

*Paleoecology and Zoogeography
of the Old World Monkeys*

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Paleoecology and Zoogeography of the Old World Monkeys

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The Cercopithecidae are perhaps the most successful family of living primates, as measured either by the number of species or by their tolerance of ecological-environmental situations, which is surpassed only by *Homo*. Moreover, the ecology and behavior of this family have been well studied, with at least some investigation of almost every genus or species-group. This quantity of data provides an excellent source for comparison and elucidation of the paleobiology of the extinct cercopithecids, while the latter can provide some interesting additions to the present diversity of the family as well as throw light on the history of its adaptations. In this paper, the dispersal and environmental history of the Cercopithecidae will be discussed in terms of the fossil record, and some types of ecoethological data useful in paleobiological reconstruction will be considered.

The analysis of mammalian paleoecology is still in its earliest developmental stages. Despite some attempts by Shotwell (1958, 1964), among others, the understanding of community relationships among fossil mammal species is far behind that for many invertebrates and even some Mesozoic vertebrates (see Olson 1952). In fact, the present state of the art for mammalian paleoecology is better considered as paleoenvironmental study, an attempt to determine the regional climate and/or ecotype by comparing the species known from a series of fossil assemblages or local faunas in the region with the ecological/environmental preferences of their nearest living relative or functional cor-

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relate. Paleobotanical (including palynological) data associated with fossil mammals are rare, but such associations, or even plant remains of similar age and distribution as mammal fossils, provide the best source of paleoenvironmental baseline information. In either case (faunal or floral), a relatively firm stratigraphic framework is a necessary prerequisite for the development of an environmental history.

THE NEOGENE TIME-SCALE

Fossil cercopithecids are known from the Miocene through Pleistocene epochs of the Tertiary, and only this time span (the Neogene "subperiod") need be considered here.¹ The most recent summaries of the correlation and calibration of time and rock units of this age are those of Berggren (1971, 1972) and Van Couvering (1972; see also Delson 1973). Only areas of conflict among these published time-scales or with my interpretations shall be discussed here. The Neogene epochs were originally defined by Lyell (1833) on the basis of aquatic (essentially marine) Euro-Mediterranean invertebrate faunas, and modern re-evaluations of the epochs and their boundaries must be based similarly on marine organisms in the type regions. Planktonic micro-organisms such as foraminifera and radiolaria have proved most useful in this endeavor, and local sequences based on assemblages of fossils and/or the evolutionary stages deduced for given lineages have been developed in or correlated to these areas of southwestern France and Italy. Several parallel sets of regional chronostratigraphic² units of lower rank than epoch have also been reinterpreted; among these stages most correlation usually is determined.

Although world-wide definition and correlation are based on these marine units, continental mammalian assemblages are more common-

¹ The Fayum catarrhines (Oligocene of Egypt) have been intentionally left out of further consideration here. The special relevance of certain of these species to cercopithecoid ancestry has been argued by Simons (e.g. 1967, 1970, 1972), but I question such a relationship for *Parapithecus* (Delson 1973, i.p.b). The environment inhabited by these animals is well reconstructed by Simons and Pilbeam (1972) as gallery forest alongside broad, sluggish, tropical rivers.

² Chronostratigraphy may be defined (see the American Code of Stratigraphic Nomenclature) as dealing with subdivisions of rocks considered solely as the record of a specific interval of geologic time; such subdivisions are tied closely to specific rock units known as stratotypes. Biostratigraphy deals with rock units as delineated by the fossils they contain and may be as formal and strictly defined as the preceding. Biochronological units, however, as presently understood for mammals at least, are less strict and may be considered as the record of geologic time as represented by organisms existing at that time.

ly considered in terms of regional sequences of biochronologic (or biostratigraphic) units known as Land Mammal Ages (Tedford 1970; Wood et al. 1941). For Europe, earlier authors usually employed the name of the supposedly time-equivalent marine stage in similar sense, but Thaler (1965) proposed a set of semiformal "biochronologic zones," based essentially on the ranges of single rodent taxa, and most recently a distinct set of terms has been employed in a manner analogous to that followed in North America (Azzaroli 1972; Tobien 1972).

In Table 1, I attempt to correlate the marine sequence with several continental and local parallels, with major fossil faunas included as reference points. As Berggren (1971: 755) has noted, the tendency to subdivide "things and events into a three-fold division on a linear scale" is a "propensity of scientists" and not necessarily a reflection of nature. The use of Early, Middle, and Late segments of the Miocene has come to imply rather specific division for modern authors, and this usage is followed in the marine ("standard") scale. The Pliocene is less certainly split into two portions, whose names are lowercased to reflect this informality; the "Astian" of many authors is probably a facies occurring throughout the epoch.

Subdivisions of the Pleistocene have previously been made by workers interested in such continental events as glaciation and mammalian or botanical evolution, with little regard for the marine sequence (Adam 1964; Butzer 1971; van der Hammen, Wijmstra, and Zagwijn 1971; Howell 1966). In order to bring the correlation of this last Tertiary epoch into balance with that of earlier ones, I suggest the equation of the beginnings of the Middle and Late Pleistocene with the bases of the Sicilian and Neotyrrenian stages, respectively. This subdivision seems more reasonable than one based either on nonbiological events (e.g. magnetic reversals) without links to paleontology or on continental evidence. Gradstein (1970) has recently shown that the early (type) Sicilian represents a relatively warm period, and although there is as yet no direct evidence, this time may be roughly correlated with the interval of warmer climate known in the Netherlands as the Waalian; the paleomagnetic work of von Montfrans (1971) suggests an age of about one million years for the beginning of the Middle Pleistocene by this definition. Much of the Sicilian has been thought correlative with the so-called Cromerian mammalian faunal interval, but the use of this term for paleontologic, lithologic, and climato-stratigraphic units is confusing. It may be replaced by the term Biharian Land Mammal Age (see Kretzoi 1969; Jánossy 1970), which begins with the first widespread presence in western Europe of eastern steppe mammals circa one million years

ago, spans the Brunhes-Matuyama magnetic reversal at 0.7 million years, and extends to the end of the Mindel glacial. The Biharian as here understood closely equates not only to the Cromerian and St. Prestian of these authors but also to the Galerian of Ambrosetti et al. (1972). For the most part, the division of the Pleistocene in this way closely approximates the accepted divisions of the authors cited above.

