

## MOLAYAN (AFGHANISTAN) AND THE KHAUR SIWALIKS OF PAKISTAN: AN EXAMPLE OF BIOGEOGRAPHIC ISOLATION OF LATE MIOCENE MAMMALIAN FAUNAS<sup>1</sup>

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### ABSTRACT

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The mammalian fauna from Molayan (Afghanistan) is compared with that of the Khaur Siwaliks of Pakistan. The detailed comparison reveals that, in spite of the geographical proximity of the two faunas, there is no recorded species in common between them. The differences cannot be attributed to a chronological gap; they can be partly explained by a difference in the palaeoenvironments. Another cause of the faunal differences must have been the existence of a mountain barrier separating the Indian subcontinent from Afghanistan. As a consequence, the Late Miocene hominoid primates from the Indian subcontinent were isolated from the Greek and Turkish ones.

### INTRODUCTION

Until 1976, the Tertiary mammals of Afghanistan were known only by scarce fossil remains which had been found in the Bamian (RAUFI & SICKENBERG, 1973) and Laghman-Jalalabad (LANG & LAVOCAT, 1968) basins. Since 1976, many mammal-bearing fossil localities have been discovered in several Neogene basins of Afghanistan (HEINTZ ET AL., 1978a; 1978b; 1978c; SEN ET AL., 1979; BRUNET ET AL., 1980; see Fig. 1). The main localities have been placed in a local biochronological sequence (Table 1), and their ages have been discussed (HEINTZ ET AL., 1979; BRUNET ET AL., 1981). Age correlations with other Neogene localities of Eurasia are proposed on Table 2.

The most important fossil locality of Afghanistan is Molayan, in the Khurd Kabul Basin. It is located 30 km southeast of Kabul, at a height of 2 300 m, at the foot of a mountain range (3 000 to 4 000 m high) which lies between Afghanistan and Pakistan. The 1 m thick fossiliferous level of Molayan yielded over 4 000 specimens. Up to now 24

mammal taxa have been identified. A Late Miocene, more precisely, Turolian age (around 8 Ma) has been established on the basis of the faunal composition, of the evolutionary stage of certain lineages, of the Afghan biochronological context, and of comparisons with faunas from Greece, Turkey, and mainly from Maragha, Iran (BERNOR ET AL., 1979; CAMPBELL ET AL., 1980).

The Molayan fossil locality is situated 3 000 km east of Maragha (Iran) as well as 300 km west of the Potwar Plateau, from which the well-known Siwalik faunas of Pakistan have been recovered. The geographical proximity of Pakistan invites comparison of the Molayan fauna with that of the Pakistan Siwaliks rather than with faunas geographically much more distant. This has led us to take part in the field work of the Geological Survey of Pakistan and Harvard University in the Siwaliks of the Potwar Plateau. There, the sedimentary formations, over 3 000 m thick, cover a time interval – Pinjor to Chinji – ranging from 1 to 12.5 Ma. The number of palaeontological records, and especially the amount of fossil material which has been collected over the past twelve years, are impressive but the biostratigraphy is not yet fully resolved, so it is difficult to find a faunal unit that would be restricted enough to allow a strict comparison with the fauna from the Molayan fossiliferous level. The faunal list which, for the time being, is the more suited to meet that requirement, is the one which has been published by BADGLEY

