FIELDIANA

Zoology

NEW SERIES, NO. 45

Taxonomy and Evolution of the *Sinica* Group of Macaques: 6. Interspecific Comparisons and Synthesis

Jack Fooden

June 30, 1988
Publication 1389

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

Information for Contributors to Fieldiana

General: *Fieldiana* is primarily a journal for Field Museum staff members and research associates, although manuscripts from nonaffiliated authors may be considered as space permits. The Journal carries a page charge of $65 per printed page or fraction thereof. Contributions from staff, research associates, and invited authors will be considered for publication regardless of ability to pay page charges, but the full charge is mandatory for nonaffiliated authors of unsolicited manuscripts. Payment of at least 50% of page charges qualifies a paper for expedited processing, which reduces the publication time.

Manuscripts should be submitted to Dr. James S. Ashe, Scientific Editor, *Fieldiana*, Field Museum of Natural History, Chicago, Illinois 60605-2496, USA. Three complete copies of the text (including title page and abstract) and of the illustrations should be submitted (one original copy plus two review copies which may be machine copies). No manuscripts will be considered for publication or submitted to reviewers before all materials are complete and in the hands of the Scientific Editor.

Text: Manuscripts must be typewritten double-spaced on standard-weight, 8½- by 11-inch paper with wide margins on all four sides. For papers longer than 100 manuscript pages, authors are requested to submit a "Table of Contents," a "List of Illustrations," and a "List of Tables." In most cases, the text should be preceded by an "Abstract" and should conclude with "Acknowledgments" (if any) and "Literature Cited." All measurements should be in the metric system. The format and style of headings should follow those of recent issues of *Fieldiana*. For more detailed style information, see *The Chicago Manual of Style* (13th ed.), published by The University of Chicago Press, and also recent issues of *Fieldiana*.

In "Literature Cited," authors are encouraged to give journal and book titles in full. Where abbreviations are desirable (e.g., in citation of synonymies), authors *consistently* should follow *Botanico-Periodicum-Huntianum* and *TL-2 Taxonomic Literature* by F. A. Stafleu & R. S. Cowan (1976 *et seq.*) (botanical papers) or *Serial Sources for the Biosis Data Base* (1983) published by the BioSciences Information Service.

References should be typed in the following form:

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif., 943 pp.

Grubb, P. J., J. R. Lloyd, and T. D. Pennington. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. Journal of Ecology, **51**: 567–601.

Langdon, E. J. M. 1979. Yagé among the Siona: Cultural patterns in visions, pp. 63–80. *In* Browman, D. L., and R. A. Schwarz, eds., Spirits, Shamans, and Stars. Mouton Publishers, The Hague, Netherlands.

Murra, J. 1946. The historic tribes of Ecuador, pp. 785–821. *In* Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

Stolze, R. G. 1981. Ferns and fern allies of Guatemala. Part II. Polypodiaceae. Fieldiana: Botany, n.s., **6**: 1–522.

Illustrations: Illustrations are referred to in the text as "figures" (not as "plates"). Figures must be accompanied by some indication of scale, normally a reference bar. Statements in figure captions alone, such as "× 0.8," are not acceptable. Captions should be typed double-spaced and consecutively. See recent issues of *Fieldiana* for details of style.

Figures as submitted should, whenever practicable, be 8½ by 11 inches (22 × 28 cm) and may not exceed 11½ by 16½ inches (30 × 42 cm). Illustrations should be mounted on boards in the arrangement you wish to obtain in the printed work. This original set should be suitable for transmission to the printer as follows: Pen and ink drawings may be originals (preferred) or photostats; shaded drawings should be originals, but within the size limitation; and photostats should be high-quality, glossy, black and white prints. All illustrations should be marked on the reverse with author's name, figure number(s), and "top." Original illustrations will be returned to the author upon publication unless otherwise specified. Authors who wish to publish figures that require costly special paper or color reproduction must make prior arrangements with the Scientific Editor.

Page Proofs: *Fieldiana* employs a two-step correction system. Each author will normally receive a copy of the edited manuscript on which deletions, additions, and changes can be made and queries answered. Only one set of page proofs will be sent. All desired corrections of type must be made on the single set of page proofs. Changes in page proofs (as opposed to corrections) are very expensive. Author-generated changes in page proofs can only be made if the author agrees in advance to pay for them.

FIELDIANA

Zoology

NEW SERIES, NO. 45

Taxonomy and Evolution of the *Sinica* Group of Macaques: 6. Interspecific Comparisons and Synthesis

Jack Fooden

Research Associate
Division of Mammals
Field Museum of Natural History
Chicago, Illinois 60605-2496

Accepted for publication September 23, 1987
June 30, 1988
Publication 1389

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

Library of Congress Catalog Card Number: 87-83733
ISSN 0015-0754
PRINTED IN THE UNITED STATES OF AMERICA

For Elizabeth

Table of Contents

List of Illustrations

List of Tables

Taxonomy and Evolution of the *Sinica* Group of Macaques: 6. Interspecific Comparisons and Synthesis

Abstract

The *sinica* group of macaques comprises four species and six subspecies: *Macaca sinica* (with subspecies *M. s. sinica* and *M. s. aurifrons*), *M. radiata* (*M. r. radiata, M. r. diluta*), *M. assamensis* (*M. a. assamensis, M. a. pelops*), and *M. thibetana.* The geographic ranges of these species are allopatric or parapatric and extend from Sri Lanka to east-central China. In this paper, *sinica*-group species are compared with respect to pelage, external measurements, cranial characters, caudal vertebrae, glans penis and baculum, female reproductive tract, blood proteins, karyology, and hybridization. A hypothetical reconstruction of major developments in the evolutionary history of this group is proposed. New locality records of *sinica*-group macaques are documented in a gazetteer.

Introduction

This is the concluding part in a series of papers that systematically review the *sinica* group of macaques. Five previous publications in this series present accounts of the four recognized species in the *sinica* group and an overview of the natural history of these species (Fooden, 1979, 1981, 1982, 1983, 1986). The present paper provides comparative studies of external characters, skeletal characters, genital characters, blood proteins, karyology, and hybridization, and a hypothetical reconstruction of major developments in the evolutionary history of this group. A gazetteer presents details of *sinica*-group locality records discovered subsequent to publication of previous species accounts.

Four species and six subspecies are recognized in the *sinica* group:

1. *Macaca sinica* (Linnaeus, 1771)
   - *M. s. sinica* (Linnaeus, 1771)
   - *M. s. aurifrons* Pocock, 1931
2. *Macaca radiata* (E. Geoffroy, 1812)
   - *M. r. radiata* (E. Geoffroy, 1812)
   - *M. r. diluta* Pocock, 1931
3. *Macaca assamensis* McClelland in Horsfield, [1840]
   - *M. a. assamensis* McClelland in Horsfield, [1840]
   - *M. a. pelops* Hodgson, 1841
4. *Macaca thibetana* A. Milne-Edwards, 1870

Taxa in the *sinica* group, as in other species groups of macaques, are allopatric or parapatric (fig. 1; Fooden, 1980, p. 4). Allocation of *sinica*-group taxa to specific or subspecific rank therefore is somewhat arbitrary. Plausible arguments can be made, for example, for regarding *M. a. pelops* as specifically distinct from *M. a. assamensis* or, conversely, for regarding *M. sinica* and *M. radiata* as conspecific. However, because available evidence is equivocal, the classification given above is retained as reasonable and widely accepted.

In references to specimens cited in this paper, institutional names are abbreviated as indicated below:

AIUZ — Anthropologisches Institut der Universität Zürich, Zurich, Switzerland

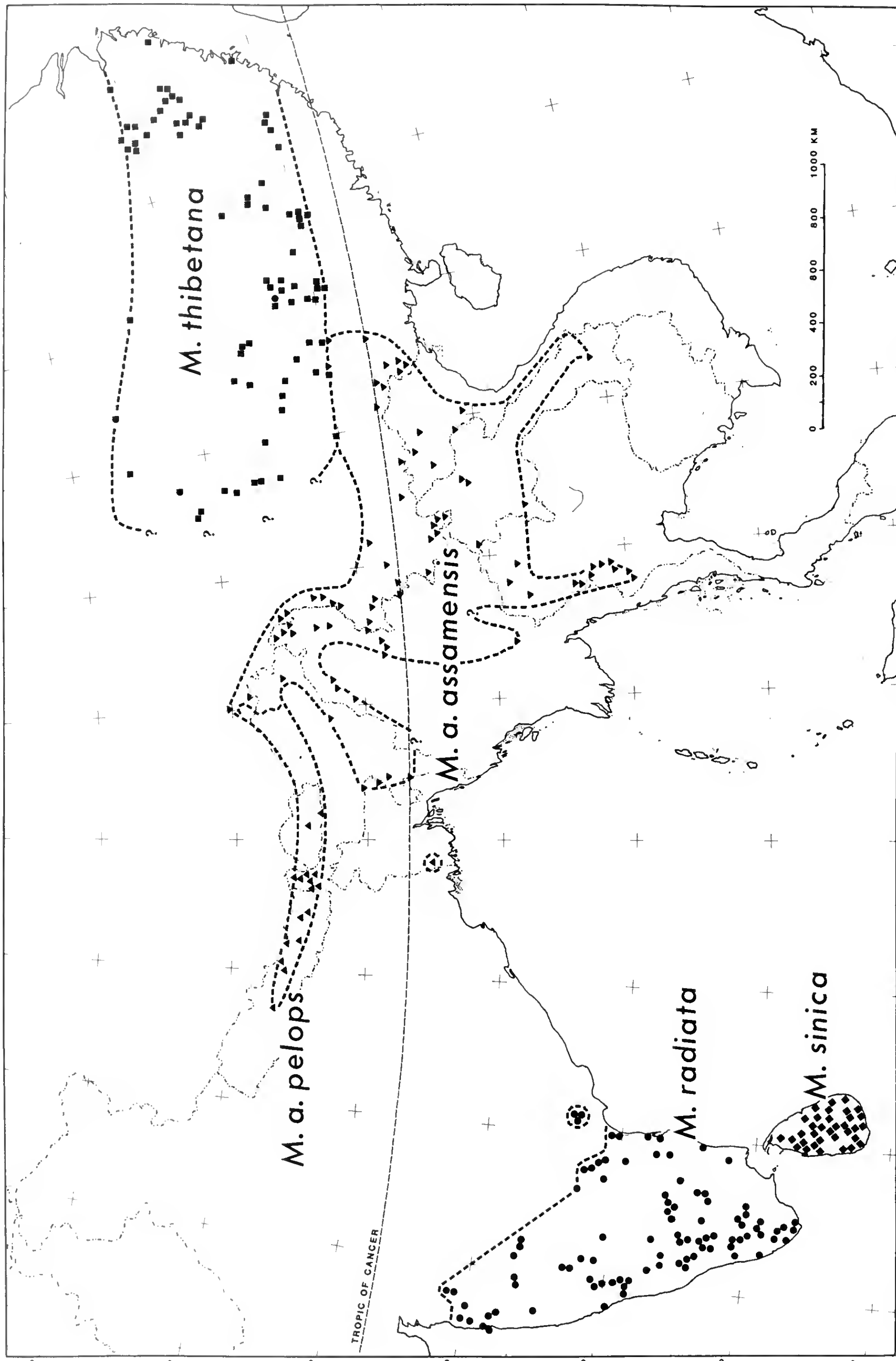

FIG. 1. Locality records (solid symbols) and inferred limits of natural distribution (dashed lines) of *sinica*-group macaques. For documentation of locality records, see Gazetteer and Fooden (1986, p. 2).

AMNH American Museum of Natural History, New York
BJMNH Beijing Museum of Natural History, Beijing
BM British Museum (Natural History), London
ECNU East China Normal University, Shanghai
FMNH Field Museum of Natural History, Chicago
GIFID Guangxi Institute of Forest Investigation and Design, Nanning, Guangxi Province, China
GZ Ganzhou Zoo, Ganzhou, Jiangxi Province, China
HZ Hangzhou Zoo, Hangzhou, Zhejiang Province, China
IMMZAM Institute of Medical Microbiology, Zhejiang Academy of Medicine, Hangzhou, Zhejiang Province, China
IRSN Institut Royal des Sciences Naturelles de Belgique, Brussels
IZCAS Institute of Zoology, Chinese Academy of Sciences, Beijing
JNRB Jinggangshan Nature Reserve Bureau, Jinggangshan, Jiangxi Province, China
JUBD Jiangxi University, Biology Department, Nanchang, Jiangxi Province, China
KIZ Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, Yunnan Province, China
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MNHN Muséum National d'Histoire Naturelle (Mammifères), Paris
NHMB Naturhistorisches Museum, Basel, Switzerland
NMSL National Museum, Sri Lanka, Colombo, Sri Lanka
NWPIB Northwest Plateau Institute of Biology, Xining, Qinghai Province, China
NZ Nanchang Zoo, Nanchang, Jiangxi Province, China
QNR Qinxidong Nature Reserve, Ruyuan, Guangdong Province, China
RCFB Ruyuan County Forest Bureau, Ruyuan, Guangdong Province, China
RMNH Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands
SCIEA South China Institute of Endangered Animals, Guangzhou, Guangdong Province, China
SMNH Shanghai Museum of Natural History, Shanghai
SZG Shanghai Zoological Garden, Shanghai
USNM National Museum of Natural History, Washington, D.C.
ZMB Zoologisches Museum des Humboldt-Universität, Berlin
ZMNH Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China
ZRCNUS Zoological Reference Collection, National University of Singapore, Singapore

Comparisons

Pelage

Dorsal pelage color in adults is variably brownish in *sinica*-group macaques (fig. 2; Fooden, 1979, p. 110; 1981, p. 2; 1982, p. 6; 1983, p. 7; Fooden et al., 1985, p. 15). Pelage color is relatively pale and bright in *Macaca sinica* and *M. radiata diluta* (yellowish brown to golden brown), darker in *M. assamensis* (golden brown to dark brown), and darkest in *M. thibetana* (dark brown to blackish). The grayish brown dorsal pelage in *M. r. radiata* is distinctly drabber than in other *sinica*-group species and subspecies; this may be related to the relative dryness of the habitat of *M. r. radiata*. Erythrism occurs sporadically in *M. sinica* and, apparently less commonly, in *M. assamensis*. Albinism has been reported as a rare anomaly in *M. sinica, M. radiata,* and *M. thibetana*. Seasonal molting has been locally documented in late spring, at the beginning of the rainy season, in *M. radiata* and *M. assamensis,* and in late summer, near the end of the rainy season, in *M. thibetana*; seasonal molting has not been reported in *M. sinica*. Interscapular hair length varies from about 50 mm in *M. sinica* to 90 mm in *M. thibetana*.

Crown hairs in *Macaca sinica* are elongated and radiate from a central whorl to form a conspicuous oval cap that extends anteriorly as far as the brow ridges; in *M. s. sinica* the entire cap is golden brown, whereas in *M. s. aurifrons* the anterior part of the cap is clearly defined yellowish. A conspicuous cap also is present in *M. radiata,* but in this species the anterior hairs of the cap are much shorter than

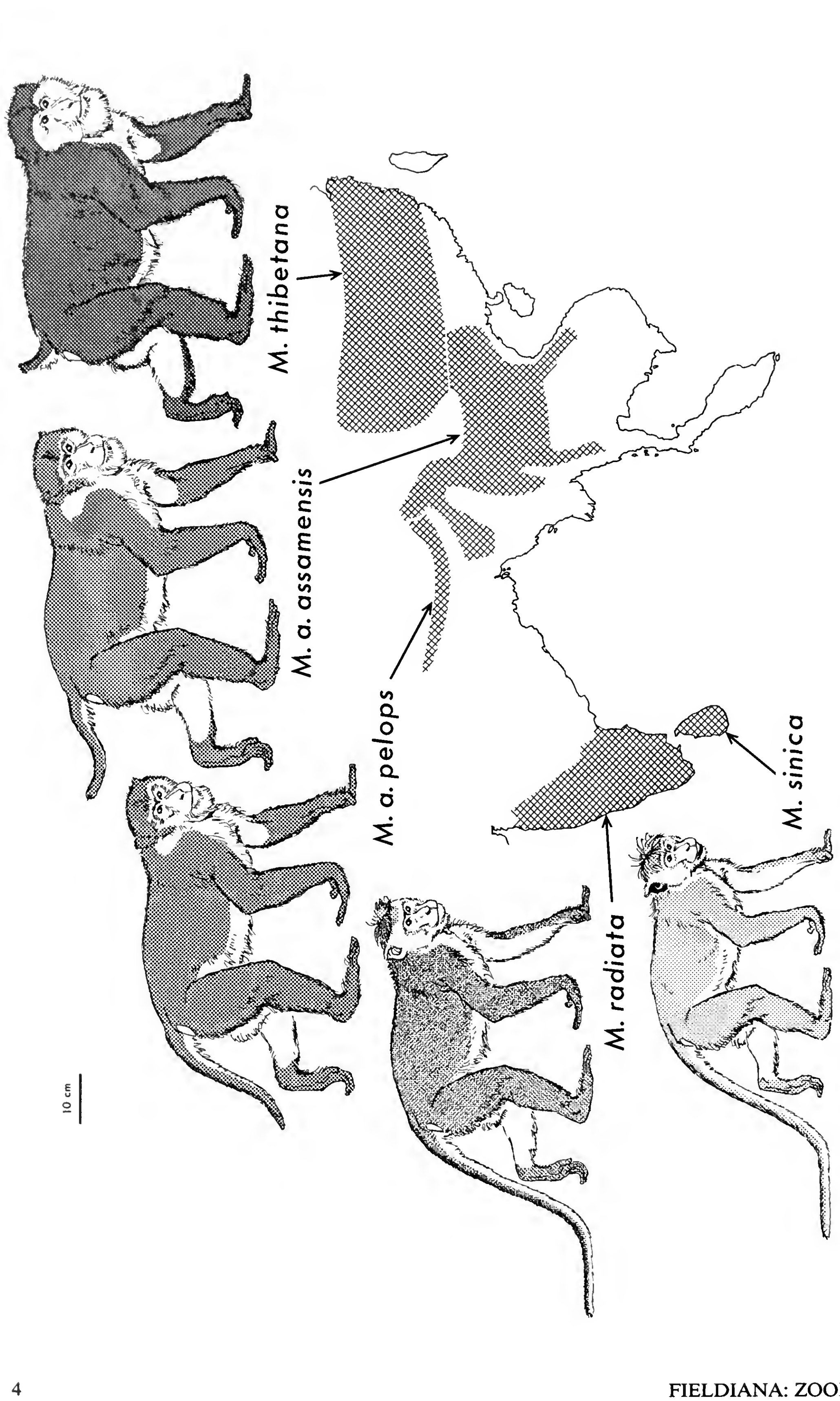

FIG. 2. External characters and distribution of *sinica*-group macaques. (Illustration by Kevin Royt.)

the posterior hairs, so that the cap extends anteriorly only to midway between the vertex and the brow ridges; the exposed frontal area in *M. radiata* is covered with short hairs that diverge laterally to form a median part. Crown hair arrangement in *M. assamensis* is variable; in some specimens there is a rudimentary cap centered at the vertex, in others there is an irregular tuft or cowlick, and in still others a whorl is absent and crown hairs are smoothly directed posteriorly. In *M. thibetana* specimens examined, a rudimentary cap is consistently present. Side-whiskers and beard are relatively inconspicuous in *M. sinica* and *M. radiata*, moderately developed in *M. assamensis*, and prominent in *M. thibetana*.

Facial skin color in *sinica*-group adults is buffy in adult males and variably buffy to pinkish to red in adult females. In *M. sinica*, ears and lips are blackish; in other *sinica*-group species, they are buffy.

External Measurements

Body size is sexually dimorphic in *sinica*-group species (table 1; fig. 3), as in other macaques. Length of head and body in adult males averages 5%–23% greater than in adult females, and weight averages 47%–70% greater. Sexual dimorphism in *Macaca thibetana* and *M. a. assamensis* apparently exceeds that in *M. radiata* and *M. sinica*; this generally accords with previous indications that sexual dimorphism increases with body size (Rensch, 1960, p. 157; Clutton-Brock et al., 1977, p. 798; Albrecht, 1980, p. 148). *Macaca assamensis pelops*, however, is represented by a sample of five exceptionally large adult females and apparently is the least dimorphic taxon in the *sinica* group.

Mean length of head and body and mean body weight of species in the *sinica* group increase with increasing latitude of the ranges of these species (fig. 3; table 1; Fooden, 1971, p. 72). In *Macaca thibetana*, the northernmost species in the group, mean length of head and body in adults is about 30% greater than in *M. sinica*, the southernmost species, and mean weight is more than 200% greater. This relationship between body size and latitude conforms to Bergmann's rule (Mayr, 1963, p. 320) and probably indicates that size in these species is adapted to temperature of habitat. The progressive increase of head and body length of *sinica*-group species is gradual, with measurements broadly overlapping in neighboring species.

Within *sinica*-group species, the relationship between latitude and head and body length may be analyzed by least squares linear regression (Albrecht, 1980, p. 144). Available data are adequate to establish that regression of head and body length on latitude is statistically significant for male specimens of *Macaca a. assamensis* and for female specimens of *M. radiata* (table 2). This intrataxon trend is particularly evident in *M. a. assamensis* males, known from a sample of 24 adults that span 15 degrees of latitude. Head and body length in *M. a. assamensis* males collected in the northern part of the subspecific range apparently exceeds that in males of *M. a. pelops* and *M. thibetana* collected at the same latitude.

Mean tail length of species in the *sinica* group generally decreases with increase in latitude of the specific range (figs. 4–5; table 1), in broad agreement with Allen's rule (Mayr, 1963, p. 323). The pattern of tail length decrease, however, is not symmetrical with the pattern of head and body length increase. Mean tail length is approximately equal in *Macaca sinica* and *M. radiata*, despite the difference in latitude of their ranges. Mean tail length then decreases successively in *M. a. pelops*, *M. a. assamensis*, and *M. thibetana*, with little or no overlap of this measurement in neighboring species or subspecies. Within species or subspecies, there is no significant tendency for tail length to decrease with latitude (table 2; the only significant regression is in *M. radiata* males, where the slope is positive). Relative tail length in immatures in *sinica*-group species apparently is approximately the same as in adults (fig. 5). Although tail reduction is sometimes associated with increased terrestriality, this does not apply to *M. assamensis*, which apparently is at least as arboreal as *M. radiata* (Fooden, 1986, p. 3).

In *Macaca sinica*, *M. radiata*, and *M. assamensis*, mean ear length, like mean tail length, tends to decrease with increase in latitude of specific ranges (table 1). *Macaca thibetana*, however, has ears that are relatively large and thus departs from the general pattern of the other three species.

Cranial Characters

Species in the *sinica* group differ markedly in skull size (figs. 6–7; table 3). In available samples of adults, mean skull length varies from 97.1 mm in female *Macaca sinica* to 130.2 mm in female *M. thibetana* and from 113.0 mm in male *M. sinica* to 156.2 mm in male *M. thibetana*. Sexual dimorphism of skull length in *sinica*-group species

TABLE 1. External measurements and proportions in *sinica*-group macaques.

Species or subspecies	HB (mm)	Tail: Length (mm)	Tail: T/HB	Ear: Length (mm)	Ear: (E/HB) × 100	Weight (kg)
			ADULT MALES			
M. sinica[1]	468 ± 30 (21) 418–528	564 ± 42 (22) 495–650	1.21 ± .11 (21) 1.00–1.39	43 ± 5 (15) 37–52	9.1 ± 1.2 (15) 7.1–11.8	4.70 ± .66 (12)[2] 3.97–6.12
M. radiata[1]	527 ± 38 (12) 450–590	562 ± 61 (12)[3] 475–675	1.07 ± .09 (12) 0.94–1.26	41 ± 3 (12) 35–48	7.7 ± .5 (12) 6.9–8.9	6.67 ± .85 (13) 5.44–8.85
M. a. pelops[1]	581 ± 30 (8) 550–635	324 ± 24 (8) 283–360	0.56 ± .05 (8) 0.50–0.63	40 ± 1 (8) 38–42	6.8 ± .4 (8) 6.0–7.3	11.5 ± 1.0 (5) 10.4–12.7
M. a. assamensis[4]	616 ± 48 (24) 532–730	212 ± 18 (22) 190–250	0.35 ± .04 (21) 0.29–0.44	37 ± 4 (20) 30–41	6.0 ± .8 (20) 4.6–7.5	11.3 ± 2.5 (16) 7.9–16.5
M. thibetana[5]	620 ± 35 (6) 580–660	71 ± 11 (5) 55–80	0.12 ± .02 (4) 0.09–0.14	46 ± 3 (4) 44–50	7.4 ± .3 (4) 6.9–7.6	15.0 ± 1.3 (6) 14.0–17.5
			ADULT FEMALES			
M. sinica[1]	413 ± 20 (12) 400–447	521 ± 40 (13) 448–559	1.28 ± .12 (12) 1.02–1.44	35 ± 2 (9) 31.5–38	8.4 ± .7 (9) 7.6–9.8	3.17 ± .71 (5)[2] 2.49–4.30
M. radiata[1]	455 ± 32 (11) 400–515	503 ± 69 (10)[3] 350–571	1.10 ± .13 (10) 0.88–1.36	37 ± 3 (10) 35–45	8.3 ± .9 (11) 7.4–10.7	3.85 ± .50 (14) 2.93–4.99
M. a. pelops[1]	552 ± 26 (5) 530–587	266 ± 25 (5) 236–293	0.48 ± .05 (5) 0.44–0.55	34 ± 3 (5) 29.2–36	6.1 ± .6 (5) 5.0–6.7	7.8 ± .8 (3) 7.0–8.6
M. a. assamensis[6]	501 ± 30 (17) 437–555	196 ± 17 (17) 170–225	0.40 ± .05 (16) 0.31–0.47	34 ± 5 (14) 25–45	6.7 ± 1.1 (13) 4.5–8.4	6.7 ± 1.1 (12) 4.86–8.75
M. thibetana[7]	523 ± 28 (5) 490–555	68 ± 10 (5) 56–80	0.13 ± .02 (4) 0.11–0.15	39 ± 4 (3) 35–42	7.7 ± .5 (3) 7.1–8.3	10.1 ± .9 (2) 9.5–10.75

HB = Head and body length; T/HB = relative tail length; E/HB = relative ear length. Mean, standard deviation, and sample size (in parentheses) reported in first line of each entry; extremes, in second line.

