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

Jack Fooden

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

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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
NPWIB  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. Erythism 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 Rojt.)
the posterior hairs, so that the cap extends ante-
riorly only to midway between the vertex and the
brow ridges; the exposed frontal area in *M. radiata*
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 con-
sistently present. Side-whiskers and beard are rel-
atively 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 di-
morphism increases with body size (Rensch, 1960,
p. 157; Clutton-Brock et al., 1977, p. 798; Al-
however, is represented by a sample of five ex-
ceptually 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% great-
er. This relationship between body size and lati-
titude 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 measure-
ments 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 (Al-
brecht, 1980, p. 144). Available data are adequate
to establish that regression of head and body length
on latitude is statistically significant for male spec-
imens of *Macaca a. assamensis* and for female
specimens of *M. radiata* (table 2). This intrataxon
trend is particularly evident in *M. a. assamensis*
male, 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 agree-
ment 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 subspe-
cies, there is no significant tendency for tail length
to decrease with latitude (table 2; the only signif-
ican t regression is in *M. radiata* males, where the
slope is positive). Relative tail length in immatures
in *sinica*-group species apparently is approxi-
mately 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. ra-
diata* (Fooden, 1986, p. 3).

In *Macaca sinica*, *M. radiata*, and *M. assam-
ensis*, 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. sin-
ica* to 156.2 mm in male *M. thibetana*. Sexual
dimorphism of skull length in *sinica*-group species
<table>
<thead>
<tr>
<th>Species or subspecies</th>
<th>HB (mm)</th>
<th>Tail</th>
<th>Ear</th>
<th>Weight (kg)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Length (mm)</td>
<td>t/</td>
<td>Length (mm)</td>
<td>(e/HB) × 100</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HB</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. sinica¹</td>
<td>468 ± 30 (21)</td>
<td>564 ± 42 (22)</td>
<td>1.21 ± .11 (21)</td>
<td>43 ± 5 (15)</td>
</tr>
<tr>
<td></td>
<td>418-528</td>
<td>495-650</td>
<td>1.00-1.39</td>
<td>37-52</td>
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<tr>
<td>M. radiata¹</td>
<td>527 ± 38 (12)</td>
<td>562 ± 61 (12)³</td>
<td>1.07 ± .09 (12)</td>
<td>41 ± 3 (12)</td>
</tr>
<tr>
<td></td>
<td>450-590</td>
<td>475-675</td>
<td>0.94-1.26</td>
<td>35-48</td>
</tr>
<tr>
<td>M. a. pelops⁴</td>
<td>581 ± 30 (8)</td>
<td>324 ± 24 (8)</td>
<td>0.56 ± .05 (8)</td>
<td>40 ± 1 (8)</td>
</tr>
<tr>
<td></td>
<td>550-635</td>
<td>283-360</td>
<td>0.50-0.63</td>
<td>38-42</td>
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<tr>
<td>M. a. assamensis⁵</td>
<td>616 ± 48 (24)</td>
<td>212 ± 18 (22)</td>
<td>0.35 ± .04 (21)</td>
<td>37 ± 4 (20)</td>
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<td>532-730</td>
<td>190-250</td>
<td>0.29-0.44</td>
<td>30-41</td>
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<tr>
<td>M. thibetana⁶</td>
<td>620 ± 35 (6)</td>
<td>71 ± 11 (5)</td>
<td>0.12 ± .02 (4)</td>
<td>46 ± 3 (4)</td>
</tr>
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<td>580-660</td>
<td>55-80</td>
<td>0.09-0.14</td>
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<td>Adult Females</td>
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<td></td>
<td></td>
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<tr>
<td>M. sinica¹</td>
<td>413 ± 20 (12)</td>
<td>521 ± 40 (13)</td>
<td>1.28 ± .12 (12)</td>
<td>35 ± 2 (9)</td>
</tr>
<tr>
<td></td>
<td>400-447</td>
<td>448-559</td>
<td>1.02-1.44</td>
<td>31.5-38</td>
</tr>
<tr>
<td>M. radiata¹</td>
<td>455 ± 32 (11)</td>
<td>503 ± 69 (10)³</td>
<td>1.10 ± .13 (10)</td>
<td>37 ± 3 (10)</td>
</tr>
<tr>
<td></td>
<td>400-515</td>
<td>350-571</td>
<td>0.88-1.36</td>
<td>35-45</td>
</tr>
<tr>
<td>M. a. pelops⁴</td>
<td>552 ± 26 (5)</td>
<td>266 ± 25 (5)</td>
<td>0.48 ± .05 (5)</td>
<td>34 ± 3 (5)</td>
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<td>530-587</td>
<td>236-293</td>
<td>0.44-0.55</td>
<td>29.2-36</td>
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<tr>
<td>M. a. assamensis⁵</td>
<td>501 ± 30 (17)</td>
<td>196 ± 17 (17)</td>
<td>0.40 ± .05 (16)</td>
<td>34 ± 5 (14)</td>
</tr>
<tr>
<td></td>
<td>437-555</td>
<td>170-225</td>
<td>0.31-0.47</td>
<td>25-45</td>
</tr>
<tr>
<td>M. thibetana⁶</td>
<td>523 ± 28 (5)</td>
<td>68 ± 10 (5)</td>
<td>0.13 ± .02 (4)</td>
<td>39 ± 4 (3)</td>
</tr>
<tr>
<td></td>
<td>490-555</td>
<td>56-80</td>
<td>0.11-0.15</td>
<td>35-42</td>
</tr>
</tbody>
</table>