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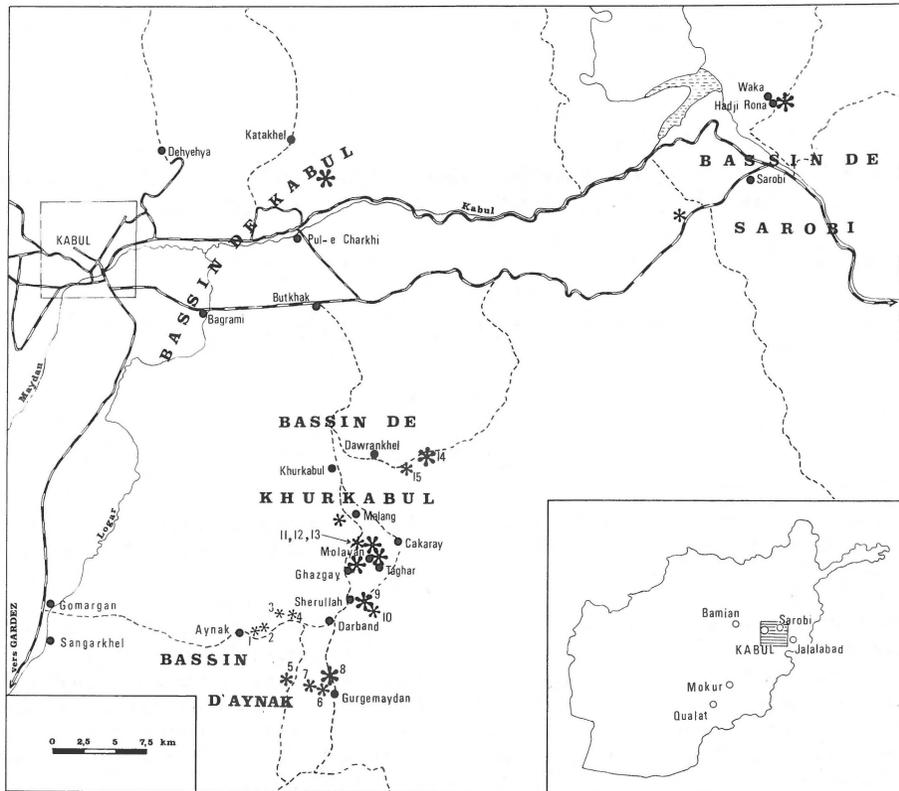


Fig. 1.

Map of the mammal-bearing Neogene localities of the Kabul, Aynak, Khurd Kabul and Sarobi Basins. The sizes of the stars indicate the richness and importance of the localities.

& BEHRENSMEYER (1980), based on data, sometimes new, contributed by many scientists. That list deals with the fauna recovered in the Khaur region from a stratigraphic sequence characterized by a marker sandstone called the 'U sandstone', the age of which is now estimated at about 8 Ma according to TAUXE's (1979) palaeomagnetic data.

Consequently, the most precise comparison possible here proposed concerns a fauna collected in Afghanistan from a sediment layer, only 1 m thick, and, in Pakistan, a fauna collected from a 160 m thick sedimentary deposit, that thus probably corresponds to a longer time interval. Moreover, in Molayan, the fossiliferous concentration is spread over an area of 800 m<sup>2</sup>, whereas the more scattered fauna from the 'U' interval has been collected from a band of sediment about 30 km long and varying in width according to the dip of strata – that is to say, from a much larger area.

## COMPARISON

### Primates

In Molayan, the primates are represented by an incomplete lower jaw and a P<sub>3</sub> of *Mesopithecus pentelicus* (HEINTZ ET AL., 1981). Lorisidae (JACOBS, 1981) and hominoid primates (*Ramapithecus*, *Sivapithecus*, *Gigantopithecus*), which are well represented in Pakistan (PILBEAM ET AL., 1980), are unknown from Afghanistan.

### Insectivora

In Molayan only a lower jaw of *Erinaceus* has been found. In the Potwar Plateau the presence of Erinaceids has been reported without further detail, hence it is impossible for the time being to determine the differences or similarities between these forms. In the Potwar fauna, the families Soricidae and Tupaiidae have been reported; they are not known from Molayan.

### Tubulidentata

Unknown in Molayan; represented in the Potwar Plateau by *Orycteropus browni*.

### Rodentia

In the Potwar Plateau, the families Sciuridae (4 taxa), Gliridae, Ctenodactylidae (*Sayimys*) and Rhyzomyidae (*Kanisamys* and *Rhyzomyides*) are represented. None of them is known in Molayan. However, rhyzomyids represented by *Rhyzomyides carbonnelli* (BRANDY, 1979) have been collected for the first time in Afghanistan, in the early Pliocene deposits of Pul-e-Charkhi, approximately 5 Ma in age (BRUNET ET AL., 1980). In contrast, the gerbillid *Pseudomeriones* n. sp. and the hystricid *Hystrix* n. sp., which exist in Molayan, are lacking in the Potwar fauna, about 8 Ma ago.

