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The Mio-Pliocene European primate fossil record: dynamics and habitat tracking

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Abstract

We present here a study of European Neogene primate occurrences in the context of changing humidity. We studied the differences of primate localities versus non-primate localities by using the mammal communities and the ecomorphological data of the taxa present in the communities. The distribution of primates is influenced by humidity changes during the whole Neogene, and the results suggest that the primates track the changes in humidity through time. The exception to this is the Superfamily Cercopithecoidea which shows a wider range of choices in habitats. All primate localities seem to differ from non-primate localities in that the mammal community structure is more closed habitat oriented, while in non-primate localities the community structure changes towards open-habitat oriented in the late Neogene. The differences in primate and non-primate localities are stronger during the times of deep environmental change, when primates are found in their preferred habitats and non-primate localities have faunas better able to adapt to changing conditions.

Keywords: fossil primates; Cercopithecoidea; herbivore humidity proxy; hypsodonty; community structure; habitat tracking; Late Neogene; Europe

Introduction

The Primate record of Europe is comparatively well known, but there have been few attempts to look at the paleoecological scenarios for the temporal and geographical variation of different primate families and genera (e.g. Andrews, 1982; Bernor, 1983; Andrews et al., 1996). Most of the earlier work does not deal specifically with primates (e.g. Fortelius et al., 1996, Jernvall and Fortelius, 2002), or uses just some of the taxa (e.g. most papers in De Bonis et al., 2001). We present here a study of the Mio-Pliocene European

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primate fossil record framed within paleoprecipitation maps in successive time slices.

The primary goal of the present paper is to characterize the spatial and temporal variation of different primate families and their relationship to changing environments of the Mio-Pliocene. We are interested in the relationships of different primate families in relation to changes in humidity and how this affects their distribution. Andrews (1982) studied the phylogeography of higher primates, and concluded that the ancestral ecological condition is tropical forest. According to him, hominoids retain this character while the Cercopithecoidea are more derived with a preference to savannah habitat.

Since most geographical variation we appreciate is in the Superfamily Cercopithecoidae, special attention is devoted to this group including a genus-level analysis to show the full variation in that superfamily.

Our second goal is to seek an answer to the question "are primate localities different from penecontemporaneous non-primate localities?". Analysing the trophic context of Miocene western Eurasia hominoids, Fortelius and Hokkanen (2001) found that there were spurious differences between hominoid and non-hominoid localities that disappeared when the data was analysed geographically and temporally. Our attempt here is to enlighten our knowledge about what contrasts exist between these localities, and to offer possible reasons for these contrasts.

Material and methods

This investigation is based on the Neogene Old World Database (NOW). This database, based at this time on the Schloss Reisensberg Initiative, was released to the public by Mikael Fortelius (NOW Coordinator) in December 1996 on the day that "The Evolution of Eurasian Neogene Mammal Faunas" (Bernor et al., 1996a) was published. Since 1996 there has been a substantial increase in the number and geographic coverage of localities and taxa, and much additional ecomorphological information has been added. The latest public NOW dataset can be downloaded from the NOW website (www.helsinki.fi/science/now/). The dataset used for this study was derived from a file downloaded from the NOW database on January 7, 2003. For the purposes of the present analysis, the NOW dataset has been herein integrated with data recently published on Sinap formation, a late Miocene (MN 9) hominid-bearing succession in Turkey (Fortelius et al., 2003). The dataset used in this study is available from the authors.

Paleoprecipitation maps

The paleoprecipitation maps are produced according to a technique recently developed by Fortelius et al. (2002). We selected a data subset defining a geographical range that includes the whole of Europe (the eastern limit being selected at 60°E, and the limit between East and West is 20°E). The timespan we are interested in is the late Neogene, from MN5 to MN17 biochronological units according to the chronological scheme of Steininger et al. (1996) with updates from more recent papers (e.g. Andrews and Bernor, 1999; Agustí et al., 2001). The whole correlation scheme for European Neogene in the NOW is based on Steininger et al. (1996), although the NOW advisory board is responsible for updating the biochronologic frame. The MN system, developed in the 1970's by Pierre Mein (Lyon) has been used and updated with different perspectives by various authors. It is now clear that it does not entirely account for the provinciality that characterizes the evolutionary and dispersal dynamics in mammal assemblages (Fortelius et al., 1996; Andrews and Bernor, 1999; Agustí et al., 2001). Its use, however, still represent a good tool for broad correlations across western Eurasia.

For this study we used all available herbivore crown height data from the database. Three classes of crown height are recorded in the NOW database: brachydont, mesodont and hypsodont. The criteria for assigning species to these classes are ultimately up to the taxonomic coordinators of the NOW advisory board (see NOW website), but the rule of thumb is based on the ratio of height to length of the second molar (upper or lower). Brachydont teeth have a ratio of less than 0.8, mesodont teeth a ratio of 0.8–1.2, and hypsodont teeth a ratio more than 1.2. For this study, the hypsodonty classes were assigned values of 1 (brachydont), 2 (mesodont) and 3 (hypsodont). The mean crown height value was calculated for each locality by averaging these ordinated scores, and the mean values were plotted on maps using interpolated colours to indicate regional differences. We also present the approximate precipitation values corresponding to hypsodonty values (based on extant data, Damuth and Fortelius, 2001; and pers. comm. with John Damuth and Mikael Fortelius).

The hypsodonty maps were produced using MapInfo 6.0 Desktop GIS using the inverse distance weighted (IDW) algorithm and the following settings: cell size 10 km, search radius 1000 km, grid border 1000 km, number of inflections 10, values rounded to 1 decimal.

All small mammals (Orders Lagomorpha, Rodentia, Insectivora and Chiroptera) have been excluded from the analysis. In order to see their environmental context we have excluded all the primates and only plotted them on the maps to show where the mentioned primate localities are. All singletons, i.e. species having only a single occurrence, and localities with only one occurrence, were also omitted from the analysis. This is based on the practice of Alroy (1992, 1994, 1996) that removal of singletons is a minimum requirement for occurrence matrices. Only localities that have an age-definition that falls inside one MN unit in the NOW database were taken into account. All other localities were omitted. Also all singletons within the MN zones were deleted, excluding the primate localities.

