

Chapter 2

Fossil Macaques, Phyletic Relationships and a Scenario of Deployment

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INTRODUCTION

The macaques, genus *Macaca*, comprise all of the living cercopithecine Old World monkeys of Eurasia and northern Africa. Today, there are between 13 and 19 species which may be arranged in four or five larger units (species groups or perhaps subgenera), as discussed especially by Fooden (1976 and this volume) and below. The modern zoogeographic pattern is by no means typical for all of the Pleistocene, as macaques have inhabited Europe for most of the past five million years, and one or two large-bodied highly terrestrial relatives of *Macaca* (*Procynocephalus* in Asia and *Paradolichopithecus* in Europe) are also known from the earlier Pleistocene and Pliocene. All three genera may be classified as the subtribe Macacina, in the tribe Papionini of the subfamily Cercopithecinae¹. After a brief review of some aspects of skeletal morphology, this chapter will concentrate on the distribution and relationships of past and present species of macaques.

MORPHOLOGY

In many ways, *Macaca* is a conservative genus, retaining numerous features which characterized the early cercopithecines, as well as they can be recon-

¹ In addition to specifically cited publications, Szalay and Delson (1979) provide detailed information on skeletal morphology, fossils, distribution, adaptation and phylogeny of macaques and other primates mentioned here.

structed. Delson (1975a) considered the basic adaptations of the Cercopithecidae and its subtaxa, following Napier's (1970) suggestion that the Old World monkey "bilophodont" dentition originated as a response to a habitat in which the ability to eat leaves when fruit was less plentiful may have been selectively advantageous. It is clear that the cheek teeth of colobines (with their derived deep lingual notches and short trigonids on lowers, and overall greater crown relief) are even better adapted to the processing of leaves than those of cercopithecines (see also Walker and Murray, 1975; Kay, 1978), which lends credence to Delson's view that the latter represent the ancestral condition for the family.

The cheek teeth of macaques (Figs. 2-1 and 2-2) were used by Delson as a model for those of early monkeys, as they present neither the increased lateral "flare" of some mangabeys and baboons, nor the reduced flare and loss of M_3 hypoconulid of the tribe Cercopithecini. On the other hand, macaques share with other papionins relatively enlarged incisors and reduced lingual enamel on lowers. In this area of the dentition, the colobine pattern of small incisors with "conical" I^2 and fully enameled lowers was probably ancestral for cercopithecids, although macaques are less "specialized" than some baboons and mangabeys.

The cranium of *Macaca* (Figs. 2-3 and 2-4) is also conservative among cercopithecines, lacking facial fossae or great elongation, but presenting such typical features of the subfamily as a vomerine contribution to the medial orbit wall, lacrimal fossa completely within the lacrimal bone, narrow interorbital area and high, narrow choanae. Modern macaques are mostly arboreal to semiterrestrial animals, and their skeleton reflects this behavior pattern both in proportions and morphology. The smaller macaques probably are rather similar in size, proportions and joint morphology to the earliest cercopithecines, which may have separated from the ancestral colobines about 15 million years ago (MYA).

PALEONTOLOGY

Miocene Papionin Diversification

Little is known of the earliest stages of cercopithecine radiation, but Delson (1975a, b) has suggested that by about 10 MYA the ancestral, semiterrestrial papionins had diverged from early cercopithecines, which entered the higher canopy to compete with the arboreal colobines. Other, more terrestrial colobines had by this time entered Eurasia. Two sets of probably Late Miocene (11-5 MYA) fossil monkeys are known which may relate to the origin of the macaques, although both consist of dental remains only, and as has been said, the teeth of *Macaca* are conservative ("primitive") within the Papionini. A single M_3 was reported by Hooijer (1963) from Ongoliba, Zaire, in a horizon

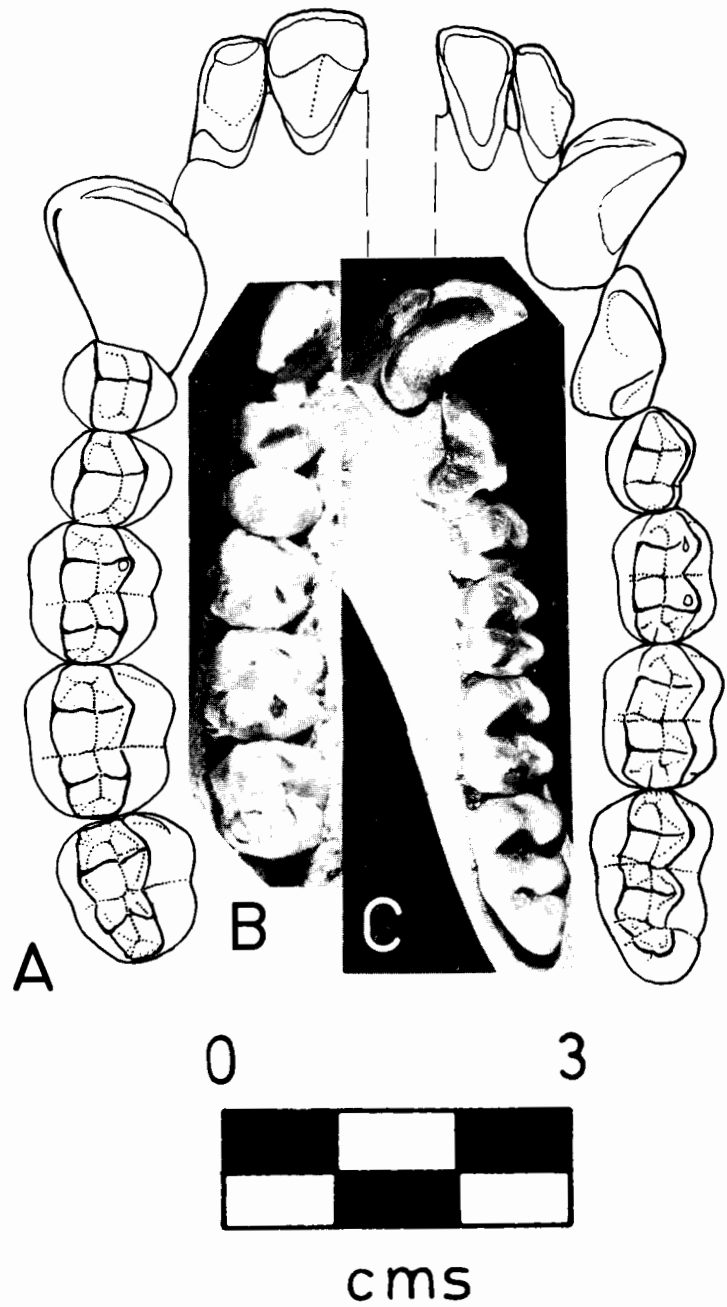


Fig. 2-1. Occlusal views of macaque dentition. A: *M. thibetana*, modern, drawing of male right, upper (to left) and lower (to right) I1-M3; B: *M. anderssoni*, Honan, China, right C'-M³ of male face (see fig. 2-3B, E); C: *M. sylvanus florentina*, Upper Val d'Arno, Italy, right C1-M3, male.

