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Source: Fieldiana Zoology, :1-43.

Published By: Field Museum of Natural History

DOI: [http://dx.doi.org/10.3158/0015-0754\(2006\)107\[1:CROFSM\]2.0.CO;2](http://dx.doi.org/10.3158/0015-0754(2006)107[1:CROFSM]2.0.CO;2)

URL: [http://www.bioone.org/doi/](http://www.bioone.org/doi/full/10.3158/0015-0754%282006%29107%5B1%3ACROFSM%5D2.0.CO%3B2)

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Comparative Review of *Fascicularis*-Group Species of Macaques (Primates: *Macaca*)

Jack Fooden

Abstract

The *fascicularis* group of macaques comprises four species: *Macaca fascicularis*, *M. mulatta*, *M. cyclopis*, and *M. fuscata*. The geographic ranges of *M. fascicularis* and *M. mulatta* are parapatric or marginally sympatric, with the former species widely distributed in insular and peninsular Southeast Asia and the latter species widely distributed in southern Asia; *M. cyclopis* is restricted to Taiwan, and *M. fuscata* is restricted to the Japanese archipelago. The four species in this group are compared with respect to pelage, external measurements and proportions, cranial characters, caudal vertebrae, molecular biology and genetics, natural history, and reproductive anatomy and behavior. In these species, head and body length and skull length generally increase with latitude, and tail length generally decreases with latitude; in shorter-tailed species, the number and length of caudal vertebrae is progressively reduced. Morphology of the glans penis in *fascicularis*-group species is uniquely derived among macaque species; morphology of the female tract in this group is similar to that in *silenus*-group species. Based on morphology and fossil history, a hypothesis is proposed concerning the evolution and dispersal of the *fascicularis* group.

Introduction

The *fascicularis* group of macaques, which is defined by unique morphology of male external genitalia (see below, Species Composition of *Fascicularis* Group), comprises four recognized species and 12 recognized subspecies, as follows:

1. *Macaca fascicularis* (Raffles, 1821 ["1822"]), p. 246; 10 subspecies
 - M. f. fascicularis* (Raffles, 1821 ["1822"]), p. 246
 - M. f. aurea* I. Geoffroy, 1830 ("1834"), pp. 58, 76, pl. 2
 - M. f. philippinensis* I. Geoffroy, 1843 ("1841"), p. 568
 - M. f. umbrosa* Miller, 1902, p. 789

- M. f. fusca* Miller, 1903, p. 476
 - M. f. lasiae* (Lyon, 1916), p. 453
 - M. f. atriceps* Kloss, 1919, p. 347
 - M. f. condorensis* Kloss, 1926, p. 357
 - M. f. tua* Kellogg, 1944, p. 75
 - M. f. karimondjavae* Sody, 1949, p. 132
2. *Macaca mulatta* (Zimmermann, 1780), p. 195; monotypic
 3. *Macaca cyclopis* Swinhoe, 1863 ("1862"), p. 350; monotypic
 4. *Macaca fuscata* (Gray, 1870), p. 32; two subspecies
 - M. f. fuscata* (Gray, 1870), p. 32
 - M. f. yakui* Kuroda, 1940, p. 273

The four recognized species have been systematically reviewed in a series of five previous publications (Fooden, 1991; 1995; 2000; Fooden & Wu, 2001; Fooden & Aimi, 2005). The purpose of the present publication is to compare

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and contrast characters of these species and to formulate hypotheses concerning the group's evolutionary history.

Materials and Methods

This survey of *fascicularis*-group species is based on (1) study of 4540 specimens listed in five previous publications (cited in Introduction), (2) study of additional specimens (caudal vertebrae sets, $n = 31$, Appendix II; female reproductive tracts, $n = 4$, Table 5; male external genitalia, $n = 5$, Table 6; bacula, $n = 12$, Table 7), and (3) review of relevant literature (cited in each section below). Microsoft Excel 2000 was used to prepare graphs and to calculate regression statistics. Reported cranial measurements (Table 2) are defined as follows (cf. Fooden, 1969, p. 40): Greatest length of skull—Most anterior point on rostrum to most posterior point on skull Postrostral length—Most inferior point on either orbital margin to most posterior point on skull Rostral length—Most anterior point on rostrum to most inferior point on either orbital margin Zygomatic breadth—Distance between most lateral points on zygomatic arches

Names of institutions in which cited specimens are preserved are abbreviated as follows:

AMNH	American Museum of Natural History, New York
FMNH	Field Museum of Natural History, Chicago
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels
JMC	Japan Monkey Centre, Inuyama
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MZB	Museum Zoologicum Bogoriense, Bogor, Indonesia
NDHU	National Dong Hwa University, Hualien, Taiwan
NHRM	Naturhistoriska Riksmuseet, Stockholm
NMNS	National Museum of Natural Science, Taichung, Taiwan
PRIKU	Primate Research Institute, Kyoto University, Inuyama, Japan
RMNH	Nationaal Natuurhistorisch Museum, Leiden
USNM	National Museum of Natural His-

tory, Washington, D.C.

ZMB Museum für Naturkunde, Berlin
ZMUZ Zoologisches Museum der Universität Zürich

Species Composition of *Fascicularis* Group

Macaca fascicularis, *M. mulatta*, *M. cyclopis*, and *M. fuscata* are unique among macaques in possessing a glans penis that is bluntly bilobed and relatively long and narrow (Figs. 13, 15; cf. Fooden, 1975, p. 33). Comparison with other cercopithecines (Pocock, 1926 [“1925”], p. 1557; Dixson, 1983, p. 86; 1987, p. 426) indicates that glans morphology in the four named species is more derived than that in *M. sylvanus*, *M. silenus*, *M. nemestrina*, and Sulawesi species but less derived than that in *M. sinica*, *M. radiata*, *M. assamensis*, *M. thibetana*, and *M. arctoides*. Based on shared derived penial morphology, *M. fascicularis*, *M. mulatta*, *M. cyclopis*, and *M. fuscata* have been collectively referred to the *fascicularis* species group (Fooden, 1976, p. 225). Monophyly of the *fascicularis* group is weakly supported by three of eight relevant DNA sequencing studies (Fig. 11).

Based primarily on results of a restriction fragment length polymorphism study published by Morales and Melnick (1998, p. 16), Groves (2001, p. 221) has proposed that the concept of the *fascicularis* group should be radically revised by including *M. arctoides* in the group and by excluding *M. mulatta*, *M. cyclopis*, and *M. fuscata* from it; the excluded species would be allocated to a newly proposed *mulatta* group. However, no recent DNA study—including the study of Tosi et al. (2003, figs. 4–8)—supports monophyly of a clade that exclusively unites *M. fascicularis* and *M. arctoides* (Fig. 11).

Geographic Distribution; Total Population Estimates

The *fascicularis* group of macaques is widely and relatively continuously distributed in southern and eastern Asia, from ca. 10°S to 40°N and from ca. 70°E to 140°E (Fig. 1). Within this broad area, the only major hiatuses in the distribution of the group are in southwestern peninsular India and adjacent Sri Lanka and in

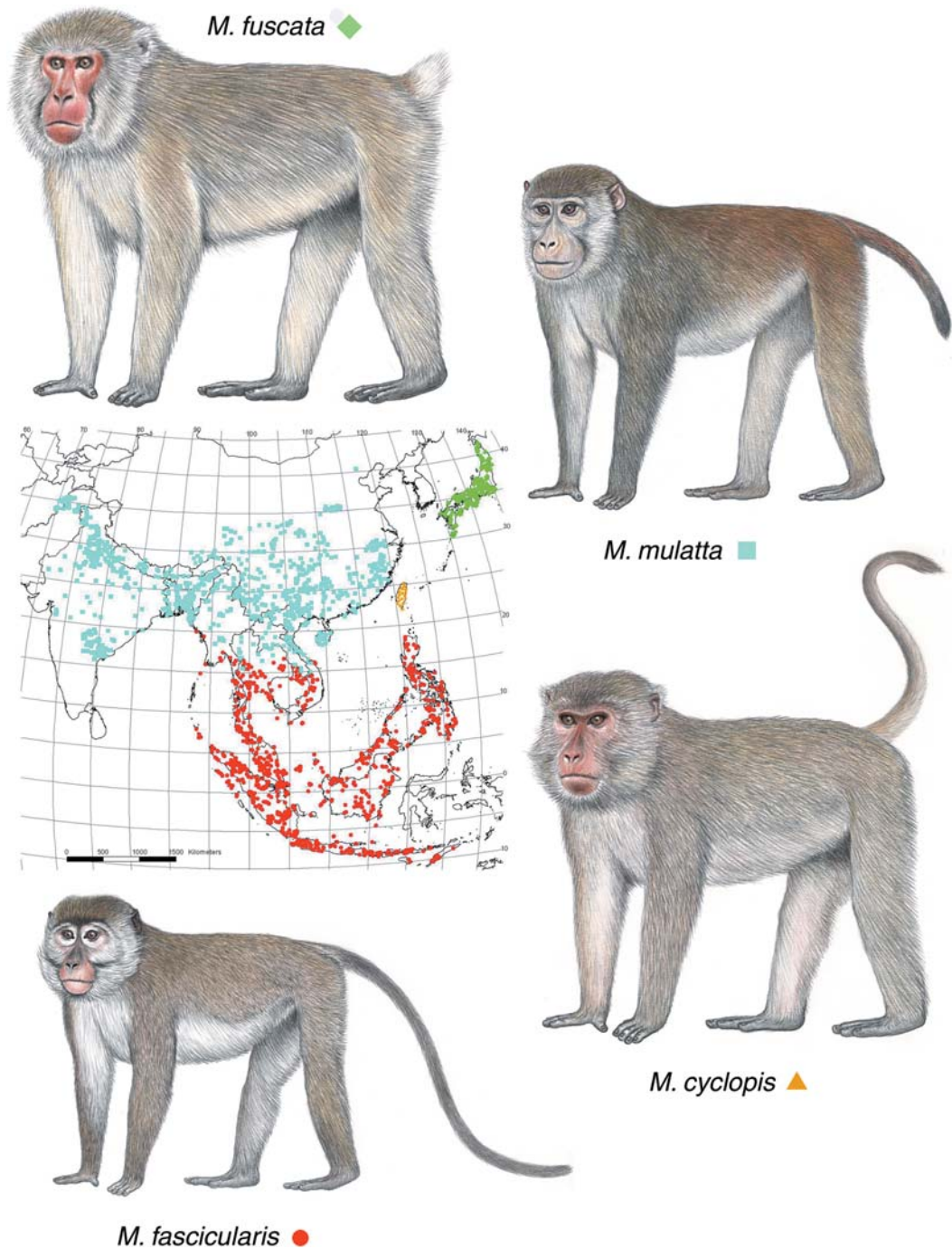


FIG. 1. Geographic distribution of *fascicularis*-group species of *Macaca* and external characters of adult males. Depicted distributions are based on known locality records and include a recently extinct population of *M. mulatta* in northeastern China (Zhang et al., 1989, p. 380) and recently extinct populations of *M. fuscata* on three small Japanese islands (Fooden & Aimi, 2005, p. 3); for an enlarged map of locality records in the *M. fascicularis*/*M. mulatta* contact zone, see Figure 2. (References: *M. fascicularis*—Fooden, 1991, p. 2; 1995, p. 2; 1996, p. 855; 1997, p. 226; Appendix I. *M. mulatta*—Fooden, 1997, p. 226; 2000, p. 2; Appendix I. *M. cyclopis*—Fooden & Wu, 2001, p. 6 [abridged]. *M. fuscata*—Fooden & Aimi, 2005, p. 113.) Illustration by Stephen D. Nash, Conservation International.

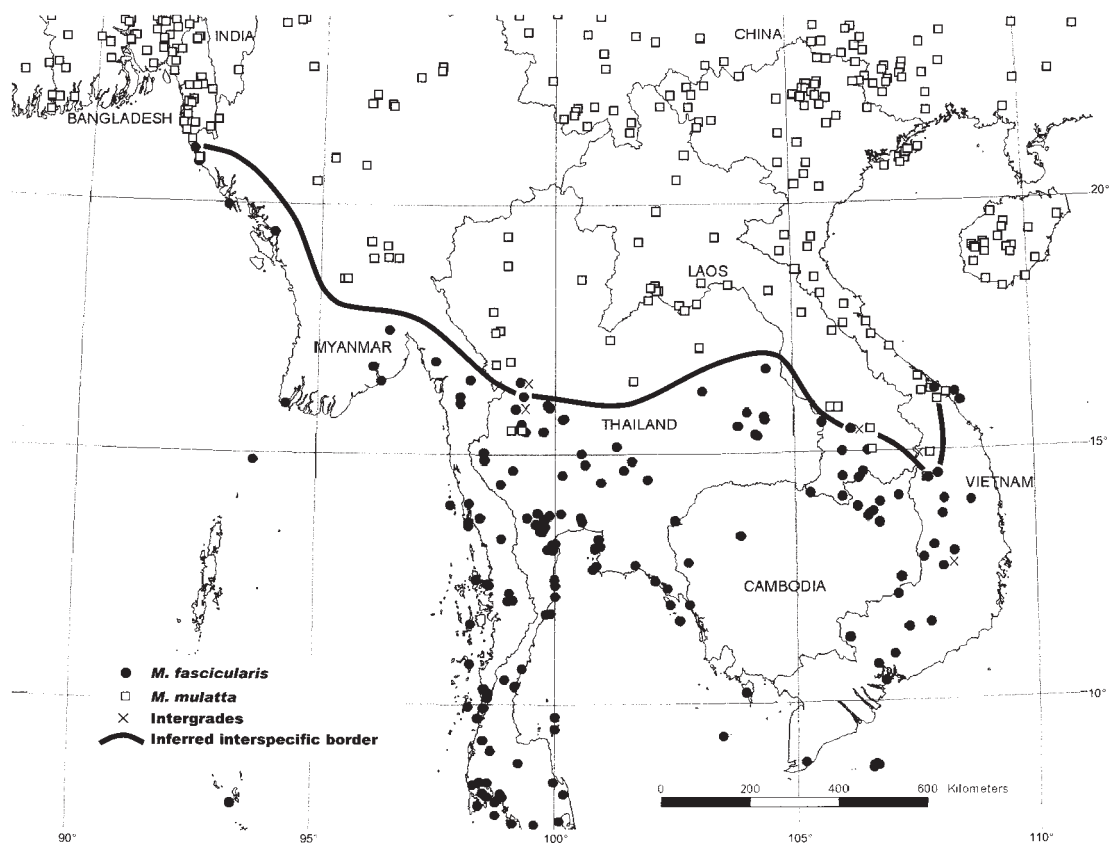


FIG. 2. Locality records of *M. fascicularis* and *M. mulatta* in their interspecific contact zone (for references, see Fig. 1); the interspecific border is interpolated. Intergrade records indicated in this figure are based on specimens in which known relative tail length (tail length/head and body length) varies between 0.70 and 0.80 (see Fooden, 1997, p. 226); specimens in which relative tail length equals or exceeds 0.80 are allocated to *M. fascicularis*, and those in which relative tail length is less than 0.70 are allocated to *M. mulatta*.

four deep-water islands or island groups—namely, Andaman and northern Nicobar Islands (between Myanmar and southern Nicobar Islands), Mentawai Islands (southwest of Sumatra), Sulawesi (east of Borneo), and Ryukyu Islands (between Taiwan and Japanese archipelago). Of these areas that are uninhabited by *fascicularis*-group macaques, southwestern peninsular India and/or Sri Lanka are inhabited by *silenus*-group and *sinica*-group macaques (Fooden, 1975, p. 79; 1988, p. 2), and the Mentawai Islands and Sulawesi are inhabited by *silenus*-group macaques (Fooden, 1969, p. 9; 1975, p. 96); the Andaman and northern Nicobar Islands and the Ryukyu Islands are totally devoid of native nonhuman primates (Kloss, 1903, p. 114; Imaizumi, 1970, p. 281; Fooden, 1975, p. 111; Corbet, 1992, p. 5).

Of the four species in the *fascicularis* group, two—*M. fascicularis* and *M. mulatta*—are

broadly distributed, and two—*M. cyclopis* and *M. fuscata*—are narrowly distributed (Fig. 1). *Macaca fascicularis* inhabits insular and peninsular Southeast Asia, from southeasternmost Bangladesh to the Philippines and Pulau Timor (probably artificially introduced in the Nusa Penida–Timor island chain, east of Bali [Fooden, 1995, p. 96; van den Bergh et al., 2001, p. 397]), and *M. mulatta* inhabits southern Asia, from easternmost Afghanistan to eastern China and northern Vietnam. *Macaca cyclopis* and *M. fuscata* are insular species, the former restricted to Taiwan and the latter restricted to the Japanese archipelago, south of Hokkaido.

On the Indochinese peninsula, the geographic ranges of *M. fascicularis* and *M. mulatta* apparently are parapatric or marginally sympatric (Fig. 2). The inferred interspecific border, which extends ca. 2000 km from southeastern Bangladesh to central Vietnam (ca. 15–20°N),

roughly corresponds to the physiographic transition from southern Indochinese lowlands to northern Indochinese highlands (Fooden, 1997, p. 226). It probably is ecologically significant that the border between long-tailed *M. fascicularis* and short-tailed *M. mulatta* on the Indochinese peninsula is latitudinally similar to the border between long-tailed *M. radiata* and short-tailed *M. mulatta* on the Indian peninsula (Fooden, 1980, p. 6; 1982, p. 576); *M. fascicularis* and *M. radiata* apparently are adapted to a tropical climate, and *M. mulatta* apparently is adapted to a subtropical climate.

Close-lying locality records of *M. fascicularis* and *M. mulatta* indicate that these two species are marginally sympatric in southeastern Bangladesh, west-central Thailand, southern Laos, and central Vietnam (Fig. 2). Specimens with intermediate tail length provide evidence of hybridization along the interspecific border in west-central Thailand, southern Laos, and central Vietnam (Fooden, 1964, p. 363; 1997, p. 227). Possible evidence of hybridization is also indicated by geographic variation in dorsal pelage color, lateral facial crest pattern, head and body length, and skull length (Fooden, 1995, p. 91; 1997, p. 227); all these characters in *M. fascicularis* populations north of the Isthmus of Kra (ca. 10°N) tend to be intermediate between those in *M. fascicularis* populations south of the Isthmus of Kra and those in *M. mulatta*. Y-chromosomal evidence indicates that *M. mulatta* haplotypes have spread into *M. fascicularis* territory at least 400 km south of the interspecific border (ca. 12.5°N) (Tosi et al., 2002, pp. 168, 173).

Judging from limited available information, the total extant populations of the two widely distributed *fascicularis*-group species, *M. fascicularis* and *M. mulatta*, are ca. 3,000,000 and <2,000,000, respectively (Fooden, 1995, p. 54; 2000, p. 7; cf. Zhang et al., 2002, p. 20). As expected, the total extant populations of the two narrowly distributed species apparently are much smaller—ca. 250,000 for *M. cyclopis* and ca. 100,000 for *M. fuscata* (Fooden & Wu, 2001, p. 2; Fooden & Aimi, 2005, p. 5).