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: Fòoden, 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); females, 557 ± 49 (8), 482-634.

⁴ References: Dào, 1978, p. 378; Fòoden, 1982, p. 10 (excluding one questionable value, HB/t = 0.26); IMCAS, 3 specimens; KIZ, 7 specimens.

⁵ References: AMNH, 1 specimen; FMNH, 1 specimen (excluding questionable measurement, HB = 710 mm); IMCAS, 3 specimens (excluding two questionable tail length measurements); KIZ, 1 specimen; SCMB, 1 specimen; Hu et al., 1982, p. 201, 2 specimens, weight only. Cf. Fòoden et al., 1985, p. 18, Table 2 (now revised).

⁶ References: Dào, 1967, p. 117; Fòoden, 1982, p. 10 (corrections to original table: Lc. No. 45, delete footnote; e/HB, mean ± SD = 7.1 ± 4; weight (kg), mean ± SD = 6.1 ± .9); BMNH, 1 specimen; IMCAS, 3 specimens; KIZ, 5 specimens.

⁷ References: Fòoden et al., 1985, p. 18 (excluding two questionable values, HB = 630 mm and t/HB = 7.2%); ZMNH, 1 specimen.

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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).

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

* = .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).
Open symbols—females; solid symbols—males. Larger symbols—adults; smaller symbols—immatures.