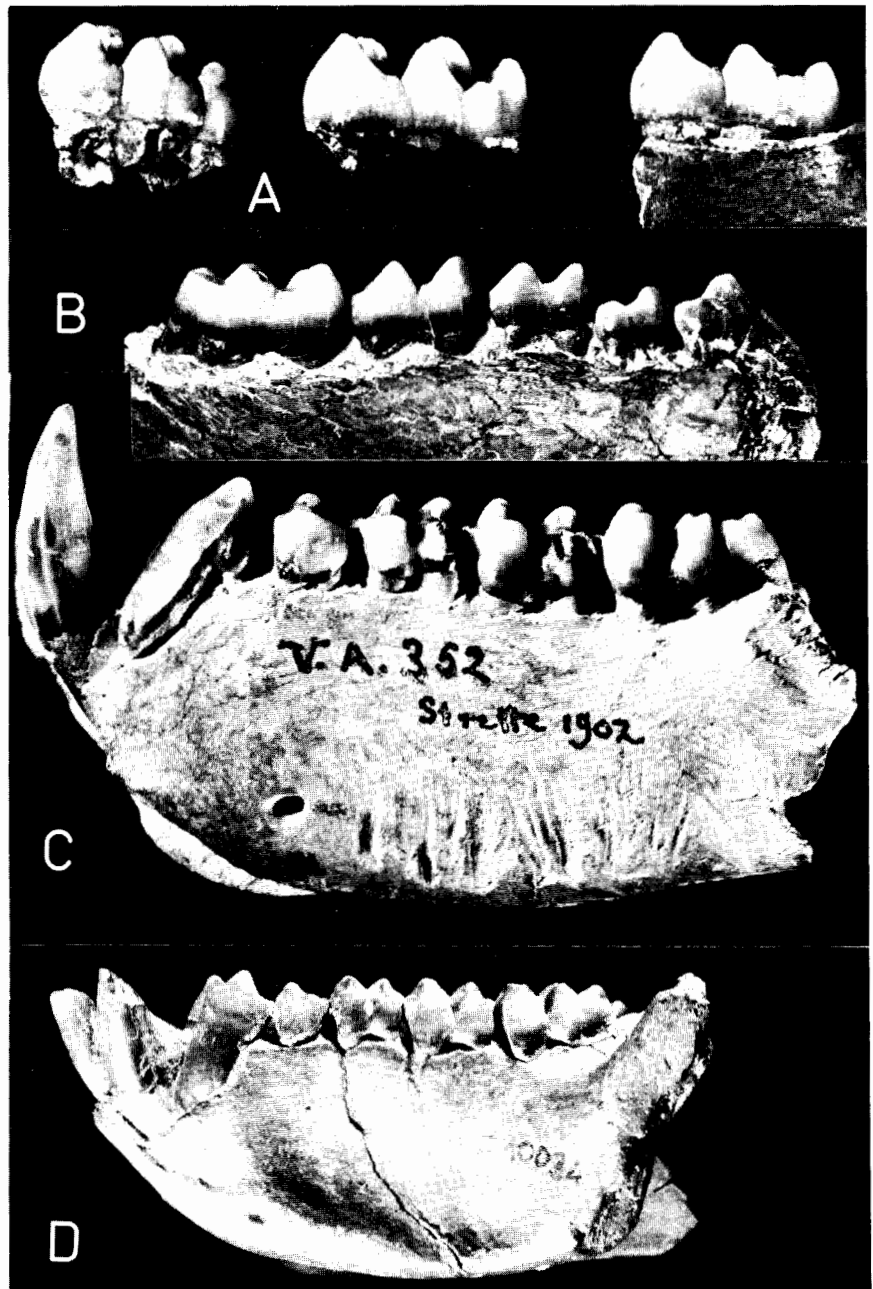


Fig. 2-2. Side views of macaque lower teeth and jaws. A: ?*Macaca* sp., Marceau, Algeria, lingual view of three right M_1 (indicating morphology and size range; B, C, D: *M. sylvanus florentina*, Upper Val d'Arno, Italy, lingual view of male left P_3 - M_3 , left lateral views of two male mandibles with C_1 - M_3 . Note lack of mandibular corpus fossa in C, presence in D (holotype). Not to same scales.

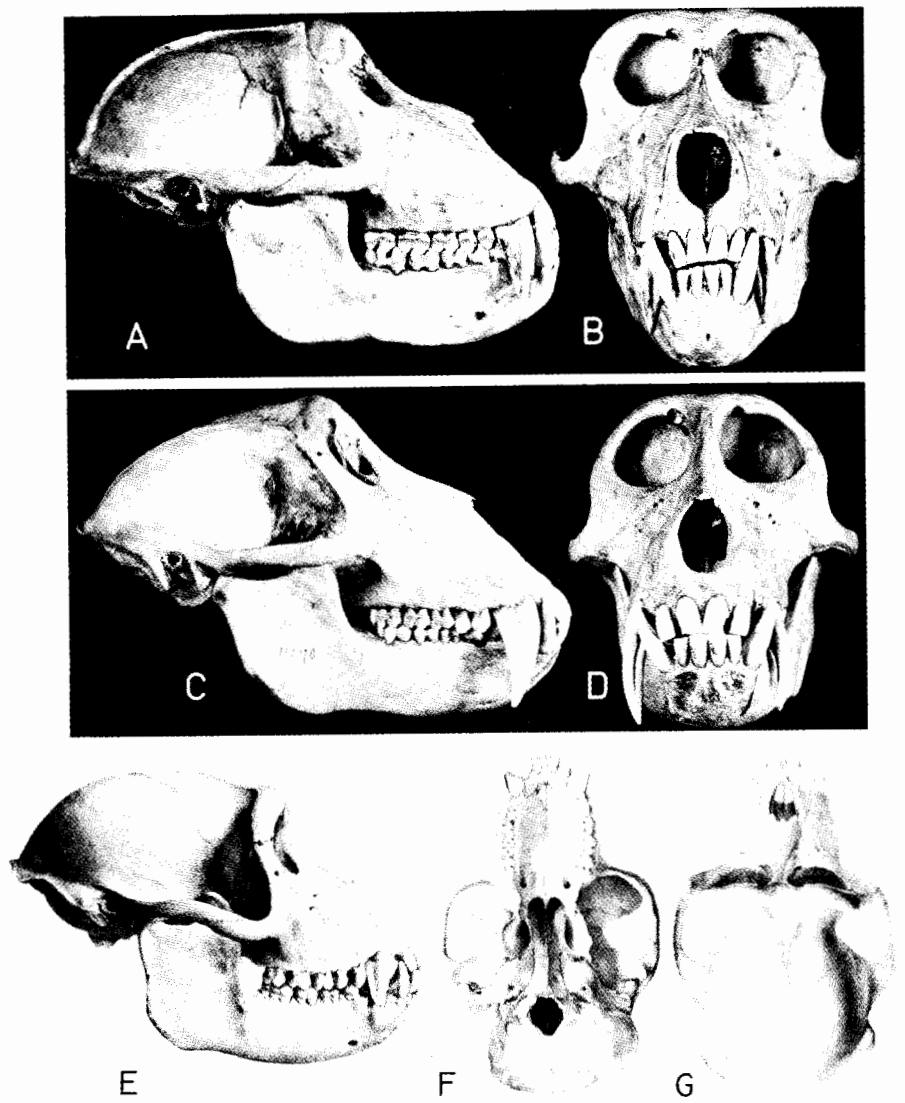


Fig. 2-3. Crania of modern macaque species. A, B: *M. thibetana*, right lateral and frontal views (from Elliot, 1913); C, D: *M. nemestrina*, right lateral and frontal views (from Elliot, 1913); E, F, G: *M. arctoides*, right lateral, basal and dorsal views (from de Blainville, 1839).

which is probably Late Miocene in age. Originally identified as “Cf. *Mesopithecus* cq. *Macaca*”, it is clearly of cercopithecine rather than colobine morphology, but is not readily allocated beyond the tribe Papionini. From the