A number of primate localities not present in the NOW, or primate localities with wide age-definition (i.e. ranging more than one MN unit) have been taken in consideration for a more extensive documentation of the primate record within our paleoprecipitation history of Europe. Among primate localities not present in the NOW database we note the following sites with the relative bibliographic references: Balaruc 2 (MN16; Michaux, 1966, 1969), Beremend 4 (MN16; Kórmos, 1937; Kretzoi, 1959), Mugello (MN17; Abbazzi et al., 1995), Orosei (MN 17; Abbazzi et al., in press); Vatera (MN 17; De Vos et al., 2002).

When the age assignment of a locality does not fit exactly within a MN unit, the NOW database allows us to introduce a wider age range. In order to maintain the information, we have decided to put the assignment to the most probable MN unit for the primate record of the following localities according to the relative references: Grebeniki (MN11, Andrews et al., 1996), Middle Maragheh (MN11; Bernor et al., 1996a,b), Vathylakkos (MN 11; De Bonis and Koufos, 1999; Andrews and Bernor, 1999), Kalimanci 2 (MN12; Spassov, 2002), Kromidovo 2 (MN12; Spassov, 2002), Baccinello V3 (MN13; Benvenuti et al., 2001), Maramena (MN13; Kullmer and Doukas, 1995), Layna (MN15 Moyà-Solà et al., 1990). A complete list of primate localities (and occurring primates) used in the present study is given in Table 1.

The locality data were assigned to MN-units and maps were produced for each MN–unit. To construct the hypsodonty maps, we used the occurrences of all species with above mentioned constrains for the analysis. This was also the practice of Fortelius and Hokkanen (2001), so our results are readily comparable with those.

On the hypsodonty maps we plotted the primate localities using the following groupings: Pliopithecidae, Hominidae, Primates indet., Cercopithecoidea *Mesopithecus*, Cercopithecoidea *Macaca*, Cercopithecoidea *Dolichopithecus*, Cercopithecoidea *Paradolichopithecus*, Cercopithecoidea indet., *Homo* sp. These groupings are based on our observation during this work that shows there is greatest variation (in relation to changing humidity) in the superfamily Cercopithecoidea and interestingly not within the Hominidae.

Primate vs. non-primate localities

For the statistical analysis the data was separated in two groups: primate and non-primate localities. Then primates were, also in this case, excluded from the primate localities for the analysis. We define primate locality as a fossil assemblage having at least one primate species. Furthermore, it has to contain at least one other mammal species in order to be included in the

Table 1
The European Neogene primate localities and the occurring species

Locality	MN age	Country	Family	Species
Pontlevoy	MN05	France	Pliopithecidae	*Pliopithecus antiquus*
Esvres Marine Faluns	MN05	France	Pliopithecidae	*Pliopithecus antiquus*
Faluns of Touraine & Anjou	MN05	France	Pliopithecidae	*Pliopithecus antiquus*
Manthelan	MN05	France	Pliopithecidae	*Pliopithecus antiquus*
La Condoue	MN05	France	Pliopithecidae	*Pliopithecus antiquus*
Ziemetshausen 1b	MN05	Germany	Pliopithecidae	*Pliopithecus antiquus*
Göriach	MN05	Austria	Pliopithecidae	*Pliopithecus platyodon*
Candir	MN06	Turkey	Hominidae	*Griphopithecus alpani*
Klein Hadersdorf	MN06	Austria	Hominidae	*Griphopithecus darwini*
Neudor Sandberg	MN06	Slovakia	Hominidae	*Griphopithecus darwini*
Hambach 6C	MN06	Germany	Pliopithecidae	indet.
Sansan	MN06	France	Pliopithecidae	*Plesiopliopithecus auscitanensis*
Trimmelkam	MN06	Austria	Pliopithecidae	*Plesiopliopithecus lockeri*
Liet	MN06	France	Pliopithecidae	*Pliopithecus antiquus*
Stätzling	MN06	Germany	Pliopithecidae	*Pliopithecus antiquus*
Kreutzlingen	MN06	Switzerland	Pliopithecidae	*Pliopithecus antiquus*
Stein am Rhein	MN06	Switzerland	Pliopithecidae	*Pliopithecus antiquus*
Diessen am Ammersee	MN06	Germany	Pliopithecidae	*Pliopithecus antiquus*
Hambach 6C	MN06	Germany	Pliopithecidae	*Pliopithecus antiquus*
Rümikon	MN06	Switzerland	Pliopithecidae	*Pliopithecus* cf. *antiquus*
Neudorf Sandberg	MN06	Slovakia	Pliopithecidae	*Pliopithecus* cf. *antiquus*
Elgg	MN06	Switzerland	Pliopithecidae	*Pliopithecus platyodon*
Neudorf Spalte	MN06	Slovakia	Pliopithecidae	*Pliopithecus vindobonensis*
St. Stephan im Lavanttal	MN07/8	Austria	Hominidae	*Dryopithecus carinthiacus*
La Grive St. Alban	MN07/8	France	Hominidae	*Dryopithecus fontani*
St. Gaudens	MN07/8	France	Hominidae	*Dryopithecus fontani*
Sant Quirze	MN07/8	Spain	Hominidae	*Dryopithecus laietanus*
Castell de Barberà	MN07/8	Spain	Hominidae	*Dryopithecus laietanus*
Can Mata 1	MN07/8	Spain	Hominidae	*Dryopithecus laietanus*
Can Vila	MN07/8	Spain	Hominidae	*Dryopithecus laietanus*
La Grive St. Alban	MN07/8	France	Pliopithecidae	*Plesiopliopithecus rhodanica*
La Grive L7	MN07/8	France	Pliopithecidae	*Plesiopliopithecus rhodanica*
La Grive St. Alban	MN07/8	France	Pliopithecidae	*Pliopithecus antiquus*
Castell de Barberà	MN07/8	Spain	Pliopithecidae	*Pliopithecus* cf. *antiquus*
Przeworno 2	MN07/8	Poland	Pliopithecidae	*Pliopithecus* cf. *antiquus*
Gorna Susica	MN09	Bulgaria	Cercopithecidae	*??? Mesopithecus pentelicus*
Sinap AS_12	MN09	Turkey	Hominidae	*Ankarapithecus meteai*
Mariathal	MN09	Austria	Hominidae	*Dryopithecus brancoi*
Rudabánya	MN09	Hungary	Hominidae	*Dryopithecus brancoi*
Can Ponsic	MN09	Spain	Hominidae	*Dryopithecus crusafonti*
Can Ponsic I	MN09	Spain	Hominidae	*Dryopithecus crusafonti*
Seu d'Urgel	MN09	Spain	Hominidae	*Dryopithecus fontani*
Salmendingen	MN09	Germany	Hominidae	*Dryopithecus fontani*
Eppelsheim	MN09	Germany	Hominidae	*Dryopithecus* indet.
Wissberg	MN09	Germany	Hominidae	*Dryopithecus* indet.
Kalfa	MN09	Moldova	Hominidae	indet.
Eppelsheim	MN09	Germany	indet.	cf. *Semnopithecus eppelsheimensis*
Götzendorf	MN09	Austria	Pliopithecidae	*Anapithecus hernyaki*
Rudabánya	MN09	Hungary	Pliopithecidae	*Anapithecus hernyaki*
Esvres Upper Faluns	MN09	France	Pliopithecidae	*Pliopithecus antiquus*
Doué la Fontaine	MN09	France	Pliopithecidae	*Pliopithecus* indet.
Meigné le Vicomte	MN09	France	Pliopithecidae	*Pliopithecus* indet.
Priay II	MN09	France	Pliopithecidae	*Pliopithecus priensis*

