of northern populations apparently die of exposure or malnutrition (Pearl et al., 1987, p. 37; Qu et al., 1993, p. 613).

Annual Mortality Rate

Annual mortality rates apparently are locally variable in natural populations of *M. mulatta*. In northern India, the annual mortality rate was approximately 2.2% in Aligarh District (Imam & Yahya, 1995, p. 7), 3.6% at Asarori Forest (Lindburg, 1971, p. 17), 3.7% at Tughlaqabad (3-year average; Malik et al., 1984, p. 317), and 9.6% at Dehra Dun (Lindburg, 1971, p. 17; cf. Southwick & M. F. Siddiqi, 1988, p. 190); in Nepal, the mortality rate was 19.0% at Swayambhu and 22.3% at Pashupati (3-year averages; Teas et al., 1981a, p. 119). In the free-ranging Cayo Santiago colony, male is known to have produced a living infant is ca. 28.5 years (Dyke et al., 1986, p. 264).

Males are known to remain capable of copulatory ejaculation to age ca. 30 years (Phoenix & Chambers, 1988, p. 159). However, in another series of copulatory tests of six healthy males age ca. 21 to 31 years (mean = 25 years), four (67%) failed to ejaculate (Chambers & Phoenix, 1992, p. 15; cf. Ouyang & Ma, 1992, p. 14).

The maximum reported longevity in captive *M. mulatta* is 37 years (Uno et al., 1998, p. 21; cf. Davis, 1985, p. 57; Erschler et al., 1988, p. 182).

Population Growth Rate

Population growth rate estimates are available for 28 natural populations of *M. mulatta* (Table 28; cf. Ross, 1988, p. 218); for 14 of these populations, the census interval is 1 year, and for the remaining 14 the census interval is 3 to 32 years. In 12 of 14 populations with 1-year census intervals, annual growth rates vary from 3.8% to 26.9% (mean ± SD = 14.8% ± 6.8%); growth rates of the remaining two of these populations are outlier negative values (−9.5%, −15.9%). In the 14 populations with multiyear census inter-
vals, annualized growth rate tends to be greater in populations with shorter census intervals; in eight populations with census intervals less than 7 years, the mean annualized growth rate is 12.3% ± 5.9% (extremes, 0.9% and 19.1%), and in six populations with census intervals greater than 22 years, the mean annualized growth rate is 3.5% ± 4.5% (extremes, −0.4% and 9.1%). In three Nepalese populations, annualized growth rate tends to be low regardless of census interval length (3 years, 0.9%; 23 years, −0.3% and −0.4%); the explanation for this low rate of population increase in Nepal is unclear (Teas et al., 1981a, p. 120; Johnson et al., 1988, p. 179). In two areas on Hainan Dao, China, population growth rates apparently began to decline after optimum population densities were reached (Jiang et al., 1998, p. 101). In two free-ranging colonies introduced in Puerto Rico, the combination of relatively high population growth rates (13.5%, 16.5%) and relatively short census intervals (7 years, 9 years) is concordant with the norm for natural populations (see above).

**Fossils and Subfossils**

Published data concerning *M. mulatta* fossils and subfossils are meager and fragmentary (Table 29; cf. Szalay & Delson, 1979, pp. 356, 363; Delson, 1980, p. 20; Pan & Jablonski, 1987, p. 63; Jablonski & Pan, 1988, p. 859; Jablonski, 1990, p. 39; Xue & Zhang, 1991, p. 357). The most important implication of these data probably is that a macaque similar or identical to *M. mulatta* had become established within the present range of *M. mulatta* in China and Vietnam during or prior to Late Pleistocene (>40 Ka).

**Systematics**

**Geographic Variation and Subspecific Recognition**

Given the broad distribution and diverse habitats of *M. mulatta* (see above), it is not surprising that this species exhibits great variation in numerous characters. Based on individual or geographic variation, 15 species-group names have been proposed for application to this taxon (Fig. 21). In the first comprehensive subspecific revision of *M. mulatta*, six subspecies were recognized (Pocock, 1932, p. 533); in subsequent classifications, various combinations of 10 subspecies have been recognized (Table 30).

Although geographic variation in *M. mulatta* is clearly evident (see above), the differentiation of local and regional populations is now regarded as inadequate to warrant formal recognition of subspecies (cf. Fooden, 1995, p. 65). Where character-state transitions are gradual or irregular, as in *M. mulatta*, the delimitation of subspecies is arbitrary (cf. Mayr et al., 1953, p. 147), and unambiguous diagnosis of subspecies is virtually impossible. Problems concerning the delimitation of subspecies in *M. mulatta* have been discussed by Pocock (1932, p. 530), Napier (1981, p. 20), Corbet (1992, p. 170), Jiang Xuelong et al. (1995, p. 46), and Yu et al. (1996, p. 153). Unless future research reveals a pattern of geographic differentiation of characters that is much more coherent than is now known in *M. mulatta*, it appears unlikely that taxonomically useful subspecies can be defined in this species.

The principal characters that previously have been used in defining subspecies of *M. mulatta* are overall size, tail length, pelage color and length, and molecular diversity. The pattern of geographic variation in these characters has been discussed in detail above and is briefly summarized here.

**Size**—Overall size usually is measured as the combined length of head and body (based on flesh measurements recorded by the collector). Overall size presumably may also be inferred from greatest length of skull, excluding incisors; although skull length is not a direct measure of overall size, compared with head and body length, skull length usually is available for more specimens, and it is subject to less interobserver variability. Meaningful comparisons of size require measurements of fully adult specimens, segregated according to sex.

In *M. mulatta*, both head and body length and skull length tend to increase from south to north (Figs. 8, 17; Tables 3, 9). The large size of specimens collected north of 30°N in Afghanistan, Pakistan, and India in the west and disjunctly in China in the east is particularly striking. However, the latitudinal size gradient is gradual, and size distributions in local samples generally overlap (cf. Jiang Xuelong et al., 1991, p. 242). Size in insular samples is generally similar to that in continental samples collected at the same latitude (Figs. 8, 17).

FOODEN: SYSTEMATIC REVIEW OF THE RHESUS MACAQUE, *MACACA MULATTA* 79
### Population growth rate in *Macaca mulatta.*

<table>
<thead>
<tr>
<th>Sample area</th>
<th>No. of groups observed</th>
<th>Census interval</th>
<th>Initial census</th>
<th>Final census</th>
<th>Annual/annualized population growth rate (%)</th>
<th>References²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>One-year census intervals</strong></td>
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<td></td>
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</tr>
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<td>Pakistan</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Dunga Gali</td>
<td>3</td>
<td>1978–79</td>
<td>105</td>
<td>95</td>
<td>−9.5</td>
<td>1</td>
</tr>
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<td>India</td>
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<tr>
<td>Jammu and Kashmir</td>
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</tr>
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<td>Jammu</td>
<td>1</td>
<td>1983–84</td>
<td>123</td>
<td>156</td>
<td>26.9</td>
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<tr>
<td>Himachal Pradesh</td>
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<td>1983–84</td>
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<td>89</td>
<td>108</td>
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<td>Bhiwani</td>
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<td>Hissar</td>
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<td>Jind</td>
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<td>854</td>
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<tr>
<td>Rohtak</td>
<td>28</td>
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<td>932</td>
<td>8.8</td>
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<td>Delhi</td>
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<td>Alwan</td>
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<td>1983–84</td>
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<td>Jaipur</td>
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<td>1983–84</td>
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<td>Uttar Pradesh</td>
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<tr>
<td>Aligarh vicinity</td>
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<td>1990–91</td>
<td>651</td>
<td>669</td>
<td>2.8</td>
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<td>Dehra Dun</td>
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<td>597</td>
<td>688</td>
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<td>Ghaziabad</td>
<td>17</td>
<td>1983–84</td>
<td>705</td>
<td>785</td>
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<tr>
<td>Saharanpur</td>
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<td>1983–84</td>
<td>448</td>
<td>524</td>
<td>17.0</td>
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<td><strong>Multyear census intervals</strong></td>
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</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Delhi</td>
<td>1–5</td>
<td>1965–90 (25 yr)</td>
<td>68</td>
<td>~600</td>
<td>~9.1</td>
<td>4</td>
</tr>
<tr>
<td>Rajasthan</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bandipur</td>
<td>1</td>
<td>1976–80 (4 yr)</td>
<td>86</td>
<td>140</td>
<td>13.0</td>
<td>5</td>
</tr>
<tr>
<td>Jaipur</td>
<td>2</td>
<td>1976–80 (4 yr)</td>
<td>74</td>
<td>113</td>
<td>11.2</td>
<td>5</td>
</tr>
<tr>
<td>Marot</td>
<td>2</td>
<td>1976–80 (4 yr)</td>
<td>87</td>
<td>128</td>
<td>10.1</td>
<td>5</td>
</tr>
<tr>
<td>Uttar Pradesh</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aligarh District</td>
<td>8–21</td>
<td>1959–91 (32 yr)</td>
<td>~287</td>
<td>267</td>
<td>~0.2</td>
<td>6</td>
</tr>
<tr>
<td>Chhatari-do-Raha³</td>
<td>2</td>
<td>1959–91 (32 yr)</td>
<td>~50</td>
<td>178</td>
<td>~4.0</td>
<td>6</td>
</tr>
<tr>
<td>Dehra Dun</td>
<td>2</td>
<td>1976–80 (4 yr)</td>
<td>57</td>
<td>113</td>
<td>18.7</td>
<td>5</td>
</tr>
<tr>
<td>Khair</td>
<td>2</td>
<td>1976–80 (4 yr)</td>
<td>96</td>
<td>171</td>
<td>15.5</td>
<td>5</td>
</tr>
<tr>
<td>Nepal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pushpati³,⁴</td>
<td>6–10</td>
<td>1975–98 (23 yr)</td>
<td>358</td>
<td>330</td>
<td>−0.4</td>
<td>7, 8</td>
</tr>
<tr>
<td>Swayambhu⁵</td>
<td>5–7</td>
<td>1975–98 (23 yr)</td>
<td>328</td>
<td>308</td>
<td>−0.3</td>
<td>7, 8</td>
</tr>
<tr>
<td>Tripureswor</td>
<td>1–72</td>
<td>1995–98 (3 yr)</td>
<td>37</td>
<td>38</td>
<td>0.9</td>
<td>8</td>
</tr>
<tr>
<td>China</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hainan: Nanwan⁴,⁶</td>
<td>5–20</td>
<td>1965–94 (29 yr)</td>
<td>~115</td>
<td>~1,300</td>
<td>~8.7</td>
<td>9</td>
</tr>
<tr>
<td>Henan: Jiuyuan⁵</td>
<td>~26</td>
<td>1982–88 (6 yr)</td>
<td>~700</td>
<td>~2,000</td>
<td>~19.1</td>
<td>11</td>
</tr>
<tr>
<td>U.S.A.: Puerto Rico</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cayo Santiago⁵</td>
<td>5–6</td>
<td>1976–83 (7 yr)</td>
<td>479</td>
<td>1,161</td>
<td>13.5</td>
<td>12</td>
</tr>
<tr>
<td>La Parguera⁵</td>
<td>4–7</td>
<td>1963–72 (9 yr)</td>
<td>106</td>
<td>418</td>
<td>16.5</td>
<td>13</td>
</tr>
</tbody>
</table>

1 Annualized growth rate = [(C₂/C₁)⁽Y⁾ − 1, where Y = years in census interval, C₁ = initial census, and C₂ = final census.


³ Provisioned.
<table>
<thead>
<tr>
<th>Locality</th>
<th>Province/State</th>
<th>Latitude (N)</th>
<th>Longitude (E)</th>
<th>Epoch</th>
<th>Approximate age (Ka)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>China</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Yin ruins</td>
<td>Henan</td>
<td>36°07'</td>
<td>114°19'</td>
<td>Holocene</td>
<td>2.5</td>
<td>1, 2, 3</td>
</tr>
<tr>
<td>Xiawanggang</td>
<td>Henan</td>
<td>~33°15'</td>
<td>~111°27'</td>
<td>Holocene</td>
<td>4.5–5.2</td>
<td>2, 4, 5</td>
</tr>
<tr>
<td>Zhengpiyan</td>
<td>Guangxi</td>
<td>~25°17'</td>
<td>~110°17'</td>
<td>Holocene</td>
<td>6.6</td>
<td>2, 5, 6</td>
</tr>
<tr>
<td>Hemudu</td>
<td>Zhejiang</td>
<td>~30°03'</td>
<td>~121°00'</td>
<td>Holocene</td>
<td>6–7</td>
<td>2, 7</td>
</tr>
<tr>
<td>Baoshan</td>
<td>Yunnan</td>
<td>25°05'</td>
<td>99°05'</td>
<td>Holocene</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Shuanglong Cave</td>
<td>Zhejiang</td>
<td>29°12'</td>
<td>119°37'</td>
<td>Holocene</td>
<td>7.8</td>
<td></td>
</tr>
<tr>
<td>Xianren Cave</td>
<td>Jiangxi</td>
<td>28°45'</td>
<td>117°09'</td>
<td>Holocene</td>
<td>8.5</td>
<td>2, 3, 10</td>
</tr>
<tr>
<td>Shexian Cave</td>
<td>Jiangsu</td>
<td>~31°38'</td>
<td>~119°02'</td>
<td>Holocene/Pleistocene</td>
<td>11.2</td>
<td>2, 5, 11</td>
</tr>
<tr>
<td>Luoding</td>
<td>Guangdong</td>
<td>22°40'</td>
<td>111°30'</td>
<td>Pleistocene5</td>
<td>10–120</td>
<td>12</td>
</tr>
<tr>
<td>Jiandaqian Shan</td>
<td>Fujian</td>
<td>~24°30'</td>
<td>~117°30'</td>
<td>Pleistocene6</td>
<td>40–120</td>
<td>13</td>
</tr>
<tr>
<td>Vietnam</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Keo Leng</td>
<td>Lang Son</td>
<td>~21°57'</td>
<td>~106°23'</td>
<td>Pleistocene</td>
<td>20–30</td>
<td>14, 15</td>
</tr>
<tr>
<td>Lang Trang</td>
<td>Than Hoa</td>
<td>20°21'</td>
<td>105°13'</td>
<td>Pleistocene</td>
<td>?</td>
<td>15, 16</td>
</tr>
<tr>
<td>India</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Goalpara (= Gulpara)</td>
<td>Assam</td>
<td>26°10'</td>
<td>90°37'</td>
<td>Holocene</td>
<td>?</td>
<td>17</td>
</tr>
</tbody>
</table>

1 Ka = thousands of years ago.
3 Species identification provisional.
4 Xiashan Cave and Shanbeiyan Cave.
5 “[P]robable Late Pleistocene.”
6 “[E]arly Late Pleistocene.”

TAIL LENGTH—Like head and body length, tail length in adults of both sexes of Macaca mulatta generally tends to increase from south to north (Fig. 9; Table 4). However, relatively long-tailed specimens collected in the Indo-Chinese peninsula, near the southeastern limit of distribution of Macaca mulatta, constitute an important exception to this generalization; these aberrant specimens have been interpreted as the result of hybridization between Macaca mulatta and M. fascicularis (Fooden, 1997, p. 228). Because of the generally parallel latitudinal variation of tail length and head and body length in Macaca mulatta, relative tail length (tail length/head and body length) is relatively constant latitudinally, except in the extreme southeast, where it increases at lower latitudes (Fig. 11; Table 5). Longitudinally, tail length and relative tail length in Macaca mulatta tend to decrease east of ca. 105°E, again except in the extreme southeast (Fig. 12; Table 5). Both latitudinally and longitudinally, variation in tail length and relative tail length is gradual (Figs. 11, 12). In insular samples, tail length and relative tail length are similar to corresponding lengths in nearby continental samples (Figs. 9, 11).

PELAGE—Analysis of geographic variation in pelage color and pelage length in Macaca mulatta is complicated by age variation and particularly by seasonal variation (see above). However, when comparisons are restricted to postinfantile speci-
mens in prime pelage, individual variation in pelage color apparently exceeds geographic variation in this species. Pelage color frequently differs strongly in individuals collected at the same locality (Fig. 3B), and pelage color frequently is similar or identical in individuals collected at localities separated by thousands of kilometers (see discussion above. “Pelage—Geographic Varia-

tion—Summary,” p. 25; cf. Jiang Xuelong et al., 1991, p. 242). Although pelage length, both on body and appendages, tends to increase from south to north, the latitudinal transition is gradual (Figs. 6, 7).

Molecular Diversity—Although mtDNA haplotypes in M. mulatta generally are unique at each locality sampled, haplotypes in neighboring
Table 30. Subspecies recognized (x) in published classifications of *Macaca mulatta*, 1932–95. Italicized code numbers indicate recognized subspecies to which unrecognized subspecies are referred in cited classifications; dash (—) indicates that proposed subspecies is not considered in cited classification.

<table>
<thead>
<tr>
<th>Proposed subspecies</th>
<th>Authors2 and dates of classifications</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>mulatta</td>
</tr>
<tr>
<td>2</td>
<td>sancijohannis</td>
</tr>
<tr>
<td>3</td>
<td>lasiotus</td>
</tr>
<tr>
<td>4</td>
<td>techeniensis</td>
</tr>
<tr>
<td>5</td>
<td>vestitis</td>
</tr>
<tr>
<td>6</td>
<td>villosus</td>
</tr>
<tr>
<td>7</td>
<td>littoralis</td>
</tr>
<tr>
<td>8</td>
<td>breviceadus</td>
</tr>
<tr>
<td>9</td>
<td>sianica</td>
</tr>
<tr>
<td>10</td>
<td>mcmahoni</td>
</tr>
</tbody>
</table>

1 Allen (1930, p. 1; 1938, p. 284), who did not publish a formal classification of subspecies of *M. mulatta*, expressed doubt concerning the distinctness of all proposed subspecies, with the possible exception of *M. m. vestitis* and *M. m. villosus*: Corbet’s (1992, p. 170) opinion is similar (“it is unlikely that discrete subspecies can be recognized”).


3 Termination as in original spelling of name.

4 Allocation of unrecognized subspecies inferred from geographic distributions given for recognized subspecies.

5 Unrecognized subspecies allocated provisionally.

6 Cited by synonym or incorrectly spelled name.

7 Recognized provisionally.

populations tend to be more similar than those in widely separated populations (see “Mitochondrial DNA” above); somewhat unexpectedly, known haplotypes in eastern *M. mulatta* are more similar to those in *M. cyclopis* and *M. fuscata* than they are to those in western *M. mulatta*. Further evaluation of the bearing of mtDNA data on subspecies determination in *M. mulatta* will require additional samples from precisely known, geographically intermediate localities. Few data are available concerning geographic variation of nuclear DNA in *M. mulatta* (see above). Available blood-protein allele frequency data (see above) also are inadequate for delimitation of subspecies in *M. mulatta*.

**Synonymy**

*Maca* *mulatta*  
(Zimmermann, 1780, p. 195)

Tawny [Monkey]: Pennant, 1771, p. 120—based on menageric animal, not preserved: “Inhabits India.”

*Cercopithecus* [sp.]: Erxleben, 1777, p. 43—generic allocation of Tawny Monkey: Pennant, 1771.

*Cercopithecus* (Mulatta) Zimmermann, 1780, p. 195—based solely on Tawny Monkey: Pennant, 1771: origin “Osindien.”

*Cercopithecus mulatta*: Anderson, 1879, p. 56—incorrect spelling, not an available name.

*Simmia Mulatta*: Goldfuss, 1809, p. 61—new combination.

*Macaca mulatta*: Hinton & Wroughton, 1921, p. 668—new combination; taxonomic history.

*Macaca mulatta*: Tate, 1947, p. 132—incorrect spelling, not an available name.

*Maca mulatta*: Khajuria, [1955], p. 114—incorrect spelling, not an available name.


*Maca mulatta mulatta*: Pocock, 1932, p. 533—new rank; type locality restriction.

*Maca mulatta mulatta*: Khajuria, [1955], p. 113—incorrect spelling, not an available name.


Hinton & Wroughton, 1921, p. 668—synonym of *Cercopithecus mulatta* Zimmermann, 1780.


Macaca rhesus: Daudin, 1802, p. 148—new combination.


Cynocephalus rhesus: Latreille, 1804, p. 292—new combination.


Inuus Rhesus: Schinz, 1821, p. 113—incorrect spelling of generic name.


Papio Rhesus: Ogilby, [1840], p. lix—new combination.

Papio Rhesus: Percy, 1844, p. 83—incorrect spelling, not an available name.


[Inuus (Maimon) erythraeus: Anderson, 1879, p. 56—incorrect spelling of generic name.

Pitheicus (Macacus) erythraeus: Dahlbom, 1856, p. 116—new combination.


Wrinkled Baboon: Shaw, 1800, p. 33—based on Macaque à queue courte: Buffon, 1789, and Simia erythraeus Schreber, [1800].

Macacus radiatus: Hodgson, 1834, p. 96 (not É. Geoffroy, 1812)—misidentification. Ogilby, [1840], p. ix—synonym of Simia rhesus Audebert, [1799].


Macaca cimops: Chiarelli, 1972, p. 208—incorrect spelling, not an available name.


Inuus pelops: Hutton, 1865, p. xiii (not Hodgson, 1841)—misidentification.


Inuus sancti-johannis: Matschie, 1912, p. 306—incorrect spelling of generic name.

Inuus sancti-johannis: Pocock, 1932, p. 546—incorrect spelling of generic name.

Macacus sancti-johannis: Swinhoe, 1870, p. 615—new combination.

Pitheus sancti-johannis: Elliot, 1913, p. 198—new combination.