[1] References: Fooden, 1979, p. 111; 1981, p. 3; 1982, p. 10. [2] Cf. Dittus (1975, p. 143), who reports mean weight in 40 adult *M. sinica* specimens at one locality: males, 5.72 kg (N = 16); females, 3.59 kg (N = 24). [3] Cf. Hartman (1938, p. 468), who reports tail length (mm) in 14 adult *M. radiata* specimens of unknown origin: males, 587 ± 43 (6), 534–660; females, 557 ± 49 (8), 482–634.

[4] References: Dào, 1978, p. 378; Fooden, 1982, p. 10 (excluding one questionable value, HB/T = 0.26); IZCAS, 3 specimens; KIZ, 7 specimens. [5] References: AMNH, 1 specimen; FMNH, 1 specimen (excluding questionable measurement, HB = 710 mm); IZCAS, 3 specimens (excluding two questionable tail length measurements); KIZ, 1 specimen; SCIEA, 1 specimen; Hu et al., 1982, p. 201, 2 specimens, weight only. Cf. Fooden et al., 1985, p. 18, Table 2 (now revised).

[6] References: Dào, 1967, p. 117; Fooden, 1982, p. 10 (corrections to original table: Loc. No. 45, delete footnote; E/HB, mean ± SD = 7.1 ± .4; weight (kg), mean ± SD = 6.1 ± .9); BJMNH, 1 specimen; IZCAS, 3 specimens; KIZ, 5 specimens. [7] References: Fooden et al., 1985, p. 18 (excluding two questionable values, HB = 630 mm and T/HB = 7.2%); ZMNH, 1 specimen.

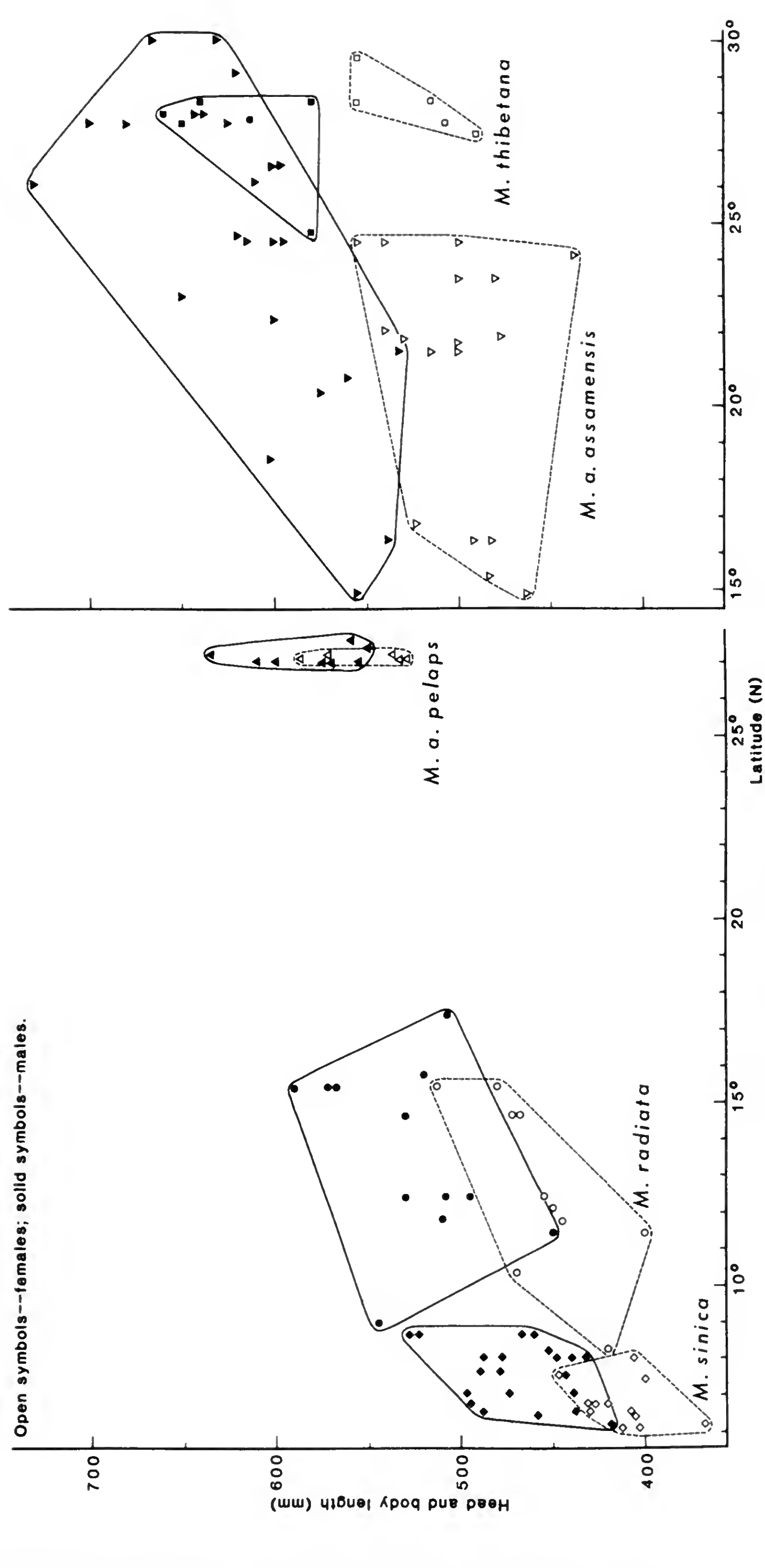

FIG. 3. Latitudinal variation of head and body length in adult *sinica*-group macaques (cf. table 2).

TABLE 2. Regression statistics for latitudinal variation of external measurements in *sinica*-group macaques (cf. figs. 3–4).

Species or subspecies	Sex	No. of specimens	No. of localities	*Y*-intercept	Slope	SE slope	*P* slope
				HEAD AND BODY LENGTH			
M. sinica	♂	21	10	379.6	11.69	7.85	.10–.25
	♀	12	9	343.4	10.29	11.46	.25–.50
M. radiata	♂	12	9	451.8	5.52	5.51	.25–.50
	♀	11	8	334.0	9.75	3.50	.025–.05*
M. a. pelops	♂	8	5	1,609.4	−37.83	59.85	.50–.75
	♀	5	2	−559.5	40.91	...	...
M. a. assamensis	♂	24	18	426.9	7.70	2.03	.001–.005**
	♀	17	12	448.7	2.51	2.46	.25–.50
M. thibetana	♂	6	5	275.0	12.56	10.10	.25–.50
	♀	5	5	−307.1	29.29	14.97	.10–.25
				TAIL LENGTH			
M. sinica	♂	22	11	676.4	−14.92	11.51	.10–.25
	♀	13	9	504.3	2.40	24.32	> .75
M. radiata	♂	12	9	348.5	15.61	6.36	.025–.05*
	♀	10	8	491.5	0.87	11.82	> .75
M. a. pelops	♂	8	6	−1,123.8	53.26	43.37	.25–.50
	♀	5	2	−2,162.7	89.39	...	...
M. a. assamensis	♂	22	16	228.2	−0.66	1.07	.50–.75
	♀	17	13	236.2	−1.88	1.24	.10–.25
M. thibetana	♂	5	5	164.7	−3.41	3.30	.25–.50
	♀	5	5	55.4	0.45	7.31	> .75

* = .05 > *P* > .01. ** = .01 > *P* > .001.

apparently is greater than sexual dimorphism of head and body length (cf. figs. 3, 7). The progressive increase of mean skull length in *sinica*-group species, like the corresponding increase of mean head and body length, is correlated with increasing latitude of the specific ranges. Unlike head and body length variation, however, skull length variation is not continuous between all four species. Skull length variation in both sexes of the two smaller species (*M. sinica, M. radiata*) is discontinuous from that in the two larger species (*M. assamensis, M. thibetana*); even at the same latitude, the largest *M. radiata* skull in each sex is smaller than the smallest *M. assamensis* skull. Skull length tends to increase with latitude within species as well as between species; within species or subspecies, regression of skull length on latitude is statistically significant in males of *M. radiata, M. a. assamensis,* and *M. thibetana* and in females of *M. a. assamensis* (table 4). Relative to head and body length, skull length in *M. thibetana* is exceptionally large (cf. figs. 3, 7).

Although species in the *sinica* group differ in skull size, they are remarkably similar in general proportions (fig. 6; table 3; Albrecht, 1978, p. 76). Relative zygomatic breadth averages approximately 0.67 in both sexes of all four species. Rostral/postrostral ratio, a measure of the ratio of facial length to cranial length, increases only slightly with increasing skull size, from 0.47 in female *M. sinica* to 0.51 in female *M. thibetana* and from 0.55 in male *M. sinica* to 0.59 in male *M. thibetana.* The two smaller species (*M. sinica, M. radiata*) tend to differ from the two larger species (*M. assamensis, M. thibetana*) in morphology of the temporal lines and sagittal crest in adult males; in the smaller species the temporal lines usually are separate, whereas in the larger species the temporal lines often converge to produce a prominent sagittal crest in adult males (cf. Pocock, 1939, pp. 35, 40, 53; Kurup, 1966, p. 74). Width of the rostrum tends to be relatively smaller in *M. sinica* and *M. radiata* than in *M. assamensis* and *M. thibetana* (fig. 6). No known cranial character uniquely distinguishes *sinica*-group species from those in other species groups.

Ontogenetic allometry of rostral length relative to postrostral length apparently differs among species in the *sinica* group (fig. 8; table 5). In a composite log-log plot of rostral length against postrostral length, data points for immature and mature specimens are approximately collinear

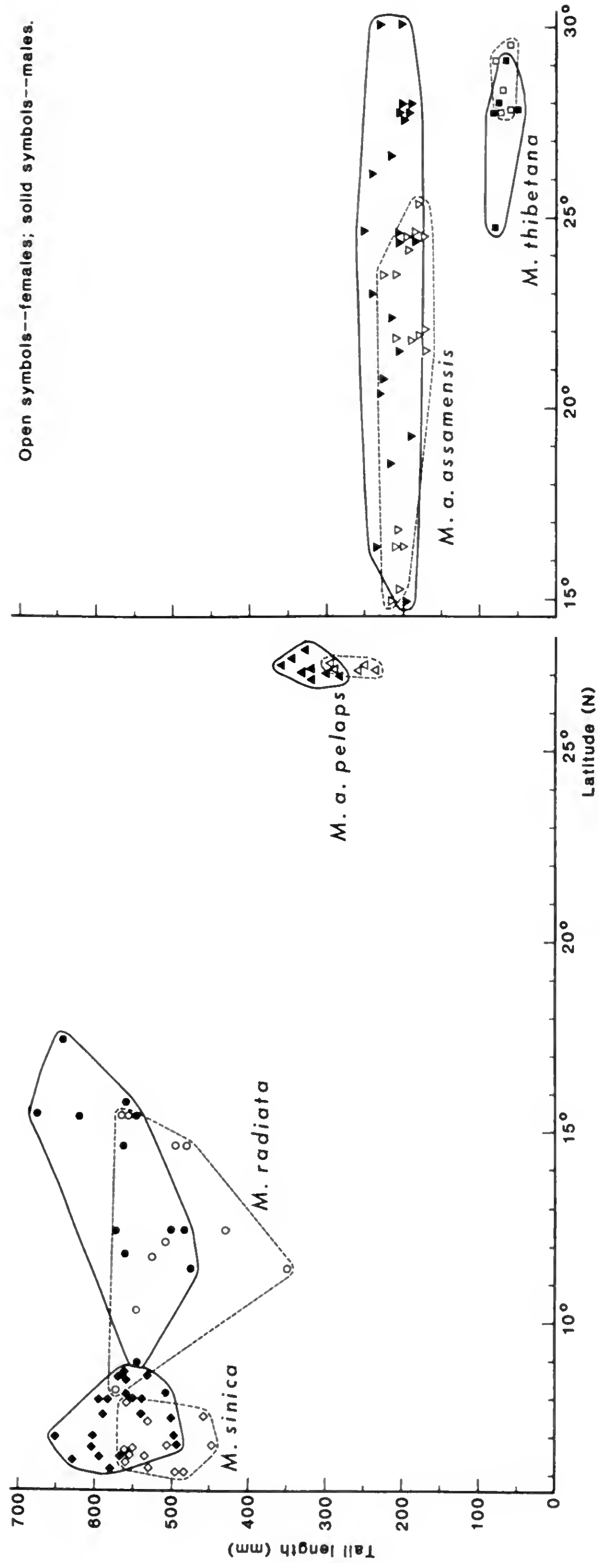

FIG. 4. Latitudinal variation of tail length in adult *sinica*-group macaques (cf. table 2).

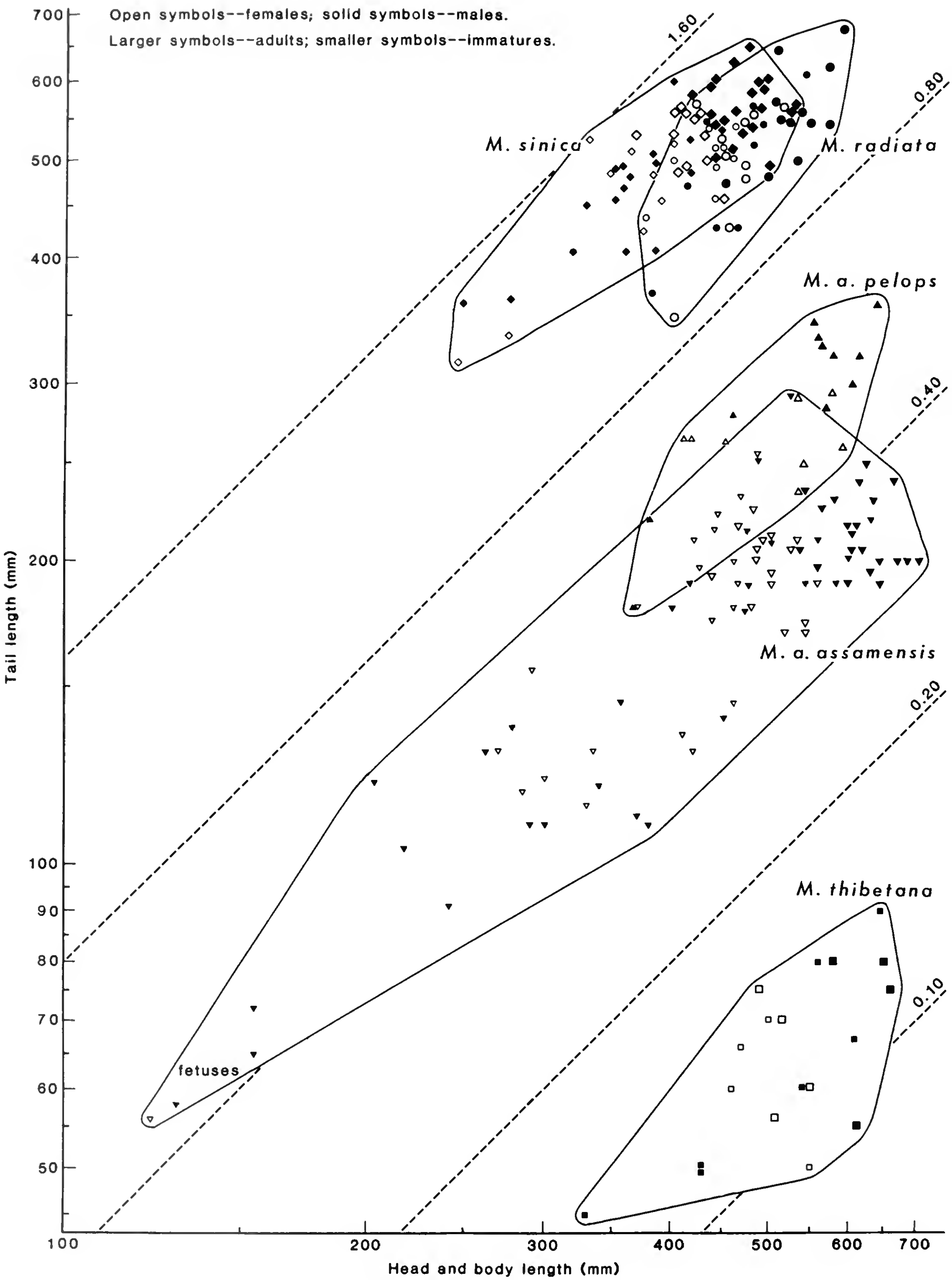

FIG. 5. Tail length vs. head and body length in immature and adult *sinica*-group macaques.

TABLE 3. Cranial measurements and proportions in *sinica*-group macaques.

Species or subspecies	GL (mm)	ZB/GL	Postrostral length (mm)	RL/PL
		ADULT MALES		
M. sinica[1]	113.0 ± 4.2 (21) 106.7–119.8	.69 ± .02 (20) .65–.71	77.8 ± 3.0 (21) 72.7–83.1	.55 ± .03 (21) .50–.60
M. radiata[1]	120.0 ± 4.0 (12) 114.6–127.9	.67 ± .02 (12) .65–.71	83.1 ± 2.6 (12) 80.2–86.5	.54 ± .02 (12) .51–.57
M. a. pelops[1]	142.1 ± 6.5 (11) 131.9–154.1	.66 ± .03 (11) .63–.70	97.3 ± 3.6 (10) 89.9–101.1	.57 ± .03 (10) .51–.62
M. a. assamensis[2]	146.9 ± 5.8 (28) 138.1–160.3	.66 ± .03 (28) .62–.70	99.4 ± 4.0 (26) 93.9–107.8	.58 ± .04 (25) .50–.65
M. thibetana[3]	156.2 ± 6.1 (18) 146.1–167.5	.67 ± .02 (18) .62–.71	105.7 ± 3.2 (15) 102.0–112.1	.59 ± .02 (15) .53–.62
		ADULT FEMALES		
M. sinica[1]	97.1 ± 3.6 (15) 93.0–104.9	.66 ± .02 (13) .63–.69	71.3 ± 2.2 (15) 68.6–75.9	.47 ± .03 (15) .43–.53
M. radiata[1]	104.4 ± 2.4 (10) 99.0–107.7	.65 ± .03 (10) .60–.69	76.9 ± 2.0 (10) 73.4–78.6	.46 ± .02 (10) .43–.50
M. a. pelops[4]	121.6 ± 5.5 (8) 116.0–131.5	.67 ± .03 (8) .63–.71	88.8 ± 2.9 (7) 85.5–93.6	.49 ± .04 (7) .45–.58
M. a. assamensis[5]	121.2 ± 6.2 (23) 113.1–138.5	.66 ± .02 (23) .63–.71	88.1 ± 4.3 (21) 81.0–97.9	.49 ± .03 (21) .41–.55
M. thibetana[6]	130.2 ± 5.3 (10) 120.7–140.0	.67 ± .01 (10) .65–.68	93.8 ± 2.6 (8) 91.0–97.3	.51 ± .02 (8) .46–.53

GL = Greatest length of skull, excluding incisors; ZB/GL = relative zygomatic breadth; RL/PL = rostral/postrostral ratio. Mean, standard deviation, and sample size (in parentheses) reported in first line of each entry; extremes, in second line. For explanation of measurements, see Fooden, 1969, p. 41.

[1] References: Fooden, 1979, p. 114; 1981, p. 14; 1982, p. 14. [2] References: Fooden, 1982, p. 14 (excluding GL = 129.6, subadult); IZCAS, 6 specimens; KIZ, 5 specimens; NWPIB, 2 specimens. [3] References: Fooden et al., 1985, p. 19 (excluding 1 AMNH specimen of unknown origin); IZCAS, 2 newly acquired specimens; SCIEA, 3 specimens.

[4] References: Fooden, 1982, p. 14; FMNH 94089, Jiri, Nepal. [5] References: Fooden, 1982, p. 14; IZCAS, 2 specimens; KIZ, 8 specimens. [6] References: Fooden et al., 1985, p. 19; SCIEA, 1 specimen; ZMNH, 1 specimen.

within each species, but data points for larger species generally are shifted to the right of those for smaller species. Evolutionary changes of size in *sinica*-group species evidently have been accompanied by compensating transformations of the allometric growth curves, with the result that these species differ only slightly in rostral/postrostral ratios of adults. In this respect, *sinica*-group

TABLE 4. Regression statistics for latitudinal variation of greatest length of skull in *sinica*-group species or subspecies (cf. fig. 7).

Species or subspecies	Sex	No. of specimens	No. of localities	*Y*-intercept	Slope	SE slope	*P* slope
M. sinica	♂	21	12	104.8	1.11	1.40	.25–.50
	♀	15	12	84.2	1.77	0.80	.05–.10
M. radiata	♂	12	9	104.3	1.12	0.41	.025–.05*
	♀	10	8	108.8	−0.37	0.31	.25–.50
M. a. pelops	♂	11	8	100.8	1.54	1.65	.25–.50
	♀	8	5	495.3	−13.72	7.22	.10–.25
M. a. assamensis	♂	28	21	129.1	0.73	0.23	.005–.01**
	♀	23	17	103.7	0.81	0.36	.025–.05*
M. thibetana	♂	18	15	115.0	1.49	0.58	.01–.025*
	♀	10	10	82.8	1.68	1.02	.10–.25

* = $.05 > P > .01$. ** = $.01 > P > .001$.

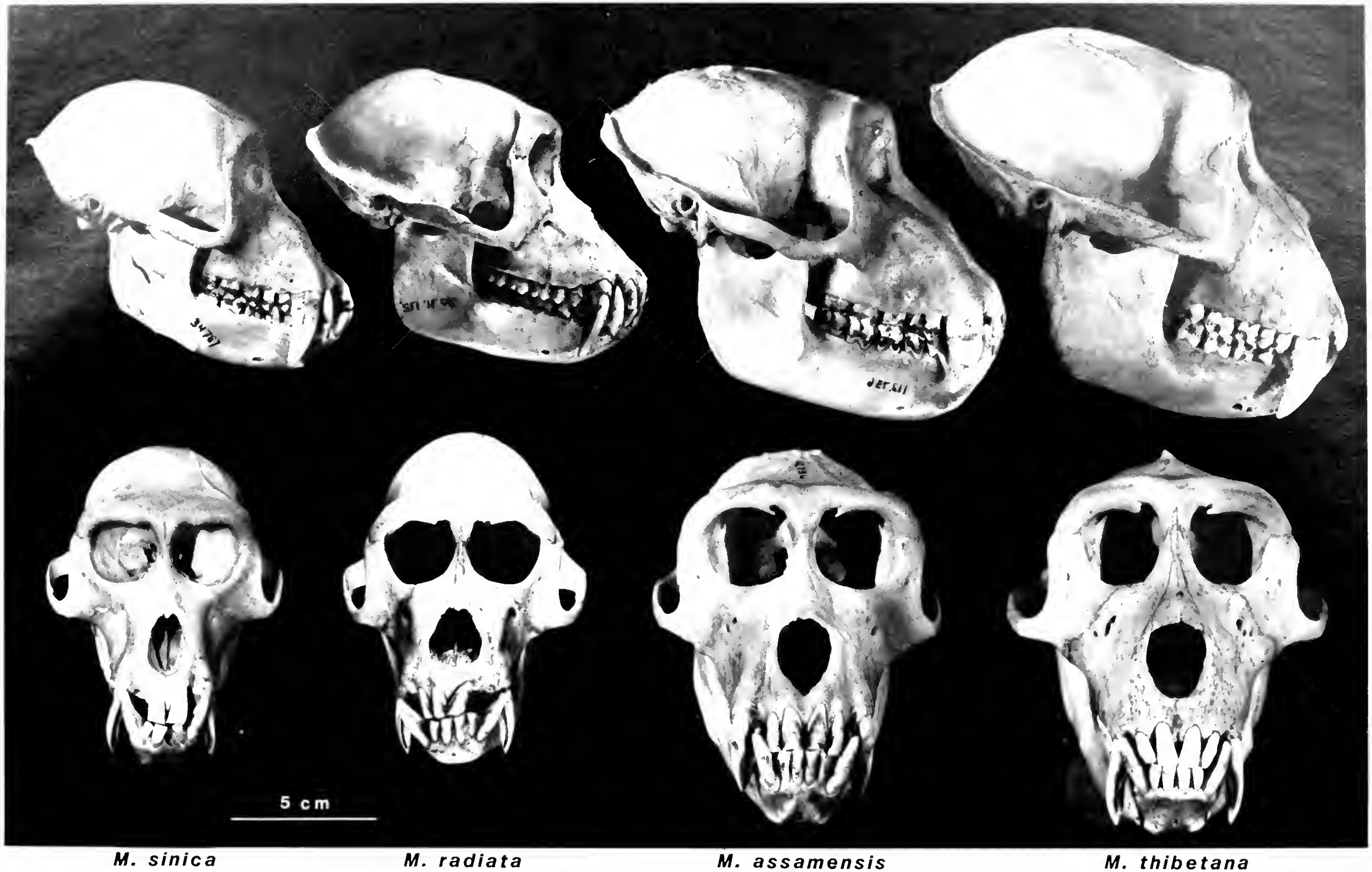

FIG. 6. Skulls of *sinica*-group macaques, adult males: *M. sinica*—MCZ 34787, Kalawewa, North Central Province, Sri Lanka; *M. radiata*—BM 30.11.1.15, Dharwar, Karnataka State, India; *M. assamensis*—AMNH 112736, Jantang-Dagung Hka, Sagaing Division, Burma (side view photographically reversed); *M. thibetana*—FMNH 39499, Hsiao Yang Chi, Sichuan Province, China. (Photos by Ron Testa, Division of Photography, Field Museum of Natural History).