Table 1 (*continued*)

Locality	MN age	Country	Family	Species
Grossulovo	MN10	Ukraine	Cercopithecidae	*??? Mesopithecus pentelicus*
Can Llobateres I	MN10	Spain	Hominidae	*Dryopithecus laietanus*
Polinya II	MN10	Spain	Hominidae	*Dryopithecus laietanus*
Ravin de la Pluie (RPL)	MN10	Greece	Hominidae	*Ouranopithecus macedoniensis*
Xirochori 1 (XIR)	MN10	Greece	Hominidae	*Ouranopithecus macedoniensis*
Terrassa	MN10	Spain	Pliopithecidae	*Anapithecus* sp.
Vathylakkos 2 (VTK)	MN11	Greece	Cercopithecidae	*Mesopithecus* cf. *pentelicus*
Vathylakkos 2 (VTK)	MN11	Greece	Cercopithecidae	*Mesopithecus* cf. *pentelicus*
Mollon	MN11	France	Cercopithecidae	*Mesopithecus* indet.
Vathylakkos 3 (VAT)	MN11	Greece	Cercopithecidae	*Mesopithecus* indet.
Vathylakkos 3 (VAT)	MN11	Greece	Cercopithecidae	*Mesopithecus* indet.
Grebeniki	MN11	Ukraine	Cercopithecidae	*Mesopithecus pentelicus*
Maragheh (Middle beds)	MN11	Iran	Cercopithecidae	*Mesopithecus pentelicus*
Ravin des Zouaves 5	MN11	Greece	Cercopithecidae	*Mesopithecus pentelicus*
Nikiti 1 (NKT)	MN11	Greece	Hominidae	*Ouranopithecus macedoniensis*
Kalimanci 2	MN12	Bulgaria	Cercopithecidae	*Mesopithecus pentelicus*
Kromidovo 2	MN12	Bulgaria	Cercopithecidae	*Mesopithecus pentelicus*
Pikermi MNHN (PIK)	MN12	Greece	Cercopithecidae	*Mesopithecus pentelicus*
Chomateres	MN12	Greece	Cercopithecidae	*Mesopithecus pentelicus*
Molayan	MN12	Afghanistan	Cercopithecidae	*Mesopithecus pentelicus*
Baccinello V2	MN12	Italy	Hominidae	*Oreopithecus bambolii*
Casteani	MN12	Italy	Hominidae	*Oreopithecus bambolii*
Montemassi	MN12	Italy	Hominidae	*Oreopithecus bambolii*
Ribolla	MN12	Italy	Hominidae	*Oreopithecus bambolii*
Fiume Santo	MN12	Italy	Hominidae	*Oreopithecus bambolii*
Serrazzano	MN12	Italy	Hominidae	*Oreopithecus bambolii*
Pyrgos Vassilissis	MN12	Greece	Hominidae	*Ouranopithecus macedoniensis*
Udabno I	MN12	Georgia	Hominidae	*Udabnopithecus garedziensis*
Casablanca M	MN13	Spain	Cercopithecidae	*Macaca* cf. *sylvana*
Dytiko 1 (DTK)	MN13	Greece	Cercopithecidae	*Mesopithecus* cf. *monspessulanus*
Dytiko 2 (DIT)	MN13	Greece	Cercopithecidae	*Mesopithecus* cf. *monspessulanus*
Polgardi	MN13	Hungary	Cercopithecidae	*Mesopithecus* cf. *pentelicus*
Brisighella	MN13	Italy	Cercopithecidae	*Mesopithecus* cf. *pentelicus*
Dytiko 1 (DTK)	MN13	Greece	Cercopithecidae	*Mesopithecus* cf. *pentelicus*
Dytiko 2 (DIT)	MN13	Greece	Cercopithecidae	*Mesopithecus* cf. *pentelicus*
Dytiko 3 (DKO)	MN13	Greece	Cercopithecidae	*Mesopithecus* cf. *pentelicus*
Maramena	MN13	Greece	Cercopithecidae	*Mesopithecus pentelicus*
Casino	MN13	Italy	Cercopithecidae	*Mesopithecus pentelicus*
Hatvan	MN13	Hungary	Cercopithecidae	*Mesopithecus pentelicus*
Baltavar	MN13	Hungary	Cercopithecidae	*Mesopithecus pentelicus*
Baccinello V3	MN13	Italy	Cercopithecidae	*Mesopithecus* sp.
Gravitelli	MN13	Italy	Cercopithecidae	*Mesopithecus* sp.
Pestlorinc	MN14	Hungary	Cercopithecidae	*Dolichopithecus ruscinensis*
Megalo Emvolon (MEV)	MN14	Greece	Cercopithecidae	*Dolichopithecus ruscinensis*
Montpellier	MN14	France	Cercopithecidae	*Dolichopithecus ruscinensis*
Osztramos 1	MN14	Hungary	Cercopithecidae	*Macaca* indet.
Montpellier	MN14	France	Cercopithecidae	*Macaca sylvana*
Montpellier	MN14	France	Cercopithecidae	*Mesopithecus monspessulanus*
Layna	MN15	Spain	Cercopithecidae	*Dolichopithecus ruscinensis*
Wölfersheim	MN15	Germany	Cercopithecidae	*Dolichopithecus ruscinensis*
Perpignan	MN15	France	Cercopithecidae	*Dolichopithecus ruscinensis*
Csarnota 2	MN15	Hungary	Cercopithecidae	*Macaca* cf. *sylvana*
Orrios 7	MN15	Spain	Cercopithecidae	*Macaca* indet.