Table 1  
Biochronology of the Neogene mammal-bearing fossil localities of Afghanistan.

	Ma	Continental stages		Afghan fossil localities
LOWER and MIDDLE Pliocene	3	Ruscinian	U.	Sarobi (Sarobi) HADJI RONA (Sarobi) ? Laghman-Jalalabad ? Bamian Dawrankhel 14 (Khordkabal) DAWRANKHEL 15 (Khordkabal)
			L.	PUL-E CHARKHI (Kabul)
UPPER MIOCENE	5.5	Turolian	U.	Gurgemaydan 5, 6, 7, 8 (Aynak) MALANG (Khordkabal)
			M.	Ghazgay 12 & 13 (Khordkabal) MOLAYAN (Khordkabal)
			L.	GHAZGAY (Khordkabal) Ghazgay (Khordkabal) TAGHAR (Khordkabal)
	9	Vallésian	U.	SHERULLAH 9 (Khordkabal) Sherullah 10 (Khordkabal)

Table 2  
Correlation of the main mammal-bearing Neogene localities of Afghanistan with other Eurasian localities.

	Ma	Continental stages		Main Afghan fossil localities	Correlations
LOWER AND MIDDLE Pliocene	3	Ruscinian	U.	HADJI RONA DAWRANKHEL 15 & 14	CALTA (Turkey) MARITSA (Greece) D.P. 13 (Pakistan)
			M.		
			L.	PUL-E CHARKHI	
UPPER MIOCENE	5.5	Turolian	U.	MALANG	PIKERMI (Greece) U SANDSTONE (Pakistan) MIDDLE MARAGHA (Iran)
			M.	MOLAYAN	
			L.	GHAZGAY TAGHAR	
	9	Vallésian	U.	SHERULLAH 9	YGSP 450 & 311 (Pakistan)

Table 3  
List of the mammals from Molayan (Afghanistan), compared with that of the 'U sandstone', Potwar Siwaliks, Pakistan.

