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TAXONOMY AND EVOLUTION OF LIONTAIL AND PIGTAIL MACAQUES (PRIMATES: CERCOPITHECIDAE)

JACK FOODEN

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TAXONOMY AND EVOLUTION OF
LIONTAIL AND PIGTAIL MACAQUES
(PRIMATES: CERCOPITHECIDAE)

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TAXONOMY AND EVOLUTION OF LIONTAIL AND PIGTAIL MACAQUES (PRIMATES: CERCOPITHECIDAE)

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Dedicated to the memory of Kitti Thonglongya (1930-1974), zoologist, friend, colleague and field companion during 1973 collecting trip to peninsular Thailand.

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INTRODUCTION

Liontail macaques inhabit southwestern India, and three well-defined forms of pigtail macaques inhabit Southeast Asia from eastern Assam to Borneo (fig. 1). No two of these macaques are sympatric. The geographic ranges of liontail macaques and pigtail macaques are separated by a 2000 km. gap; the ranges of recognized forms of pigtail macaques are adjacent but not overlapping. Current taxonomic practice, following Kloss (1919b, p. 138), is to regard liontails as one species (*Macaca silenus* Linnaeus, 1758) and various forms of pigtail macaques as subspecies of another species (*M. nemestrina* Linnaeus, 1766). Although available evidence is not as conclusive as generally assumed (see below), this usage is retained in the present revision.

Liontails (*M. silenus*) and Sundaic pigtails (*M. nemestrina nemestrina*), both described in the eighteenth century, are the best known members of this group. Indochinese pigtails (*M. n. leonina*), described in 1863, are less widely known and are frequently confused with *M. n. nemestrina*. Kepulauan Mentawai pigtails (*M. n. pagensis*), described in 1903 and represented in collections by a total of nine museum specimens, are known only to a few specialists.

The present revision is based on study of 462 museum specimens and review of relevant literature. Specimens examined are preserved in the museums listed below. I am deeply grateful to officials of these institutions for permission to study material in their custody.

- AIUZ Anthropologisches Institut der Universität Zürich
- AMNH American Museum of Natural History, including
Archbold Collection (AMNH-AC), New York
- BM British Museum (Natural History), London
- BNHS Bombay Natural History Society, Bombay
- CTNRC Centre for Thai National Reference Collections,
Applied Scientific Research Corporation of Thailand, Bangkok

FMNH	Field Museum of Natural History, Chicago
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHN	Museum National d'Histoire Naturelle, Paris
MZB	Museum Zoologicum Bogoriense, Bogor
NHMB	Naturhistorisches Museum, Basel
NHMBe	Naturhistorisches Museum, Bern
NHRM	Naturhistoriska Riksmuseet, Stockholm
NMS	Natur-Museum Senckenberg, Frankfurt
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
SMK	Sarawak Museum, Kuching
SMTD	Staatliches Museum für Tierkunde, Dresden
USNM	United States National Museum of Natural History, Washington, D.C.
ZMB	Zoologisches Museum der Humboldt-Universität, Berlin
ZMUZ	Zoologisches Museum der Universität, Zürich
ZRCS	Zoological Reference Collection, University of Singapore (This collection was formerly housed in the Singapore National Museum, also known as Raffles Museum.)
ZSBS	Zoologisches Sammlung des Bayerischen Staates, Munich
ZSI	Zoological Survey of India, National Zoological Collection, Calcutta

Early stages in this research were supported by U.S. Public Health Service Grant No. GM-13113. Final stages were partially supported by Minorities Schools Biomedical Support Grant No. RR-08043 (National Institutes of Health) to Chicago State University. For skillful assistance I thank the following persons: Mr. Kevin Royt, illustrations; Mr. John Bayalis and Mr. Fred Huysmans, Division of Photography, Field Museum of Natural History, photographs; Mrs. Nancy Shortall, typing.

NOTE ADDED IN PROOF: Volume 7 of *Primates: Comparative Anatomy and Taxonomy* by W. C. Osman Hill (John Wiley and Sons, 1974), which includes a discussion of liontail and pigtail macaques (pp. 652-687), was published after the present work had been submitted for publication; no evidence presented by Hill requires modification of the present work.

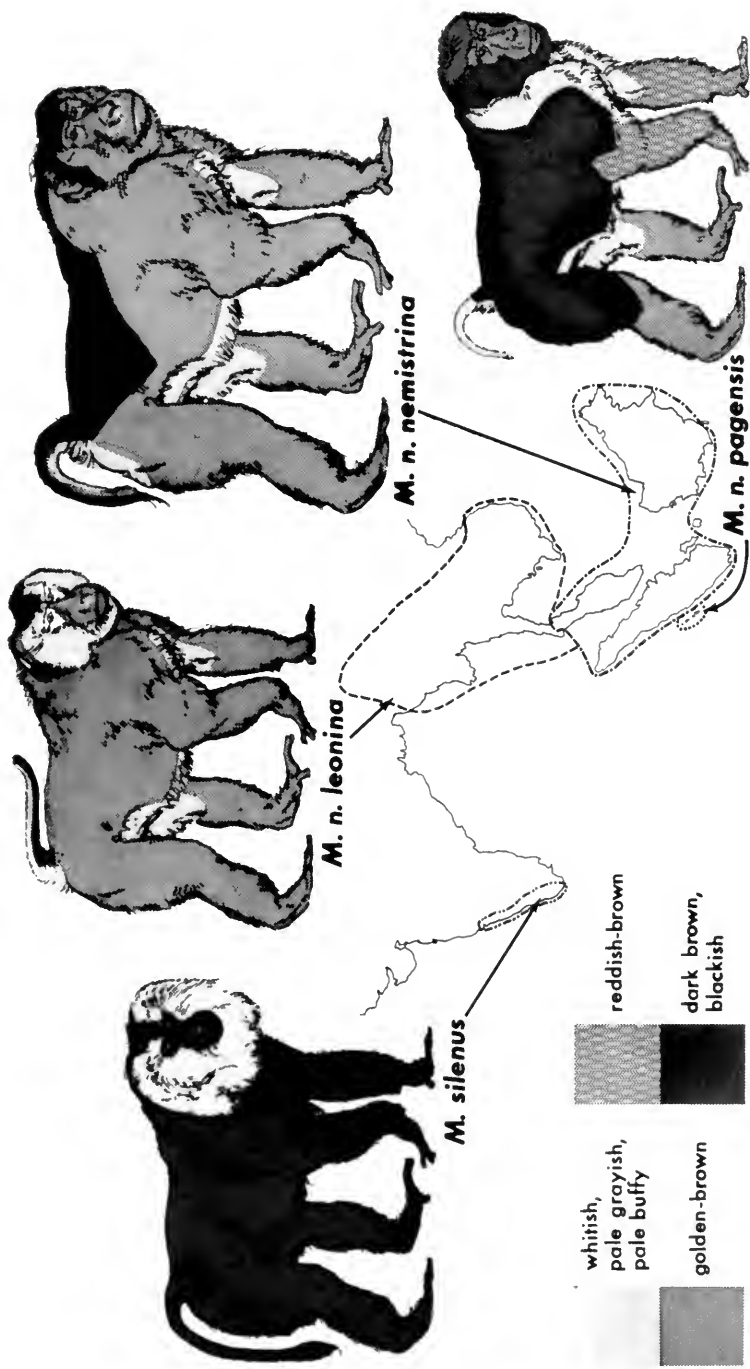


FIG. 1. External characters and geographic distribution in liontail and pigtail macaques; for details of distribution, see maps, Figures 20, 25, 28. Tail carriage in *M. n. pagensis* is unknown and depicted arbitrarily.

GENERIC NAMES APPLIED TO LIONTAIL AND PIGTAIL MACAQUES

- Macaca* Lacépède, 1799, p. 4 – first applied to pigtail macaques by Daudin, [1802], p. 148; synonyms listed below are those applicable to liontail and pigtail macaques only.
- Silenus* Goldfuss, 1820, pp. xxiv, 479 – subgenus of *Cynocephalus*; included species, *C. silenus* (= *Macaca silenus*), type-species by monotypy and tautonymy. Lesson, [1830], p. 101 – subgenus of *Macacus*; included species, *Macacus silenus*, type-species by original designation. Lesson, 1839, p. 70 – genus. J. A. Allen, 1916, p. 51 – genus; selected to replace *Macaca*. Fiedler, 1956, p. 177 – subgenus; external characters.
- Les Maimons: I. Geoffroy, 1826, p. 588 – one of three subdivisions (“petite groups”) recognized within *Macacus*; included species, *M. silenus*, *M. erythraeus* (= *Macaca mulatta*), *M. nemestrinus* (“Le Maimon”), *M. libidinosus* (= *Macaca n. nemestrina*), *M. speciosus* (= *M. fuscata*), *M. maurus*.
- Maimon* Wagner, [1839], p. 141 – subgenus of *Inuus* (= *Macaca*); included species, *I. silenus*, *I. erythraeus* (= *M. mulatta*), *I. nemestrinus* (type-species by tautonymy; Maimon of Buffon cited in synonymy, p. 144), *I. arctoides*, *I. speciosus* (= *M. fuscata*), *I. niger*. J. A. Allen, 1916, p. 50 – invalid designation of *I. erythraeus* as type-species.
- Vetulus* Reichenbach, 1862, p. 125 – genus; included species, *V. silenus* (type-species by tautonymy, synonym), *V. nestor*, *V. ursinus*, *V. priamus*, *V. thersites*.
- Nemestrinus* Reichenbach, 1862, p. 139 (not Latreille, 1802), subgenus of *Macacus*; included species, *M. nemestrinus* (type-species by tautonymy), *M. libidinosus* (= *Macaca n. nemestrina*); preoccupied by *Nemestrinus* Latreille, 1802, p. 437, a genus of Diptera.

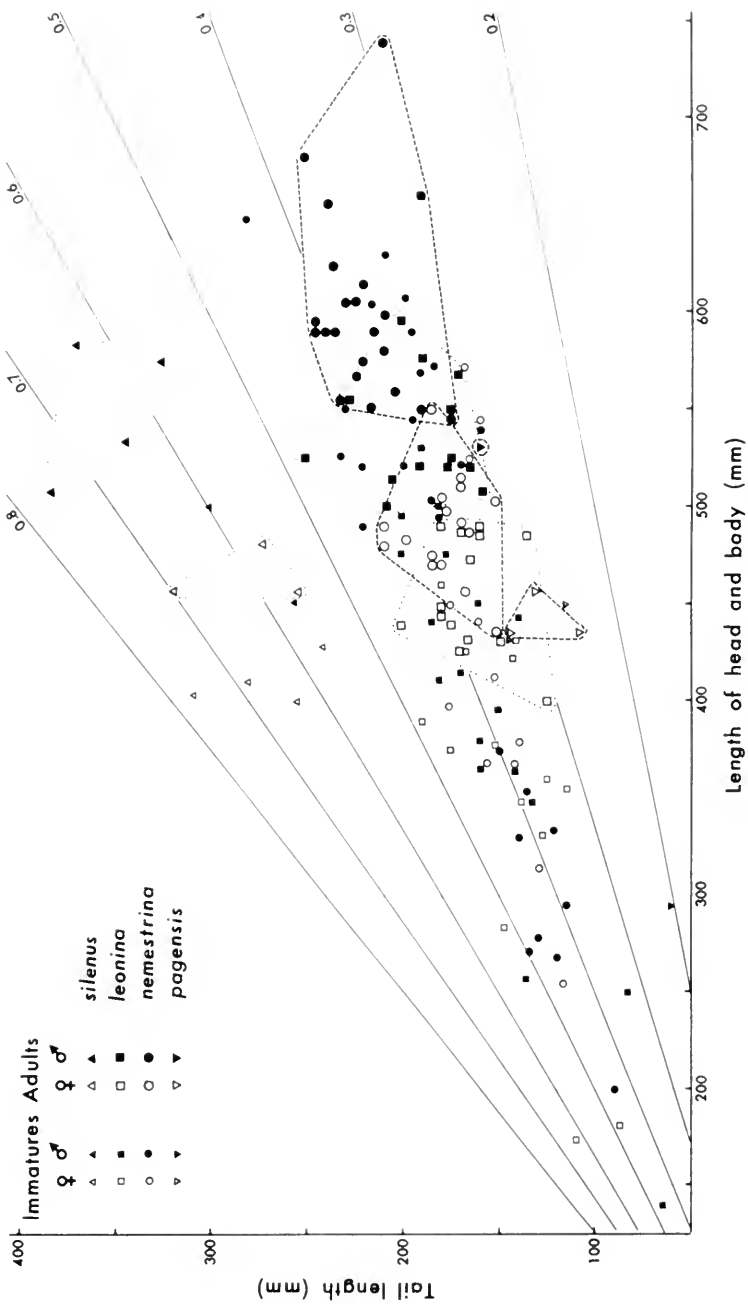


FIG. 2. Relative tail length in immature and adult liontails and pigtails; adult measurements in each species and sex are enclosed by dashed or dotted lines. Included in this graph in addition to measurements of specimens examined, are measurements of six specimens reported by Blanford (1888b, p. 16), Kao Yueh-ting et al. (1962, p. 188), and Pocock (1939, p. 67), and those of two unexamined specimens of *M. n. nemestrina* collected at Abai, Sabah (MCZ, Asiatic Primate Expedition records). The smallest specimen represented in this graph is a fetus (FMNH 99688, mother) of estimated conception age 4 months.

KEY TO EXTERNAL CHARACTERS

Conspicuous external characters of adult male liontail and pigtail macaques (fig. 1) are contrasted in the following key. Details of individual, sexual and ontogenetic variation are discussed in species and subspecies accounts. Although length of head and body averages about 10-20 per cent greater in adult *M. n. nemestrina* than in other members of this group, this character is not absolutely diagnostic because of species overlap (figs. 2, 22).

1. Tail length greater than 50 per cent of combined length of head and trunk. Trunk and limbs blackish; crown patch blackish, narrow anteriorly; cheek ruff and beard prominent, pale grayish-brown; muzzle relatively short.....*Macaca silenus*

Tail length less than 50 per cent of combined length of head and trunk.

Macaca nemestrina, 2

2. Tail thinly furred, skin of tail clearly visible through sparse downy pelage. Trunk chocolate-brown non-agouti dorsally, becoming pale brown ventrally; hind limbs brown, forelimbs reddish-brown; crown patch brown, broad anteriorly; cheek hairs short, lateral surface of throat region sharply defined pale ochraceous-buff; muzzle relatively short*M. n. pagensis*

Tail densely furred, skin of tail completely covered by hair.....3

3. Mid-dorsal region of trunk golden-brown agouti, similar in color to lateral surface of trunk and limbs. Crown patch dark brown, narrow anteriorly; cheek ruff moderately long, pale ochraceous-buff; reddish streaks extending laterally from external angles of eyes; muzzle relatively short; tail carried arched forward over back, tip of tail directed upward and forward.....*M. n. leonina*

Mid-dorsal region of trunk blackish, contrasting with golden-brown agouti color of lateral surface of trunk and limbs. Crown patch blackish, broad anteriorly; cheek hairs short, pale basally, blackish at tips; muzzle long; tail carried arched rearward, tip of tail directed downward.....*M. n. nemestrina*

CRANIAL COMPARISONS

(Figures 3-6)

Cranial characters that appear to be of greatest taxonomic importance in liontail and pigtail macaques are (1) greatest length of skull (excluding incisors), (2) relative zygomatic breadth, (3) relative length of rostrum, (4) length of incisor-canine field and premolar-molar field, (5) morphology of supraorbital ridges, and (6) morphology of malar region. These characters are discussed in the following paragraphs and their variation is graphed in Figures 7-9, 22. The method of measurement, except for dental-field measurements defined below, is described and illustrated elsewhere (Fooden, 1969a, p. 40).

As usual in catarrhines, taxonomic differences in liontails and pigtails are more distinct in skulls of adult males than in skulls of females and immatures. Since only a few adult specimens of *M. n. pagensis* and wild-collected *M. silenus* are available, no attempt has been made to construct a formal key to cranial characters. Two male and three female skulls of *M. silenus* have previously been compared with an unspecified number of skulls of *M. n. nemestrina* (Kurup, 1963, p. 249).

Greatest length of skull averages about 15 per cent larger in *M. n. nemestrina* than in *M. n. leonina*, *M. n. pagensis*, and *M. silenus*, which are approximately equal in this measurement (figs. 7, 22). Overlap between *M. n. nemestrina* and the three smaller subspecies or species is minimal. In specimens examined of *M. n. leonina*, *M. n. pagensis*, and *M. silenus*, the range of greatest skull length is 102.3-121.1 mm. in adult females and 124.1-140.1 mm. in adult males; in *M. n. nemestrina* these ranges are 115.4-138.9 mm. in adult females (only slightly smaller than in adult male *M. n. leonina*, *M. n. pagensis*, and *M. silenus*) and 139.5-174.5 mm. in adult males. Predictably, variation of skull length generally parallels variation of length of head and body in these subspecies and species (figs. 2, 7, 22).



FIG. 3. Anterior and lateral views of adult skulls: *M. silenus* — a, female, RMNH 1314, zoo specimen; b, c, male, FMNH 47322, zoo specimen; *M. n. leonina* — d, female, FMNH 99677, Loc. No. 31; e, f, male, FMNH 99691, Loc. No. 21. Approx. $\frac{1}{2}$ nat. size. (Photos FMNH)

For locality numbers see Figures 20, 25, and 28.

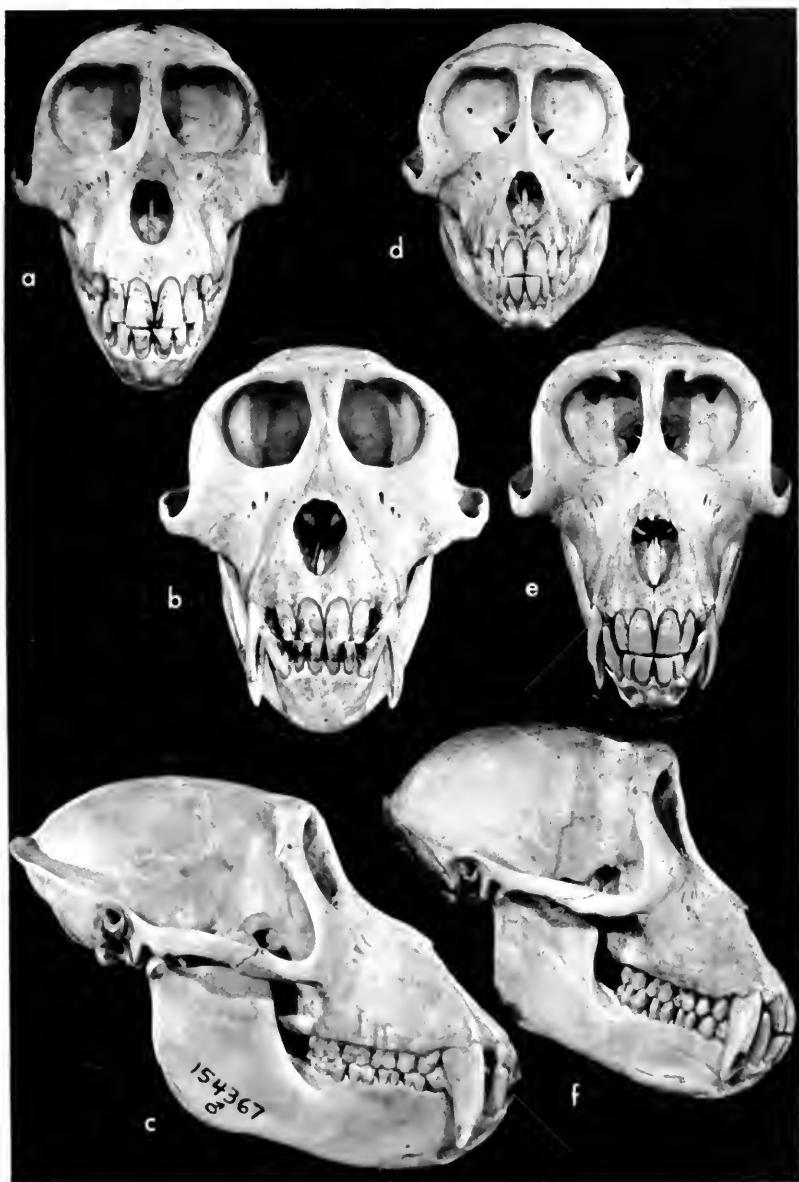


FIG. 4. Anterior and lateral views of adult skulls: *M. n. nemestrina* — a, female, USNM 114502, Loc. No. 30; b, c, male, USNM 154367, Loc. No. 69; *M. n. pagensis* — d, female, AMNH-AC 103398, Loc. No. 93; e, f, male, AMNH-AC 103394, Loc. No. 92. Approx. $\frac{1}{2}$ nat. size. (Photos FMNH)

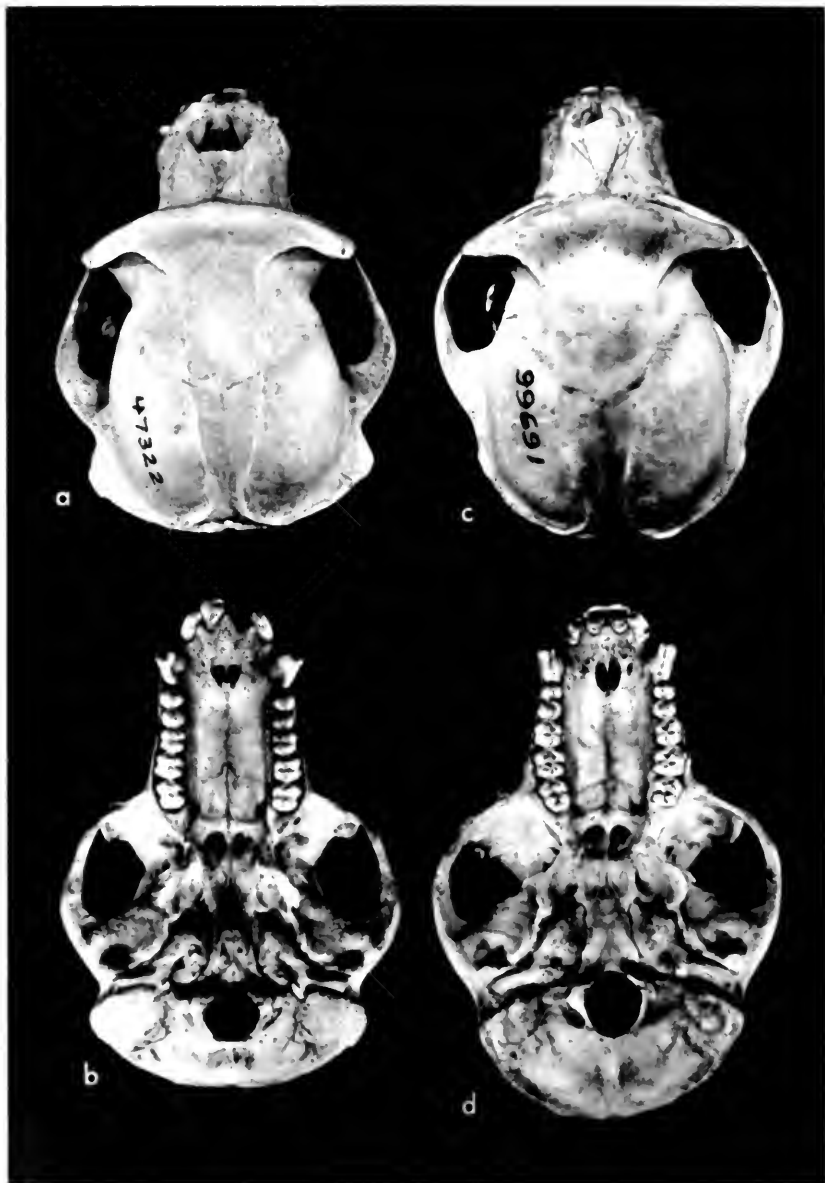


FIG. 5. Dorsal and ventral views of adult male skulls: a, b, *M. silenus*, FMNH 47322, zoo specimen; c, d, *M. n. leonina*, FMNH 99691, Loc. No. 21. Approx. $\frac{1}{2}$ nat. size. (Photos FMNH)

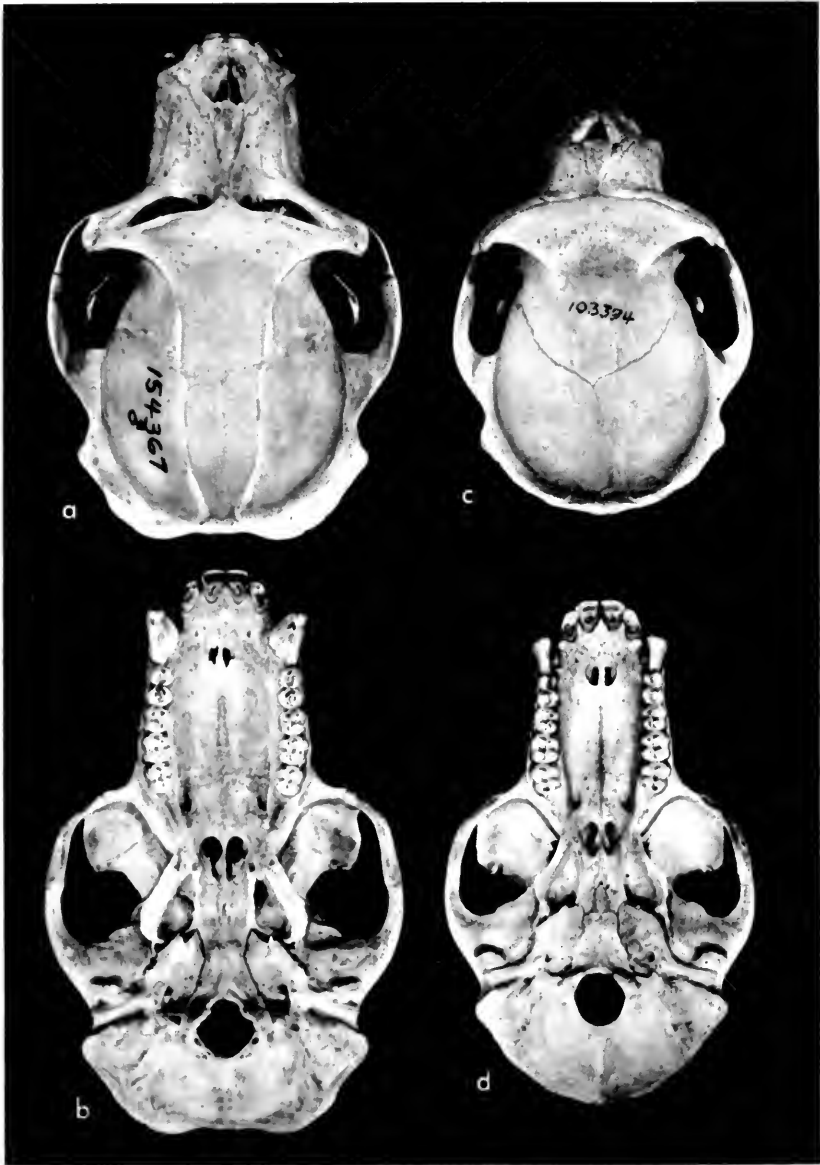


FIG. 6. Dorsal and ventral views of adult male skulls: a, b, *M. n. nemestrina*, USNM 154367, Loc. No. 69; c, d, *M. n. pagensis*, AMNH-AC 103394, Loc. No. 92. Approx. $\frac{1}{2}$ nat. size. (Photos FMNH)

Relative zygomatic breadth (zygomatic breadth/greatest length excluding incisors) in *M. silenus* and *M. n. leonina* tends to be somewhat greater than in *M. n. nemestrina* and *M. n. pagensis* (fig. 7, table 1). Within each subspecies or species this ratio is about the

TABLE 1. Relative zygomatic breadth (zygomatic breadth/greatest skull length x 100) in liontail and pigtail macaques.

Species or subspecies	Mean \pm standard error; sample size indicated by figure in parenthesis		
	Infants and juveniles	Adult females	Adult males
<i>M. silenus</i>	66.43 \pm 0.65 (6)	68.40 \pm 0.88 (7)	68.84 \pm 0.68 (6)
<i>M. n. leonina</i>	64.88 \pm 0.43 (23)	67.39 \pm 0.60 (19)	70.15 \pm 0.58 (17)
<i>M. n. nemestrina</i>	63.26 \pm 0.36 (50)	63.82 \pm 0.39 (35)	64.49 \pm 0.32 (76)
<i>M. n. pagensis</i>	62.89 \pm 1.07 (2)	64.24 \pm 0.68 (3)	63.11 (1)

same in both sexes. In adult specimens examined relative zygomatic breadth varies from 0.58 to 0.71 in *M. n. nemestrina* and *M. n. pagensis* and from 0.63 to 0.75 in *M. silenus* and *M. n. leonina*. In infant and juvenile specimens of all four subspecies and species, zygomatic breadth is relatively narrow, approximately as in adult *M. n. nemestrina* and *M. n. pagensis*. Zygomatic proportions in 12 *M. n. nemestrina* specimens (without locality data) measured by Khajuria (1954, p. 118) fall within the range of variation in specimens examined of that subspecies (fig. 7).

In liontail and pigtail macaques, as in many other catarrhines (Vogel, 1966, p. 21) relative length of rostrum (rostral length/postrostral length) is strongly correlated with skull size (figs. 7, 8). In adult female skulls examined of *M. silenus*, *M. n. leonina*, and *M. n. pagensis*, which are the smallest adult skulls measured, relative rostral length is 0.40-0.55; in adult female skulls of *M. n. nemestrina*, the next larger size class, relative rostral length is 0.47-0.61; in adult male skulls of *M. silenus*, *M. n. leonina*, and *M. n. pagensis*, which average slightly larger than those of female *M. n. nemestrina*, relative rostral length is 0.55-0.61; in adult male skulls of *M. n. nemestrina*, the largest size class in this group of subspecies and species, relative rostral length is 0.62-0.78.

Although relative rostral length in liontails and pigtails varies ontogenetically, sexually, and taxonomically, the composite log-log plot of all measurements available for immature and adult males and females is approximately linear (fig. 8). This indicates that there probably is a constant allometric relationship between rostral

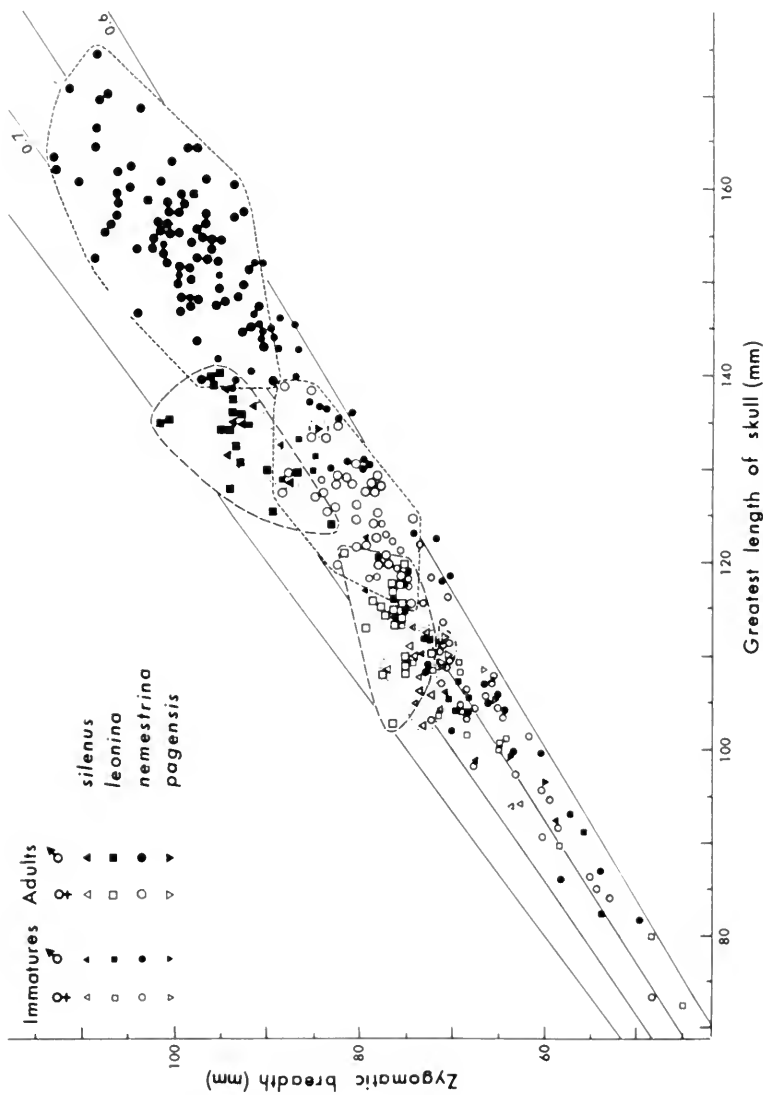


FIG. 7. Relative zygomatic breadth in immature and adult liontails and pigtails; adult measurements for each species or subspecies and sex are enclosed by dashed or dotted lines. This figure, unlike Figure 22, includes measurements of specimens without accurate locality data.

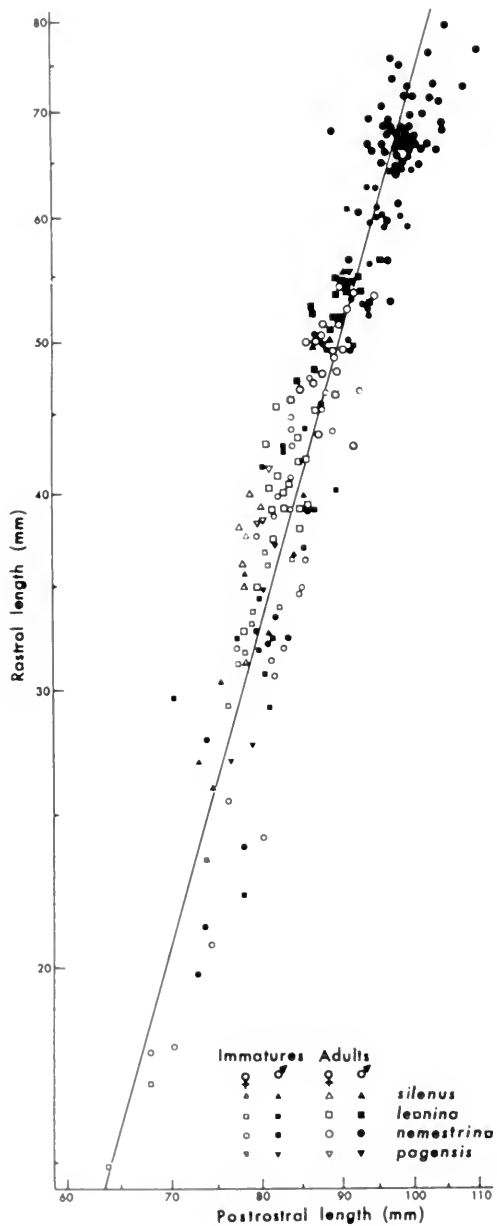


FIG. 8. Allometry of rostral length v. postrostral length in immature and adult liontails and pigtails. Log-log scales; slope = 3.543.

length (y) and post-rostral length (x) in these macaques. The power function equation for this relationship computed (with generous assistance of Dr. Gary E. Eertmoed, Chicago State University) by the method of principal axes is $\log y = 3.543 \log x - 5.222$; 95 per cent confidence limits for the slope are $L_1 = 3.381$ and $L_2 = 3.720$. Numerical values in this power function equation are comparable to those in equations for the relationship between muzzle length and calvaria length in species of baboons studied by Freedman (1962, pp. 121-125); as in the baboon scattergrams, points in Figure 8 for very young specimens tend to lie to the right of the regression line (relative rostral lengths less than expected). The conspicuous sexual and taxonomic differentiation of relative rostral length in adult liontails and pigtails appears, as in baboons (Freedman, 1962, p. 127), to be a result of differential rates of ontogenetic development of a constant allometric relationship between growth of rostrum (facial skeleton) and growth of postrostrum (braincase). Since cranial dimensions are known to be approximately equal in immature male and female *M. n. nemestrina* up to age three years (Swindler et al., 1973, p. 229), the rate differential that results in adult sexual dimorphism of relative rostral length apparently develops (at least in this subspecies) sometime between age three years and the age of physical maturity (probably about age six or seven years).

Rostral length and postrostral length, although allometrically related to each other, are each linearly related to length of component parts of the adult maxillary dental arch (fig. 9). Relevant measurements taken of the dental arch are: (1) total length of arch—perpendicular distance from most anterior point on premaxilla to line passing through most posterior points on alveoli of third molars; (2) length of premolar-molar field—alveolar distance from front of first premolar to rear of last molar (measured on right side, wherever possible); (3) length of incisor-canine field—difference between total length of arch and length of premolar-molar field.

Length of the premolar-molar field typically is 35-40 per cent of postrostral length in both sexes of all four subspecies and species of adult liontails and pigtails (fig. 9a); similarly, length of the incisor-canine field typically is 30-40 per cent of rostral length (fig. 9b). From the allometric relationship that exists between rostral length and postrostral length, it follows that length of the incisor-canine field is allometrically related to length of the premolar-molar field.

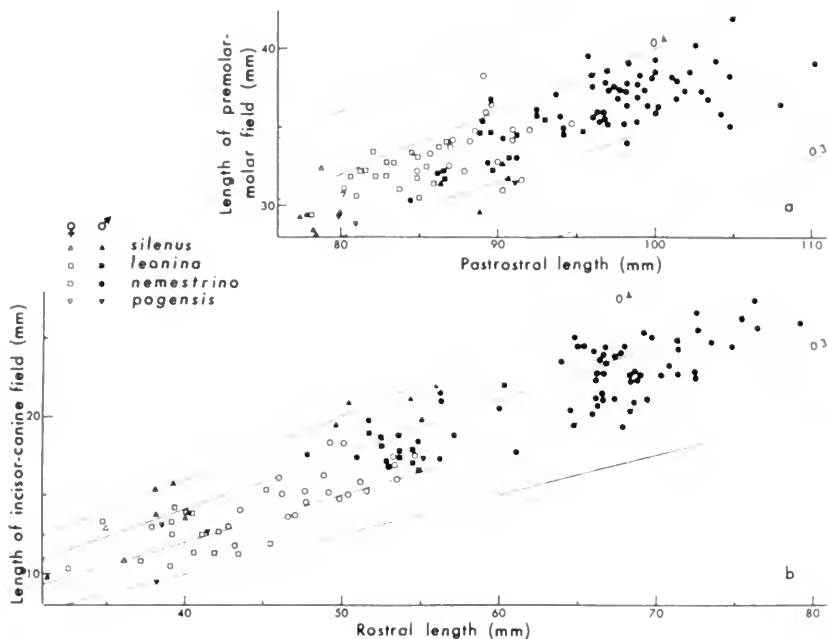


FIG. 9. Relative length of dental fields in adult liontails and pigtailed macaques; a, length of premolar-molar field *v.* postrostral length (linear scales); b, length of incisor-canine field *v.* rostral length (linear scales).

In specimens examined of *M. silenus*, relative length of the incisor-canine field tends to be slightly greater (fig. 9b) and relative length of the premolar-molar field tends to be slightly less (fig. 9a) than in the three subspecies of *M. nemestrina*.

Supraorbital ridges (fig. 3) in *M. silenus* are strongly projecting, although relatively thin (about 5 mm. thick in adult males). In *M. n. leonina* and *M. n. pagensis* these ridges are somewhat thicker (7-8 mm.), but they tend to recede laterally. In *M. n. nemestrina* supraorbital ridges are relatively thin (5 mm.), especially dorsolaterally, and strongly receding. In *M. n. leonina*, *M. n. nemestrina*, and *M. n. pagensis* the malar region is flat to weakly convex; in *M. silenus* well-developed intraorbital concavities are present in this region. In none of these macaques do the temporal ridges meet in the midline to form a sagittal crest.

Size, relative rostral length, and relative dental field proportions evidently constitute a complex of interrelated elements in the cranial evolution of liontail and pigtail macaques. Greatest length of skull is trigonometrically related to rostral length and postrostral length; rostral length is allometrically related to postrostral length; and rostral length and postrostral length are linearly related to length of incisor-canine field and premolar-molar field. It is not clear which of these interrelated cranial elements are primary factors in evolution and which are secondary. Cranial differentiation in these macaques may be the result of selective forces that act primarily on overall size, size of the braincase, size of the facial skeleton, size of the incisors and canines, size of the premolars and molars, on some combination of these, or on none. Present evidence does not appear adequate to indicate a clear choice among these alternative evolutionary possibilities.

TAIL – PROPORTIONS, PELAGE, VERTEBRAE, CARRIAGE

Relative tail length (tail/head and body) in adult male and female specimens examined varies from 0.24 - 0.34 in *M. n. pagensis*, from 0.28 - 0.45 in *M. n. nemestrina*, from 0.30 - 0.46 in *M. n. leonina*, and from 0.57 - 0.75 in *M. silenus* (fig. 2). (The denominator used in computing these ratios is the standard linear distance from tip of nose to base of tail, as measured by mammalogists, not the crown-rump height customarily employed by anthropologists.) The short, thin tail in the three subspecies of *M. nemestrina* is, of course, the basis for their collective designation as "pigtail" macaques. Judging from the few known specimens of *M. n. pagensis*, relative tail length in this subspecies averages slightly less than in the other two pigtail subspecies, which are essentially similar in tail proportions, although different in overall size. In *M. n. leonina* and *M. n. nemestrina*, the two subspecies for which reasonably adequate samples are available, relative tail length tends to be greater in infants (head and body length less than 300 mm.; probably less than one year old) than in juveniles and adults (cf. Lumer and Schultz, 1941, p. 297). The rate of growth of the tail relative to that of the head and body also is known to decline with age, at least until age two or three years, in *M. mulatta* (Schultz, 1933, p. 18) and *M. fascicularis* (Karrer, 1970, p. 174).

In *M. silenus* the fur of the tail is uniformly blackish, like that of the trunk; guard hairs at the tip of the tail usually are elongated to form a well-defined terminal tuft—hence, the "liontail" (fig. 21). In *M. n. leonina* and *M. n. nemestrina* the fur of the tail is sharply defined bicolor, dark brown to blackish dorsally and buffy ventrally; in *M. n. nemestrina* the hairs at the tip frequently are slightly elongated and reddish-brown to ochraceous, forming a weakly defined tuft. In *M. n. pagensis* the tail is virtually naked, superficially resembling that of an opossum. The dark chocolate-brown fur of the lower back in this subspecies extends only to the base of the dorsal surface of the tail; more distally, for 80-90 per cent of its length, the tail is sparsely covered by inconspicuous short

TABLE 2. Reported caudal vertebrae counts in *M. n. leonina* and *M. n. nemestrina*.