The dates and some of the stage/age assignments of Table 1 may not be familiar to those accustomed to the correlations of North American (and in fact most English- and German-speaking) vertebrate paleontologists (for example, Thenius 1958, 1959; Evernden et al. 1964; Simons 1972) and who have not followed recent developments. This time-scale does not imply changes in the "absolute" or radiometric ages assigned to such events as the appearance of *Hipparion* or the beginning of the Villafranchian Land Mammal Age; it merely reflects better understanding of the position of these continental events in a sequence based on marine fossils. Recently, deep drilling has clarified the most important event in the Mediterranean marine realm — namely, the closing of the straits of Gibraltar by tectonic activity related to the drifting of northwestern Africa into contact with Europe at a time that corresponds to the gap between Lyell's Miocene and Pliocene. Following this, the Mediterranean basin became completely desiccated several times, to depths of more than 10,000 feet (3,000+ meters) below present sealevel, until Atlantic water cut first a waterfall and then a deep contact through the straits and renewed oceanic circulation (Ryan et al. 1970; Hsü 1972; Cita and Ryan 1972; Hsü, Ryan, and Cita 1973).

This event, cataclysmic in terms of its effect on marine faunas, certainly merits recognition as the cause of a stratigraphic gap at the Miocene–Pliocene boundary, and thus the first sediment deposited by the refilling Atlantic water may be considered earliest Pliocene in age; the salt deposits formed subaerially by Late Miocene evaporation compose much of the rocks assigned to the Messinian stage, which is thus assigned to the end of the Late Miocene. Note that the first appearance of *Hipparion* has nothing whatsoever to do with this boundary redefinition but must instead be correlated to the marine sequence somehow.

This correlation is in fact quite important, because it aids in determining and calibrating another marine boundary. *Hipparion* first occurs in the late Barstovian Mammal Age in North America before 12 million years ago, but it is morphologically distinct (having less complex cheek teeth and a different facial structure) from the oldest Eurasian forms, known from the Vallesian Mammal Age of Europe (and apparently the lower part of the Nagri Formation in the Siwaliks [Hussain 1971, per-

sonal communication]). It is generally assumed that *Hipparion* of Old World type did evolve in North America (possibly in the Pacific Northwest) and upon crossing a Bering "filter-bridge" migrated rapidly across Eurasia, reaching all available regions within a geological "instant." Van Couvering and Miller (1969) noted that a date of 12.4 million years has been reported in close association with a very early *Hipparion*-including assemblage at Höwenegg, Germany, and they suggested a date of some 12.5 million years for the first appearance of this genus in Eurasia and thus the beginning of the Vallesian. However, they neither note the 1.1 million-year error range provided for this date by Lippolt, Gentner, and Wimmenauer (1963) nor consider that although this may be a technically "good" or accurate date, it is still a single determination at the top of a concordant series of ages (and thus could conceivably be too old). There is by definition a 33 percent chance that the actual date is within the range 12.4 to 11.3 million years (or, of course, between 12.4 and 13.5, but this is negated by other data), and the younger range agrees better with North American results. I thus suggest an age of 12.0 to 11.5 million years for the first widespread occurrence of *Hipparion* and the base of the Vallesian.

Few correlations exist between assemblages of mammals and marine fossils well placed with regard to their respective relative-age sequences, but two have recently been reported from Crete. De Bruijn, Sondaar, and Zachariasse (1971) recorded the association of very early Tortonian foraminifera and rodents of late Vallesian age (at Kastellios Hill), while de Bruijn and Meulenkamp (1972) noted that the *Plakia* assemblage of late pre-Vallesian rodents was found in rocks of late pre-Tortonian age (greater precision is not yet possible). These observations would seem to indicate a rather close concordance between the beginnings of the Tortonian stage and the Vallesian Mammal Age. Similar but less precise intercalations have been reported in France between mammals and molluscs: Mein and Truc (1966) recorded late Vallesian contemporaneous with "middle" Tortonian, while Guérin et al. (1972) reported *Hipparion* teeth in seemingly pre-Tortonian rocks, although both of these marine placements are questionable. From these data and in conjunction with published (and personal) communications from Berggren and Van Couvering, I would estimate that the Vallesian may have begun slightly before the Tortonian (on present definitions), and thus I assign an age of about 11 million years to the base of the Late Miocene (Tortonian).

The locality of Hauterives, southern France, yields a mammalian assemblage of probably earliest Ruscinian age (Guérin and Mein 1971)

and has been shown by Ballesio (1971) to postdate the deep cutting of the Rhone valley brought on by the drop in Mediterranean baselevel at the end of the Miocene. It may thus be suggested that the base of the Ruscian as here understood closely corresponds to the base of the Pliocene. This also agrees well with eastern and central European (Paratethys) evidence, for the type Pontian is generally equated roughly with part of the Messinian (e.g. Cicha and Senes 1972), and the immediately post-Pontian or latest Pontian local faunas of Baltavar and Polgardi in Hungary (Kretzoi 1969; Kertai 1968) may be of early Ruscian age (Mein and Michaux 1970; Mein, personal communication). Interpretations of the Villafranchian in terms of the epoch time-scale have varied greatly, but it is now generally agreed that its position must be determined with respect to marine stages, not defined *a priori* (e.g. as earliest Pleistocene). Radiometric dates and marine correlations (Savage and Curtiss 1970) indicate that the type (earliest) Villafranchian is of mid-Pliocene age (approximately 4 million years), while latest Villafranchian and latest Calabrian appear contemporaneous (Azzaroli and Ambrosetti 1970; Azzaroli and Berzi 1971). Dates and paleomagnetic results from Senèze (Prévot and Dalrymple 1970), a crater lake at whose top is a late Villafranchian mammal fauna, suggest that the middle/late Villafranchian "boundary" approximates that between the Pliocene and the Pleistocene at about 1.9 million years (Delson 1973). Given these independent calibrations of the mammalian sequence, it is possible to consider environmental evidence from the continental record and to correlate this with other events.