*Macacus lasiotus*: Gray, 1868, figure caption—inaudient misspelling (cf. text), not an available name.

*Macacus loriolus*: Mollendorf, 1889, p. 9—incorrect spelling, not an available name.

*Macaca johannis*: Blyth, 1875, p. 5—new combination.

*Pithecus lasiotus*: Elliot, 1913, p. 198—new combination.


*[Macacus lasiotis] teheliensis*: Trouessart, 1897, p. 27—new rank.

*Macaca lasiotis teheliensis*: de Beaux, 1923, p. 28—incorrect spelling, not an available name.


*Pitheus vestitus*: Elliot, 1913—new combination.


*[Macacus] villosus*: Trouessart, 1897, p. 27—new rank.

*Pitheus villosus*: Elliot, 1913, p. 200—new combination.


*Pitheus littoralis*: Elliot, 1909, p. 250—holotype, BM(NH) 1900.5.8.1 (Coll. No. a), adult female, skin and skull, collected at Kuator, Fujian Province, China, by C. B. Rickett, November 1898; paratypes, BM(NH) 1898.11.1.29 (juvenile male, skin and skull, purchased at Kuator, Fujian Province, China, by J. de la Touche, 12 May 1898), BM(NH) 1871.3.5 (juvenile female, menagerie animal, skin and skull, obtained from Zoological Society of London before 1872, provenance reportedly “Kashmir”). Allen, 1930, p. 2—synonym of *Cercopithecus mulatta* Zimmermann, 1780. Pocock, 1932, p. 546—synonym of *Macaca mulatta sanctijohannis* (Swinhoe, [1867]). Kellogg, 1945, p.

Macaca mulatta littoralis: Jiang Xuelong et al., 1991, p. 244—new rank.

Pithecus brachyurus Elliot, 1909, p. 251 (not Macacus brachyurus Smith, 1842)—holotype, AMNH 27577, adult male, skin and skull, collected at Mr. Wachi (= Wuzhi Shan), Hainan Dao, China by A. Owston, 10 October 1905; paratypes (incidentally cited in original description), AMNH 26646 (Coll. No. 13/16, adult male, skin and skull, collected at Henron, Hainan Dao, China by A. Owston, 10 May 1904), AMNH 27568 (infant male, 1 October), 27569 (juvenile female, 2 October), 27570 (juvenile female, 3 October), 27571 (adult female, 4 October), 27572 (subadult male, 5 October), 27573 (adult female, 5 October), 27574 (adult female, 6 October), 27575 (juvenile female, 7 October), 27578 (subadult female, 30 October). BM(NH) 1909.7.11.1 (Coll. No. 13, AMNH 27576, juvenile male, 10 October), collected at Wuzhi Shan, Hainan Dao, China by A. Owston, 1905. Elliot, 1913, p. 217—homonym of Macacus brachyurus Smith, 1842; replaced by Pithecus brevicaudatus Elliot, 1913.

Macaca mulatta brachyurus: Xu et al., 1983, p. 312—new rank.


Pithecus brevicaudatus: Fiedler, 1956, p. 179—incorrect spelling, not an available name.

Macaca brevicaudata: Mell, 1922, p. 11—new combination.

Macaca brevicaudata: Tate, 1947, p. 134—new combination; incorrect spelling, not an available name; “doubtfully valid form.”


Macaca simica: Yang & Chou, 1984, p. 56—incorrect spelling, not an available name.


Macaca mulatta momahoni Pocock, 1932, p. 544—holotype, BM(NH) 1920.6.11.1, adult male, skin and skull, collected at Kootai, lower Chitrals, 3600 ft (= Kateo, lower Kunar River, 1100 m), Pakistan, by F. D. Stirling, early February 1914; paratype, BM(NH) 1931.9.1.1, [adult male], skin only, obtained alive in eastern Nurestan, Pakistan, by H. McMahon, received at Regents Park Zoo 3 April 1906, died 19 January 1910. Napier, 1981, p. 24—type series cataloged.


M [mulatta] momahori: Peng et al., 1993, p. 5—incorrect spelling, not an available name.

Type

Cercopithecus mulatta Zimmermann, 1780 (p. 195), is expressly based on Pennant’s (1771, p. 120) brief characterization of a menagerie captive that he observed, presumably in London, “in Mr. Brook’s exhibition.” No part of the captive, which Pennant designated as the Tawny Monkey, is known to have been preserved.

In an addendum, Pennant (1771, p. xxiii, pl. XIII.A, fig. II) characterized and figured a second monkey (unpreserved, species unidentified) that he regarded as a “variety” of the Tawny Monkey. This second monkey also is cited as a “Spielart” in Zimmermann’s (1780, p. 195) original description of Cercopithecus mulatta. As an acknowledged variant, the second monkey does not qualify as a syntype of Cercopithecus mulatta (International Code of Zoological Nomenclature, 1985, Article 72[b]:i). Although the holotype of Cercopithecus mulatta Zimmermann appears not to have been preserved, designation of a neotype is not appropriate here. Article 75(a) of the International Code of Zoological Nomenclature (1985) specifies that a neotype is to be designated “only in exceptional circumstances when a neotype is necessary in the interests of stability of nomenclature.” Because such circumstances do not apply to M. mulatta, designation of a neotype for this species would have no standing (Article 75[c]).

Type Locality

Concerning the geographic origin of the Tawny Monkey, Pennant (1771, p. 120) merely commented, “Inhabits India” (italics in original). Zimmermann (1780, p. 195) rephrased this comment as “Er kam aus Ostindien.” Based on the type locality of Macacus oïnops Hodgson, 1841, a subjective synonym of Cercopithecus mulatta Zimmermann, 1780. Pocock (1932, p. 533) restricted the type locality of M. mulatta to “Nepal Tarai”—that is, the belt of Nepalese lowlands.
(Terai) that extends along the border between Nepal and India (Fig. 21).

Evolution and Dispersal

Fossil evidence indicates that a macaque similar or identical to *M. mulatta* inhabited Vietnam ca. 20 to 30 Ka and inhabited eastern China ca. 40 to 120 Ka (Table 29). This evidence establishes minimum dates for the existence of *M. mulatta*, or a close relative, in eastern Asia; the actual date of first appearance of this species in this region may of course be much earlier. Following is a hypothetical interpretation of the evolutionary and geographical history of this species, based primarily on variation in relative tail length (Fig. 22).

*M. mulatta* is a member of the *fascicularis* group of macaques, which also includes *M. fascicularis* in peninsular and insular Southeast Asia, *M. cyclopis* in Taiwan, and *M. fuscata* in Japan (cf. Fooden & Albrecht, 1999, p. 432; Morales & Melnick, 1998, p. 17). In these species, relative tail length generally decreases as latitude increases, in accord with Allen’s rule (Table 31).

Assuming that reduced relative tail length is a shared derived character state in the *fascicularis* group, *M. fascicularis* may be regarded as the primitive sister group of *M. cyclopis*, *M. mulatta*, and *M. fuscata*. Initial reduction of relative tail length and splitting of the derived species from *M. fascicularis* presumably occurred before ca. 40 Ka, in or near the northern part of the Indochinese peninsula (Fig. 22A); reduction of relative tail length in this area probably was an evolutionary response to lower ambient temperatures encountered by a *fascicularis* group population as it dispersed northward from its ancestral tropical habitat. The latitudinal range of the northward-dispersing *fascicularis* group population eventually extended to at least ca. 40°N in eastern Asia.

Although relative tail length in the *fascicularis* group generally decreases with increasing latitude, this correlation does not apply to southern populations of *M. mulatta* (ca. 15°-25°N), in which relative tail length is similar to that in conspecific northern populations (Fig. 11) and therefore is less than expected according to Allen’s rule. This suggests that southern populations of *M. mulatta* did not originate within their present latitudinal zone but instead dispersed there relatively recently from farther northward (cf. Fooden & Albrecht, 1999, p. 438). Judging from the general relationship between latitude and relative tail length in the *fascicularis* group, relative tail length in the population of this group that originally inhabited the 15 to 25°N latitudinal zone probably was similar to that in *M. cyclopis*. This interpretation assumes that evolutionary shortening of a long tail in response to cooler climate occurs more readily than evolutionary lengthening of a short tail in response to warmer climate (cf. *M. fuscata*, Figs. 22 A, B; *M. a. assamensis*, Fooden, 1988, pp. 4, 9).

Mean relative tail length in the northward-dispersing *fascicularis* group population apparently varied from ca. 0.90 at ca. 20°N to ca. 0.30 at ca. 40°N; conversely, body size and pelage length and density presumably increased at higher latitudes (Figs. 6, 8). At this evolutionary stage, the progenitors of *M. cyclopis* (mean relative tail length ca. 0.90) presumably dispersed from the mainland to Taiwan, and the progenitors of *M. fuscata* (mean relative tail length ca. 0.30) dispersed from the mainland to the Japanese islands. There is no evidence that the southern *fascicularis* group population (15°-25°N) with mean relative tail length ca. 0.90 dispersed northwest of the Indochinese peninsula; this suggests that a barrier to northwestward dispersal may have existed during this stage in the evolution of the *fascicularis* group.

As indicated above, the evidence of relative tail length suggests that an *M. mulatta* population (mean relative tail length <0.50) dispersed southward and replaced the *cyclopis*-like population (mean relative tail length ca. 0.90) that is postulated to have originally inhabited the 15°-25°N latitudinal zone in mainland eastern Asia (Fig. 22B); as a result of this replacement, *M. cyclopis* became relictual in Taiwan. The southward dispersal of *M. mulatta* and the correlated replacement of the aboriginal mainland *cyclopis*-like population may have occurred during the last glacial maximum (ca. 18 Ka), when climatic deterioration rendered the northern part of the present range of *M. mulatta* unsuitable for habitation by this species (Xu, 1988, p. 875; Tong & Shao, 1991, p. 65; Tong & Zhang, 1991, p. 389; Winkler & Wang, 1993, p. 245; Zheng & Lei, 1999, p. 357). Before or during the southward shift of the range of *M. mulatta* in eastern Asia, a west-east gradient of declining relative tail length apparently had become established in this species (100°E, mean relative tail length ca. 0.45; 120°E, mean relative tail length ca. 0.30) (Fig. 12); the factors
**A: ≥40 Ka**

Boldface numbers indicate approximate mean relative tail length in local populations.

**B: 18 Ka**

**C: <18 Ka**

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FIELDIANA: ZOOLOGY
Table 31. Latitudinal range and relative tail length (tail length/head and body length) in *fascicularis*-group species of macaques (Fooden & Albrecht, 1999, fig. 2).

<table>
<thead>
<tr>
<th>Species</th>
<th>Latitudinal range</th>
<th>Mean ± SD</th>
<th>Extremes</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. fascicularis</em></td>
<td>10°S–21°N</td>
<td>116.9 ± 14.4</td>
<td>69.2–149.5</td>
<td>393</td>
</tr>
<tr>
<td><em>M. cyclops</em></td>
<td>22°N–25°N</td>
<td>82.9 ± 6.3</td>
<td>69.2–94.7</td>
<td>26</td>
</tr>
<tr>
<td><em>M. mulatta</em></td>
<td>15°N–41°N</td>
<td>44.4 ± 8.9</td>
<td>20.0–72.1</td>
<td>120</td>
</tr>
<tr>
<td><em>M. fascata</em></td>
<td>30°N–41°N</td>
<td>13.5 ± 2.7</td>
<td>9.5–18.6</td>
<td>7</td>
</tr>
</tbody>
</table>

In addition to displacing the *cyclops*-like population that formerly inhabited mainland eastern Asia, the southward dispersal of *M. mulatta* to the 15°–25°N latitudinal zone apparently had three further zoogeographic consequences: (1) Eastern members of the *M. mulatta* population (mean relative tail length ca. 0.30) apparently dispersed to Hainan and two groups of smaller shallow-water islands in the South China Sea (Fig. 22B; cf. Pan et al., 1992, p. 42); during the last glacial maximum, these present-day islands were connected to continental Asia by dry land (Fooden, 1995, p. 12). (2) Western members of the *M. mulatta* population (mean relative tail length ca. 0.45) may have dispersed westward, perhaps marking the entrance of *M. mulatta* into the Indian subregion, which ultimately may have contributed to local disappearance of *sinica*-group species of macaques (Fooden, 1989, p. 42); a Holocene fossil of *M. mulatta* has been reported in the Madras region (ca. 80°E; Table 29), and archaeological evidence indicates that this species was known at Moenjo Daro (27°19’N, 68°07’E) ca. 4 Ka (see “Geographic Distribution,” pp. 2 ff.). (3) In the south, *M. mulatta* contacted *M. fascicularis*; this contact apparently has resulted in limited hybridization between *M. mulatta* and *M. fascicularis* (Fooden, 1997, p. 226).

Subsequent to the last glacial maximum, as the climate at higher latitudes ameliorated, *M. mulatta* in eastern Asia apparently dispersed northward and reoccupied the northern area it had previously vacated (Fig. 22C). The western population of *M. mulatta* also dispersed to higher latitudes in the Indian subregion, apparently retaining the relative tail length (ca. 0.45) of its putative founders (Table 5). Eastern and western populations of *M. mulatta* at higher latitudes are similar in their enhanced body size, pelage length, and pelage density (Figs. 6, 8; Table 3); this similarity presumably is the result of parallel adaptation to cool temperature.

The above scenario is compatible with major findings concerning geographic variation in mtDNA haplotypes in *M. mulatta* and other *fascicularis* group species (see above). The similarity of haplotypes in eastern *M. mulatta*, *M. cyclops*, and *M. fascata* may be attributable to the common origin of these three groups from *M. fascicularis* (Fig. 22A). The divergence of haplotypes in western *M. mulatta* and, independently, in Hainanese *M. mulatta* from those in eastern *M. mulatta* may be attributable to the presence of distinctive haplotypes in founders of the western and Hainanese populations (Fig. 22B).

Acknowledgments

For access to specimens and generous cooperation, I am deeply grateful to curators and staff members of institutions cited above (see “Introduction”). For helpful discussions, useful supplementary information, and other assistance, I also thank D. Brandon-Jones and P. D. Jenkins (British Museum [Natural History]); D. J. Melnick and J. C. Morales (Columbia University); J. Bates, L. R. Heaney, J. C. Kerbs Peterhans, B. D. Patterson, and J. Weinstein (Field Museum of Natural History); Zhang Yongzu (Institute of Geography, Chinese Academy of Sciences); Liu Wanfu (Forestry Department of Guangxi); Wu Mingchuan (Forestry Designing Center of Guangxi); Feng

Fig. 22. Hypothetical stages in the evolution and dispersal of *Macaca mulatta*, based primarily on variation in relative tail length in *fascicularis*-group species.

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Zuojian and Quan Guoqiang (Institute of Zoology, Chinese Academy of Sciences); E. Delson (Lehman College, City University of New York); and M. K. Chalise (Natural History Society of Nepal). Preparation of this monograph was partly supported by the Barbara E. Brown Fund for Mammal Research.

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Note Added in Proof

Listed below are relevant supplementary publications that appeared while this monograph was in press.

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JOHNSON, E. 1999. Food-aphobia in semi-free ranging rhesus macaques: Effects of food limitation and food source. American Journal of Primatology, 50: 25–35. (For date of publication, see outside back cover.)


Appendix 1: Specimens Examined (Total 638)

SKINS AND SKULLS, 342

AFGHANISTAN, 1. Konarha (1), Chigha Sarai, north of—FMNH 102839.


INDIA, 60. Arunachal Pradesh (2): Dening—BM(NH) 1931.1.11.13, 1931.1.11.14, Assam (7): Bogra Nadi—BM(NH) 1931.1.11.6; Golaghat—BM(NH) 1931.1.11.12; Hot Springs—BNHS 5087, Kulsi [River]—BNHS 5088; Lamsakhang—BM(NH) 1921.7.9.4; Rajapara—BM(NH) 1921.7.9.3; locality unknown—ZSI 11928. Bihar (3): Liana—BM(NH) 1915.4.3.1, 1915.4.3.2; BNHS 5089. Gujarat (3): Dangs District—BM(NH) 1931.1.11.1-1931.1.11.3. Himachal Pradesh (6): Dharamsala—BNHS (BM(NH) 1933.12.12, Kangra—BNHS 5112, 5114; Kangra Fort—BM(NH) 1923.9.1.118; Samayala—BN (NH) 1931.1.11.34, 1931.1.11.35. Jammu & Kashmir (11): Dunwein—P-CM T4/2(skin), T4/8 (skull); Kashmir—BNHS 1871.3.3.5, USNM 63471; Kothiar—USNM 173812, 173813; Lolab—USNM 20120-20124; Lolab Valley—USNM 173814. Manipur (3): Bishenpur—BM(NH) 1943.60, 1943.61; Imphal, ca. 4 mi northeast of—ZSI 11187. Meghalaya (1): Nangpoh—BM(NH) 1931.1.11.15. Nagaland (2): Changchang Pani—AMNH 83431, 83432. Tripura (2): Ampi Bazar, ca. 3 km southeast of resthouse—ZSI Coll. No. TM4; Charilam resthouse—ZSI Coll. No. TM18. Uttar Pradesh (10): Bageshwar—BM(NH) 1914.7.10.1-1914.7.10.3; Jharna—ZSI 12091; Ramnagar—BNHS 5108; Ratighat—BM(NH) 1914.7.10.4, 1914.7.10.5; BNHS 5109; Sita Bani—BM(NH) 1931.1.11.31, BM(NH) 1931.1.11.32. West Bengal (8): Bharnabari—BM(NH) 1931.1.11.8. Hasimara—BM(NH) 1916.7.29.1, 1916.7.29.2, 1931.1.11.9; Mangpu—FMNH 35448, 35449; Narbong—BM(NH) 1915.9.11; Sukna—ZSI 7294. State unknown (2): INDIA—BM(NH) 1841.12.25.1, BM(NH) 1842.4.29.55.

INDIA or BANGLADESH, 2. Bengal—NHMB 29, 31.

LAOS, 8. Louangphrabang or Phongsali (1):

MYANMAR. 72. Chin (2): Ali Cha—BNH(N) 1931.11.11.22. Kindat, 20 mi northwest of—BNH(N) 1931.11.11.26. Irrawaddy (1): Pye (= Prome), 30 mi southeast of—BNHS 5081. Kachin (19): Bawnwiang—BNH(N) 1950.373; Bhamo—BNH(N) 1936.12.26.4; Htingnan Triangle; BNH(N) 1950.372; Karen Chaung—BNH(N) 1937.12.3.75; N'Changyang—BNH(N) 1936.154; Nanyaseik—AMNH 112722–112725; Singkaling Hkamti—BNH(N) 1931.1.11.25; Singkaling Hkamti, 50 ft—BNHS 5093; Singkaling Hkamti, left (east) bank—ZSI 12088; Singkaling Hkamti, right (west) bank—AMNH 112988; Taga Hka—AMNH 112734, 112971; Tang Hpre—USNM 279191; Tanga-Shingaw—AMNH 114547; Taro—AMNH 112732, 112732. Karen (3): Toungoo, 13 mi east of—BNH(N) 1931.1.11.20, BNHS 5105; Toungoo, 13 mi north of—BNH(N) 1927.11.18.1. Mandalay (14): Kokkoang—BNH(N) 1937.12.3.76; Lethan Hka—BNH(N) 1936.12.26.3; Maymyo—AMNH 163616; Popa Hill, 1000 m—AMNH 163610–163615; Popa Hill, 4961 ft—BNH(N) 1914.7.19.2, BNHS 5102–5104, 5106. Pegu (6): Pye (= Prome). 35 mi southeast of—BNH(N) 1931.1.11.21; Toungoo, 30 mi northwest of—BNH(N) 1931.1.11.17, BNHS 5101; Toungoo, east side of Sittang River—BNH(N) 1931.1.11.16, 1931.1.11.18, 1931.1.11.19. Sagaing (20): Hein-sun—AMNH 112739, 112972; Hisweht—BNH(N) 1931.1.11.24; Homalin—BNH(N) 1915.5.5.3, 1915.5.5.4, BNHS 5094 Kin—BNHS 5095; Maungkan—AMNH 112741; Mingun—BNH(N) 1914.7.19.1, Moklok—AMNH 112740; Tatkon, east bank of Chindwin River—BNHS 5091; Tatkon, west bank of Chindwin River—BNH(N) 1915.5.5.6, BNHS 5090; Yin, east bank of lower Chindwin River—BNH(N) 1915.5.5.7; BNHS 5097; FMNH 82806, 82807; Yin, lower Chindwin River—BNHS 5096, 5098, 5099. Shan (7): Mansam Falls—BNH(N) 1931.1.11.28, BNHS 5082, 5083, 5085; Pyun-gaung—BNH(N) 1931.1.11.30, BNHS 5084; Se-eng—BNH(N) 1931.1.11.29.


SKINS ONLY. 154


INDIA or BANGLADESH. 1. "(Bengal)"—ANSP 3950.


NEPAL. 4. Bagmati (4): Gokarna—UPs Coll. No. 529 (formerly FMNH 104163); Trisuli Bazar, 4 mi southeast of—FMNH 135427—135429 (all three in alcohol).


SKULLS ONLY, 142.