(continued on next page)

Table 1 (*continued*)

Locality	MN age	Country	Family	Species
Perpignan	MN15	France	Cercopithecidae	*Mesopithecus monspessulanus*
Malushteni	MN15	Romania	Cercopithecidae	*Mesopithecus monspessulanus*
Wölfersheim	MN15	Germany	Cercopithecidae	*Mesopithecus monspessulanus*
Malushteni	MN15	Romania	Cercopithecidae	*Paradolichopithecus* cf. *arvernensis*
Hajnácka	MN16	Slovakia	Cercopithecidae	indet.
Triversa (Fornace RDB)	MN16	Italy	Cercopithecidae	*Macaca* cf. *sylvana*
Gundersheim 1	MN16	Germany	Cercopithecidae	*Macaca* cf. *sylvana*
Cova Bonica	MN16	Spain	Cercopithecidae	*Macaca* cf. *sylvana*
Balaruc	MN16	France	Cercopithecidae	*Macaca* sp.
Beremend 4	MN16	Hungary	Cercopithecidae	*Macaca* sp.
Hajnácka	MN16	Slovakia	Cercopithecidae	*Mesopithecus monspessulanus*
Triversa (Fornace RDB)	MN16	Italy	Cercopithecidae	*Mesopithecus monspessulanus*
Vialette	MN16	France	Cercopithecidae	*Paradolichopithecus* cf. *arvernensis*
Cova Bonica	MN16	Spain	Cercopithecidae	*Paradolichopithecus* sp.
Moreda	MN16	Spain	Cercopithecidae	*Paradolichopithecus* sp.
Saint Vallier	MN17	France	Cercopithecidae	*Macaca* cf. *sylvana*
La Puebla de Valverde	MN17	Spain	Cercopithecidae	*Macaca* cf. *sylvana*
Senèze	MN17	France	Cercopithecidae	*Macaca* cf. *sylvana*
Tegelen	MN17	Netherlands	Cercopithecidae	*Macaca florentina*
Mugello	MN17	Italy	Cercopithecidae	*Macaca florentina*
Capo Figari	MN17	Italy	Cercopithecidae	*Macaca majori*
Orosei	MN17	Italy	Cercopithecidae	*Macaca majori*
Vatera	MN17	Greece	Cercopithecidae	*Paradolichopithecus arvenensis*
Senèze	MN17	France	Cercopithecidae	*Paradolichopithecus arvenensis*
La Puebla de Valverde	MN17	Spain	Cercopithecidae	*Paradolichopithecus* cf. *arvernensis*
Kuruksaj	MN17	Tadzhikistan	Cercopithecidae	*Paradolichopithecus sushkini*
Dmanisi	MN17	Georgia	Hominidae	*Homo* sp.

analysis (see above for criteria of excluding singletons). Those primate localities which do not fall within one MN-zone were excluded from the analysis, even those included in the maps. The sample sizes for both sets of localities can be found in Table 2.

For dietary comparison we used "diet_3" assignment from the NOW database: plant-dominated omnivory (plant_dom), browsing (browse), mixed feeding (br/gr), and grazing (graze). In the diet_3 assignments the emphasis is not entirely on hypsodonty, but it uses dental wear patterns (Janis, 1990; Fortelius and Solounias, 2000) and cranial proportions (Solounias and Moelleken, 1993; Janis, 1995) to deduce the dietary behaviour of species.

We made two kinds of comparisons. One based on diet and other based on mean crown height value of primate and non-primate communities. Both comparisons were made between primate and non-primate localities using the same dataset as the hypsodonty comparison. The dietary comparison was made with both absolute and relative values. The statistical significance of differences in diets in primate and non-primate localities (for absolute values) can be seen in Table 3 and the statistical significance of differences in mean crown height values between primate and non-primate localities are given in Table 4.

Results

Primates and humidity

Fortelius et al. (2002) demonstrated that ungulate crown height can be used as a proxy for approximate humidity. Damuth and Fortelius (2001) also showed that it can be crudely connected to rainfall and used as paleoprecipitation proxy. One must be warned that relative crown

Table 2
The sample sizes with mean hypsodonty values (that are same as in fig. 3) for primate and non-primate datasets

	Number of species in primate localities	Number of primate localities	Mean hypsodonty in primate localities
MN05	113	5	1,125
MN06	135	10	1,1529
MN07/8	104	6	1,0943
MN09	239	15	1,4672
MN10	101	5	1,4068
MN11	56	3	1,6619
MN12	63	10	1,6666
MN13	70	7	1,7051
MN14	29	2	1,8
MN15	59	5	1,6551
MN16	43	4	1,28
MN17	70	3	1,9714
	Number of species in non-primate localities	**Number of non-primate localities**	**Mean hypsodonty in non-primate localities**
MN05	208	31	1,2047
MN06	112	19	1,2025
MN07/8	158	32	1,1717
MN09	206	31	1,2186
MN10	121	18	1,6117
MN11	204	19	1,5853
MN12	320	24	1,6836
MN13	125	16	2,1506
MN14	90	15	1,7735
MN15	85	11	1,5952
MN16	195	18	1,8977
MN17	124	9	2,0377