Descriptions of specimens	Sex	Number of caudal vertebrae/frequency						
		14	15	16	17	18	19	20
<i>M. n. leonina</i>								
Skeletons ¹	♀				1	1		1
Skeletons ¹	♂				1	1		
Cadavers ²	♀					1		2
Cadavers ²	♂				2	1	3	
<i>M. n. nemestrina</i>								
Skeletons ¹	♀							1
Skeletons ¹	♂					3	2	
(?) <i>M. n. leonina</i> or <i>M. n. nemestrina</i> ³								
Living	♀			1		1	1	
Living	♂		1		1		2	
Skeletons	♀	2	2		1			
Skeletons	♂	1	1	2	2		1	1

1. See Table 3.

2. In collection of Dr. Russell H. Tuttle, Department of Anthropology, The University of Chicago; vertebral counts reported by Wilson (1970, p. 186).

3. Reported by Wilson (1970, p. 186; 1972, p. 245), who does not distinguish between *M. n. leonina* and *M. n. nemestrina*.

buffy hairs (2-3 mm. long) through which the corrugated surface of the epidermis is plainly visible.

The number of caudal vertebrae evidently averages about 21 or 22 in *M. silenus* and about 18 or 19 in *M. n. leonina* and *M. n. nemestrina* (tables 2, 3; Schlegel, 1876, p. 111; Anderson, 1879, p. 55). Caudal vertebrae counts in specimens examined of *M. n. leonina* and *M. n. nemestrina* apparently agree with those in specimens studied by Schultz (1938, p. 6), who reports an average of 18.7 caudal vertebrae in six pigtail macaques, all or most of which probably are *M. n. nemestrina* (G. M. Allen and Coolidge, 1940, p. 147). A group of aberrantly low caudal vertebrae counts of uncertain validity is reported by Wilson (1970, p. 187; 1972, p. 245) in inadequately identified skeletal material (table 2).

The length of each of the proximal three caudal vertebrae (Ca1, Ca2, Ca3) is approximately 10.5 mm. in adult male *M. n. leonina* and *M. n. nemestrina* and approximately 12.5 mm. in adult male *M. silenus* (table 3). The next four vertebrae (Ca4-Ca7) usually become successively longer in all three of these macaques. Vertebra Ca7,

TABLE 3. Length (mm.) of caudal vertebrae in liontail and pigtail macaques; italicized figure indicates longest vertebra in series.

Specimen No.	Sex	Vertebra No.											
		1	2	3	4	5	6	7	8	9	10	11	12
<i>M. silenus</i> , adults													
FMNH 47322	♂	—	12.7	12.7	13.3	17.4	25.0	<i>30.0</i>	28.7	28.0	26.6	25.6	22.8
NHMB 3931	♂	12.7	12.5	12.5	15.1	20.8	26.1	27.2	26.5	25.8	24.6	22.5	19.7
FMNH 47387 ²	♀	11.4	11.0	11.9	16.3	21.3	23.2	24.5	23.8	22.6	22.2	20.2	17.9
RMNH d	♀	10.3	9.7	10.6	13.1	17.8	22.5	23.5	22.8	22.6	21.9	20.3	17.3
RMNH 4a	♀	11.6	10.4	10.7	13.9	17.0	21.5	23.8	<i>24.0</i>	23.9	21.6	21.8	18.3
<i>M. silenus</i> , immature													
RMNH 5b ³	♀	10.0	11.0	13.4	10.7	18.0	23.0	<i>25.4</i>	21.6 ¹				
<i>M. n. leonina</i> , adults													
FMNH 99673	♂	11.3	10.4	10.5	10.5	12.8	14.7	<i>18.0</i>	18.0	16.7	15.5	13.9	11.8
FMNH 99691	♂	10.8	10.3	10.6	11.7	15.1	19.5	<i>20.1</i>	19.4	18.1	16.7	14.2	11.9
RMNH b/b	♂	11.5	9.6	10.6	11.0	13.9	18.3	<i>20.3</i>	20.1	18.3	15.8	13.8	12.3
Means	♂	11.2	10.1	10.6	11.1	13.9	17.5	<i>19.5</i>	19.2	17.7	16.0	14.0	12.0
FMNH 99688	♀	9.3	8.9	8.5	9.2	10.7	10.5	14.6	<i>15.6</i>	15.4	14.9	12.7	11.7
RMNH a/E	♀	8.4	8.2	7.9	9.2	11.4	15.0	<i>15.7</i>	15.1	15.0	14.4	10.0	8.2

TABLE 3. (continued)

Specimen No.	Vertebra No.										
	13	14	15	16	17	18	19	20	21	22	23
	<i>M. silenus</i> , adults										
FMNH 47322	20.2	17.2	15.1	12.0	8.8	9.3	7.6	4.9	4.6	4.1	1.0
NHMB 3931	15.9	14.9	12.7	10.5	8.7	6.8	6.1	4.5	3.01		
FMNH 473872	16.2	13.9	11.2	10.2	8.6	7.1	6.11				
RMNH d	15.3	13.1	11.0	10.1	7.6	6.2	5.5	3.01			
RMNH 4a	15.9	14.3	12.7	10.8	9.0	7.2	5.4	4.71			
	<i>M. n. leonina</i> , adults										
FMNH 99673	9.1	7.4	6.0	4.9	3.7						
FMNH 99691	9.41										
RMNH b/b	9.6	7.8	7.0	4.3	6.0	2.2					
Means	9.4	7.6	6.5	4.6	4.8	2.2					
FMNH 99688	10.0	8.4	6.7	5.1	4.2	3.5	2.3	1.8			
RMNH a/E	7.6	6.6	5.3	2.5	2.0						

TABLE 3. (continued)

Specimen No.	Sex	Vertebra No.											
		1	2	3	4	5	6	7	8	9	10	11	12
NHRM 1/384	♀	11.5	10.0	10.1	11.1	13.7	20.4	18.9	18.2	15.0	15.1	13.5	11.1
		<i>M. n. leonina</i> , immature											
IRSN 6464	♂	9.1	9.1	11.3	16.9	16.6	16.5	15.6	13.5	11.9	10.0	8.2	7.0
IRSN 9323	♂	10.5	10.0	10.0	11.8	15.4	20.4	20.6	14.6	18.2	17.3	16.0	14.6
IRSN 18896	♂	11.9	11.0	11.0	12.5	14.0	19.7	20.9	19.9	19.0	18.8	17.0	14.2
MCZ 7090	♂	10.5	10.2	10.6	10.1	15.3	16.7	18.8	18.8	17.4	17.0	15.2	13.0
RMNH 10a	♂	9.3	9.3	9.3	9.4	13.6	15.4	17.0	18.7	18.0	17.0	16.0	13.8
RMNH 11b	♂	9.4	10.7	9.7	9.6	11.2	15.0	17.2	17.0	16.0	15.4	13.2	13.2
RMNH 12c	♂	12.5	10.1	9.1	8.8	11.3	15.6	18.1	18.5	18.0	16.1	15.1	13.5
RMNH 13d	♂	15.0	11.9	9.4	13.2	15.7	16.7	21.0	21.3	21.4	20.3	14.7	16.3
RMNH 14e	♂	9.6	10.0	8.9	9.5	11.3	14.7	16.1	16.8	15.6	14.1		
ZMUZ 11611	♂	11.4	10.3	10.8	11.5	14.1	18.0	18.7	18.1	16.7	15.6	14.3	12.0
Means	♂	10.9	10.3	10.0	11.3	13.8	16.9	18.4	17.7	17.2	16.1	14.4	13.1
		<i>M. n. nemestrina</i> , immatures											
FMNH 542525	♂	11.0	9.5	8.0	9.9	13.5	17.6	21.3	19.6	19.6	18.6	15.4	14.1
FMNH 543054	♀	7.3	7.0	8.2	10.3	12.7	15.4	15.4	15.0	14.0	13.1	12.2	11.0
RMNH 15f	♀	6.9	5.8	5.8	7.8	8.0	10.2	10.7	12.8	10.7	11.3	9.6	9.6

TABLE 3. (continued)

Specimen No.	Vertebra No.									
	13	14	15	16	17	18	19	20		
NHRM 1/384	6.9	7.1	5.0	3.8	2.8	1.7				
			<i>M. n. leonina</i> , immature							
			<i>M. n. nemestrina</i> , adults							
IRSN 6464	6.3	5.6 ¹								
IRSN 9323	12.9	10.6	8.8 ¹							
IRSN 18896	12.2	10.9	8.4	6.6	4.5	3.5	5.2			
MCZ 7090	11.6	9.1	8.0	6.1	4.6 ¹					
RMNH 10a	11.3	9.1	7.9 ¹							
RMNH 11b	10.8	9.0	7.7	5.3	5.3	2.8	2.6			
RMNH 12c	11.9	10.7	8.5	6.3	4.9	4.1				
RMNH 13d	14.2	10.7	9.2	7.1	4.3	3.8				
ZMUZ 11611	10.1	8.3	7.2	5.7	4.9	3.8				
Means	11.3	9.3	8.2	6.2	4.8	3.6	3.9			
			<i>M. n. nemestrina</i> , immatures							
FMNH 542525	12.6	11.0	9.3	8.1 ¹						
FMNH 543054	9.6	8.1	6.6	5.4	4.7	4.0	3.1	2.5		
RMNH 15f	8.1	7.1	5.3	5.1	3.5	4.1	2.3			

1. Terminal vertebrae missing.
2. Presumably adult; dentition not examined.
3. Juvenile; M2, deciduous ml.
4. Subadult; C incompletely erupted, M3 unerupted.
5. Subadult; M3 erupted, C incompletely erupted.

which tends to be the longest member of the series, averages about 19 mm. long in adult male *M. n. leonina* and *M. n. nemestrina* and about 28.5 mm. long in adult male *M. silenus*. More distal vertebrae typically become successively shorter, about 2 mm. per vertebra, to a terminal vertebral length of 1-5 mm. The pattern of caudal vertebral length variation presented here for adult males is essentially similar to that in a series of 10 males and females, many of which apparently are immature, that is reported by Wilson (1970, p. 198). Comparing *M. silenus* with *M. n. leonina* and *M. n. nemestrina*, the greatest reduction in vertebral length is at the longest vertebra in the series, which, as noted, is usually Ca7. This vertebra also appears to be at or near the focus of evolutionary tail reduction in Celebesian stump-tail macaques (Fooden, 1969a, p. 17) and in crab-eating and rhesus macaques (Wilson, 1970, p. 60).

In adult male *M. silenus* the relaxed tail is carried hanging posteriorly (fig. 21; Karr, 1973, p. 191), in what apparently is the typical manner in most long-tailed monkeys. In adult male *M. n. leonina* the base of the tail normally is inflected anteriorly, and the tail is carried arched over the back with the tip directed upward and forward. Judging from published illustrations (Sclater, [1870], pl. 35; Yerkes Newsletter, 1971, p. 14) and observation of captive specimens (fig. 29), the tail in adult male *M. n. leonina* is seldom, if ever, dropped posteriorly (Tickell, 1863-1875, MS., p. 139; Heck, 1916, p. 552). In adult male *M. n. nemestrina* the tail is carried arched rearward, with the base inflected dorsally and the distal part inflected downward (fig. 26; Wilson, 1970, p. 115). The manner of tail carriage in *M. n. pagensis* has not been recorded.

I have attempted to investigate the anatomical basis for the difference of tail carriage in *M. n. leonina* and *M. n. nemestrina*. Material available for detailed study consists of embalmed cadavers of three adult males of *M. n. leonina* (kindly lent by Dr. Russell H. Tuttle, Department of Anthropology, The University of Chicago; spec. nos. NM6, PM1, PM2), caudal vertebrae of three wild-caught adults of *M. n. leonina* (FMNH 99673 ♂, 99688 ♀, 99091 ♂), and caudal vertebrae of two captive subadults of *M. n. nemestrina* (FMNH 54252 ♂, 54305 ♀). Judging from cadavers examined, the first two or three postsacral vertebrae, although osteologically "caudal," are, in fact, located in the sacral region of the trunk, dorsal to the rectum and anterior to the anus (fig. 10). The vertebra at the base of the external tail is Ca3 or Ca4 (Wilson, 1970, p. 48). The upward inclination of the tail base that is evident in living *M.*

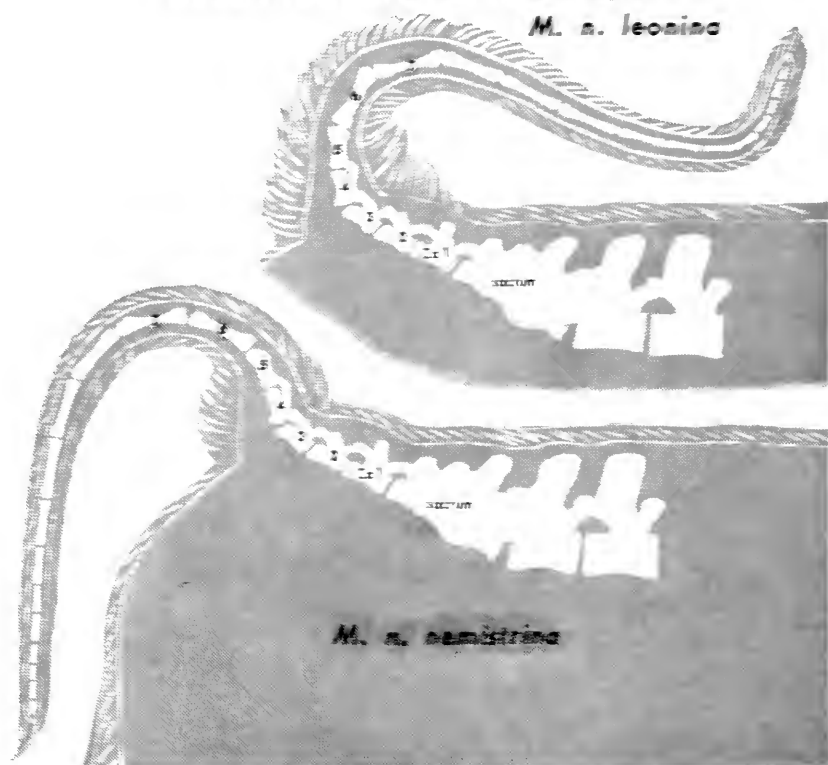


FIG. 10. Relationship between tail carriage and orientation of caudal vertebrae in *M. n. leonina* and *M. n. nemestrina*.

n. leonina (fig. 29) and *M. n. nemestrina* (fig. 26) evidently is a result of dorsal hyperextension of intervertebral joints C₂-3 and C₃-4. In *M. n. leonina* intervertebral joints C₄-5, C₅-6, and C₆-7 also are hyperextended to form the anteriorly directed tail flexure in this subspecies (fig. 10). In *M. n. nemestrina*, by contrast, intervertebral joints C₄-5, C₅-6, and C₆-7 apparently are ventriflexed to form the proximal part of the downward directed tail flexure, and intervertebral joints C₇-8 and C₈-9 also are flexed to complete the tail arch (fig. 10). The characteristic difference of tail carriage in these two subspecies appears, consequently, to depend on habitual dorsal hyperextension of intervertebral joints C₄-5, C₅-6, and C₆-7 in *M. n. leonina* as contrasted with habitual ventriflexion of these joints in *M. n. nemestrina*.

Although intervertebral joints C₄-5, C₅-6, C₆-7 are oppositely inflected in *M. n. leonina* and *M. n. nemestrina*, in specimens

examined there seems to be no consistent difference between these subspecies in the structure of vertebrae Ca4-Ca7, which are the vertebrae directly affected. However, in vertebra Ca3 the transverse processes in *M. n. leonina* are consistently broader, relatively and

TABLE 4. Breadth (mm.) of transverse processes of first seven caudal vertebrae in subadult and adult specimens of *M. silenus*, *M. n. leonina*, and *M. n. nemestrina*; figure in parenthesis is ratio of breadth of transverse processes to length of vertebral centrum (see Table 3).

FMNH No.;		Vertebra No.						
sex		1	2	3	4	5	6	7
<i>M. silenus</i>								
47322	♂	—	ca. 21.2	20.0	16.3	13.8	10.3	8.7
			(1.67)	(1.57)	(1.23)	(0.79)	(0.41)	(0.29)
47387	♀	17.4	18.4	15.7	12.2	8.7	8.0	6.8
		(1.53)	(1.67)	(1.32)	(0.75)	(0.41)	(0.34)	(0.28)
<i>M. n. leonina</i>								
99673	♂	ca. 24.0	ca. 24.0	23.0	16.2	13.8	8.1	7.1
		(2.12)	(2.31)	(2.19)	(1.54)	(1.08)	(0.55)	(0.39)
99691	♂	23.5	25.4	21.7	15.0	9.3	6.9	5.5
		(2.18)	(2.47)	(2.05)	(1.28)	(0.62)	(0.35)	(0.27)
99688	♀	19.4	18.2	15.7	10.8	7.6	5.8	5.1
		(2.09)	(2.04)	(1.85)	(1.17)	(0.71)	(0.55)	(0.35)
<i>M. n. nemestrina</i>								
54252 ¹	♂	19.8	19.0	13.2	11.8	10.0	6.8	5.7
		(1.80)	(2.00)	(1.65)	(1.19)	(0.74)	(0.39)	(0.27)
54305 ¹	♀	17.4	15.8	11.8	11.1	7.3	5.9	5.0
		(2.38)	(2.25)	(1.44)	(1.08)	(0.57)	(0.38)	(0.32)

1. Subadult (see Table 3).

usually absolutely (table 4), than in *M. n. nemestrina* (and *M. silenus*). Reduction of these transverse processes in specimens of *M. n. nemestrina* has been noted previously by Wilson (1970, p. 53, fig. 3). These transverse processes receive the tendons of insertion of m. ischiocaudalis, which acts to abduct and depress the base of the tail (Wilson, 1970, p. 78; Trevor-Jones, 1970, pp. 320, 323). Enlargement of these transverse processes in *M. n. leonina* may be a function of increased abductor and ventriflexor tension. This, in turn, may stabilize the base of the tail against increased extensor tension (of m. extensor caudae medialis) that apparently is exerted more distally to effect the characteristic dorsal hyperextension of joints Ca4-5, Ca5-6, and Ca6-7.

A more complete explanation of the structural basis for the difference of tail carriage in *M. n. leonina* and *M. n. nemestrina* probably will require further comparative study employing more adequate skeletal and cadaver material of *M. n. nemestrina*. The evolutionary significance of the tail carriage difference between these subspecies, like that of many conspicuous and taxonomically important differences between primates subspecies and species, remains obscure.

FEMALE GENITALIA

Cyclical estrous swelling of the circumanal sexual skin is well known in *M. n. nemestrina* (F. Cuvier, 1816-1817, pl. 5, fig. 2; Pocock, 1926, fig. 68b; Zuckerman, 1937, p. 319; Kuehn et al., 1965, figs. 1, 2; White et al., 1973, p. 189). This swelling typically develops gradually, beginning during or immediately after the menstrual period and reaching maximal tumescence usually in about 15 days. At its maximum, the engorged pinkish hairless area extends dorsoventrally from the base of the tail to the ventral border of the ischial callosities, which are partly buried in the swelling, and extends laterally over an area twice the breadth of both callosities (fig. 11). Ventral to the callosities the thinly haired skin anterior to the vulva (mons pubis) is less conspicuously swollen. Following ovulation, usually within one or two days after maximal tumescence, the swelling rapidly subsides. Detumescence persists for about 15 days, until the next menstrual period. In laboratory mating tests, maximal female perineal tumescence in *M. n. nemestrina* is directly correlated with maximal sexual behavior in females (Goldfoot, 1971, p. 330) and with maximal incidence and rate of ejaculation in males (Bullock et al., 1972, p. 230).

Sexual skin in *M. silenus* has been cursorily described in an unspecified number of specimens by Pocock (1926, p. 1547) and more precisely characterized in one specimen by W. C. O. Hill (1937, p. 210, figs. 2a, 2b). Judging from these accounts, the general pattern of sexual skin morphology is similar in *M. silenus* and *M. n. nemestrina*, although swelling is much less distended in estrous *M. silenus* (fig. 11). In this species the swelling does not form a continuous pillowlike mass, as in *M. n. nemestrina*, but instead is subdivided into five separate swollen areas—one large subcaudal swelling, a pair of smaller swellings dorsolateral to the anus, and a pair of broad swellings that surround the ischial callosities, lateral to the vulva. (The ventral margin of the vulva in one *M. silenus* adult female that I observed at Lincoln Park Zoo, Chicago, is approximately in line with the lower border of the ischial callosities,

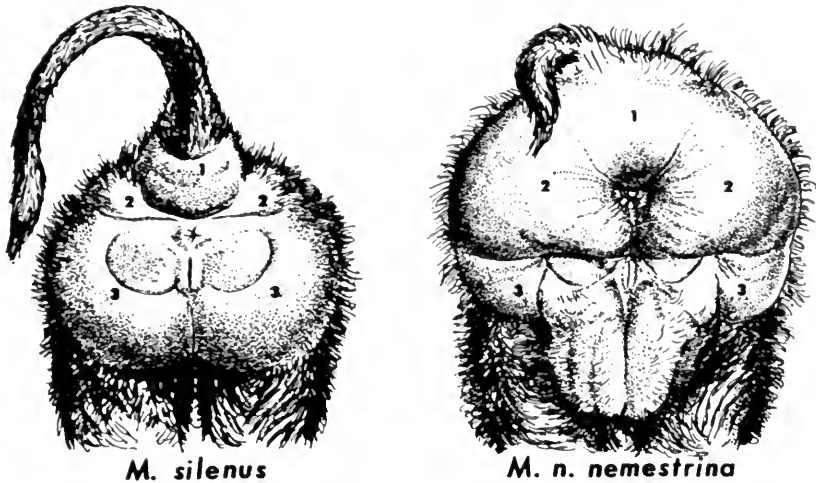


FIG. 11. Female sexual swellings in *M. silenus* (modified from W. C. O. Hill, 1937, p. 214) and *M. n. nemestrina* (Kuehn et al., 1965, p. 253): 1, subcaudal swelling; 2, para-anal swellings; 3, para-vulval swellings.

as in other species of macaques; the vulva is not especially high between the callosities, as described and figured by W. C. O. Hill, loc. cit.) The paired swellings dorsolateral to the anus in *M. silenus* are particularly less developed than in *M. n. nemestrina*, where these para-anal swellings fuse with the subcaudal swellings dorsally, extend over the gluteal region dorsolaterally, and overlap the ischial callosities ventrally.

Morphology of sexual swelling has not been reported in estrous specimens of *M. n. leonina* and *M. n. pagensis*. In non-estrous *M. n. leonina* specimens examined (FMNH 99674, 99687, subadults; 99685, 99688, pregnant adults; 99677, 99678, 99679, lactating adults), the hairless area of sexual skin seems to be less extensive than in corresponding non-estrous specimens of *M. n. nemestrina*, more nearly resembling that in *M. silenus*.

Internal female reproductive structures have been previously investigated in three specimens of *M. n. nemestrina* (Hafez and Jaszczak, 1972, pp. 297, 300). The present account is based on study of 12 alcohol-preserved reproductive tracts of *M. n. leonina* immatures and adults (table 5). The female tract in *M. n. leonina* (fig. 12) is essentially similar to that in *M. n. nemestrina* (Hafez and Jaszczak, op. cit.). It is also generally similar to that in *M.*

TABLE 5. Measurements (mm.) of female reproductive tracts in *Macaca n. leonina*.

FMNH No.	Head and body length		Dental stage ¹	Estimated age ² (yr.)	Vagina		Cervix D-V Length diam.	Main cervical collicle, height	Uterine body		D-V D-V Breadth diam.
	Length	D-V diam.			Length	D-V diam.			Length	Breadth	
99682	174	dec i2	0.1	19.8	3.1	5.0	3.0	1.8	9.5	5.5	1.8
99692	284	dec m2	1	22.5	4.1	6.7	3.1	1.6	7.6	7.6	2.0
99689	378	(11)	2.5	25.0	3.8	8.0	3.8	1.2	10.5	8.2	3.6
99681	348	M2	3.5	ca. 25.0	4.2	8.0	3.2	1.5	10.5	8.4	2.1
99687	390	(P)	4	35.2	13.7	19.9	16.7	6.2	14.0	12.3	6.5
99674	423	M2/M3	6	28.3	12.0	14.3	10.0	4.6	18.7	12.8	7.7
NM43	—	M2/M3	6	38.8	11.0	13.9	8.8	4.0	13.7	10.8	6.3
996854	432	M3	>6	31.5	18.3	27.2	14.5	5.6	37.0	31.9	23.5
996885	473	M3	>6	35.3	18.2	42.7	22.1	5.2	108.6	119.8	76.5
996796	488	M3	>6	35.0	11.4	18.8	12.4	3.0	18.2	20.8	7.1
996787	448	M3	>6	27.2	—	13.3	10.5	3.0	22.2	13.0	6.9
99677	484	M3	>6	29.5	ca. 15.0	13.9	9.8	2.6	18.1	13.1	7.0

TABLE 5. (continued)

FMNH No.	Ovaries	
	Right	Left
99682	4.8x3.0x1.5	5.6x2.8x1.1
99692	6.6x3.7x2.0	5.3x4.2x2.0
99689	—	8.0x5.6x3.1
99681	6.7x4.9x2.0	7.1x4.0x1.7
99687	9.9x6.5x3.6	9.4x4.2x2.8
99674	8.3x6.2x3.0	7.9x6.6x2.8
NM43	5.9x3.1x2.1	6.5x5.5x2.3
996854	7.3x6.0x2.4	8.2x7.5x4.5
996885	12.0x9.4x2.6	12.1x7.6x3.2
996796	10.6x8.0x3.1	10.7x7.5x2.6
996787	8.4x5.9x2.6	8.3x6.1x2.6
99677	12.4x6.9x3.0	11.6x9.0x2.2

1. Parentheses indicate incompletely erupted teeth.
2. Based on dental emergence norms for *M. mulatta* (Hurme, 1960, p. 797).
3. Collection of Dr. Russell H. Tuttle, Department of Anthropology, The University of Chicago.
4. Blastocyst diameter 20 mm.; estimated conception age 1 month.
5. Sitting height of fetus 150 mm.; estimated conception age 4 months.
6. Estimated age of infant (FMNH 99683) 1 month.
7. Estimated age of infant (FMNH 99682) 1.5 months.

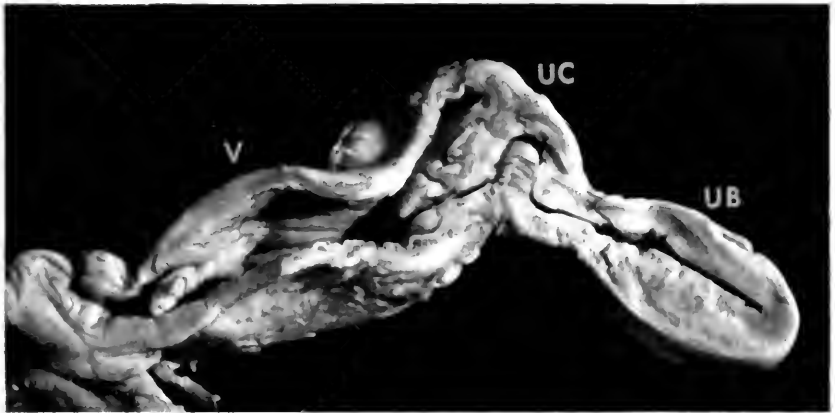


FIG. 12. Sagittal section of female reproductive tract in subadult *M. n. leonina*, FMNH 99674; $\times 2$. UB: uterine body, UC: uterine cervix, V: vagina (distortion of wall is artifact of preservation). (Photo FMNH)

fascicularis (Jainudeen et al., 1972, p. 473) and *M. mulatta* (Wislocki, 1933, p. 239; Eckstein and Zuckerman, 1956, p. 138; Cuadros, 1971, p. 139). However, the uterine cervix in *M. n. leonina* evidently is somewhat smaller than at corresponding stages in *M. mulatta*. Judging from specimens examined (table 5), the cervix in *M. n. leonina* enlarges markedly approximately at puberty (FMNH 99687), regresses during adolescence (FMNH 99674; NM4), reaches maximal size during pregnancy (FMNH 99685, 99688), and regresses during lactation (FMNH 99677, 99679).

Structure of the female tract in *M. n. leonina* is distinctly different from that in the *M. sinica*-group (*M. sinica*, *M. radiata*, *M. assamensis*, *M. thibetana*), which is characterized by presence of cornified vaginal spines and a hypertrophied endocervical chamber (Fooden, 1971b, p. 67). It also differs from that in *M. arctoides*, in which a large dorsal vestibular collicle is present and cervical colliculi are absent (Fooden, 1967, p. 939; Demers et al., 1972, p. 529; Hafez and Jaszczak, 1972, p. 302).

NOTE ADDED IN PROOF: Cf. Eaton, G. G. and J. A. Resko, 1974, Ovarian hormones and sexual behavior in *Macaca nemestrina*, *J. Comp. Physiol. Psychol.*, **86**, pp. 919-925.

GLANS PENIS AND BACULUM

This account is based on study of 30 specimens of penises or bacula of liontail and pigtail macaques (*M. silenus*, 3; *M. n. leonina*, 19; *M. n. nemestrina*, 8; tables 6, 9) and review of relevant literature (Daubenton, in Buffon and Daubenton, 1766, p. 179; F. Cuvier, 1820, p. 1; F. Cuvier, 1822a, p. 2; DeBeaux, 1917, p. 10; 1923, p. 34; Pocock, 1921, p. 227; 1926, p. 1559; Pohl, 1928, p. 103; W. C. O. Hill, 1937, p. 213; 1958, p. 655).

In liontail and pigtail macaques the glans penis is helmet shaped and bluntly bilobed (fig. 13), closely resembling that in Celebesian macaques (Fooden, 1969a, p. 20) and *M. sylvanus* (Daubenton, in Buffon and Daubenton, 1766, p. 119; W. C. O. Hill, 1958, p. 655, fig. 18a) and generally similar to that in the *mulatta*-group (*M. fascicularis*, *M. mulatta*, *M. cyclopis*, *M. fuscata*; Fooden, 1972, p. 310). The bluntly rounded glans in macaque groups listed above is distinctly different from the apically elongate subpyramidal glans in the *sinica*-group (*M. sinica*, *M. radiata*, *M. assamensis*, *M. thibetana*; Fooden, 1971b, p. 72) and the even more elongate lanceolate glans in *M. arctoides* (Fooden, 1967, p. 939). These three sharply defined glans types in the genus *Macaca* (fig. 14) were first recognized by Pocock (1921, p. 229); subsequent authors, including Pocock (1926, p. 1557), have tended to obscure the basic penial trichotomy of macaques. The bluntly rounded glans type seems to be the most common form in macaques and other cercopithecids (Pocock, 1926, p. 1557) and, therefore, probably is primitive in the genus and family.

The three subdivisions of the genus *Macaca* that are defined by structure of the glans penis exactly correspond, as far as presently known, to three subdivisions defined by structure of the uterine cervix. In *M. n. leonina*, *M. fascicularis*, and *M. mulatta*, all with glans bluntly rounded, the cervix and cervical colliculi are moderately large (see above); in *M. sinica*, *M. radiata*, and *M. assamensis*, with glans apically elongate, the cervix is enormously inflated and cervical colliculi are hypertrophied (Fooden, 1971b, p.

TABLE 6. Measurements (mm.) of glans penis¹ and baculum in adult liontail and pigtail macaques.

Specimen No.	Glans			Baculum			Distal process, length
	Length	Relative breadth	Greatest length	Least D-V diam. of shaft	Shaft length	Distal process, length	
			<i>M. silenus</i>				
BM 41.1.15.12, 3	—	—	21.1	2.5	18.4	5.5	
NMS 26302, 4	11.05	0.78	21.2	2.6	18.9	4.3	
RMNH 13082, 4	15.45	0.69	24.2	2.7	21.1	5.1	
			<i>M. n. leonina</i>				
BM 55.1505	—	—	19.7	2.5	14.9	7.0	
FMNH 99673	18.9	0.72	26.7	3.0	21.6	6.2	
FMNH 99691	17.2	0.73	22.9	2.5	19.2	6.1	
NM26	18.4	0.68	21.9	2.5	17.4	7.4	
NM56	16.9	0.72	21.0	2.6	17.7	6.0	
NM66	17.9	0.63	24.9	2.2	17.5	9.2	
NM76	17.8	0.74	22.4	3.2	18.5	7.2	
PM16	—	—	24.9	2.5	19.0	8.0	
USNM 241022	13.15	0.80	21.5	2.8	17.8	7.8	
USNM 258868	15.85	0.68	26.4	3.2	20.6	9.9	

TABLE 6. (continued)

Specimen No.	Glans		Relative breadth	Greatest length	Baculum		Distal process, length
	Length	Breadth			Least diam. of shaft	Shaft length	
				<i>M. n. nemestrina</i>			
AMNH 119514 ² , 7	—	—	—	18.3	2.5	16.8	3.8
BM 55.707	—	—	—	21.1	2.2	19.1	3.8
BM 55.1503	—	—	—	16.1	2.1	14.9	3.0
FMNH 687033	—	—	—	16.9	1.6	15.4	3.4
MCZ 35670	13.15	0.60	0.60	17.5	1.7	15.2	4.2
NMS 26292	9.45	0.89	0.89	18.6	2.5	16.1	4.7
RMNH 2000 ² , 4	14.65	0.71	0.71	21.1	2.2	19.2	3.8
(unknown) ⁸	10	—	—	19	2	18	3

35

1. All specimens fluid-preserved except as noted.
2. Zoo specimen.
3. Subadult; canines and last molars incompletely erupted.
4. Subadult or adult; skin only.
5. Dry specimen reconstituted in fluid.
6. Collection of Dr. Russell H. Tuttle, Department of Anthropology, The University of Chicago.
7. Baculum deformed (fig. 15s).
8. Pohl, 1928, p. 108, pl. 3, fig. 18.

67); in *M. arctoides*, with glans lanceolate, cervical colliculi are absent and columnar epithelium extends unusually far distally (Fooden, 1967, p. 940; Demers et al., 1972, p. 532; Hafez and Jaszczak, 1972, p. 304). Information on cervical structure in other species of the genus has not been recorded.



FIG. 13. Penis in adult *M. n. leonina* (FMNH 99691), left lateral view and dorsal view. $\times 1.5$. (Photo FMNH)

Patterns of copulatory behavior apparently also are distinctive in each of the three subdivisions of macaques that are defined by male and female genital morphology (Michael et al., 1973, p. 248; Nadler and Rosenblum, 1973a, p. 18; 1973b, p. 217). In *M. n. nemestrina*, *M. mulatta*, and *M. fuscata* (glans rounded, cervix moderately large), copulation usually consists of a series of non-ejaculatory mounts that precede the ejaculatory mount (median 7-11 mounts per ejaculation); although evidence concerning *M. fascicularis* is ambiguous, copulatory behavior in this species seems to be basically similar to that in *M. mulatta* (Goustard, 1968, p. 468; Kanagawa et al., 1972, p. 453; Kanagawa and Hafez, 1973, p. 234). In *M. radiata* (glans apically elongate, cervix inflated) copulation usually is completed in one mount (maximum four mounts) with 5-30 intromissive thrusts to ejaculation. In *M. arctoides* (glans lanceolate, cervix simplified) copulation also usually is completed in one or a few mounts, but with about 60-70 thrusts to ejaculation.

The correlated variation of male genitalia, female genitalia, and copulatory behavior in these three macaque subgroups undoubtedly is related, in a way not yet understood, to the history of evolutionary differentiation and reproductive isolation in the genus.

Although the bluntly rounded form of the glans penis in liontail and pigtail macaques is generally similar to that in the *mulatta*-group, and length of the glans is broadly overlapping in the two groups, diameter of the glans in the liontail-pigtail group averages nearly twice as great as in the *mulatta*-group. In specimens examined, the ratio of glans breadth to glans length is 0.60-0.89 in liontail and pigtail macaques (tables 6, 9) as contrasted with 0.36-0.55 in the *mulatta*-group (table 7). Relative glans breadth in Celebesian macaques appears to be about the same as in liontail

TABLE 7. Relative breadth of glans penis in fluid-preserved specimens¹ of *M. fascicularis*, *M. mulatta*, and *M. fuscata*.

Dental stage ²	Estimated age ³ (years)	Glans length ⁴ (mm.)	Relative breadth
<i>M. fascicularis</i>			
dec. m2	1	6.2, 7.7, 8.5	0.44, 0.45, 0.52
(M ₁)	1.5	7.4, 7.7	0.41, 0.42
(I ₁)	2.5	7.0	0.43
(P)	4	7.4, 12.3	0.47, 0.53
(C, M3)	6	12.9	0.49
M3	>6	14.4, 15.2, 16.6	0.55, 0.46, 0.41
<i>M. mulatta</i>			
M1	2	11.8 (10.6-13.1) ⁵	0.42 (0.36-0.50) ⁵
(I2, M2)	3	13.5	0.36
(C)	4.5	9.5	0.47
M3	>6	18.7	0.54
<i>M. fuscata</i> ⁶			
—	3	17.0, 17.1	0.38, 0.40
(C)	5	18.3	0.40
—	>5	15.9	0.39
—	>6	20.0	0.40
—	>7	20.0	0.48

1. Specimens in FMNH.

2. Parentheses indicate incompletely erupted teeth.

3. Based on dental emergence norms for *M. mulatta* (Hurme, 1960, p. 797).

4. Measured parallel to long axis of glans; differs slightly from greatest length reported previously (Fooden, 1972, p. 306).

5. Mean and extremes in eight specimens.

6. For age estimates see Fooden, 1972, p. 306.

and pigtail macaques, judging from measurements of dry specimens reconstituted in fluid (table 8).

TABLE 8. Relative breadth of glans penis in reconstituted dry specimens of Celebesian macaques.

Species	Specimen No.	Glans length (mm.)	Relative breadth
<i>M. brunnescens</i>	NMS 1017, 1020	13.8, 15.2	0.59, 0.63
<i>M. hecki</i>	RMNH 1099, 3801	14.9, 17.3	0.66, 0.51
<i>M. maura</i>	RMNH 751 (2363, 2484)	8.4, 13.3	0.83, 0.66
<i>M. nigra</i>	RMNH 13, MCZ 34459	7.9, 9.8	0.87, 0.72
<i>M. ochreata</i>	NMS 1022	13.2	0.61
<i>M. tonkeana</i>	NMS 16838	13.2	0.64

In liontail and pigtail macaques (fig. 13), as in *M. mulatta*, the dorsal part of the glans extends back over the shaft about twice as far as the ventral part, the glans is bilobed, the urethral orifice opens between the lobes, and the baculum protrudes into the left lobe, which is somewhat larger than the right. Also as in *M. mulatta*, the glans and distal part of the shaft are densely studded with tiny epidermal papillae about 0.05 mm. in diameter; these are much smaller than the epidermal spines (0.3 mm. diameter) present on corresponding penial surfaces in the *sinica*-group (fig. 14). In early accounts (Daubenton, *in* Buffon and Daubenton, 1766, p. 179; F. Cuvier, 1822a, p. 2) the glans in *M. n. nemestrina* is characterized, somewhat confusingly, as three-lobed; this evidently is a result of counting as a lobe a small variably defined V-shaped dorsomedian eminence that is situated between the bases of the right and left lobes, proximal to the urethral cleft (fig. 13).

In living specimens of *M. silenus*, color of the detumescent glans is dark gray (W. C. O. Hill, 1937, p. 214; personal observation, one adult, Lincoln Park Zoo, Chicago) and color of the tumescent glans is "bright purple" (W. C. O. Hill, loc. cit). In *M. n. leonina*, the glans is pinkish (DeBeaux, 1923, p. 35; personal observation, one adult, National Zoological Park, Washington, D.C.). In *M. n. nemestrina* the color of the "penis" (?glans) is recorded as "pale crimson" (field tag of BM 55.1503, Sungai Renggam, West Malaysia).

The external similarity in structure of the glans in liontail and pigtail macaques conceals unexpected internal differences in size and structure of the baculum (fig. 15; table 6). Comparing species for which reasonably adequate samples are available, length of the



FIG. 14. Basic glans types in genus *Macaca*, left lateral and dorsal views: a, b, bluntly rounded type, *M. fascicularis*, FMNH 99642; c, d, subpyramidal type, *M. h.*, 99691, > 6 yr.; i, 99673, >> 6 yr. Natural size. (Courtesy Chicago Zoological Park, Brookfield, Ill.)

baculum in *M. n. leonina* (21.0-26.7 mm. in 10 adults) averages about 25 per cent greater than in *M. n. nemestrina* (16.1-21.1 mm. in seven adults; cf. Kinzey, 1971, p. 102). This is somewhat surprising, considering that head and body length in *M. n. leonina* averages about 15 per cent less than in *M. n. nemestrina* (fig. 2). The bacular length difference in *M. n. leonina* and *M. n. nemestrina* is due principally to a difference in length of the downward inflected distal process (fig. 15). In *M. n. leonina* this process is sharply defined, and its length is 29-51 per cent of that of the proximal bacular shaft (10 specimens); in *M. n. nemestrina* the inflected distal process is more weakly defined, and its length is 20-30 per cent of that of the proximal shaft (seven specimens). The dorsoventral diameter of the bacular shaft also is notably greater in *M. n. leonina* than in *M. n. nemestrina*; as a result, the shaft is bilaterally flattened in *M. n. leonina* and more nearly cylindrical in *M. n. nemestrina*.

One baculum of *M. n. leonina* and one of *M. n. nemestrina* are anomalous. In the anomalous *M. n. leonina* specimen (NM6; fig. 15k) the shaft is unusually slender, the basal end is studded with small tuberosities, and the distal process, which is weakly inflected, terminates in three vertically arrayed lobules, in place of a simple ventrally directed tip. In the anomalous *M. n. nemestrina* baculum (AMNH 119514, zoo animal) the bone is unusually thickened and porous (fig. 15s). As indicated previously (Fooden, 1969a, p. 25), the abnormal structure of this baculum may be a result of captivity-induced bone pathology. However, bacular structure in two other captive specimens examined (NMS 2629; RMNH 2000; figs. 15p, 15q) is essentially similar to that in wild-collected specimens.