AFGHANISTAN -MOLAYAN	PAKISTAN-U. SANDSTONE (C. Badgley & A.K. Behrens- meyer, 1980)	AFGHANISTAN -MOLAYAN	PAKISTAN-U. SANDSTONE (C. Badgley & A.K. Behrens- meyer, 1980)
	PRIMATES		PROBOSCIDEA
Cercopithecidae <i>Mesopithecus pentelicus</i>	Lorisidae (Jacobs, L. 1981) <i>Nycticeboides simpsoni</i> Ramapithecidae <i>Gigantopithecus</i> cf. <i>bilaspur- ensis</i> <i>Sivapithecus indicus</i> <i>Ramapithecus punjabicus</i>	Gomphotheriidae Tetralophodont gomphotheriid indet. Deinotheriidae <i>Deinotherium</i> sp. of very large size	Gomphotheriidae <i>Choerolophodon corrugatus</i> <i>Stegolophodon</i> sp. Deinotheriidae
	INSECTIVORA		HYRACOIDEA
Erinaceidae <i>Erinaceus</i> sp.	Erinaceidae Soricidae Tupaïidae	<i>Pliohyrax</i> n.sp.	
	TUBULIDENTA		PERISSODACTYLA
	Orycteropidae <i>Orycteropus browni</i>	Chalicotheriidae <i>Ancylotherium pentelicum</i> Rhinocerotidae <i>Dicerorhinus orientalis</i>	Chalicotheriidae <i>Chalicotherium salinum</i> Rhinocerotidae <i>Brachypotherium perimense</i> <i>Chilotherium intermedium</i> <i>Gaindatherium browni</i>
	RODENTIA	Equidae <i>Hipparion</i> sp.	Equidae <i>Cormohipparion theobaldi</i> ' <i>Hipparion</i> ' <i>antilopinum</i> ? <i>Hipparion</i> sp.
Muridae  <i>Karnimata</i> n.sp.	Muridae <i>Progonomys</i> sp. <i>P. debruijni</i> <i>Karnimata darwini</i> <i>Parapodemus</i> sp. Rhizomyidae <i>Kanisamys sivalensis</i> <i>Rhizomyides</i> cf. <i>R. nagrii</i>	Suidae <i>Microstonyx major</i>	ARTIODACTYLA Suidae <i>Tetradocodon magnus</i> <i>Hippopotamodon sivalense</i> <i>Lophochoerus nagrii</i> <i>Propotamochoerus hysudricus</i> Tayassuidae <i>Schizochoerus gandakasensis</i> Anthracotheriidae <i>Anthracotherium punjabiense</i> <i>Merycopotamus dissimilis</i> Tragulidae <i>Dorcabune nagrii</i> <i>Dorcatherium majus</i> <i>D.</i> sp. indet. (small)
Hystricidae <i>Hystrix</i> n.sp. Gerbillidae <i>Pseudomeriones</i> n.sp.	CREODONTA <i>Metapterodon</i> n.sp.	Cervidae Absent in Molayan Present in Taghar cf. text) Giraffidae <i>Palaeotragus</i> sp.  Bovidae <i>Miotragocerus</i> n.sp.  <i>Gazella</i> sp. cf. <i>Graccokeryx</i> sp. <i>Protoryx</i> n.sp. cf. <i>Prostrepsiceros</i> n. sp. Bovid indet. (small size).	Cervidae Absent Giraffidae <i>Bramatherium megagephalum</i> <i>Giraffokeryx punjabiensis</i> Bovidae <i>Miotragocerus punjabicus</i> <i>Selenoportax vexillarius</i> ? <i>Pseudotragus</i> sp. <i>Elachistoceras khauristani</i> <i>Gazella</i> sp.
	CARNIVORA		
Hyaenidae <i>Adcrocuta eximia</i> <i>Ictitherium</i> ( <i>Ictitherium</i> ) 'robustum group' <i>Ictitherium</i> ( <i>Pallhyaena</i> ) 'hipparionum group'	Amphicyonidae <i>Amphicyon</i> sp. <i>Agnotherium</i> n.sp. Hyaenidae <i>Percrocuta carnifex</i> <i>P. grandis</i>  <i>Progenetta</i> (2 species)		
Felidae <i>Felis attica</i> cf. <i>Dinofelis abeli</i>	Felidae <i>Paramachaerodus</i> sp.  Mustelidae <i>Eomellivora</i> sp. <i>Sivaonyx</i> sp. cf. <i>Ischyrictis</i> Viverridae <i>Viverra chinjiensis</i> Paradoxurinae Herpestinae Gen. nov.		

The situation is more complicated for the Muridae. *Progonomys*, represented by two species in Pakistan, is unknown in Afghanistan. *Parapodemus* sp. has been described from locality YGSP 182A in the Potwar Plateau. This genus has not been found in Molayan, but has been recovered in Afghanistan from more ancient (Sherullah and Ghazgay) and more recent (Malang) localities (BRUNET ET AL., 1981).

The genus *Karnimata* is known in Pakistan as well as in Afghanistan. However, the *K. darwini*–*K. huxleyi* lineage of Potwar is independent from the *K. minima* (Sherullah)–*K. intermedia* (Ghazgay)–*K. n. sp.* (Molayan) lineage of Afghanistan.

#### Creodonta

Unknown in Afghanistan; represented in the Potwar Plateau by the genus *Metapterodon*.

#### Carnivora

The Amphicyonidae (two genera), Mustelidae (three genera) and Viverridae (at least four genera) exist in the Potwar Plateau but are not known in Afghanistan. The Hyaenidae are represented in both regions, but with different genera, namely: *Adcrocuta eximia*, *Ictitherium* (*Ictitherium*) of the *robustum* group and *Ictitherium* (*Palhyaena*) of the *hipparionum* group in Molayan, and *Percrocuta carnifex*, *P. grandis* and *Progenetta* (two species) in the Potwar Plateau.