Fig. 5. Tail length vs. head and body length in immature and adult *sinica*-group macaques.
<table>
<thead>
<tr>
<th>Species or subspecies</th>
<th>GL (mm)</th>
<th>ZB/GL</th>
<th>Postrostral length (mm)</th>
<th>RL/PL</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ADULT MALES</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>M. sinica</em>¹</td>
<td>113.0 ± 4.2 (21)</td>
<td>.69 ± .02 (20)</td>
<td>77.8 ± 3.0 (21)</td>
<td>.55 ± .03 (21)</td>
</tr>
<tr>
<td></td>
<td>106.7-119.8</td>
<td>.65-.71</td>
<td>72.7-83.1</td>
<td>.50-.60</td>
</tr>
<tr>
<td><em>M. radiata</em>¹</td>
<td>120.0 ± 4.0 (12)</td>
<td>.67 ± .02 (12)</td>
<td>83.1 ± 2.6 (12)</td>
<td>.54 ± .02 (12)</td>
</tr>
<tr>
<td></td>
<td>114.6-127.9</td>
<td>.65-.71</td>
<td>80.2-86.5</td>
<td>.51-.57</td>
</tr>
<tr>
<td><em>M. a. pelops</em>¹</td>
<td>142.1 ± 6.5 (11)</td>
<td>.66 ± .03 (11)</td>
<td>97.3 ± 3.6 (10)</td>
<td>.57 ± .03 (10)</td>
</tr>
<tr>
<td></td>
<td>131.9-154.1</td>
<td>.63-.70</td>
<td>89.9-101.1</td>
<td>.51-.62</td>
</tr>
<tr>
<td><em>M. a. assamensis</em>²</td>
<td>146.9 ± 5.8 (28)</td>
<td>.66 ± .03 (28)</td>
<td>99.4 ± 4.0 (26)</td>
<td>.58 ± .04 (25)</td>
</tr>
<tr>
<td></td>
<td>138.1-160.3</td>
<td>.62-.70</td>
<td>93.9-107.8</td>
<td>.50-.65</td>
</tr>
<tr>
<td><em>M. thibetana</em>³</td>
<td>156.2 ± 6.1 (18)</td>
<td>.67 ± .02 (18)</td>
<td>105.7 ± 3.2 (15)</td>
<td>.59 ± .02 (15)</td>
</tr>
<tr>
<td></td>
<td>146.1-167.5</td>
<td>.65-.71</td>
<td>102.0-112.1</td>
<td>.53-.62</td>
</tr>
<tr>
<td><strong>ADULT FEMALES</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>M. sinica</em>¹</td>
<td>97.1 ± 3.6 (15)</td>
<td>.66 ± .02 (13)</td>
<td>71.3 ± 2.2 (15)</td>
<td>.47 ± .03 (15)</td>
</tr>
<tr>
<td></td>
<td>93.0-104.9</td>
<td>.63-.69</td>
<td>68.6-75.9</td>
<td>.43-.53</td>
</tr>
<tr>
<td><em>M. radiata</em>¹</td>
<td>104.4 ± 2.4 (10)</td>
<td>.65 ± .03 (10)</td>
<td>76.9 ± 2.0 (10)</td>
<td>.46 ± .02 (10)</td>
</tr>
<tr>
<td></td>
<td>99.0-107.7</td>
<td>.60-.69</td>
<td>73.4-78.6</td>
<td>.43-.50</td>
</tr>
<tr>
<td><em>M. a. pelops</em>¹</td>
<td>121.6 ± 5.5 (8)</td>
<td>.67 ± .03 (8)</td>
<td>88.8 ± 2.9 (7)</td>
<td>.49 ± .04 (7)</td>
</tr>
<tr>
<td></td>
<td>116.0-131.5</td>
<td>.63-.71</td>
<td>85.3-93.6</td>
<td>.45-.58</td>
</tr>
<tr>
<td><em>M. a. assamensis</em>³</td>
<td>121.2 ± 6.2 (23)</td>
<td>.66 ± .02 (23)</td>
<td>88.1 ± 4.3 (21)</td>
<td>.49 ± .03 (21)</td>
</tr>
<tr>
<td></td>
<td>113.1-138.5</td>
<td>.63-.71</td>
<td>81.0-97.9</td>
<td>.41-.55</td>
</tr>
<tr>
<td><em>M. thibetana</em>³</td>
<td>130.2 ± 5.3 (10)</td>
<td>.67 ± .01 (10)</td>
<td>93.8 ± 2.6 (8)</td>
<td>.51 ± .02 (8)</td>
</tr>
<tr>
<td></td>
<td>120.7-140.0</td>
<td>.65-.68</td>
<td>91.0-97.3</td>
<td>.46-.53</td>
</tr>
</tbody>
</table>

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.


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

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

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

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

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FOODEN: COMPARISONS AND SYNTHESIS IN *SINICA* MACAQUES

11
Fig. 7. Latitudinal variation of greatest skull length in adult *sinica*-group macaques (cf. table 4).

Open symbols—females; solid symbols—males.
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).

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

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).


The 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).