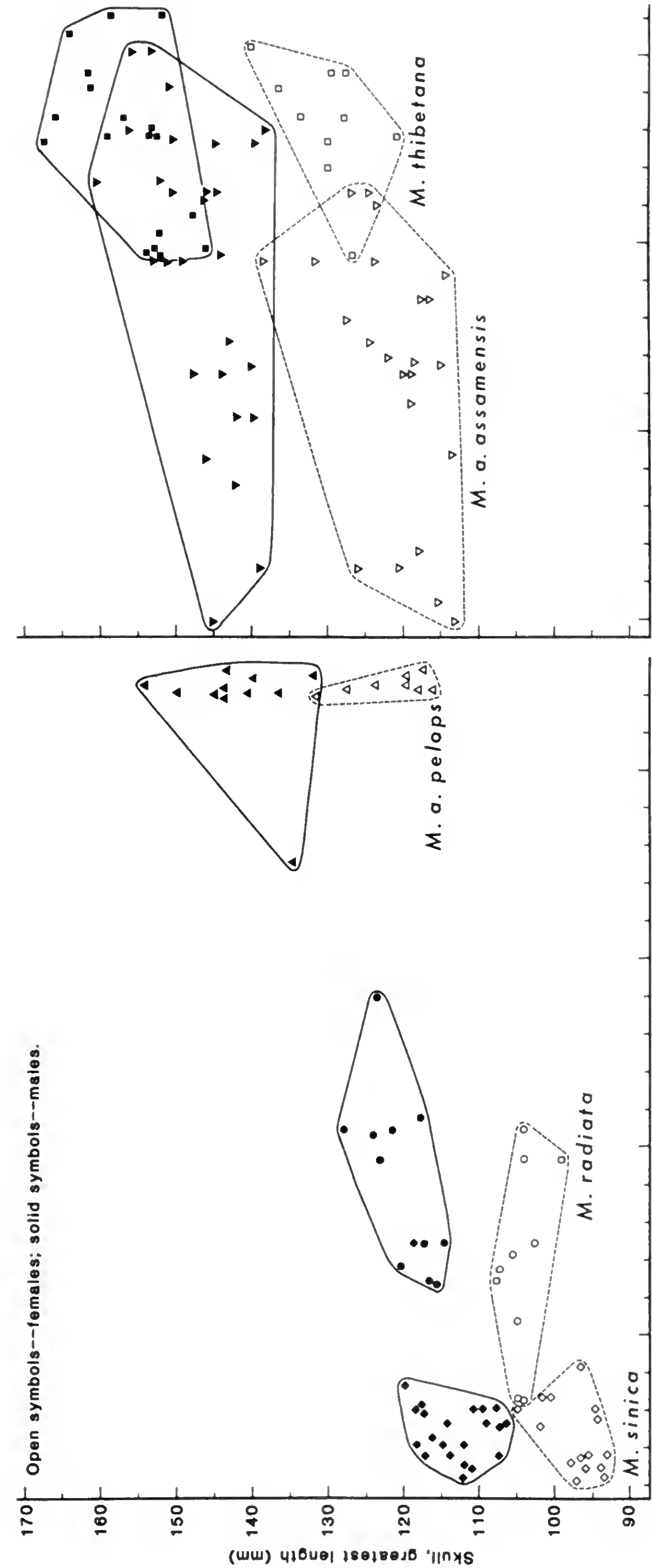

FIG. 7. Latitudinal variation of greatest skull length in adult *sinica*-group macaques (cf. table 4).

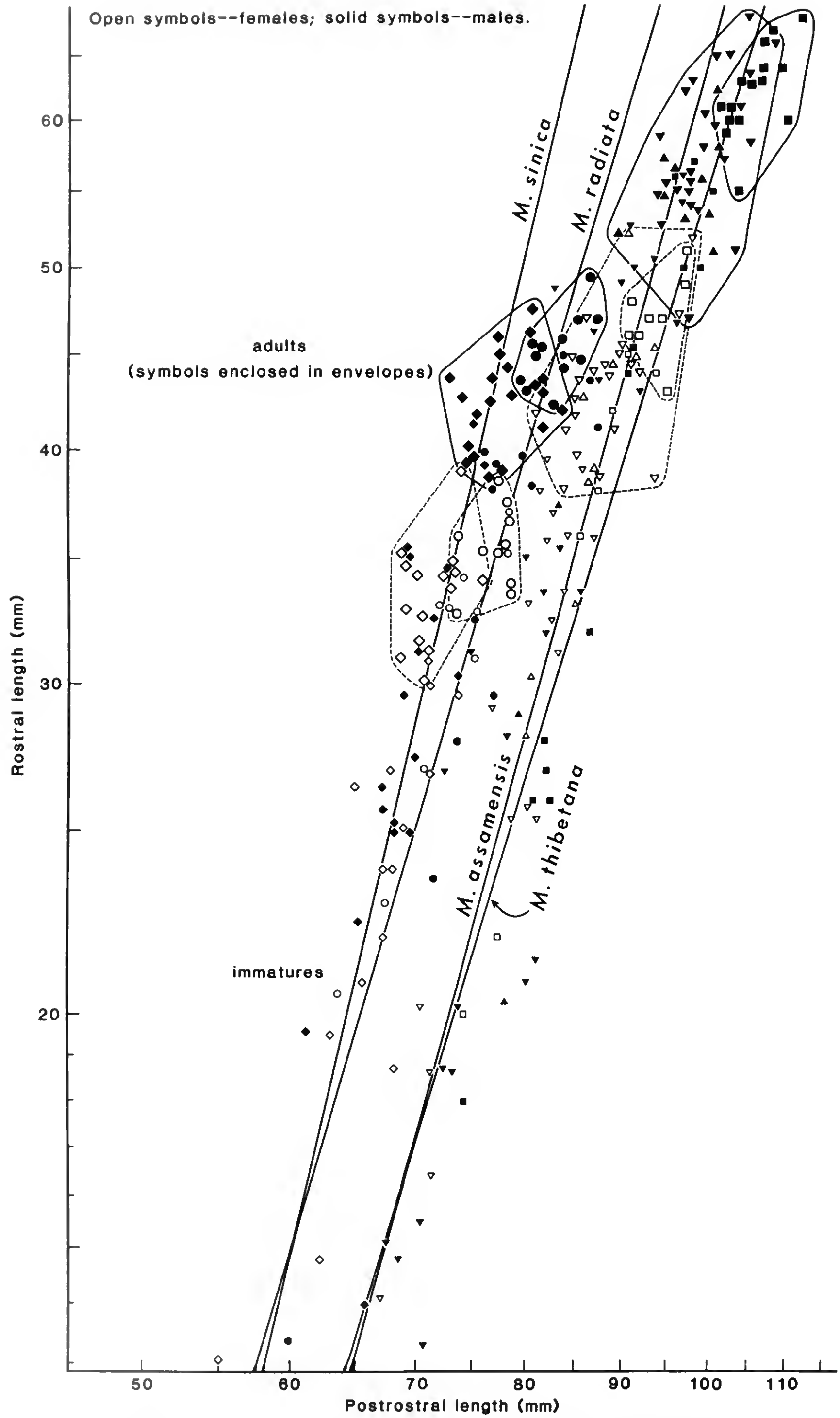

FIG. 8. Ontogenetic allometry of rostral length (y) vs. postrostral length (x) in *sinica*-group macaques. Principal axis equations: *M. sinica*, log y = 4.317 log x − 6.507; *M. radiata*, log y = 3.395 log x − 4.860; *M. assamensis*, log y = 3.711 log x − 5.610; *M. thibetana*, log y = 3.297 log x − 4.851 (table 5).

TABLE 5. Ontogenetic and interspecific allometry of rostral length (y) relative to postrostral length (x) in *sinica*-group macaques (cf. fig. 8).

Species/sex	N	Line-fitting technique	Slope	95% confidence limits	*Y*-intercept	*r*
			ONTOGENETIC ALLOMETRY			
M. sinica[1]	69[2]	ma	4.317	3.830–4.937	−6.507	0.882
		rma	3.861	3.417–4.305	−5.661	...
		lsr	3.405	2.961–3.849	−4.816	...
M. radiata[1]	45[2]	ma	3.395	3.019–3.865	−4.860	0.925
		rma	3.181	2.809–3.553	−4.456	...
		lsr	2.942	2.570–3.314	−4.005	...
M. assamensis[3]	117[2]	ma	3.711	3.457–4.003	−5.610	0.928
		rma	3.482	3.243–3.721	−5.165	...
		lsr	3.232	2.993–3.471	−4.679	...
M. thibetana[4]	43[2]	ma	3.297	3.040–3.598	−4.851	0.964
		rma	3.200	2.950–3.450	−4.659	...
		lsr	3.086	2.819–3.353	−4.434	...
			INTERSPECIFIC ALLOMETRY			
Adult males	4[5]	ma	1.291	1.182–1.412	−0.816	0.998
		rma	1.290	1.040–1.540	−0.815	...
		lsr	1.287	1.037–1.537	−0.809	...
Adult females	4[5]	ma	1.312	1.119–1.549	−0.914	0.993
		rma	1.309	0.847–1.771	−0.909	...
		lsr	1.301	0.839–1.763	−0.893	...

ma = Major axis; rma = reduced major axis; lsr = least squares regression. For discussion of these techniques, see Sokal and Rohlf (1981, p. 549) and Steudel (1985, p. 462).

[1] References: Fooden, 1979, p. 115; 1981, p. 11. [2] Both sexes, all ages. [3] Cf. Fooden, 1982, p. 16, N = 74. [4] Cf. Fooden, 1983, p. 11, N = 20.

[5] Bivariate means for each species; see table 3.

species contrast with *silenus*-group species *Macaca silenus* and *M. nemestrina,* which apparently follow a common allometric growth curve and, as adults, exhibit conspicuous size-related differentiation of rostral/postrostral ratio (Fooden, 1975, p. 12). In *M. silenus* and *M. nemestrina,* interspecific allometry of adults is an extension of intraspecific growth allometry; in *sinica*-group species, interspecific allometry follows a trajectory different from that of intraspecific allometry. Macaque species groups evidently are not isomorphic in their patterns of rostral-postrostral evolution.

Caudal Vertebrae

Interspecific variation of caudal (Cd) vertebral morphology is of particular interest in macaques because tail reduction is a conspicuous evolutionary trend in this genus. Sets of caudal vertebrae of *sinica*-group species are available for long-tailed *Macaca sinica* and *M. radiata,* for short-tailed *M. a. assamensis,* and for stump-tailed *M. thibetana* (table 6). No caudal vertebral specimens are available for *M. a. pelops,* in which tail length is intermediate between that in *M. radiata* and *M. a. assamensis.*

In *Macaca sinica* and *M. radiata,* tail length is approximately equal (table 1); the number of caudal vertebrae is similar, averaging about 25 or 26 in both species; and lengths of corresponding caudal vertebrae also are similar (table 6; Schultz & Straus, 1945, p. 623). In adult males of both species, caudal vertebral length increases rapidly from about 12 mm in Cd1 to about 30 mm in Cd5, reaches a peak of about 36 mm in Cd6–9, and then decreases somewhat more gradually to about 5 mm in the terminal vertebra (fig. 9). In six adult males, Cd7 is the longest caudal vertebra in three specimens, Cd8 in two specimens, and Cd9 in one specimen. Neural arches are present in Cd1–5, which thus constitute the proximal caudal region as defined by Ankel (1972, p. 232); all other caudal vertebrae lack neural arches and constitute the distal caudal region. Vertebral length reaches its maximum in the first section of the distal caudal region in *M. sinica* and *M. radiata,* as in most long-tailed mammals (Lessertisseur & Saban, 1967, p. 632). In adult females and in immatures of both sexes, the number of caudal vertebrae and the vertebral

TABLE 6. Length (mm) of centrum of caudal vertebrae in *sinica*-group macaques; italicized figure indicates longest vertebra in series (cf. fig. 9).

Specimen no.	Vertebra no.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
***M. sinica*, adult males**														
FMNH 95021	11.2	12.9	17.9	25.1	31.1	35.5	36.3	*36.4*	35.6	34.9	33.6	31.5	29.1	27.1
FMNH 98261	10.3	12.1	16.9	23.2	28.4[2]	33.3[2]	34.7	*35.3*	34.8	33.6	32.7	31.0	28.7	26.4
Means	10.8	12.5	17.4	24.2	29.8	34.4	35.5	*35.8*	35.2	34.2	33.2	31.2	28.9	26.8
***M. radiata*, adult male**														
FMNH 54041	11.9	14.3	18.8	26.6	32.9	37.1	*37.8*	37.5	37.1	36.3	35.0	33.7	30.9	28.9
***M. sinica* or *M. radiata*, skeletons only, adult males**														
AIUZ 7083	11.4	13.1	17.2	23.2	28.3	32.6	*33.4*	33.2	32.0	31.6	29.8	27.9	25.6	24.2
AIUZ PAL52	13.2	14.0	17.5	22.9	30.3[3]	36.3[3]	*39.5*	39.4	39.3	38.5	37.4	34.9	33.2	30.7
RMNH 12c	14.3	13.4	16.0	21.0	25.9	26.3	33.2	30.9[2]	*36.5*	35.3	34.2	33.1	31.7	27.2
Means	13.0	13.5	16.9	22.4	28.2	31.7	35.4	34.5	*35.9*	35.1	33.8	32.0	30.2	27.4
***M. sinica* or *M. radiata*, skeleton only, adult female**														
AIUZ PAL50	8.5	9.9	16.2	22.3	27.1	31.6	*34.2*	34.1	28.9[2]	33.6	32.3	31.5	29.3	27.1
***M. sinica* or *M. radiata*, skeletons only, immatures[4]**														
AIUZ AS1811	10.0	11.4	14.5	18.4	26.9	30.2	*32.2*	31.8	32.1	31.6	30.5	29.5	28.0	25.7
IRSN 8877	7.0	9.9	11.7	15.3	18.2	23.0	25.4	*26.6*	*26.6*	23.1[2]	23.3	22.0	20.8	19.3
IRSN 9065	11.5	11.3	12.4	20.6	24.1	29.4	29.4	29.5	*29.6*	27.5	26.7	25.8	24.6	22.5
IRSN 9071	8.5	9.2	10.8	16.7	21.8	23.9	*25.4*	25.1	*25.4*	25.0	24.2	22.6	22.6	19.4
***M. a. assamensis*, adult males**														
FMNH 99622	11.5[3]	10.3	10.4	10.8	12.3	15.6	18.9	*20.1*	20.0	19.1	16.8	14.6	12.0	9.8
FMNH 99631	12.1	11.1	10.8	12.4	16.0	20.2	*22.9*	*22.9*	22.6	20.5	18.7	17.3	13.7	11.6
Means	11.8	10.7	10.6	11.6	14.2	17.9	20.9	*21.5*	21.3	19.8	17.8	16.0	12.8	10.7
***M. a. assamensis*, immatures[5]**														
FMNH 99621	8.4	8.2	8.7	9.2	12.1	15.2	*18.5*	17.4	15.6	15.0	14.2	11.0	9.1	7.8
FMNH 99629	4.2	3.8	3.6	3.4	3.9	5.7	*6.1*	5.9	5.0	4.7	4.0	3.3	2.4	1.8
FMNH 99633	10.5	11.0	13.1	15.3	18.4	21.0	*21.7*	20.3	19.2	17.5	15.5	13.3	11.0	8.5
***M. thibetana*, adult males**														
IZCAS 20000	*13.0*	11.1	10.5	m[1]	...	...	...	...	...	...	...	...	...	...
IZCAS 20002	10.5[3]	10.0	10.5	10.4	*11.5*	10.5	10.2	9.2	6.4	5.5	m[1]	...	...	...
SCIEA (1960)	*14.8*[3]	11.0	14.2	11.5	11.9	10.8	10.6	7.0	5.6	5.3	4.1	3.0	...	...
Means	*12.8*	10.7	11.7	11.0	11.7	10.6	10.4	8.1	6.0	5.4	4.1	3.0	...	...
***M. thibetana*, adult female**														
IZCAS 20001	8.6[3]	8.9	9.0	8.6	9.7	*10.0*	*10.0*	8.8	6.7	2.0	...	...	...	...

TABLE 6. *Continued.*

Specimen no.	Vertebra no.												
	15	16	17	18	19	20	21	22	23	24	25	26	27
***M. sinica*, adult males**													
FMNH 95021	24.2	22.8	20.2	17.3	14.3	12.2	10.5	m[1]	...	...	...	...	...
FMNH 98261	24.3	21.9	20.8	18.5	15.7	13.0	11.0	8.7	m[1]	...	...	...	...
Means	24.2	22.4	20.5	17.9	15.0	12.6	10.8	8.7	...	...	...	...	...
***M. radiata*, adult male**													
FMNH 54041	26.8	24.0	22.2	19.2	17.0	14.1	12.2	9.6	m[1]	...	...	...	...
***M. sinica* or *M. radiata*, skeletons only, adult males**													
AIUZ 7083	22.0	19.8	18.3	17.0	14.8	12.7	10.6	8.9	7.2	3.8	...	...	...
AIUZ PAL52	26.0[3]	25.0[3]	24.1	m[1]	...	...	...	...	...	...	...	...	...
RMNH 12c	25.6	24.8	20.5	19.2	16.5	16.3	12.6	10.8	10.1	8.3	7.3	4.9	m[1]
Means	24.5	23.2	21.0	18.1	15.6	14.5	11.6	9.8	8.6	6.0	7.3	4.9	...
***M. sinica* or *M. radiata*, skeleton only, adult female**													
AIUZ PAL50	25.6	24.0	22.1	19.8	18.1	m[1]	...	...	...	...	...	...	...
***M. sinica* or *M. radiata*, skeletons only, immatures[4]**													
AIUZ AS1811	23.6	22.1	20.2	18.6	15.8	m[1]	...	...	...	...	...	...	...
IRSN 8877	13.7[2]	14.7	13.5	10.8	9.7	8.4	6.5	5.5	4.2	...	...	...	...
IRSN 9065	20.3	18.9	16.9	15.0	m[1]	...	...	...	...	...	...	...	...
IRSN 9071	18.6	17.9	15.2	14.8	13.0	9.6[2]	9.6	8.0	m[1]	...	...	...	...
***M. a. assamensis*, adult males**													
FMNH 99622	7.3	5.0	3.6	2.3	1.8	...	...	...	...	...	...	...	...
FMNH 99631	7.2	5.7	3.5	2.5	2.0	...	...	...	...	...	...	...	...
Means	7.2	5.4	3.6	2.4	1.9	...	...	...	...	...	...	...	...
***M. a. assamensis*, immatures[5]**													
FMNH 99621	6.1	4.1	2.1	1.4	...	...	...	...	...	...	...	...	...
FMNH 99629	0.5	...	...	...	...	...	...	...	...	...	...	...	...
FMNH 99633	5.3	2.7	m[1]	...	...	...	...	...	...	...	...	...	...
***M. thibetana*, adult males**													
IZCAS 20000	...	...	...	...	...	...	...	...	...	...	...	...	...
IZCAS 20002	...	...	...	...	...	...	...	...	...	...	...	...	...
SCIEA (1960)	...	...	...	...	...	...	...	...	...	...	...	...	...
Means	...	...	...	...	...	...	...	...	...	...	...	...	...
***M. thibetana*, adult female**													
IZCAS 20001	...	...	...	...	...	...	...	...	...	...	...	...	...

[1] Terminal vertebrae missing. [2] Vertebra deformed. [3] Vertebra fused to adjacent vertebra; for Cd1, the fusion is to S1.

[4] AIUZ AS1811, juvenile female; IRSN 8877, subadult male; IRSN 9065 and IRSN 9071, juvenile males. [5] FMNH 99621, juvenile female; FMNH 99629, fetal male, sitting height 170 mm, estimated conception age 4.5 months (Fooden, 1982, p. 20), measurements taken on radiograph of fetus (radiograph courtesy Dr. K. Doi, University of Chicago Medical Center); FMNH 99633, subadult female.

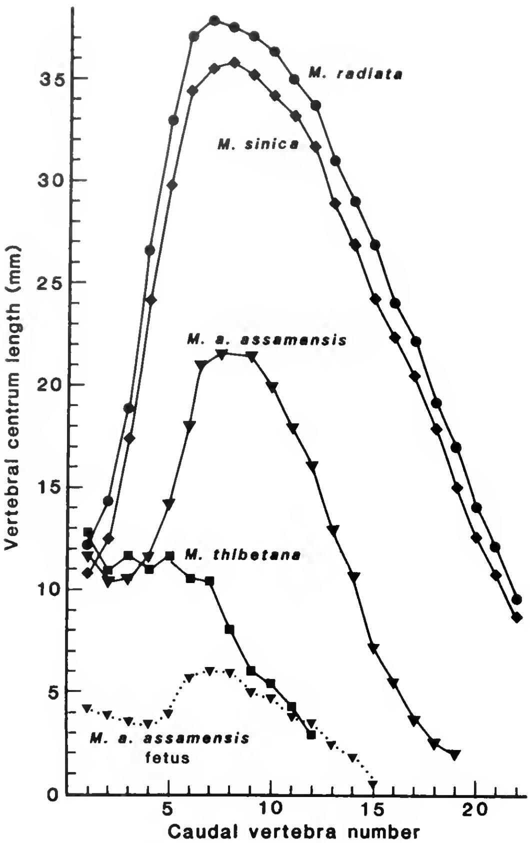

FIG. 9. Mean length of vertebral centrum in successive caudal vertebrae of *sinica*-group macaques: adult male *M. sinica, M. radiata, M. a. assamensis,* and *M. thibetana*; fetal male *M. a. assamensis* (table 6).

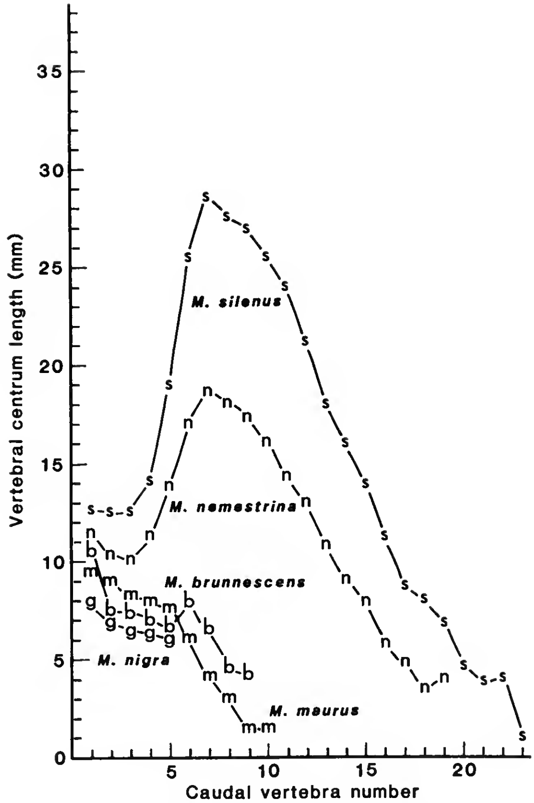

FIG. 10. Mean length of vertebral centrum in successive caudal vertebrae of adult male *silenus*-group macaques (Fooden, 1969, p. 18; 1975, p. 20).

length gradient apparently are similar to those in adult males.

In *Macaca a. assamensis,* caudal vertebrae are reduced both in number and length relative to those in *M. sinica* and *M. radiata*; the morphology of corresponding vertebrae is generally similar, however, in all three species. The number of caudal vertebrae in five specimens of *M. a. assamensis* is 17–19 (table 6; Schultz, 1938, p. 6). In adult males, vertebral length decreases slightly from about 12 mm in Cd1 to about 10 mm in Cd2 and Cd3, increases rapidly to about 18 mm in Cd6, reaches a peak of about 21 mm in Cd7–9, and decreases somewhat more gradually to about 2 mm in the terminal vertebra. In a near-term fetus of *M. a. assamensis,* the vertebral length gradient characteristic of this subspecies is already apparent (fig. 9).

In *Macaca thibetana,* the number of caudal vertebrae is reduced to 10–12 (table 6). Vertebral length in adult males decreases irregularly from about 13 mm in Cd1 to about 10 mm in Cd7 and then decreases more abruptly to about 3 mm in the terminal vertebra.

The caudal vertebral length gradient in *Macaca sinica* and *M. radiata* probably is primitive in this species group. In *M. a. assamensis,* peak vertebral length in the first section of the distal caudal region is reduced by about one-third; in *M. a. pelops,* the reduction in this region presumably is somewhat less. Although the length of Cd1 is approximately the same in *M. a. assamensis* as in *M. sinica* and *M. radiata,* the length of Cd2 and Cd3 in *M. a. assamensis* is reduced. Beginning at Cd4, each caudal vertebra in adult male *M. a. assamensis* averages 10–16 mm shorter than the corresponding vertebra in adult male *M. sinica* and *M. radiata.* In *M. thibetana,* the length of vertebrae in the first section of the distal caudal region is reduced by about one-half, relative to *M. a. assamensis*; this reduction completely eliminates the length peak that characterizes this caudal vertebral section in *M. sinica, M. radiata,* and *M. a. assamensis.* The

FIG. 11. Male external genitalia of *M. a. assamensis* (FMNH 99622, adult; Ban Muang Baw Ngam, Kanchanaburi Province, Thailand).

length of Cd1 in *M. thibetana* remains about the same as in other species in the group. Beginning at Cd7, each caudal vertebra in adult male *M. thibetana* averages 10–16 mm shorter than the corresponding vertebra in adult male *M. a. assamensis*; this parallels the relationship noted above between *M. sinica/M. radiata* and *M. a. assamensis.* The caudal vertebral length gradient in stump-tailed *M. thibetana* clearly is not a paedomorphic retention of the fetal gradient in short-tailed *M. a. assamensis* (fig. 9). Caudal vertebral length gradients in the *sinica* group are generally similar to those in the *silenus* group (fig. 10) and, judging from data available for *M. fascicularis* and *M. mulatta,* also to those in the *fascicularis* group (Ankel, 1962, p. 156; Wilson, 1970, pp. 196–197).