Although examination of three available specimens of *M. silenus* (fig. 15a-c, table 6) suggests that bacular structure is

Opposite:

FIG. 15. Bacula in adult liontail and pigtail macaques; left lateral view, dorsal surface of baculum at top, distal end at left; italicized figures below indicate locality numbers as in distribution maps, Figures 25, 28. a, b, c, *M. silenus* (zoo specimens): BM 41.1.15.1 (subadult), NMS 2630 (subadult or adult), RMNH 1308 (subadult or adult); d-k, *M. n. leonina*: BM 55.1505 47, NM 5 ("Thailand"), NM 7 ("Thailand"), USNM 241022 25, NM2 ("Thailand"), PM1 ("Thailand"), USNM 258868 36, NM6 ("Thailand"); l-s, *M. n. nemestrina*: BM 55.1503 12, MCZ 35670 89, FMNH 68703 90 (subadult), NMS 2629 (zoo), RMNH 2000 (subadult or adult, zoo), BM 55.707 58, FMNH 105676 4 (subadult), AMNH 119514 (captive, deformed). × 2. (Photos FMNH)

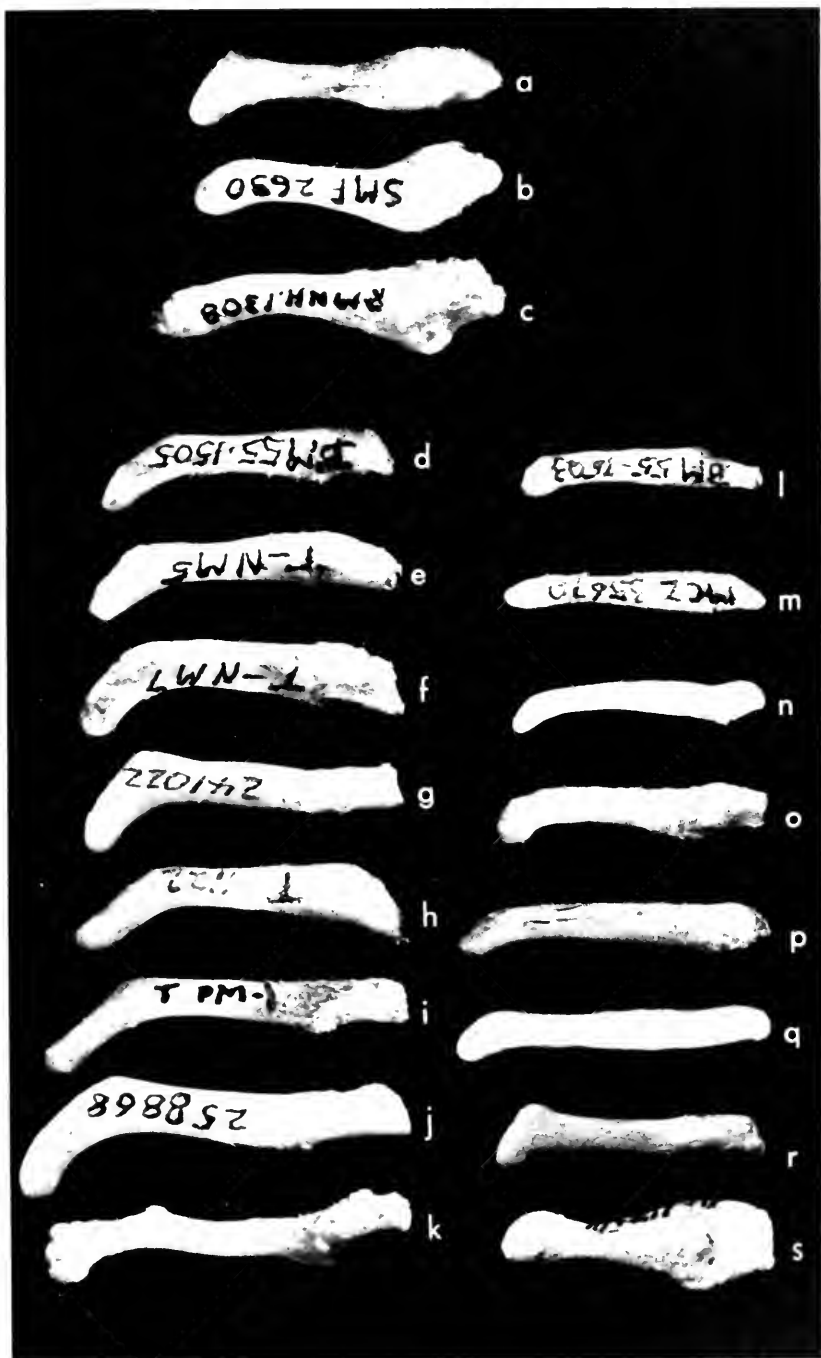


TABLE 9. Measurements (mm.) of glans penis and baculum in *M. n. leonina* immatures and adults collected in western Thailand.

FMNH No.	Head and body length	Skull greatest length	Dental stage ¹	Estimated age (yr.) ²	Length	Glans		Baculum		
						Relative breadth	Greatest length	Least D-V diam. of shaft	Shaft length ³	Distal process, length
99690	257	91.3	dec.m2	1	8.0	0.68	11.1	0.7	9.7	1.3
99680	366	—	I1, (I2)	2.5	7.7	0.78	10.1	0.7	9.4	1.1
99676	366	104.2	(M2)	3	7.0	0.81	8.7	0.5	7.9	1.9
99675	380	107.5	M2	3.5	8.6	0.74	11.0	0.8	10.0	1.8
99686	414	112.4	(C)	4.5	12.2	0.70	15.7	1.6	14.2	3.5
99684	441	114.9	(C, M3)	6	14.6	0.70	19.6	2.1	16.1	6.0
99672	476	119.7	(C, M3)	6	15.3	0.78	19.7	2.3	17.4	5.4
99691	—	139.2	M3 sl. worn	>6	17.2	0.73	22.9	2.5	19.2	6.1
99673	514	136.3	M3 worn	>>6	18.9	0.72	26.7	3.0	21.6	6.2

1. Parentheses indicate incompletely erupted teeth.

2. Based on dental emergence norms for *M. mulatta* (Hurme, 1960, p. 797).

3. Measured from proximal extremity of shaft to dorsal inflection point at base of distal process.

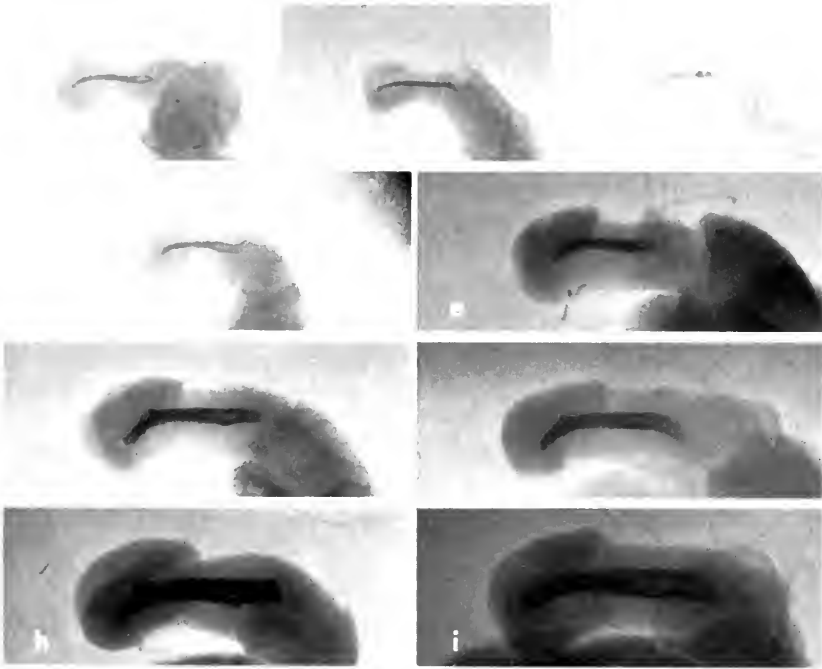


FIG. 16. Radiographs of glans penis in immature and adult *M. n. leonina* showing ontogenetic development of baculum: **a**, FMNH 99690, estimated age 1 yr.; **b**, 99680, 2.5 yr.; **c**, 99676, 3 yr.; **d**, 99675, 3.5 yr.; **e**, 99686, 4.5 yr.; **f**, 99684, 6 yr.; **g**, 99672, 6 yr.; **h**, 99691, > 6 yr.; **i**, 99673, >> 6 yr. Natural size. (Courtesy Chicago Zoological Park, Brookfield, Ill.)

taxonomically distinctive in this macaque, as in *M. n. leonina* and *M. n. nemestrina*, the evidence is imperfect and should be interpreted with caution. All three bacula are from zoo animals, which introduces the possibility of captivity-induced deformation. In addition, one of these specimens is from a known subadult, and the other two are from animals of unknown age. In these three *M. silenus* bacula, the bases are exceptionally thick, the proximal shafts are stout and cylindrical, and the distal processes are short and weakly defined. Bacular form in these specimens is more like that in *M. n. nemestrina* than in *M. n. leonina*; however, overall size exceeds that in *M. n. nemestrina*, and diameter of the base is disproportionately greater than in *M. n. nemestrina*.

A series of nine *M. n. leonina* specimens collected in a restricted area in western Thailand in 1967 (Fooden, 1971a, p. 32) provides an opportunity for investigation of ontogenetic devel-

opment of penial structure in this subspecies. Estimated ages of these nine specimens are: 1 year (infant), 1; 3 years (juvenile), 3; 4-5 years (late juvenile), 1; 6 years (subadult), 2; > 6 years (adult), 2 (table 9). Judging from available evidence (table 9, fig. 16), size of glans and baculum remains approximately constant from about age one year to age three years, while length of head and body is increasing by nearly 50 per cent. Beginning about age 4.5 years, when permanent canines emerge and puberty begins, size of glans and baculum increases rapidly, at a rate about five times that of head and body (linear dimensions). This pattern of development suggests that penial growth in *M. n. leonina* is controlled primarily by sex hormones, rather than by pituitary growth hormones. Similar indications for *M. fuscata* were reported previously (Fooden, 1972, p. 309). The characteristic prolongation of the downward inflected distal process of the baculum appears relatively late in ontogenetic development of *M. n. leonina* (fig. 16; table 9). As a result, bacular form in juvenile *M. n. leonina* (fig. 16), resembles that in adult *M. n. nemestrina* (fig. 15), which therefore is pedomorphic for this character.

BLOOD PROTEINS

Data suitable for serological comparison of *M. n. leonina* and *M. n. nemestrina* are provided by a recent series of studies of blood protein polymorphism in various macaques (table 10). Although authors of the studies do not explicitly recognize these two subspecies of pigtailed macaques, adequate information is given on the geographic origin of specimens to permit subspecific identification. No blood protein data are available for *M. n. pagensis* or for *M. silenus*.

Blood protein phenotypes are variably differentiated in *M. n. leonina* and *M. n. nemestrina* (table 10), although none of these phenotypes are absolutely diagnostic and characteristic in these or other macaque subspecies and species. *M. n. leonina* and *M. n. nemestrina* are essentially similar in frequency distributions of phenotypes of haptoglobin, acid phosphatase, albumin, thyroxine-binding prealbumin, alkaline phosphatase, plasma phosphohexose isomerase, 6-phosphogluconate dehydrogenase, and phosphoglucomutase. These two subspecies differ slightly to moderately in frequency distributions of phenotypes of α_1 -antitrypsin, carbonic anhydrase II, erythrocyte phosphohexose isomerase, transferrin, and carbonic anhydrase I. These subspecies differ strikingly in frequency distributions of phenotypes of plasma agglutinin and hemoglobin. The ratio of anti-A to anti-A + B agglutinin phenotypes is about 3:1 in *M. n. leonina*, and about 1:9 in *M. n. nemestrina*; the ratio of FS to F hemoglobin phenotypes (determined electrophoretically) is about 3:1 in *M. n. leonina*, while in *M. n. nemestrina* F is the only hemoglobin so far detected electrophoretically. Since all studies in this series evidently are based on blood samples from many or most of the same monkeys, differences in the frequency distributions presumably indicated that at least some of these blood protein phenotypes are inherited independently; however, the loci for carbonic anhydrase I and carbonic anhydrase II probably are linked in these macaques

TABLE 10. Frequency distribution (per cent) of polymorphic blood protein phenotypes in *M. n. leonina* and *M. n. nemestrina*.

Plasma proteins	Phenotypes and frequencies								
Haptoglobin¹	H_p 1-1								
<i>M. n. leonina</i> (85 specimens)	100.0								
<i>M. n. nemestrina</i> (158 specimens)	100.0								
Albumin¹	Single			Double					
<i>M. n. leonina</i> (85)	98.8			1.2					
<i>M. n. nemestrina</i> (158)	98.1			1.8					
Thyroxine-binding prealbumin²	PA^{ff}			PA^{fs}					
<i>M. n. leonina</i> (36)	100.0			0					
<i>M. n. nemestrina</i> (128)	97.2			2.8					
Phosphohexose isomerase³	1	6-1	Unidentified						
<i>M. n. leonina</i> (25)	100.0	0	0						
<i>M. n. nemestrina</i> (73)	94.5	1.4	4.1						
Alkaline phosphatase¹	A			AC					
<i>M. n. leonina</i> (85)	100.0			0					
<i>M. n. nemestrina</i> (158)	94.3			5.7					
Alpha₁-antitrypsin⁴	AB	B	AC	BC	C	CD	BD	D	
<i>M. n. leonina</i> (64)	0	1.6	0	7.8	68.7	14.1	1.6	6.2	
<i>M. n. nemestrina</i> (151)	0.7	6.6	1.3	32.4	58.3	0.7	0	0	
Transferrin⁵	BG	CC	CD	CF	CG	D'D	DD	DF	
<i>M. n. leonina</i> (85)	1.2	1.2	3.5	4.7	12.9	1.2	8.2	3.5	
<i>M. n. nemestrina</i> (158)	0	0.6	3.2	4.5	2.5	0	13.9	17.7	
	DG	F'G	F'F'	F'G	FF	FG	GG		
<i>M. n. leonina</i> (cont.)	17.7	0	0	0	3.5	10.6	31.8		
<i>M. n. nemestrina</i> (cont.)	23.4	0.6	1.3	0.6	7.6	17.7	6.4		
Agglutinin⁶	Anti-A			Anti-B			Anti-A+B		
<i>M. n. leonina</i> (82)	74.4			1.2			24.4		
<i>M. n. nemestrina</i> (144)	9.0			2.1			88.9		
Erythrocyte proteins	Phenotypes and frequencies								
NADH diaphorase⁷	A			AB			AC		
<i>M. n. nemestrina</i> (25)	92.0			4.0			4.0		
Acid phosphatase⁸	A								
<i>M. n. leonina</i> (40)	100.0								
<i>M. n. nemestrina</i> (127)	100.0								
6-phosphogluconate dehydrogenase⁹	AS			A			AF		
<i>M. n. leonina</i> (36)	2.8			97.2			0		
<i>M. n. nemestrina</i> (110)	0			97.3			2.7		
Phosphoglucomutase⁸	I			V					
<i>M. n. leonina</i> (23)	95.7			4.3					
<i>M. n. nemestrina</i> (111)	92.8			7.2					
Carbonic anhydrase II¹⁰	b			a₂			a₂b		
<i>M. n. leonina</i> (17)	52.9			17.7			29.4		
<i>M. n. nemestrina</i> (12)	66.6			16.7			16.7		

TABLE 10. (continued)

Erythrocyte proteins	Phenotypes and frequencies					
Phosphohexose isomerase ³	1	5-1	6-1			
<i>M. n. leonina</i> (11)	81.8	18.2	0			
<i>M. n. nemestrina</i> (34)	97.1	0	2.9			
Carbonic anhydrase 1 ¹⁰	a	b	ab	c	d	o
<i>M. n. leonina</i> (63)	7.9	57.1	1.6	0	6.4	27.0
<i>M. n. nemestrina</i> (165)	32.1	23.7	9.1	1.2	1.2	32.7
Hemoglobin ¹¹	F	FS	S			
<i>M. n. leonina</i> (85)	24.7	72.9	2.4			
<i>M. n. nemestrina</i> (160)	100.0	0	0			

1. Ishimoto, 1972a, pp. 260, 273.
2. Weiss et al., 1971, p. 78.
3. Ishimoto and Kuwata, 1972, p. 161; enzyme activity stronger in red cells than in plasma.
4. Omoto et al., 1970, p. 220.
5. Ishimoto, 1972a, p. 255; cf. Prychodko et al., 1971, p. 180.
6. Nakajima et al., 1970, p. 246.
7. Ishimoto, 1971, p. 385; *M. leonina* specimens not included in this study.
8. Ishimoto, 1972b, pp. 339, 341.
9. Ishimoto, 1972b, p. 342; cf. Prychodko et al., 1971, p. 176.
10. Tashian et al., 1971, p. 190.
11. Ishimoto et al., 1970, p. 235, phenotypes determined electrophoretically; hemoglobin polymorphism in *M. n. nemestrina* has subsequently been detected chromatographically (Nute and Pataryas, 1974a, p. 21).

(DeSimone, Linde, and Tashian, 1973, p. 55; Magid et al., 1973, p. 157; DeSimone, Magid, and Tashian, 1973, p. 165).

Blood protein data published for subspecifically indeterminate pigtailed of unknown geographic origin are generally concordant with data summarized above for subspecifically identifiable specimens. In 40 adult pigtailed of unknown geographic origin studied by Nute and Stamatoyannopoulos (1971a, p. 145; 1971b, p. 109), hemoglobin phenotype is monomorphic, which indicates that these specimens probably were *M. n. nemestrina* (see table 10). In 75 pigtailed studied by Crawford (1966, p. 398), the frequency distribution of hemoglobin phenotypes is 57.3 per cent F (type 2 of Crawford), 26.7 per cent FS (types 3 and 4), and 16.0 per cent S (type 1), which suggests that this may have been a mixed group of *M. n. leonina* and *M. n. nemestrina*, approximately as later suspected by Crawford (1971, p. 706; cf. Nute and Pataryas, 1974a, p. 17). In a general review of ABO blood groups in primates, Moor-Jankowski and Wiener (1971, p. 240) report that B and O are characteristic of pigtailed (subspecifically indeterminate), which is compatible with the

observed preponderance of agglutinin anti-A in *M. n. leonina* and anti-A + B in *M. n. nemestrina* (table 10). Transferrin polymorphism reported in subspecifically indeterminate pigtailed (Goodman et al., 1965, p. 885; Goodman, 1967, p. 8; Prychodko et al., 1969, p. 104) is likewise compatible with transferrin polymorphism in identifiable *M. n. leonina* and *M. n. nemestrina* (table 10).

In a captive multi-male colony of 16 pigtailed of unknown geographic origin, nine blood proteins were studied in an attempt to determine paternity of five infants (Simons and Crawford, 1969, p. 255). Since hemoglobin phenotype was monomorphic, the colony probably consisted exclusively of *M. n. nemestrina* (see table 10). This colony also was monomorphic for phenotypes of phosphoglucomutase (PGM-M), acid phosphatase (pm), erythrocyte glucose-6-phosphate dehydrogenase (Gd^A), erythrocyte 6-phosphogluconate dehydrogenase (6PGD^A; cf. table 10) and haptoglobin (Hp1). The same colony was polymorphic for phenotypes of serum pseudocholinesterase (E₂; E₁^S, E₁^U, hypothesized), transferrin (Tf^A, Tf^B, Tf^D), and blood groups (14 reagents). In a mixed group of *M. n. leonina* and *M. n. nemestrina*, MN and Lewis blood groups were studied by Nakajima et al. (1970, p. 248); 39 individuals tested were positive for M or M-like antigens, 236 tested were negative for Le^a antigens, and 12 of 123 tested were positive for Le^b antigens. In 13 pigtailed of unknown geographic origin, erythrocyte isoantigen polymorphism was studied with taxonomically inconclusive results (LaSalle, 1969, p. 120). The amino acid composition of the β - hemoglobin chain in *M. n. nemestrina* has been compared with that in *M. fascicularis*, *M. mulatta*, and *M. fuscata* (Nute and Pataryas, 1974b, p. 79); the composition of this chain in *M. n. leonina* is unknown.

In Indochinese populations of *M. n. leonina*, *M. mulatta*, and *M. fascicularis*, similarities in frequency distributions of transferrin phenotypes and 6-phosphogluconate dehydrogenase phenotypes have been construed as evidence of interspecific gene exchange (Goodman, 1967, p. 9; Prychodko et al., 1969, p. 108; Prychodko et al., 1971, p. 181). *M. arctoides* (= *M. speciosa* of authors) formerly was also included in this hypothetical group of interbreeding "semispecies" (Goodman, 1965, p. 255; Goodman et al. 1965, p. 886), but in recent reports this macaque apparently is regarded as a well-isolated species (Prychodko et al., 1969, p. 107; Prychodko et al., 1971, p. 179). However, regardless of the disposition of *M. arctoides*, available evidence does not support the assumption that similarity

of blood protein phenotype frequencies necessarily implies gene exchange. Transferrin phenotypes, for example, are more similar in Thai *M. n. leonina* and Thai *M. mulatta* (index of dissimilarity 0.360; Prychodko et al., 1969, p. 107), which are members of two different species, than in Thai *M. mulatta* and northeast Indian *M. mulatta* (index of dissimilarity 0.546), which are local populations in one continuously distributed species. Since gene exchange usually is assumed to be greater within species than between species, it follows that similar blood protein phenotypic frequencies are not a reliable indicator of gene exchange.

If interspecific gene exchange has occurred in Indochinese macaques with similar transferrin and 6-phosphogluconate dehydrogenase phenotypes, this probably should be also be evident in non-hematological characters of these specimens. However, no such non-hematological evidence of gene exchange has been observed or reported in these critical specimens. In fact, there is no indication that other blood protein phenotypes in these specimens support the hypothesis of gene exchange, and one published analysis of their phenotypic frequencies of alpha₁ - antitrypsin definitely fails to demonstrate such gene exchange (Omoto et al., 1970, p. 226). As previously indicated by Jolly (1971, p. 197), it seems likely that reported similarities in blood protein phenotype frequency distributions in Indochinese macaque species probably are the result of common inheritance and/or convergent evolution, not gene exchange (cf. Weiss et al., 1973, p. 225).

Frequency distributions of blood protein phenotypes also have provided the basis for a computer-generated dendrogram of hypothetical interrelationships among macaque species and infraspecific populations (Goodman, 1971, p. 83; cf. Weiss et al., 1973, pp. 220-223 and Ishimoto, 1973, p. 9). (It should be noted that this dendrogram is based on the implicit assumption that similar blood protein phenotype frequencies are the result of common inheritance, not of gene exchange.) Judging from the dendrogram, hematological evidence apparently indicates that *M. n. leonina* and *M. n. nemestrina* diverged from the common ancestral macaque lineage subsequent to the divergence of Celebesian macaques and that *M. mulatta* diverged subsequent to the divergence of *M. fuscata*. However, these phylogenetic inferences are contrary to those derived from non-hematological characters, which indicate that short-tailed Indochinese *M. n. leonina* and Sundaic *M. n. nemestrina* probably represent the stock that is ancestral to (hence

diverged prior to) stump-tailed Celebesian macaques (fig. 18c; Fooden, 1969a, p. 61) and that short-tailed continental *M. mulatta* probably represents the stock ancestral to stump-tailed insular *M. fuscata* (Fooden, 1972, p. 310). Judging from non-hematological characters, it is likewise difficult to accept the hematologically supported assertion (Goodman, 1971, p. 86) that "human beings are very generalized mammals"; compared with Mesozoic stem mammals and with primitive marsupials and insectivores (Romer, 1966, pp. 193-211), humans obviously are highly specialized, except for retention of pentadactyly (cf. Clark, 1972, p. 473).

COMPARATIVE ECOLOGY AND BEHAVIOR

As discussed in detail in species and subspecies accounts (see below), liontail macaques and pigtail macaque subspecies appear to be essentially similar in habitat, diet, and troop size. The usual or exclusive habitat of liontails and pigtails is dense evergreen rain forest, and their geographic distribution closely coincides with the distribution of this habitat in tropical Asia (fig. 17). The food of these macaques evidently consists chiefly of fruits and seeds, occasionally augmented by young tender leaves, insects (larvae and adults), spiders, and, probably, birds eggs and small vertebrates. Troop size in these macaques typically is about 5 to 20. Most troops probably are composed of 1-3 adult males, 2-10 adult females, and 2-10 immatures. Solitary adult males are fairly common; this presumably is correlated with the unbalanced ratio of male and female adults within troops.

Altitudinal distribution is not uniform in liontails and pigtail subspecies (table 11). Of the three relatively well-known species or subspecies, *M. silenus*, with known altitudinal range 300-1300 m., is restricted to upper elevations; *M. n. leonina*, with altitudinal range 75-1250 m., is limited to the vicinity of foothills of major mountain chains; and *M. n. nemestrina*, with altitudinal range 0-1700 m., is relatively widespread and inhabits lowland areas as far as 150 km. distant from the nearest mountains. These differences in altitudinal range probably are determined by regional temperature and rainfall patterns (Koeppel and DeLong, 1958, pl. 2), which, in turn, determine rain forest distribution (fig. 17).

Liontails and pigtail subspecies also appear to differ in population density and arboreal-terrestrial preference. Population density in *M. silenus* seems to be much lower than in *M. n. leonina* and *M. n. nemestrina*, judging from frequency of reported encounters. *M. silenus* and *M. n. leonina* apparently are much more arboreal than *M. n. nemestrina*; *M. silenus* and *M. n. leonina* are rarely encountered on the forest floor, whereas such sightings of *M. n. nemestrina* are commonplace. When alarmed, *M. silenus* and *M.*

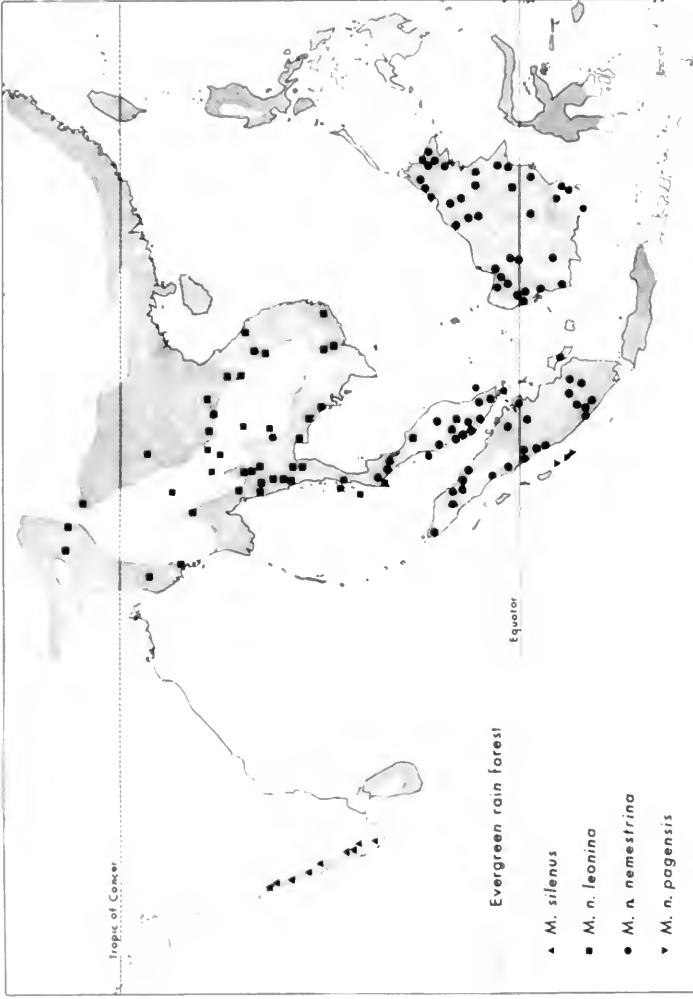


FIG. 17. General distribution of broadleaf evergreen rain forest in tropical Asia (shaded area; Küchler, 1964, pp. 17, 141) and locality records of liontail and pigtail macaques (black symbols, see figs. 20, 25, 28). The few locality records shown here slightly outside of shaded areas probably indicate the existence of isolated tracts of rain forest that are too small to have been included in the reference vegetation map.

TABLE 11. Altitudinal distribution of accurately known localities of lion-tail and pigtail macaques. Locality numbers (italicized) as in Figures 20, 25, 28; for details, see Gazetteer of Collecting Localities.

Altitude (m.)	Species or subspecies; locality numbers			
	<i>M. silenus</i>	<i>M. n. leonina</i>	<i>M. n. nemestrina</i>	<i>M. n. pagensis</i>
1600-1799	—	—	82	—
1400-1599	—	—	—	—
1200-1399	—	6	—	—
1000-1199	7, 10, 13, 17	—	16, 75	—
800-999	—	8, 32	66	—
600-799	—	30	16, 17, 25	—
400-599	8	—	43, 82	—
200-399	1	21, 22, 23, 25	50, 56	—
0-199	—	1, 2, 29, 31, 46	11, 44, 46, 88	92, 93

n. leonina usually flee into the canopy, while *M. n. nemestrina* typically descends from the trees and flees on the ground.

Except for *M. n. pagensis* in Kepulauan Mentawai, the geographic ranges of liontails and pigtail subspecies overlap those of several other species of macaques. *M. silenus* inhabits forest tracts in southwestern India that also are inhabited by *M. radiata*. The combined range of *M. n. leonina* and *M. n. nemestrina* broadly overlaps that of *M. fascicularis*; however, these species are at least partly segregated ecologically by the preference of *M. n. leonina* and *M. n. nemestrina* for inland evergreen rain forest and that of *M. fascicularis* for marginal mixed secondary growth habitats. The same ecological segregation may also apply to the relationship between *M. n. leonina* and *M. mulatta* where their ranges narrowly overlap (cf. below, fig. 28, and Fooden, 1971a, fig. 2). The combined range of *M. n. leonina* and *M. n. nemestrina* narrowly overlaps that of *M. arctoides*, which has been collected in the same forests as *M. n. leonina*. Although the range of *M. n. leonina* is almost completely allopatric with that of *M. assamensis*, these species have been collected together in a few forest tracts along the frontier between their ranges.

HYBRIDIZATION

Information available concerning hybrid matings that involve liontails or pigtail subspecies indicates a relatively low level of hybrid viability and fertility (table 12). Of five reported intergeneric matings, one failed to produce conceptions, three produced hybrids that died in infancy, and one produced a hybrid that survived less than two years. Of 48 interspecific and intersubspecific hybrid conceptions reported, at least nine resulted in stillbirths or produced young that died in infancy; 11 of the hybrids are known to have reached the age of sexual maturity, and only three of these are known to have produced living offspring.

All intergeneric crosses that involve liontail or pigtail macaques are restricted to members of the 42 chromosome group of cercopithecine genera (Chiarelli, 1967, p. 162). All interspecific crosses are restricted to macaque species in which the glans penis is bluntly rounded and the uterine cervix and cervical colliculi are moderately large (see above). Because of the size difference between sexes in catarrhine monkeys, it is not surprising that most hybrid matings of *M. n. nemestrina* with smaller-sized monkeys (*M. silenus*, *M. n. leonina*, *M. fascicularis*, *Cercocebus* sp.) are between a female of *M. n. nemestrina* and a male of the smaller species or subspecies; conversely, all four crosses with larger-sized species (*Papio* spp., *Mandrillus* sp.) involve a male *M. n. nemestrina* and a female of the larger species. The high incidence of hybrid matings reported between pigtail macaques and either *M. fascicularis* or *M. mulatta* may merely reflect the fact that *M. fascicularis* and *M. mulatta* are the macaque species most frequently kept in captivity.

Available evidence concerning F₁ phenotypes is limited and of varying precision and reliability (table 13). This deficiency is unfortunate because such evidence would be useful in interpreting the genetics and evolution of taxonomic characters in liontail and pigtail macaques. Although relevant data are somewhat ambiguous, the following genetic inferences are probably valid: (1) dorsal pelage color in *M. fascicularis* is dominant to that in *M. silenus* and *M. n.*

TABLE 12. Reported hybridizations involving liontail and pigtail macaques.

Parental species or subspecies ¹	Sex of offspring	Longevity of offspring	Reference
Intergeneric crosses			
<i>M. n. nemestrina</i> x <i>Papio anubis</i> ♀	—	frequent matings during 4 mo.; no conceptions	1. Zuckerman, 1933, p. 100
<i>P. ursinus</i> ♀	?	infant	2. Blyth, 1863, p. 455
<i>P. hamadryas</i> ♀	♀	4 days	3. Mangili in Chiarelli, 1971, p. 5
<i>Mandrillus leucophaeus</i> ♀	?	infant	4. Knottnerus-Meyer, 1904, p. 61
<i>Cercocebus fuliginosus</i> ♂	♂	1 yr. 10 mo.	5. Montagu, 1950, p. 150
Interspecific and intersubspecific crosses			
<i>M. silenus</i> x			
<i>M. n. nemestrina</i> ♀	♂	?	6. Bernstein in Chiarelli, 1971, p. 4
<i>M. n. nemestrina</i> ♀	♀	8 mo.	7. Montagu, 1950, p. 150
<i>M. n. nemestrina</i> ♀	♀	7 yr. 2 mo.	8. Zukowsky, 1952, p. 3, figs. 1-16, 19, 22, 25, 26-28
<i>M. n. nemestrina</i> ♀	♀	>5 yr. 10 mo.	8. Zukowsky, 1952, p. 3, figs. 1-16, 19, 22, 25, 26-28
<i>M. n. nemestrina</i> ♀	♂	>4 yr. 10 mo.	8. Zukowsky, 1952, p. 3, figs. 1-16, 19, 22, 25, 26-28
<i>M. n. nemestrina</i> ♀	♀	1 yr. 1 mo.	8. Zukowsky, 1952, p. 3, figs. 1-16, 19, 22, 25, 26-28
<i>M. n. nemestrina</i> ♀	♂	adult	9. Chicago Zool. Pk., Brookfield, Ill. ²
" <i>Celebes-Makak</i> " ♂	?	?	10. Hecke, 1916, p. 558
<i>M. fascicularis</i> ♂	♀	>5 yr.	11. Linke, 1971, p. 163, figs. 1-3
<i>M. fuscata</i> ³	♀	?	12. Int. Zoo Yearb., 1971, p. 265
<i>M. n. nemestrina</i> x			
<i>M. n. leonina</i> ♂	♀	adult	13. Nat. Zool. Pk., Wash., D.C. ⁴
<i>M. n. leonina</i> ♂	?	> infant	13. Nat. Zool. Pk., Wash., D.C. ⁴

TABLE 12. (continued).

Parental species or subspecies ¹	Sex of offspring	Longevity of offspring	Reference
<i>M. n. leonina</i> ♂	♀	adult ⁵	14. Soc. R. Zool. Anvers, 1968, p. 3
<i>M. n. leonina</i> ♂	♀	?	14. Soc. R. Zool. Anvers, 1968, p. 3
? <i>M. maura</i> ³	♂	ca. 12 yr.	15. Schwarz, 1934, p. 44; BM 33.11.9.1
<i>M. nigra</i> ♀	?	stillborn	16. Ridley, 1906, p. 140
<i>M. nigra</i> ♂	?	4 stillbirths (1 premature, 3 full-term)	17. Bernstein in Gray, 1971, p. 12
<i>M. nigra</i> ♂	♀	"viable"	17. Bernstein in Gray, 1971, p. 12
<i>M. nigra</i> ♀	♀	"viable"	18. Bernstein in Chiarelli, 1971, p. 4; Bernstein in Gray, 1971, p. 12
<i>M. fascicularis</i> ♂	♂	stillborn	19. Pocock, 1906, p. 563
<i>M. fascicularis</i> ♀	?	infant	20. Gentry, 1872, p. 122
<i>M. fascicularis</i> ♂	♂	3 yr. 8 mo.	21. Montagu, 1950, p. 150
<i>M. fascicularis</i> ♂	♂	12 yr.	22. Ridley, 1906, p. 140; BM 31.1.9.2
<i>M. fascicularis</i> ♂	?	?	23. Flower, 1929, p. 23
<i>M. fascicularis</i> ♂	?	?	24. Heck, 1916, p. 553
<i>M. fascicularis</i> ♂	♀	adult ⁶	25. Bernstein, 1968, p. 131, fig. 3; Bernstein in Chiarelli, 1971, p. 6; Bernstein in Gray, 1971, p. 14
<i>M. fascicularis</i> ♂	1 ♂, 1 ♀	?	25. Bernstein, 1968, p. 131, fig. 3; Bernstein in Chiarelli, 1971, p. 6; Bernstein in Gray, 1971, p. 14
<i>M. fascicularis</i> ³	?	?	26. Flower, 1929, p. 23
? <i>M. fascicularis</i> ^{3, 7}	♂	adult	27. Bernstein, 1966, p. 1559, fig. 3; 1968, p. 121, fig. 1-2
? <i>M. fascicularis</i> ^{3, 7}	♀	adult	27. Bernstein, 1966, p. 1559, fig. 3; 1968, p. 121, fig. 1-2

TABLE 12. (continued)

Parental species or subspecies ¹	Sex of offspring	Longevity of offspring	Reference
<i>M. mulatta</i> ³	1 ♂, 5 ♀, 4?	2 died in infancy, 8 unknown	28. Int. Zool., Yearb., 1963, p. 223; 1966, p. 388; 1967, p. 304; 1969, p. 220; 1970, p. 254; 1971, p. 264; 1972, p. 317
<i>M. mulatta</i> ♀	?	infant or juv.	29. Antonius, 1951, p. 106
<i>M. mulatta</i> ³	♂	adult ⁸	30. Nesturkh, 1959, p. 44
<i>M. mulatta</i> ³	?	adult ⁹	31. Int. Zool. Yearb., 1968, p. 292
<i>M. mulatta</i> ♂	♀	?	32. Bernstein in Chiarelli, 1971, p. 6; Bernstein in Gray, 1971, p. 16

1. In some matings the pigtail parent may be *M. n. leonina* instead of *M. n. nemestrina*; authors do not always distinguish between these two pigtail subspecies.
2. Unpublished zoo records.
3. Sex unknown.
4. Information kindly supplied by H. J. Egoscue, Manager of Division of Small Mammals and Primates, letter February 17, 1971.
5. Hybrid apparently produced one offspring.
6. Hybrid female was backcrossed to *M. fascicularis* male; mating produced two stillbirths, one premature and one full-term.
7. Conjectural hybridization; inferred from phenotype of presumed hybrid, parents not observed.
8. Hybrid male was mated with *Papio hamadryas* female; mating produced two female offspring, one of which reportedly showed characters of both parents.
9. Hybrid was backcrossed to *M. mulatta*; mating produced one male offspring.

TABLE 13. F₁ phenotypes in hybridizations involving liontail or pigtail macaques.

Parental species or subspecies	F ₁ phenotype ¹						Ref. No. ²
	Face	Pelage of head	Dorsal pelage color	Tail length	Tail carriage	Remarks	
<i>M. silenus</i> x							
<i>M. n. nemestrina</i> ♀ 3	skin color: <i>n.n.</i>	facial ruff: int.	int.	<i>n.n.</i>	<i>n.n.</i>	<i>n.n.</i> characters predominant	8
"Celebes-Makah" ♂	—	—	—	<i>sil.</i>	—	—	10
<i>M. fascicularis</i> ♂	skin color: <i>fasc.</i> orbital patch: <i>fasc.</i>	facial ruff: int. crown patch: <i>sil.</i>	<i>fasc.</i>	int.	—	sexual swellings: <i>fasc.</i>	11
<i>M. n. nemestrina</i> x							
<i>M. n. leonina</i> ♂	—	crown patch: <i>n.n.</i>	—	—	—	—	13
? <i>M. maura</i>	—	crown patch: <i>n.n.</i>	<i>maura</i>	<i>maura</i>	—	—	15
<i>M. nigra</i> ♀	—	—	—	—	—	characters of both parents	16
<i>M. fascicularis</i> ♂	facial length: <i>n.n.</i>	—	<i>fasc.</i>	int.	<i>n.n.</i>	—	22
<i>M. fascicularis</i> ♂	—	—	—	int.	<i>fasc.</i>	—	25
? <i>M. fascicularis</i> ⁴	—	—	—	int.	<i>fasc.</i>	—	27
<i>M. mulatta</i> ♀	—	—	—	—	—	<i>n.n.</i> characters predominant	29
<i>Papio ursinus</i> ♀	—	—	—	<i>urs.</i>	—	<i>n.n.</i> characters predominant	2

1. In phenotype columns, an abbreviated specific or subspecific name indicates that the hybrid is phenotypically similar to the parental species or subspecies indicated; the abbreviation "int." indicates that the phenotype of the hybrid is intermediate between the parental phenotypes.

2. See Table 12.

3. Four hybrid offspring were produced by this pair.

4. Two presumed hybrids.

nemestrina; (2) tail length and carriage in *M. n. nemestrina* is dominant to that in *M. silenus*; (3) tail length in *M. fascicularis* is not dominant to that in *M. silenus* and *M. n. nemestrina* (hybrids intermediate). The number of genetic loci or alleles that underlie each of these characters is uncertain.

FOSSIL RECORD

All known fossils and subfossils that are referable to the liontail-pigtail group have been collected in Quaternary deposits in the Malay Peninsula and Greater Sunda Islands, in or near the range of living *M. n. nemestrina*. In the Malay Peninsula, macaque subfossils are part of human food remains collected in floor deposits in a rock shelter (Gua Madu) in southern Kelantan, West Malaysia. According to Chasen (*in* Tweedie, 1940, p. 7), these food remains, which are not individually described or listed, include bones and teeth of *M. n. nemestrina*, langurs (2 spp.), bamboo rat, Malay bear, wild pigs (2 spp.), barking deer, sambar deer, and wild ox; no specimens of *M. fascicularis* are reported. Associated Hoabinhian artifacts indicate that the floor deposit in this shelter was formed about 4000-10,000 B.P.

In the Greater Sunda Islands, identified macaque subfossils and fossils consist exclusively of fragments of jaws and teeth. Specific determination of these specimens depends essentially on tooth size. Based on macaque species and subspecies that now inhabit the area, subfossils or fossils with large teeth are identified as *M. n. nemestrina*, and those with small teeth are identified as *M. fascicularis*. Most specimens with intermediate size teeth are indeterminable.

In west-central Sumatra, 124 isolated subfossil teeth have been collected in three caves (Djamboe, Lida Ajer, Sibrambang) in the Padang highlands. Of these, 102 are identified as *M. n. nemestrina* (82 per cent), 7 are identified as *M. fascicularis* (6 per cent), and 15 are indeterminable (12 per cent) (Hooijer, 1962a, p. 57); species proportions are reasonably consistent in all three caves. The age of these cave deposits is estimated to be prehistoric Holocene (Hooijer, 1962a, p. 4). The agency responsible for assembling the large accumulations of teeth of macaques and other mammals in these caves is unknown (Hooijer, 1948, p. 187).

In Borneo (Niah Caves, northern Sarawak) 76 identifiable subfossil macaque jaws and teeth have been collected in strata with

TABLE 14. Stratification of *M. n. nemestrina* and *M. fascicularis* subfossils collected in Niah Caves, northern Sarawak (Hooijer, 1962b, pp. 441-443).

Depth below surface (inches) ¹	Approximate C14 age (B.P.) ²	Number of subfossils	
		<i>M. n. nemestrina</i>	<i>M. fascicularis</i>
0 - 24	0 - 10,000	4 (16%)	21 (84%)
25 - 49	10,000 - 20,000	0	37 (100%)
50 - 74	20,000 - 30,000	0	7 (100%)
75 - 102	30,000 - 40,000	1 (17%)	5 (83%)
	Totals	5 ³ (7%)	70 (93%)

1. Specimens tabulated according to midpoint value of depth interval reported.
2. See Harrison, 1958, p. 563.
3. Excludes one specimen without stratigraphic data.