Pelage (Fig. 1)

Dorsal pelage color is more variable in *M. fascicularis* than in the other three *fascicularis*-

group species. In *M. fascicularis*, dorsal pelage color varies geographically from buffy to yellowish gray to golden brown to reddish brown to dark brown to blackish (Fooden, 1995, p. 11; Vo, 2003a, p. 10). In *M. mulatta*, dorsal pelage color varies from yellowish gray to golden brown cranially and becomes variably intensely burnt orange caudally (Fooden, 2000, p. 16); in the northern part of the Indochinese peninsula, where the geographic range of *M. fascicularis* is contiguous with that of *M. mulatta* (Fig. 2), dorsal pelage color in the former species tends to approach that in the latter (Fooden, 1995, p. 11; 1997, p. 227). In *M. cyclopis*, dorsal pelage color is yellowish brown to golden brown cranially, becoming slightly brighter caudally (Fooden & Wu, 2001, p. 2). And in *M. fuscata*, dorsal pelage color varies from pale yellowish brown to grayish brown to dark golden brown (Fooden & Aimi, 2005, p. 5). Summer molting has been reported in *M. mulatta*, *M. cyclopis*, and *M. fuscata* but not in *M. fascicularis*. In newborn infants in all four species, dorsal pelage is dark brown to blackish, conspicuously darker than in adults.

The lateral facial crest (side whiskers) in *M. fascicularis* usually sweeps upward from near the angle of the jaw to the lateral margin of the crown (transzygomatic crest), but in some individuals or populations of this species, the crest is restricted to the posterior mandibular region (infrazygomatic crest; Fooden, 1995, pp. 19, 66). In *M. mulatta*, the lateral facial crest usually is infrazygomatic (80.3% of 244 specimens examined; Fooden, 2000, p. 7), and it is infrazygomatic in all *M. cyclopis* and *M. fuscata* specimens examined (Fooden & Wu, 2001, p. 2; Fooden & Aimi, 2005, p. 5). The thinly haired facial skin is brownish to pinkish in *M. fascicularis* (cf. Vo, 2003a, p. 10), pale brown to reddish in *M. mulatta*, and pinkish to reddish in *M. cyclopis* and *M. fuscata*. For a discussion of sexual skin variation in *fascicularis*-group species, see below, Reproduction.

External Measurements and Proportions

In the *fascicularis* group, as in other macaque species groups, body size in adult males generally exceeds that in adult females (Table 1). In available samples, mean head and body length in males exceeds that in females by 13% in *M. fascicularis* and *M. mulatta*, by 14% in *M.*

TABLE 1. External measurements and proportions in *fascicularis*-group species of *Macaca*¹; values in each cell indicate mean \pm SD (where $n > 2$), extremes, and sample size (italicized figures in parentheses).

Species	Head and body length (mm)	Body weight (kg)	Tail length (mm)	Relative tail length (T/HB)
Adult females				
<i>M. fascicularis</i>	412.2 \pm 36.85 315–545 (162)	3.6 \pm 0.68 2.4–5.4 (47)	476.5 \pm 53.55 315–628 (163) ²	1.163 \pm 0.1555 0.704–1.484 (160) ²
<i>M. mulatta</i>	470.6 \pm 48.34 370–580 (74)	5.3 \pm 1.33 3.0–10.0 (36)	204.5 \pm 30.19 125–280 (73)	0.440 \pm 0.0889 0.278–0.608 (73)
<i>M. cyclopis</i> ³	472.0 \pm 40.14 420–600 (22)	7.2 \pm 1.19 5.5–9.5 (15)	383.5 \pm 19.18 350–410 (22)	0.816 \pm 0.0617 0.650–0.942 (22)
<i>M. fuscata</i>	522.8 \pm 30.50 464–601 (53)	8.5 \pm 1.62 4.0–13.8 (150) ⁴	80.8 \pm 13.21 22–106 (72)	0.156 \pm 0.0309 0.044–0.228 (53)
Adult males				
<i>M. fascicularis</i>	465.6 \pm 42.48 370–630 (238)	5.4 \pm 1.44 3.4–12.0 (69)	544.2 \pm 53.28 360–715 (242) ⁵	1.176 \pm 0.1337 0.692–1.495 (232) ⁵
<i>M. mulatta</i>	533.2 \pm 55.36 410–660 (48)	7.7 \pm 2.33 4.0–14.1 (25)	228.9 \pm 35.77 125–310 (49)	0.433 \pm 0.0797 0.200–0.620 (48)
<i>M. cyclopis</i> ³	540.0 \pm 58.09 475–650 (7)	8.4 \pm 0.34 8.1–8.8 (3)	466.4 \pm 31.59 435–530 (7)	0.870 \pm 0.0881 0.692–0.947 (7)
<i>M. fuscata</i>	570.1 \pm 42.30 472–650 (41)	11.2 \pm 2.53 5.6–18.4 (87) ⁴	87.4 \pm 19.69 21–121 (53)	0.151 \pm 0.0399 0.035–0.217 (40)

¹ Cf. Fooden (1995, p. 21; 2000, p. 26), Fooden and Wu (2001, p. 3), and Fooden and Aimi (2005, p. 8).

² Excludes bobtailed specimen collected in West Malaysia: T = 215 mm, T/HB = 0.53 (cf. Fooden, 1995, p. 22).

³ Includes captive specimens.

⁴ Includes mean values published by Hamada et al. (1996, pp. 101, 102).

⁵ Excludes two bobtailed specimens collected in Thailand and Java, respectively: T = 269 mm, 250 mm; T/HB = 0.67, 0.46 (cf. Fooden, 1995, p. 22).

cyclopis, and by 9% in *M. fuscata*. Predictably, the sexual difference in mean body weight (a volumetric measure) is greater than that in mean head and body length (a linear measure); mean body weight in males exceeds that in females by 50% in *M. fascicularis*, by 45% in *M. mulatta*, by 17% in *M. cyclopis*, and by 32% in *M. fuscata* (cf. Thierry et al., 2000, p. 718; Vo, 2003a, p. 9).

Among species in this group, body size is smallest in *M. fascicularis*, intermediate in *M. mulatta* and *M. cyclopis*, and greatest in *M. fuscata* (Table 1). In adult females, mean head and body length varies from 412 mm in *M. fascicularis* to 523 mm in *M. fuscata*, and mean body weight varies from 3.6 kg in *M. fascicularis* to 8.5 kg in *M. fuscata*. In adult males, mean head and body length varies from 466 mm in *M. fascicularis* to 570 mm in *M. fuscata*, and mean body weight varies from 5.4 kg in *M. fascicularis* to 11.2 kg in *M. fuscata*.

Within and between species in the *fascicularis* group, head and body length in females and males tends to increase with latitude, both south and north of the equator (Fig. 3). This pattern of latitudinal variation, which also applies to body

weight (Fig. 4), is in accord with Bergmann's rule (cf. Mayr, 1963, p. 319).

Tail length in *fascicularis*-group species tends to decrease as head and body length increases (Table 1). Mean tail length in adult females varies from 476 mm in *M. fascicularis* to 81 mm in *M. fuscata*, and mean tail length in adult males varies from 544 mm in *M. fascicularis* to 87 mm in *M. fuscata*. Tail length in females and males generally decreases as latitude increases (Fig. 5), in accord with Allen's rule (cf. Mayr, 1963, p. 323); however, data points for *M. cyclopis* tend to lie above the composite interspecific tail length vs. latitude curve, and data points for lower-latitude *M. mulatta* (<25°N) tend to lie below the composite curve.

Relative tail length (T/HB) is an index value that facilitates comparison of tail length in specimens of varying body size (Fooden & Albrecht, 1999, p. 434). Mean relative tail length in adult females varies from 1.16 in *M. fascicularis* to 0.16 in *M. fuscata*, and mean relative tail length in adult males similarly varies from 1.18 in *M. fascicularis* to 0.15 in *M. fuscata* (Table 1). Latitudinal variation in relative tail length is

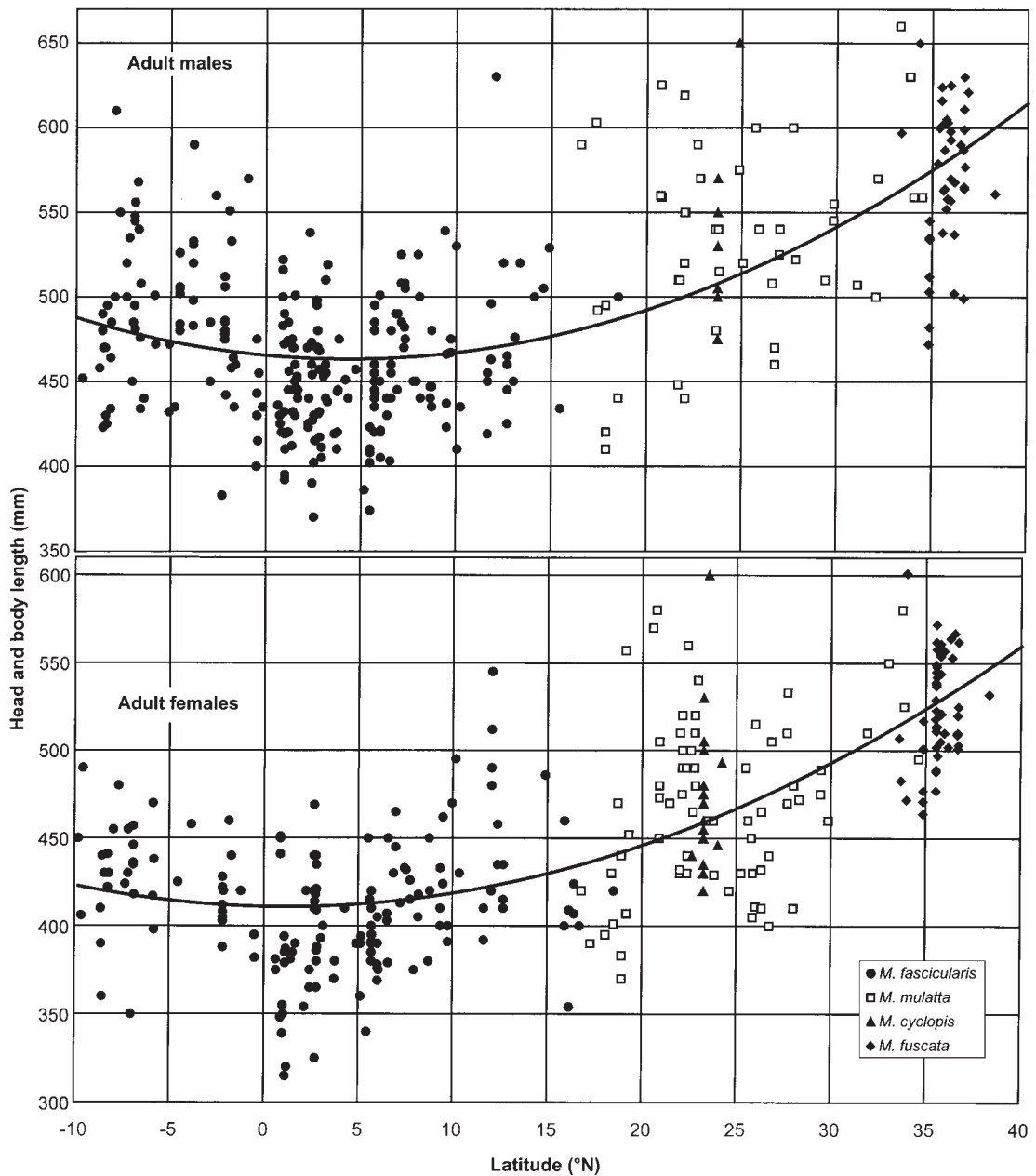


FIG. 3. Latitudinal variation in head and body length in adults of *fascicularis*-group species of *Macaca* (cf. Table 1); specimens are wild-collected, except those of *M. cyclopis*, which include captives. Regression statistics: Females—equation, $y = 0.099x^2 - 0.226x + 411.0$; $r^2 = 0.552$; $n = 311$; $P < 0.01$. Males—equation, $y = 0.119x^2 - 1.044x + 465.4$; $r^2 = 0.451$; $n = 334$; $P < 0.01$.

similar to corresponding variation in tail length (Figs. 5, 6). For details concerning Indochinese specimens in which relative tail length is intermediate between that in *M. fascicularis* and *M. mulatta*, see Fooden (1997, p. 227).

Cranial Characters (Fig. 7)

In available adult samples of both sexes of *fascicularis*-group species, mean greatest length of the skull increases progressively in the series

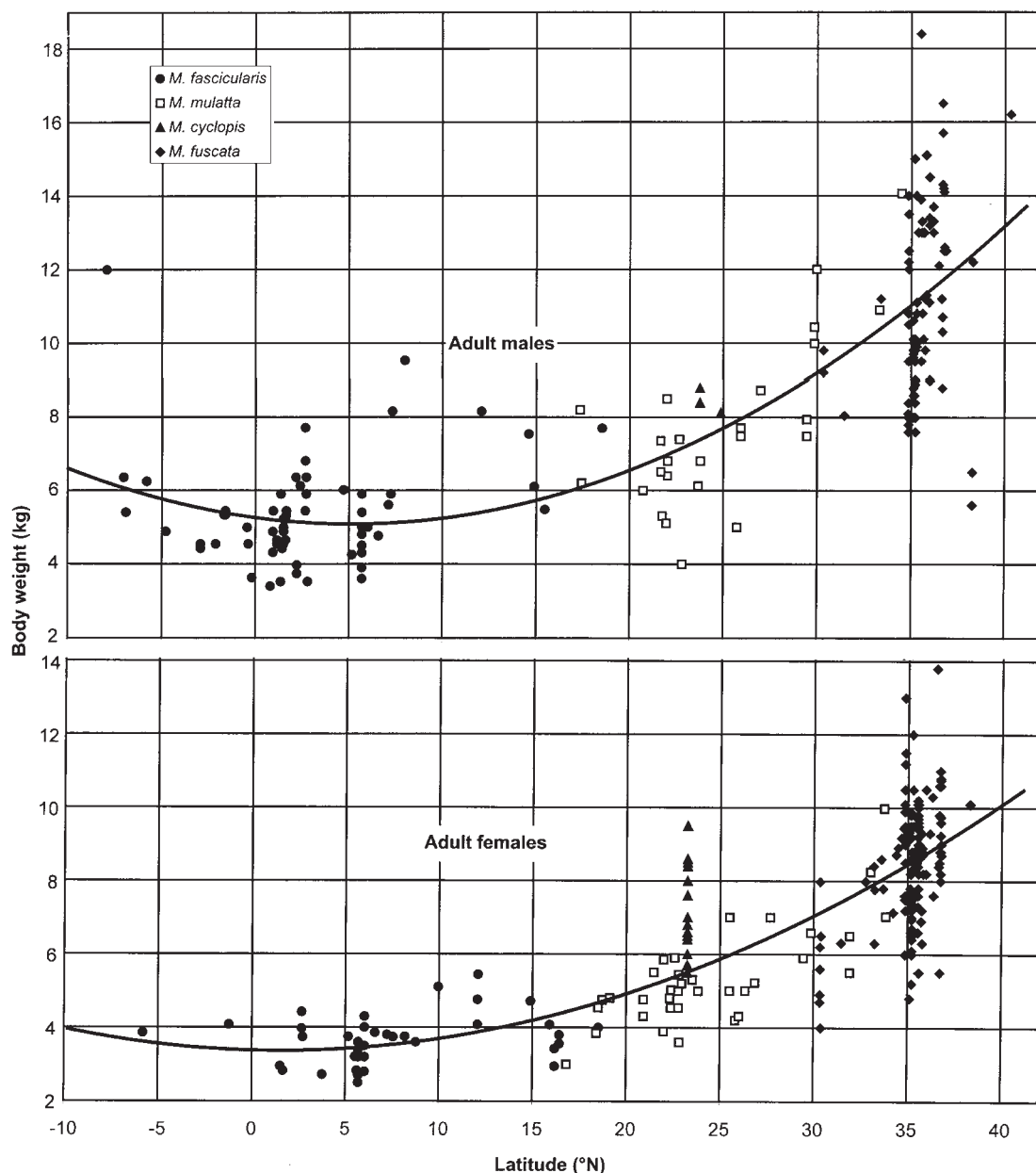


FIG. 4. Latitudinal variation in body weight in adults of *fascicularis*-group species of *Macaca* (cf. Table 1); specimens are wild-collected, except those of *M. cyclopis*, which include captives; values for *M. fuscata* include means published by Hamada et al. (1996, pp. 101–102). Regression statistics: Females—equation, $y = 0.0045x^2 - 0.0137x + 3.3777$; $r^2 = 0.699$; $n = 248$; $P < 0.01$. Males—equation, $y = 0.0067x^2 - 0.0681x + 5.2539$; $r^2 = 0.677$; $n = 184$; $P < 0.01$.

M. fascicularis, *M. mulatta*, *M. cyclopis*, and *M. fuscata* (Table 2), which is the same pattern of interspecific variation that applies to mean head and body length (Table 1). In adult females, mean greatest length of skull varies from

100.5 mm in *M. fascicularis* (cf. Vo, 2003a, p. 10) to 119.4 mm in *M. fuscata*; in adult males, mean greatest length of skull varies from 118.6 mm in *M. fascicularis* to 133.1 mm in *M. fuscata*.