Glans Penis and Baculum

The form of the glans penis in the *sinica* group is highly distinctive (fig. 11; Cuvier, 1820, p. 1; Cuvier, 1846, p. 220; De Beaux, 1917, p. 6; Pocock, 1921, p. 228; Hill & Bernstein, 1969, p. 6; Fooden, 1971, p. 72). In this group, the glans is strongly inflected relative to the shaft of the penis, the dorsal margin of the corona is thickened and reflected anteriorly, the subterminal urethral meatus opens anterodorsally, and the apex of the glans is subacute. In other macaques, except *Macaca arctoides,* the glans is only slightly inflected relative to the shaft, the corona is relatively simple, the urethral meatus is terminal, and the apex of the glans is bilobed and bluntly rounded, approximately as in humans and most catarrhine monkeys (Pocock [1926], p. 1557; Hill, 1958, p. 650; Fooden, 1975, p. 33); in aberrant *M. arctoides,* the glans is more than twice as long as in the *sinica* group and the urethral meatus opens ventral to the apex of the glans (Fooden et al., 1985, p. 18). Although difficult to measure, the glans and shaft of the penis in the *sinica* group also seem to be relatively larger than in most other macaques; judging from specimens examined, the dorsoventral diameter of the distal part of the shaft is about 50% greater in *sinica*-group species than in other

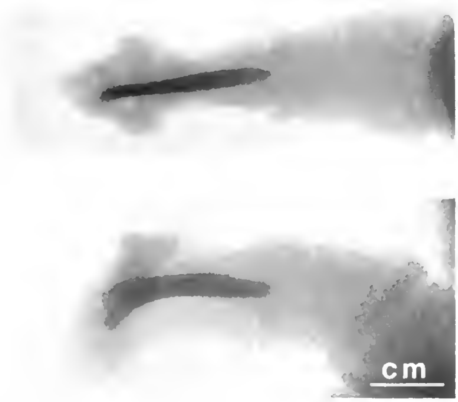

FIG. 12. Radiographs of penis of *M. a. assamensis,* dorsal and lateral views, showing position of baculum (FMNH 99632, subadult; Ban Pong Nam Ron, ca. 25 km W, Kamphaeng Phet Province, Thailand). (Radiographs courtesy Chicago Zoological Park, Brookfield, Illinois.)

macaque species of corresponding head and body length. Glans morphology in the *sinica* group evidently is derived relative to that in most macaques.

The thickened dorsal margin of the corona in the *sinica* group forms a horseshoe-shaped swelling that surrounds almost half of the glans. Between this swelling and the dorsal end of the urethral meatus is a well-defined semicircular concavity. The urethral meatus is a dorsoventrally oriented slit that extends about one-third the length of the glans and terminates dorsal to the apex of the glans. The left lip of the meatus is about twice as thick as the right lip and contains the distal inflected process of the baculum (fig. 12). Proximal to the glans, the skin of the distal part of the shaft of the penis is densely studded with prominent spines, the tips of which are recurved toward the base of the shaft. The length of these spines ranges up to about 0.5 mm in fluid-preserved adult specimens of *Macaca sinica* and up to about 0.7 mm in similarly preserved adult specimens of *M. a. assamensis*; the basal diameter of the spines is about half of their length. Spines also are present on the margin of the corona, particularly dorsally, where they cover about half of the horseshoe-shaped swelling. The color of the glans is pinkish in living *M. sinica, M. radiata,* and *M. a. assamensis* and buffy in living *M. thibetana.*

Size of the glans in *sinica*-group species apparently is approximately proportional to head and body length. Measurements in millimeters of glans length (apex to middorsal margin of corona) and breadth are 17.5 × 10.5 and 18.5 × 11.0 in two fluid-preserved adult specimens of *Macaca sinica* (FMNH 57720, 57721), 22.5 × 16.0 and 22.5 × 16.5 in two fluid-preserved adult specimens of *M. a. assamensis* (FMNH 99622, 99631) (cf. Hill & Bernstein, 1969, p. 7); measurements in one living adult specimen of *M. thibetana* are 25 × 20 (Fooden et al., 1985, p. 19). These measurements suggest that relative breadth of the glans may be greater in the larger species.

Variation of form of the glans within and between species is relatively minor. The distinctive form is readily recognized even in infants less than one year old (prior to eruption of the first permanent teeth). However, in one specimen of *M. sinica* (FMNH 57723, ?adult), the glans is abnormal. The meatal cleft in this specimen is prolonged ventrally and extends through the ventral border of the corona of the glans to the right of the apex. This extension of the meatal cleft subdivides the distal end of the glans into two lobes, the left lobe larger than the right, which brings the form of this part of the glans somewhat closer to that in most non-*sinica*-group species of macaques. However, the horseshoe-shaped dorsal swelling and semicircular concavity in this specimen are as in typical *sinica*-group specimens.

The baculum, which provides skeletal support for the glans, is stocking-shaped and bilaterally flattened in *sinica*-group macaques (figs. 12–13; Daubenton, 1766, p. 306; De Beaux, 1917, p. 6; Chaine [1927], p. 15; Pohl, 1928, p. 102; Fooden [1966], p. 160). The shaft of the baculum is rooted in the corpora cavernosa of the penis. The distal inflected process, variably subdivided into a dorsal and ventral lobe, projects into the left lip of the urethral meatus, where it terminates to the left of the navicular fossa near the ventral end of the meatal cleft; the baculum does not extend into the apex of the glans (fig. 12).

Bacular size in *sinica*-group species is roughly proportional to body size (tables 1, 7). Bacular length averages 12.2% of mean skull length in four adult specimens of *Macaca sinica,* 16.6% of skull length in four adult specimens of *M. a. assamensis,* and 16.0% of skull length in two adult specimens of *M. thibetana.* Length of the distal inflected process relative to length of the shaft averages greater in *M. sinica* and *M. radiata* than in *M. a. assamensis* and *M. thibetana.* Size and form of the baculum in *M. a. assamensis* and *M. thibetana* tend toward those in *M. nemestrina leonina* (Fooden, 1975, p. 41).

Bacular variation within and between species in the *sinica* group appears to be greater than variation of glans morphology (see above). A parallel situation previously was noted in the *silenus* group, where subspecies *Macaca n. nemestrina* and *M. n. leonina* are similar in glans morphology but differ in bacular morphology (Fooden, 1975, p. 38). Three bacula examined exhibit special peculiarities: *M. radiata* ZMB 124 (?adult) has a large fossa on the left side of the shaft of the baculum immediately proximal to the distal inflected process (fig. 13, *M. radiata*: *b*); *M. a. assamensis* FMNH 99622 (adult), has an exceptionally short shaft (fig. 13, *M. assamensis*: *a*); and *M. thibetana* AMNH 84475 (infant) has a distal inflected process which curves gradually into the shaft instead of being set off at an abrupt angle.

The functional relationship between specialized morphology of the penis in the *sinica* group and specialized morphology of the female tract (see below) is unknown. Copulatory behavior in this group has been reported in detail only for *Macaca*

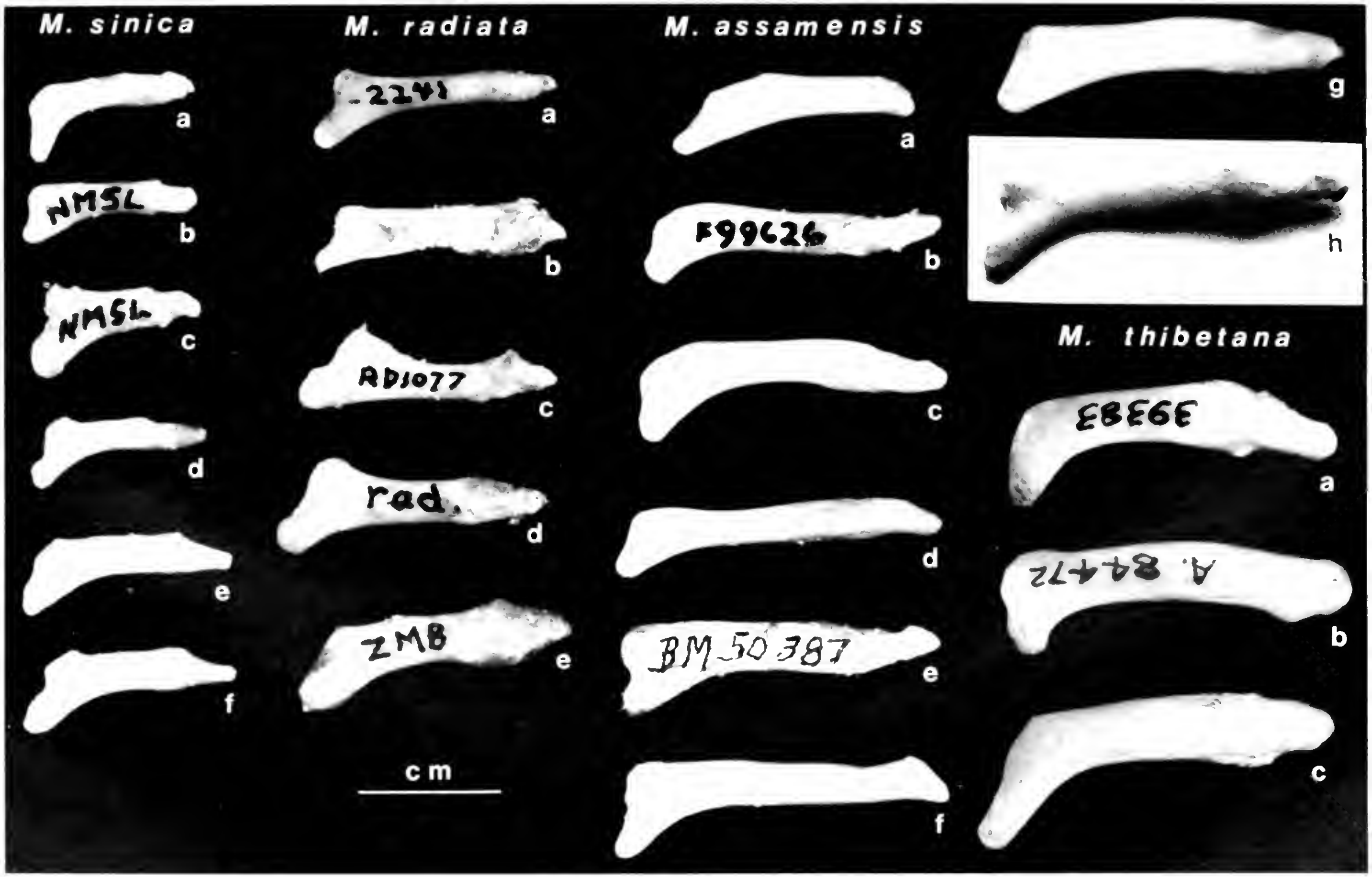

FIG. 13. Bacula of subadult and adult *sinica*-group macaques (cf. table 7); left lateral view, dorsal surface of baculum at top, distal end at left. *Macaca sinica*: **a,** FMNH 57723 (?ad.); **b,** NMSL 2-X-A (ad.); **c,** NMSL 2 D (ad.); **d,** FMNH 95021 (ad.); **e,** FMNH 57721 (?ad.); **f,** FMNH 95022 (ad.). *Macaca radiata*: **a,** RMNH 2241 (?ad.); **b,** ZMB 124 (?ad.); **c,** RMNH RD1077 (?ad.); **d,** RMNH 1 a (?ad.); **e,** ZMB unnumbered (?ad.). *Macaca assamensis* (all *M. a. assamensis*): **a,** FMNH 99622 (ad.); **b** FMNH 99626 (subad.); **c,** FMNH 99632 (subad.); **d,** FMNH 99627 (subad.); **e,** BM 50.387 (?ad.); **f,** FMNH 99631 (ad.); **g,** FMNH 31765 (ad.); **h,** IZCAS 26681 (ad.). *Macaca thibetana*: **a,** FMNH 39383 (subad.); **b,** AMNH 84472 (ad.); **c,** FMNH 39499 (ad.). (Photos, except IZCAS 26681, by Ron Testa, Division of Photography, Field Museum of Natural History.)

TABLE 7. Male external genitalia: specimens examined and measurements of baculum.

Specimen no./ref. no.	Age	Dental stage[1]	Skull, greatest length (mm)	Baculum measurements (mm): Greatest length	Least dorsoventral diameter of shaft	Shaft length[2]	Distal process length[3]	Penis preservation[4]
			Macaca sinica					
FMNH 57722	Immature	...	...	9.3	1.1	7.6	2.9	Fluid
Ref. 5	"Adult"	...	...	11	...	...	...	...
RMNH 1a	Immature	...	...	11.3	2.1	9.8	3.7	Dry
Ref. 6	Immature	...	...	12	...	...	...	...
Ref. 7	Immature	...	...	14.6	ca. 2	...	...	...
MCZ 34789	Subadult	M3, (C)	94.0	16.9	1.9	14.3	4.6	...
FMNH 57720	?Adult	...	...	13.8	2.7	11.7	5.3	Fluid
FMNH 57721	?Adult	...	...	15.4	2.7	12.6	5.9	Fluid
FMNH 57723	?Adult	...	...	12.6	2.2	10.6	5.2	Fluid
FMNH 95021	Adult	M3, C	109.0	12.9	2.2	10.0	5.3	...
FMNH 95022	Adult	M3, C	114.2	15.6	2.7	11.8	6.7	...
NMSL 2D	Adult	M3, C	111.6	12.8	2.9	10.9	6.6	Dry
NMSL 2-X-A	Adult	M3, C	107.3	12.7	2.2	11.6	4.1	Dry
Mean ± SD (N = 7)	Adult			13.7 ± 1.3				
			Macaca radiata					
RMNH 1474	Infant/juvenile	...	...	8.2	0.8	6.5	2.0	Dry
RMNH 2229	Juvenile	(M1)	90.4	10.8	0.9	9.0	3.3	Dry
NHMB 3360	Juvenile	M1, (I)	91.3	9.5	1.0	7.7	2.8	Dry
BM 30.11.1.25	Juvenile	(M2, P3)	98.8	12.0	1.6	10.8	3.6	Dry
AMNH 18043	Juvenile	M2	99.3	12.7	1.6	12.1	3.3	...
RMNH 1a	?Adult	...	...	19.1	3.0	14.9	7.5	Dry
RMNH RD1077	?Adult	...	...	18.2	2.6	14.0	7.2	Dry
RMNH 2241	?Adult	...	...	17.5	2.3	14.8	5.9	Dry
ZMB 124	?Adult	...	...	17.9	2.9	15.0	4.7	Dry
ZMB –	?Adult	...	...	19.8	3.3	16.2	6.2	Dry
Ref. 8	?Adult	...	...	20	2.5	...	...	...
Ref. 9	?Adult	...	...	20	2.0	...	...	...
Mean ± SD (N = 7)	Adult			18.9 ± 1.1				
			Macaca assamensis pelops[10]					
BM 79.11.21.302	Juvenile	P4, (C)	...	20.2	2.1	17.4	6.5	...
			Macaca a. assamensis					
BM 50.378	Infant	(dec. c, m1)	78.3	9.6	1.6	9.6	2.7	...
FMNH 99630	Infant	dec. m2	86.5	10.8	1.7	9.9	2.9	Fluid

Table 7. *Continued.*

Specimen no./ref. no.	Age	Dental stage[1]	Skull, greatest length (mm)	Baculum measurements (mm): Greatest length	Least dorsoventral diameter of shaft	Shaft length[2]	Distal process length[3]	Penis preservation[4]
BM 50.381	Juvenile	(I, M1)	104.4	10.1	1.6	9.3	3.4	...
FMNH 99625	Juvenile	I2	93.0	10.8	1.1	9.8	2.7	Fluid
FMNH 99624	Juvenile	I2, M2	97.0	14.8	1.9	13.5	4.0	Fluid
FMNH 99627	Subadult	(M3, C)	122.1	23.5	2.5	21.7	4.9	Fluid
FMNH 99626	Subadult	M3, (C)	123.8	21.5	3.0	17.8	6.3	Fluid
FMNH 99632	Subadult	M3, (C)	121.9	22.4	3.1	18.7	7.4	Fluid
BM 50.387	?Adult	...	...	23.0	3.4	21.3	6.6	...
FMNH 31765	Adult	M3, C	139.9	25.2	3.7	22.5	6.5	...
FMNH 99622	Adult	M3, C	145.0	17.6	2.7	10.6	8.1	Fluid
FMNH 99631	Adult	M3, C	138.9	24.2	3.0	21.9	6.8	Fluid
IZCAS 26681	Adult	M3, C	144.0	26.9	3.6	24.9	8.1	...
Mean ± SD (N = 5)	Adult			23.4 ± 3.5				
			Macaca thibetana					
AMNH 84475	Infant	...	...	8.8	1.3	7.1	2.7	...
FMNH 39383	Subadult	M3, (C)	143.9	23.7	3.7	21.9	7.3	...
AMNH 84472	Adult	M3, C	...	24.9	3.9	23.3	7.4	...
FMNH 39499	Adult	M3, C	161.3	26.3	4.3	21.0	9.9	Dry
Ref. 11	Adult	...	...	...	...	...	...	Living
Mean ± SD (N = 2)	Adult			25.6 ± 1.0				

[1] Abbreviation indicates latest teeth in dental arch, parentheses indicate incomplete eruption; ellipsis indicates unavailability of skull.
[2] Measured from proximal extremity of shaft to dorsal inflection point at base of distal process. [3] Measured from dorsal inflection point at base of distal process to distal extremity. [4] For study, dry specimens were reconstituted in fluid.
[5] Pohl, 1928, p. 102. [6] De Beaux, 1917, p. 6. [7] Daubenton, 1766, p. 306. [8] Chaine [1927], p. 15; specimen misidentified as *M. sinicus.* [9] Chaine [1927], p. 16; specimen identified as *M. pileatus,* illustration apparently inverted.
[10] Bacular length in 3 adult *M. assamensis* specimens that probably belong to this subspecies has been reported by Dixson (1987, p. 53; for subspecies indication, see Napier, 1981, p. 32): 25.4, 25.8, and 26.2 mm (25.8 ± 0.4 mm). [11] Fooden et al., 1985, p. 21.

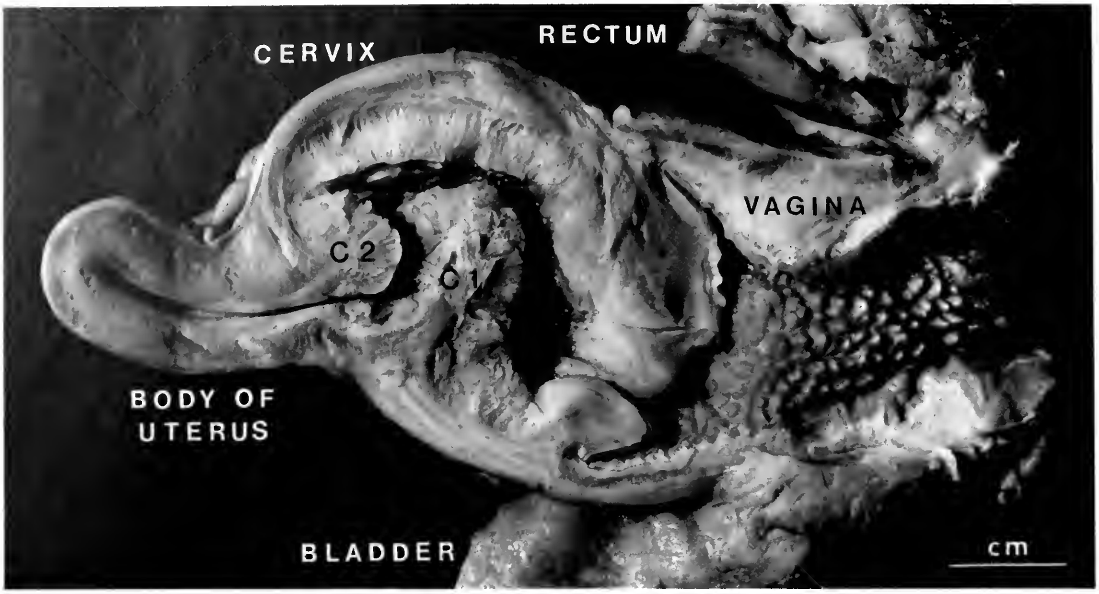

FIG. 14. Sagittal section of female reproductive tract of *M. a. assamensis* (FMNH 99628, adult; Ban Mae Lamao, Tak Province, Thailand). (Photo by John Bayalis, Division of Photography, Field Museum of Natural History.)

radiata, in which ejaculation usually is accomplished in a single mount with an average of 17 thrusts and a mean total duration of 10 seconds (Shively et al., 1982, p. 376). The greater variation of bacular morphology than of glans morphology suggests that glans morphology is subject to more rigorous selection pressure.

Female Reproductive Tract

Cyclical estrous swelling of the sexual skin in *sinica*-group females is relatively modest (Zuckerman, 1930, p. 705; Hartman, 1938, p. 468; Hill, 1939, p. 25; Fooden, 1971, p. 63; Dittus, 1974, chap. 1, p. 52; McArthur et al., 1972, p. 118; Hill, 1974, pp. 697, 729; Fooden et al., 1985, p. 23), compared with that in *silenus*-group females (Fooden, 1969, p. 13; 1975, p. 28). In *Macaca sinica* and *M. radiata,* slight swelling of the subcaudal, circumanal, or labial area has been observed occasionally; in *M. thibetana,* swelling and reddening of the perineal region apparently are common in estrous females (Xiong, 1984, p. 6); no information is available concerning estrous swelling in *M. assamensis.* During pregnancy, a subcaudal swelling has been noted in *M. radiata* and *M. assamensis.* Gray, blue, or purple coloration of the sexual skin has been noted in all four species in this group: in *M. sinica,* a dark gray or bright purple color that extends from tail root to labia develops with age in adult females and may persist through the entire menstrual cycle; in *M. radiata,* the circumanal area is dark purple in nonpregnant females and becomes even darker during pregnancy; in *M. assamensis,* a bluish perineal streak has been reported in a pregnant female, and a dark blue circumanal triangle has been reported in a lactating female; and in *M. thibetana,* a bluish perineal streak has been reported in one nonpregnant female.

The vaginal lining is distinctively spinose in two nonpregnant nonlactating female specimens of *Macaca a. assamensis* (fig. 14; Fooden, 1971, p. 67). Similar coarse spines are present in the vaginal lining of one nonpregnant female specimen of *M. thibetana* (Fooden et al., 1985, p. 22). No information is available concerning presence or absence of vaginal spines in *M. sinica* or *M. radiata.* Cyclical desquamation of cells from the vaginal lining in *M. radiata* is only about 10% of that in *M. mulatta* (Hartman, 1938, p. 473).

The uterine cervix in *sinica*-group species is greatly enlarged (fig. 14; Zuckerman, 1930, p. 704; Hartman, 1938, p. 473; Hill, 1939, p. 28; Fooden, 1971, p. 67; Ovadia et al., 1971, p. 128; Jainudeen et al., 1972, p. 471; Fooden et al., 1985, p. 23). In nonpregnant nonlactating adults, the interdigitating dorsal and ventral colliculi, which partly obstruct the cervical canal, are more than twice as large in *sinica*-group species than in other macaque species groups (Fooden, 1980, p. 3). The

TABLE 8. Blood protein electrophoresis: monomorphism in *Macaca* spp., including *sinica*-group species (not studied in *M. thibetana*).

Monomorphic protein locus	No. of specimens studied				Ref. nos.
	M. sinica	*M. radiata*	*M. assamensis*	Other species of *Macaca*	
			PLASMA PROTEINS		
Alp	131	22	28	2,106[1] (13 spp.)	2–9
Amy	131	19	28	2,062 (13 spp.)	3–9
Cat	131	19	28	1,397 (5 spp.)	3–4, 7
LAP	131	19	28	2,127[10] (13 spp.)	2–9
PA	0	19	28	1,807 (6 spp.)	3–6
α_2	131	19	28	2,062[11] (13 spp.)	3–9
			ERYTHROCYTE PROTEINS		
G6PD	131	19	28	2,128 (13 spp.)	2–9
PGI	0	1	0	28 (5 spp.)	2
TO	131	19	28	2,062 (13 spp.)	3–9

Alp = Alkaline phosphatase; Amy = amylase; Cat = catalase; LAP = leucine aminopeptidase; PA prealbumin; α_2 = slow α_2-macroglobulin; G6PD = glucose-6-phosphate dehydrogenase; PGI = phosphoglucoisomerase; TO = tetrazolium oxidase.

[1] Variant allele in 3 of 477 *M. fascicularis* specimens and in 2 of 255 Sulawesi macaque specimens.

