FIELDIANA

Zoology

NEW SERIES, NO. 113

Systematic Review of the Barbary Macaque, *Macaca sylvanus* (Linnaeus, 1758)

Jack Fooden

October 26, 2007

Publication 1547

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

FIELDIANA

Zoology

NEW SERIES, NO. 113

Systematic Review of the Barbary Macaque, *Macaca sylvanus* (Linnaeus, 1758)

Jack Fooden

*Division of Mammals
Department of Zoology
Field Museum of Natural History
1400 South Lake Shore Drive
Chicago, Illinois 60605-2496
U.S.A.*

Accepted July 20, 2007
Published October 26, 2007
Publication 1547

PUBLISHED BY FIELD MUSEUM OF NATURAL HISTORY

© 2007 Field Museum of Natural History

ISSN 0015-0754

PRINTED IN THE UNITED STATES OF AMERICA

Table of Contents

ABSTRACT. 1

INTRODUCTION. 1

MATERIALS AND METHODS 1

GEOGRAPHIC DISTRIBUTION 2

TOTAL POPULATION ESTIMATES. 2

PELAGE 3

EXTERNAL MEASUREMENTS AND PROPORTIONS 4

CAUDAL VERTEBRAE. 6

CRANIAL CHARACTERS 6

MOLECULAR BIOLOGY AND GENETICS 8

 DNA variation 8

 Karyology 12

NATURAL HISTORY. 13

 Habitats. 13

 Terrestriality/Arboreality 14

 Group Size and Composition 14

 Group Fission 15

 Home Range Area and Population Density. 15

 Diet. 15

 Predators 17

 Intergroup Migration 18

REPRODUCTION 18

 Seasonality 18

 Sexual Maturation 19

 Reproductive Anatomy Notes 19

 Female Sexual Cycles 20

 Consortships. 20

 Copulation 21

 Male Dominance Rank and Reproductive Success. 21

 Inbreeding/Outbreeding 21

 Gestation 22

 Parturition 22

 Birth Rate 23

 Neonatal Sex Ratio. 23

 Twinning 23

 Stillbirths; Infant Mortality 24

 Weaning. 25

 Male-Infant Interactions 25

 Longevity; Reproductive Senescence; Death Rate. 26

 Population Growth Rate 26

FOSSILS 27

SYSTEMATICS 28

 Synonymy 28

 Type Series. 30

 Type Locality 30

 Distribution 30

 Diagnosis 30

 Remarks 30

 Specimens Examined. 31

EVOLUTION AND DISPERSAL 31

ACKNOWLEDGMENTS. 32

LITERATURE CITED. 32

APPENDIX I: SPECIMENS EXAMINED (DETAILS)	42
APPENDIX II: GAZETTEER OF <i>MACACA SYLVANUS</i> LOCALITIES	42
APPENDIX III: CENTRUM LENGTH AND VERTEBRAL COUNT OF CAUDAL VERTEBRAE IN <i>MACACA SYLVANUS</i>	52
APPENDIX IV: GROUP SIZE AND ADULT SEX COMPOSITION IN <i>MACACA SYLVANUS</i> POPULATIONS.	53
APPENDIX V: COORDINATES, GEOLOGICAL AGE, AND REPORTED IDENTIFICATION OF CIRCUM-MEDITERRANEAN MACAQUE FOSSILS.	54

List of Illustrations

1. Map of northwestern Africa showing extant and Holocene localities of <i>Macaca sylvanus</i>	3
2. Adult pelage in <i>Macaca sylvanus</i>	
A. Male, pre-molt	5
B. Male, molting.	5
C. Estrous female, post-molt	5
3. Tail vestige in <i>Macaca sylvanus</i>	7
4. Ventral view of sacrum and caudal vertebrae in <i>Macaca sylvanus</i>	9
5. Skull of adult female <i>Macaca sylvanus</i>	10
6. Skull of adult male <i>Macaca sylvanus</i>	11
7. Phylogenetic relationships among Moroccan and Algerian populations of <i>Macaca sylvanus</i> as indicated by mtDNA haplotypes	13
8. Copulation posture in <i>Macaca sylvanus</i>	22
9. Geographic distribution of circum-Mediterranean macaque fossils compared with geographic distribution of extant populations and Holocene extinct populations of <i>Macaca sylvanus</i>	28

List of Tables

1. Frequency distribution of elevation records of <i>Macaca sylvanus</i>	4
2. External measurements and proportions in wild-collected <i>Macaca sylvanus</i>	6
3. Tail length and relative tail length in <i>Macaca sylvanus</i> specimens collected near Azrou, Moyen Atlas, Morocco	8
4. Cranial measurements and proportions in wild-collected <i>Macaca sylvanus</i>	12
5. Mitochondrial DNA haplotype frequencies in Gibraltar and North African samples of <i>Macaca sylvanus</i>	12
6. Estimated dates of divergence of <i>Macaca sylvanus</i> sister groups	13
7. Habitats of <i>Macaca sylvanus</i>	14
8. Frequency of terrestriality in <i>Macaca sylvanus</i> populations.	15
9. Home range area in natural populations of <i>Macaca sylvanus</i>	16
10. Population density in <i>Macaca sylvanus</i>	16
11. Number of gymnosperm and angiosperm species consumed by <i>Macaca sylvanus</i> populations.	17
12. Allocation of feeding time to various dietary components by <i>Macaca sylvanus</i> groups in Grande Kabylie, Algeria	18
13. Seasonal mating periods and birth periods reported in <i>Macaca sylvanus</i> populations.	19
14. Mean annual birth rate in <i>Macaca sylvanus</i> groups	23
15. Neonatal sex ratio in <i>Macaca sylvanus</i>	24
16. Twinning frequency reported in semi-natural populations of <i>Macaca sylvanus</i>	24
17. Stillbirth frequency in semi-natural populations of <i>Macaca sylvanus</i>	25
18. Infant mortality rate in natural and semi-natural populations of <i>Macaca sylvanus</i>	25
19. Mean annual death rate in semi-natural populations of <i>Macaca sylvanus</i>	27
20. Demographic growth rate in natural and semi-natural populations of <i>Macaca sylvanus</i>	27
21. Evolution and dispersal of circum-Mediterranean macaques: hypothetical chronology.	31

Systematic Review of the Barbary Macaque, *Macaca sylvanus* (Linnaeus, 1758)

Jack Fooden

Abstract

The Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758), is systematically reviewed, based on a study of 103 specimens and survey of relevant literature. This review includes analyses of external characters, cranial characters, DNA variation, and karyology. Information also is presented concerning natural history, reproduction, fossils, and taxonomic history. Current knowledge of geographic variation in *M. sylvanus* is insufficient to warrant recognition of subspecies. Although *M. sylvanus* is now restricted to northwestern Africa, fossil evidence suggests that this species is a relict of the ancestral macaque stock that originated in Africa ca. 7–6 million years ago (Ma) and dispersed to Eurasia ca. 6–5 Ma. Macaques formerly were widely distributed in Europe, but became extinct there ca. 0.100–0.020 Ma; macaques have survived in Asia and are now represented there by ca. 20 species. An annotated gazetteer lists 166 localities where *M. sylvanus* has been collected, observed, or reported.

Introduction

The Barbary macaque, *Macaca sylvanus*, is unique within its genus in two obvious respects: (1) it is the only macaque species that is distributed outside of Asia, and (2) it is the only macaque species in which the tail is reduced to an inconspicuous boneless vestige or is completely absent. Probably as a result of its juxta-Mediterranean distribution and its distinctive tail reduction, the Barbary macaque was well known to ancient Phoenicians, Etruscans, Egyptians, and Greeks—including Aristotle (McDermott, 1938, pp. 28, 29, 38, 88; Goudsmit & Brandon-Jones, 1999, p. 49). This species is the first primate listed in Gesner's (1551, p. 957) classic *Historiae Animalium*, from which it was cited by Linnaeus (1758, p. 25).

Materials and Methods

This review of *M. sylvanus* is based on study of 103 specimens (Appendix I) and review of relevant literature. ArcView GIS was used to prepare maps, and Microsoft Excel was used to calculate summary statistics. Reported cranial measurements (Table 4) are defined as follows (cf. Fooden, 1969, p. 40): Greatest length of skull—Most anterior point on rostrum to most posterior point on skull. Postrostral length—Most inferior point on either orbital margin to most posterior point on skull. Rostral length—Most anterior point on rostrum to most inferior point on either orbital margin. Zygomatic breadth—Distance between most lateral points on zygomatic arches.

Names of institutions in which cited specimens are preserved are abbreviated as indicated below; the number of *M. sylvanus* specimens studied at each institution is indicated by a parenthetical notation:

AMNH	American Museum of Natural History, New York (7)
------	--

Division of Mammals, Department of Zoology, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605–2496, U.S.A.

BM(NH)	The Natural History Museum, London (8)
CMNH	Carnegie Museum of Natural History, Pittsburgh (1)
FMNH	Field Museum of Natural History, Chicago (4)
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels (17)
ISR	Institut Scientifique, Rabat (7)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (2)
MNHN	Muséum National d'Histoire Naturelle, Paris (10)
NHMBa	Naturhistorisches Museum, Basel (1)
NHMBe	Naturhistorisches Museum, Bern (1)
NMS	Natur-Museum Senckenberg, Frankfurt (4)
RMNH	Nationaal Natuurhistorisch Museum, Leiden (10)
USNM	National Museum of Natural History, Washington, D.C. (19)
ZMB	Museum für Naturkunde, Berlin, (3)
ZMUZ	Zoologisches Museum der Universität Zürich (4)
ZSBS	Zoologisches Staatsammlung, Munich (5)

Geographic Distribution

Extant natural populations of *M. sylvanus* are disjunctly distributed in the Atlas and Rif Mountain ranges in Morocco and Algeria (Fig. 1); latitudinally the geographic range extends from ca. 31°15'N to 36°45'N, and longitudinally it extends from ca. 7°45'W to 5°35'E. Moroccan and Algerian populations are separated by a gap that is ca. 700 km wide, and narrower gaps separate disjunct populations within these two countries. Holocene extinction records (Fig. 1, 28 populations) indicate that distributional gaps were narrower within historic times and further indicate that the range of the species recently extended east of Algeria to ca. 10°E in neighboring Tunisia; an early reference to *M. sylvanus* in Tunisia has been provided by Herodotus (ca. 484–425 B.C.E.) (McDermott, 1938, p. 56). The known elevational distribution of *M. sylvanus* is 400–2300 m (Table 1); half of the 62

available elevational records are at or above 1800 m. No other nonhuman primate is known to have ever been sympatric with *M. sylvanus*.

The population of *M. sylvanus* that currently inhabits Gibraltar apparently is not native. There is no mention of this species in ancient commentaries on Gibraltar (Joleaud, 1931a, p. 138; McDermott, 1938, p. 56). Instead, the oldest known reference to monkeys on Gibraltar is in an 18th century document preserved in the British Museum (Sayre, 1862, p. 454; cf. Buffon, 1789, p. 36); this document indicates that “a great quantity” of Barbary macaques were introduced into the British garrison in 1740 (cf. Busk, 1877, p. 129; Trouessart, 1905, p. 359; Morris & Morris, 1966, p. 15; Fa, 1981, p. 74). Additional introductions occurred in 1813 and 1860 (Fa & Lind, 1996, p. 235), but the population in 1925 was reduced to three individuals (Kenyon, 1938, p. 115), and in 1938–1945 major restocking occurred (Fa, 1984b, p. 266). A recent study of mtDNA variation in the existing Gibraltar population indicated that this population includes individuals of both Moroccan and Algerian ancestry (Modolo et al., 2005, p. 7397).

Lydekker (1893–1894, p. 118) and Forbes (1894, p. 5) indicated that during the 19th century, *M. sylvanus* inhabited southern Spain in the vicinity of Gibraltar. This appears to have been an error (cf. Kelaart in Newman, 1846, p. 1292; Joleaud, 1931a, p. 138), and, in a subsequent publication, Lydekker (1916, p. 7) omitted Spain from the species distribution.

An introduced population of *M. sylvanus* was recently established in Morocco in 1985, when more than 40 formerly captive individuals were deliberately released near Nador, a northern coastal town at ca. 35°00'N, 3°00'W (Aulagnier & Thevenot, 1986, p. 56; cf. Chivers, 1984, p. vii; Anonymous, 1988, p. 50).

Total Population Estimates

In 1984, Fa et al. (1984, pp. 86, 91, 99, 101) estimated the total extant natural population of *M. sylvanus* to be 14,000–23,000 individuals (9,000–17,000 in Morocco, 5,000–6,000 in Algeria). In 1992, Lilly and Mehlman (1993, p. 327; cf. Mehlman & Lilly, 1993, p. 334) indicated that the population had declined to 10,000–16,000, and, in 2005, Modolo et al. (2005, p. 7392; cf.

FIG. 1. Map of northwestern Africa, showing extant and Holocene localities of *Macaca sylvanus*; for documentation, see Gazetteer, Appendix II. **Key to Locality Numbers:** **MOROCCO and U.K.** 1. Goundafa. 2. Ourika, Jebel; Ourika, Oued; Tourchte; Zaclia Si Fatma; Zaclia Si Fatma, S of. 3. Ouzoud, Cascades d'. 4. Aït Mehammed, S of. 5. Tillouguit N'Aït Isha, S of. 6. Ouaouizahrt, MF de. 7. Ighrem, Jebel. 8. Asker, Zaouia; Idrous, Jebel; Kousser, Massif du; Tsemair. 9. Aït Sokhmane forest; Azrar; Boutferda vicinity; Haounet, Forêt d'El; Ijbertene. 10. El Kisba vicinity; Komuch. 11. Asserdoun. 12. Khenifra area. 13. Ajdir, Plateau d'; Ali ou Zrou, Jebel; Annocer; Arhbalou N'Irkraouen; Azigza. Aguelmane; Bou Cèdre; Bou Igaouerh, Jebel; Imi Ourarn; Kerrouchene; Khenifra, 22 km E; Mimejad; Senoual region; Tafecnna; Tiguerouguine. 14. Abid, Oued el, gorge; Arhbala, N of; Tizi M'Isly, N of. 15. SidiYahya ou Youssef, 8–10 km W of; SidiYahya ou Youssef, S and W of. 16. Tounfit, 15–20 km SSE of. 17. Tounfit, N and W of. 18. Tagoulelt vicinity. 19. Itzer, 10–15 km E of; Itzer, W of. 20. Assaka N'Ouam; Zad region. 21. Seheb. 22. Afennourir; Aïn Kahla; Aïn Leuh; Azrou, 18 km S; El Hammam; Ouiouane; Oum Er Rbia, Oued, source; Sidi Mguid vicinity; Zaouia de Ifrane. 23. Azrou; Azrou, 5 km S; Azrou, above; Azrou Forest; Azrou region; Bou Jirih; Cèdre Gouraud; Ifrane; Michlifene; Ras El Ma. 24. Imouzzert du Kandar, vicinity. 25. Taffert; Tahar Souk, N of. 26. Bou Iblane, Jebel; Tamjilt, below. 27. Tahafourt. 28. Rhiata mountains. 29. U.K.: Gibraltar; Gibraltar, N end of mountain. 30. Moussa, Jebel. 31. Fath Lemhar. 32. Ahfa-Timesh; Buzeitune, Jebel; Derti-Na, N of; El Haouz region; Kelti, Jebel; Sidichmim; Tétouan vicinity; Zarka cascade vicinity. 33. Bouhassim, Jebel. 34. Adelma, Oued; Beni Mohammed; Chechaouene, Jebel; El Kelaa; Farda, Oued; Kaiat, Jebel; Lakraa, Jebel; Magoo, Jebel; Sidi Salah, Jebel; Sidi Siah; Talaat, Ardhouse; Talasemtane; Tasaot, Jebel; Tilljida, Oued; Tisouka, Jebel. 35. Tisirene, Jebel. 36. Targa vicinity. 37. Besene, Bab. 38. Ketama vicinity. 39. Tidirhine, Jebel. 40. Tizi Ifri. 41. Al Hoceima. 42. Beni Touzine vicinity. 43. Nador vicinity. **ALGERIA.** 44. Rond-Point des Cèdres. 45. Tighret forestry post. 46. Chiffa, Gorges de la. 47. Chiffa, Gorges de la, ca. 15 km S of Blida. 48. Chrea. 49. Bou Zegza, Djebel. 50. Palestro, Gorges de; Tala Kitane. 51. Aït Oubane, Forêt d'; Cheminot; Djurdjura, Djebel; Guessig, Mount; Hotel; Icetcifène; Ras Timedouine; Source des Singes; Tala Gulief; Tala Rana; Tigounatine; Tikjda. 52. Akfadou, Forêt de; Beni Rhobri, Forêt des; Taourirt Irhil, Forêt de. 53. Bouak, Cap-Cap Carbon, between; Pic des Singes National Park. 54. Akra, Chabet El; Borj Mira; Darguinah; Kherrata, Gorges de; Takoucht, Djebel. 55. Babor, Djebel. 56. Adendoun, Djebel; Dar El Oued; Guerrouh, Forêt Domaniale de; Ziam Mansouria, E of. 57. Kebir, Oued El, gorge. 58. Constantine. 59. Collo, Kabylie de. 60. Stora, "Oran"; Stora vicinity. 61. Azzaba, W of. 62. Edough, Djebel. **TUNISIA.** 63. Tabarqah. 64. Zaghwan.

Camperio Ciani & Palentini, 2003, p. 63) reported a further decline to 10,000. The main factor responsible for population decline apparently is anthropogenic destruction of habitat (Fa. 1986a, p. 250; Camperio Ciani et al., 2005, p. 640; Waters et al., 2007, p. 107). *M. sylvanus* has been designated as Vulnerable on the IUCN Red List of Threatened Species (IUCN, 2006).

Pelage (Fig. 2)

In *M. sylvanus* adults and subadults, prime pelage coloration on the dorsal surface of the trunk typically is strongly variegated (Fig. 2C), pale (pale buffy to golden brown to burnt orange) and dark (blackish). This variegation is a result of conspicuous banding of individual dorsal hairs: in one adult male (USNM 255979,

TABLE 1. Frequency distribution of elevation records of *Macaca sylvanus* (see Gazetteer, Appendix II).¹

Elevation (m)	Number of records
400–599	2
600–799	2
800–999	1
1000–1199	7
1200–1399	9
1400–1599	4
1600–1799	6
1800–1999	21
2000–2199	9
2200–2300	1
Total	62

¹ Where elevations were originally reported as a range of values, the midpoint of these values is tabulated here.

Gibraltar, zoo specimen), interscapular hair length is ca. 80 mm, the basal 50 percent of each hair is dark brown, the middle 30 percent is pale buffy, and the distal 20 percent is blackish; in other adults and subadults, the pale intermediate band often is more brightly colored. Premolt pelage is faded and drab (Fig. 2A).

The pelage in one exceptional adult or subadult female (USNM 258206, Gibraltar, zoo specimen) is strikingly erythristic—reddish brown on crown, trunk, and appendages. Moroccan specimens that apparently are similarly erythristic have been reported by Panouse (1957, p. 25: “franchement au roux”) and Aulagnier and Thevenot (1986, p. 56: “brun-roux sur le dos”). According to Bédé (1927, p. 28), specimens obtained in Morocco were generally more erythristic than those obtained in Algeria, but the purported geographic difference remains to be adequately documented (Didier & Rode, 1936, p. 13; Rode, 1937, p. 158).

Pelage on the crown is variegated like that on the back, but crown hairs tend to be more brightly colored. The sides of the face are bounded by streaks of dark brown hair, whereas the face itself is thinly haired and lightly pigmented. The lateral facial crests in 13 specimens examined are restricted to the posterior mandibular region (infrazygomatic crests; Fooden, 1995, p. 19). On outer surfaces of the pectoral and pelvic appendages, variegation tends to decrease from proximal to distal segments, generally becoming pale brown to medium brown on dorsal surfaces of the hands and feet. The ventral surfaces of the trunk and

appendages are thinly haired, pale buffy to whitish.

At birth, dorsal pelage is blackish, and ventral pelage, which is thin, is slightly paler (Fa, 1984c, p. 338; cf. Carpentier, 1931, p. 275; Deag & Crook, 1971, p. 188; MacRoberts & MacRoberts, 1971, p. 39). The gradual transition from blackish infantile pelage to variegated brownish juvenile pelage begins about age 45 days and is completed by about age 145 days. Pelage length in juveniles is less than in subadults and adults, but the coloration is generally similar.

Molting occurs during spring and summer and usually is complete by September or October (Fig. 2C; cf. MacRoberts & MacRoberts, 1971, p. 39; Merz, 1976, p. 59; Deag, 1984, p. 124). In females with new infants, molting usually begins about two months after parturition (Fa, 1984c, p. 339). The bright new fur appears first on the head, arms and forearms; subsequently, it appears more caudally and ventrally.

External Measurements and Proportions

Head and body length measurements are available for a small sample of wild-collected *M. sylvanus* specimens, all of which originated near Azrou, Moyen Atlas, Morocco (Table 2). In this sample, mean head and body length is 556.8 mm in four adult females and 634.3 mm in three adult males; the female/male dimorphism ratio is 87.8%. Sexual dimorphism of head and body length is similar in six captive specimens or specimens of unknown history—573.0 mm in four adult females (AMNH 19014, BM[NH] 11.11.11.1, USNM 258206, 502460) and 630.5 mm in two adult males (Cabrera, 1932, p. 201; MCZ 15296); in these specimens, the female/male length ratio is 90.9%. No information is available concerning geographic variation of head and body length in *M. sylvanus*.

Mean body weight in wild-collected adults is 9.9 kg in 18 females and 14.5 kg in 33 males (Table 2; cf. Roberts, 1978, p. 233; Fa, 1984c, pp. 341–346; 1989, p. 58); the female/male dimorphism ratio for this volumetric measurement is 68.3%. Mean weight in four adult females collected in Morocco (9.2 ± 0.82 kg) is not significantly different ($P > 0.05$, *t*-test) from that in 14 females probably trapped in Algeria (10.1 ± 1.03 kg); weights of Moroccan adult males are unavailable (cf. Table 2, footnote 4).

FIG. 2. Adult pelage in *Macaca sylvanus*. A. Male, premolt. B. Male, molting (note new pelage on head and shoulders). C. Estrous female, postmolt. Photographed 29 September 2006 at Cèdre Gouraud, Morocco, by G. Fooden; image in figure B is photographically reversed.

Relative to adult size in *M. sylvanus*, ears in infants are larger than hind feet (Table 2). Length of the ear in infants is ca. 80% of that in adults, whereas length of the hind

foot in infants is only ca. 60% of that in adults.

An inconspicuous vestigial tail is variably present in *M. sylvanus* (Fig. 3; Table 3; cf.

TABLE 2. External measurements and proportions in wild-collected *Macaca sylvanus*.^{1,2}

Age/sex class ³	Head and body length (mm)	Weight (kg)	Hind foot length (mm)	Relative hind foot length (HF/HB × 100)	Ear length (mm)	Relative ear length (E/HB × 100)
Infants	266.5 246–287 (2)	1.0 0.9–1.0 (2)	101.5 96–107 (2)	38.2 37.3–39.0 (2)	40.0 36–44 (2)	15.0 14.6–15.3 (2)
Juveniles	521.0 ± 28.16 500–553 (3)	7.1 ± 1.31 6.2–8.6 (3)	159.0 ± 13.89 150–175 (3)	30.5 ± 1.10 29.4–31.6 (3)	45.0 ± 6.24 38–50 (3)	8.6 ± 1.00 7.5–9.4 (3)
Subadult males	604.0 559–649 (2)	—	182 (1)	28.0 (1)	51 (1)	7.9 (1)
Adult females	556.8 ± 11.47 540–566 (4)	9.9 ± 1.04 8.0–12.0 (18)	167.8 ± 1.71 166–170 (4)	30.1 ± 0.68 29.3–30.9 (4)	48.8 ± 1.26 47–50 (4)	8.8 ± 0.10 8.7–8.9 (4)
Adult males	634.3 ± 25.72 605–653 (3)	14.5 ± 1.75 10.0–18.0 (33) ⁴	179.0 ± 7.94 170–185 (3)	28.3 ± 1.85 26.4–30.1 (3)	51.3 ± 1.15 50–52 (3)	8.1 ± 0.42 7.8–8.6 (3)

¹ Mean ± SD (where $n > 2$), extremes, and sample size (italicized figures in parentheses).

² Most measurements are of specimens collected near Azrou, Morocco (BM(NH), USNM). Exceptions are weights of 14 adult females and 33 adult males that were reported by Delson et al. (2000, pp. 144–145); these 47 adults probably were trapped and weighed in Algeria (cf. Scheffrahn et al., 1993, p. 383; 1996, abstract no. 240). Measurements of USNM specimens are from specimen tags and collectors' field catalogs.

³ Dental specifications: infants, deciduous teeth only; juveniles, some permanent teeth erupted; subadults, M3 in females or C in males incompletely erupted; adults, all permanent teeth completely erupted.

⁴ Excludes USNM 476781 (juvenile) and USNM 476791 (weight recorded as ">10 kg") (cf. Delson et al., 2000, p. 144).

Lydekker, 1893–1894, pp. 117–119); Aristotle (d'A. W. Thompson translation, 1984, p. 799) accurately described the tail vestige in this species as "... a very small one—a sort of hint of a tail." In a series of 13 Moroccan specimens that were carefully examined by the collectors, a tail vestige, varying in length from 4 mm to 22 mm, was detected in eight individuals (62%); although the sample size is small, the data suggest that the tail vestige might be more frequent in males (86%) than in females (33%). Tail vestiges of similar length are known to occur in three captive males (Hill, 1974, p. 622, 18.7 mm; FMNH 60716, 9 mm [Fig. 3]; MCZ 15206, 22 mm). Relative tail length probably is greater in infants than in postinfants (Table 3), which suggests that the postnatal growth rate of the tail is less than the postnatal growth rate of the head and body.

Caudal Vertebrae

Caudal vertebrae also are vestigial in *M. sylvanus* (Fig. 4), and, as previously noted by

Waldeyer (1896, p. 783) and Schultz (1925, pp. 249–250), these vertebrae do not extend into the external tail; for this reason, Waldeyer and Schultz have characterized the tail vestige in *M. sylvanus* as "soft." The number of caudal vertebrae in this species varies from two to five (Appendix III), with a modal number of three (13 of 29 specimens reported). Reduction in number of caudal vertebrae in *M. sylvanus* apparently exceeds that in humans, where the modal number of caudal vertebrae is four (Schultz & Straus, 1945, p. 613).

Cranial Characters

Mean greatest length of skull in wild-collected *M. sylvanus* is 118.7 mm in four adult females and 135.5 mm in five adult males (Figs. 5, 6; Table 4); the female/male dimorphism ratio is 0.88. Available evidence does not permit analysis of geographic variation of skull size in this species (cf. Table 4, footnote 4).

In wild-collected *M. sylvanus*, mean relative zygomatic breadth increases from 60.9% in

FIG. 3. Tail vestige (indicated by arrow) in *Macaca sylvanus* (FMNH 60716, infant male, zoo specimen); tail length is 9 mm. (Photograph by R. Banasiak.)

infants to 69.2% in adult males, and mean rostral–postrostral ratio increases from 23.8% in infants to 59.0% in adult males (Table 4). As in other macaques, postnatal relative growth of the rostrum greatly exceeds that of the zygomatic arches.

A sagittal crest is relatively rare in *M. sylvanus*. In adult male skulls examined, this crest is absent in four wild-collected specimens and present in only two (MCZ 15296, MNHN CG 1831/835) of nine captive specimens or specimens of unknown history (overall frequency, 2/13 = 15.4%).

TABLE 3. Tail length and relative tail length in *Macaca sylvanus* specimens collected near Azrou, Moyen Atlas, Morocco: measurements from specimen tags and collectors' field catalogs.

USNM No.	Age ¹	Sex	Head and body length (mm)	Tail length ² (mm)	Relative tail length (T/HB × 100)
476788	Infant	Male	246	15	6.1
476789	Infant	Male	287	15	5.2
476790	Juvenile	Female	510	0	—
478329	Juvenile	Female	500	15	3.0
476781	Juvenile	Male	553	15	2.7
476784	Subadult	Male	649	22	3.4
476782	Adult	Female	561	0	—
476783	Adult	Female	566	4	0.7
476786	Adult	Female	540	0	—
476787	Adult	Female	560	0	—
476780	Adult	Male	605	20	3.3
476785	Adult	Male	653	22	3.4
476791	Adult	Male	645	0	—

¹ For dental specifications, see Table 2.

² Cf. MacRoberts and MacRoberts, 1971, p. 39; Burton and de Pelham, 1979, p. 109 (apparent decimal point placement errors in this publication; tail length reported as “0.5 mm” and “0.53 mm” in two infant specimens).

Based on analyses of 27 cranial dimensions, Pan and Oxnard (2004, p. 367) have reported that cranial differences between *M. sylvanus* (21 adult specimens) and 10 Asian macaque species (303 adult specimens) greatly exceed corresponding differences among the 10 Asian species. Unfortunately, the provenance of the *M. sylvanus* specimens (and non-*M. sylvanus* specimens) studied in this research project is not specified (cf. Table 4); some artificially provisioned individuals might have been included (cf. Fooden & Aimi, 2005, p. 17).

Molecular Biology and Genetics

DNA Variation

Virtually all studies of interspecific DNA variation within the genus *Macaca* have indicated that *M. sylvanus* is the sister group of Asian macaque species (Hayasaka et al., 1996, p. 1050; Morales & Melnick, 1998, pp. 15–16; Deinard & Smith, 2001, p. 50; Tosi et al., 2003, pp. 1427, 1430; Modolo et al., 2005, p. 7394; Liu & Pearl, 2007, p. 411; Ziegler et al., 2007, p. 811). A recent exception is Tosi et al.'s (2003, p. 1426) study of Y-chromosomal DNA, in which the phylogenetic relationship of *M. sylvanus* was unresolved.