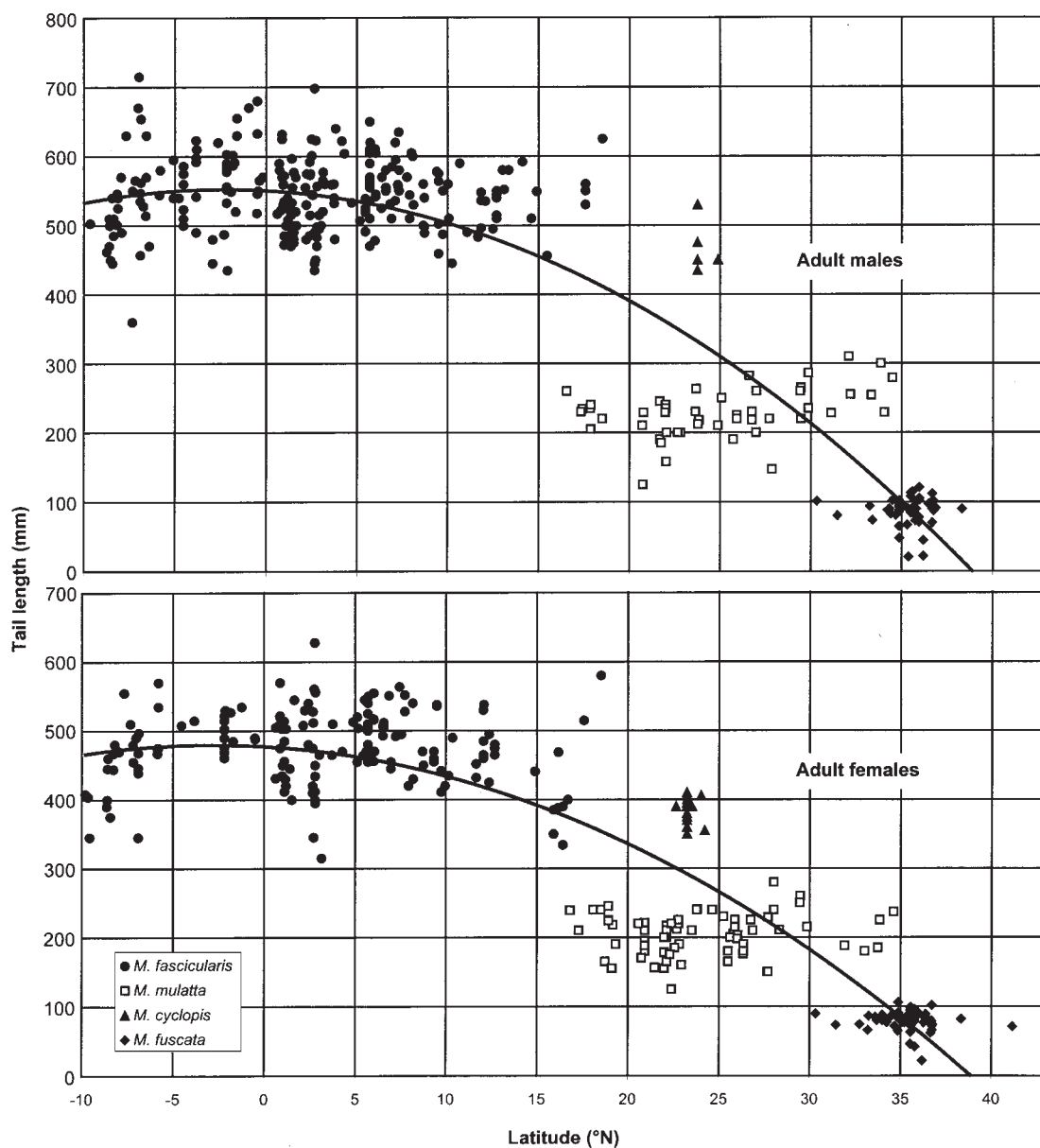


FIG. 5. Latitudinal variation in tail length in adults of *fascicularis*-group species of *Macaca* (cf. Table 1); specimens are wild-collected, except those of *M. cyclopis*, which include captives; values for *M. fuscata* include means published by Hamada et al. (1996, pp. 101–102). Regression statistics: Females—equation, $y = -0.276x^2 - 1.580x + 477.4$; $r^2 = 0.826$; $n = 330$; $P < 0.01$. Males—equation, $y = -0.326x^2 - 1.493x + 550.6$; $r^2 = 0.838$; $n = 351$; $P < 0.01$.

The patterns of variation in postrostral length, rostral length, and zygomatic breadth in *fascicularis*-group species are generally similar to the pattern of variation in greatest length of skull (Table 2), with two exceptions: (1) mean rostral length (and mean rostral–postrostral ratio) is conspicuously large in *M. fascicu-*

laris—equaling or exceeding that in *M. mulatta*—and (2) mean zygomatic breadth (and mean relative zygomatic breadth) is conspicuously large in *M. mulatta*—equaling or exceeding that in *M. cyclopis*.

As suggested by the above interspecific comparison of mean greatest length of skull (Table 2),

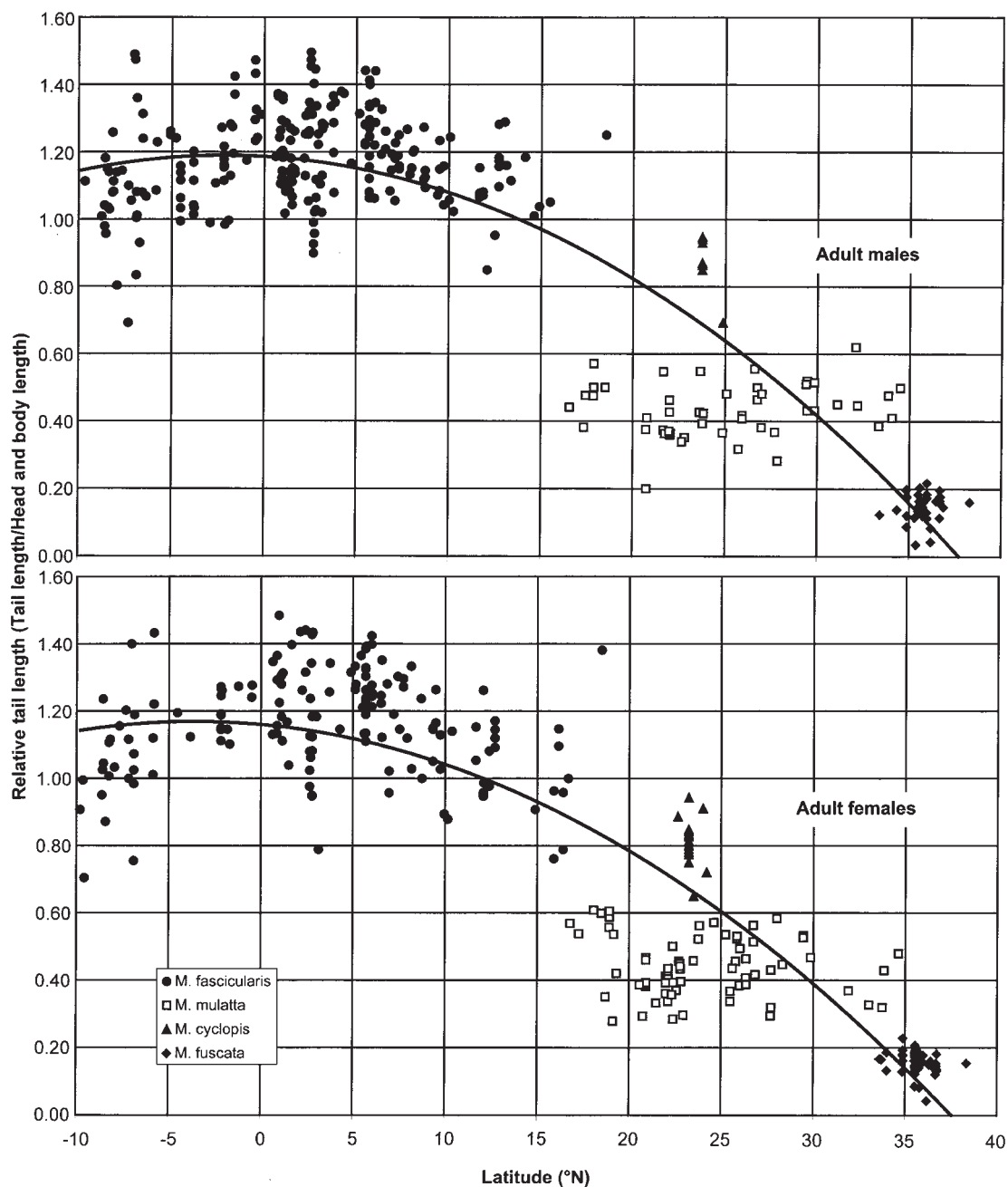


FIG. 6. Latitudinal variation in relative tail length (tail length/head and body length) in adults of *fascicularis*-group species of *Macaca* (cf. Table 1; Fooden, 1997, p. 225; Fooden & Albrecht, 1999, p. 433); specimens are wild-collected, except those of *M. cyclopis*, which include captives. Regression statistics: Females—equation, $y = -0.000691x^2 - 0.004977x + 1.160$; $r^2 = 0.810$; $n = 308$; $P < 0.01$. Males—equation, $y = -0.000748x^2 - 0.003216x + 1.186$; $r^2 = 0.830$; $n = 327$; $P < 0.01$.



FIG. 7. Skulls of *fascicularis*-group macaques, adult males. *M. fascicularis*—AMNH 106566, Indonesia: Sumatra, Bukit Sanggul (photos by James L. Balodimas, Division of Photography, FMNH). *M. mulatta*—FMNH 99669, Thailand: Tak Province, Huai Ap Nang (photos by John Weinstein, Division of Photography, FMNH). *M. cyclopis*—USNM 399111, Taiwan: Taipei Hsien, Hsiao (photos by John Weinstein, Division of Photography, FMNH). *M. fuscata*—PRIKU 5414, Japan: Fukui Prefecture, Naka (photos by Minoru Kinoshita, PRIKU).

greatest length of skull in *fascicularis*-group adults is positively correlated with latitude (Fig. 8) and therefore generally follows Bergmann's rule (cf. Mayr, 1963, p. 319); a similar correlation with latitude also applies to head and body length (Fig. 3). It should be noted, however, that greatest length of skull apparently decreases with latitude in *M. fascicularis* specimens collected on the Indochinese peninsula north of ca. 14°N (Fooden & Albrecht, 1993, p. 526).

Ontogenetically, rostral growth is allometric relative to postrostral growth in *fascicularis*-group species (Fig. 9). In a composite log-log plot of rostral length vs. postrostral length, data points for larger species in this group tend to lie to the right of those for smaller species. This relationship between size and rostral-postrostral allometry is similar to that previously reported among species in the *sinica* group of macaques (Fooden, 1988, p. 14).

A median sagittal crest, which develops as a result of ontogenetic convergence of the temporal lines and which presumably functions to accommodate an expanded origin of the temporalis muscle, is variably present in adult

males (but not in adult females) of *fascicularis*-group species (Fooden, 1995, p. 30; 2000, p. 44; Fooden & Wu, 2001, p. 9; Fooden & Aimi, 2005, p. 21; cf. Mouri, 1982, p. 220; Mouri et al., 2004, p. 26). In adult male specimens examined, the frequency of this crest is greatest in *M. fascicularis* (59.0%, $n = 400$), least in *M. mulatta* (4.2%, $n = 71$), and intermediate in *M. cyclopis* (20.0%, $n = 15$) and *M. fuscata* (14.6%, $n = 158$).

Caudal Vertebrae

As indicated above (Table 1), mean tail length in *fascicularis*-group adults varies from >475 mm in *M. fascicularis* to <90 mm in *M. fuscata*. This tail length variation is correlated with variation in both the number and the length of caudal vertebrae (Appendix II; Fig. 10; Table 3). The mean number of caudal vertebrae in this group declines from 25.5 in *M. fascicularis* to 22.1 in *M. cyclopis* to 17.1 in *M. mulatta* to 9.5 in *M. fuscata*. In *M. fascicularis* adult males, the mean length of successive caudal vertebral

TABLE 2. Cranial measurements¹ and proportions in *fascicularis*-group species of *Macaca*²; values in each cell indicate mean \pm SD (where $n > 2$), extremes, and sample size (italicized figures in parentheses).

Species	Greatest length of skull (mm)	Postrostral length (mm)	Rostral length (mm)	Rostral–postrostral ratio (R/PR \times 100)	Zygomatic breadth (mm)	Relative zygomatic breadth (ZB/GL \times 100)
<i>M. fascicularis</i>	100.5 \pm 5.70 84.0–119.2 (429)	74.0 \pm 3.25 64.3–87.2 (242)	Adult females 35.3 \pm 4.02 24.2–46.5 (246)	47.6 \pm 4.25 36.9–61.0 (242)	66.2 \pm 4.13 56.8–81.1 (433)	65.9 \pm 2.41 59.4–74.1 (429)
<i>M. mulatta</i>	108.0 \pm 7.10 92.9–126.5 (122)	80.7 \pm 4.46 71.3–92.6 (106)	35.5 \pm 4.02 28.1–46.9 (109)	44.0 \pm 3.72 37.6–59.4 (106)	74.4 \pm 5.25 64.0–88.2 (124)	69.0 \pm 2.17 60.1–73.9 (122)
<i>M. cyclops</i>	110.4 \pm 2.40 107.7–114.5 (12)	82.5 \pm 2.28 78.7–85.1 (6)	40.0 \pm 2.55 36.8–42.8 (5)	48.6 \pm 2.79 44.7–51.1 (5)	74.6 \pm 2.14 72.0–78.7 (12)	67.6 \pm 1.75 64.7–70.4 (12)
<i>M. fuscata</i>	119.4 \pm 4.93 109.0–133.7 (155)	86.7 \pm 3.07 79.1–94.8 (149)	44.2 \pm 3.20 36.4–52.0 (155)	51.0 \pm 3.02 43.4–57.5 (148)	84.5 \pm 4.10 75.7–94.7 (160)	70.8 \pm 2.09 64.3–77.9 (155)
<i>M. fascicularis</i>	118.6 \pm 7.29 97.4–140.1 (439)	80.9 \pm 3.98 70.6–93.1 (314)	Adult males 45.9 \pm 4.43 30.4–57.6 (318)	56.7 \pm 3.93 41.9–66.3 (314)	80.5 \pm 4.96 66.3–95.1 (444)	67.9 \pm 2.65 59.8–76.4 (427)
<i>M. mulatta</i>	122.3 \pm 8.51 107.1–143.1 (81)	86.5 \pm 4.28 77.8–96.9 (67)	43.8 \pm 4.16 35.0–56.4 (70)	50.6 \pm 3.06 41.3–58.2 (67)	86.7 \pm 6.45 71.3–101.0 (84)	70.8 \pm 2.62 65.0–76.1 (81)
<i>M. cyclops</i>	125.2 \pm 5.39 114.6–133.4 (14)	88.0 \pm 4.48 77.8–93.1 (10)	47.2 \pm 4.19 39.7–53.0 (10)	53.6 \pm 3.90 45.6–58.2 (10)	86.7 \pm 4.42 77.6–94.5 (14)	69.2 \pm 2.59 64.4–73.6 (14)
<i>M. fuscata</i>	133.1 \pm 5.89 116.2–148.3 (115)	92.1 \pm 3.05 83.0–98.8 (115)	53.2 \pm 3.90 44.5–64.7 (113)	57.8 \pm 3.52 50.3–66.1 (110)	95.4 \pm 4.62 80.8–109.0 (122)	71.6 \pm 2.40 65.5–78.0 (115)

¹ For definition of measurements, see Materials and Methods.

² Cf. Fooden (1995, p. 38; 2000, p. 44), Fooden and Wu (2001, p. 13), and Fooden and Aimi (2005, pp. 30, 37).

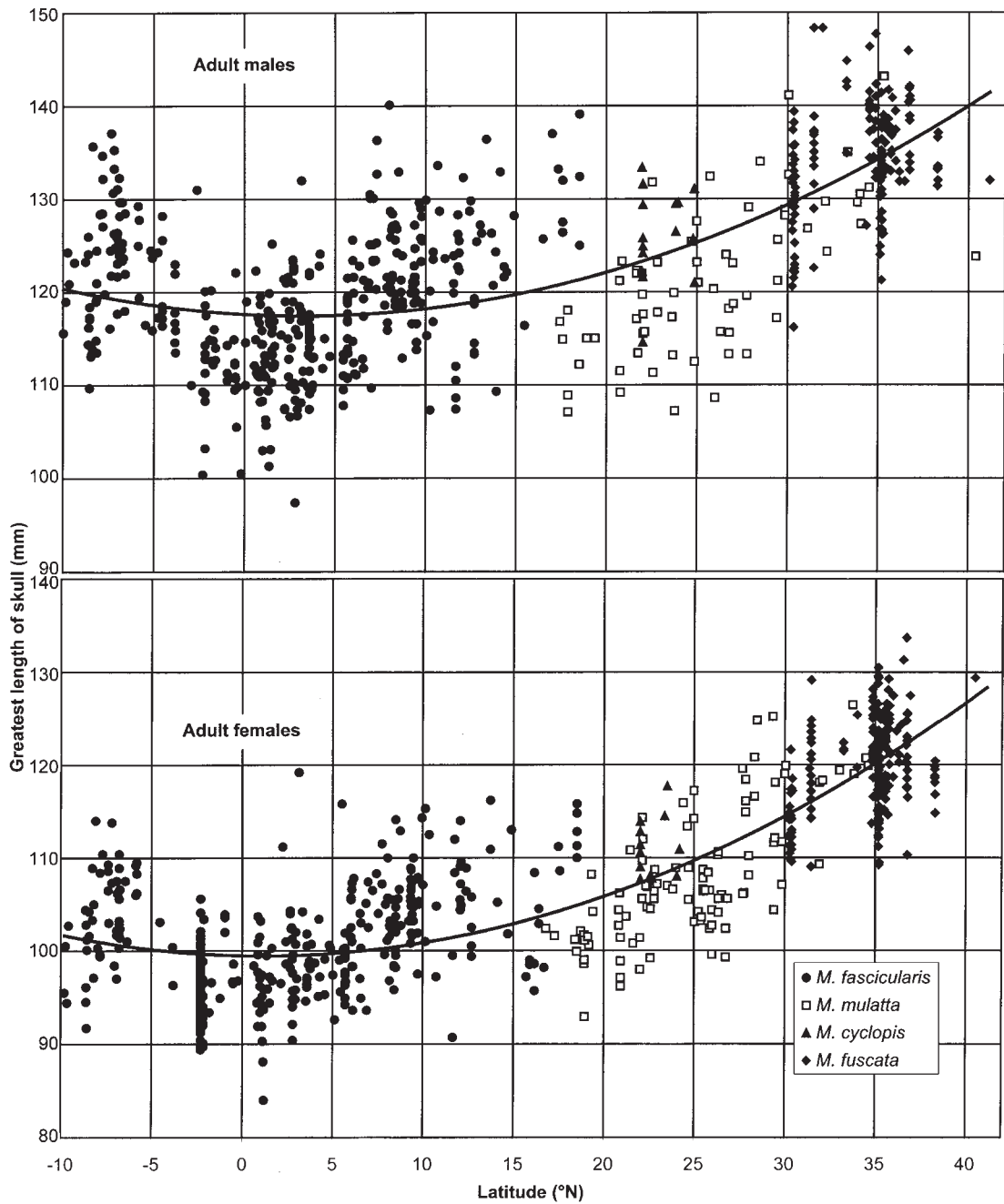


FIG. 8. Latitudinal variation in greatest length of skull in adults of *fascicularis*-group species of *Macaca* (cf. Table 2). Regression statistics: Females—equation, $y = 0.0181x^2 - 0.0437x + 99.5$; $r^2 = 0.734$; $n = 718$; $P < 0.01$. Males—equation, $y = 0.0167x^2 - 0.110x + 117.6$; $r^2 = 0.451$; $n = 649$; $P < 0.01$.

centra increases in proximal vertebrae from 11.8 mm in Cd 1 to 36.9 mm in Cd 6 and Cd 7 and then gradually decreases in more distal vertebrae to 1.25 mm in Cd. 28. In *M. cyclopis*

adult males, mean centrum length decreases slightly from 15.2 mm in Cd 1 to 14.2 mm in Cd 2, increases to 34.0 mm in Cd 8, and decreases to 3.3 mm in Cd 24. In *M. mulatta*