Carbon 14 dates extending back to about 40,000 B. P. (Harrison, 1958, p. 563). Of these subfossils, six are identified as *M. n. nemestrina* (8 per cent) and 70 as *M. fascicularis* (92 per cent) (Hooijer, 1962b, p. 440). *M. fascicularis* specimens strongly preponderate at all stratigraphic levels (table 14). All of these specimens apparently are human food remains (Medway, 1964, p. 34).

In eastern Java 28 fragments of macaque jaws and teeth have been collected in early Holocene deposits in three caves (Gua Djimbe, Gua Ketjil, cave near Wadjak; Hooijer, 1962a, pp. 41, 54). All tooth dimensions in these specimens closely correspond to those in *M. fascicularis mordax*, the living Javan subspecies of crab-eating macaque (tables 16, 17). The agency responsible for accumulation of these subfossils is unknown.

The composition of subfossil macaque faunules in the Sunda area is compared with that of modern faunas in Table 15. In

TABLE 15. Relative abundance of *M. n. nemestrina* (*n*) and *M. fascicularis* (*f*) in modern faunas and in subfossil faunules (see text).

Age of fauna	Malay Peninsula	Sumatra	Borneo	Java
Modern	$f > n$	$f > n$	$f > n$	$f > (n)^1$
0-10,000 B.P. ²	$n > (f)^1$	$n > f$	$f > n$	—
10,000-20,000 B.P. ³	—	—	$f > (n)^1$	$f > (n)^1$
20,000-30,000 B.P.	—	—	$f > (n)^1$	—
30,000-40,000 B.P.	—	—	$f > n$	—

1. Species absent.
2. Includes prehistoric Holocene
3. Includes early Holocene.

TABLE 16. Measurements¹ (mm.) of upper teeth in Pleistocene, Holocene, and living macaques; italic figure in parenthesis indicates number of specimens, where known.

Sample	C(a-p)	C (tr)	P3 (tr)	P4 (tr)	M1 (tr)	M2 (tr)	M3 (tr)
<i>Macaca</i> , Pleistocene Java							
Dub. No. 3785 ♂ 2	>9.0	—	5.9	6.9	7.6	9.4	9.2
Misc. isolated teeth ³	7.0	6.0	—	7.0	—	8.5	>6.7, >7.7
<i>Macaca</i> , Holocene Java ⁴	♂ 10.6	♀ 4.9, ♂ 6.4	5.5-6.1(4)	6.1-6.9 (7)	6.4-7.4(8)	7.3-8.4(5)	6.6-8.3(4)
<i>M. fascicularis mordax</i> ⁴	♀ 4.7-6.3	♀ 3.9-5.3	5.0-6.5	5.5-6.9	6.0-7.5	6.7-8.6	6.5-8.5
	♂ 8.5-11.2	♂ 5.7-7.9					
<i>M. n. leonina</i> ⁵	♀ 5.7-6.2(7)	♀ 4.5-5.1(7)	5.6-6.5(12)	6.1-7.1(12)	7.0-8.1(17)	8.1-9.3(13)	7.9-9.2(8)
	♂ 7.9-9.4(4)	♂ 6.4-7.2(4)					
<i>M. n. nemestrina</i> ⁶	♀ 6.1-8.0	♀ 4.9-6.7	5.5-8.5	6.3-7.9	6.5-7.8	7.6-9.3	7.2-9.7
	♂ 11.8-14.3	♂ 6.3-9.2					

1. Abbreviations: a-p, anteroposterior diameter; tr, transverse diameter.

2. Hooijer, 1962a, pp. 51, 53.

3. Badoux, 1959, p. 88; Hooijer, 1962a, p. 53, 1964, p. 76.

4. Hooijer, 1962a, p. 55.

5. AMNH 83434; FMNH 65994, 99672-78, 99680-81, 99685-89, 99691.

6. Hooijer, 1962a, p. 58.

TABLE 17. Measurements¹ (mm.) of lower teeth in Pleistocene, Holocene, and living macaques; italic figure in parenthesis indicates number of specimens, where known.

Sample	C (a-p)	C (tr)	P ₃ (h)	P ₃ (tr)	P ₄ (tr)	M ₁ (tr)	M ₂ (tr)	M ₃ (a-p)	M ₃ (tr)
<i>Macaca</i> , Pleistocene Java									
Dab. No. 37862	—	—	—	—	—	6.2	7.3	11.1	7.2
Dab. No. 37882	—	—	—	—	—	—	6.6	10.4	7.6
Dab. No. 37932	—	—	—	—	—	5.9	6.5	—	—
Misc. isolated teeth ³	± 5.7-6.9(5)	± 3.5-4.9(5)	± 7.9	± 1.1-1.1, 1.1	5.4-5.4	—	—	9.0, 10.2	6.5, 7.2
	± 8.7, 9.0	± 4.5, 5.3	—	—	—	—	—	—	—
<i>Macaca</i> , Holocene, Java ⁴	± 6.3	± 3.5	± 7.5-8.0(1)	± 3.6-4.3(3)	1.6-5.0(10)	5.0-6.0(10)	6.0-7.2(10)	9.3-10.5(7)	5.7-7.1(9)
	± 7.1-9.7(5)	± 4.6-5.4(5)	± 9.7-12.4(6)	± 4.2-4.5(6)	—	—	—	—	—
<i>M. fascicularis mordax</i> ²	± 5.3-7.0	± 2.9-3.7	± 7.0-8.6	± 3.5-4.1	1.4-5.7	4.8-6.3	5.8-7.6	8.7-12.5	5.7-7.9
	± 7.7-11.3	± 4.7-6.2	± 9.7-14.5	± 4.0-4.9	—	—	—	—	—
<i>M. n. leonina</i> ⁵	± 5.3-5.9(7)	± 3.3-4.2(7)	± 7.8-9.2(7)	± 3.6-4.5(7)	4.7-5.7(11)	5.5-6.6(17)	6.5-8.2(11)	9.8-11.2(8)	7.2-8.2(8)
	± 9.0-14.9(6)	± 5.2-5.2, 5.3	± 12.8-13.8(1)	± 4.5-5.5(4)	—	—	—	—	—
<i>M. n. nemestrina</i> ⁶	± 5.9-8.4	± 4.0-4.9	± 8.8-10.7	± 4.0-4.6	4.8-7.8	5.4-7.4	6.4-9.2	9.8-13.8	6.4-9.5
	± 9.8-12.5	± 5.7-7.8	± 12.8-19.5	± 4.8-7.7	—	—	—	—	—

1. Abbreviations: a-p = anteroposterior diameter; tr = transverse diameter; h = height measured from base of anteroexternal enamel extension to posterior border of crown.

- Hooijer, 1962a, p. 53.
- Dentinger, 1910, p. 3; Stremme, 1911, p. 140; Badoux, 1959, p. 89; Hooijer, 1962a, p. 53.
- Hooijer, 1962a, pp. 56-57.
- AMNH 83434; FMNH 65994, 99672-78, 99680-81, 99685-89, 99691.
- Hooijer, 1962a, p. 58.

modern Malayan, Sumatran, and Bornean faunas, *M. fascicularis* is approximately 10 times more abundant than *M. n. nemestrina* (below p. 103). In Java *M. fascicularis* is the only macaque now present (Chasen, 1940a, p. 65). Subfossil faunules collected in Borneo (late Pleistocene-subrecent) and Java (early Holocene) are similar in composition to the respective modern faunas; those collected in the Malay Peninsula and Sumatra (prehistoric Holocene) are not. Taken at face value, the Malayan and Sumatran subfossil data would indicate that, within the past 10,000 years, *M. n. nemestrina* was more abundant than *M. fascicularis* in the western part of the Sunda area, which is the reverse of the present situation in this area. However, this indication of recent local reversal of relative abundance may be misleading, if the accumulation of macaque remains in the Malay Peninsula and Sumatra has been subject to some unknown selective bias (cf. Hooijer, 1962b, p. 447). Hopefully, further collecting in Sunda area caves and rock shelters may help to resolve this intriguing and important problem in macaque paleogeography.

In addition to Holocene subfossils, mid-Pleistocene fossils that are referable to *Macaca* also have been collected in eastern Java (Bangle, Punung, Sangiran, Saradan, Trinil; Deninger, 1910, p. 1; Stremme, 1911, p. 140; Badoux, 1959, p. 88; Hooijer, 1962a, p. 50; Hooijer, 1964, p. 76). These Pleistocene fossils, some of which originate in fissure deposits with those of *Homo erectus*, are among the oldest known macaque remains in Southeast Asia. Dental measurements in 14 recorded specimens (tables 16, 17) are not completely consonant with measurements in either living Javan *M. fascicularis mordax* or living Sumatran and Bornean *M. n. nemestrina* (and still less with those in living Sumatran and Bornean *M. fascicularis*; Hooijer, 1962a, p. 58). Although dimensions of anterior teeth in these Pleistocene Javan fossils are approximately the same as in living *M. f. mordax* (and in Holocene subfossil *M. f. mordax*; tables 16, 17), breadth of the last premolar and all three molars is nearer to that in *M. n. nemestrina*. In the best preserved Pleistocene specimen (Dub. No. 3785, see table 16), breadth of the last two molars is 8-9 per cent greater than in the largest measured specimens of *M. f. mordax* and well within the range of molar breadths in *M. n. nemestrina*.

The relationship of the Pleistocene Javan fossil macaque to living *M. n. nemestrina* and *M. f. mordax* has been carefully reviewed by Hooijer (1962a, p. 51). In interpreting these data,

Hooijer notes that the ratio of premolar breadth to molar breadth in the fossil macaque is less than in living *M. n. nemestrina* and postulates that this would not be true in the Pleistocene ancestor of *M. n. nemestrina*. Accordingly, he rejects a relationship to *M. n. nemestrina* and concludes that the fossil macaque probably is an ancestral form of *M. f. mordax*, in which the premolar-molar breadth ratio was greater than in the living form.

However, the *a priori* assumption that the ratio of premolar breadth to molar breadth in the Pleistocene ancestor of *M. n. nemestrina* would not be less than in living *M. n. nemestrina* may not be valid. The relatively broad premolars in living *M. n. nemestrina* may be a recently evolved condition that is related to allometric increase in size of the rostrum and anterior part of the dental arch (figs. 8, 9). Cranial and dental characters in the stock ancestral to *M. n. nemestrina* may have been similar to those in *M. n. leonina*, which has tooth proportions that are fairly close to those in the Pleistocene Javan fossil macaque (tables 16, 17).

Available evidence permits two plausible interpretations of the Javan fossil macaque. This Pleistocene macaque may be ancestral to Holocene and living *M. f. mordax*, in which case relative premolar breadth in this line has undergone evolutionary decrease; this interpretation implies that the pigtail stock was absent from Java during the Pleistocene, as well as during the Holocene and present. Alternatively, the Pleistocene macaque may be ancestral to living *M. n. nemestrina*, in which case relative premolar breadth has undergone evolutionary increase from proportions similar to those in living *M. n. leonina*; this interpretation implies that the pigtail stock inhabited Java during the Pleistocene and subsequently became locally extinct, as did the siamang, orangutan, Malay bear, elephant, and tapir (Badoux, 1959, p. 129).

EVOLUTION AND DISPERSAL

Liontails, pigtail subspecies, and Celebesian stumptail species are allopatric and apparently constitute a closely interrelated phylogenetic unit, the *silenus*-group. (If subgeneric recognition of this group is warranted, the tautonym *Silenus* Goldfuss, 1820, is available and valid.) The close relationship between liontails and pigtails originally was inferred from similarities in pattern of hair growth, morphology of female sexual swelling, and structure of tail (Pocock, 1926, p. 1571). The relationship between Sundaic pigtails (*M. n. nemestrina*) and Celebesian stumptails was inferred from evidence of external proportions, structure of baculum, and geographic distribution (Fooden, 1969a, p. 61). The present study further indicates that species and subspecies in the *silenus*-group are similar in form and proportions of the glans penis (above, p. 33); these macaques also are similar in general form of estrous sexual skin swelling (above, fig. 11; Pocock, 1926, p. 1547; Fooden, 1969a, p. 13). Judging from penial and cervical morphology, the *silenus*-group probably is more closely related to *M. sylvanus* and to the *fascicularis*-group (*M. fascicularis*, *M. mulatta*, *M. cyclops*, *M. fuscata*) than to either the *sinica*-group (*M. sinica*, *M. radiata*, *M. assamensis*, *M. thibetana*) or *M. arctoides* (above, pp. 32, 33).

The close relationship of species in the *silenus*-group evidently is not revealed by their chromosome morphology. Karyologically, *M. silenus* and *M. nemestrina* are less similar to each other than each is to other macaque species (Chiarelli, 1962, pp. 408-412; Schmager, 1972, p. 481).

Geographic distribution of species and subspecies in the *silenus*-group (fig. 18f) closely corresponds to major subdivisions of the Oriental faunal region (Sclater and Sclater, 1899, p. 131, pl. 5). The range of *M. silenus* is in the Indian Subregion, that of *M. n. leonina* is in the Indochinese Subregion (extended to include the Isthmus of Kra), and that of *M. n. nemestrina* is in the Sundaic Subregion (for name of this subregion, see Johnson, 1964, p. 69; Bullock, 1964, p. 212). The insular range of *M. n. pagensis* in Kepulauan Mentawai is

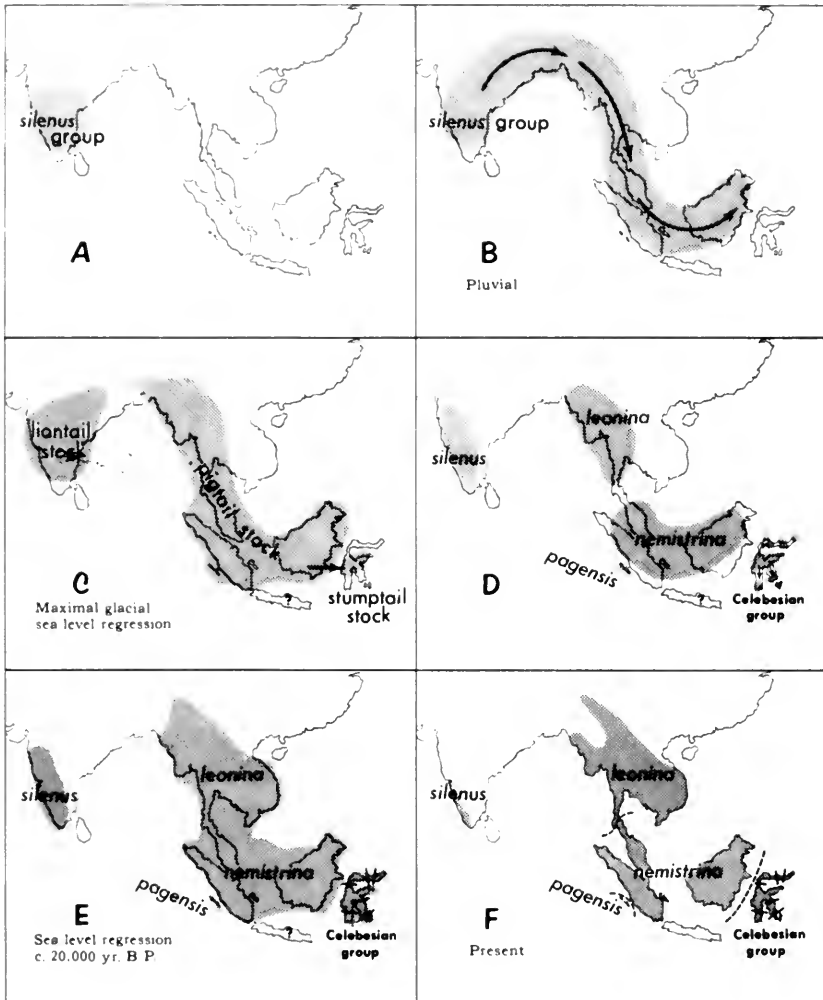


FIG. 18. Hypothetical stages in evolution and dispersal of species and subspecies in the *silenus*-group.

at the edge of the Sunda Shelf, marginal to the Sundaic Subregion. The range of Celebesian stumptail species is in the transition zone between the Oriental Region and the Australian Region.

The zoogeographic hypothesis presented below (schematically illustrated in fig. 18) is proposed as a first approximation of the Quaternary history of the *silenus*-group. Obvious problems in zoogeographic interpretation are posed by deficiencies in the fossil

record of this group (see above, p. 60) and by incomplete information concerning Pleistocene changes in the geography, climate, and vegetation of the Oriental Region. Major topics considered in the following discussion are:

1. Center of origin of *silenus*-group; main pattern of dispersal.
2. Disjunct distribution of liontails and pigtails.
3. Dispersal of *silenus*-group to zoogeographically peripheral Kepulauan Mentawai and Celebes (Sulawesi).
4. Geographic contiguity and morphological discontinuity between *M. n. leonina* and *M. n. nemestrina*.
5. Geographic isolation and morphological similarity within *M. n. nemestrina*.

In species and subspecies of the *silenus*-group there is a clear geographic pattern of progressive decrease of tail length from west to east. Relative tail length is 0.57-0.75 in *M. silenus*, 0.28-0.46 in *M. n. leonina* and *M. n. nemestrina*, 0.24-0.34 in *M. n. pagensis*, 0.05-0.12 in southern and central Celebesian species, and 0.03-0.07 in northern and northeastern Celebesian species (fig. 2; Fooden, 1969a, p. 15). Assuming that a long tail is primitive in macaques, as in other monkeys, this west-to-east trend may be interpreted as a trend from primitive to derived. Similarly, the relatively short rostrum in skulls of *M. silenus* and *M. n. leonina* probably is more primitive than the long rostrum in *M. n. nemestrina* (fig. 8); the most specialized skulls in this group, or in any species of macaque, are those of *M. nigrescens* and *M. nigra* in northeastern Celebes (Fooden, 1969a, p. 30). The geographic pattern of morphological variation of skull and, especially, of tail length tends to suggest that, among living species and subspecies, Indian *M. silenus* is morphologically most similar to the ancestral stock of the *silenus*-group and that Indochinese and Sunda area species and subspecies represent successive stages in evolutionary development of the group. Accordingly, the starting point of the present hypothesis is that the *silenus*-group originated in the Indian Peninsula (fig. 18a) and subsequently dispersed to the Indochinese Peninsula and the Sunda area (fig. 18b).

The initial direction of dispersal from the Indian Peninsula presumably was northward (fig. 18b). This may have given impetus to tail reduction in the *silenus*-group, since higher latitudes are known to be correlated with shorter tails in two previously studied groups of macaques (Fooden, 1971b, p. 72; 1972, p. 310). However,

relative tail length in the unknown original progenitor of the *silenus*-group probably was greater than in *M. silenus* (0.57-0.75), judging from external proportions in most monkeys (Napier and Napier, 1967, p. 413). *M. fascicularis*, which is the only living macaque with a long tail (relative length 0.79-1.48; Fooden, 1971a, p. 27) and a rounded glans penis (see above) may serve as a morphological model of the unknown pre-*silenus* ancestor of the group.

The present range of *M. silenus* in southwestern India is separated from the western border of the range of *M. n. leonina* in Assam and Burma by a gap that is about 2000 km. broad. At present, natural vegetation in the intervening area is deciduous or semi-deciduous forest (Küchler, 1964, pp. 17, 141), which evidently is not suitable habitat for the *silenus*-group (fig. 17). Past dispersal of the *silenus*-group across this area, as assumed in the present hypothesis (fig. 18b), probably implies that the area formerly supported evergreen forest, which, in turn, implies more continuous rainfall than at present.

It seems likely, therefore, that dispersal of the *silenus*-group from the Indian Peninsula to the Indochinese Peninsula occurred during a Pleistocene pluvial interval (fig. 18b), and that subsequent disjunction of Indian and Indochinese sections of the group dates from a succeeding arid interval (fig. 18c). The same series of Pleistocene climate changes probably also accounts for similar disjunct distributions in Indian and Indochinese species of langurs, lorises, giant squirrels, civets, and mouse deer (Pocock, 1939, p. xxvi; cf. Kurup, 1966, p. 19). Analogous zoogeographic interpretations based on Pleistocene rainfall variation previously have been proposed to account for distributions of tropical bird species in Southeast Asia (Stresemann, 1939, p. 416) and South America (Haffer, 1969, p. 131). Recent human interference with natural vegetation patterns probably has played a relatively minor role in exaggerating disjunction of the ranges of *M. silenus* and *M. n. leonina*.

Isolation of Indian and Indochinese sections of the *silenus*-group presumably led to morphological differentiation of ancestral liontails and pigtails. Populations of the ancestral pigtail stock evidently dispersed to Kepulauan Mentawai and to Celebes, where subsequent isolation resulted in differentiation of a stumptail stock (fig. 18c). In Kepulauan Mentawai, *M. n. pagensis* is part of a strikingly peculiar mammal fauna (Kloss, [1928], p. 806) that also

includes an endemic species of gibbon, *Hylobates klossii*. Because dispersal of gibbons evidently is strongly inhibited by water barriers (Groves, 1967, p. 281; Fooden, 1969b, p. 640), it seems likely that ancestral populations of the distinctive Kepulauan Mentawai fauna, including ancestors of *M. n. pagensis* and *H. klossii*, reached this island group by way of a transitory land connection with the adjacent Sunda Shelf. Conversely, absence of gibbons from Celebes, and the generally depauperate character of the Celebesian mammal fauna (Darlington, 1957, p. 519), suggests that original dispersal of the *silenus*-group to this island was across a water gap, probably by rafting (Fooden, 1969a, p. 64).

Dispersal of the *silenus*-group to Kepulauan Mentawai and Celebes probably occurred during maximal Pleistocene glacial lowering of sea level, to about 200 m. below present sea level (Jongsma, 1970, p. 151), when the Sunda Shelf was most extensively exposed. Relative richness of mammal faunas in Kepulauan Mentawai and Celebes evidently has been controlled by depth of the straits that separate these insular areas from the Sunda Shelf. Minimum depth of the strait between the Sunda Shelf and Kepulauan Mentawai is about 200 m., and that between the Sunda Shelf and Celebes is about 600 m. (Atlas van Tropisch Nederland, 1938, pl. 3). The absence of otherwise widespread *M. fascicularis* from both Kepulauan Mentawai and Celebes suggests that this macaque had not yet arrived in the Sunda area at the time that maximal Pleistocene lowering of sea level made possible dispersal of the *silenus*-group to these outlying islands (cf. Dorst, 1953, p. 312).

The border between the ranges of *M. n. leonina* and *M. n. nemestrina* almost exactly coincides with the location of the Khlong Marui Fault (Garson and Mitchell, 1970, p. 45), which cuts across the sharp bend in the Thai-Malay Peninsula. Significantly, the Khlong Marui Fault area is a border zone for many groups of animals and plants. Zoological evidence places the subregional boundary between the Indochinese and Sundaic vertebrate faunas about 250 km. north of the Khlong Marui Fault (Chasen, 1940a, p. ix), and botanical evidence places the corresponding boundary between the Continental Southeast Asiatic and Malesian floras about 250 km. south (Kloss, 1920, p. 79; van Steenis, 1950, p. lxxii; Keng, 1970, p. 51).

The broad pattern of faunal and floral differentiation, including differentiation of *M. n. leonina* and *M. n. nemestrina*, that centers around the Khlong Marui Fault probably implies the former

existence in this area of a physical barrier that blocked genetic exchange between populations on either side of the barrier. Geographic considerations suggest that this barrier may have been a local marine transgression that transected the Thai-Malay Peninsula; this transgression may have been either eustatic or tectonic in origin. Geological evidence pertaining to such a transgression is ambiguous (Scrivenor, 1911, p. 9; 1949, p. 114; Viji Stresthaputra et al., 1951, p. 40; Ho, 1960, p. 18; Kobayashi, 1960, p. 142).

Judging from degree of morphological differentiation, isolation of the *M. n. pagensis* pigtail stock in Kepulauan Mentawai probably dates from about the same time as disjunction and isolation of the *M. n. leonina* and *M. n. nemestrina* pigtail stocks. Dispersal of the ancestral Celebesian stump-tail stock to peripheral islands in the hypothetical Pleistocene Celebesian archipelago (Fooden, 1969a, p. 64) may have occurred during this same stage in the evolution of the *silenus*-group (fig. 18d).

Subsequent to the morphological differentiation of *M. n. leonina* and *M. n. nemestrina*, the postulated former barrier between their ranges evidently disappeared, bringing these two pigtail stocks into secondary contact (fig. 18e). Judging from the present restricted distribution of morphological intermediates (table 20), it appears that only limited gene exchange has subsequently occurred between these two subspecies. The geographic change that brought *M. n. leonina* and *M. n. nemestrina* into secondary contact may also have provided an opportunity for the apparently recent entry of *M. fascicularis* into the Sunda region (see above).

About 20,000 years ago, during the latest Wisconsin/Würm glacial advance, sea level in the Sunda area evidently was at least 120 m. lower than at present (Van Andel et al., 1967, p. 743; Emery, 1969, p. 114; Jongsma, 1970, p. 150). As a result of this most recent (but not most extensive) exposure of the Sunda Shelf, the Malay Peninsula, Sumatra, Bangka, and Borneo, which are now isolated parts of the range of *M. n. nemestrina*, were interconnected by dry land (fig. 18e). This relatively recent continuity of range presumably promoted partial homogenization of the gene pool of *M. n. nemestrina*, which is evident in the morphological similarity of now disjunct insular and peninsular population of the subspecies (fig. 22).

With the postglacial rise of sea level, ranges of species and subspecies in the *silenus*-group attained their present configuration

(fig. 18f). Two negative features of these ranges are somewhat difficult to interpret. These two enigmatic features are (1) the absence of *M. n. leonina* from apparently suitable evergreen forest habitats (fig. 17) in central and northern Laos and North Vietnam (Osgood, 1932, pp. 208-211) and (2) the absence of *M. n. nemestrina* from similar suitable habitats in Java, which is on the Sunda Shelf. These absences may indicate that unknown past physical or biological barriers prevented the *silenus*-group from dispersing to the northeastern part of the Indochinese Peninsula and Java or, alternatively, that populations of the group formerly inhabited either or both of these areas and subsequently became locally extinct. Problematical fossils that may record the presence in Pleistocene Java of a population ancestral to *M. n. nemestrina* are discussed above (p. 64).

SPECIES ACCOUNTS

Macaca silenus (Linnaeus, 1758)

[*Simia*] *Silenus* Linnaeus, 1758, p. 26 – part, subsequently restricted by Buffon (1766, p. 169); external characters; distribution, Asia: Ceylon, Java, etc; the specific name is a nominative singular masculine noun (Latin name of bearded woodland diety) standing in apposition to the feminine generic name.

Simia Silenus [variety A]: Schreber, 1774, pp. 87, 186, pl. 11 (animal ex Buffon) – part (also includes references to *Presbytis* sp.); external characters; habits; distribution, Ceylon, Coromandel Coast, possibly East Indies.

Sim [ia] silenus: G. Cuvier, 1817, p. 108 – species included among “Les Macaques”; distribution, Ceylon.

Simia silanus [sic]: F. Cuvier, 1822b, p. 2, pl. (animal) – external characters of captive, origin unknown; Indian name, Nil-Bandar.

Cercopithecus silenus: Kerr, 1792, pp. 32d, 64-part, liontail macaque assigned to subspecies *Cercopithecus silenus albibarbatus* Kerr, 1792.

Papio silenus: E. Geoffroy, 1803, p. 27 – zoo specimen listed; distribution, Ceylon. [Ogilby], 1838, pp.364, 386, fig. (animal) – external characters; taxonomic relationships.

Pithecus silenus: Desmarest, 1817, p. 321 – external characters; distribution, Ceylon and neighboring lands.

P[ithecus] silenus: Blainville, 1839, p. 30 – citation of possible reference in ancient Greek literature.

Macacus silenus: Desmarest, 1820, p. 63, pl. 10 (animal ex Buffon) – external characters; distribution, Ceylon. Bennett, 1829, p. 20, fig. (animals) – external characters; habits in captivity; distribution, Malabar Coast, Ceylon. Blyth, 1851, p. 154 – vernacular name not Wanderoo, which instead applies to *Presbytis* sp. Anderson, 1879, p. 93 – external and cranial characters; distribution, Western Ghats from near Goa to Cape Comorin. Blanford, 1888b, p. 16, fig. 5 (head) – external characters; nomenclature; distribution, Western Ghats northward to 14°N.

[*Macaca*] *Silenus*: Thomas, 1911, p. 126 – nomenclature.

[*Macaca*] *silenus*-group: Miller, 1933, p. 5 – key to external characters.

Macaca silenus: Pocock, 1939, p. 66, pl. 4 (animals), figs. 16 (head ex Blanford, 1888b), 17 (skull) – external and cranial characters; taxonomy, closely related to *M. nemestrina leonina*: Pocock, 1939; ecology; distribution, Western Ghats in Travancore and Cochin, reportedly from Cape Comorin northward to 14°N.

- Cynoceph [alus] Silenus*: Schinz, 1821, p. 114 — new combination; taxonomy; distribution, Ceylon.
- I[nuus] Silenus*: Wagner, [1839], p. 141 — part (also includes references to *Presbytis* sp.); external characters taxonomy; distribution, Ceylon. Blyth, 1847, p. 731 — not native to Ceylon according to Colombo resident Dr. R. Templeton; said to be abundant in Travancore and Cochin.
- Inuus silenus*: Jerdon, 1867, p. 10 — external characters; taxonomy; field observations; distribution, Western Ghats northward to 14°N.
- V[etulus] Silenus*: Reichenbach, 1862, p. 125, figs. 321-325 (animals ex authors) — external characters; habits in captivity; distribution, Malabar.
- Ouanderou: Buffon and Daubenton, 1766, p. 169, pl. 18 — part (also includes references to *Presbytis* sp.); restriction of species and virtual designation of neotype; external characters and measurements; habits; distribution, Ceylon, Malabar Coast (implied). F. Cuvier, 1837, liv. 70, pl. (animal) — taxonomic history; distribution, peninsular India.
- Lion tailed monkey [variety α]: Pennant, 1771, p. 109, pl. 13a (animal) — characters and habits of captive exhibited in London; compared with neotype of *M. silenus* (Linnaeus, 1758).
- [*Cercopithecus*] *Vetulus* Erxleben, 1777, p. 25 — new name based on (1) *Simia silenus* Linnaeus, 1758, (2) Ouanderou: Buffon, 1766, (3) Lion tailed monkey: Pennant, 1771, (4) various characterizations of *Presbytis* sp. and *Colobus* sp.; type-locality, "Zeylona, Asia, Africa." Boddaert, 1785, p. 57 — restricted to liontail macaque; distribution, Ceylon, Coromandel Coast. Fischer, 1829, p. 28 — a synonym of *Simia silenus* Linnaeus, 1758.
- Simia ferox* Shaw, 1792, p. 69, pl. opposite p. 71 (animals) — new name based on (1) *Simia silenus* Linnaeus, 1758, (2) Ouanderou: Buffon, 1766, (3) Lion tailed monkey; Pennant; 1771, (4) characterization by Ray (1693, p. 158) of *Presbytis senex*; type locality, "East Indies, ... Ceylon...also said to be found in the interior parts of Africa." Shaw, 1800, p. 30, pl. 16 (animal ex Buffon) — external characters; taxonomy. Blanford, 1888b, p. 16 — a synonym of *Macacus silenus*.
- [*Simia*] *Ferox*: Griffith, 1821, p. 105, pl. (animal) — a synonym of *Simia silenus* Linnaeus, 1758.
- M[acaca] ferox*: Wroughton, 1918, p. 554 — nomenclature; external characters; type-locality, Ceylon.
- Cercopithecus silenus albibarbatus* Kerr, 1792, pp. 32d, 64 — new subspecific name based on (1) *Simia silenus* Linnaeus, 1758, (2) Ouanderou: Buffon, 1766, (3) Lion tailed monkey: Pennant, 1771, (4) characterization by Ray (1693, p. 158) of *Presbytis senex*; type-locality, "Ceylon and the rest of India."
- Pithecus albibarbatus*: Elliot, [1913], p. 218, pl. 8 (animal; not cranial pl. 24, misidentified skull of *Macaca radiata*; see Pocock, 1939, p. 68) — external characters; taxonomic history.
- Silenus albibarbatus*: DeBeaux, 1923, p. 34 — external characters.
- [*Simia*] *Veter*: Audebert, 1798-1800, Fam. 4, p. 4 (not Linnaeus, 1766) — said to be a variety of Ouanderou: Buffon, 1766.
- Silenus veter*: J. E. Gray, 1843, p. 8 (not Linnaeus, 1766) — specimens listed.

[*Simia*] *leonina*: G. Cuvier, 1817, p. 108 (not Shaw, 1800) — external characters; name incorrectly attributed to Linnaeus and Gmelin; distribution, Ceylon.

Type. — None preserved. A captive specimen (fig. 19) described and figured by first reviser Buffon (*in* Buffon and Daubenton, 1766, p. 169, pl. 18) is now regarded as neotype (see discussion below).

As previously noted (Blanford, [1888a], p. 620; Thomas, 1911, p. 126; Elliot, 1913, p. 219; J. A. Allen, 1916, p. 50; Pocock, 1939, p. 66), it is difficult or impossible to identify with certainty the original objective basis of *Simia silenus* Linnaeus, 1758 as described in the tenth edition of *Systema Naturae* (p. 26). Linnaeus' concept of this taxon apparently was derived solely from published accounts of earlier naturalists, not from direct examination of a specimen. In the original description, quoted in full below, Linnaeus (1758, p. 26) explicitly acknowledges that the species is obscure and that most of its characters are unknown:

Silenus. 5. S[imia] caudata barbata, corpore nigro, barba nivea proluxa.

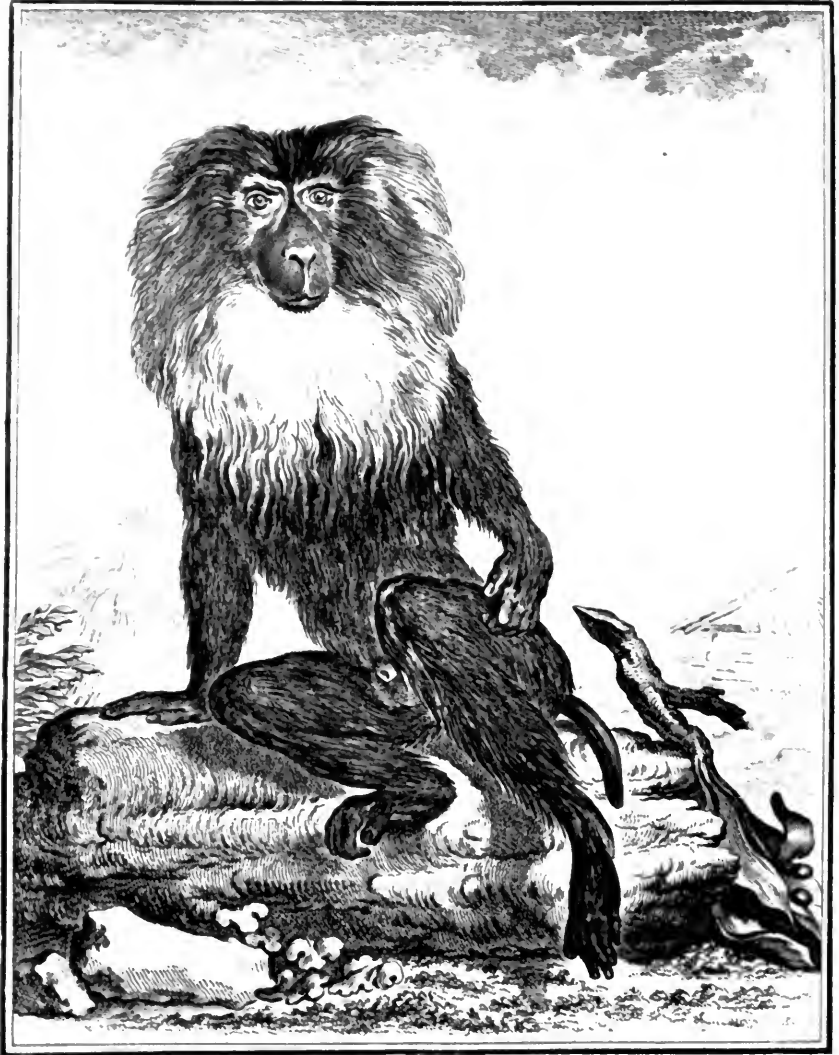
Simia Callitriches magnitudine cynocephalorum. Alp. aegypt. 242?

Habitat in Asia: Zeylona, Java & c.

Species obscurior, ignotis Pedum unguibus aliisque plurimis attributis.

In this account the skimpy diagnosis (tailed monkey with black body and full white beard) is generally applicable to the Indian liontail macaque. However, the bibliographic citation and the assigned geographic range refer to at least two other species of cercopithecids. The doubtful synonym cited (with a question mark) from Alpinus (1735, *Historiae Aegypti naturalis*) is based on a figure of a *black*-bearded monkey or baboon that reportedly originated in Egypt. The indefinite geographic distribution given by Linnaeus (Asia: Ceylon, Java, etc.) may have been partly influenced by Ray's (1693, p. 158) characterization of a monkey in Ceylon as "*Cercopithecus niger barba incana promissa*" (= *Presbytis senex*); it should be noted, however, that Ray's account of this Ceylonese monkey is not explicitly cited by Linnaeus, although Ray's work is cited in synonymies of eight other monkey species described in the tenth edition of *Systema Naturae*.

The earliest known unequivocal association of *Simia silenus* Linnaeus, 1758, with an actual specimen is in Buffon's (*in* Buffon and Daubenton, 1766, p. 169, pl. 18) account of the "Ouanderou" or "Lowando." This report is based on a captive liontail (fig. 19) that was exhibited at a fair in France. Although the owner of the captive



De Sève Del.

OUANDEROU.

Dupont Scul

FIG. 19. Ouanderou: Buffon (*in* Buffon and Daubenton, 1766, pl. 18), neotype of *M. silenus* Linnaeus, 1758.

asserted that it originated in South America, Buffon dismissed this assertion as mere showmanship. He surmised instead that the monkey probably was native to Ceylon. The sources of this erroneous geographic conjecture evidently are the faulty account of *Simia silenus* given by Linnaeus (1758, p. 26) and misinterpreted characterizations of *Presbytis senex* published by Knox (1681, p. 41, [1911 ed.]) and Ray (1693, p. 158), all of which are cited by Buffon in the synonymy of the "Ouanderou"; Buffon derived the name "Ouanderou" from the Ceylonese vernacular name cited by Knox for *Presbytis senex*. Along with the mistaken reference to Ceylon, Buffon (*in* Buffon and Daubenton, 1766, p. 171) also refers to the true geographic range of the liontail ("Malabar") in a footnote abstract of field notes published by Père Vincent Marie, who observed this species while serving as a missionary in southwestern India.

In the same year that Buffon published his account of the "Ouanderou," Linnaeus (1766, p. 36), in the twelfth edition of *Systema Naturae*, published a radically modified characterization of *Simia silenus*. In an obvious attempt to eliminate discrepancies between the characters and range of *Simia silenus* and those of the monkey cited from Alpinus, Linnaeus emended the diagnosis of *Simia silenus* in the twelfth edition to "S[im]ia] caudata barbata nigra, barba nigra prolixa" (beard black, not white, as in the tenth edition) and changed the distribution to "Habitat in Egypto" (not Asia: Ceylon, Java etc., as in the tenth edition).

However, despite ambiguity in the original characterization of this species, and despite Linnaeus' subsequent contradictory redefinition, the name *silenus* has been applied to the Indian liontail macaque by virtually all authors since Buffon. To preserve stability of the specific name, Buffon (*in* Buffon and Daubenton, 1766, p. 169, pl. 18) may be regarded as first reviser of the imprecisely characterized composite nominal species *Simia silenus* Linnaeus, 1758, and Buffon's restriction of this species to the Indian liontail macaque, represented by a described and figured captive specimen (neotype, fig. 19), may be regarded as decisive. According to this interpretation, *Simia silenus* Linnaeus, 1766, which is based on a black-bearded African monkey, is an unavailable junior homonym of *Simia silenus* Linnaeus, 1758, as restricted to the Indian liontail macaque by first reviser Buffon (1766).

Type-locality. — Geographic origin initially given as "Asia: Zeylona, Java & c." (Linnaeus, 1758, p. 26); restricted to "Ceylan"

and "Malabar" by first reviser Buffon (*in* Buffon and Daubenton, 1766, pp. 169-171); "No exact typical locality available," according to Thomas (1911, p. 126); type-locality designated "Egypt" by Elliot ([1913], p. 219); now corrected to Western Ghats, inland from Malabar Coast, southwestern India (see above).

Distribution. — Restricted to the Western Ghats, a low mountain chain in southwestern peninsular India (fig. 20); known altitudinal range 300-1300 m. (Loc.1, 12). The northernmost known locality is Anshi Ghat (14°55'N), near Goa, and the southernmost is Kalakkadu Hills (8°25'N), near Cape Comorin. The range of this species evidently has been narrowly restricted at least since the middle of the nineteenth century (see below). Recently the range has been further reduced, almost to nil, as a result of local deforestation caused by man (Sugiyama, 1968, p. 284; C. A. Hill, 1971, p. 35).

External characters (fig. 21). — Head and body length 457-481 mm. in 3 adult females, 508-584 mm. in 4 adult males; relative tail length (T/HB) 0.56-0.69 in 3 adult females, 0.57-0.75 in 4 adult males (table 18; fig. 2); weight 6.75 kg. in one male, presumably adult (Napier and Napier, 1967, p. 406). Fur blackish on crown, dorsal surface of trunk, arms, legs, hands, feet, and tail; side whiskers and beard long, pale ochraceous-gray, forming a conspicuous facial ruff; crown patch narrow anteriorly; skin of muzzle blackish, thinly covered with inconspicuous short whitish hairs; ventral surface of trunk thinly haired, grayish brown to brown.

In adults the dorsal pelage is long and dense, 8-10 cm. long on the scapular region and 4 cm. long on the lumbosacral region. The fur at the tip of the tail in adult specimens examined consists exclusively of coarse guard hairs, which are sparsely distributed elsewhere in the pelage. These hairs usually are elongated and form a more or less distinct terminal caudal tuft (fig. 21), on which Pennant (1781, p. 183) based the name "lion tailed monkey." Hairs on the crown are 2-3 cm. long and form a whorl radiating from the vertex. More anteriorly, the dark frontal hairs are about 2 cm. long, posteriorly directed, and form a sharply defined wedge-shaped patch that is bordered anteriorly and laterally by short pale hairs of the lateral supraorbital region and long pale hairs of the facial ruff. In adults, pale hairs of the facial ruff may attain a length of 10-15 cm.