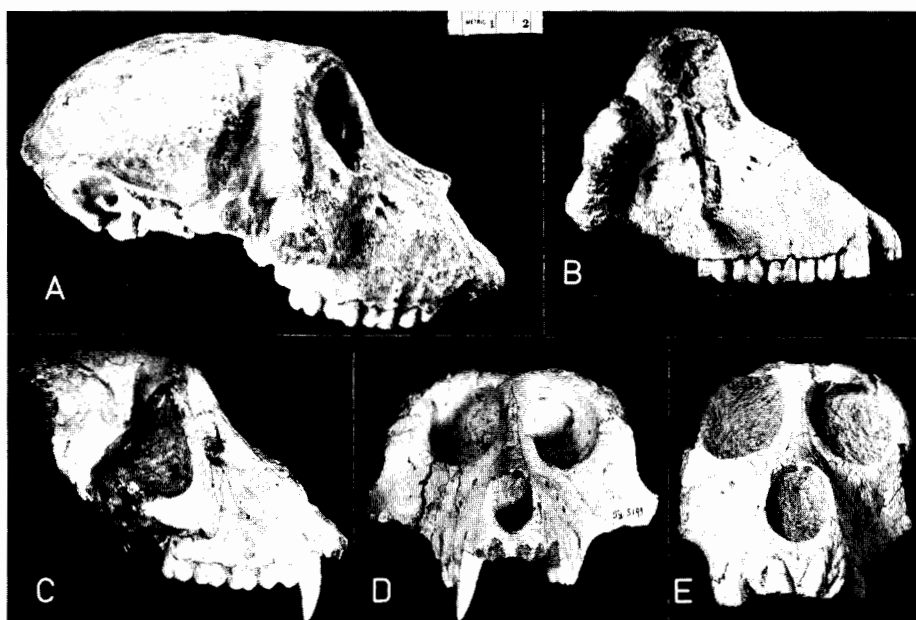


Fig. 2-4. Crania of fossil macaques. A: *M. anderssoni* (= "*robusta*"), Choukoutien, China, male cranium (cast) in right lateral view; B, E: *M. anderssoni*, Honan China, male face in right lateral and frontal views; C, D: *M. ?sylvanus majori*, Capo Figari, Sardinia, male face in right lateral and frontal views.

probably later Turolian (ca. 7 MYA) locality of Marceau, Algeria, Arambourg (1959) reported a number of isolated cercopithecoid teeth which he named *Macaca flandrini*. The type and several other specimens are colobine, from a taxon which Delson (1975a) has provisionally called *?Colobus flandrini*, using the modern term as a "form-genus" for African colobines. In the same way, the majority of the Marceau teeth (about 40) can be termed *?Macaca* sp. It is possible that more than one species is represented, as there is a wide range of size present (e.g., in M_3 , see Fig. 2-2A), but my detailed study of the material is not yet completed. The Ongoliba specimen is similar in form to those from Marceau, and the two populations might represent what Delson (1975b) has postulated to have been a wide-ranging, possibly polytypic species of early papionin present in much of Africa in the Late Miocene.

At the end of the Miocene, the Mediterranean almost completely dried up as a result of tectonic movements, and this desiccation might have aggravated the general trend toward aridity seen in southern Europe earlier in the Late Miocene, eventually leading to the formation of a semidesertic barrier across the Sahara (see extended discussion and references in Delson, 1975b). Such a

barrier might have led to the differentiation of the Papionini into the three known groups (subtribes): *Theropithecus* in wet lowlands; *Papio*, *Cercocebus* and extinct allies in more forested regions, eventually invading the plains; and *Macaca* to the north, in a variety of habitats. The earliest known papionins (other than *Theropithecus*) south of the Sahara are nearly impossible to allocate generically without cranial material, and the distinctive crania of the conservative *Parapapio* are in many ways similar to those of *Macaca*, lacking the steep anteorbital drop of *Papio* and the infraorbital and mandibular-corpus fossae of modern African papionins.

North African and European Fossil Macaques

The fossil macaques of the circum-Mediterranean region have been given about a dozen nominally distinct species designations, but in fact only a few, if any, are significantly distinguishable morphologically from the living *M. sylvanus*, let alone from each other. It seems probable at present that almost all of this Mediterranean record reflects the sampling of a single evolving lineage, with no major cladogenesis having taken place. If that is indeed the case, it is biologically most meaningful to designate the various taxa accepted here as subspecies, rather than full species, thus not implying more than genetically controlled fluctuation in size or proportion about an evolutionary mean. Only cranial or perhaps postcranial remains could clarify this point, as the dentition of macaques (and all other papionins) is of course highly stereotyped, but such fossils are rare. Revision is currently under way, but a provisional scheme may recognize six temporo-geographic forms, most tentatively ranked as subspecies of *M. sylvanus*.

The oldest of these is *Macaca libyca* (Stromer, 1920), represented only by a collection of dental remains, some in partial jaws, from the Late Miocene (ca. 6 MYA) locality of Wadi Natrun, in northern Egypt. As are almost all the European and north African fossils, these teeth are within the size range of *M. sylvanus* and may be referred to *Macaca* on the basis of geography and the (ancestral) condition of absence of mandibular corpus fossae on one well-preserved and several poorly preserved specimens. This taxon *may* predate the division of the genus into Asian and Mediterranean lineages, and thus is recognized as a full species. No facial regions are preserved, and in any event, it would be most difficult to distinguish a macaque of this age from the hypothetical common ancestor of the Papionini.

More interesting, if equally little-known, is the first macaque from Europe, probably the oldest cercopithecine outside Africa. *Macaca sylvanus prisca* (Gervais, 1859) is a slightly smaller form than *M. libyca*, known from a number of localities in southern Europe dating from the Ruscinian (5–4 MYA) and perhaps the early Villafranchian (4–3 MYA) mammal ages. The type locality

is Montpellier, in southern France, where several teeth and partial jaws (see Fig. 2-5F) are found associated with the large terrestrial colobine *Dolichopithecus ruscinensis* and the smaller, perhaps more arboreal *Mesopithecus monspessulanus* in a moist forested habitat. A juvenile mandible of similar age from Hungary was named *M. praeinus* by Kormos (1914), but it is probably referable to *M. s. prisca*. Additional fragmentary dental remains are known from definite or probable early Villafranchian local faunas in Italy, France, Hungary, Spain and Germany; these may also be tentatively referred to *M. s. prisca* as they appear somewhat smaller than the later Villafranchian *M. s. florentina*. These early specimens are most important in documenting the first extension of the cercopithecines out of Africa, probably by a crossing of, or circuit around, the Mediterranean during its desiccated phase at the end of the Miocene (see Azzaroli, 1975; Delson, 1975b).

A roughly contemporaneous but morphologically distinct population is known only from the cave breccia at Capo Figari, Sardinia, previously thought to be of "postglacial" age. From here come over 100 specimens, mostly dental, but including several partial crania and numerous postcranial elements (see Figs. 2-4C,D; 2-5A,D). Azzaroli (1946) described a few of these fossils as the "dwarf" species *M. majori*, named after the excavator Forsyth Major; it is here recognized tentatively as another subspecies of *M. sylvanus*. Preliminary comparisons suggest dental size differences from living *M. s. sylvanus* on the order of 5–10 percent (even less from *M. s. prisca*), statistically different at the 95 percent confidence level in most cases, but not as extreme as might be implied by the term dwarf (compared to other Pleistocene insular mammals). Moreover, the cheek teeth appear a bit more inflated or "puffy" than those of either *M. s. sylvanus* or *M. s. prisca*. Further studies of cranial and joint morphology may reveal additional diagnostic features to support a provisional suggestion that this is the most distinctive of the European macaque populations, potentially meriting status as a distinct species.

