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TAXONOMY AND EVOLUTION
OF THE *SINICA* GROUP OF MACAQUES:
4. SPECIES ACCOUNT OF *MACACA THIBETANA*

JACK FOODEN

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INTRODUCTION

Macaca thibetana is one of two species of stumptail macaques that are native to China; the other is M. arctoides (= M. speciosa of many authors; Fooden, [1966], p. 153). These two macaques differ strikingly in form and size of the glans penis and baculum, which are about half as long in M. thibetana as in M. arctoides, and presumably also in structure of the female reproductive tract (Fooden, 1967, p. 939; 1971b, p. 72). Vernacular names proposed for these species are "Père David's stumptail macaque" for M. thibetana, in reference to the collector of the type-specimen, and "bear macaque" for M. arctoides (Fooden, 1976, p. 226). Despite conspicuous differences between M. thibetana and M. arctoides, they frequently are confused and often have erroneously been assumed to be conspecific because both species are large, stumptailed, and generally brownish in dorsal pelage color.

Based on reproductive anatomy, *M. thibetana* is assigned to the *sinica* group of macaques (Fooden, 1971b, p. 72), which also includes *M. sinica*, *M. radiata*, and *M. assamensis*. The tail length morphocline and pattern of geographic distribution in this group suggests that *M. thibetana* is the most derived of the four species. Accounts of the other three species in the *sinica* group have been published recently (Fooden, 1979, p. 109; 1981, p. 1; 1982, p. 1). A comprehensive comparative overview of the group is in preparation.

The present account of *M. thibetana* is based on a study of 29 available museum specimens and review of relevant literature. The most important previous works on the taxonomy of this species are those of Milne-Edwards ([1872], p. 244), Matschie (1912, p. 305), Allen (1930, p. 3; 1938, p. 289), Dobroruka (1967, p. 305) and Hill (1974, pp. 760, 763). Specimens examined by me are preserved in the following institutions, whose officials and staffs I thank for their generous cooperation:

| AMNH | American Museum of Natural History, New York (7 specimens) |
|-------------|---|
| FMNH | Field Museum of Natural History, Chicago (4 specimens) |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge (1 specimen) |
| MNHN | Muséum National d'Histoire Naturelle (Mammifères), Paris (5 specimens) |
| USNM | U.S. National Museum of Natural History, Washington, D.C. (11 specimens) |
| ZMB | Zoologisches Museum der Humboldt-Universität, Berlin (1 specimen) |

Only 13 localities are recorded for *M. thibetana*, and little is known of its natural history. Interest in wildlife and conservation, however, is growing in China (Zhang et al., 1981, p. 223), and we may therefore anticipate further research that ultimately will lead to better understanding of this unique, rare, and intriguing element of the Chinese primate fauna.

SPECIES ACCOUNT

Macaca thibetana A. Milne-Edwards, 1870

singe d'assez grande taille: David, 1869, p. 11—announcement of discovery; assigned to genus *Macacus* (= *Macaca*); inhabits cold mountainous region, "principauté thibetaine . . . de Mou-pin."

M[acacus] Thibetanus: A. Milne-Edwards, 1870, p. 341—external characters, taxonomic comparisons; provenance, "Thibet oriental." A. Milne-Edwards, 1892, p. 671—distribution, "la vallée de Moupin."

Macacus thibetanus: Blanchard, 1871, p. 619—external characters and habitat of specimen reported by David (1869, p. 11).

[Macacus (Macacus)] thibetanus: Trouessart, 1878, p. 126—distribution, Mouping.

M[acaca] thibetanum: Pocock, [1926], p. 1571—tentatively allocated to Lyssodes group. Rode, 1938, p. 223—type-specimens catalogued.

Macaca thibetana: Fooden, [1966], p. 160, fig. 3 (bacula)—external characters; bacular anatomy; taxonomic comparisons; zoogeography. Fooden, 1971a, p. 38—taxonomic comparison with M. arctoides. Fooden, 1971b, p. 72, fig. 5 (glans penis)—penial anatomy; external measurements ex Allen, 1938, p. 292; taxonomic comparisons.

Pithecus thibetanum: Elliot, [1913], p. 196, cranial pl. 21 (skull)—external and cranial characters of type-specimen.

Pithecus thibetanus: Howell, 1929, p. 34—external characters of three specimens; locality, Emei Shan: Si Gi Pin.

Lyssodes speciosus thibetanus: Allen, 1938, p. 290—external and cranial characters ex literature; taxonomy; distribution, "western Yunnan northwestward into central Szechwan." Sowerby, 1941, p. 263, fig. opp. (photo of adult and young)—external characters; distribution, "Moupin . . . Mount Omei . . . no specimens . . . from Tibet Proper."

Lyssodes s[peciosa] thibetanus: Tate, 1947, p. 135—distibution, "Tibet and Szechwan."

Macaca speciosa thibetana: Kellogg, 1945, p. 124—distribution ex Allen, 1938, p. 291. Bertrand, 1969, p. 5—taxonomy; distribution, "high mountains of Szechwan."

[Macaca speciosa] thibetanus: Buettner-Janusch, 1963, p. 52—listed.

Macaca (Lyssodes) speciosa thibetana: Dobroruka, 1967, p. 312, fig. 1 (photo of female), fig. 2 (photo of head of male), fig. 5 (map of distribution)—external characters; taxonomic comparisons and history; natural history; distribution, "Von Nan-Ling-Gebirge nach Szetschwan."

Macacus tibetanus: A. Milne-Edwards, [1872], p. 244, pl. 34 (animal, in color), pl. 35 (skull)—unjustified emendation; external and cranial characters of two specimens collected by David (1869, p. 11); natural history; taxonomic comparisons; measurements; provenance, "Tibet oriental . . . principautè de Moupin." David, 1874, p. 9—details of collection of type-specimen. David, 1875, p. 267—first record in Fujian: "Koatén."

[Macacus (Macacus) arctoides] tibetanus: Trouessart, 1897, p. 27—distribution, Mouping. Macacus arctoides tibetanus: Lydekker, [1907], p. 997—zoogeography.

Macaca arctoides: Forbes, 1894, p. 8 (not. I. Geoffroy, 1831, p. 61)—part, included in synonymy.