Sample sizes given for both total amount of localities and species in each MN-unit.

height as a humidity/aridity proxy does not differentiate between seasonal or continuous aridity (Fortelius et al., in press). It is best described by generalised water stress (Fortelius et al., 2002) or by generalised humidity that is not only rainfall, but also the moisture in the soil and other factors (M. Fortelius, pers. comm.). Here we use the term "humidity level" for the differences that we are seeing. We do not presume that our humidity values would be anything else but a crude measure of the actual values. In the recent EEDEN (Environments and Ecosystem Dynamics of the Eurasian Neogene, http://www.esf.org/eeden/) Working Group meeting (Micheels et al., 2003) it was concluded that all the available proxies are quite consistent with each other and all have the same kind of uncertainty limits (between 100 and 300 mm/year, plus or minus). We have plotted occurrences of Neogene primates on hypsodonty maps (Figs. 1 and 2) in order to look at the environmental requirements between different families of primates and their development in time.

A basic pattern evident from the map succession (Figs. 1 and 2) is that primates generally occur in areas where the humidity is highest. This is particularly true for pliopithecids and hominids during Late Miocene (MN5–MN12), while Cercopithecoidea instead show exceptions to this rule, especially during latest Miocene and Pliocene.

A clear pattern emerging from the map succession is one of environmental changes that start from the East. The phenomenon of provinciality in the Neogene of Europe (in the broadest sense) has been stressed in several papers, especially by Bernor (1983, 1984), Bernor et al. (2001, 2004), Fortelius et al. (1996).

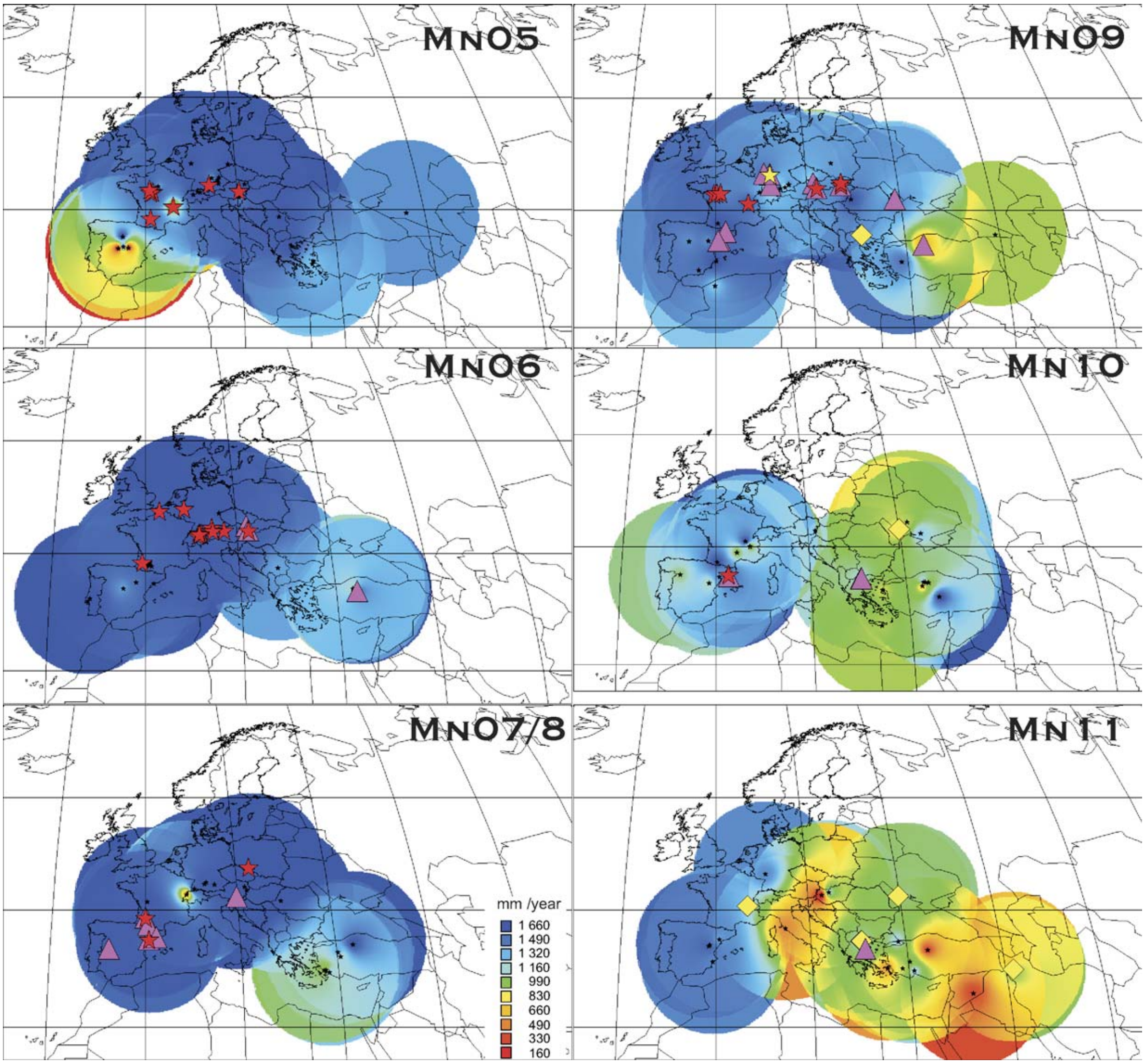

Fig. 1. Humidity maps with primate occurrences for the age range of MN5–MN11. Different colours indicates rainfall estimates (mm/year) based on herbivore hypsodonty (see text for explanation). The asterisks marking the primate occurrences are the following: **Pliopithecus site**: red star; **Hominidae site**: pink triangle; **Primates indet**.: yellow star; **Cercopithecidae *Mesopithecus***: yellow ruby; **C. *macaca***: white upside triangle; **C. indet**.: blue ball; **C. *Dolichopithecus***: pink ball; **C. *Paradolichopithecus***: black triangle; ***Homo* sp.**: blue star.