Seven localities or "fields" have yielded macaque fossils of middle and late Villafranchian age (later Pliocene, ca. 3–1.6 MYA); no material is definitively known from the Early Pleistocene, 1.6–1 MYA. The largest collection of remains, including some half-dozen mandibles, an equal number of partial tooththrows or isolated teeth, and one partial ulna, derives from the Montevarchi Group of the Upper Val d'Arno, upstream of Florence, Italy. This unit spans a long time, perhaps the last 0.5 MY of the late Villafranchian, and many localities have yielded individual specimens. The first (and still most complete) specimen found was named *Macaca florentina* (Cocchi, 1872), which can be employed subspecifically for all populations of this age. These other samples are known mostly by isolated specimens from Spain, France, the Netherlands, Italy (earlier than Val d'Arno) and Yugoslavia. The Val d'Arno specimens are variable in both size and morphology, but essentially comparable to *M. s.*

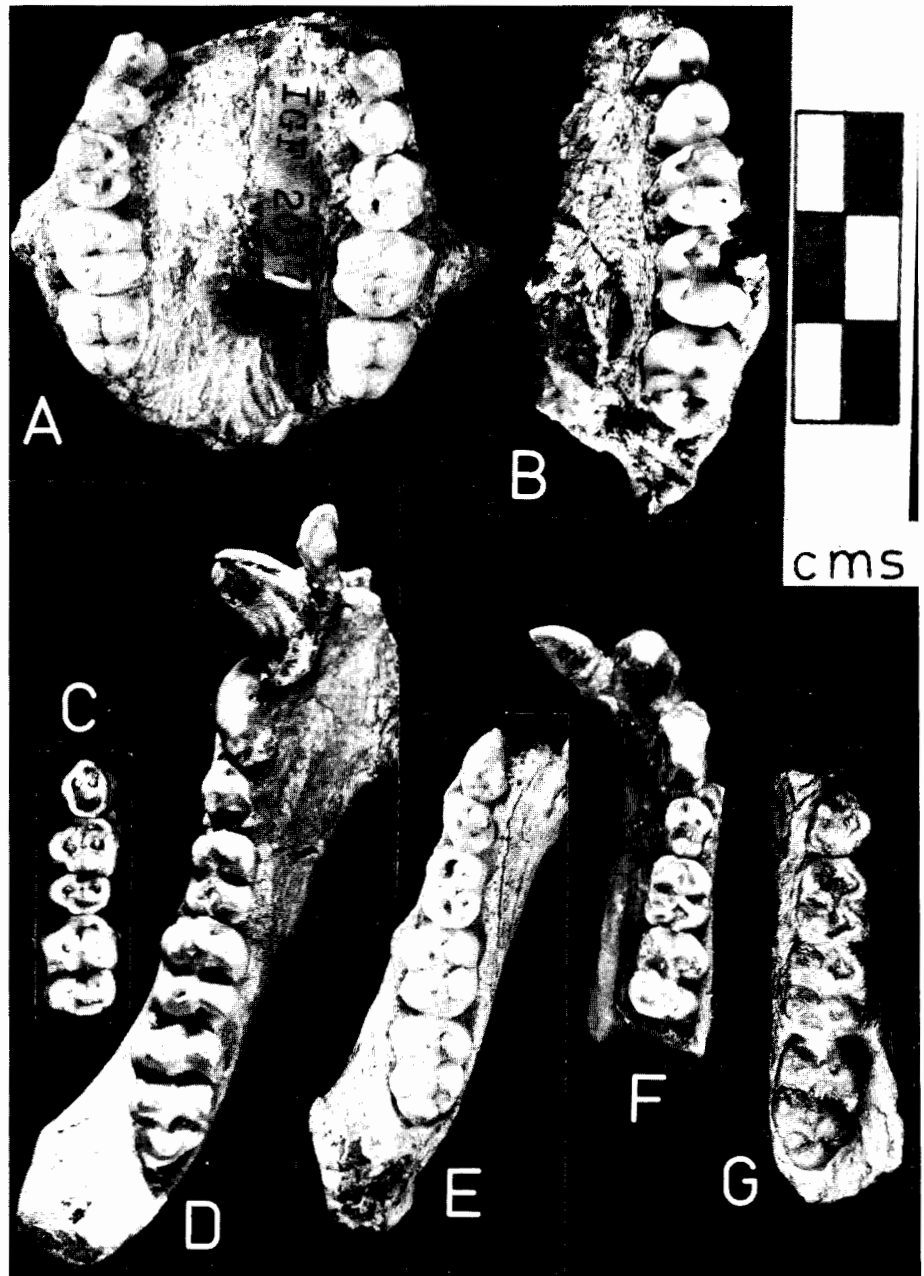


Fig. 2-5. Dentitions of fossil macaques. A: *M. ?sylvanus majori*, Capo Figari, Sardinia, male palate with right and left P³-M³; B: *M. sylvanus pliocena*, Heppenloch, Germany, left P³-M³; C: *?Macaca* sp., Marceau, Algeria, composite left P₄-M₂ (isolated teeth); D: *M. sylvanus florentina*, Upper Val d'Arno, Italy, male left I₂-M₃; E: *M. ?s. majori*, male left P₃-M₃; F: *M. s. prisca*, Montpellier, France, male right I₂-M₂; G: *?M. palaeindica*, Siwaliks, India, right P₄-M₃, sex unknown. All occlusal view.

sylvanus, larger than preceding *M. s. prisca*. The type mandible (Fig. 2-2D, 2-5D) of *M. s. florentina* possesses deep fossae on the corpus, but at least one other male specimen (Fig. 2-2C) does not, emphasizing the uncertainty of drawing morphological distinctions without even the cranium.

A number of sites across Europe have yielded Middle Pleistocene (ca. 1–0.125 MYA) macaque fossils, once again mostly fragmentary dentitions. The oldest name for these is *Macaca sylvanus pliocena* (Owen, 1845), for a single upper molar from an early warm phase of the “Riss” glacial stage at Grays Thurrock, near London. The nominal taxa *M. suevica* (Hedinger, 1891) and *M. tolosana* Harlé, 1892, from caves in Germany and France, are synonyms (see Fig. 2-5B). Over a dozen other localities have produced specimens, indicating a range from central Spain to East Anglia, Czechoslovakia, Italy, the Caucasus and Israel. All appear to be dated to warm phases, perhaps including the Last or Eemian Interglacial (125–75 thousand years ago). Although the local environments of these macaques varied between forest and steppe, they did seem to require a temperate climate to prosper; in the colder intervals, macaques may have retreated to the Mediterranean littoral (although they are not known from there except during warmer phases) or even out of Europe altogether, perhaps via the Near East. Morphologically, these specimens are nearly identical to the earlier *M. s. florentina*, but the cheek teeth may be slightly wider. Such refuges appear to have failed during the last glacial, if not earlier, as no monkeys occur in any of the numerous “postglacial” faunal assemblages from Europe or the Levant.

In the Pliocene and Pleistocene of northern Africa, a few fossil macaques are known, all of which can tentatively be termed *M. sylvanus* aff. *sylvanus*. In Tunisia, a humerus from Ichkeul is Ruscinian in age, while two molars from Ain Brimba are Villafranchian. An incorrect association of the latter with two incisors of a saber-tooth “cat” led Arambourg (1969–1970) to suggest the name “*Anomalopithecus bicuspidatus*” for this “aberrant” monkey, without formally describing the specimens or designating a type; the name is thus, happily, unavailable. Other sites are generally later Late Pleistocene (younger than 20,000 years old and thus clearly linked to the living Maghreb *M. sylvanus*), but Ain Mefta, Algeria, may be later Middle Pleistocene. From this site come a number of postcranial elements on which Pomel founded two species, *M. trarensis* and *M. proinuus*, in 1892 and 1896, respectively. It must be assumed that he simply changed his mind about the name, in ignorance of the practices of zoological nomenclature (not yet formalized in the Règles), as the later monograph does not even cite the first, short paper.

Asian Fossil Macaques

The potential proliferation of names for circum-Mediterranean *Macaca* should not confuse what is most probably a single closely knit lineage, with no

evidence for more than one species at any given time, except perhaps for the apparently short-lived *M. ?sylvanus majori*. In Asia, on the other hand, there are today at least a dozen species in several distinct groups. In the past, the evidence for coexistence of two or more forms is unclear, but the record is even less complete than in Europe. As in the Mediterranean region, the earliest known Asian cercopithecids are colobine, a few dental remains being known from the Late Miocene (Dhok Pathan) of Pakistan. These specimens have been variously named *Macaca sivalensis* and *Cercopithecus* or *Semnopithecus asnoti*, but as Simons (1970) partly suggested, they are all referable to a single colobine species best termed *?Presbytis sivalensis*.