CERCOPITHECID PALEOENVIRONMENT AND DISPERSAL

In the discussion that follows, all Old World monkeys are considered to belong to a single family, Cercopithecidae, of the "infraorder" Catarrhini. The leaf-eating monkeys may be separated as the subfamily Colobinae, while the nominate subfamily may be further divided into tribes: Cercopithecini for *Cercopithecus* and its allies ("*Miopithecus*," *Allenopithecus*, and *Erythrocebus*) and Papionini for the baboon/macaque/mangabey/gelada group and their extinct relatives. Geladas (*Theropithecus*) are clearly members of this tribe, although their "specialized" dentition tends to isolate them somewhat.

The Earliest Monkeys

The oldest fossils that can undoubtedly be allocated to Cercopithec-

idae are known from the East African Early Miocene. Pilbeam and Walker (1968) have reported an upper molar of cercopithecine aspect and a partial frontal bone said to be most similar to those of platyrrhines or juvenile colobines. On the basis of this association (at Napak, Uganda, dated to about 19 million years), they suggested a prior separation of the two modern subfamilies. In fact, however, the specimens merely reflect the expected ancestral cercopithecoid conditions for the known parts; that is, on the basis of comparative morphology irrespective of geologic age (see Schaeffer, Hecht, and Eldredge 1972), the ancestral cercopithecoid would be expected to have cercopithecine-like molars and a colobine-gibbon type of facial skull (Delson 1973, 1975).

More complete remains from the probably Middle Miocene Maboko Island local fauna suggest the presence of more than one "morph," although the distinction of two species of *Victoriapithecus* in this material by von Koenigswald (1969) is mostly based on incorrect interpretation of a portion of the sample. Further study in progress suggests that both colobine and cercopithecine specializations, as well as moderate adaptation to terrestrial life on the part of some cercopithecids (?early cercopithecines), had been developed by this time. No undoubted monkeys are known from Fort Ternan (L. Leakey 1968, to the contrary), but Hooijer (1963, 1970) reported a tooth of cercopithecine form from Ongoliba (Zaire, previously Congo) and Simons (1969) discussed *Prohylobates* from Wadi Moghara, Egypt; the latter is possibly close to *Victoriapithecus*. Little is known about the environment of the last two Miocene localities (Simons and Pilbeam 1972).

No complete study has yet been made of the main East African Early and Middle Miocene assemblages either, but rather more is known of the probable environment, especially for Rusinga Island. Much of the Lake Victoria region was dominated by large volcanoes rising 2,000 to 4,000 feet (about 1,000 meters) above the lake. The floral remains were interpreted by Chesters (1957) as indicative of gallery forest along streams, with more open country farther back, but Andrews and Van Couvering (1975) suggest that denser forest is more likely in light of both fauna and topography, as nearby volcanoes are heavily forested today. The majority of the cercopithecoid fossils are from Maboko, whose fauna is poorly known but appears somewhat distinct from Rusinga on the one hand and Fort Ternan on the other. It may be intermediate in age, but the dominance (among primates) of monkeys suggests a different local environment, possibly drier lowland savanna with deciduous groves.

Circum-Mediterranean Province

During the Late Miocene, further differentiation and dispersal of cercopithecids may have occurred in sub-Saharan Africa (see below), but the record is essentially restricted to the circum-Mediterranean region (Delson 1973). The best-known fossil cercopithecoid is *Mesopithecus pentelici*, hundreds of specimens of which have been recovered from the early Turolian locality of Pikermi, near Athens. Local faunas of similar age in Macedonia (Greek, Bulgarian, and Yugoslavian) and the Ukraine have also yielded *M. pentelici*, and single individuals are known from the possibly late Turolian assemblage at Maragha, Iran, and the possibly late Vallesian local faunas at Wissberg, Germany, and Baccinello, Italy (youngest vertebrate horizon). This species is clearly a colobine in terms of cranio-dental morphology, which suggests at least beginning development of the colobine digestive tract specializations for processing leaves; the postcranial remains indicate a habitus as terrestrial as that of *Presbytis entellus*.

Two different colobine species characterize the European Pliocene: the larger and even more terrestrial *Dolichopithecus rusciniensis* and the slightly smaller and probably more arboreal *Mesopithecus monspessulanus*. These two often occur in the same assemblages, spread across southern Europe from northern Spain to the Crimea; neither is found after the early Villafranchian, except for one tooth referred to *M. monspessulanus* from the probably middle Villafranchian Red Crag of England.

In northern Africa, two further colobine species are known in Late Miocene deposits, both associated with cercopithecines. At Marceau, Algeria, a small local fauna is dominated by cercopithecoid teeth: most are cercopithecine (macaque-like, but not clearly referable to *Macaca*), but the type of Arambourg's *Macaca flandrini* (1959) and some other teeth are in fact colobine, of apparently African affinity. The latest Turolian, (about 6 million years old, Cooke and Maglio 1972) assemblage from Wadi Natrun, Egypt, contains the skull and one isolated tooth of *Libypithecus markgrafi*, an African-type colobine, as well as numerous dental remains of a macaque (named *M. libyca*).

The slightly younger early Ruscian local faunas of Europe contain the first cercopithecines outside Africa, which also seem to be identifiably *Macaca*. This group gains in importance with time, becoming the only cercopithecoid in Europe during most of the Pleistocene and persisting apparently until the last interglacial (? Borgio, Italy), perhaps into the "postglacial" (*M. majori*, a small form at Capo Figari,

Sardinia). European fossil macaques ranged from England to the Caucasus and probably are closely linked phylogenetically to the modern populations of *Macaca sylvanus* of the Maghreb. A larger more terrestrial form (*Paradolichopithecus*) is known in France and Romania during the late Villafranchian; possible early members of this lineage occur in the same areas during the early Villafranchian (Delson 1971). More complete locality data on all circum-Mediterranean occurrences are given by Delson (1973, i.p.a.).