Macacus (Magus) arctoides esau: Matschie, 1912, pp. 305, 309—holotype, adult male, skin and skull (ZMB 16179), collected alive at "Yao-tze Berge" W of Lo-ch'ang (border area between Guangdong, Hunan, and Guangxi) by R. Mell some time before 9 Feb. 1911, transported to Berlin Zoological Garden, died in captivity 16 March 1912; subspecific name based on proper name applied to captive monkey; external and cranial characters; taxonomic comparisons. Allen, 1930, p. 4—regarded as a synonym of Macacus (Magus) arctoides melli Matschie, 1912. Fooden, [1966], p. 160—regarded as a synonym of Macaca thibetana Milne-Edwards, 1870. Dobroruka, 1967, p. 312—regarded as a synonym of Macaca thibetana Milne-Edwards, 1870.

- Simia arctoides esau: Heck, 1916, p. 547, pl. "Affen III," fig. 9 (captive, photograph; type-specimen according to Dobroruka, 1967, p. 309, footnote 2)—natural history ex Matschie (1912, p. 309). Petzold, 1964, p. 330, fig. 21 (captives, photograph)—tentative identification of zoo specimens.
- Macacus arctoides esau: Mell, 1922, pp. 4, 10, pl. 1, fig. 2 (type-specimen photographed alive), fig. 3 (referred specimen photographed alive)—type history; temperament in captivity.
- Pithecus pullus: Howell, 1928, p. 41—holotype, subadult male, skin and skull (USNM 252157), collected at Kuatun by F. T. Smith (Coll. No. 850), 16 May–24 June 1926; external and cranial characters; taxonomic comparisons. Howell, 1929, p. 34, pl. 5 (skull of type)—pelage comparison with Pithecus thibetanus. Allen, 1930, p. 4—said to be a synonym of Macacus (Magus) arctoides melli Matschie, 1912.
- Lyssodes speciosus melli: Allen, 1930, p. 3 (not Matschie, 1912, p. 308)—misidentification of specimens collected at Chong'an Xian near Kuatun; external characters; taxonomy. Allen, 1938, p. 291 (not Matschie, 1912, p. 308)—external and cranial characters; measurements; taxonomy; natural history; distribution, "northwestern Fukien southward along the coast region of China, . . . Kwangtung and Kwangsi."
- Macaca speciosa melli: Kellogg, 1945, p. 124 (not Matschie, 1912, p. 308)—part, Macacus (Magus) arctoides esau Matschie, 1912, and Pithecus pullus Howell, 1928, included in synonymy; distribution ex Allen, 1938, p. 292.
- Macaca (Lyssodes) speciosa melli: Dobroruka, 1967, p. 312 (not Matschie, 1912, p. 308)—part, Pithecus pullus Howell, 1928, included in synonymy and distribution.
- Macaca arctoides melli: Hill, 1974, p. 760 (not Matschie, 1912, p. 308)—external and cranial characters; measurements, most ex Allen, 1938, p. 292.
- Macaca [(Lyssodes)] speciosa: Fiedler, 1956, p. 179 (not F. Cuvier, 1825, p. 2, or I. Geoffroy, 1826, p. 589)—part, Macacus thibetanus Milne-Edwards, 1870, included in synonymy.
- Macaca speciosa speciosa: Pocock, 1939, p. 71 (not F. Cuvier, 1825, p. 2, or I. Geoffroy, 1826, p. 589)—part, [Macacus (Magus) arctoides] esau Matschie, 1912, and Pithecus pullus Howell, 1928, included in synonymy.
- M[acaca] speciosa: Zhang et al. 1981, pp. 215, 221 (not 1. Geoffroy, 1826, p. 589)—part, included in distribution. Mao Jiangsen et al., 1981, p. 1590—specimens used in hepatitis research, collected in Zhejiang Province.

TYPES

The type-series available to Milne-Edwards (1870, p 341; [1872], p. 244) evidently consisted of two mounted skins with skulls: an adult male (MNHN 329/282A, 1870 No. 1, Type Cat. No. 60a), collected by A. David (1874, p. 9), 11 March 1869 (fig. 1); and an adult female (MNHN 330/282B, 1870 No. 527, Type Cat. No. 60b, Coll. No. 109), acquired from a local hunter by A. David (1874, p. 19), 31 March 1869. Both skins are preserved, but the skulls are missing, as previously noted by Rode (1938, p. 223). The male skull is last known to have been examined by Elliot ([1913], p. 197).

Rode (1938, p. 223) designated the male specimen as lectotype ("Holotype") and the female specimen as paralectotype ("Allotype"). The lectotype skin and skull were figured by Milne-Edwards ([1872], pls. 34, 35), who also published measurements of the skulls and dry skins.

Type-Locality

The lectotype of *M. thibetana* was collected ca. 20 km NNW of Baoxing (= Moupin or Mu-ping), central Sichuan Province, China (David, 1874, p. 9). In the original description (Milne-Edwards, 1870, p. 341), the geographic origin is imprecisely given as "Thibet oriental." The paralectotype (female) also was collected in the vicinity of Baoxing, where David (1874, p. 19) received it from a local hunter.

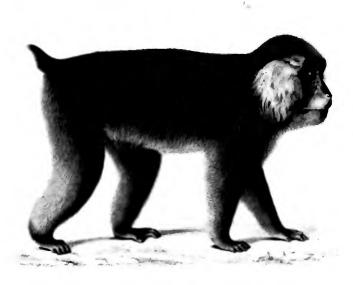


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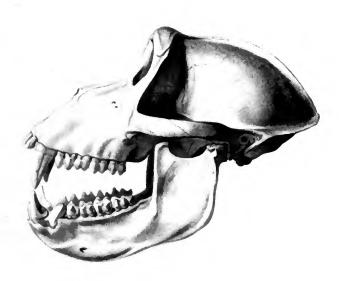


Fig. 1. Macaca thibetana, lectotype skin and skull (A. Milne-Edwards, [1872], pls. 34–35; skull ca. 0.45 natural size), adult male collected by A. David, ca. 20 km NNW of Baoxing (= Moupin), central Sichuan, China, 11 March 1869.

Distribution (Fig. 2)

East-central China, ca. 25°00′N–33°00′N, 102°30′E–119°30′E. The 13 known locality records are restricted to upland areas in central Sichuan, southern Shaanxi, western Hubei, northwestern Guangdong, eastern Jiangxi, northern and eastern Fujian, and southwestern Zhejiang. The known altitudinal range is from ca. 1,000 m (Fuqing Xian; Hsiao Yang Chi; "Yao-tze Berge") to ca. 2,500 m (Baoxing, NNW; David, 1871, p. 84, 1874, p. 9).