The "colobine" genus *Mesopithecus* seems to have its first occurrence quite early in MN 9 (Gorna Susica in Bulgaria) in a humid scenario, while the only occurrence in the following time slice (MN10, Grossulovo in Ukraine) appears to occur in a more arid area, however, surrounded by a wide humid area. The basis of the MN correlation for these sites is not very firm and should be taken cautiously. The first sure occurrence of the genus *Mesopithecus* is in MN 11 sites correlative with Maragheh (Andrews et al., 1996). The genus then maintains a distribution limited to localities with humid environments until its last occurrence in the Pliocene (MN16). The wider

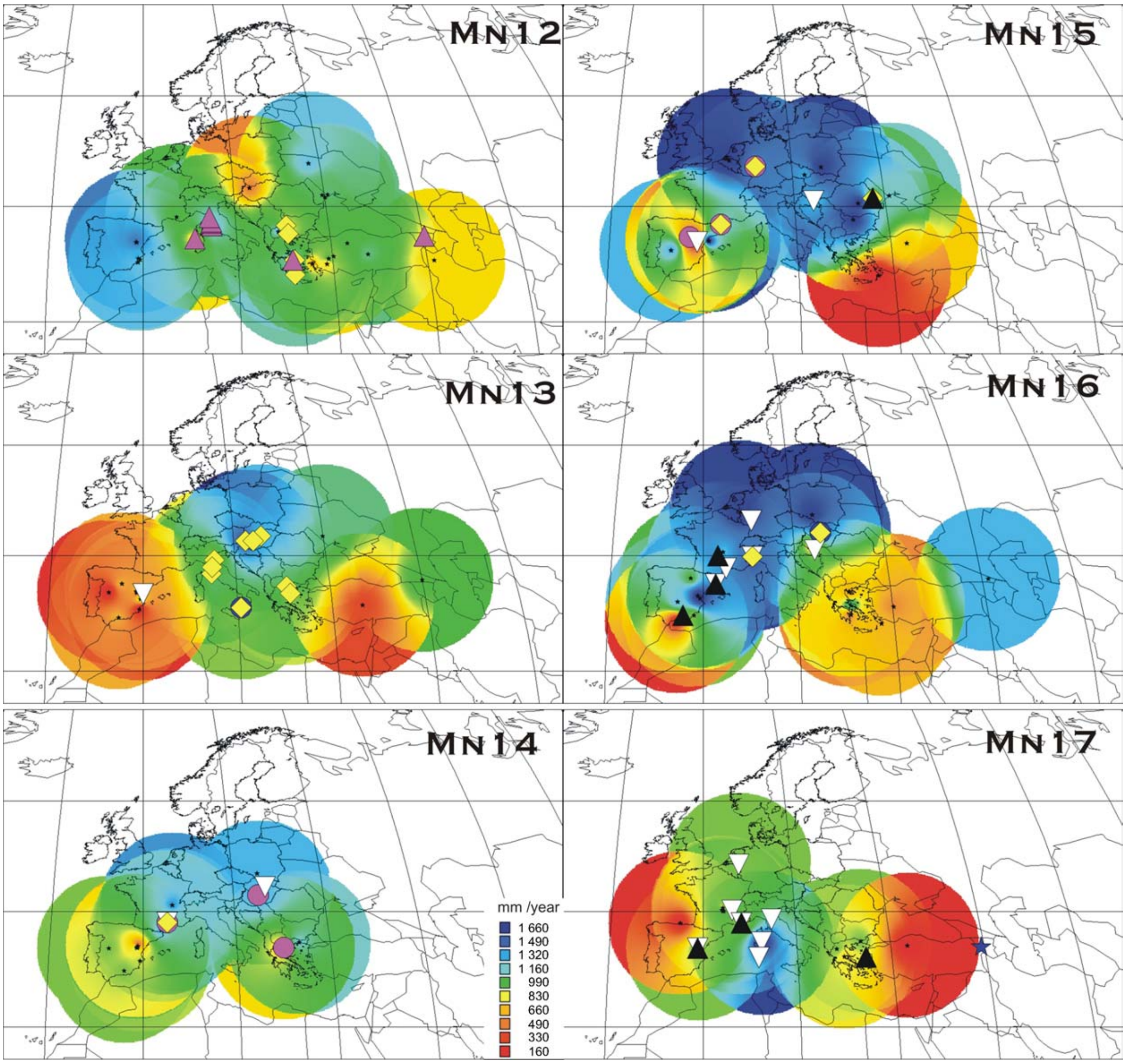

Fig. 2. Humidity maps with primate occurrences for the age range of MN12–MN17. Different colours indicates rainfall estimates (mm/year) based on herbivore hypsodonty (see text for explanation). The asterisks marking the primate occurrences are the following: **Pliopithecus site**: red star; **Hominidae site**: pink triangle; **Primates indet**.: yellow star; **Cercopithecidae *Mesopithecus***: yellow ruby; **C. *Macaca***: white upside triangle; **C. indet**.: blue ball; **C. *Dolichopithecus***: pink ball; **C. *Paradolichopithecus***: black triangle; ***Homo* sp.**: blue star.

spectrum of its distribution is seen in the late Miocene (MN11–MN13) with a large geographic range occurring also in habitats characterized by lower humidity.