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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.
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
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...
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 metatal 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 metatal 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 stocky 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 metatal 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.)
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</tr>
<tr>
<td>ZMB 124</td>
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<td></td>
<td>19.8</td>
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<td>6.2</td>
<td>Dry</td>
</tr>
<tr>
<td>ZMB 124</td>
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<td></td>
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<tr>
<td>Ref. 8</td>
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<td>20</td>
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</tr>
<tr>
<td>Mean ± sd (N = 7)</td>
<td>Adult</td>
<td></td>
<td></td>
<td>18.9 ± 1.1</td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Specimen no./ref. no.</th>
<th>Age</th>
<th>Dental stage¹</th>
<th>Skull, greatest length (mm)</th>
<th>Greatest length</th>
<th>Least dorsoventral diameter of shaft</th>
<th>Shaft length²</th>
<th>Distal process length³</th>
<th>Penis preservation⁴</th>
</tr>
</thead>
<tbody>
<tr>
<td>BM 79.11.21.302</td>
<td>Juvenile</td>
<td>P4, (C)</td>
<td>...</td>
<td>20.2</td>
<td>2.1</td>
<td>17.4</td>
<td>6.5</td>
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<table>
<thead>
<tr>
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<th>Age</th>
<th>Dental stage¹</th>
<th>Skull, greatest length (mm)</th>
<th>Greatest length</th>
<th>Least dorsoventral diameter of shaft</th>
<th>Shaft length²</th>
<th>Distal process length³</th>
<th>Penis preservation⁴</th>
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</thead>
<tbody>
<tr>
<td>BM 50.378</td>
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<td>(dec. c, m1)</td>
<td>78.3</td>
<td>9.6</td>
<td>1.6</td>
<td>9.6</td>
<td>2.7</td>
<td>...</td>
</tr>
<tr>
<td>FMNH 99630</td>
<td>Infant</td>
<td>dec. m2</td>
<td>86.5</td>
<td>10.8</td>
<td>1.7</td>
<td>9.9</td>
<td>2.9</td>
<td>Fluid</td>
</tr>
<tr>
<td>Specimen no./ref. no.</td>
<td>Age</td>
<td>Dental stage</td>
<td>Skull, greatest length (mm)</td>
<td>Greatest length</td>
<td>Least dorsoventral diameter of shaft</td>
<td>Shaft length</td>
<td>Distal process length</td>
<td>Penis preservation</td>
</tr>
<tr>
<td>----------------------</td>
<td>---------</td>
<td>--------------</td>
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<td>-----------------</td>
<td>--------------------------------------</td>
<td>-------------</td>
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</tr>
<tr>
<td>BM 50.381</td>
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<td>I, M1</td>
<td>104.4</td>
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<td>9.3</td>
<td>3.4</td>
<td>Fluid</td>
</tr>
<tr>
<td>FMNH 99625</td>
<td>Juvenile</td>
<td>I2</td>
<td>93.0</td>
<td>10.8</td>
<td>1.1</td>
<td>9.8</td>
<td>2.7</td>
<td>Fluid</td>
</tr>
<tr>
<td>FMNH 99624</td>
<td>Juvenile</td>
<td>12, M2</td>
<td>97.0</td>
<td>14.8</td>
<td>1.9</td>
<td>13.5</td>
<td>4.0</td>
<td>Fluid</td>
</tr>
<tr>
<td>FMNH 99627</td>
<td>Subadult</td>
<td>(M3, C)</td>
<td>122.1</td>
<td>23.5</td>
<td>2.5</td>
<td>21.7</td>
<td>4.9</td>
<td>Fluid</td>
</tr>
<tr>
<td>FMNH 99626</td>
<td>Subadult</td>
<td>M3, (C)</td>
<td>123.8</td>
<td>21.5</td>
<td>3.0</td>
<td>17.8</td>
<td>6.3</td>
<td>Fluid</td>
</tr>
<tr>
<td>FMNH 99632</td>
<td>Subadult</td>
<td>M3, (C)</td>
<td>121.9</td>
<td>22.4</td>
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<td>18.7</td>
<td>7.4</td>
<td>Fluid</td>
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<tr>
<td>BM 50.387</td>
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<td>...</td>
<td>...</td>
<td>23.0</td>
<td>3.4</td>
<td>21.3</td>
<td>6.6</td>
<td>Fluid</td>
</tr>
<tr>
<td>FMNH 31765</td>
<td>Adult</td>
<td>M3, C</td>
<td>139.9</td>
<td>25.2</td>
<td>3.7</td>
<td>22.5</td>
<td>6.5</td>
<td>...</td>
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<tr>
<td>FMNH 99622</td>
<td>Adult</td>
<td>M3, C</td>
<td>145.0</td>
<td>17.6</td>
<td>2.7</td>
<td>10.6</td>
<td>8.1</td>
<td>Fluid</td>
</tr>
<tr>
<td>FMNH 99631</td>
<td>Adult</td>
<td>M3, C</td>
<td>138.9</td>
<td>24.2</td>
<td>3.0</td>
<td>21.9</td>
<td>6.8</td>
<td>Fluid</td>
</tr>
<tr>
<td>IZCAS 26681</td>
<td>Adult</td>
<td>M3, C</td>
<td>144.0</td>
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<td>3.6</td>
<td>24.9</td>
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</tr>
<tr>
<td>Mean ± SD (N = 5)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