The oldest Asian cercopithecines, on the other hand, have erroneously been thought colobine by all previous workers who even considered them, until Delson (1975a) indicated that they were papionin and could be termed *?Macaca palaeindica* (Lydekker, 1884). The specimens involved are two mandibular fragments (see Fig. 2-5G) from the "Tatrot-equivalent" (Late Pliocene, ca. 3 MYA) of northern India, which are clearly cercopithecine in dental morphology, although the type specimen has a deep and narrow corpus. The teeth are similar in size to those of *M. sylvanus*, that is, rather large for Asian macaques. It is worth noting that there may be a still older specimen of macaque-like cercopithecoid in Asia, as yet unpublished; this damaged mandible is said to be associated with a northeastern Chinese local fauna of Late Miocene age (see Delson, 1977).

All other Asian fossil macaques are Pleistocene in age, and a number of them can be referred to living species. A partial mandible of an old male from the ?Early Pleistocene Pinjor beds of northern India was originally termed *Cynocephalus* (= *Papio*) *falconeri*, but Jolly (1967) suggested it to be a large macaque. I now consider that it more probably represents *Procynocephalus*, known by two other jaws from the same horizon. In China, a male face (Figs. 2-1B, 2-4B,E) from the ?Early Pleistocene of Honan was named *M. anderssoni* by Schlosser (1924), while Young (1934) coined *M. robusta* for a series of mostly dental specimens (but see Fig. 2-4A) from the Middle Pleistocene of Choukoutien, near Peking. These two taxa are probably not distinguishable at the specific level. Moreover, *M. anderssoni* (sensu lato) is cranially similar to the modern *M. thibetana* and *M. arctoides* (placed in different species groups by Fooden, but see below), though all are rather different in shape and relative tooth size from the equally large-skulled *M. nemestrina* (see Fig. 2-3).

Additional, less complete fossil remains have been reported from Chinese sites ranging in age from later Early Pleistocene (the "*Gigantopithecus*-cave" at Liucheng, far to the southwest) through Late Pleistocene. The youngest of these may refer to *M. mulatta*, known in south and central China today, but few details have been published (for discussion, see Delson, 1977). Farther south, in the Indochinese peninsula, macaque remains have been recovered from a number of localities, most of which are probably later Middle Pleistocene in

age (as are the majority of the Chinese sites). Until these are reported in more detail, their specific identity will remain uncertain. The most complete specimen is a partial skull from Tung-Lang, northern Vietnam, described by Jouffroy (1959) as *M. speciosa subfossilis*, after comparison especially with *M. speciosa* (sic) *thibetana*. The cranium does closely resemble *M. thibetana* and might belong to this species, or to *M. arctoides* or even to *M. anderssoni*, so similar is the morphology among these taxa.

Hooijer (1962) and Fooden (1975) discussed fossil macaques from Java ranging in age back into the Middle Pleistocene. These suggest that populations of *M. fascicularis* and/or *M. nemestrina* were present, but as cranial remains are lacking, precise identification is not yet possible. *Macaca* is also known in the fossil record of Japan, but here the age of the specimens is even less certain, none being clearly older than Late Pleistocene. Iwamoto (1975) has reviewed most of the previous work and described a new skull which he considered to share some features with *M. "robusta."* The Japanese fossils are most probably a distinct subspecies of the living *M. fuscata* (of the *fascicularis* species group), and thus it seems unlikely that they would be closely related to the early Chinese fossils, which may belong to the *sinica* species group (see below). Macaque fossils are also known from caves in South Korea.

PHYLOGENY

Review of Published Data

This brief review of the fossil record of *Macaca* does not directly lead to further inference as to the evolutionary relationships within the genus. But if the insightful studies of Fooden (see this volume for summary) on reproductive organ morphology and other external characters are combined with the fossils and with scattered additional comments on macaque relationships and Asian biogeography by Albrecht (1978), and Brandon-Jones and Hiemae (unpublished ms) among others, a dim picture begins to emerge. A review of this nonpaleontological data leads to the formulation of a set of testable phylogenetic hypotheses, which may then be extrapolated further with the incorporation of time and adaptational factors.

Following Fooden, the male and female genital morphology seen in the *silenus-sylvanus* group of macaque species is ancestral for the genus. Female genital morphology and the presumably ancestral multiple-mount copulation pattern is shared with the *fascicularis* group, which differs in having a narrow, rather than a broad, glans penis. The *sinica* group is distinguished by a broad but acute or sagittate glans, hypertrophied uterine cervix and colliculi and a

single-mount copulation pattern. Finally, *M. arctoides*, placed in its own species group by Fooden, is characterized by an acute, elongate (lanceolate) glans, lack of cervical colliculi but presence of a vestibular collicle and single-mount copulation with an increased number of intromissive thrusts. At least the male morphology and behavior pattern appear to form a three-pole morphocline with one trend from the ancestral (*silenus*) condition through the *sinica* to the *arctoides* (in which the female genital tract may show an evolutionary reversal), and a second to the *fascicularis* group's quite distinctive mosaic. Within each group, tail length, long thought to be a valuable taxonomic character, appears to have reduced convergently, as populations moved northward and body size increased. If Fooden's four groups are recognized, such convergent reduction would have occurred five times, or perhaps six if there were two episodes within the *fascicularis* group.

New Interpretations

Considering this evidence along with the early date of entry into Europe of macaques apparently related to *M. sylvanus*, it seems likely that this species is more distinctive than Fooden has previously admitted (as recognized also by Albrecht, 1978, p. 18). It is linked to *M. silenus* and its relatives (Fooden, 1975) essentially by retention of ancestral conditions, not by any shared derived states which would uphold its placement within the same species group. It may thus be tentatively recognized as a separate group, monotypic today but possibly containing one or more fossil species noted above (see also Cronin, *et al.*, this volume).

On the other hand, *M. arctoides* could well be placed within the *sinica* group. Although more derived than other members of that group, it appears to be on the same morphocline trend in penial morphology and copulation pattern. The female reproductive tract of *M. arctoides* is certainly specialized (reciprocally with that of the male) in a different way than is that of the rest of the *sinica* group. But Fooden (1967) suggested that this was an adaptation to ensure reproductive isolation from neighboring relatives—I suggest the *assamensis/thibetana* subgroup for this role. Hill and Bernstein (1969) also thought that *M. assamensis* was less derived in penial morphology and cranial hair-flow pattern than *M. sinica* or *M. radiata*, thus supporting the long separation of these subgroups. More detailed comparisons among all five species are needed to refute or confirm this hypothesis of their relationship. The cranial similarity of *M. arctoides* to *M. thibetana* (and *M. assamensis*) is another important link, as is the distribution pattern of the three species. *M. assamensis* is basically a smaller, slightly longer-tailed, more southerly version of *M. thibetana*, and the two are clearly closely related and parapatric. *M.*

arctoides is quite close in size (especially of skull) and relative tail length to *M. thibetana*, and it is widely distributed in southern Indochina, an area unoccupied by any other *sinica*-group member. However, *M. arctoides* also ranges northward to overlap fairly extensively with *M. assamensis* and slightly with *M. thibetana*; Albrecht (1978, p. 20) also considered that this distribution suggested "an ecological and/or evolutionary relationship between these" taxa. In sum, *Macaca arctoides* would appear to be related to the *assamensis*/*thibetana* pair, but to have developed more extreme (uniquely derived) conditions since its origin; it is thus included formally in the *sinica* group.

The hypothesis of relationships resulting from these inferences is presented in Fig. 2-6. It differs slightly from one which might reflect Fooden's published views, but the overall agreement is obvious. Some of the character states discussed above are shown on this cladogram (which has no simple time axis), as is relative tail length. According to this hypothesis, only one major tail reduction trend is required for each species group (four in all): *M. arctoides* and *M. thibetana* underwent continued reduction from an already short-tailed ancestor, and a similar canalization may have occurred in the *fascicularis* group (see below). Some fossils are tentatively indicated on the cladogram, although only one (*M. anderssoni*) is of any importance. An indication of the zoogeographic model presented below is also indicated. The seven taxa of macaques of Sulawesi (the Celebes) which Fooden consistently recognizes as species, are here indicated as a single unit. Albrecht (1978) basically accepted Fooden's ranking, but included comments by Groves (p. 87) which suggested some intergradation in the north. I imagine that perhaps four full species may eventually be recognized (see Groves, this volume), but any number from one to seven is feasible.