The most comprehensive survey of intraspecific DNA variation in *M. sylvanus* has been

published by Modolo et al. (2005, p. 7393). In this study, a 468-bp sequence of hypervariable region 1 of the mtDNA control region was analyzed in 68 samples of Gibraltar monkeys (artificially introduced population; see above, Geographic Distribution), 116 samples of Moroccan monkeys (3 localities), and 96 samples of Algerian monkeys (4 localities) (Table 5). Of the 24 haplotypes detected in non-Gibraltar samples, nos. 1–15 were restricted to Morocco and nos. 16–24 were virtually restricted to Algeria (cf. Pastorini et al., 2000, p. 166; Crouau-Roy et al., 2001, p. 157; von Segesser, 2002, p. 161); the sole exception is haplotype no. 16, which was detected in 25 Akfadou (Algeria) samples and four Rif (Morocco) samples. Modolo et al. (2005, pp. 7394, 7397) plausibly concluded that the anomalous geographic distribution of haplotype no. 16 probably is a result of Algerian monkeys having been artificially transported and released in the Rif mountains. Haplotype evidence (Table 5) also indicated that the Gibraltar population has resulted from artificial introduction of monkeys from the Rif (Morocco) and Akfadou (Algeria) regions (Modolo et al., 2005, p. 7397).

Phylogenetic analysis indicates that Algerian mtDNA haplotypes are more divergent than Moroccan haplotypes (Fig. 7); in fact, Algerian haplotypes at Pic des Singes (haplotype no. 18) and Kherrata (haplotypes nos. 19–22) are more similar to Moroccan haplotypes than they are to other Algerian haplotypes (cf. Scheffrahn et al.,

FIG. 4. Ventral view of sacrum and caudal vertebrae (Cd 1–Cd 3) in *Macaca sylvanus* (FMNH 47398, adult male, zoo specimen); vestigial Cd 3 is asymmetrically fused to Cd 2. (Photograph by J. Weinstein.)

1996, abstract no. 240). Modolo et al. (2005, p. 7396) have indicated that the present disjunct clustering of mtDNA haplotypes could be a product of Pleistocene and Holocene climate

changes that resulted in periodic forest fragmentations and interconnections. Based on fossil evidence and the date of the Messinian Salinity Crisis (Delson, 1980a, p. 16; Tosi et al., 2003,

FIG. 5. Skull of adult female *Macaca sylvanus*: USNM 476782, Azrou, 18 km S of, Morocco. (Photographs by E. M. Santana.)

p. 1424), Modolo et al. (2005, p. 7393) have postulated that *M. sylvanus* originated ca. 5.5 million years ago (Ma) and have inferred that extant clades and subclades of *M. sylvanus*

differentiated within the past 1.85 million years (Table 6).

Microsatellite variation within and between four isolated Algerian populations of *M. sylvanus*

FIG. 6. Skull of adult male *Macaca sylvanus*: USNM 476785, Azrou, 18 km S of, Morocco. (Photographs by E. M. Santana.)

TABLE 4. Cranial measurements^{1,2} and proportions in wild-collected *Macaca sylvanus*; except for one adult male obtained at Gorges de la Chiffa, Algeria, all specimens were collected near Azrou, Morocco (see footnotes 4 and 5).

Age/sex class ³	Greatest length of skull (mm)	Relative zygomatic breadth (ZB/GL × 100)	Postrostral length (mm)	Rostral-postrostral ratio (R/PR × 100)
Infants	80.3	60.9	71.1	23.8
	77.6–83.0	60.4–61.4	68.4–73.7	23.3–24.4
Juveniles	(2)	(2)	(2)	(2)
	113.0	66.6	82.6	48.0
	109.8–116.3	65.7–67.5	81.2–83.9	43.7–52.2
Adult females	(2)	(2)	(2)	(2)
	118.7 ± 5.48	69.4 ± 2.05 ⁴	85.9 ± 1.66	49.6 ± 3.12
	113.7–125.7	68.2–72.4	84.1–87.5	47.4–54.2
Subadult males	(4)	(4)	(4)	(4)
	124.3	67.6	90.7	56.5
	118.2–130.5	66.0–69.2	(1)	(1)
Adult males	(2)	(2)	(1)	(1)
	135.5 ± 2.27 ⁴	69.2 ± 1.00 ⁵	91.7 ± 0.95	59.0 ± 2.47
	132.7–137.7	68.0–70.5	90.5–92.7	55.6–61.6
	(5)	(5)	(4)	(4)

¹ For definition of measurements, see above, Materials and Methods.
² Mean ± SD (where sample size exceeds two), extremes, and sample size (italicized figures in parentheses).
³ Dental specifications: infants, deciduous teeth only; juveniles, some permanent teeth erupted; subadults, M3 in females or C in males incompletely erupted; adults, all permanent teeth completely erupted.
⁴ 135.3 ± 2.58 mm in four adult males collected in Morocco; 136.2 mm in one adult male collected in Algeria (measurement of Algerian specimen provided by D. Brandon-Jones).
⁵ Zygomatic breadth of Algerian specimen estimated by D. Brandon-Jones.

nus was studied by von Segesser et al. (1999, p. 436). In a sample of 159 monkeys, six of the seven loci tested were found to be polymorphic, with 4–12 alleles per locus. Populations and population subgroups were genetically differentiated with respect to these loci. Genetic distance was significantly correlated with geographic distance within a population—but not between populations. Crouau-Roy et al. (2001, p. 157), who also studied microsatellite variation in *M.*

sylvanus, found 12 alleles specific to Moroccan samples and 21 alleles specific to Algerian samples.

Karyology

The chromosomes of *M. sylvanus* have been studied—with partly divergent results—by Stan-
yon et al. (1980, p. 150), Dutrillaux et al. (1982, p. 97), Tihy et al. (1996, p. 10), and Morescalchi

TABLE 5. Mitochondrial DNA haplotype frequencies in Gibraltar and North African samples of *Macaca sylvanus* (Modolo et al., 2005, p. 7393).

Locality	N	Haplotype code numbers																															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24								
Gibraltar	68	24		U.K.										36																			
Rif	28	4		Morocco										4																			
Moyen Atlas	69	4	16																							3	1		12	10	1	16	2
Haut Atlas	19	6		6		3	4		Algeria										25														
Akfadou	25																																
Djurdjura	54																							45		9							
Pic des Singes	12																																
Kherrata	5																			7		5		2				1		1		1

FIG. 7. Phylogenetic relationships among Moroccan (Mor.) and Algerian (Alg.) populations of *Macaca sylvanus*, as indicated by mtDNA haplotypes (maximum likelihood tree, condensed from Modolo et al., 2005, p. 7394); the Pic des Singes sample includes two haplotype subgroups.

et al. (1998, p. 102). Stanyon et al. (1980, p. 150) found that chromosomes in *M. sylvanus* are generally similar to those in *M. mulatta*, except that banding patterns in four chromosomes (nos. 1, 4, 9, and 16) are polymorphic in *M. sylvanus* but not in *M. mulatta*. Dutrillaux et al. (1982, p. 107) reported that chromosomes in *M. sylvanus* are similar to those in other macaques (except *M. fascicularis*) and also are similar to those in species of *Papio* and *Lophocebus*. Tihy et al. (1996, p. 10) reported that chromosome no. 18 in *M. sylvanus* is homologous to chromosome no. 13 in humans; a centromeric shift probably occurred during the course of this chromosomal transition. And Morescalchi et al.

(1998, p. 103) reported that chromosome no. 2 in *M. sylvanus* has a clear band adjacent to the centromere that does not occur in other species of *Macaca* but does occur in species of *Papio*; these authors also found that human chromosome probes nos. 7 and 21 hybridized to *M. sylvanus* chromosome no. 2 (cf. Wienberg et al., 1990, p. 347).

As in other members of the tribe Papionini, the diploid chromosome number in *M. sylvanus* is 42.

Natural History

Habitats

Habitats occupied by *M. sylvanus* include cedar, fir, and oak forests (evergreen oak and deciduous oak), scrub, grasslands, and rocky ridges dominated by herbaceous vegetation (Table 7); although most extant *M. sylvanus* populations inhabit cedar forests, this might reflect current habitat availability rather than habitat preference (Fa, 1984e, pp. 281, 284). Climate in the range of this species is Mediterranean, with warm dry summers and relatively wet winters (Trewartha, 1978, p. 8); at elevations above 1500 m—i.e., well within the elevational range of *M. sylvanus* (Table 1)—snow falls in winter, and snow accumulations can persist on mountain summits until mid-May (Fa, 1982, p. 50; Mehlman, 1984, p. 172). Alvarez and Hiraldo (1975, p. 256) have reported that monkey populations in the Rif mountains migrate to lower elevations during winter.

TABLE 6. Estimated dates of divergence of *Macaca sylvanus* sister groups, based on mtDNA haplotype relationships (Modolo, 2005, p. 7394, table 4).

Sister groups (see Fig. 7)		Estimated divergence dates (Ma) ¹
Morocco/Kherrata/Pic des Singes (hapl. no. 18) clade (Morocco + Algeria)	Djurdjura/Akfadou/Pic des Singes (hapl. no. 17) clade (Algeria)	1.24–1.85
Morocco clade	Kherrata/Pic des Singes (hapl. no. 18) clade (Algeria)	1.22–1.62
Djurdjura clade (Algeria)	Akfadou/Pic des Singes (hapl. no. 17) clade (Algeria)	0.78–1.01
Kherrata subclades (Algeria)		0.064–0.359
Morocco subclades		0.110–0.282
Akfadou subclades (Algeria)		0.070–0.078
Djurdjura subclades (Algeria)		0.070–0.078

¹ Million years ago.

TABLE 7. Habitats of *Macaca sylvanus*.

Geographic area	Dominant vegetation	Scientific name	References ¹
Morocco	Scrub	—	1, 2
Haut Atlas	Atlantic cedar	<i>Cedrus atlantica</i>	1, 3, 4
Moyen Atlas	Holm oak ²	<i>Quercus ilex</i>	—
	Mixed cedar-oak	—	—
	Grassland	—	—
Rif	Spanish fir	<i>Abies pinsapo</i>	2, 5, 6, 7, 8
	Atlantic cedar	<i>Cedrus atlantica</i>	—
	Holm oak ²	<i>Quercus ilex</i>	—
	Mixed oak	—	—
	Scrub	—	—
Algeria			
Chiffa	Holm oak ²	<i>Quercus ilex</i>	6
	Mixed oak	—	—
Tigounatine	Mixed cedar-oak ²	—	9, 10
Icefcifère	Herbaceous	—	9, 10
Akfadou	Mixed oak ³	—	10, 11
Kerrata	Holm oak ²	<i>Quercus ilex</i>	6
	Mixed oak	—	—

¹ Key to reference numbers: 1. Deag and Crook, 1971, p. 186. 2. Taub, 1977, p. 110. 3. Ménard, 2002, p. 95. 4. Camperio Ciani et al., 2005, p. 639. 5. Alvarez and Hiraldo, 1975, pp. 254–257. 6. Fa et al., 1984, pp. 86, 100, 105. 7. Mehlman, 1984, p. 165. 8. Fa, 1986a, p. 222. 9. Ménard and Vallet, 1986, pp. 173, 174. 10. Ménard, 2002, p. 95. 11. Ménard, 1985, p. 452; 2002, p. 95.

² Evergreen.

³ Deciduous.

Terrestriality/Arboreality

Macaca sylvanus spends most of the daylight hours on the ground (Table 8); reported mean frequency of daytime terrestriality varied from 68% to 83% in Morocco and from 58% to nearly 100% in Algeria. Infants and juveniles tended to be less terrestrial than adults (Merz, 1976, p. 60; Deag, 1985, p. 408; Ménard, 1985, p. 466; Ménard, & Vallet, 1986, p. 176; Machairas et al., 2003, p. 189); in populations studied at Afennourir and Cèdre Gouraud (=Gouroud), Morocco, juveniles were 70% terrestrial and adult males were 81% terrestrial (Machairas et al., 2003, p. 189). Frequency of terrestriality also varied seasonally (Deag, 1985, pp. 408–409; Ménard & Vallet, 1986, p. 190; 1997, p. 292). This species flees into trees to escape danger (Merz, 1976, p. 60; Deag, 1985, p. 408), and it sleeps in trees (Taub, 1977, p. 128; de Turkheim & Merz, 1984, p. 247; Mehlman, 1989, p. 285; Hammerschmidt et al., 1994, p. 279) or in caves on rocky cliffs (MacRoberts & MacRoberts, 1971, p. 45; Alvarez & Hiraldo, 1975, p. 258; Fa et al., 1984, p. 94; Mehlman, 1984, pp. 190–191).

Group Size and Composition

Reported size in 68 natural groups of *M. sylvanus* averaged 27.1 individuals and varied from seven to 88 individuals (Appendix IV). Limited available evidence has suggested that group size might average smallest (18.3 individuals) in the Moroccan Rif, largest (50.2 individuals) in the Algerian Grande Kabylie, and intermediate (28.6 individuals) in the Moroccan Moyen Atlas (Appendix IV). Group size generally is fairly stable in this species, but it was unstable in an Algerian population that inhabits a rocky habitat in the Djurdjura mountains (Ménard et al., 1985, p. 72; 1990, p. 169; Ménard, 2002, pp. 96, 98); in this marginal habitat, groups frequently split into subgroups that subsequently reunite in various combinations. Solitary males, as far as 7 km distant from the nearest group, have been reported in the Moroccan Rif (Mehlman, 1985, p. 204; 1986, p. 75). Provisioned semi-free-ranging groups, which sometimes have included as many as 200 members (de Turkheim & Merz, 1984, p. 243; Kuester & Paul, 1992, p. 194), apparently can become larger than natural groups.

TABLE 8. Frequency of terrestriality in *Macaca sylvanus* populations.

Locality	Sample size	Mean frequency of terrestriality	References ¹
	Morocco: Moyen Atlas		
Aïn Kahla (cedar)	11,202 observations	83%	1
Afennourir (cedar)	317 hr	68%	2
Cèdre Gouraud ² (cedar-oak)	267 hr	77%	2
	Algeria: Grand Kabylie		
Tigounatine (cedar-oak)	2,587 scans	68%	3
Akfadou (oak)	2,608 scans	58%	3
Icefcifère (mountain ridge)	—	~100%	4
	France: semi-free-ranging		
Kintzheim (mixed European forest)	—	>50%	5

¹ Key to reference numbers: 1. Deag, 1985, p. 409. 2. Machairas et al., 2003, p. 189. 3. Ménard and Vallet, 1997, p. 292; cf. Ménard, 1985, p. 466; Ménard and Vallet, 1986, p. 176. 4. Ménard and Vallet, 1986, p. 190. 5. Merz, 1976, p. 60.

² Alternate locality name: Gouroud.

Within natural groups of *M. sylvanus*, the number of adult males apparently averages only slightly less than the number of adult females (Appendix IV). The known ratio of adult males to adult females averaged 0.70 in the Moroccan Moyen Atlas, 0.99 in the Moroccan Rif, and 0.84 in the Algerian Grande Kabylie.

Group Fission

A *M. sylvanus* group in the Algerian Grande Kabylie that increased in size from 38 members in 1983 to 88 members in 1988 permanently subdivided in 1989 into three daughter groups (50, 24, and 13 members; 1 member disappeared) (Ménard & Vallet, 1993a, p. 483; 1993b, p. 105; Lathuillière et al., 2004, p. 176). As noted above, 88 is the maximum group size known in natural groups of *M. sylvanus*, which suggests that fission could be inevitable in groups that approach this size.

Fission also has been reported in semi-free-ranging European groups of *M. sylvanus* (Prud'Homme, 1991, p. 10; Fa & Lind, 1996, p. 237; Kuester & Paul, 1997, p. 946; Fischer, 1998, p. 800; Kümmerli & Martin, 2005, p. 1232). Female matriline generally remained intact during the course of these fission events, which usually began during the mating seasons.

Home Range Area and Population Density

Available evidence suggests that home range area in natural groups of *M. sylvanus* averages smallest (18.4 ha) in the Moroccan Moyen Atlas,

largest (804.5 ha) in the Moroccan Rif, and intermediate (279.7 ha) in the Algerian Grand Kabylie (Table 9). Home ranges of adjacent groups frequently overlapped—100% overlap reported for some groups—in all three areas (Deag & Crook, 1971, p. 188; Rumsey & Whiten, 1972, p. 562; Menard et al., 1986, p. 37; Mehlman, 1989, p. 282). Of 13 observed visual contacts between neighboring groups, only three (23%) were agonistic (Mehlman & Parkhill, 1988, p. 33; cf. Deag & Crook, 1971, p. 189). Linear day ranges of >2 km have been reported for two Algerian groups (Ménard & Vallet, 1997, p. 297).

Population density in *M. sylvanus* apparently attains its maximum in relatively undisturbed cedar or mixed cedar/oak habitats, where densities of 19–70 individuals per km² have been reported (Table 10). As expected, degraded habitats, particularly those in the Moroccan Rif, support population densities that are much lower—0.37–4.50 individuals per km² (cf. Mehlman, 1989, p. 286; Dell'Amico et al., 2006, p. 292). Two semi-natural populations maintained in France have reached densities of 1,500 and 2,600 individuals per km² (de Turckheim & Merz, 1984, p. 245).

Diet

The diet of natural populations of *M. sylvanus* includes a wide variety of gymnosperms and angiosperms (Fa, 1984d, pp. 348–355) (Table 11). In the Moroccan Moyen Atlas, 107 species of food plants have been reported

TABLE 9. Home range area in natural populations of *Macaca sylvanus*.

Sample area	Group size	Home range area (ha)	References ¹
Morocco: Moyen Atlas			
Aïn Kahla	32 ² (25–39)	15.1 ² (11.7–18.6)	1
Bou Jirirh	40	25.0	2
Means (weighted)	34.7	18.4	—
Morocco: Rif ³			
Beni Hessane: Bouhassim	27	1200.0	1
Rhomara: Talssemtane	28.8 ⁴ (12–59)	725.4 ⁴ (307–901)	3
Means (weighted)	28.5	804.5	—
Algeria: Grande Kabylie			
Akfadou	39–45	424	4
Djurdjura: Mount Guessig	≥37	39	5
Djurdjura: Tigounatine	46–73	376	4
Means (weighted)	≥46.2	279.7	—

¹ Key to references: 1. Fa, 1986d, p. 202. 2. Drucker, 1984, p. 139; Fa, 1986d, p. 202. 3. Mehlman, 1989, p. 282. 4. Ménard and Vallet, 1996, pp. 123–124. 5. Ménard et al., 1990, p. 169.

² Mean value of two groups; extreme values indicated in parentheses.

³ Cf. Rumsey and Whiten, 1972, p. 562.

⁴ Mean value of five groups; extreme values indicated in parentheses.

(Drucker, 1984, p. 142; cf. Deag, 1983, p. 573); in the Moroccan Rif, 100 species have been reported (Mehlman, 1988, pp. 472, 477; cf. Fa, 1983a, p. 84); and in the Algerian Grand Kabylie, 130 species have been reported (Ménard

& Vallet, 1986, pp. 180, 190; 1996, pp. 120, 125; cf. Ménard, 1985, pp. 460–463). The 100 species exploited as food in the Moroccan Rif constituted 51% of 195 species of seed plants identified as present in that area, and, similarly, the 130

TABLE 10. Population density in *Macaca sylvanus*.

Sample area	Dominant vegetation	Survey year	Density (individuals/km ²)	References ¹
Morocco: Moyen Atlas				
Afennourir	Cedar (protected)	1994–1995	19.3	1
Aïn Kahla	Mixed cedar/oak	1968–1969	60–70	2
Aïn Kahla	Mixed cedar/oak	1973–1974	40	3
Azrou vicinity	Mixed cedar/oak	1994	28.19	4
Azrou vicinity	Mixed cedar/oak (degraded)	2002	7.26	4
Bou Jirirh	Cedar (undamaged)	1980–1981	50	5
Cèdre Gouraud ²	Mixed cedar/oak (degraded)	1994–1995	7.8	1
Oued-el-Abid	Mixed oak/juniper	1984	~11	6
Morocco: Rif				
Anjera: Moussa, Jebel	Scrub	1980	1.09	7
Beni Hessane: Bouhassim	Mixed oak	1980	0.37	7
Beni Zaid	Scrub	1980	0.60	7
Rhomara	Various	1980	1.08–4.50	7
Rhomara: Talassemtane	Fir	1981–1982	8.3	8
Algeria: Grande Kabylie				
Akfadou	Deciduous oak	1990	12.5	9
Djurdjura: Tigounatine	Mixed cedar/oak	1990	28.2	9

¹ Key to references: 1. Machairas et al., 2003, p. 189; cf. Camperio Ciani and Machairas, 2003, p. 124. 2. Deag, 1977, p. 269; 1984, p. 123. 3. Taub, 1977, p. 110. 4. Camperio Ciani et al., 2005, p. 638. 5. Drucker, 1984, p. 136; Fa, 1986d, p. 202. 6. Fa, 1986b, p. 33. 7. Fa, 1982, p. 62. 8. Mehlman, 1984, p. 175. 9. Ménard and Vallet, 1996, p. 124.

² Alternate locality name: Gouroud.

TABLE 11. Number of gymnosperm and angiosperm (seed-plant) species consumed by *Macaca sylvanus* populations.

Sample area	Number of seed-plant species eaten	References
Aïn Kahla	70	Morocco: Moyen Atlas Deag, 1983, p. 573
Bou Jirirh	107	Drucker, 1984, p. 142 Morocco: Rif
Djebala region	46	Fa, 1983a, p. 84
Lakraa, Jebel	100 ¹	Mehlman, 1988, pp. 472, 477 Algeria: Grande Kabylie
Akfadou	77	Ménard, 1985, pp. 460–463; Ménard & Vallet, 1996, pp. 120, 125
Icetcifère	31	Ménard & Vallet, 1986, p. 190
Tigounatine	130 ²	Ménard & Vallet, 1996, pp. 120, 125

¹ Total seed-plant species identified as present in this sample area: 195 (51.3% consumed).

² Total seed-plant species identified as present in this sample area: 271 (48.0% consumed).

species exploited in the Algerian Grand Kabylie constituted 48% of 271 species identified as present in that area. Barbary macaques also consume fungi, lichens, mosses, and animal prey (Deag, 1983, p. 571; Fa, 1984d, p. 355; Ménard, 1985, p. 452). Agricultural crops are known to have been raided by Barbary macaques at least since the early 16th century (Leo Africanus, 1896 edition, p. 948; cf. Mehlman, 1988, p. 477).

Plant parts that are eaten by *M. sylvanus* include flowers, fruits, seeds, seedlings, leaves, buds, bark, gum, stems, roots, bulbs, and corms (Fa, 1984d, p. 348; Mehlman, 1988, p. 472; Ménard & Qarro, 1999, p. 130). Because dietary composition varies seasonally (Deag, 1983, p. 571; Mehlman, 1984, p. 192; Ménard, 1985, p. 455; Ménard & Vallet, 1986, p. 177), comparative quantitative evaluation of dietary components requires study periods that extend over at least 12 months. Studies of that duration have indicated that seeds and leaves are the main foods (ca. 60–75%) of Barbary macaques in the Algerian Grande Kabylie (Table 12). Other studies have suggested that fruits could constitute a more significant part of the diet in the Moroccan Moyen Atlas (Deag, 1983, p. 574; Drucker, 1984, p. 142; Ménard & Qarro, 1999, p. 130).

Animal prey consumed by *M. sylvanus* includes snails, earthworms, scorpions, spiders, centipedes, millipedes, grasshoppers, termites, water striders, scale insects, beetles, butterflies, moths (including larvae), ants (including nests), and tadpoles (Fa, 1983a, p. 84; 1984d, p. 355;

Mehlman, 1984, p. 193; 1988, p. 476; Ménard & Vallet, 1986, p. 187). Semi-free-ranging monkeys have been observed to pursue and/or catch birds, squirrels, and young rabbits, but never to eat them (Kaumanns, 1978, p. 59; de Turckheim & Merz, 1984, p. 248); mice apparently are ignored.

Feeding reportedly occupied an average of 24% and 25% of daytime hours at two localities in the Moroccan Moyen Atlas (Machairas et al., 2003, p. 193; cf. Fa, 1986c, p. 216) and also occupied 24% and 25% of daytime hours at two localities in the Algerian Grande Kabylie (Ménard & Vallet, 1997, p. 291).

In winter, water has been obtained by eating snow (de Turckheim & Merz, 1984, p. 249; Mehlman, 1988, p. 482). During other times of water shortage, *M. sylvanus* has stripped the bark of cedar trees in order to obtain retained moisture (Camperio Ciani et al., 2001, p. 263).

Predators

Under natural conditions, the leopard probably was a major predator of *M. sylvanus* when these two species were broadly sympatric (Aulagnier & Thevenot, 1986, p. 56; cf. Fa, 1986b, p. 31). Large eagles presumably also were and are predators, because Barbary macaques respond to eagles' approach with alarm calls (Mehlman, 1984, p. 191); domestic dogs elicit a similar response, but foxes and jackals do not (cf. Ménard et al., 1986, p. 36).

In semi-free-ranging European populations, *M. sylvanus* gave alarm calls in response to the appearance of snakes, raptorial birds, and dogs

TABLE 12. Allocation of feeding time to various dietary components by *Macaca sylvanus* groups in Grande Kabylie, Algeria (Ménard, 1985, p. 454; Ménard & Vallet, 1986, p. 175; cf. Ménard & Vallet, 1996, p. 122).

Dietary component	Feeding time (%)	
	Akfadou ¹ (Deciduous oak forest)	Tigounatine ² (Cedar/evergreen oak forest)
Seeds	32.2	26.7
Leaves ³	27.3	48.1
Lichens	14.2	1.9
Invertebrates	10.5	5.6
Roots	6.9	7.7
Fungi	4.1	1.5
Flowers	3.4	1.6
Fruits	0.8	4.3
Other	0.6	2.6
Totals	100.0	100.0

¹ Study period: February 1983–September 1984.

² Study period: April 1983–March 1985.

³ Includes herbs.

(Paul & Kuester, 1988, p. 200; Fischer & Hammerschmidt, 2002, p. 37). In a European zoo, an infant Barbary macaque was killed by a hawk (Salzert, 1978, p. 39).

Intergroup Migration

Transfer of males between *M. sylvanus* groups apparently is reduced or postponed relative to intergroup transfer in other macaque species (K[ue]ster & Paul, 1984a, p. 70; Paul & Kuester, 1984, p. 372; Taub, 1984b, p. 52; Kuester & Paul, 1986, p. 317; 1997, p. 962; Ménard & Vallet, 1996, p. 118; Kümmerli & Martin, 2005, p. 1232). At two localities in the Algerian Grande Kabylie, 50% of sexually mature males remained in their natal groups (Ménard & Vallet, 1996, p. 118; cf. Scheffrahn et al., 1993, p. 383), and, in a semi-free-ranging European population, ca. 67% of sexually mature males remained in their natal groups (Kuester & Paul, 1999, p. 91; cf. 1989, p. 94). In the Algerian groups, the age of migrating males usually was >5 years (78–100%); in the European groups, the age of migrating males usually was 3–4 years (extremes, 1.75–11.75 years). Migration most frequently occurred during the fall–winter mating season (Ménard & Vallet, 1996, p. 119; Kuester & Paul, 1999, p. 91). Females rarely migrated (Paul & Kuester, 1988, p. 216; Kuester & Paul, 1989, p. 95; Ménard & Vallet, 1993b, p. 110; cf. Ménard et al., 1986, p. 36).

Reproduction

Seasonality

Reported matings in natural populations of *M. sylvanus* were restricted to the period September–April (wet season), with a mating peak during the period November–January (Table 13). The mating seasons of semi-natural and captive populations were of generally similar duration, but they might extend slightly longer than those in natural populations. In the Salem semi-natural population, onset of the mating period of individual females was related to age and reproductive history (K[ue]ster & Paul, 1984a, p. 71; 1984b, p. 193); older females (>10 years) began mating earlier in the year than younger females, and adult females without young of the previous year began mating earlier than adult females with young of the previous year.

Births in natural populations of *M. sylvanus* were restricted to the period February–September, and births in semi-natural and captive populations were restricted to the period January–November (Table 13). The timing of birth seasons can vary locally; the observed median birth date at Akfadou (3 May) was significantly earlier than that at nearby Tigounatine (19 May) (Ménard & Vallet, 1996, p. 109), and the birth season at Kintzheim apparently occurs earlier than at Rocamadour and Salem (de Turckheim & Merz, 1984, p. 257).

TABLE 13. Seasonal mating¹ periods (m) and birth periods (b) reported in *Macaca sylvanus* populations.

Sample area	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	References ²
Morocco: Moyen Atlas													
Aïn Kahla		m	m	m	m	m	m/b	m/b	b	b	b		1
Cèdre Gouraud ³				m	m			b	b	b	b		2
Afenmourir	b				m	m					b	b	2
Morocco: Rif													
Talassemtane			m	m	m	m	m	m	m/b	b	b		3
Lakraa, Jebel	b	b		m	m	m	m	m		b	b	b	4
Algeria: Grande Kabylie													
Icetitère					m ⁴			b		b	b		5
Tigounatine					m ⁴				b	b	b	b	5
Akfadou			m	m	m	m	m	m	b	b	b	b	5
Semi-natural or captive populations													
U.K.: Gibraltar	b	m/b	m	m	m	m	m	m	m/b	m/b	b	b	6
France: Rocamadour		m	m	m	m	m		b	b	b	b	b	7
France: Kintzheim		m	m	m	m	m/b	m/b	m/b	m/b	b	b	b	8
Germany: Salem	m/b	m	m	m	m	m	m	m/b	b	b	b	b	9
Germany: Rheine	b	b								b	b	b	10
U.K.: Jersey										b	b	b	11
U.S.A.: Nat. Zoo	b	b	m/b	b				b	b	b	b	b	12

¹ Mating is defined as ejaculatory copulation.

² Key to references: 1. Deag and Crook, 1971, pp. 183, 189; Deag, 1984, pp. 124–125. 2. Machairas et al., 2003, p. 189. 3. Mehlman, 1984, p. 176; 1986, p. 69; 1989, p. 276. 4. Rumsey and Whiten, 1972, p. 562. 5. Ménard et al., 1985, p. 73; Ménard and Vallet, 1993b, p. 108; 1996, p. 109. 6. Zeuner, 1952, p. 271; MacRoberts and MacRoberts, 1966, p. 300; 1971, p. 39; Burton, 1972, pp. 45, 52; Burton and Sawchuk, 1974, p. 275; Fa, 1984b, p. 279; 1986c, p. 152; Semple, 1998, p. 288. 7. Small, 1990a, p. 86; Hammerschmidt and Ansoerge, 1989, p. 79; Ansoerge et al., 1992, p. 272; Will and Todt, 1997, p. 66. 8. de Turckheim and Merz, 1984, p. 256; Prud'Homme, 1991, p. 11. 9. Paul and Thommen, 1984a, pp. 4, 6; K[ue]ster and Paul, 1984a, p. 71; de Turckheim and Merz, 1984, p. 256; Paul and Kuester, 1987, p. 120; 1988, p. 207. 10. Salzert, 1978, p. 39. 11. Mallinson, 1979, p. 37. 12. Roberts, 1978, p. 231.