Dolichopithecus, is a "colobine" larger in size than *Mesopithecus* and limited to the Early Pliocene (MN14 and MN15). During MN14 it occurs either in a mid-arid assemblage (Megalo Emvolon in Greece) or in mid-humid assemblages (Montpellier in southern France and Pestlorinc in Hungary). It disappears from the fossil record in the end of MN15 when it is distributed in localities of contrasting paleoprecipitations (Layna, mid-arid assemblage in Spain; Perpignan and

Table 3
The significance values of dietary comparison (figs. 4 and 5) between primate and non-primate localities for each MN-unit (Pearson Chi-square test)

MN-Unit	Chi-Square value	DF	Significance (*p*)
5	1,777	3	0.7585
6	1,101	3	0.777
7/8	7,644	3	0.54
9	1,591	3	0.6614
10	0,894	3	0.8269
11	3,184	3	0.3642
12	6,672	3	0.0831
13	**14,639**	3	**0.0022**
14	1,165	3	0.7614
15	1,143	3	0.7667
16	10,5	3	0.0148
17	2,331	3	0.5066
MN5–MN17	13,84	3	0.0031

Significant values are marked by bold characters.

Wölfersheim, mid-humid assemblages of southern France and Germany respectively).

The very large cercopithecid *Paradolichopithecus* appears during MN15 at Malushteni (Romania), in a quite humid environment. During the following time slice (MN16) it is still distributed in France and northern Spain in sites with comparable humidity, while at Moreda (Southern Spain) it appears to be present in much more arid mammal community. During MN17 *Paradolichopithecus* is distributed in quite arid localities at Mediterranean latitudes (Spain-France-Greece). Out of the range of our maps this primate occurs in MN17 at Kuruksaj in Tadzhikistan (in an arid assemblage).

Table 4
The significance values for mean hypsodonty value comparison (fig. 3) between primate and non-primate localities for each MN-unit (Pearson Chi-square test)

MN unit	Chi-square value	DF	Significance (*p*)
MN5	1,254	2	0.5342
MN6	0,441	2	0.802
MN7/8	2,949	2	0.2289
MN9	0,848	2	0.6546
MN10	7,867	2	0.0196
MN11	0,113	2	0.9452
MN12	0,224	2	0.8942
MN13	**10,721**	**2**	**0.0047**
MN14	0,299	2	0.8612
MN15	1,79	2	0.4085
MN16	**15,665**	2	**0.004**
MN17	0,64	2	0.726
MN5–MN17	3,097	2	0.2126

Significant values are marked by bold characters.

Finally, the genus *Macaca* has its first occurrence on the latest Miocene (MN13) in Spain as an isolate primate finding within an arid area. In successive time slices the genus is widespread over Europe in relatively humid areas, with again an exception in Spain during MN15 occurring at the locality Orrios-7. In the final phases of the Pliocene (MN17) the genus *Macaca* is distributed over localities with wide range of humidities and reaching its northernmost distribution (Tegelen, The Netherlands).

Primate versus non-primate localities

In order to look if the primate localities differ from non-primate ones we used a dataset where the localities have been separated into primate and non-primate localities (see Material and Methods). By plotting the mean crown height values of both locality sets in the same diagram, three different stages in the development of mean crown height through time can be recognized (Fig. 3, data is also shown in Table 2): Middle Miocene (MN5–MN7 + 8), Late Miocene to the beginning of the Pliocene (MN9–MN14) and the late Early to Late Pliocene (MN15–MN17). Within the late Neogene there are two time units (MN11 and MN14) where the mean hypsodonty does not show difference between the primate and non-primate localities.

Mean crown height values are rather similar during the middle Miocene (MN5–MN7/8). The primate localities show consistently lower values than non-primate localities, but the differences are small.

In terms of crown height proxy (Fig. 1), Europe appears to have been rather homogeneous vis-à-vis its paleoclimate during MN9. The exception is central Turkey and Georgia. Especially the Turkish locality of Sinap seems to have had arid conditions compared to other regions in our study. Particularly significant is the occurrence of the hominid *Ankarapithecus* under these conditions. This is not the case in mean crown height values

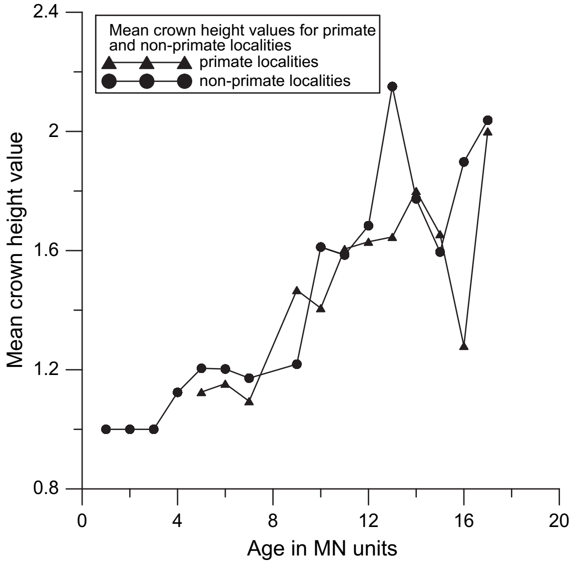

Fig. 3. Mean ordinated hypsodonty for primate and non-primate localities. Age refers to MN-units.

(Fig. 3). In MN9 the primate localities have higher mean value than non-primate ones.

During the interval MN7/8–MN11 the non-primate localities seem to "lag" one MN-unit behind the primate localities, while after that the primate localities appear to "lag" one MN-unit behind the non-primate localities in mean hypsodonty values, and in contrast to the non-primate localities there is no sharp rise in mean hypsodonty value in MN13.

The mean hypsodonty rises in non-primate localities from MN9 almost constantly until MN13, after which there is a sharp decline. In primate localities, the mean hypsodonty rises between MN7/8 and MN11, and remains quite stable after that until MN14. (During MN9 the primate localities have higher mean hypsodonty value than non-primate localities.)

It is noteworthy that overall the mean hypsodonty value is very stable in primate localities in the time period MN11–MN13 (MN14). During this period the hypsodonty values of non-primate localities varies greatly. This is also a time period when vast areas are without primate occurrences, representing presumably tendency towards aridification in the latest Miocene (Messinian; MN13). It is interesting to note that the highest mean hypsodonty value in primate localities before MN17 is seen in MN14, right after the end of the Messinian stage (earliest Pliocene).