Contrary to the implication of the specific name, *M. thibetana* does not occur within the currently recognized boundaries of the Tibetan Autonomous Republic (now officially known as Xizang), as previously noted by Sowerby (1941, p. 263). The type-locality of this species is 350 km east of the present border of Tibet (Xizang), but this place was close to the Tibetan border as understood by David (1874, p. 4) when he collected the type specimens.

External Measurements (Table 1)

Although it is clear from the evidence of dry skins that *M. thibetana* is a large macaque, probably the largest species in the genus, and that tail length is about 10 percent of head and body length, actual flesh measurements recorded by collectors are available for only 10 specimens, and of these only six are adults; at least one set of adult measurements probably is invalid (Table 1). Recorded

TABLE 1. External measurements recorded by collectors for 10 specimens of Macaca thibetana.

| Locality No.1 | Province | Head and body length (mm) | Tail length (mm) | Relative tail length (T/HB) |
|------------------|----------|---------------------------------|------------------------|-----------------------------------|
| | | Adult males ² | | |
| 1 | Sichuan | 710 | 65 | 0.09 |
| 5 | Sichuan | [?]950 | [?]90 | [?]0.09 |
| 10 ³ | Fujian | ca. 700 | ca. 50 | ca. 0.07 |
| 11 | Fujian | 613 ⁴ | 55 | 0.09 |
| | | Adult females | 5 | |
| 1 | Sichuan | 630 | 80 | 0.13 |
| 11 | Fujian | 507 ⁶ | 56 | 0.11 |
| | | Subadult male | 2 | |
| 10 | Fujian | 607 | 67 | 0.11 |
| | | Subadult femal | es | |
| 1 | Sichuan | 650 | 60 | 0.09 |
| 5 | Sichuan | 600 | 55 | 0.09 |
| | | Juvenile male | | |
| 5 | Sichuan | 584 | 75 | 0.13 |

For key to locality numbers, see distribution map (fig. 2).

²Cf. dry skin measurements recorded by Milne-Edwards ([1872], p. 244) for lectotype male, Sichuan: Loc. No. 4, HB 800 mm, T 100 mm, T/HB 0.13.

³Measurements from Sowerby, 1941, p. 263.

⁴Ear length 46 mm.

⁵Cf. dry skin measurements recorded by Milne-Edwards ([1872], p. 245) for paralectotype female, Sichuan: Loc. No. **3**, HB 540 mm, T 60 mm, T/HB 0.11.

⁶Ear length 42 mm.

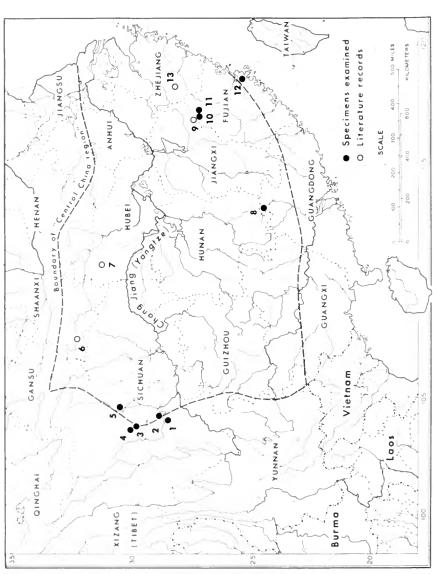


Fig. 2. Macaca thibetana, distribution of known locality bers-SICHUAN: 1, Hsiao GUANGDONG: 8, "Yao-tze 12, Fuqing Xian. 13, Suichang spondence with boundary of Key to locality num-Yang Chi. 2, Si Gi Pin; Emei Shan. 3, Baoxing vicinity. 4, Baoxing, ca. 20 km NNW. 5, Yin Shiu Wan. SHAANXI: 6, Shaanxi, southern. HUBEI: 7, Berge." JIANGXI: 9, Kuatun, Kuatun. 11, Chong'an Xian. Xian. (For details, see Gazetrecords; note general correzoogeographic area designated as "Central China region" (Zhang et al., 1981, p. Shennongjia Mountains. ca. 20 km NW]. FUJIAN: 10, 217).

head and body lengths are 507 mm and 630 mm in two adult females (650 mm reported in one subadult) and 613 mm, ca. 700 mm, and 710 mm in three adult males. Relative tail lengths (T/HB) are 0.11 and 0.13 in the adult females and ca. 0.07, 0.09, and 0.09 in the adult males. Ear length is 42 mm in one adult female (E/HB \times 100 = 8.3) and 46 mm in one adult male (E/HB \times 100 = 7.5). Body weight information has not been recorded for museum specimens examined, but Hu Xiaosu et al. (1982, p. 200) report that two large laboratory specimens (presumably adult males) obtained in Sichuan weighed 15 kg and 17.5 kg.

Pelage (Figs. 1, 3)

Dorsal surface of trunk dark brown, frequently with a diffuse blackish wash caudally, hairs dense and long in prime pelage (5–10 cm long on scapular region in adult males), hair banding indistinct or absent; dorsal surface of limbs colored like back proximally, becoming paler distally, to pale brown on dorsum of hands and feet; crown brown, paler than back, with hairs radiating to form a small whorl (5 cm diameter) centered at vertex; skin of muzzle region pale brownish; circumorbital skin color possibly sexually dimorphic, whitish in immatures and adult males, pinkish in adult females (judging from color slides of Emei Shan troop members kindly provided by Dr. J. D. Lazell, Jr., The Conservation Agency, 22 Dec. 1982); side-whiskers buffy, prominent (hairs 3–6 cm long), concealing ears in anterior view; beard usually prominent, buffy to brown; hairs on ventral surface of trunk and limbs pale buffy to pale gray, contrastingly paler and less dense than on back.