Cranial characters (figs. 3, 5). — Skull relatively small (greatest length excluding incisors 102.3-112.6 mm. in 7 adult females, 128.5-

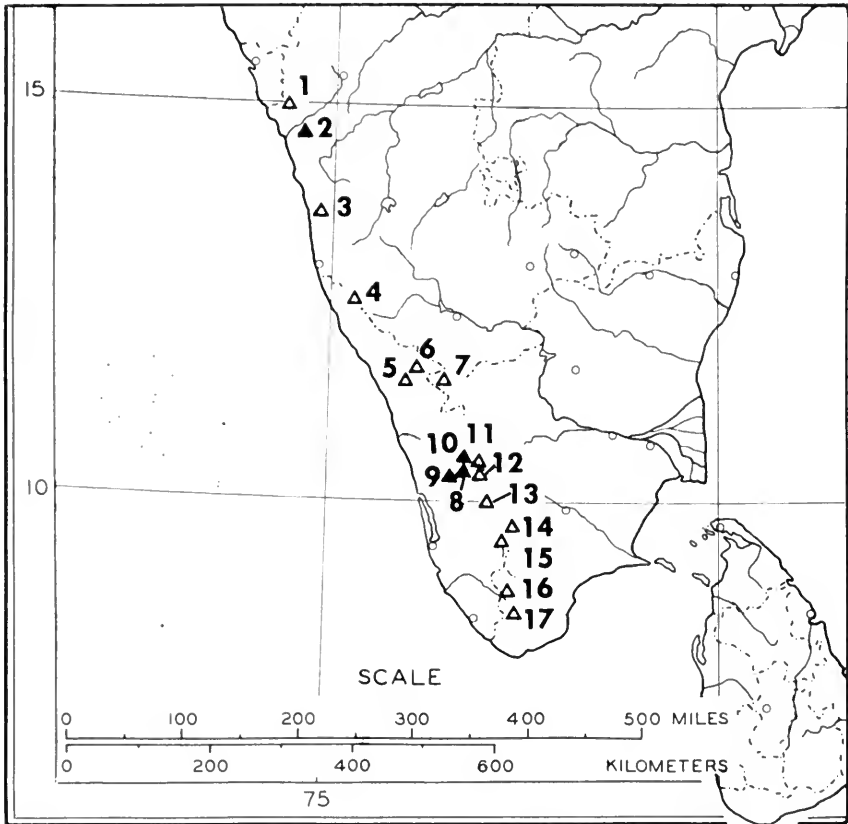


FIG. 20. Locality records of *Macaca silenus*: closed triangles = specimens examined, open triangles = literature records. For details, see Gazetteer of Collecting Localities.

Key to localities: 1. Anshi Ghat; Goa, near. 2. North Kanara. 3. South Kanara. 4. Coorg. 5. Kuttyadi Pass. 6. Wynaad. 7. Nilgiri Hills, 800-1300 m; Nilgiri Hills, western slopes. 8. Parambikulam Valley. 9. Cochin. 10. Cotengady Estate; Nelliampathy Hills; Palagapandy; Seetagundy Estate. 11. Anaimalai Hills, northern. 12. Anaimalai Hills, 800-1300 m.; Grass Hills; Varagaliyar. 13. Panniar. 14. High Wavy Mountain; Varushnaad Valley. 15. Periyar Lake, northern shore; Periyar Lake, south. 16. Manjolai Tea Estate. 17. Kalakkadu Hills; Naraikkadu Estate.

138.5 mm. in 7 adult males), rostrum relatively short, zygomatic arches broad (table 19; figs. 7, 8); supraorbital ridges thick and prominent; anterior surface of malar with a clearly defined infraorbital concavity.

Habits and habitats. — This account is based on field observations published by authors listed below. Authors are cited

TABLE 18. External variation in *M. silenus* adults; collecting localities unknown except as indicated.

Specimen No. or reference	Head and body (mm.)	Relative tail length (T/HB)
Females		
FMNH 98163	481	0.57
ZSBS 1959/264	? 610	? 0.39
Blanford, 1888 ^b , p. 16 ¹	457	0.69
Blanford, 1888 ^b , p. 16 ¹	457	0.56
Males		
AMNH 54837 ²	575	0.57
Anderson, 1879, p. 93	? 610	? 0.42
Blanford, 1888 ^b , p. 16 ¹	533	0.64
Blanford, 1888 ^b , p. 16 ¹	508	0.75
Pocock, 1939, p. 67	ca. 584	0.63

1. Collected at Travancore.

2. Collected at Nelliampathy Hills.

TABLE 19. Cranial variation in *M. silenus* adults (permanent dentition completely erupted); collecting localities unknown except as indicated.

Specimen No.	Greatest length (mm.)	Relative zygomatic breadth ¹	Rostral-postrostral ratio
Females			
BM 10 b	111.1	0.67	0.51
BNHS 5283 ²	ca. 106.2	ca. 0.69	ca. 0.46
NHRM Z4288	108.4	0.71	—
RMNH 1314	110.0	0.67	0.49
ZSBS 1959/264	112.6	0.65	0.49
ZSI 7752	102.3	0.71	0.40
ZSI 7753	105.7	0.62	0.45
Means	108.0	0.67	0.47
Males			
BNHS 5059/5064 ³	134.8	0.69	0.61
BNHS 5062 ²	128.5	0.68	0.57
FMNH 47322	135.4	0.69	0.60
MNHN 1925/8	136.6	0.67	—
NHMB 1610/3931	138.5	0.68	—
RMNH 2122	131.3	0.72	0.57
Means	134.2	0.69	0.59

1. Zygomatic breadth/greatest length.

2. Collected at North Kanara.

3. Collected at Palagapandy.

by means of the indicated abbreviations. Of these authors, Sugiyama (1968) provides the most detailed and useful information.

B	Baker in Blyth, 1859, p. 283
H	Hutton, 1949, p. 690
J	Jerdon, 1867, p. 10
Ka	Karr, 1973, pp. 191-192
Ki	Kinloch in Pocock, 1939, p. 68
Kr	Krishnan, 1972, pp. 542-543
O'B	O'Brien in Pocock, 1939, p. 69
P	Poirier, 1970, p. 261
Sp	Spence, 1921, p. 970
St	Stonor, 1944, p. 591
Su	Sugiyama, 1968, pp. 283-292
W-P	Webb-Peploe, 1947, p. 629

M. silenus is a hill species restricted to dense evergreen forest (B, H, J, Ki, Kr, P, Sp, Su, W-P) or semi-evergreen forest in which trees are more than 20 m. tall (Su) at elevations between 300 m. (Anshi Ghat) and 1300 m. (Su). Within this limited habitat, the distribution of troops of *M. silenus* is sparse (H, Kr, O'B, St, Su, W-P). As early as 1867, an observer (J) noted that this monkey "frequents the most dense and unfrequented parts of the forest, . . . and I had often traversed the Malabar forests before I first fell in with it." In 1968 the total living wild population was estimated at fewer than 1000 individuals (Su) in a maximum habitat area of 50 km. × 750 km.

The maximum number of individuals reported in a troop of *M. silenus* is 22 (Su). Other reports of troop size are: "four or five" (St), 6+ (Ka), "about a dozen" (Ki), 16 (Su), "twelve to twenty or more" (J), and "about twenty" (W-P). In two carefully studied troops, one with 16 members included 2 adult males and 7 adult females, and another with 22 members included 2 adult males and 10 adult females (Su). Solitary adult males have been observed fairly frequently (H, St, Su).

Although *M. silenus* is primarily arboreal (Su), it occasionally descends to the ground:

Once several were seen climbing slowly down one tree and walking along the ground to the next tree. This they climbed, investigated and came down to earth to repeat the process. (W-P)

Similar terrestrial excursions also are reported by two other observers (H, Su). *M. silenus* may occasionally venture into streams, since captive specimens are said to be fond of water and to swim well (H). In the trees *M. silenus* evidently is somewhat

deliberate in its locomotor behavior (Ka), moving more leisurely and with less leaping than sympatric *M. radiata*, for example (H, Kr, W-P). When disturbed, *M. silenus* flees high into the canopy (Su).

Like other macaques, *M. silenus* feeds chiefly on fruit, but augments its diet with a variety of other plant and animal foods. The species has been observed to eat wild figs (St). Another observer (Su) reports:

The only important food...during the study period was a...chestnut-like fruit...In addition...they ate other fruits, nuts, flowers and young buds of many kinds of trees, insect larvae living under tree-bark, pith of cardamon stems and so on.

In one troop that also fed on fruit, behavior apparently directed at locating arthropod food is described (Ka) as follows:

Another adult climbed to the uppermost branches of a tall emergent tree where several dead branches projected above the surrounding canopy. Pieces up to a foot long were broken off and torn apart, presumably in search of arthropods in the rotting wood. The macaque moved lower in the tree before dismantling the branch and then moved to the upper branches again, peered into the broken stub and tore off another dead branch.

During its morning feeding session, this troop evidently was dispersed over several hectares of forest (Ka).

Information on breeding periodicity is ambiguous. A birth peak in January is indicated by observation (Su) in that month of three new-born infants and also by observation (Ka) in early March of one or two young about two months old. However, another observer (W-P) asserts that females carrying young are seen regularly in September. Likewise difficult to interpret is a report (Su) of 12 instances of sexual behavior, including four copulations, observed in January and February; if these were fertile matings, the young presumably would have been born in June or July.

Encounters between adjacent troops of *M. silenus* apparently are usually hostile and characterized by aggressive vocal challenges:

As the overlapping part of the ranges of the two troops had many food trees...both troops frequently came to them, and contact between the two troops was observed many times. They were antagonistic and troop 2 was dominant. When they came near, large adult males in each troop displayed by whooping loudly but no direct fighting was seen. Usually, troop 1 moved away after a short time of vocalization. (Su)

Contradictory reports concerning interactions of *M. silenus* with sympatric primate species are discussed below. These reports



FIG. 21. *Macaca silenus*, external characters. (Photos courtesy San Diego Zoo)

are not readily harmonized. According to one observer (Su), *M. silenus* is tolerant of and subordinate to *M. radiata*:

A troop of bonnet macaque [*M. radiata*] moved among liontailed macaques and sometimes even travelled following the latter. Liontailed macaques usually did not react to the appearance of bonnet macaques but sometimes moved away slowly from them. Although smaller, bonnet macaques were dominant.

However, another observer (W-P) reports that *M. radiata* "will keep out of the way when the Lion-tailed Monkey is about." This report agrees with an early anecdotal account by Vincent Marie (*in Buffon*, 1766, p. 171), which also implies that *M. silenus* is dominant to *M. radiata*.

Similarly, three observers (Ka, St, Su) indicate that *M. silenus* associates amicably with the Nilgiri langur, *Presbytis johnii*, while two others (H, W-P) report that contacts between these species are hostile:

In the Animalais there are about as many Lion-tailed as Black monkeys [*P. johnii*] and some trespassing on each others' territory is inevitable. On these occasions some terrific battles take place in the trees, and there are casualties on both sides (W-P).

These contradictory reports may signify that interspecific behavior is variable in these monkeys.

Like other macaques (Fooden, 1969a, p. 52), *M. silenus* may form symbiotic associations with some species of birds. One observer (St) noted a troop of these monkeys "in a *Ficus* tree, oddly enough in company with the Great Indian Hornbill (*Dichoceros bicornis*)." A giant squirrel, *Ratufa indica*, that approached a female *M. silenus* with infant was responded to aggressively (Ka).

Specimens examined — Total 59. INDIA: Cochin, 1 (skull only, BM); Cotengady Estate, 1 (BM); Malabar, 5 (1, NMS; 4, skins only, RMNH); Malabar Coast ?, 1 (skin only, ZSI); Nelliampathy Hills, 2 (skins only, AMNH); North Kanara, 2 (skull only, BNHS); Palagapandy, 1 (BNHS); Parambikulam, 1 (skin only, BM); Seetagundy Estate, 1 (skin only, BNHS). Imprecise localities: 5 (2 skins only, AMNH), 6 (3 skins only, BM), 3 (1 skin and postcranial skeleton only, 1 skin only, FMNH), 2 (skulls in skins, IRSN), 5 (2 skulls in skins, 1 skull only, MNHN), 1 (skull only, NHRM), 1 (skin only, NMS), 7 (3 skins only, RMNH), 3 (1 skin only, USNM), 1 (ZSBS), 10 (4 skins only, 1 skull only, ZSI).

Macaca nemestrina (Linnaeus, 1766). (Synonymies under subspecies headings)

Taxonomy. — Compared with liontail macaques, the three recognized allopatric forms of pigtail macaques (*Inuus leoninus* Blyth, *Simia nemestrina* Linnaeus, *Macaca pagensis* Miller) are obviously similar in tail proportions and general brownish pelage hue. These three forms of pigtails are dissimilar in pelage pattern, average size, cranial characters, bacular structure, arboreal-terrestrial preference, facial markings, tail carriage, and plasma protein frequencies. Whether to regard these three pigtails (*leonina*, *nemestrina*, *pagensis*) as species or as subspecies depends ultimately on analysis of geographic variation of the characters that distinguish them (Mayr, 1963, p. 194). In the following paragraphs, overall geographic variation of adequately known characters in parapatric *leonina* and *nemestrina* is considered first. This is followed by detailed discussion of diagnostic characters in critical specimens of *leonina* and *nemestrina* that have been collected near the common border between their ranges. The taxonomic status of insular *pagensis* is considered last.

Pelage pattern is relatively constant and distinctive in *leonina* and *nemestrina*. The pale dorsal surface and anteriorly narrow crown patch in all *leonina* specimens examined is readily distinguishable from the dark dorsal surface and broad crown patch in all but four geographically marginal specimens of *nemestrina* (see below). In *leonina* specimens, preauricular sidewhisker hairs are elongate and pale from base to tip; in *nemestrina* specimens, these hairs are short and dark tipped. Although pelage pattern varies individually in *leonina* and *nemestrina*, this variation is not geographic. There is no apparent overall geographic tendency for pelage pattern in either of these pigtails to approach that of the other.

External size, measured as the combined length of head and body, apparently follows a continuous latitudinal cline in adult *leonina* and *nemestrina* (fig. 22), with geographic variation parallel in males and females. Judging from specimens examined, external size is relatively constant in Indochinese populations of *leonina* south to about 10°N in peninsular Thailand. Farther southward, length of head and body in local populations of *leonina* and *nemestrina* gradually increases, by about 100 mm. over 15 degrees of latitude, to reach a maximum in Sumatran *nemestrina*. It is significant that geographically isolated populations of *nemestrina* in Sumatra, Borneo, and the Malay Peninsula apparently all conform

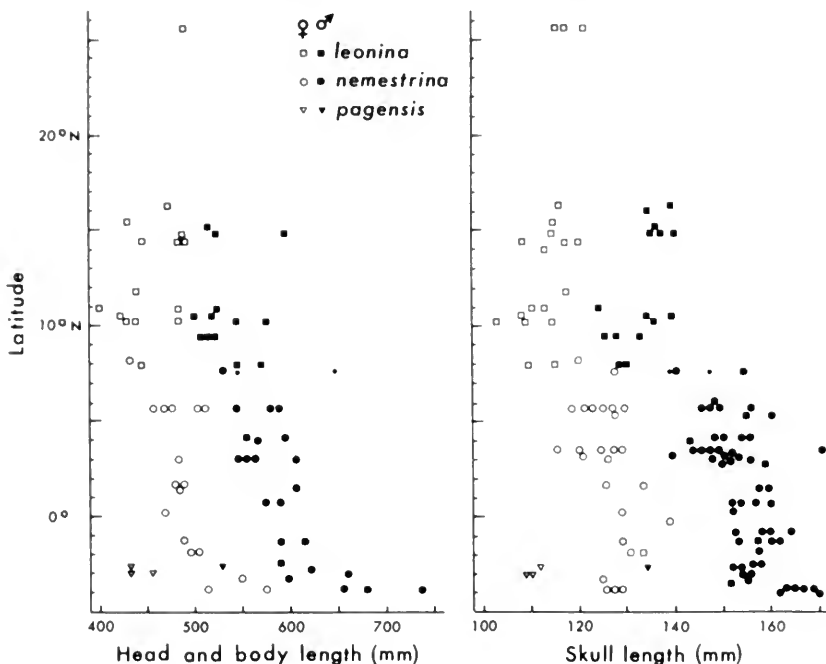


FIG. 22. Latitudinal variation of head and body length and skull length in adult specimens examined of *leonina*, *nemestrina*, and *pagensis*; specimen locality numbers (figs. 25, 28) as follows: *leonina* (fig. 28), 1, 21-26, 29, 31, 32, 37, 39, 42, 44 (for measurements of one female skull, see Pocock, 1932, p. 308), 45-47, Chamchay (unnumbered locality, see "Gazetteer of Collecting Localities"); *nemestrina* (fig. 25), 1-4, 6, 9, 10, 12, 18, 24, 26, 28-30, 33, 34, 36-39, 42-52, 55, 56, 58, 64, 66, 68, 69, 76, 77, 82-84, 87, 89, Banang, Trang (unnumbered localities, see Gazetteer); *pagensis* (fig. 25), 92, 93. Small symbols represent measurements in two subadult *nemestrina* males (canines incompletely erupted).

to the same latitudinal size cline. Over the entire range, external size is broadly overlapping in *leonina* and *nemestrina*.

Cranial size, measured as greatest length of skull excluding incisors, evidently follows a step cline in *leonina* and *nemestrina* (fig. 22). The *leonina* curve and the *nemestrina* curve appear to be abruptly discontinuous about 8°N, and known overlap of greatest skull length in these two pigtailed species is minimal. In adult males, skull length exceeds 142 mm. in 56 of 58 *nemestrina* specimens examined and in none of 15 *leonina* specimens; in adult females, skull length exceeds 120 mm. in 24 of 27 *nemestrina* specimens and in only one of 19 *leonina* specimens. Other aspects of cranial morphology (zygomatic breadth, rostral-postrostral proportions, relative length

of dental fields; see above) are directly or allometrically related to skull length and therefore have a similar pattern of geographic variation.

The geographic ranges of *leonina* and *nemestrina* are contiguous in peninsular Thailand (8-9°N) at the southern end of the Isthmus of Kra (fig. 23). Available from this area are 13 pigtail specimens (table 20), of which six are referred to *leonina* and seven to *nemestrina*. In five insular specimens collected at Klong Tung Sai and Telok Poh, virtually all known external and cranial characters are those of *leonina*; the only exception is external size in one adult male (570 mm.), which is in the range of overlap of *leonina* and *nemestrina*. A baculum of the Telok Poh specimen also is available (fig. 15d, table 6); although this is the shortest adult *leonina* baculum examined (greatest length 19.7 mm.), its form is clearly that of *leonina* (distal process length/shaft length = 0.47). One mainland specimen collected at Ban Nong Kok (skin only, subadult or adult male) likewise is a typical example of *leonina* in all available characters, as previously noted by Chasen (1935, p. 38, "Ghirbi" specimen).

The northernmost pigtail specimen that clearly exhibits pelage characters of *nemestrina* is an adult female recently collected by me at Khao Si Kaeo, which is about 10 km. north of Ban Nong Kok (mainland *leonina* locality mentioned above). Critical characters in this specimen are a mixture of those of *nemestrina* and *leonina*, with *nemestrina* characters considered to predominate. The dorsal surface is dark brown as in *nemestrina*, distinctly darker than in the Ban Nong Kok *leonina* specimen and in all other *leonina* specimens examined. Skull length (119.9 mm.) is in the range of overlap of adult female *nemestrina* and *leonina*. The crown patch is narrow anteriorly, as in *leonina*, and length of head and body (434 mm.) is within the range of female *leonina* (less than in any other adult female *nemestrina*). When encountered by hunters who took the specimen, the troop to which this female belonged was 20-25 m. above the ground in dipterocarp trees; in response to gunfire, some members of the troop descended and fled on the ground, as in *nemestrina*, and others fled in the treetops, as in *leonina*.

In one adult female and one adult male collected at Sathani Lam Phura, about 100 km. southeast of Khao Si Kaeo, the dorsal surface is dark and the crown patch is broad, both as in typical *nemestrina*. Skull length in the female (127.7 mm.) also is typical of

TABLE 20. Critical characters in pigtail specimens collected in *leonina-nemestrina* border area; l = *leonina* character state, n = *nemestrina* character state, l/n = intermediate.

Locality, Specimen No.	Age, Sex	Year collected	Dorsal pelage	Crown patch	Length of head and body	Skull length	Bacular structure	Arboreal- terrestrial preference
Klong Tung Sai, Ko Phuket								
BM 55.1506	ad. ♀	1917	l	l	l	l	—	—
ZRCS44	juv. ♂	1917	l	l	—	—	—	—
ZRCS53	ad. ♀	1917	l	l	—	l	—	—
ZRCS111	ad. ♂	1917	l	l	l	l	—	—
Telok Poh, Ko Yao Yai								
BM 55.1505	ad. ♂	1918	l	l	l/n	l	l	—
Ban Nong Kok								
ZRCS170	subad. or ad. ♂	1918	l	l	—	—	—	—
Khao Si Kaeo								
FMNH 105658	ad. ♀	1973	n	l	l	l/n	—	l/n
Sathani Lam Phura								
ZRCS3469	ad. ♂	1910	n	n	l	l/n	—	—
ZRCS3473	ad. ♀	1910	n	n	—	n	—	—
Chong								
BM 55.1504	subad. ♂	1909	l/n	l	n	n	—	—
Huai Lian								
FMNH 105676	subad. ♂	1973	n	l	l/n	l/n	l/n	l
FMNH 105678	juv. ♀	1973	n	l	—	—	—	l
“Trang”								
ZRCS1215/10	ad. ♂	—	—	—	—	n	—	—

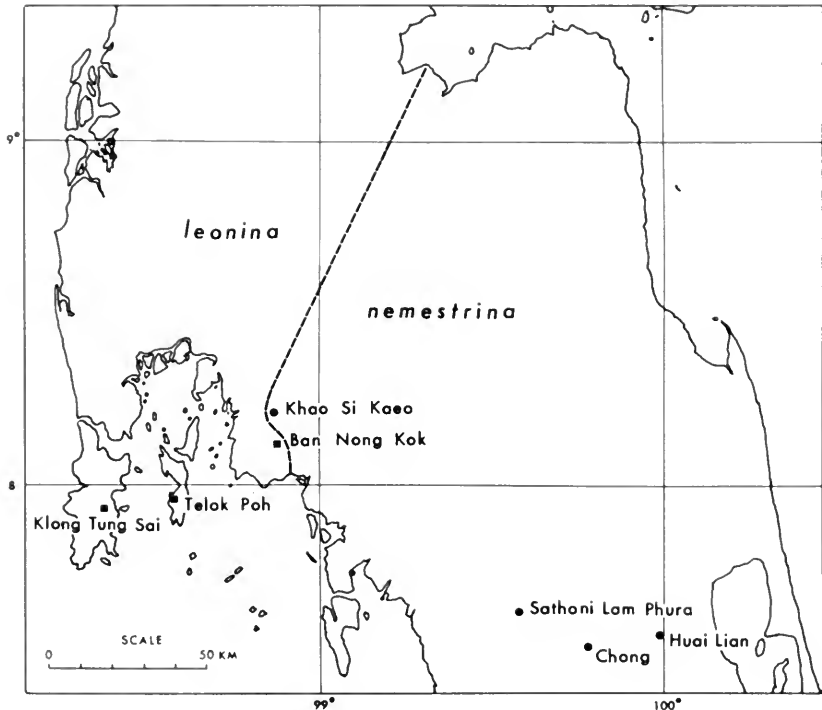


FIG. 23. Map of peninsular Thailand showing marginal collecting localities of Indochinese pigtailed macaques (*leonina*, squares) and Sundaic pigtailed macaques (*nemestrina*, circles).

nemestrina. (Length of head and body given on the tag of this specimen is 590 mm., which is highly improbable; this may be a lapsus for 490 mm.) Skull length in the male (139.6 mm.) is at the lower limit of the *nemestrina* range (upper limit of *leonina* range) and length of head and body (532 mm.) also is at the lower limit of the *nemestrina* range (well within *leonina* range).

In one subadult male (canines not quite fully erupted) collected at Chong, 25 km. southeast of Sathoni Lam Phura, the crown patch is narrow anteriorly, as in *leonina*, and the dorsal surface is pale golden-brown agouti with a weakly defined median dark streak (about 5 cm. broad), approximately intermediate between typical *leonina* and *nemestrina*. Hairs in the side-whisker region are short and dark-tipped, as in *nemestrina*. Skull length in this subadult (147.7 mm.) is within the range of adult male *nemestrina*, and length of head and body (648 mm.) approaches

that in the largest known adult male specimens of *nemestrina* collected in southern Sumatra. This Chong subadult appears to have been the specimen on which Kloss (1919b, p. 344) based his influential decision to regard *leonina* and *nemestrina* as conspecific.

In one subadult male (upper canines about 75 per cent erupted) and one juvenile female that I collected near Huai Lian, 17 km. east of Chong, the dorsal surface is dark brown to blackish, approximately as in typical *nemestrina*, and the crown patch is narrow, as in *leonina*. In the subadult male, skull length (139.6 mm.) is about equal to the maximum known in adult male *leonina* and to the minimum known in adult male *nemestrina*. Length of head and body in this subadult (548 mm.) is in the range of overlap of adult male *leonina* and *nemestrina*. In the baculum of this subadult, relative length of the distal process (0.30; fig. 15r) is slightly greater than the maximum known in adult *nemestrina* (0.29; table 6, NMS 2629) and slightly smaller than in a less mature subadult *leonina* (0.31; table 9, FMNH 99672); on balance, bacular structure in this subadult seems slightly closer to that in *nemestrina* than in *leonina*. These Huai Lian specimens were collected on successive days and belonged to different troops; in response to gunfire, both troops fled in the treetops, as in *leonina*.

Also collected in the general area of Sathani Lam Phura, Chong, and Huai Lian, is an isolated adult male skull with locality given merely as "Trang" (province). This is a typical, large *nemestrina* skull (greatest length 154.3 mm.). Another male specimen of *nemestrina* collected in this area is briefly mentioned in passing by Kloss (1919b, p. 344); this may be the Sathani Lam Phura male discussed above.

In summary, typical *leonina* specimens have been collected as far south as Klong Tung Sai, Telok Poh, and Ban Nong Kok. Within 10-150 km. of Ban Nong Kok, at Khao Si Kaeo, and in the Trang area (Sathani Lam Phura, Chong, Huai Lian), seven pigtailed have been collected in which *nemestrina* characters—most conspicuously, dark dorsal pelage color—are variably mixed with *leonina* characters, especially the narrow crown patch. This accords well with Kloss' (1919b, p. 344) observation, based on two specimens available to him, that "Trang may therefore be regarded as the locality where intermediates between the two forms occur." About 400 km. farther south, Malayan pigtail specimens exhibit characters that are unambiguously those of typical *nemestrina*.

The mixture of characters in geographically marginal specimens referred above to *nemestrina*, taken together with the continuous clinal distribution of external size in *leonina* and *nemestrina* tends to support classification of these two pigtailed macaques as conspecific subspecies, which, following Kloss (1919b, p. 344), has been the usual recent taxonomic practice. However, the narrow geographic distribution of known specimens with mixed or intermediate pelage and bacular characters and the step cline in cranial size probably indicate that genetic exchange between *leonina* and *nemestrina* is relatively restricted. On balance, despite some evidence of partial genetic discontinuity, it seems appropriate to follow a conservative course and continue to regard these two pigtailed macaques as subspecies of the species *M. nemestrina*.

The geographic isolation of Kepulauan Mentawai *pagensis* precludes the possibility of interbreeding or intergradation with neighboring Sumatran *nemestrina*. Since the degree of morphological differentiation between *pagensis* and *nemestrina* is comparable to that between *nemestrina* and *leonina*, it seems reasonable to accord equivalent taxonomic status to all three of these forms. Accordingly, *pagensis* is also treated in this revision as a subspecies of *M. nemestrina*.

Macaca nemestrina nemestrina (Linnaeus, 1766)

Pig-tailed Monkey: Edwards, 1758, p. 8, pl. 214 (animal in color) — external characters of two captives; distribution, Sumatra.

Le Maimon: Buffon and Daubenton, 1766, p. 176, pl. 19 (animal) — external characters and measurements of captive, origin unknown; internal anatomy; osteology; taxonomy; distribution, Sumatra and probably elsewhere in East Indies.

[*Simia*] *Nemestrina* Linnaeus, 1766, p. 35 — external characters ex Edwards (1758); distribution, Sumatra; the specific name is an adjective (derived from Latin name of god of groves) agreeing in gender with the feminine generic name.

Simia Nemestrina: Schreber, 1774, p. 79, pl. 9 (animal ex Edwards, 1758) — external characters; distribution, Sumatra.

[*Papio*] *Nemestrina*: Erxleben, 1777, p. 20 — external characters; distribution, Sumatra, Japan.

Papio nemestrinus: [Olgby], 1838, pp. 363, 373 — taxonomy. Cantor, 1846, p. 176 — first record of pigtailed macaque in Malay Peninsula (Pulau Pinang).

Macaca nemestrina: Daudin, [1802], p. 148 — listed; new combination. Miller, 1906, p. 556, pls. 13-20 (skin, skulls) — external and cranial characters; range restricted to Sumatra. Grimm, 1967, p. 361 — vocalizations. Blakley, Morrow, and Morton, 1973, p. 120 — serum cholesterol higher in Sumatran specimens than in West Malaysian specimens.

- Macacus nemestrinus*: Desmarest, 1820, p. 66, pl. 10 (animals ex Edwards and Buffon) – external characters; distribution, Java Sumatra. Anon., 1851, p. 444 – distribution, Sumatra, Borneo, Pinang, Malacca. Bleeker, 1851, p. 527 – first record of pigtail macaque in Pulau Bangka. Hagen, 1890, p. 82 – field observations. Sclater, 1893, p. 325 – report of aberrantly colored Bornean specimen. Thomas and Hartert, 1894, p. 654 – field observations; introduced in Kepulauan Natuna.
- Macaca nemestrina nemestrina*: Kloss, 1919b, p. 345 – external characters; said to intergrade with Indochinese pigtail macaque at Trang, peninsular Thailand. J. R. Napier and P. H. Napier, 1967, p. 403 – listed.
- Macacus nemestrinus nemestrinus*: Davis, 1958, p. 126 – external characters; field notes.
- Pithecus nemestrinus*: E. Geoffroy, 1803, p. 25 – external characters of two museum specimens; distribution, "L'Inde méridionale."
- Cynocephalus nemestrinus*: Latreille, 1804, p. 291 – external characters.
- Inuus nemestrinus*: E. Geoffroy, 1812, p. 101 – external characters, distribution, Java, Sumatra.
- [*Inuus*] *nemestrinus*: Wagner, [1839], p. 143 – external characters; distribution, Sumatra, Borneo.
- Macacus (Inuus) nemestrinus*: Müller, 1839-1840, p. 14 – field observations; distribution, Sumatra and Borneo, transported from Sumatra to Java.
- S[almacis] nemestrina*: Gloger, [1841], p. 36 – new combination.
- Nemestrinus nemestrinus*: Schneider, 1905, p. 73 – field observations.
- Rhesus nemestrinus*: DeBeaux, 1923, p. 36 – external and cranial characters.
- Pig-tail [Baboon]: Pennant, 1771, p. 105 – part (also includes references to *Macaca fuscata*); external characters; distribution, Sumatra, Japan.
- New Baboon: Pennant, 1771, p. xxiii, pl. 13 (animal) – external characters, based on figure of specimen of unknown origin.
- Simia platypygos* Schreber, 1774, p. 74, pl. 5b (animal, head) – syntypes, male and female of unknown origin observed in captivity by D. Hermann; external characters; habits; characteristic pigtail grimace noted. Erxleben, 1777, p. 629 – external characters. Zimmermann, 1780, p. 181 – possibly a synonym of *Papio nemestrina* Erxleben, 1777. E. Geoffroy, 1812, p. 101 – a synonym of *Simia nemestrina* Linnaeus, 1766.
- Papio platypygos*: Kerr, 1792, pp. 32d, 62 – listed.
- Brown Baboon: Pennant, 1781, pl. 20 (animal) – replacement name for New Baboon: Pennant, 1771; *Simia platypygos* Schreber, 1774, cited in synonymy.
- Babouin à longues jambes: Buffon, 1789, p. 41, pl. 8 (ex Pennant, 1781) – external characters and habits of captive specimen, origin unknown; *Simia platypygos* Schreber, 1774, cited in synonymy.
- S[imia] Longicruris* Link, 1795, p. 62 – based on Babouin à longues jambes: Buffon, 1789. J. E. Gray, 1843, p. 7 – synonym of *Macacus nemestrinus* Desmarest, 1820.

- S[im]ia fusca* Shaw, 1800, p. 24, pl. 13 (animal ex Pennant, 1781) – type, Brown Baboon: Pennant, 1781; *Simia platypygos* Schreber, 1774, cited as a possible synonym. E. Geoffroy, 1812, p. 101 – a synonym of *Simia nemestrina* Linnaeus, 1766.
- Macaca sphinx* [Variété C]: Daudin, [1802], p. 149 (not Linnaeus, 1758) – applied to Babouin à longues jambes: Buffon, 1789.
- Macaque, Espèce inédite: F. Cuvier, 1816-1817, pl. 5 (animal) – figure of tumescent female, origin unknown.
- Singe à queue de cochon: F. Cuvier, 1820, liv. 19, p. 1, pl. (animal) – taxonomy, referred to *Simia nemestrina* Linnaeus; external characters; reproductive biology, sexual swelling, gestation 7 months 20 days; distribution, Sumatra. F. Cuvier, 1822a, liv. 36, p. 1, pl. (animal, head) – taxonomy; distribution, Sumatra.
- Simia carpolegus* Raffles, [1821], p. 243 – based on specimens collected and observed in Sumatra by T. S. Raffles between 1818 and 1820; syntypes formerly preserved in collections of Zoological Society of London (Waterhouse, 1838, p. 8) and East India Company (Horsfield, 1851, p. 19); external characters and variation; M₃ 5-cusped; trained to pick coconuts; Malay name, Bruh; type-locality, Bencoolen (=Bengkulu), southwestern Sumatra. Fischer, 1829, p. 30 – a synonym of *Simia nemestrina* Linnaeus, 1766.
- Cynocephalus carpolegus*: [Vigors], 1829, p. 13 – specimen listed.
- Macacus libidinosus* I. Geoffroy, 1826, p. 589 – based on illustration of Macaque, Espèce inédite: F. Cuvier, 1816-1817, origin unknown.
- S[im]ia libidinosa*: Fischer, 1829, p. 30 – doubtfully distinguishable from *Simia nemestrina* Linnaeus, 1766.
- P[ithecus] maimon* Blainville, 1839, pl. 10 (dentition of adult male) – new name used in figure caption.
- Macaca nemestrina* var. *leoninus*: Oudemans, 1890, p. 266 – captive juvenile received from Sumatra.
- Macaca broca* Miller, 1906, p. 558 – external and cranial characters; holotype, adult male, skin and skull (USNM 34930, Coll. No. 19211), collected at Sungai Sapagaya, Sabah by C. F. Adams, Nov. 21, 1887; distribution, Borneo. Lyon, 1907b, p. 566 – cranial comparison with Bornean *M. nemestrina*. Elliot, [1913], p. 205 – a synonym of *Simia nemestrina* Linnaeus, 1766; synonymy said to be concurred in by G. S. Miller, original author of *broca*.
- P[ithecus] broca*: Lyon, 1911, p. 136 – cranial comparison with Bornean *M. nemestrina*.
- Macaca nemestrina broca*: Myers and Kuntz, 1969, p. 420 – nematode parasite.
- Macaca nemestrina nucifera* Sody, 1936, p. 42 – based on skin (head only) and skull of adult male collected at Pulau Bangka by H. J. V. Sody (Coll. No. Bk 75), date and museum unknown; external and cranial characters; taxonomic comparisons. Sody, 1937, p. 248 – taxonomic comparison. Chasen, 1940a, p. 65 – a synonym of *Macaca nemestrina nemestrina*.

Type. – None preserved. Linnaeus' (1766, p. 35) description of this species is based solely on Edwards' (1758, p. 8) illustrated



FIG. 24. Pig-tailed Monkey: Edwards (1758, p. 8), holotype of *M. nemestrina nemestrina* (Linnaeus, 1766).

account of a captive juvenile male (fig. 24) that was brought from Sumatra to England on a British warship in 1752 and was subsequently purchased by Edwards. In Edwards' account, the holotype juvenile is compared with an older captive female (paratype) that was then on exhibit at a fair in London. Neither holotype nor paratype is known to have been preserved.

Type-locality. — Sumatra (Edwards, 1758, p. 8).

Distribution (fig. 25). — Sunda area from Surat Thani-Krabi depression in peninsular Thailand (8-9°N) southeastward through West Malaysia, Sumatra, Bangka, and Borneo; known altitudinal range 0-1700 m. (table 11). *M. n. nemestrina* apparently is native to the offshore islets Pulau Pinang (west coast of West Malaysia), Pulau Tioman (east coast of West Malaysia), and Pulau Batam (Riau Archipelago, southern tip of West Malaysia) (see Gazetteer). Other offshore islets generally are excluded from the natural range of the subspecies, although it often is present as an introduced element. A captive specimen said to have been obtained in the Nicobar Islands (Corner, 1941, p. 14) probably represents such an introduction (see Kloss, 1928, p. 802).

Anomalous locality information is recorded on the museum tag of one captive adult male specimen of *M. n. nemestrina* (AMNH 119514, skin and skeleton; blackish dorsal streak, greatest length of skull 144.8 mm.) that died in the New York Zoological Park on June 18, 1937 and was catalogued at the museum on the same day. According to the tag, this monkey was born about December, 1931 and was obtained by the Legendre Indo-China Expedition (date unspecified) at Plateau des Bolovens, Laos, which, however, is far outside the indicated range of *M. n. nemestrina* (fig. 25). It is known that the Legendre expedition collected a series of *M. n. leonina* skins (AMNH 87268 ♂, 87269 ♂, 87273 ♀, 87274 ♀; immatures) at Plateau des Bolovens in February 1932 and also obtained a living specimen that was donated to the New York Zoological Park later the same year (Berger, 1932, p. 329; Legendre, 1932, p. 495; New York Zoological Society Annual Report, 1933, p. 109). It seems likely that geographic information properly applicable to Legendre's captive Indochinese pigtail (whereabouts now unknown) was inadvertently transferred to a captive Sundaic specimen (AMNH 119514); this may have occurred while both were being kept at the New York Zoological Park.

External characters (fig. 26). — Head and body length 434-576 mm. in 17 adult females, 532-738 mm. in 23 adult males (excluding

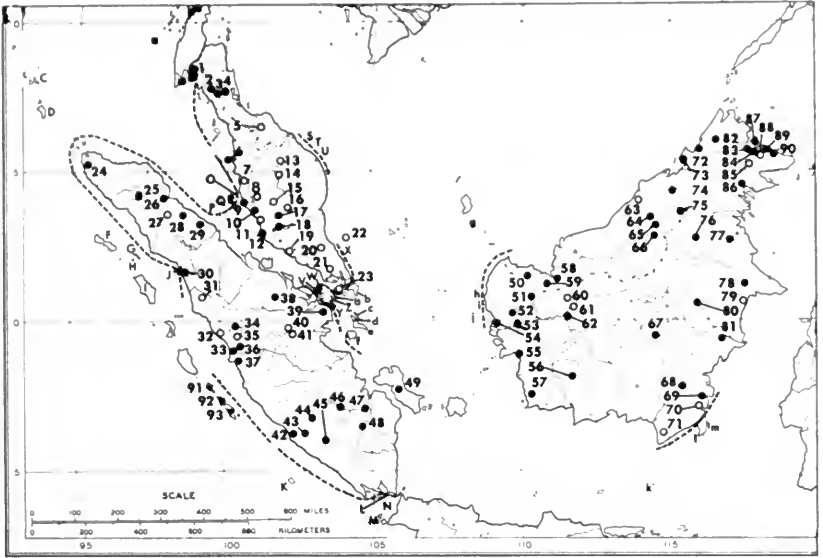


FIG. 25. Locality records of *M. n. nemestrina* (circles) and *M. n. pagensis* (inverted triangles); closed symbols = specimens examined, open symbols = literature records; squares = marginal records of *M. n. leonina*; letters and heavy broken lines indicate negative reports. For details, see "Gazetteer of Collecting Localities."

M. n. nemestrina localities: 1. Khao Si Kao. 2. Lam Phura. 3. Chong. 4. Huai Lian. 5. Biserat. 6. Pinang. 7. Larut; Perak, Upper. 8. Gedong; Keroh Forest Reserve. 9. Hantu, Tanjong; Simpang Empat Rungkup. 10. Jeram; Lima Belas Estate. 11. Sungai Buloh. 12. Kelang; Meru; Sungai Renggam. 13. Galas, Sungai. 14. Gua Madu. 15. Bukit Fraser, 5 km. S; Bukit Fraser, northern slopes. 16. Kuala Lompat; G. Benom. 17. Bentong; Bentong, 6-9 miles W. 18. Ampang; Kepang; ? Kuala Lumpur; Kuala Lumpur, Cheras Road, 7th mile; Ulu Gombak Forest Reserve. 19. Melaka. 20. Janing, Gunong. 21. Johor, southeast. 22. Tioman, Pulau. 23. Batam, Pulau. 24. Pasi. 25. Leuser Reserve; Pulau Munteh. 26. Aru, Teluk; Bukit Tinggi; Langsa; Pangkalanberandan; Pulutelang. 27. Borohok; Langkat; Serapit. 28. Batangkuwis; Deli; Dolok-Oelve; Medan; Tandjungmorawa. 29. Bedagi; Lauttador; Padang [district]; Paguruan, Sungai; Serdang; Tebingtinggi; Tandjung. 30. Sibolga, Teluk. 31. Sirambas. 32. Lubukbasung. 33. Padang. 34. Lida Ajer cave; Pajakumbuh. 35. Djamboe Cave; Sibrambang Cave. 36. Kajutanam; Solok. 37. Tarusan, Teluk. 38. Siak, Sungai. 39. Kateman, Sungai. 40. Baru, Danau. 41. Kota, Danau; Rengat. 42. Bengkulu. 43. Sanggul, Bukit. 44. Lubuklinggau; Muarabeliti. 45. Pagaralam. 46. Babat; Kluang; Loeboek Karet; Palembang [district]. 47. Palembang. 48. Ogan, Air. 49. Bangka, Pulau. 50. Kuching; Sidong, Gunong. 51. Sekajam, Sungai. 52. Landak, Sungai. 53. Kapuas, Sungai. 54. Pontianak. 55. Sukadana. 56. Riam. 57. Kendawangan, Sungai. 58. Pulo Paku. 59. Entawa-Samarahan. 60. Roema Manoeal. 61. Semitau. 62. Sintang. 63. Niah Caves. 64. Salai, Sungai. 65. Kalulong, Bukit. 66. Sut. 67. Puruktjahu. 68. Tandjung. 69. Pamukan, Teluk. 70. Klumpeng, Teluk. 71. Pelaihari. 72. Papar. 73. Labuan, Pulau, mainland opposite. 74. Madihit, Sungai. 75.

improbable measurements: adult female, 590 mm., ZRSC 1214/10, Loc. No. 2; adult male, 469 mm., ZRSC 2592/10, Loc. No. 10) (fig. 22) relative tail length (T/HB) 0.30-0.44 in 16 adult females (0.16 in one aberrant adult female, AMNH-AC 106562, Loc. No. 43, largest female specimen examined), 0.28-0.42 in 22 adult males (fig. 2); weight 5.4-7.6 kg. in 10 adult females, 10.0-13.6 kg. in 8 adult males (table 21). Pelage of trunk yellowish-brown agouti to golden-brown agouti laterally, with a variably developed blackish mid-dorsal streak or patch (about 4-20 cm. broad) that becomes more or less indistinct anteriorly on the scapular region; crown hairs short (1 cm.), blackish, radiating to form a whorl centered at the vertex; crown patch broad anteriorly, extending laterally on supraorbital region approximately as far as lateral angle of each eye; side whiskers relatively short (2-3 cm.), with buffy bases and blackish tips that collectively form a pair of dark preauricular streaks or sideburns; skin of muzzle pale brownish, thinly covered with inconspicuous short whitish hairs; outer surface of arms, legs, hands and feet yellowish-brown to golden-brown, approximately like flanks; posterior surface of shanks frequently with indistinct dark streaks; tail thin, bicolor, sharply defined blackish dorsally, pale ochraceous-buff ventrally, frequently with terminal hairs elongate and weakly defined ochraceous to dark reddish-brown, forming an inconspicuous tuft; underparts thinly haired whitish to ochraceous-buff anteriorly, often becoming darker (buffy to pale brown) on the epigastric region.