³ Alternate locality name: Gouroud.

⁴ Cycling females (but no copulations) observed in other months.

Sexual Maturation

In natural populations in the Algerian Grand Kabylie, females typically were at least 5 years old before they produced their first infants (18 of 32 females), which indicates that the minimal age for female sexual maturity (capability of pregnancy) generally was ca. 4.5 years (Ménard et al., 1985, p. 68; Ménard & Vallet, 1996, p. 114); only 1 of 37 females (3%) in this population produced an infant at age 4 years, and none of 43 females produced an infant at age 3 years. Males in the Algerian Grand Kabylie were capable of ejaculatory copulation at age 5–7 years, although they were not yet full grown (Ménard et al., 1985, p. 68); the same was true of males at age 5–7 years in the Moroccan Moyen Atlas (Deag, 1980, p. 57).

The chronology of sexual maturation in provisioned semi-natural populations apparently

was generally similar to that in natural populations (Burton, 1972, p. 48; de Turckheim & Merz, 1984, p. 257; Fa, 1984c, pp. 341, 343). However, maturation might have been somewhat accelerated in semi-natural populations: Paul and Kuester (1996b, p. 298) reported that, in the semi-natural Salem population, 55 of 157 females (35%) produced their first infants at age 4 years (see above).

Reproductive Anatomy Notes

Although morphology of the glans penis and uterine cervix provides important taxonomic characters relevant to species relationships in the genus *Macaca* (Fooden, 2006, p. 27), little information is available concerning these structures in *M. sylvanus*. Illustrations of the glans penis published by Daubenton (in Buffon & Daubenton, 1766, p. 119, plate 11; slightly

revised in Buffon & Daubenton, 1833, plate 415, fig. 1) and Hill (1958, p. 654; 1974, p. 207) indicate that the glans in *M. sylvanus* is bilobed and relatively broad, as in the *silenus* group (Fooden, 1975, p. 33). Hill (1974, p. 621) also has provided measurements of two *M. sylvanus* bacula: length—11.2 mm, 11.5 mm; dorsoventral diameter—3.1 mm, 3.5 mm; and transverse diameter—2.2 mm, 2.0 mm.

Illustrations of the female reproductive tract have been published by Daubenton (in Buffon & Daubenton, 1766, p. 121, plate 12) and Rouget and Sabatier (1866, plate 8, fig. 2), but, unfortunately, neither of these figures depicts critical characters of the uterine cervix.

Female Sexual Cycles

During the mating season, *M. sylvanus* females exhibit coordinated reproductive cycles of sexual skin swelling, estrus behavior, and menstruation. The sexual skin cycle consists of prominent tumescence and detumescence of two areas of perineal sexual skin—one located around the anus (Fig. 2C) and the other located bilateral to the vulval cleft (Burton, 1972, p. 49; de Turkheim & Merz, 1984, p. 256; Fa, 1984c, p. 343; K[ue]ster & Paul, 1984a, p. 75). Developmentally, these circumanal and lateral vulval swellings are first evident as slight pinkish bulges that appear in females at age ca. 2.5 years. During subsequent mating seasons, the swellings increase in area and thickness—and often become bluish-gray—until age ca. 7–15 years, after which the swellings gradually decrease in size, ultimately becoming inconspicuous beyond age ca. 20 years. At the stage of maximal development, the area of the circumanal swelling (ca. 200 cm²) is approximately four times as large as the area of the lateral vulval swellings (Fa, 1984c, p. 345; Möhle et al., 2005, pp. 355, 359).

Of 12 females in the Gibraltar *M. sylvanus* population that were closely monitored during the 2001–2002 mating season, ten exhibited two cycles of tumescence and detumescence, and two exhibited three cycles (Möhle et al., 2005, p. 358; cf. Roberts, 1978, p. 231); tumescence was associated with an increasing fecal estrogen level, and detumescence was associated with an increasing fecal progesterone level. Ten of the monitored females became pregnant during one of their cycles, and all ten of these females exhibited a postconception tumescence. The

median interval between successive tumescence peaks was ca. 32 days (extremes, 27–44 days).

The estrus cycle consists of a period of female proceptive/receptive sexual behavior, marked by gradually increasing copulation rate, abruptly followed by a period of female sexual inactivity (K[ue]ster & Paul, 1984a, pp. 73, 75; Ménard et al., 1985, p. 73; Paul & Kuester, 1987, p. 125; Kuester & Paul, 1989, p. 96; cf. Small, 1990b, p. 272); maximal copulation rate in an estrus cycle is correlated with maximal sexual swelling/tumescence. Most females exhibit two estrus cycles per mating season; of 58 mature females in the Salem semi-natural population, 38 (65.5%) had two estrus cycles during the 1982–1983 mating season, 9 (15.5%) had one estrus cycle, and only one female had a maximum of five estrus cycles during this season (cf. Small, 1990b, p. 271; Semple, 1998, p. 288). A female's first estrus cycle of the season tends to be the longest, including 2–4 weeks (rarely 6 weeks) of sexual activity and ca. 2 weeks of sexual inactivity; subsequent estrus cycles include about one week of sexual activity. Most females probably are fertilized during the first estrus cycle of the season (K[ue]ster & Paul, 1984b, p. 194). During an estrus cycle, several females in the same group (5 of 13 in one group; 6 of 14 in another) were sexually active concurrently (Semple, 1998, p. 288; cf. Ménard et al., 1985, p. 73).

The menstrual cycle in *M. sylvanus* has a median length of ca. 32 days, including a median duration of menstrual bleeding of 4 days (extremes, 1–9 days) (Panouse, 1957, p. 28; Möhle et al., 2005, p. 360). The median interval between the last day of maximal sexual skin swelling and the first day of menstruation was 16 days (extremes, 12–18 days; $n = 11$) (Möhle et al., 2005, p. 358). Postconception bleeding in *M. sylvanus* has been reported to occur ca. three weeks after fertilization (K[ue]ster & Paul, 1984a, p. 75; Möhle et al., 2005, p. 361).

Consortships

During the mating season of *M. sylvanus*, pairs of males and estrous females form consortships—temporary sexual associations in the course of which copulations occurred (Taub, 1978b, unpaginated; 1980b, p. 292; de Turkheim & Merz, 1984, p. 257; Fa, 1986c, p. 151). The reported duration of consortships varied from <1 minutes to 93 minutes (median = 13 minutes, $n = 297$ consortships) in the Moroccan

Moyen Atlas (Taub, 1980b, p. 308) and from ca. 1 minute to 240 minutes (85% less than 8 minutes) on Gibraltar (Fa, 1986c, p. 153). In Morocco, the formation of most consortships was initiated by females (55%; males, 28%; mutually originated, 17%), and females also were responsible for the termination of most consortships (72%) (Taub, 1980b, pp. 299, 302; cf. Todt & Pohl, 1984, p. 225; Small, 1992, p. 142). The mean rate of exchange of consortship partners by females in the Moroccan Moyen Atlas was one per 19.9 minutes (Taub, 1980b, pp. 306, 308; cf. Small, 1992, p. 144; Paul et al., 1993b, p. 498). In the studied group, which included six mature females and 11 mature males, females consorted with a mean of 6.1 males per day (extremes, 3–10 males) (cf. Fa, 1986c, p. 151; Small, 1993, p. 84; Ménard et al., 2001, p. 606). In this group, a single copulation occurred during most consortships ($198/278 = 71\%$); two copulations occurred during nine consortships ($9/278 = 3\%$); and 71 consortships were nonejaculatory ($71/278 = 26\%$) (Taub, 1980b, p. 314).

Copulation

As in other macaques, a *M. sylvanus* male typically mounts a *M. sylvanus* female dorsoventrally by gripping her trunk and shanks with his hands and feet, respectively (Fig. 8; cf. Fooden & Aimi, 2005, p. 60). This species is a single-mount ejaculator—that is, copulations usually are restricted to a single mount–dismount sequence, during which the participating male ejaculates following a brief series of pelvic thrusts (Taub, 1980b, p. 313; 1982, p. 110; Mehlman, 1986, p. 72; Kuester & Paul, 1989, p. 99; 1992, p. 208; van den Bergh, 1991, p. 40; Semple, 1998, p. 288). In the Aïn Kahla group, studied in Morocco, the mean ($\pm$ SD) duration of 205 observed copulations was 8.7 ± 1.1 seconds (extremes, 6–14 seconds), and the mean number of pelvic thrusts to ejaculation was 9.1 ± 1.8 (extremes, 5–21) (Taub, 1980b, pp. 313, 314; cf. Mehlman, 1986, p. 72; Kuester & Paul, 1989, pp. 99, 100; 1992, p. 208); the mean interval between consortship formation (see above) and onset of copulation was 2.3 minutes (extremes, <1–16 minutes). Although harassment of copulating pairs by other group members was not observed at Aïn Kahla (Taub, 1980b, p. 296), 100 incidents of harassment by females were observed in the Salem semi-natural population

(Kuester & Paul, 1996, p. 770); of these harassment incidents, only 5% resulted in successful displacement of the harassed target. During the peak mating season at three Algerian localities, Ménard et al. (1985, p. 73) observed an average of 1.1–1.3 copulations per hour.

During the concluding phase of a copulation, the female partner utters a characteristic series of loud, low-frequency grunts (Taub, 1980b, p. 296; Todt & Pohl, 1984, p. 225; Paul, 1989, p. 463; van den Bergh, 1991, p. 40; Small, 1992, p. 142; Todt et al., 1995, p. 153; Semple, 1998, p. 288). Males apparently are able to detect differences between copulation calls produced by females at different stages of the estrous cycle (Pohl & Todt, 1984, p. 373; Semple & McComb, 2000, p. 710; Fischer & Hammerschmidt, 2002, p. 40; cf. Pfefferle et al., 2006, abstract no. 579).

Male Dominance Rank and Reproductive Success

Early studies of the relationship between male dominance rank and reproductive success in *M. sylvanus* were based on observation of copulation frequency (mating success), whereas more recent studies have been based on genetic determination of paternity (fertilization success). Of ca. 234 copulations observed in a natural group at Aïn Kahla, 76.6% were accumulated by four high-ranking males, and only 23.4% were accumulated by seven low-ranking males (Taub, 1980b, p. 320). Similarly, in the semi-natural population at Salem, mating success was strongly dependent on dominance rank (Paul, 1989, p. 467).

The results of paternity determination studies—in semi-natural groups—are equivocal. Although a positive overall relationship between rank and fertilization success was found in the Salem population (Paul & Kuester, 1996b, p. 302) and in the Rheine Zoo population (Witt et al., 1981, p. 207), no such relationship was found in the Gibraltar Middle Hill population (Kümmerli & Martin, 2005, p. 1238).

Inbreeding/Outbreeding

Male emigration and group fission tend to separate maternally related *M. sylvanus* males and females and thereby tend to reduce the possibility for inbreeding to occur (Kuester & Paul, 1999, p. 101; Lathuillière et al., 2004, p. 175; see above, Natural History). Even when *M. sylvanus* males became sexually mature while

FIG. 8. Copulation posture in *Macaca sylvanus*. Photographed 29 September 2006 at Cèdre Gouraud, Morocco, by G. Fooden.

still in their natal group, matrilineal inbreeding apparently was rare (Taub, 1980b, p. 334; Paul & Kuester, 1984, p. 372; cf. Merz, 1976, p. 62); in the Salem semi-natural population, incestuous copulations were observed in only 15 of 371 possible matrilineal male-female pairs (Kuester et al., 1994, p. 1186; cf. Paul & Kuester, 1985, p. 320). Avoidance of inbreeding in the Salem population was inferred to be a proximate effect of close association of maternal relatives during early life (Kuester et al., 1994, p. 1190).

Gestation

In the Salem semi-natural population, gestation length was measured as the interval between the date of an infant's birth and the date of its mother's last copulation during a conceptional estrus (Paul & Kuester, 1987, p. 126; cf. Didier & Rode, 1936, p. 11; MacRoberts & MacRoberts, 1966, p. 302; K[ue]ster & Paul, 1984a, p. 77).

The mean ($\pm$ SD) gestation period determined for 67 female infants was 165.3 ± 4.55 days (extremes, 145–178 days), and that for 56 male infants was 163.2 ± 5.38 days (extremes, 145–177 days). The difference between the mean gestation periods of female infants and male infants is statistically significant ($P < 0.02$, t -test).

Parturition

Details have been reported concerning one *M. sylvanus* parturition that was observed in 1987 in the semi-natural Rocamadour population (Hammerschmidt & Ansorge, 1989, p. 79). The observed parturition was one of 24 that occurred in this group—all apparently at night or early in the morning—during the March–June birth season. The prepartum female, already mother of a 1-year-old male, drew the attention of observers at 2125 hours (exact date in 1987 unspecified), when she remained sitting alone on the ground while other group members moved into sleeping

TABLE 14. Mean annual birth rate (births/reproductive years) in *Macaca sylvanus* groups.

Sample area	Observation period	Births	Reproductive years ¹	Mean annual birth rate	References ²
Natural groups					
Rhomara, Morocco	1980–1983	43	74	0.58	1
Tigounatine, Algeria	1982–1990	99 ³	173	0.57	2
Akfadou, Algeria	1982–1990	67 ⁴	105	0.64	2
Totals	—	209	352	0.59	—
Semi-natural groups					
Queen's Gate, Gibraltar	1936–1994	130	268	0.49	3
Middle Hill, Gibraltar	1946–1994	129	204	0.63	3
Middle Hill, Gibraltar	1995–2001	57	64	0.89	4
Rocamadour, France	1987	26	48	0.54	5
Salem, Germany	1978–1988	730	952	0.77	6
Totals	—	1072	1536	0.70	—

¹ Potential reproductive years of sexually mature females in each group.

² Key to references: 1. Mehlman, 1989, p. 277. 2. Ménard and Vallet, 1993b, p. 107; 1996, pp. 107, 109. 3. Fa, 1984b, p. 275; Fa and Lind, 1996, pp. 238, 240; cf. Burton and Sawchuk, 1982, p. 142. 4. Kümmerli and Martin, 2005, p. 1240. 5. Small, 1990c, p. 297. 6. Paul et al., 1993a, p. 110.

³ Midpoint value in range of uncertainty (97–101) specified in source.

⁴ Midpoint value in range of uncertainty (66–68) specified in source.

trees ca. 30 m distant; during the next 38 minutes, the solitary prepartum female manually inspected her perineum and emitted regular, low-amplitude vocalizations. Meanwhile, at 2145, after the female had moved on the ground ca. 15 m toward other group members, a liquid—suspected to be amniotic fluid—was noted on her hindquarters. At 2203, the neonate was rapidly delivered directly into the mother's hands, and, immediately following its birth, the infant emitted at least 12 screams. At 2211, after the mother had licked the infant for a few minutes, the placenta was expelled, and, by 2215, it was completely consumed by the mother. During this stage, the female and infant were joined by a young juvenile, which might have been the female's 1-year-old offspring. Finally, by 2219, the mother, carrying her infant, and the accompanying juvenile had climbed into a sleeping tree.

Birth Rate

The mean annual birth rate in *M. sylvanus* was 0.59 in three natural groups and 0.70 in five semi-natural groups (Table 14), which suggests that births every year are relatively uncommon in females of this species—particularly in natural groups (cf. Deag, 1980, p. 57; 1984, p. 125). Among factors known to affect the birth rate are natural food supply fluctuations (Ménard &

Vallet, 1993b, p. 111), age and parity of sexually mature females (Paul & Thommen, 1984b, p. 186; Paul & Kuester, 1988, p. 207; Paul et al., 1993a, pp. 109, 110; Ménard & Vallet, 1996, p. 109); and human disturbance of semi-natural groups (Fa, 1988, p. 77).

Neonatal Sex Ratio

Of 1040 reported *M. sylvanus* neonates, 538 were males and 502 were females (male/female ratio = 1.07) (Table 15); although the overall difference was not statistically significant ($P > 0.10$, chi-square test), the number of male neonates equaled or exceeded that of female neonates in five of the seven available samples. Neonatal sex ratio was related to maternal rank in the Salem sample (Paul & Kuester, 1990, p. 288): the male/female ratio among infants produced by high-rank mothers ($102/74 = 1.38$) significantly exceeded the ratio among infants produced by low-rank mothers ($86/95 = 0.91$; $P < 0.05$, chi-square test); the ratio among infants produced by mid-rank mothers was intermediate ($92/96 = 0.96$).

Twinning

In a composite sample of 874 births reported in semi-natural populations of *M. sylvanus*,

TABLE 15. Neonatal sex ratio in *Macaca sylvanus*.

Sample area	Observation period	Number of births			Ratio: males/females	References ¹
		Females	Males	Total		
Natural groups						
Tigounatine, Algeria	1982–1990	53	43	96	0.81	1
Akfadou, Algeria	1982–1990	29	34	63	1.17	1
Subtotals	—	82	77	159	0.94	—
Semi-natural groups						
Queen's Gate, Gibraltar	1936–1981	59	62	121	1.05	2
Middle Hill, Gibraltar	1936–1981	52	71	123	1.37	2
Middle Hill, Gibraltar	1995–2001	31	35	66	1.13	3
Rocamadour, France ²	1987	13	13	26	1.00	4
Salem, Germany ²	1977–1988	265	280	545	1.06	5
Subtotals	—	420	461	881	1.10	—
Totals	—	502	538	1,040	1.07	—

¹ Key to references: 1. Ménard and Vallet, 1996, p. 114. 2. Fa, 1984b, p. 283; 1986c, p. 292; cf. Burton and Sawchuk, 1982, p. 142. 3. Kümmerli and Martin, 2005, p. 1240. 4. Small, 1990c, p. 299. 5. Paul and Kuester, 1990, p. 288.

² Cf. de Turckheim and Merz, 1984, p. 257.

twinning frequency was 0.80% (Table 16). Viability of *M. sylvanus* twins was relatively low; of the 10 pairs reported, 6 pairs were stillborn, 2.5 pairs died within 8 days after birth, and only 1.5 pairs survived.

Geissmann (1990, p. 390) has shown that observed twinning frequency in primates tends to decrease as sample size increases to ca. 1,500 births. This indicates that larger samples will be required in order to provide a more reliable estimate of twinning frequency in *M. sylvanus*.

Stillbirths, Infant Mortality

Stillbirth frequency (stillbirths/total births) in four semi-natural populations varied from 0.02 to 0.07 (Table 17). Infant mortality rate (infant deaths/infant births)—reported for varying post-natal periods—varied from 0.23 to >0.80 in four natural populations and from 0.04 to 0.10 in four semi-natural populations (Table 18). The conspicuously lower infant mortality rate reported in semi-natural populations presumably is primarily attributable to artificial provisioning.

TABLE 16. Twinning frequency reported in semi-natural populations of *Macaca sylvanus*.

Sample area	Observation period	Births reported	Twin births reported	Twinning frequency	References ¹
Queen's Gate, Gibraltar	1936–1981	130	3 ²	2.3%	1
Middle Hill, Gibraltar	1946–1981	129	1 ²	0.78%	1
Rocamadour, France	1986	?	2 ³	—	2
Rocamadour, France	1987	25	1	4.0%	2, 3
Salem, Germany	1978–1985	615	3 ⁴	0.49%	2, 4
Gibraltar/Salem totals	—	874 ⁵	7 ⁵	0.80%	—

¹ Key to references: 1. Fa, 1984b, p. 276; cf. Burton and Sawchuk, 1974, p. 276; Burton and de Pelham, 1979, p. 106. 2. Schaub, 1988, p. 109. 3. Hammerschmidt and Ansorge, 1989, p. 79; Small, 1990c, p. 299. 4. Paul and Kuester, 1988, p. 207; cf. Paul and Kuester, 1987, p. 120.

² Stillborn.

³ One pair stillborn; one pair died 3–4 days after birth.

⁴ One pair stillborn; three of remaining four individuals died 2–8 days after birth.

⁵ Rocamadour samples omitted because of small number of births reported.

TABLE 17. Stillbirth frequency (stillbirths/total births) in semi-natural populations of *Macaca sylvanus*.

Sample area	Study period	Total births	Stillbirths	Stillbirth frequency	References ¹
Gibraltar: Queen's Gate	1936–1981	130	9 ²	0.07	1
Gibraltar: Middle Hill	1948–1981	129	6 ³	0.05	1
France: Rocamadour	1987	26	1	0.04	2
Germany: Salem	1977–1985	615	12	0.02	3

¹ Key to references: 1. Fa, 1986c, p. 292; cf. Burton and Sawchuk, 1974, p. 276. 2. Small, 1990c, p. 299. 3. Paul and Kuester, 1988, p. 207.

² Includes three twin stillbirths.

³ Includes one twin stillbirth.

In the Salem semi-natural population, neonatal mortality was greater in males than in females (Paul & Kuester, 1988, p. 213), and the rate of stillbirths and infant mortality was greater in primiparous females than in multiparous females (Paul and Kuester, 1996, p. 301).

Weaning

Macaca sylvanus infants begin to experiment with solid foods at age ca. 45 days, and, during the next few months, mothers often begin to resist nursing attempts by their infants (Burton, 1972, pp. 38, 39; Rumsey & Whiten, 1972, p. 562; Fa, 1984c, p. 339). Although an infant generally continues to nurse sporadically until age ca. 1 year—or longer, if its mother does not produce a new infant—an orphan in a natural population was seen to be fully capable of feeding itself at age 6–8 months (Deag, 1980,

p. 57; K[ue]ster & Paul, 1984a, p. 78; Paul & Thommen, 1984a, p. 12; 1984b, p. 188; Ménard et al., 1985, p. 68). In the Salem semi-natural population, older mothers reportedly wean their infants later than younger mothers (Paul et al., 1993a, p. 117).

Carpentier (1931, p. 275) reported that a young captive *M. sylvanus* infant (with blackish pelage) was successfully nursed by a female dog.

Male–Infant Interactions

Interactions between infants and older males apparently are more frequent in *M. sylvanus* than in most other species of macaques and baboons (Fa, 1984a, p. 8; Taub, 1985, p. 863; Maestri-pieri, 1998, p. 250; Thierry, 2000, p. 119). Nineteenth century observers noticed that *M. sylvanus* infants on Gibraltar frequently were carried by older males (Lydekker, 1893–1894, p. 121;

TABLE 18. Infant mortality rate (infant deaths/infant births) in natural and semi-natural populations of *Macaca sylvanus*.

Sample area	Study period	Infant births	Infant deaths	Infant mortality rate	Length of infant death interval	References ¹
Natural populations						
Morocco: Azrou vicinity	1994	?	?	>0.80	6 mo	1
Morocco: Cèdre Gouraud ²	1995	18	13	0.72	~6 mo	2
Algeria: Tigounatine	1983–1990	78–82	?	0.23–0.27	12 mo	3
Algeria: Akfadou	1983–1990	58–60	?	0.38–0.40	12 mo	3
Semi-natural populations						
Gibraltar: Queen's Gate	1936–1981	130	7	0.05	6 mo	4
Gibraltar: Middle Hill	1948–1981	129	9	0.07	6 mo	4
Gibraltar: Middle Hill	1995–2001	57	2	0.04	3 mo	5
Germany: Salem	1978–1988	706	70	0.10	12 mo	6

¹ Key to references: 1. Camperio Ciani et al., 1996, p. 71. 2. Machairas et al., 2003, p. 189. 3. Menard and Vallet, 1996, p. 116. 4. Fa, 1984b, p. 291; cf. Burton and Sawchuk, 1982, p. 143. 5. Kümmerli and Martin, 2005, p. 1240. 6. Paul et al., 1993a, p. 110.

² Alternate locality name: Gouroud.

Forbes, 1894, p. 7; cf. Sanderson, 1957, p. 133), and, subsequently, Stewart (1958, p. 340) reported that infants that were carried often were taken from their mothers immediately after birth. Lahiri and Southwick (1966, p. 260) studied two newborn infants in captive groups at the National Zoological Park, Washington, D.C., for 12 weeks and found that the infants consistently were associated with the dominant males in their respective groups for ca. 8% of the observation hours; during these interactions, the infants were held, groomed, or carried by the dominant males. Generally similar interactions between infants and adult males (without grooming, however) were observed by MacRoberts (1970, p. 93; cf. MacRoberts & MacRoberts, 1971, p. 46; Burton, 1972, p. 33) during a six-month study conducted on Gibraltar.

In addition to dyadic male-infant interactions as described above, Deag and Crook (1971, p. 191; cf. Rumsey & Whiten, 1972, p. 562; Deag, 1980, p. 57), who studied natural *M. sylvanus* groups for two months in the Moyen Atlas, Morocco, observed triadic interactions involving one infant and two older males. In these interactions, one of the males—typically lower ranking—carried an infant to another male—typically higher ranking—and presented the infant to the higher ranking male. Deag and Crook hypothesized that presence of the infant tended to reduce tension that would otherwise exist between a low-ranking male and a nearby high-ranking male; accordingly, Deag and Crook designated dyadic interactions as “male care” and triadic interactions as “agonistic buffering.”

Evidence concerning possible harm to infant participants in male-infant interactions is equivocal. Although Taub (1980a, p. 189) reported that older males handled infants carefully and that no injuries were sustained by infants in 535 interactions that he observed in the Moyen Atlas, Fa (1986c, p. 75) indicated that three infant deaths on Gibraltar were the result of “kidnapping” by the dominant male, and Paul and Kuester (1988, p. 216) attributed at least nine infant deaths at Salem, Germany, to a similar cause. At Kintzheim, France, males have been observed to carry and otherwise interact with dead infants in approximately the same way that they interact with living infants (Merz, 1978, p. 750).

The functional significance of triadic male-infant interactions has been vigorously debated.

On one side of this debate, an exploitative agonistic-buffering function has been assigned to these triadic interactions by Deag and Crook (1971, p. 191; cf. Deag, 1980, p. 57; Small, 1993, p. 162; Paul & Kuester, 1996a, p. 36); on the other side, an altruistic kin-investment function (i.e., males caring for their kin) has been proposed by Taub (1975, p. 333; 1978b, unpaginated; 1980a, p. 196; 1984b, p. 36; 1990, p. 340; Taub & Redican, 1984, p. 381; cf. Smith & Pfeffer-Smith, 1982, p. 105; Riechelmann et al., 1994, p. 285). Significantly, recent genetic studies have not indicated that male-infant triads preferentially consist of closely related individuals (Kuester & Paul, 1986, p. 322; 2000, p. 92; Paul et al., 1992, p. 96; 1996, p. 163; Ménard et al., 1992, p. 170; 2001, p. 607).

Longevity, Reproductive Senescence, Death Rate

The greatest life span reported for *M. sylvanus* females is ca. 30 years, in the semi-natural population at Salem (Paul et al., 1993a, p. 113; cf. Burton & Sawchuk, 1974, p. 275; 1982, p. 141), and the greatest life span reported for males is ca. 25 years, also at Salem (Kuester et al., 1995, p. 467, cf. Burton, 1972, p. 54; Burton & Sawchuk, 1974, p. 275). The mean postreproductive life span for females is ca. 6 years (extremes 3–8 years) in seven individuals at Salem that died after reaching estimated ages of at least 25 years (Paul et al., 1993, p. 113; cf. K[ue]ster & Paul, 1984a, p. 71; Paul & Thommen, 1984b, p. 186; Paul & Kuester, 1988, p. 208; 1996b, p. 307); in this group, females continued to cycle for 1–3 years after ceasing to produce infants. The reported postreproductive life span in the 25-year-old male at Salem (see above) was one year (Kuester et al., 1995, p. 467).

The mean annual death rate in three semi-natural populations of *M. sylvanus* varied from 3.4% to 5.8% (Table 19; cf. Fa, 1984b, p. 294).

Population Growth Rate

The mean annual population growth rate in two natural Algerian populations of *M. sylvanus* varied from 4.8% in a deciduous oak forest at Akfadou to 14.6% in a cedar-oak forest at Tigounatine (Table 20). The growth rate in the Tigounatine population approached that reported in the provisioned captive population maintained at Salem, Germany (18.3% growth rate).

TABLE 19. Mean annual death rate in semi-natural populations of *Macaca sylvanus*.

Sample area	Study period	Mean annual death rate (%)	References
Rocamadour	1976–1981	5.8	de Turckheim & Merz, 1984, p. 258
Kintzheim	1976–1981	3.4	de Turckheim & Merz, 1984, p. 258
Salem	1977–1985	3.6 ¹	Paul & Kuester, 1988, p. 212

¹ Cf. de Turckheim and Merz, 1984, p. 258.

Fossils

Circum-Mediterranean macaque fossils—most of which were identified as *M. sylvanus* or *M. cf. sylvanus*—have been reported from ca. 70 localities in a broad area that includes the present North African range of *M. sylvanus* and also includes much of Europe (Fig. 9, Appendix V). The European records extend as far north as southern England and southern Germany and extend as far east as Romania and the Caucasus; isolated southeastern Mediterranean records also have been reported in Israel, Egypt, and Libya. Contrastingly, only one macaque fossil has been reported south of the present North African range—in central Tunisia. It also is noteworthy that no macaque fossils have been reported from Gibraltar (Szalay & Delson, 1979, pp. 355–356; cf. Imrie, 1798, pp. 198, 201; Busk, 1877, p. 129; Calderon, 1877, p. 128).

The oldest circum-Mediterranean macaque fossils were collected at four localities that probably are of Late Miocene age, ca. 7–5.5 million years ago (Ma). These Late Miocene localities are: Almenara-M, east-central Spain, fossils equivocally identified as *M. cf. sylvanus* (cf. Köhler et al., 2000, p. 450; Eronen & Rook,

2004, p. 327); Menacer (=Marceau), northern Algeria, fossils identified as *Macaca* sp.; Sahabi area, northeastern Libya, fossils identified as cf. *Macaca*; and Wadi Natrun, northeastern Egypt, fossils identified as *M. libyca* (Appendix V). These circum-Mediterranean macaque fossils apparently are older than the oldest known Asian macaque fossils (Yushe Basin, Hubei, China, probably Early Pliocene (ca. 4.5–4.0 Ma) (Delson, 1980a, p. 20; 1996, p. 40; pers. comm. 1 January 2007).