HISTORICAL ZOOGEOGRAPHY

A final step which can be taken here is to suggest an overall scenario of deployment for the genus, again based extensively on Fooden's work, but also on the phylogeny developed above. Fooden has suggested that the strongly disjunct distribution pattern of the *silenus-sylvanus* group(s) suggests early dispersal, followed by that of the moderately disjunct *sinica* group, after which the contiguously ranging *fascicularis* group may have dispersed. Each successive dispersal probably was closely linked to the disjunction of previous group(s), as well as Pleistocene climatic alternations.

After an origin in northern Africa, early macaques spread into Eurasia, probably via the Near East. One line entered southern Europe by the beginning of the Pliocene, here recognized as a succession of temporal subspecies of *Macaca sylvanus*. North African Late Miocene *M. libyca* and Sardinian later Pliocene *M. ?s. majori* might be distinct species, referred to the

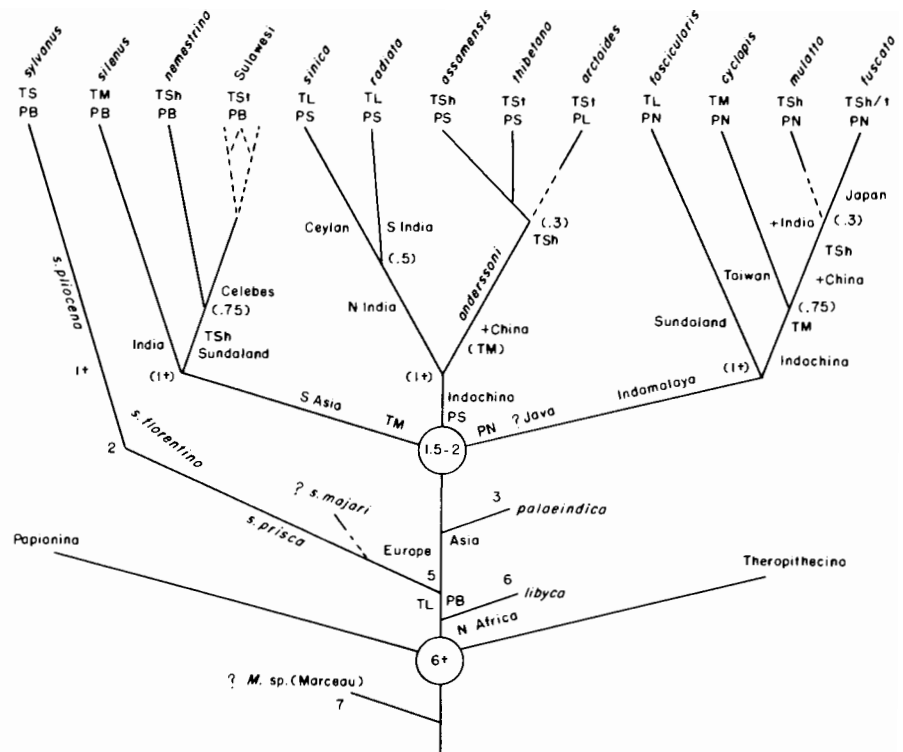


Fig. 2-6. Phylogram of macaque evolution. This diagram can be read in two ways. As a simple cladogram, the lines indicate relationships among the species of *Macaca* (all Sulawesi forms being treated as an indivisible monophyletic group). In a cladogram, there is no simple time axis; branching points along any lineage are more recent toward the top of the diagram, but nodes at a similar height along different lineages are not necessarily of similar age. All species are of the genus *Macaca*, and some fossil species are placed as independent lineages, as are the two other subtribes of the Papionini. Due to uncertainty as to their relationships, the two additional genera of the Macacina, *Procynocephalus* and *Paradolichopithecus*, are not included at all. The distribution and inferred history of two characters, tail length and penial glands shape, are also included. TL=tail long (\geq head + body length[HB], the inferred ancestral condition; TM=medium (between 1.0 and 0.5 HB); TSH=short (between 0.5 and 0.2 HB); and TSSt=stump tail (less than 0.1 HB); TSh/t is intermediate between the last two. These classes are arbitrary, merely to indicate an approximate pattern, data from Fooden, this volume, PB=glans blunt and broad, the inferred ancestral pattern; PS=sagittate (acute and broad); PL=lanceolate (acute and elongate); PN=narrow (and blunt) (data from Fooden). The two large circles represent unresolved trichotomies. Note: TS at *M. sylvanus* should read TSSt.

With further extrapolation, as described in the text, time, geography and character evolution may be added. Thus, the numbers indicate the ages of branching points and fossil taxa (those in parentheses being relatively less certain); nodes of similar age have been brought to equivalent heights. Changes from the inferred ancestral conditions of TL and PB are indicated by the newly derived condition on the segment involved, except that no changes are indicated for terminal segments. Several fossil species and subspecies are placed along segments which they might actually represent. Based on Fig. 2-7, an indication is given to the geographic dispersal of the various lineages: a "+" indicates the extension of a range; new terms following a node represent the subdivision of a range, and no term indicates continuity.

sylvanus species group on geographic grounds alone at present. *M. sylvanus* apparently flourished in Europe only during the warmer phases of the Pliocene and Pleistocene, eventually retreating from the continent entirely. Continuous occupation of the north African littoral, especially in the west, is likely.

A second line of macaques moved eastward, reaching India by the later Pliocene, if not earlier (Fig. 2-7). This group, like early *M. sylvanus*, would have been long-tailed, with *silenus*-type reproductive organs. The ancestral species presumably spread from southern India, along the coast (and perhaps inland) to Burma and into Malaya. As in Europe, climatic fluctuations affected southern Asia and "Sundaland" (a collective term for Indonesia and the neighboring margins of the Sunda shelf, see Medway, 1970). Brandon-Jones and Hiiemae (unpublished ms) suggest that cool/arid phases (linked to drops in sea-level and thus to island connections permitting migration of suitably adapted species) led to restriction of forest in relict areas within this region (see also Eudey, this volume). Such phases would have alternated, several times during the past two million years and more rapidly after 0.5 MYA, with episodes of warmer and moister climate during which islands and their species were isolated from one another. The timing of these oscillations is quite unclear, but the relative sequence of evolutionary events postulated for *Macaca* is estimated to best agree with the underlying phylogeny, known fossils and rare biogeographic evidence (in part suggested by Brandon-Jones and Hiiemae). Fig. 2-7 depicts, in a very tentative manner, six stages in the deployment of Asian macaques.

An early drop in sea level permitted entry into Sundaland, after which I suggest that ancestors of the *fascicularis*-group became isolated in Indonesia (perhaps Java) and a proto-*sinica*-group species arose in or west of Burma; later, *M. nemestrina* or its ancestor speciated from the *silenus*-like stock in Malaya or Sumatra. This isolation is thought to have been younger both because of the overall closer relationship between *M. silenus* and *M. nemestrina* (mostly based on conservative retentions) and because these two show some tail reduction, suggesting that the trend had already commenced between the time the other two groups diverged and the point when these species became isolated.

With alternating climatic amelioration and decay, the several Asian macaque groups came into contact and competition. Long-tailed early *sinica*-group populations moved south and west into peninsular India, perhaps competing strongly with indigenous *M. silenus*. The former also moved north toward China, where they would have become larger and shorter-tailed, perhaps being represented by some of the earlier fossils of *M. cf. anderssoni*. Later, *M. silenus* may have been restricted to its present southwest Indian relict distribution, while the northern and southern members of the *sinica* group may have become (partly) genetically isolated. Ceylon may have been colonized by the southern form at this time (circa early Middle Pleistocene).