In Molayan, there is a *Felis* close to *Felis attica* from Pikermi and a *Dinofelis* close to *Dinofelis abeli* from the 'Pontian' of Honan. In the Potwar Plateau, the Felidae are represented only by the genus *Paramachaerodus*.

#### Hyracoidea

This group, totally absent in Pakistan, is represented by *Pliohyrax* in Molayan.

#### Proboscidea

In Molayan a bunodont, tetralophodont, tetrabelodont and longirostral gomphotheriid have been found. Owing to the too fragmentary character of the remains, it has not been possible to make a more precise determination. In the Potwar Plateau the Gomphotheriidae are represented by *Choerolophodon corrugatus* and *Stegolophodon* sp.

In Pakistan, the presence of Deinotheriidae has been reported. In Molayan, a few carpal bones indicate the presence of a huge *Deinotherium*, comparable in size with the largest individuals of *D. bozazi* from the east African Plio-Pleistocene.

As far as the Proboscidea are concerned, it is thus impossible to point out the similarities or differences between the two faunas.

#### Perissodactyla

In Molayan, the family Chalicotheriidae is represented by an *Ancylotherium* close to *A. pentelici* known in Pikermi, Samos, Maragha and in Tito Veles. In the Potwar Plateau, the representative of the family is *Chalicotherium salinum*. It is noteworthy that the genus *Chalicotherium* is common in the Eurasian Middle Miocene localities and that it survived with *Chalicotherium goldfussi* in the Late Miocene of eastern Europe and Anatolia.

In Molayan, the only representative of the family Rhinocerotidae is *Dicerorhinus orientalis* known also from eastern Europe (Pikermi, Samos, Salonica, etc.) and from Asia (Honan, Shansi—but not Maragha). In the Potwar Plateau, the Rhinocerotidae are represented by three forms which differ from that of Molayan, namely: *Brachypotherium perimense*, *Chilotherium intermedium*, *Gaindatherium browni*. The type localities of these three species are all situated in the Indian subcontinent.

In Molayan, the family Equidae is represented by an important number of specimens belonging to only a few individuals. It is therefore concluded that equids are not common in the locality. The 400 specimens which have been recorded up to now cannot be distinguished into different species; we thus refer them all to one species of *Hipparion*. As far as is possible to judge from the shape of the preorbital fossae of a distorted skull, the *Hipparion* from Molayan would belong to group III (WOODBURNE & BERNOR, 1980). According to its features, taken as a whole, and more particularly to the features of the metapodials, the *Hipparion* from Molayan closely resembles certain medium-sized forms from Maragha and Pikermi, and differs from those described from the Potwar Siwaliks where, depending on the authors, there would be three or four taxa: *Cormohipparion theobaldi*, '*Hipparion*' *antilopinum*, *H. nagriensis* and *H. sp.* The Siwalik hipparionines would have differentiated locally from a single wave of immigrants (HUSSAIN, 1971). This hypothesis could explain the particularism of the Potwar hipparionines.

#### Artiodactyla

*Suidae*—In Molayan, the Suidae are rare, and the few specimens which have been collected, including in particular two skulls, all belong to one taxon, *Microstonyx major*. That species, which is widespread from Western Europe to China in the Late Miocene, has not been found in the Potwar Plateau, where the suids are otherwise abundantly represented. Indeed, although BADGLEY & BEHRENSMEYER (1980) mention only five genera (four suids and one tayassuid) during the time interval associated with the 'U sandstone' sequence, it must be recalled that thirteen genera (PICKFORD, in PILBEAM ET AL., 1977) and fourteen species (MOONEN ET AL., 1978) of Suidae and Tayassuidae have been reported from Chinji, Nagri and Dhok Pathan, taken together.