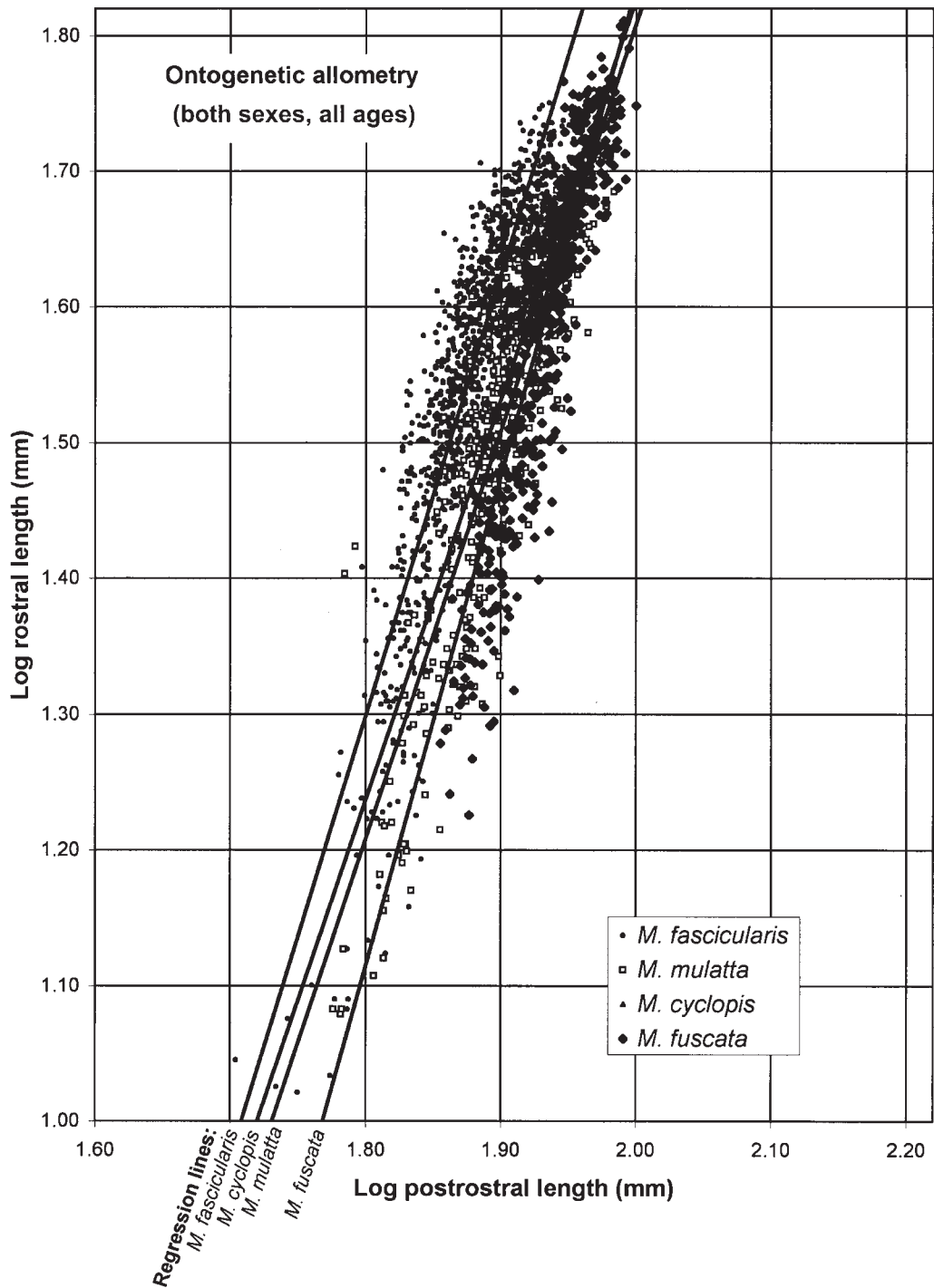


FIG. 9. Ontogenetic allometry of rostral length (y) vs. postrostral length (x) in *fascicularis*-group species of *Macaca* (cf. Table 2). Regression statistics: *M. fascicularis*—equation, $y = 3.246x - 4.545$; $r^2 = 0.794$; $n = 1015$; $P < 0.01$. *M. mulatta*—equation, $y = 3.005x - 4.201$; $r^2 = 0.779$; $n = 367$; $P < 0.01$. *M. cyclopis*—equation, $y = 2.946x - 4.067$; $r^2 = 0.768$; $n = 28$; $P < 0.01$. *M. fuscata*—equation, $y = 3.605x - 5.375$; $r^2 = 0.757$; $n = 633$; $P < 0.01$.

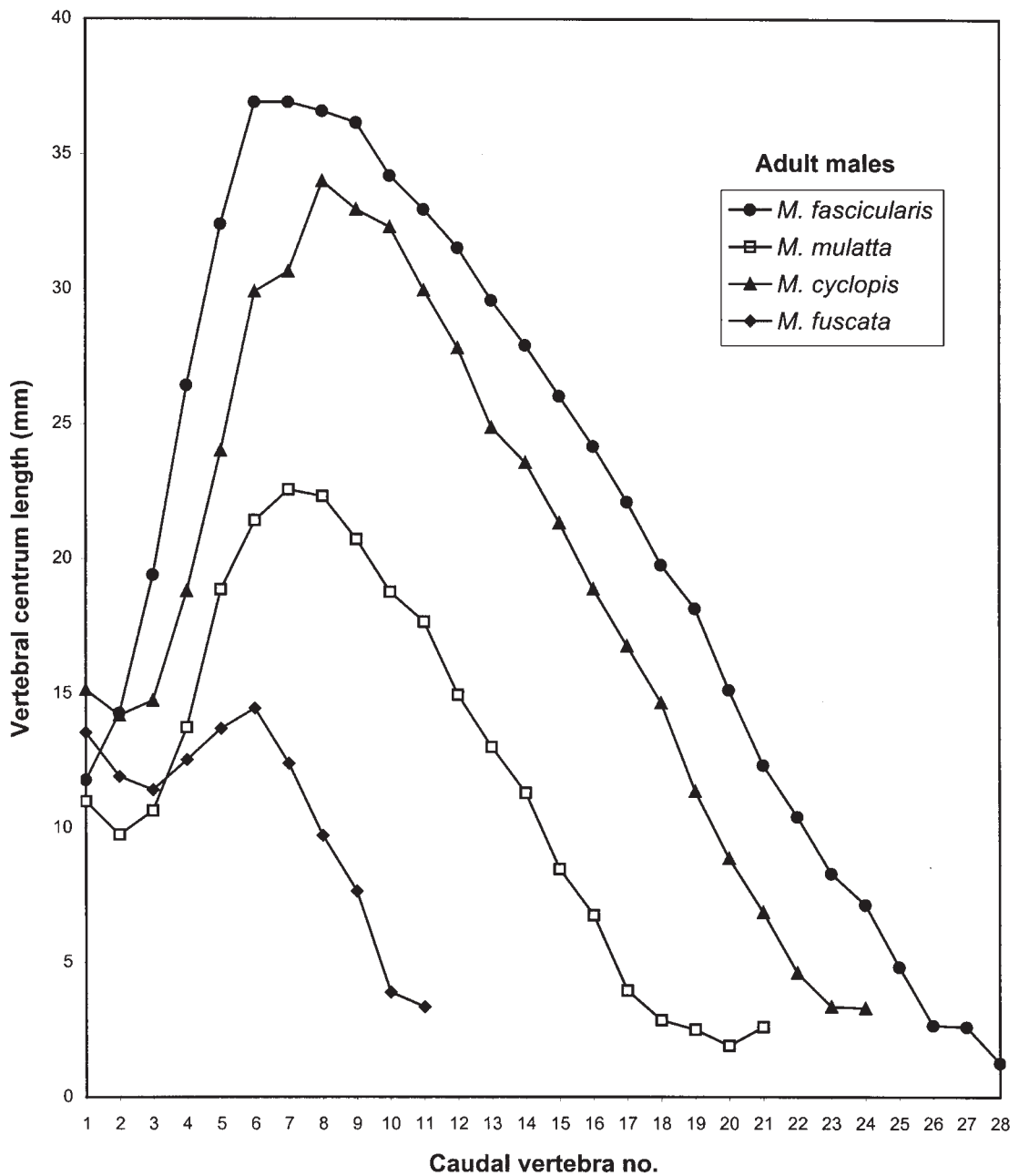


FIG. 10. Mean length of vertebral centrum in successive caudal vertebrae in adult males in *fascicularis*-group species of *Macaca* (cf. Appendix II).

adult males, mean centrum length decreases from 11.0 mm in Cd 1 to 10.6 mm in Cd 3, increases to 22.6 mm in Cd 7, and decreases to 1.9 mm in Cd 20 (2.6 mm in Cd 21). In *M. fuscata* adult males, mean centrum length decreases from 13.6 mm in Cd 1 to 11.4 mm

in Cd 3, increases to 14.5 mm in Cd 6, and decreases to 3.4 mm in Cd 11. The focus of vertebral length reduction in *fascicularis*-group species apparently is in the region of Cd 6–Cd 8 (Fig. 10). A similar pattern of caudal vertebral length reduction was previously noted in the

TABLE 3. Number of caudal vertebrae (No. Cd vert.) reported in *fascicularis*-group species of *Macaca*; values indicated are means and extremes, except where $n < 3$.

References ¹	<i>M. fascicularis</i> ²		<i>M. mulatta</i> ³		<i>M. cyclopis</i> ⁴		<i>M. fuscata</i>	
	No. Cd vert.	<i>N</i>	No. Cd vert.	<i>N</i>	No. Cd vert.	<i>N</i>	No. Cd vert.	<i>N</i>
1	—	—	17	1	—	—	10 ⁵	3
2	25.9 (21–28) ⁶	25	16.6 (13–20)	92	—	—	—	—
2	23.3 (20–27) ⁷	13	—	—	—	—	—	—
3	26.3 (25–27)	12	18.3 (17–20) ⁸	31	—	—	—	—
4	—	—	—	—	20, 22	2	—	—
5	—	—	—	—	—	—	9.4 (7–11)	69
6	27.3 (26–29)	6	18, 21	2	22.5 (21–24)	6	11.0 (11–11)	4
Totals	25.5 (20–29)	56	17.1 (13–21)	126	22.1 (20–24)	8	9.5 (7–11)	76

¹ Key to reference numbers: 1. Schlegel, 1876, pp. 112, 114. 2. Schultz & Straus, 1945, p. 623; cf. Schultz, 1938, p. 6; Ankel, 1965, pp. 265, 270; 1972, p. 233. 3. Wilson, 1972, p. 244; cf. Wilson, 1970, pp. 184–185. 4. Hill, 1974, p. 222. 5. Aimi, 1994, p. 5. 6. Appendix II.

² Excludes caudal vertebrae count of 22 reported for sample of unknown size by Blanford (1888, p. 21).

³ Excludes caudal vertebrae counts of “usually 17 or 18” reported by Blanford (1888, p. 13) and “about twenty” reported by Sullivan (1933, p. 57), both for samples of unknown size.

⁴ Excludes improbable caudal vertebrae count of 16 reported by Murie (1873 [“1872”], p. 775).

⁵ Extreme values not reported.

⁶ Non-Philippine *M. fascicularis*.

⁷ Philippine *M. fascicularis*.

⁸ Excludes improbable caudal vertebrae count of 11 reported for one *M. mulatta* specimen.

silenus and *sinica* groups of macaques (Wilson, 1970, p. 60; Fooden, 1988, p. 18); this suggests that homologous genetic factors may control tail length reduction in the *fascicularis*, *silenus*, and *sinica* groups.

Molecular Biology and Genetics

DNA Studies

Recent molecular research concerning the phylogenetic interrelationships of *fascicularis*-group species includes sequencing studies of mitochondrial DNA, Y-chromosomal DNA, and autosomal DNA (Fig. 11). These three kinds of DNA studies help clarify the evolutionary effects of different modes of inheritance and different patterns of population dispersal (Tosi et al., 2003, p. 1420): mtDNA is maternally inherited, and its haplotypes disperse slowly as a result of macaque female philopatry; Y-chromosomal DNA is paternally inherited, and its haplotypes disperse relatively rapidly as a result of subadult male emigration from natal groups; and autosomal DNA is biparently inherited. In the phylogenetic trees of *fascicu-*

laris-group interrelationships that are presented here (Fig. 11), the species *M. arctoides* is included because of its purported close relationship to *M. fascicularis* (Groves, 2001, p. 229).

Earlier studies of restriction fragment length polymorphism and blood-protein variation in macaques (Hayasaka et al., 1988, p. 278; Fooden and Lanyon, 1989, p. 224; Melnick et al., 1993, p. 92; Zhang and Shi, 1993, p. 13; Morales and Melnick, 1998, p. 16; Vernesi et al., 2000, p. 188) have been largely superseded by sequencing studies.

MITOCHONDRIAL DNA—The *fascicularis* group is indicated as monophyletic in only one of three relevant mtDNA trees (Fig. 11A, 11C, 11D; the mtDNA tree published by Mouri et al. [2000] does not include non-*fascicularis*-group species). In all four mtDNA trees, *M. mulatta*, *M. cyclopis*, and *M. fuscata* are indicated as more closely related to each other than to *M. fascicularis*, and *M. mulatta* is indicated as paraphyletic relative to *M. cyclopis*, and *M. fuscata*. *Macaca arctoides* is not indicated as a sister group to *M. fascicularis* in any of the three relevant studies. Tosi et al. (2000, p. 138; 2003, p. 1430) have interpreted mtDNA paraphyly that is indicated for *M. mulatta* as a probable result of incomplete lineage sorting.

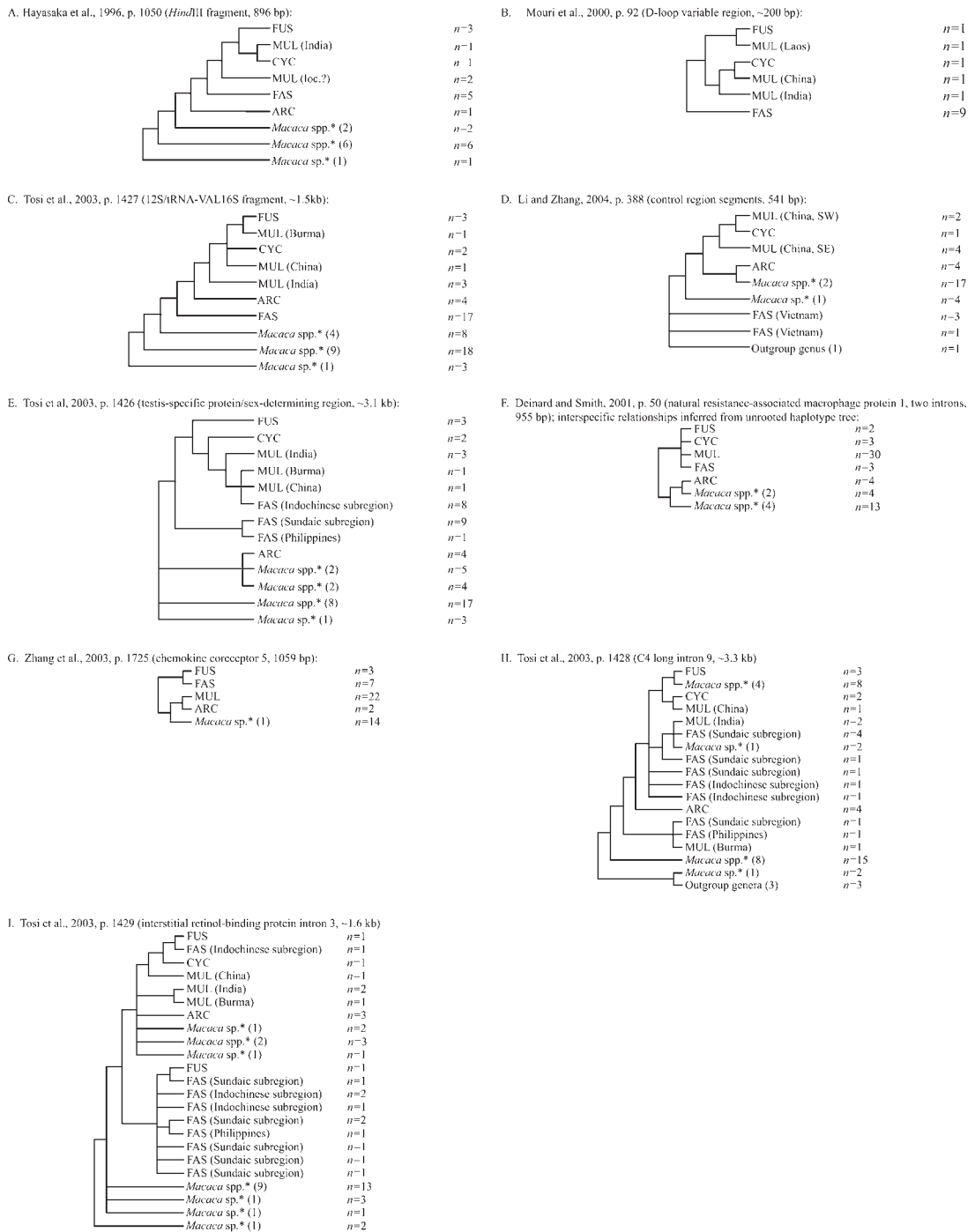


FIG. 11. Phylogenetic relationships among *Macaca fascicularis* (FAS), *M. mulatta* (MUL), *M. cyclopis* (CYC), *M. fuscata* (FUS), and *M. arctoides* (ARC), as determined by DNA sequencing studies; asterisks (*) indicate macaque species excluded from detailed consideration here. (A–D) Mitochondrial DNA studies. (E) Y-chromosomal DNA study. (F–I) Autosomal DNA studies.