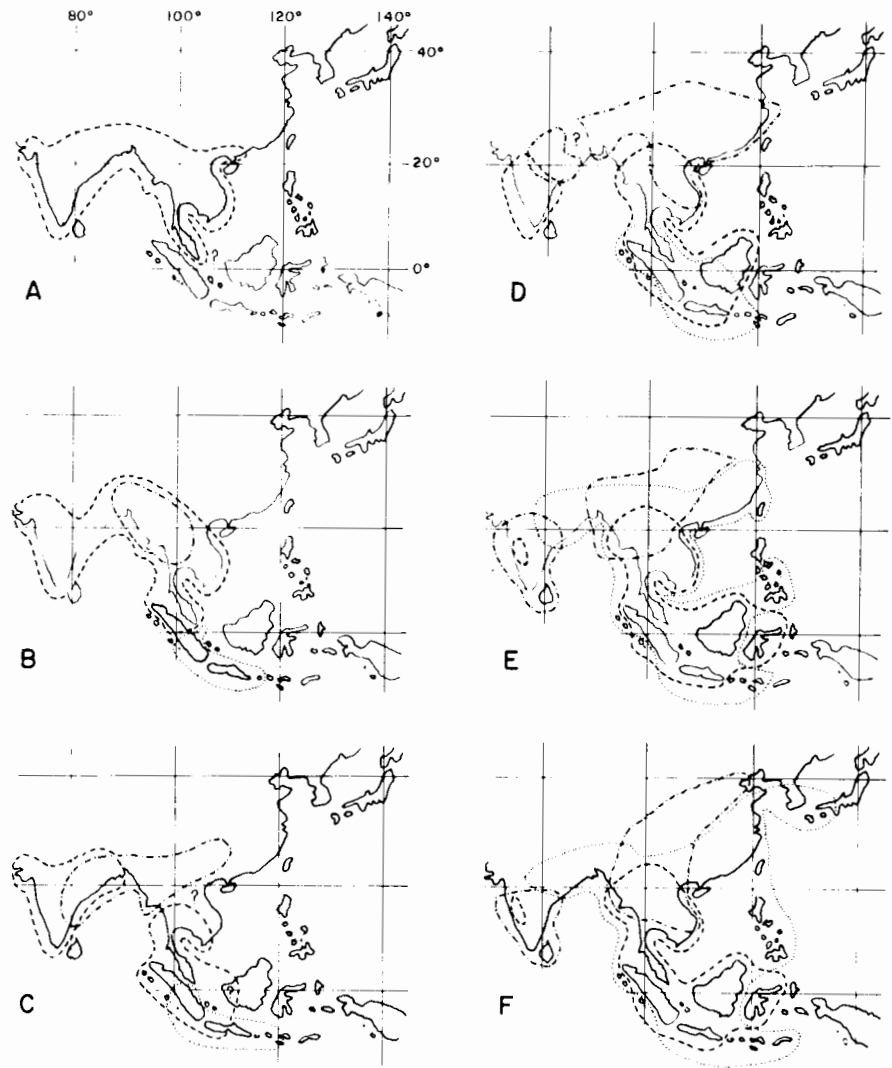


Fig. 2-7. Hypothetical dispersal pattern of Asian macaques. On the same base map used by Fooden (this volume) to present modern distributions, the inferred ranges of the three species groups are given for six time periods: A, later Pliocene (2.5–2.0 MYA); B, Early Pleistocene (1.5–1.3 MYA); C, late Early Pleistocene (ca. 1.1 MYA); D, early Middle Pleistocene (ca. 0.9 MYA); E, mid Middle Pleistocene (ca. 0.6 MYA); F, late Middle Pleistocene (ca. 0.25 MYA). ----- *silenus* group (and ancestral dispersal pattern) *fascicularis* group - . - . *sinica* group. The boundaries are, of course, extremely questionable, but do include all known fossils (see text); the maps themselves are somewhat schematized.

In Sundaland, a population of *M. cf. nemestrina* may have entered Sulawesi from Borneo, while early *fascicularis* group populations began to spread onto various islands and up the Malayan peninsula. Succeeding mid-Pleistocene climatic fluctuations allowed the colonization of the Mentawai Islands by and divergence of a northern and southern major subspecies of *M. nemestrina* (Fooden, 1975); the diversification of the Sulawesi macaques from a *M. maura*-like ancestor (Fooden, 1969; Albrecht, 1978); the spread of *M. fascicularis* into the many islands of Indonesia and the Philippines; and the isolation, perhaps relatively early, of a northern member of the *fascicularis* group in Burma or eastern India (proto-rhesus).

The presence of *M. fascicularis* today in the Philippines and on small islands near the Mentawai group, but not on the latter (more distant from Sumatra) or on Sulawesi, suggests that *M. nemestrina* may have reached the last two areas early on, but that they were inaccessible by the time *M. fascicularis* pushed northward after colonizing the eastern islands (which lack *nemestrina* or relatives). Fossils of mid Pleistocene age on Java document the presence of at least one of these two species, but which one is yet uncertain; perhaps relative tooth size data may answer this question. Previously, Fooden has argued that the *fascicularis* group was the last to disperse, but as Albrecht (1978, p.20) noted, its distribution with respect to *M. nemestrina* in Sundaland is difficult to interpret on this premise; other authors (e.g., Medway, 1970) have suggested that *M. fascicularis* in fact arrived first. If it is postulated that *M. fascicularis* originated and diversified in southeastern Sundaland, but only entered the mainland at a later date, some of the opposing interpretations are reconciled.

Once a northern member of the *fascicularis* group invaded southern Asia, it may have spread rapidly both east and west. If tail length is considered, parsimoniously, to have reduced only once in the group, it must be suggested that *M. cyclopis* reached and became isolated on Taiwan at a relatively early stage, as its tail is longer than that of *M. mulatta*. On the other hand, being farther north and larger than the rhesus, *M. cyclopis* would be expected to have a shorter tail. Perhaps it penetrated into eastern China in a warm phase and then retreated to Taiwan during a glacial, without altering its tail/body proportions after subsequent isolation. Meanwhile, a population like modern *M. mulatta*, very ecologically adaptable, may have entered the Indian region and displaced *sinica*-group populations from the northern zones. *M. sinica* itself became isolated on Ceylon, while modern *M. radiata* developed in southern peninsular India, overlapping only partly with *M. silenus*. The presence of *M. mulatta* effectively completed the isolation of the southern and northern lines of the *sinica* group, whose territory it overlapped eastward. Japan was colonized by a form presumably like *M. mulatta* by the later Middle

Pleistocene. During the earlier Middle Pleistocene, *M. anderssoni* (= *M. robusta*) inhabited China, and its resemblance to *M. arctoides* and *M. thibetana* suggests that these species were not yet distinct. A search for derived cranial features among these taxa should prove useful. At some point, *M. arctoides* would have become isolated in southeastern Indochina (?), while *M. thibetana* and *M. assamensis* would have diverged even later in time, with tail length reducing in the first two of these.

Brandon-Jones and Hiiemae (unpublished ms) and Albrecht (1978) have noted that similar patterns of dispersal and distribution are known in various mammalian, avian and floral taxa over the same geographic range. Most interesting is the pattern seen by Brandon-Jones and Hiiemae for the Asian colobines. They argue that the south Indian-Ceylonese "*Kas*" *senex* is closely related to the Indochinese-Indonesian *Trachypithecus* group; a possible sister of this taxon is "*Semnopithecus*" *entellus* of India. If this hypothesis were accepted, *Trachypithecus* might be recognized as a subgenus of *Semnopithecus*. In Sundaland, the smaller bodied species of *Presbytis* (sensu stricto) occur widely. There are also two groups of more distinctive colobines: *Pygathrix* [and *P. (Rhinopithecus)*] in southern China and eastern Indochina; and *Nasalis* [and *N. (Simias)*] on Borneo and the Mentawai Islands, respectively. The link between *S. (Trachypithecus)* of southern India and Indochina, separated by the highly adaptable and successful *S. (S.) entellus* in India recalls the pattern of *M. mulatta* separating members of both the *sinica* and *silenus* groups. Moreover, the distribution of *Pygathrix* parallels that of *M. arctoides*, compared to their respective "ancestral stocks" of *Semnopithecus* and *M. assamensis/M. thibetana*.