FOODEN: SYSTEMATIC REVIEW OF THE RHESUS MACAQUE, MACACA MULATTA
Binh (1): Bo Trach District—IEBR 1431. Quang
Nam-Da Nang (2); Son Tra, Mt—USNM 356978
(mandible missing), 356979 (external measurements
in collector's fieldbook). Quang Ninh (4): Quan Lan,
Dao—IEBR T15; Van Canh, Dao—IEBR T13, 14
(identification tentative); Van Hai, Dao—ZMVNU
178/3.152.Pc27. Vinh Phu (1); Thanh Son—ZMVNU
18, T19; Thuong Bang La—IEBR 835/36/199. Pro-
vince unknown (26): Tu Chi—ZMVNU 189/34;
VIETNAM—FCXM 028 (identification tentative),
IEBR 440, 2311, 2335, 2358, 2359, unnumbered (4),
ZMVNU 179/3.157.Pc46, 181/3.164.0 (identification
tentative), 182/3.166.0, 183/3.167.0, 187/3.168.0,
190/35, 191/36, 192/37, 193/38, 194/39, 195/40,
541/3.156. Pc45, unnumbered; [VIETNAM]—ZMVNU

Appendix 2: Gazetteer of Macaca mulatta Localities

Locality names listed as primary entries in this
gazetteer preferentially are official names approved
in gazetteers published by the U.S. Board on
Geographic Names (USBGN; Afghanistan,
1971; Bangladesh, 1976; Burma [= Myanmar],
1966a; China, 1979; India [includes Bhutan and
Nepal], 1952; Laos, 1973; Pakistan, 1983; Thai-
lnd, 1966b; Vietnam, 1986). In addition, supplen-
tary references have been consulted for loca-
talities in China (Administrative Divisions of the
People's Republic of China—1980, 1981; Zong-
hua Renmin Gongheguo Fen Sheng Dituji, 1983),
India (National Atlas of India, 1979; Census of
India 1981—various district census handbooks),
and Vietnam (Cuc Ban Do-Bo Tong Tham Muu,
Quan Doi Nhan Dan Viet Nam, 1980–88). Locali-
talities of M. mulatta that were not found in
USBGN gazetteers or supplementary references
are spelled here as in the original sources. Sec-
condary entries, with cross references to corre-
sponding primary entries, indicate variant spell-
ings or alternate locality names that appear on
specimen tags, in published literature, or in un-
published notes concerning M. mulatta.

The sequence of information presented in
primary entries is as follows:

1. Locality name. (Note: Chinese locality names
frequently include the following generic geo-
graphic terms: Dao = Island; Shan = Moun-
tain; Xian = County.)
2. Altitude, if reported by collector or observer.
3. Name of province, state, or other first-order administrative division, in italics.
4. Name of country, in capital letters.
5. Coordinates of locality (principal sources: USBGN gazetteers, supplementary references indicated above, published or unpublished field notes of collectors or observers).
6. Date of collection or observation.
7. Name of collector or observer.
8. Bibliographic reference (in parentheses) to published or unpublished field notes, if any.
9. Abbreviated name of museum (see "Introduction") where specimens are preserved.
10. Number of specimens available (with indication of part preserved, if skin and skull are not both present).
11. Locality code as indicated in distribution maps (Figs. 2A–C).

<table>
<thead>
<tr>
<th>Number</th>
<th>Abbreviated Name</th>
<th>Number</th>
<th>Abbreviated Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Imam</td>
<td>2</td>
<td>Imam</td>
</tr>
<tr>
<td>111</td>
<td>Allahabad</td>
<td>273</td>
<td>Allahabad</td>
</tr>
<tr>
<td>102</td>
<td>Akbarabad</td>
<td>33</td>
<td>Akbarabad</td>
</tr>
<tr>
<td>128</td>
<td>Agra</td>
<td>69</td>
<td>Agra</td>
</tr>
</tbody>
</table>
Amber. See Amer.


Ampi Bazar, ca. 3 km southeast of resthouse; Tripura, INDIA; ca. 26°40'N, 91°38'E; collected 18 Jan. 1971 by V. C. Agrawal (Agrawal & Bhattacharyya, 1977, p. 137); zsm, l. B:1-40.


Anganganj. See Khair, Tahsil.


Anhui, CHINA; 29°–35°N, 115°–120°E; collected 1959–1960 by museum collectors; SMNH, 8 (7 skins only, 1 skull only). Not mapped.

Anji Xian; Zhejiang, CHINA; ca. 30°40'N, 119°40'E; ca. 50 captures acquired 1950–1959 from Local Products Supply Co. by Hangzhou Zoo (Fu Yiyuan, Director, pers. comm., 25 Oct. 1985). C:C-56.


Anlong; Guangzhou, CHINA; 25°06'N, 105°31'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-157.

Annapurna Conservation Area. See Pokhara.


Anyuan; Jiangxi, CHINA; 25°09′N, 115°21′E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-98.

Arbesi. See Basirhat Reserve Forest.

Arunachal Pradesh, INDIA; 26°55′–29°30′N, 91°35′–97°25′E; reported during “past few years” by A. Borang and G. S. Thapliyal (1993, p. 839). Not mapped.


Ashi; Yunnan, CHINA; ca. 26°53′N, 100°00′E; collected in 1921 (see USNM catalog) by J. F. Rock (1925, p. 447; 1926, p. 139; Chock, 1963, p. 93); USNM. 2. B:C-44.


Asmar, east of; Konarha, AFGHANISTAN; ca. 35°00′N, 71°30′E; reported before 1972 by A. Puget (1971, p. 201). A:A-1.


Assam, INDIA; 24°10′–28°00′N, 89°40′–96°00′E; acquired before 1859 by Zoological Society of London; BMN(H), 1 (skull only). Acquired before 1956 by Calcutta Zoological Garden (Khajuria, [1955], pp. 113, 114); ZSM, 1. Not mapped.

Assembly. See Simla.


Babuwali, Jasalmier District; Rajasthan, INDIA; ca. 26°47′N, 69°44′E; falsely reported 4 Sept.

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Bac Can. Tonkin region, 500 ft (= 150 m); Bac Thai, VIETNAM; 22°08’N, 105°49’E; collected 13 Dec. 1926–14 Jan. 1927 by J. Delacour and W. P. Lowe (Delacour & Jobouille, 1927, p. 302); BM(NH), 3 (including 1 skin only): MNHN, 1. C:V-10.

Bachepalli. See Dachepalle.

Bachi. Pingyuan [Xian], Guangdong, CHINA; 24°46’N, 115°49’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-97.


Bac Tan Trai (= Bac Tan Tray), Tonkin region; Lai Chau, VIETNAM; 22°24’N, 103°12’E; collected 5 Nov. 1931 by T. D. Carter (Legendre, 1936, p. 83); ANSP, 1. C:V-1.

Badu. See Batu.


Baima; Qinghai, CHINA; ca. 33°02’N, 100°04’E; collected 11 Sept. 1967 by Wang Zongyi; IZCAS, 1. B:C-23.

Bairaglia. See Hazaria Patherghatta.


Baihuijiang Natural Reserve, 1700–2900 m and 3000–3400 m; Shaanxi, CHINA; ca. 33°35’N, 105°54’E; reported before 1989 by Ma Guoyao (1988, p. 27). C:C-18.


Bak shi mun. See Luofu Shan.


Bamo village, near, Bamo Subcounty, Tiané Xian; Guangxi, CHINA; 24°55’N, 107°21’E; collected in 1987 by Yang Runqiang, subsequently purchased by Huang Runqiang (pers. comm., 24 Oct. 1992); IZCAS, 1 (skull only). C:C-173.


Bandhavgarh National Park; Madhya Pradesh, INDIA; ca. 23°40’N, 81°02’E; reported Feb.–


Bangma: Sichuan, CHINA; not located, 26°00'-34°10'N, 97°40'-110°05'E; reported before 1992 by Jiang Xuelong, Wang Yingxiang, and Ma Shilai (1991, p. 243). Not mapped.

Bangram. See Dhaka.

Bangsal. See Dhaka.


Ban Mak Nao, Camp No. 34; Vientiane, LAOS; 18°00'N, 102°58'E; collected 16 Feb. 1920 by J. Bangassar (Weitzel et al., 1988, p. 116); ZRC, 1. B:L-8.

Ban Manao. See Ban Mak Nao.

Bannabari. See Bharnabhari.


Ban Thi, Cho Don District; Bac Thai, VIETNAM; 22°14'N, 105°31'E; collected 2 May 1970 by Nguyen Trong Tien; ZMVNU, 1 (skull only; species identification tentative). Collected 20 May 1970 by Mr. Nhe; ZMVNU, 1 (skin only). C:V-6.

Ban Umphang, 28 mi (= 45 km) southeast of, 1750 ft (= 530 m); Kamphaeng Phet, THAILAND; ca. 15°28'N, 99°04'E; collected 4 Feb. 1924 by A. S. Vernay (Lowe, 1932, p. 197; 1933, p. 260); AMNH, 1. B:T-8.


Bapon, Fusui Xian; Guangxi, CHINA; ca. 22°35'N, 107°57'E; collected Aug. 1986 by Wu Mingchuan (pers. comm., 27 Nov. 1992); FDGC, 1 (skull only). C:C-219.

Bara Math Temple. See Chitrakut.

Barami. See Barmi.


Barautha. See Barotha.

Bar Chanrai Hill, lower Swat Valley opposite Malakand; North-West Frontier, PAKISTAN; ca. 34°34'N, 71°56'E; reported before 1902 by A. H. McMahon (1901b, p. 9). A:P-6.

Bardia National Park. See Babai River vicinity.


Barikowt (= Baricot), southeast of; Konaraha, AF-GHANISTAN; ca. 35°10'N, 71°35'E; reported before 1972 by A. Puget (1971, p. 201). A:A-1.


Bashgal Valley. See Kaotai.


Baska Nadi. See Bogra Nadi.

Batang vicinity, 2200-3000 m; Sichuan, CHINA; ca. 30°00'N, 99°00'E; reported 1914--1916 by H. Weigold (1924, p. 71). Purchased at Batang market in 1961 by unknown collector; izcA, 1 (skin only). B:C-32.

Batu, Pinglang District, Tianlin Xian; Guangxi,
CHINA; ca. 24°18'N, 106°13'E; collected 31 July 1978 and ca. Oct. 1978 by Neuong Shihua (Quan Guoqiang, pers. comm., 29 Nov. 1985); FDCG, 2 (1 skin only, 1 skull only). C:C-170.

Bawangling, Changjiang Xian, Hainan Dao, 500–600 m; Hainan, CHINA; 19°07'N, 109°05'E; collected 1 Jan. 1964 by Liu Zhenhe; SCIEA. 1. C:C-234.

Bawmwang, 3200 ft (= 975 m); Kachin, MYANMAR (= BURMA); 26°39'N, 97°50'E; collected 6 Feb. 1939 by R. Kaulback; BM(NH). 1. B: M-1.

Beichuanshan, Taishan Xian, Shangchuan Dao, 0–500 m; Guangdong, CHINA; 21°45'N, 112°50'E; observed Apr.–May 1981 by Liu Zhenhe, SCIEA (pers. comm., 25 Nov. 1985). C: C-213.

Beijing (= Pekin), monastery outside of: Beijing, CHINA; 39°56'N, 116°24'E; erroneous locality information (Morris & Morris, 1966, p. 18; Hill, 1974, p. 583) for monkeys (presumably either M. mulatta or M. thibetana) observed ca. 1325 at monastery in Hangzhou vicinity by Odorico of Pordenone (1928, pp. 232, 234). Not mapped.

Benaras. See Varanasi.

Benares. See Saktesgarh; Varanasi.

Bengal. See West Bengal.

“(Bengal)”, INDIA or BANGLADESH; 22°–27°N, 86°–93°E; date and collector unknown; captive, Zoological Society of Philadelphia; ANSP. 1 (skin only). Not mapped.

Bengalen; INDIA or BANGLADESH; 22°–27°N, 86°–93°E; collected in 1859 by unknown collector; NHMB. 2. Captive obtained (date unknown) in Sumatra by Prof. Neisser, reportedly imported from “Bengalen”; MZB, 1 (skull only). Not mapped.


Bhalagpur District; Bihar, INDIA; ca. 25°15'N, 87°00'E; reported 1810–1811 by F. Buchanan (1939, p. 285; posthumous publication). B: I-5.

Bhamo, 600 ft (= 180 m); Kachin, MYANMAR (= BURMA); 24°16'N, 97°14'E; collected 15 Feb. 1936 by P. E. Garthwaite; BM(NH). 1. B: M-15.


Bharnabhari (= Bharnabhavi), Bhutan Duars, 600 ft (= 180 m); West Bengal, INDIA; ca. 26°45'N, 89°23'E; collected 21 Feb. 1916 by N. A. Baptista (H. V. O'Donel in Wroughton, 1917, p. 63); BM(NH). 1. B: I-9.

Bheri River; Saliyana, NEPAL; ca. 28°30'N, 82°00'E; observed Feb. 1977 by P. Byrne (1979, p. 70). A: N-7.

Bherian. See Tinsukia.


Bhopal, east of; Madhya Pradesh, INDIA; ca. 23°20'N, 77°40'E; reported ca. 1922 by B. C. Ellison (1922, p. 1100; cf. Fooden. 1989, p. 44). A: I-96.

Bhowal area. See Naini Tal.

Bhotan Duars. See Bharnabhari; Hasimara.

Bhutan Duars. See Bharnabhari; Hasimara.


Bijnor, 1000 ft (= 300 m); Uttar Pradesh, INDIA; 29°22'N, 78°08'E; collected before 1927 by B. B. Osmaston (Napier, 1981, p. 23); BM(NH). 1 (skull only). A: I-34.


Biloxi River, near Nuijiang (= Salween River). Bijiiiang Xian; 3000 m; Yunnan, CHINA; ca. 26°35'N, 99°05'E; collected 19 Oct. 1978 by Ma Shilai (pers. comm., 1 Sept. 1983); KIZ, 1 (skull only). B: C-43.

Bishenpur (= Bistenpur), 3000 ft (= 900 m); Manipur, INDIA; 24°38'N, 93°46'E; collected 20 Feb. 1940 by W. J. C. Frost; BM(NH). 2. B: I-38.

Biyun, ca. 30 km north of; Anhui, CHINA; ca. 30°25'N, 118°20'E; observed before 1973 by

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Xiong Chenpei (Wada et al., 1986, p. 82). C:C-53.

Biyun, Jingde Xian, 300–400 m; Anhui, CHINA; ca. 30°10'N, 118°20'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-62.

Boai; Henan, CHINA; 35°10'N, 113°04'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-11.

Boga Juli. See Bogra Nadi.

Bogra Nadi (? = Boga Juli), North Kamrup, 2000 ft (= 600m); Assam, INDIA; ca. 26°48'N, 91°35'E; collected 5 Jan. 1921 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BM(NH), 1. B:1-16.

Bohea. See Kuatun.


Boluo, Yingde Xian; Guangdong, CHINA; 24°25'N, 113°00'E; reported in 1970 by local residents to Liu Zhenhe, SCIEA (pers. comm., 25 Nov. 1985). C:C-205.

Bolovens. See Muang Thateng.

Bombay. See Mumbai.


Borajan. See Tinsukia.


Borribazar. See Borome.

Boska Nadi. See Bogra Nadi.

Bo Trach District; Quang Binh, VIETNAM; ca. 17°35’N, 106°33’E; collected 25 Mar. 1976 by unknown collector; IEBR, 1 (skull only). C:V-30.

Bouzini, Katmandu Valley; Bagmati, NEPAL; ca. 27°41’N, 85°11’E; collected 18 June 1922 by N. A. Baptista (Hinton & Fry, 1923, p. 403); BM(NH), 1. A:N-12.

Brindaban. See Vrindavan.
1964 by Hien Hao; ZMVNU, 3 (skulls only). C: V-14.


Cehong; Guizhou, CHINA; 24°58’N, 105°49’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-159.


Chaibasa. See Luia.


Chakmanki. See Chamkani.


Chamkani, southeast of; Pakitia, AFGHANISTAN; ca. 33°45’N, 70°05’E; reported before 1972 by A. Puget (1971, p. 201). A:A-12.


Changchang Pani; Nagaland, INDIA; 26°36’N, 94°26’E; collected 15–18 Feb. 1930 by C. McCann (1933a, p. 395); AMNH, 2. B:J-31.

Changde; Hunan, CHINA; 29°02’N, 111°41’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-108.

Changhua vicinity, Lin’an Xian; Zhejiang, CHINA; ca. 30°10’N, 119°13’E; skin collected locally in 1979 observed Apr. 1980 by Tang Ziyi-

Changjiang. See Yichang.

Changlung. See Nu Jiang.

Changning [Xian]; Yunnan, CHINA; ca. 24°50’N, 99°36’E; blood sample obtained before 1999 by Ding Bo, Zhang Yaping, and Hou Yidi (1998, p. 172). B:C-64.

Changshun; Guizhou, CHINA; 25°59’N, 106°25’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-146.


Chapai. See Nawabganj vicinity.

Charilam resthouse, ca. 25 km south of Agartala; Tripura, INDIA; 23°38’N, 91°18’E; collected 16 Nov. 1969 by V. C. Agrawal (Agrawal & Bhattacharyya, 1977, p. 137); zsi, 1. B:1-40.


Chengbu; Hunan, CHINA; 26°26’N, 110°21’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-186.


Chengli. 2 mi (= 3 km) west of Ghurkha; Gandaki, NEPAL; ca. 28°00’N, 84°35’E; collected 7 Dec. 1922 by N. A. Baptista; BM(NH), 1. A: N-9.

Chengxian; Gansu, CHINA; 33°42’N, 105°36’E;
reported before 1998 (Zhang et al., 1997, p. 58).


Chhota Assam, H. S. A. Siddiqi; 28°00'–30°00'N, 92°00'–94°40'E; collected 1923–1924 by F. R. Wulsin (letter, 9 Jan. 1925; USNM archives, no. 85377); MCZ, 2. Not mapped.

China; northern; 30°–45°N, 100°–125°E; obtained date unknown by Mr. Gerrard; ZMB, 1. Not mapped.


China, North; 20°–30°N, 100°–120°E; collected 1929–1942 by F. R. Wulsin (letter, 9 Jan. 1925; USNM archives, no. 85377); MCZ, 2. Not mapped.

Chinhewa River; Sagaing, MYANMAR (= BURMA); 21°35'–27°00'N, 94°20'–97°10'E; collected ca. 1914 by G. C. Shortridge; BM(NH), 1 (skull only). Not mapped.

Chin Hills. See Kindat, 20 mi (=32 km) northwest of.


Chitralt. See Nurestan, eastern.

Chitralt, lower. See Kaotai; Kunar River; Mirk- hani.


Chittagong, southern; Cox’s Bazar, BANGLADESH; ca. 21°50’N, 92°00'E; observed early in 1980 by S. P. Gittins and A. W. Akonda (1982, p. 278). B:Ba-38.


Chittagong Hill Tracts; Chin, MYANMAR (= BURMA); ca. 21°40’N, 92°40'E; collected before 1927 by B. B. Osman (Napier, 1981, p. 21); BM(NH), 1 (skull only). B:M-25.


Chittagong Hill Tracts, northern, BANGLADESH; ca. 23°20’N, 92°10'E; observed early in 1980 by S. P. Gittins and A. W. Akonda (1982,

Chitwan National Park. See Dudurhani; Simri. Narayani River.

Cho Don District; Bac Thai. VIETNAM; ca. 22°10'N. 105°36'E; collected Oct. 1989 by unknown collector; FCXM, 1 (skull only). C:V-6.

Chokoria Sunderbans; Cox's Bazar. BANGLADESH; ca. 21°45'N, 92°00'E; reported early in 1980 by S. P. Gittins and A. W. Akonda (1982, p. 278). B:Ba-38.


Chokoria Sunderbans; Cox's Bazar. BANGLADESH; ca. 22°10'N, 105°36'E; observed 1989 by unknown collector; FCXM, 1 (skull only). C:V-6.

Chokoria Sunderbans; Cox's Bazar. BANGLADESH; ca. 21°45'N, 92°00'E; reported early in 1980 by S. P. Gittins and A. W. Akonda (1982, p. 278). B:Ba-38.


Chunabati. See Sukna-Kurseong.

Chunar. See Saktesgarh.


Chungan Hsien. See Chong'an Xian.

Chungtia, 4000 ft (= 1200 m); Nagaland, INDIA; 26°24'N, 94°28'E; collected ca. Sept. 1919 by J. P. Mills (1923, p. 222); museum unknown, 2 (not seen). B:J-32.


Chuxiong; Yunnan. CHINA; 25°02'N, 101°33'E; tissue sample obtained ca. 1991 by Zhang Yaping and Shi Liming (1993b, p. 589). B:C-52.


Cotgai. See Kotgai.


Cox's Bazar, Forest Division (South); Cox's Bazar. BANGLADESH; 20°45'–21°30'N, 92°00'–92°20'E; reported May 1982–Dec. 1983 by S. M. A. Rashid, A. Khan, and M. A. R. Khan (1990, p. 64). Not mapped (see B:Ba-38).


Dacca. See Dhaka.


Dahao Dao; Xianggang (= Hong Kong). CHINA; ca. 22°15'N, 114°00'E; reported 1908–1921 by R. Mell (1922, p. 10). C:C-210.

Dahe, Xixiang Xian, 800 m; Shaanxi. CHINA;


Dainkog (= Dengke); Sichuan, CHINA; 32°32′N, 97°55′E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-19.

Daiyun Shan; Fujian, CHINA; ca. 25°50′N, 118°15′E; reported Nov. 1983 by Zhen Xueqing (1984, p. 145). C:C-86.


Dalimkhola. See Gorubathan Forest.

Dalingxia, Gangcun, She Xian, 400–700 m; Anhui, CHINA; ca. 30°00′N, 118°10′E; observed 1973–1986 by Xiong Chenpei, K. Wada, and Wang Qishan (Wada et al., 1986, pp. 83, 88). C:C-62.

Dalu. See Taro.