TABLE 4. Interspecific comparison of natural history variables in *fascicularis*-group species of *Macaca*.¹

Natural history variable	Species		
	<i>M. fascicularis</i>	<i>M. mulatta</i>	<i>M. cyclops</i>
Latitudinal range	10°S–21°N	14°–40°N ²	22°–25°N
Elevational range	0–2300 m	0–4000 m ³	100–3400 m
Forest habitats	Mangrove; broadleaf; mixed broadleaf–needleleaf ~75% ⁷ (~400 troops)	Mangrove ⁵ ; broadleaf; mixed broadleaf–needleleaf; needleleaf ~25% (19 localities) 1000 m	Broadleaf; mixed broadleaf–needleleaf; needleleaf ~80% (1 locality) Swims well
Arboreality ⁶		~30 (2 to ~250) ~1/90	~40 (10–161) 1/7
Swimming ability ⁸	100 m	0.39 (0.08–1.43) 9/9	0.58 (0.20–1.33) 3/5
Troop size ⁹	~20 (3 to ~100) 1/58	~195 (16 to ≥2020) 1/29 ¹²	~130 (≤37 to ≥200) ~27
Adult sex ratio ^{9,11}	0.60 (0.14–1.67) 3/4		
Home range area (ha) ⁹	~55 (<12 to ≥300) ≥55		~220 (24–780) 1/3 ¹³

¹ For documentation, see Fooden (1991, p. 13; 1995, 49; 2000, p. 54), Fooden and Wu (2001, p. 21), and Fooden and Aimi (2005, p. 50).² Includes recently extinct northeastern Chinese population (Fooden, 2000, p. 3).³ Includes Gokavaram (Fooden, 2000, p. 138).⁴ Includes Kojima (Fooden & Aimi, 2005, p. 51).⁵ See Mandal (1964, p. 154).⁶ Percent of daylight hours spent in trees.⁷ ~75% arboreal in coastal and riverbank areas; ~97% arboreal in inland areas (3 localities).⁸ Indicated values are maximum swimming distances reported.⁹ Nonprovisioned or minimally provisioned troops; indicated values are means, extremes (in parentheses), and sample sizes (italicized).¹⁰ Cf. Lee and Lin (1991, p. 34), who indicate that mean troop size is ca. 12.2 individuals in ca. 121 troops concerning which they received reports.¹¹ Adult sex ratio = number of sexually mature males ÷ number of sexually mature females.¹² These values are for forest troops (nonprovisioned); corresponding values for nonforest troops (nonprovisioned) are ~65 (3 to ≥162) 3/23.¹³ See Takasaki (1981, p. 278). Indicated values are for broadleaf evergreen forest; corresponding values for deciduous broadleaf forest are ~800 (160–2670) 1/7.

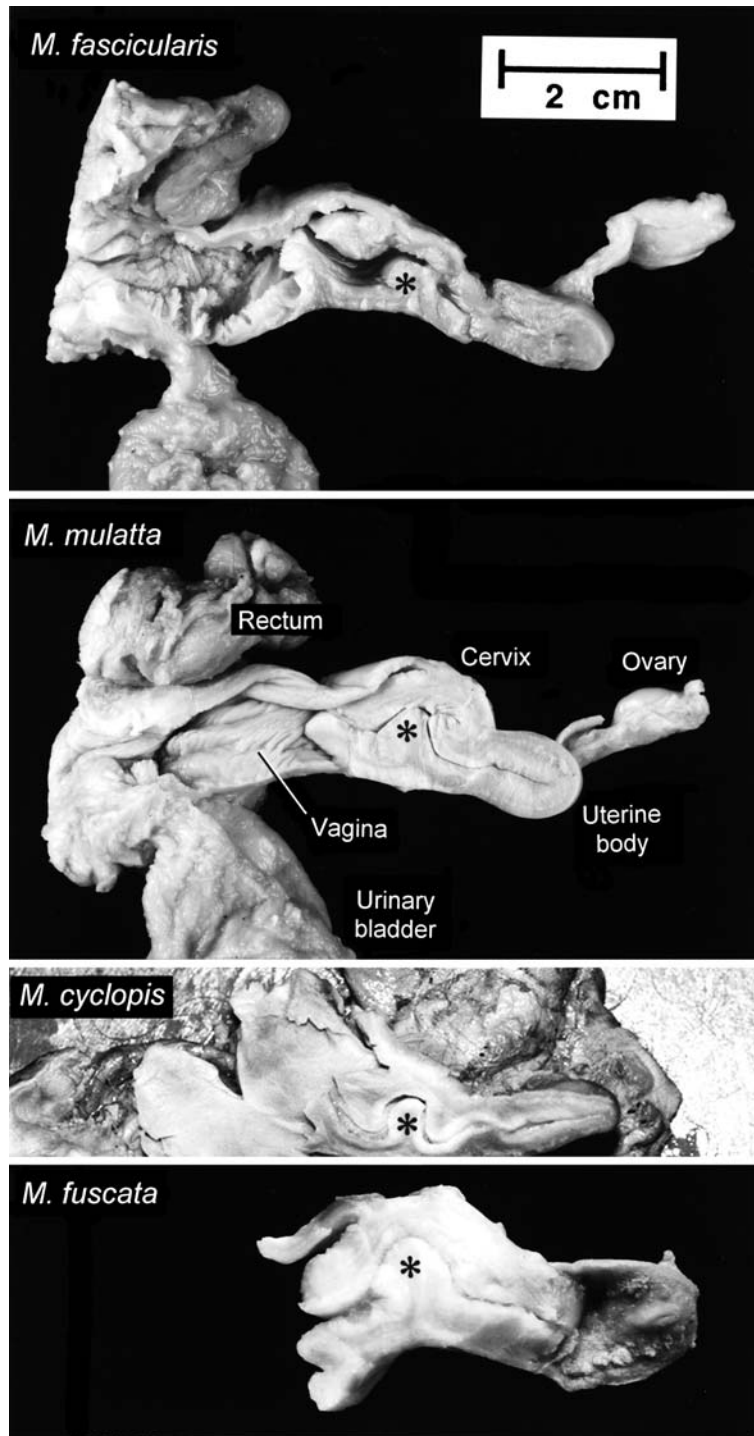


FIG. 12. Female reproductive tract (midsagittal section) in *fascicularis*-group species of *Macaca* (*M. cyclopis* and *M. fuscata* specimens incomplete). Asterisk (*) indicates ventral cervical collicle; other structures labeled in *M. mulatta* specimen. Specimen numbers (cf. Table 5): *M. fascicularis*—FMNH 99659 (lactating); *M. mulatta*—FMNH 99668 (lactating); *M. cyclopis*—NMNS T-3909; *M. fuscata*—PRIKU 533 (age 24 yr, probably postreproductive). Photo credits: *M. fascicularis* and *M. mulatta*—John Weinstein, Division of Photography, FMNH; *M. cyclopis*—Hai-Yin Wu, NDHU; *M. fuscata*—Mitsuru Aimi, PRIKU.

TABLE 5. Measurements (mm) of female reproductive tract in adult specimens of *fascicularis*-group species of *Macaca* (cf. Fig. 12).

Dimension	<i>M. fascicularis</i> ¹ (FMNH 99659)	<i>M. mulatta</i> (FMNH 99668)	<i>M. cyclopis</i> (NMNS T-3909)	<i>M. fuscata</i> ² (PRIKU 533)
Head and body length	407	420	448	—
Vagina length	30	32	40	—
		Uterine cervix		
Length	22	22	20	29
Breadth	14	16	—	22
Dorsoventral diameter	12	15	10	20
		Ventral cervical collicle		
Height	4	5	4	8
Craniocaudal diameter	6	7	4	10
		Uterine body		
Length	20	13	18	25
Breadth	15	16	—	—
Dorsoventral diameter	8	10	8	15

¹ Cf. Fooden (1971a, p. 26).

² For photographs of an unmeasured female reproductive tract of *M. fuscata*, see Makita (1992, p. 84).

Y-CHROMOSOMAL DNA—Although the *fascicularis* group is indicated as monophyletic in the single available Y-chromosomal DNA tree (Fig. 11E), *M. fascicularis* and *M. mulatta* are each indicated as paraphyletic in this tree. *Macaca arctoides* is not indicated as a sister group to *M. fascicularis*. The paraphyly that is indicated for *M. fascicularis* has been interpreted by Tosi et al. (2003, p. 1425) as a probable result of hybridization between Indochinese *M. fascicularis* and adjacent populations of *M. mulatta*.

AUTOSOMAL DNA—The *fascicularis* group is indicated as monophyletic in only one of four available studies of autosomal DNA (Fig. 11F–11I). *Macaca fascicularis* and *M. mulatta* are indicated as paraphyletic in two of these trees, and *Macaca arctoides* is not indicated as a sister group to *M. fascicularis*. The level of resolution is relatively low in the autosomal DNA studies of Tosi et al. (2003, p. 1431).

INFERRED AGE OF DIVERGENCE—The age of divergence (Ma = millions of years ago) of the *fascicularis* group inferred in Hayasaka et al.'s (1996, p. 1052) study is ca. 2.2 Ma, and that of the *fascicularis* group plus *M. arctoides* inferred in Tosi et al.'s (2003, p. 1431) study is ca. 3.2 Ma (cf. Melnick & Hoelzer, 1993, p. 4; Melnick et al., 1993, p. 290).

SUMMARY—The *fascicularis* group is indicated as monophyletic in three of eight relevant DNA studies. Incomplete lineage sorting and/or hybridization may explain apparent paraphyly within *M. fascicularis* and *M. mulatta* samples. No sequencing evidence indicates that the species

M. fascicularis and *M. arctoides* constitute a monophyletic unit. Future research on supplementary loci may be expected to further illuminate phylogenetic relationships of the *fascicularis* group and its included species (Disotell, 2000, p. 39; Deinard & Smith, 2001, p. 57; Rokas et al., 2003, p. 801; Tosi et al., 2003, p. 1433; Smith & McDonough, 2005, p. 8).

Karyology

The karyotype of *fascicularis*-group macaques apparently is generally similar to that in other species of *Macaca* (Stanyon et al., 1988, p. 11; Fooden & Wu, 2001, p. 15). Within the *fascicularis* group, *M. fascicularis* is distinguished by a unique clear band on chromosome 5, and *M. fuscata* is distinguished by a small pericentric inversion on chromosome 15.

Natural History

Macaca fascicularis and *M. mulatta*—the two widely distributed *fascicularis*-group species—inhabit tropical and subtropical climate zones, respectively (Fig 1; Table 4). Of the more narrowly distributed species, *M. cyclopis*—like *M. mulatta*—inhabits the subtropical zone, and *M. fuscata*, the northernmost of these species, occupies a marginal subtropical/temperate habitat. As previously indicated (see above, External Measurements and Proportions, Cranial Char-

acters), body size and tail length in species of this group apparently are adapted to their respective climate-zone habitats. Thermoregulatory physiology in these species apparently also is adapted to the climates of their habitats (Okada et al., 1975, p. 199; Tokura et al., 1975a, p. 175; Tokura et al., 1975b, p. 151).

The elevational distribution of all four of these species extends from lowland forests near sea level to the highest montane forests (2000–4000 m) that exist within each of their geographic ranges (Table 4). Inland broadleaf evergreen forests and broadleaf deciduous forests are the most common habitats of all four species, but *M. fascicularis* and *M. mulatta* are known also to inhabit coastal mangrove forests, and *M. mulatta*, *M. cyclopis*, and *M. fuscata* are known to inhabit needleleaf (coniferous) forests. Fragmentary data suggest that daytime activity of *M. fascicularis* and *M. cyclopis* is mainly arboreal ($\geq 75\%$), that daytime activity of *M. mulatta* is mainly terrestrial (ca. 25% arboreal), and that daytime activity of *M. fuscata* is intermediate (ca. 50% arboreal); all four species usually sleep in trees. *Macaca mulatta* is capable of swimming across ocean gaps that are at least 1000 m wide, and the remaining three species reportedly also swim well.

In nonprovisioned troops, mean troop size varies from ca. 20 individuals in *M. fascicularis* to ca. 40 individuals in *M. fuscata* (Table 4; excludes unverified mean troop size of ca. 12 individuals indicated for *M. cyclopis* by Lee & Lin, 1991, p. 34). The mean ratio of sexually mature males to sexually mature females varies from ca. 0.40 in *M. mulatta* troops to ca. 0.60 in *M. fascicularis* and *M. fuscata* troops. Mean home range area apparently is smallest in *M. fascicularis* (ca. 55 ha), intermediate in *M. cyclopis* (ca. 130 ha), and largest in *M. mulatta* and *M. fuscata* (ca. 200 ha); within species, the size of a troop's home range apparently is strongly influenced by the quality of the troop's habitat (Table 4, footnotes 12–13).

All four of these macaque species consume a wide variety of plant and animal foods, of which fruits and seeds probably are most important (Fooden, 1991, p. 18; 1995, p. 54; 2000, p. 57; Fooden & Wu, 2001, p. 23; Fooden & Aimi, 2005, p. 52; cf. Vo, 2003b, p. 1). Known natural predators on *M. fascicularis* and/or *M. mulatta* include crocodiles, giant monitors, snakes, raptorial birds, dogs, weasels, leopards, and tigers; known natural predators on *M.*

cyclopis and/or *M. fuscata* are limited to eagles, dogs, possibly raccoon dogs, and clouded leopards.

Reproduction

Seasonality

Birth seasonality—the most intensively studied aspect of reproductive seasonality—is weakly developed in *M. fascicularis* and strongly developed in *M. mulatta*, *M. cyclopis*, and *M. fuscata* (cf. Thierry et al., 2000, p. 718); the interspecific difference presumably is attributable to limited seasonal variation of temperature in the tropical regions inhabited by *M. fascicularis*. In 21 broadly distributed samples of natural populations of *M. fascicularis*, births have been reported in every month of the year, but births apparently tend to peak during late summer–early autumn (Fooden, 1995, p. 201; cf. Fooden, 1991, p. 18). Of 289 births recorded in these natural populations, 58% occurred during the four-month period July–October, when the number of births per month varied from 34 to 58, and only 42% occurred during the remaining eight months of the year, when the number of births per month varied from 9 to 21. Birth peaks in *M. fascicularis* may vary locally and annually (Fooden, 1995, p. 58).

In natural populations of *M. mulatta*, *M. cyclopis*, and *M. fuscata*, most births apparently occur during spring and summer. In 16 samples of natural populations of *M. mulatta*, most births reportedly occurred during the period March–August, few occurred during the period September–November, and none occurred during the period December–February (Fooden, 2000, p. 69). In eight samples of natural populations *M. cyclopis*, births reportedly were restricted to the period February–October (Fooden & Wu, 2001, p. 27). In 20 samples of natural populations of *M. fuscata*, births reportedly were restricted to the period March–October, with local birth seasons generally tending to occur earlier at higher latitudes (Fooden & Aimi, 2003, p. 113).

Copulation frequency tends to peak 5–6 months before the indicated birth peaks (Fooden, 1995, p. 200; 2000, p. 69; Fooden & Wu, 2001, p. 27), which is in accord with the ca. 165-day gestation period in macaques (Table 9).

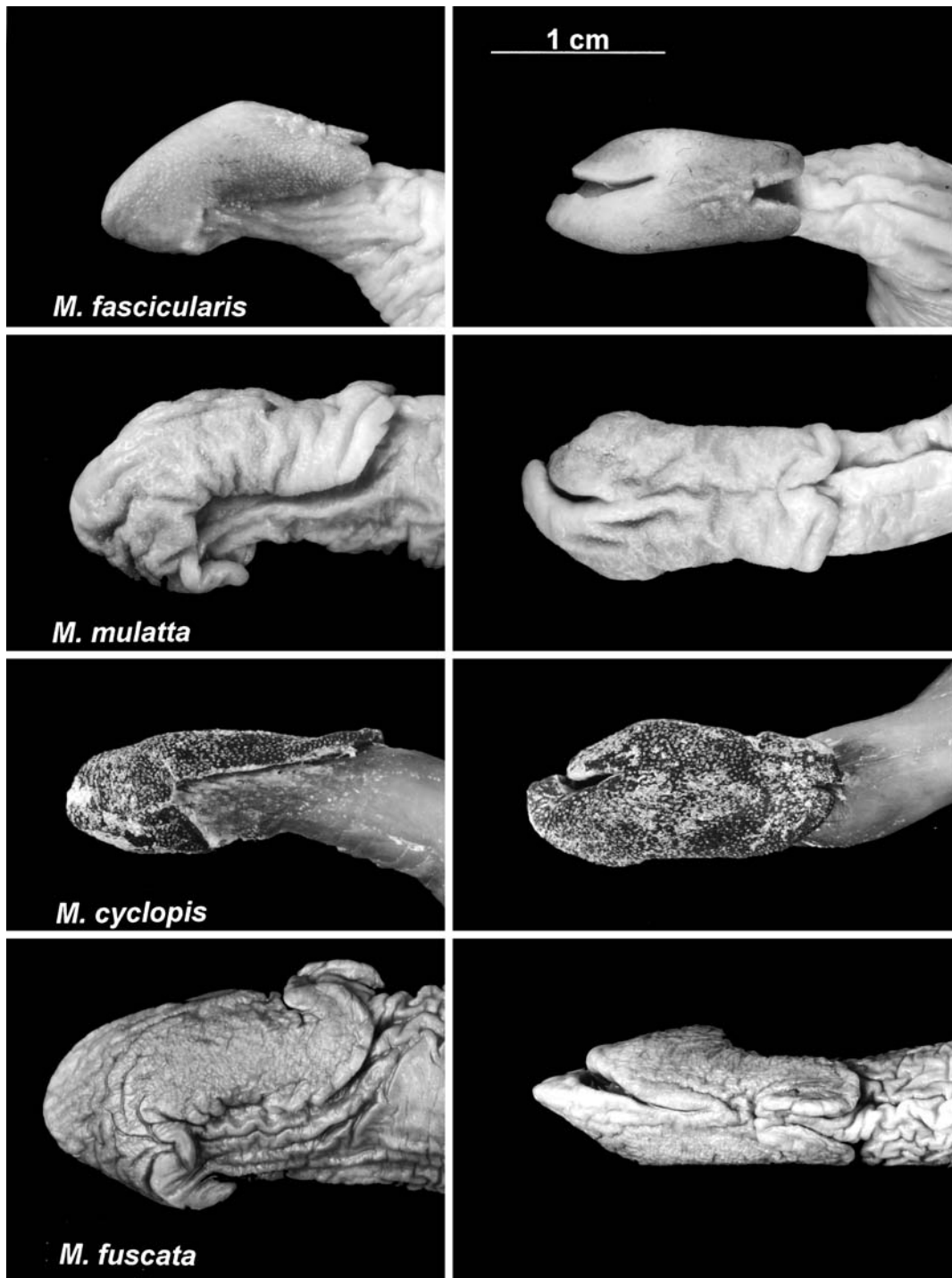


FIG. 13. Glans penis (left lateral and dorsal views) in adult specimens of *fascicularis*-group species of *Macaca*. Specimen numbers (cf. Table 6): *M. fascicularis*—FMNH 99642; *M. mulatta*—FMNH 99669 (conspicuous postmortem wrinkling); *M. cyclopis*—ZMB 26479 (dry specimen, reconstituted in fluid); *M. fuscata*—FMNH 57995. Photos by John Weinstein, Division of Photography, FMNH.

TABLE 6. Glans penis measurements in fluid-preserved adult specimens of *fascicularis*-group species of *Macaca* (cf. Fig. 13).

Species	Glans penis measurements (mm)			Head and body length (mm)	Body weight (kg)	Source of data ¹
	Length	Breadth	Dorsoventral diameter			
<i>M. fascicularis</i>	15.3	6.8	8.6	529	6.1	1
<i>M. mulatta</i>	19.0 ²	9.4	10.7	492	6.2	2
<i>M. cyclopis</i>	18.2	8.1	7.4	—	—	3
<i>M. fuscata</i>	20.9	8.8	11.4	—	17.1	4

¹ Key to data sources: 1. FMNH 99642. 2. FMNH 99669. 3. MZB 26479 (dry specimen, reconstituted in fluid). 4. Fooden, 1972 ("1971"), p. 306—mean values in two adults, age >6 yr (cf. Hill, 1958, p. 656).