**Macaca thibetana**

<table>
<thead>
<tr>
<th>Specimen no./ref. no.</th>
<th>Age</th>
<th>Dental stage</th>
<th>Skull, greatest length (mm)</th>
<th>Greatest length</th>
<th>Least dorsoventral diameter of shaft</th>
<th>Shaft length</th>
<th>Distal process length</th>
<th>Penis preservation</th>
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</thead>
<tbody>
<tr>
<td>AMNH 84475</td>
<td>Infant</td>
<td>...</td>
<td>...</td>
<td>8.8</td>
<td>1.3</td>
<td>7.1</td>
<td>2.7</td>
<td>...</td>
</tr>
<tr>
<td>FMNH 39383</td>
<td>Subadult</td>
<td>M3, (C)</td>
<td>143.9</td>
<td>23.7</td>
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<td>21.9</td>
<td>7.3</td>
<td>...</td>
</tr>
<tr>
<td>AMNH 84472</td>
<td>Adult</td>
<td>M3, C</td>
<td>...</td>
<td>24.9</td>
<td>3.9</td>
<td>23.3</td>
<td>7.4</td>
<td>...</td>
</tr>
<tr>
<td>FMNH 39499</td>
<td>Adult</td>
<td>M3, C</td>
<td>161.3</td>
<td>26.3</td>
<td>4.3</td>
<td>21.0</td>
<td>9.9</td>
<td>Dry</td>
</tr>
<tr>
<td>Ref. 11</td>
<td>Adult</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
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<td>Living</td>
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<td>Mean ± SD (N = 2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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. For study, dry specimens were reconstituted in fluid.
5. 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). Fooden et al., 1985, p. 21.
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).
TABLE 8. Blood protein electrophoresis: monomorphism in *Macaca* spp., including *sinica*-group species (not studied in *M. thibetana*).

<table>
<thead>
<tr>
<th>Monomorphic protein locus</th>
<th><em>M. sinica</em></th>
<th><em>M. radiata</em></th>
<th><em>M. assamensis</em></th>
<th>Other species of <em>Macaca</em></th>
<th>Ref. nos.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PLASMA PROTEINS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alp</td>
<td>131</td>
<td>22</td>
<td>28</td>
<td>2,106 (13) spp.</td>
<td>2–9</td>
</tr>
<tr>
<td>Amy</td>
<td>131</td>
<td>19</td>
<td>28</td>
<td>2,062 (13) spp.</td>
<td>3–9</td>
</tr>
<tr>
<td>Cat</td>
<td>131</td>
<td>19</td>
<td>28</td>
<td>1,397 (3) spp.</td>
<td>3–4, 7</td>
</tr>
<tr>
<td>LAP</td>
<td>131</td>
<td>19</td>
<td>28</td>
<td>2,127 (13) spp.</td>
<td>2–9</td>
</tr>
<tr>
<td>PA</td>
<td>0</td>
<td>19</td>
<td>28</td>
<td>1,807 (6) spp.</td>
<td>3–6</td>
</tr>
<tr>
<td>(\alpha_2)</td>
<td>131</td>
<td>19</td>
<td>28</td>
<td>2,062 (13) spp.</td>
<td>3–9</td>
</tr>
<tr>
<td><strong>ERYTHROCYTE PROTEINS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G6PD</td>
<td>131</td>
<td>19</td>
<td>28</td>
<td>2,128 (13) spp.</td>
<td>2–9</td>
</tr>
<tr>
<td>PGI</td>
<td>0</td>
<td>19</td>
<td>0</td>
<td>28 (5) spp.</td>
<td></td>
</tr>
<tr>
<td>TO</td>
<td>131</td>
<td>19</td>
<td>28</td>
<td>2,062 (13) spp.</td>
<td>3–9</td>
</tr>
</tbody>
</table>