Geographic variation of pelage color is negligible in specimens of *M. thibetana* examined; adult specimens collected in Sichuan Province closely match those collected in Fujian Province, 1,500 km to the east. Adult males and females generally are similar in color, but the side-whiskers and beard are more prominent in males. In one adult female (FMNH 39500, Hsiao Yang Chi), the ventral surface of the tail is marked by a small bright patch of chestnut-colored fur. An





FIG. 3. Pelage variation in *Macaca thibetana*, adult males (left—photographed by G. Fournier at Emei Shan, August 1982, transmitted by Dr. J. D. Lazell, Jr., The Conservation Agency; right—reproduced from Heck, 1916, pl. Affen III, fig. 9).

albino captive specimen of this species reportedly was kept in a village in Guangdong Province, close to a natural habitat (Mell, 1922, p. 10).

Pelage color apparently darkens with age in *M. thibetana*. The smallest specimen examined (AMNH 84475 &, Chong'an Xian, skin only), an infant probably only a few months old, is pale grayish brown on crown and back, buffy on the sides and virtually hairless on the ventral surface. A larger infant (AMNH 60161 \$\frac{2}{3}\$, same locality, M1 visible in alveoli), probably about one year old, is buffy brown on crown and back, paler on the sides and pale buffy on the ventral surface. A young juvenile (USNM 259030 &, Si Gi Pin, M1 erupting), probably about 18 months old, is golden brown (near reddish brown) on crown and back. Two older juveniles (USNM 241161 &, Si Gi Pin, I2 and M2 erupting; USNM 258687 &, Yin Shiu Wan, skin only), probably both about three years old, are respectively pale medium brown and dark medium brown on crown and back. Older juveniles and subadults are only slightly paler than adults.

Seasonal molting in *M. thibetana* in late summer is suggested by pelage condition in a series of four specimens collected in August (1925, 1929) at Si Gi Pin, central Sichuan, as previously noted by Hill (1974, p. 765). In an adult female (USNM 241162) collected 16 August 1925 and a subadult male (USNM 254800) collected 6 August 1929, most of the dorsal hairs are only 2–3 cm long, but a scattering of longer hairs (6–7 cm long) also is present. It appears that the longer hairs in these specimens were in the process of being shed, thus revealing the short (? new) fur. In a juvenile male (USNM 241161) collected 6 August 1925, only short (? new) dorsal hairs are present. An adult male (USNM 241163) collected 17 August 1925 is in prime pelage.

As previously indicated, *M. thibetana* frequently is confused with *M. arctoides* because of the similar brown color, large size, and stump tail of these two species. Living specimens of these species may be distinguished by conspicuous genital characters (see Introduction). Dry museum specimens may be distinguished by pelage characters, particularly around the face and on the ventral surface. In *M. thibetana*, the forehead (to the brow ridges) and cheeks are thickly covered with dense fur and the buffy side-whiskers are prominent; in *M. arctoides*, the forehead and cheeks are only thinly covered by very short hairs (superficially, forehead and cheeks appear bald) and hairs of the side-whisker region are indistinguishable in color and length from those of adjacent regions on the head. Fur on the ventral surface in *M. thibetana* is pale buffy to pale gray, distinctly paler than that on the back; fur on the ventral surface in *M. arctoides* is dark brown, similar in color to that on the back. Texture of the dorsal pelage also seems to differ in these two species; dorsal hairs appear coarser in *M. thibetana* (woolly) than in *M. arctoides* (silky).

CRANIAL CHARACTERS (Fig. 4; Table 2)

Skull large, greatest length 130.9 ± 7.6 mm in five adult females, 157.1 ± 5.4 mm in nine adult males (cf. Albrecht, 1978, p. 129); relative zygomatic breadth (ZB/GL) $0.67 \pm .01$ and $0.67 \pm .02$ in the same males and females; rostral-postrostral ratio $0.52 \pm .01$ in three adult females, $0.58 \pm .03$ in seven adult males; supramaxillary ridges weakly developed in adult males; supraorbital ridges thick in adult males (10–13 mm); sagittal crest and nuchal crest prominent (6–8 mm) in old adult males.

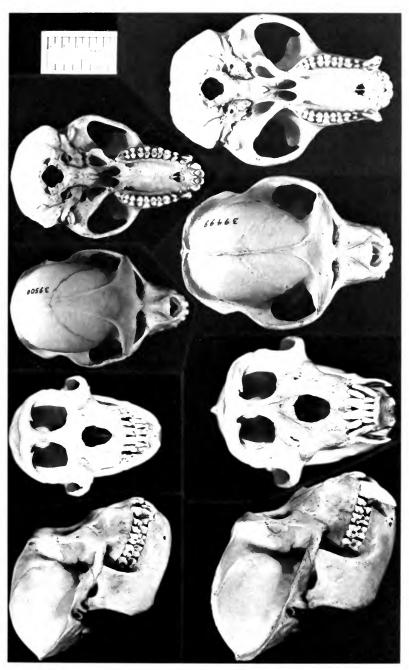


Fig. 4. Cranial morphology in Macaca thibetana, adult female (above, FMNH 39500) and adult male (below, FMNH 39499), both collected at Hsiao Yang Chi, Loc. No. 1. (Photos by Ron Testa, Division of Photography, Field Museum of Natural History.)

TABLE 2. Cranial measurements¹ and ratios in 25 specimens of Macaca thibetana².