Most Pliocene macaque fossil localities in Europe are south of 46°N (Fig. 9); the sole exception is Gundersheim, Germany, which is at 49°35'N. Pleistocene macaque fossils in Europe have been reported as far north as ca. 53°N. The youngest macaque fossils reported in Europe are from Solano del Zamborino (Spain), Grotta degli Orsi Volanti (Italy), Torre in Pietra (Italy), and Kugelsteinhöhle (Austria)—all Late Pleistocene, probably Eemian interglacial, ca. 0.120 Ma—and from Cova Negra (Spain)—Late Pleistocene, last glacial, probably <0.100 Ma (Appendix V). Most Pleistocene macaque fossils in Europe date from interglacial phases (Kurtén, 1968, p. 59; Delson, 1975b, p. 48; 1980a, p. 19).

The above discussion ignores an isolated cercopithecine lower third molar, probably of

TABLE 20. Demographic growth rate in natural and semi-natural populations of *Macaca sylvanus*.

Demographic factors	Natural populations ¹		Semi-natural population ²
Sample area	Algeria: Akfadou	Algeria: Tigounatine	Germany: Salem
Forest type	Deciduous oak	Cedar-oak	Beech-spruce
Study period	1983–1990	1983–1990	1976–1983
Initial census	33	38	164
Terminal census	53	106 ³	533
Increase factor	1.61 ⁴	2.79 ⁴	3.25
Mean annual growth rate	4.8% ⁵	14.6% ⁵	18.3%

¹ Reference: Ménard and Vallet, 1993b, p. 105.

² Reference: Paul and Kuester, 1988, pp. 202, 203.

³ Three daughter groups: 55 + 30 + 21 individuals.

⁴ Includes immigration/emigration balance.

⁵ Excludes immigration/emigration balance.

FIG. 9. Geographic distribution of circum-Mediterranean macaque fossils (cf. Appendix V) compared with geographic distribution of extant populations and Holocene extinct populations of *Macaca sylvanus* (cf. Fig. 1)

Late Miocene age, which was collected in Congo (Zaire), central Africa (Hooijer, 1963, p. 26; 1970, p. 166). Although this tooth was originally identified equivocally as "Cf. *Macaca* c.q. *Mesopithecus* spec.," its generic allocation remains problematic (Delson, 1980a, p. 11).

Systematics

Synonymy

Macaca sylvanus (Linnaeus, 1758)

[Πιθηκος (=Pithekos)]: Aristotle, 384–322 B.C.E., (1984 edition), p. 798 (see McDermott, 1938, p. 88)—external characters; pre-Linnaean, unavailable name. Galen, 129–200 C.E. (see McDermott, 1938, p. 97)—anatomy.

Babuini: Leo Africanus, 1526 (1896 edition), p. 948—external characters; behavior; distri-

bution, Mauritania, Bejaïa and Constantine mountains; pre-Linnaean, unavailable name.

Simia: Gesner, 1551, p. 957—external characters; behavior; pre-Linnaean, unavailable name. Brisson, 1756, p. 188—habitat, Africa.

Simia cynocephalus alter: Alpini, ca. 1609 (1979 edition), p. 241, pl. 16 (see Linnaeus, 1758, p. 25)—pre-Linnaean, unavailable name.

Cercopithecus: Jonston, 1650 (1657 edition), plate 59, fig. (lower right corner) (see Linnaeus, 1758, p. 25)—pre-Linnaean, unavailable name.

Simia ecaudata, *clunibus tuberosis*: Linnaeus, 1748, p. 3—pre-Linnaean (=pre-1758), unavailable name.

Simia Cynocephala: Brisson, 1756, p. 191—pre-Linnaean (=pre-1758), unavailable name.

Le Pithèque: Buffon, 1766, p. 84—vernacular, unavailable name. Buffon, 1789, pp. 30–36—external characters; behavior.

Le Magot: Buffon, 1766, p. 109—vernacular, unavailable name; external characters; behav-

- ior; distribution, Tartary, Arabia, Ethiopia, Malabar, Barbary, Mauritania, Cape of Good Hope. F. Cuvier, 1819, pp. 1–4—behavior, measurements; distribution, Barbary, Egypt, southern Spain.
- Pygmy Ape: Pennant, 1771, p. 98—vernacular, unavailable name.
- Barbary Ape: Pennant, 1771, p. 100—vernacular, unavailable name.
- Le Petit Cynocéphale: Buffon, 1789, p. 37—vernacular, unavailable name; compared with Le Magot. Daudin in Lacépède and Daudin, 1802, p. 149—recognized as a distinct species of *Macaca*, but not named.
- [*Simia*] *Sylvanus* Linnaeus, 1758, p. 25. Type localities “Africa, Zeylonica.” Müller, 1773, p. 120—external characters. Latreille, 1804a, p. 178; 1804b, p. 294—taxonomic relationship to *S. inuus* uncertain. G. Cuvier, 1817, p. 108—external characters; taxonomy; distribution, “Barbarie” (=Barbary Coast). Virey, 1819, p. 275—taxonomy; distribution, juxta-Mediterranean Africa, Gibraltar.
- Simia Silvanus*: Schreber, 1774, p. 68—incorrect subsequent spelling of specific name.
- [*Simia*] *siluanus* Erxleben, 1777, p. 11—unjustified emendation of specific name; synonymy; distribution, Africa, India, Jamaica.
- Macaca sylvanus*: Daudin in Lacépède & Daudin, 1802, p. 149—new combination; listed as “Variété A” of *Macaca inuus*.
- Magus sylvanus*: Lesson, 1827, p. 43—new combination; taxonomy; distribution, Barbary, Egypt, introduced on Gibraltar.
- Inuus sylvanus*: Jardine, 1833, pp. 149, 214—new combination; taxonomy; behavior, external characters; distribution, warmer parts of Africa and India.
- Pithecus* [(*Pithecus*)] *sylvanus*: Dahlbom, 1856, p. 121—new combination; taxonomy; external characters; distribution, North Africa, Gibraltar.
- Macacus sylvanus*: Schlegel, 1876, p. 115—incorrect subsequent spelling of generic name; external characters; distribution, Morocco, Gibraltar, Algeria.
- [*Macacus* (*Pithecus*)] *sylvanus*: Trouessart, 1882 (“1878”), p. 126—new combination; distribution, Algeria, Morocco, Gibraltar.
- [(*Simia* or) *Macaca*] *sylvanus*: Thomas, 1911, pp. 121, 125—nomenclature; designated type species of *Simia* by “Linnaean tautonymy” (cf. International Code of Zoological Nomenclature, 1999, Art. 68.5).
- Macaca sylvana*: Flower, 1931, p. 155—new combination; unwarranted change of gender ending of specific name; longevity in captivity.
- [*Macaca*] *sylvanus*—group: Müller, 1933, p. 5—new rank; external characters.
- [*Simia*] *Inuus* Linnaeus, 1766, p. 35. Type locality unknown; name based on “*Simius cynocephalus alter*” of Alpinus (ca. 1609, p. 241, pl. 16) and *Simia cynocephala* of Brisson (1756, p. 191); external characters said to be similar to those of *S. sylvanus*. Müller, 1773, p. 121—distribution, Africa. Blumenbach, 1788, p. 66—said to be difficult to distinguish from *S. sylvanus*; distribution identical to that of *S. sylvanus*. Audebert, 1797–1798, p. 1—possibly a synonym of *S. sylvanus*. Desmarest, 1804, p. 8—species allocated to genus *Cynocephalus*.
- Macaca inuus*: Lacépède, 1799, p. 4—new combination. Stiles and Orleman, 1927, p. 24—validly designated as type species of genus by monotypy; now regarded as a synonym of *M. sylvanus* (Linnaeus, 1758).
- Pithecus inuus*: É. Geoffroy, 1803, p. 26—new combination; distribution, Africa.
- Cyn[occephalus] inuus*: Latreille, 1804b, p. 293—new combination; said to be a degenerate “variété” of Le Magot.
- [*Macacus*] *inuus*: Desmarest, 1820, p. 67—incorrect subsequent spelling of generic name.
- Macacus inuus*: Desmarest, 1823, p. 470—incorrect subsequent spelling of generic and specific names.
- [*Simia*] [*Pithecus*] *inuus*: Griffith, 1827, p. 19—new combination.
- Simia Innuus*: Wagler, 1830, p. 5—incorrect subsequent spelling of specific name.
- [*Macacus*] *Innuus*: Gulliver, 1842, p. 68—incorrect subsequent spelling of generic and specific names.
- [*Macacus* (*Pithecus*)] *inuus*: Trouessart, 1897, p. 26—new combination; incorrect subsequent spelling of generic and specific names.
- [*Macacus* (*Innuus*)] *inuus*: Trouessart, 1904, p. 17—new combination; incorrect subsequent spelling of generic and specific names.
- [*Cynocephalus Inuus*, variety] *α. natatorius* Fischer, 1813, p. 539. Type localities “Arabia, India, Malabar, Bucharia?”; new variety, based on specimen with membranes between pedal digits.
- Simia Pithecia* Link, 1795, p. 60 (not Linnaeus, 1766, p. 40)—invalid junior homonym of

[*Simia*] *Pithecia* Linnaeus, 1766, p. 40 (= *Pithecia pithecia*, white-faced saki).

Simia Pithecius Schreber, [1800], suppl. plate 4B. Type locality unknown; name incorrectly attributed to Bufl[on] (cf. Wagner, 1839 [“1840”], p. 149).

Inuus pithecius: Lesson, 1840, p. 99—new combination; distribution, Barbary coast, Gibraltar, Alexandria, Cairo, Morocco. I. Geoffroy, 1851, p. 31—said to be indigenous on Gibraltar.

[*Simia*] *Anomela* Link, 1795, p. 60. Type locality unknown; name based on Le Petit Cynocephale of Buffon, 1789, p. 37.

Simia Cynopsis Goldfuss, 1809, p. 53. Type locality unknown; name based on Le Petit Cynocephale of Buffon, 1789, p. 37.

[*Lasiopyga*] *ecaudis* Illiger, 1811, p. 68—Type locality unknown; name based on Le Petit Cynocephale: Buffon, 1789, p. 37.

Inuus ecaudatus É. Geoffroy, 1812, p. 100—Type locality “toute la partie d’Afrique qui cotoie la Méditerranée, et en Europe, Gibraltar”; external characters; pelage color variation.

Inuus ecaudatus: Schinz, 1821, p. 112—new combination; incorrect subsequent spelling of generic name.

[*Macacus*] *ecaudatus*: Schinz, 1844, p. 60—new combination.

[*Inuus* (*Inuus*)] *ecaudatus*: Wagner, 1855, p. 59—new combination.

Inuus macacus Rüppell, 1835, p. 8. Type locality “ganzen Küste der Barbarie bis nach Marocco”; name based on captives transported to Egypt.

Macacus magots Smith, 1842, p. 103. Type locality “Barbary”; name based on the Barbary Ape, probably of Pennant (1771, p. 100).

[*pithecius*] *Pygmaeus* Reichenbach, 1862, p. 145. Type locality unknown; name based on the Pygmy Ape of Pennant (1771, p. 98) and a menagerie animal, both of unknown origin; taxonomic comparison.

Type Series

Although no type specimen was specified in Linnaeus’ (1758, p. 25) original description of *Simia sylvanus*, four bibliographic references were cited. Accordingly, the specimens discussed or figured in these references are syntypes that collectively constitute the type series of *Simia sylvanus* (International Code of Zoological

Nomenclature [ICZN], 1999, Art. 72.4.1). The four cited references are: (1) Gesner, 1551, p. 957—includes figure of tailless monkey; (2) Alpini, ca. 1609, pp. 241–242, plates 15, 16—includes figures of captives transported from Alexandria to Venice; (3) Jonston, 1650 (1657 ed.), pl. 59, fig. (lower right corner)—unnumbered figure of tailless monkey labeled “Cercopithecq”; and (4) Linnaeus, 1748, p. 3, plate 1, fig. 1 (this publication includes another citation of Alpini, ca. 1609, p. 241)—possibly includes ambiguously captioned figure of skull. None of the syntypes is known to have been preserved.

At present, designation of a lectotype from among the available syntypes would serve no useful taxonomic purpose (cf. ICZN, 1999, Art. 74.7.3).

Type Locality

Originally given as “Africa, Zeylona”; corrected to “Africa” by Elliot (1913, p. 174); restricted to “Barbary Coast” by Allen (1939, p. 156).

Distribution

Disjunct areas in the Atlas and Rif Mountains of Morocco and Algeria, extending from ca. 31°15’N, 7°45’W to ca. 36°45’N, 5°20’E (Fig. 1).

Diagnosis

Prime dorsal pelage color in adults strongly variegated, buffy to reddish mixed with blackish (Fig. 2C). Mean head and body length 556.8 mm in four adult females and 634.3 mm in three adult males. Tail reduced to an inconspicuous fleshy vestige (4–22 mm long) or completely absent. Mean greatest length of skull 118.7 mm in four adult females and 135.5 in five adult males.

Remarks

Linnaeus (1758, p. 25) originally allocated the Barbary macaque to the genus *Simia*, but this generic name was subsequently suppressed by the International Commission on Zoological Nomenclature (1929, p. 26; cf. Stiles & Orleman, 1927, p. 1). The next oldest available generic name applicable to the Barbary macaque is

TABLE 21. Evolution and dispersal of circum-Mediterranean macaques: hypothetical chronology.

Approximate age ¹	Evolutionary event
13–10 Ma	Origin of Papionini (in Africa)
7–6 Ma	Origin of <i>Macaca</i> (in northern Africa)
6–5 Ma	Dispersal of <i>Macaca</i> from Africa to Eurasia ²
0.100–0.020 Ma	Extinction of <i>Macaca</i> in Europe
<0.010 Ma	Anthropogenic reduction of North African habitats of <i>Macaca</i>

¹ Ma = million years ago.

² Subsequent radiation of *Macaca* in Asia.

Macaca Lacépède, 1799, p. 4. The specific name *sylvanus* (Latin, woodland god) is a noun standing in apposition to the generic name and therefore is not required to agree in gender with the generic name (ICZN, 1999, Art. 34.2.1). Because available information concerning geographic variation in *M. sylvanus* is deficient (see above), recognition of subspecies in this species is currently unwarranted.

Specimens Examined

Total 103: skins and skulls, 33; skins only, 37; skulls or skeletons only, 33 (see Appendix I).

Evolution and Dispersal

The most comprehensive studies of the evolutionary history of *M. sylvanus* and its relatives have been published by E. Delson (1973, pp. 140, 667, 685; 1975a, p. 207; 1975b, p. 44; 1980a, p. 11; 2000, p. 170; Szalay & Delson, 1979, p. 354). These publications provide the primary basis for the present discussion (Table 21).

Although only one species of macaque—*M. sylvanus*—inhabits Africa, and ca. 20 species of macaques inhabit Asia, fossil evidence indicates that the genus *Macaca* originated in Africa and that *M. sylvanus* is a geographic relict of that origin (Simons, 1970, p. 109; Delson, 1973, p. 689; 1980a, p. 23; Szalay & Delson, 1979, p. 334; Stewart & Disotell, 1998, p. R585; Groves, 2001, p. 221). The tribe Papionini—which includes macaques (subtribe Macacina) and baboons, mandrills, mangabeys, and geladas (subtribe Papionina)—probably originated in Africa ca. 13–10 million years ago (Ma) (Raaum et al., 2005, p. 250; cf. Szalay & Delson, 1979, p. 327; Delson, 1980a, p. 24; 2000, pp. 168, 170). Through much of the history of these subtribes,

their distributions apparently have been allopatric, with macaques inhabiting northern Africa and baboons, mandrills, mangabeys, and geladas inhabiting central and southern Africa; an inter-subtribal barrier in the vicinity of the present Sahara Desert appears to have been operative.

The earliest known macaque or near-macaque fossils date from the Late Miocene (ca. 7–6 Ma) in Algeria, Libya, and Egypt (see above, Fossils). Between ca. 6–5.3 Ma, the Mediterranean Sea became desiccated as a result of tectonic movements isolating it from the Atlantic Ocean (Loget et al., 2005, p. 414); Delson (1975b, p. 40) has suggested that this might have facilitated dispersal of ancestral macaques from Africa to Eurasia. The earliest known macaque fossils in Europe (Spain) date from ca. 5.5 Ma, and the earliest macaque fossils in Asia date from ca. 4.5–4.0 Ma in China (see above, Fossils) and from ca. 3 Ma in India (Delson, 1980a, p. 20).

DNA evidence supports a sister-group relationship between *M. sylvanus* and all species of Asian macaques (see above, DNA Variation). Judging from tail length variation in extant Asian macaques (Fooden, 2006, p. 27), the ancestral macaque stock that dispersed from Africa to Eurasia probably was long-tailed; if so, this stock probably would not be regarded as conspecific with extant *M. sylvanus*. After dispersal of macaques from Africa to Eurasia, tail reduction in North African and Eurasian macaques apparently evolved independently at least four times—probably as an adaptation to cool climate (cf. Fooden, 1988, p. 4; 2006, p. 3).

Macaques survived in Italy—and perhaps Austria—at least until the Eemian interglacial interval (ca. 0.120 Ma), and they survived in Spain at least until the beginning of the last glaciation (<0.100 Ma) (see above, Fossils). During cyclical glacial advances, the geographic distribution of macaques in Europe probably was restricted to more temperate southern areas

(Kurtén, 1968, p. 59; Delson, 1980a, p. 19); macaques might have finally become extinct in Europe as a result of inability to tolerate the most severe stage of the last glaciation (ca. 0.020 Ma). During the Holocene (<0.010 Ma), the population of *M. sylvanus* in North Africa has been reduced as a result of anthropogenic habitat modification (Mehlman, 1984, p. 182; Thirgood, 1984, p. 36; Camperio Ciani et al., 2005, p. 637).

Acknowledgments

For access to specimens and generous assistance, I am deeply grateful to officials and staff members of institutions cited above (see Materials and Methods). Valuable supplementary help and advice were provided by R. Banasiak (FMNH), D. Brandon-Jones (Richmond, Surrey), G. Fooden (Los Angeles), S. B. McLaren (CMNH), M. Mouna (ISR), C. L. Richardson (FMNH), E. M. Santana (USNM), W. Stanley (FMNH), R. W. Thorington, Jr. (USNM), J. Weinstein (FMNH), and J. R. Wible (CMNH). I also thank E. Delson (AMNH), J. E. Fa (Durrell Wildlife Conservation Trust), L. Hlusko (University of California, Berkeley), J. Voight (FMNH), and one anonymous reviewer for their careful reviews of a previous draft of the manuscript. This research was partly supported by the Barbara E. Brown Fund for Mammal Research.

Literature Cited

ALLEN, G. M. 1939. A Checklist of African Mammals. Museum of Comparative Zoology, Cambridge, Massachusetts, 763 pp.

ALPINI, P. ca. 1609. *Historiae Aegyptiacae Naturalis* (French translation by R. de Feñoyí, 1979). L'Institut Français d'Archéologie Orientale du Caire, Cairo, xxxi + 583 pp.

ALVAREZ, F., AND F. HIRALDO. 1975. Distribution and habitat of the Barbary macaque (*Macaca sylvana*) in North Morocco. Doñana—Acta Vertebrata, 2: 253–259.

ANONYMOUS. 1988. Barbary macaques reintroduced. Oryx, 22: 50.

ANSORGE, V., K. HAMMERSCHMIDT, AND D. TODT. 1992. Communal roosting and formation of sleeping clusters in Barbary macaques (*Macaca sylvanus*). American Journal of Primatology, 28: 271–280.

ARDITO, G., AND A. MOTTURA. 1987. An overview of the geographic and chronologic distribution of West European cercopithecoids. Human Evolution, 2: 29–45.

ARISTOTLE. 384–322 B.C.E. History of animals, pp. 774–993 (English translation by d'A. W. Thompson, 1984). In The Complete Works of Aristotle. Princeton University Press, Princeton.

AUDEBERT, J. B. 1797–1798. *Simia inuus*, part 3, pp. 1–4. In Audébert, J. B., Histoire Naturelle des Singes et des Makis. Desray, Paris.

AULAGNIER, S., AND M. THIEVENOT. 1986. Catalogue des mammifères sauvages du Maroc. Travaux de l'Institut Scientifique, 41: 2–163.

BAILEY, J. F., M. HENNEBERG, I. B. COLSON, A. CIARALLO, R. E. M. HEDGES, AND B. SYKES. 1999. Monkey business in Pompeii—unique find of a juvenile Barbary macaque skeleton in Pompeii identified using osteology and ancient DNA techniques. Molecular Biology and Evolution, 16: 1410–1414.

BÉDÉ, P. 1927. Notes sur l'ornithologie du Maroc. Mémoires de la Société des Sciences Naturelles du Maroc, 16: 25–150.

BLUMENBACH, J. F. 1788. Handbuch der Naturgeschichte, 3rd ed. Johann Christian Dieterich, Göttingen, xvi + 715 pp. + 3 plates.

BRISSEN, M.-J. 1756. Regnum Animale in Classes IX Distributum ... Cl. Joannem-Baptistam Bauche, Paris, vi + 382 pp.

BUFFON, G. L. L. DE. 1789. Histoire Naturelle, Générale et Particulière, Servant de Suite à l'Histoire des Animaux Quadrupèdes, suppl. vol. 7. L'Imprimerie Royale, Paris, xx + 364 pp.

BUFFON, G. L. L. DE, AND L.-J.-M. DAUBENTON. 1766. Histoire Naturelle, Générale et Particulière, avec la Description du Cabinet du Roi, vol. 14. L'Imprimerie Royale, Paris, 411 pp.

———. 1833. Œuvres Complètes de Buffon ... Buffon et Daubenton, Planches, vol. 4. Th. Lejeune, Bruxelles, plates 304–467.

BURTON, F. D. 1972. The integration of biology and behavior in the socialization of *Macaca sylvana* of Gibraltar, pp. 29–62. In Poirier, F. E., ed., Primate Socialization. Random House, New York.

BURTON, F. D., AND A. DE PELHAM. 1979. A twinning event in *Macaca sylvanus* of Gibraltar. Journal of Medical Primatology, 8: 105–112.

BURTON, F. D., AND L. A. SAWCHUK. 1974. Demography of *Macaca sylvanus* of Gibraltar. Primates, 15: 271–278.

———. 1982. Birth intervals in *M. sylvanus* of Gibraltar. Primates, 23: 140–144.

BUSK, G. 1877. On the ancient or Quaternary fauna of Gibraltar, as exemplified in the mammalian remains of the ossiferous breccia. Transactions of the Zoological Society of London, 10: 53–136 + 27 plates.

CABRERA, A. 1932. Los mamíferos de Marruecos. Trabajos del Museo Nacional de Ciencias Naturales, Serie Zoológica, 57: 1–208.

- CALDERON, S. 1877. On the fossil Vertebrata hitherto discovered in Spain. *Quarterly Journal of the Geological Society of London*, **33**: 124–133.
- CAMPERIO CIANI, A., M. ARAHOU, AND M. MOUNA. 1996. *Macaca sylvanus* as a biological indicator to monitor cedar forests of Morocco: The model works! *Folia Primatologica*, **67**: 71. (abstract only)
- CAMPERIO CIANI, A., AND I. MACHAIRAS. 2003. Frequency of aggressive behavior and a case of mortal attack in wild *Macaca sylvanus* in the Middle Atlas region (Morocco). *Human Evolution*, **18**: 123–130.
- CAMPERIO CIANI, A., L. MARTINOLI, C. CAPILUPPI, M. ARAHOU, AND M. MOUNA. 2001. Effects of water availability and habitat quality on bark-stripping behavior in Barbary macaques. *Conservation Biology*, **15**: 259–265.
- CAMPERIO CIANI, A., AND L. PALENTINI. 2003. La desertificazione in Marocco: uso degli indicatori biologici nel monitoraggio della desertificazione delle foreste del Medio Atlante. *Antropologia Mediterranea*, **1**: 57–68.
- CAMPERIO CIANI, A., L. PALENTINI, M. ARAHOU, L. MARTINOLI, C. CAPILUPPI, AND M. MOUNA. 2005. Population decline of *Macaca sylvanus* in the Middle Atlas of Morocco. *Biological Conservation*, **121**: 635–641.
- CARPENTIER, J.-C. 1931. Allaitement d'un magot par une chienne. *Bulletin de la Société Nationale d'Acclimatation de France*, **78**: 275–276.
- CHIVERS, D. J. 1984. Forward, pp. vii–viii. *In* Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- CROUAU-ROY, B., M. LATHUILLERE, F. VON SEGESSER., R. D. MARTIN, AND N. MÉNARD. 2001. Conservation and evolution of human microsatellite loci in Barbary macaques (*Macaca sylvanus*) and genetic diversity of Moroccan and Algerian populations. *Folia Primatologica*, **72**: 156–157. (abstract only).
- CUVIER, F. 1819. Le Magot, Livraison 2, pp. 1–4. *In* Geoffroy Saint-Hilaire, E., and F. Cuvier, eds., *Histoire Naturelle des Mammifères*, vol. 1. A. Belin, Paris. (For authorship, see Introduction, *Histoire Naturelle des Mammifères*, vol. 1, p. 8.)
- CUVIER, G. 1817. Le Règne Animal Distribué d'Après Son Organisation ..., vol. 1. Deterville, Paris, xxxvii + 540 pp.
- DAHLBOM, A. G. 1856. *Studia Zoologica* ..., vol. 1, fasc. 1. Berlingianis, Lund, 240 pp.
- DEAG, J. M. 1977. The status of the Barbary macaque *Macaca sylvanus* in captivity and factors influencing its distribution in the wild, pp. 267–287. *In* H. S. H. Prince Rainier III of Monaco, and G. H. Bourne, eds., *Primate Conservation*. Academic Press, New York.
- . 1980. Interactions between males and unweaned Barbary macaques: Testing the agonistic buffering hypothesis. *Behaviour*, **75**: 54–81.
- . 1983. Feeding habits of *Macaca sylvanus* (Primates: Cercopithecinae) in a commercial Moroccan cedar forest. *Journal of Zoology*, **201**: 570–574.
- . 1984. Demography of the Barbary macaque at Ain Kahla in the Moroccan Moyen Atlas, pp. 113–133. *In* Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- . 1985. The diurnal patterns of behaviour of the wild Barbary macaque *Macaca sylvanus*. *Journal of Zoology, Series A*, **206**: 403–413.
- DEAG, J. M., AND J. H. CROOK. 1971. Social behaviour and "agonistic buffering" in the wild Barbary macaque *Macaca sylvana* L. *Folia Primatologica*, **15**: 183–200.
- DE HEINZELIN, J., AND A. EL-ARNAUTI. 1987. The Sahabi Formation and related deposits, pp. 1–21. *In* Boaz, N. T., A. El-Arnauti, A. W. Gaziry, J. de Heinzelin and D. D. Boaz, eds., *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss, New York.
- DEINARD, A., AND D. G. SMITH. 2001. Phylogenetic relationships among the macaques: Evidence from the nuclear locus *NRAMP1*. *Journal of Human Evolution*, **41**: 45–59.
- DELL'AMICO, M., M. MOUNA, AND A. CAMPERIO CIANI. 2006. Demography and density of *Macaca sylvanus* in relation to habitat quality in the Middle Atlas region of Morocco. *Folia Primatologica*, **77**: 292. (abstract only)
- DELSON, E. 1973. Fossil colobine monkeys of the circum-Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia). Ph.D. dissertation, Columbia University, New York, 856 pp.
- . 1974. Preliminary review of cercopithecoid distribution in the circum-Mediterranean region. *Mémoires du Bureau de Recherches Géologiques et Minières (France)*, **78**: 131–135.
- . 1975a. Evolutionary history of the Cercopithecidae, pp. 167–217. *In* Szalay, F., ed., *Approaches to Primate Paleobiology, Contributions to Primatology*, vol. 5. Karger, Basel.
- . 1975b. Paleogeology and zoogeography of the Old World monkeys, pp. 37–64 + table. *In* Tuttle, R. H., ed., *Primate Functional Morphology and Evolution*. Mouton, The Hague.
- . 1980a. Fossil macaques, phyletic relationships and a scenario of deployment, pp. 10–30. *In* Lindburg, D. G., ed., *The Macaques: Studies in Ecology, Behavior and Evolution*. Van Nostrand Reinhold, New York.
- . 1980b. A study of fossil Old World monkeys of the circum-Mediterranean region. *National Geographic Society Research Reports*, **12**: 125–128.
- . 1996. The oldest monkeys in Asia, p. 40. *In* Takenaka, O., ed., abstracts of proceedings of International Symposium: Evolution of Asian Primates, August 5–8. Freude and Kyoto University Primate Research Institute, Inuyama, Japan.
- . 2000. Cercopithecinae, pp. 166–171. *In* Delson, E., I. Tattersall, J. A. Van Couvering and A. S. Brooks, eds., *Encyclopedia of Human Evolution and Prehistory*, 2nd ed. Garland, New York.
- DELSON, E., C. J. TERRANOVA, W. L. JUNGERS, E. J. SARGIS, N. G. JABLONSKI, AND P. C. DECHOW. 2000. Body mass in Cercopithecidae (Primates, Mammalia): Estimation and scaling in extinct and extant taxa. *Anthropological Papers of the American Museum of Natural History*, **83**: 1–159.