*Anthracotheriidae*—No representative of the family Anthracotheriidae has been recovered up to now from Molayan or from any other fossil locality in Afghanistan. Once again, there is a striking contrast with the Potwar Plateau, where at least two species are frequently found in the vicinity of the 'U sandstone'. In addition, anthracotheriids are present almost everywhere in the Potwar stratigraphic sequence.

*Tragulidae*—No tragulid has been found up to now in Molayan or elsewhere in Afghanistan. This absence contrasts with the abundance of the *Tragulidae* in the Potwar Plateau, where at least three forms (four to five according to other authors) have been identified.

*Giraffidae*—In Molayan, the family Giraffidae is represented by about one hundred specimens corresponding to ten individuals at least, that is to say approximately the same number as for *Hipparion*. All these specimens are referred to only one species of the genus *Palaeotragus*. This genus has never been recorded in the Potwar Plateau, where BADGLEY & BEHRENSMEYER (1980) indicated the presence, during the 'U sandstone' time interval, of two forms, a large one, *Bramatherium megacephalum*, and a small one, *Giraffokeryx punjabiensis*. According to BARRY in PILBEAM ET AL., 1979, *Giraffokeryx* would have been restricted to biozones 2 and 3, corresponding approximately to the Chinji. The replacement of *Giraffokeryx* by a large size giraffid would have occurred in biozone 4, that is to say approximately at the beginning of the Nagri, 9 to 10 Ma ago according to the tables of LINDSAY ET AL., 1980. Consequently, *Giraffokeryx* no longer exists in the 'U sandstone' time interval (approximately 8 Ma ago). Moreover, we could check in the field that, in the Nagri (e.g. loc. 450, Padhri region) as well as in the Dhok Pathan (e.g. loc. 452, near Padhri) only specimens of the large size giraffid were found.

*Cervidae*—Although the Molayan fossil locality has not yielded any cervid remains, it is still worthwhile to discuss this family. At least, one cervid is present in Afghanistan i.e. in the Lower Turolian of Taghar. This fossil locality is situated 500 m from Molayan, 30 m lower in the stratigraphic sequence (BRUNET ET AL., 1981). The presence of this cervid stands in striking contrast to the absence of *Cervidae* in the Chinji, Nagri and Dhok Pathan of the Potwar Plateau; in the Siwaliks, the *Cervidae* appeared only very late around 2 Ma, or perhaps 2.9 Ma ago (BARRY ET AL., 1982).

*Bovidae*—The comparison between the bovids from Molayan and the ones from the Potwar Plateau is complicated, since detailed studies are lacking. Our general impression is that the Molayan bovids are different, on the whole, from the ones of the Potwar Plateau. Three out of the five genera which have been recorded from the 'U sandstone' sequence, *Selenoportax*, ? *Pseudotragus* and *Elachistoceras*, clearly do not exist in Molayan. The problem with *Miotragocerus* is more difficult,

since it is known that this genus, widespread over entire Eurasia and during the complete Late Miocene, embraces a large number of taxa which are hard to distinguish from each other at present (THOMAS, 1979). The assignment of all these forms to one genus is satisfactory for the time being, it may however not reflect the actual complexity of the group. In any case, the Molayan *Miotragocerus* differs from *M. punjabiensis* from the Potwar Plateau. It must also be emphasized that *Miotragocerus* is the most abundant animal in the Molayan fauna. About a thousand specimens, including many skulls, have been recorded. They belong to approximately a hundred individuals, representing at least 50% of the total number of individuals in the fauna.

As far as the genus *Gazella* is concerned, the comparison is even more difficult because the attribution of bovids to this genus was mainly on the basis of size criteria. In Molayan, there is a relative abundance of material which can be referred to the genus *Gazella*. This material, and especially the horn cores, differs from the material known from the Potwar Plateau.

In addition, there are in Molayan four other genera of bovids which are unknown in the Potwar Plateau:

- one form, similar in size to *Miotragocerus*, but with horn cores of the *Graecoryx* type. Up to now, it is known only by a frontlet;
- a smaller form (male and female skulls), which can be referred to cf. *Protoryx*;
- an antelope with spiraled horn cores, which can be provisionally attributed to the *Prostrepsiceros* group;
- an antelope, smaller than the gazelle, but larger than *Elachistoceras* (THOMAS, 1977) from the Potwar Plateau, and differing considerably from the latter.

