

## Preliminary review of Cercopithecoid distribution in the Circum Mediterranean Region

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RÉSUMÉ: Cette note a pour but de présenter les résultats provisoires d'une étude en cours, qui concerne l'histoire naturelle des Singes Cynomorphes (Cercopithecidae, Primates) de l'Europe et de l'Afrique du Nord.

On décrira brièvement les espèces qui ont été reconnues dans les dépôts néogènes de cette région, en accompagnant chaque espèce de la liste des localités fossilifères (local faunas) où l'on rencontre ces espèces. La rareté des Cynomorphes fossiles en général, et la faible quantité qu'on en trouve dans chaque gisement - sauf exception - ne permettent pas d'établir une « zonation biostratigraphique » fondée sur la présence de ces animaux. On peut cependant noter que la présence sur toute l'Europe de *Dolichopithecus rusciniensis* - Singe distinctif par rapport à toutes les autres espèces étudiées - est limitée au Ruscinién et au Villafranchien ancien, périodes qui sont marquées en Europe par le retour de conditions plus forestières.

In recent years, reviews have been presented of the mammalian biostratigraphy of Europe during the Pliocene and Pleistocene. Some were based on large mammals (eg by TOBIEN and by AZZAROLI) while others considered micro-mammals (eg works by MICHAUX, CHALINE and MEIN). The primates have been ignored in these discussions, fitting comfortably into neither group and as yet offering no good biostratigraphical indications. A study of the fossil cercopithecoid monkeys of the circum-mediterranean region, now in progress, allows me to complement the above reviews with a summary of the spatio-temporal distribution of these animals.

In order to place the localities yielding monkey fossils in age relation to each other, I have tentatively subdivided the time between the present and the first appearance of *Hipparion* in Europe into eleven informal and unequal (and partly artificial) "time blocks", solely for the convenience of the reader. This subdivision is presented below, with some well-known Mediterranean local faunas listed for each block. These faunas do not either define or delimit the blocks (which are, it must be repeated, still informal) but merely illustrate them. As I have been

unable to subdivide time on the basis of cercopithecoid morphological evolution, the relative ages of the local faunas and time blocks are based on the literature and on discussion with numerous colleagues whom I thank here. The terms Miocene, Pliocene and Pleistocene are based on marine invertebrate stratigraphy and their suggested boundaries are one of several possibilities. The abbreviations of each block will be used below to place each local fauna with monkeys in one such block. Finally, the temporal ranges of the several cercopithecoid species are noted (see table I).

Eight major types of cercopithecoid fossils are known from mediterranean Neogene deposits. Each can be briefly characterized as follows.

The most common are the macaques, known from many localities but in nearly all cases only from dental remains. At least twelve species have been proposed to receive these fragmentary specimens, but only the oldest forms can plausibly be separated from the living *Macaca sylvanus* of western North Africa at this stage of the study. The many local populations sampled in time and space may be provisionally considered as demes of *M. sylvanus*. It is hoped that

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TABLE I. — Mediterranean Neogene "time blocks" and cercopithecoid distribution

EPOCH	"TIME BLOCK"	Abbrev.	ILLUSTRATIVE LOCALITIES	DISTRIBUTION OF CERCOPITHECID SPECIES
PLEISTOCENE	LATE		Flandrian ("Holocene", "Recent")	<i>Macaca sylvanus</i>
	PLEISTOCENE	LP	Wurmian	<i>Macaca</i> sp.
			Eemian (Riss-Wurm)	
	MIDDLE	MP	Rissian	<i>Macaca</i> sp.
			Holsteinian (Hoxnian)	
	PLEISTOCENE		Cromer	<i>Theropithecus</i> sp.
			Biharian Eburonian	
			Les Valerots	
	LATE (AND FINAL)		Farneta	<i>Macaca</i> sp.
	VILLAFRANCHIAN	LVi	Senèze	" <i>Dolichopithecus</i> " <i>arvernensis</i>
			? <i>Mesopithecus monspessulanus</i> (?)	
MIDDLE		Saint Vallier	<i>Macaca</i> sp.	
VILLAFRANCHIAN	MVi	Roccaneyra		
PLIOCENE	EARLY		North African Early Villafranchian	<i>Macaca</i> sp.
	VILLAFRANCHIAN	EVi	Etouaires	<i>Theropithecus</i> sp.
			Villafranca d'Asti	<i>Dolichopithecus ruscinensis</i>
				? <i>Mesopithecus monspessulanus</i>
				" <i>Dolichopithecus</i> " <i>arvernensis</i>
	LATE (AND FINAL)		Perpignan (Serrat d'En Vacquer)	<i>Macaca</i> sp.
	RUSCINIAN	LR		<i>Dolichopithecus ruscinensis</i>
			Csarnota-2	? <i>Mesopithecus monspessulanus</i>
				" <i>Dolichopithecus</i> " <i>arvernensis</i> (?)
	EARLY AND MIDDLE		Montpellier	<i>Macaca</i> sp.
RUSCINIAN	EMR		<i>Dolichopithecus ruscinensis</i>	
			? <i>Mesopithecus monspessulanus</i>	
LATE		Sahabi	<i>Libypithecus markgrafi</i>	
		Arquillo La Fontana	<i>Dolichopithecus ruscinensis</i> (?)	
TUROLIAN	LT	Pontian (typical, USSR)	<i>Macaca</i> sp.	
		Melka el Ouidane (Camp Berteaux)	? <i>Mesopithecus monspessulanus</i> (?)	
			<i>Colobinae</i> , sp. indet.	
LATE MIOCENE	EARLY	ET	Los Mansuetos	<i>Mesopithecus pentelici</i>
	TUROLIAN		Meotian	
			Samos 1-4	
			Pikermi	
	LATE		Mollon	
	VALLESIAN	LVa		<i>Mesopithecus pentelici</i> (?)
		Masia del Barbo		
EARLY		Oued el Hammam (Bou Hanifia)		
VALLESIAN	EVa	Can Llobateres		
		Höwenegg		