- DESMAREST, A. G. 1804. Tableau méthodique des mammifères, pp. 5–38. In *Nouveau Dictionnaire d'Histoire Naturelle* ..., vol. 24. Deterville, Paris.
- . 1820. *Mammalogie ou Description des Espèces de Mammifères. Première Partie* ... Veuve Agasse, Paris, viii + 276 pp.
- . 1823. Macaque, pp. 463–473. In *Dictionnaire de Sciences Naturelles*, vol. 27. F. G. Levrault, Strasbourg.
- DE TURCKHEIM, G., AND E. MERZ. 1984. Breeding Barbary macaques in outdoor open enclosures, pp. 241–261. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- DIDIER, R., AND P. RODE. 1936. *Mammifères, Étude Systematique par Espèces: Macaca sylvanus*. Paul Lechevalier, Paris, 13 pp. + 3 plates + Bibliographie.
- DRUCKER, G. R. 1984. The feeding ecology of the Barbary macaque and cedar forest conservation in the Moroccan Moyen Atlas, pp. 135–164. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- DUTRILLAUX, B., J. COUTURIER, M. MULIERIS, M. LOMBARD, AND G. CHIAUVIER. 1982. Chromosomal phylogeny of forty-two species or subspecies of cercopithecoids (Primates Catarrhini). *Annales de Genetique*, **25**: 96–109.
- ELLIOT, D. G. 1913. A Review of the Primates, vol. 2. American Museum of Natural History, New York, xviii + 382 + xxvi pp. (For date of publication, see Correction, between pp. ii–iii.)
- ERONEN, J. T., AND L. ROOK. 2004. The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *Journal of Human Evolution*, **47**: 323–341.
- ERXLEBEN, C. P. 1777. *Systema Regni Animalis* ... , Classis I: Mammalia. Impensis Weygandianis, Lipsiae, xlviii + 636 pp. + 66 unnumbered pp.
- FA, J. E. 1981. Apes on the Rock. *Oryx*, **16**: 73–76.
- . 1982. A survey of population and habitat of the Barbary macaque *Macaca sylvanus* L. in North Morocco. *Biological Conservation*, **24**: 45–66.
- . 1983a. An analysis of the status of the Barbary macaque (*Macaca sylvanus*, L.) in the wild—steps towards its conservation, pp. 58–85. In Harper, D., ed., *Conservation of Primates and Their Habitats, Volume I: Primate Conservation in the Wild*. University of Leicester, Department of Adult Education, Leicester.
- . 1983b. The Barbary macaque—the future. *Oryx*, **17**: 62–67.
- . 1984a. The Barbary macaque, pp. 3–15. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- . 1984b. Structure and dynamics of the Barbary macaque population in Gibraltar, pp. 263–306. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- . 1984c. Appendix I. Definition of age-sex classes for the Barbary macaque, pp. 335–346. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- . 1984d. Appendix II. Diet of the Barbary macaque in the wild, pp. 347–355. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- . 1984e. Habitat distribution and habitat preference in Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology*, **5**: 273–286.
- . 1986a. On the ecological status of the Barbary macaque *Macaca sylvanus* L. in North Morocco: habitat influences versus human impact. *Biological Conservation*, **35**: 215–258.
- . 1986b. An important new locality for the Barbary macaque (*Macaca sylvanus*) in Morocco. *Primate Conservation*, **7**: 31–34.
- . 1986c. Use of time and resources by provisioned troops of monkeys: Social behaviour, time and energy in the Barbary macaque (*Macaca sylvanus* L.) at Gibraltar. *Contributions to Primatology*, **23**: xii + 377 pp.
- . 1986d. Balancing the wild/captive equation—the case of the Barbary macaque (*Macaca sylvanus* L.), pp. 197–211. In Benirschke, K., ed., *Primates: the Road to Self-Sustaining Populations*. Springer-Verlag, New York.
- . 1988. Supplemental food as an extranormal stimulus in Barbary macaques (*Macaca sylvanus*) at Gibraltar—its impact on activity budgets, pp. 53–78. In Fa, J. E. and C. H. Southwick, eds., *Ecology and Behavior of Food-Enhanced Primate Groups*, *Monographs in Primatology*, vol. 11. Alan R. Liss, New York.
- . 1989. The genus *Macaca*: A review of taxonomy and evolution. *Mammal Review*, **19**: 45–81.
- FA, J. E., AND R. LIND. 1996. Population management and viability of the Gibraltar Barbary macaques, pp. 235–262. In Fa, J. E. and D. G. Lindburg, eds., *Evolution and Ecology of Macaque Societies*. Cambridge University Press, Cambridge.
- FA, J. E., D. M. TAUB, N. MÉNARD, AND P. J. STEWART. 1984. The distribution and current status of the Barbary macaque in North Africa, pp. 79–111. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- FISCHER, G. 1813. *Zoognosia Tabulis Synopticis Illustrata*, vol. 2. Nicolai Sergeidis Vsevolozsky, Moscow, 605 pp.
- FISCHER, J. 1998. Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, **55**: 799–807.
- FISCHER, J., AND K. HAMMERSCHMIDT. 2002. An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire. *Folia Primatologica*, **73**: 32–45.
- FLADERER, F. A. 1987. *Macaca* (Cercopithecidae, Primates) im Altpleistozän von Deutsch-Altenburg, Niederösterreich. *Beiträge zur Paläontologie von Österreich*, **13**: 1–24.
- . 1989. Höhlenschutz und Eiszeitforschung Erstnachweis von Affen (Gattung *Macaca*) im Jungpleistozän Mitteleuropas. *Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark*, **119**: 23–26.

- . 1991. Der erste Fund von *Macaca* (Cercopithecidae, Primates) im Jungpleistozän von Mitteleuropa. *Zeitschrift für Säugetierkunde*, **56**: 272–283.
- FLOWER, S. S. 1931. Contributions to our knowledge of the duration of life in vertebrate animals.—V. Mammals. *Proceedings of the Zoological Society of London*, **1931**: 145–234.
- FOODEN, J. 1969. Taxonomy and evolution of the monkeys of Celebes (Primates: Cercopithecidae). *Bibliotheca Primatologica*, **10**: 1–148.
- . 1975. Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana: Zoology*, **67**: 1–168.
- . 1988. Taxonomy and evolution of the *sinica* group of macaques: 6. Interspecific comparisons and synthesis. *Fieldiana: Zoology, new series*, **45**: vi + 44 pp.
- . 1995. Systematic review of Southeast Asian longtail macaques, *Macaca fascicularis* (Raffles, [1821]). *Fieldiana: Zoology, new series*, **81**: v + 206 pp.
- . 2006. Comparative review of *fascicularis*-group species of macaques (Primates: *Macaca*). *Fieldiana: Zoology, new series*, **107**: iv + 43 pp.
- FOODEN, J., AND M. AIMI. 2005. Systematic review of Japanese macaques, *Macaca fuscata* (Gray, 1870). *Fieldiana: Zoology, new series*, **104**: vi + 200 pp.
- FORBES, H. O. 1894. A Hand-Book to the Primates, vol. 2. W. H. Allen and Co., London, xv + 296 pp.
- GEISSMANN, T. 1990. Twinning frequency in catarrhine primates. *Human Evolution*, **5**: 387–396.
- GENTILI, S., A. MOTTURA, AND L. ROOK. 1998. The Italian fossil primate record: Recent finds and their geological context. *Geobios*, **31**: 675–686.
- GEOFFROY SAINT-HILAIRE, É. 1803. Catalogue des Mammifères du Muséum National d'Histoire Naturelle. Muséum National d'Histoire Naturelle, Paris, 272 pp.
- . 1812. Tableau des quadrumanes, ou des animaux composant le premier ordre de la classe des mammifères. *Annales du Muséum National d'Histoire Naturelle*, Paris, **19**: 85–122.
- GEOFFROY SAINT-HILAIRE, I. 1851. Catalogue Méthodique de la Collection des Mammifères Gide et Baudry, Paris, xv + [vii] + 96 pp.
- GERAADS, D. 1987. Dating the northern African cercopithecoid fossil record. *Human Evolution*, **2**: 19–27.
- GESNER, C. 1551. *Historiae Animalium Lib. I. De Quadrupedibus Utiuiparis*. Christ. Froschover Vm, Zurich, 1104 + unnumbered pp.
- GIEBEL, C. G., AND W. LECHE. 1874–1900. Säugethiere: Mammalia, Sechster Band, V. Abtheilung, 1169 pp. + 121 plates. In Dr. H. G. Bronn's Klassen und Ordnungen des Thier-Reichs C. F. Winter'sche Verlagshandlung, Leipzig.
- GOLDFUSS, G. A. 1809. Vergleichende Naturbeschreibung der Säugethiere. Verlag des Waltherschen Kunst- und Buchhandlung, Erlangen, xxi + 314 + 2 unnumbered pp. + 36 plates.
- GOUDSMIT, J., AND D. BRANDON-JONES. 1999. Mummies of olive baboons and Barbary macaques in the Baboon Catacomb of the sacred animal necropolis at North Saqqara. *The Journal of Egyptian Archaeology*, **85**: 45–53 + 2 plates.
- GRIFFITH, E. 1827. *The Animal Kingdom Arranged in Conformity with its Organization ...*, vol. 5. Geo. B. Whittaker, London, 392 pp.
- GROVES, C. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, D.C., viii + 350 pp.
- GULLIVER, G. 1842. Observations on the muscular fibers of the oesophagus and heart in some of the vertebrate animals. *Proceedings of the Zoological Society of London*, **1842**: 63–72.
- HAMMERSCHMIDT, K., AND V. ANSORGE. 1989. Birth of a Barbary macaque (*Macaca sylvanus*): Acoustic and behavioural features. *Folia Primatologica*, **52**: 78–87.
- HAMMERSCHMIDT, K., V. ANSORGE, J. FISCHER, AND D. TODT. 1994. Dusk calling in Barbary macaques (*Macaca sylvanus*): Demand for social shelter. *American Journal of Primatology*, **32**: 277–289.
- HAYASAKA, K., K. FUJII, AND S. HORAI. 1996. Molecular phylogeny of macaques: Implications of nucleotide sequences from an 896-base pair region of mitochondrial DNA. *Molecular Biology and Evolution*, **13**: 1044–1053.
- HILL, W. C. O. 1958. External genitalia, pp. 630–704. In Hofer, H., A. H. Schultz and D. Starck, eds., *Primatologia*, vol. 3, pt 1. Karger, Basel.
- . 1974. *Primates: Comparative Anatomy and Taxonomy*. VII. Cynopithecinae: *Cercocebus*, *Macaca*, *Cynopithecus*. John Wiley & Sons, New York, xxi + 934 pp.
- HOOIJER, D. 1963. Miocene Mammalia of Congo. *Annales, Musée Royal de Afrique Centrale, Sciences Géologiques*, **46**: 77 pp. + 10 plates.
- . 1970. Miocene Mammalia of Congo, a correction. *Annales, Musée Royal de Afrique Centrale, Sciences Géologiques*, **67**: [161]–167.
- ICZN. See INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE.
- ILLIGER, C. 1811. *Prodromus Systematis Mammalium et Avium Sumptibus C. Salfeld, Berolini*, xviii + 302 pp.
- IMRIE, MAJOR. 1798. A short mineralogical description of the mountain of Gibraltar. *Transactions of the Royal Society of Edinburgh*, **4**: 191–202.
- INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE, 4th Edition. 1999. International Trust for Zoological Nomenclature, London, xxix + 306 pp.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1929. Opinion 114: Under suspension *Simia*, *Simia satyrus* and *Pithecus* are suppressed. *Smithsonian Miscellaneous Collections*, **73**: 25–26.
- INTERNATIONAL TRAVEL MAPS, MOROCCO, 1:900,000. 2000. Vancouver.
- IUCN. 2006. 2006 Red List of Threatened Species. IUCN, Gland, Switzerland, <http://www.iucnredlist.org>.

- JARDINE, W. 1833. The Naturalists Library: Mammalia, vol. 1. Monkeys. W. H. Lizars and Sterling and Kenney, Edinburgh, 230 pp.
- JOLEAUD, L. 1926. Les vestiges des anciennes associations biologiques de la Berbérie, pp. 128–134. In *Compte Rendu Publié par le Secrétaire Général du Congrès, Congrès International de Géographie*, Cairo, April 1925, vol. 4, part 2.
- . 1931a. La role des singes dans les traditions populaires Nord-Africaines. *Journal de la Société des Africaniste*, 1: 117–150.
- . 1931b. Le magot de Berbérie. *Bulletin de la Société Nationale d'Acclimatation de France*, 78: 153–155.
- . 1933. Études de géographie zoologique sur la Berbérie. Les Primates: le magot, pp. 851–863. In *Comptes Rendus du Congrès International de Géographie*, Paris, 1931, vol. 2, fasc. 2, Travaux de la Section III.
- JOHNSTON, J. 1650 (1657 ed.). *Historiae Naturalis de Quadeupedibus*. Ioannem Iacobi Fil. Schipper, Amstelodami, 163 pp. + unpaginated index.
- KÄHLKE, R. D., AND S. GAUDZINSKI. 2005. The blessing of a great flood: Differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. *Journal of Archaeological Science*, 32: 1202–1222.
- KARTOGRAFIAI VALLALAT, ALGERIA, 1:1,000,000. 1991. Budapest.
- KAUMANN, W. 1978. Berberaffen (*Macaca sylvana*) im Freigehege Salem. *Zeitschrift des Kölner Zoo*, 21: 57–66.
- KENYON, E. R. 1938. Gibraltar under Moor, Spaniard, and Briton. Methuen and Co., London, xviii + 136 pp. + fold-out map.
- KÖHLER, M., S. MOYÀ-SOLÀ, AND D. M. ALBA. 2000. *Macaca* (Primates, Cercopithecidae) from the Late Miocene of Spain. *Journal of Human Evolution*, 38: 447–452.
- KJUESTER, J., AND A. PAUL. 1984a. Female reproductive characteristics in semifree-ranging Barbary macaques (*Macaca sylvanus* L. 1758). *Folia Primatologica*, 43: 69–83.
- . 1984b. Zum zeitlichen Verlauf der reproduktiven Aktivität weiblicher Berberaffen (*Macaca sylvanus*). *Anthropologischer Anzeiger*, 42: 191–196.
- KUESTER, J., AND A. PAUL. 1986. Male–infant relationships in semifree-ranging Barbary macaques (*Macaca sylvanus*) of Affenberg Salem/FRG: testing the “male care” hypothesis. *American Journal of Primatology*, 10: 315–327.
- . 1989. Reproductive strategies of subadult Barbary macaque males at Affenberg Salem, pp. 93–109. In Rasa, A. E., C. Vogel and E. Volland, eds., *The Sociobiology of Sexual and Reproductive Strategies*. Chapman and Hall, London.
- . 1992. Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). *Behaviour*, 120: 192–217.
- . 1996. Female–female competition and male mate choice in Barbary macaques (*Macaca sylvanus*). *Behaviour*, 133: 763–790.
- . 1997. Group fission in Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *International Journal of Primatology*, 18: 941–966.
- . 1999. Male migration in Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *International Journal of Primatology*, 20: 85–106.
- . 2000. The use of infants to buffer male aggression, pp. 91–93. In Aureli, F. and F. B. M. de Waal, eds., *Natural Conflict Resolution*. University of California Press, Berkeley.
- KUESTER, J., A. PAUL, AND J. ARNEMANN. 1994. Kinship, familiarity and mating avoidance in Barbary macaques (*Macaca sylvanus*). *Animal Behaviour*, 48: 1183–1194.
- . 1995. Age-related and individual differences of reproductive success in male and female Barbary macaques (*Macaca sylvanus*). *Primates*, 36: 461–476.
- KÜMMERLI, R., AND R. D. MARTIN. 2005. Male and female reproductive success in *Macaca sylvanus* in Gibraltar: no evidence for rank dependence. *International Journal of Primatology*, 26: 1229–1249.
- KURTÉN, B. 1968. Pleistocene Mammals of Europe. Weidenfeld and Nicolson, London, vii + 317 pp.
- LACÉPÈDE, B. G. E. 1799. Tableau des divisions, sous-divisions, ordres et genres des mammifères, pp. 1–18. In Lacépède, B. G. E., ed., *Discours d'Ouverture et de Clôture du Cours d'Histoire Naturelle Donné dans le Muséum National d'Histoire Naturelle* Plassan, Paris.
- LACÉPÈDE, B. G. E., AND F. M. DAUDIN. 1802. Tableau des Divisions, Sous-Divisions, Ordres et Genres des Mammifères P. Didot & Firmin Didot, Paris, 346 pp. + 23 plates.
- LAHIRI, R. K., AND C. H. SOUTHWICK. 1966. Parental care in *Macaca sylvana*. *Folia Primatologica*, 4: 257–264.
- LATHIULLIÈRE, M., B. CROUAY-ROY, E. PETIT, W. SHEFFRAHN, AND N. MÉNARD. 2004. Influence of group fission on gene dispersion in the Barbary macaque (*Macaca sylvanus*). *Folia Primatologica*, 75: 175–176. (abstract only)
- LATREILLE, P. A. 1804a. Pitheque, pp. 176–178. In Sonnini, C. S., ed., *Histoire Naturelle Générale et Particulière*, par Leclerc de Buffon, vol. 35. De L'Imprimerie de F. Dufart, Paris.
- . 1804b. Tableau méthodique des singes, pp. 275–298. In Sonnini, C. S., ed., *Histoire Naturelle Générale et Particulière*, par Leclerc de Buffon, vol. 36. De L'Imprimerie de F. Dufart, Paris.
- LEO AFRICANUS. 1526 (1896 edition). *The History and Description of Africa ...*, vol. 3. Hakluyt Society, London, pp. 699–1119. Translated by J. Pory.
- LESSON, R.-P. 1827. *Manuel de Mammalogie, ou Histoire Naturelle des Mammifères*. Roret, Paris, xv + 442 pp.
- . 1840. *Species des Mammifères Bimanes et Quadrumanes; Suivi d'un Mémoire sur les Oryctéropes*. J. B. Ballière, Paris, xiv + 292 pp.

- LILLY, A. A., AND P. T. MEHLMAN. 1993. Conservation update on the Barbary macaque. I. Declining distribution and population size in Morocco. *American Journal of Primatology*, **30**: 327. (abstract only)
- LINK, H. F. 1795. *Beyträge zur Naturgeschichte*, vol. 2. Karl Christoph Stiller, Rostock, 126 pp.
- LINNAEUS, C. 1748. *Systema Naturae* ..., 6th ed. Impensis Godofr. Kiesewetteri, Stockholm, 4 + 224 + 27 pp. + 8 plates.
- . 1758. *Systema Naturae* ..., 10th ed, vol. 1. Impensis Direct. Laurentii Salvii, Holmiae, 823 + 1 + 3 pp.
- . 1766. *Systema Naturae* ..., 12th ed, vol. 1. Impensis Direct. Laurentii Salvii, Holmiae, 532 pp.
- LIU, L., AND D. K. PEARL. 2007. Species trees from gene trees: Restructuring Bayesian posterior distributions of a species phylogeny using estimated gene tree distributions. *Systematic Biology*, **56**: 504–514.
- LOGET, N., J. VAN DEN DRIESSCHE, AND P. DAVY. 2005. How did the Messinian Salinity Crisis end? *Terra Nova*, **17**: 414–419.
- LYDEKKER, R. 1893–1894. *The Royal Natural History*, vol. 1. Frederick Warne and Co., London, 583 pp.
- . 1916. *Wildlife of the World: A Descriptive Survey of the Geographical Distribution of Animals*, vol. 3. Frederick Warne and Co., London, 457 pp.
- LYNES, H. 1920. Ornithology of the Moroccan "Middle-Atlas." *The Ibis*, 11th series, **2**: 260–301 pp. + 12 plates.
- MACHAIRAS, I., A. CAMPERIO CIANI, AND S. SGARDELIS. 2003. Interpopulation differences in activity patterns of *Macaca sylvanus* in the Moroccan Middle Atlas. *Human Evolution*, **18**: 185–202.
- MACROBERTS, B. R., AND M. H. MACROBERTS. 1971. The apes of Gibraltar. *Natural History*, **80**: 38–47.
- MACROBERTS, M. H. 1970. The social organization of Barbary apes (*Macaca sylvana*) on Gibraltar. *American Journal of Physical Anthropology*, **33**: 83–99.
- MACROBERTS, M. H., AND B. R. MACROBERTS. 1966. The annual reproductive cycle of the Barbary ape (*Macaca sylvana*) in Gibraltar. *American Journal of Physical Anthropology*, **25**: 291–304.
- MAESTRIPIERI, D. 1998. The evolution of male–infant interactions in the tribe Papionini (Primates: Cercopithecidae). *Folia Primatologica*, **69**: 247–251.
- MALLINSON, J. C. 1979. The birth season of mammals at the Jersey Wildlife Preservation Trust. *Dodo, Journal of the Jersey Wildlife Preservation Trust*, **16**: 36–40.
- MASCHENKO, E. N., AND G. F. BARYSHNIKOV. 2002. The taxonomic status of a macaque (Primates, Cercopithecidae) from the Middle Pleistocene of Georgia. *Paleontological Journal, English Translation of Paleontologicheskii Zhurnal*, **36**: 403–413.
- MAZZA, P., M. RUSTIONI, S. AGOSTINI, AND A. ROSSI. 2005. An unexpected Late Pleistocene macaque remain from Grotta degli Orsi Volanti (Rapino, Chieti, central Italy). *Geobios*, **38**: 211–217.
- MCDERMOTT, W. C. 1938. *The Ape in Antiquity*. Johns Hopkins Press, Baltimore, ix + 338 pp. + 10 plates.
- McLAREN, S., D. A. SCHLITTER, AND H. H. GENOWAYS. 1984. Catalog of the Recent Scandentia and Primates in the Carnegie Museum of Natural History. *Annals of Carnegie Museum*, **53**: 463–525.
- MEHLMAN, P. T. 1984. Aspects of the ecology and conservation of the Barbary macaque in the fir forest habitat of the Moroccan Rif Mountains, pp. 165–199. *In* Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- . 1985. Intergroup dynamics of the Barbary macaque, *Macaca sylvanus* L., Ghomaran Rif, Morocco. *American Journal of Physical Anthropology*, **66**: 204. (abstract only)
- . 1986. Male intergroup mobility in a wild population of the Barbary macaque (*Macaca sylvanus*), Ghomaran Rif Mountains, Morocco. *American Journal of Primatology*, **10**: 67–81.
- . 1988. Food resources of the wild Barbary macaque (*Macaca sylvanus*) in high-altitude fir forest, Ghomaran Rif, Morocco. *Journal of Zoology*, **214**: 469–490.
- . 1989. Comparative density, demography, and ranging behavior of Barbary macaques (*Macaca sylvanus*) in marginal and prime conifer habitat. *International Journal of Primatology*, **10**: 269–292.
- MEHLMAN, P. T., AND A. A. LILLY. 1993. Conservation update on the Barbary macaque. II. Prospects for future survival in Algeria and Morocco. *American Journal of Primatology*, **30**: 334–335.
- MEHLMAN, P. T., AND R. S. PARKHILL. 1988. Intergroup interactions in wild Barbary macaques (*Macaca sylvanus*), Ghomaran Rif Mountains, Morocco. *American Journal of Primatology*, **15**: 31–44.
- MEIKLE, W. E. 1987. Fossil Cercopithecidae from the Sahabi Formation, pp. 119–127. *In* Boaz, N. T., A. El-Arnauti, A. W. Gaziry, J. de Heinzelin and D. D. Boaz, eds., *Neogene Paleontology and Geology of Sahabi*. Alan R. Liss, New York.
- MÉNARD, N. 1985. Le régime alimentaire de *Macaca sylvanus* dans différents habitats d'Algérie: I.— Régime en chenaie décidue. *Revue d'Ecologie*, **40**: 451–466.
- . 2002. Ecological plasticity of Barbary macaques (*Macaca sylvanus*). *Evolutionary Anthropology*, **11**: 95–100.
- MÉNARD, N., M. AMROUN, R. MOHAMED SAID, AND A. GAUTIER-HION. 1986. Status of the Barbary macaque (*Macaca sylvanus*) in Tikjda Forest, Algeria. *Primate Conservation*, **7**: 35–38.
- MÉNARD, N., R. HECHAM, D. VALLET, H. CHIKHI, AND A. GAUTIER-HION. 1990. Grouping patterns of a mountain population of *Macaca sylvanus* in Algeria—a fission-fusion system? *Folia Primatologica*, **55**: 166–175.
- MÉNARD, N., AND M. QARRO. 1999. Bark stripping and water availability: a comparative study between Moroccan and Algerian Barbary macaques (*Macaca sylvanus*). *Revue d'Ecologie*, **54**: 123–132.

- MÉNARD, N., W. SCHEFFRAHN, D. VALLET, C. ZIDANE, AND C. REBER. 1992. Application of blood protein electrophoresis and DNA fingerprinting to the analysis of paternity and social characteristics of wild Barbary macaques, pp. 155–174. In Martin, R. D., A. F. Dixson and E. J. Wickings, eds., *Paternity in Primates: Genetic Tests and Theories, Implications of Human DNA Fingerprinting*. Karger, Basel.
- MÉNARD, N., AND D. VALLET. 1986. Le régime alimentaire de *Macaca sylvanus* dans différents habitats d'Algérie: II.—Régime en forêt sempervirente et sur les sommets rocheux. *Revue d'Ecologie*, **41**: 173–192.
- . 1993a. Dynamics of fission in a wild Barbary macaque group (*Macaca sylvanus*). *International Journal of Primatology*, **14**: 479–500.
- . 1993b. Population dynamics of *Macaca sylvanus* in Algeria: an 8-year study. *American Journal of Primatology*, **30**: 101–118.
- . 1996. Demography and ecology of Barbary macaques (*Macaca sylvanus*) in two different habitats, pp. 106–131. In Fa, J. E. and D. G. Lindburg, eds., *Evolution and Ecology of Macaque Societies*. Cambridge University Press, Cambridge.
- . 1997. Behavioral responses of Barbary macaques (*Macaca sylvanus*) to variations in environmental conditions in Algeria. *American Journal of Primatology*, **43**: 285–304.
- MÉNARD, N., D. VALLET, AND A. GAUTIER-HION. 1985. Démographie et reproduction de *Macaca sylvanus* dans différents habitats en Algérie. *Folia Primatologica*, **44**: 65–81.
- MÉNARD, N., F. VON SEGESSER., W. SCHEFFRAHN, J. PASTORINI, D. VALLET, B. GACI, R. D. MARTIN, AND A. GAUTIER-HION. 2001. Is male-infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? *Comptes Rendus de l'Académie des Sciences, Série III, Sciences de la Vie*, **324**: 601–610.
- MERZ, E. 1976. Beziehungen zwischen Gruppen von Berberaffen (*Macaca sylvana*) auf La Montagne des Singes. *Zeitschrift des Kölner Zoo*, **19**: 49–67.
- . 1978. Male-male interactions with dead infants in *Macaca sylvanus*. *Primates*, **19**: 749–754.
- MICHELIN, MOROCCO, 1:1,000,000. No date. Mohammedia.
- MILLER, G. S. Jr. 1933. The groups and names of macaques, pp. 1–9. In Hartman, C. G. and W. L. Straus, Jr., eds., *The Anatomy of the Rhesus Monkey (*Macaca mulatta*)*. Williams and Wilkins, Baltimore.
- MIVART, ST. G. 1865. Contributions toward a more complete knowledge of the axial skeleton in primates. *Proceedings of the Zoological Society of London*, **1865**: 545–592.
- MODOLO, L., W. SALZBURGER, AND R. D. MARTIN. 2005. Phylogeography of Barbary macaques (*Macaca sylvanus*) and the origin of the Gibraltar colony. *Proceedings of the National Academy of Sciences of the United States of America*, **102**: 7392–7397.
- MÖHLE, U., M. HEISTERMANN, J. DITTAMI, V. REINBERG, AND J. K. HODGES. 2005. Patterns of anogenital swelling size and their endocrine correlates during the ovulatory cycles and early pregnancy in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. *American Journal of Primatology*, **66**: 351–368.
- MOIGNE, A.-M., M. R. PALOMBO, V. BELDA, D. HERIECH-BRIKI., S. KACIMI, F. LACOMBAT, M.-A. DE LUMLEY., J. MOUTOUSSAMY, F. RIVALS, J. QUILÈS, AND A. TESTU. 2006. Les faunes de grands mammifères de la Caune de l'Arago (Tutavel) dans le cadre biochronologique des faunes du Pléistocène moyen italien. *L'anthropologie*, **110**: 788–831.
- MORALES, J. C., AND D. J. MELNICK. 1998. Phylogenetic relationships of the macaques (Cercopithecidae: *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *Journal of Human Evolution*, **34**: 1–23.
- MORESCALCHI, A. M., A. CAMPERIO CIANI, AND R. STANYON. 1998. Chromosome banding and molecular cytogenetics of the Barbary macaque, *Macaca sylvanus*. *Italian Journal of Zoology*, **65**: 101–107.
- MORRIS, R., AND D. MORRIS. 1966. *Men and Apes*. McGraw-Hill, New York, 271 pp.
- MÜLLER, P. L. S. 1773. Des Ritters Carl von Linné ... *Natursystem* Gabriel Nicolaus Raspe, Nürnberg, 508 pp. + index + 32 plates.
- NAPIER, P. H. 1981. *Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles. Part II. Family Cercopithecidae, Subfamily Cercopithecinae*. British Museum (Natural History), London, 203 pp.
- NEWMAN, E. 1846. The apes of Gibraltar. *The Zoologist: A Popular Miscellany of Natural History*, **4**: 1292–1293.
- OUAHBI, Y., M. ABERKAN, AND F. SERRE. 2001. Climatic effect on Late Pleistocene mammals from the northern Rif Mountains, northern Morocco. *Paleontological Journal, English Translation of Paleontologicheskii Zhurnal*, **35**: 641–646.
- OUDAHMANE, M., AND B. ASSELAH. 2005. What does the future hold for the Barbary macaque (*Macaca sylvanus*) in Algeria? *Primate Report*, **72**–1: 31. (abstract only)
- PAN, R.-L., AND C. OXNARD. 2004. Craniodental variation in the African macaque, with reference to various Asian species. *Folia Primatologica*, **75**: 355–375.
- PANOUSE, J. B. 1957. Les mammifères du Maroc: Primates, carnivores, pinnipèdes, artiodactyles. *Travaux de l'Institut Scientifique Chérifien, Série Zoologie*, **5**: pp. 9–206 + Addendum and Corrigenda + 11 plates.
- PASTORINI, J., J. T. EPPLER, AND R. D. MARTIN. 2000. Multilocus DNA fingerprinting using oligonucleotide probes in 5 macaque species. *Folia Primatologica*, **71**: 161–168.
- PAUL, A. 1989. Determinants of male mating success in a large group of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Primates*, **30**: 461–476.