Damoh. See Kakara.

Danba; Sichuan, CHINA; 30°57′N, 101°55′E; collected before 1992 by unknown collector (Jiang Xuelong et al., 1991, p. 243); museum unknown, 4 (not seen). B:C-26.

Dangao Dao (= North Lena Island); Guangdong, CHINA; ca. 22°02′N, 114°18′E; observed 5 May 1854 by W. Stimpson (unpublished journal, p. 131; R. Vasile, letters, 2 and 13 May 1887). Collected in 1866 by Commander St. John (in Swinhoe, [1867], p. 556); BM(NH), 1 (holotype of Inius sancti-johannis Swinhoe, [1867]). Reported ca. 1951 by G. A. C. Herklotz (1951, p. 83). C:C-211.

Dangao Dao, Zhuhai Xian, 150 m; Guangdong, CHINA; 22°02′N, 114°18′E; collected 2 and 25 Mar. 1981 by Liu Zhenhe and Xu Longhui (Liu Zhenhe, sciea, pers. comm., 26 Nov. 1985); SCIEA, 2. C:C-211.

Dangien Island. See Dangian Dao.


Dangs District; Gujarat, INDIA; ca. 20°35′–21°00′N, 73°30′–73°55′E; collected 1922–1923 (date discrepancy between original tags and museum tags) by A. C. Miller; BM(NH), 3. Not mapped (see A:1-99).

Dan Sai District; Loei, THAILAND; ca. 17°17′N, 101°09′E; collected 31 Mar. 1954 by R. E. Elbel; USNM, 3. B:T-10.

Danzhou, Hainan Dao; Hainan, CHINA; 19°43′N, 109°17′E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-228.


Dareh Nur. See Khyber Pass vicinity.

Darjeeling. See Darbong; Sukna.


Dashashmedh Ghat. See Varanasi.

Dashuping, 400 m; Shaanxi, CHINA; 32°26′N, 107°27′E; observed July 1974 by Yao Jianchu, siz (pers. comm., 10 Oct. 1985). C:C-32.

Datang, Lunshuihe (river), Tengchong Xian; Yunnan, CHINA; ca. 25°30′N, 98°45′E; collected Dec. 1976 by Ma Shilai (pers. comm., 1 Sept. 1983); KIZ, 6. B:C-57.


Deep Water Bay. See Sam Shui Wan Valley.

Defu Water Regulation Forest Reserve; Guangxi, CHINA; 23°17′N, 105°47′E; observed 1976,

Dége’ vicinity: Sichuan, CHINA; 31°49’N, 98°40’E; purchased in Dége by unknown collector. 15 July 1961; ICAS, 1 (skin only). B:C-22.


Dela, ca. 8 mi (= 13 km) west of Ramnagar; Kumaun region, 1500 ft (= 460 m); Uttar Pradesh, INDIA; 29°26’N, 79°00’E; collected 7 Jan. 1914 by C. A. Crump (in Wroughton, 1914, p. 284; Napier, 1981, p. 24); BM(NH), 1 (skin only). A:I-33.


Dengke. See Dainkong.

Dening, Mishmi Hills, 2240—2250 ft (= 685 m); Arunachal Pradesh, INDIA; 28°01’N, 96°14’E; collected 29 Mar. and 6 Apr. 1921 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BM(NH), 3 (including 1 skin only). B:I-28.

Deogarh, Sambalpur District; Orissa, INDIA; 21°32’N, 84°44’E; collected 30 Dec. 1972 by A. K. Mandal; zsi, 1 (skin only). A:I-104.

Déqên; Yunnan, CHINA; 28°30’N, 98°52’E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-36.


Dhalar. See Narkanda, ca. 1 km north of. Dhaleswari River. See Nagorhenga.


Dharmsala, 4500 ft (= 1370 m); Himachal Pradesh, INDIA; 32°13’N, 76°19’E; collected 5 Feb. 1922 by H. W. Wells (Lindsay, 1926, p. 599); BM(NH), 1. A:I-12.

Dhaulikot Forest, Dehra Dun region; Uttar Prah...
Dhela. See Dela.
Dhikala. See Ramganga River.
Dhulokot. See Dhaulokot Forest.


Diggi Road. See Aligarh.


Dimapur. See Imphal, ca. 4 mi (= 6.5 km) north of.


Dinh Ca. Thai Nguyen region, 300 m; Bac Thai, VIETNAM; 21°45'N, 106°03'E; collected 20 Dec. 1956 by unknown collector (Dao, 1961, p. 302; 1985, p. 64); museum unknown. 1 (skull only; cranial measurements cited by Dao). C:V-11.

Dir District. See Dokudusra; Gwaldri Valley; Landrai Valley.


Ditin, Jingxi Xian; Guangxi, CHINA; ca. 23°10'N, 106°30'E; collected Nov. 1982 by Wei Zhanyi; FDGC. 1 (Skull only). C:C-167.


Dongfang, Hainan Dao; Hainan, CHINA; ca. 19°04'N, 108°51'E; collected 7 Feb. 1957 by Tang Ziying; USBD. 2 (1 skin only, 1 skull only). Collected 9 May 1957 by Wang Sung; ICAS. 1. C:C-235.

Dong He. See Wa Shan.

Dongmen, Xianan Subcounty, Huanjiang Xian, 460 m; Guangxi, CHINA; ca. 25°09'N, 107°53'E; collected 21 Oct. 1992 by Tan Nenrui (pers. comm. 5 Nov. 1992); ICAS. 1 (skin only). C:C-177.

Dongshan, 5 km south of Xianan. Huanjiang Xian, 440 m; Guangxi, CHINA; ca. 24°52'N, 107°57'E; captured ca. 15 Oct. 1992 by Gung Lao (pers. comm., 5 Nov. 1992); captive observed 5 Nov. 1992 at Xianan. C:C-177.

Dowok, above 9500 ft (>2900 m); Xizang (= Tibet), CHINA; ca. 29°22'N, 94°18'E; reported July–Aug. 1913 by F. M. Bailey (1914, map; 1915, p. 74). B:C-9.

Doza. See Narkanda, ca. 1 km north of.


Dunga Gali vicinity, Hazara District. 2000–2800 m; North-West Frontier, PAKISTAN; 34°03'N, 73°22'E; collected 12 Sept. 1963 at 8100 ft (= 2470 m) by R. L. Amouraux; USNM. 1. Observed 1978–1981 at 2000–2800 m by S. J.


Durga Temple. See Varanasi.

Dushan; Guizhou, CHINA; 25°50'N, 107°32'E; tissue samples obtained ca. 1991 by Zhang Yapin and Shi Liming (1993b, p. 589). C:C-123.

Dzo La, southeast of; Xizang (= Tibet), CHINA; ca. 29°13'N, 97°07'E; observed 12–24 July 1935 by R. Kauback (1938, p. 91). B:C-33.


East BURMA. See MYANMAR (= BURMA), eastern.

Eastern Mausoleum. See Xinglong Xian, southern.

Eastern Mausoleum. See Xinglong Xian, southern.

Eastern Tombs. See Xinglong Xian, southern.

East Sichuan. See Sichuan, eastern.

Emei Shan (= Mount Omei); Sichuan, CHINA; ca. 29°32'N, 103°21'E; collected before 1930 by unknown collector (Howell, 1929, p. 35); USNM, 1 (specimen not located). Reported before 1942 by A. de C. Sowerby (1941, p. 261). C:C-139.


Erzhou Dao; Guangdong, CHINA; ca. 22°00'N, 114°11'E; reported in 1981 by Liu Zhenhe and Yuan Xicai (Zhang et al., 1991, p. 177; 1997, p. 58). Population possibly artificially intro-
duced >100 years ago (Zhang Yongzu, letter, 3 July 1996). C:C-211.


Fameng, Xingyi Xian, 1580 m; Guizhou, CHINA; ca. 24°45'N, 104°45'E; collected 11 July 1963 by Wang Yixiang (pers. comm., 1 Sept. 1983); Kiz, 1 (skull only). C:C-155.


Fanjingshan; Guizhou, CHINA; 27°57'N, 108°50'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-116.


Fengxingshan, Jing'an Xian; Jiangxi, CHINA ca. 8°52'N, 115°22'E; trapped and released May 1984 (Tan, 1985, p. 73). C:C-77.

Fokien Occid. See Kuatun.

Forest Research Institute. See Dehra Dun.

Fugong; Yunnan, CHINA; 26°58'N, 98°54'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-42.

Fuhai. See Menghai.


Funing; Yunnan, CHINA; 23°37'N, 105°36'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-163.

Fuqing vicinity; Fujian, CHINA; ca. 25°43'N, 119°22'E; purchased Aug. 1963 by unknown collector; IZCAS, 2. C:C-85.


Fuxi, She Xian, 400–700 m; Anhui, CHINA; ca.


Ganges. See Ganges River.

Ganges River, forests along banks (“forêts des bords du Gange”); Bihar, Uttar Pradesh, or West Bengal, INDIA; 23°–31°N, 78°–88°E; reported before 1820 by F. Cuvier (1819, p. 2). Not mapped.


Garampani. See Hot Springs.

Garidwaha. See Simulbari-Pankhabari.


Garo Hills, foot; Sherpur, BANGLADESH; ca. 25°00'N, 90°00'E; observed before 1982 by M. A. R. Khan (1981, p. 13). B:Ba-6.

Garubathan. See Garubathan Forest.


Gegong, Dongzhi Xian, 400–600 m; Anhui, CHINA; 30°05'N, 117°11'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-49.

Gejiu; Yunnan, CHINA; 23°23'N, 103°09'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-149.


Getou, Leishan Xian, 1200 m; Guizhou, CHINA; ca. 26°20'N, 108°10'E; collected 4 Sept. 1963 by unknown collector; KIZ, 3. C:C-121.


Ghazipur; Comilla, BANGLADESH; 23°32'N, 91°08'E; introduced population, reported before 1986 by M. A. R. Khan (1985, p. 31). Not mapped.


Ghori Dhaka, 1 mi (= 1.6 km) east of, Hazara District; North-West Frontier, PAKISTAN; 34°02'N, 73°26'E; collected 18 Sept. 1962 by H. W. Setzer; USNM, 1. A:P-12.


Gin Keo Ho (= Giakoeho), cliff above; Sichuan, CHINA; 29°20'N, 103°05'E; collected 18 July 1925 by D. G. Graham (1926–29, p. 31; unpublished map, USNM, archives, no. 89413); USNM, 1. C:C-140.

Gokarna, King’s Forest, 5 mi (= 8 km) northeast of Katmandu, 4500 ft (= 1370 m); Bagmati, NEPAL; ca. 27°43'N, 85°23'E; collected 24 Dec. 1966 by C. O. Maser; FMNH, 1; UPS, 1 (skin only). A:N-12.


Gokteik. See Pyaunggaung.

Golaghat, Sibsagar District, 300 ft (= 90 m); Assam, INDIA; 26°31'N, 93°58'E; collected 4 Jan. 1920 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BM(NH), 1. B:1-22.


Gorkha. See Chengli.


Government Press. See Aligarh.


Guangdong or Guangxi. CHINA; 20°–27°N, 104°–117°E; collected 1923–1924 by F. R. Wulsin (letter, 9 Jan. 1925; USNM archives, no. 85377); MCZ, 1. Not mapped.


Guangnan; Yunnan. CHINA; 24°03’N, 105°03’E: reported before 1998 (Zhang et al., 1997, p. 58). C:C-153.

Guangxi. CHINA; 21°–27°N, 104°–112°E; purchased in Shanghai Nov. 1922 by F. R. Wulsin; USNM, 4 (including 1 skin only). Collected 1951–1980 by museum collectors; SMNH, 22 (including 16 skins only, 2 skulls only). Not mapped.


Guanyuan; Sichuan. CHINA; 31°00’N, 103°37’E: reported before 1998 (Zhang et al., 1997, p. 58). C:C-30.


Guidong; Hunan. CHINA; 26°12’N, 114°00’E: reported before 1998 (Zhang et al., 1997, p. 58). C:C-102.

Guixi; Guangxi. CHINA ca. 21°50’N, 109°40’E: reported before 1998 (Zhang et al., 1997, p. 58). C:C-216.

Guiyang; Guizhou. CHINA; 26°35’N, 106°43’E: reported before 1998 (Zhang et al., 1997, p. 58). C:C-125.


Gunujjung, Shitai-Qimen Xian; <700 m; Anhui. CHINA: ca. 30°05’N, 117°30’E: observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-48.

Guoelo Prefecture. See Golog Zangzu Zizhizhou.


Gurkha. See Chengli.


Gyaca Xian; Xizang (= Tibet). CHINA; ca. 29°25’N, 92°40’E: observed 1979–1982 by

Gyala, above, 2800 m; *Xizang (= Tibet), CHINA*; ca. 29°38’N, 94°56’E; observed 17 July 1913 by F. M. Bailey (1914, map; 1915, p. 74; 1957, p. 122). B:C-12.


Harbajwala. See Dehra Dun vicinity.


Haripur, Kheri District; *Uttar Pradesh, INDIA*; ca. 28°07’N, 80°43’E; collected Mar. 1932 by C. McCann; BM(NH), 1 (skin only). A:1-55.

Harparan Mohalla. See Khair, Tahsil.

Hasimara, Bhutan Duars, 550 ft (= 170 m); *West Bengal, INDIA*; ca. 26°45’N, 89°20’E; collected 1–10 Jan. 1916 by N. A. Baptista (H. V. O’Donel in Wroughton, 1917, p. 63); BM(NH), 3; BM(NH), mounted skin, on exhibit. A:1-9.

Hastings Road. See Cuttack.


Hazara District, southern; *North-West Frontier, PAKISTAN*; ca. 34°00’N, 73°00’E; observed 1914–1916 by R. W. G. Hingston ([1920], p. 243). A:P-8.

Hazaribagh; *Chittagong, BANGLADESH*; ca. 22°20’N, 92°00’E; observed Feb. 1990–June 1991.
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Hechi Prefecture; Guangxi, CHINA; ca. 24°42′N, 108°02′E; acquired in 1992 from Chinese Medicine Division, Hechi; izcas, 3 (skulls only). B: C-178

Heinsun (= Heinsum; Heinzun), east bank of Chindwin River; Sagaing, MYANMAR (= BURMA); 25°52′N, 95°35′E; collected 11 Mar. 1935 by H. C. Raven (in Carter, 1943, p. 100; Morris, 1936, p. 665); AMNH, 2. B:M-9.


Hekou; Yunnan, CHINA; 22°36′N, 103°58′E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-152.


Hindan Bridge Temple. See Delhi.


Hisweht (= Hiswet), west bank of Nantaleik Chaung, above Tamanthi, upper Chindwin River, 460 ft (= 140 m); Sagaing, MYANMAR (= BURMA); ca. 25°22′N, 95°16′E; collected 25 Aug. 1914 by G. C. Shortridge and S. A. Macmillan (Shortridge in Wroughton, 1916a, p. 293); BM(NH), 1. B:M-12.

Hitaura, 0.5 mi (= 1 km) west, 1450 m; Chisapani, NEPAL; 27°27′N, 85°02′E; recorded 12 Feb. 1967 by C. O. Maser (field notebook, FMNH, p. 39); specimen not located. A:N-10.

Hkamti. See Singkaling Hkamti.

Hkandau, 2000 ft (= 610 m); Kachin, MYANMAR (= BURMA); 26°01′N, 97°50′E; collected 8 Aug. 1939 by R. Kaulback; BM(NH), 1 (skin only). B:M-2.

Hoa Bình; Hòa Bình, VIETNAM; ca. 20°49′N, 105°22′E; collected 1 June 1972 by Dang Huy Huynh and Truong Van Le; ieb, 1. C:V-20.

Hoa Bình, VIETNAM; 20°20′–21°00′N, 104°50′–105°50′E; collected 19 July 1960 by unknown collector; zmvnu, 1 (skin only). Not mapped.

Hoi Xuan, Quan Hoa District; Thành Hoa, VIETNAM; 20°23′N, 105°06′E; collected Mar. 1964 by unknown collector (Dao, 1985, p. 196); museum unknown (not seen), 2. C:V-22.

Homalin, west bank of upper Chindwin River, 400 ft (= 120 m); Sagaing, MYANMAR (= BURMA); 24°52′N, 94°55′E; collected 14–15 July 1914 by G. C. Shortridge and S. A. Macmillan (Shortridge in Wroughton, 1916a, p. 293); BM(NH), 2. B:NHS, 1. B:M-14.

Hong Kong. See Xianggang.

Hongshui He, between Tien’e and Hai Zhou, 4–5 km northwest of Tien’e, Tian’e Xian; Guangxi, CHINA; ca. 25°01′N, 107°07′E; captured Apr. 1990 by Luo Mengfei (pers. comm., 15 Oct. 1992); captive observed 15 Oct. 1992 at Tian’e. C:C-173.


Hongshui He, right bank, 500 m below Heke, Tian’e Xian, 260 m; Guangxi, CHINA; 25°14′N, 106°58′E; observed 19 Oct. 1992 by J. Fooden (cf. Fooden et al., 1994, p. 623). C: C-173.

Hopeh. See Xinglong Xian, southern.

Hoshangabad. See Sohagpur.

Hot Mix Plant. See Aligarh.

Hot Springs (= Garampani). Jaintia Hills, 2400 ft (= 730 m); Assam, INDIA; 25°31′N, 92°34′E; collected 18 July 1920 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BNHS, 1. B:1-19.

Hotha Valley; Yunnan, CHINA; ca. 24°25′N, 97°55′E; captured purchased July 1868 by J. Anderson (1876, p. 275; 1879, pp. xvi, 56); zsi, 1. B:C-61.

Houmda. See Ngamda.

Hsignolo. See Xi Golog.

Hsi-Kiang. See Xi Jiang.

Hsi-o-lo. See Xi Golog.

Htingnan Triangle, 3500 ft (= 1070 m); Kachin, MYANMAR (= BURMA); 26°36′N, 97°53′E; collected 28 Jan. 1939 by R. Kaulback; BM(NH), 1. B:M-1.

Huai Ap Nang, right bank of Mae Nam Ping. 350 m; Tak, THAILAND; 17°25'N, 98°43'E; collected 29 Mar. 1967 by J. Fooden (1971, p. 18); FMNH, 1. B:T-5.

Huaiji; Guangdong, CHINA; 23°55'N, 112°10'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-207.

Huai Kwang Pah. left bank of Mae Nam Ping. 350 m; Tak, THAILAND; 17°28'N, 98°50'E; collected 29 Mar. 1967 by J. Fooden (1971, p. 18); CTNRGC, 1; FMNH, 1 (in alcohol). B:T-5.


Huaping [Xian]; Yunnan, CHINA; ca. 26°37'N, 101°13'E; blood sample obtained before 1999 by Ding Bo, Zhang Yaping, and Hou Yidi (1998, p. 172). B:C-47.

Huashi, north of; Hebei, CHINA; ca. 40°24'N, 117°30'E; reported 1940–1980 by local residents (Zhang et al., 1989, p. 379). C:C-1.


Hue, 0 m; Thu Ha Thienn-Hue, VIETNAM; 16°28'N, 107°36'E; collected Oct.–Dec. 1925 by J. Delacour, P. Jabouille, and W. P. Lowe (Delacour et al., 1927, p. 132; Delacour, 1940, pp. 21, 24); ?MNHN, 1–2 (not seen). C:V-33.

Huidong; Guangdong, CHINA; 22°58'N, 114°44'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-209.

Huishui; Guizhou, CHINA; 26°08'N, 106°36'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-124.

Huixian; Gansu, CHINA; 33°46'N, 106°06'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-17.


Hui-yao; Yunnan, CHINA; ca. 25°15'N, 98°30'E; collected 26 Apr. 1917 by R. C. Andrews (in Andrews & Andrews, 1918, pp. 298, 305); AMNH, 2; MCZ, 1. B:C-58.

Hule (= Huleu), Ningguo Xian. 200–500 m; Anhui, CHINA; ca. 30°21'N, 118°47'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-55.


Huong Binh. See Song-Ta-Voy.

Huong Him. See Song-Ta-Voy.

Huon Son (= Muong Son) District; Ha Tinh, VIETNAM; ca. 18°31'N, 105°28'E; collected 19 June 1985 by Nguyen Van Dung; FCXM, 1 (skull only). C:V-27.


Hwang Liang Commune. See Huangliangping.


Ichang. See Yichang.

Imphal, ca. 4 mi (= 6.5 km) north of milestone 129 [km] on Dimapur Road. 3000 ft (= 900 m); Manipur, INDIA; 24°52'N, 93°56'E; collected 6 Nov. 1945 by M. L. Roonwal (1949, p. 84; 1950, p. 16 [misidentified as M. assamensis]); ZSI, 1. B:I-37.


Indian Museum compound. See Calcutta.

Imperial Hunting Grounds. See Xinglong Xian, southern.
INDIA: 15°–35°N, 71°–97°E; collected before 1843 by Mr. Cross; BM(NH), 1 (skin only). Collected before 1844 by B. H. Hodgson; BM(NH), 1 (skull only). Collected before 1852 by unknown collectors; BM(NH), 2. Collected 15 Dec. 1925 by R. P. Page; BM(NH), 1 (skin only). Date and collector unknown; ZSI, 2 (skull only). Not mapped.


Irrawaddy River, left bank, below Yenangyaung; Magwe, MYANMAR (= BURMA); ca. 20°27’N, 94°52’E; observed before 1879 by J. Anderson (1879, p. 57). B:M-26.

Jagannath Temple. See Puri.


Jagvedi Temple. See Chitrakut.

Jaintia Hills. See Hot Springs; Narpur Reserved Forest.