Alp = Alkaline phosphatase; Amy = amylase; Cat = catalase; LAP = leucine aminopeptidase; PA prealbumin; \(\alpha_2\) = slow \(\alpha_2\)-macroglobulin; G6PD = glucose-6-phosphate dehydrogenase; PGI = phosphoglucomerase; TO = tetrazolium oxidase.

1 Variant allele in 3 of 477 *M. fascicularis* specimens and in 2 of 255 Sulawesi macaque 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; Foden, 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; Shiotake, 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* (Shiotake, 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

<table>
<thead>
<tr>
<th>Monomorphic protein locus</th>
<th><em>M. sinica</em></th>
<th><em>M. radiata</em></th>
<th><em>M. assamensis</em></th>
<th>Ref. nos.</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of <em>sinica</em>-group specimens studied</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>CP</td>
<td>131</td>
<td>22</td>
<td>28</td>
<td>2-5</td>
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<tr>
<td>GC1</td>
<td>131</td>
<td>0</td>
<td>0</td>
<td>5</td>
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<tr>
<td>Hp</td>
<td>131</td>
<td>28</td>
<td>28</td>
<td>2-5</td>
</tr>
<tr>
<td>PI</td>
<td>131</td>
<td>19</td>
<td>28</td>
<td>3-5</td>
</tr>
</tbody>
</table>

**PLASMA PROTEINS**

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>AcP</td>
<td>131</td>
<td>19</td>
<td>28</td>
</tr>
<tr>
<td>CA-I</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>CA-I control</td>
<td>55</td>
<td>52</td>
<td>0</td>
</tr>
<tr>
<td>Cell Es9</td>
<td>131</td>
<td>19</td>
<td>28</td>
</tr>
<tr>
<td>EsD1</td>
<td>131</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Got</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Hb-β</td>
<td>202</td>
<td>6810</td>
<td>28</td>
</tr>
<tr>
<td>LDH-A</td>
<td>131</td>
<td>35</td>
<td>28</td>
</tr>
<tr>
<td>MDH</td>
<td>131</td>
<td>44</td>
<td>28</td>
</tr>
<tr>
<td>6-PGD</td>
<td>188</td>
<td>8911</td>
<td>28</td>
</tr>
</tbody>
</table>

**ERYTHROCYTE PROTEINS**

1 Two proteins listed here, GC and EsD, have been studied only in *M. sinica.*
6 Nozawa (ref. 3) and Shotake (ref. 4) indicate that the π allele frequency in *M. radiata* is 1.00 C (N = 19).
However, Lucotte et al. (1984, p. 340) indicate that the π allele frequency in this species is 0.96 B (N = 96). The explanation for this discrepancy is unclear.
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, 135).

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* to *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-a) and is not intermediate at three loci (ADA, IDH, PGMM-1). 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. sinica* and *M. radiata* is intermediate.
**Table 10. Blood protein electrophoresis: dimorphism in *sinica*-group species (not studied in *M. thibetana*).**