FIG. 25. *continued*

Bareo; Pa Umore. 76. Bahau, Sungai. 77. Badang; Peleben. 78. Karangan, Sungai. 79. Kutai Reserve. 80. Tabang. 81. Djembajan, Sungai. 82. Lumu Lumu; Ranau. 83. Betotan; Lungmanis Station. 84. Sapagaya, Sungai. 85. Ulu Segama Forest Reserve. 86. Tibas, Sungai. 87. Sandakan. 88. Kinabatangan, Sungai. 89. Abai. 90. Kretam Kechil, Sungai; Segama, Sungai.

M. pagensis localities: 91. Sioban. 92. Pagai Utara, Pulau. 93. Pagai Selatan, Pulau.

Negative reports: C. Nicobar Islands, northern. D. Nicobar Islands, southern. E. Klet Kaeo, Ko (fig. 28). F. Simeulue, Pulau. G. Bangkajene, Kepulauan. H. Bangkaru, Pulau. I. Nias, Pulau. J. Musala, Pulau. K. Enggano, Pulau. L. Sebesi, Pulau. M. Panaitan, Pulau. N. Krakatau, Kepulauan. O. Pangkor, Pulau. P. Berhala, Pulau. Q. Jarak, Pulau. R. Sembilan, Kepulauan. S. Perhentian Besar, Pulau. T. Redang, Pulau. U. Bidong Laut, Pulau. V. Kundur, Pulau. W. Karimun, Pulau. X. Tinggi, Pulau. Y. Durian, Pulau. Z. Sugi, Pulau. a. Bulan, Pulau. b. Bintan, Pulau. c. Sebangka, Pulau. d. Bakung, Pulau. e. Lingga, Pulau. f. Singkep, Pulau. g. Natuna, Kepulauan. h. Lemukutan, Pulau. i. Temadju, Pulau. j. Datuk, Pulau. k. Masalembu-Besar. l. Laut, Pulau. m. Sebuku.



FIG. 26. *Macaca nemestrina nemestrina*, external characters. (Photo courtesy Japan Monkey Centre)

TABLE 21. Weight in wild collected adult specimens of *M. n. nemestrina*.

Locality Nos. ¹	Weight (kg.)	
	Females	Males
1	5.45	—
26	—	10.9, 11.8
30	7.3, 7.6	—
37	7.3	13.6
38, 39	6.4	10.9, 11.0
55, 69	—	10.9, 10.9
89	5.4, 5.7, 6.4, 6.4, 6.8	10.0
Means	6.5	11.2

1. See map, Figure 25.

In adult males dorsal hairs are longest (7-9 cm. long) on the scapular region, where the blackish median streak is least distinct. The basal quarter of each of these scapular hairs is pale buffy, and the distal three-quarters is annulated with about ten alternating bands of yellowish or golden and blackish, with the blackish bands generally broader than the yellowish bands. More posteriorly, hairs in the blackish median streak are 3-4 cm. long, with the basal half of each hair pale buffy and the distal half blackish, rarely with an indistinct narrow pale annulation.

In three subadult or adult males collected at localities less than 150 km. apart in west-central West Malaysia, width of the blackish mid-dorsal streak varies from about 8 cm. (BM 55.1502, subadult, Bentong) to 12 cm. (BM 55.1503, adult, Sungai Renggam) to 18 cm. (BM 50.1501, adult, Rungkup). Anterior extent of the dorsal streak is roughly correlated with its width. In the West Malaysian specimen with the narrowest dorsal streak (BM 55.1502), the streak is separated from the blackish patch on the crown and nape by a clearly defined zone of golden-brown on the scapular region; in the specimen with the broadest dorsal streak (BM 55.1501), a virtually uninterrupted blackish band extends from the crown to the dorsal surface of the tail, with only a slight tinge of brownish on the scapular region. The darkest of these West Malaysian specimens (BM 55.1501) is closely matched by an adult specimen collected in southeastern Sumatra (BM 1938.11.30.6, Palembang), near the southern limit of the range of the subspecies, and by another collected in northeastern Sarawak (BM 93.6.2.2, Bukit Kalulong), near the northeastern limit of the range. In a very old male collected in Sabah (USNM 34930, Sungai Sapagaya, type of *broca*

Miller), the dorsal ground color is drab-yellowish-brown, with unusually indistinct annulations on individual hairs.

In adult females and in immatures of both sexes the dark dorsal streak is generally somewhat more restricted and dilute than in adult males, the hair on the flanks is paler and drabber than in adult males, and the agouti pattern is less conspicuous. In one adult female (BM 93.4.29.1, Sungai Baram, Sarawak) that reportedly lived in captivity in Sarawak for about five years (Sclater, 1893, p. 325), the dorsal fur, which is unusually fine and silky, is pale golden-brown non-agouti laterally, with a narrow and indistinct darker brown streak medially. Pocock (1931, p. 310) has speculated that this exceptionally pale specimen is a captive-bred *M. mulata*-*M. n. nemestrina* hybrid; alternatively, it may merely be a albinistic specimen of *M. n. nemestrina*. Two albinistic Bornean specimens have been reported by Banks (1931, p. 111).

As previously noted (fig. 22), length of head and body generally increases from north to south in *M. n. nemestrina*, with the same clinal pattern of increase evident in all three isolated components of the range (Malay Peninsula, Sumatra, Borneo). However, one exceptionally large subadult male (BM 55.1504) has been collected at Chong, peninsular Thailand, near the northern limit of the range (fig. 22). Relative tail length tends to be somewhat less in the largest specimens examined than in smaller ones (fig. 2).

Cranial characters (figs. 4, 6, 27). — Skull relatively large, greatest length excluding incisors 115.4-138.9 mm. in 35 adult females, 139.5-174.5 mm. in 77 adult males (fig. 7); rostrum long (fig. 8); zygomatic arches relatively narrow (fig. 7); supraorbital ridges relatively thin, especially laterally, and somewhat receding; anterior surface of malar flat to weakly convex.

Skull length in specimens collected in the northern part of the range of *M. n. nemestrina* (Malay Peninsula; Sumatra and Borneo north of 3°N) averages about 10 mm. less than in those collected in the southern part of the range (Bangka; Sumatra and Borneo south of 3°N) (fig. 22). However, one large specimen (NMS 16640, skull only, greatest length 170.7 mm.) reportedly collected at "Dolok-Oelve," Deli, northern Sumatra, appears to be an exception to this generalization (fig. 22).

Habits and habitats. — This account is based primarily on field observations published by authors listed below; authors are cited by means of indicated abbreviations.



FIG. 27. Cranial variation in adult male *M. n. nemestrina*: a, AMNH-AC 106037, Badang; b, MZB 6501, Pulau Bangka (possible captive); c, AMNH-AC 106563, Bukit Sanggul. $\times \frac{1}{2}$ (Photos FMNH)

A	Abbott <i>in</i> Lyon, 1907b, p. 566
Ba	Banks, 1931, p. 110
Be-a	Bernstein, 1967a, pp. 198-207
Be-b	Bernstein, 1967b, pp. 217-228
C	Chivers, 1971, pp. 78, 84
D	Davis, 1962, p. 58
Hg	Hagen, 1890, p. 82
Hrt	Hartert, 1902, p. 193
Hrt/T	Hartert <i>in</i> Thomas and Hartert, 1894, pp. 654-655
Hs	Harrison, 1969, p. 175
Hss/D	Harrison <i>in</i> Davis, 1958, p. 126
Hss/M	Harrison <i>in</i> Medway, 1965, p. 85
K	Kawabe, 1970, p. 286
K/M	Kawabe and Mano, 1972, p. 216
Ku	Kurt, 1973, pp. 64-65
L	Lim Boo Liat, 1969, p. 127
McC	McClure, [1965], p. 57
Me	Medway, 1970, p. 527
Me/W	Medway and Wells, 1971, p. 247
Mü	Müller, 1839-1840, pp. 17-18
R	Rodman, 1973, pp. 655-659
Sch	Schneider, 1905, p. 73
So/C	Southwick and Cadigan, 1972, p. 8
St	Stott, 1964, p. 12

These published field observations have been supplemented by brief unpublished notes recorded on field tags of four museum specimens collected in Sumatra by M. Boogaarts in 1929 (SMF 16640, ad ♂, "Dolok-Oelve") and J. J. Menden in 1933 (AMNH-AC 102203, ad ♂, Lubuklinggau; AMNH-AC 102201-02, juv. ♂, ad. ♀, Muarabeliti). For a detailed study of activity cycles in a captive colony of *M. n. nemestrina*, see Bernstein (1972, p. 390) and works cited therein.

Observers agree that the principal habitat of *M. n. nemestrina* is dense evergreen rainforest (Be-a, Be-b, D, Hg, Hss/D, K/M, L, McC, Mü, So/C; Menden specimens). The known altitudinal range of this subspecies extends from near sea level (Sumatra: Sungai Kateman, Sungai Siak) to upland elevations of 550-750 m. in Sumatra (Pulau Munteh), 1000 m. in West Malaysia (Me), and 1700 m. in Borneo (Lumu Lumu). In West Malaysia *M. n. nemestrina* is rare in coastal areas (C, L, So/C). In East Malaysia one author (Ba) has reported that coastal areas are a preferred habitat; but this has not been confirmed by more recent observers (K/M). *M. n. nemestrina* seems to be a rare visitor in some suitable habitats; one tract of inland forest in West Malaysia evidently was visited by this subspecies only twice in two years (McC). Recent persecution by

man has completely eliminated *M. n. nemestrina* from some areas that it formerly inhabited (Be-b, Hss/M).

Reported counts or estimates of troop size in this subspecies are: 3, 5 (Me); 6, 9 (McC); seldom more than a dozen (Hg); 6-15 (Sch); 5-20 (L); 20-30 (Ku); 30, 47 (Be-a). The two largest troops reported (30 and 47 individuals) were confined to a relatively small and isolated forest tract and therefore may not be typical. Solitary males are encountered frequently (Ba, Be-b, K, Me, St; Boogaarts specimen).

The population density of *M. n. nemestrina* in suitable habitats in West Malaysia has been estimated at 0.13 troops per square mile (So/C). Throughout its range this macaque is distinctly less abundant than sympatric *M. fascicularis* (D, Hg, Hrt, K/M, L, Me). In West Malaysia, the reported ratio of *M. n. nemestrina* to *M. fascicularis* in three local population surveys (Hs, Me/W, So/C) is 19:148 individuals (0.13), 3:22 individuals (0.14), and 1:13 troops (0.08). In eastern Kalimantan, the reported ratio of *M. n. nemestrina* to *M. fascicularis* in one study (R) is 40:268 groups (0.15).

M. n. nemestrina is often encountered on the forest floor (Ba, Be-b, Hg, Hrt/T, Hss/D, Mü, R, Sch, St). However, the subspecies also has frequently been observed to move through the branches of trees (Be-a, D, Hg, McC; also see Chivers, 1973, p. 130). In East Malaysia, two young males (FMNH 85923, 85924; Sungai Tibas) were collected 50 ft. (15 m.) above the ground in secondary growth. In domestication *M. n. nemestrina*'s skillfulness as a climber has long been exploited for harvesting coconuts (Raffles, 1821, p. 243; Bertrand, 1967, p. 484) and recently also for collecting botanical specimens (Corner, 1946, p. 89). One observer (Be-b) in West Malaysia estimates that free-ranging *M. n. nemestrina* spends about 15 per cent of its waking hours on the ground; another observer (R) in Kalimantan reports that 67 per cent of 40 contacts with *M. n. nemestrina* were with groups that were on the ground.

In fleeing from danger, *M. n. nemestrina* habitually descends to the forest floor (Be-a, C, Mü, R), as described below:

The usual response to humans was flight, and the troop typically descended to the ground and fled as a unit. In descending from the trees, animals leapt to the ground from as high as 10 meters and then succeeded in fleeing silently into good cover. The few successful efforts to track troops fleeing on the ground revealed the troop to be in a compact mass with individuals often shoulder to shoulder moving quietly and rapidly along the forest floor (Be-b).

Fruits and seeds evidently are the principal food of this subspecies (Be-b, D, McC; Spiller and Rahlman, 1970. p. 496). Other reported natural foods are young leaves, leaf stems, fungi, insects, spiders, and lizards, including geckos (Be-b, Hrt/T; Harrison, 1961, p. 7). Under semi-natural conditions, *M. n. nemestrina* also is reported (Corner, 1941, p. 12) to eat the following: plant shoots, buds, flowers, rotan-palm hearts, plant sap, snails (except giant garden snails), slugs, caterpillars, maggots, insect nests, honey, frogs eggs, birds eggs, baby birds, baby squirrels; items apparently not eaten under these conditions are: poisonous mushrooms (which are distinguished from non-poisonous), gallfigs, earthworms, centipedes, millipedes, dragonflies, and cockroaches. In an experimental study of food preference in captive *M. n. nemestrina*, insect larvae and raw birds eggs were found to be highly acceptable, while live earthworms, raw meat, raw fish, and raw shellfish were completely rejected (Spiller and Rahlman, 1970, p. 496). In Sarawak *M. n. nemestrina* often raids rice fields (Hss/D), and in Sumatra it raids maize fields (Hg).

Data concerning possible breeding seasonality are minimal. One author (Be-b) notes a concentration of births in the period November-March and mentions isolated births in other months. Another observer (McC) reports two females with suckling young in March and one female with a small infant in May, which is compatible with a birth peak in the period November-March.

Observed contacts between neighboring troops of *M. n. nemestrina* reportedly are peaceful (Be-b). In West Malaysia peaceful contacts also have been reported with sympatric *M. fascicularis*, *Presbytis obscurus*, *P. melalophus*, and *Hylobates lar* (Be-a; also see Chivers, 1973, p. 122). However, in eastern Kalimantan, *M. n. nemestrina* and *M. fascicularis* were found to be highly segregated, with the former species occupying inland habitats and the latter restricted to the vicinity of a major river (R). In one reported contact with a giant squirrel, *Ratufa affinis*, a pigtail troop drove the squirrel out of a food tree (McC).

Remarks. — *Macaca nemestrina nucifera* Sody, 1936 (p. 42) is based on the skull and part of the skin (head only) of a specimen collected at Pulau Bangka (between Sumatra and Borneo) by H. J. V. Sody (Coll. No. Bk 75, date unspecified). The present whereabouts of the type skull and skin fragment is unknown. Although some of Sody's specimens were deposited in the Museum Zoologicum Bogoriense and others in the Rijksmuseum van

Natuurlijke Historie, Leiden, the type material of *nucifera* has not been found in either of these institutions (RMNH collection searched by Dr. A. M. Hussen, Curator of Mammals, and myself in June, 1965; MZB collection searched by Dr. P. F. D. Van Peenen, U. S. Naval Medical Research Unit No. 2, Djakarta Detachment, in March 1971 and by me in August, 1973).

According to Sody (1936, p. 42), the type of *nucifera* is an adult male, and the greatest length of the skull is 136.5 mm. (table 22). This would be well outside the range of cranial measurements in southern Sumatran adult male *M. n. nemestrina* (fig. 22) and comparable to those in adult male *M. silenus*, *M. n. leonina*, and *M. n. pagensis* (fig. 7). Pelage of the head of *nucifera* evidently is indistinguishable from that in Bornean and Sumatran *M. n. nemestrina* (Sody, 1936, p. 42).

The only other known museum specimen of a pigtail collected in Bangka is an isolated skull (MZB 6501, adult ♂, fig. 27b), for which, unfortunately, the collector, date of collection, and exact locality of origin in Bangka are unknown. Judging from the abruptly truncated canines and unworn molars, the skull may be that of a captive animal. Greatest length of the skull is 157.5 mm., which is within the size range of *M. n. nemestrina* in southern Sumatra and southern Borneo (fig. 22).

Although available evidence is not conclusive, *M. n. nucifera* Sody is now provisionally regarded as indistinguishable from *M. n. nemestrina* (Linnaeus). The missing type of *nucifera* may have been mis-sexed or incorrectly measured (but see table 22). Additional properly documented specimens of pigtails collected in Bangka are required for definitive resolution of this problem.

Specimens examined. — Total 306. INDONESIA (Kalimantan): Badang, 4 (AMNH-AC); Bahau, 1 (skull only, MNHN); Banang, 1 (ZSBS); Djembajan, Sungai, 1 (USNM); Kapuas, Sungai, 1 (skull in skin, RMNH); Karangan, Sungai, 2 (USNM); Kendawangan, Sungai, 1, skull only (USNM); Landak, Sungai, 1 (skull only, USNM); Pamukan, Teluk, 1 (USNM); Peleben, 3 (2, AMNH-AC; 1, MZB); Pontianak, 1 (skin only, RMNH); Puruktjahu, 1 (skin only, BM); Riam, 2 (AMNH-AC); Sekajam, Sungai, 2 (USNM); Sintang, 1 (skull only, ZSBS); Sukadana, 1 (USNM); Tabang, 2 (MZB); Tandjung, 1 (skull only, mandible lacking, NHMB); southwestern Kalimantan, 5 (3 skins only, 2 skulls only, ZSBS); no locality, 1 (AMNH), 1 (NHMB), 1 (skull only, ZMB); 2

TABLE 22. Cranial measurements (mm.) reported by Sody (1936, p. 42) for type-specimen of *Macaca nemestrina nucifera*.

Greatest length of skull	136.5
Basal length	98.5
Postrostral length	90
Palatal length	60
Zygomatic breadth	89
Braincase breadth	63.5
Interorbital constriction	8
Postorbital constriction	48
Upper toothrow (P-M3)	44.5
Canine, alveolar diameter	10.5
Crown of upper M3	8.5 x 8.3
Mandibular length	99.5
Lower toothrow	50.5

(1 skull only, MZB). INDONESIA (Sumatra); Aru, Teluk, 3 (USNM); Babat, 2 (MZB); Bangka, 1 (skull only, MZB); Batangkuwis, 3 (1 skins only, ZSBS); Bengkulu, 2 (skulls only (RMNH); Brandan, 2 (skins only, ZMB); Deli, 1 (skeleton only, NMS); 1 (skin only, ZSBS); "Dolok-Oelwe," 1 (skull only, NMS); Kajutanam, 2 (skulls only, MZB); Kateman, Sungai, 5 (1 skull only, USNM); Kluang, 3 (2 skulls only, MZB); Lampoengsche Distrikten, 1 (MZB); Langsa, 1 (skull only, MZB); Loeboek Karet, 1 (MZB); Lubuklinggau, 1 (AMNH-AC); Medan vicinity, 8 (2 skins only, ZSBS); Muarabeliti, 2 (AMNH-AC); Ogan, Air, 3 (FMNH); Padang, 1 (NMS), 3 (skulls in skins, RMNH), 1 (ZMUZ); Pagaralam, 2 (skulls only, MZB); Pajakumbuh, 1 (skull and limb bones only, RMNH); Palembang, 2 (skulls only, NHMBe), 1 (RMNH); Palembang district, 1 (BM); Pasi, 1 (skull only, MZB); Pulau Munteh, 1 (MZB); Pulutelang, 1 (skeleton only, NHMB); Sanggul, Bukit, 8 (6, AMNH-AC; 2 MZB); Siak, Sungai, 2 (USNM); Sibolga, Teluk, 2 (USNM); Solok, 1 (RMNH); Tandjungmorawa, 1 (skull only, RMNH), 2 (ZSBS); Tarusan, Teluk, 2 (USNM); Tebingtinggi, 3 (1 skin only, 1 skull only MZB); no locality, 2 (skulls only, BM), 1 (FMNH), 2 (skins only, MNHN), 3 (1 skull in skin, RMNH), 7 (4 skulls only, AMNH), 1 (MZB), 4 (2 skulls only, ZMB), 3 (skulls only, ZSBS). MALAYSIA, EAST: Abai, 10 (1 skin only, 4 skulls only, MCZ); Bareo, 1 (FMNH); Betotan, 2 (ZRCS); Entawa-Samarahan, 1 (BM); Kalulong, Bukit, 1 (BM); Kretam Kechil, Sungai, 1 (FMNH); Kuching, 3 (1 skull in skin, SMK) Labuan, Pulau, mainland opposite, 1 (skin only, BM); Lumu Lumu, 7 (5 skulls only, MCZ); Madihit, Sungai, 1 (skull in skin, SMK); Papar,

1 (USNM); Pa Umor, 1 (FMNH); Pulo Paku, 2 (BM); Ranau, 1 (AMNH); Salai, Sungai, 4 (1, BM; 3, skins only, SMK); Sandakan, 1 (skeleton only, MCZ); Sapagaya, Sungai, 1 (type of *broca*, USNM); Segama, Sungai, 1 (skin only, ZMB); Sidong, Gunong, 1 (skin only, SMK); Sut, Sungai, 1 (FMNH); Tibas, Sungai, 2 (FMNH). MALAYSIA, WEST: Bentong, 1 (BM); Hantu, Tanjong, (ZRCS); Jeram, 1 (ZRCS); Kelang, 1 (skin only, ZRCS); Kepong, 2 (ZRCS); “?Kuala Lumpur,” 1 (ZRCS); Kuala Lumpur, Cheras Road, 1 (skin only, ZRCS); Kuala Lumpur, Weld’s Hill, 2 (ZRCS); Pinang, Pulau, 1 (BM), 2 (skulls only, NHMB), 1 (skin only, NHRM), 2 (skeletons only, USNM); Simpang Empat Rungkup, 1 (BM); Sungai Renggam, 1 (BM). THAILAND: Chong, 1 (BM), Huai Lian, 2 (FMNH); Khao Si Kaeo, 1 (FMNH); Lam Phura, Sathani, 2 (ZRCS); “Trang,” 1 (skull only, ZRCS). Imprecise localities: 9 (1 skin only, 1 skeleton only, 1 skull only, AMNH), 6 (3 skins only, BM), 1 (FMNH), 8 (3 skins only, 5 skeletons only, IRSN), 10 (3 skins only, 3 skulls only, MNHN), 16 (skulls only, NHMBe), 7 (3 skins only, 3 skulls only, NMS), 26 (2 skulls in skins, 6 skins only, 15 skulls only, RMNH), 3 (skins only, USNM), 18 (16 skins only, ZMB), 5 (1 skin only, 1 skeleton only, 1 skull only, ZMUZ), 4 (2 skulls only, ZRCS), 3 (skulls only, ZSBS), 16 (9 skins only, 5 skulls only, 2 skeletons only, ZSI).

***Macaca nemestrina leonina* (Blyth, 1863)**

Another species of *Cercopithecus*: Helfer, 1838, p. 858 – reported to inhabit limestone buttes in northern Tenasserim.

Macacus nemestrinus (?): Blyth, 1844, p. 473 – external characters of specimens collected in Arakan district, Burma, by A. P. Phayre; probable distribution, Arakan, Tenasserim.

Macacus nemestrinus: Morice, 1875, p. 41 – recorded in South Vietnam.

Macaca nemestrina sub. sp.: McCann, 1933b, p. 808 – external characters; field observations.

Macaca nemestrina: Yin, 1954, p. 269 – sight record in Burma. Fooden, 1971a, p. 32, pl. 5a (head), pl. 5b (animal) – report on specimens collected in Thailand; possibly specifically distinct from Sundaic *M. nemestrina*; nasal deformity in adult female.

[Inuus] arctoides (? Is. Geoff.): Blyth, 1847, p. 731 – revised identification of specimens earlier identified as *Macacus nemestrinus* (?): Blyth, 1844.

Inuus pileolatus Tickell, 1854-1863, MS., pp. 109, 111 – unavailable manuscript name based on captive immature male (pl. 23) collected by R. S. Tickell in forest near Ye, Burma, Nov. 1854; subsequently regarded as a synonym of *Silenus nemestrinus* (Tickell, 1863-1875, MS., p. 139).

- [Inuus] leoninus* Blyth, 1863, p. 7 – new species based on specimens previously identified as *Macacus nemestrinus* (?): Blyth (1844, p. 473) and *Inuus arctoides*: Blyth (1847, p. 731); specific name is an adjective, presumably alluding to the lionlike mane and cheek ruff; subsequently considered identical with *Inuus nemestrinus* (Blyth, 1863, appendix, p. [189]). Blyth, 1875, p. 4 – redescription of syntypes; zoogeography.
- Macacus leoninus* Sclater, [1871], p. 663, pl. 35 (animals) – taxonomic history. Anderson, 1879, p. 52, figs. 1, 2 (skull of type of *M. andamanensis* Bartlett, 1869) – external characters; cranial characters and measurements; osteology; relationships; distribution, southern Arakan, Irrawaddy Valley. Anderson, 1881, p. 71 – part (also includes reference to misidentified female specimen of *Macaca assamensis* collected near Bhamo); redescription of holotype. Sclater, 1898, p. 280 – first record in Thailand. Elliot, [1913], pp. 208, 209 – incorrectly rejected as a junior homonym of *Simia leonina* Shaw, 1800, which is a langur, not a macaque.
- Macacus coininus*: Kloss, 1903, pp. 322, 325 – lapsus for *Macacus leoninus*.
- M[acaca] leonina*: Wroughton, 1918, p. 555 – external characters; type-locality, Arakan. Kloss, 1919, p. 344 – redescription of holotype; regarded as a synonym of *Macacus andamanensis* Bartlett, 1869.
- Macacus nemestrinus*, var. *leonina*: Schlegel, 1876, p. 356 – specimen received from “?Arracan.”
- Macaca nemestrina leonina*: Pocock, 1939, p. 59 – external and cranial characters; taxonomy; field observations; distribution, upper Burma to Tenasserim, Mergui Archipelago, Thailand. Fiedler, 1956, p. 177 – external characters. J. R. Napier and P. H. Napier, 1967, p. 403 – listed.
- Pithecus leoninus*: Wroughton, 1916a, p. 296 – external characters; taxonomic comparisons.
- Nemestrinus leoninus*: Heck, 1916, p. 551 – external characters; taxonomic comparisons; facial expressions of captive; distribution, Arakan, Irrawaddy region, upper Burma, possibly Thailand.
- Rhesus (Nemestrinus) leoninus*: DeBeaux, 1923, p. 34 – external and cranial characters.
- Macacus andamanensis* Bartlett, 1869, p. 57, fig. (animal) – holotype B.M. 71.5.19.2 (skin, skull), subadult female obtained alive in 1864 by Capt. T. A. Brown, R.N., at Port Blair, South Andaman Island, presented to Menagerie of Zoological Society of London on July 8, 1869. Sclater, [1870], p. 467, fig. (captive holotype) – type history. Hamilton, 1870, p. 220 – holotype said to have been transported to Andaman Islands from Burma. Sclater, [1871], p. 663 – a synonym of *Inuus leonina* Blyth.
- Pithecus andamanensis*: Elliot, [1913], p. 208, pl. 2 (animals ex Sclater, 1870) – redescription of holotype of *Inuus Lioninus* Blyth, 1863; distribution, Arakan, Irrawaddy Valley, possibly Thailand, introduced in Andaman Islands.
- Macaca andamanensis*: Kloss, 1916a, p. 30 – external and cranial characters; taxonomic comparisons; nomenclature. Kloss, 1916b, p. 2 – external and cranial characters; taxonomic comparisons.

[*Macaca nemestrina*] *andamanensis*: Kloss, 1919b, p. 345 – key to external characters. Pocock, 1931, p. 302 – external characters and variation; cranial characters; distributions, “Arakan and Upper Burma to Tenasserim, including the Mergui Archipelago, and the adjoining districts of Siam.”

Macaca nemestrina andamanensis: Pocock, 1939, p. 60 – junior synonym of *Macaca nemestrina leonina*: Pocock, 1939.

Macaca adusta Miller, 1906, p. 559, pls. 13-17 (skin and skull of holotype) – external and cranial characters; holotype, adult male skin and skull (USNM 124023) collected at Champang, Tenasserim Div., Burma, by W. L. Abbott, Dec. 22, 1903; distribution: “Malay Peninsula. Limits of range unknown.” Pocock, 1931, p. 303 – a synonym of *Macacus leoninus* Blyth, 1863.

Macaca nemestrina adusta: Kloss, 1908, p. 147 – included in provisional list of mammals of southern Malay Peninsula. Gyldenstolpe, 1919, p. 130 – reported in peninsular Thailand. Kloss, 1919b, p. 343 – key to external characters; distribution, southern Tenasserim.

Pithecus adusta: Elliot, [1913], p. 206 – redescription of holotype; zoogeography; distribution, Tenasserim. Robinson and Kloss, 1914a, p. 392 – doubtfully distinguishable from Sumatran *Macaca nemestrina*.

Macaca insulana Miller, 1906, p. 560 – external and cranial characters; holotype, adult male, skin and skull (USNM 104441, Coll. No. 199) collected at Chance Island (=Ko Chan), Mergui Archipelago, Thailand, by W. L. Abbott, Jan. 1, 1900; distribution, Ko Chan. Pocock, 1931, p. 303 – a synonym of *Macacus leoninus* Blyth, 1863.

Pithecus insulanus: Elliot, [1913], p. 207 – redescription of type; zoogeography.

Macaca nemestrina indochinensis Kloss, 1919b, p. 343 – external and cranial characters; holotype, adult male, skin and skull (USNM 236623, Coll. No. 2148) collected at Lat Bua Khao, southeastern Thailand, by C. B. Kloss, Oct. 12, 1916. Pocock, 1931, p. 303 – a synonym of *Macacus leoninus* Blyth, 1863. Chasen, 1935, p. 38 – external characters; taxonomic comparisons.

[*Macaca nemestrina*] *blythii* Pocock, 1931, p. 305 – external and cranial characters; holotype, adult male, skin and skull (BM 72.11.18.2; Orig. No. 1552B), captive specimen of unknown origin, originally identified as *Macacus leoninus* (Sclater, [1871], p. 663, pl. 35), acquired by British Museum (Natural History) in 1872; distribution unknown.

Macaca nemestrina blythii: Pocock, 1939, p. 63, fig. 15 (animal ex Slater, [1871]) – external and cranial characters of holotype; type history; hypothetical distribution, “?Naga Hills in Assam.” J. R. Napier and P. H. Napier, 1967, p. 403 – listed.

Macaca fascicularis subsp.: Delacour, 1940, p. 24 – said to be common in vicinity of Húe and Sai Gon, South Vietnam.

Type. – Adult male, skin only (ZSI 11823/I.M. 43a), preserved in the National Zoological Collection, Zoological Survey of India, Calcutta; collected by A. P. Phayre, 1844. The type-series originally also included an immature specimen, which was also collected by

Phayre (Blyth, 1863, p. 8), but the whereabouts of this syntype is now unknown.

Type-locality. — “Mountainous and rocky situation,” Arakan district, southeastern Burma (Blyth, 1844, p. 473).

Distribution (fig. 28). — Indochinese Peninsula, from eastern Assam (India), extending southeastward through Burma, southwestern Yunnan (China), Thailand, southern Laos, South Vietnam, Cambodia (inferred), south to Surat Thani-Krabi depression in peninsular Thailand (8-9°N); known altitudinal range about 75-1250 m. (table 11). The lack of records of *M. n. leonina* in central Burma, an area reasonably well collected by the Bombay Natural History Society's Mammal Survey (Ryley, 1914, p. 710; Wroughton, 1915a, p. 460; 1916a, p. 291; 1916b, p. 758; 1921, p. 549; Fry, 1928, p. 545; 1929, p. 636), suggests that this area may constitute a natural hiatus within the range of the subspecies; Tickell (1854-1863, MS., p. 112) likewise indicates that this subspecies is rare or absent in central Burma. Known insular records of *M. n. leonina* are restricted to Lanbi Kyun, Ko Chan, Ko Phuket, and Ko Yao Yai, all off the west coast of peninsular Burma and Thailand.

Two erroneous locality records of *M. n. leonina* have been published by Anderson (1881). A female specimen (ZSI 11909/I.M. 43c) collected 20-25 miles below Bhamo in northeastern Burma was referred to *M. n. leonina* (Anderson, 1881, p. 72) after having been originally identified as *M. assamensis* (Anderson, 1879, p. 65); the correct identification of this specimen is *M. assamensis*, as previously indicated by Khajuria (1954, p. 115). Anderson (1881, p. 72) also records a male specimen of *M. n. leonina* (ZSI 11926/I.M.43e) that was presented to the Indian Museum by O. L. Fraser, Jan. 6, 1878, and was said to have originated in “Perak,” which presumably refers to the state of that name in West

FIG. 28 — *continued*:

15. Thakhek. 16. Savannahket. 17. Pakse; Plateau des Bolovens. 18. Saravane. 19. Húe. 20. Kawkareik. 21. Ban Pong Nam Ron. 22. Khlung, Khlung; Ko Keow. 23. Samnak Rabam. 24. Hin Lap, Sathani. 25. Pak Chong, Sathani. 26. Lat Bua Khao, Sathani. 27. Phu Kheo Forest Reserve. 28. Ye. 29. Ban Kerng Chada. 30. Chongkrong. 31. Ban Huai Maenam Noi. 32. Paungdaw power station. 33. Rat Buri. 34. Phet Buri. 35. Ban Nong Kho. 36. Chantaburi; Sa Bap, Khao. 37. Ban Huang Som. 38. Tay Ninh. 39. Trang Bom. 40. Sai Gon. 41. Da Ban. 42. Lanbi Kyun. 43. Red Point. 44. Bankachon; Champang; Telok Besar. 45. Chan, Ko. 46. Ban Khlung Wan; Ban Tha San. 47. Klong Tung Sai; Telok Poh. 48. Ban Nong Kok.

Negative Reports: A. Andaman Islands. B. Barren Island. C. Nicobar Islands, northern. D. Nicobar Islands, southern. E. Klet Kao, Ko.

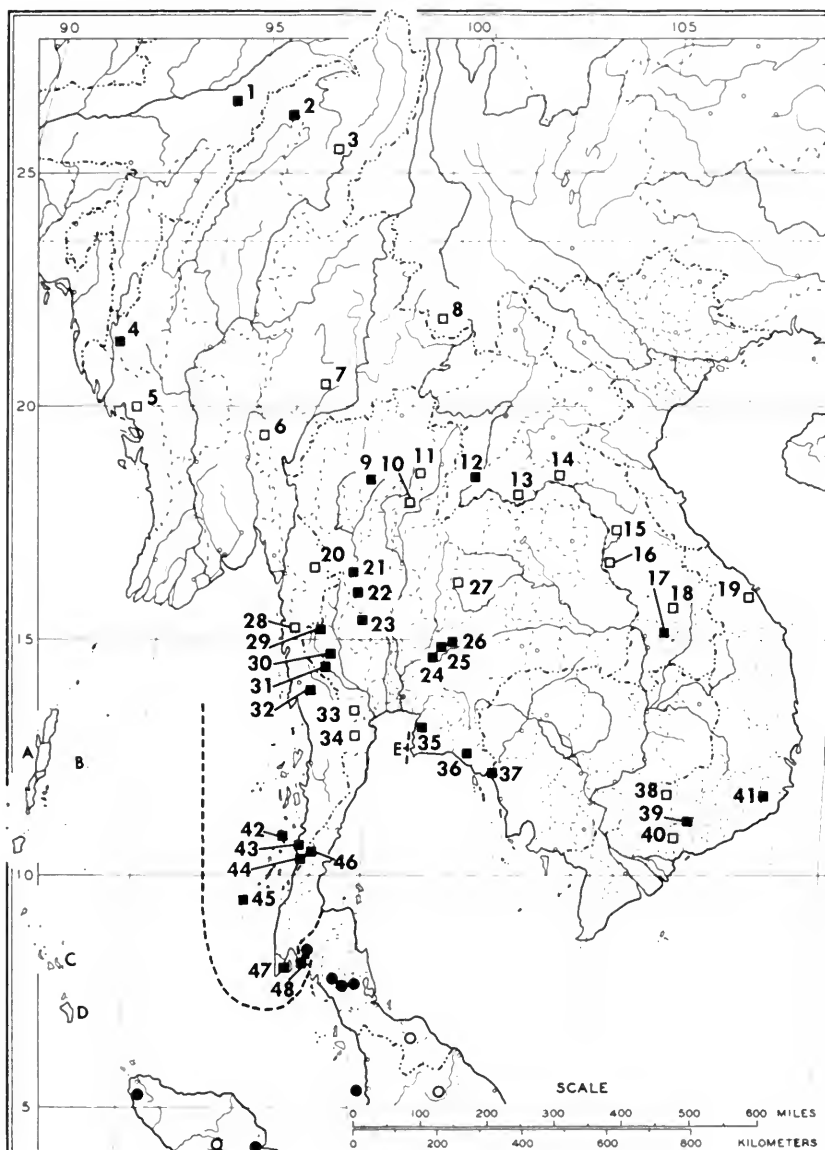


FIG. 28. Locality records of *M. n. leonina*; closed squares = specimens examined; open squares = literature records; circles = marginal records of *M. n. nemestrina*; letters and heavy broken lines indicate negative reports. For details, see "Gazetteer of Collecting Localities."

Key to localities: 1. Changchang Pani. 2. Singkaling Hkamti. 3. Pidaung Game Sanctuary. 4. Arakan. 5. Sittwe. 6. Tabo. 7. Mông Nai. 8. Meng-hai. 9. Khun Tan. 10. Ban Hue Hom. 11. Meh Lem river. 12. Muang Liap. 13. Vientiane. 14. Paksane.

Malaysia. However, this state is more than 300 km. beyond the apparent range of *M. n. leonina* (fig. 28). The tail of this specimen is mutilated and the fur seems to have been worn off in life, suggesting that the monkey was a captive; the Malaysian locality is undoubtedly spurious (Blanford, 1888b, p. 20; cf. Chasen, 1940a, p. 65).

According to Dollman (1932, p. 9), Lord Cranbrook supposedly collected a pigtail macaque at Nam Tamai, a tributary of the upper Irrawady River in northernmost Burma. However, this report probably is based on misidentification of a juvenile male specimen of *M. assamensis* (BM 32.11.1.2; Pocock, 1939, p. 54) obtained by Lord Cranbrook on April 8, 1931 at Adung Valley, which is another name for the same tributary of the Irrawady River (Cranbrook *in* Kinnear, 1934, p. 348).

External characters (fig. 29). — Head and body length 400-490 mm. in 15 adult females (excluding improbable measurement of 555 mm. recorded for BNHS 5068, Loc. No. 1; McCann, 1933b, p. 809), 500-595 mm. in 13 adult males; relative tail length (T/HB) 0.28-0.45 in 14 adult females, 0.30-0.48 in 13 adult males (fig. 2); weight 4.4-5.7 kg. in 7 adult females, 6.2-9.1 kg. in 6 adult males (table 23). Dorsal pelage yellowish-brown agouti to golden-brown agouti anteriorly, becoming slightly drabber posteriorly, with an indistinct median dark streak (about 2 cm. broad) on the lumbosacral region; crown short-haired, usually somewhat darker golden-brown than back; anterior part of crown patch narrow, extending laterally approximately as far as middle of each eye, sharply defined anterolaterally by contrast with pale ochraceous-buff lateral supraorbital patches; side whiskers long, pale ochraceous-buff, forming a well-defined facial ruff that tends to conceal the ears from anterior view; skin of muzzle pale brownish, densely covered with short buffy hairs; outer surface of arms above elbows colored approximately like back, outer surface of forearms, hands, thighs, shanks and feet slightly paler and drabber; tail thin, bicolor, sharply defined blackish dorsally, pale ochraceous-buff ventrally; base of tail set off by a pair of dorsolaterally projecting tufts of whitish fur; throat, chest and anterior surface of shoulders pale ochraceous-buff; underparts thinly haired pale yellowish-brown to whitish. (See Addenda, p. 168.)

In adult males hairs on the scapular region are 7-10 cm. long, the distal two-thirds of each of these hairs is conspicuously annulated with about 15 alternating bands (each 3-4 mm. broad) of



FIG. 29. *Macaca nemestrina leonina*, external characters. (Photos by J. Fooden at Calcutta Zoo)

TABLE 23. Weight in wild-collected adult specimens of *M. n. leonina*.

Locality Nos. ¹	Weight (kg.)	
	Females	Males
21, 23	4.71, 5.48	8.5
29, 31	4.40, 4.65, 4.96	8.1
44	4.6, 5.7	8.2, 9.1
45	—	6.2, 6.2
Means	4.9	7.7

¹. See map, Figure 28.

yellowish or golden and dark brown, and the basal third of each hair is pale ochraceous-buff. Laterally on the lumbosacral region, where individual hairs are 3-4 cm. long, the number of pale and dark annulations is reduced to 3-5, and the pale ochraceous-buff unannulated basal portion is about 1 cm. long. Medially on the lumbosacral region, individual hairs in the faintly defined median dark streak lack the pale basal portion and are about 1 cm. shorter than hairs lateral to the streak. In two living adult male specimens examined (National Zoological Park, Washington, D.C.; Calcutta Zoological Gardens), the skin of the perineal area is marked with a clearly defined red streak that extends ventrally along the median raphe from the anus to the prepuce, both of which are red.