- PAUL, A., AND J. KUESTER. 1984. Incest avoidance in semifree-ranging Barbary macaques, *Macaca sylvanus*. *International Journal of Primatology*, **5**: 372. (abstract only)
- . 1985. Intergroup transfer and incest avoidance in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem (FRG). *American Journal of Primatology*, **8**: 317–322.
- . 1987. Sex ratio adjustment in a seasonally breeding primate species: Evidence from the Barbary macaque population at Affenberg Salem. *Ethology*, **74**: 117–132.
- . 1988. Life history patterns of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem, pp. 199–228. In Fa, J. E. and C. H. Southwick, eds., *Ecology and Behavior of Food-Enhanced Primate Groups*, Monographs in Primatology, vol. 11. Alan R. Liss, New York.
- . 1990. Adaptive significance of sex ratio adjustment in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem. *Behavioral Ecology and Sociobiology*, **27**: 287–293.
- . 1996a. The sociobiology of the Barbary macaque (*Macaca sylvanus*): A summary of the "Salem" project. *Primate Report*, **44**: 35–36. (abstract only)
- . 1996b. Differential reproduction in male and female Barbary macaques, pp. 293–317. In Fa, J. E. and D. G. Lindburg, eds., *Evolution and Ecology of Macaque Societies*. Cambridge University Press, Cambridge.
- PAUL, A., J. KUESTER, AND J. ARNEMANN. 1992. DNA fingerprinting reveals that infant care by male Barbary macaques (*Macaca sylvanus*) is not paternal investment. *Folia Primatologica*, **58**: 93–98.
- . 1996. The sociobiology of male–infant interactions in Barbary macaques (*Macaca sylvanus*). *Animal Behaviour*, **51**: 155–170.
- PAUL, A., J. KUESTER, AND D. PODZUWEIT. 1993a. Reproductive senescence and terminal investment in female Barbary macaques (*Macaca sylvanus*) at Salem. *International Journal of Primatology*, **14**: 105–124.
- PAUL, A., J. KUESTER, A. TIMME, AND J. ARNEMANN. 1993b. The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). *Primates*, **34**: 491–502.
- PAUL, A., AND D. THOMMEN. 1984a. Timing of birth, female reproductive success and infant sex ratio in semifree-ranging Barbary macaques (*Macaca sylvanus*). *Folia Primatologica*, **42**: 2–16.
- . 1984b. Differentieller Reproduktionserfolg und Reproduktionsstrategien weiblicher Berberaffen (*Macaca sylvanus*). *Anthropologischer Anzeiger*, **42**: 185–190.
- PENNANT, T. 1771. *Synopsis of Quadrupeds*, vol. 1. J. Monk, Chester, xxv + 382 pp.
- PFEFFERLE, D., K. BRAUCH, M. HEISTERMANN, K. HODGES, AND J. FISCHER. 2006. On the influence of sexual hormones on acoustic structures of female Barbary macaque (*Macaca sylvanus*) copulation calls. *International Journal of Primatology*, **27** (suppl. 1): abstract no. 579. (abstract only, unpaginated)
- POHL, R., AND D. TODT. 1984. Significance of mating calls and gestures in the Barbary macaque and their relation to the estrous cycle of females (*Macaca sylvanus*). *International Journal of Primatology*, **5**: 373. (abstract only)
- POMEL A. 1892. Sur un macaque fossile des phosphorites quaternaires de l'Algérie. *Macacus traensis*. *Comptes Rendus de l'Académie des Sciences, Série III, Sciences de la Vie*, **115**: 157–160.
- . 1896. *Carte Géologique de l'Algérie, Paléontologie—Monographies: Singe et Homme*. Imprimerie P. Fontana, Alger, 34 pp. + 8 plates.
- PRUD'HOMME, J. 1991. Group fission in a semifree-ranging population of Barbary macaques, (*Macaca sylvanus*). *Primates*, **32**: 9–22.
- RAAUM, R. L., K. N. STERNER, C. M. NOVIELLO, C.-B. STEWART, AND T. R. DISOTELL. 2005. Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. *Journal of Human Evolution*, **48**: 237–257.
- REICHENBACH, H. G. L. 1862. *Die Vollständigste Naturgeschichte der Affen. Expedition der vollständigsten Naturgeschichte*, Dresden und Leipzig, 204 pp.
- RIECHELMANN, C., H. HULTSCH, AND D. TODT. 1994. Early development of social relationships in Barbary macaques, (*Macaca sylvanus*): Trajectories of alloparental behaviour during an infant's first three months of life, pp. 279–285. In Roeder, J. J., B. Thierry, J. R. Anderson and N. Herrenschmidt, eds., *Current Primatology II*. Université Louis Pasteur, Strasbourg.
- ROBERTS, M. S. 1978. The annual reproductive cycle of captive *Macaca sylvana*. *Folia Primatologica*, **29**: 229–235.
- RODE, P. 1937. *Les Primates de l'Afrique*. Librairie Larousse, Paris, xi + 223 pp. + 13 plates.
- ROOK, L., L. ABBAZZI, C. ANGELONE, M. ARCA, G. BARISONE, C. BEDETTI, M. DELFINO, T. KOTSAKIS, F. MARCOLINI, M. R. PALOMBO, M. PAVIA, P. PIRAS, D. TORRE, C. TUVERI, A. M. F. VALLI, AND B. WILKENS. 2003. Osservazioni preliminari sui vertebrati fossili Plio–Pleistocenici nati del Monte Tuttavista (Orosei, Sardegna). *Sardinia, Corsica et Baleares Antiquae—International Journal of Archaeology*, **1**: 11–29.
- ROOK, L., A. MOTTURA, AND S. GENTILI. 2001. Fossil *Macaca* remains from RDB quarry (Villafranca d'Asti, Italy): New data and overview. *Journal of Human Evolution*, **40**: 187–202.
- ROOK, L., AND P. O'HIGGINS. 2005. A comparative study of adult facial morphology and its ontogeny in the fossil macaque *Macaca majori* from Capo Figari, Sardinia, Italy. *Folia Primatologica*, **76**: 151–171.
- ROUGET, C., AND A. SABATIER. 1866. Note sur les organes érectiles utéro-ovariens d'une femelle de magot (*Pithecius inuus*). *Annales des Sciences Naturelles, Cinquième Série: Zoologie et Paléontologie*, **5**: pp. 219–225 + plate 8.
- RUMSEY, T. J., AND A. WHITEN. 1972. Baby care in Barbary apes. *Animals*, **14**: 561–563.

- RÜPPELL, W. P. E. S. 1835. Neue Wirbelthiere zu der Fauna von Abyssinien Gehörig: Säugethiere. Siegmund Schmerber, Frankfurt am Main, 40 pp. + 14 plates.
- SALZERT, W. 1978. Magotpark im Tierpark Rheine. Zoologische Garten, N. F., **16**: 33–40.
- SANDERSON, I. T. 1957. The Monkey Kingdom. Hanover House, Garden City, New York, 200 pp.
- SAYRE, F. 1862. The History of Gibraltar and of Its Political Relation to Events in Europe Saunders, Otley, and Co., London, viii + 520 pp.
- SCHAUB, S. 1988. The world's first surviving *Macaca sylvanus* twins in a semifree-ranging colony. Folia Primatologica, **49**: 106–110. (For date of publication, see outside front cover.)
- SCHIEFFRAHN, W., N. MÉNARD, D. VALLET, AND B. GACI. 1993. Ecology, demography, and population genetics of Barbary macaques in Algeria. Primates, **34**: 381–394.
- SCHIEFFRAHN, W., N. SERRIDA, J. PASTORINI, N. MÉNARD, AND B. GACI. 1996. Field studies of population genetics in *Macaca sylvanus* of Algeria, abstract no. 240. In Abstracts: XVIIth Congress of the International Primatological Society, 11–16 August 1996, University of Wisconsin–Madison. (abstract only, unpaginated)
- SCHINZ, H. R. 1821. Das Thierreich Eingetheilt nach dem Bau der Thiere vol. 1. J. G. Cotta'schen Buchhandlung, Stuttgart und Tübingen, xxxviii + 894 pp.
- . 1844. Systematischen Verzeichniss Aller bis Jetzt Bekannten Säugethiere vol. 1. Verlag von Jent und Gassmann, Solothurn. xvi + 587 pp.
- SCHLEGEL, H. 1876. Monographie 40: Simiae. Revue Méthodique, Muséum Naturelle des Pays-Bas, **7**: 1–356.
- SCHREIBER, J. C. D. 1774. Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen, Theil I. Wolfgang Walther, Erlangen, pp. 1–190. (For date of publication, see C. D. Sherborn, [1892], Proceedings of the Zoological Society of London, **1891**: 588.)
- . 1800. Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen, Theil V. Wolfgang Walther, Erlangen, pp. 937–968 + supplementary plate 4B (“IIII B”). (For date of publication, see C. D. Sherborn, [1892], Proceedings of the Zoological Society of London, **1891**: 590.)
- SCHULTZ, A. H. 1925. Embryological evidence of the evolution of man. Journal of the Washington Academy of Sciences, **15**: 247–263.
- SCHULTZ, A. H., AND W. L. STRAUS, Jr. 1945. The numbers of vertebrae in primates. Proceedings of the American Philosophical Society, **89**: 601–626.
- SLATER, P. L. 1888. The Barbary ape in Algeria. Nature, **39**: 30.
- SEMPLE, S. 1998. The function of Barbary macaque copulation calls. Proceedings of the Royal Society of London, **B265**: 287–291.
- SEMPLE, S., AND K. MCCOMB. 2000. Perception of female reproductive state from vocal cues in a mammal species. Proceedings of the Royal Society of London, **B267**: 707–712.
- SIMONS, E. L. 1970. The deployment and history of Old World Monkeys (Cercopithecidae, Primates), pp. 97–128. In Napier, J. R. and P. H. Napier, eds., Old World Monkeys: Evolution, Systematics, and Behavior. Academic Press, New York.
- SINGER, R., R. G. WOLFF, B. G. GLADFELTER, AND J. J. WYMER. 1982. Pleistocene *Macaca* from Hoxne, Suffolk, England. Folia Primatologica, **37**: 141–152.
- SMALL, M. F. 1990a. Social climber: independent rise in rank by a female Barbary macaque (*Macaca sylvanus*). Folia Primatologica, **55**: 85–91.
- . 1990b. Promiscuity in Barbary macaques (*Macaca sylvanus*). American Journal of Primatology, **20**: 267–282.
- . 1990c. Alloparental behaviour in Barbary macaques, *Macaca sylvanus*. Animal Behaviour, **39**: 297–306.
- . 1992. Female choice in mating. American Scientist, **80**: 142–151.
- . 1993. Female Choices: Sexual Behavior of Female Primates. Cornell University Press, Ithaca, xi + 245 pp.
- SMITH, C. H. 1842. The Naturalists Library: Introduction to the Mammalia, vol. 13. W. H. Lizars, Edinburgh, 313 pp.
- SMITH, E. O., AND P. G. PFEFFER-SMITH. 1982. Triadic interactions in captive Barbary macaques (*Macaca sylvanus*, Linnaeus, 1758): “Agonistic buffering.” American Journal of Primatology, **2**: 99–107.
- STANYON, R., W. H. PATTON, J. A. KURLAND, AND D. M. TAUB. 1980. G-banding in the Barbary macaque (*Macaca sylvanus*, Linnaeus, 1758) of Morocco. Journal of Human Evolution, **9**: 147–152.
- STEWART, C.-B., AND T. R. DISOTELL. 1998. Primate evolution—in and out of Africa. Current Biology, **8**: R582–R588.
- STEWART, J. D. 1958. The apes of Gibraltar. Corona, **10**: 338–342.
- STILES, C. W., AND M. B. ORLEMAN. 1927. The nomenclature for man, the chimpanzee, the orangutan, and the Barbary ape. Hygienic Laboratory Bulletin, **145**: 1–66.
- SZALAY, F. S., AND E. DELSON. 1979. Evolutionary History of the Primates. Academic Press, New York, xiv + 580 pp.
- TAUB, D. M. 1975. Paternalism in free-ranging Barbary macaques, *Macaca sylvanus*. American Journal of Physical Anthropology, **42**: 333–334. (abstract only)
- . 1977. Geographic distribution and habitat diversity of the Barbary macaque *Macaca sylvanus* L. Folia Primatologica, **27**: 108–133.
- . 1978a. The Barbary macaque in North Africa. Oryx, **14**: 245–253.
- . 1978b. Does “agonistic buffering” buffer agonism? The dynamics of membership in the triadic interaction. In Abstracts: Second Annual Meeting of the American Society of Primatologists. (abstract only, unpaginated).
- . 1980a. Testing the ‘agonistic buffering’ hypothesis: I. The dynamics of participation in the triadic interaction. Behavioral Ecology and Sociobiology, **6**: 187–197.

- . 1980b. Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus* L.), pp. 287–344. In Lindburg, D. G., ed., *The Macaques: Studies in Ecology, Behavior and Evolution*. Van Nostrand Reinhold, New York.
- . 1982. Sexual behavior of wild Barbary macaque males (*Macaca sylvanus*). *American Journal of Primatology*, 2: 109–113.
- . 1984a. A brief historical account of the recent decline in geographic distribution of the Barbary macaque in North Africa, pp. 71–78. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- . 1984b. Male caretaking behavior among wild Barbary macaques (*Macaca sylvanus*), pp. 20–55. In Taub, D. M., ed., *Primate Paternalism*. Van Nostrand Reinhold, New York.
- . 1985. Male–infant interactions in baboons and macaques: A critique and reevaluation. *American Zoologist*, 25: 861–871.
- . 1990. The functions of primate paternalism: A cross-species review, pp. 338–377. In Feerman, J. R., ed., *Pedophilia: Biosocial Dimensions*. Springer-Verlag, New York.
- TAUB, D. M., AND W. K. REDICAN. 1984. Adult male–infant interactions in Old World monkeys and apes, pp. 377–406. In Taub, D. M., ed., *Primate Paternalism*. Van Nostrand Reinhold, New York.
- THIERRY, B. 2000. Covariation of conflict management patterns across macaque species, pp. 106–128. In Aureli, F. and F. B. M. de Waal, eds., *Natural Conflict Resolution*. University of California Press, Berkeley.
- THIRGOOD, J. V. 1984. The demise of Barbary macaque habitat—past and present forest cover of the Maghreb, pp. 19–69. In Fa, J. E., ed., *The Barbary Macaque: A Case Study in Conservation*. Plenum, New York.
- THOMAS, O. 1911. The mammals of the tenth edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. *Proceedings of the Zoological Society of London*, 1911: 120–158.
- TIHY, F., N. LEMIEUX, M. LOMBARD, AND B. DUTRILLAUX. 1996. Comparative RFLP gene mapping in *Homo sapiens*, *Pithecia pithecia*, *Macaca sylvana*, and *Cercopithecus aethiops tantalus*. *Cytogenetics and Cell Genetics*, 72: 9–11.
- TODT, D., K. HAMMERSCHMIDT, V. ANSORGE, AND J. FISCHER. 1995. The vocal behavior of Barbary macaques (*Macaca sylvanus*): Call features and their performance in infants and adults, pp. 141–160. In Zimmermann, E., J. D. Newman and U. Jürgens, eds., *Current Topics in Primate Vocal Communication*. Plenum, New York.
- TODT, D., AND R. POHL. 1984. Communicative strategies in estrous Barbary ape females (*Macaca sylvanus* L.) during copulation behaviour: Advertising, triggering, affiliating. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 77: 225. (abstract only)
- TOSI, A. J., J. C. MORALES, AND D. J. MELNICK. 2003. Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution*, 57: 1419–1435.
- TREWARTHA, G. T. 1978. Climatic regions, pp. 8–9. In Espenshade, E. B., Jr., and J. L. Morrison, eds., *Goode's World Atlas*, 15th ed. Rand McNally and Co., Chicago.
- TROUSSERT, E.-L. 1882 (“1878”). *Catalogue des mammifères vivants et fossiles*. *Revue et Magasin de Zoologie Pure et Appliquée*, ser. 3, 6: 108–140.
- . 1897. *Catalogus Mammalium Tam Viventium Quam Fossilium*. Nova Editio (Prima Completa). Fasciculus I. Primates, Prosimiae, Chiroptera, Insectivora. R. Friedländer und Sohn, Berlin, v + 218 pp.
- . 1904. *Catalogus Mammalium Tam Viventium Quam Fossilium*, Suppl. 5. R. Friedländer und Sohn, Berlin, iv + 929 pp.
- . 1905. La faune des mammifères de l'Algérie, du Maroc et de la Tunisie. *Causeries Scientifiques de la Société Zoologique de France*, 1: 353–410.
- U.S. BOARD ON GEOGRAPHIC NAMES (USBGN). 1970. *Morocco*. Washington, D.C., ix + 923 pp.
- . 1972. *Algeria*, Washington, D.C., xiii + 754 pp.
- VAN DEN BERGH, U. 1991. Signal exchange among Barbary macaques during mating season. *Primate Report*, 31: 40. (abstract only)
- VIREY, J.-J. 1819. Singes, pp. 257–299. In *Nouveau Dictionnaire d'Histoire Naturelle ...*, vol. 31. Deterville, Paris.
- VON SEGESSER, F. 2002. Conservation genetics of Barbary macaques (*Macaca sylvanus*). *Evolutionary Anthropology*, 11(Suppl. 1): 159–161.
- VON SEGESSER, F., N. MÈNARD, B. GACI, AND R. D. MARTIN. 1999. Genetic differentiation within and between isolated Algerian subpopulations of Barbary macaques (*Macaca sylvanus*): Evidence from microsatellites. *Molecular Ecology*, 8: 433–442.
- VROLIK, W. 1841. *Recherches d'Anatomie Comparée sur le Chimpanzé*. Johannes Müller, Amsterdam, 51 pp. + 7 plates.
- WAGLER, J. 1830. *Natürliches System der Amphibien, mit Vorangehender Classification der Säugethiere und Vögel*. Ein Beitrag zur Vergleichenden Zoologie. J. G. Cotta'schen Buchhandlung, München, Stuttgart und Tübingen, vi + 354 pp.
- WAGNER, J. A. 1839 (“1840”). *Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber*, Supplementband 1, Heft 90–94. Expedition des Schreber'schen Säugethier- und des Esper'schen Schmetterlingswerkes und in Commission der Palm'schen Verlagsbuchhandlung, Erlangen. (For date of publication, see C. D. Sherborn, [1892], *Proceedings of the Zoological Society of London*, 1891: 591.)
- . 1855. *Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen von Dr. Johann Christian Daniel von Schreber*, Supplementband 5, Heft 136–146. T. O. Weigel, Leipzig (For date of publication, see C. D. Sherborn, [1892], *Proceedings of the Zoological Society of London*, 1891: 592.)
- WALDEYER, W. 1896. *Die Caudalanhänge des Menschen*. *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1896 (Halbband 2): 775–784.

- WATERS, S. S., M. AKSISSOU, A. EL HARRAD, M.-E. HOBELINK, AND J. E. FA. 2007. Holding on in the Djebela: Barbary macaque *Macaca sylvanus* in northern Morocco. *Oryx*, **41**: 106–108.
- WHITEN, A., AND T. J. RUMSEY. 1974 ("1973"). "Agonistic buffering" in the wild Barbary macaque, *Macaca sylvana* L. *Primates*, **14**: 421–425. (For date of publication, see outside back cover.)
- WIENBERG, H., A. JAUCH, R. STANYON, AND T. CREMER. 1990. Molecular cytotoxicity of primates by chromosomal *in situ* suppression hybridization. *Genomics*, **8**: 347–350.
- WILL, A., AND D. TODT. 1997. Exploration and social use of handy objects in Barbary macaques (*Macaca sylvanus*). *Primate Report*, **47**: 65–72.
- WITT, R., C. SCHMIDT, AND J. SCHMITT. 1981. Darwinian fitness in a multimale group of Barbary macaques (*Macaca sylvana* Linnaeus, 1758): Dominance reversals and male reproductive success. *Folia Primatologica*, **36**: 201–211.
- ZEUNER, F. E. 1952. Monkeys in Europe, past and present. *Oryx*, **1**: 265–273.
- ZIEGLER, T., C. ABEGG, E. MEIJARD, D. PERWITASARI-FARAJALLAH, L. WALTER, J. K. HODGES, AND C. ROOS. 2007. Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group. *Molecular Phylogenetics and Evolution*, **42**: 807–816.

Appendix I. Specimens Examined (Details), Total 103

SKINS AND SKULLS, 33

ALGERIA, 3. Region unknown (3): BM(NH) 1939.1048, IRSN IG 16871, NHMBE 1268.

MOROCCO, 8. *Central Moyen Atlas* (5): Azrou—BM(NH) 1919.8.19.1; Azrou, 5 km S—USNM 476786 (external measurements from field catalog), 476788; Azrou, 18 km S—USNM 476789; Khenifra, 22 km E—USNM 476790 (tail measurement from field catalog). Region unknown (3): IRSN IG 16696, MNHN CG 1831/835, USNM 196984 (locality "Herrata," not located).

U.K., 5. Gibraltar (5): FMNH 47398, 47409, 47410, USNM 255979, ZMUZ 11600.

Country unknown, 17. AMNH 17408, 17409, 19014, 70269 (mounted skin, not seen), IRSN IG 16696, IG 16701/7108, IG 16701/7825, IG 17058/7586, IG 17058/8587, IG 9295, MCZ 15296, MNHN CG 1939/173, CG 1939/1118, NMS 1621, RMNH 4152, ZMUZ 11601, ZSBS 1959/4.

SKINS ONLY, 37

ALGERIA, 2. *Skikda* (1): Stora—BM(NH) 49b (skull in skin). Region unknown (1): MNHN 283 (skull in skin).

MOROCCO, 7. *Central Moyen Atlas* (4): Aïn Leuh—ISR 123.001 (listed as ISR 123.002 by Aulagnier & Thevenot, 1986, p. 154); Azrou—ISR 123.002 (mounted specimen, on exhibit; listed as ISR 123.001 by Aulagnier & Thevenot, 1986, p. 154), 132.007; Azrou, 18 km S—USNM 478329 (in fluid; external measurements from field catalog). Region unknown (3): ISR 100.037, RMNH 5-e, 6-f.

U.K., 3. Gibraltar (3): BM(NH) 1939.551, 1939.1049, USNM 258206 (in fluid).

Country unknown, 25. AMNH 6316/7951, BM(NH) 1842.12.29.1, 1911.11.11, unnumbered (old collection; skull in skin), FMNH 60716 (in fluid), IRSN IG 10743, IG 9323 MB, stand no. 40 (mounted specimen), stand no. 80 (mounted specimen), MNHN 55a (skull in skin), 55b (skull in skin), 286, 287, 290, CG 1930/72, NHMBA 27, NMS 16837, RMNH 1-a, 2-f, 3 (skull in skin), 4-d, 4153, USNM 200951, 502460 (in fluid), ZSBS (unnumbered, mounted specimen).

SKULLS OR SKELETONS ONLY, 33.

MOROCCO, 13. *Central Moyen Atlas* (9): Azrou, 18 km S—CMNH 45290, USNM 476780, 476781, 476782, 476783, 476784, 476785, 476787 (external measurements from field catalog for all seven USNM specimens from this locality); Khenifra, 22 km E—USNM 476791. Region unknown (4): ISR 500 031, 500 032 (probably listed as ISR 100.078 by Aulagnier & Thevenot, 1986, p. 154), 500.03[?] (probably listed as ISR 100.072 by Aulagnier & Thevenot, 1986, p. 154), ZSBS 1961/188.

U.K., 1. Gibraltar (1): IRSN IG 17073.

Country unknown, 19. AMNH 19178, 2060/5484, IRSN IG 9071, IG 9165/4218, IG 9165/4219, IG 9295, MCZ 7098, NMS 1551, 1552, RMNH 7-a, 9-c, USNM 543429, ZMB 8264, 8271, 16492, ZMUZ 11602, 11742 (skull size indicates that this specimen is a female), ZSBS unnumbered female, unnumbered male.

Appendix II. Gazetteer of *Macaca sylvanus* Localities

Locality names listed as primary entries in this gazetteer preferentially are official names ap-

proved in gazetteers published by the U.S. Board on Geographic Names—USBGN: Algeria, 1972 and USBGN: Morocco, 1970. (Note that the Arabic word for “mountain” is consistently spelled “djebel” in USBGN: Algeria and “jebel” in USBGN: Morocco.) Supplementary references that have been consulted are: Kartografiai Vallalat, Algeria map, 1991; International Travel Maps, Morocco map, 2000; and Michelin, Morocco map, no date. Localities of *M. sylvanus* that were not found in USBGN gazetteers or in supplementary references are spelled here as in the original sources. Secondary entries, with cross references to corresponding primary entries, indicate variant spellings or alternate locality names that occur in published literature.

For each primary entry in this gazetteer, the sequence of information presented is as follows: 1. Locality name. 2. Elevation, if reported by collector or observer. 3. Name of region (in italics). 4. Name of country (in capital letters). 5. Coordinates of locality (principal source: USBGN gazetteers). 6. Date of collection or observation. 7. Name of collector or observer. 8. Bibliographic reference (in parentheses), if any. 9. Abbreviated name of museum (see above, Materials and Methods) where specimens, if any, are preserved. 10. Number of specimens available, if any (with indication of part preserved, if skin and skull are not both present). 11. Locality number (italicized), as indicated in distribution map (Fig 1).

Abid, Oued el, gorge, Bou Tferda vicinity; *Southern Moyen Atlas*, MOROCCO; ca. 32°24'N, 5°40'W; observed 20–24 Nov. 1984 by J. E. Fa (1986b, p. 32). 14.

Adelma, Oued, 400 m; *Rif*, MOROCCO; 35°13'N, 5°03'W; observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 87). 34.

Adelmane, Oued. See Adelma, Oued.

Adendoun, Djebel, SSW of Jijel, 800–1200 m; *Petite Kabylie*, ALGERIA; ca. 36°40'N, 5°35'E; observed 1973–1975 by D. M. Taub (1977, p. 122). 56.

Afennourir; *Central Moyen Atlas*, MOROCCO; 33°16'N, 5°16'W; observed Oct. 1994–Sep. 1995 by I. Machairas (Machairas et al., 2003, p. 186). 22.

Agfadou. See Akfadou, Forêt de.

Aguelmame Aziga. See Azigza, Aguelmane.

Ahfa-Timesh, N of Oued Laou; *Rif*, MOROCCO; ca. 35°22'N, 5°17'W; observed be-

fore 1976 by F. Alvarez and F. Hiraldo (1975, p. 253; cf. Fa., 1983a, p. 79). 32.

Aïn Kahla, 2010 m; *Central Moyen Atlas*, MOROCCO; 33°15'N, 5°13'W; observed Jul.–Aug. 1968 by J. M. Deag and J. H. Crook (1971, p. 186). Observed Jun. 1973–Dec. 1974 by D. M. Taub (1977, pp. 110, 116). 22.

Aïn Leuh, 1200–1450 m and 1750 m; *Central Moyen Atlas*, MOROCCO; 33°17'N, 5°23'W; collected 20 Dec. 1923 by Prince L. Murat (cf. Aulagnier & Thevenot, 1986, p. 154); isr. 1 (skin only). Reported before 1932 by L. Joleaud (1933, p. 852). Observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 91). 22.

Aït Mehammed, S of; *Southern Moyen Atlas*, MOROCCO; ca. 31°53'N, 6°28'W; observed 1973–1975 by D. M. Taub (1977, p. 119; cf. Fa et al., 1984, p. 97). 4.

Aït Mgild. See Sidi Mgild.

Aït M'Hammed. See Aït Mehammed.

Aït Oubane, Forêt d', Djebel Djurdjura, 1750–2300 m; *Grande Kabylie*, ALGERIA; 36°28'N, 4°17'E; observed 1982–1983 by N. Ménard (in Fa et al., 1984, p. 103). 51.

Aït Sokhmane forest, right bank of Oued El Abid; *Southern Moyen Atlas*, MOROCCO; ca. 32°15'N, 5°50'W; reported in 1931 by L. Joleaud (1933, p. 852). 9.

Aït Sokmane. See Aït Sokhmane.

Ajdır, Plateau d', 1600–2000 m; *Central Moyen Atlas*, MOROCCO; 32°56'N, 5°25'W; observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 91). 13.

Akfadou, Forêt de, 500–1600 m and 800–1300 m; *Grande Kabylie*, ALGERIA; 36°43'N, 4°33'E; observed 1973–1975 by D. M. Taub (1977, pp. 118, 122; cf. Fa et al., 1984, p. 104). Observed 1983–1984 by N. Ménard (1985, p. 452). Blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). Tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393). 52.

Akra, Chabet El, N of Kherrata, 1500 m; *Petite Kabylie*, ALGERIA; 36°32'N, 5°18'E; reported in 1931 by L. Joleaud (1933, p. 853). Observed 1973–1975 by D. M. Taub (1977, p. 122; cf. Fa et al., 1984, p. 105). Tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393). 54.

Al Hoceima, *Rif*; MOROCCO; 35°15'N, 3°56'W; reported present in 1920s (Taub, 1978a, p. 249). Reported locally extinct before 1979 by D. M. Taub (1978a, p. 249). 41.