Jakka. See Sungri, ca. 2 km south of.


Jalpaiguri. See Bramhabhiri; Hasimara.


Jäntschin. See Yanjing.


Jaypore Agency. See Malkangiri.


Jegu Xiang, Yushu Xian; Qinghai, CHINA; 32°42’N, 97°15’E; collected 30 May and 10 June 1963 by Shou Zhongchan; NWPB, 2 (including 1 skin only). B:C-18.

Jenli, 2–3 km north of, Mulun Subcounty, Huanjiang Xian, 670 m; Guangxi, CHINA; ca. 25°07’N, 108°01’E; collected fall 1991 by Hu Huguan (pers. comm., 5 Nov. 1992); skeleton examined 5 Nov. 1992 at Jenli. C:C-177.


Jeypore Agency. See Malkangiri.

Jiuzi. See Jigzhi.

Jixi: *Anhui*, CHINA; 30°05'N, 118°36'E; reported before 1988 (Zhang et al., 1997, p. 58). C:C-60.


Kaeng Mae Hat (rapids), Mae Nam Ping (river), below Chiang Mai, 850 ft (= 260 m); *Chiang Mai*, THAILAND; 17°51'N, 98°41'E; collected 14 Apr. 1916 by K. G. Gairdner (Kloss, 1917, p. 247); ZRC, 1 (holotype of *Macaca siamica*). B:T-4.

Kafirstan. See Nuristan.


Kakara, Damoh District, 1200 ft (= 370 m); *Madhya Pradesh*, INDIA; ca. 23°50'N, 79°27'E; collected 12 May 1912 by C. A. Crump (in Wroughton & Ryley, 1913, p. 46); BM(NH), 1 (skin only). A:1-94.

Kakhyen Hills. See Tengchong.


Kali Bari Temple. See Simila.


Kamdech. See Landay Sind.


Kanding (= K’ang-ting; Tausin Lou); *Sichuan*, CHINA; 30°03'N, 102°02'E; collected June–July 1890 by H. d’Orleans (Bonvalot, 1891, vol. 2, p. 210; 1892, p. 506); MNHN, 1 (holotype of *Macacus vestitus*). B:C-27.


Kangra Fort. 2450 ft (= 750 m); *Himachal Pradesh*, INDIA; ca. 32°05'N, 76°16'E; collected 18 Mar. 1921 by H. W. Wells (Lindsay, 1926, p. 599); BM(NH), 1. A:1-12.


Kangxian; *Gansu*, CHINA; 33°26'N, 105°37'E;

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Kanti vicinity, Chitral District; North-West Frontier, PAKISTAN; ca. 35°35'N, 71°41'E; reported before 1978 by T. J. Roberts (1977, p. 86). A:P-1.

Kaotai (= Kootai), lower Kunar (= Chitral) River, 3600 ft (= 1100 m); North-West Frontier, PAKISTAN; ca. 35°20'N, 71°35'E; collected early Feb. 1914 by F. D. Stirling (Wroughton, 1918, p. 553); BM(NH), 1 (holotype of *Macaca mulatta mcmahoni*). A:P-1.

Kao Tien. See Kutun.


Kaptai, south of; Chittagong, BANGLADESH; ca. 22°00'N, 92°00'E; tentatively reported July–Nov. 1976 by K. M. Green (1978, p. 146). B: Ba-38.


Karen Chaung, Pidaung Reserve, Myitkyina District, 500 ft (= 150 m); Kachin, MYANMAR (= BURMA); ca. 25°25’N, 97°15’E; collected 25 May 1936 by H. C. Smith (Napier, 1981, p. 21); BM(NH), 2 (including 1 skin only). B:M-5.


Karkara. See Kakara.


Karrachi (= Karachi). See PAKISTAN.


Kathmandu. See Katmandu.


Katmandu; Katmandu Valley, NEPAL; 27°43’N, 85°18’E; observed before 1979 by B. Marriott (1978b, p. [27]). A:N-12.

[Katmandu Valley], NEPAL; 27.5°–28°N, 85°–85.5°E; collected before 1845 by B. H. Hodgson (Scully, 1888, p. 234; Napier, 1981, p. 24); BM(NH), 7 (including 3 skulls only [1 not seen]); probably includes part of type series of *Macacus ounops*. Not mapped.

Kaukori. See Kakori.


Kemga. See Gengma.

Kerwada Forest. See Kherwada Forest.


Khair Inter College. See Khair. Taishi.


Khali Hills. See Nongpho.


Kheiber. See Khyber Pass vicinity.

Kheo Ting-Ta Ke. See Tat Ke vicinity.


Khirganga. See Pulga.

Khyber Pass vicinity; North-West Frontier, PAKI-

STAN: ca. 34°05’N, 71°10’E; reported ca. 1525 by Z. M. Bābur (1921 [translation], p. 218). A: P-4.

Kiang-ka: Sichuan, CHINA: ca. 30°00’N, 99°00’E; reported 31 Aug. 1877 by local residents (Gill, 1883, p. 230). B:C-32.

Kiangsu. See Guangxi.

Kian Tatie. See Ngaruma.

Kia-ting. See Leshan.


Kin. west bank of lower Chindwin River: Saya-


Kindat. 20 mi (= 32 km) northwest of, Chin Hills, 600 ft (= 180 m); Chin, MYANMAR (= BURMA); ca. 23°50’N, 94°10’E; collected 20 Jan. 1915 by J. M. Mackenzie (Wroughton, 1916c, p. 759); BM(NH). 1. B:M-16.

King’s Forest. See Gokarna.

Kintachiet. See Ngamda.

Kistawar. See Dunwein.

Klosterv Nam miu. See Luofo Shan.


Koh-e-Sefid. See Khyber Pass vicinity.

Kokara. See Kakara.

Kokoanrg (= Kokhoanig), 500 ft (= 150 m); Mandalay, MYANMAR (= BURMA): 20°47’N, 95°56’E; collected 14 June 1937 by H. C. Smith (cf. Moore & Tate, 1965, p. 323; Napier, 1981, p. 21); BM(NH). 1. BM(M).-28.

Keoladeo Ghana National Park. See Bharatpur.


Kondapalle, Krishna District, 70 m; Andhra Pra-

desh, INDIA: 16°37’N, 80°33’E; observed 13


Kongbo; Xizang (= Tibet), CHINA; ca. 29°30'N, 94°45'E; captive observed at Lu, 19 Aug. 1913, by F. M. Bailey (1914, map; 1957, p. 171; cf. Fooden, 1982a, p. 52). B:C-10.

Kootai. See Kaotai.

Kosi River, left bank; Saptari, NEPAL; ca. 26°35'S, 86°55'E; collected Mar. 1887 by H. d'Orleans (1889, pp. 225, 379); museum unknown (not seen). B:N-3.


Kotgay (= Cogtai), east of; Nangarhar, AFGHANISTAN; ca. 34°00'N, 70°20'E; reported before 1972 by A. Puget (1971, p. 201) A:A-10.

Kotgay (= Cogtai), northeast of; Nangarhar, AFGHANISTAN; ca. 34°04'N, 70°00'E; reported before 1972 by A. Puget (1971, p. 201). A:A-9.


Kothiara, 7000 ft (= 2100 m); Jammu & Kashmir, INDIA ca. 33°45'N, 75°10'E; collected 3 and 18 Oct. 1910 by W. L. Abbott; USNM, 2. A:1-3.


Kounar. See Landay Sind, left bank, near confluence with Kunar River.

Kowloon; Xianggang (= Hong Kong), CHINA; ca. 22°15'–22°30'N, 114°10'–114°25'E; reported in 1992 by J. R. Fellowes (Southwick & M. F. Siddiqi, 1994b, p. 52). Not mapped.

Kowloon Reservoir vicinity. See Eagle’s Nest Trail; Kam Shan Entrance.


Kullu Valley. See Kulu Valley.

Kulsi [River], South Kamrup, 750 ft (= 230 m); Assam, INDIA; ca. 26°00'N, 91°23'E; collected 25 Aug. 1920 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BNHS, 1. B:1-15.


Kumaun (= Kumaon) Hills; Uttar Pradesh, INDIA; ca. 29°20'N, 79°30'E; observed before
Kumtachie. See Ngama.
Kunar River, lower; *North-West Frontier*, PAKISTAN ca. 35°25'N, 71°40'E; reported before 1902 by A. H. McMahon (1901a, p. 4). A:P-1.
Kuo-Lo. See Golot Zanzu Zizhuzhou.
Kyroong. See Gyirong.
Lai Chau, VIETNAM; 20°50'–22°50'N, 102°10'–103°50'E; collected in 1963 by unknown collector; IEIBR, 1 (skin only). Not mapped.
Lakhimpur. See Margherita.
Lamsakhang, Cachar District, 200 ft (= 60 m); *Assam*, INDIA; 25°48'N, 93°06'E; collected 10 Sept. 1920 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BM(NH), 1. B:1-20.
Lancang Jiang (= Mekong River), Lincang District; *Yunnan*, CHINA; ca. 24°00'N, 100°23'E; reported before 1996 by Lan Daoying and Guo Guang (1995, p. 6). B:C-70.
Landrai Valley, northern Dir District; *North-West Frontier*, PAKISTAN; ca. 35°30'N, 72°00'E; reported before 1978 by T. J. Roberts (1977, p. 86). A:P-2.
Lang Son, VIETNAM; 21°25'–22°50'N, 106°05'–107°20'E; collected 1962 by unknown collector; ZMVNU, 1 (skin only). C:V-12.
Lan-tao. See Dahao Dao.
Ledhan hla. See Lethan Hla.
Leibo; *Sichuan*, CHINA; 28°15'N, 103°34'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-142.
Lema Islands. See Dangan Dao.
Lena Island. See Dangan Dao.
Leshan (= Kia-ting), mountains 30 mi southwest
of. 2900 ft (= 880 m): Sichuan, CHINA; ca. 29°28'N, 103°18'E; collected 6 Feb. 1911 by M. P. Anderson; BM(NH). I. C:C-139.

Lethan Hka, Maymyo F. D., 300 ft (= 90 m): Mandalay, MYANMAR (= BURMA); ca. 22°00'N, 96°30'E; collected 22 Dec. 1935 by H. C. Smith; BM(NH). I. B:M-21.

Le Thuy. See Xuan Ninh.

Lhasa. See CHINA.


Liangiang: Gansu, CHINA; 33°56'N, 106°12'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-16.

Liangping: Guangdong, CHINA; 24°22'N, 114°30'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-96.

Lian Xian. See Lianzhou.


Libo: Guizhou, CHINA; 25°25'N, 107°53'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-175.

Lijiang: Yunnan, CHINA; 26°48'N, 100°16'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-45.

Lina. See Dangan Dao.


Lingling Island. See Neilingdingdao Dao.

Lingjun. See Longjun.

Lingrui. See Longrui.

Lin Thong, Dinh Hoa: Bac Thai, VIETNAM; 22°00'N, 105°42'E; collected 22 June 1967 by Truong Van La; ZMVNUL, 2 (skins only). C:V-10.

Lintin Dao. See Neilingdingdao Dao.


Litang-Batang: Sichuan, CHINA; ca. 30°00'N, 100°00'E; reported 23 Aug. 1877 by local residents (Gill 1883, p. 212). B:C-31.

Liukou, Qimen Xian. 300 m: Anhui, CHINA; 29°55'N, 117°30'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-48.

Liukou, Xiuning Xian. 400 m: Anhui, CHINA; 29°34'N, 117°49'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-63.

Liulipenshan: Hebei, CHINA; ca. 40°24'N, 117°30'E; reported fall 1987 by local hunters (Zhang et al., 1989, p. 380). C:C-1.


Lofau. See Luofu Shan.

Lolab, 7500 ft (= 2300 m): Jammu & Kashmir, INDIA; ca. 34°30'N, 74°35'E; collected 8–9 Sept. 1891 by W. L. Abbott (True, 1894, p. 3; Blanford, 1898, p. 361); USNM, 5 including holotype of Macacus rhesus villosus). A:I-1.

Lolab Valley: Jammu & Kashmir, INDIA; ca. 34°30'N, 74°35'E; collected 11 Feb. 1911 by W. L. Abbott; USNM, 1. A:I-1.


Longhua Water Regulation Forest Reserve: Guangxi, CHINA; ca. 23°17'N, 105°34'E; observed 1976, 1986, and 1993 by Liu Wanfu and


Loshan. See Leshan.

Longsheng; Guangxi, CHINA; 25°48'N, 110°00'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-185.

Longxi (prefecture); Fujian, CHINA; ca. 24°31'N, 117°40'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-93.


Louangphrabang, downstream; Louangphrabang, LAOS; ca. 19°52'N, 102°08'E; reported before 1964 by J. Deuve and M. Deuve (1963, p. 59). B:L-3.

Lower Bazar. See Simla.

Lu. See Kongbo.

Luang-Prabang. See Louangphrabang.

Luchun; Yunnan, CHINA; 23°19'N, 102°10'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-76.


Lula, Chaibasa vicinity, Singhbhum District, 1000 ft (= 300 m); Bihar, INDIA; 22°23'N, 85°32'E; collected 1 Aug. 1914 by C. A. Crump (in Wroughton, 1915b, p. 99); BM (NH), 3. A:1-105.


Luocheng; Guangxi, CHINA; 24°47'N, 108°54'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-179.

Luofu Shan, 800–1100 m; Guangdong, CHINA; ca. 23°17'N, 114°03'E; reported 1908–1921 by R. Mell (1922, pp. 10, 11). C:C-208.

Luquan; Yunnan, CHINA; 25°35'N, 102°30'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-50.

Luyuan, Taihe Xian; Jiangxi, CHINA; ca. 26°50'N, 114°40'E; reported Oct. 1979 by local residents (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985). C:C-104.

Ly Bon, Bao Lac District; Cao Bang, VIETNAM; ca. 22°57'N, 105°41'E; collected 5 June 1965 by unknown collector (Dao, 1985, p. 38); IEBR, 4 (3 skins only, 1 skull only [possibly belongs with one of the skins]). C:V-7.

Machayara Game Reserve; Azad Kashmir, PAKI-

STAN; ca. 34°00'N, 73°35'E; reported before 1984 by M. Nawaz (1983, p. 6). A:P-12.


Madaya, Maymyo Reserve; Mandalay, MYAN-

MAR (= BURMA); 22°13'N, 96°07'E; collected 15 Feb. 1936 by P. F. Garthwaite; BM (NH), 1 (skin only). B:M-22.

Madhupur. ca. 100 km west of; Natore, BANGLADESH; ca. 24°30'N, 89°00'E; tentatively reported July–Nov. 1976 by K. M. Green (1978, p. 146). B:Ba-5.

Madhupur National Park; Tangail, BANGLADESH; ca. 24°45'N, 90°08'E; observed July–


Makalu-Barun Conservation Area. See Sankhuwa Khola.

Makehe Plantation, 3100–4000 m; Qinghai, CHINA; ca. 33°00’N, 96°20’E; purchased ca. 1982 at Baima Xian by Liao Yianfa, Director of Xining Zoo (pers. comm., 6 Oct. 1985); captive observed 6 Oct. 1985. B:C-16.


Malakand. See Bar Chanrai Hill.

Malipur. See Kair, Tahsil.


Malua, Seoni Tank; Madhya Pradesh, INDIA; ca. 21°00’N, 79°59’E; collected before 1974 by S. W. Prater; BNHS, 1 (skin only). A:I-103.

Maluling; Xizang (= Tibet), CHINA; ca. 32°40’N, 97°20’E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-18.

Mamsam Falls. See Mansam Falls.


Manas. See Royal Manas National Park.


Mandal. See Kedarnath Sanctuary.


Mangpu, 3000 ft and 3500 ft (= 910 m and 1070 m); West Bengal, INDIA; 26°58’N, 88°24’E; collected 5 and 12 Dec. 1930 by H. Stevens; FMNH, 2. B:I-6.

Manipomplaa. See Munipamula.


Manpa, Mengla Xian, 650–750 m; Yunnan, CHINA; ca. 21°40’N, 101°37’E; collected 14 May 1959 by Deng Xiangfu; KIZ. 2 (skulls only). Collected 19 Jan. and 8 May 1962 by Quan Guoqiang (pers. comm., 25 Aug. 1983); ICAS, 2. B:C-85.

Mansam Falls, Nam Yao (river), 2000 ft (= 610 m); Shan, MYANMAR (= BURMA); 22°48’N, 97°32’E; collected 6 June 1913 by G. C. Shortridge (in Ryley, 1914, p. 713); BM(NH), 2 (including 1 skin only); BNHS, 3. B:M-19.

Mansar Patwar. See Surinsar.


Maowen; Sichuan, CHINA; 31°41'N, 103°52'E; tentatively reported 1914–1916 by H. Weigold (1924, p. 71). C:C-25.

Marco River. See Golgo Zangzu Zishizhou.

Mardan. See Pajka Hill.


Margherita, Lakhimpur District, 200 ft (= 60 m); Arunachal Pradesh, INDIA; 27°17'N, 95°41'E; collected 14 Nov. 1919 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); zst. 1 (skin only). B:1-29.


Mar Qu. See Golgo Zangzu Zishizhou.


Mathura District (= Muttra); Uttar Pradesh, INDIA; 27°15'–28°00'N, 77°15'–77°50'E; laboratory animals obtained in 1891 by W. Heape (1897, p. 135). Not mapped.


Matlab, southeast of; Noakhali BANGLADESH; ca. 23°00'N, 91°00'E; tentatively reported July–Nov. 1976 by K. M. Green (1978, p. 146). B:Ba-30.

Maungkan, east bank of Chindwin River; Sagaing, MYANMAR (= BURMA); 25°05'N, 95°02'E; collected 20 Mar. 1935 by H. C. Raven and R. C. Morris (Raven in Carter, 1943, p. 100; Morris, 1936, p. 667); AMNH, 1. B:M-13.

Maure, near. 1.6 km north of Jamduar; Assam, INDIA; ca. 26°44'N, 89°53'E; observed 19 Nov.–1 Dec. 1959 by E. P. Gee (1961, p. 6). B:1-10.

Mautschou. See Maowen.

Maymo F. D. See Lethan Hka.

Maymoy (= Maymo), 800 m; Mandalay, MYANMAR (= BURMA); 22°02'N, 96°28'E; collected 3 Dec. 1937 by G. Heinrich; AMNH, 1. B: M-21.

Maymo Reserve. See Madaya.

Médog Xian; Xizang (= Tibet), CHINA; ca. 29°15'N, 95°15'E; observed 1979–1982 by Zhang Cizu, Director, Shanghai Zoo (pers. comm. 18 Oct. 1985). B:C-13.


Meigu; Sichuan, CHINA; 28°20'N, 103°04'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-141.


Meitan, near; Guizhou, CHINA; ca. 27°40'N, 107°30'E; captive purchased 7 Nov. 1960 by Quan Guoqiang (pers. comm. 25 Aug. 1983); IZCAS, 1 C:C-128.

Mekong River. 90 km above Viangchian; Vientiane, LAOS; 18°05'N, 101°57'E; collected 7 July 1924 by F. R. Wulsin (field catalog and map, USNM archives); USNM, 1. B:L-5.


Meng-ban; Yunnan, CHINA; ca. 21°45'N, 100°10'E; collected 30 May 1958 by Ye Zongyao (Bannikov, 1958, p. 68; Kao et al., 1962, p. 188; Quan Guoqiang, pers. comm., 25 Aug. 1983). IZCAS, 1. B:C-80.

Menghai; Yunnan, CHINA; 21°58'N, 100°28'E; collected 27 Nov. 1957 and 17 Apr. 1958 by Ye Zongyao (Bannikov, 1958, p. 68; Kao et al., 1962, p. 188); IZCAS, 2 (1 skin only; 1 skull only).
Mengla; Menghun; Mesogarh; Me.
Midwest
Mikir
Minglang; 154
by reported skull B:C-81.
Mishmi Hills. See Dening.
Miyi; Sichuan, CHINA; 26°50'N, 102°03'E; reported before 1998 (Zhang et al., 1997, p. 58).
B:C-48.
Moenjodaro. See Moenjo Daro.
Moklok, east bank of Chindwin River; Sagaing, MYANMAR (= BURMA); ca. 25°37'N, 95°25'E; collected 16 Mar. 1935 by H. C. Raven (in Carter, 1943, p. 100; Morris, 1936, p. 666); AMNH. 1. B:M-10.
Mollur. See Mallur.
Momien. See Tengchong.
Mong Moen. See Muong Muon.
Mong Moun. See Muong Pon.
Monkey Bridge. See Lucknow vicinity.
Monkey hill, <10 mi (<16 km) south of Jing-gangshan; Jiangxi, CHINA; ca. 26°30'N,


Morang region; *Morang*, NEPAL; ca. 26°30'N, 87°30'E; reported 1920–1921 by N. A. Baptista (in Hinton & Fry, 1923, p. 403). B:N-4.

Morit forest. See Kokkaoing.

Moshemien; *Sichuan*, CHINA; ca. 30°00'N, 102°00'E; reported 24 June–7 July 1929 by local residents (Stevens, 1934, p. 132). B:C-27.

Motionling, Dehao Xian; *Guangxi*, CHINA; ca. 23°20'N, 106°37'E; collected ca. Oct. 1979 by unknown collector (Quan Guoqiang, pers. comm., 13 Dec. 1985); FDCCG, 1 (mounted skin with skull inside; specimen not seen). C:C-167.

Muong Boum. See Muong Boum.

Muong Mouen. See Muong Muon.

Muong-moun. See Muong Moun.

Mount Everest. See Sagarmatha.

Mount Omei. See Emei Shan.