The climate record of the later Neogene in Europe is relatively well-known, at least on a large scale. The Middle Miocene would appear to have been characterized in general by a well-watered woodland environment (except perhaps at the end of this interval, in the typical Sarmatian of north-central Europe, where Thenius [1960] reported drier elements of flora and fauna). The typical Vallesian and Turolian succeed one another in two Spanish local basins, in which the former assemblage reflects continuity with the preceding Middle Miocene (with the addition of *Hipparion* and then murid rodents), while the latter evidences drying and replacement of "forest" by "steppe" mammals.

Tobien (1970b) has questioned whether this picture is typical of all of Europe or whether these two facies could have coexisted throughout the Late Miocene (his "Pontian") in different regions. He noted that most southern European assemblages (e.g. Pikerimi) were of predominantly open-country type and thus associated with the Turolian, but that at least some North African "steppe-savanna" local faunas (e.g. Oued el Hammam; no monkeys) were of Vallesian-equivalent age on the basis of mammalian stage-of-evolution. Tobien further suggested that most central European local faunas were of woodland or Vallesian aspect, but that if some could be shown to be Turolian in age, this would suggest that the two facies were time-successive all over the Mediterranean region.

Various small pieces of evidence do imply both earlier woodland assemblages in the south and later steppe/parkland in the north along with woodland. Thenius (1955) reported a forest-dwelling suid (Hünemann 1969) from central Greece; Hünemann (1968) indicated that some German sites (Wissberg) contain a suid indicative of more open country; and the latest vertebrate horizon (V-3) at Baccinello may be interpreted best as a late Vallesian intermediate environment. Both of the last two assemblages contain isolated teeth attributed to *Mesopithecus pentelici*, associated in the Balkans with an open-country fauna. Moreover, Kretzoi (1969) has reported late Turolian Hungarian assemblages with a woodland character but late mammalian and inverte-

brate species. Finally, the Austrian local fauna of Eichkogel is interstratified with molluscs of latest Pannonian (late Pontian, latest Turolian) age but includes many mammalian species similar to those of the Franco-Spanish early Turolian as well as more "advanced" ones (Daxner-Hock and Rabeder 1971; Daxner-Hock 1972); this seems best understood as a mixture of evidence from age and ecology, the latter leading to similarities with older environmental equivalents to the south and west, despite a younger actual age.

Taken together, the mammalian evidence indicates that the Vallesian was characterized throughout Europe by a continuation of faunas adapted to rather well-watered and well-wooded environments, but during the Turolian the climate generally became drier, as was the case in Spain (and as had been the situation in North Africa during at least part of the Vallesian). In northern and central Europe, however, woodland faunas persisted nearly to the end of the Miocene. At any given time, therefore, there would have been a gradient from well-watered deciduous (or even evergreen) woodland in the north, through parkland, scrub, and into a steppelike vegetation similar to that of the western Soviet Union, but more thermophilous and with gallery forests along watercourses; the dominant factor was probably a relative decrease in moisture (Butzer 1971: 71-75).

This suggestion from mammalian evidence is supported by the rarer paleobotanical results available. Grassland with moderately developed coniferous forest has been reported from the Turolian of Macedonia (Gillet and Faugères 1970), while a picture of progressive decrease in hygrophilous plants but retention of some evergreen forest on higher slopes has been painted for central Europe (see Knobloch 1970; Nagy 1970; Planderova 1971). On the other hand, the apparently late Turolian local fauna from Marceau (Algeria) was recovered from lignite deposits indicating relatively humid woodlands. It may finally be suggested that the tectonically controlled Mediterranean desiccation at the end of the Miocene accentuated the independent dehumidification of southern Europe (which had gone on for some time already) through removal of the potential evaporation source for precipitation.

At the beginning of the Pliocene, the situation reversed somewhat, with the peri-Mediterranean lands becoming much more humid, while the drying trend may have persisted longer in the north. Kretzoi (1969) has suggested that the mammal fauna of the Ruscinian (and the early Villafranchian, following Tobien [1970a]) is of monsoon-forest aspect. Michaux (1971) also considered that the great abundance of murid rodents in Spain and southern France at this time was due to high humid-

ity, and that a drying during the Pleistocene led to the reduction of this group in Europe; although this seems to have been the case, it leaves unexplained the great increase of murids during the equally dry later Turolian. Furthermore, Lobreau-Callen and Suc (1972) have been able to determine a pollen spectrum closely analogous to that of the monsoon/dry season climate of North Vietnam, at a middle Ruscinian locality (Celleneuve/Montpellier) where *Macaca*, *?Mesopithecus*, and *Dolichopithecus* have been recovered.³ The earliest Villafranchian locality of Vialette (with "*Paradolichopithecus*" and dated to earlier than 3.8 million years) has recently yielded a pollen flora of more modern aspect than earlier sites, indicating a relatively open forest with pine, juniper, and beech, perhaps on neighboring slopes (Meon-Vilain 1972). Levels above and below the mammal-bearing horizon were more densely wooded, but grasses were quite common (35 percent) in the matrix surrounding the bones, despite the quantities of forest-dwelling tapir, deer, and mastodont recovered (Viret 1954; Guérin 1972). Finally, both *Dolichopithecus rusciniensis* and *?Mesopithecus monspessulanus* have been found in the contemporaneous lignites of Baraolt-Capeni (Romania), further suggesting a forest facies at this time.