- Ali ou Zrou, Jebel, 1600–2000 m; *Central Moyen Atlas*, MOROCCO; 32°55'N, 5°25'W; observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 91). 13.
- Andjera. See Moussa, Jebel.
- Anjra massif. See Moussa, Jebel.
- Annaba. See Edough, Djebel.
- Annocer, ca. 10 km SW of Aguelmane Azigza; *Central Moyen Atlas*, MOROCCO; 32°54'N, 5°30'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 94). 13.
- Aqfadou. See Akfadou, Forêt de.
- Arhbal, N of; *Southern Moyen Atlas*, MOROCCO; 32°29'N, 5°39'W; observed 1973–1975 by D. M. Taub (1977, p. 119; cf. Fa et al., 1984, p. 97). 14.
- Arhbalou N'Irkraouen, above Lake Miami, 1600–2000 m; *Central Moyen Atlas*, MOROCCO; ca. 32°54'N, 5°22'W; observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, pp. 91, 94). 13.
- Ari Bou Iblan. See Bou Iblane, Jebel.
- Asker, Zaouia, Taguelft region; *Southern Moyen Atlas*, MOROCCO; 32°10'N, 6°10'W; observed 1973–1975 by D. M. Taub (1977, p. 119). 8.
- Asru. See Azrou.
- Assaka N'Ouam, NE of Bekrit; *Central Moyen Atlas*, MOROCCO; 33°06'N, 5°10'W; reported before 1978 by Mr. Arnoud (Deag, 1977, p. 276). 20.
- Assaka-n-Quam. See Assaka N'Ouam.
- Asserdoun, Zaïan circle; *Central Moyen Atlas*, MOROCCO; 32°41'N, 5°46'W; infant captured 30 Apr. 1929 by local residents (Carpentier, 1931, p. 275). 11.
- Azigza, Aguelmane, 1600–2000 m; *Central Moyen Atlas*, MOROCCO; 32°58'N, 5°26'W; collected May 1950 by A. Kalfleche (Aulagnier & Thevenot, 1986, p. 154); ISR 150.011 (not seen); the *M. sylvanus* specimen collected at this locality is now missing (searched for on 25 Sep. 2006); the monkey currently tagged with this number has a tail that is longer than the extended hind leg. Observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 91). 13.
- Azrar, Taguelft region; *Southern Moyen Atlas*, MOROCCO; 32°18'N, 6°00'W; observed 1973–1975 by D. M. Taub (1977, p. 119). Population extant 1982–1984 (Fa et al., 1984, p. 96). 9.
- Azrou, 1600–2200 m and 1890 m; *Central Moyen Atlas*, MOROCCO; 33°26'N, 5°13'W; collected 15 Jun. 1919 by H. Lynes (cf. Napier 1981, p. 6); BMNH, 1. Collected 19 Dec. 1923 by Prince L. Murat (cf. Aulagnier & Thevenot, 1986, p. 154); ISR 1 (skin only). Collected in 1932 by J. Surcouf (cf. Aulagnier & Thevenot, 1986, p. 154); ISR, 1 (skin only). Observed 1973–1975 by D. M. Taub (1977, p. 117; cf. Fa et al., 1984, p. 91). 23.
- Azrou, 5 km S; *Central Moyen Atlas*, MOROCCO; 33°24'N, 5°13'W; collected 21 Jun. 1970 by M. G. Hearst; USNM, 1. Collected 21 Jun. 1970 by L. W. Robbins; USNM, 1. 23.
- Azrou, 18 km S; *Central Moyen Atlas*, MOROCCO; 33°16'N, 5°12'W; collected 22 Jun. 1970 by M. G. Hearst (cf. McLaren et al., 1984, p. 513); CMNH, 1 (skull only), USNM, 4 (skulls only). Collected 22 Jun. 1970 by L. W. Robbins; USNM, 5 (1 in fluid, 1 skeleton only, 2 skulls only, 1 skin and skeleton). 22.
- Azrou, above, 1520–1700 m (5000–5600 ft); *Central Moyen Atlas*, MOROCCO; 33°25'N, 5°10'W; observed 2 May–17 Jul. 1919 by H. Lynes (1920, p. 273, pl. 12). 23.
- Azrou Forest; *Central Moyen Atlas*, MOROCCO; ca. 33°26'N, 5°13'W; tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393). 23.
- Azrou region, *Central Moyen Atlas*, MOROCCO; ca. 33°26'N, 5°13'W; tissue samples collected from captives before 2006 by L. Modolo et al. (2005, p. 7393; cf. de Turekheim & Merz, 1984, p. 242). 23.
- Azzaba, W of; *Azzaba*, ALGERIA; ca. 36°44'N, 7°06'E; unconfirmed local report in 1914 (Joleaud, 1933, p. 853), beyond modern eastern limit of distribution (Fa et al., 1984, p. 107). 61.
- Bab Barred. See Tisirene, Jebel.
- Bab Besen. See Besene, Bab.
- Bab Bessen. See Besene, Bab.
- Babor, Djebel, Kherrata gorge, 1500 m; *Petite Kabylie*, ALGERIA; 36°30'N, 5°28'E; reported in 1925 by L. Joleaud (1926, p. 129; 1933, p. 853). Observed 1973–1975 by D. M. Taub (1977, p. 122; cf. Fa et al., 1984, p. 105). 55.
- Babors. See Babor.
- Bab Taza. See Lakraa, Jebel.
- Bejaia. See Pic des Singes National Park.
- Bekrit. See Assaka N'Ouam.
- Beni Ghobri. See Beni Rhobri.
- Beni Hosmar. See Buzeitune, Jebel; Sidichmim.
- Beni Hozmar. See Zarka cascade.
- Beni M'hamed. See Beni Mohammed.

- Beni Mohammed, Rhomara tribal area, 1300 m; *Rif*, MOROCCO; 35°09'N, 5°07'W; reported Jul.–Sep. 1980 by J. E. Fa (1982, p. 53; cf. Fa et al., 1984, p. 87; Mehlman, 1984, p. 168). 34.
- Beni Rhobri, Forêt des, 500–1600 m; *Grande Kabylie*, ALGERIA; 36°44'N, 4°28'E; Observed 1973–1975 by D. M. Taub (1977, p. 122; cf. Fa et al., 1984, p. 104). 52.
- Beni Touzin. See Beni Touzine.
- Beni Touzine vicinity, between Metalsa and Ourighel; *Rif*, MOROCCO; ca. 35°00'N, 3°42'W; reported present before 1932 by L. Joleaud (1933, p. 852). Reported present before 1962 and locally extinct in 1973–1975 by D. M. Taub (1977, p. 113; 1984a, p. 73). 42.
- Beni Ziat. See Targa.
- Besene, Bab, *Rif*, MOROCCO; ca. 35°00'N, 4°45'W; reported present in mid-1960s and locally extinct subsequently (J. Chitty in Taub, 1977, p. 113; 1984a, p. 73). 37.
- Blida. See Chiffa, Gorges de la; Chrea.
- Bône. See Edough, Djebel.
- Borj Mira; *Petite Kabylie*, ALGERIA; ca. 36°34'N, 5°18'E; reported by forestry officials as locally extinct before 1962 (D. M. Taub, 1977, p. 122; cf. Fa et al., 1984, p. 105). 54.
- Bouak, Cap and Cap Carbon, between; *Grande Kabylie*, ALGERIA; ca. 36°47'N, 5°06'E; reported in 1931 by L. Joleaud (1933, p. 853; cf. Fa et al., 1984, p. 105). 53.
- Bou Cèdre, between Azigza Aguelmame and Senoual, 1800 m; *Central Moyen Atlas*, MOROCCO; ca. 32°58'N, 5°20'W; observed 1973–1975 by D. M. Taub (1977, p. 116; Fa et al., 1984, pp. 91, 93). 13.
- Bougie. See Pic des Singes National Park.
- Bouhachem. See Bouhassim, Jebel.
- Bouhassim, Jebel, 1300 m; *Rif*, MOROCCO; 35°14'N, 5°26'W reported before 1933 by A. Cabrera (1932, p. 202). Observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 253). Observed 1973–1975 by D. M. Taub (1977, p. 112). Observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 53; cf. Fa et al., 1984, p. 86). Observed Oct.–Nov. 2004 by S. S. Waters et al. (2007, p. 107). 33.
- Bou Iblane, Jebel, between El Mers and Missouri; *Eastern Moyen Atlas*, MOROCCO; 33°39'N, 4°06'W; reported present before 1932 by L. Joleaud (1933, p. 852). Reported locally extinct before 1978 by D. M. Taub (1977, p. 115). 26.
- Bou Igaoerh, Jebel; *Central Moyen Atlas*, MOROCCO; 32°57'N, 5°16'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 94). 13.
- Bou Jirirh, *Central Moyen Atlas*, MOROCCO; 33°30'N, 5°09'W; observed Oct. 1980–Oct. 1981 by G. R. Drucker (1984, pp. 136, 138). 23.
- Bou Tferda. See Abid, Oued el.
- Boutferda vicinity, Aït Abdi; *Southern Moyen Atlas*, MOROCCO; ca. 32°22'N, 5°51'W; reported in 1931 by L. Joleaud (1933, p. 852). 9.
- Bouzega, Djebel. See Bou Zegza, Djebel.
- Bou Zegza, Djebel, *Grande Kabylie*, ALGERIA; ca. 36°36'N, 3°27'E; observed in 2005 by M. Oudahmane and B. Asselah (2005, p. 31), locality recolonized by *M. sylvanus*. 49.
- Buhasen. See Bouhassim, Jebel.
- Bu Haxen. See Bouhassim, Jebel.
- Buseitun. See Buzeitune, Jebel.
- Buzeitune, Jebel, Beni Hozmar, 1300 m; *Rif*, MOROCCO; ca. 35°30'N, 5°20'W; observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 253; cf. Fa., 1983a, p. 79). Reported before 1985 by J. E. Fa et al. (1984, pp. 85, 86). 32.
- Carbon, Cap. See Bouak, Cap.
- Cèdre Gouraud, 1800 m; *Central Moyen Atlas*, MOROCCO; 33°25'N, 5°10'W; observed Oct. 1994–Sep. 1995 by I. Machairas (Machairas et al., 2003, p. 186). Observed 29 Sep. 2006 by J. Fooden. 23.
- Ceuta. See Moussa, Jebel.
- Chabet El Akra. See Akra, Chabet El.
- Chechaouene (?=Xauen), Jebel; *Rif*, MOROCCO; 35°10'N, 5°16'W; observed 1955–1975 by Mr. Valverde, subsequently extinct at this locality (Alvarez & Hiraldo, 1975, p. 258). 34.
- Cheminot, Djebel Djurdjura; *Grande Kabylie*, ALGERIA; ca. 36°26'N, 4°07'E; blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). 51.
- Chiffa. See Chiffa.
- Chiffa, Gorges de la; *Chiffa*, ALGERIA; 36°30'N, 2°45'E; collected before 1940 by unknown collector (Napier, 1981, p. 6); BM(NH), 1 (not seen; cranial measurements kindly provided by D. Brandon-Jones). 46.
- ?Chiffa, Gorges de la (locality uncertain); *Chiffa*, ALGERIA; 36°30'N, 2°45'E; date and collector unknown (Napier, 1981, p. 6); University Museum of Zoology, Cambridge, 2 (skulls only; not seen). 46.
- Chiffa, Gorges de la, ca. 15 km S of Blida, 1630 m; *Chiffa*, ALGERIA; ca. 36°21'N,

- 2°45'E; observed 28 Oct. 1888 by P. L. Selater (1888, p. 30). Reported in 1925 by L. Joleaud (1926, p. 129; cf. 1933, p. 852). Observed in 1975 by D. M. Taub (1977, pp. 119, 121; cf. Fa et al., 1984, p. 99). 47.
- Chrea, 5 km S of Blida, National Park of the Cedars; *Chiffa*, ALGERIA; 36°25'N, 2°53'E; reported present ca. 1954–1973 and absent in 1974 by J. Chitty and J. P. Thomas (Taub, 1984a, p. 75). 48.
- Collo, Kabylie de, vicinity; region unknown, ALGERIA; ca. 37°00'N, 6°30'E; reported present in 1931 by L. Joleaud (1933, p. 853). Reported to be beyond eastern limit of species distribution in 1978 by D. M. Taub (1978a, p. 249; 1984a, p. 75). 59.
- Constantina. See Constantine.
- Constantine; *Constantine*, ALGERIA; 36°22'N, 6°37'E; reported before 1527 by Leo Africanus (1896 edition, p. 948). Reported to be beyond eastern limit of species distribution in 1978 by D. M. Taub (1978a, p. 249; 1984a, p. 75). 58.
- Dar El Oued, SSW of Jijel, 800–1200 m; *Petite Kabylie*, ALGERIA; ca. 36°40'N, 5°35'E; observed 1973–1975 by D. M. Taub (1977, p. 122). 56.
- Darguina. See Darguinah.
- Darguinah; *Petite Kabylie*, ALGERIA; 36°34'N, 5°18'E; reported by forestry officials to be locally extinct before 1962 (D. M. Taub, 1977, p. 122; cf. Fa et al., 1984, p. 105). 54.
- Derti-Na, N of, Oued Laou; *Rif*, MOROCCO; ca. 35°22'N, 5°17'W; observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 253; cf. Fa., 1983a, p. 79). 32.
- Djebel Bouzega. See Bou Zegza, Djebel.
- Djidjelli. See Ziam Mansouria.
- Dijel. See Adendoun, Djebel; Dar El Oued; Guerrouch, Forêt Domaniale de.
- Djurdjura, Djebel; *Grande Kabylie*, ALGERIA; ca. 36°27'N, 4°15'E; tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393). 51.
- Djurdjura, Djebel. See Aït Oubane, Forêt d'; Irlit Aimet; Tala Guilef; Tigounatine; Tikjda.
- Edough, Djebel, Annaba vicinity; *Annaba*, ALGERIA; 36°52'N, 7°39'E; reported present in historic times and locally extinct before 1932 by L. Joleaud (1931b, p. 154). 62.
- El Hammam, 1200–1450 m; *Central Moyen Atlas*, MOROCCO; 33°28'N, 5°13'W; observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 91). 22.
- El Haouz region; *Rif*, MOROCCO; ca. 35°30'N, 5°20'W; observed Jan. 2005 by A. El Harrad (Waters et al., 2007, p. 107). 32.
- El Kelaa; *Rif*, MOROCCO; ca. 35°10'N, 5°15'W; reported present before 1933 by A. Cabrera (1932, p. 202). Reported locally extinct before 1984 by J. E. Fa (1983a, pp. 69, 79). 34.
- El Ksiba vicinity, 1800–2000 m; *Southern Moyen Atlas*, MOROCCO; ca. 32°35'N, 6°02'W; observed 1973–1975 by D. M. Taub (1977, p. 119; cf. Fa et al., 1984, p. 96). 10.
- Farda, Oued, Rhomara tribal area; *Rif*, MOROCCO; 35°13'N, 4°10'W; frequent local reports in 1981–1982 to P. T. Mehlman (1984, pp. 166, 170). 34.
- Fath Lemhar, Jebel El Haouz survey area; 700 m; *Rif*, MOROCCO; ca. 35°39'N, 5°29'W; observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 52; cf. Fa et al., 1984, p. 86). 31.
- Gargide Chiffa. See Chiffa, Gorges de la.
- Gibraltar, ca. 400 m; *Gibraltar*, U.K.; ca. 36°08'N 5°21'W; introduced repeatedly, including in or before 1740 (cf. Busk, 1877, p. 130; Kenyon, 1938, pp. 1, 4, 111, 116; Fa, 1984b, p. 266; Modolo et al., 2005, p. 7397). Collected before 1865 by unknown collector; ZMUZ, 1. Collected before 1910 by unknown collector (cf. Napier, 1981, p. 6); BM(NH), 2 (skins only). Collected 11 Dec. 1930 by unknown collector; USNM, 1. Collected Feb. 1937 by unknown collector; FMNH, 3. Collected 11 Nov. 1949 by R. Henry; IRSN, 1 (skeleton only). 29.
- Gibraltar, N end of mountain; *Gibraltar*, U.K.; ca. 36°09'N, 5°21'W; unfossilized skulls, tentatively identified as *M. sylvanus* (introduced), collected before 1798 by miners (Imrie, 1798, pp. 198, 201), museum unknown, 2 (skulls only). 29.
- Gorges de la Chiffa. See Chiffa, Gorges de la.
- Goundafa; *Haut Atlas*, MOROCCO; 31°00'N, 8°05'W; reported present before 1926 by L. Joleaud (1926, p. 129). Reported locally extinct in 1973–1975 by D. M. Taub (1977, p. 111). 1.
- Gouraya, Djebel. See Pic des Singes National Park.
- Gouroud. See Cèdre Gouraud.
- Guerrouch, Forêt Domaniale de, SSW of Jijel, 800–1200 m; *Petite Kabylie*, ALGERIA; 36°42'N, 5°37'E; observed 1973–1975 by D. M. Taub (1977, p. 122; cf. Fa et al., 1984, p. 107). 56.

- Guessig, Mount, Djurdjura National Park, 1480–2100 m; *Grande Kabylie*, ALGERIA; 36°27'N, 4°08'E; observed Apr. 1983–Jul. 1988 by N. Ménard et al. (1990, pp. 167, 169). 51.
- Haounet, Forêt d'El, vicinity, Aït Abdi; *Southern Moyen Atlas*, MOROCCO; ca. 32°13'N, 5°56'W; reported in 1931 by L. Joleaud (1933, p. 852). 9.
- Haouz, Jebel El. See Fath Lemhar.
- Herrata; region unknown, MOROCCO; not located; collected 20 Apr. 1904 by W. Schlüter; USNM, 1. Not mapped.
- Hotel, Jebel Djurdjura; *Grande Kabylie*, ALGERIA; ca. 36°26'N, 4°08'E; blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). 51.
- Icefcifène, Jebel, ca. 2 km from Tigounatine. Jebel, Jebel Djurdjura, 1600–2100 m; *Grande Kabylie*, ALGERIA; ca. 36°27'N, 4°08'E; observed 1983–1985 by N. Ménard and D. Vallet (1986, p. 174). 51.
- Icefcifere. See Icefcifène, Jebel.
- Idjberten. See Ijbertene, Arhbalou.
- Idrous, Jebel; *Southern Moyen Atlas*, MOROCCO; ca. 32°08'N, 6°04'W; reported in 1931 by L. Joleaud (1933, p. 852). 8.
- Ifrane, 1650 m; *Central Moyen Atlas*, MOROCCO; 33°32'N, 5°06'W; observed 1973–1975 by D. M. Taub (1977, p. 116). 23.
- Ighrem, [Jebel], Kasba Tadla-Beni Mellal region; *Southern Moyen Atlas*, MOROCCO; ca. 32°20'N, 6°15'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 96). 7.
- Iirilt Aimet, Jebel Djurdjura, 1750–2300 m; *Grande Kabylie*, ALGERIA; not precisely located; ca. 36°27'N, 4°15'E; observed 1982–1983 by N. Ménard (in Fa et al., 1984, p. 103). Not mapped.
- Ijbertene, Arhbalou; *Southern Moyen Atlas*, MOROCCO; 32°10'N, 5°46'W; reported in 1931 by L. Joleaud (1933, p. 852). 9.
- Illjida, Oued. See Tilljida, Oued.
- Imi Ourarn, above Lake Miami, 1600–2000 m; *Central Moyen Atlas*, MOROCCO; ca. 32°54'N, 5°22'W; observed 1973–1975 by D. M. Taub (1977, p. 118; cf. Fa et al., 1984, pp. 91, 94). 13.
- Immouzer-du-Kandar. See Imouzzet du Kandar.
- Imouzzet du Kandar, vicinity; *Central Moyen Atlas*, MOROCCO; ca. 33°44'N, 5°01'W; observed 1973–1975 by D. M. Taub (1978a, p. 246). 24.
- Itzer, 10–15 km E of; *Central Moyen Atlas*, MOROCCO; ca. 32°53'N, 4°55'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 95). 19.
- Itzer, W of; *Central Moyen Atlas*, MOROCCO; ca. 32°53'N, 5°03'W; observed 1973–1975 by D. M. Taub (1977, p. 118; cf. Fa et al., 1984, p. 95). 19.
- Itzere. See Itzer.
- Jemmapes. See Azzaba.
- Jirrir; Jirigh. See Bou Jirirh.
- Kaiat, Jebel, 1300 m; *Rif*, MOROCCO; 35°18'N, 5°09'W; observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 254). Observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 52; cf. Fa et al., 1984, p. 86). 34.
- Katama. See Ketama.
- Kebir, Oued El, gorge, S of El Milia; *El Milia*, ALGERIA; ca. 36°40'N, 6°15'E; reported in 1931 by L. Joleaud (1933, p. 853), beyond modern eastern limit of distribution (Taub, 1984a, p. 75). 57.
- Kelti, Jebel, 1300 m; *Rif*, MOROCCO; 35°22'N, 5°17'W; observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 253). Observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 86). 32.
- Kerrata. See Akra, Chabet El; Babor, Jebel.
- Kerrouchene; *Central Moyen Atlas*, MOROCCO; 32°49'N, 5°20'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 95). 13.
- Ketama vicinity, Senhaja de Sraïr region; *Rif*, MOROCCO; ca. 34°47'N, 4°40'W; reported present before 1932 by L. Joleaud (1933, p. 852). Reported present in mid-1960s and absent in 1973–1975 by J. Chitty (in Taub, 1977, p. 113; 1984a, p. 73). 38.
- Khenifra, 22 km E, 1600 m; *Central Moyen Atlas*, MOROCCO; 32°58'N, 5°27'W; collected 8 Jul. 1970 by R. E. Vaden; USNM, 2 (including 1 skull only). 13.
- Khenifra area, *Central Moyen Atlas*, MOROCCO; ca. 32°56'N, 5°40'W; blood samples collected Aug. 1977 (Stanyon et al., 1980, p. 149). 12.
- Kherrata. See Akra, Chabet El; Babor, Jebel.
- Kherrata, Gorges de; *Petite Kabylie*, ALGERIA; ca. 36°29'N, 5°17'E; observed 1982–1991 by N. Ménard et al. (1992, p. 156). Blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). 54.
- Komuch, El Ksiba vicinity; *Southern Moyen Atlas*, MOROCCO; ca. 32°35'N, 6°02'W; observed 1973–1975 by D. M. Taub (1977, p. 119; Fa et al., 1984, p. 97). 10.
- Koucer. See Kousser, Massif du.

- Kousser, Massif du; *Southern Moyen Atlas*, MOROCCO; 32°03'N, 6°02'W; reported in 1931 by L. Joleaud (1933, p. 852). 8.
- Ktama. See Ketama.
- Lakraa, Jebel, 1600–2160 m; *Rif*, MOROCCO; 35°08'N, 5°09'W; observed 17 Oct.–27 Nov. 1971 by A. Whiten and T. J. Rumsey (1974, p. 421). Observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 257). Observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 86). 34.
- Lau. See Derti-Na, Sidi Siah.
- Maggó. See Magoo, Jebel.
- Magoo, Jebel; *Rif*, MOROCCO; ca. 35°10'N, 5°15'W; reported present before 1933 by A. Cabrera (1932, p. 202). Reported locally extinct before 1984 by J. E. Fa (1983a, p. 69). 34.
- Mansouria. See Ziama Mansouria.
- Mauretania; region unknown, MOROCCO and/or ALGERIA; ca. 34–37°N, 3°W–5°E; reported before 1527 by Leo Africanus (1896 edition, p. 948). Not mapped.
- Mauritania. See Mauretania.
- Merhraoua. See Tahafourt.
- Miami, Lake. See Arhbalou N'Irkraouen; Imi Ourarn.
- Michlifene, 2000 m; *Central Moyen Atlas*, MOROCCO; 33°25'N, 5°07'W; observed 1973–1975 by D. M. Taub (1977, p. 116). 23.
- Mimejab. See Mimejad.
- Mimejad; *Central Moyen Atlas*, MOROCCO; 33°00'N, 5°16'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 94). 13.
- Mischlifin. See Michlifene.
- MOROCCO (locality and region unknown); collected 7 Aug. 1931 by Dr. Lionville; MNHN. 1. Not mapped.
- Mouça. See Moussa, Jebel.
- Moussa, Jebel, Anjra massif, W of Ceuta, 800 m; *Rif*, MOROCCO; ca. 35°54'N, 5°24'W; reported before 1932 by L. Joleaud (1933, p. 852). Observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 254). Observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 86). Observed Oct.–Nov. 2004 by S. S. Waters et al. (2007, p. 107). 30.
- Muça. See Moussa, Jebel.
- Musa. See Moussa, Jebel.
- Nador vicinity; *Rif*, MOROCCO; ca. 35°00'N, 3°00'W; population introduced in 1985 (Aulagnier & Thevenot, 1986, p. 56). 43.
- National Park of the Cedars. See Chrea.
- North Saqqara; EGYPT; ca. 29°53'N, 31°15'E; mummified captives (introduced), ca. 400–0 B.C.E. (Goudsmit & Brandon-Jones, 1999, p. 51). Not mapped.
- Ouaouezarht. See Ouaouizarht.
- Ouaouizarht, MF de; *Southern Moyen Atlas*, MOROCCO; 32°10'N, 6°21'W; observed 1973–1975 by D. M. Taub (1977, p. 119; cf. Fa et al., 1984, p. 96). 6.
- Oued el Rbia. See Oum Er Rbia, Oued.
- Ouiouane; *Central Moyen Atlas*, MOROCCO; 33°07'N, 5°22'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 93). 22.
- Oum Er Rbia, Oued, source; *Central Moyen Atlas*, MOROCCO; 33°04'N, 5°25'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 93). 22.
- Ourika Valley. See Ourika, Oued; Tourchte; Zaclia Sti Fatma.
- Ourika, Jebel; *Haut Atlas*, MOROCCO; ca. 31°15'N, 7°47'W; reported before 1926 by L. Joleaud (1926, p. 129). 2.
- Ourika, Oued; *Haut Atlas*, MOROCCO; ca. 31°15'N, 7°38'W; reported in 1926 by P. Bédé (1927, p. 28). Observed in 1981 by G. R. Drucker (Fa et al., 1984, pp. 80, 99). Tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393). 2.
- Ouzoud, Cascades d', Oud-el-Abid gorge, Azilal district; *Southern Moyen Atlas*, MOROCCO; ca. 32°02'N, 6°47'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 97). Observed in 1981 by G. R. Drucker (Fa et al., 1984, p. 97). Reported before 1985 by G. de Turckheim (Taub, 1984a, p. 73; Fa et al., 1984, p. 97). Tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393; cf. Fa et al., 1984, p. 97). 3.
- Palestro, Gorges de, Bou Zegza; *Grande Kabylie*, ALGERIA; 36°36'N, 3°35'E; reported in 1925 and 1931 by L. Joleaud (1926, p. 129; 1933, p. 853). Reported absent before 1985 by D. M. Taub (1984a, p. 75). 50.
- Philippeville. See Stora vicinity.
- Pic des Singes National Park, Djebel Gouraya, near Bejaïa, 600 m; *Grande Kabylie*, ALGERIA; 36°46'N, 5°05'E; reported before 1527 by Leo Africanus (1896 edition, p. 948). Reported in 1925 by L. Joleaud (1926, p. 129). Observed in 1931 by L. Joleaud (1933, p. 853). Observed in 1975 by D. M. Taub (1977, p. 120; cf. Fa et al., 1984, p. 102). Blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). Tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393). 53.