² Cf. Dixon and Nevison (1997, p. 132); means \pm SEM in four sedated captives—20.5 \pm 0.7 mm, early mating season; 21.4 \pm 0.5 mm, late mating season.

Female Reproductive Tract

Judging from available specimens, the structure of the female tract is basically similar in all four species of the *fascicularis* group (Fig. 12; Table 5; cf. Demers et al., 1972, p. 530; Jainudeen et al., 1972, p. 473). In nonpregnant females, the vagina probably is ca. 30–40 mm long, the uterine cervix is ca. 20–30 mm long, and the uterine body is ca. 15–25 mm long. As in other macaques, the cervical canal in *fascicularis*-group species is not straight but instead is sinuously deflected dorsally by a prominent ventral collicle that protrudes from the ventral wall of the cervix (Keith, 1900, p. xlvi; Franke, 1902, p. 358; Clark & Corner, 1935, p. 250; Makita, 1992, p. 84). All species in the *fascicularis* group possess a moderately large uterine cervix, which resembles that in *M. nemestrina* (Fooden, 1971b, p. 71; 1975, p. 32; Jainudeen et al., 1972, p. 473) and differs strikingly from the much larger uterine cervix in *M. sinica*, *M. radiata*, *M. assamensis*, *M. thibetana*, and *M. arctoides* (Fooden, 1967, p. 940; 1971b, p. 71; 1990, p. 662). The vaginal wall is rugose in nonpregnant *fascicularis*-group females (Fig. 12; Makita, 1992, p. 84), not spinose as apparently is true in nonpregnant *M. sinica*, *M. radiata*, *M. assamensis*, and *M. thibetana* females (Fooden, 1971b, p. 67; 1988, p. 24).

Cyclical changes in uterine anatomy in *M. mulatta* have been described by Hartman (1932, pp. 61, 67).

Glans Penis and Baculum

In *fascicularis*-group macaques, the glans penis is helmet shaped and relatively long and narrow;

the dorsal portion of the glans extends approximately twice as far proximally as the ventral portion (Fig. 13; Dixon, 1987, p. 432). Although the glans also is helmet shaped in *silenus*-group macaques and *M. sylvanus*, it is relatively much broader in these species than in *fascicularis*-group species (Fooden, 1976, p. 227). Distally, the apex of the glans is asymmetrically cleft into two unequal lobes by the urethral meatus, a vertical slit situated to the right of the midline; the left lobe of the glans, into which the baculum protrudes (see below), is approximately twice as large as the right lobe. Proximally, the free dorsal margin of the glans is notched medially. The surface of the glans and shaft is covered by minute epidermal papillae, each ca. 0.1 mm in diameter; unlike *sinica*-group species (Fooden, 1988, p. 20), *fascicularis*-group species lack penial spines. Measurements of the glans in one fluid-preserved adult of *M. fascicularis*, the smallest species in this group, are 15.3 mm (length) \times 6.8 mm (breadth) \times 8.6 mm (dorsoventral diameter); means of corresponding measurements in two fluid-preserved adults of *M. fuscata*, the largest species in the group, are 20.9 mm \times 8.8 mm \times 11.4 mm (Table 6).

The baculum (penis bone) is a slender ossified distal extension of the fused corpora cavernosa (Wislocki, 1933, p. 239). The proximal end of the baculum is rooted within the fused corpora cavernosa at a level immediately proximal to the dorsal margin of the glans; the distal end terminates within the left lobe of the glans at a level ca. 5 mm proximal to the tip of this lobe (Fig. 14). In adult and late subadult *fascicularis*-group specimens examined, the baculum is a gently curved arcuate or sigmoid rod, with its distal end inclined ventrally; in these specimens,

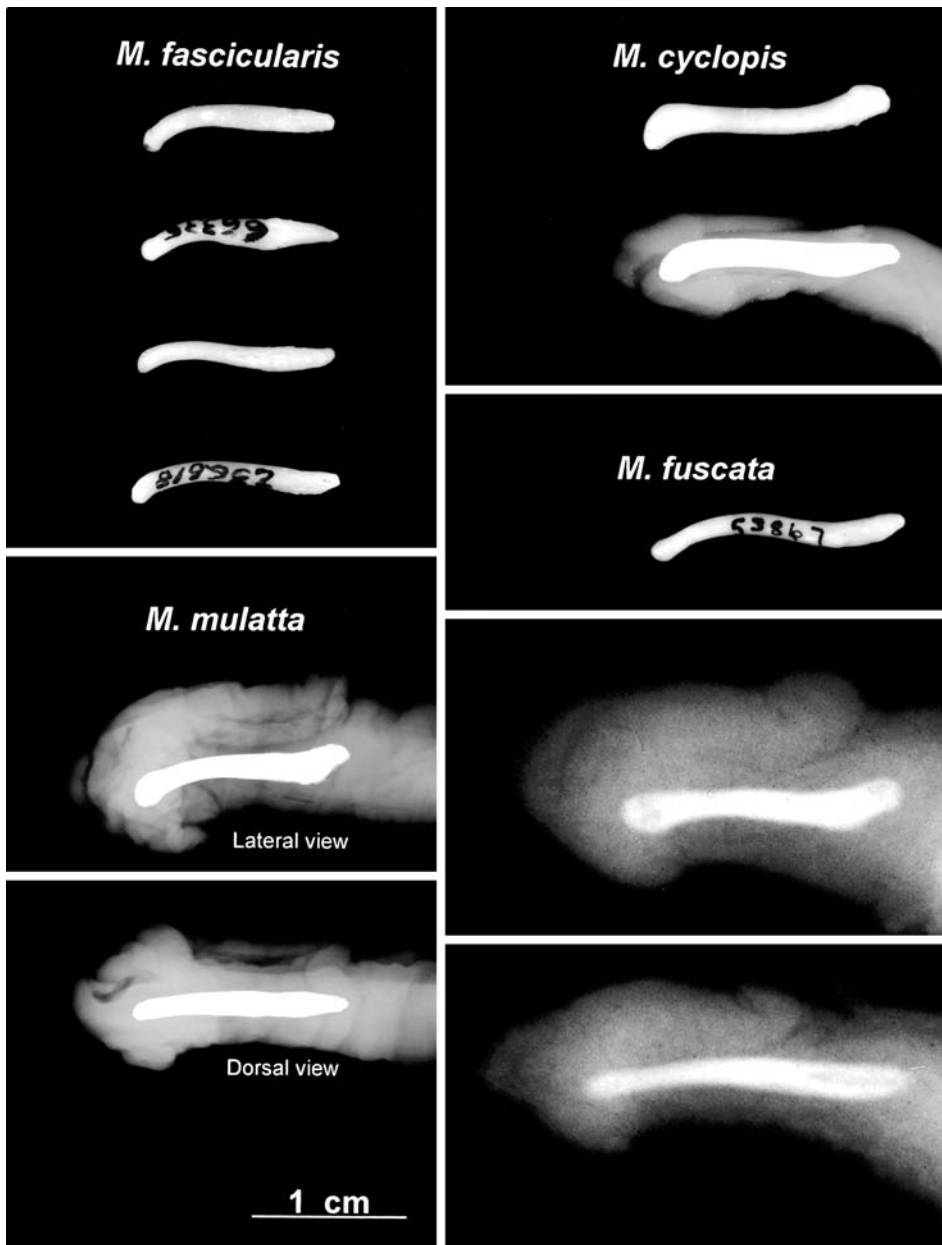


FIG. 14. Bacula, extracted and in situ (radiographic images), in adult and late subadult specimens of *fascicularis*-group species of *Macaca* (left lateral view; dorsal view supplement for *M. mulatta*). Specimen numbers (cf. Table 7): *M. fascicularis* (top to bottom)—FMNH 66336, USNM 83944, USNM 236618, FMNH 67733 (subadult); *M. mulatta*—FMNH 99669; *M. cyclopis* (top to bottom)—USNM 296795 (subadult), ZMB 26479 (dry specimen, reconstituted in fluid); *M. fuscata* (top to bottom)—FMNH 53867 (captive), FMNH 57995, FMNH 57994. Photos by John Weinstein, Division of Photography, FMNH.

the baculum measures ca. 12–19 mm in length and ca. 1–2 mm in dorsoventral diameter (Fig. 14; Table 7). Judging from limited available

data, length of the baculum in *M. fascicularis* (mean, 13.3 mm) is less than that in the three larger species (means, 16.1–17.4 mm); these data

TABLE 7. Baculum length in adults and late subadults (see footnote 3) of *fascicularis*-group species of *Macaca* (cf. Fig. 14).

Specimen No.	Geographic origin	Greatest length of skull (mm)	Baculum length ¹ (mm)
		<i>M. fascicularis</i> ²	
FMNH 66336	Philippines: Negros	129.6	13.0 (10.0%)
FMNH 67733 ³	Philippines: Mindanao	120.5	13.0 (10.8%)
MCZ 35294	Philippines: Mindoro	127.2	13.4 (10.5%)
MZB 2387	Indonesia: Flores	116.2	12.3 (10.6%)
USNM 83944	Malaysia: Sarawak	113.3	12.7 (11.2%)
USNM 236618	Thailand: Ko Khram Yai	113.3	13.8 (12.2%)
(Dixson, 1987, p. 53)	—	—	13
(Pohl, 1928, p. 103)	—	—	15
Mean ± SD	—	—	13.28 ± 0.826
		<i>M. mulatta</i> ⁴	
FMNH 99669	Thailand: Huai Ap Nang	116.8	14.3 ⁵ (12.2%)
(De Beaux, 1917, p. 4)	—	—	17
(Pohl, 1928, p. 104)	—	—	18
Mean ± SD	—	—	16.43 ± 1.914
		<i>M. cyclopis</i> ⁶	
USNM 296795 ³	Taiwan: Shou Shan	122.6	16.1 (13.1%)
ZMB 26479	Taiwan: Manchoutsun	124.2	16.2 ⁵ (13.0%)
Mean	—	—	16.15
		<i>M. fuscata</i> ⁷	
FMNH 53867	(captive)	126.2	16.8 (13.3%)
FMNH 57994	Japan: Shodoshima	—	18.8 ⁵
FMNH 57995	Japan: Kyushu	—	16.6 ⁵
Mean ± SD	—	—	17.40 ± 1.217

¹ Parenthetical notation indicates ratio of baculum length to greatest length of skull.

² Excludes baculum length measurements published by Retterer and Neuville (1914, p. 535: 10 mm), De Beaux (1917, p. 7: 11 mm), and Chaine (1927 [“1926”], p. 17: 10 mm, 12 mm; cf. Kinzey, 1971, p. 101); these may be measurements of immature specimens.

³ Late subadult.

⁴ Excludes baculum length measurements published by the following authors: Chaine (1927 [“1926”], p. 18: 10 mm; apparently based on an immature specimen); Kinzey (1971, p. 102: $n = 7$, mean = 15.1 mm, extremes 12.4–17.2 mm; sample apparently includes immature specimens); Dixson and Nevison (1997, p. 132, $n = 4$, mean = 21.8; large measurements, obtained by palpation of baculum in sedated living captives).

⁵ Measured on radiograph.

⁶ In one late juvenile captive (USNM 296796), greatest length of skull is 122.4 mm, and baculum length is 16.2 mm.

⁷ Excludes immature specimen cited by Hill (1974, p. 598, length = 10 mm). Also excludes specimen figured as “*L. fuscatus*” by Pocock (1921, p. 225); this actually is *M. arctoides* (Fooden, 1990, p. 610).

also suggest an allometric relationship in which the ratio of baculum length to skull length is less in *M. fascicularis* than in the larger species.

Sexual Skin

At puberty, various areas of sexual skin become swollen and/or red in *fascicularis*-group females (Table 8); this adolescent swelling apparently is most conspicuously developed in

M. cyclopis (Sclater, 1865, p. 710; Murie, 1873, p. 772; Hsu, 1990, pp. 52, 60). During subsequent mating seasons, swelling of the sexual skin is reduced, but the color of the sexual skin continues to undergo cyclical variation in redness, which becomes most intense during the estrous phase of the reproductive cycle; redness of sexual skin in adult females is least conspicuous in *M. fascicularis* (cf. Thierry et al., 2000, p. 718). Reduced swelling in *fascicularis*-group

TABLE 8. Sexual skin reported in females and males of *fascicularis*-group species of *Macaca*.¹

Species	Females		Adult males ²	References ³
	Pubertal, subadult	Adult ²		
<i>M. fascicularis</i>	Subcaudal swelling, perivulval reddening	Swelling and reddening reduced or absent	Sexual skin not reported	1
<i>M. mulatta</i>	Pubic swelling; subsequent paravulval swelling	Swelling reduced; reddening of area from tail to thighs; red face and nipples	Red face and perineum	2
<i>M. cyclopis</i>	Prominent swelling and reddening of perineum and posterior surface of thighs	Swelling reduced; red face, nipples, and perineum	Red face and scrotum	3
<i>M. fuscata</i>	Para-anal swellings; subsequent subcaudal or paravulval swellings	Swelling reduced; red face, nipples, and perineum	Red face, perianal region, scrotum	4

¹ Cf. Napier (1981, p. 5).

² Sexual skin becomes red during the mating season; intensity of the redness varies cyclically during the mating season in adult females but apparently not in adult males.

³ Key to references: 1. Fooden, 1995, p. 59. 2. Fooden, 2000, p. 71. 3. Fooden & Wu, 2001, p. 26. 4. Fooden & Aimi, 2005, p. 57.

adult females has been interpreted as a derived character state (Dixon, 1983, pp. 81, 87; 1998, p. 211; Thierry et al., 2000, p. 722).

In *fascicularis*-group males, reddening of the face and hindquarters during the mating season has been reported in *M. mulatta*, *M. cyclopis*, and *M. fuscata* but not in *M. fascicularis* (Table 8). Intensity of redness of the sexual skin in males apparently remains relatively constant throughout the mating season.

Copulatory Behavior

Copulations in *fascicularis*-group species apparently usually occur in the context of consortships (temporary male-female associations of varying durations) during a female's estrous period, approximately midway between successive menstrual periods (Fooden, 1995, p. 59; 2000, p. 71; Fooden & Wu, 2001, p. 28; Fooden & Aimi, 2005, p. 59). During copulations in

TABLE 9. Summary comparison of reproductive parameters in *fascicularis*-group species of *Macaca*.¹

Reproductive variable	<i>M. fascicularis</i>	<i>M. mulatta</i>	<i>M. cyclopis</i>	<i>M. fuscata</i>
Age at sexual maturity, ² nonprovisioned females	3.5 yr	4.5 yr	3.5–4.5 yr	4.5–5.5 yr ³
Age at sexual maturity, nonprovisioned males	ca. 5.5 yr	6.5 yr	ca. 5.5 yr ⁴	8.5 yr ⁵
Menstrual cycle length, mode	28 days	ca. 28 days	ca. 28 days ⁶	27 days ⁶
Gestation length, mean	163.5 days	165.8 days	162 days	171.7 days
Annual birth rate, ⁷ nonprovisioned groups	0.58	0.67	0.69	0.38

¹ For details, see Fooden (1995, p. 58; 2000, p. 68), Fooden and Wu (2001, p. 26), and Fooden and Aimi (2005, pp. 57–68).

² Age at first fertile copulation.

³ Provisioned groups.

⁴ Estimated.

⁵ Full sociosexual maturity.

⁶ Mean value.

⁷ Live births/sexually mature females.

TABLE 10. Estimated age of earliest *fascicularis*-group fossils in various geographic areas; species identifications are those of authors cited.

Country: island	Estimated age (Ka)	References
		<i>M. fascicularis</i> ¹
Philippines: Palawan	≤11	Reis & Garong, 2001, pp. 413–417
Indonesia: Timor ²	4.5	Glover, 1986, pp. 159, 192
Indonesia: Flores ²	3.5	Hooijer, 1967, p. 160; Musser, 1981, p. 72
Indonesia: Java	900	van den Bergh et al., 2001, p. 389
Indonesia: Sumatra	60–80	Hooijer, 1962a, p. 58; van den Bergh et al., 2001, p. 392
Malaysia: Borneo	30–40	Hooijer, 1962b, p. 440; Fooden, 1975, p. 61
Malaysia (peninsular)	7	Tweedie, 1940, p. 7
		<i>M. mulatta</i> ³
Vietnam	20–30	Olsen & Ciochon, 1990, pp. 764–766 ⁴
China	40–120	You & Cai, 1996, p. 341
India	≤10	Lydekker, 1880, pp. 32–33
		<i>M. cyclopis</i>
Taiwan	~300	Fooden & Wu, 2001, p. 31
		<i>M. fuscata</i>
Japan: Honshu	430–630	Fooden & Aimi, 2005, p. 72
		<i>Macaca</i> sp.
Korea	400–600	Fooden & Aimi, 2005, p. 72

¹ Cf. Fooden (1995, p. 62).

² Probably introduced by humans (Fooden, 1995, p. 96; van den Bergh et al., 2001, p. 397).

³ Cf. Fooden (2000, p. 81).

⁴ Cf. Bacon et al. (2004, p. 310).

fascicularis-group species, as in other species of macaques, a male typically mounts a female dorsoventrally by grasping her hips and calves with his hands and feet, respectively (Fooden, 1995, p. 59; 2000, p. 72; Fooden & Wu, 2001,

p. 29; Fooden & Aimi, 2005, p. 60). Ejaculation in all four species in this group species may be accomplished either in a single mount (SME = single-mount ejaculation) or in a series of mounts and dismounts (MME = multiple-mount

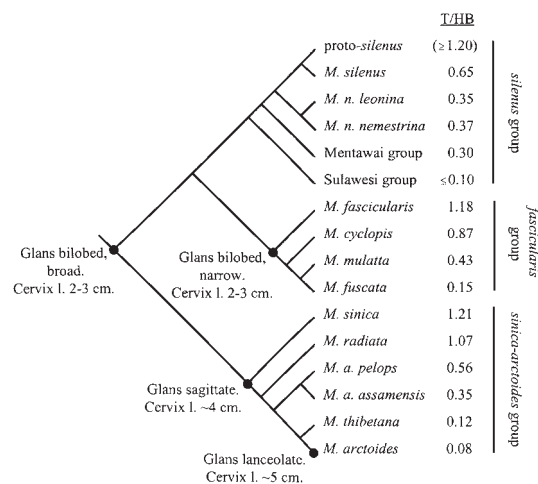


FIG. 15. Phylogenetic interrelationships among Asian macaques, inferred from glans penis morphology, uterine cervix length, and relative tail length ($T/HB = \text{tail length}/\text{head and body length}$). Relative tail length values specified for extant species and subspecies are mean values in samples of adult males; the value specified for *proto-silenus* is hypothetical. References: Reproductive morphology—Fooden, 1975, p. 28; 1980, p. 1; 1988, p. 19; 1990, pp. 627, 659; see above, Reproduction. Relative tail length—Fooden, 1975, pp. 5, 80, 119; 1980, p. 7; 1988, p. 6; 1990, p. 620; see above, External Measurements.