TABLE II. — Cercopithecoid distribution in Mediterranean Neogene local faunas

AGE	LOCALITY, COUNTRY	NOMINAL PREVIOUS SPECIES	COMMENT
<i>Macaca cf. sylvanus</i>			
LVa +	Mollon, France		NS <sup>1</sup>
LT +	Marceau, Algeria	<i>M. flandrini</i>	
LT +	Wadi Natrun, Egypt	<i>M. libyca</i>	
EMR +	Montpellier, France	<i>M. prisca</i>	
LR	Csarnota-2, Hungary	<i>M. praeinuus</i>	
EVi +	Villafranca d'Asti (Fornace), Italy		
EVi +	Balaruc-2, France		
Evi	Beremend-4, Hungary		
Evi?	Lac Ichkeul, Tunisia		
Evi?	Ain Brimba, Tunisia	"Anomalopithecus bicuspidatus"	
Evi? +	Cova Bonica, Spain		
Evi?	Gundersheim, Germany		NSP
MVi?	Sandalja, Yugoslavia		NS
MVi	Saint-Vallier, France		
MVi	Puebla de Valverde, Spain		
MVi	Mugello, Italy		
LVi	Tegelen, Holland		
LVi	Upper Val d'Arno (Montevarchi), Italy	<i>M. florentina</i> , " <i>M. ausonius</i> "	
LVi +	Senèze, France		
MP	'Ubeidiya, Israël		
MP ?	Vallonnet, France		
MP	Puspukfurdo (Beftia-2), Romania		
MP	Hohensülzen, Germany		
MP	Voigtstedt, Germany		
MP	Gombasek, Czechoslovakia		
MP	Zlaty Kun, Czechoslovakia		
MP	West Runton, England		
MP	Mosbach-2, Germany		
MP	Saint-Estève-Janson (L'Escale), France		
MP	Torralba, Spain		
MP	Heppenloch, Germany	<i>M. suevica</i>	
MP	Montsaunès, France	<i>M. tolosana</i>	
MP	San Vito di Leguzzano, Italy		
MP ?	Rome, Italy		
LP ?	Grays Thurrock, England	<i>M. pliocena</i>	
LP ?	Capo Figari, Sardinia, Italy	<i>M. majori</i>	
LP ?	Ain Mefta, Algeria	<i>M. trarensis</i> ; <i>M. proinuus</i>	
LP	Affalou-Bou-Rhummel & Tamar Hat, Algeria		
LP	Amud, Israel		NS <sup>2</sup>
LP	Kudaro-1, USSR (Caucasus)		NSP
LP	Living today in North Africa		T
<i>"Dolichopithecus" arvernensis</i>			
EVi	Vialette, France		Cf.
EVi? +	Malusteni, Romania		Cf.
Evi ? +	Cova Bonica, Spain		Cf.
LVi ?	Graunceanu, Romania	<i>Paradolichopithecus geticus</i>	
LVi +	Senèze, France		T
<i>Theropithecus sp.</i>			
Evi ?	Ain Jourdel, Algeria	<i>Cynocephalus atlanticus</i>	
MP	Ternifine, Algeria		