As Tobien (1970a), Azzaroli (1970), and Kretzoi (1969), among others, have noted, the major environmental break in the Villafranchian is neither at its beginning nor at the middle/late transition which approximates the Plio-Pleistocene boundary, but at the early/middle transition when the humid forest retreated again to allow the spread of holarctic open-country environments. At this time, also, it becomes feasible to attempt correlation with the Netherlands pollen sequences most recently summarized by van der Hammen, Wijmstra, and Zagwijn (1971). They noted that the first important cooling in the paleobotanical record occurred during the Pretiglian (roughly middle Villafranchian), at which time many of the older, southeast Asian forms disappear from Europe for the last time. There may also have been tundra in the North Sea-Baltic region at this time, but mammal faunas do not clearly reflect such conditions. The Tiglian of the Netherlands is essentially the late Villafranchian of this scheme, as Tegelen also yields mammals of that age, including macaque. Floras from Tegelen and from Senèze (Elhaï 1969) indicate relatively warm climate and de-

³ On the other hand, Heintz (1971) has reported the strongly open-country gazelle from the same locality. More complete review of the total mammalian assemblage at some Ruscinian localities might indicate which animals were most common, at least in the vicinity of the recovered death assemblages.

ciduous forest, with periods of open-country parkland ("steppe").

During the Pleistocene in Europe, macaque (the only cercopithecoid known) is widespread in relatively warm, interglacial or "interstadial" times but never present in faunas of distinctly cold aspect. This feature has been especially discussed by Bartolomei (1969)⁴, as well as by Hinton (1908), Bernsen (1930), and Viret (1954). The corresponding assumption made by Kurtén (1963) and Forsten (1968) that the presence of monkeys also implies forest or woodland is not supported by faunal evidence. The mammals associated with macaque, as with earlier monkeys in Europe, may be of forest or steppe type, and the latter seems more common during the Pleistocene (as well as the Late Miocene).

Asia

An essentially similar climatic history seems to have characterized much of Asia, although details differed. This region is treated more specifically by Prasad (1975), but a few comments may be made here. Comparison of *Hipparion* stage-of-evolution in particular and of total faunal aspect in general (Hussain i.p.) suggests that the Vallesian is closely time-equivalent with the Nagri "age" in the Siwalik region. The subsequent Dhok Pathan probably equates not only to the Turolian, but to the Ruscinian and possibly part of the Villafranchian as well (Maglio, personal communication). Tattersall (1969a 1969b; Leakey and Bazett 1969) has indicated that the Nagri mammals are of woodland type, as are those of the Chinji; moreover, he noted lithological evidence (from Krynine 1937) for seasonal rainfall in a forested environment during Nagri time, with development of prairie and aridification during Dhok Pathan time. Prasad (1971) has confirmed these results with paleobotanical evidence. It must be recalled, however, that the Siwalik "faunas" each derive from units of rock thousands of feet (more than 1,000 meters) thick, as opposed to the relatively brief spans sampled by isolated European localities. On the one hand, it is possible to speak of "Nagri time," represented by a continuous sequence of rock and a faunal assemblage, but on the other hand, direct associations between specimens or taxa are usually not certain.

⁴ Bartolomei's paper is a useful contribution reviewing the distribution of macaque and porcupine (*Hystrix*) in the European Plio-Pleistocene and concluding that both forms are good indicators of a relatively warm climate. Two minor errors in his distribution list for macaques may be corrected here: neither Villany-3 nor Sutto (both Hungary) have yielded any cercopithecoid. Other taxonomic errors in terms of Ruscinian and older localities and a more complete listing may be found in Delson (i.p.a.).

The earliest known cercopithecoid fossils from the Siwalik sequence are of Dhok Pathan age, subsequent to any certainly placed hominoids. Although these few specimens have been variously assigned to *Macaca*, *Semnopithecus*, and *Cercopithecus*, Simons (1970, 1972) correctly identified several of them as colobine. All specimens from the Dhok Pathan published or known to me can be referred to a single colobine species, which may be termed *?Presbytis sivalensis* (Lydekker). This form may have been quite similar to *Mesopithecus pentelici*, of equivalent age and (probably) environment in Europe, but as yet only dental fragments are known. The two partial mandibles from the next younger Tatrot Formation have previously been identified as colobines (or ignored, as by Simons [1970, 1972]), but they in fact represent the oldest cercopithecine in Asia, *Macaca paleindicus* (Lydekker). Without further study and revision of both the mammal species and their relative stratigraphic placement, little can be said about the environments of either the Tatrot or the succeeding Pinjor.

Younger Asian cercopithecoid fossils are known from India, China, Vietnam, Laos, Indonesia, and Japan. The most interesting of these are a maxilla from the Pinjor and some dental and postcranial specimens from China which may be referred to the genus *Procynocephalus*. Jolly (1967) has shown that the long bones and foot indicate a highly terrestrial adaptation, while the dentition is clearly cercopithecine. This form may have evolved locally from *Macaca* in parallel with *Paradolichopithecus* of similar age, or the two lineages may be specially related (Simons 1970, 1972). From the same horizons and also from Tung-Lang, North Vietnam, the Chou-Kou-Tien caves, and the *Gigantopithecus* caves come specimens of one or more large species of *Macaca* which seem closest to the modern *M. thibetana*-*M. assamensis* group (of Fooden 1971), possibly indicating a wider range for this type than today. Most other specimens are smaller and appear closely related to the modern inhabitants of the local regions.

Africa

Although *Libypithecus* and the Marceau colobine (*?Colobus flandrini*) are apparently of African aspect and relationship, sub-Saharan Africa is as yet nearly barren of cercopithecids from the Middle Miocene until the Pliocene (one tooth has been reported from the early Late Miocene of Ngorora by Bishop and Chapman [1970] and the isolated cercopithecine tooth from Ongoliba may also be of Late Miocene age).

Moreover, very little can yet be discussed about the paleoenvironments of the regions producing fossil monkeys in the Pliocene and Pleistocene, in part because many East African localities are still being worked intensively and no complete faunal lists are available and in part because of the lack of comprehensive studies of the long-known southern African cave sites. The few papers reviewing the fossil mammals of the latter area (e.g. Sampson 1971) have not attempted specific environmental reconstructions, but most do tend to agree with the granulometric-petrographic work of Brain (1967) in suggesting a ranking of relative aridity of the major sites from Taung (dry) through Sterkfontein, Makapan, Swartkrans, and Kromdraai (see also Peabody 1954). This is also approximately a time order, with Sterkfontein or Makapan the oldest, but it is unlikely (although possible) that a single drying trend occurred through the time span represented (perhaps 3 to 1.5 million years [Cooke and Maglio 1972]).