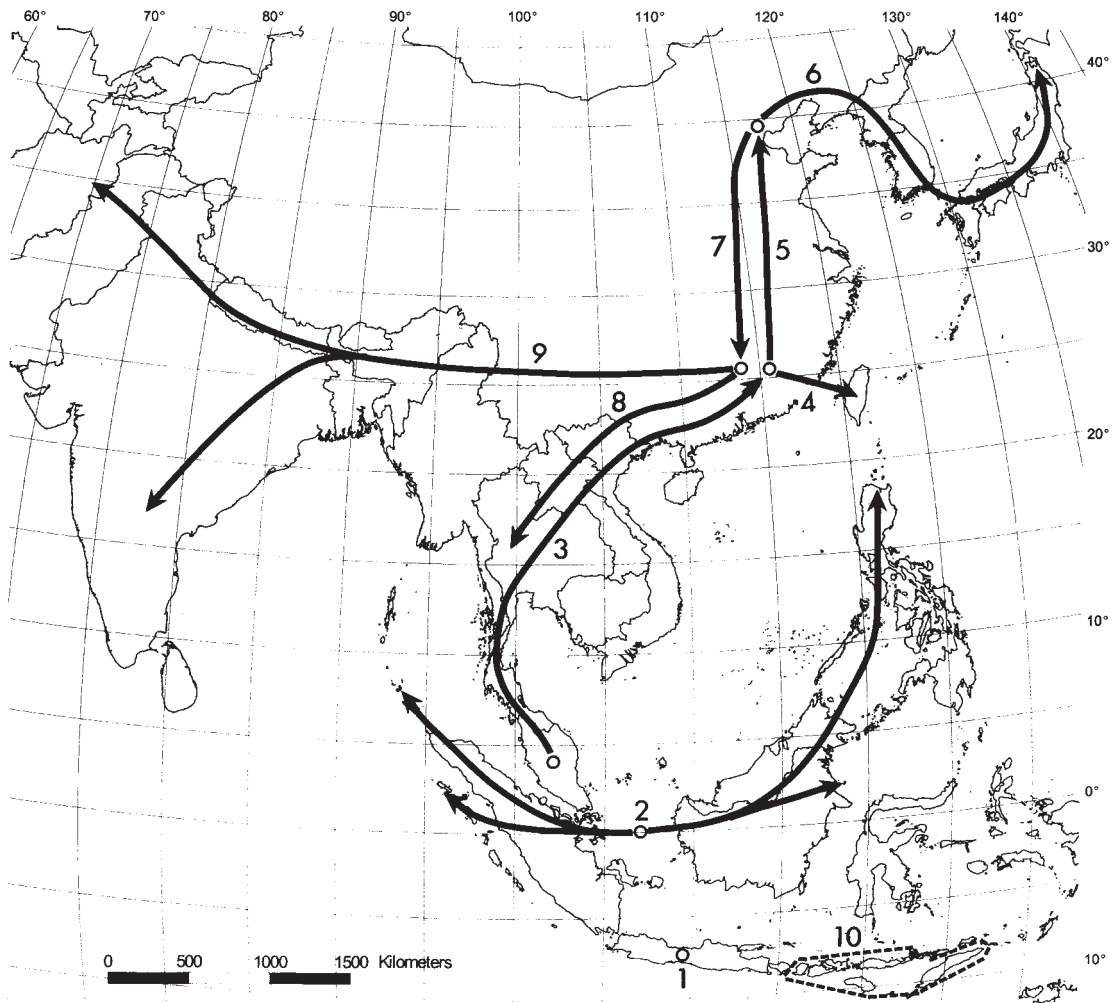


FIG. 16. Hypothetical stages in evolution and dispersal of *fascicularis*-group species of *Macaca* (cf. Figs. 1, 15; Fooden, 1995, p. 87; 2000, p. 87; Fooden & Wu, 2001, p. 36; Fooden & Aimi, 2005, p. 83). Key to indicated dispersal stages: (1) Java—earliest known occurrence of *M. fascicularis* (or close relative) and *fascicularis* group (900 Ka). (2) Dispersal of *M. fascicularis* to deep-water islands on Sunda Shelf; numerous dispersals to shallow-water islands not indicated. (3) Northward dispersal of *M. cyclopis* progenitor to latitude of Taiwan. (4) Dispersal of *M. cyclopis* progenitor to Taiwan (≥ 300 Ka). (5) Northward dispersal of *M. mulatta* progenitor to latitude of Korean peninsula. (6) Dispersal of *M. fuscata* progenitor to Japanese archipelago (430–630 Ka). (7) Southward dispersal of *M. mulatta* to latitude of Taiwan; displacement of *M. cyclopis* progenitor. (8) Southward dispersal of *M. mulatta* to Indochinese peninsula; hybridization with *M. fascicularis*. (9) Westward dispersal of *M. mulatta* to Indian peninsula and Hindu Kush; displacement of *M. radiata* and/or *M. assamensis*. (10) Human introduction of *M. fascicularis* on Nusa Penida–Pulau Timor island chain (ca. 4 Ka).

ejaculation). Although available evidence indicates that MME is the more common copulatory type in *M. mulatta* and *M. fuscata*, evidence is insufficient to indicate which type—if either—is more common in *M. fascicularis* and *M. cyclopis* (cf. Thierry et al., 2000, p. 718). The reported number of intromissive thrusts per mount in both SME and MME copulations varies from 1

to ca. 30, and the duration of each mount is less than 1 minute—probably usually less than 15 seconds. In *M. fascicularis*, the reported number of mounts per sequence in MME copulations varies from 2 to 6, and the duration of MME sequences varies from 2 to 85 minutes; in *M. mulatta* and *M. fuscata*, the reported number of mounts per sequence may be much

greater—as many as 59 and 100 mounts per sequence, but the reported duration of MME sequences is similar—up to 60 minutes or more; comparable information for *M. cyclopis* is unavailable.

Copulation frequency and fertilization success apparently are generally correlated with male dominance rank in studied groups of *M. fascicularis*, *M. mulatta*, and *M. cyclopis* (Fooden, 1995, p. 60; 2000, p. 73; Fooden & Wu, 2001, p. 29). Published evidence concerning the possibility of such correlations in *M. fuscata* is equivocal (Fooden & Aimi, 2005, p. 60).

Reproductive Rate Factors

Limited available evidence suggests that *M. fuscata* may differ from other *fascicularis*-group species in age at sexual maturity (greater in *M. fuscata*), gestation length (greater in *M. fuscata*), and annual birth rate (lower in *M. fuscata*) (Table 9). These differences may indicate that *M. fuscata* is more K-selected than other *fascicularis*-group species (cf. Gould, 1977, p. 290); if so, the greater K-selection presumably is related to *M. fuscata*'s relatively cool habitat, which is the northernmost of any species in the *fascicularis* group—or in the genus *Macaca*.

In females in nonprovisioned populations of *fascicularis*-group species, biennial births apparently are more frequent than annual births (Table 9).

Fossils

Tentatively assuming that relevant fossils have been correctly identified by their reporters, it may be hypothesized that *M. fascicularis* (or a closely related species) inhabited the Sundaic subregion (Java) by 900 Ka (thousand of years ago), that *M. mulatta* inhabited the Indochinese subregion 40–120 Ka, that *M. cyclopis* inhabited Taiwan at least ca. 300 Ka, and that *M. fuscata* inhabited Honshu at least 430 Ka (Table 10). It should be emphasized that all these ages are minimum values for the existence of the respective species; although the oldest known fossils of *M. mulatta*, for example, are dated at ≤ 120 Ka, this species presumably was actually extant before 430 Ka because *M. fuscata* apparently is descended from an *M. mulatta*-like ancestor (cf. Fooden, 2000, p. 88). Evolution

and dispersal of the *fascicularis* group (see below) apparently has been in progress at least since the late Early Pleistocene and presumably was profoundly influenced by the global cooling and sea-level depression that accompanied at least five major glacial episodes (Rohling et al., 1998, p. 163).

Evolution and Dispersal

The *fascicularis* group of macaques is defined by distinctive morphology of the glans penis (Figs. 13, 15). Judging from intragroup variation in relative tail length ($T/HB = \text{tail length/head and body length}$), the least-derived extant species in the group is *M. fascicularis* ($T/HB \sim 1.20$) (Figs. 1, 6; Table 1), which is distributed mainly in the Sundaic subregion (Fig. 1). More derived species in this group are allopatrically, parapatrically, or marginally sympatrically distributed north of *M. fascicularis*, which suggests a relatively simple scenario, outlined below, concerning the group's evolution and dispersal (Fooden, 1972 [“1971”], p. 310; 1980, p. 6; cf. Delson, 1980, p. 26; Abegg & Thierry, 2002, p. 570; Chu & Lin, 2004, p. 101).

The progenitor of the *fascicularis* group presumably was a now-extinct long-tailed ($T/HB \geq 1.20$) member of the *silenus* group (Fig. 15, “proto-*silenus*”), but available evidence is insufficient to indicate the location and date of the *fascicularis* group's origin. Wherever and whenever this group originated, Javanese fossils of *M. fascicularis* (or a close relative) indicate that the group had become established within its present Sundaic geographic range at or before 900 Ka (Fig. 16, stage 1; Table 10; Hooijer, 1962a, p. 50; van den Bergh et al., 2001, p. 389), and this presumably implies prior sea-level depression and exposure of a land bridge to Java (van den Bergh et al., 2001, p. 399; cf. Woodruff, 2003, p. 558; de Bruyn et al., 2005, p. 374). Relative tail length in ancestral *M. fascicularis* probably was ca. 1.20 (Fig. 15). From the Sunda Shelf, *M. fascicularis* apparently was able to disperse—to unknown dates, probably by rafting—to surrounding deep-water islands (southern Nicobars; Pulau Simeulue; P. Lasia; P. Maratua; Philippines) (Fig. 16, stage 2; Fooden, 1995, p. 88). Dispersal to shallow-water islands on the Sunda Shelf presumably occurred intermittently during Pleistocene glacial episodes of sea-level depres-

sion (Fooden, 1995, p. 95). The geographic range of *M. fascicularis* also includes deep-water Lesser Sunda islands, east of Bali, but this probably is the result of relatively recent (ca. 4 Ka) introduction by humans (Fig. 16, stage 10; Fooden, 1995, p. 96; van den Bergh et al., 2001, p. 397).

The *M. fascicularis* stock apparently also dispersed northward into eastern Asia, where it encountered cooler temperatures—to which it became adapted, in part by tail length reduction (Fig. 16, stage 3; Fooden, 2000, p. 87); this would be in accord with Allen's rule (Mayr, 1963, p. 323). An early stage in *fascicularis*-group tail length reduction is probably represented by relative tail length in *M. cyclopis* (T/ HB ~0.90), which apparently dispersed from the mainland opposite Taiwan to Taiwan by ca. 300 Ka (Fig. 16, stage 4; Table 10). The mainland progenitors of *M. cyclopis* apparently were subsequently replaced at that latitude by a southward-dispersing population of *M. mulatta* (see below).

Further northward dispersal in eastern Asia, to the latitude of the Korean peninsula, apparently was accompanied by further tail length reduction and differentiation of *M. mulatta* (T/ HB ~0.45) (Fig. 16, stage 5; Fooden, 2000, p. 87). During one or two glacial episodes of sea-level depression ca. 430–630 Ka, an *M. mulatta*-like population apparently dispersed via the Korean peninsula to the Japanese archipelago (Fig. 16, stage 6; Fooden & Aimi, 2005, p. 83); this dispersal apparently was accompanied by further tail length reduction and differentiation of *M. fuscata* (T/ HB ~0.15). Like most other endemic species of Japanese nonvolant terrestrial mammals, *M. fuscata* apparently has not been able to disperse northward across the Tsugaru Strait, from Honshu to Hokkaido (Fooden & Aimi, 2005, p. 83).

Subsequently, perhaps during a glacial episode, *M. mulatta* apparently dispersed southward and supplanted the mainland progenitor of *M. cyclopis* (Fig. 16, stage 7). As a result of further southward dispersal to the Indochinese peninsula (Fig. 16, stage 8), marginal contact between *M. mulatta* and *M. fascicularis* apparently became established, and interspecific hybridization has subsequently occurred (Fooden, 1997, p. 228; 2000, p. 89; Tosi et al., 2002, p. 172). *Macaca mulatta* also has dispersed westward to the Indian peninsula and the Hindu Kush mountains (Fig. 16, stage 9) and, concom-

itantly, has probably supplanted *M. radiata* and/or *M. assamensis* in the northern part of the Indian peninsula (Fooden, 1988, p. 34; cf. Wada, 2005, p. 118); the southward dispersal of *M. mulatta* on the Indian peninsula apparently has been subject to ecological constraints similar to those that have controlled the southward dispersal of this species on the Indochinese peninsula (see above, Geographic Distribution; Total Population Estimates).

As *fascicularis*-group populations dispersed northward, their body size apparently tended to increase as an adaptation to cooler temperatures (Figs. 3, 4, 8; Tables 1, 2); this is in accord with Bergmann's rule (Mayr, 1963, p. 320). Molting and reproductive seasonality, both of which are conspicuous in *M. cyclopis*, *M. mulatta*, and *M. fuscata* but are weak or absent in *M. fascicularis*—the only tropical member of this species group—may also be adaptations to cooler and more seasonal climates. As indicated above (see Reproduction), the K-selection attributes of *M. fuscata* (late sexual maturity, long gestation period, low annual birth rate) may be adaptations to the northern geographic distribution of this species.

Facial skin coloration and sexual skin development are relatively inconspicuous in *M. fascicularis* (see above, Pelage; Table 8); the evolutionary significance of minimization in *M. fascicularis* of these characters—which presumably serve a signaling function—is unclear (cf. Dixon, 1983, p. 87). Also unclear is the significance of the relatively long rostrum and—presumably correlated—the high frequency of sagittal crest development in adult male *M. fascicularis* (see above, Cranial Variation).

Acknowledgments

For valuable advice and assistance, I thank M. Aimi (PRIKU), S. O. Bober (FMNH), S. D. Nash (Conservation International), R. J. Timmins (Wildlife Conservation Society), H. K. Voris (FMNH), J. Weinstein (FMNH), and H.-Y. Wu (NDHU). I also thank E. Delson (AMNH), S. Frost (University of Oregon, Eugene), C. Groves (Australian National University, Canberra), and J. R. Voight (FMNH) for their careful reviews of a previous draft of the manuscript. This

research was partly supported by the Barbara E. Brown Fund for Mammal Research.

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Appendix I. Supplementary Locality Records of *Macaca fascicularis* and *M. mulatta*

Abbreviations of Generic Terms

NBCA National Biodiversity Conservation Area

PNBCA Proposed National Biodiversity Conservation Area

Macaca fascicularis

(Supplement to Fooden, 1991, p. 2; 1995, p. 2; 1996, p. 855; 1997, p. 226)

CAMBODIA

Kan Chan, O; Stoeng Treng Prov.; ca. 13°40'N, 106°31'E; observed 16 May 1998 by R. J. Timmins and Men Soriyun (1998, p. 35).

Kong River, N bank; Stoeng Treng Prov.; 13°53'N, 106°18'E; observed 11 Nov. 2002 by R. J. Timmins, Pech Bunnat, and Prum Sovanna (2003, p. 16).

Kong River, S bank; Stoeng Treng Prov.; 13°52'N, 106°18'E; observed 11 Nov. 2002 by R. J. Timmins, Pech Bunnat, and Prum Sovanna (2003, p. 16).

Senmonorom; Mondol Kiri Prov.; ca. 12°27'N, 107°12'E; captive observed in market 8 May 2000 by R. J. Timmins and Ou Ratanak (2001, p. 194).

Tonle San, N bank, above Phum Svay Rieng; Stoeng Treng Prov.; 13°42'N, 106°32'E; observed 14 May 1998 by R. J. Timmins and Men Soriyun (1998, p. 35).

Tonle San, N of Taveng area; Rotanokiri Prov.; ca. 14°05'N, 107°10'E; captive observed 10 May–13 June 1998 by R. J. Timmins and Men Soriyun (1998, p. 35).

Tonle San, S bank, 500 m below Phum Talat; Stoeng Treng Prov.; 13°46'N, 106°37'E; observed 13 May 1998 by R. J. Timmins and Men Soriyun (1998, p. 35).

Tonle San, S bank, below Phum Pakalan; Rotanokiri Prov.; 13°57'N, 106°46'E; observed 17 May 1998 by R. J. Timmins and Men Soriyun (1998, p. 35).

Tonle Stripok, S bank, Camp Island vicinity; Rotanokiri Prov.; 13°33'N, 106°45'E; observed 1 June 1998 by R. J. Timmins and Men Soriyun (1998, p. 35).

INDIA

Great Nicobar Island; Andaman & Nicobar Islands (territory); ca. 6°45'–7°14'N, 93°38'–93°57'E; 53 groups observed Dec. 1999–Feb. 2000 by G. Umapathy et al. (2003, pp. 286, 287).

Katchal Island; Andaman & Nicobar Islands (territory); ca. 7°52'–8°02'N, 93°18'–93°28'E; 18 groups observed Dec. 1999–Feb. 2000 by G. Umapathy et al. (2003, pp. 286, 289).

Little Nicobar Island; Andaman & Nicobar Islands (territory); ca. 7°14'–7°26'N, 93°37'–93°45'E; 17 groups observed Dec. 1999–Feb. 2000 by G. Umapathy et al. (2003, pp. 286, 288).

LAOS

Dong Hua Sao NBCA; Champasak Prov.; ca. 15°00'N, 106°00'E; reported present 1992–1998 by J. W. Duckworth et al. (1999, p. 170).

Dong Kalo, Xe Pian NBCA; Champasak Prov.; ca. 14°05'N, 106°00'E; observed Nov. 1992–May 1993 by J. W. Duckworth et al. (1994, p. 187).

Dong Khanthung PNBCA; Champasak Prov.; ca. 14°10'N, 105°20'E; reported present 1992–1998 by J. W. Duckworth et al. (1999, p. 170).

Phou Xiang Thong NBCA; Champasak Prov.; ca. 15°35'N, 105°35'E; reported present 1992–1998 by J. W. Duckworth et al. (1999, p. 170).

Xe Kong, Xe Pian NBCA, ≤844 m; Champasak Prov.; ca. 14°35'N, 106°25'E; observed Nov. 1992–May 1993 by J. W. Duckworth et al. (1994, p. 187).

Xe Pian, lower, 80 m; Champasak Prov.; ca. 14°27'N, 106°20'E; observed Mar.–May 1995 by T. D. Evans et al. (2000, pp. 71, 77).

Xe Pian NBCA, main block, degraded; Champasak Prov.; ca. 14°30'N, 106°00'E; observed Nov. 1992–May 1993 by J. W. Duckworth et al. (1994, p. 187).

Xe Pian river, near Ban Houayko, Bolovens Southwest PNBCA, 320–340 m; Champasak Prov.; ca. 15°00'N, 106°31'E; observed 10–22 Apr. 1995 by T. D. Evans et al. (2000, p. 77; cf. Duckworth et al., 1999, p. 170).