AGE	LOCALITY, COUNTRY	NOMINAL PREVIOUS SPECIES	COMMENT
<i>Mesopithecus pentelici</i>			
LVa ?	Baccinello V-3, Italy		Cf.
LVa ?	Wissberg, Germany		Cf.
ET	Pikermi, Greece		T
ET	Saloniki, Greece		
ET	Titov Veles, Yugoslavia		
ET	Kalimanci, Kromidovo & Gorna Susica, Bulgaria		
ET	Grebeniki, USSR		
ET	Taraklia & Grossulovo, USSR		NS <sup>1</sup>
LT ?	Maragha, Iran		
LT ?	Hatvan, Hungary		Cf.
EMR ?	Polgardi, Hungary		Cf.
<i>?Mesopithecus monspessulanus</i>			
LT ?	Gravitelli, Italy		NSP
LT ?	Casino, Italy		Cf.
EMR ?	Baltavar, Hungary		
EMR +	Montpellier, France		T
EMR	Celleneuve, France	<i>Anthropodus rouvillei</i>	
LR +	Perpignan (Serrat d'En Vacquer), France		
LR	Ivanovce, Czechoslovakia		
LR +	Wölfersheim, Germany		
EVi +	Villafranca d'Asti (Fornace), Italy		
EVi	Hajnacka, Czechoslovakia		
EVi +	Malusteni, Romania		
EVi ? +	Barot-Kopec (Baraolt-Capeni), Romania		
MVi ?	Red Crag, England		Cf.
<i>Dolichopithecus ruscinensis</i>			
LT ?	Pesztentlorinc, Hungary		Cf.
EMR +	Montpellier, France		Cf.
LR +	Perpignan (Serrat d'En Vacquer), France		T
LR +	Wölfersheim, Germany		
LR	Layna, Spain		
EVi +	Balaruc-2, France		
EVi	Malusteni, Romania		
EVi +	Beresti, Romania		
EVi ? +	Barot-Kopec (Baraolt-Capeni), Romania		
EVi	Novopetrovka, USSR		NSP
EVi	Budey, USSR		NSP-CP.
EVi ?	"Odessa", USSR	<i>"Adelopithecus hypsilophus"</i>	NS-CF.
<i>Libypithecus markgrafi</i>			
LT +	Wadi Natrun, Egypt		T
<i>Colobinae, sp. indet.</i>			
LT +	Marceau, Algeria	<i>Macaca flandrini</i>	T

Notes : 1 Specimens report but not illustrated, presumed lost, identifications uncertain.

2 Specimen illustrated, but identification as primate questioned.

further study will permit formal grouping of some of these demes into biologically meaningful sub-species; a small Sardinian form, probably subfossil, may prove...

A rare and much larger animal appears to have been derived *in situ* from Mediterranean macaques. Originally named *Dolichopithecus arvernensis*, it is in fact distinct from the genotype of *Dolichopithecus*, *D. ruscinensis*, at the subfamily level. As yet no limb bones are known which could permit behavioral or ecological interpretations.

Rare representatives of the living genus *Theropithecus* are found in Algeria. This animal is today restricted to the Ethiopian highlands where its ecology is unique among primates; fossil relatives were widespread during post-Ruscinian times in eastern and southern Africa.

The second subfamily of the Cercopithecidae, the Colobinae, is today represented by rather arboreally adapted forms in sub-Saharan Africa and eastern Asia. Five types at least are known from the Mediterranean Neogene. *Mesopithecus pentelici* is best represented at Pikermi where remains of over a hundred individuals may be preserved. More terrestrial than living colobines morphologically, *Mesopithecus pentelici* is found only in those faunas of "savannah" type, that is neither densely forested nor very arid. Its absence from Spain suggests an ecological "barrier" of some type. Similar specimens, mostly dental fragments, are known from deposits as young as the Middle Villafranchian. The post-Turolian specimens have been termed "*Semnopithecus*" *monspessulanus*, but they are dentally indistinguishable from *Mesopithecus pentelici* except (perhaps) by statistical techniques. Until skull morphology of this form is known, or until limb bones allow functional morphological comparison, I consider the later populations referable provisionally to *Mesopithecus*. They are given specific rank tentatively, partly on as yet subjective bases, but localities of intermediate age yield specimens not readily attributable either to ?*Mesopithecus monspessulanus* or to *M. pentelici*.

A single skull and some dental fragments of *Libypithecus markgrafi* are known from an isolated locality. It is clearly distinct from *Mesopithecus* (of which no specimen is as complete) but dental size and morphology are similar between the two genera. A derivation of *Libypithecus* from *Mesopithecus* is

possible, and in fact some of the isolated European dental remains could represent the former genus.

Another possible derivative from a *Mesopithecus* stock is *Dolichopithecus ruscinensis*, which is now rather well known at its type locality. Larger than any living colobine, *D. ruscinensis* shows morphological features in its appendicular skeleton which parallel those of some terrestrial African baboons. These monkeys inhabited the forested regions of the Ruscinian and Early Villafranchian, and it can be suggested that they were convergent onto the ecological niche of the forest baboons or mandrills. Its size and the distinctiveness of its bones and teeth make *D. ruscinensis* a useful indicator in a relatively broad temporal span; but its absence in any local fauna cannot yet be given a meaningful interpretation.

Finally, a few teeth of a colobine are known in Algeria which are not close to any of the above four species and which may indicate affinities with sub-Saharan lineages.

The spatio-temporal distribution of these cercopithecoid species in the local faunas of the Mediterranean Neogene is summarized in the preceding list. No attempt is made here to order localities temporally within the "time blocks", and some localities may have to be translocated one block in either direction.

For each species, a list is given of those localities in which it occurs. For each locality, its proposed time block is given by an abbreviation. The following comments may appear alongside a locality as well: cf. implies uncertain referral of the specimens to the relevant taxon; NS indicates published reports of specimens not seen by me; NSP refers to those cases where published photographs satisfactorily confirm the suggested identification; a plus (+) indicates the presence of more than one cercopithecoid species at the locality; (T) indicates the type-locality of each species; and a species name alongside indicates a nominal species of doubtful validity (see table II).

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