[2] Bruce, 1977, pp. 144, 152, 157, 162. [3] Nozawa et al., 1977, pp. 16, 18, 22. [4] Shotake, 1979, pp. 444, 447–448. [5] Kawamoto et al., 1981, pp. 18, 20. [6] Kawamoto et al., 1982, p. 58. [7] Shotake and Santiapillai, 1982, pp. 81–82. [8] Kawamoto and Suryobroto, 1985, p. 35. [9] Kawamoto et al., 1985, pp. 46, 49.

[10] Variant allele in 1 of 29 *M. arctoides* specimens and in 1 of 255 Sulawesi macaque specimens. [11] Protein absent in 2 of 1,063 *M. fuscata* specimens.

highly developed endocervical epithelium in *sinica*-group species is richly glandular; regulated by ovarian hormones, this epithelium secretes large quantities of mucus (Percy, 1844, p. 83; Xiong, 1984, p. 6) that apparently functions as a sex pheromone (Rahaman & Parthasarathy, 1971, p. 98; Fooden, 1981, p. 29).

Recent histological study of the ovary of *Macaca radiata* has revealed that the preovulatory Graafian follicle in this species is remarkably different from that in most mammals, including *M. fascicularis* and *M. mulatta* (Barnes et al., 1978, p. 538). Unlike the smooth-walled spherical preovulatory follicle that is typical of mammals, the follicle in *M. radiata* has walls that are deeply folded, giving the follicle a collapsed appearance. The form of the preovulatory follicle in other *sinica*-group species has not been reported.

Blood Proteins

ELECTROPHORESIS—Thirty-seven blood protein loci have been investigated electrophoretically in three *sinica*-group species and in other macaques (tables 8–12). The three *sinica*-group species that have been studied are *Macaca sinica* (32 loci), *M. radiata* (35 loci), and *M. assamensis* (30 loci). Blood proteins in *M. thibetana* have not been studied.

Comprehensive analyses of electrophoretic evidence from adequate samples of *sinica*-group specimens agree with previous determinations, originally based on reproductive tract morphology, that species in the *sinica* group are more closely related to each other than to other species of macaques (Darga et al., 1975, p. 803; Shotake, 1979, p. 447; Melnick & Kidd, 1985, p. 138). Although preliminary study of one specimen of *Macaca assamensis* appeared to indicate that this species was serologically closer to *M. mulatta* than to *M. sinica* and *M. radiata* (Cronin & Meikle, 1979, p. 262; Cronin et al., 1980, pp. 44, 46; Cann et al., 1979, p. 425; Pope & Cronin, 1984, p. 384), subsequent study of 28 specimens of *M. assamensis* has established that the serologic distance of this species from *M. mulatta* is about three times as great as its distance from *M. radiata* (Shotake, 1979, p. 447). Because of the possibility of convergent evolution of blood proteins, study of a small number of loci may not detect the close interrelationship of *sinica*-group species that is revealed by more comprehensive analysis. A recent study of transferrin allele frequencies in macaques indicates that, with respect to alleles at this locus, *M. sinica* is convergently similar to *M. mulatta,* and *M. radiata* is convergently similar to *M. cyclopis* (Hazout et al., 1986, p. 245).

Of the 37 blood protein loci that have been studied in *sinica*-group species and in other macaques, nine loci (6 plasma proteins, 3 erythrocyte pro-

TABLE 9. Blood protein electrophoresis: monomorphism in *sinica*-group species (not studied in *M. thibetana*), polymorphism in other species of macaques.[1]

Monomorphic protein locus	No. of *sinica*-group specimens studied: *M. sinica*	*M. radiata*	*M. assamensis*	Ref. nos.
PLASMA PROTEINS				
CP	131	22	28	2–5
GC[1]	131	0	0	5
Hp	131	28	28	2–5
PI	131	19[6]	28	3–5
ERYTHROCYTE PROTEINS				
AcP	131	19	28	3–5
CA-II	0	22	0	7
CA-I control	55	52	0	8
Cell Es[9]	131	19	28	3–5
EsD[1]	131	0	0	5
GOT	0	26	0	2
Hb-β	202	68[10]	28	4–5, 8
LDH-A	131	35	28	2–5
MDH	131	44	28	2–5
6-PGD	188	89[11]	28	2–5, 8

CP = Ceruloplasmin; GC = group-specific component; Hp = haptoglobin; PI = protease inhibitor; AcP = acid phosphatase; CA-II = carbonic anhydrase II; CA-I control = carbonic anhydrase I control; Cell Es = cell esterase; EsD = esterase D; GOT = glutamate oxalate transaminase; Hb-β = hemoglobin beta; LDH-A = lactate dehydrogenase A; MDH = malate dehydrogenase; 6-PGD = 6-phosphogluconate dehydrogenase.

[1] Two proteins listed here, GC and EsD, have been studied only in *M. sinica.*

[2] Bruce, 1977, pp. 145, 149–150, 155, 158, 161. [3] Nozawa et al., 1977, pp. 16, 19, 22–23. [4] Shotake, 1979, pp. 444, 447–448. [5] Shotake and Santiapillai, 1982, pp. 81–82.

[6] Nozawa (ref. 3) and Shotake (ref. 4) indicate that the PI allele frequency in *M. radiata* is 1.00 *C* (N = 19). However, Lucotte et al. (1984, p. 340) indicate that the PI allele frequency in this species is 0.96 *B* (N = 96). The explanation for this discrepancy is unclear.

[7] Weiss et al., 1973, pp. 214, 219. [8] Darga et al., 1975, pp. 800, 803–804. [9] Cf. Bruce, 1977, pp. 33, 159–160. [10] Cf. Bruce (1977, pp. 25, 146) and Ahaley et al. (1978, p. 52).

[11] Excludes 1 specimen with variant allele (Bruce, 1977, pp. 31, 155).

teins) are monomorphic in all 16 macaque species investigated, including *M. sinica, M. radiata,* and *M. assamensis* (table 8). Some or all of these monomorphic alleles may be genus-level (or higher category) taxonomic characters. Fourteen blood protein loci (4 plasma proteins, 10 erythrocyte proteins) are monomorphic in all three *sinica*-group species that have been studied, but are polymorphic between or within other macaque species (table 9). Some of these alleles may be species-group characters. Fourteen blood protein loci (4 plasma proteins, 10 erythrocyte proteins) are polymorphic within the *sinica* group; 10 of these loci are dimorphic (table 10), three are trimorphic (table 11), and one (transferrin) exhibits seven alleles in *sinica*-group species (table 12).

Judging from evidence available for *sinica*-group macaques, it appears that plasma proteins may vary more at higher taxonomic levels and erythrocyte proteins may vary more at lower taxonomic levels (cf. Palmour et al., 1980, p. 806). Local variation of polymorphic blood protein allele frequencies in natural populations of *Macaca sinica* has been investigated in detail by Shotake and Santiapillai (1982, p. 82).

The pattern of interspecific variation of allele frequencies at polymorphic blood protein loci in *Macaca sinica, M. radiata,* and *M. assamensis* deviates from the pattern of variation of external and cranial morphology in these species. Morphological variation (head and body length, tail length, skull length; figs. 3–4, 7) follows a consistent gradient from *M. sinica* through *M. radiata* to *M. assamensis,* and the morphological distance from *M. sinica* to *M. radiata* is consistently less than the distance from *M. radiata* to *M. assamensis.* The sequence of species and the relative interspecific distances in these morphological gradients exactly parallel the geographic interrelationships of these species (geographic range of *M. sinica* at one extreme and geographic range of *M. assamensis* at the other extreme; range of *M. radiata* nearer that of *M. sinica* than that of *M. assamensis*; fig. 1). Variation of blood protein allele frequencies does not conform to this pattern, either with respect to the sequence of species or with respect to relative interspecific distances.

There is no tendency for blood protein allele frequencies in *M. radiata* to be intermediate between those in *M. sinica* and *M. assamensis* (comparisons and abbreviations in tables 10–12). For example, of five dimorphic loci at which allele frequencies in *M. radiata* differ from those in *M. sinica* and *M. assamensis,* the frequency in *M. radiata* is intermediate between that in *M. sinica* and *M. assamensis* at two loci (TBPA, Hb-α) and is not intermediate at three loci (ADA, IDH, PGM-I). Allele frequency differences between *M. sinica* and *M. radiata* may be compared with those between *M. radiata* and *M. assamensis* for nine of the dimorphic loci (all except AK, which has not been studied in *M. assamensis*): at three loci (Dia, IDH, LDH-B), the allele frequency difference between *M.*

TABLE 10. Blood protein electrophoresis: dimorphism in *sinica*-group species (not studied in *M. thibetana*).

Dimorphic protein locus	Major allele	Minor allele	Frequency of major allele (sample size in parentheses) *M. sinica*	*M. radiata*	*M. assamensis*	Ref. nos.
			PLASMA PROTEIN			
TBPA	F	S	0.287[1] (196)	0.661[2] (171)	0.966 (28)	3–6
			ERYTHROCYTE PROTEINS			
ADA[7]	1	3	0.996 (131)	0.526 (19)	0.639 (18)	4–5
AK	1	3	0.965 (131)	1.000 (14)	··· (0)	5, 8
CA-I	C	A	0.667[9] (186)	1.000 (71)	1.000 (28)	3–5
Dia	A	C	1.000 (131)	1.000 (21)	0.722 (28)	4–5, 8
Hb-α[10]	1[11]	2[11]	0.947[12] (202)	0.736[13] (68)	0.618 (28)	3–5
IDH	1	2	0.902 (131)	0.963[14] (27)	0.471 (28)	4–5, 8
LDH-B	1	3	1.000 (131)	1.000 (35)	0.912 (28)	4–5, 8
PGM-I[7]	1	5	1.000 (131)	0.773[15] (22)	1.000 (28)	4–5
PGM-II[7]	1	7	0.677 (131)	1.000 (22)	1.000 (28)	4–5, 8

TBPA = Thyroxine-binding prealbumin; ADA = adenosine deaminase; AK = adenylate kinase; CA-I = carbonic anhydrase I; Dia = NADH diaphorase; Hb-α = hemoglobin alpha; IDH = isocitrate dehydrogenase; LDH-B = lactate dehydrogenase B; PGM-I = phosphoglucomutase I; PGM-II = phosphoglucomutase II.

[1] Weighted mean of 0.385 (N = 65; ref. 3) and 0.2385 (N = 131; ref. 5). [2] Weighted mean of 0.705 (N = 56; ref. 3), 0.6842 (N = 19; ref. 4), and 0.63 (N = 96; ref. 6).

[3] Darga et al., 1975, pp. 800, 802, 804. [4] Shotake, 1979, pp. 444, 448. [5] Shotake and Santiapillai, 1982, pp. 83, 89, 91. [6] Lucotte et al., 1984, p. 340. [7] Cf. Palmour et al., 1980, pp. 800, 805. [8] Bruce, 1977, pp. 141, 147–148, 151, 153–154.

[9] Weighted mean of 0.510 (N = 55; ref. 3) and 0.7323 (N = 131; ref. 5). [10] Cf. Bruce (1977, pp. 25, 146), Ahaley et al. (1978, p. 52), and Matsuda (1985, p. 360).

[11] Major allele designated *H* and minor allele designated *M* by Darga et al. (ref. 3).

[12] Weighted mean of 0.951 (N = 71; ref. 3) and 0.9449 (N = 131; ref. 5). [13] Weighted mean of 0.725 (N = 49; ref. 3) and 0.7632 (N = 19; ref. 4). [14] Weighted mean of 1.000 (N = 19; ref. 4) and 0.875 (N = 8; ref. 8). [15] Weighted mean of 0.737 (N = 19; ref. 4) and 1.000 (N = 3; ref. 8).

sinica and *M. radiata* is less than that between *M. radiata* and *M. assamensis*; at five loci (TBPA, ADA, CA-I, Hb-α, PGM-II), the difference between *M. sinica* and *M. radiata* is greater; and at one locus (PGM-I), the difference is equal. For these nine dimorphic loci, the mean allele frequency difference between *M. sinica* and *M. radiata* is 0.222 ± 0.170 (SD) and that between *M. radiata* and *M. assamensis* is 0.180 ± 0.161. The sequence and distance of allele frequency variations at the trimorphic loci (Alb, Ch-Es, PHI) and the polymorphic transferrin locus exhibit the same lack of concordance with the sequence and distance of morphological variation (tables 11–12).

Blood protein allele frequencies in the *sinica* group evidently have evolved independently of external and cranial morphology (cf. King & Wilson, 1975, p. 114). Hazout et al. (1984, p. 346) have suggested that blood protein allele frequencies are partly determined by natural selection in response to climatic and geographic factors. Part of the allele frequency divergence of *M. sinica* may be a consequence of insular genetic drift (cf. Prychodko et al., 1969, p. 105; Nozawa et al., 1977, p. 26).

TABLE 11. Blood protein electrophoresis: trimorphism in *sinica*-group species (not studied in *M. thibetana*).

Alleles	Allele frequencies *M. sinica*[1] (N = 131)	*M. radiata*[2] (N = 19)	*M. assamensis*[2] (N = 28)
		Alb	
A	0	0	0.161
B	0.980	1.000[3]	0.839
D'	0.020	0	0
		Ch-Es	
1	0.988	0.808	1.000
4	0	0.192	0
5	0.012	0	0
		PHI	
1	0.752	1.000	1.000
15	0.228	0	0
16	0.020	0	0

Alb = Plasma albumin; Ch-Es = plasma cholinesterase; PHI = cell phosphohexoseisomerase.

[1] Reference: Shotake and Santiapillai, 1982, p. 83. [2] Reference: Shotake, 1979, p. 448. [3] N = ca. 50; Shotake (ref. 2)—19 specimens; Bruce, 1977, p. 156—5 specimens; Weiss et al., 1973, p. 214—20–30 specimens (estimate).

TABLE 12. Blood protein electrophoresis: polymorphism of plasma transferrin (Tf) in *sinica*-group species (not studied in *M. thibetana*).

		Tf allele frequencies						
Ref. nos.	N	*B*	*C*	*D*	*E*	*F*	*F''*	*G*
				M. sinica				
1	69	.058	.246	.051	.283	.022	.007	.333
2	131	.181	.185	0	.291	0	0	.343
3	39	.08	.30	.06	.19	0	0	.37
Means	239	.129	.221	.025	.272	.006	.002	.345
				M. radiata[4]				
1	59	0	.568	0	0	.407	0	.025
3	51	.14	.59	0	.01	.26	0	.01
5	19	0	.921	0	.079	0	0	0
Means	129	.054	.628	0	.015	.288	0	.015
				M. assamensis				
5	28	0	.146	.146	.708	0	0	0
6	7	.071	.214	.571	0	.071	0	.071
Means	35	.014	.160	.231	.567	.014	0	.014

[1] Darga et al., 1975, p. 801. [2] Shotake and Santiapillai, 1982, p. 83; note that allele *E* is designated D^3 in this study (see p. 82). [3] Hazout et al., 1986, p. 244; cf. Lucotte et al., 1984, p. 340. [4] Cf. Devor, 1977, p. 127. [5] Shotake, 1979, pp. 444, 448. [6] Annenkov, 1974, pp. 60, 62; in this work, allele *F* of other authors apparently is designated as *F'*.

AGGLUTINATION—*Macaca radiata* is the only *sinica*-group species in which blood group agglutination has been investigated. Two studies of human-type blood groups indicate that groups *A, B,* and *AB* are all fairly common in *M. radiata* and that group *O* is rare or absent. One study suggests that *M. radiata* is monomorphic for group *M* in the *M-N* series (table 13).

In a study of simian-type blood groups, erythrocytes of 52 specimens of *Macaca radiata* were tested for agglutinogens by using isoimmune sera of 10 rhesus monkeys (*M. mulatta*) (Socha et al., 1976, p. 489; Moor-Jankowski & Socha, 1978, p. 139). Unlike erythrocytes of some other macaque species, erythrocytes of *M. radiata* were either uniformly positive (5 sera) or uniformly negative (5 sera) when tested with the isoimmune rhesus sera. A similar monomorphic response previously had been obtained when erythrocytes of six *M. radiata* specimens were tested with one rhesus isoimmune serum (LaSalle, 1969, p. 127). Intraspecific cross-testing of erythrocytes and sera from a series of *M. radiata* specimens yielded results that were mostly negative, but responses to two sera were polymorphic (Socha & Ruffié, 1983, p. 168). Additional agglutination studies of other species in the *sinica* group will be required in order to evaluate the possible systematic significance of human-type and simian-type blood group characters in this species group.

Karyology

Classically stained karyotypes are known for *Macaca sinica, M. radiata,* and *M. assamensis* (Ardito, 1979, pp. 255–258). Banded karyotypes are known for *M. radiata* (Stanyon, 1982, p. 72;

TABLE 13. Blood protein agglutination: human-type blood groups in *Macaca radiata* (not studied in other *sinica*-group species).

References	N	Blood group frequencies			
		O	A	B	AB
Socha & Ruffié, 1983, p. 47	52	0	0.40	0.27	0.33
More & Banerjee, 1979, p. 1331	25	0	0.44	0.56	0
Means	77	0	0.42	0.36	0.22
		M	N	MN	
More & Banerjee, 1979, p. 1331	25	1.00	0	0	

1983, p. 58; Brown et al., 1984, p. s14; 1986, p. 168; Krishna-Murthy et al., 1984a, p. 195; 1984b, p. 179), *M. assamensis* (Chen et al., 1980, p. 92; 1981, p. 37; Cao et al., 1981, p. 120), and *M. thibetana* (Chen et al., 1981, pp. 92–115; Chen & Luo, 1985, p. 83). The diploid chromosome number is 42 in all macaques, including *sinica*-group species. Chromosome number and morphology are remarkably similar in *Macaca, Papio, Theropithecus,* and *Cercocebus* (Chiarelli, 1966, p. 168; Dutrillaux et al., 1982, p. 100; Muleris et al., 1986, p. 40).

Based on classically stained karyotypes, Schmager (1972, p. 481) analyzed chromosome lengths in *sinica*-group species and other macaques. The reported morphometric karyological similarities generally do not agree with relationships indicated by nonkaryological evidence; for example, chromosome length unites *Macaca sinica, M. radiata,* and *M. silenus* in one group and separates these species from another group that includes *M. assamensis* and *M. nemestrina* (cf. Fooden, 1980, p. 7). Banded karyotypes of *M. radiata, M. assamensis,* and *M. thibetana* reportedly are generally similar to those of other macaque species. No direct comparison has been made of the banded karyotypes of these three *sinica*-group species.

Hybridization

Species in the *sinica* group have been reported as participants in 15 hybrid matings, all in captivity (table 14). Of these matings, one—of questionable reliability—is intergeneric, nine are with macaques in other species groups (intergroup), and five are with other species in the *sinica* group (intragroup).

Intergeneric Hybridization—The questionable intergeneric record is based on ambiguous evidence of infantile pelage and skin color in a male offspring born to a *Cercopithecus aethiops* female (Gunning, 1910, p. 54; Gray, 1972, pp. 6, 11, listed four times under various specific names; Chiarelli, 1973, p. 301, listed twice; Hill, 1974, p. 470, listed four times). More than six months prior to birth of the infant, the *C. aethiops* female had been caged with a *M. radiata* male. No information is available as to whether other male monkeys may also have had access to this female. Paternity of the infant is suspect.

Successful hybridization between *Cercopithecus* and *Macaca* would be surprising because these genera belong to karyologically divergent subgroups in the subfamily Cercopithecinae (Ardito, 1979, p. 251; Chiarelli, 1979, p. 28; Bernstein & Gordon, 1980, pp. 138, 145). In one of these subgroups (*Cercopithecus, Erythrocebus*) the chromosome number is 2n = 48–72, whereas in the other (*Macaca, Cercocebus, Papio, Theropithecus*) the chromosome number is 2n = 42.

Two other reports of hybridization between the karyologically divergent subgroups, in addition to the questionable *Cercopithecus aethiops* × *Macaca radiata* record cited above, are listed in Gray's (1972) checklist of mammalian hybrids, but both of these reports also are suspect. Gray's tentative record of hybridization ("presumed hybrid") between *Cercopithecus sabaeus* and *Macaca mulatta* (p. 11; also listed as *C. aethiops* × *M. mulatta,* p. 6) is cited from Zuckerman (1931, p. 338; 1933, p. 96; 1953, p. 942); Zuckerman himself characterizes this record as "supposed" (1931), "doubtful" (1933), and "uncertain" (1953). Gray's record of hybridization between a *Cercocebus torquatus* female and a *Cercopithecus mitis* male (p. 5) is cited from Montagu (1950, p. 150) and Chiarelli (1961, table 1; secondary source). No such intergeneric cross is listed by Montagu. Gray and Chiarelli appear to have misinterpreted a hybridization record, explicitly labeled "Interspecific", that Montagu lists as "*Cercocebus aethiops* ♀ × *Cercocebus mitas* ♂"; this evidently is a lapsus for *Cercopithecus aethiops* ♀ × *Cercopithecus mitis* ♂ (interspecific not intergeneric). No known record reliably documents hybridization between the 48–72-chromosome cercopithecine subgroup and the 42-chromosome subgroup.

Intergroup Hybridization—Nine hybridizations are reported between species in the *sinica* group (*Macaca radiata,* 5 hybridizations; *M. assamensis,* 4) and species in the *fascicularis* (*M. fascicularis,* 1, inferred; *M. mulatta,* 4), *silenus* (*M. nemestrina,* 1), and *arctoides* (*M. arctoides,* 3) groups (table 14). Male and female reproductive organs in the *sinica* group are strikingly different from those in the *fascicularis, silenus,* and *arctoides* groups (Fooden, 1980, p. 2), but these anatomical differences evidently do not prevent intergroup copulation and fertilization, at least in captivity.

Attempts to form mixed-species social groups by confining together members of *sinica*-group species (*Macaca radiata, M. assamensis*) with members of *fascicularis*-group and *silenus*-group species generally have been unsuccessful (Bernstein & Gordon, 1980, pp. 135, 137). However, Stynes et al. (1975, p. 822, abstract only) report a

TABLE 14. Hybridizations reported for *sinica*-group species.[1]

Parental species (sexes indicated where known)	Sex of hybrid[2]	Birth date	Survival of hybrid	Location	Reference[3]
		INTERGENERIC(?)			
1. ?*M. radiata*[4] ♂ × *Cercopithecus aethiops* ♀	♂[2]	1 Oct. 1909	≧ 1 mo	Pretoria	Gunning, 1910, p. 54
		INTERGROUP			
2. *M. radiata*[4] ♂ × *M. fascicularis* ♀	♀[2]	12 May 1864	≧ 3 mo	Munich	Fitzinger, 1864, p. 335
3. *M. radiata* × *M. mulatta*	?	8 Feb. 1846	14.5 mo	London	Flower, 1929, p. 24
4. *M. radiata* ♂ × *M. mulatta* ♀	♂	6 Jan. 1881	4 yr	Leipzig	Westermann, in Landois, 1896, p. 156
5. *M. radiata* × *M. mulatta*	?[2]	ca. 1960	?	Teheran	Krumbiegel, 1965, p. 32
6. *M. radiata* × *M. mulatta*	?[2]	ca. 1960	?	Jaipur	Krumbiegel, 1965, p. 32
7. *M. assamensis* ♂ × *M. nemestrina* ♀	?	26 July 1970	Stillborn	Atlanta	Bernstein & Gordon, 1980, p. 128
8. *M. assamensis* ♀ × *M. arctoides* ♂	♂	18 Sept. 1964	≧ 5 yr	E. Berlin	Int. Zoo Yearb., 1966, p. 389; Petzold, 1968, p. 408[5]
9. *M. assamensis* ♀ × *M. arctoides* ♂	♂	1966	≧ 3 yr	E. Berlin	Int. Zoo Yearb., 1968, p. 292[5]
10. *M. assamensis* ♀ × *M. arctoides* ♂	♂	1967	≧ 2 yr	E. Berlin	Int. Zoo Yearb., 1969, p. 220[5]
		INTRAGROUP			
11. *M. sinica* × *M. radiata*	?	1860 or before	?	London	Flower, 1929, p. 23
12. *M. sinica* ♀ × *M. radiata* ♂	♀[2]	27–28 June 1935	≧ 19 mo	Colombo	Hill, 1937, p. 382, pl. 18
13. *M. sinica* × *M. radiata*	♀	1967	?	Tokyo	Int. Zoo Yearb., 1969, p. 219
14. *M. radiata* ♂ × *M. assamensis* ♀	♂[2]	9 March 1975	> 6 yr	Barang (India)	Acharjyo & Misra, 1977, p. 521, fig. 1; 1982, p. 376
15. *M. radiata* ♂ × *M. assamensis* ♀	♀[2]	27 March 1977	> 4 yr	Barang (India)	Acharjyo & Misra, 1982, p. 376

[1] Includes all valid records cited by Gray (1972, pp. 12–19), Chiarelli (1973, pp. 301–302), and Hill (1974, pp. 469–473); misidentifications and duplications in these three works have been corrected or eliminated.

[2] Phenotypic data are available for seven hybrids, as follows: No. 1, ?*M. radiata* × *Cercopithecus aethiops*—pelage brown with blackish tips; face flesh-colored. No. 2, *M. radiata* × *M. fascicularis*—forehead hairs parted (as in *M. radiata*); face reddish flesh-colored (close to *M. radiata*); dorsal surface dark olive-brown, becoming blackish medially (close to *M. fascicularis*); ventral surface whitish (both parental species); hands bare, blackish (as in *M. fascicularis*). Nos. 5 and 6, *M. radiata* × *M. mulatta*—crown hair growth pattern as in *M. radiata*; tail length and iris color intermediate between *M. radiata* and *M. mulatta*. No. 12, *M. sinica* × *M. radiata*—dorsal pelage slightly more yellowish than in *M. radiata* (tending somewhat toward *M. sinica*); crown hair growth pattern, cheek whorl pattern, and facial skin pigmentation as in *M. radiata*. Nos. 14 and 15, *M. radiata* × *M. assamensis*—crown hair growth pattern, ear shape, and tail length as in *M. radiata*; pelage color as in *M. assamensis*.