Hairs on the crown are about 1.5 cm. long posteriorly and 0.5 cm. long anteriorly and form a whorl radiating from the vertex. On the midfrontal region the anteriorly directed golden-brown crown hairs meet the posteriorly directed pale ochraceous-buff hairs of the lateral supraorbital region to form a low but sharply defined wedge-shaped crest that marks the anterior border of the crown patch. The pale side whiskers in front of the ears are about 4 cm. long. The skin around the eyes is sharply defined pale bluish white. In most adult males a pair of clearly defined narrow reddish streaks extend laterally from the outer corner of each eye to the side whiskers (Tickell, [1863]-1875, MS., p. 139; Sclater, [1871], colored pl. 35, republished in Elliot, [1913], colored pl. 2). Brown (1896, p. 485) reports that the red color of these eye streaks became intensified during excitement in one young captive specimen. These streaks seem to be absent in an adult male observed at the National Zoological Park, Washington, D. C.

In adult females the pelage is generally similar to that in males, but the fur is somewhat shorter and averages somewhat

paler and drabber — pale yellowish-brown instead of golden-brown. Although the anterior margin of the crown patch is sharply defined in females, as in males, there usually is little contrast between the color of the crown and that of the upper back in females. The sparse hairs on the ventral surface of adult females are whitish instead of pale yellowish-brown agouti as in males. Immatures are generally paler and drabber than adult females, and the agouti pattern tends to be less developed in immatures.

A series of three small adult male specimens collected at Ko Chan (Loc. No. 45), Mergui Archipelago, is the basis of *Macaca insulana* Miller, 1906; this may be an instance of insular dwarfism (fig. 22). Two adult females (BNHM 5068, 5069) collected at Changchang Pani are somewhat darker golden-brown than a third adult female (AMNH 83434) collected at the same place and also darker than most other specimens examined of *M. n. leonina*.

Cranial characters (figs. 3, 5). — Skull relatively small, greatest length excluding incisors 103.0-121.1 mm. in 19 adult females, 124.1-140.1 mm. in 17 adult males (fig. 2); rostrum short (fig. 8); zygomatic arches broad (fig. 7); supraorbital ridges thick and prominent; anterior surface of malar flat to weakly convex. In specimens examined, skull length in northern populations of *M. n. leonina* (north of about 11°N) averages slightly greater than in southern populations (fig. 22). (See Addenda, p. 168.)

Habits and habitats. — This account is based on field observations published by the following authors, who are cited by means of indicated abbreviations:

F	Fooden, 1971a, p. 32
H	Helfer, 1838, p. 858
McC	McCann, 1933b, p. 808
P/B	Phayre <i>in</i> Blyth, 1844, p. 473
S/W	Shortridge <i>in</i> Wroughton, 1915b, p. 700
T	Tickell, 1854-1863, MS., p. 112

Information in these published reports is supplemented by brief notes on field tags of two museum specimens, one collected by M. Pierre in 1874 (MNHN 1878/1126, ad. ♂, Chamchay, South Vietnam) and the other collected by W. L. Abbott in 1903 (USNM 124022, ad. ♂, Champang, Burma).

All known specimens of this subspecies have been collected in the foothills of Southeast Asian mountain ranges (fig. 28; H, P/B, T) at elevations ranging from about 75 m. (Ban Huai Maenam Noi,

Thailand) to 1200-1300 m. (Taho, Burma) (table 11). All but one troop for which type of forest is known were observed in dense evergreen forest (F, McC, T); the exceptional troop was observed in deciduous dipterocarp forest (F). Within its range this species is fairly abundant, although not as common as gibbons and langurs (F, S/W, T).

Reported troop size in eight troops is: 12, 15, 20, 20, 20, 20+, 30+, 40 (F). Of two solitary males that have been collected (F; Pierre specimen), one is a subadult and the other an adult.

M. n. leonina is almost exclusively arboreal (F, McC). However, in at least part of the range, troops are known to descend to the ground in order to raid rice fields (S/W). When frightened, this macaque flees into the canopy (F, McC). Although *M. n. leonina* is naturally more arboreal than *M. n. nemestrina*, this subspecies does not seem to be domesticated and used as a trained coconut harvester, as is frequently done with *M. n. nemestrina* (see above).

The diet of *M. n. leonina* consists predominantly of fruit (F, McC), although leaves (McC), caterpillars and adult insects (F), and rice (S/W) also are eaten, at least occasionally.

Information on breeding seasonality in *M. n. leonina* is scanty. A tumescent female, evidently in prime breeding condition, was collected in September (Abbott specimen). Pregnant females collected in February and in April apparently would have given birth in April-May (McC) or June-July (F). Young infants collected in February appeared to have been born in the preceding December (F). These meager data may indicate that there are semi-annual birth peaks in this subspecies, approximately in June and December.

There are no known reports of encounters between *M. n. leonina* and other species of primates, although species of gibbons and langurs inhabit the same forests and probably pass through the same trees (F). *M. arctoides* also inhabits the same forests, but encounters with *M. n. leonina* presumably are infrequent since *M. arctoides* is primarily terrestrial and *M. n. leonina* is primarily arboreal (F, McC). *M. assamensis*, which seems to be very similar to *M. n. leonina* in habits and ecological requirements (F), is almost completely allopatric in geographic distribution; known areas of overlap of *M. n. leonina* and *M. assamensis* are restricted to a narrow zone in west-central Thailand (F) and another in the Assam-Burma border area (Changchang Pani, Singkaling Hkamti).

M. fascicularis is broadly sympatric with *M. n. leonina* but seems to be ecologically segregated by its preference for lower elevations and non-evergreen habitats (F).

Remarks. — *M. nemestrina blythii* Pocock, 1931, is now regarded as inseparable from *M. n. leonina* Blyth, 1863. This is in agreement with the determinations of Blyth (*in* Sclater, [1871], p. 664) and Anderson (1879, p. 52), but contrary to the opinion of Pocock (1931, p. 304; 1939, p. 62), who is followed by authors of recent checklists.

The type and only known specimen of *blythii* is the skin and skull (BM 72.11.18.2) of an adult male pigtail without locality data that was purchased by the Menagerie of the Zoological Society of London from an animal dealer on June 14, 1870 (Sclater, [1871], p. 663; 1883, p. 19). Within three or four months of acquisition, the living captive was examined by Blyth (*in* Sclater, [1871], p. 664), who identified it as *Macacus leoninus* (= *M. n. leonina*), and it also was depicted in an excellent colored illustration by the animal artist J. Wolf (*in* Sclater, [1871], pl. 35; republished in Elliot, [1913], vol. 2, colored pl. 2). This illustration clearly shows the V-shaped crown patch, the red lateral orbital streaks and the anteriorly directed tail arch that are characteristic of *M. n. leonina*. After about 2½ years of captivity in the London Zoo, the monkey died and its skin and skull were acquired by the British Museum (Natural History), probably in mid-November, 1872, judging from the catalog number.

The stuffed skin is in relatively poor condition with much of the fur missing from the sacral and buttock regions. What fur remains generally resembles that in *M. n. leonina*, but is much darker and drabber — brown to golden-brown agouti dorsally, instead of pale golden-brown agouti. The skull is indistinguishable from that in adult male *M. n. leonina* (Anderson, 1879, figs. 1,2; Pocock, 1931, p. 306; 1939, p. 65); a transverse eminence on the left parietal lateral to the temporal ridge appears to be the result of an old healed fracture.

The dark pelage color at the type-specimen of *blythii* is the sole basis for Pocock's (1931, 1939) opinion that it represents a form distinct from *M. n. leonina*; Pocock's (1939, p. 65) unfounded speculations concerning the hypothetical geographic origin of the specimen are irrelevant. In view of the otherwise near-perfect identity of characters of the museum specimen with those of *M. n.*

leonina, and in view of Blyth's identification of the living animal as *M. n. leonina*, the significance of the dark coloration is suspect. This coloration may be an individual variable, it may be a result of conditions of captivity, or it may be an artifact of past conditions of storage; a captive specimen of *M. n. nemestrina* (BM 42.2.20.7) is similarly darkened as compared with wild-collected specimens of that subspecies. In any event, the ambiguous coat color evidence of this tattered zoo specimen of unknown origin does not appear adequate to warrant continued recognition of *blythii* as a valid taxonomic entity.

Specimens examined. — Total 89. BURMA: Arakan, 2 (1 skull only, ZMB; 1 skin only, type of *leonina*, ZSI); Bankachon, 8 (3 skins only, 1 skull only, BM; 3, BNHS; 1 skin only, ZSI); Champang, 2 (including type of *adusta*, USNM); Lanbi Kyun, 1 (BM); Paungdaw, 1 (BM); Red Point, 1 (USNM); Singkaling Hkamti, 1 (BM); Telok Besar, 2 (1 skull only, USNM); no locality, 1 (ZMB). INDIA: "Assam," 1 (IRSN); Changchang Pani, 4 (2, AMNH; 2, BNHS); "Ross Island, Andaman Islands," 1 (type of *andamanensis*, BM). LAOS: Muang Liap, 1 (ZRCS); Plateau des Bolovens, 4 (skins only, AMNH). SOUTH VIETNAM: Chamchay, 1 (skull only, MNHN); Da Ban, 1 (ZRCS); Trang Bom, 3 (2, USNM; 1, ZRCS). THAILAND: Ban Huai Maenam Noi, 7 (1, CTNRC; 6, FMNH); Ban Huang Som, 1 (BM); Ban Kerng Chada, 4 (FMNH); Ban Khlong Wan, 1 (ZRCS); Ban Nong Kho, 2 (USNM); Ban Nong Kok, 1 (skin only, ZRCS); Ban Pong Nam Ron, 7 (1 fetus, FMNH); Ban Tha San, 2 (ZRCS); Chan, Ko, 3 (including type of *insulana*, USNM); Chantaburi, 2 (ZRCS); Chongkrong, 1 (FMNH); Hin Lap, 1 (USNM); Khlung, Khlong, 1 (FMNH); Khun Tan, 1 (NHRM); Klong Tung Sai, 4 (1, BM; 3, ZRCS); Ko Keow, 1 (FMNH); Lat Bua Khao, 1 (type of *indochinensis*, USNM); Pak Chong, 2 (1, BM; 1, USNM); Sa Bap, Khao, 1 (USNM); Samnak Rabam, 2 (1, CTNRC; 1, FMNH); Telok Poh, 1 (BM); no locality, 1 (skin only, AMNH). Imprecise localities: 1 (AMNH), 1 (type of *blythii*, BM), 1 (skull in skin, MNHN), 2 (skins only, RMNH); 2 (skins only, ZSI).

***Macaca nemestrina pagensis* Miller, 1903b**

Macacus nemestrinus: Thomas, 1895, pp. 661, 664 — report of specimen collected at Sioban, Pulau Sipura; said to be possibly introduced.

Macaca nemestrina: Medway, 1970, pp. 527, 528 — part; distribution, Pagi Islands, said to be possibly introduced.

Macacus pagensis Miller, 1903b, p. 61, pls. 11-13 (skull of holotype) – external and cranial characters; distribution, Pulau Pagi Selatan; specific name is adjective derived from name of locality.

Macaca pagensis: Miller, 1906, p. 557, pls. 18-20 (skull of holotype) – redescription of type; distribution, "probably confined to the Pagi Islands."

Macaca nemestrina pagensis: Chasen, 1940a, p. 66 – distribution, Pagi Islands. J. R. Napier and P. H. Napier, 1967, p. 403 – listed.

Pithecus pagensis: Elliot, [1913], p. 200 – external and cranial characters of holotype.

Rhesus nemestrina mentaveensis DeBeaux, 1923, p. 37 – provisionally proposed subspecies; external and cranial characters; holotype, juvenile male, skin and skull in collection of Museo Civico di Storia Naturale "Giacomo Doria," Genova, collected at Sioban, Pulau Sipura, by E. Modigliani, 1894.

Type. – The holotype is an adult female skin (fig. 30) and skull preserved in the United States National Museum (USNM 121653, Coll. No. 2053), collected by W. L. Abbott, November 17, 1902 (Miller, 1903b, p. 61, pl. 11-13, skull). A juvenile paratype, offspring of the holotype (Miller, 1903b, p. 63), cannot now be located.

Type locality. – South Pagi Island (=Pulau Pagai Selatan), southwest of Sumatra, Indonesia.

Distribution (fig. 25). – Known only from Pulau Sipura, Pulau Pagi Utara (North Pagi Island), and Pulau Pagai Selatan (South Pagi Island), all in Kepulauan Mentawai (Mentawi Islands), southwest of Sumatra. The range probably also includes Pulau Siberut, which is the largest and northernmost island in the Kepulauan Mentawai chain and which has a mammalian fauna generally similar to that in the three southern islands (Chasen and Kloss, 1928, pp. 808-840). (See Addenda, p. 168.)

External characters (figs. 30, 31). – Head and body length 435-456 mm. in 3 adult females, 530 mm. in 1 adult male (fig. 22); relative tail length (T/HB) 0.25-0.33 in 3 adult females, 0.30 in 1 adult male (fig. 2); weight 4.5 kg. in 1 adult female (USNM 121653). Dorsal surface chocolate-brown non-agouti, becoming pale brown non-agouti on flanks; crown golden-brown, slightly paler than back; side whiskers and beard short (about 1 cm. long), dark brown; skin of muzzle brownish, thinly covered with inconspicuous short buffy hairs; throat, sides of neck and anterior surface of shoulders clearly defined pale ochraceous-buff; outer surface of upper arm (deltoid region) drab brown, similar to adjacent region of back; outer surface of elbows, forearms and hands contrastingly pale reddish-brown; outer surface of legs chocolate-brown proximally, becoming pale

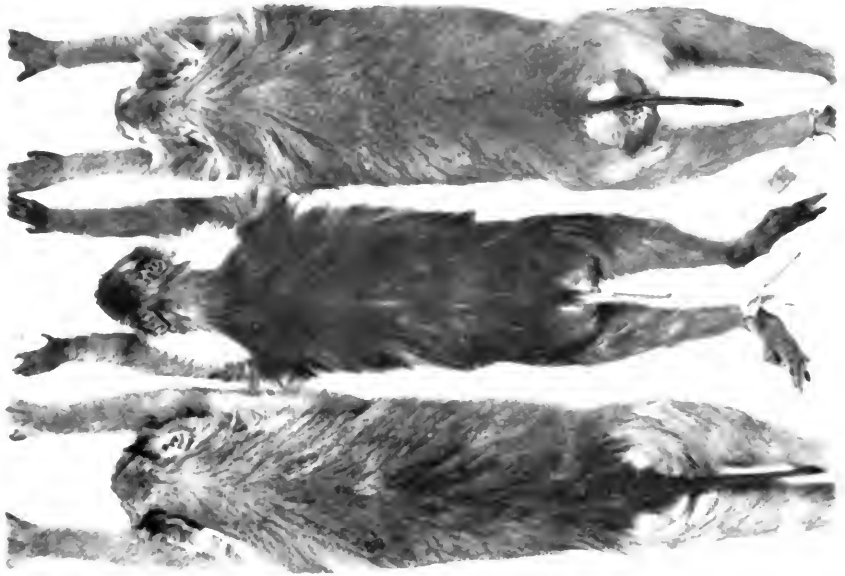


FIG. 30. Type specimen of *Macaca nemestrina pagensis* Miller (1903b) (center; USNM 121653, adult female) compared with adult female specimens of *M. n. leonina* (above) and *M. n. nemestrina* (below). (Photo by J. Fooden)

brown distally; dorsal surface of basal 10-20 per cent of tail covered with dark brown fur, balance of tail virtually naked, thinly covered with inconspicuous short buffy hairs; underparts thinly haired, buffy to pale brown.

The non-agouti dorsal pelage in *M. n. pagensis* is strikingly different from the agouti pelage in *M. n. leonina* and *M. n. nemestrina*, particularly in adult males (figs. 30, 31). Crown hairs in *M. n. pagensis* are relatively long (3-4 cm.) and radiate to form a broad whorl centered at the vertex; this cap of radiating hairs extends notably farther anteriorly and laterally than in *M. n. leonina* and *M. n. nemestrina*. The large pale patches on the sides of the neck in *M. n. pagensis* constrict the dark area on the nape to a relatively narrow band (about 5 cm. broad) which joins the broader dark area on the crown to that on the dorsal surface of the trunk. The nearly hairless condition of the distal 80-90 per cent of the tail, which superficially resembles that of an opossum, is consistent in all eight specimens examined and therefore apparently is normal in the subspecies. The color of the dorsal surface of the hands and feet is about the same as that of the forearms and

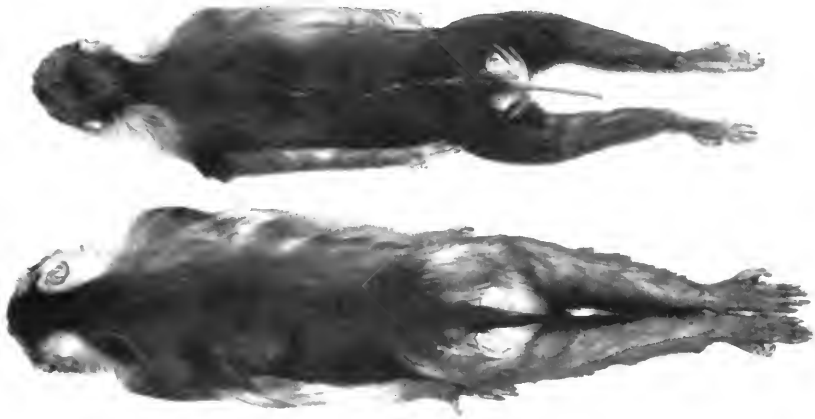


FIG. 31. Dorsal pelage in adult male *M. n. pagensis* (above; AMNH-AC 103394, Pulau Pagai Utara) compared with that in adult male *M. n. nemestrina* (below; FMNH 33643, Sumatra: Air Ogan); in *M. n. pagensis* note broad crown whorl, pale lateral throat patches, dark non-agouti dorsum, contrastingly colored (reddish-brown) forearms, and thinly haired tail. (Photo FMNH)

shanks. Miller (1903b, p. 62) indicates that the hands and feet are contrastingly darker than the arms and legs, but this seems to be based on misinterpretation of grease stains on the hands and feet of the type-specimen (USNM 121653).

Cranial characters (figs. 4, 6). — Skull relatively small, greatest length excluding incisors 109.1-112.1 mm. in 3 adult females, 134.2 mm. in 1 adult male (fig. 22); rostrum short (fig. 8); zygomatic arches narrow (fig. 7); supraorbital ridges thick, somewhat receding; anterior surface of malar weakly convex.

Habits and habitats. — The only information available concerning behavior or ecology in *M. n. pagensis* is that three specimens collected at Pulau Pagai Utara and three collected at Pulau Pagai Selatan were taken in primary forest at sea level (J. J. Menden, notes on field tags of AMNH-AC 103394-103399).

Specimens examined. — Total 8. INDONESIA, Sumatra: Pulau Pagai Selatan, 3 (AMNH-AC), 1 (type of *pagensis*, USNM); Pulau Pagai Utara, 3 (AMNH-AC). Imprecise locality: 1. (MZB).

GAZETTEER OF COLLECTING LOCALITIES

Locality names listed as primary entries in this gazetteer generally are the standard names approved in U. S. Board on Geographic Names gazetteers (No. 10: Malaysia, Singapore, and Brunei, 1970; No. 13: Indonesia and Portugese Timor, 1968; No. 22: Mainland China, 1968; No. 58: South Vietnam, 1971; No. 73: Laos, 1973; No. 96: Burma, 1966; No. 97: Thailand, 1966). For localities in India, *The Imperial Gazetteer of India* (1907-1909) is used as the standard reference. In primary entries for localities not included in U. S. Board on Geographic Names gazetteers or in the *Imperial Gazetteer of India*, spellings given below follow those in the original source. Secondary entries, with cross references to corresponding primary entries, provide a key to variant spellings and alternate names that have been applied to liontail and pigtail localities. In alphabetizing primary and secondary entries, generic geographic terms have been treated as in U. S. Board on Geographic Names gazetteers; these gazetteers provide comprehensive glossaries to local generic geographic terms.

Primary entries include the following information: locality name; altitude, if known; country; state or other administrative division; coordinates (taken from standard references listed above, unless otherwise indicated); name of collector or observer; date of collection or observation; abbreviated name of museum in which specimens examined are preserved, or bibliographic reference to literature records. If field notes have been published concerning a locality, this is indicated by a bibliographic citation following the name of the collector or observer. Numbers in italics at the end of primary entries are locality numbers used in distribution maps (figs. 20, 25, 28); letters in italics at the end of primary entries indicate negative reports as shown in distribution maps.

Macaca silenus**Map, Figure 20**

Anaimalai Hills, 800-1300 m.; INDIA: Kerala and Tamil Nadu; 10°15'-10°31'N, 76°51'-77°20'E; observed by A. F. Hutton (1949, p. 690), date unknown, and Y. Sugiyama (1968, p. 284), Sept., 1961-Feb., 1962. 12

Anaimalai Hills, northern area, 1500-3000 ft., Cochin district; INDIA: Kerala; ca. 10°30'N, 77°00'E; observed by C. H. Stonor (1944, p. 591), Feb. 12-March 10, 1944. 11

Anshi Ghat, 1000 ft., North Kanara district between Kadra (14°55'N, 74°20'E) and Kumbharwada (15°07'N, 74°24'E); INDIA: Mysore; ca. 15°00'N, 74°20'E; observed by R. S. Dharmakumarsinhji, Dec. 20, 1955 (Ali and Santapau, 1956, p. 687). 1

Cardamon Range. See Panniar.

Cochin district; INDIA: Kerala; 9°48'-10°49'N, 76°00'-76°55'E; collected by F. Colyer, 1937 (BM). 9

Coorg district, western border; INDIA: Kerala; ca. 12°30'N, 75°30'E; reported by G. C. Shortridge (*in* Ryley, 1913, p. 490). 4

Cotengady Estate, 3500 ft., Nelliampathy Pleateau, 24 miles from Palghat (Lindsay, 1926, p. 592); INDIA: Kerala; ca. 10°30'N, 76°45'E; collected by F. R. O'Brien, April 28, 1921 (BM). 10

Cotiaddy Pass. See Kuttyadi Pass.

Courtallam. See Kuttalam.

Dohnavur. See Naraikkadu Estate.

Goa district, near; INDIA: 15°-16°N, 74°E; reported by Rev. H. Baker, Jr. (*in* Blyth, 1859, p. 283). 1

Grass Hills; INDIA: Tamil Nadu; 10°21'N, 77°03'E; reported by E. R. C. Davidar (1971, p. 353), April 3-8, 1971. 12

High Range. See Panniar.

High Wavy Mountain, 4000-5100 ft.: INDIA: Tamil Nadu; ca. 9°40'N, 77°25'E; observed by A. F. Hutton (1949, p. 690). 14

Kadra. See Anshi Ghat.

Kalakkadu Hills; INDIA: Tamil Nadu; ca. 8°25'-8°32'N, 77°30'E; reported by J. C. Daniel (1970, p. 541). 17

Kellengode. See Seetagundy Estate.

Kollangod. See Seetagundy Estate.

Kumbharwada. See Anshi Ghat.

Kuriarkutti. See Parambikulam Valley.

Kuttalam, near; INDIA: Tamil Nadu; ca. 8°56'N, 77°16'E; observed by M. Krishnan ([1972], p. 542), about 1935; species subsequently exterminated at this locality. 16

Kuttyadi Pass, top of, between Malabar and Wynaad; INDIA: Kerala; ca. 11°30'N, 76°00'E; observed by T. C. Jerdon (1867, p. 10). 5

Madura. See High Wavy Mountain.

Malabar Coast?; INDIA: Kerala; 10°15'-12°18'N, 75°00'-76°00'E; J. McClelland, 1848 (ZSI).

Malabar [district]; INDIA: Kerala; 10°15'-12°18'N, 75°11'-76°51'E; collector unknown, 1887 (NMS); collector and date unknown (RMNH); reported by Père Vincent Marie (*in* Buffon and Daubenton, 1766, p. 171).

Manjolai Tea Estate, ca. 1000 m.; INDIA: Tamil Nadu; ca. 8°38'N, 77°25'E; observed by J. R. Karr (1973, p. 191), March 2-3, 1972. 17

Naraikkadu Estate, vicinity, 2500-5000 ft.; INDIA: Tamil Nadu; ca. 8°30'N, 77°30'E; observed by C. G. Webb-Peploe (1947, p. 629). 17

Nelliampathy Plateau. See Cotengady Estate.

Nelliampathy Hills, 3500 ft.; INDIA: Kerala; 10°26'-10°42'N, 76°31'-76°52'E; collected by A. P. Kinloch, March 19, 1923 (AMNH). 10

Nilgiri Hills, 800-1300 m; INDIA: Kerala and Tamil Nadu; 11°12'-11°40'N, 76°14'-77°00'E; observed by Y. Sugiyama (1968, p. 284) Sept., 1961-Feb. 1962. 7

Nilgiri Hills, western slopes, 3000-4000 ft.; INDIA: Tamil Nadu; ca. 11°25'N, 76°30'E; observed by F. E. Poirier (1970, pp. 258, 260), Sept., 1965-Aug., 1966. 7

North Kanara [district]; INDIA: Mysore; ca. 14°45'N, 74°30'E; collected by W. F. Jardine, March 7, 1906 (BNHS). 2

Palghat. See Cotengady Estate.

Palagapandy; Nelliampathy Hills; INDIA: Kerala; ca. 10°35'N, 76°45'E; collected by A. M. Kinloch, March 25, 1920 (BNHS; also see Anon., 1921, p. 411). 10

Panniar, 1000-1250 m., High Range, Cardamon Hills; INDIA: Kerala; ca. 10°00'N, 77°00'E; observed by Y. Sugiyama (1968, p. 284), Jan. 5-Feb. 27, 1963. 13

Parambikulam Valley, 1600 ft., near Kuriarkutti; INDIA: Kerala; 10°25'N, 76°43'E; collected by C. H. Biddulph, catalogued 1953 (BM). 8

Periyar Lake, northern shore; INDIA: Kerala; 9°36'N, 77°11'E; reported by J. Tanaka (1965, p. 111), Jan. 7-Feb. 5, 1963. 15

Periyar Lake, south of, 800-1300 m.; INDIA: Kerala; ca. 9°25'N, 77°20'E; observed by Y. Sugiyama (1968, p. 284), Sept., 1961-Feb., 1962. 15

Seetagundy Estate, Kollangode district, Nelliampathy Plateau (Lindsay, 1926, p. 592); INDIA: Kerala; ca. 10°35'N, 76°45'E; collected by A. M. Kinloch, Nov. 29, 1920 (BNHS; also see Spence, 1921, p. 971). 10

South Kanara [district], northern border; INDIA: Mysore; ca. 13°55'N, 74°40'E; reported by G. C. Shortridge (*in* Ryley, 1913, p. 490). 3

Tinnevely. See Naraikkadu Estate.

Travancore district; INDIA: Kerala; 8°04'-10°21'N, 76°14'-77°37'E; collected by F. W. Bourdillon, date and museum unknown (Blanford, 1888b, p. 17). (not mapped)

Vaigai River. See High Wavy Mountain.

Varagaliyar, Anaimalais; INDIA: Kerala or Tamil Nadu; not precisely located, 10°15'-10°31'N, 76°51'-77°20'E; observed by M. Krishnan ([1972], p. 542), April 30, 1960. 12

Varushnaad Valley, south of, 3000-6000 ft.; INDIA: Tamil Nadu; ca. 9°35'N, 77°30'E; observed by A. F. Hutton (1949, p. 690). 14

Wynaad district; INDIA: Kerala; 11°27'-11°58'N, 75°47'-76°27'E; reported by A. F. Hutton (1949, p. 690). 6

Macaca nemestrina nemestrina

Map, Figure 25

Abai; EAST MALAYSIA: Sabah; 5°42'N, 118°23'E (Coolidge, 1940, pp. 123, 129); collected by S. L. Washburn and A. H. Schultz, June 27-July 26, 1937 (MCZ). 89

Ampang; WEST MALAYSIA: Selangor; 3°09'N, 101°46'E; observed by I. S. Bernstein (1967b, p. 220), May 4-14, 1965. 18

Aru, Teluk; INDONESIA: Sumatra; 4°09'N, 98°12'E; collected by W. L. Abbott (*in* Lyon, 1908, p. 620), Nov. 29-Dec. 11, 1905 (USNM). 26

Atjeh. See Langsa, Atjeh.

Babat; INDONESIA: Sumatra; 2°46'S, 104°06'E; collected by Soekarno, Oct. 17-Nov. 2, 1933 (MZB). 46

Badang; INDONESIA: Kalimantan; not precisely located; ca. 3°N, 117°E; collected by V. von Plessen, May 12-25, 1935 (AMNH-AC). 77

Bagan Datoh. See Simpang Empat Rungkup.

Bahau, Sungai; INDONESIA: Kalimantan; 2°50'N, 115°57'E; collected by P. Pfeffer (letter June 22, 1972), May 21, 1957 (MNHN). 76

Bakong. See Bakung, Pulau.

Bakung, Pulau; INDONESIA: Sumatra; 0°04'N, 104°27'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). *d*

Banang, Sungai; INDONESIA: Kalimantan; not precisely located, on west coast between 2°N and 3°S; collected by C. Bruegel, Feb. 27, 1909 (ZSBS). (not mapped)

Bangka, Pulau; INDONESIA: Sumatra; 2°S, 106°E; reported by Bleeker (1851, p. 527); collected by H. J. V. Sody (1936, p. 45), date and museum unknown; collector and date unknown (MZB). 49

Bangka, Pulau, north coast or west coast; INDONESIA: Sumatra; 1°30'-2°40'S, 105°20'-106°00'E; observed by W. L. Abbott (*in* Lyon, 1906, p. 611), May 20-July 4, 1904. 49

Bangkaru, Pulau; INDONESIA: Sumatra; 2°04'N, 97°07'E; pigtail macaques reportedly absent (Abbott *in* Miller, 1903a, p. 480). *H*

Banjak, Kepulauan; INDONESIA: Sumatra; 2°10'N, 97°15'E pigtail macaques absent (Kloss, [1928], p. 802). *G*

Banka. See Bangka, Pulau.

Baram River. See Salai, Sungai.

Bareo, 3700 ft.; EAST MALAYSIA: Sarawak; 3°45'N, 115°27'E; collected by T. Harrisson, Nov. 28, 1947 (FMNH). 75

Bario. See Bareo.

Barito River. See Puruktjahu.

Baru, Danau; INDONESIA: Sumatra; 0°22'S, 102°23'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 40

Batam, Pulau; INDONESIA: Sumatra; 1°05'N, 104°03'E; reported by C. B. Kloss (*in* Lyon, 1907a, p. 657), based on information supplied by local residents. 23

Batangkuwis; INDONESIA: Sumatra; 3°36'N, 98°47'E (Atlas Trop. Ned, pl. 12a); collected by Widmann, April, 1907-Aug., 1908 (ZSBS). 28

Bedagi [district]; INDONESIA: Sumatra; ca. 3°20'N, 99°05'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 29

Bedung, Pulau. See Bidong Laut, Pulau.

Bencoolen. See Bengkulu.

Benkoelen. See Bengkulu.

Bengkulu, vicinity; INDONESIA: Sumatra; ca. 3°48'S, 102°16'E; observed by T. S. Raffles (1821, p. 243), 1817-1820; collected by E. Dubois, date unknown (RMNH), and H. J. V. Sody, date unknown (RMNH). 42

Benom, Gunung, northeast slope, 2400 ft. and 3600 ft.; WEST MALAYSIA: Pahang; 3°51'N, 102°10'E; reported by Lord Medway (1972, p. 120), 1967-1968. 16

Bentong; WEST MALAYSIA: Pahang; 3°22'N, 101°55'E; collector unknown, Dec. 16, 1912 (BM). 17

Bentong, 6-9 miles W; WEST MALAYSIA: Pahang; 3°32'N, 101°50'E; collected by C. B. Kloss (1911a, p. 146), June, 1910 (museum unknown). 17

Berhala, Pulau; INDONESIA: Sumatra; 3°46'N, 99°31'E; *M. n. nemestrina* absent (Harrison and Hendrickson, 1963, p. 548). *P*

Bernam, Sungei. See Lima Belas Estate.

Betong. See Pulo Paku.

Betotan; EAST MALAYSIA: Sabah; 5°47'N, 117°52'E; collected by F. N. Chasen and C. B. Kloss (1931, p. 50), Aug. 14-15, 1927 (ZRCs). 83

Bettotan. See Betotan.

Bidong Laut, Pulau; WEST MALAYSIA: Terengganu; 5°37'N, 103°04'E; *M. n. nemestrina* introduced (Kloss, 1911b, p. 176). *U*

Bintan, Pulau; INDONESIA: Sumatra, 1°05'N, 104°30'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). *b*

Biserat, vicinity; THAILAND: Yala; ca. 6°35'N, 101°20'E; observed by H. C. Robinson (*in* Bonhote, 1903, p. 3), 1901-1902. 5

Bohorok, vicinity; INDONESIA: Sumatra; 3°30'N, 98°12'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 27

Brandan. See Pangkalanberandan.

Btg. Kwis. See Batangkuwis.

Bukit Cheraka Klang. See Jeram.

Bukit Fraser, 5 km. S; WEST MALAYSIA: Selangor; 3°41'N, 101°45'E; observed by M. Kawabe (1970, p. 286), Aug., 1966-March, 1967. 15

- Bukit Fraser, northern slopes; WEST MALAYSIA: Pahang; ca. 3°45'N, 101°45'E; observed by D. Chivers (1971, p. 80; 1973, p. 130) 1968-1970. 15
- Bukit Tinggi; INDONESIA: Sumatra; 3°57'N, 98°18'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 26
- Bulan, Pulau; INDONESIA: Sumatra; 0°58'N, 103°55'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). a
- Bulu Telang. See Pulutelang.
- Charas Road. See Kuala Lumpur, Cheras Road, 7th mile.
- Cheras Road. See Kuala Lumpur, Cheras Road, 7th mile.
- Chong; THAILAND: Trang; 7°33'N, 99°47'E; collected by H. C. Robinson and C. B. Kloss (1910, p. 669), Dec. 14, 1909 (BM). 3
- Datu, Pulo. See Datuk, Pulau.
- Datuk, Pulau; INDONESIA: Kalimantan; 0°10'N, 108°32'E; monkeys absent (Abbott *in* Lyon, 1911, p. 59). j
- Deli district; INDONESIA: Sumatra; ca. 3°30'N, 98°30'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown); Geryun, 1904 (ZSBS); collector unknown, 1952 (RMNH); observed by E. Hartert, date unknown (Thomas and Hartert, 1894, p. 655). 28
- Dewhurst Bay. See Kretam Kechil, Sungai.
- Dindings. See Hantu, Tanjong.
- Djambajan, Sungai. See Djembajan, Sungai.
- Djamboe cave, near Tapisello, Padang highlands (Hooijer, 1946, p. 17); INDONESIA: Sumatra; ca. 0°25'S, 100°30'E; subfossils, prehistoric Holocene; collected by E. Dubois, 1888-1890 (presumably in RMNH; Hooijer, 1962a, p. 58). 35
- Djembajan, Sungai; INDONESIA: Kalimantan; ca. 0°35'S, 116°45'E (Deignan, 1959, p. 269); collected by H. C. Raven, May 13, 1914 (USNM). 81
- "Dolok-Oelve, Deli"; INDONESIA: Sumatra; not precisely located, ca. 3°30'N, 98°30'E; collected by M. Boogaarts, March 3, 1929 (NMS). 28
- Durian, Pulau; INDONESIA: Sumatra; 0°42'N, 103°43'E; *M. n. nemestrina* absent (Dammerman, 1926, pp. 285, 302). Y
- East Perhentian Island. See Perhentian Besar, Pulau.
- Engano Id. See Enggano, Pulau.
- Enggano, Pulau; INDONESIA: Sumatra; 5°24'S, 102°16'E; pigtail macaques absent (Kloss, [1928], p. 802). K
- Entawa-Samarahan; EAST MALAYSIA: Sarawak; ca. 1°15'N, 111°00'E; collected by H. C. Robinson, Nov. 23, 1919 (BM). 59
- Etawa. See Entawa-Samarahan.
- Fraser's Hill. See Bukit Fraser.
- Galas, Sungai, west of; WEST MALAYSIA: Kelantan; ca. 5°15'N, 102°00'E; reported by D. Chivers (1971, p. 80). 13
- Gasip, Sungai. See Siak, Sungai.

- Gedong; WEST MALAYSIA: Perak; 4°07'N, 101°18'E (Annandale and Robinson, 1903, map); observed by N. Annandale (*in* Bonhote, 1903, p. 3). 8
- Geram. See Jeram.
- Great Redang Group. See Redang, Pulau.
- Gua Madu; WEST MALAYSIA: Kelantan; ca. 4°50'N, 101°57'E; remains of monkeys eaten by humans, ca. 8000-2000 B. C.; collected by M. W. F. Tweedie (1940, p. 7), July-Aug., 1939 (probably in National Museum, Singapore). 14
- Hantu, Tanjung; WEST MALAYSIA: Perak; 4°19'N, 100°34'E; collected by Langgi, Aug. 2, 1918 (ZRCS). 9
- Huai Lian; THAILAND: Phatthalung; ca. 7°30'N, 100°00'E; collected by J. Fooden, June 28-29, 1973 (FMNH). 4
- Jalan Kebun. See Kelang, Jalan Kebun, 7th mile.
- Janeng, Gunong. See Janing, Gunong.
- Janing, Gunong; WEST MALAYSIA: Johor; 2°31'N, 103°25'E; observed by H. J. Kelsall (1894, pp. 4, 16), Oct. 20, 1892. 20
- Jarak, Pulau; WEST MALAYSIA: Perak; 3°59'N, 100°06'E; *M. n. nemestrina* absent (Harrison and Hendrickson, 1963, p. 548). Q
- Jeram; WEST MALAYSIA: Selangor; 3°13'N, 101°19'E; collector unknown, Nov. 16, 1910 (ZRCS). 10
- Johor, southwest; WEST MALAYSIA: Johor; ca. 1°30'N, 103°30'E; reported by D. Chivers (1971, p. 80). 21
- Kajan, Sungai. See Peleben.
- Kajutanam; INDONESIA: Sumatra; 0°33'S, 100°20'E; collected by P. Ouruans, 1911 (MZB). 36
- Kalabakan. See Tibas, Sungai.
- Kalulong, Bukit; EAST MALAYSIA: Sarawak; 3°14'N, 114°39'E; collected by C. Hose, Feb. 1893 (BM). 65
- Kampong Durian bei Medan. See Medan.
- Kapuas, Sungai; INDONESIA: Kalimantan; ca. 0°, 110°E; collected by L. A. C. M. Schwaner, May, 1845 (RMNH). 53
- Karagan, Sungai. See Karangan, Sungai.
- Karangan, Sungai; INDONESIA: Kalimantan; ca. 1°19'N, 117°42'E (Deignan, 1959, p. 269); collected by H. C. Raven, Dec. 2, 1913 (USNM). 78
- Karimon. See Karimun, Pulau.
- Karimun, Pulau; INDONESIA: Sumatra; 1°03'N, 103°22'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). W
- Kateman, Sungai; INDONESIA: Sumatra; ca. 0°12'N, 103°20'E; collected by W. L. Abbott, Aug. 15-27, 1903, Dec. 11, 1905 (USNM). 39
- Kelabit Plateau. See Bareo and Pa Umor.