It is hoped that this set of hypotheses will be tested in the future through studies of morphologic and molecular systematics of macaque species (giving due consideration to the great ranges of variation within many species), as well as by finds of new fossils and studies of stereotyped behavior patterns and Pleistocene climatic shifts. This is a first step, built upon the groundwork of others and probably far too detailed, but it is offered in the hope of arousing interest and thus a desire to test and refute, among my colleagues.

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REFERENCES

- Albrecht, Gene H. The Craniofacial Morphology of the Sulawesi Macaques. Multivariate Approaches to Biological Problems. *Contributions to Primatology*, **13**: 1–151. Basel : S. Karger (1978).
- Arambourg, Camille. Vertébrés continentaux du Miocène supérieur de l'Afrique du nord. *Publications Serv. Carte Geol. Algérie* (nouv. série), *Paléontologie*, **4**: 5–159 (1959).
- _____. Les vertébrés du Pleistocène de l'Afrique du nord. *Arch. Mus. Nat. Hist. Nat.*, Paris, sér. 7, **10**: 1–126 (1969–1970).
- Azzaroli, Augusto. La scimmia fossile della Sardegna. *Riv. Sci. Preist.*, **1**: 168–176 (1946).
- _____. Late Miocene interchange of terrestrial faunas across the Mediterranean. In M. T. Alberdi and E. Aguirre (eds.), *Actas I Coloquio Internacional sobre Biostratigrafía Continental del Neogeno Superior y Cuaternario Inferior*, 1974. Madrid: Instituto Lucas Mallada (CSIC), pp. 67–72 (1975).
- Blainville, H. M. D. de. *Ostéographie des Mammifères. I. Primates, Atlas*. Paris: Baillière (1839).
- Brandon-Jones, Douglas and Hiimae, Karen. Present primate distributions as a guide to Quaternary climatic change in Asia (Unpublished ms).
- Cocchi, I. Su di due Scimmie fossili italiane. *Boll. Comitato Geol. Italia*, **3**: 59–71 (1872).
- Delson, Eric. Evolutionary history of the Cercopithecidae. *Contributions to Primatology*, **5**: 167–217. Basel: S. Karger (1975a).
- _____. Paleoecology and zoogeography of the Old World monkeys. In R. Tuttle (ed.), *Primate Functional Morphology and Evolution*. The Hague: Mouton, pp. 37–64 (1975b).
- _____. Vertebrate paleontology, especially of non-human primates, in China. In W. W. Howells and P. J. Tsuchitani (eds.), *Paleoanthropology in the People's Republic of China*. Washington, D. C. : National Academy of Sciences, pp. 40–65 (1977).
- Elliot, D. G. *A Review of the Primates*. Monographs, Amer. Mus. Nat. Hist., 3 vols., New York (1913).
- Fooden, Jack. Complementary specialization of male and female reproductive structures in the bear macaque, *Macaca arctoides*. *Nature*, **214**: 939–941 (1967).
- _____. Taxonomy and evolution of the monkeys of Celebes (Primates: Cercopithecidae). *Bibliotheca Primatologica*, **10**: 1–148, Basel: S. Karger (1969).
- _____. Taxonomy and evolution of liontail and pigtail macaques (Primates: Cercopithecidae). *Fieldiana: Zoology*, **67**: 1–169 (1975).
- _____. Provisional classification and key to living species of macaques (Primates: *Macaca*) *Folia primatol.*, **25**: 225–236 (1976).
- Harlé, Edouard. Une mandibule de singe du repaire des hyènes de Montsaunès (Haute-Garonne). *Bull. Soc. Hist. Nat. Toulouse*, **26**: ix–xi (1892).
- Hedinger, A. Über den Pliocänen Affen des Heppenlochs. *N. Jb. Min., Geol., Paläont.*, **1**: 169–177 (1891).
- Hill, William Charles Osman and Bernstein, Irwin. On the morphology, behaviour and systematic status of the Assam macaque (*Macaca assamensis* McClelland, 1839). *Primates*, **10**: 1–17 (1969).
- Hooijer, Dirk Albert. Quaternary langurs and macaques from the Malay archipelago. *Zool. Verhandelingen Mus. Leiden*, **55**: 3–64 (1962).
- _____. Miocene Mammalia of Congo. *Ann. Mus. Roy. Afr. Centr.*, sér. in 8^{vo}, sci. Géol., **46**: 1–71 (1963).

- Jolly, Clifford J. The evolution of the baboons. In H. Vagtborg, (ed.), *The Baboon in Medical Research*, vol. 2. Austin: Univ. Texas Press, pp. 427-457 (1967).
- Jouffroy, Françoise Kyou. Un crâne subfossile de Macaque du Pleistocène du Viet Nam. *Bull. Mus. Nat. Hist. Nat., Paris*, sér. 2, **31**: 209-216 (1959).
- Kay, Richard F. Molar structure and diet in extant Cercopithecidae. In P. M. Butler and K. Joysey (eds.), *Studies in the development, function and evolution of teeth*. London: Academic Press, pp. 309-339 (1978).
- Kormós, Theodor. Die phylogenetische und zoogeographische Bedeutung praeglazialer Faunen. *Verhandlungen K.-K. Zool.-bot. Gesell., Wien*, **64**: 218-238 (1914).
- Lydekker, Richard. Rodents and new ruminants from the Siwaliks, and synopsis of Mammalia. *Mem. Geol. Survey India, Paleont. Indica*, ser. X, **3**: 105-134 (1884).
- Medway, Lord. The monkeys of Sundaland: ecology and systematics of the cercopithecids of a humid equatorial environment. In J. R. Napier and P. H. Napier (eds.), *Old World Monkeys*. London: Academic Press, pp. 513-553 (1970).
- Napier, John R. Paleoecology and catarrhine evolution. In J. R. Napier and P. H. Napier (eds.) *Old World Monkeys*. London: Academic Press, pp. 55-95 (1970).
- Owen, Richard. Notice sur la découverte, faite en Angleterre, de restes fossiles d'un quadruman du genre Macaque, dans une formation d'eau douce appartenant au nouveau pliocène. *C. R. Acad. Sci. (Paris)*, **21**: 573-575 (1845).
- Pomel, A. Sur un macaque fossile des phosphorites quaternaires de l'Algérie. *C. R. Acad. Sci. (Paris)*, **115**: 157-160 (1892).
- . Singe et Homme. *Publ. Serv. Carte Geol. Algérie, Paléont. Monogr.*, **11**: 1-32 (1896).
- Schlosser, Max. Fossil primates from China. *Palaeont. Sinica*, **1** (2): 1-16 (1924).
- Simons, Elwyn L. The deployment and history of Old World monkeys (Cercopithecidae, Primates). In J. R. Napier and P. H. Napier, (eds.), *Old World Monkeys*. London: Academic Press, pp. 97-137 (1970).
- Stromer, Ernst. Mitteilungen über Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten). 5. Nachtrag zu 1. Affen. *Sitz.-ber. Bayerischen Akad. Wiss., Math.-phys. Kl.* 1920, pp. 345-370 (1920).
- Szalay, Frederick S. and Delson, Eric. *Evolutionary History of the Primates*. New York: Academic Press (1979).
- Walker, Phillip and Murray, Peter. An assessment of masticatory efficiency in a series of anthropoid primates with special reference to the Colobinae and Cercopithecinae. In R. H. Tuttle, (ed.), *Primate Functional Morphology and Evolution*. The Hague: Mouton, pp. 135-150 (1975).
- Young, Chung-chien. On the Insectivora, Chiroptera, Rodentia and Primates other than *Sinanthropus* from locality 1 at Choukoutien. *Palaeont. Sinica*, ser. C, **8**(3): 1-160 (1934).