- Pompeii; ITALY; 40°31'N, 14°29'E; skeletal fragments of introduced captive, radiocarbon dated 50 B.C.E.–140 C.E. (Bailey et al., 1999, p. 1413). Not mapped.
- Ras El Ma, 1800 m; *Central Moyen Atlas*, MOROCCO; 33°28'N, 5°07'W; observed 1973–1975 by D. M. Taub (1977, p. 116). 23.
- Ras Timedouine, Djebel Djurdjura; *Grande Kabylie*, ALGERIA; ca. 36°27'N, 4°14'E; observed 1982–1983 by N. Ménard (in Fa et al., 1984, p. 103). 51.
- Ras Timedouire. See Ras Timedouine.
- Rass El Ma. See Ras El Ma.
- Rhiata mountains, SW of Taza; *Eastern Moyen Atlas*, MOROCCO; ca. 34°10'N, 4°07'W; reported present before 1932 by L. Joleaud (1933, p. 852). Reported locally extinct 1973–1975 by D. M. Taub (1977, p. 115; 1984a, p. 73). 28.
- Riata. See Rhiata mountains.
- Rif (imprecise locality); *Rif*, MOROCCO; ca. 35°N, 4°W; tissue samples collected before 2006 by L. Modolo et al. (2005, p. 7393). Not mapped.
- Rond-Point des Cèdres; *Theniet el Had*, ALGERIA; 35°52'N, 1°57'E; reported present in 1954 and absent in 1974 (J. Chitty and J. P. Thomas in Taub, 1984a, p. 75). 44.
- Ruisseau des Singes. See Chiffa, Gorges de la.
- Seheb, ca. 15 km SE of Azrou, 1700 m; *Central Moyen Atlas*, MOROCCO; ca. 33°20'N, 5°05'W; observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 91). 21.
- Senoual region, 1800 m, *Central Moyen Atlas*, MOROCCO; ca. 32°58'N, 5°13'W; observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 91). 13.
- Setti Fatma. See Zaclia Sti Fatma.
- Sidichmim, Beni Hozmar; *Rif*, MOROCCO; ca. 35°30'N, 5°20'W; observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 253; cf. Fa., 1983a, p. 79). 32.
- Sidi Mguid vicinity; *Central Moyen Atlas*, MOROCCO; ca. 33°13'N, 5°16'W; reported before 1932 by L. Joleaud (1933, p. 852). Observed 1973–1975 by D. M. Taub (1977, p. 116; cf. Fa et al., 1984, p. 90). 22.
- Sidi M'Guild. See Sidi Mguid.
- Sidi Salah, Jebel, 1300 m; *Rif*, MOROCCO; 35°17'N, 5°09'W; observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 86). 34.
- Sidi Siah, at confluence of Oued Laou and Uad Talambot, *Rif*, MOROCCO; 35°17'N, 5°14'W; observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 253). 34.
- Sidi Yahia ou Youssef. See Sidi Yahya ou Youssef.
- Sidi Yahya ou Youssef, 8–10 km W of, 1900 m; *Southern Moyen Atlas*, MOROCCO; ca. 32°24'N, 5°28'W; observed 1973–1975 by D. M. Taub (1977, p. 119; cf. Fa et al., 1984, p. 96). 15.
- Sidi Yahya ou Youssef, S and W of, 1900 m; *Southern Moyen Atlas*, MOROCCO; ca. 32°24'N, 5°22'W; observed 1973–1975 by D. M. Taub (1977, p. 119; cf. Fa et al., 1984, p. 96). 15.
- Sokmane. See Aït Sokhmane forest.
- Source des Singes, Djebel Djurdjura; *Grande Kabylie*, ALGERIA; ca. 36°25'N, 4°13'E; blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). 51.
- Spain, [southern]; *Andalusia*, SPAIN; ca. 37°N, 5°W; spurious reports (I Geoffroy, 1851, p. 31; Lydekker, 1893–1894, p. 118; cf. 1916, p. 7; Forbes, 1894, p. 5; cf. Drinkwater in Kenyon, 1938, p. 112). Not mapped.
- Stora, “Oran”; probably *Skikda*, ALGERIA; probably ca. 36°54'N, 6°52'E; collector and date unknown (Napier, 1981, p. 6); BM(NH), 1 (skin only, skull inside). 60.
- Stora vicinity, W of Skikda; *Skikda*, ALGERIA; ca. 36°54'N, 6°52'E; reported present in 1925 by L. Joleaud (1926, p. 129). Population reported near extinction in 1931 by L. Joleaud (1931b, p. 154; 1933, p. 853). Population reported extinct before 1978 by D. M. Taub (1977, p. 123). 60.
- Tabarca. See Tabarqah.
- Tabarqah; *Beja*, TUNISIA; 36°57'N, 8°45'E; reported present in historic times by L. Joleaud (1931b, p. 154). 63.
- Tafechna, ca. 10 km SW of Aguelmane Azigza; *Central Moyen Atlas*, MOROCCO; ca. 32°54'N, 5°30'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 94). 13.
- Taffert, at Tine M'lilt, 1700–2000 m; *Eastern Moyen Atlas*, MOROCCO; ca. 33°45'N, 4°17'W; observed 1973–1975 by D. M. Taub (1977, pp. 111, 115). 25.
- Tagoulelt vicinity; *Southern Moyen Atlas*, MOROCCO; ca. 32°32'N, 4°48'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 96). 18.
- Taguelft region. See Asker; Azrar; Tsemair.
- Tahafourt, 4 km S of Merhraoua, 1400–1700 m; *Eastern Moyen Atlas*, MOROCCO; 33°52'N,

- 4°04'W; observed 1973–1975 by D. M. Taub (1977, pp. 111, 115; cf. Fa et al., 1984, p. 80). 27.
- Tahar Souk, N of; *Rif*, MOROCCO; ca. 34°40'N, 4°15'W; reported before 1958 to M. Ricard by Moroccan informants (Panouse, 1957, p. 28). 25.
- Takoucht, Djebel; *Petite Kabylie*, ALGERIA; 36°31'N, 5°13'E; population reported extinct before 1962 by forestry officials (Taub, 1977, p. 122; cf. Fa et al., 1984, p. 105). 54.
- Talaat Ardhouse, 1300 m; *Rif*, MOROCCO; ca. 35°16'N, 5°08'W; observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59). 34.
- Tala Guiléf. See Tala Gulief.
- Tala Gulief, Djebel Djurdjura, 1750–2300 m; *Grande Kabylie*, ALGERIA; ca. 36°29'N, 4°00'E; observed 1982–1983 by N. Ménard (in Fa et al., 1984, p. 103). Blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). 51.
- Tala Kitane, Akfadou vicinity, 900–1278 m; *Grande Kabylie*, ALGERIA; 36°41'N, 3°34'E; observed 1982–1983 by N. Ménard (in Fa et al., 1984, p. 104). 50.
- Talambot. See Sidi Siah.
- Tala Rana, Djebel Djurdjura; *Grande Kabylie*, ALGERIA; ca. 36°25'N, 4°15'E; blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). 51.
- Talassemtane, Rhomara tribal area, 2100 m; *Rif*, MOROCCO; ca. 35°09'N, 5°07'W; observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 86). Observed 1981–1982 by P. T. Mehlman (1984, p. 170). Observed Oct.–Nov. 2004 by S. S. Waters et al. (2007, p. 107). 34.
- Tamjilt, below, 1700–2000 m; *Eastern Moyen Atlas*, MOROCCO; 33°39'N, 4°00'E; observed 1973–1975 by D. M. Taub (1977, pp. 111, 115). 26.
- Taurirt Irhil, Forêt de, 500–1600 m, *Grande Kabylie*, ALGERIA; 36°41'N, 4°40'E; observed 1973–1975 by D. M. Taub (1977, p. 122; cf. Fa et al., 1984, p. 104). 52.
- Targa vicinity, Beni Ziat area; *Rif*, MOROCCO; ca. 35°24'N, 5°01'W; reported before 1932 by L. Joleaud (1933, p. 852; cf. Fa, 1983a, p. 79). 36.
- Tarhzirt. See Ouzoud, Cascades d'.
- Tasaot, Jebel, Rhomara tribal area, 1700–2000 m; *Rif*, MOROCCO; 35°14'N, 5°06'W; observed 1973–1975 by D. M. Taub (1977, p. 111). Observed before 1976 by F. Alvarez and F. Hiraldo (1975, p. 254). Observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 87; Mehlman, 1984, p. 170). 34.
- Tazaot. See Tasaot, Jebel.
- Tazaoute. See Tasaot, Jebel.
- Tazonte, Djebel. See Tasaot, Jebel.
- Tétouan vicinity; *Rif*, MOROCCO; ca. 35°34'N, 5°22'W; reported present before 1926 by L. Joleaud (1926, p. 129). Reported locally extinct before 1983 by J. E. Fa (1982, p. 48). 32.
- Theniet el Had. See Rond-Point des Cèdres.
- Tidiquin. See Tidirhine.
- Tidirhine, Jebel; *Rif*, MOROCCO; 34°51'N, 4°31'W; reported present in mid-1960s and locally extinct subsequently by J. Chitty and local forestry official (Taub, 1984a, p. 73). 39.
- Tighret forestry post, 25 km NW of Miliana; *Chiffa*, ALGERIA; ca. 36°25'N, 2°00'E; reported present in 1954–1973 and locally extinct in 1974 by J. Chitty and J. P. Thomas (Taub, 1978a, p. 249; 1984a, p. 75). 45.
- Tigounatine, Djebel Djurdjura, 1750–2300 m; *Grande Kabylie*, ALGERIA; 36°27'N, 4°08'E; observed 1973–1975 by D. M. Taub (1977, p. 120; cf. Fa et al., 1984, p. 102). Observed 1983–1984 by N. Ménard et al. (1985, p. 66). Blood samples collected before 2000 by F. von Segesser et al. (1999, p. 435). 51.
- Tiguerouguine, Plateau d'Ajdir; *Central Moyen Atlas*, MOROCCO; ca. 32°55'N, 5°25'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 94). 13.
- Tijjida, Oued. See Tilljida, Oued.
- Tikjda, Djebel Djurdjura, 1200–1900 m; *Grande Kabylie*, ALGERIA; 36°27'N, 4°08'E; observed 1983–1985 by N. Ménard et al. (Fa et al., 1984, p. 103; Ménard et al., 1986, p. 35). 51.
- Tilljeda, Oued. See Tilljida, Oued.
- Tilljida, Oued, Rhomara tribal area, 400 m; *Rif*, MOROCCO; 35°11'N, 5°06'W; observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 58; cf. Fa et al., 1984, p. 87; Mehlman, 1984, p. 170). 34.
- Tillouguit N'Aït Isha, S of; *Southern Moyen Atlas*, MOROCCO; ca. 32°02'N, 6°13'W; observed 1973–1975 by D. M. Taub (1977, p. 119; cf. Fa et al., 1984, p. 97). 5.
- Tilougguite. See Ouzoud, Cascades d'; Tillouguit N'Aït Isha.
- Tine M'lilt. See Taffert.
- Tirizene, Djebel. See Tisirene, Jebel.
- Tisirene, Jebel, above Bourçit, 1800 m; *Rif*, MOROCCO; 35°01'N, 4°55'W; observed 1973–1975 by D. M. Taub (1977, pp. 111,

- 112). Reported in 1984 by J. E. Fa et al. (1984, p. 87; cf. Fa, 1983b, p. 62). 35.
- Tisouka, Jebel, Rhomara tribal area, 2100 m; *Rif*, MOROCCO; 35°10'N, 5°13'W; observed Jul.–Sep. 1980 by J. E. Fa (1982, p. 59; cf. Fa et al., 1984, p. 87; Mehlman, 1984, p. 170). 34.
- Tissouka, Djebel. See Tisouka, Jebel.
- Tiz Ifni. See Tizi Ifri.
- Tizi Ifri (?=Tiz Ifni); *Rif*, MOROCCO; 34°51'N, 4°15'W; reported present in mid-1960s and locally extinct subsequently by J. Chitty and local forestry official (Taub, 1984a, p. 73). 40.
- Tizi M'Isly, N of; *Southern Moyen Atlas*, MOROCCO; ca. 32°28'N, 5°46'W; observed 1973–1975 by D. M. Taub (1977, p. 119). 14.
- Tizirane, Djebel. See Tisirene, Jebel.
- Tounfit, 15–20 km SSE of; *Southern Moyen Atlas*, MOROCCO; ca. 32°20'N, 5°10'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 96). 16.
- Tounfit, N and W of; *Southern Moyen Atlas*, MOROCCO; ca. 32°30'N, 5°15'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 96). 17.
- Tounfite. See Tounfit.
- Tourchte, Oued Ourika; *Haut Atlas*, MOROCCO; 31°15'N, 7°38'W; multiple reports in Jul.–Aug. 1968 received by J. M. Deag and J. H. Crook (1971, p. 186). 2.
- Tsemair, Taguelft region; *Southern Moyen Atlas*, MOROCCO; ca. 32°15'N, 6°08'W; observed 1973–1975 by D. M. Taub (1977, p. 119). Possibly locally extinct 1974–1982 (Fa et al., 1984, p. 96). 8.
- Xauen. See Chechaouene.
- Zaclia Sti Fatma, 50 km SSE of Marrakesh, ca. 1900 m; *Haut Atlas*, MOROCCO; 31°18'N, 7°47'W; collected 15 Aug. 1968 by unknown collector (Napier, 1981, p. 6; cf. Deag & Crook, 1971, p. 186); BM(NH), 1 (skull only; not seen). 2.
- Zaclia Sti Fatma, S of, Oued Ourika, 1900 m; *Haut Atlas*, MOROCCO; ca. 31°13'N, 7°42'W; observed Jul.–Aug. 1968 by J. M. Deag and J. H. Crook (1971, p. 186; cf. Napier, 1981, p. 6). 2.
- Zad region, 2300 m; *Central Moyen Atlas*, MOROCCO; ca. 33°01'N, 5°04'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 95). 20.
- Zaghwan. See Zaghwan.
- Zaghwan; *Zaghwan*, TUNISIA; 36°24'N, 10°09'E; reported present in historic times (Joleaud, 1931b, p. 154). 64.
- Zaouia de Ifrane; *Central Moyen Atlas*, MOROCCO; ca. 33°14'N, 5°25'W; observed 1973–1975 by D. M. Taub (Fa et al., 1984, p. 94). 22.
- Zarka cascade vicinity, Beni Hozmar area; *Rif*, MOROCCO; ca. 35°28'N, 5°20'W; reported before 1932 by L. Joleaud (1933, p. 852). 32.
- Ziama Mansouria, E of, Jijel, W of; *Petite Kabylie*, ALGERIA; ca. 36°40'N, 5°30'E; reported in 1931 by L. Joleaud (1933, p. 853). 56.

Appendix III. Centrum Length and Vertebral Count of Caudal Vertebrae in *Macaca sylvanus*

Specimen No.	Length (mm) of indicated caudal vertebrae					Inferred caudal vertebral count ¹
	1	2	3	4	5	
Juvenile females						
FMNH 47410	8.0	11.5	m ²	—	—	3
IRSN 9165♀	10.9	15.2 ³	—	—	—	≥3
IRSN 9071	9.6	7.8	7.1	—	—	3
ZMUZ 11602 ⁴	8.1	8.1	11.9	1.4	—	4
ZSBS 1959/4	10.3	17.7 ³	—	—	—	≥3
Juvenile males						
IRSN 9165♂	10.5	7.5 ³	—	—	—	3
IRSN 16701	10.5	10.9	10.8	—	—	3
IRSN 16696	7.8	8.1	8.0	—	—	3
NMS 1552	9.7	10.3	7.5	—	—	3
ZMB 8264	8.5	10.5	9.2	—	—	3
Adult females						
FMNH 47409	11.1	>5.9 ⁵	—	—	—	≥2
IRSN 9295	10.9	10.4	5.3	m ²	—	≥4
IRSN 17073	11.1	8.5	7.2	—	—	3
IRSN 17058	9.9	8.7	6.3	—	—	3
IRSN 16871	10.8	11.7	14.2 ³	—	—	≥4
RMNH 9c	11.9	13.1	11.4	13.1	3.0	5
USNM 476786	10.0	11.7	4.0	—	—	3
ZMB 16492	12.0	18.9 ³	—	—	—	≥3
Means ⁶	10.96	10.68	6.84	13.1	3.0	—
Adult males						
FMNH 47398	16.2	21.3 ³	—	—	—	≥3
MCZ 7098	13.1	11.3	10.3	—	—	3
RMNH 7a	13.2	18.9 ³	—	—	—	≥3
USNM 476785	12.7	8.9	m ²	—	—	≥3
ZMB 8271	11.3	11.9	6.1	—	—	3
Means ⁶	13.30	10.70	8.20	—	—	—

¹ Supplementary counts from literature (age, sex, and/or measurements of specimens usually not specified): Vrolik, 1841, p. 10—2 caudal vertebrae; Mivart, 1865, p. 583—3, 4, and 4 caudal vertebrae; Giebel and Leche, 1874—1900, p. 241—4 caudal vertebrae; Didier and Rode, 1936, p. 3—generally 2 caudal vertebrae; A. W. Todd in Schultz and Straus, 1945, p. 613—2 caudal vertebrae.

² Terminal vertebra/vertebrae missing.

³ Cd2 and Cd3 fused; values excluded from calculation of means.

⁴ Sex uncertain.

⁵ Vertebra broken.

⁶ For adult specimens only.

Appendix IV. Group Size and Adult Sex Composition in *Macaca sylvanus* Populations

Sample area	No. of groups	Group size			Adult composition			References ¹
		Mean	Mini- mum	Maxi- mum	Males	Fe-males	M/F ratio	
Morocco: Moyen Atlas								
Afennourir	9	37.8	—	—	—	—	1.21	1
Aïn Kahla	1	39	—	—	7	9	0.78	2
Aïn Kahla	16	24.1	12	39	66	94	0.70	3
Aïn Kahla	1	35	—	—	—	—	—	4
Bou Jirirh	1	40	—	—	—	—	—	5
Cèdre Gouraud ²	3	23.7	—	—	—	—	0.96	1
Oued-el-Abid	1	18	—	—	3	5	0.60	6
Sidi Mguid	1	15	—	—	—	—	—	7
Regional summary	33	28.6	12	39	76	108	0.70 ³	—
Morocco: Rif								
Anjera: Moussa, Jebel ⁴	1	12	—	—	1	2	0.50	8
Beni Hessane: Bouhassim ⁴	5	13.6	8	27	15	11	1.36	8
Beni Zaid: Kelti, Jebel	1	12	—	—	3	2	1.50	8
Beni Zaid: Sidi Salah, Jebel	1	14	—	—	2	3	0.67	8
Beni Zaid: Talaat Ardhouse	1	10	—	—	2	4	0.50	8
Rhomara: Adelma, Oued	2	11	10	12	6	6	1.00	8
Rhomara: Lakraa, Jebel	4	16.8	12	28	11	11	1.00	8
Rhomara: Lakraa, Jebel	2	27.5	25	30	18	9	2.00	9
Rhomara: Talasemtane ⁴	1	27	—	—	4	4	1.00	8
Rhomara: Talasemtane	6	27.0	12	59	29 ⁵	40	0.72	10
Rhomara: Tazoute, Jebel	1	19	—	—	4	4	1.00	8
Rhomara: Tisouka, Jebel	2	13.5	7	20	5	5	1.00	8
Regional summary	27	18.3	7	59	100	101	0.99	—
Algeria: Grande Kabylie								
Akfadou ⁶	1	53	—	—	—	—	1.00	11
Djurdjura: rocky mountains ⁷	4	45.2	36	58	—	—	0.89	12
Djurdjura: Tigounatine ⁸	1	88	—	—	—	—	1.00	11
Djurdjura: Tikjda ⁹	2	40.0	36	44	~14	~17	~0.82	13
Regional summary	8	50.2	36	88	~14	~17	~0.82	—
Composite	68	27.1	7	88	~190	~226	~0.84	—

¹ Key to references: 1. Machairas et al., 2003, p. 189; Camperio Ciani and Machairas, 2003, p. 125. 2. Taub, 1980b, p. 290. 3. Deag, 1984, p. 119. 4. Ménard and Qarro, 1999, p. 124. 5. Drucker, 1984, p. 139. 6. Fa, 1986b, p. 32. 7. Hammerschmidt et al., 1994, p. 279. 8. Fa, 1982, p. 59. 9. Whiten and Rumsey, 1974, p. 423. 10. Mehlman, 1989, p. 272. 11. Ménard and Vallet, 1993b, pp. 105, 108. 12. Ménard et al., 1990, p. 169. 13. Ménard et al., 1986, p. 37.

² Alternate locality name: Gouroud.

³ Excludes undocumented Afennourir and Cèdre Gouraud ratios.

⁴ New censuses of these groups were conducted in 2004 (Waters et al., 2007, p. 107).

⁵ Focal group apparently includes 11 (not 12) adult males.

⁶ 1990 census; in 1983 group size was 33.

⁷ Group size in this area is unstable—subject to subgroup fusion and fission (cf. Ménard et al., 1985, p. 72; Menard, 2002, pp. 96, 98).

⁸ 1988 census; in 1983 group size was 38, and in 1989 the group subdivided into three daughter groups.

⁹ December 1985 census; excludes data for group T1 (=Tigounatine group).

Appendix V: Coordinates, Geological Age, and Reported Identification of Circum-Mediterranean Macaque Fossils¹

Fossil localities	Coordinates (approximate)	Epoch	Remarks ²	References ³
ALBANIA Gajtan	42°03'N 19°34'E	Pleistocene	Cf. <i>M. sylvanus pliocena</i> ; Mid-Pleist.	1
ALGERIA Afalou bou Rummel	36°30'N 5°20'E	Pleistocene	<i>M. cf. sylvanus</i> ; Late Pleist.	2
Menacer (Marceau)	36°30'N 5°00'E	Miocene	? <i>Macaca</i> sp.; probably Late Mio., ca. 7 Ma	2, 3, 4, 5
Tamar Hat	36°30'N 5°20'E	Pleistocene	<i>M. cf. sylvanus</i> ; Late Pleist.	2, 3
Taya, Djebel, grottos ⁴	36°30'N 7°08'E	Pleistocene	<i>M. sylvanus</i>	6
Traras, Monts des, Nedroma	35°02'N 1°40'W	Pleistocene	<i>M. sylvanus</i> ; Mid- or Late Pleist., 0.2 Ma	4, 5, 6, 7, 8
AUSTRIA Deutsch-Altenburg ⁵	48°10'N 16°55'E	Pleistocene	<i>M. sylvanus</i> ; Early Pleist.	9
Kugelsteinhöhle, 22 km N of Graz	47°13'N 15°20'E	Pleistocene	<i>M. sylvanus</i> group; Late Pleist., probably Eemian	10
CROATIA Sandalja	45°05'N 14°00'E	Pliocene	<i>M. cf. sylvanus</i> ; Mid-Villafranchian	2, 3, 4, 11
CZECH REPUBLIC Zlatý Kun, Cave C718	49°35'N 14°45'E	Pleistocene	<i>M. sylvanus</i> ; Mid-Pleist.	2, 3, 4
EGYPT Wadi Natrun	30°25'N 30°13'E	Miocene	<i>M. libyca</i> ; Late Mio., ca. 6 Ma	2, 3, 4, 5
ENGLAND, U.K. Grays Thurrock	51°29'N 0°20'E	Pleistocene	<i>Macaca</i> sp.; probably late Middle Pleist.	2, 3, 4, 5, 11
Hoxne	52°21'N 1°12'E	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	12
Swanscombe (Barnfield Pit)	51°26'N 0°18'E	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	11
West Runton	52°45'N 1°05'E	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	2, 3, 4, 11
FRANCE Balaruc-2	43°35'N 3°45'E	Pliocene	<i>M. cf. sylvanus</i> ; Early Villafranchian	2, 4, 11
Caune de l'Arago	42°33'N 3°00'E	Pleistocene	<i>M. sylvanus</i> ; Mid-Pleist, 0.23 Ma	13
Montpellier	43°38'N 3°53'E	Pliocene	<i>M. cf. sylvanus</i> ; Early/Mid-Ruscinian	2, 3, 4, 5, 11
Montsaunès	43°20'N 0°55'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist.	2, 3, 4, 11
Orgnac-3	43°50'N 5°00'E	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	3, 11
Saint-Estève-Janson	43°30'N 5°40'E	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	2, 3, 4, 11
Saint-Vallier	45°10'N 4°50'E	Pliocene	<i>M. cf. sylvanus</i> ; Mid-Villafranchian	2, 3, 4, 11
Senèze	44°30'N 3°00'E	Pleistocene	<i>M. cf. sylvanus</i> ; Late Villafranchian	2, 3, 4, 11

Appendix V: Continued.

Fossil localities	Coordinates (approximate)	Epoch	Remarks ²	References ³
Vallonet	43°45'N 7°40'E	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	2, 3, 4, 11
GEORGIA				
Kudaro-1	42°30'N 43°40'E	Pleistocene	<i>Macaca</i> sp. ⁶ ; interglacial, ca. 0.350 Ma	2, 3, 4, 5, 14
GERMANY				
Gundersheim	49°35'N 10°45'E	Pliocene	<i>M. cf. sylvanus</i> ; Early Villafranchian	2, 3, 4, 11
Heppenloch	48°15'N 9°25'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist.	2, 3, 4, 11
Hohensülzen	50°00'N 8°15'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist.	3, 4, 11
Hunas	49°30'N 11°32'E	Pleistocene	cf. <i>M. sylvanus pliocena</i> ; Mid- Pleist.	1
Mosbach-2	49°21'N 9°09'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist.	2, 3, 4, 11
Untermassfeld, 2 km S of Meiningen	50°33'N 10°25'E	Pleistocene	<i>M. sylvanus</i> ; late Early Pleist., 1.07 Ma	15
Voigtstedt	50°40'N 11°40'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist.	2, 3, 4, 11
GREECE				
Tourkobounja (Athens)	38°00'N 23°40'E	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	11
HUNGARY				
Beremend-4	45°45'N 18°25'E	Pliocene	<i>M. sylvanus</i> ; Early Villafranchian	2, 3, 4
Csarnota-2	45°45'N 18°25'E	Pliocene	<i>M. sylvanus</i> ; Late Ruscianian	2, 3, 4, 5
Somssichhegy 2	45°52'N 18°26'E	Pleistocene	cf. <i>M. sylvanus pliocena</i> ; Mid- Pleist.	1
ISRAEL				
Ubeidiya	32°05'N 36°05'E	Pleistocene	<i>M. sylvanus</i> ; Mid-Pleist.	2, 3, 4
ITALY				
Bristie II (Carso Triestino)	45°40'N 13°45'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid.-Pleist.	11
Cavo Pompei	41°40'N 13°20'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid.-Pleist.	11
Figari, Capo (Sardinia)	41°00'N 9°35'E	Pleistocene	<i>M. majori</i> ; Early to Mid-Pleist.	5, 16
Fontana Ranuccio	41°45'N 13°10'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist., 0.458 Ma	11
Fornace RDB, Villafranca d'Asti	44°54'N 8°12'E	Pliocene	<i>M. cf. sylvanus</i> ; Early Villafranchian	2, 3, 4, 5, 17
Grotta degli Orsi Volanti	42°14'N 14°09'E	Pleistocene	<i>M. cf. sylvanus</i> ; Late Pleist., probably Eemian	18
Monte Peglia	42°45'N 12°10'E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist., Cromerian G	11
Monte Sacro (="Rome")	41°56'N 12°32'E	Pleistocene	<i>M. cf. sylvanus</i> ; Early Pleist.?	11
Mugello	43°50'N 10°55'E	Pliocene	<i>M. cf. sylvanus</i> ; Mid- Villafranchian	2, 3, 4, 11
Orciano	43°28'N 10°30'E	Pliocene	<i>M. cf. sylvanus</i> ; Late Plio.	11
Pietrafitta	42°55'N 12°20'E	Pleistocene	<i>M. cf. sylvanus</i> ; Early Pleist.	19
Pofi	41°34'N 13°25'E	Pleistocene	cf. <i>M. sylvanus pliocena</i> ; Mid- Pleist.	1

Appendix V: Continued.

Fossil localities	Coordinates (approximate)	Epoch	Remarks ²	References ³
San Vito di Leguzzano	45° 45' N 11° 40' E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist.	2, 3, 4, 11
Torre in Pietra	41° 55' N 12° 30' E	Pleistocene	<i>M. cf. sylvanus</i> ; Late Pleist., probably Eemian	11
Tuttavista, Monte	40° 22' N 9° 41' E	Pleistocene	<i>M. cf. majori</i> ; probably Early Pleistocene	20
Val d'Arno, Upper	43° 45' N 11° 10' E	Pleistocene	<i>M. cf. sylvanus</i> ; Late Villafranchian	2, 3, 4, 5, 11
Valdemino (Borgio Verezzi)	44° 10' N 8° 20' E	Pleistocene	<i>M. sylvanus</i> ; Mid-Pleist.	3, 5, 11
Zoppega II, Soave	45° 45' N 11° 45' E	Pleistocene	<i>M. cf. sylvanus</i> ; Mid-Pleist., Cromerian G	11
LIBYA				
Sahabi area	30° 00' N 21° 00' E	Miocene?	cf. <i>Macaca</i> ; Mio.-Plio.	8, 21
MOROCCO				
Chrafate	33° 50' N 5° 05' W	Pleistocene	<i>M. sylvanus</i> ; Late Pleist.	22
Ez Zarka	34° 25' N 5° 45' W	Pleistocene	<i>M. sylvanus</i> ; Late Pleist.	22
NETHERLANDS				
Steyl ⁷	51° 20' N 6° 08' E	Pleistocene	<i>M. cf. sylvanus</i> ; age uncertain	11
Tegelen ⁷	51° 19' N 6° 09' E	Pleistocene	<i>M. cf. sylvanus</i> ; Late Villafranchian	2, 3, 4, 11
ROMANIA				
Betfia-2 [also infillings 9 and 13]	46° 05' N 22° 50' E	Pleistocene	<i>M. sylvanus</i> ; Mid-Pleist.	2, 3, 4
SLOVAKIA				
Gombasek	48° 50' N 21° 35' E	Pleistocene	<i>M. sylvanus</i> ; Mid-Pleist.	2, 3, 4
Vcelare 2	48° 35' N 20° 48' E	Pleistocene	cf. <i>M. sylvanus pliocena</i> ; Mid- Pleist.	1
SPAIN				
Almenara-M (=Casablanca-M)	39° 44' N 0° 13' W	Miocene	<i>M. cf. sylvanus</i> ; Late Mio.	23, 24
Ambrona	40° 50' N 2° 25' W	Pleistocene	<i>Macaca</i> sp.; Mid-Pleist.	2, 3, 4, 11
Cova Bonica	41° 25' N 2° 15' E	Pliocene	<i>M. cf. sylvanus</i> ; Early Villafranchian	2, 3, 4, 11
Cova Negra	38° 53' N 0° 08' W	Pleistocene	<i>Macaca</i> sp.; Late Pleist, beginning last glaciation ⁸	11
La Puebla de Valverde	40° 13' N 0° 56' W	Pliocene	<i>M. cf. sylvanus</i> ; Mid- Villafranchian	2, 3, 4, 11
Solano del Zamborino	36° 50' N 2° 50' W	Pleistocene	<i>Macaca</i> sp.; Late Pleist, probably Eemian	11
TUNISIA				
Aïn Brimba	36° 45' N 8° 30' E	Pliocene	<i>M. sylvanus</i> ; Mid-Villafranchian, 3 Ma	2, 3, 4, 5, 8
Ichkeul, Garaet (lake)	33° 40' N 8° 50' E	Pliocene	<i>M. sylvanus</i> ; Ruscinian, 3 Ma	2, 3, 4, 5, 8, 25

¹ See Fig. 9.

² Fossil identifications indicated in this column are those specified in the cited references; Ma = million years ago.

³ Key to references: 1. E. Delson, pers. comm., 11 Jan. 2007. 2. Delson (1974, p. 133). 3. Szalay and Delson (1979, pp. 355, 356). 4. Delson (1973, p. 140). 5. Delson (1980a, pp. 16–19). 6. Joleaud (1926, p. 129). 7. Pomel (1892, p. 157; 1896, p. 11). 8. Geraads (1987, pp. 22, 25). 9. Fladerer (1987, p. 2). 10. Fladerer (1989, p. 25; 1991,

Appendix V: *Continued.*

p. 272). 11. Ardito and Mottura (1987, pp. 34–40). 12. Singer et al. (1982, p. 144). 13. Moigne et al. (2006, p. 793). 14. Maschenko and Baryshnikov (2002, p. 411). 15. Kahlke and Gaudzinski (2005, pp. 1208, 1212, 1213). 16. Rook and O'Higgins (2005, p. 169). 17. Rook et al. (2001, p. 188). 18. Mazza et al. (2005, p. 212). 19. Gentili et al. (1998, p. 683). 20. Rook et al. (2003, p. 18). 21. de Heinzelin and El-Arnauti (1987, p. 17); Meikle (1987, p. 126). 22. Ouahbi et al. (2001, p. 641). 23. Köhler et al. (2000, p. 450). 24. Eronen and Rook (2004, p. 327). 25. Delson (1980b, p. 126).

⁴ Hammam Meskoutine vicinity.

⁵ Ca. 50 km SE of Vienna.

⁶ Delson (1973, p. 140) and Szalay and Delson (1979, p. 356) regarded these fossils as closely related to *M. sylvanus*; Maschenko and Baryshnikov (2002, p. 411) regarded them as more closely related to Asian macaques.

⁷ Possibly two names for the same locality.

⁸ Probably <0.100 Ma (E. Delson, pers. commun., 1 Jan. 2007).

Note Added in Proof

For further discussion relevant to dessication of the Mediterranean Sea (see above, Evolution and Dispersal), consult the following:

- ROUCHY, J. M., J.-P. SUC, J. FERRANDINI, AND M. FERRANDINI 2006. Editorial: The Messinian Salinity Crisis revisited. *Sedimentary Geology*, **188-189**: 1-8.
- SUC, J.-P., J. M. ROUCHY, M. FERRANDINI, AND J. FERRANDINI. 2007. Editorial: The Messinian Salinity Crisis revisited. [bis]. *Geobios*, **40**: 231-232.

Field Museum of Natural History
1400 South Lake Shore Drive
Chicago, Illinois 60605-2496
Telephone: (312) 665-7055