Mt. Wuchi. See Wuzhi Shan.

Muang Khoua. See Ou, Nam, between Muang Khoua and Muang Ngoy.

Muang Ngoy. See Ou, Nam, between Muang Khoua and Muang Ngoy.

Muang Pakxan; *Vientiane*, LAOS; ca. 18°22'N, 103°39'E; reported before 1964 by J. Deuve and M. Deuve (1963, p. 59). C:L-2.


Municipal Corporation Building. See Aliagarh.


Muong Boum, Tonkin region; *Lai Chau*, VIETNAM; 22°23'N, 102°49'E; collected 27 Mar. 1929 by R. W. Hendee (Bangs & Van Tyne, 1931, p. 37; Coolidge, 1933, p. 94); FMNH, 1. B:V-1.

Muong Cha; *Lai Chau*, VIETNAM; 21°58'N, 102°51'E; collected 27 Apr. 1963 by unknown collector (Dao, 1985, p. 147); museum unknown (not seen), B:V-3.


Muong Moun. Tonkin region; *Lai Chau*, VIETNAM; 21°42'N, 103°01'E; collected 15 Mar. 1929 by R. E. Wheeler (Bangs & Van Tyne, 1931, p. 34); FMNH, 1. C:V-3.

Muong Muon. Tonkin region; *Lai Chau*, VIETNAM; 21°40'N, 103°04'E; captive purchased Nov. 1931 by T. D. Carter (Legembre, 1936, p. 125); died in zoo 15 June 1932; AMNH, 1. C:V-2.

Muong Pon (= Muong Poun), Tonkin region; *Lai Chau*, VIETNAM; 21°33'N, 103°01'E; collected 18 Nov. 1931 by T. D. Carter (Legembre, 1936, p. 125); AMNH, 1. C:V-2.

Muong Son. See Huang Son.

Murree, outskirts; *Punjab*, PAKISTAN; 33°54'N, 73°22'E; reported in 1964 by T. J. Roberts (1977, p. 87). A:P-12.
Mussoorie (= Mussooree) vicinity; Uttar Pradesh, INDIA; ca. 30°27’N, 78°05’E; reported before 1866 by T. Hutton (1865, p. xii [misidentified as Inuus pelops]; cf. Fooden, 1982a, p. 2). A:I-27.


Muttra. See Mathura.


MYANMAR (= BURMA), upper; Kachin, MYANMAR; 26°00’–26°40’N, 97°50’–97°55’E; collected ca. 1939 by R. Kaulback (Pocock, 1941, p. v); BM(NH), 1 (skull only). Not mapped (see B:M-1).

Myitykina; Kachin, MYANMAR (= BURMA); 25°23’N, 97°24’E; captive purchased June–Dec. 1945 by M. L. Roomwal (1950, p. 16 [misidentified as M. assamensis]). B:M-5.


Na chaka. See Yajiang.

Nachuka. See Yajiang.


Nagarjunakonda Valley, See Siddeldar Hill.

Nagarokot (= Nagarcoat), 8000 ft (= 2400 m); Bagmati, NEPAL; 27°42’N, 85°31’E; collected 15 Oct. 1920 by R. L. Kennion (Hinton & Fry, 1923, p. 403); BM(NH), 2. A:N-12.

Nagchuka. See Yajiang.


Nai Basti. See Khair, Tahsil.


Nam Co (= Tengri-Nor); Xizang, CHINA; 30°42’N, 90°35’E; erroneous record (Elliot, 1913, p. 197; cf. Milne-Edwards, 1892, p. 670). Not mapped.

Nam Fong. See Nanfeng.

Nam hou. See Ou, Nam.

Nam miu. See Luofu Shan.

Nam Ngap, Luc Yen District, Yen Bai, VIETNAM; ca. 22°07’N, 104°47’E; collected Dec. 1971 and date unknown by unknown collector; IEBR, 2 (skulls only). C:V-4.

Nam U. See Ou, Nam.

Nam Yao. See Mansam Falls.

Nam Yu. See Ou, Nam.


Nanding He (= Namting River), Lincang District; Yunnan, CHINA; ca. 24°00’N, 99°44’E; reported before 1996 by Lan Daoying and Guo Guang (1995, p. 6). B:C-68.


Nangamora; Assam, INDIA; ca. 27°00’N, 94°46’E; reported 9 Mar. 1987–16 Feb. 1988 by A. Choudhury ([1991a], p. 31). B:J-25.

Nangpoh. See Nongpoh.

Nang Pon. See Nongpoh.

Nang Xian; Xizang (= Tibet), CHINA; ca. 29°05’N, 93°05’E; observed 1979–1982 by Zhang Cizu, Director, Shanghai Zoo (pers. comm., 18 Oct. 1985). B:C-6.

Nanhuai; Yunnan, CHINA; 25°13’N, 101°21’E; reported before 1998 (Zhang et al., 1997, p. 58).
Nanjian; **Yunnan**, CHINA; 25°04′N, 100°32′E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-54.
Nanjiang; **Sichuan**, CHINA; 32°21′E; 106°50′E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-33.
Nanning; **Guangxi**, CHINA; ca. 22°49′N, 108°19′E; captive purchased Jan. 1964 by unknown collector; KIZ, 1. C:C-220.
Nanping; **Sichuan**, CHINA; 33°14′N, 104°06′E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-22.
Nantaleik Chaung. See Hisweht.
Nanting River. See Nanding He.
Nanyaseik, 480 ft (= 145 m): **Kachin**, MYANMAR (= BURMA); ca. 25°37′N, 96°36′E; collected 7 and 11 Jan. 1935 by H. C. Raven (in Carter, 1943, p. 100; Morris, 1936, p. 648); ANNH, 4, B:M-6.
Narong, Darjeeling District, 2000 ft (= 600 m); **West Bengal**, INDIA; 26°51′N, 88°20′E; collected 11 Mar. 1915 by C. A. Crump (Wroughton, 1916b, p. 472); BM(NH), 1. B:1-6.
Narma. See Narva.
Nathia Gali; **North-West Frontier**, PAKISTAN; 34°04′N, 73°24′E; reported in 1964 by T. J. Roberts (1977, p. 87). A:P-12.
Nawakot. See Trisuli Bazar.
N’Changyang, 1500 ft (= 460 m); **Kachin**, MYANMAR (= BURMA); 25°50′N, 97°48′E; collected 4 and 19 July 1939 by R. Kaubal; BM(NH), 2 (including 1 skin only). B:M-3.


NEPAL. See [Katmandu Valley].

Nepal Tarai. See Terai.

Newakot. See Trisuli Bazar.

New Forest Estate. See Dehra Dun vicinity.

Ngamba (?) = Kintachié; ? = Houmda; Xizang (= Tibet), CHINA; ca. 31°05’N, 96°43’E; captive purchased 7 May 1890 by G. Bonvalot and H. d’Orleáns (Bonvalot, 1891, vol. 2, pp. 149, 156; 1892, p. 505; Bonvalot et al., 1891, map); captive living in menagerie of MHN. 22 Aug. 1892 (Milne-Edwards, 1892, p. 671); skin possibly in MHN (see below, Tibet). B:C-14.

Nghe An, VIETNAM; 18°35’–20°00’N, 103°50’–105°50’E; collected in 1959 and Nov. 1961 by unknown collectors; zMVN, 3 (skulls only). Not mapped (see C:V-24 through C:V-26).

Nghia Dan (= Nghia Hung, Phu Qui), 100 ft (= 30 m); Nghe An, VIETNAM; 19°19’N, 105°25’E; collected 28 Feb. 1928 by J. Delacour and W. P. Lowe (Delacour, 1929, p. 198); BM(NH), 1. C:V-24.


Nghia Hung. See Nghia Dan.

Nghia Lo. See Yen Bai.


Nheri. See Narkanda, ca. 1 km north of.


Ningdu; Jiangxi, CHINA; 26°22’N, 115°48’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-100.

Ninggang; Jiangxi, CHINA; 26°45’N, 113°58’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-103.

Ningming; Guangxi, CHINA; 22°12’N, 107°05’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-227.


Nodoa. See Nada.

Nong Khaï (= Nong Kay; Nong Khaï), Camp No. 28; Nong Khaï, THAILAND; 17°52’N, 102°44’E; collected 9 Feb. 1920 by J. Bangasar (C. B. Kloss, unpublished itinerary notes, ZRC); ZRC, 2. B:T-11.

Nonglin, Mengla Xian, 670 m; Yunnan, CHINA; ca. 21°28’N, 101°35’E; collected 19 Dec. 1959 by Deng Xiangfu; KIZ, 1 (skull only). B:C-86.

Nongpoh, Khasi Hills, 1200 ft (= 370 m); Meghalaya INDIA; 25°54’N, 91°53’E; collected 27 May 1920 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BM(NH), 1. B:1-17.


Nordchina. See CHINA, northern.


North District, northeastern; Tripura, INDIA; ca. 24°20’N, 92°25’E; reported May–June 1978 by


North Kamrup. See Bogra Nadi.

North Lena Island. See Dangan Dao.


Nuguvedu. See Yeppuru.

Nu Jiang (= Salween River), above Changlung; Yunnan, CHINA; ca. 24°15′N, 99°05′E; tentatively reported Mar. 1917 by R. C. Andrews (in Andrews & Andrews, 1918, p. 279). B:C-65.

Nurestan (= Nuristan), eastern; Konarha, AFGHANISTAN; ca. 35°30′N, 71°30′E; captive obtained in 1906 by H. McMahan (Pocock, 1932, p. 543); died 19 Jan 1910 in Regents Park Zoo; BM(NH), 1 (skin only). A:A-1.

Nurestan (region), densely wooded districts; Konarha, Laghman, or Nangarhar; AFGHANISTAN; 34°–36°N, 70°–72°E; reported before 1860 by H. G. Raverty (1859, p. 332). Not mapped.

Nurestan vicinity; Laghman, AFGHANISTAN; 35°00′N, 70°20′E; reported before 1972 by A. Puget (1971, p. 201); A:A-4.

Nur Valley. See Khyber Pass vicinity.

Nyachuka. See Yajijian.

Nyainqentanglha Sheng (region); Xizang (= Tibet), CHINA; ca. 29°–32°N, 90°–96°E; reported before 1964 by Shen Xiaozhou (1963, p. 140; cf. Fooden, 1982a, pp. 26, 51; 1989, p. 44). Not mapped (see B:C-1, B:C-3, and B:C-6 through B:C-13).

Nychoy (= Yao-cheng) vicinity; Hainan Dao; Hainan, CHINA; ca. 18°22′N, 109°08′E; collected Mar. 1868 by R. Swinhoe (1870, p. 226; Napier, 1981, p. 22); BM(NH), 1. C:C-237.

Old Chandpur Bazar. See Chandpur Bazar, old.

Olongche (= Wolongshi); Sichuan, CHINA; ca. 30°03′N, 101°21′E; collected {21 Jun. 1890} by G. Bonvalot and H. d’Orleans (Bonvalot, 1892, p. 506); MNHM, 1 (including 1 skull only). B:C-28.

Omei. Mount. See Emei Shan.


Ou, Nam (= Nam hou); Louangphabang, LAOS; ca. 20°30′N, 102°35′E; collected ca. Apr. 1892 by H. d’Orleans (Gagnepain, 1944, map 1, p. 45); MNHN, 1 (skull only). B:L-2.

Ou, Nam, between Muang Khoua and Muang Ngoy; Louangphabang or Phongsali, LAOS; ca. 21°00′N, 102°45′E; collected 20 May 1929 by R. W. Hendee (field catalog, FMNH, p. 49; Bangs & Van Tyne, 1931, p. 37; Osgood, 1932, p. 195) FMNH, 1. B:L-1.

Ououlongtche. See Olongche.

Outapour, south of; Konarha, AFGHANISTAN; ca. 34°50′N, 70°50′E; reported before 1972 by A. Puget (1971, p. 201). A:A-7.

Ovra (= Overa) Sanctuary, proposed. 2135 m; Jammu & Kashmir, INDIA; ca. 34°00′N, 75°00′E; observed Apr.–May 1981 by P. C. Tak and G. Kumar (1984, p. 203; Roonwal & Tak, 1981, p. 96). A:1-2.


Pahalgam vicinity. See Ovra (= Overa) Sanctuary.

Pata, ca. 6 mi (= 10 km) east of Shogran, Hazara Division, 8700 ft (= 2650 m); North-West Frontier, PAKISTAN; 34°37′N, 73°33′E; collected 5 Aug. 1964 by M. Iqbal (Roberts, 1977, p. 343); USNM, 1. A:P-10.

Pajja Hill, north of Mardan; North-West Frontier,
PAKISTAN; ca. 34°12′N, 72°02′E; observed 1899–1901 by unidentified British officers (McMahon, 1901b, p. 9), A:P-7.


Pakhal Wild Life Sanctuary; *Andhra Pradesh*, INDIA; 17°50′–18°05′N, 79°55′–80°10′E; reported Nov. 1966 by J. J. Spillett (1968, p. 8). Not mapped (see A:I-133).


Paksane. See Muang Pakxan.

Palamau; *Bihar*, INDIA; ca. 23°50′N, 84°10′E; observed 22 Feb. 1970 by M. Krishnan (1972, p. 540), A:I-92.


Pang Nam Un; *Nan*, THAILAND; 18°30′N, 100°33′E; collected 25 Jan. 1953 by R. E. Elbel and Prasit Seecharong (Moore & Tate, 1965, p. 329), USNM, 1. B:T-5.

Panighatta; *West Bengal*, INDIA; 26°48′N, 88°15′E; observed in 1962 by C. H. Southwick, A. Ghosh, and C. D. Louch (1964, p. 446), B: I-6.

Panipat-Rhotak, highway between; *Haryana*, INDIA; ca. 29°05′N, 76°40′E; observed 1964–1965 by R. P. Mukherjee and G. D. Mukherjee (1972, p. 67), A:I-37.

Pankhabari. See Simulbari-Pankhabari.

Paras vicinity, lower Kaghan Valley; *North-West Frontier*, PAKISTAN; ca. 34°39′N, 73°31′E; reported before 1978 by T. J. Roberts (1977, p. 86), A: P-10.


Patang. See Batang vicinity.


Patria, Murree region, 7150 ft (= 2180 m); *Punjab*, PAKISTAN; 33°51′N, 73°29′E; collected 14–15 June 1923 by H. W. Wells (in Lindsay, 1926, p. 608); BM(NH), 1; BNHS, 1. A:P-12.

Peak. See [Victoria] Peak.

Pekin. See Beijing.

Phala/Kutbor Game Reserve; *Azad Kashmir*, PAKISTAN; ca. 34°00′N, 73°35′E; reported before 1984 by M. Nawaz (1983, p. 6), A:P-12.


Phu Qui. See Nghia Dan.

Phu Vach, Tan Lac District; *Hoa Binh*, VIETNAM; ca. 20°35′N, 105°18′E; collected 21 Jan. 1973 by Pham Trong Anh; IEBR, 1 (skin only), C: V-21.

Piangzu, 3.5 km northeast of Banli, Luoshan Sub-county, Jinxian Xian; *Guangxi*, CHINA; ca. 24°02′N, 110°15′E; captive purchased ca. 1987 by Zhong Changwan (pers. comm., 21 Nov. 1992); died in 1991; skeleton examined 21 Nov. 1992 at Banli. C:C-195.

Pidaung Reserve. See Karen Chaung.


Pina, forests above, Rara Daha (= Lake) vicinity;


Pinglang. See Batu.

Pingnan Xian; Fujian, CHINA; ca. 26°56'N, 119°03'E; reported Sept. 1980 by Zheng Xueqing (1984, p. 146). C:C-70.

Pingwu; Sichuan, CHINA; 32°25'S, 104°36'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-24.

Pinxiang vicinity; Jiangxi, CHINA; ca. 27°37'N, 113°51'E; captured in 1983 for Pinxiang Zoo; observed at zoo in summer 1984 by Sheng He-lin, ECNU (pers. comm., 19 Oct. 1985). C:C-106.


Plateau des Bolovens. See Muang Thateng.

Pochuan, 6–7 km west of, Xianan Subcounty. Huanxian Xian, 460 m; Guangxi, CHINA; ca. 25°00'N, 107°52'E; collected 25 Oct. 1992 by Tan Nenrui (pers. comm., 5 Nov. 1992); IZCAS, 1. C:C-177.

Podumoni. See Tinsukia.


Po Lu, Ba Be vicinity; Cao Bang, VIETNAM; ca. 22°24'N, 105°38'E; collected 6 Aug. 1967 by Vo Quy; ZMVNU, 1 (skull only). C:V-8.


Popa Hill, 1000 m; Mandalay, MYANMAR (= BURMA); 20°55'N, 95°15'E; collected 21 Oct.–5 Nov. 1937 by G. Heinrich; AMNH, 6. B: M-27.

Popa Hill, 4961 ft (= 1512 m); Mandalay, MYANMAR (= BURMA); 20°55'N, 95°15'E; collected July–Oct. 1913 by G. C. Shortridge (in Wroughton, 1915a, p. 461); BM(NH), 1; BNHS, 5 (including 1 skull only). B:M-27.

Prag Oil Mill. See Aligarh.

Prome. See Pye.

Pu'er Xian; Yunnan, CHINA; ca. 23°05'N, 101°03'E; immunological survey conducted before 1996 by Duan Xingsheng, Liu Yuanwei, Wu Jing, Dao Weiying, and Liu Jianghai (1995, p. 411). B:C-77.


Pulareddi. See Siddeldar Hill.


Puquan Road Maintenance Station, Zhongliang Subcounty, Jinxian Xian, 850 m; Guangxi, CHINA; 24°11'N, 110°19'E; observed in 1991 by Mo Cailein and Mo Xiuzhen, road maintenance workers (pers. comm., 14 Nov. 1992). C:C-195.


Pyauunggaung, 2794 ft (= 852 m); Shan, MYANMAR (= BURMA); 22°35'N, 97°05'E; collected 8 and 14 May 1913 by G. C. Shortridge (in Ryley, 1914, p. 713; Moore & Tate, 1965, p. 330); BM(NH), 2 (including 1 in alcohol); BNHS, 2 (including 1 skull only). B:M-20.

Pye (= Prome), 30 mi (= 50 km) southeast of, 200 ft (= 60 m); Irrawaddy, MYANMAR (= BURMA); ca. 18°30'N, 95°30'E; collected 2 Feb. 1917 by J. M. D. Mackenzie (Wroughton, 1921, p. 553); BNHS, 1. B:M-34.

Pye (= Prome), 35 mi (= 55 km) southeast of, 800 ft (= 240 m); Pegu, MYANMAR (= BURMA); ca. 18°30'N, 95°35'E; collected 25 Oct. 1916 by J. M. D. Mackenzie (Wroughton, 1921, p. 553); BM(NH), 1. B:M-34.

Qamdo; Xizang (= Tibet), CHINA; 31°10'N, 97°14'E; reported before 1992 by Jiang Xuelong, Wang Yingxiang, and Ma Shilai (1991, p. 245). B:C-21.


Qianjiandong Water Regulation Forest Reserve; Guangxi, CHINA; ca. 25°26'N, 111°16'E; ob-

Qianxian. See Yixian.

Qiasui, Huaijii Xian; Guangdong, CHINA; ca. 24°06'N, 112°20'E; reported Apr. 1982 by local residents (Liu Zhenhe, SCIEA, pers. comm., 26 Nov. 1985). C:C-107.

Qigong, Yangshan Xian; Guangdong, CHINA; 24°18'N, 112°34'E; reported July 1982 by local residents (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985). C:C-206.

Qihong, Qimen Xian, 200–600 m; Anhui, CHINA; ca. 29°35'N, 117°40'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-63.

Qingchuan; Sichuan, CHINA; 32°36'N, 105°09'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-23.

Qingliangfeng, Jixi Xian, 800 m; Anhui, CHINA; ca. 30°10'N, 118°50'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-55.


Qizhen; Guizhou, CHINA; 26°33'N, 106°28'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-145.

Qinyang; Henan, CHINA; 35°06'N, 112°57'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-11.

Qionglai; Sichuan, CHINA; 30°25'N, 103°29'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-29.

Quan Lan, Dao; Quang Ninh, VIETNAM; ca. 20°52'N, 107°30'E; collected 3 June 1969 by unknown collector; IBIR, 1 (skull only). C:V-13.

Quang Ninh. See Xuan Ninh.

Quanzhou; Guangxi, CHINA; 25°57'N, 111°04'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-188.

Qusum Xian; Xizang (= Tibet), CHINA; ca. 29°05'N, 92°10'E; observed 1979–1982 by Zhang Cizu, Director, Shanghai Zoo (pers. comm., 18 Oct. 1985). B:C-3.

Quxian; Zhejiang, CHINA; 28°58'N, 118°52'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-64.


Railway Station. See Aligarh.


Raj Bhavan compound. See Mumbai.


Rajapara, South Kamrup. 600 ft (= 180 m); Assam, INDIA; ca. 25°55'N, 91°15'E; collected 21 and 25 Nov. 1920 by H. W. Wells (Hinton & Lindsay, 1926, p. 385); BM(NH), 2 (including 1 skin only). B: I-15.

Rajendrapur forest. See Ghazipur.


Rama Pass. See Xi Golong.


Ramnagar, Kumaun region, 1100 ft (= 340 m); Uttar Pradesh, INDIA; ca. 29°24'N, 79°07'E; collected Aug. 1913–Mar. 1914 by C. A. Crump (in Wroughton, 1914, p. 284; Napier, 1981, p. 24); BM(NH), 3 (1 skin only, 2 skulls only); BNHS, 1. A:I-33.