## CONCLUSIONS

At the end of this comparison, it appears that, about 8 Ma ago, the faunas in Afghanistan and in the Potwar Plateau, although geographically close (less than 300 km) were distinct. From a taxonomic point of view, this is reflected by differences which range from the specific to the ordinal level. At present it is impossible to be certain that even one species is common to both faunas. How can we explain such important differences between two faunas which are geographically so close to one another?

At first sight, we can be tempted to explain these differences as resulting from a chronological gap between Molayan and the 'U sandstone' time interval. It must be emphasized, however, that, in the present case, the faunal differences are not related to the degree of precision of the proposed correlation. If one compares the Molayan fauna with those of Chinji, Nagri or Dhok Pathan (lists in MOONEN ET AL., 1978)—i.e. with the three faunal complexes which, in the Pakistan Siwaliks, follow one another from 12.5 to 5.5 Ma, the differences remain. Consequently, the explanation must be sought elsewhere.

First of all the palaeoenvironment can be examined. The composition of the Molayan fauna – its taxa as well as their comparative frequency – denotes, on the whole, an open environment of the grassland to savannah type, with sparsely scattered woodlands. This is substantiated by the abundance of bovids and, among the latter, by the large number of tragocerines, which probably lived in herds. The hipparionines, though relatively rare, also indicate an open environment. On the contrary, the chalicotheres, the rhinocerotids and the giraffids indicate the presence of trees. The herbivorous primate *Mesopithecus* had an appendicular skeleton with a front limb slightly shorter than the hind limb: such a morphology suggests that it was partly terrestrial and partly arboreal, which is consistent with the environmental interpretation. Among the rodents, the comparative abundance of the gerbillid relative to the very rare murid indicates a dry environment. The present-day *Hystrix* dwells in dry lands and mountain slopes. The absence of crocodiles, tortoises, amphibians and fishes, the remains of which are common in the Potwar Plateau, is also an indication of an, at least temporarily, very dry environment. It must also be noted that an attempt at finding sporomorphs proved unsuccessful. The faunal complex thus seems to denote a dry and open environment. Besides, it must be remembered that the lithological succession of the Molayan hill shows a rhythmic sedimentation, corresponding to a tropical climate with alternate dry and humid seasons (HEINTZ ET AL., 1978a).

The environment of the Siwalik 'U sandstone' of the Pakistan Potwar Plateau has been defined as follows (BADGLEY ET AL., 1980, p. 154): 'The members of the community inhabited a diverse set of fluvial environments, probably characterized by a mosaic of vegetation types from forest to woodland to open grassland'. This implies the existence of more closed zones in a region perhaps subjected to the monsoon, to a climate that on the whole was warmer and more humid than in Afghanistan. The faunal elements which indicate such an environment are the tragulids, the anthracotheriids, the suids, the primates, the crocodiles, the aquatic tortoises, etc. The differences in climate and environment which are observed at present between the high plateaus in Afghanistan (about 2 000 m) and the lowlands of the Punjab in Pakistan (about 500 m) can, to a certain extent, provide a model for the differences which existed between Molayan and the Potwar Plateau during the Late Miocene.

Therefore, certain faunal differences between Molayan and the Potwar Plateau can be explained by differences in palaeoenvironment. The latter, however, do not account for all the faunal differences. If they did, the existence of open environments in Molayan as well as in the Potwar Plateau should logically have resulted in a greater taxonomic similarity of the bovids, equids, giraffids, rhinocerotids, etc. Moreover, this does not explain the absence in the subcontinent of the suid *Microstonyx*, an ubiquitous genus, known throughout the Late Miocene in other parts of Eurasia. Similarly, the Afghan *Mesopithecus* could have found a favourable environ-

ment in the Potwar Plateau. The same holds for the hyracoids and others. Finally, the cervids, present in Afghanistan about 8 Ma ago, could also have found a favourable environment in the Potwar Plateau.