<table>
<thead>
<tr>
<th>Dimorphic protein locus</th>
<th>Major allele</th>
<th>Minor allele</th>
<th>Frequency of major allele (sample size in parentheses)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td><strong>M. sinica</strong></td>
</tr>
<tr>
<td><strong>PLASMA PROTEIN</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TBPA</td>
<td>F</td>
<td>S</td>
<td>0.287(^1) (196)</td>
</tr>
<tr>
<td>ADA(^7)</td>
<td>I</td>
<td>3</td>
<td>0.996 (131)</td>
</tr>
<tr>
<td>AK</td>
<td>I</td>
<td>3</td>
<td>0.965 (131)</td>
</tr>
<tr>
<td>CA-I</td>
<td>C</td>
<td>A</td>
<td>0.667(^6) (186)</td>
</tr>
<tr>
<td>Dia</td>
<td>A</td>
<td>C</td>
<td>1.000 (131)</td>
</tr>
<tr>
<td>Hb-α(^10)</td>
<td>I(^11)</td>
<td>2(^11)</td>
<td>0.947(^10) (202)</td>
</tr>
<tr>
<td>IDH</td>
<td>I</td>
<td>2</td>
<td>0.902 (131)</td>
</tr>
<tr>
<td>LDH-B</td>
<td>I</td>
<td>3</td>
<td>1.000 (131)</td>
</tr>
<tr>
<td>PGM-I</td>
<td>I</td>
<td>5</td>
<td>1.000 (131)</td>
</tr>
<tr>
<td>PGM-II</td>
<td>I</td>
<td>7</td>
<td>0.677 (131)</td>
</tr>
</tbody>
</table>

**ERYTHROCYTE PROTEINS**

<table>
<thead>
<tr>
<th>Major allele</th>
<th>Minor allele</th>
<th>Frequency of major allele (sample size in parentheses)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><strong>M. sinica</strong></td>
</tr>
<tr>
<td>ADA(^7)</td>
<td>I</td>
<td>3</td>
</tr>
<tr>
<td>AK</td>
<td>I</td>
<td>3</td>
</tr>
<tr>
<td>CA-I</td>
<td>C</td>
<td>A</td>
</tr>
<tr>
<td>Dia</td>
<td>A</td>
<td>C</td>
</tr>
<tr>
<td>Hb-α(^10)</td>
<td>I(^11)</td>
<td>2(^11)</td>
</tr>
<tr>
<td>IDH</td>
<td>I</td>
<td>2</td>
</tr>
<tr>
<td>LDH-B</td>
<td>I</td>
<td>3</td>
</tr>
<tr>
<td>PGM-I</td>
<td>I</td>
<td>5</td>
</tr>
<tr>
<td>PGM-II</td>
<td>I</td>
<td>7</td>
</tr>
</tbody>
</table>

* 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 trisomic 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. Prchodko 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*).**

<table>
<thead>
<tr>
<th>Alleles</th>
<th><strong>M. sinica</strong></th>
<th><strong>M. radiata</strong></th>
<th><strong>M. assamensis</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Alb</td>
<td>0</td>
<td>0</td>
<td>0.161</td>
</tr>
<tr>
<td>B</td>
<td>0.980</td>
<td>1.000(^1)</td>
<td>0.839</td>
</tr>
<tr>
<td>D'</td>
<td>0.020</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ch-Es</td>
<td>0.988</td>
<td>0.808</td>
<td>1.000</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>0.192</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>0.012</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>PHI</td>
<td>0.752</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>15</td>
<td>0.228</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>16</td>
<td>0.020</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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

\(^1\) Reference: Shotake and Santiapillai, 1982, p. 83.

**FOODEN: COMPARISONS AND SYNTHESIS IN SINICA MACAQUES**

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

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

1 Darga et al., 1975, p. 801. 2 Shotake and Santiapillai, 1982, p. 83; note that allele E is designated D 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 isimmune 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 isimmune rhesus sera. A similar monomorphic response previously had been obtained when erythrocytes of six *M. radiata* specimens were tested with one rhesus isimmune 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 & Ruffi, 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;...

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).

INTEGRGENERIC 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 sabaenus 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 mitis"; this evidently is a lapsus for Cercopithecus aethiops × Cercocebus 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

<table>
<thead>
<tr>
<th>Parental species (sexes indicated where known)</th>
<th>Sex of hybrid ²</th>
<th>Birth date</th>
<th>Survival of hybrid</th>
<th>Location</th>
<th>Reference ³</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. ?M. radiata ⁴ ♂ × Cercopithecus aethiops ♀</td>
<td>♂</td>
<td>1 Oct. 1909</td>
<td>≥ 1 mo</td>
<td>Pretoria</td>
<td>Gunning, 1910, p. 54</td>
</tr>
<tr>
<td>INTERGENERIC (?)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. M. radiata ⁴ ♂ × M. fascicularis ♀</td>
<td>♀</td>
<td>12 May 1964</td>
<td>≥ 3 mo</td>
<td>Munich</td>
<td>Fitzinger, 1864, p. 335</td>
</tr>
<tr>
<td>INTRAGROUP</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. M. sinica × M. radiata</td>
<td>?</td>
<td>1860 or before</td>
<td>?</td>
<td>London</td>
<td>Flower, 1929, p. 23</td>
</tr>
</tbody>
</table>

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.