[3] Primary-source references only; for numerous secondary-source references to these hybridizations, see Gray (1972, pp. 12–19).

[4] Paternal species inferred by author of original report based on phenotype of offspring—mating not observed; female parent may also have had access to males of other species.

[5] For data on sex and survival of hybrids, see Gray (1972, p. 12), who further indicates that the *M. assamensis* parent probably was female. A report by Dathe (1983, p. 126) of hybridization in 1968 between *M. assamensis* and *M. arctoides* is now known to be erroneous (R. Dathe, pers. comm., 3 Nov. 1987).

tendency toward increased social interaction and sexual behavior (details unspecified) between *M. radiata* and *M. nemestrina* after several individuals of these species had been kept together for more than 12 weeks.

Natural intergroup contacts between *Macaca radiata* (*sinica* group) and *M. mulatta* (*fascicularis* group) have been observed in India at four localities along the border between the ranges of these two species (Fooden et al., 1981, p. 465; Fooden, 1986, p. 14). In one village, a troop of *M. radiata* remained within 10–50 m of a troop of *M. mulatta* for about an hour without overt social interaction between the troops. At three other localities, *M. radiata* males apparently were closely integrated into *M. mulatta* troops and interacted amicably with *M. mulatta* females. No matings—interspecific or intraspecific—were seen during the course of these observations, which were made outside of the peak breeding season (September–November) of both *M. radiata* and *M. mulatta* (Roonwal & Mohnot, 1977, p. 110; Fooden, 1981, p. 27). Recognizable hybrids of *M. radiata* and *M. mulatta* were not observed in this border area. Although *M. radiata* and *M. mulatta* hybridize in captivity (table 14) and apparently are compatible in naturally occurring mixed-species troops, an unknown behavioral or physiological barrier, previously also postulated by Bernstein and Gordon (1979, p. 271; 1980, p. 146), evidently restricts gene flow between these species in the interspecific contact zone.

INTRAGROUP HYBRIDIZATION—Three reported intragroup hybridizations are between *Macaca sinica* and *M. radiata*, and two are between *M. radiata* and *M. assamensis* (table 14). Not surprisingly, these two hybridizing species pairs are composed of species that are near each other in body size (table 1).

Intragroup hybridization may occur more readily than intergroup hybridization. A captive *M. assamensis* female who had easy access to *M. nemestrina* and *M. arctoides* males and more difficult access to a *M. radiata* male preferentially associated with the *M. radiata* male, despite repeated efforts by keepers to separate them (Acharjyo & Misra, 1977, p. 521; 1982, p. 376); this pair ultimately produced two hybrid offspring. For another account of compatibility of captive *M. assamensis* and *M. radiata*, see Dathe (1983, p. 127).

Natural intragroup hybridization is now impossible between *Macaca sinica* and *M. radiata*, the ranges of which are separated by the Palk Strait, and between *M. radiata* and *M. assamensis*, separated by a 1,300-km gap. Natural hybridization may occasionally occur between *M. assamensis* and *M. thibetana* in northern Guangxi Province, China, where the ranges of these two species are in close proximity (fig. 1).

PHENOTYPES OF HYBRIDS—Phenotypic data are available for six intrageneric hybrids (table 14). Based on these limited data, tentative inferences may be drawn concerning relative dominance of certain taxonomic character states in *Macaca*. (1) Crown hair growth pattern: The pattern in *M. radiata* (large whorl with short anterior hairs, exposed forehead hairs parted) apparently is dominant to that in *M. sinica* (large whorl with long anterior hairs), *M. assamensis* (whorl small or absent), *M. fascicularis* (whorl small and irregular or absent), and *M. mulatta* (whorl absent). (2) Tail length: The long tail in *M. radiata* apparently is dominant to the shorter tail in *M. assamensis*, but it is incompletely dominant (hybrids intermediate) to the short tail in *M. mulatta*; tail length dominance in intragroup hybridization may differ from that in intergroup hybridization. (3) Facial skin color: Pale lips and ears in *M. radiata* apparently are dominant to blackish lips and ears in *M. sinica*. (4) Dorsal pelage color: The saturate brown color in *M. assamensis* apparently is dominant to the drab brown color in *M. radiata*. Judging from available evidence, character states in *M. radiata* generally tend to be dominant over those in other macaque species; this was previously indicated by Hill (1937, p. 384), based on study of one *M. sinica* × *M. radiata* hybrid.

Evolution and Dispersal

The following reconstruction of the evolutionary history of the *sinica* group is based mainly on inferences from morphology, distribution, and natural history of living species and subspecies. Only one known fossil has been unequivocally referred to the *sinica* group (Delson, 1980, p. 19; Ha, 1985, p. 82).

Macaques probably reached southern Asia about Late Pliocene (Delson, 1980, p. 25), which implies that evolution of the *sinica* group occurred mainly during the Pleistocene. This was an epoch of great changes in the topography, climate, sea level, and plant distribution of southern and eastern Asia (Liu & Ding, 1984, p. 14; Sharma, 1984, p. 58; Vishnu-Mittre, 1984, p. 499), and undoubtedly

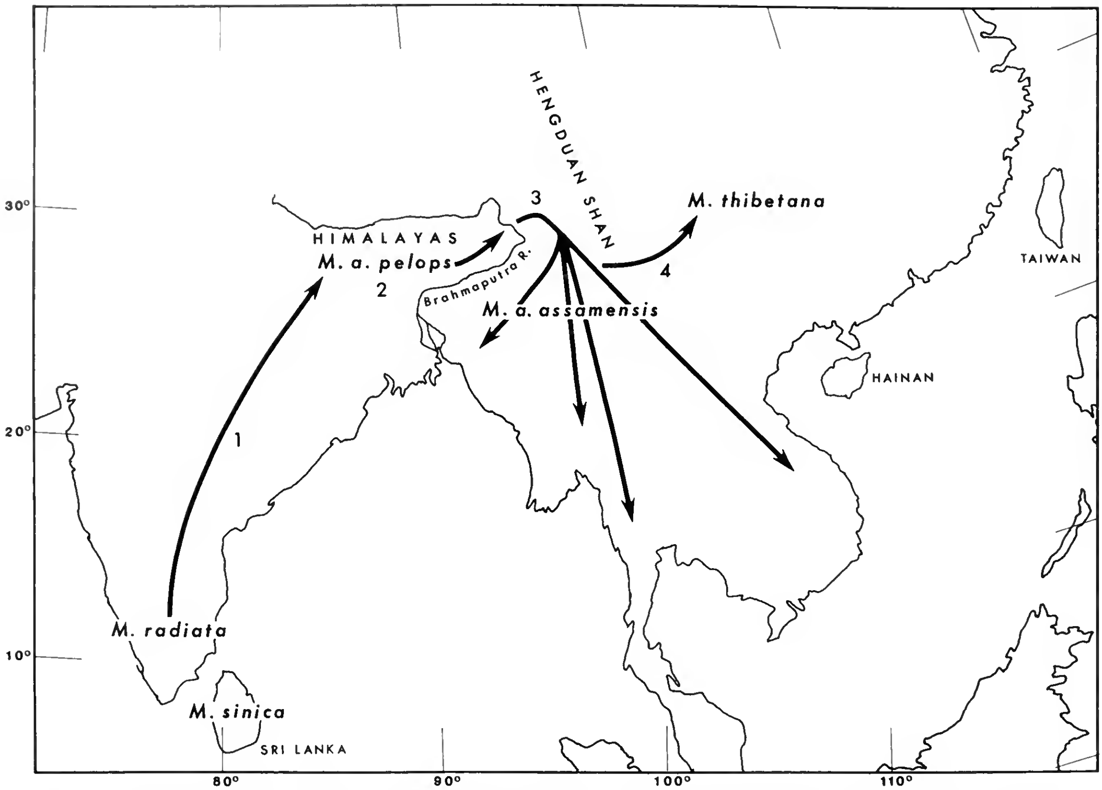

FIG. 15. Hypothetical reconstruction of principal stages in evolution and dispersal of *sinica*-group macaques.

these changes strongly influenced the evolutionary history of the *sinica* group. Unfortunately, knowledge of the details of these environmental changes generally is not sufficiently precise to permit specific environmental changes to be associated with specific evolutionary events in the history of the *sinica* group. Such association is attempted here only for Late Pleistocene and Holocene, the last two of six evolutionary stages discussed below.

1. Origin and Early Dispersal of *sinica* Group: *Macaca sinica/M. radiata*

Species and subspecies in the *sinica* group constitute an orderly morphological and geographic series that extends from small-bodied, long-tailed *M. sinica* and *M. radiata* in Sri Lanka and peninsular India at one extreme, to large-bodied, short-tailed *M. thibetana* in east-central China at the other extreme (fig. 2). The regularity of this series suggests that these species and subspecies originated sequentially as a result of successive episodes of dispersal, isolation, and differentiation. The evolutionary polarity in this series presumably is from longer-tailed species with many caudal vertebrae to shorter-tailed species with few caudal vertebrae, since a long tail generally is the primitive condition in monkeys. This implies that *M. sinica* and *M. radiata* probably are closest to the ancestral stock of the *sinica* group and that the center of origin of the group probably was in the area of Sri Lanka and peninsular India (fig. 15; cf. Hill & Bernstein, 1969, p. 13; Delson, 1980, p. 25; Eudey, 1980, p. 64; Wada, 1985, p. 38).

The *silenus* group of macaques apparently also originated in the area of Sri Lanka and peninsular India (Fooden, 1975, p. 68). The morphology of male and female genitalia is more derived in the *sinica* group (see pp. 19, 24) than in the *silenus* group (Fooden, 1975, p. 28). The *sinica* group may have originated as an offshoot of the *silenus* group in the Sri Lanka-peninsular India area. If so, the *silenus* group ancestor presumably was an unknown, extinct species in which the tail was longer than in living *M. silenus.* The origin of the *sinica* group probably occurred fairly early in the Pleistocene, judging from the number of subsequent speciation events that are inferred to have occurred in this group. The underlying cause of the original splitting, which presumably inaugurated the distinctive genital specializations of the *sinica* group, is unclear.

From the Sri Lanka-peninsular India area, the *sinica* group, at the stage of ancestral *Macaca sinica* or *M. radiata,* evidently spread northward and ultimately reached the foothills of the Himalayas (which were then lower than at present). Whether this northward dispersal occurred simultaneously with the parallel dispersal of the *silenus* group (Fooden, 1975, p. 68) is unknown; at present, species in these two groups are almost completely segregated from one another, either ecologically or geographically (Fooden, 1986, p. 14), and they may have been similarly segregated in the past. As the *sinica-radiata* stock moved northward, its body size apparently increased (fig. 3), in accord with Bergmann's rule, but its tail length apparently remained approximately constant—about 550 mm (fig. 4).

2. Origin of *Macaca assamensis pelops*

A major evolutionary discontinuity evidently occurred when an offshoot of the *sinica-radiata* stock colonized midelevation evergreen forest on the slopes of the east-west trending Himalayas (Fooden, 1982, p. 17). Tail length in the Himalayan population shortened, apparently abruptly, from about 550 to 300 mm (fig. 4). This shortening of the tail, which marked the origin of *M. assamensis pelops,* may have been an adaptation to the cooler climate of the new habitat, as predicated by Allen's rule. The *M. a. pelops* stock apparently spread from west to east through the belt of Himalayan midelevation evergreen forest.

3. Origin of *Macaca assamensis assamensis*

The next important change in the morphology of the *sinica* group evidently occurred when an offshoot of the *M. a. pelops* stock gained access to the foothills of the north-south trending mountains in Southeast Asia (Hengduan Shan) and became isolated there; this isolation may have been caused by a glacial advance in the region of the Brahmaputra gap at the eastern end of the Himalayan chain. Tail length in the isolated Hengduan Shan population decreased, again apparently abruptly, from about 300 to 200 mm (fig. 4), marking the origin of *M. a. assamensis.* Eastward spread of the newly evolved *M. a. assamensis* stock apparently was obstructed by the high north-south ranges of Hengduan Shan. Blocked from northward and eastward spread by high mountains, this stock evidently spread southward via midelevation forest accessible on the relatively low mountain chains that extend into the Indochinese Peninsula. As the *M. a. assamensis* stock spread southward, its head and body length apparently decreased, in accord with Bergmann's rule, but its tail length remained approximately constant (figs. 3–4). Ultimately, southward spread of the *M. a. assamensis* stock in the Indochinese Peninsula apparently was stopped by competition with *M. nemestrina leonina,* which has similar habitat requirements and is almost perfectly parapatric with *M. a. assamensis* (Fooden, 1982, p. 24). Fossil evidence indicates that *M. a. assamensis* reached northern Vietnam (Vo Nhai District, ca. 21°45′N, 106°00′E) before 18,600 YBP (Ha, 1985, p. 82).

4. Origin of *Macaca thibetana*

An offshoot of the *M. a. assamensis* stock apparently dispersed around the southern end of Hengduan Shan and became isolated in the region of upper Chang Jiang (Yangtze River). This isolation may have been caused by a glacial advance at the divide between the drainage basins of upper Lancang Jiang and Yuan Jiang (Mekong and Red rivers) and the drainage basin of upper Chang Jiang. Tail length in the isolated upper Chang Jiang population decreased, again abruptly, from about 200 mm to less than 100 mm (fig. 4), marking the origin of *M. thibetana.* Head and body length in the *M. thibetana* stock evidently has remained approximately the same as in the northern population of *M. a. assamensis* from which it was derived (fig. 3).

5. Late Pleistocene

During the period of the most recent glaciation, climaxing about 18,000 years ago, air temperature was reduced and sea level was lowered. Both of these environmental changes presumably affected species and subspecies of the *sinica* group: (1) Northern species and subspecies were forced southward or to lower altitudes along with their forest habitats (see Liu & Ding, 1984, p. 34). During this period, the altitudinal range of *Macaca a. pelops* presumably was lower on the slopes of the Himalayas than at present; the northern limit of

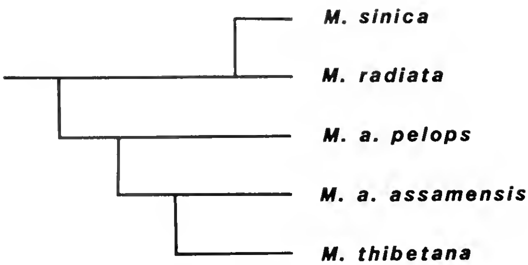

FIG. 16. Phylogenetic relationships inferred among *sinica*-group macaques. Note that *M. a. assamensis* and *M. thibetana* are shown as sharing a common ancestor more recently than *M. a. assamensis* and *M. a. pelops*; this is incongruous but unavoidable when a particular subspecies of one species is identified as the probable ancestor of another species.

the range of *M. thibetana* was farther south; the boundary between *M. thibetana* and *M. a. assamensis* was farther south; and the boundary between *M. a. assamensis* and *M. nemestrina leonina* was farther south and/or at lower altitudes. (2) As a consequence of glacially induced sea-level regression, the present range of *M. sinica* in Sri Lanka was connected to the present range of *M. radiata* in peninsular India (Jacob, 1949, p. 341; Sahni & Mitra, 1980, p. 56). The step-cline color gradient that now extends through both recognized subspecies of *M. sinica* and both recognized subspecies of *M. radiata* (Fooden, 1981, p. 9), transcending the specific boundary, suggests that the *M. sinica* and *M. radiata* stocks may have been genetically continuous—hence not specifically distinct—when their ranges were geographically continuous during the most recent glaciation. Hainan and Taiwan also were connected to the mainland during the same glaciation (Liu & Ding, 1984, p. 16), but neither of these islands is now inhabited by *sinica*-group macaques, although both are inhabited by macaques belonging to the *fascicularis* group (Fooden, 1980, p. 5). If *M. a. assamensis* or *M. thibetana* colonized Hainan or Taiwan during the late Pleistocene sea-level regression, they evidently subsequently became locally extinct.

6. Holocene

During the Holocene, as a consequence of postglacial warming, vegetation zones have shifted northward (with some oscillations), and the ranges of *Macaca a. pelops, M. a. assamensis,* and *M. thibetana* have correspondingly shifted northward and upward to their present latitudes and altitudes. Holocene sea-level elevation has separated Sri Lanka from peninsular India, thereby isolating the *sinica* stock from the *radiata* stock and presumably promoting their genetic divergence. The Holocene may also be the epoch when *M. mulatta* dispersed westward into northern peninsular India and disrupted the presumed former contiguity of the ranges of *M. radiata* and *M. a. pelops* (Fooden, in press). An isolated population of *M. radiata* within the range of *M. mulatta* in east-central peninsular India suggests that the advance of *M. mulatta* and disappearance of *M. radiata* in this area have occurred relatively recently (Fooden et al., 1981, p. 472; Saha, 1984, p. 164). The isolated Sundarbans population of *M. a. pelops* (Fooden, 1982, p. 2) may be another indication of recent contraction of the range of the *sinica* group in this area.

Phylogenetic relationships among *sinica*-group macaques that are implied by the proposed evolutionary reconstruction are depicted in Figure 16.

Acknowledgments

For facilitating this research, I am deeply grateful to officials and staff members of the institutions listed in the Introduction. I am also grateful to the Committee on Scholarly Communication with the People's Republic of China for supporting my study of *Macaca assamensis* and *M. thibetana* in China in 1985. Valued collaborators in the research project in China were Quan Guoqiang and Luo Yining, Institute of Zoology, Chinese Academy of Sciences, Beijing. I also thank James W. Koeppl and Peter Lowther, Field Museum of Natural History, for statistical advice and assistance, and Bruce D. Patterson, Field Museum of Natural History, for helpful comments on parts of the manuscript.

Gazetteer

This list of *sinica*-group macaque localities supplements previously published lists, as specified below for each species or subspecies. For specimens examined, a parenthetical notation indicates the abbreviated name of the institution where specimens are preserved (see Introduction), the number of specimens available, and the part that is preserved, if skin and skull are not both present.

Macaca sinica
(supplement to Fooden, 1979, p. 133; 1986, p. 2)

SRI LANKA

Ruhunu National Park; Southern Prov.; 06°21′N, 81°27′E; observed 1968–1975 by W. P. J. Dittus (1977, p. 242).

Udawatakelle Sanctuary; Central Prov.; 07°18′N, 80°39′E; observed 1968–1975 by W. P. J. Dittus (1977, pp. 239, 257).

Macaca radiata
(supplement to Fooden, 1981, p. 37; 1986, p. 2; Fooden et al., 1981, p. 469)

INDIA

Parambikulam Wildlife Sanctuary, ca. 600 m; Kerala State; ca. 10°25′N, 76°43′E; observed 1972–1978 by V. S. Vijayan (1979, p. 890); observed 1981–1983 by M. Balakrishnan and P. S. Easa (1986, p. 196).

Thambraparni and Servalar rivers, Mundanthurai Sanctuary, 180 m; Tamil Nadu State; ca. 08°40′N, 77°28′E; observed Feb. 1977–Apr. 1978 by R. Ali (1986, p. 98).

Udevara, NE, 960 m; Hassan District, Karnataka State; 13°01′N, 75°50′E; observed Apr. 1972–Aug. 1973 by H. Rahaman and M. D. Parthasarathy (1979, p. 406).

Macaca assamensis pelops
(supplement to Fooden, 1982, p. 35; 1986, p. 22)

CHINA

Xizang

Zhangmu; Nyalam Co.; 28°02′N, 85°55′E; collected by Scientific Mountaineering Team of China, 1974 (NWPIB, 1, skin only).

Macaca assamensis assamensis
(supplement to Fooden, 1982, p. 35; 1986, p. 22)

CHINA

Guangxi

Chongzuo Co., ca. 22°24′N, 107°21′E; reported by Tan (1985, p. 73).

Daming Shan (mt.); probably Shanglin Co.; ca. 23°23′N, 108°30′E; reported by Shen Lantian (in Tan, 1985, p. 73).

Daxin Co.; ca. 22°50′N, 107°12′E; reported by Wu (1983, p. 16).

Jingxi Co.; ca. 23°08′N, 106°25′E; reported by Wu (1983, p. 16). Comment: misspelled "Jiangxi" by Fooden (1986, p. 22).

Ningming Co.; ca. 22°07′N, 107°02′E; reported by Tan (1985, p. 73).

Guizhou

Jiangkou Co.; ca. 27°41′N, 108°49′E; apparently erroneous report (Editorial Committee of Guizhou Fauna, 1979, p. 110), probably based on misidentified *M. thibetana* (see Fooden et al., 1985, p. 15). Not mapped in Figure 1.

Xizang

Beibeng, 900 m; Medog Co.; 29°15′N, 95°30′E; collected by Cai Guiquan and Feng Zuojian, 3 Aug. 1977 (NWPIB, 1). Comment: locality previously recorded as "Medog" (Fooden, 1982, p. 41).

Yigong, 2250 m and 2750 m; Bomi Co.; 30°08′N, 95°02′E; collected by Feng Zuojian and Zheng Changlin, 21 June and 9 Sep. 1973 (IZCAS, 2 [including 1 skull at NWPIB]). Comment: locality previously recorded as "Bomi" (Fooden, 1982, p. 39).

Yunnan

Lengsuihe; Datang Dist., Tenchong Co.; 25°39′N, 98°38′E; collected by Fang Lixiang, Apr. 1960 (BJMNH, 2, skins only).

Lijiang Co.; 26°51′N, 100°13′E; apparently erroneous report (Tan, 1985, p. 73). Comment: according to Wang Yingxiang, KIZ, the only species of macaque in Lijiang Co. is *M. mulatta* (pers. comm., 11 Dec. 1985). Not mapped in Figure 1.

Longling Co. (Li & Lin, 1983, p. 113). See Xiaoheshan (Fooden, 1986, p. 22).

Luchun Co. (Li & Lin, 1983, p. 113). See Dahongshan (Fooden, 1986, p. 22).

Menglian Co.; ca. 22°21′N, 99°36′E; reported by Tan (1985, p. 73).

Pingbian Co. (Li & Lin, 1983, p. 113). See Dawei Shan (Fooden, 1986, p. 22).

Xishuangbanna Prefecture (Li & Lin, 1983, p. 113). See Lancang Jiang, Menglun, Menghan, Xiangming, Manpa, and Mengla Xian (Fooden, 1986, p. 22).

INDIA

Proposed Dhaleswari Wildlife Sanctuary; Assam State; 24°10′–24°40′N, 92°20′–93°10′E; reported by Choudhury (1983, p. 14).

THAILAND

Huai Nua Pla, 2500 ft [760 m]; Tak Prov.; 16°54′N, 98°48′E; collected by J. H. Chambai, 9 May 1924 (ZRCNUS, 1). Comments: for locality notes and coordinates, see Chasen and Kloss (1930, p. 62) and Moore and Tate (1965, p. 321); specimen previously misidentified as *M. mulatta* (Fooden, 1982, p. 52).
Hue Nya Pla. See Huai Nua Pla.
Hue Yah Pla. See Huai Nua Pla.

Macaca thibetana
(supplement to Fooden, 1983, p. 14; Fooden et al., 1985, p. 15)

CHINA

Anhui

Banqiao, 700–1000 m; Ningguo Co.; ca. 30°38′N, 118°58′E; hunter's pelt observed in farmhouse, 1973–1985 (Wada et al., 1986, pp. 81, 83). Not mapped in Figure 1.
Chimen Co. See Qimen Co.
Gegong, 600–800 m; Dongzhi Co.; 30°05′N, 117°11′E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).
Guimenguan, 500 m; Huang Shan, Shexian Co.; ca. 30°03′N, 118°09′E; troop captured Nov. 1972 (Wada et al., 1986, p. 89).
Guniujiang, 1000–1500 m; Shitai-Qimen Cos.; ca. 30°05′N, 117°30′E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).
Huanghuajian, 600–1200 m; Shitai Co.; ca. 30°08′N, 117°20′E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).
Jilian, 600–800 m; Yixian Co.; ca. 30°00′N, 118°00′E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).
Jiuhua Shan, 1000–1200 m; Qingyang Co.; ca. 30°27′N, 117°48′E; 6 troops reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, pp. 83, 90).
Lianhuafeng, 800–1600 m; Huang Shan, Shexian Co.; ca. 30°07′N, 118°10′E; observed 1976 by Xiong Chengpei (Wada et al., 1986, p. 89).
Pailou, 600 m; Guichi Co.; 30°21′N, 117°18′E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).
Qihong, 200–600 m; Qimen Co.; ca. 29°35′N, 117°40′E; one monkey captured 1964, apparently now extinct at locality (Wada et al., 1986, p. 83).
Qimen Co.; ca. 29°53′N, 117°43′E; reported by Tan (1985, p. 75).
Quliting, 1000–1400 m; Huang Shan, Shexian Co.; ca. 30°08′N, 118°11′E; observed 1976 by Xiong Chengpei (Wada et al., 1986, p. 89).
Rucun, 500–1000 m; Xiuning Co.; ca. 29°55′N, 118°07′E; observed 1960–1965, apparently now extinct at locality (Wada et al., 1986, p. 83).
Shangyangjian, 800–1200 m; Jixi Co.; ca. 30°05′N, 118°20′E; hunter's pelt observed in farmhouse, 1973–1985 (Wada et al., 1986, pp. 81, 83). Not mapped in Figure 1.
Songguan, 890–1700 m; Huang Shan, Shexian Co.; ca. 30°11′N, 118°10′E; observed 1976 and 1977 by Xiong Chengpei (Wada et al., 1986, p. 89).
Tanglingguan, 800–1350 m; Huang Shan, Shexian Co.; ca. 30°07′N, 118°09′E; observed 1977 by Xiong Chengpei (Wada et al., 1986, p. 89).
Tianbangshi, 700–1100 m; Huang Shan, Shexian Co.; ca. 30°07′N, 118°09′E; one troop captured Nov. 1972; another troop observed 1975–1977 by Xiong Chengpei, 1985 by Wada et al. (1986, p. 89).
Xiancun, 600–900 m; Taiping Co.; ca. 30°08′N, 118°05′E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).
Xiangrupeng, ca. 800 m; Huang Shan, Shexian Co.; ca. 30°08′N, 118°06′E; 15 monkeys captured 1980 (Wada et al., 1986, p. 89).
Xinglong, 600–800 m; Jingde Co.; ca. 30°19′N, 118°31′E; hunter's pelt observed in farmhouse, 1973–1985 (Wada et al., 1986, pp. 81, 83). Not mapped in Figure 1.
Yixian Co.; ca. 29°55′N, 117°55′E; reported by Tan (1985, p. 75).
Yulingkeng, 800–1100 m; Huang Shan, Shexian Co.; ca. 30°04′N, 118°08′E; observed 1973–1977 and 1980 by Xiong Chengpei; 27 monkeys captured 1974 and 1977; observed 1985 by Wada et al. (1986, p. 89).
Yungusi, 570–1000 m; Huang Shan, Shexian Co.; ca. 30°07′N, 118°13′E; observed 1973 and 1975 by Xiong Chengpei (Wada et al., 1986, p. 89).
Yunwaifeng, ca. 1000 m; Huang Shan, Shexian Co.; ca. 30°08′N, 118°09′E; observed 1977 by Xiong Chengpei (Wada et al., 1986, p. 89).