As at most African localities, the dominant groups of cercopithecids at these sites are the baboons and geladas – the large Papionini. The moderately large, probably (semi-) arboreal colobine *Cercopithecoides*, however, is represented in almost all of the caves. Several taxa allocated to the genus *Parapapio* are most common at the older localities, where a range of sizes has been divided into three “species” (Freedman and Stenhouse 1972). Animals with more typically *Papio*-like facial morphology are more abundant at the three younger sites (and at several others of less certain age, e.g. Bolts Farm), ranging from small species to the very large forms with baboon- (not gelada-) type teeth, *Dinopithecus* and “*Gorgopithecus*.” True geladas, *Theropithecus* (*Simopithecus*) species, have been reported only from Makapan and Swartkrans as yet.

In eastern Africa, the same taxonomic dominance occurs. Small monkeys, both cercopithecines of the *Cercopithecus* or true *Cercocebus* type and colobines (?*Colobus* sp.) have been noted from East Rudolf (Cooke and Maglio 1972), Omo (Eck and Howell 1972), and Kanam (Delson 1975). *Theropithecus* species are common (only or most abundant form) at most East African localities; the majority of these are of waterside environment (Jolly 1972), with the exception of the two sites lacking gelada, Kanam and Laetotil (Delson 1975). As yet no very large baboons have been reported, but *Papio* or *Parapapio* spp. are known from many localities, spanning an age range from Lothagam (latest Miocene or earliest Pliocene) to the present. The possible replacement of gelada-like forms by *Papio* baboons has been discussed by Jolly (1970, 1972) in an environmental framework

for East Africa and may be reflected in the more sketchy South African evidence as well. Large colobines are also present at some eastern localities: *?Cercopithecoides* in the Omo and the probably related *Paracolobus* in the upper Chemeron Formation and probably at Laetolil and East Rudolf (R. Leakey 1969; M. Leakey, personal communication; Delson 1975).

The distinction between the moister, possibly more open environments favored by the early *Theropithecus* and the drier mixed parkland in which fossil *Papio* and *Parapapio* are found is interesting but may reflect only part of the story. The African Papionini today include mangabeys and mandrills of denser woodland as well, and all four of these "types" are distinct both geographically and morphologically from the more adaptable Asian (and northwest African) macaques. The latter, it will be recalled, first appeared in North Africa during the latest Miocene, then in Europe in the early Pliocene, and in Asia in the late Pliocene, or Pleistocene. Possibly at the same time that the peri-Mediterranean lands suffered great aridity as a result of the combination of tectonically caused Mediterranean desiccation and the previously begun Late Miocene deterioration of climate, the region of the present Sahara also suffered a drying, perhaps to the extent of forming a temporary barrier to migration between northern and east-central Africa. The Sahara has generally been considered to be of much younger age (Moreau 1963; Monod 1963), but there is little evidence for its earlier condition; Beucher (1967) described a flora of "Pliocene" age in the northwest Sahara that included elements of both tropical and circum-Mediterranean affinity but was dominated by desertic types. A hypothesis of an ecological barrier across the region of the present Sahara in the Late Miocene would explain the differentiation of African and Eurasian cercopithecines at approximately this date and could be tested by comparison with other groups.

Historical Zoogeography

The dispersal pattern of cercopithecids has been discussed briefly by Napier (1970), who has suggested that the early cercopithecids were essentially colobines, one group of which gave rise to cercopithecines in Eurasia during the early Miocene. This hypothesis appears to be based mostly on the view that "colobines are essentially arboreally adapted in locomotion and diet and it is well-nigh inconceivable, on anatomical and physiological grounds alone, that they should have evolved from

a ground-living stock" (Napier 1970: 79). This argument agrees neither with the fossil evidence nor with morphological considerations suggesting that colobine teeth (and related digestive tract features) are more "specialized" than those of cercopithecines. Moreover, because of their behaviorally linked plasticity, postcranial elements are notoriously dangerous to use in studying relationship or ancestry. Finally, there is nothing to require that the common ancestor of colobines and cercopithecines had to be effectively one or the other already.

A more realistic approach to the historical pattern of Old World monkey deployment might begin with Napier's (1970) suggestion that the eating of leaves as well as fruits in a deciduous forest environment would prolong the time during which food was plentifully available, thus conferring a selective advantage. Ancestral (as yet unknown) monkeys that occupied this mixed leaf-and-fruit niche in the early Miocene might by the mid-Miocene have diverged into the source groups for the two subfamilies: early colobines concentrating on leaves and developing specialized dentitions and digestive tracts, and early cercopithecines retaining the earlier food preferences or re-emphasizing fruits, as well as concentrating on development of terrestrial locomotion with concomitant evolution of longer faces and cheek pouches.

As partly discussed by Van Couvering (1972, personal communication) and others, it is possible to envisage the dispersal of catarrhines in general as a series of sequentially replacing migrations out of Africa. The small apes such as *Pliopithecus* (and *Limnopithecus*) first occur in the earliest Miocene of Africa and appear in Europe by the early Middle Miocene, becoming most common late in this period, before waning to a last occurrence in the late Vallesian. *Dryopithecus* species are first found late in the African Early Miocene, entering Europe by mid-Middle Miocene, and having a widest Eurasian distribution in the late Middle and early Late Miocene (Chinji-Nagri), but probably not lasting into the Turolian/Dhok Pathan of temperate regions. Both of these genera were basically forest-adapted, *Dryopithecus* possibly semiarboreal to as terrestrial as chimpanzees; the presence of *Ramapithecus* at this time implies that it may not have been closely linked to the still rare open country.