| Locality No.3 | Province | Skull, greatest length (mm) | Relative zygomatic breadth (ZB/GL) | Postrostral length (mm) | Rostral- postrostral ratio | | |
|--|-----------------------------|--------------------------------------|---|-------------------------------|----------------------------------|--|--|
| Adult males ⁴ | | | | | | | |
| 1 | Sichuan | 161.3 | 0.68 | 109.5 | 0.58 | | |
| 2 | Sichuan | 161.7 | 0.68 | 107.4 | 0.61 | | |
| 45 | Sichuan | 164.0 | 0.65 | | | | |
| 5 | Sichuan | 151.7,158.5 | 0.68,0.67 | 102.1,105.9 | 0.59,0.59 | | |
| -6 | ?Sichuan | 157.8 | 0.65 | 107.0 | 0.61 | | |
| 8 | Guangdong | | 0.65 | | | | |
| 11 | Fujian | 159.1 | 0.65 | 110.1 | 0.55 | | |
| 12 | Fujian | 147.7 | 0.69 | 103.7 | 0.53 | | |
| | $\bar{x} \pm S.D.(n)$ | $157.1 \pm 5.4(9)^7$ | $0.67 \pm .02(9)$ | $106.5 \pm 2.7(7)$ | $0.58 \pm .03(7)$ | | |
| Adult females | | | | | | | |
| 1 | Sichuan | 136.4 | 0.68 | 97.3 | 0.53 | | |
| 2 | Sichuan | 127.6 | 0.66 | 91.3 | 0.51 | | |
| 3 ⁵ | Sichuan | 140.0 | 0.67 | | | | |
| 11 | Fujian | 120.7 | 0.68 | | | | |
| _8 | ?Fujian | 129.9 | 0.65 | 92.8 | 0.52 | | |
| | $\bar{x} \pm S.D.(n)$ | $130.9 \pm 7.6(5)^{9}$ | $0.67 \pm .01(5)$ | $93.8 \pm 3.1(3)$ | $0.52 \pm .01(3)$ | | |
| | | S | ubadult males | | | | |
| 2 | Sichuan | 142.1 | 0.61 | 95.9 | 0.58 | | |
| 10 | Fujian | 140.3 | 0.64 | 98.8 | 0.51 | | |
| 11 ¹⁰ | Fujian | 143.9 | 0.69 | 98.1 | 0.58 | | |
| | $\bar{x} \pm \hat{S}.D.(n)$ | $142.1 \pm 1.8(3)$ | $0.65 \pm .04(3)$ | $97.6 \pm 1.5(3)$ | $0.56 \pm .04(3)$ | | |
| Subadult females | | | | | | | |
| 1 | Sichuan | 125.1 | 0.68 | 90.3 | 0.50 | | |
| 5 | Sichuan | 127.8 | 0.66 | 93.7 | 0.48 | | |
| _ | $\hat{x} \pm S.D.(n)$ | $126.4 \pm 1.9(2)$ | $0.67 \pm .01(2)$ | $92.0 \pm 2.4(2)$ | $0.49 \pm .01(2)$ | | |
| Juveniles: 4 males, 1 female (Loc. No. 10) | | | | | | | |
| 2 | Sichuan | 98.2,110.2 | 0.67,0.66 | 80.8,86.5 | 0.32,0.37 | | |
| 5 | Sichuan | 138.2 | 0.65 | 96.9 | 0.53 | | |
| 10 | Fujian | 120.0 | 0.63 | | | | |
| ?1011 | Fujian | 125.8 | 0.67 | 91.2 | 0.5 | | |
| . = - | $\bar{x} \pm S.D.(n)$ | $118.4 \pm 15.2(5)$ | $0.66 \pm .02(5)$ | $88.8 \pm 6.8(4)$ | $0.43 \pm .10(4)$ | | |
| | Infant male | | | | | | |
| 11 | Fujian | 86.0 | 0.68 | 74.1 | 0.28 | | |
| * * | i ujian | 00.0 | 0.00 | /4.1 | 0.20 | | |

¹For detailed explanation of measurements, see Fooden, 1969, p. 41.

²Includes all specimens tabulated by Allen (1938, p. 292), Hill (1974, p. 761) and Albrecht (1978, p. 114).

For key to locality numbers, see distribution map (Fig. 2).

^{&#}x27;Age class criteria: adults—last molars and permanent canines completely erupted; sub-adults—last molars in females or permanent canines in males emergent but not completely erupted; juveniles—one or more permanent teeth erupted, but prior to subadult stage; infants—deciduous teeth only.

Measurements from Milne-Edwards ([1872], p. 247).

^{*}Locality: "Chinese Thibet."

Sichuan specimens, 159.2 \pm 4.3(6); Guangdong and Fujian specimens, 153.0 \pm 5.7(3).

^{*}Locality: "China? No data."

Sichuan specimens, $134.7 \pm 6.4(3)$; Fujian specimens, $125.3 \pm 6.5(2)$.

¹⁰Specimen reported as adult by Albrecht (1978, p. 114); locality listed as "Fu-ching", based on label error.

[&]quot;Locality: "probably Kuatun."

In the western part of the range (Sichuan), skull length in *M. thibetana* may average somewhat greater than in the eastern part (Guangxi, Fujian), judging from the few adult specimens available (Table 2). Dental anomalies occur in two of five skulls (USNM 258649, USNM 258651, both adult males) collected at Yin Shiu Wan, Central Sichuan: both of these specimens lack right and left lower lateral incisors, and one (USNM 258651) also lacks left upper and lower third molars; no trace of alveoli for these teeth is evident.

Ontogenetically, relative zygomatic breadth remains approximately constant from infancy to adulthood, while rostral-postrostral ratio increases allometrically (Table 2; fig. 5). The power function equation for the ontogenetic relationship between rostral length (y) and postrostral length (x) determined by the method of principal axes is:

$$\log y = 3.103 \log x - 4.468.$$

The 95 percent confidence limits for the slope are $L_1 = 2.723$ and $L_2 = 3.591$.

NATURAL HISTORY

Available information concerning the natural history of *M. thibetana* is meager. Brief field notes have been recorded by four collectors (Table 3). Two other observers have published notes that may refer either to *M. thibetana* or to *M. mulatta*, or to both (La Touche in Thomas, [1899], p. 770; Wilson, 1913, vol. 1, p. 198).

The known limits of distribution of *M. thibetana* roughly correspond to the boundaries of the zoogeographic area designated by Zhang et al. (1981, p. 217) as the "Central China region." In this area the temperature remains above 10° C for 225–280 days per year, and the climax vegetation generally is subtropical broadleaf evergreen forest (Zhang et al., 1981, p. 216); *Quercus*, *Castanopsis* and *Pasania* are the dominant forest genera (Wang, 1961, p. 133; Sochava & Lukicheva, 1964, p. 110). Long-continued intensive agriculture has reduced the natural forest to scattered remnants on unarable uplands (Zhang et al., 1981, p. 222).

Most observers agree that *M. thibetana* is restricted to forested areas within its range (David, 1871, p. 88; David, 1875, p. 324; Wilson, 1913, vol. 1, p. 224; Smith in Sowerby, 1929, p. 315; Pope, 1932, p. 495). Only Mell (in Matschie, 1912, p. 309), who observed this species in northwestern Guangdong, reports that it inhabits rocky cliffs, not forests; perhaps the monkeys encountered by Mell were at the edge of a forested area. Within forests, this species has been sighted both in trees and on the ground (David, 1875, p. 256; Smith in Sowerby, 1929, p. 315); available evidence is inadequate to assess the relative degree of arboreality or terrestriality. Footprints in the snow followed by David (1874, p. 9) indicate that one old male walked on the ground for some distance; this individual subsequently hid in a rocky hollow.