Fujian

Dadongken; Shangang Dist., Chong'an Co.; 27°50′N, 117°48′E; collected by Qin Yaoling, 1960 (SCIEA, 1).
Guangze Co.; ca. 27°31′N, 117°19′E; observed Sep. 1981 (Zheng, 1984, p. 145), cited as *M. arctoides.*

Longyan Co.; ca. 25°06′N, 117°00′E; tentative identification; observed Oct. 1982, cited as *M. arctoides* by Zheng (1984, p. 146), who applies the same name to the stumptail macaque of Chong'an Co. (= *M. thibetana*; AMNH, FMNH, MCZ, MNHN, SCIEA, USNM).

Meihua Shan (mts.); ca. 25°15′N, 116°45′E; tentative identification; reported as *M. arctoides* by Zheng (1984, p. 146), who applies the same name to the stumptail macaque of Chong'an Co. (= *M. thibetana*; AMNH, FMNH, MCZ, MNHN, SCIEA, USNM).

Pucheng Co.; ca. 27°54′N, 118°31′E; observed Aug. 1980 (Zheng, 1984, p. 145), cited as *M. arctoides.*

Shanghang Co.; ca. 25°02′N, 116°23′E; tentative identification; observed Sep. 1982, cited as *M. arctoides* by Zheng (1984, p. 146), who applies the same name to the stumptail macaque of Chong'an Co. (= *M. thibetana*; AMNH, FMNH, MCZ, MNHN, SCIEA, USNM).

Shaowu Co.; ca. 27°19′N, 117°29′E; observed June 1983 (Zheng, 1984, p. 145), cited as *M. arctoides.*

Gansu

Southern Gansu; ca. 32°50′N, 104°40′E; reported by Tan (1985, pp. 75, 80).

Guangdong

Bibei Qu, 100–200 m; Ruyuan Co.; ca. 25°01′N, 113°17′E; collected by unknown Yao hunter, 9 Nov. 1985, not preserved (Ling Wenfeng, RCFB, pers. comm., 10 Nov. 1985).

Da'ao, 500–600 m; Luoyang Dist., Ruyuan Co.; 24°43′N, 113°05′E; traces observed Feb. 1983 by Ling Wenfeng, RCFB (pers. comm., 10 Nov. 1985).

Dapingding, ca. 1000 m; Longnan Dist., Ruyuan Co.; 24°48′N, 113°06′E; observed 2 Oct. 1985 by Ling Wengfeng, RCFB (pers. comm., 10 Nov. 1985).

Goujiken, 700 m; Ruyuan Co.; 24°56′N, 113°04′E; observed 8 Nov. 1985 by Huang Mingyan (Ling Wengfeng, RCFB, pers. comm., 10 Nov. 1985).

Gouweizhang, < 1684 m; Dongpin Dist., Ruyuan Co.; 24°57′N, 113°14′E; observed 15 Oct. 1985 by vice-director of district (Ling Wengfeng, RCFB, pers. comm., 10 Nov. 1985).

Gumudong, 600–700 m; Gumushui Dist., Ruyuan Co.; 24°36′N, 113°03′E; crop raid June 1985 reported by local farmers (Ling Wengfeng, RCFB, pers. comm., 10 Nov. 1985).

Julongpin, ca. 1400 m; Lianxian Co.; 24°52′N, 112°41′E; living captive observed 25 Oct. 1985 by Cheng Xinzhou (pers. comm., 13 Nov. 1985).

Jushonglou, 1000 m; Fucheng Dist., Ruyuan Co.; 24°49′N, 113°17′E; > 300 monkeys shot by local hunter in 1969–1971; observed 3 Nov. 1985 by officials of county construction bureau (Ling Wengfeng, RCFB, pers. comm., 10 Nov. 1985).

Laopengeyiduei, 0.7 km NNE, 1100 m; Ruyuan Co.; 24°56′N, 113°01′E; collected by Mr. Zhang, Forest Ranger, Qinxidong Nature Reserve, 11 June 1985 (QNR headquarters, living captive observed 9 Nov. 1985).

Leyang, ca. 800 m; Ruyuan Co.; 24°40′N, 113°03′E; collected by Liu Zhenhe and Xu Longhuei, June 1970 and 15 July 1981 (SCIEA, 3, including 1 skull only).

Longnan Dist.; Ruyuan Co.; ca. 24°50′N, 113°05′E; collected by Quan Guoqiang, 10 Nov. 1985 (IZCAS, 2, skulls only).

Pingxi, ca. 800 m; Ruyuan Co.; 24°45′N, 113°00′E; collected by Xu Longhuei, 15 July 1981 (SCIEA, 1).

Qinxidong Nature Reserve, Tract No. 25, ca. 700 m; Ruyuan Co.; 24°58′N, 113°02′E; collected by Ling Wenfeng, RCFB, Oct. 1983, two specimens, not preserved (pers. comm., 10 Nov. 1985).

Qinxidong Nature Reserve, Tract No. 37, ca. 1100 m; Ruyuan Co.; 24°57′N, 113°03′E; calls of two monkeys heard 6 Nov. 1985 by Ling Wenfeng, RCFB (pers. comm., 10 Nov. 1985).

Qinxidong Nature Reserve, Tract No. 44, ca. 1000 m; Ruyuan Co.; 24°56′N, 113°03′E; observed Oct. 1983 by Ling Wenfeng, RCFB (pers. comm., 10 Nov. 1985).

Shijiaoken, 700 m; Ruyuan Co.; 24°57′N, 113°05′E; observed Oct. 1983 by Ling Wenfeng, RCFB (pers. comm., 10 Nov. 1985).

Tianjinshan, 800–1000 m; Luoyang Dist., Ruyuan Co.; 24°42′N, 112°53′E; observed July 1983 by local officials (Ling Wenfeng, RCFB, pers. comm., 10 Nov. 1985).

Yao Shan (mts.), 800–1200 m; Lechang Co.; ca. 25°15′N, 113°15′E, collected by R. Mell, Sep. 1908–Feb. 1911 (ZMB, 1). Comment: type locality of *M. arctoides esau* Matschie, 1912; previously reported as "Yao-tze Berge" (Mell in Matschie, 1912, p. 309; Mell, 1922, pp. 4, 10; Fooden, 1983, pp. 2, 17).

Guangxi

Chuanzhou Co. See Quanzhou Co.

Lingui Co.; ca. 25°12′N, 110°11′E; reported by Shen Lantian (in Tan, 1985, p. 75).

Lipu Co.; ca. 24°30′N, 110°24′E; reported by Shen Lantian (in Tan, 1985, p. 75).

Longsheng Co.; ca. 25°43′N, 110°01′E; reported by Shen Lantian (in Tan, 1985, p. 75).

Luoyiang; Huanjiang Co.; 24°58′N, 108°12′E; collected by local people in 1981, not preserved (reported 29 Nov. 1985 by Wu Mingchuan, GIFID, to Quan Guoqiang, IZCAS; pers. comm., 12 Dec. 1985).

Quanzhou Co.; ca. 25°56′N, 111°02′E; reported by Shen Lantian (in Tan, 1985, p. 75).

Xunle, Huanjiang Co.; 25°25′N, 108°15′E; present in 1981 (reported 29 Nov. 1985 by Wu Mingchuan, GIFID, to Quan Guoqiang, IZCAS; pers. comm., 12 Dec. 1985).

Yangshuo Co.; ca. 24°46′N, 110°29′E; reported by Shen Lantian (in Tan, 1985, p. 75).

Yangso Co. See Yangshuo Co.

Yongfu Co.; ca. 24°57′N, 109°58′E; reported by Shen Lantian (in Tan, 1985, p. 75).

Youngfu Co. See Yongfu Co.

Yueli; Nandan Co.; 25°25′N, 107°15′E; specimen collected Nov. 1981 by local people, not preserved (reported 29 Nov. 1985 by Wu Mingchuan, GIFID, to Quan Guoqiang, IZCAS; pers. comm., 12 Dec. 1985).

Ziyaan Co. See Ziyuan Co.

Ziyuan Co.; ca. 26°01′N, 110°39′E; reported by Shen Lantian (in Tan, 1985, p. 75).

Guizhou

Chingzhen Co. See Qingzhen Co.

Guiding Co.; ca. 26°34′N, 107°13′E; reported by Editorial Committee of Guizhou Fauna (1979, p. 110).

Jiangkou Co. (Editorial Committee of Guizhou Fauna, 1979, p. 110). See Fooden et al. (1985, p. 15).

Qingzhen Co.; ca. 26°33′N, 106°28′E; reported by Editorial Committee of Guizhou Fauna (1979, p. 110).

Sandu Co.; ca. 25°58′N, 107°51′E; reported by Editorial Committee of Guizhou Fauna (1979, p. 110).

Suiyang Co.; ca. 27°56′N, 107°10′E; reported by Editorial Committee of Guizhou Fauna (1979, p. 110).

Xingyi Co.; ca. 25°05′N, 104°53′E; reported by Editorial Committee of Guizhou Fauna (1979, p. 110).

Zheng'an Co.; ca. 28°33′N, 107°26′E; reported by Editorial Committee of Guizhou Fauna (1979, p. 110).

Zhijin Co.; ca. 26°39′N, 105°46′E; reported by Editorial Committee of Guizhou Fauna (1979, p. 110).

Hunan

Chengbu Co.; ca. 26°20′N, 110°19′E; reported by local people, Nov. 1980 (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985).

Guidong Co., E; ca. 26°00′N, 113°53′E; reported by local people, Oct. 1979 (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985). Comment: cited as *M. arctoides* by Tan (1985, p. 74; pers. comm., 16 Dec. 1985).

Huangshuang Nature Reserve; Suining Co.; 26°25′N, 110°03′E; reported by local people, Nov. 1980 (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985). Comment: cited as *M. arctoides* by Tan (1985, p. 74; pers. comm., 16 Dec. 1985).

Lanshan Co.; 25°21′N, 112°10′E; living captive obtained 1982 (observed in Lianxian, Guangdong Prov., 13 Nov. 1985).

Shunhuangshan Plantation, ca. 1000 m; Xinning Co.; ca. 26°30′N, 110°55′E; reported by local people, Nov. 1980 (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985). Comment: cited as *M. arctoides* by Tan (1985, p. 74; pers. comm., 16 Dec. 1985).

Xinning Co.; ca. 26°31′N, 110°48′E; collected 24 Dec. 1984 by local residents (Zhou, 1986, p. 109).

Zhezhiping, 1200 m; Mangshan Dist., Yizhang Co.; ca. 24°56′N, 112°53′E; collected by Liu Zhenhe, 9 Nov. 1980 (SCIEA, 1). Comment: cited as *M. arctoides* by Tan (1985, p. 74; pers. comm., 16 Dec. 1985).

Zhiyunshan Nature Reserve, ca. 1000 m; Xinning Co.; ca. 26°35′N, 111°05′E; reported by local people, Nov. 1980 (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985). Comment: cited as *M. arctoides* by Tan (1985, p. 74; pers. comm., 16 Dec. 1985).

Jiangxi

Guixi Co.; Wuyi Shan (mts.); ca. 28°18′N, 117°12′E; living captives collected, Winter 1983, not preserved (Sheng Helin, ECNU, pers. comm., 19 Oct. 1985).

Hexilong, 700–1000 m; Jinggangshan Co.; ca. 26°32′N, 114°09′E; collected by Zheng Xianhuai, 25 Dec. 1982 (JNRB, 1, mounted skin with skull inside).

Jingzhushan, 1000 m; Jinggangshan Co.; 26°31′N, 114°06′E; collected by Long Dizong, 1 April 1980 (JUBD, 1, mounted skin with skull inside).

NE Jiangxi, "near the Anhui border"; probably Jingdezhen Co.; ca. 29°00′N, 118°00′E; reported by Tan (1985, pp. 75, 80).
Pingxiang (town), vicinity; Pingxiang Co.; ca. 27°38′N, 113°50′E; living captive collected 1983, observed in Pingxiang Zoo by Sheng Helin, ECNU (pers. comm., 19 Oct. 1985) and Huang Zhangsen, NZ (pers. comm., 28 Oct. 1985).
Shangyou Co.; ca. 25°48′N, 114°30′E; living captive obtained May–June 1978 by Ma Jielun, Ganzhou Zoo (captive observed at GZ, 6 Nov. 1985). Comment: probably collected at Wuzhifeng, Shangyou Co.
Shanbaishan; Xunwu Co.; ca. 25°00′N, 115°45′E; collected in 1976 by local people, not preserved (Liu Zhenhe, SCIEA, pers. comm., 25 Nov. 1985).
Yanshan Co.; ca. 28°18′N, 117°42′E; two living captives collected by Huang Zhangsen, 1980 (captives observed at NZ, 28 Oct. 1985); living captives collected by local people, Winter 1983 (Sheng Helin, ECNU, pers. comm., 19 Oct. 1985). Comment: misspelled "Qianshan" by Fooden et al. (1985, p. 15).
Yushan Co., probably; ca. 28°41′N, 118°13′E; living captive obtained in late 1970s by Wu Fuhai, Hangzhou Zoo, Zhejiang Prov. (captive observed at HZ, 25 Oct. 1985). Comment: obtained from local people in Jiangshan, Zhejiang; reportedly collected across provincial boundary in nearby Jiangxi Prov.

Sichuan

Bao Guo Si (temple), near; Emei Shan (mt.), Emei Co.; ca. 29°32′N, 103°21′E; collected by Quan Guoqiang, Aug. 1959 (IZCAS, 1, skull only).
Chiu-lao-tung; Emei Shan (mt.), Emei Co.; ca. 29°32′N, 103°21′E; observed Aug. 1982 by J. D. Lazell, Jr. (1983, p. 61).
Xiang Feng, ca. 1900 m; Emei Shan (mt.), Emei Co.; ca. 29°32′N, 103°21′E; observed Aug. 1982 by J. D. Lazell, Jr. (1983, p. 62).
"Western Sichuan", 43 counties; 27°–33°N, 98°–103°E; questionable report (Tan, 1985, pp. 75, 80). Comment: hitherto, only *M. mulatta* has been reported or collected in this area (Wilson, 1913, p. 192; Weigold, 1935, p. 233). Not mapped in Figure 1.

Xizang

"Eastern Tibet"; ca. 28°40′N, 97°00′E; improbable report (Tan, 1985, pp. 75, 80). Comment: apparently in range of *M. a. assamensis* (see Fooden, 1982, p. 27). Not mapped in Figure 1.
Xizang Prov.; improbable locality datum (SMNH, 1, skin only). Comment: specimen received 8 June 1962 from Shanghai Zoological Garden, which now has no record of it (Zhang Cizu, SZG, pers. comm., 18 Oct. 1985). Not mapped in Figure 1.

Yunnan

Yongshan Co.; ca. 28°10′N, 103°40′E; collected Aug. 1984 by local hunter, not preserved (Wang Yingxiang, KIZ, pers. comm., 11 Dec. 1985).

Zhejiang

Beiyandangshan; Yueqing Co.; 28°23′N, 121°04′E; collected by Chai Weixi, 1960 (ZMNH, 2, mounted skins with skulls inside).
Daoshiwu; Lin'an Co.; ca. 30°13′N, 119°43′E; living captives collected Feb. 1985 by local people (Wu Fuhai, HZ, pers. comm., 25 Oct. 1985).
Jiulong Shan. See Zhuanxian.
Wangcunkou; Suichang Co.; 28°24′N, 118°59′E; collected by Mao Jiangsen, June 1979 (IMMZAM, 1).
Zhoucun, ca. 1000 m; Jiangshan Co.; 28°22′N, 118°37′E; collected by Kang Ximin, 23 Mar. 1985 (ZMNH, 1).
Zhuanxian, near Jiulong Shan (mt.); Suichang Co.; ca. 28°20′N, 119°00′E; collected by villagers, 23 May 1957 (Zhou, 1984, p. 58).
Zhidaikou, ca. 1000 m; Suichang Co.; 28°16′N, 118°46′E; observed Aug. 1985 by Kang Ximin, ZMNH (pers. comm., 24 Oct. 1985).

Literature Cited

ACHARJYO, L. N., AND R. MISRA. 1977. Notes on a young hybrid macaque. Journal of the Bombay Natural History Society, **73**: 521–522.

———. 1982. Further notes on the birth of hybrid macaque *Macaca radiata* × *Macaca assamensis* at Nandankanan Biological Park, Orissa. The Indian Forester, **108**: 376. (Reprinted in The Indian Forester, **108**: 464.)

AHALEY, S. K., M. K. GOVERDHAN, AND N. S. GANDHI. 1978. Hemoglobin types in *Presbytis entellus* and *Macaca radiata*. Indian Journal of Heredity, **10**: 51–57.

ALBRECHT, G. H. 1978. The craniofacial morphology of the Sulawesi macaques: Multivariate approaches to biological problems. Contributions to Primatology, **13**: 1–151.

———. 1980. Latitudinal, taxonomic, sexual, and insular determinants of size variation in pigtail macaques. International Journal of Primatology, **1**: 141–152.

ALI, R. 1986. Feeding ecology of the bonnet macaque at the Mundanthurai Sanctuary, Tamilnadu. Journal of the Bombay Natural History Society, **83:** 98–110.

ANKEL, F. 1962. Vergleichende Untersuchungen über die Skelettmorphologie des greifschwanzes südamerikanischer Affen (Platyrrhina). Zeitschrift für Morphologie und Ökologie der Tiere, **52:** 131–170.

———. 1972. Vertebral morphology of fossil and extant primates, pp. 223–240. *In* Tuttle, R. H., ed., The Functional and Evolutionary Biology of Primates. Aldine-Atherton, Chicago.

ANNENKOV, G. A. 1974. Proteins of the Blood Serum of Primates. Meditsina, Moscow. (In Russian.)

ARDITO, G. 1979. Primate chromosome atlas, pp. 211–281. *In* Chiarelli, B., A. L. Koen, and G. Ardito, eds., Comparative Karyology of Primates. Mouton, The Hague.

BALAKRISHNAN, M., AND P. S. EASA. 1986. Habitat preferences of the larger mammals in the Parambikulam Wildlife Sanctuary, Kerala, India. Biological Conservation, **37:** 191–200.

BARNES, R. D., B. L. LASLEY, AND A. G. HENDRICKX. 1978. Midcycle ovarian histology of the bonnet monkey, *Macaca radiata.* Biology of Reproduction, **18:** 537–553.

BERNSTEIN, I. S., AND T. P. GORDON. 1979. Inter- and intraspecific sexual behavior in two species of macaque: A possible behavioral barrier to gene flow. Behavioural Processes, **4:** 265–272.

———. 1980. Mixed taxa introductions, hybrids, and macaque systematics, pp. 125–147. *In* Lindburg, D. G., ed., The Macaques: Studies in Ecology, Behavior and Evolution. Van Nostrand Reinhold, New York.

BROWN, C. J., V. G. DUNBAR, AND D. A. SHAFER. 1984. A comparison of the karyotypes of 5 species of the genus *Macaca* and a species of the genus *Cercocebus.* Genetics, **107:** s14. (Abstract only.)

———. 1986. A comparison of the karyotypes of six species of the genus *Macaca* and a species of the genus *Cercocebus.* Folia Primatologica, **46:** 164–172.

BRUCE, E. J. 1977. A study of the molecular evolution of primates using the techniques of amino acid sequencing and electrophoresis. Ph.D. thesis, University of California, Davis.

CANN, R., J. E. CRONIN, AND V. M. SARICH. 1979. Molecular approaches to the study of systematics in the macaques. American Journal of Physical Anthropology, **50:** 425. (Abstract only.)

CAO XIAOMEI, CHEN YIFENG, LUO LIHUA, AND SHAN XIANGNIAN. 1981. A comparative study on the nucleolus organizer regions in chromosomes of eleven species of primates. Zoological Research, **2:** 119–123. (In Chinese, English abstract; English abstract reprinted in Biological Abstracts, **75:** 8168 [1983].)

CHAINE, J. [1927]. L'os pénien: Étude descriptive et comparative. Actes de la Société Linnéenne de Bordeaux, **78:** 5–195.

CHASEN, F. N., AND C. B. KLOSS. 1930. On mammals from the Raheng district, western Siam. The Journal of the Siam Society, Natural History Supplement, **8:** 61–78.

CHEN YIFENG AND LUO LIHUA. 1985. Comparative studies on G- and C-banded chromosomes of three subspecies of the stump-tailed monkey (*Macaca speciosa*), pp. 83–85. *In* Kawamichi, T., ed., Contemporary Mammalogy in China and Japan. Mammalogical Society of Japan, Tokyo.

CHEN YIFENG, LUO LIHUA, SHAN XIANGNIAN, AND CAO XIAOMEI. 1980. A comparative study of the karyotypes of the four species of the genus *Macaca.* Zoological Research, **1:** 91–99. (In Chinese, English abstract; English abstract reprinted in Antropologia Contemporanea, **3:** 292 [1980].)

———. 1981. Chromosomes of the Primates in China. Academic Press, Beijing. (In Chinese.)

CHIARELLI, B. 1961. Ibridologia e systematica in primati: I. Raccolta di dati. Atti Associazione Genetica Italiana, **6:** 213–220.

———. 1966. Caryology and taxonomy of the catarrhine monkeys. American Journal of Physical Anthropology, **24:** 155–169.

———. 1973. Check-list of Catarrhina primate hybrids. Journal of Human Evolution, **2:** 301–305.

———. 1979. Problems of primate karyology, pp. 27–28. *In* Chiarelli, B., A. L. Koen, and G. Ardito, eds., Comparative Karyology of Primates. Mouton, The Hague.

CHOUDHURY, A. U. 1983. Plea for a new wildlife refuge in eastern India. Tigerpaper, **10**(4): 12–15.

CLUTTON-BROCK, T. H., P. H. HARVEY, AND B. RUDDER. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature, **269:** 797–800.

CRONIN, J. E., R. CANN, AND V. M. SARICH. 1980. Molecular evolution and systematics of the genus *Macaca,* pp. 31–51. *In* Lindburg, D. G., ed., The Macaques: Studies in Ecology, Behavior and Evolution. Van Nostrand Reinhold, New York.

CRONIN, J. E., AND W. E. MEIKLE. 1979. The phyletic position of *Theropithecus*: Congruence among molecular, morphological, and paleontological evidence. Systematic Zoology, **28:** 259–269.

CUVIER, F. 1820. Le toque mâle, liv. 18, pp. 1–2. *In* Geoffroy Saint-Hilaire, E., and F. Cuvier, Histoire Naturelle des Mammifères, vol. 1. Belin, Paris.

CUVIER, G. 1846. Leçons d'Anatomie Comparée, 2nd ed., vol. 8. Fortin, Masson, Paris.

DÀO VAN TIÊN. 1967. Notes sur une collection de mammifères de la région de Yên-bai (Nord-Vietnam). Mitteilungen aus dem Zoologischen Museum in Berlin, **43:** 117–125.

———. 1978. Sur une collection de mammifères du plateau de Môc châu (Province de So'n-la, Nord-Vietnam). Mitteilungen aus dem Zoologischen Museum in Berlin, **54:** 377–391.

DARGA, L. L., M. GOODMAN, M. L. WEISS, G. W. MOORE, W. PRYCHODKO, H. DENE, R. TASHIAN, AND A. KOEN. 1975. Molecular systematics and clinal variation in macaques, pp. 797–812. *In* Markert, C. L., ed., Isozymes IV: Genetics and Evolution. Academic Press, New York.

DATHE, R. 1983. Haltungsrekord eines weiblichen Bartrhesus (*Macaca assamensis* M'Clelland, 1839) im Tierpark Berlin. Der Zoologische Garten (NF), **53:** 125–132.

DAUBENTON, L. J. M. 1766. Description de la partie du cabinet qui a rapport à l'histoire naturelle des guenons, pp. 304–310. *In* Buffon, G. L. L. de, and L. J. M. Daubenton, Histoire Naturelle Générale et Particulière, avec la Description du Cabinet du Roi, vol. 14. L'Imprimerie Royale, Paris.

DE BEAUX, O. 1917. Osservazioni morfologiche e sistematiche sul penis de "*Macacus arctoides*" Is. Geoffr. e di cinque altre specie di macachi. Giornale per la Morfologia dell'Uomo e dei Primati, **1**: 1–12.