By the later Vallesian, semiarboreal colobines had entered Eurasia, developing further terrestrial adaptations in Europe during the Turolian (*M. pentelici*) and present but of uncertain habit in Asia during Dhok Pathan time. It was probably the most terrestrial colobines that departed Africa, leaving more arboreal types to radiate as an African natural group, still connected across the Sahara region. Drying on both sides

of the Mediterranean at the end of the Miocene may have led to a tripartite division of the Papionini, which had already diverged from the more arboreal Cercopithecini.

The ancestral macaques were able to enter Europe by the earliest Pliocene, reaching Asia late in the epoch. Ancestral *Theropithecus* (first known as fossils in eastern and northern Africa by 4 million years ago) may have diverged from other African Papionini as a wet-lowland adaptation, leaving *Parapapio*-like forms to diversify into the several living and extinct dentally typical genera. The late exit of papionins suggests that they may have been too terrestrially committed by the Vallesian to follow the colobines across a semiforested Afro-Asian corridor at that time, while cercopithecines were too arboreal.

Finally, a fifth catarrhine group, early man (already *Homo* cf. *erectus*?), may not have been able to depart Africa until the earliest Pleistocene because of the return of wooded conditions in western Asia during the Pliocene.

PROGNOSIS FOR PALEOBIOLOGY

Research of the type summarized here obviously draws upon, but also may contribute to, studies of modern relatives. The comparative anatomical study of joint surfaces and limb-element proportions provides quantifiable data that may indicate similarities between fossil forms and living analogues in terms of postcranial adaptations and the possible range of movements and thus behaviors of which the animals were capable.

Five fossil cercopithecoid species are sufficiently represented by postcranial specimens to suggest something of their way of life. The European Late Miocene (Turolian) *Mesopithecus pentelici* is best known in this respect, and preliminary studies of its limbs indicate not only colobine affinities, but terrestrial adaptations as pronounced as in the most terrestrial living colobine, *Presbytis entellus* (Delson 1973; Gaudry 1862; Gabis 1960). Its occurrence at Pikermi and elsewhere in association with a fauna and flora of open parkland type suggests that *Mesopithecus* may have slept in gallery forests, traveling terrestrially between isolated stands of deciduous feeding-trees and foraging on ground products as well. The analogy with *Presbytis entellus* as studied by Beck and Tuttle (1972) and others (reviewed by Dolhinow 1972) may be rather close.

The larger European colobine *Dolichopithecus ruscinensis*, of the

Pliocene (Ruscinian and early Villafranchian), was even more terrestrially adapted (Delson 1973). Although the mosaic of character states seen in this form is not the same as that found in any known cercopithecine, it might have been as agile terrestrially as a mandrill or Barbary ape. Its presence in the "monsoon forest" of the Ruscinian suggests further ecological similarity with large semiterrestrial cercopithecines. On the other hand, an even larger extinct colobine, East African *Paracolobus chemeroni*, shows a few morphological parallels with terrestrial forms, but its feet and limb proportions indicate a fully arboreal habitus, although more complete study is required to draw further analogies.

Two fossil cercopithecines have also been studied (Jolly 1967, 1972) in terms of postcranial adaptations: Asian *Procynocephalus* and African "*Simopithecus*." The former genus is represented by limb bones published by Teilhard de Chardin (1938) from locality 12 of Chou-Kou-Tien, which Jolly interpreted as being about as terrestrially inclined as those of *Papio* species. "*Simopithecus*" includes the most ground-adapted species of cercopithecoid yet known, especially the late large forms of East Africa with massive limbs and lengthened humerus. These animals went well beyond the modern gelada in their morphological adjustments to terrestrial life and probably represent the mainstream of *Theropithecus* evolution, as opposed to the relict-refuge distribution of *T. gelada* today.

It is clear that none of these observations on the habits of fossil animals could be made without study of the skeletons of modern forms by both paleontologists and anatomists. But the right sorts of observations on the activity patterns of living, behaving primates are also of great importance, especially as they cannot usually be made by the paleontologist himself. Studies of cineradiographic films of monkeys chewing or locomoting are also useful, but they do not necessarily reflect an animal's natural range of actions in its own habitat. For that information, we must rely on ecoethologists (in the widest sense).

Among the types of observations that might be most useful in interpreting fossils and their anatomy (as well as relationships and taxonomy of both living and extinct species) we can list:

1. Percentages of time spent by animals in different locomotory modes — either typical classes (e.g. terrestrial quadrupedalism, branch-walking, arm-support stance, etc.) or species-specific modes employed by the animals as observed and delimited *a posteriori*.
2. The activities that employ these modes — feeding, travel, play, sleep, etc. Observation of the use of the thumb or other body elements,

such as those made by Lorenz (1971), could be of great use in deciphering relationships, as of colobines with differentially reduced thumbs (*Mesopithecus*, for example, has an ancestrally long thumb, intermediate between those of *Nasalis* and macaques, at the extremes of their respective subfamilies).

3. Inter- and intraspecific differences in feeding behavior (e.g. in mastication time and concentration of effort for different food items); food preferences among differing consistencies; types of food preparation (husking, shelling, stripping) required; the use of fingers, teeth, etc., in holding, preparing, and transporting food objects.

4. Especially important, the range of activities and variations observed. The ecological variability found in *Presbytis entellus* (or *Papio* of the *cynocephalus* group), for example, has been shown to be reflected in its behavior, yet it would appear that its morphology is constant. On the other hand, even that statement needs to be checked, for although Simons (1970: 110) states that *P. entellus* is "fully arboreally adapted," my examination of a limited number of skeletons suggests that it is certainly more terrestrially adapted than any other living colobine, as in fact has been observed of its behavior. The interaction, feedback, and reinforcement of paleontological-anatomical observations and ethological ones will eventually allow for a true understanding of primate paleobiology.