- Kelang, Jalan Kebun, 7th mile; WEST MALAYSIA: Selangor; ca. 3°02'N, 101°27'E; collector unknown, July 22, 1935 (ZRCS). 12
- Kendawangan, Sungai; INDONESIA: Kalimantan; ca. 2°15'S, 110°30'E; collected by W. L. Abbott (*in* Lyon, 1911, p. 54), June 17-Sept. 29, 1908. 57
- Kenepai, Gunung. See Roema Manoel.
- Kepong; WEST MALAYSIA: Selangor; 3°13'N, 101°38'E; collected by A. L. Butler, date unknown (ZRCS). 18
- Keroh Forest Reserve; WEST MALAYSIA: Perak; 4°13'N, 101°07'E; collected by R. C. Morris (1936, p. 443), June 1-12, 1935 (museum unknown). 8
- Khao Si Kaeo; THAILAND: Krabi; ca. 8°12'N, 98°52'E; collected by J. Fooden, June 6, 1973 (FMNH). 1
- Kinabalu, Mount. See Lumu Lumu.
- Kinabatangan district. See Kretam Kechil, Sungai.
- Kinabatangan R[iver]. See Abai.
- Kinabatangan, Sungai, 0-245 m; EAST MALAYSIA: Sabah; ca. 5°30'N, 118°00'E; observed by M. Kawabe, Oct., 1968-March, 1969 (Kawabe and Mano, 1972, p. 216). 88
- Klang. See Kelang, Jalan Kebun, 7th mile.
- Kluang; INDONESIA: Sumatra; 2°41'S, 103°54'E; collected by Soekarno, Aug. 21-29, 1933 (MZB). 46
- Klumpeng, Teluk, NW; INDONESIA: Kalimantan; ca. 2°45'S, 116°00'E; observed by W. L. Abbott (*in* Lyon, 1911, p. 58), Jan. 8-March 13, 1908. 70
- Kota, Danau; INDONESIA: Sumatra; 0°23'S, 102°25'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 41
- Kotawaringin. See Riam
- Krakatau, Kepulauan; INDONESIA: Sumatra; 6°07'S, 105°25'E; primates absent (Dammerman, 1922, p. 65). N
- Kretam Kechil, Sungai; EAST MALAYSIA: Sabah; 5°31'N, 118°33'E; collected by D. D. Davis (1962, p. 58), June 3, 1950 (FMNH). 90
- Kroh Reserve. See Keroh Forest Reserve.
- Kuala Lompat Post, vicinity; WEST MALAYSIA: Pahang; ca. 3°40'N, 102°20'E; observed by Lord Medway and D. R. Wells (1971, p. 246), Feb. 22-26, 1970; observed by D. Chivers (1971, p. 80; 1973, p. 122), 1968-1970. 16
- Kuala Lumpur, Cheras Road, 7th mile; WEST MALAYSIA: Selangor; 3°05'N, 101°45'E; collector unknown, Feb. 8, 1929 (ZRCS). 18
- Kuala Lumpur, 22 miles E. See Ulu Gombak Forest Reserve.
- ?Kuala Lumpur; WEST MALAYSIA: Selangor; ca. 3°10'N, 101°42'E; collector and date unknown (ZRCS). 18
- Kuching, vicinity; EAST MALAYSIA: Sarawak; ca. 1°33'N, 110°20'E; collected by O. Beccari (1904, p. 30) and G. Doria, 1865 (Museo Civico di Storia Naturale

- "Giacomo Doria," Genova [DeBeaux, 1923, p. 36]; collected by Bukong, Nov. 23, 1891, March 31, 1892 (SMK); collector unknown, Oct. 2, 1931 (SMK). 50
- Kundur, Pulau; INDONESIA: Sumatra; 0°45'N, 103°26'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). V
- Kutai Reserve; INDONESIA: Kalimantan; ca. 0°40'N, 117°40'E; observed by P. S. Rodman (1973, p. 655), May, 1970-July, 1971. 79
- Labuan, Pulau, mainland opposite; EAST MALAYSIA: Sabah; ca. 5°30'N, 115°30'E; collected by H. Low, 1848-1877 (BM). 73
- Lamukotan, Pulo. See Lemukutan, Pulau.
- Landak, Sungai; INDONESIA: Kalimantan; ca. 0°15'N, 109°45'E; collected by W. L. Abbott (*in* Lyon, 1907b, p. 548), June-Sept., 1905 (USNM). 52
- Lam Phura, Sathani; THAILAND: Trang; 7°40'N, 99°35'E; collected by museum collectors (Robinson and Kloss, 1910, p. 670), Jan. 20, 1910 (ZRCS). 2
- Lampoengsche Distrikten; INDONESIA: Sumatra 4°-6°S, 104°-106°E; zoo specimen, Aug. 17, 1937 (MZB). (not mapped)
- Lam-ra. See Lam Phura, Sathani (Moore and Tate, 1965, p. 324).
- Lang Island. See Krakatau, Kepulauan.
- Langkat district; INDONESIA: Sumatra; 3°20'-4°20'N, 98°00'-98°40'E; observed by E. Hartert, date unknown (Thomas and Hartert, 1894, p. 655). 27
- Langsa, Atjeh; INDONESIA: Sumatra; 4°28'N, 97°58'E; collected by Berthold, Feb. 15, 1935 (MZB). 26
- Lankat. See Langkat district.
- Larut; WEST MALAYSIA: Perak; 4°48'N, 100°45'E; collector and date unknown (Taiping Museum [Flower, 1900, p. 315]). 7
- Laut. See Lauttador.
- Laut, Pulau; INDONESIA: Kalimantan; 3°40'S, 116°10'E; *M. n. nemestrina* absent (Abbott *in* Lyon, 1911, p. 62). l
- Lauttador; INDONESIA: Sumatra; 3°18'N, 99°15'E; collected by G. Schneider (1905, p. 73) 1897-1899 (museum unknown). 29
- Lemukutan, Pulau; INDONESIA: Kalimantan; 0°45'N, 108°43'E; *M. n. nemestrina* absent (Abbott *in* Lyon, 1911, p. 59). h
- Leuser Reserve; INDONESIA: Sumatra; 2°10'-4°00'N, 97°10'-97°25'E; observed by F. Kurt (1973, p. 64), April-Aug., 1970. 25
- Lida Ajer cave, near Pajakumbuh, Padang highlands (Hooijer, 1946, p. 17); INDONESIA: Sumatra; ca. 0°14'S, 100°38'E; microfossils, prehistoric Holocene; collected by E. Dubois, 1888 (presumably in RMNH; Hooijer, 1962a, p. 58). 34
- Lima Belas Estate, Sungei Bernam; MALAYSIA: Selangor; 3°46'N, 101°21'E; observed by I. S. Bernstein (1967a, p. 198), 1965-1966. 10
- Lima Blas Estate. See Lima Belas Estate.
- Lingga, Pulau; INDONESIA: Sumatra; 0°12'S, 104°35'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). e

- Little Kretam River. See Kretam Kechil, Sungai.
- Little Redang Island. See Bidong Laut, Pulau.
- Loeboe Basong. See Lubukbasung.
- Loeboek Karet; INDONESIA: Sumatra; 2°52'S, 104°18'E (Atlas van Nederlandsch Oost-Indië. 1901. p. 8); collected by Soekarno, May 5, 1933 (MZB). 46
- Loeboek Linggun. See Lubuklinggau.
- Long Salai. See Salai, Sungai.
- Lubukbasung, vicinity; INDONESIA: Sumatra; ca. 0°20'S, 100°04'E; collected by F. von Feber, date unknown, (International Colonial Exhibition, Amsterdam [Jentink, 1883, p. 171]). 32
- Lubuklinggau, sea level; INDONESIA: Sumatra; 3°18'S, 102°52'E; collected by J. J. Menden, Nov. 30, 1933 (AMNH-AC). 44
- Lumu Lumu, 5500 ft.; EAST MALAYSIA: Sabah; ca. 6°02'N, 116°34'E; collected by J. A. Griswold, Jr. (1939, pp. 403, 506), July 20, 1937 (MCZ). 82
- Lungmanis Station; EAST MALAYSIA: Sabah; ca. 5°40'N, 117°45'E; observed by K. Stott, Jr. (1964, p. 12), date unknown. 83
- Madihit, Sungai; EAST MALAYSIA: Sarawak; 4°11'N, 115°08'E; museum collector, June, 1911 (SMK). 74
- Malacca. See Melaka.
- Mansalar Id. See Musala, Pulau.
- Mara. See Peleben.
- Masalembo-Besar; INDONESIA: Kalimantan; 5°34'S, 114°26'E; monkeys absent (Abbott *in* Lyon, 1911, p. 61). *k*
- Masolombo Besar. See Masalembo-Besar.
- Medan, vicinity; INDONESIA: Sumatra; ca. 3°35'N, 98°40'E; collected by H. Dürk. Dec. 29, 1904-Jan. 5, 1905 (ZSBS); Widmann, 1908 (ZSBS). 28
- Melaka; WEST MALAYSIA: Melaka; ca. 2°12'N, 102°15'E; reported by N. Annandale (*in* Bonhote, 1903, p. 3) and E. J. H. Corner (1941, p. 14). 19
- Meru; WEST MALAYSIA: Selangor; 3°08'N, 101°26'E; observed by I. S. Bernstein (1967b, p. 220), May 4, 1965-Feb. 28, 1966. 12
- Moyen Bahau. See Bahau, Sungai.
- Muarabeliti, sea level; INDONESIA: Sumatra; 3°15'S, 103°02'E; collected by J. J. Menden, Nov. 26, 1933 (AMNH-AC). 44
- Muarabliti. See Muarabeliti.
- Musala, Pulau; INDONESIA: Sumatra; 1°38'N, 98°32'E; pigtail macaques absent (Kloss, [1928], p. 802). *J*
- Natuna, Kepulauan; INDONESIA: Sumatra; 4°00'N, 108°15'E; *M. n. nemestrina* introduced (Thomas and Hartert, 1894, p. 654). *g*
- Niah Caves; EAST MALAYSIA: Sarawak; 3°49'N, 113°47'E; subfossils, late Pleistocene-subrecent; collected by Sarawak Museum, 1954-1962 (Hooijer, 1962b, p. 445). 63

- Nias, Pulau; INDONESIA: Sumatra; 1°05'N, 97°35'E; pigtail macaques absent (Kloss, [1928], p. 802). *I*
- Nicobar Islands, northern. See under *Macaca n. leonina. C*
- Nicobar Islands, southern. See under *Macaca n. leonina. D*
- Ogan, Air, upper; INDONESIA: Sumatra; ca. 3°30'S, 104°40'E; collected by Chancellor Stuart Exp., 1929 (FMNH). 48
- Padang; INDONESIA: Sumatra; 0°57'S, 100°21'E; collected by S. Müller, 1836 (RMNH); H. Meyer, 1890 (ZMUZ); I. Hagenbeck, May 2, 1925 (NMS). 33
- Padang [district]; INDONESIA: Sumatra; ca. 3°15'N, 99°15'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 29
- Padang highlands. See Djamboe cave, Lida Ajer cave, and Sibrambang cave.
- Pagar, Tanjong. See Singapore Island.
- Pagaralam; INDONESIA: Sumatra; 4°01'S, 103°16'E; collected by A. V. A. Coulin, June 19, 1941 (MZB). 45
- Pagurawan. See Paguruan, Sungai.
- Paguruan, Sungai; INDONESIA: Sumatra; 3°26'N, 99°20'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 29
- Pajakombo. See Pajakumbuh.
- Pajakumbuh; INDONESIA: Sumatra; 0°14'S, 100°38'E; collected by E. Dubois, date unknown (RMNH). 34
- Pajakumbuh, near. See Lida Ajer cave.
- Palembang; INDONESIA: Sumatra; 2°55'S, 104°45'E; collector unknown, Feb. 4, 1921 (RMNH); collector unknown, March 12, 1924 (NHMBE). 47
- Palembang [district], sea level; INDONESIA: Sumatra; "3°S, 104°E(app)"; collected by W. J. Frost, April 20, 1938 (BM). 46
- Pamarkang Bay. See Pamukan, Teluk.
- Pamukan, Teluk; INDONESIA: Kalimantan; ca. 2°30'S, 116°15'E; collected by W. L. Abbott (*in* Lyon, 1911, p. 58), March 25, 1909 (USNM). 69
- Panaitan, Pulau; INDONESIA: Java; 6°32'-6°40'S, 105°04'-105°14'E; *M. n. nemestrina* apparently absent (Hoogerwerf, 1953, p. 492). *M*
- Pangkalanberandan; INDONESIA: Sumatra; 4°01'N, 98°17'E; collected by Wilhelm Th. A. H. Volz (1912, p. 22), Oct. 14-Nov. 10, 1904 (ZMB). 26
- Pangkor, Pulau; WEST MALAYSIA: Perak; 4°13'N, 100°34'E; *M. n. nemestrina* absent (Harrison and Hendrickson, 1963, p. 548). 0
- Papar; EAST MALAYSIA: Sabah; 5°44'N, 115°56'E; collected by R. E. Kuntz, Sept. 12, 1960 (USNM). 72
- Pasi; INDONESIA: Sumatra; 5°12'N, 95°17'E; collected by Lt. v. d. Rest, date unknown (MZB). 24
- Pa Umor, 3400 ft.; EAST MALAYSIA: Sarawak; 3°44'N, 115°31'E; collected by T. Harrison, Jan. 3, 1948 (FMNH). 75

Pa Umur. See Pa Umor.

Pelaihari; INDONESIA: Kalimantan; 3°48'S, 114°45'E; collected by J. H. F. Kohlbrugge (1896, p. 181), Dec 15-21, 1894 (museum unknown). 71

Peleben [on Sungai Kajan near Mara; MS notes in AMNH, reported by Dr. Joseph Curtis Moore, personal communication]; INDONESIA: Kalimantan; ca. 2°45'N, 117°15'E; collected by V. von Plessen, June 24-July 21, 1935 (AMNH-AC; ZMB). 77

Pendeng. See Pulau Munteh.

Penang. See Pinang, Pulau.

Pennan, Koh. See Phangan, Ko.

Perak, Upper; WEST MALAYSIA: Perak; ca. 5°00'N, 101°00'E; reported by N. Annandale (*in* Bonhote, 1903, p. 3). 7

Perhentian Besar, Pulau; WEST MALAYSIA: Terengganu; 5°54'N, 102°46'E; macaques absent (Kloss, 1911b, p. 180). S

Phangan, Ko; THAILAND: Surat Thani; 9°45'N, 100°00'E; "*M. n. nemestrina* is stated on native authority to be found...Captive specimens were seen but their provenance was uncertain and they had not improbably been brought from the mainland" (Robinson and Kloss, 1914b, p. 130). (not mapped)

Pinang, Pulau; WEST MALAYSIA: Pinang; 5°24'N, 100°14'E; collected by T. Cantor (1846, p. 177; museum unknown); v. Düben, 1846 (NHRM); W. Rüttimeyer, 1880 (NHMB); Wistar Inst. of Anat., 1900 (USNM); collector and date unknown (BM). 6

Pleihari. See Pelaihari.

Pohorok. See Bohorok.

Pontianak; INDONESIA: Kalimantan; 0°02'S, 109°20'E; collected by P. Diard, [1826], (RMNH). 54

Priaman [district]. See Lubukbasung.

Pulau Munteh, 550-750 m.; INDONESIA: Sumatra, 4°05'N, 97°30'E (Chasen, 1941, map opp. p. 1); collected by A. Hoogerwerf (*in* Chasen, 1940b, p. 485), May 1, 1937 (MZB). 25

Pulo Paku, Betong Saribas; EAST MALAYSIA: Sarawak; ca. 1°30'N, 111°15'E; collected by H. C. Robinson, Oct. 15-Nov. 25, 1916 (BM). 58

Pulutelang; INDONESIA: Sumatra; 3°53'N, 98°20'E; collected by G. Schneider (1905, p. 73), 1897-1899 (NHMB). 26

Puruktjahu; INDONESIA: Kalimantan; 0°35'S, 114°35'E; collected by G. C. Shortridge, Sept. 3, 1909 (BM). 67

Ranau, 1350 ft.; EAST MALAYSIA: Sabah; 5°58'N, 116°41'E; collected by R. E. Kuntz, Sept., 1960 (USNM). 82

Redang, Pulau, group; WEST MALAYSIA: Terengganu; 5°47'N, 103°01'E; *M. n. nemestrina* absent (Kloss, 1911b, p. 177). T

Rengam. See Sungai Renggam.

- Rengat, inland; INDONESIA: Sumatra; ca. 0°24'S, 102°33'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 41
- Riam, Kotawaringin district, 300 m.; INDONESIA: Kalimantan; 1°50'S, 111°54'E; collected by J. J. Menden, Nov. 6, 1935 (AMNH-AC). 56
- Ringat. See Rengat.
- Roema Manoeal; INDONESIA: Kalimantan; 0°46'N, 111°39'E; collected by J. Buttikofer (1897, p. 12), Dec. 26, 1893 (RMNH; specimen not seen, data from Jentink, 1897, p. 39). 60
- Rungkup. See Simpang Empat Rungkup.
- Sagamafluss. See Segama, Sungai.
- Sakaïam River. See Sekajam, Sungai.
- Salai, Sungai; EAST MALAYSIA: Sarawak; ca. 3°30'N, 114°30'E; captive presented to London Zoo by F. Day in 1892, originally obtained about 1888 (Sclater, 1893, p. 325) (BM); collected by C. Hose, Feb.-June, 1891 (SMK). 64
- Samarahan. See Entawa-Samarahan.
- Sandakan, vicinity; EAST MALAYSIA: Sabah; ca. 5°50'N, 118°07'E; collected by H. G. Deignan, June 10, 1937 (MCZ). For note on locality, see Coolidge (1940, p. 130). 87
- Sanggul, Bukit, 500 m.; INDONESIA: Sumatra; 3°50'S, 102°37'E; collected by J. J. Menden, Aug. 20-Sept. 2, 1936 (AMNH-AC; MZB). 43
- Sapagaya, Sungai; EAST MALAYSIA: Sabah; ca. 5°39'N, 118°06'E; collected by C. F. Adams, Nov. 21, 1887 (USNM). 84
- Saribas. See Pulo Paku.
- Sebang. See Sebangka Pulau.
- Sebangka, Pulau; INDONESIA: Sumatra; 0°07'N, 104°36'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). c
- Sebesi, Pulau; INDONESIA: Sumatra; 5°57'S, 105°30'E; primates absent (Dammerman, 1922, p. 75). L
- Sebesy. See Sebesi, Pulau.
- Sebuku, Pulau; INDONESIA: Kalimantan; 3°30'S, 116°22'E; *M. n. nemestrina* absent (Abbott *in* Lyon, 1911, p. 62). m
- Segama, Sungai; EAST MALAYSIA: Sabah; ca. 5°30'N, 118°30'E; collected by Dr. Pagel, Aug. 22, 1907 (ZMB). 90
- Sekajam, Sungai; INDONESIA: Kalimantan; probably about 0°50'N, 110°25'E; collected by W. L. Abbott (*in* Lyon, 1907b, pp. 548, 566), June-Sept., 1905 (USNM). 51
- Sembilan, Kepulauan; WEST MALAYSIA: Perak; 4°02'N, 100°33'E; *M. n. nemestrina* absent (Harrison and Hendrickson, 1963, p. 548). R
- Semitau, vicinity; INDONESIA: Kalimantan; ca. 0°33'N, 111°58'E; observed by J. Buttikofer (1897, p. 11; *in* Jentink, 1897, p. 39) Nov.-Dec., 1893. 61

- Serapit; INDONESIA: Sumatra 3°34'N, 98°19'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 27
- Serdang [district]; INDONESIA: Sumatra; ca. 3°30'N, 98°50'E; observed by E. Hartert, date unknown (Thomas and Hartert, 1894, p. 655). 29
- Siak, Sungai, lower, at mouth of Sungai Gasip; INDONESIA: Sumatra; 0°43'N, 101°42'E; collected by W. L. Abbott, Jan. 1, 1907 (USNM). 38
- Sibolga, Teluk; INDONESIA: Sumatra; 1°38'N, 98°45'E; collected by W. L. Abbott (in Miller, 1903a, p. 482), Feb. 19-March 25, 1902 (USNM). 30
- Sibrambang cave, Padang highlands; INDONESIA: Sumatra; not precisely located, ca. 0°30'S, 100°30'E; subfossils, prehistoric Holocene; collected by E. Dubois, 1888-1890 (presumably in RMNH; Hooijer, 1962a, p. 58). 35
- Sidong, Gunong, 1200 ft.; EAST MALAYSIA: Sarawak; ca. 1°05'N, 110°25'E (Medway, 1965, map); collector unknown, Oct. 10, 1910 (ZRCS). 50
- Simeulue, Pulau; INDONESIA: Sumatra; 2°33'N, 95°55'E; pigtail macaques absent (Abbott in Miller, 1903a, p. 479). F
- Simpang Empat Rungkup; WEST MALAYSIA: Perak; 3°57'N, 100°43'E; collected by E. S[eimund], Nov. 28, 1913 (BM). 9
- Singapore Island; SINGAPORE: 1°20'N, 103°50'E; *M. n. nemestrina* introduced (Ridley, 1895, p. 26; Annandale in Bonhote, 1903, p. 3). (not mapped)
- Singkep, Pulau; INDONESIA: Sumatra; 0°30'S, 104°25'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). f
- Sintang; INDONESIA: Kalimantan; 0°04'N, 111°30'E; collected by C. Bruegel, March 18, 1907 (ZSBS). 62
- Sintass. See Sekajam.
- Sirambas; INDONESIA: Sumatra; 0°49'N, 99°32'E; collected by E. Modigliani, date unknown (Museo Civico di Storia Naturale "Giacomo Doria," Genova [DeBeaux, 1923, p. 36]). 31
- Si-Rambè. See Sirambas.
- Smitau. See Semitau.
- Solok; INDONESIA: Sumatra; 0°48'S, 100°39'E; collected by P. O. Stolz, July 17, 1915 (RMNH). 36
- Solombo. See Masalembo-Besar.
- Sugi, Pulau; INDONESIA: Sumatra; 0°50'N, 103°47'E; *M. n. nemestrina* absent (Dammerman, 1926, p. 316). Z
- Sukadana; INDONESIA: Kalimantan; 1°15'S, 109°57'E; collected by W. L. Abbott (in Lyon, 1911, p. 54), June 10, 1907 (USNM). 55
- Sungai Buloh, 150-300 ft.; WEST MALAYSIA: Selangor; 3°12'N, 101°35'E; collected by Institute for Medical Research, 1947-1957 (Harrison and Hendrickson, 1963, p. 548; Harrison, 1969, p. 176). 11
- Sungai Renggam; WEST MALAYSIA: Selangor; 3°03'N, 101°32'E; collector unknown, May 28, 1923 (BM). 12

Sungei Rengam. See Sungai Renggam.

Sut, [Sungai], 3000 ft.; EAST MALAYSIA: Sarawak; 2°42'N, 114°39'E; collected by T. A. Chavasse, Sept. 27, 1955 (FMNH). 66

Tabong; INDONESIA: Kalimantan; 0°34'N, 116°02'E; collected by A. M. R. Wegner, Sept. 13, 1956 (MZB). 80

Tandjung. See Tandjung.

Tandjung; INDONESIA: Kalimantan; 2°11'S, 115°23'E; collected by A. Buxtorf, 1905 (NHMB). 68

Tandjung; INDONESIA: Sumatra; 3°17'N, 99°19'E; collected by G. Schneider (1905, p. 73), 1897-1899 (museum unknown). 29

Tandjungmorawa; INDONESIA: Sumatra; 3°30'N, 98°47'E (Atlas Trop. Ned., pl. 12a); collected by B. Hagen (1890, pp. 80, 82), 1882-1883 (RMNH; also see Jentink, 1887, p. 26); C. Bruegel, 1906 (ZSBS). 28

Tanjong Antu. See Hantu, Tanjong.

Tapanuli Bay. See Sibolga, Teluk.

Tapisello. See Djamboe cave.

Tarusan, Teluk; INDONESIA: Sumatra; 1°13'S, 100°25'E; collected by W. L. Abbott, Dec. 31, 1904 (USNM). 37

Tawau district. See Tibas, Sungai.

Tebingtinggi, Deli; INDONESIA: Sumatra; 3°20'N, 99°09'E; collected by J. A. Coenraad, Nov., 1931, Feb., 1932 (MZB). 29

Temadju, Pulau; INDONESIA: Kalimantan; 0°29'N, 108°52'E; monkeys absent (Abbott *in* Lyon, 1911, p. 59). *i*

Temaju, Pulo. See Temadju, Pulau.

Tibas, Sungai; EAST MALAYSIA: Sabah; 4°26'N, 117°29'E (Davis, 1962, p. 127); collected by R. F. Inger, June 9, 1956 (FMNH). 86

Tinggi, Pulau; WEST MALAYSIA: Johor; 2°18'N, 104°07'E; *M. n. nemestrina* absent (Robinson, 1919, p. 325). *X*

Tioman, Pulau; WEST MALAYSIA: Pahang; 2°48'N, 104°11'E; *M. n. nemestrina* said to be absent (Abbott *in* Miller, 1900, p. 246); collected by J. L. Harrison and J. R. Hendrickson (1963, p. 548), May, 1958 (museum unknown). 22

Trang. See Chong.

Trang [province]; THAILAND: Trang; ca. 7°30'N, 99°30'E; collector and date unknown (ZRCS). (not mapped)

Ulu Gombak Forest Reserve, 2000 ft.; WEST MALAYSIA: Selangor; ca. 3°20'N, 101°50'E; observed by H. E. McClure ([1965], p. 57), May 20, 1961, March 10, 1962; reported by D. Chivers (1971, p. 80). 18

Ulu Madihih. See Madihit, Sungai.

Ulu Segama Forest Reserve, 800-5000 ft.; EAST MALAYSIA: Sabah; ca. 5°11'N, 117°53'E; observed by J. MacKinnon (1971, p. 153), 1968-1970. 85

Ulu Sempan, Raub. See Bukit Fraser.

Verlaten Island. See Krakatau, Kepulauan.

Macaca nemestrina leonina

Map, Figure 28

Adung Valley. See Nam Tamai.

Akyab. See Sittwe.

Andaman Islands; INDIA: Andaman and Nicobar Islands; 10°-14°N, 92°-93°E; monkeys not indigenous, *M. n. leonina* introduced (Hamilton, 1870, p. 220). *A*

Annam. See Da Ban.

Arakan district, northern hills; BURMA: Arakan Div.; ca. 21°30'N, 93°00'E; collected by A. P. Phayre, 1844 (ZSI); Darling, date unknown (ZMB); collector and date unknown (RMNH); reported by Sclater ([1881], p. 537). *4*

Arracan. See Arakan.

Assam [state]; INDIA: Assam; 25°-27°N, 90°-95°E; obtained by Mr. Gerrard, purchased March 17, 1885 (IRSN). (not mapped)

Bang Hue Hom. See Ban Hue Hom.

Ban Huai Maenam Noi, vicinity, ca. 75 m.; THAILAND: Kanchanburi; ca. 14°25'N, 98°51'E; collected by J. Fooden (1971a, p. 32), Feb. 16, 1967 (CTNRC, FMNH). *31*

Ban Huang Som; THAILAND: Trat; 11°51'N, 102°50'E; collected by C. B. Kloss, (1916a, pp. 30, 66), Jan. 11, 1915 (BM). *37*

Ban Hue Hom, hill forests north of; THAILAND: Phrae; ca. 17°55'N, 100°10'E; reported by N. Gyldenstolpe (1914, p. 5). *10*

Bankachon, Victoria Point; BURMA: Tenasserim Div.; 10°09'N, 98°36'E; collected by G. C. Shortridge (*in* Wroughton, 1915b, p. 696), Nov. 11-Dec. 29, 1913 (BM; BNHS; ZSI). *44*

Bankasun. See Bankachon.

Ban Kerng Chada, ca. 150 m.; THAILAND: Kanchanaburi; 15°08'N, 98°31'E; collected by J. Fooden (1971a, p. 32), Feb. 5, 1967 (FMNH). *29*

Ban Khlong Wan; THAILAND: Ranong; 10°30'N, 98°49'E; collected by H. C. Robinson and C. B. Kloss (1921, p. 9), March 16, 1919 (ZRCS). *46*

Ban Nong Kho; THAILAND: Chon Buri 13°09'N, 101°04'E; collected by H. M. Smith, Nov. 13, 1926 (USNM). *35*

Ban Nong Kok; THAILAND: Krabi; 8°06'N, 98°52'E; collected by H. C. Robinson and C. B. Kloss (1919, p. 88), Jan. 7, 1918 (ZRCS). *48*

Ban Pong Nam Ron, 8-12 km. W and 10 km. NW, ca. 250-300 m.; THAILAND: Kamphaeng Phet; ca. 16°20'N, 99°15'E; collected by J. Fooden (1971a, p. 32), April 12-23, 1967 (FMNH). *21*

Ban Tha San, 220 ft.; THAILAND: Chumphon; 10°29'N, 98°55'E; collected by H. C. Robinson and C. B. Kloss (1921, p. 10), March 14, 1919 (ZRCS). *46*

Barren Island; INDIA: Andaman and Nicobar Islands; 12°15'N, 93°50'E; monkeys absent (Kloss, 1903, p. 14). *B*

- Bhamo, 20-25 miles below; BURMA: Kachin State; ca. 24°10'N, 97°00'E; erroneous record (Anderson, 1881, p. 72) of *M. n. leonina* (see above, p. 110).
- Bien Hoa. See Trang Bom.
- Bolovens, Plateau des; LAOS: 14°45'-15°30'N, 106°00'-106°50'E; collected by T. D. Carter, Legendre Indo-China Expedition, Feb. 3-13, 1932 (AMNH). For locality note, see Legendre (1932, p. 495). 17
- Chamchay, Cochinchine; SOUTH VIETNAM: not precisely located, 8°30'-12°30'N, 104°30'-107°30'E; collected by M. Pierre, April 1874 (MNHN). (not mapped)
- Champang; BURMA: Tenasserim Div.; 10°13'N, 98°31'E; collected by W. L. Abbott, Dec. 21-22, 1903 (USNM). 44
- Chan, Ko; THAILAND: Ranong, Mergui Archipelago; 9°25'N, 97°50'E (Moore and Tate, 1965, p. 323); collected by W. L. Abbott, Dec. 30, 1899-Jan. 1, 1900 (USNM). 45
- Chance Island. See Chan, Ko (Moore and Tate, 1965, p. 317).
- Changchang Pani, 500 ft.; INDIA: Nagaland; 26°35'N, 94°25'E; collected by C. McCann (1933a, p. 395), Feb. 7-19, 1930 (AMNH; BNHS). 1
- Chantabun. See Chantaburi.
- Chantaburi; THAILAND: Chantaburi; 12°36'N, 102°09'E; collected by C. J. Aagaard, Dec. 16-17, 1926 (ZRCS). 36
- Chongkrong, 600-900 m.; THAILAND: Kanchanaburi; 14°41'N, 98°52'E; collected by J. Fooden (1971a, p. 32), Jan. 28, 1967. 30
- Cochinchine. See Chamchay.
- Da Ban; SOUTH VIETNAM: Ninh Thuan; ca. 11°45'N, 108°45'E, collected by C. B. Kloss (1919a, p. 395), March 24, 1918 (ZRCS). 41
- Ghirbi. See Ban Nong Kok.
- Hin Lap, Sathani; THAILAND: Sara Buri; 14°40'N, 101°09'E; collected by H. M. Smith, Oct. 2, 1932 (USNM). 24
- Hkamti. See Singkaling Hkamti.
- Hué, vicinity; SOUTH VIETNAM: Thua Thien; 16°28'N, 107°36'E; reported by J. Delacour (1940, p. 24). 19
- Junk Seylon. See Klong Tung Sai.
- Kao Sabab. See Sa Bap, Khao.
- Kawkareik; BURMA: Kawthule State; 16°33'N, 98°14'E; collected by L. Fea, May 1887 (Museo Civico di Storia Naturale "Giacomo Doria," Genova [Thomas, 1892, p. 916; DeBeaux, 1923, p. 34]). 20
- Khlung, Khlong, upper; THAILAND: Kamphaeng Phet; ca. 16°05'N, 99°20'E; collected by C. C. Sanborn (1952, p. 2) and F. C. Wonder, July 2, 1949 (FMNH). 22
- Khun Tan, mountains; THAILAND: Lamphun; ca. 18°30'N, 99°15'E; collected by N. Gyldenstolpe ([1917], p. 7), June 7, 1914 (NHRM). 9
- Klet Kaeo, Ko; THAILAND: Chon Buri; 12°46'N, 100°51'E; pigtail macaques absent (Berkson et al., 1971, p. 237). F

- Klong Klung. See Khlung, Khlong.
- Klong Menao. See Ban Huang Som (Moore and Tate, 1965, p. 323).
- Klong Tundai. See Klong Tung Sai.
- Klong Tung Sai, Ko Phuket; THAILAND: Phuket; 7°98'N, 98°22'E (Robinson and Kloss, 1919, p. 88); collected by C. B. Kloss, Dec. 20-26, 1917 (BM; ZRCS). For comment on locality, see Chasen, 1935, p. 38. 47
- Klong Tun Sai. See Klong Tung Sai.
- Klong Wan. See Ban Khlong Wan.
- Kokareet. See Kawkareik.
- Ko Keow, vicinity, ca. 200 m.; THAILAND: Kamphaeng Phet; ca. 15°55'N, 99°25'E; J. Fooden (1971a, p. 32), March 9, 1967 (FMNH).22
- Koon Tan. See Khun Tan.
- Krabi. See Ban Nong Kok.
- Lampi Island. See Lanbi Kyun.
- Lanbi Kyun; BURMA: Tenasserim Div., Mergui Archipelago; 10°50'N, 98°15'E; collected by C. Primrose, March 3, 1922 (BM). 42
- Lat Bua Kao. See Lat Bua Khao.
- Lat Bua Khao, Sathani, north of; THAILAND: Nakhon Ratchasima; 14°52'N, 101°36'E; collected by C. B. Kloss (1919b, p. 343), Oct. 12, 1916 (USNM). 26
- Meh Lem river, north of; THAILAND: Phrae; ca. 18°25'N, 100°20'E (Gyldenstolpe, 1913, p. 4; 1916, pl. 1); observed and tentatively identified by N. Gyldenstolpe (1914, p. 4), March 5-27, 1912. 11
- Meng-hai; CHINA: Yunnan; 21°52'N, 100°28'E; collected by Kao Yüeh-ting et al. (1962, p. 188), 1957-1958 (probably in collection of Institute of Zoology, Academia Sinica, Peking). 8
- Möng Nai; BURMA: Shan State; 20°31'N, 97°52'E; collected by Dr. Griggs, in or before April, 1894 (Brown, 1896, p. 485). 7
- Muang Leip. See Muang Liap.
- Muang Liap; LAOS: Xaignabouri; 18°29'N, 101°40'E; collected by J. Bangga, Jan. 15, 1920 (ZRCS). 12
- Nam Tamai; BURMA: Kachin State; 27°42'N, 97°54'E (Moore and Tate, 1965, p. 328); probably erroneous record (Dollman, 1932, p. 9; see above p. 112).
- Nicobar Islands, northern; INDIA: Andaman and Nicobar Islands; 8°-10°N, 92°-94°E; monkeys absent (Kloss, 1903, p. 114). C
- Nicobar Islands, southern; INDIA: Andaman and Nicobar Islands; 7°-8°N, 93°-94°; pigtail macaques absent (Kloss, [1928], p. 802). D
- Nong Khor. See Ban Nong Kho (Chasen, 1935, p. 32; Moore and Tate, 1965 p. 329).
- Nong Kok. See Ban Nong Kok.
- Pak Chong, Sathani, 900 ft.; THAILAND: Nakhon Ratchasima; 14°42'N, 101°25'E;

- collected by E. G. Herbert and M. Smith, Dec. 4, 1915 (BM; Kloss, 1916b, p. 2) and H. M. Smith, March 2, 1924 (USNM). 25
- Pak Jong. See Pak Chong, Sathani.
- Paksane (province); LAOS: ca. 18°30'N, 104°00'E; collected by J. Deuve and M. Deuve (1963, p. 60), date and museum unknown. 14
- Pakse (province); LAOS: ca. 15°00'N, 106°00'E; collected by J. Deuve and M. Deuve (1963, p. 60), date and museum unknown. 17
- Panjang, Pulau. See Telok Poh.
- Pan-na-meng-hai. See Meng-hai.
- Paungdaw power station, hill NW, 3000 ft.; BURMA: Tenasserim Div.; ca. 14°00'N, 98°30'E; collected by J. Keenan, July 12, 1961 (BM). 32
- "Perak"; WEST MALAYSIA: Perak; ca. 5°00'N, 101°00'E; presented by O. L. Fraser, Jan. 6, 1878 (ZSI). Erroneous locality (see above, p. 110).
- Petchaburi. See Phet Buri.
- Phet Buri [province]; THAILAND: Phet Buri; 12°35'-13°10'N, 99°15'-100°05'E; reported by K. G. Gairdner (1914, p. 36). 34
- Phu Kheo Forest Reserve; THAILAND: Chaiyaphum; ca. 16°15'N, 101°30'E; remains of monkeys eaten by humans, reported by J. A. McNeely and E. W. Cronin (1972, p. 459), Jan. 1972. 27
- Phuket, Ko. See Klong Tung Sai.
- Pidaung Game Sanctuary; BURMA: Kachin State; 25°25'N, 97°09'E; observed by U Tun Yin (1954, p. 269), March, 1951-Feb., 1952. 3
- Plateau des Bolovens. See Bolovens, Plateau des.
- Puket. See Klong Tung Sai.
- Rat Buri [province]; THAILAND: Rat Buri; 13°10'-13°45'N, 99°20'-100°05'E; reported by K. G. Gairdner (1914, p. 36). 33
- Red Point; BURMA: Tenasserim Div.; 10°40'N, 98°30'E (Moore and Tate, 1965, p. 331); collected by W. L. Abbott, Feb. 20, 1904 (USNM). 43
- Ross Island. See Andaman Islands.
- Sa Bap, Khao; THAILAND: Chanthaburi; 12°31'N, 103°13'E; collected by H. M. Smith, Nov. 5, 1933 (USNM). 36
- Sai Gon; SOUTH VIETNAM: Gai Dinh; 10°45'N, 106°40'E; reported by J. Delacour (1940, p. 24). 40
- Salanga. See Klong Tung Sai.
- Samnak Rabam, 10 km. SE, ca. 200 m.; THAILAND: Uthai Thani; 15°25'N, 99°30'E; collected by J. Fooden (1971a, p. 32), Feb. 26, 1967 (CTNRC, FMNH). 23
- Saravane (province); LAOS: ca. 15°45'N, 106°45'E; collected by J. Deuve and M. Deuve (1963, p. 60), date and museum unknown. 18
- Savannahket (province); LAOS: ca. 16°30'N, 104°45'E; collected by J. Deuve and M. Deuve (1963, p. 60), date and museum unknown. 16

Selok Poh. See Telok Poh.

"Siam"; THAILAND: no exact locality; collected by R. C. Bulkeley, date unknown (AMNH). (not mapped)

Singkaling Hkamti, about 20 miles north [east], W bank of Chindwin River, 500 ft.; BURMA: Sagaing Div.; ca. 26°10'N, 96°00'E; collected by G. C. Shortridge and S. A. Macmillan, July 26, 1914 (BM). For locality note, see Wroughton, 1916a, p. 293. 2

Sittwe, hills inland; BURMA: Arakan Div.; ca. 20°00'N, 93°30'E; reported by S. R. Tickell (1854-1863, MS., p. 112; Pocock, 1939, p. 60) and E. Blyth (1863, appendix p. [189]; in Dunn, 1864, p. 370). 5

Sullivan's Island. See Lanbi Kyun.

Taho, 1200-1300 m.; BURMA: Shan State; 19°27'N, 96°53'E; collected by L. Fea (1888, pp. 855, 859), Feb. 29, 1888 (Museo Civico di Storia Naturale "Giacomo Doria," Genova [Thomas, 1892, p. 916; DeBeaux, 1923, p. 34]). 6

Tapli. See Ban Khlong Wan.

Tasan. See Ban Tha San.

Tavoy. See Ye.

Tay Ninh; SOUTH VIETNAM: Tay Ninh; 11°18'N, 106°05'E, reported by A. Morice (1875, p. 41). 38

Telok Besar; BURMA: Tenasserim Div.; 10°22'N, 98°35'E (Moore and Tate, 1965, p. 333); collected by W. L. Abbott, March 17, 1904 (USNM). 44

Telok Poh, Ko Yao Yai; THAILAND: Phangnga; 8°00'N, 98°38'E (Robinson and Kloss, 1919, p. 88); collected by C. B. Kloss, Jan. 22, 1918 (BM). For comment on locality, see Chasen, 1935, p. 38. 47

Thakhek (province); LAOS: ca. 17°30'N, 105°00'E; collected by J. Deuve and M. Deuve (1963, p. 60), date and museum unknown. 15

Thào. See Taho.

Tongha. See Klong Tung Sai.

Tongka. See Klong Tung Sai.

Trang Bom; SOUTH VIETNAM: Bien Hoa, 10°57'N, 107°00'E; collected by C. B. Kloss (1919a, p. 401), June 5, 1918 (ZRCS); M. Poilane, Sept. 4, 1932 (USNM); for locality restriction, see Van Peenen et al., 1969, p. 102). 39

Victoria Point. See Bankachon.

Vientiane (province); LAOS: ca. 18°00'N, 102°30'E; collected by J. Deuve and M. Deuve (1963, p. 60); date and museum unknown. 13

Yao Yai, Ko. See Telok Poh.

Ye, forest near; BURMA: Tenasserim Div.; ca. 15°15'N, 98°00'E; collected by S. R. Tickell (1854-1875, MS., pp. 112, 137, 139), Nov., 1854 and Jan.-Feb., 1860 (museum unknown). 28

Yey. See Ye.

Zingkalling. See Singkaling Hkamti.

Macaca nemestrina pagensis
Map, Figure 25

Mentawai, Kepulauan. See Sipura, Pulau; Pagai Utara, Pulau; Pagai Selatan, Pulau.

North Pagi. See Pagai Utara, Pulau.

Pagai Selatan, Pulau, sea level; INDONESIA: Sumatra; ca. 3°00'S, 100°20'E; collected by W. L. Abbott, Nov. 17, 1902 (USNM) and J. J. Menden, Jan. 24, 1935 (AMNH-AC). 93

Pagai Utara, Pulau, sea level; INDONESIA: Sumatra; ca. 2°42'S, 100°07'E; collected by J. J. Menden, Jan. 13-26, 1935 (AMNH-AC). 92

Pagi Islands. See Pagai Selatan, Pulau, and Pagai Utara, Pulau.

Sioban; INDONESIA: Sumatra; 2°11'S, 99°43'E; collected by E. Modigliani, 1883 (Museo Civico di Storia Naturale "Giacomo Doria," Genova [Thomas, 1895, p. 664; DeBeaux, 1923, p. 37]). 91

Sipora. See Sioban.

Sipura, Pulau. See Sioban.

South Pagi. See Pagai Selatan, Pulau.

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ADDENDA

1. While this monograph was in press, one additional adult male specimen of *Macaca nemestrina leonina* (No. 20039) collected at Khao Soi Dao, Thailand (see below) was examined at the Academy of Natural Sciences, Philadelphia. Significant measurements (mm.) of this specimen are: head and body length, 574; tail length, 162 (relative tail length, 0.28); greatest length of skull excluding incisors, 141.5; zygomatic breadth, 99.6; rostral length, 56.3; postrostral length, 95.5; length of incisor-canine field, 18.1; length of premolar-molar field, 37.8. These new measurements slightly extend the range of relative tail length and greatest skull length specified above (pp. 7, 18, 112, 115) for this subspecies; inclusion of these measurements in graphs of dimensional characters (figs. 2, 7, 8, 9, 22) would have relatively minor effects.

2. Three recent publications, listed below, provide valuable morphological information concerning growth changes and sex differences in *Macaca nemestrina*.

GARN, S. M., D. R. SWINDLER, and P. E. MINNIS

1975. The sex difference in dimensional communalities in *Macaca nemestrina*. Amer. J. Phys. Anthropol., **43**, pp. 19-22.

SIRIANNI, J. E., D. R. SWINDLER, and L. H. TARRANT

1975. Somatometry of newborn *Macaca nemestrina*. Folia primatol., **24**, pp. 16-23.

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1975. Postnatal growth in the pig-tailed monkey (*Macaca nemestrina*). Ph. D. Thesis. Univ. of Washington, Seattle, ii + 113 pp.

3. Supplementary locality records (unmapped) to be added to the Gazetteer of Collecting Localities (pp. 112-142) are documented below.

Macaca silenus

Shimoga Dist., 2000 ft., INDIA: Mysore; ca. 14°00'N, 75°30'E; observed by R. Whitaker, Mar., 1972 (Pruett, C., 1974, J. Bombay Nat. Hist. Soc., **70**, p. 547).

Silent Valley, ca. 4200 ft.; INDIA: Kerala; ca. 11°10'N, 76°30'E; troop including 11-12 adults (2 females with young infants) observed by C. Pruett (*ibid.*, pp. 546-547) and D. Hayles, Mar., 1972.

Singampatti Hills (*ibid.*, p. 546). See Manjulai Tea Estate.

Macaca nemestrina nemestrina

Kenangan, near; INDONESIA: Kalimantan; ca. 1°05'S, 116°45'E; observed by C. C. Wilson and W. L. Wilson (1975, *Folia primatol.*, **23**, pp. 252, 253), March, 1973.

Macaca nemestrina leonina

Soi Dao, Khao, 3500 ft.; THAILAND: Nakhon Sawan; 15°30'N; 100°44'E; collected by R. M. de Schauensee (1946, *Proc. Acad. Nat. Sci. Philad.*, **98**, p. 5), May 25, 1938 (Academy of Natural Sciences, Philadelphia, 1, skin and skeleton).

Macaca nemestrina pagensis

Tei-Tei Peleigei, near; INDONESIA: Sumatra (Pulau Siberut); ca. 1°24'S, 99°01'E; reported by R. R. Tenaza (1975, *Folia primatol.*, **24**, p. 67), July 1-Oct. 7, 1972.





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