DELSON, E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment, pp. 10–30. *In* Lindburg, D. G., ed., The Macaques: Studies in Ecology, Behavior and Evolution. Van Nostrand Reinhold, New York.

DEVOR, E. J. R. 1977. Genetic differentiation in the genus *Macaca*. American Journal of Physical Anthropology, **47**: 127. (Abstract only.)

DITTUS, W. P. J. 1974. The ecology and behavior of the toque monkey, *Macaca sinica*. Ph.D. thesis, University of Maryland, College Park.

———. 1975. Population dynamics of the toque monkey, *Macaca sinica*, pp. 125–151. *In* Tuttle, R. H., ed., Sociobiology and Psychology of Primates. Mouton, The Hague.

———. 1977. The socioecological basis for the conservation of the toque monkey (*Macaca sinica*) of Sri Lanka (Ceylon), pp. 237–265. *In* Prince Ranier III and G. H. Bourne, eds., Primate Conservation. Academic Press, New York.

DIXSON, A. F. 1987. Baculum length and copulatory behavior in primates. American Journal of Primatology, **13**: 51–60.

DUTRILLAUX, B., J. COUTURIER, M. MULERIS, M. LOMBARD, AND G. CHAUVIER. 1982. Chromosomal phylogeny of forty-two species or subspecies of cercopithecoids (Primates Catarrhini). Annales de Génétique, **25**: 96–109.

EDITORIAL COMMITTEE OF GUIZHOU FAUNA. 1979. Distribution List of Vertebrates of Guizhou. Guizhou People's Publishing Co., Guiyang. (In Chinese.)

EUDEY, A. A. 1980. Pleistocene glacial phenomena and the evolution of Asian macaques, pp. 52–83. *In* Lindburg, D. G., ed., The Macaques: Studies in Ecology, Behavior and Evolution. Van Nostrand Reinhold, New York.

FITZINGER, L. J. 1864. Nachrichten aus dem zoologischen Garten in München. Der Zoologische Garten, **5**: 335–338.

FLOWER, S. S. 1929. A List of the Vertebrated Animals Exhibited in the Gardens of the Zoological Society of London, 1828–1927. I, Mammals. Zoological Society, London.

FOODEN, J. [1966]. Identification of the stump-tailed monkey, *Macaca speciosa* I. Geoffroy, 1826. Folia Primatologica, **5**: 153–164.

———. 1969. Taxonomy and evolution of the monkeys of Celebes (Primates: Cercopithecidae). Bibliotheca Primatologica, **10**: 1–148.

———. 1971. Female genitalia and taxonomic relationships of *Macaca assamensis*. Primates, **12**: 63–73.

———. 1975. Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). Fieldiana: Zoology, **67**: 1–169.

———. 1979. Taxonomy and evolution of the *sinica* group of macaques: 1. Species and subspecies accounts of *Macaca sinica*. Primates, **20**: 109–140.

———. 1980. Classification and distribution of living macaques (*Macaca* Lacépède, 1799), pp. 1–9. *In* Lindburg, D. G., ed., The Macaques: Studies in Ecology, Behavior and Evolution. Van Nostrand Reinhold, New York.

———. 1981. Taxonomy and evolution of the *sinica* group of macaques: 2. Species and subspecies accounts of the Indian bonnet macaque, *Macaca radiata*. Fieldiana: Zoology, n.s., no. **9**: 1–52.

———. 1982. Taxonomy and evolution of the *sinica* group of macaques: 3. Species and subspecies accounts of *Macaca assamensis*. Fieldiana: Zoology, n.s., no. **10**: 1–52.

———. 1983. Taxonomy and evolution of the *sinica* group of macaques: 4. Species account of *Macaca thibetana*. Fieldiana: Zoology, n.s., no. **17**: 1–20.

———. 1986. Taxonomy and evolution of the *sinica* group of macaques: 5. Overview of natural history. Fieldiana: Zoology, n.s., no. **29**: 1–22.

———. In press. Classification, distribution, and ecology of Indian macaques. *In* Seth, P. K., and S. Seth, eds., Perspectives in Primate Biology, vol. 2. Today and Tomorrow's Printers and Publishers, New Delhi.

FOODEN, J., A. MAHABAL, AND S. S. SAHA. 1981. Redefinition of rhesus macaque-bonnet macaque boundary in peninsular India (Primates: *Macaca mulatta*, *M. radiata*). Journal of the Bombay Natural History Society, **78**: 463–474.

FOODEN, J., QUAN GUOQIANG, WANG ZONGREN, AND WANG YINGXIANG. 1985. The stumptail macaques of China. American Journal of Primatology, **8**: 11–30.

GEOFFROY SAINT-HILAIRE, E. 1812. Tableau des quadrumanes, ou des animaux composant le premier ordre de la classe des mammifères. Annales du Muséum d'Histoire Naturelle, Paris, **19**: 85–122.

GRAY, A. P. 1972. Mammalian Hybrids: A Check-List with Bibliography, 2nd ed. Commonwealth Agricultural Bureaux, Farnham Royal, Slough, England.

GUNNING, J. W. B. 1910. Bastard zwischen *Macacus sinicus* und *Cercopithecus lalandei*. Zoologischer Beobachter: Der Zoologische Garten, **51**: 54.

HA VAN TAN. 1985. The late Pleistocene climate in Southeast Asia: New data from Vietnam. Modern Quaternary Research in Southeast Asia, **9**: 81–86.

HARTMAN, C. G. 1938. Some observations on the bonnet macaque. Journal of Mammalogy, **19**: 468–474.

HAZOUT, S., A. W. COOPER, AND G. LUCOTTE. 1984. Variation électrophorétique et clinale dans les différentes localités géographiques de *Macaca fascicularis*. Biochemical Systematics and Ecology, **12**: 343–347.

HAZOUT, S., F. LOIRAT, AND G. LUCOTTE. 1986. Variation électrophorétique et clinal chez les différentes espèces de Macaques asiatiques. Biochemical Systematics and Ecology, **14**: 243–247.

HILL, W. C. O. 1937. On the breeding and rearing of certain species of primates in captivity. Ceylon Journal of Science (B), **20**: 369–389.

———. 1939. The menstrual cycle of the toque macaque (*Macaca sinica* Linn.), with observations on its uterine structure, compared with that of other macaques. Ceylon Journal of Science (D), **5:** 21–36.

———. 1958. External genitalia, pp. 630–704. *In* Hofer, H., A. H. Schultz, and D. Starck, eds., Primatologica, vol. 3, pt. 1. Karger, Basel.

———. 1974. Primates: Comparative Anatomy and Taxonomy. VII. Cynopithecinae: *Cercocebus, Macaca, Cynopithecus.* John Wiley & Sons, New York.

Hill, W. C. O., and I. S. Bernstein. 1969. On the morphology, behaviour and systematic status of the Assam macaque (*Macaca assamensis* McClelland, 1839). Primates, **10:** 1–17.

Hodgson, B. H. 1841. Three new species of monkey; with remarks on the genera *Semnopithecus* et *Macacus.* Journal of the Asiatic Society of Bengal, Calcutta, pt. 2, **9:** 1211–1213.

Horsfield, T. [1840]. List of Mammalia and birds collected in Assam by John McClelland. . . . Proceedings of the Zoological Society of London, **1839:** 146–167. For date of publication, see Proceedings of the Zoological Society of London, **107**(Ser. A): 79 (1937).

Hu Xiaosu, Hu Anqi, Lin Fangqing, Yan Heping, Zhu Shenghua, and Deng Anxiao. 1982. On the infection of *Macaca thibetanus* with *Plasmodium knowlesi.* Acta Zoologica Sinica, **28:** 200–201. (In Chinese.)

International Zoo Yearbook. 1966. Species of animals bred in zoos and aquaria during 1964. **6:** 385–406.

———. 1968. Species of wild animals bred in captivity during 1966. **8:** 288–316.

———. 1969. Species of wild animals bred in captivity during 1967. **9:** 215–244.

Jacob, K. 1949. Land connections between Ceylon and peninsular India. Proceedings of the National Institute of Sciences of India, **15:** 341–343.

Jainudeen, M. R., E. S. E. Hafez, and L. Kothari. 1972. Histomorphology of the cervix uteri of toque (*M. sinica*) and bonnet macaques (*M. radiata*). Folia Primatologica, **18:** 469–476.

Kawamoto, Y., T. M. Ischak, and J. Supriatna. 1982. Gene constitution of crab-eating macaques (*Macaca fascicularis*) on Lombok and Sumbawa. Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates, **2:** 57–64.

Kawamoto, Y., K. Nozawa, and T. M. Ischak. 1981. Genetic variability and differentiation of local populations in the Indonesian crab-eating macaque (*Macaca fascicularis*). Kyoto University Overseas Research Report of Studies on Indonesian Macaque, **1:** 15–39.

Kawamoto, Y., and B. Suryobroto. 1985. Gene constitution of crab-eating macaques (*Macaca fascicularis*) on Timor. Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates, **4:** 35–40.

Kawamoto, Y., O. Takenaka, B. Suryobroto, and E. Brotoisworo. 1985. Genetic differentiation of Sulawesi macaques. Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates, **4:** 41–61.

King, M., and A. C. Wilson. 1975. Evolution at two levels in humans and chimpanzees. Science, **188:** 107–116.

Krishna-Murthy, D. S., S. Roy, and V. C. Shah. 1984a. Pattern and frequency of association of nucleolus organizer region (NOR) chromosomes in the Hanuman langur (*Presbytis entellus entellus*) and the bonnet monkey (*Macaca radiata*), pp. 193–199. *In* Roonwal, M. L., S. M. Mohnot, and N. S. Rathore, eds., Current Primate Researches. University of Jodhpur, Jodhpur, India.

Krishna-Murthy, D. S., T. S. Sundereshan, S. Roy, P. M. Contractor, B. R. Srinath, and V. C. Shah. 1984b. Banding patterns (GTG, QFM, CBG and NOR) of the chromosomes of the bonnet monkey (*Macaca radiata*): Some comparisons with the human karyotype, pp. 177–184. *In* Roonwal, M. L., S. M. Mohnot, and N. S. Rathore, eds., Current Primate Researches. University of Jodhpur, Jodhpur, India.

Krumbiegel, I. 1965. Säugetierkundliche Beobachtungen im Vorderen Orient und in Indien. Säugetierkundliche Mitteilungen, **13:** 32–39.

Kurup, G. U. 1966. A comparative study on the cranial characters of *Presbytis* and *Macaca* based on Indian species (Primates: Cercopithecidae). Mammalia, **30:** 64–81.

Landois, H. 1896. Briefliche Mitteilungen. Der Zoologische Garten, **37:** 156.

LaSalle, M. 1969. Erythrocyte isoantigens of the genus *Macaca,* pp. 120–128. *In* Hofer, H. O., ed., Proceedings of the Second International Congress of Primatology, vol. 3. S. Karger, Basel.

Lazell, J. D., Jr. 1983. The footsteps of Liu. Explorers Journal, **61:** 58–63.

Lessertisseur, J., and R. Saban. 1967. Squelette axial, pp. 584–708. *In* Grassé, P.-P., ed., Traité de Zoologie: Anatomie, Systématique, Biologie. Tom XVI (Fascicule 1), Mammifères: Téguments et Squelette. Masson, Paris.

Li Zhixiang and Lin Zhengyu. 1983. Classification and distribution of living primates in Yunnan, China. Zoological Research, **4:** 111–120. (In Chinese, English abstract.)

Linnaeus, C. 1771. Mantissa Plantarum Altera Generum Editionis VI et Specierum Editionis II. L. Salvii, Holmiae.

Liu Dongsheng and Ding Menglin. 1984. The characteristics and evolution of the palaeoenvironment of China since the Late Tertiary, pp. 11–40. *In* Whyte, R. O., ed., The Evolution of the East Asian Environment. Vol. I, Geology and Palaeoclimatology. Centre of Asian Studies, University of Hong Kong.

Lucotte, G., S. Hazout, and D. G. Smith. 1984. Distinction électrophorétique des groupes naturels d'espèces dans le genre *Macaca.* Biochemical Systematics and Ecology, **12:** 339–342.

Matschie, P. 1912. Zur Kenntnis der südchinesischen Kurzschwanz-Makaken. Sitzungbericht der Gesellschaft Naturforschender Freunde zu Berlin, **1912:** 305–310.

Matsuda, G. 1985. Phylogeny of primates as inferred from alpha-hemoglobin sequences. Proceedings of the Japan Academy, Ser. B, **61:** 359–362.

MAYR, E. 1963. Animal Species and Evolution. Harvard University, Cambridge, Massachusetts.

MCARTHUR, J. W., J. OVADIA, O. W. SMITH, AND J. BASHIR-FARAHMAND. 1972. The menstrual cycle of the bonnet monkey (*Macaca radiata*): Changes in cervical mucus secretion, vaginal cytology, sex skin and urinary estrogen excretion. Folia Primatologica, **17**: 107–121.

MELL, R. 1922. Beiträge zur Fauna sinica. I. Die Vertebraten Südchinas; Feldlisten und Feldnoten der Säuger, Vogel, Reptilien, Batrachier. Archiv für Naturgeschichte, **88**, Abt. A: 1–146.

MELNICK, D. J., AND K. K. KIDD. 1985. Genetic and evolutionary relationships among Asian macaques. International Journal of Primatology, **6**: 123–160.

MILNE-EDWARDS, A. 1870. Note sur quelques mammifères du Thibet oriental. Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences, Paris, **70**: 341–342.

MONTAGU, M. F. A. 1950. A hybrid gibbon. Journal of Mammalogy, **31**: 150–153.

MOOR-JANKOWSKI, J., AND W. W. SOCHA. 1978. Blood groups of macaques: A comparative study. Journal of Medical Primatology, **7**: 136–145.

MOORE, J. C., AND G. H. H. TATE. 1965. A study of the diurnal squirrels, Sciurinae, of the Indian and Indochinese Subregions. Fieldiana: Zoology, **48**: 1–351.

MORE, K. N., AND K. BANERJEE. 1979. Homologues of the Human A, B, O & M, N blood groups in *Macaca radiata* (Geoffroy) & *Presbytes entellus* (Dufresne) & the reaction of their erythrocytes with lectins. Indian Journal of Experimental Biology, **17**: 1330–1332.

MULERIS, M., J. COUTURIER, AND B. DUTRILLAUX. 1986. Phylogénie chromosomique des Cercopithecoidea. Mammalia, **50**(No. spécial): 38–52.

NAPIER, P. H. 1981. Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles. Part II: Family Cercopithecidae, Subfamily Cercopithecinae. British Museum (Natural History), London.

NOZAWA, K., T. SHOTAKE, Y. OHKURA, AND Y. TANABE. 1977. Genetic variations within and between species of Asian macaques. Japanese Journal of Genetics, **52**: 15–30.

OVADIA, J., J. W. MCARTHUR, L. KOPITO, AND H. ULFELDER. 1971. The cervical mucus secretion of the bonnet monkey (*M. radiata*): Anatomical basis and physiological regulation. Biology of Reproduction, **5**: 127–145.

PALMOUR, R. M., J. E. CRONIN, A. CHILDS, AND B. W. GRUNBAUM. 1980. Studies of primate protein variation and evolution: Microelectrophoretic detection. Biochemical Genetics, **18**: 793–808.

PERCY, J. 1844. Remarks on the management of various species of monkeys in confinement. Proceedings of the Zoological Society of London, part **12**: 81–84.

PETZOLD, H.-G. 1968. Im Tierpark Berlin 1964 erstmalig gehaltene Tierformen. Milu, **2**: 375–410.

POCOCK, R. I. 1921. The systematic value of the glans penis in macaque monkeys. Annals and Magazine of Natural History, ser. 9, **7**: 224–229.

———. [1926]. The external characters of the catarrhine monkeys and apes. Proceedings of the Zoological Society of London, **1925**: 1479–1579.

———. 1931. The long-tailed macaque monkeys (*Macaca radiata* and *M. sinica*) of southern India and Ceylon. Journal of the Bombay Natural History Society, **35**: 276–288.

———. 1939. The Fauna of British India, Including Ceylon and Burma. Mammalia. Vol. 1, Primates and Carnivora (in Part). Taylor and Francis, London.

POHL, L. 1928. Zur Morphologie der männlichen Kopulationsorgane der Säugetiere; insbesondere der Versuch einer vergleichend-anatomischen Studie über den Penis der Primaten, einschiesslich des Menschen. Zeitschrift für Anatomie und Entwicklungsgeschichte, **86**: 71–119.

POPE, G. G., AND J. E. CRONIN. 1984. The Asian Hominidae. Journal of Human Evolution, **13**: 377–396.

PRYCHODKO, W., M. GOODMAN, E. POULIK, T. MIKI, AND T. TANAKA. 1969. Geographic variations of transferrin allelic frequencies in continental and insular populations, pp. 103–108. *In* Hofer, H. O., ed., Proceedings of the Second International Congress of Primatology, vol. 2. S. Karger, Basel.

RAHAMAN, H., AND M. D. PARTHASARATHY. 1971. The role of the olfactory signals in the mating behavior of bonnet monkeys (*Macaca radiata*). Communications in Behavioral Biology (A), **6**: 97–104.

———. 1979. Behavioural variants of bonnet macaque (*Macaca radiata*) inhabiting cultivated gardens. Journal of the Bombay Natural History Society, **75**: 406–425.

RENSCH, B. 1960. Evolution Above the Species Level. Columbia University, New York.

ROONWAL, M. L., AND S. M. MOHNOT. 1977. Primates of South Asia: Sociobiology and Behaviour. Harvard University, Cambridge, Massachusetts.

SAHA, S. S. 1984. The present southern limit of the rhesus macaque *Macaca mulatta* in peninsular India, specially in the Godavari and the Krishna river basins, pp. 153–165. *In* Roonwal, M. L., S. M. Mohnot, and N. S. Rathore, eds., Current Primate Researches. University of Jodhpur, Jodhpur, India.

SAHNI, A., AND H. C. MITRA. 1980. Neogene palaeobiogeography of the Indian subcontinent with special reference to fossil vertebrates. Palaeogeography, Palaeoclimatology, Palaeoecology, **31**: 39–62.

SCHMAGER, J. 1972. Cytotaxonomy and geographical distribution of the Papinae. Journal of Human Evolution, **1**: 477–485.

SCHULTZ, A. H. 1938. The relative length of the regions of the spinal column in Old World primates. American Journal of Physical Anthropology, **24**: 1–22.

SCHULTZ, A. H., AND W. L. STRAUS, JR. 1945. The numbers of vertebrae in primates. Proceedings of the American Philosophical Society, **89**: 601–626.

SHARMA, K. K. 1984. The sequence of phased uplift of the Himalaya, pp. 56–70. *In* Whyte, R. O., ed., The Evolution of the East Asian Environment. Vol. I, Geology and Palaeoclimatology. Centre of Asian Studies, University of Hong Kong.

SHIVELY, C., S. CLARKE, N. KING, S. SCHAPIRO, AND G. MITCHELL. 1982. Patterns of sexual behavior in male macaques. American Journal of Primatology, **2:** 373–384.

SHOTAKE, T. 1979. Serum albumin and erythrocyte adenosine deaminase polymorphisms in Asian macaques with special reference to taxonomic relationships among *Macaca assamensis, M. radiata,* and *M. mulatta.* Primates, **20:** 443–451.

SHOTAKE, T., AND C. SANTIAPILLAI. 1982. Blood protein polymorphisms in the troops of the toque macaque, *Macaca sinica,* in Sri Lanka. Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates, **2:** 79–95.

SOCHA, W. W., J. MOOR-JANKOWSKI, A. S. WIENER, D. R. RISSER, AND H. PLONSKI. 1976. Blood groups of bonnet macaques (*Macaca radiata*), with a brief introduction to seroprimatology. American Journal of Physical Anthropology, **45:** 485–491.

SOCHA, W. W., AND J. RUFFIÉ. 1983. Blood Groups of Primates: Theory, Practice, Evolutionary Meaning. Alan R. Liss, New York.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: The Principles and Practice of Statistics in Biological Research, 2nd ed. W. H. Freeman, New York.

STEUDEL, K. 1985. Allometric perspectives on fossil catarrhine morphology, pp. 449–475. *In* Jungers, W. L., ed., Size and Scaling in Primate Biology. Plenum, New York.

STANYON, R. R. 1982. Chromosomal evolution in primates: *Macaca* to *Homo.* Ph.D. thesis, Pennsylvania State University, University Park, Pennsylvania.

———. 1983. A test of the karyotypic fissioning theory of primate evolution. BioSystems, **16:** 57–63.

STYNES, A. J., I. C. KAUFMAN, AND S. M. REISER. 1975. Social behavior in heterospecific groups of young macaque monkeys (*M. nemestrina* & *M. radiata*): Preliminary observations. American Zoologist, **15:** 822. (Abstract only.)

TAN BANGJIE. 1985. The status of primates in China. Primate Conservation, **5:** 63–81.

VIJAYAN, V. S. 1979. Parambikulam Wildlife Sanctuary and its adjacent areas. Journal of the Bombay Natural History Society, **75:** 888–900.

VISHNU-MITTRE. 1984. Floristic change in the Himalaya (southern slopes) and Siwaliks from the mid-Tertiary to recent times, pp. 483–503. *In* Whyte, R. O., ed., The Evolution of the East Asian Environment. Vol. II, Palaeobotany, Palaeozoology and Palaeoanthropology. Centre of Asian Studies, University of Hong Kong.

WADA, K. 1985. Essay on some ecological and evolutionary characteristics of the genus *Macaca,* pp. 36–38. *In* Kawamichi, T., ed., Contemporary Mammalogy in China and Japan. Mammalogical Society of Japan, Tokyo.

WADA, K., XIONG CHENPEI, AND WANG QISHAN. 1986. On the distribution of Thibetan and rhesus monkeys in southern Anhui, China. Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates, **5:** 79–94. (Reprinted in Acta Theriologica Sinica, **7:** 168–176 [1987].)

WEIGOLD, H. 1935. Südost-Tibet als Lebensraum. Jahrbuch der Geographischen Gesellschaft zu Hannover, **1934-1935:** 203–247.

WEISS, M. L., M. GOODMAN, W. PRYCHODKO, G. W. MOORE, AND T. TANAKA. 1973. An analysis of macaque systematics using gene frequency data. Journal of Human Evolution, **2:** 213–226.

WILSON, D. R. 1970. A functional morphology of the tail, ischial callosities and pelvocaudal musculature in *Macaca.* Ph.D. thesis, University of Chicago, Chicago.

WILSON, E. H. 1913. A Naturalist in Western China . . . , 2nd ed., vol. 2. Methuen, London.

WU MINGCHUAN. 1983. On the distribution and number estimation of primates in Guangxi Province. Acta Theriologica Sinica, **3:** 16. (In Chinese.)

XIONG CHENGPEI. 1984. Ecological studies of the stump-tailed macaque. Acta Theriologica Sinica, **4:** 1–9. (In Chinese, English abstract.)

ZHENG XUEQING. 1984. A preliminary survey of the resources of monkeys in Fujian, with suggestions on its conservation. Wuyi Science Journal, **4:** 145–148. (In Chinese, English abstract.)

ZHOU GUOXING. 1984. Morphological analysis of the Jiulong Mountain "manbear" (wildman) hand and foot specimens. Cryptozoology, **3:** 58–70.

———. 1986. On wildman reports and Chinese macaques. Cryptozoology, **5:** 109–111.

ZUCKERMAN, S. 1930. The menstrual cycle of the primates. Part I. General nature and homology. Proceedings of the Zoological Society of London, **1930:** 691–754.

———. 1931. The menstrual cycle of the primates. Part III. The alleged breeding season of the primates; with special reference to the chacma baboon (*Papio porcarius*). Proceedings of the Zoological Society of London, **1931:** 325–343.

———. 1933. Functional Affinities of Man, Monkeys and Apes: A Study of the Bearings of Physiology and Behaviour on the Taxonomy and Phylogeny of Lemurs, Monkeys, Apes, and Man. Keegan, Paul, Trench, Trubner, London.

———. 1953. The breeding seasons of mammals in captivity. Proceedings of the Zoological Society of London, **122:** 827–950.

Other *Fieldiana: Zoology* Titles Available in This Series

Taxonomy and Evolution of the *Sinica* Group of Macaques: 2. Species and Subspecies Accounts of the Indian Bonnet Macaque, *Macaca radiata*. By Jack Fooden. *Fieldiana: Zoology*, n.s. 3, 1981. 52 pages, 9 illus., 15 tables.

Publication 1325, $5.50

Taxonomy and Evolution of the *Sinica* Group of Macaques: 3. Species and Subspecies Accounts of *Macaca assamensis*. By Jack Fooden. *Fieldiana: Zoology*, n.s. 9, 1982. 52 pages, 10 illus., 11 tables.

Publication 1329, $5.25

Taxonomy and Evolution of the *Sinica* Group of Macaques: 4. Species Account of *Macaca thibetana*. By Jack Fooden. *Fieldiana: Zoology*, n.s. 17, 1983. 20 pages, 5 illus., 3 tables.

Publication 1345, $3.50

Taxonomy and Evolution of the *Sinica* Group of Macaques: 5. Overview of Natural History. By Jack Fooden. *Fieldiana: Zoology*, n.s. 29, 1986. 22 pages, 2 illus., 4 tables.

Publication 1367, $5.00

Order by publication number and/or ask for a free copy of our price list. All orders must be prepaid. Illinois residents add current tax. All foreign orders are payable in U.S. dollar-checks drawn on any U.S. bank or the U.S. subsidiary of any foreign bank. Address all requests to:

FIELD MUSEUM OF NATURAL HISTORY
Library - Publications Division
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2498, U.S.A.

Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2496
Telephone: (312) 922-9410