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Age in M.Y.	Worldwide epochs and sub-epochs	"Standard" (marine) stages/ages	Western — Hungary, Vienna basin	Paratethys sequences	Eastern — Crimea, U.S.S.R.	Previous European "stages" (by M.Y.) ^a	Small mammal zones & sub-zones (after Thaler et al.)	European land mammal ages (subdivisions informal)	Age in M.Y.
0	LATE PLEISTOCENE	FLANDRIAN				?		(RECENT) OLDENBURGIAN	0
1	MIDDLE PLEISTOCENE	TYRRENIAN				CROMERIAN		OLDENBURGIAN	1
2	EARLY PLEISTOCENE	SICILIAN (EMILIAN) CALABRIAN				VILLA-FRANCIAN		FINAL BIHARIAN	2
3	LATE PLEISTOCENE	PLACENZIAN				ASTIAN		VILLA-LATE	3
4	EARLY PLEISTOCENE	TABLIANIAN (ZANCIAN)	RUMANIAN DACIAN	KUJALINIKIAN			SEYNES PER-SETE PIG-NAN HAUTMAGNE ALCOY	IRAN-MIDDLE	4
5								CHIANG	5
6								EARLY	6
7	LATE							CHIANG	7
8								EARLY	8
9	MIOCENE							EARLY	9
10								EARLY	10
11								EARLY	11
12	MIDDLE	SERRAVALLIAN						EARLY	12
13								EARLY	13
14	MIOCENE							EARLY	14
15								EARLY	15
16								EARLY	16
17								EARLY	17
18	EARLY	BURDIGALIAN						EARLY	18
19								EARLY	19
20	MIOCENE							EARLY	20
21								EARLY	21
22								EARLY	22
23	LATE OLIGOCENE	CHATTIAN						EARLY	23

^a Previous terminology is general usage of early to middle 1960's, correlated by estimated ages of boundaries in M.Y.

Age in M.Y. Circum-Mediterranean climate and environment

Selected circum-Mediterranean fossil mammal assemblages

Asian (Chinese, Indonesian, Vietnamese, Siwalik) nameless, Siwalik

Selected sub-Saharan African fossil mammal assemblages (east to left, south to right)

Age in M.Y.

Localities in all capitals include fossil cercopithecoidea; others do not

0	HEM/Warm/FLANDRIAN HOLSTEIN/Riss CROMERIAN/Mindel WAALIAN/Menapian Eburonian-Cool TIGLIAN / Cool WARM PARKLAND Preiglian COOLER MIXED STEPPE & OPEN WOODLAND PARKLAND/FOREST MOIST BUT SEASONAL	CAPO FIGARI BORGIO ALGERIA MOROCCO HIPPENLOCH MONTSAUNES ORGNAC GRAYS CROMER TERMIENE ?UBEDIYA LESCALE MOSBACH VOIGTSTEDT VALLONNET BETFLA2 Simelles Farneta Imoth UPPER VALDARNO (MONTEVARCCHI) SENEZE THEGHELEN GRAUNGEANU Olivola PUEBLA DE VALVERDE Le Coupet ST. VALIER Roccaeyra BRIMBA MUGELLO ??COVA BONICA?? Ebanates ?AIN JOURDEL? MALUSTENI BALARUC-2 BAROT-KOPEC VILLAFRANCA VIALETTE HAINACKA LAYNA WOLFKESHEIM CSARNOTA-2 PERPIGNAN IVANOVCE LAC ICHKEUL MONTPELLIER CELENEUVE OSZTRAMOS-1 Alcov Hauterives BALTAVAR La Alberte CASINO POIGARDI Lisseu Eichkogel WADI NATRUN Arguillo PESTENTLORINC Sahabi GRAVITELLI HATVAN Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	C H U O K O U T E E N ^o	U.C. 2 1.3 13 12	JAPAN TRINIL TUNGLANG? KWANGSI HONAN DIETS PINJOR YUSHE TATROT	GAMBILIAN O IV L D U U V I	KANIERA Isimila OLOROESAUILE HOPEFIELD KROMDRAAI SWARTKRANS TAUNG BOLTS FARM MAKAPAN	0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
1	WELL-WATERED (?) WOODLAND—MORE GALLERY-TYPE IN CENTER/NORTH	La Grive Fissures later classic Opole ?plakin? St. Gaudens Armanes IX	Chinli (WOODLAND)				12 13 14	
2	DECIDUOUS AND MIXED FORESTS EVERGREENS	Oeningen Manchones Samsen Goriach Neudorf adM (Sundberg) Neudorf an der March (Spalte) Franzensbad Langenmoosen Pont-Levoy Mantelian Vieux Collonges La Romieu Orechov Wintershof-West Tuhorice Estrepouy Lambert Caunelle Laugnae WADI MOGHARA Cetina de Aragon St.-Germand-le-Puy Jebel Zelten Paulhac Boudry Westerwald Codelert	Kamliat ? Bugli		Fort Ternan OMBO MABOKO LOPEROT RUSINGA (?cercopithecid) NAPAK Songhor Koru Karungu Bukwa	14 15 16 17 18 19 20 21 22 23		
3	"MONSOON" FOREST MEDITERRANEAN DISJUNCTION N. EUROPE DRY??	Qued el Hammam ??Yautusee? Nombrevilla Eppelsheim Howenegg ?Upper Beglia Fm? Giggenhausen Baccinello VI-2 Anwil La Grive Fissures later classic Opole ?plakin? St. Gaudens Armanes IX	Chinli (WOODLAND)				12 13 14	
4	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
5	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
6	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
7	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
8	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
9	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
10	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
11	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
12	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
13	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
14	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
15	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
16	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
17	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
18	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
19	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
20	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
21	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
22	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		
23	SOUTHERN EUROPE DRIER TO ?ARID	Mont Leberon Samos (Upper level) ?MARGHA? MARCEAU Melka el Ouidane Kofidisch Comend Los Mansuetos Samos (Lower level-1-4)	DHOK PATHAN (RELATIVELY OPEN, DRY ENVIRONMENT)		Mpesida ONGOLIBA	7 8 9 10		

^b Warm (interglacial) periods of the "Glacial Pleistocene" are in capitals, cool or cold (glacial) ones in upper case and lower case; dashed lines separate earlier phases; indications given for Siwalik sequence when possible (see text).

^c Numbers refer to localities in Choukoutien; U.C. is Upper Cave.