The diet of *M. thibetana* has not been recorded, but presumably it consists primarily of fruit supplemented by some animal food, as in other species of macaques. At Emei Shan, central Sichuan, Wilson (1913, vol. 1, p. 224) reports that these monkeys "are fond of the blue pod-like fruit of Decaisnea, the shining black flattened seeds of which, however, I noticed they cannot digest."

Until 50–100 years ago, *M. thibetana* apparently was fairly common within its restricted habitat (David, 1873, collector's note, MNHN 1874/479, Kuatun; Mell in Matschie, 1912, p. 309; Wilson, 1913, vol. 1, p. 224; Smith in Sowerby, 1929, p. 315; Guo Zhusong, 1981, p. 65). David (1871, p. 88) encountered an old hunter

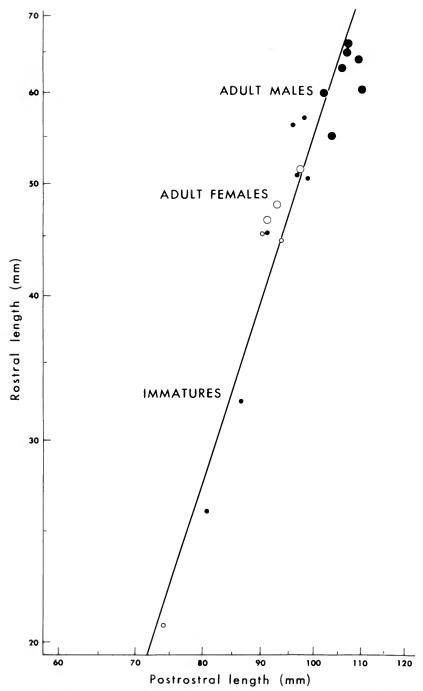


Fig. 5. Allometry of rostral length (y) vs. postrostral length (x) in 20 immature and adult specimens of *Macaca thibetana* (log-log plot; open circles = females, closed circles = males; smaller circles = immatures, larger circles = adults); principal axis, $\log y = 3.103 \log x - 4.468$.

in central Sichuan who claimed to have taken nearly 800 *M. thibetana* individuals during his lifetime. Troop size has been recorded only once (David, 1875, p. 256), in a troop that contained 10 members; among these was one that was reddish, probably a young juvenile (see above, Pelage). Solitary individuals have been reported by David (1874, p. 9) in central Sichuan and by Mell (in Matschie, 1912, p. 309) in northwestern Guangdong. Concerning possible reproductive seasonality, all that is known is that an "infant in arms" (AMNH 84475 &, skin only, Chong'an Xian), probably only a few months old, was collected by C. H. Pope in northwestern Fujian in mid-May 1926.

Three other species of nonhuman primates—Rhinopithecus (or Pygathrix) roxellanae, Macaca arctoides, M. mulatta—occur in or near the range of M. thibetana. R. roxellanae has been collected or observed near M. thibetana, along the northwestern edge of the range of M. thibetana, from central Sichuan (David, 1871, p. 88) to western Hubei (Xiao Zhi, 1979, p. 31); according to David (loc. cit.), R. roxellanae occurs at higher altitudes than M. thibetana. M. arctoides, which generally ranges to the southwest of M. thibetana, has been collected once (ZMB

TABLE 3. Field notes recorded by collectors concerning Macaca thibetana.

- 1(a). A. David (1874, p. 9), 11 March 1869, Loc. No. 4, Baoxing, 20 km NNW (translated from French)—Having walked to the upper end of our valley 5 leagues [20 km] from my living quarters, I discovered in the snow the tracks of a fairly large monkey mixed with the tracks of a leopard. By following the tracks for some time, we were able to locate in a rocky hollow an old monkey with long fur and a short tail [identified in footnote as "Macacus Tibetanus (A. Edw.)"]; a fortunate shot brought it down dead at our feet. . . This monkey lives in mountains that are quite cold where there is an abundance of large trees, firs and other gigantic conifers, of which a great number of trunks lie piled up and rotting in the mountain streams.
- 1(b). A. David (1875, pp. 255–6), 8 Oct. 1873, Loc. No. 9, Kuatun, ca. 20 km NW (translated from French)—In the morning we travel in a long cool valley that has its bordering slopes well forested; I am all eyes (as far as my illness permits) to perceive some trace of the monkeys that I am told abound in these parts. In fact, we pass some houses where people keep two or three monkeys that were captured in this region. . . . A little farther, I myself see a group of 10 of these brown-haired macaques in the trees and on the rocks; I am very surprised to see among them one individual that is pale reddish and appears to belong to a different species [possibly a juvenile; see above, Pelage]. In fact, the mountain people with me say that there are two or three different species of monkeys here [M. thibetana, M. mulatta].
- 1(c). A. David (1875, p. 324), summary of observations (translated from French)—Macacus tcheliensis [= Macaca mulatta] lives in small numbers in rocky places from the cold mountains near Beijing to Sichuan and Fujian. Macacus tibetanus lives in the center of the [Chinese] empire, from west to east, in forested regions.
- 2. R. Mell (in Matschie, 1912, p. 309), 1908–11, Loc. No. 8, "Yao-tze Berge" (translated from German)—In this mountainous region, 2000 m estimated altitude [subsequently corrected to 800–1,200 m; Mell, 1922, p. 10], this monkey is said to be not uncommon. I have only seen it solitary and, as indeed would be inferred from its short limbs, only on rocky slopes, not in forest. The same sorts of places also are inhabited by the red-faced monkey [= *M. arctoides*].
- 3. F. T. Smith (in Sowerby, 1929, p. 315), 16 May–24 June 1926, Loc. No. 10, Kuatun—... while in spots these monkeys were fairly numerous, they were exceedingly shy and difficult to approach, since they kept well hidden in the thick foliage of the trees, and could only be located by their calls. Another much smaller macaque [*M. mulatta*] was also secured at the same place....
- 4. C. H. Pope (in Allen, 1938, p. 293), July 1925–May 1926, Loc. No. 11, Chong'an Xian—. . . they prefer the more rugged precipitous sections.