The importance of the faunal differences implies, in our opinion, that, in addition to differences in palaeoenvironment, there had to be an obstacle such as a mountain barrier which considerably restrained – and perhaps even completely prevented – the faunal exchange between Molayan and the Potwar Plateau. This barrier would have been located at the site of the present-day Baluchi Range, i.e. in line, westwards, with the Indus-Tsangpo suture zone (Khost zone) (BASSOULET ET AL., 1980). Thus, about 8 Ma ago, a mountain barrier, which probably also played a part as a climatic barrier (obstacle to the monsoon?), separated two biogeographical provinces: one of them corresponded to the Indian subcontinent; the other one, which included Afghanistan or at least the eastern part, might have been connected with the Greco-Iranian Province (DE BONIS ET AL., 1979). The barrier would have perpetuated the biogeographical isolation which characterized the Indian subcontinent before it was united with Eurasia. Finally, it was classically admitted that the Dhok Pathan fauna of the Indian subcontinent Siwaliks was similar to that of the Western Asian and European Turolian (PILBEAM ET AL., 1977; MOONEN ET AL., 1978); the comparison between Molayan and the Potwar Plateau shows, on the contrary, that about 8 Ma ago, these faunas were biogeographically separated.

These biogeographical relationships provide new data for discussing a present-day problem that deals with the Miocene hominoid primates' teeth with thick enamel. These primates have experienced and still experience many taxonomic and phylogenetic vicissitudes, and no agreement seems imminent. In this respect, it seems useful to sum up a few tribulations of genera classically cited in the literature: *Sivapithecus* PILGRIM, 1910; *Ramapithecus* LEWIS, 1934; *Ankarapithecus* OZANSOY, 1957; *Kenyapithecus* LEAKEY, 1962; *Graecopithecus* VON KOENIGSWALD, 1972; *Bodvapathecus* KRETZOI, 1975; *Ouranopithecus* DE BONIS & MELENTIS, 1977 (we exclude here *Gigantopithecus* VON KOENIGSWALD, 1935). *Sivapithecus* and *Ramapithecus* have been considered as the type-genera of two subfamilies: Sivapithecinae and Ramapithecinae (PILBEAM ET AL., 1977). More recently, it has been suggested that 'the features regarded as characteristic of *Ramapithecus* might be secondary sexual characters (DE BONIS, 1981). KAY (1982) has retained only one genus, *Sivapithecus*. Regarding the phylogeny, *Ramapithecus* has been considered the most ancient hominoid, an opinion advocated by the majority of the authors. We, however, support the new idea that *Ramapithecus* belongs, together with a few other genera, to the orang-utang group, and, consequently, to the Ponginae s.s. (ANDREW, 1982). From a stratigraphic point of view, these primates are known since the Middle Miocene (Austria, Turkey, Africa), but mainly in the Late Miocene (Hungary, Greece, Turkey, China, Indian subcontinent). However, it is

in the Indian subcontinent that they remained longest, until about 7 Ma ago, while they seem to have disappeared approximately 9 Ma ago from the other parts of Eurasia. This is consistent with the biogeographical isolation as well as the hot and wet climate suggested for the Indian subcontinent; besides, no identical species has been cited in the literature for the Late Miocene. On the other hand, during the Middle Miocene, *Ramapithecus wickeri*, recorded from Turkey (Pasalar, 15 to 16 Ma) and from Africa (Fort Ternan, 12,5 to 14 Ma) reveals the first appearance of the group and the existence of faunal exchanges. During the Late Miocene, the Greek and Turkish forms must have been isolated from those of the Indian subcontinent. From a taxonomic point of view, and owing to the priority rule, we propose to keep the genus name *Ankarapithecus* to designate the former, and *Sivapithecus* to designate the latter. This would at least reflect a biogeographical reality: paleontological documents, which would provide the morphological evidence for this generic distinction, are still to be found: they will either confirm or invalidate this opinion.

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