VIETNAM

Bai Cahn, Hon; Tra Vinh Prov. (province uncertain); ca. 8°40'N, 106°41'E; observed 20

- Mar.–13 Apr. 1987 by G. Kuznetsov (2000, pp. 358, 361).
- Can Gio Mangrove Park, 0–1.8 m; Ho Chi Minh City; 10°23'N, 106°51'E; field studies conducted 1999–2001 by Vo Dinh Son (2002a, p. 4; 2002b, p. 1; 2003a, p. 9; 2003b, p. 1; 2004, p. 1).
- Cham, Cu Lao; Quang Nam–Da Nang Prov.; ca. 15°57'N, 108°30'E; observed 20 Mar.–13 Apr. 1987 by G. Kuznetsov (2000, pp. 358, 361).
- Eakar District Reserve; Dac Lac Prov.; ca. 12°56'N, 108°18'E; observed and photographed Mar. 1997 by Vu Ngoc Thanh (1998, abstract no. 087; pers. comm., Dec. 1997).
- Tho Chu, Dao; Kien Giang Prov. (province uncertain); 9°18'N, 103°29'E; observed 20 Mar.–13 Apr. 1987 by G. Kuznetsov (2000, pp. 358, 361).
- 1998 by J. W. Duckworth et al. (1999, p. 166; cf. Duckworth, 1996, p. 218).
- Theun-Hinboun dam site, few miles below Keng Maiha. Nam Kading NBCA; Khammouan Prov.; ca. 18°15'N, 104°30'E; observed 24 Dec. 1994–29 Apr. 1995 by T. D. Evans et al. (2000, p. 77; cf. Duckworth et al., 1999, p. 166).
- Xe Bang–Nouan NBCA, central hills; Saravan Prov. or Savannakhet Prov.; ca. 15°53'N, 105°55'E; observed 27 May–8 Jul. 1994 by T. D. Evans et al. (2000, p. 77; cf. Duckworth et al., 1999, p. 170).
- Xe Bang–Nouan NBCA, western lowlands; Saravan Prov. or Savannakhet Prov.; ca. 15°53'N, 105°45'E; observed 27 May–8 Jul. 1994 by T. D. Evans et al. (2000, p. 77; cf. Duckworth et al., 1999, p. 170).
- Xe Namnoy dam site vicinity, Bolovens North-east PNBCA, 800 m; Attapu Prov. or Champasak Prov.; ca. 15°02'N, 106°37'E; observed Mar. 1995 by T. D. Evans et al. (2000, p. 77; cf. Duckworth et al., 1999, p. 170).

Macaca mulatta

(Supplement to Fooden, 1997, p. 226; 2000, p. 2)

LAOS

- Hin Namno NBCA; Khammouan Prov.; ca. 17°25'N, 105°50'E; reported present 1992–1998 by J. W. Duckworth et al. (1999, p. 168).
- Nakai Plateau; Khammouan Prov.; ca. 17°48'N, 105°11'E; observed 4 Feb.–29 Apr. 1994 and 30 Jan.–17 Mar. 1995 by T. D. Evans et al. (2000, p. 77).
- Nam Leuk dam site, Muang Hom road, Phou Khaokhoay NBCA, ca. 300 m; Vientiane Prov.; ca. 18°25'N, 103°05'E; observed Oct. 1994 and 30 Jan.–17 Mar. 1995 by T. D. Evans et al. (2000, p. 76; cf. Duckworth et al., 1999, p. 166).
- Nam Ou, Phou Dendin NBCA; Phongsali Prov.; ca. 22°00'N, 102°15'E; observed 24 May–2 Jun. 1995 by T. D. Evans et al. (2000, p. 76; cf. Duckworth et al., 1999, p. 166).
- Nam Theun Extension PNBCA; Khammouan Prov.; ca. 18°40'N, 105°05'E; reported present 1992–1998 by J. W. Duckworth et al. (1999, p. 166).
- Sangthong District; Vientiane Prov.; ca. 18°20'N, 102°00'E; reported present 1992–

THAILAND

- Mai Sot Yai, Phu Khieo Wildlife Sanctuary; Chaiyaphum Prov.; 16°27'N, 101°38'E; observed Dec. 2000–Sep. 2001 by C. Borries et al. (2002, p. 80).

VIETNAM

- Ba Be, ca. 200 m; Cao Bang Prov.; 22°24'N, 105°37'E; observed Oct.–Dec. 1996 by M. Hill (1999, pp. 66, 69).
- Ba Na, ca. 300–1440 m; Quang Nam–Da Nang Prov.; ca. 16°00'N, 108°00'E; observed Jul.–Sep. 1995 by M. Hill (1999, pp. 66, 68).
- Ban Sen; Quang Ninh Prov.; ca. 20°59'N, 107°31'E; collected 1988–1992 by National Central Research Institute of Vietnam (Kuznetsov, 2000, pp. 358, 361).
- Dang Khoa, Dao; Quang Ninh Prov.; ca. 21°02'N, 107°35'E; collected 20 Mar.–13 Apr. 1987 by G. Kuznetsov (2000, pp. 358, 361, 363).
- Kaitien; Quang Ninh Prov.; ca. 21°04'N, 107°47'E; observed 1988–1992 by National Central Research Institute of Vietnam (Kuznetsov, 2000, pp. 358, 361).

Muong Nhe, 300 m and 500 m; Lai Chau Prov.; ca. 22°13'N, 102°28'E; observed Jan.–Mar. 1997 by M. Hill (1999, pp. 66, 69).

Phong Nha–Ke Bang Proposed National Park; Quang Binh Prov.; ca. 17°34'N, 106°04'E; reported present before 1996 by R. J. Timmins et al. (1999, p. 23).

Phuong Hoang, Dao; Quang Ninh Prov.; ca. 20°47'N, 107°24'E; observed 20 Mar.–13 Apr. 1987 by G. Kuznetsov (2000, pp. 358, 361).

Pu Huong, 400–1580 m; Nghe An Prov.; 19°22'N, 104°52'E; observed Apr.–Jun. 1995 by M. Hill (1999, pp. 66, 69).

Species Identifications Tentative or Uncertain

LAOS

Dakling, near, ca. 750 m; Sekong Prov.; ca. 15°44'N, 106°57'E; skulls tentatively identified as *M. fascicularis* collected in 1993–1994 by W. Bergmans (1995, pp. 287, 290).

Dong Ampham NBCA; Attapu Prov.; ca. 14°55'N, 107°20'E; uncertain report of *M. fascicularis*, 1992–1998, by J. W. Duckworth et al. (1999, p. 170).

Nam Et NBCA; Louang Houaphan Prov.; ca. 20°30'N, 103°35'E; uncertain report of *M. mulatta*, 1992–1998, by J. W. Duckworth et al. (1999, pp. 166, 170).

Nam Ha NBCA; Louang Namtha Prov.; ca. 20°50'N, 101°10'E; uncertain report of *M.*

mulatta, 1992–1998, by J. W. Duckworth et al. (1999, pp. 166, 170).

Phou Ahyon; Sekong Prov.; ca. 15°45'N, 107°05'E; uncertain report of *M. mulatta*, 1992–1998, by J. W. Duckworth et al. (1999, pp. 166, 170).

Phou Khathong PNBCA; Sekong Prov.; ca. 15°05'N, 106°55'E; uncertain report of *M. mulatta*, 1992–1998, by J. W. Duckworth et al. (1999, pp. 166, 170).

Phu Tje, mountain near Tangiung, ca. 1050 m; Sekong Prov.; ca. 15°30'N, 107°02'E; skull tentatively identified as *M. fascicularis* collected in 1993–1994 by W. Bergmans (1995, pp. 287, 290).

Xe Sap NBCA; Saravan Prov.; ca. 16°10'N, 107°00'E; uncertain report of *M. mulatta*, 1992–1998, by J. W. Duckworth et al. (1999, pp. 166, 170).

VIETNAM

Ma Da; Dong Nai Prov.; ca. 11°14'N, 106°55'E; *M. mulatta* reportedly observed Oct. 1989–Apr. 1990 by V. Y. Sokolov et al. (1991, p. 105); this and the following locality are more than 300 km south of previously known records of *M. mulatta*.

Suoi Mok; Binh Thuan Prov.; ca. 11°05'N, 108°25'E; *M. mulatta* reported in May 1990 to V. Y. Sokolov et al. (1991, p. 109); see comment in preceding entry.

Appendix II

**Appendix II. Centrum Length of Caudal
Vertebrae in *Fascicularis*-Group Species
of *Macaca*.¹**

Specimen no.	Caudal vertebra no.												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>M. fascicularis</i> , adult males													
FMNH 62273	12.6	14.3	20.0	26.8	32.3	36.3	36.6	35.2	35.3	32.5	32.5	31.0	28.3
FMNH 62275	12.0	13.8	19.5	27.8	32.9	36.8	35.7	36.1	35.1	34.3	32.5	d ²	d ²
FMNH 62276	11.2	15.6	19.5	26.4	32.5	36.9	37.0	36.9	36.1	34.9	31.7	30.6	29.7
FMNH 68701	11.4	13.4	18.6	24.7	32.0	37.6	38.3	38.1	38.1	35.1	35.1	33.0	30.7
Means	11.8	14.3	19.4	26.4	32.4	36.9	36.9	36.6	36.2	34.2	33.0	31.5	29.6
<i>M. fascicularis</i> , subadult males													
FMNH 56161	9.0	12.8	19.0	24.4	31.3	36.5	35.3	35.9	34.5	34.2	31.7	28.9	27.8
FMNH 105689	13.1	13.0	18.4	26.0	33.3	37.2	37.4	36.7	36.3	35.1	34.6	32.4	30.3
IRSN 2417	9.8	11.5	16.5	23.7	26.3	30.8	30.7	31.0	29.7	28.9	27.4	25.4	24.5
<i>M. fascicularis</i> , juvenile male													
ZMUZ 11630	7.3	10.3	11.5	15.0	20.2	21.6	24.0	24.4	24.3	22.6	21.8	21.0	20.0
<i>M. fascicularis</i> , infant female													
NHRM Z3325	5.3	7.3	6.4	9.5	11.7	15.4	16.8	16.8	16.5	15.0	16.3	15.0	14.1
<i>M. fascicularis</i> / <i>M. mulatta</i> intergrade, subadult male													
FMNH 99657	11.9	13.0	15.7	23.2	30.1	30.1	29.6	29.6	26.8	26.8	24.6	22.5	20.1
<i>M. mulatta</i> , adult males													
FMNH 54253	11.3	10.7	12.4	14.7	20.3	21.3	21.8	21.4	19.8	18.0	16.8	14.0	12.4
NHRM Z1535	10.7	8.8	8.9	12.8	17.4	21.5	23.3	23.2	21.6	19.5	18.5	15.9	13.6
ZMUZ 11728 ³	10.8	11.6	14.7	16.1	21.5	23.0	20.5	18.0	16.7	14.3	11.9	11.2	9.8
Means ³	11.0	9.8	10.7	13.8	18.8	21.4	22.6	22.3	20.7	18.8	17.6	15.0	13.0
<i>M. mulatta</i> , adult female													
NHRM Z839	8.0	9.5	11.2	14.7	20.0	21.2	20.8	18.7	18.5	15.9	14.5	12.6	10.8
<i>M. mulatta</i> , juveniles													
ZMUZ 11726	9.4	8.4	12.3	16.2	19.6	21.7	21.7	19.9	17.9	17.1	14.6	13.2	10.6
ZMUZ 11727	9.6	9.5	10.8	13.8	19.4	22.8	24.2	22.8	21.4	19.8	17.5	15.7	13.0
<i>M. cyclopis</i> , adult males													
ZMB 26554	15.5	15.0	16.0	19.8	24.0	29.1	31.5	32.4	33.1	33.1	30.5	28.8	25.6
ZMB 26556	14.8	13.4	13.5	17.8	24.0	30.7	29.8	35.6	32.8	31.5	29.4	26.8	24.1
Means	15.2	14.2	14.8	18.8	24.0	29.9	30.6	34.0	33.0	32.3	30.0	27.8	24.8
<i>M. cyclopis</i> , subadult male													
ZMB 26555	13.6	12.8	18.0	22.7	29.2	35.2	33.9	34.9	33.3	31.0	28.5	26.0	23.7
<i>M. cyclopis</i> , adult females													
NDHU ⁵	12.6	12.3	14.6	18.8	24.1	29.2	31.0	33.7	31.1	29.2	27.1	24.7	23.7
ZMB 26553	11.6	12.9	14.7	17.9	23.3	27.9	27.2	25.0	26.7	25.9	23.4	20.4	18.6

Appendix II. *Extended.*

Caudal vertebra no.															
14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
<i>M. fascicularis</i> , adult males															
27.5	25.3	24.1	23.0	20.0	18.3	16.2	12.7	10.6	8.7	7.8	5.8	2.0	2.0	0.9	—
26.7	24.4	23.2	21.2	19.5	d ²	15.6	12.1	9.6	7.6	6.6	4.9	m ⁴	—	—	—
27.8	26.5	24.1	22.0	19.4	18.9	15.0	12.4	10.4	7.8	6.6	4.4	m ⁴	—	—	—
29.6	27.9	25.2	22.1	20.1	17.2	13.7	12.1	11.0	9.0	7.5	4.2	3.3	3.2	1.6	—
27.9	26.0	24.2	22.1	19.8	18.1	15.1	12.3	10.4	8.3	7.1	4.8	2.6	2.6	1.2	—
<i>M. fascicularis</i> , subadult males															
26.8	24.0	22.5	20.2	19.1	16.8	15.0	12.0	11.7	8.5	7.8	5.3	2.8	1.8	—	—
28.0	27.8	26.0	24.4	21.7	20.0	17.5	15.3	11.7	9.0	6.4	4.5	0.8	—	—	—
21.4	20.8	18.8	17.4	14.8	12.0	9.6	8.4	5.9	4.7	m ⁴	—	—	—	—	—
<i>M. fascicularis</i> , juvenile male															
18.6	16.5	14.5	12.3	10.6	8.8	7.1	6.2	5.3	4.5	3.9	3.0	3.1	—	—	—
<i>M. fascicularis</i> , infant female															
13.1	12.2	12.3	11.4	11.1	9.5	8.3	7.0	6.1	5.5	4.6	3.2	2.6	2.2	2.0	2.0
<i>M. fascicularis</i> / <i>M. mulatta</i> intergrade, subadult male															
18.0	15.1	12.3	9.5	6.7	3.9	2.9	1.7	1.5	1.5	—	—	—	—	—	—
<i>M. mulatta</i> , adult males															
10.7	8.1	6.7	2.4	2.8	—	—	—	—	—	—	—	—	—	—	—
11.9	8.8	6.8	5.5	2.9	2.5	1.9	2.6	—	—	—	—	—	—	—	—
8.2	7.2	5.4	4.0	5.6	m ⁴	—	—	—	—	—	—	—	—	—	—
11.3	8.4	6.8	4.0	2.8	2.5	1.9	2.6	—	—	—	—	—	—	—	—
<i>M. mulatta</i> , adult female															
9.5	7.9	6.5	4.8	3.1	m ⁴	—	—	—	—	—	—	—	—	—	—
<i>M. mulatta</i> , juveniles															
8.6	7.3	5.0	m ⁴	—	—	—	—	—	—	—	—	—	—	—	—
11.1	9.0	m ⁴	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>M. cyclopis</i> , adult males															
25.9	22.8	20.8	18.8	16.3	12.5	10.2	8.8	6.1	4.2	3.3	—	—	—	—	—
21.2	19.8	16.9	14.7	13.0	10.2	7.5	4.9	3.1	2.5	—	—	—	—	—	—
23.6	21.3	18.8	16.8	14.6	11.4	8.8	6.8	4.6	3.4	3.3	—	—	—	—	—
<i>M. cyclopis</i> , subadult male															
21.4	18.6	16.7	10.8	10.1	5.2	4.4	3.3	—	—	—	—	—	—	—	—
<i>M. cyclopis</i> , adult females															
20.0	16.1	14.1	12.4	9.0	7.5	6.0	2.8	2.3	—	—	—	—	—	—	—
16.1	14.0	12.4	10.4	9.0	7.8	5.2	4.7	3.5	2.8	—	—	—	—	—	—

Appendix II. *Continued.*

Specimen no.	Caudal vertebra no.												
	1	2	3	4	5	6	7	8	9	10	11	12	13
	<i>M. cyclopis</i> , juvenile												
ZMB 26366	11.2	11.5	12.8	16.7	21.7	26.7	29.8	29.7	29.3	28.1	27.0	25.9	23.3
	<i>M. fuscata</i> , adult males												
JMC ?601	12.4	10.8	11.1	12.7	15.7	13.7	11.6	9.1	6.7	2.9	2.6	—	—
RMNH 12/a	12.3	12.4	12.7	13.8	15.2	16.2	13.9	9.7	7.5	m ⁴	—	—	—
RMNH 13/b	14.6	11.7	10.7	13.0	14.0	d ²	m ⁴	—	—	—	—	—	—
ZMB 5082	14.9	13.2	11.8	10.5	11.4	12.6	11.5	8.8	7.6	3.5	4.1	f ⁶	—
ZMB Helg1874	13.6	11.5	10.8	12.7	12.2	14.6	12.6	11.3	8.8	5.3	f ⁶	—	—
Means	13.6	11.9	11.4	12.5	13.7	14.5	12.4	9.7	7.6	3.9	3.4	—	—
	<i>M. fuscata</i> , subadult male												
JMC ?925	10.2	9.6	10.5	9.0	12.9	11.4	10.7	8.2	7.8	4.6	3.8	m ⁴	—
	<i>M. fuscata</i> , adult females												
ZMB 13 Feb 74	10.4	9.3	8.8	9.5	12.0	13.5	11.2	8.7	7.5	1.9	1.3	—	—
ZMUZ 11603a	9.9	8.5	9.4	>10.6	12.2	11.2	10.2	8.4	5.5	4.2	4.3	—	—
	<i>M. fuscata</i> , juvenile												
RMNH 5/14/c	7.4	7.4	7.5	9.0	9.2	9.7	7.8	6.4	5.0	3.9	1.8	—	—

¹ Cf. Wilson (1970, pp. 21, 58, 60, 184–185, 196–197), who reports similar measurements in mixed age samples of *M. fascicularis* and *M. mulatta* (maturity of individual specimens not specified).

² Vertebra deformed.

³ Skull deformed, apparently a captive; vertebral measurements excluded from calculation of means.

⁴ Terminal vertebrae missing.

⁵ Hai-Yin Wu collection.

⁶ Terminal vertebrae fused.

Appendix II. Continued/Extended.

Caudal vertebra no.															
14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
<i>M. cyclopis</i> , juvenile															
21.3	18.9	17.1	15.5	12.8	11.4	8.7	6.9	4.8	—	—	—	—	—	—	—
<i>M. fuscata</i> , adult males															
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
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<i>M. fuscata</i> , subadult male															
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<i>M. fuscata</i> , adult females															
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<i>M. fuscata</i> , juvenile															
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—