Rangoli Reserve Forest. See Diroi (Rangoli) Reserve Forest.


Rara Daha (= Lake). See Hutu Forest; Pina.


Ratighat, Naini Tal vicinity. Kumaun region, 3700 ft and 3800 ft (1130 m and 1160 m) Uttar Pradesh, INDIA; 29°27'N, 79°29'E; collected 1–8 Nov. 1913 by C.A. Crump (in Wroughton, 1914, p. 283); BM(NH), 2; BNHS, 1. A:I-32.

Rehnathapalli. See Raghnathapalle.


Rest House. See Dehra Dun vicinity.


Ridge. See Simla vicinity.

Ripon Hospital. See Simla vicinity.


Rongrenganji vicinity, Garo hills; Assam, INDIA; ca. 25°33'N, 90°34'E; observed Jan.–Feb. 1957 by H. Khajuria (1962a, p. 122). B:I-13.

Rongtong. See Sukna-Kurseong.

Rouetoundo (= Routeoudo); Xizang (= Tibet), CHINA; ca. 31°35'N, 97°25'E; infant captured and two specimens collected 17 May 1890 by G. Bonvalot and H. d'Orleans (Bonvalot, 1891, vol. 2, p. 156; 1892, p. 505; Bonvalot et al., 1891, map); skins possibly in MNHN (see below, Tibet). B:C-20.


Rucun, Xiuning Xian, 500–800 m; Anhui, CHINA; ca. 29°55'N, 118°07'E; observed 1973–1986 by Xiong Chenpei, K. Wada, and Wang Qishan (Wada et al., 1986, pp. 83, 88). C:C-62.


Ruicheng; Shanxi, CHINA; 34°42'N, 110°42'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-15.

Russian Camp, Birganj Forest District; Bara, NEPAL; 27°12'N, 85°04'E; observed June 1964–
S. A. Factory. See Dhaka.
Sahebgunj. Gaya; Bihar, INDIA; ca. 24°50'N, 85°00'E; reported 1811-1812 by F. Buchanan ([1936], p. 403, posthumous publication). A:I-91.
Saktesgarh; Uttar Pradesh, INDIA; 24°59'N, 82°49'E; collected before 1849 by unknown collector (Napier, 1981, p. 25); BM(NH), 1 (skull only). A:I-86.
Sala Reserve Forest; Assam, INDIA; ca. 27°00'N, 94°54'E; observed 9 Mar. 1987-16 Feb. 1988 by A. Choudhury ([1991a], p. 32). B:I-25.
Salween River. See Nu Jiang.
Samaguting; Nagaland, INDIA; 25°47'N, 93°47'E; collected before 1873 by J. Butler (Anderson, 1881, p. 69); ZSI, 1 (skull only). B: I-34.
Samayala (= Samyala), Kangra Valley, 5000 ft (= 1500 m); Himachal Pradesh, INDIA; ca. 32°10'N, 76°25'E; collected 9 May 1922 by H. W. Wells (Lindsay, 1926, p. 599); BM(NH), 2; A:1-12.
Sambalpur. See Deogarh.
Sam Shui Wan Valley; Xianggang (= Hong Kong), CHINA; ca. 22°14'N, 114°10'E; reported before 1952 by G. A. C. Herklots (1951, p. 83). C:C-210.
Sandu; Guizhou, CHINA; 25°59'N, 107°52'E; re-
ported before 1998 (Zhang et al., 1997, p. 58).
C:C-122.
Sangu/ Matamuhari; Bandarban, BANGLA-
Sangzhi; Huanan, CHINA; 29°24'N, 110°09'E; re-
ported before 1998 (Zhang et al., 1997, p. 58).
C:C-111.
Sankat Mochan Temple. See Varanasi.
Sankhuwa Khola, both banks, Makalu-Barun Conservation Area; Dhankuta, NEPAL; ca. 27°30'N, 87°05'E; observed ca. 1997, by M. K. Chalise (1997, p. 31; e-mail, 9 Nov. 1998). B: N-1.
Samming Xian; Fujian, CHINA; ca. 26°14'N, 117°35'E; reported Apr. 1981 by Zheng Xue-
Sanpihu Water Regulation Forest Reserve; Guangxi, CHINA; ca. 25°06'N, 107°13'E; ob-
C:C-173.
Santaishan, Luxi Xian; 1250 m; Yunnan, CHINA; ca. 24°15'N, 98°25'E; collected 11 Apr. 1962 by unknown collector (Wang Yingxiang, kiz, pers. comm., 1 Sept. 1983); kiz, 1; B:C-62.
Sanya, Hainan Dao; Hainan, CHINA; 18°14'N, 109°29'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-238.
Saraguri; Assam, INDIA; ca. 27°00'N, 94°29'E; reported 9 Mar. 1987-16 Feb. 1988 by A. Choudhury ([1991a], p. 31). B:I-25.
Sariska Tiger Reserve; Rajasthan, INDIA; ca. 27°20'N, 76°25'E; reported May-Oct. 1990 by C. Ross and A. Srivastava (1994, p. 362). Re-
Sarupduli. See Ramganga River.


Satkhira, southern; BANGLADESH; ca. 22°00’N, 89°10’E; observed 1951–1961 by A. K. Mandal (1964, p. 164). B:Ba-22.


Sayabouri. See Xaignabouri.

School Yard. See Chhatari-do-Raha.

Se-eng, Hsipaw District, 1411 ft (= 430 m); Shan, MYANMAR (= BURMA); 22°43’N, 97°31’E; collected 25 May 1913 by G. C. Shortridge in Ryley. (1914, p. 713); BM(NH), 1. B:M-19.

Seoni. See Malua.

Seri. See Sungri, ca. 2 km south of.

Setschuen. See Sichuan.

Sevoke. See Sivok.

Shahabad District; Bihar, INDIA; ca. 25°30’N, 84°15’E; reported 1809–1810 by F. Buchanan (1934, p. 227), posthumous publication). A:I-90.


Shakar Bazar. See Dhaka.


Shangchuan Dao. See Miwan.

Shanghai. See Sichuan.


Shangsi; Guangxi, CHINA; 22°10’N, 108°00’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-218.

Shangzhou Is. See Miwan.

Shanman, Menghai Xian; Yunnan, CHINA; ca. 21°55’N, 100°25’E; collected Nov. 1957 by unknown collector (Wang Yingxiang, kiz. pers. comm., 1 Sept. 1983); kiz 1 (skin only). B:C-81.

Shanmoji, Dabu District, Ruyuan Yaozu Zizhixian. >1000 m; Guangdong, CHINA; 24°33’N, 113°12’E; captive purchased in 1979 by district purchasing agent (Ling Wenfeng, county forest officer, photos and pers. comm., 10 Nov. 1985). C:C-203.


Shennongjia Forestry Region; Hubei, CHINA; ca. 31°44’N, 110°44’E; reported before 1980 by Xiao Zhi (1979, p. 31). C:C-43.

Shenzhen Shi. See Neilingding Dao.


Shexian; Anhui, CHINA; 29°52’N, 118°26’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-61.

Shihshahshu Temple; Sichuan, CHINA; ca. 29°32’N, 103°21’E; reported 4–8 Oct. 1929 by local residents (Stevens, 1934, p. 222; possibly misidentified M. thibetana). C:C-139.

Shimen. Qimen Xian, 300–500 m; Anhui, CHINA; ca. 29°55’N, 117°45’E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-62.

Shimla. See Simla.

Shingaw. See Tanga-Shingaw.

Shing Mun Country Park; Xianggang (= Hong Kong, MACAQUA MULATTA)...

Shiqian; Guizhou, CHINA; 27°30’N, 108°14’E; reported before 1998 (Zhang et al., 1997 p. 58). C:C-119.

Shishi, and Chaqian; Sichuan, Shuicheng (86).


Shiva. See Siva.


Shogran Valley, Himachal Pradesh; INDIA; ca. 27°10’N, 88°30’E; collected before 1892 by [L. Mandelli] (Bланфорд, 1888b, p. 14); BM (NH), 2 (skins only, 1 with skull inside). B:I-7.

Shogran vicinity, lower Kaghan Valley; North-West Frontier. PAKISTAN; ca. 34°37’N, 73°28’E; reported before 1978 by T. J. Roberts (1977, p. 86). A:P-10.


Shuangbai; Yunnan, CHINA; 24°40’N, 101°38’E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-51.


Shuicheng Xian vicinity; Guizhou, CHINA; ca. 26°50’N, 105°00’E; reported before 1989 by Tan Bangjie and F. E. Poirier ([1991], p. 131). C:C-144.

Sibsagar. See Golaghat.


Sikarwar. See Khair, Tahsil.


Simla Water Catchment Reserve; Himachal Pra-


Simulbari-Pankhabari, highway between; West Bengal, INDIA; ca. 29°05'N, 88°18'E; observed Mar.–Apr. 1985 by R. P. Mukherjee, S. Chaudhuri, and A. Murmu (1995, p. 27). B:1-6.


Singaw. See Tanga-Shingaw.

Singhbhum. See Luia.

Singkaling Hkamti, upper Chindwin River; Kachin, MYANMAR (= BURMA); ca. 26°00'N, 95°42'E; collected June–Aug. 1914 by G. C. Shortridge (in Wroughton, 1916a, p. 293). BM(NH), 3 (including 2 skulls only). B:M-8.

Singkaling Hkamti, upper Chindwin River, 500 ft (= 150 m); Kachin, MYANMAR (= BURMA); ca. 26°00'N, 95°42'E; collected 5 Aug. 1914 by G. C. Shortridge and S. A. Macmillan (in Wroughton, 1916a, p. 293); BM(NH), 1. B:M-8.

Singkaling Hkamti, upper Chindwin River, left (east) bank, 500 ft (= 150 m); Kachin, MYANMAR (= BURMA); ca. 26°00'N, 95°42'E; collected 24 July 1914 by G. C. Shortridge and S. A. Macmillan (in Wroughton, 1916a, p. 293); ZSI, 1. B:M-8.

Singkaling Hkamti, upper Chindwin River, right (west) bank; Kachin, MYANMAR (= BURMA); ca. 26°00'N, 95°42'E; collected 8 Mar. 1935 by H. C. Raven (in Carter, 1943, p. 100; Morris, 1936, p. 662); AMNH, 1. BM(NH), 1 (skin only). A:L-18.

Singolo. See Xi Golog.

Sita Bani, Ramnagar vicinity, Kumaun region. 2000 ft (= 600 m); Uttar Pradesh, INDIA; 29°24'N, 78°13'E; collected 22 Nov. 1913 by C. A. Crump (in Wroughton, 1914, p. 283); BM(NH), 2. A:I-34.


Sittang River. See Toongoo. 15 mi. (= 24 km) north of.


Sivalik Hills. See Siwalik Range.

Sivok; West Bengal, INDIA; 26°52'N, 88°27'E; collected 11 Nov. 1930 by H. Stevens; FMNH, 1 (skin only). B:1-6.

Sivok, ca. 3 km east of; West Bengal, INDIA; ca. 26°52'N, 88°30'E; observed Mar.–Apr. 1985 by R. P. Mukherjee, S. Chaudhuri, and A. Murmu (1995, p. 27). B:1-6.

Sivok, ca. 5 km east of; West Bengal, INDIA; ca. 26°52'N, 88°31'E; observed Mar.–Apr. 1985 by R. P. Mukherjee, S. Chaudhuri, and A. Murmu (1995, p. 27). B:1-6.

Sivok, ca. 6 km east of; West Bengal, INDIA; ca. 26°52'N, 88°32'E; observed Mar.–Apr. 1985 by R. P. Mukherjee, S. Chaudhuri, and A. Murmu (1995, p. 27). B:1-6.


Sohagpur, Hoshangabad District, 1000 ft (= 300 m); Madhya Pradesh, INDIA; 22°42'N, 78°12'E; collected 10 Apr. 1912 by C. A. Crump (Wroughton & Ryley, 1913, p. 45); BM(NH), 1 (skin only). A:1-95.


Sonargaon; Narayanganj; BANGLADESH;


Songtao; Guizhou, CHINA; 28°12’N, 109°12’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-114.

Song-Ta-Voi (= Song-Ta-Voi); Quang Nam Da Nang, VIETNAM; ca. 16°10’N, 107°40’E; collected [?Jan. 1899] by P. E. S. Barthélemy (1904, p. 38); MNHN, 1. C:V-34.


Son La; VIETNAM; ca. 20°35’–22°05’N, 103°15’–105°00’E; collected before 1986 by unknown collector (Dao, 1985, p. 166); museum unknown (not seen). Not mapped.


Son Tra, Mt., 3.9 km west and 0.3 km south of; 240 m; Quang Nam Da Nang, VIETNAM; ca. 16°07’N, 108°15’E; collected 14 Sept. 1967 by P. F. Ryan (Van Peenen et al., 1968, p. 609; 1971, pp. 127, 134; Fooden, 1995, p. 25); USNM, 1 (external measurements questionable). C:V-36.

South China. See CHINA, South.


South Kamrup. See Kulsi; Rajapara.

“Southwest” Yunnan. See Yunnan [northwestern].


Srinagar, ca. 22 km southeast of. See Ovra (= Overa) Sanctuary.

Suifu. See Yibin.

Suiyang; Guizhou, CHINA; 27°57’N, 107°11’E; reported before 1988 (Zhang et al., 1997, p. 58). C:C-130.

Sucktaisgur. See Saktesgarh.


Sultanpur vicinity; Uttar Pradesh, INDIA; ca. 26°16’N, 82°04’E; blood samples obtained 16–


Sundarbans (= Sunderbans, Sunderbunds); West Bengal, INDIA; 88°00’–89°00’N, 21°30’–22°30’E; reported in 1892 by E. de Poncins (1935, p. 846). Reported before 1997 by K. K. Gurung and R. Singh (1996, p. 122). Not mapped (see B:1-1 and B:1-2).

Sundarbans (= Sunderbunds), ca. 50 mi (= 80 km) east of Calcutta; Satkhira, BANGLADESH; ca. 22°35’N, 89°15’E; collected 26 Apr. 1870 by museum collector (Anderson, 1872, p. 529); zst 7 (including 1 skin only). B:Ba-21.


Surat. See Dangs District.


Suritola. See Dhaka.


Swat Valley, lower. See Bar Chanrai Hill.


Szechuan. See Sichuan.

Szechuen. See Sichuan.

Tachienlu. See Kangding.

Ta Chang Tai. See Tha Chang Tai.

Taga Hka, Chindwin River, west bank; Kachin, MYANMAR (= BURMA); 26°21’N, 96°09’E;


Tai: Jiangxi, CHINA; 26°48′N, 114°56′E; reported before 1998 (Zhang et al., 1997, p. 58); C:C-105.

Taining, Wuyishan: Fujian, CHINA; 26°55′N, 117°12′E; reported before 1998 (Zhang et al., 1997, p. 58); C:C-81.

Taining Xian: Fujian, CHINA; ca. 26°55′N, 117°12′E; reported May 1981 by Zheng Xueqing (1984, p. 145); C:C-81.

Tai Po Kau Nature Reserve: Xianggang (= Hong Kong), CHINA; ca. 22°25′N, 114°10′E; reported before 1992 by J. R. Fellowes (1992, p. 131); C:C-210.

Tai Tam Reservoir: Xianggang (= Hong Kong), CHINA; ca. 22°14′N, 114°13′E; reported in 1947 by G. A. C. Herklots (1951, p. 83); C:C-210.

Takerhat. See Dhaka.


Tamanthe. See Hisweht.


Tanbazar. See Narayanganj.

Tang Hpre (= Tang Hper); Kachin, MYANMAR (= BURMA); ca. 25°23′N, 97°14′E; collected 14 Oct. 1945 by K. E. Stager (letter, 9 Aug. 1985); USNM, 1, B:M-5.

Tanga-Shingaw (= Tang-Singaw), road between, 800 ft (= 240 m); Kachin, MYANMAR (= BURMA); ca. 25°40′N, 97°55′E; collected 9 Apr. 1939 by H. E. Anthony (1941, pp. 55, 83); AMNH, 1, B:M-4.

Tangxi. Guichi Xian, 200–560 m; Anhui, CHINA; ca. 30°20′N, 117°40′E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-50.


Tanti Road. See Dhaka.

Tara Devi. See Nhera/Tara Devi.

Tarai. See Terai.


Taro (?= Dalu); Kachin, MYANMAR (= BURMA); 26°21′N, 96°11′E; collected 5 Feb. 1935 by H.C. Raven (in Carter. 1943, p. 100; Morris, 1936, p. 653); AMNH, 2, B:M-7.

Tasin Lou. See Kangding.

Tat Ke vicinity (= Kheo Ting-Ta Ke area). Na Hang District; Tuyen Quang, VIETNAM; ca. 22°25′N, 105°25′E; captured ca. 1992 by local resident (Ratajczczak et al., 1992, p. 14). C:V-6.

Tatkon, near Kindat, east bank of Chindwin River, 250 ft (= 75 m); Sagaing, MYANMAR (= BURMA); ca. 23°47′N, 94°30′E; collected 5 July 1914 by G. C. Shortridge and S. A. Macmillan (Shortridge in Wroughton, 1916a, p. 293); BNHS, 1, B:M-18.

Tatkon, near Kindat, west bank of Chindwin River, 250 ft (= 75 m); Sagaing, MYANMAR (= BURMA); 23°47′N, 94°29′E; collected 28 June and 5 July 1914 by G. C. Shortridge (in Wroughton, 1916a, p. 293); BM(NH), 2 (including 1 skin only); BNHS, 2 (including 1 skin only). B:M-18.

Ta-tsien-lou. See Kangding.

Tatura, Chandigarh; Punjab, INDIA; not precisely located, 30°38′–30°47′N, 76°43′–76°53′E; reported 1964–1966 by D. G. Lindburg (1977a, p. 268). Not mapped.

Tay Tru. See Trai Tru.

Tché-ly, eastern mountains. See Xinglong Xian, southern.


Tenali, 5.5 km west of. Guntur District, 10 m; Andhra Pradesh, INDIA; 16°14′N, 80°37′E;

Tenasserim; MYANMAR (= BURMA): 10°-15°N, 98°-100°E; observed 4 Oct. 1912 by Sch. Med. Rat. Dömitz; locality information probably inaccurate (see above, Fig. 2B); ZMB, 1 (skull only). Not mapped.

Tengchong (= Momien); Yunnan, CHINA; ca. 25°02'N, 98°28'E; collected before 1984 by Ma Shilai; KIZ, 1 (skull only). B:C-59.

Tengchong Xian; Yunnan, CHINA; ca. 25°02'N, 98°28'E; collected before 1984 by Ma Shilai; KIZ, 1 (skull only). B:C-59.

Tengri-Nor. See Nam Co.

Teng-yue-chow. See Tengchong.

Teng-yueh. See Hui-yao.

Ten Ky. See Nghia Dung.

Terai (region); NEPAL; 26°-29°N, 80°-88°E; reported before 1842 by B. H. Hodgson (1841, p. 1212; cf. Karan, 1960, p. 92). Not mapped.

Tha Chang Tai (= Ta Chang Tai), 600 ft (= 180 m); Tak, THAILAND; 16°51'N, 99°03'E; collected 14 July 1924 by J. H. Chambray (Kloss, 1930, p. 62); ZRC, 1 (excludes ZRC 4-822, a colobine: cf. Weitzel et al., 1988, p. 116). B:T-7.

Thai Nguyen; Bac Thai, VIETNAM; ca. 21°36’N, 105°50’E; collected 30 Dec. 1956 and 17 June 1959 by unknown collectors; ZMVNU, 2 (skulls only). C:V-15.

Thana Ghazi. See Bandipul.

Thanh Son; Vinh Phu, VIETNAM; 21°13’N, 105°11’E; collected 27 June 1961 by unknown collector; ZMVNU, 1 (skull only). C:V-18.

Thanh Tuong, Na Hang District; Tuyen Quang, VIETNAM; 22°19’N, 105°24’E; collected 18 Jan. 1965 and 23 Oct. 1965 by Ma Van Dam (Dao, 1985, p. 29; external measurements published); IEBR, 2. C:V-6.

Thapathali. See Triuresworo.

Tharikella. See Tankikella.

Thateng. See Muang Thateng.

Theme. See Pye (= Prome), 35 mi (= 55 km) southeast of.

Thirumunidevipetta. See Tirumaladevipeta.

Thuong Bang La, Van Chan District; Yen Bai, VIETNAM; 21°25’N, 104°47’E; collected Mar. 1963 by unknown collector (Dao, 1985, pp. 183, 192); IEBR, 1 (skull only). C:V-17.

Tian’e Xian; Guangxi, CHINA; ca. 25°00’N, 107°10’E; purchased at traditional medicine shop 15 Oct. 1992 by Quan Guoqiang (cf. Fooden et al., 1994, p. 623); IZCAS, 3 (skulls only). C:C-173.


Tibet; Sichuan or Xizang (= Tibet), CHINA; 30°-32°N, 96°5°-102°E; collected [May–July 1890] by G. Bonvalot and H. d’Orleans (Bonvalot, 1891, vol. 2, p. 210; 1892, p. 505); possibly purchased at Ngamda (= Kintachié/Houmda) and/or collected at Rouetoundo (see above; Bonvalot, 1891, vol. 2, pp. 149, 156); MNHN, 2 (skins only). Not mapped.

Tibet Colony. See Dehra Dun vicinity.


Tipusultan Road. See Dhaka.


Tongjiang Xian; Sichuan, CHINA; ca. 31°55’N, 107°13’E; collected July 1966 by Expedition of Biological and Agricultural Resources in Qingling, Shaanxi; siz. 4. C:C-31.