**INTEGRAL HYBRIDIZATION**—Three reported intergroup 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).

Intergroup 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 (Acharyjo & 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 intergroup 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 saturated 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-Mitre, 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 (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

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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 post-glacial 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

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

Macaca radiata

INDIA
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).
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 Liang, Apr. 1960 (BMNH, 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.
Menglian Co.; ca. 22°21’N, 99°36’E; reported by Tan (1985, p. 73).

INDIA
Proposed Dhaleswari Wildlife Sanctuary; Assam State; 24°10’-24°40’N, 92°20’-93°10’E; reported by Choudhury (1983, p. 14).
Macaca thibetana

(supplement to Foeden, 1983, p. 14; Foeden et al., 1985, p. 15)

CHINA

Anhui

Baqiiao, 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).

Guijia, 500 m; Huang Shan, Shexian Co.; ca. 30°03'N, 118°09'E; troop captured Nov. 1972 (Wada et al., 1986, p. 89).

Guinuijiang, 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).

Huanghui, 600–1200 m; Shitai Co.; ca. 30°08'N, 117°20'E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).

Jilin, 600–800 m; Yixian Co.; ca. 30°00'N, 118°00'E; reported 1973–1985 by Xiong Chengpei (Wada et al., 1986, p. 83).

Jiuhe 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).

Lianhua, 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).

Qinghong, 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).

Quiting, 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).

Xianjun, 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).

Yunwhifeng, 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; Shanggang Dist., Chong'an Co.; 27°50'N, 117°48'E; collected by Qin Yaoling, 1960 (SCIEA, 1).

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**

Bibe 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 Wenfeng, 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 Wenfeng, 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 Wenfeng, 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 Wenfeng, RCFB, pers. comm., 10 Nov. 1985).


Junshonglou, 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 Wenfeng, RCFB, pers. comm., 10 Nov. 1985).

Laopengyudui, 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 Longhui, 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 (iz-cas, 2, skulls only).

Pingxi, ca. 800 m; Ruyuan Co.; 24°45'N, 113°00'E; collected by Xu Longhui, 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 Liantian (in Tan, 1985, p. 75).

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

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


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


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

Youngfu Co. See Youngfu Co.


Ziyaan Co. See Ziyuan Co.

Ziyuan Co.; ca. 26°01’N, 110°39’E; reported by Shen Liantan (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).


Pingzhen 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 Ed-

itorial Committee of Guizhou Fauna (1979, p. 110).

Hunan


Jiangxi


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).


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).


Sichuan
Bao Guo Si (temple), near; Emei Shan (mt.), Emei Co.; ca. 29°32’N, 103°21’E; collected by Quan Guoqiang, Aug. 1959 (iczcas, 1, skull only).


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

Zhejiang
Beiyandangshan; Yueqing Co.; ca. 28°23’N, 121°04’E; collected by Chai Weixi, 1960 (zmnh, 2, mounted skins with skulls inside).


Jiulong Shan. See Zhanxian.

Wangcunkou; Suichang Co.; ca. 28°24’N, 118°59’E; collected by Mao Jiangsen, June 1979 (immzam, 1).

Zhoucun, ca. 1000 m; Jiangshan Co.; ca. 28°22’N, 118°37’E; collected by Kang Xinmin, 23 Mar. 1985 (zmnh, 1).

Zhanxian, near Jiulong Shan (mt.); Suichang Co.; ca. 28°20’N, 119°00’E; collected by villagers, 23 May 1957 (Zhou, 1984, p. 58).

Zhidaiakou, ca. 1000 m; Suichang Co.; ca. 28°16’N, 118°46’E; observed Aug. 1985 by Kang Xinmin, zmnh (pers. comm., 24 Oct. 1985).

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