15925, Lien Shan [= Lianshan], NW) about 135 km southwest of a *M. thibetana* locality ("Yao-tze Berge"), near the southeastern limit of distribution of *M. thibetana*; the collector (Mell in Matschie, 1912, p. 309) indicates that *M. arctoides* (= *M. arctoides melli* Matschie, 1912) and *M. thibetana* (= *M. arctoides esau* Matschie, 1912) occupy the same kind of habitat in this area.

M. mulatta is broadly sympatric with M. thibetana, but these two species may differ in their ecological preferences. M. mulatta and M. thibetana have been collected or observed within 25 km of each other in central Sichuan, southern Shaanxi, western Hubei, and northwestern Fujian. References to the occurrence of M. mulatta in these areas are: Baoxing vicinity, David, 1871, p. 88; Emei Shan vicinity, USNM 241160 (Gin K'eo Ho), BM 11.9.8.1 (Kia-ting, SW), RMNH (Leiden) 4585/V67–W50 (Wa-shan); southern Shaanxi, David, 1875, p. 42; western Hubei, Xiao Zhi, 1979, p. 31; Kuatun vicinity, David, 1875, pp. 281, 285; Kuatun, BM 97.6.5.2, BM 98.11.1.29, MNHN 336/480, 337/481; Chong'an Xian, AMNH 84474, 84476. At Kuatun, northwestern Fujian, La Touche (in Thomas, [1899], p. 770) reports that M. mulatta is more abundant than M. thibetana (not specifically identified by La Touche), but David's (1875, p. 281) hunters at this place required almost one month longer to obtain M. mulatta than to obtain M. thibetana. Throughout the range of M. thibetana, David (1875, p. 324) asserts that it favors forested areas while M. mulatta favors more open rocky areas.

SPECIMENS EXAMINED

Total, 29.

Skins and skulls, 20—SICHUAN: Loc. Nos. 1, Hsiao Yang Chi (3—FMNH 39499 ad. &, 39500 ad. \$\, 2, 39501 subad. \$\, 2); 2, Si Gi Pin (5—USNM 241161 juv. \$\, 241162 ad. \$\, 2, 241163 ad. \$\, 6, 254800 subad. \$\, 6, 259030 juv. \$\, 6); 5, Yin Shiu Wan (4—USNM 258649 ad. \$\, 6, 258650 subad. \$\, 9, 258651 ad. \$\, 6, 258686 juv. \$\, 6). GUANGDONG: Loc. No. 8, "Yao-tze Berge" (1—ZMB 16179 ad. \$\, 6). FUJIAN: Loc. Nos. 10, Kuatun (2—MNHN 1874/479 juv. \$\, 9, USNM 252157 subad. \$\, 6); 11, Chong'an Xian (4—AMNH 60161 inf. \$\, 9, 84472 ad. \$\, 6, FMNH 39383 subad. \$\, 6, MCZ 26477 ad. \$\, 9); 12, Fuqing Xian (1—AMNH 60160 ad. \$\, 6).

Skins only, 6—SICHUAN: Loc. Nos. **3**, Baoxing, vic. (1—MNHN 1870/527 ad. ♀); **4**, Baoxing, ca. 20 km NNW (1—MNHN 1870/1 ad. ♂); **5**, Yin Shiu Wan (1—USNM 258687 juv. ♂). FUJIAN: Loc. Nos. **10**, Kuatun (2—MNHN 1874/477 ad. ♂, 1874/478 juv. ♀); **11**, Chong'an Xian (1—AMNH 84475 inf. ♂).

Skulls only, 3—"China? No data" (1—AMNH 83994 ad. $\mathfrak P$); "Chinese Thibet" (1—AMNH 129 ad. $\mathfrak P$), "probably Kuatun" (1—AMNH 60162 juv. $\mathfrak P$).

For further details, see Gazetteer.

GAZETTEER

Locality names listed in this gazetteer preferentially are Pinyin names approved by the U.S. Board on Geographic Names (USBGN) in Gazetteer of the People's Republic of China (1979). Primary entries for macaque localities that are not included in the USBGN gazetteer are spelled here as in the original source. Secondary entries, with cross references to corresponding primary entries, give variant spellings or alternate locality names that appear on specimen tags or in published literature on *M. thibetana*.

The sequence of information presented in each primary entry is as follows:

- 1. locality name
- 2. altitude, if reported by collector or observer
- 3. name of province (capitalized)
- 4. coordinates of locality

- 5. name of collector or observer followed by parenthetical reference to published locality notes, if any
- 6. date of collection or observation
- abbreviated name of museum where specimens are kept and number of specimens available (with indication of part preserved, if skin and skull are not both present) or bibliographic reference to literature record
- 8. italicized locality number as shown in distribution map (fig. 2).

Baoxing, ca. 20 km NNW; SICHUAN; ca. 30°35'N, 102°35'E; collected by A. David (1874, p. 9), 11 Mar. 1869 (MNHN, 1 [skin only]). 4

Baoxing, vicinity; SICHUAN; ca. 30°23′N, 102°50′E; obtained from local hunter by A. David (1874, p. 19), 31 Mar. 1869 (MNHN, 1 [skin only]). 3

Chensi. See Shaanxi.

"China? No data"; [probably FUJIAN]; collected by R. C. Andrews' Third Asiatic Exp., date unknown (AMNH, 1 [skull only]). Not mapped.

"Chinese Thibet"; [possibly SICHUAN]; Verreaux Coll., 1844 (AMNH, 1 [skull only]). Not mapped.

Chong'an Xian [county]; FUJIAN; ca. 27°51′N, 117°49′E (Pope, 1929, p. 345; 1932, pp. 491, 495; 1935, p. 499); collected by C. H. Pope (citations above, and 1940, p. 72), 7 July 1925, 13–16 May 1926 (AMNH, 3 [1 skin only]; FMNH, 1; MCZ, 1). 11

Chungan Hsien. See Chong'an Xian.

Daba mountain range. See Shennongjia Mountains.

Emei Shan, ca. 1,900 m; SICHUAN; ca. 29°32'N, 103°21'E; sight record, E. H. Wilson (1913, vol. 1, p. 224, vol. 2, p. 192), Oct. 1903 (also see Heim, 1932, p. 2); photograph published (Guo Zhusong, 1981, p. 62), date unknown; observed by J. D. Lazell, Jr. (letter 22 Dec. 1982), August 1982. 2

Fokien occidental. See Kuatun.