Tong Kou; Anhui, CHINA; ca. 30°05’N, 118°10’E; collected 23 May and 21 July 1959 by Wang Zeyeh; IZCAS, 2 (including 1 skin only). C:C-62.

Tonglin. mountains of. See Xinglong Xian, southern.

Tongzhi. See Tongzi.

Tongzi (= Tongzhi); Guizhou, CHINA; 28°08’N, 106°49’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-135.

Tonkin region; VIETNAM; 20°–23°N, 102°–108°E; captive obtained in 1886 by Lt. Stahl;
died in zoo 26 Jan. 1887; MNHN, 1 (skin only). Not mapped.

Toungoo, 13 mi (= 21 km) east of, 500 ft (= 150 m); Karen, MYANMAR (= BURMA); ca. 18°55'N, 96°40'E; collected 2 Sept. 1927 by J. M. D. Mackenzie (in Fry, 1929, p. 637); BM(NH), 1; B:M-31.

Toungoo, 15 mi (= 24 km) north of, east side of Sittang River, 400 ft (= 120 m); Karen, MYANMAR (= BURMA); ca. 19°10'N, 96°25'E; collected 26 Jan. 1927 by J. M. D. Mackenzie (Fry, 1928, P. 545); BM(NH), 1. B:M-30.

Toungoo, 15 mi (= 24 km) north of, east side of Sittang River, 400 ft (= 120 m); Karen, MYANMAR (= BURMA); ca. 19°15'N, 96°05'E; collected 26 Nov. and 6 Dec. 1928 by J. M. D. Mackenzie (Khajuria, [1955], p. 113); BM(NH), 1; BNHS, 1; ZSI, 1 (skin only). B:M-33.

Toungoo, 30 mi (= 48 km) northwest of, 500 ft (= 150 m); Pegu, MYANMAR (= BURMA); ca. 18°56'N, 96°27'E; collected 15 May 1927 by J. M. D. Mackenzie (in Fry, 1929, p. 637); BM(NH), 3. B:M-32.

Toungoo, east side of Sittang River, 100 ft (= 30 m); Pegu, MYANMAR (= BURMA); ca. 18°56'N, 96°27'E; collected 15 May 1927 by J. M. D. Mackenzie (in Fry, 1929, p. 637); BM(NH), 1; BNHS, 1; ZSI, 1 (skin only). B:M-29.

Trai Tru (= Tay Tru), Huong Khe District; Ha Tinh, VIETNAM; 18°11'N, 105°35'E; collected 6 Feb. 1964 by unknown collector (Dao, 1985, p. 233; external measurements published); JEIBR, 1 (skull only). C:V-28.


Trisuli Bazar, 4 mi (= 6.5 km) southeast of, Nawakot District, 1875 ft (= 570 m); Bagmati, NEPAL; ca. 27°55'N, 85°10'E; collected 9 and 13 Apr. 1967 by C. O. Masar; FMNH, 6 (3 skeletons only, 3 in alcohol); UPS, 2 (in alcohol, not seen). A:N-11.

Trung Khanh District, Cao Bang, VIETNAM; ca. 22°50'N, 106°31'E; collected 9 May 1967 by Hoang Tung; FCXM, 1 (skull only, mandible missing). C:V-9.

Tsari Chu (= Tsari Valley); Xizang (= Tibet), CHINA; ca. 28°45'N, 93°10'E; observed Sept. – Oct. 1913 by F. M. Bailey (1914, map; 1915, p. 74). B:C-5.

Tsee-Jia-Geo; Sichuan, CHINA; ca. 28°18'N, 104°12'E; collected 14 Jan. 1931 by D. G. Graham (Moore & Tate, 1965, p. 334); USNM, 1. C: C-138.

Tsingtau. See Sichuan.

Tsung he. See Luofu Shan.

Tu Chi. VIETNAM; not located, 15°–23°N, 102°–109°E; date and collector unknown; ZMVNU, 1 (skull only). Not mapped.


Tunchang Xian; Hainan; CHINA; ca. 19°22'N, 110°05'E; reported before 1986 by Xu Longhui and Liu Zhenhe (1985, p. 148). C: C-230.

Tungho. See Wu Shan.


Tung Ling. See Xinglong Xian, southern.

Tunxi; Anhui, CHINA; 29°43'N, 118°19'E; collected 23 Jan. 1959 by museum collector; SMNH, 1 (skin only). C:C-61.

Tusu River. See Hisweht.

Tuzu River. See Hisweht.

Twenty-four Parganas District; West Bengal, INDIA; 21°30'–22°20'N, 88°00'–89°00'E; observed 1951–1961 by A. K. Mandal (1964, P. 165). Not mapped (see B:I-1 and B:I-2).

U, Nam. See Ou, Nam.


United Khasi-Jaintia Hills; Meghalaya, INDIA;

Um Pang. See Ban Umphang.

Umpilagudem. See Dumpallagudem.

Uppadhyay Mohalla. See Khaire, Tahsil.

Utzun Vicinity, Chitral District 5000 ft (= 1500 m); North-West Frontier, PAKISTAN; ca. 35°30'N, 71°40'E; reported 1901–1902 by H. Fulton (1903, p. 758). Reported before 1978 by T. J. Roberts (1977, p. 86). A:P-1.

Uzipur. See Wazipur.

Vaddepalli. See Vaddepalle.

Van Canh, Dao; Quang Ninh, VIETNAM; ca. 20°52'N 107°22'E; collected 3 Apr. 1969 and June 1969 by unknown collectors; IEBR, 2 (skulls only). C.V-13.


Varanasi (= Benares) District; Uttar Pradesh, INDIA; 24°40'–25°30'N, 82°05'–83°30'E; captured once in 1891 by W. Heape (1897, p. 135). Not mapped (see A:I-87).


Vergel. See Wargel.


Viangchan; Vientiane. LAOS; ca. 17°58'N, 102°36'E; reported before 1964 by J. Deuve and M. Deuve (1963, p. 59). B:L-7.

[Victor] Peak; Xianggang (= Hong Kong), CHINA; 22°16'N, 114°08'E; reported before 1952 by G. A. C. Herklots (1951, p. 83). C:C-210.

Vientiane. See Viangchan.

VIETNAM; 15°–23°N, 102°–109°E; collected 28 Feb. 1965 by unknown collector; ZMVNU, 2 (skulls only). Collected in 1992 and 1994 by unknown collectors; IEBR, 2 (1 skull only, 1 skull only). Date and collector unknown; FCXM, 1 (skull only; identification tentative); IEBR, 14 (including 5 skins only, 8 skulls only); ZMVNU, 14 (3 skulls only, 11 skulls only [one identification tentative]). Not mapped.


Vinh Linh region, 50 m; Quang Tri, VIETNAM; ca. 17°04'N, 107°02'E; collected 28 Aug. 1956 by unknown collector (Dao, 1960, p. 228; 1962, p. 724); misidentified as M. assamensis; museum unknown. C:V-32.


Visakhapatnam. See Malkangiri.

Vizag. See Malkangiri.


Waddepalle, Banswada Taluk, Nizamabad District; Andhra Pradesh, INDIA; 18°14'N,


Wangmo; Guizhou, CHINA; 25°14'N, 105°59'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-158

Wanshien. See Wa Shan.

Wanxian; Sichuan, CHINA; 30°49'N, 108°21'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-38.

Wanyuan; Sichuan, CHINA; 32°04'N, 108°02'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-37.


Wa Shan (= Waschan), near Dong He (= Tungho), 900–2000 m; Sichuan, CHINA; ca. 29°15'N, 103°03'E; collected 29 Mar. 1915 by H. Weigold (1916, p. 74; 1922, p. iv; 1924, p. 71; 1935, p. 212; Israel, 1919, pl. 7; Jacobi, 1923, p. 1); RMNH, 2. C:C-140

Wassuland; Sichuan, CHINA; ca. 31°05'N, 103°10'E; tentatively reported 1914–1916 by H. Weigold (1924, p. 71). C:C-27.


Weixi; Yunnan, CHINA; 27°13'N, 99°16'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-41.

Wenchuan; Sichuan, CHINA; 31°28'N, 103°35'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-26.

Wenga; Guizhou, CHINA; 27°00'N, 107°32'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-126.

West Bengal, INDIA; ca. 22°–28°N, 86°–90°E; obtained before 1857 by Theobald Collection; BMNH, 1 (skull only). Collected date unknown by [C. A. Crump]; BMNH, 1 (skull only). Not mapped.


West Sichuan. See Sichuan, western.


Wonglung kun. See Luofu Shan.
Wuchi. See Wuzhi Shan.
Wudu; Gansu, CHINA; 33°24'N, 104°50'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-21.

Wuliang Shan Reserve; Yunnan, CHINA; ca. 24°00'N, 101°00'E; reported in 1990 by L. K. Sheeran and F. E. Poirier (1994, p. 21). B:C-73.

Wushan; Sichuan, CHINA; 31°02'N, 109°56'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-40.

Wu-tsao. See Xi Jiang.


Wuzhi Shan, Hainan, CHINA; ca. 18°54'N, 109°40'E; collected 1–30 Oct. 1905 by A. Owston. AMNH, 10 (including holotype of Pithecus brachyurus and Pithecus brevicaudus); BM(NH), 1. C:C-232.

Wuzhou; Guangxi, CHINA; 23°29'N, 111°19'E; tissue sample obtained ca. 1991 by Zhang Yap ing and Shi Liming (1993b, p. 589). C:C-197.


Xin Xian. See Huangjiangping.


Xianan-Mulun, Huanjiang Xian; Guangxi, CHINA; ca. 25°03'N, 107°57'E; collected ca. 1991 by local resident (Tan Yulung, pers. comm., 5 Nov. 1992); skull examined 5 Nov. 1992 at Mulun. C:C-177.

Xiangcheng; Sichuan; CHINA; 29°00'N, 99°46'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-37.


Xiangkoang, LAOS; ca. 19°20’N, 103°22’E; reported before 1964 by J. Deuve and M. Deuve (1963, p. 59). C:L-1.


Xieng-Khouang. See Xiangkoang.

Xi Golog (= Singolo); Sichuan, CHINA; 30°00’N, 100°42’E; collected 31 Oct. 1931 by Dolan West China Expedition (Schäfer, 1933, p. 191; 1942, p. 257; Stone, 1933, p. 170; Dolan, 1939, p. 178); ANSP (skin) / MCZ (skull), 1. B:C-30.

Xi Jiang (= Hsi-kiang; river), near Wuzhou (= Wu-tsao); Guangxi, CHINA; ca. 23°29’N, 111°19’E; collected 27 Apr. 1912 by R. Mell (Matschie, 1912, p. 305); ZMH, 1. C:C-197.


Xindeng, Fuyang Xian, <500 m; Zhejiang, CHINA; 29°58’N, 119°44’E; collected 2 Feb. 1963 by museum collector; ZMNH, 1 (skin with skull inside). C:C-58.


Xinglung. See Xinglong Xian, southern.

Xining; Guangdong, CHINA; 24°08’N, 115°43’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-95.

Xingyi; Guizhou, CHINA; 25°03’N, 104°59’E; re-
ported before 1998 (Zhang et al., 1997, p. 58). C:C-156.

Xinlong, Wanning Xian, 500–600 m; Hainan Dao; Hainan, CHINA; 18°45’N, 110°12’E; collected 3 July 1960 by Wu Luping (Liu Zhenhe, SCIEA, pers. comm., 26 Nov. 1985); SCIEA, 1. C: C-240.


Xinning, Xinluwan, Xinlong. Xishuangbanna; Xishui; C:C-240. Dao; C:C-156.ported comm..

CHINA; 35°19’N, Nov. before Xu

(= Xinxiang) Xinlong. Xinlong. Xishuangbanna; Xishui; C:C-235.

Xi Xia, Dongfang Xian, Hainan Dao; Hainan, CHINA; ca. 19°00’N, 108°55’E; collected 13 and 14 April 1960 by Quan Guoqiang (pers. comm., 25 Aug. 1983); IZCAS, 3 (including 2 skulls only). C:C-235.

Xiashuangbanna (perfecture); Yunnan, CHINA; 21°–23°N, 99°–102°E; collected in 1960 and 1964 by unknown collectors; KIZ, 2 (skins only). Not mapped (see B:C-80 through B:C-86).

Xishui; Guizhou, CHINA; 28°24’N, 106°15’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-134.


Yadong Xian; Xizang (= Tibet), CHINA; ca. 27°30’N, 89°00’E; reported before 1964 by Shen Xiaozhou (1963, p. 140; Zhang et al., 1989, p. 379; 1991, p. 177; Zhang Yongzu, letter, 3 July 1996). B:C-1.

Yai-cheng. See Nychow.

Yajiang, 10000 ft (= 3050 m); Sichuan, CHINA; 30°02’N, 101°02’E; collected 26 Aug. 1908 by W. R. Zappey (Henshaw, 1912, p. 109; Dolan, 1939, p. 177); MCZ, 1. B; C-29.

Yangcheng; Shaxi, CHINA; 35°32’N, 112°36’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-5.

Yangliupu (= Yangliu), Xuancheng Xian, 200–400 m; Anhui, CHINA; ca. 29°07’N, 98°33’E; reported 1914–1916 by H. Weigold (1924, p. 71). B:C-35.

Yangshan; Guangdong, CHINA; 24°29’N, 112°38’E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-202.

Yangzte Gorges. See Yichang (= Ichang).

Yanjiang vicinity; Xizang (= Tibet), CHINA; ca. 29°07’N, 98°33’E; reported 1914–1916 by H. Weigold (1924, p. 71). B:C-35.

Yanyuan; Sichuan, CHINA; 27°25’N, 101°33’E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-40.

Yao, Nam. See Mansam Falls.


Yenangyaung. See Irrawaddy River.

Yen Bai, VIETNAM; 21°15’–22°20’N, 103°55’–105°10’E; collected in 1963 by unknown collector; IEBR, 1 (skin only). Not mapped.


Yiajia, Bawangling District, Changjiang Xian, 1000 m; Hainan Dao; Hainan, CHINA; 19°05’N, 109°08’E; collected 24 Oct. 1964 by Liu Zhenhe, SCIEA (pers. comm., 26 Nov. 1985); SCIEA, 1. C:C-234.

Yibin (= Suifu); Sichuan, CHINA; 28°46’N, 104°34’E; collected 10 Oct. 1922 by D. G. Graham; USNM, 1. C:C-137.

Yichang; Hubei, CHINA ca. 30°42’N, 111°18’E; reported before 1989 by Hu Hongxing (Zhang et al., 1989, p. 379; 1991, p. 177; Zhang Yongzu, letter, 3 July 1996). C:C-46.

Yichang (= Ichang), Chang Jiang (= Yangtze) gorges above; Hubei, CHINA; ca. 30°45’N,
111°15'E; reported before 1942 by A. de C. Sowerby (1941, p. 262). C:C-46.
Yicheng: Shanxi, CHINA; 35°42'N, 111°40'E; reported before 1998 (Zhang et al., 1997, p. 58).
C:C-2.
Yigong, Bomi Xian 2250 m; Xizang (= Tibet), CHINA; 30°08'N, 95°02'E; collected 24 June 1973 by Zheng Changlin and Cat Guiqué (pers. comm., 7 Oct. 1985; Feng et al., 1984, p. 344); NWPHB. 1. B:C-11.
Yigong Forest Reserve, Bomi Xian; Xizang (= Tibet), CHINA; 30°08'N, 95°02'E; captures obtained 1979–1982 by Zhang Cizu. Director, Shanghai Zoo (pers. comm. 18 Oct. 1985); captured observed 18 Oct. 1985. B:C-11.
Yiliang; Yunan, CHINA; 27°35'N, 104°01'E; tissue sample obtained ca. 1991 by Zhang Yaping and Shi Liming (1993b, p. 589). C:C-143.
Yin, east bank of lower Chindwin River; Sagaing, MYANMAR (= BURMA); 22°47'N, 94°42'E; collected 9–18 June 1914 by G. C. Shortridge (in Wroughton. 1916a, p. 294); BNHS, 1; BM(nh), 1; BNHS, 1; FMNH, 2; ZSI, 1 (skin only). B:M-24.
Yin, lower Chindwin River; Sagaing, MYANMAR (= BURMA); 22°47'N, 94°42'E; collected 15 and 18 June 1914 by G. C. Shortridge and S. A. Macmillan (Shortridge in Wroughton, 1916a, p. 294); BNHS, 3. B:M-24.
Yingde; Guangdong, CHINA; 24°10'N, 113°24'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-204.
Yingjiang; Yunan, CHINA; 24°48'N, 98°05'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-60.
Yinjiang; Guizhou, CHINA; 28°01'N, 108°24'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-118.
Yixian (= Qianxian); Anhui, CHINA; 29°53'N, 117°57'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-62.
Yongchun; Fujian, CHINA; 25°19'N, 118°17'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-87.
Yongde vicinity; Yunan, CHINA; ca. 24°00'N, 99°15'E; purchased in market Aug. 1964 by Quan Guoqiang (pers. comm., 25 Aug. 1983); IZCAS, 1 (skin only). B:C-66.
Yongshan; Yunnan, CHINA; 28°11'N, 103°35'E; tissue sample obtained ca. 1991 by Zhang Yaping and Shi Liming (1993b, p. 589). C:C-142.
Yongsheng [Xian]; Yunnan, CHINA; ca. 26°42'N, 100°45'E; blood sample obtained before 1999 by Ding Bo, Zhang Yaping, and Hou Yidi (1998, p. 172). B:C-46.
Yongshun; Hunan, CHINA; 29°00'N, 109°54'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-112.
Yongtai Xian; Fujian, CHINA; ca. 25°52'N, 118°55'E; reported Nov. 1983 by Zheng Xueqing (1984, p. 146). C:C-84.
Yongyap Chu (= Yongyap Valley), 9500 ft (= 2900 m); Arunachal Pradesh, INDIA; ca. 29°10'N, 95°37'E; observed May–June 1913 by F. M. Bailey (1914, map; 1915, p. 74). B:1-27.
Yu, Nam. See Ou, Nam.
Yuanmou; Yunan, CHINA; 25°42'N, 101°52'E; reported before 1998 (Zhang et al., 1997, p. 58). B:C-49.
Yuanqu; Shanxi, CHINA; 35°18'N, 111°41'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-14.
Yung-ling. See Xinglong Xian, southern.
Yunlong [Xian]; Yunnan, CHINA; ca. 25°50'N, 99°28'E; blood sample obtained before 1999 by Ding Bo, Zhang Yaping, and Hou Yidi (1998, p. 172). B:C-55.
Yunnan, CHINA; 21°–29°N, 98°–106°E; collected in 1957 by Quan Guoqiang; IZCAS, 1 (skull only). Date and collector unknown; IZCAS, 1 (skull only). Not mapped.
Yunnan, [northwestern]. CHINA; 25°–29°N, 97°–102°E; tissue samples obtained ca. 1991 by
Zhang Yaping and Shi Liming (1993b, p. 589. fig. 1). Not mapped (see B:C-36).

Yunnan border; *Sichuan*, CHINA; ca. 28°20'N, 104°20'E; collected 17 Sept. 1928 by D. G. Graham; USNM, (skull only). C:C-138.

Yunnan border, south of Yibin (= Suifu) 3000 ft (= 910 m); *Sichuan*, CHINA; ca. 28°20'N, 104°20'E; collected 19 Feb. and 25 Mar. 1932 by D. G. Graham; USNM, 2. C:C-138.

Yuqing; *Guizhou*, CHINA; 27°12'N, 107°56'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-120.


Zackala. See Yanjing vicinity.

Zaya Xian; *Xizang* (= Tibet), CHINA; ca. 28°28'N, 97°04'E; collected in 1973 by Feng Zuojian (Feng et al., 1984, p. 344; Quan Guoqiang, letter, 30 Oct. 1995); *IZCAS*, 3 (including 1 skull only). Purchased Aug. 1973 at traditional medicine shop. Qamdo, by Zheng Changlin (pers. comm., 7 Oct. 1985); *NWPIB*, 3 (skulls only). C:C-34.


Zhaojia (Zhaojia), Dongzhi Xian, 200–500 m; *Anhui*, CHINA; ca. 29°39'N, 116°49'E; observed 1973–1986 by Xiong Chenpei (Wada et al., 1986, p. 83). C:C-47.


Zhongzhou; *Guangxi*, CHINA; ca. 22°40'N, 107°05'E; collected 24 Mar. 1982 by Wu Mingchuan (pers. comm., 27 Nov. 1992); FDG, 1 (skull with skull inside). C:C-223.


Zhuaihui Xian. See Dangan Dao.

Zhusuan; *Hubei*, CHINA; 32°13'N, 110°24'E; tissue sample obtained ca. 1991 by Zhang Yaping and Shi Liming (1993b, p. 589). C:C-42.


Zigu; *Hubei*, CHINA; 31°01'N, 110°35'E; reported before 1998 (Zhang et al., 1997, p. 58). C:C-45.

Zixi Xian; *Jiangxi*, CHINA; ca. 27°45'N, 117°00'E; trapped in 1982 for Nanchang Zoo (Huang Zhangsen, pers. comm., 28 Oct. 1985); captives observed 28 Oct. 1985. C:C-78.


Zunyi vicinity; *Guizhou*, CHINA; ca. 27°42'N, 106°55'E; purchased in market Nov. 1960 by Quan Guoqiang (pers. comm., 25 Aug. 1983); *IZCAS*, 1 (skull only). Collected 30 and 31 May 1964 by Fang Lixiang; BMNH, 4 (skulls only). C:C-129.
Specific and subspecific names referable to *Macaca mulatta* are spelled here as they were originally proposed.

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