Fu-ch'ing Hsien. See Fuqing Xian.

Fukien. See Fuqing Xian.

Fuqing Xian [county]; FUJIAN; ca. 25°44′N, 119°24′E (Pope, 1935, p. 494); collected by C. H. Pope (1929, p. 345; 1932, p. 493; 1935, p. 11), 6 Oct. 1925 (AMNH, 1). 12

Futsien. See Fuqing Xian.

Futsing Hsien. See Fuqing Xian.

Hokow. See Yalong Jiang.

Hong-chan-tin. See Baoxing, ca. 20 km NNW.

Hsiao Yang Chi; SICHUAN; 29°07'N, 103°18'E (unpublished map, Division of Birds, FMNH); collected by F. T. Smith, 10 June 1932 (FMNH, 3). 1

Hung Shan Ting. See Baoxing, ca. 20 km NNW.

Jalungfluss. See Yalong Jiang.

Jao-tze Bergen. See "Yao-tze Berge."

Ju-juen. See "Yao-tze Berge."

Ju-juen, village near. See Ruyuan.

Kaoten. See Kuatun.

Koaten. See Kuatun.

"Kuangsi" (= GUANGXI); province uncertain; unreliable record based on alleged origin of captive specimen observed in Canton (= Guangzhou) market by R. Mell (1922, p. 10), 1908–21. Not mapped.

Kuangtung, Hunan, Kuangsai: Grenzgebiete zw. See "Yao-tze Berge."

Kuatun; FUJIAN; ca. 27°51′N, 117°48′E (La Touche, 1892, p. 402; Pope, 1929, p. 343, 1935, p. 496); collected by A. David (1875, p. 267), 20 Oct. 1873 (MNHN, 3 [2 skins only]); F. T. Smith (1926, p. 131), [16 May–24 June 1926] (USNM, 1; another specimen retained in Shanghai according to Sowerby, 1929, p. 315). For additional locality notes see La Touche (1899, p. 173; in Thomas, [1899], p. 769 and Pope (1932, p. 490). 10

Kuatun, [ca. 20 km NW]; JIANGXI; ca. 28°00'N, 117°40'E; observed by A. David (1875, p. 256), 8 Oct. 1873. 9

Kuatun, "probably"; FUJIAN; ca. 27°51'N, 117°48'E; collected by C. H. Pope (1932, p. 490), prior to 1 Feb. 1926 (AMNH, 1 [skull only]). Not mapped.

Kuei-yung, S; SICHUAN; ca. 30°30′N, 102°00′E; questionable record (Hill, 1974, p. 766), based on inconclusive field note of E. H. Wilson (1913, vol. 1, p. 198: "The men who were in front of me saw several troupes of monkeys [species unreported] . . . , but I saw no animals."), 1908. Not mapped.

Lien-dsau. See "Yao-tze Berge."

Lihn-dsau. See "Yao-tze Berge."

Log-dsong. See "Yao-tze Berge."

Lo-tschang-ho, W. See "Yao-tze Berge."

Mapienting, [WNW]. See Hsiao Yang Chi.

Mount Emei. See Emei Shan.

Mount Omei. See Emei Shan.

Moupin. See Baoxing.

Muping. See Baoxing.

Nan-Ling-Gebirge. See "Yao-tze Berge."

Omei, Mt. See Si Gi Pin.

Ra-ma-la. See Yalong Jiang.

Ruyuan, village near; GUANGDONG; ca. 24°46'N, 113°16'E; captive observed by R. Mell (1922, p. 10), 1908–21. Not mapped.

San Chiang. See Chong'an Xian.

Shaanxi, southern; SHAANXI; ca. 33°N, 107°E; observed by A. David (1875, p. 42), Oct. 1872–Apr. 1873. 6

Shennongjia Mountains; HUBEI; ca. 31°45'N, 110°45'E; reported by Xiao Zhi (1979, p. 31), date unknown. 7

Shensi, See Shaanxi,

Shin Kai Si. See Si Gi Pin.

Sichuan Province; SICHUAN; ca. 26°-34° N, 98°-110° E; imprecise origin of laboratory specimens, reported by Hu Xiaosu et al., p. 200. Not mapped.

- Si Gi Pin, 6,000 ft [1,800 m]; SICHUAN; ca. 29°30′N, 103°30′E (unpublished map in Smithsonian Institution archives, Accession No. 89413, 1925); collected by D. C. Graham and Yang Fong Tsang, 11–17 Aug. 1925, 6 Aug. 1929, 7 July 1934 (USNM, 5). 2
- Singolo. See Yalong Jiang.
- Suichang Xian [county], "mountainous country"; ZHEJIANG; ca. 28°35'N, 119°15'E; origin of captive laboratory specimens, reported by Mao Jiangsen et al., 1981, p. 1590 (county data in letter 4 June 1982). 13
- Wa Shan, region; SICHUAN; ca. 29°20′N, 103°05′E; tentative report, E. H. Wilson (1913, vol. 2, p. 192), July 1903. Not mapped.
- Wen Chuan, near. See Yin Shiu Wan.
- Yalong Jiang; SICHUAN; ca. 30°N, 101°E; misleading report (Schäfer, 1942, pp. 208, 257; cf. Schäfer, 1933, pp. 192, 280), "Tibetmakaken" (= *M. mulatta*, not *M. thibetana*), collected by E. Schäfer, 31 Oct. 1931 (Academy of Natural Sciences, Philadelphia, 1 [skin], MCZ [skull]). Not mapped.
- "Yao-tze Berge", 800–1,200m; GUANGDONG; ca. 25°15'N, 113°15'E; collected by R. Mell (in Matschie, 1912, p. 309; 1922, pp. 4, 10), 26 Sep. 1908–9 Feb. 1911 (ZMB, 1). 8
- Yin Shin Wan. See Yin Shiu Wan.
- Yin Shiu Wan, ca. 6,000 ft [1,800m]; SICHUAN; ca. 31°05'N, 103°31'E (Helde, 1923, map); collected by D. C. Graham and Yang Fong Tsang, 10 Apr.–4 Nov. 1933 (USNM, 5 [1 skin only]). 5
- Yin Shu Wan. See Yin Shiu Wan.

Zhejiang Province. See Suichang Xian.

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