After MN14 mean hypsodonty value of primate localities begins to decline sharply. The lowest value is seen in MN16, and the difference between primate and non-primate localities is the same magnitude as in MN13. In MN17 the values come again close to each other.

The dietary comparison (Figs. 4 and 5) complements the pattern. Until MN9 both sets of localities have same kinds of communities: Browsers dominate with mixed feeders. From MN9 onwards the number of browsers diminishes, and also their relative abundance declines (see also Janis et al., 2000). Beginning from MN11, and continuing thereon, the primate and non-primate localities show some differences in diet structure.

From MN11 onwards the relative abundance of grazers starts to rise in non-primate localities (Fig. 5A). This is followed by reduction in the frequency of browsers in MN12 and MN13 mammal localities. In primate localities (Figs. 4A and 4B) there is only a slight decline in the abundance of browsers during this time. While the dietary structure is quite similar in both sets of localities in MN11 (Figs. 4 and 5), there are differences in MN12 even while it is not statistically significant. The number of grazers starts to rise in non-primate localities whereas in primate localities the number of grazers stay low.

In MN13 faunas the diets are different (Table 3). In the primate localities there are still only few grazers while in the non-primate localities the number of grazers is high. In MN14 the dietary structure is again quite similar in both primate and non-primate localities. MN15 is almost the same as MN14. The number of browsers rises in both while other dietary categories remain almost constant (Figs. 4 and 5). In MN16 the number of grazers rises in non-primate localities, while in primate localities there is almost no change. The rise in grazers is seen in primate localities in MN17. The dietary structures are different in MN16, but almost the same in MN17.

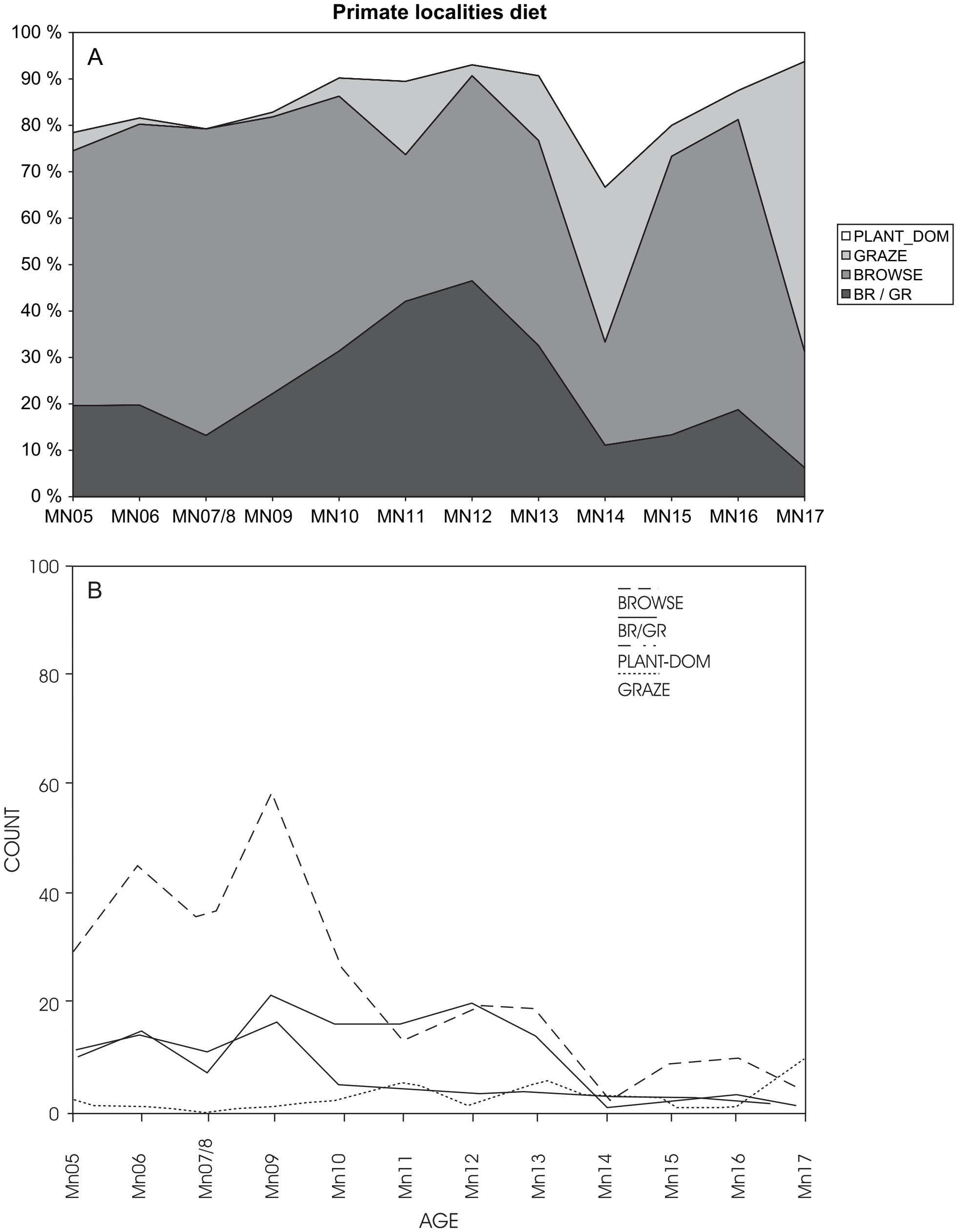

Fig. 4. a. Relative proportions of different dietary behaviours in primate localities. Age refers to MN-units 4b. Absolute numbers of different dietary behaviours in primate localities. Age in the X-axel is in MN-units.

Discussion

From MN5, where we record the first appearance of catarrhine Primates in Europe, until MN7/8 the humidity pattern is quite stable. It is well known that the Middle Miocene of Europe was humid and warm (e.g. Kovar-Eder et al., 1996; Esu, 1999; Utescher et al., 2000; Ivanov et al., 2002). This is in

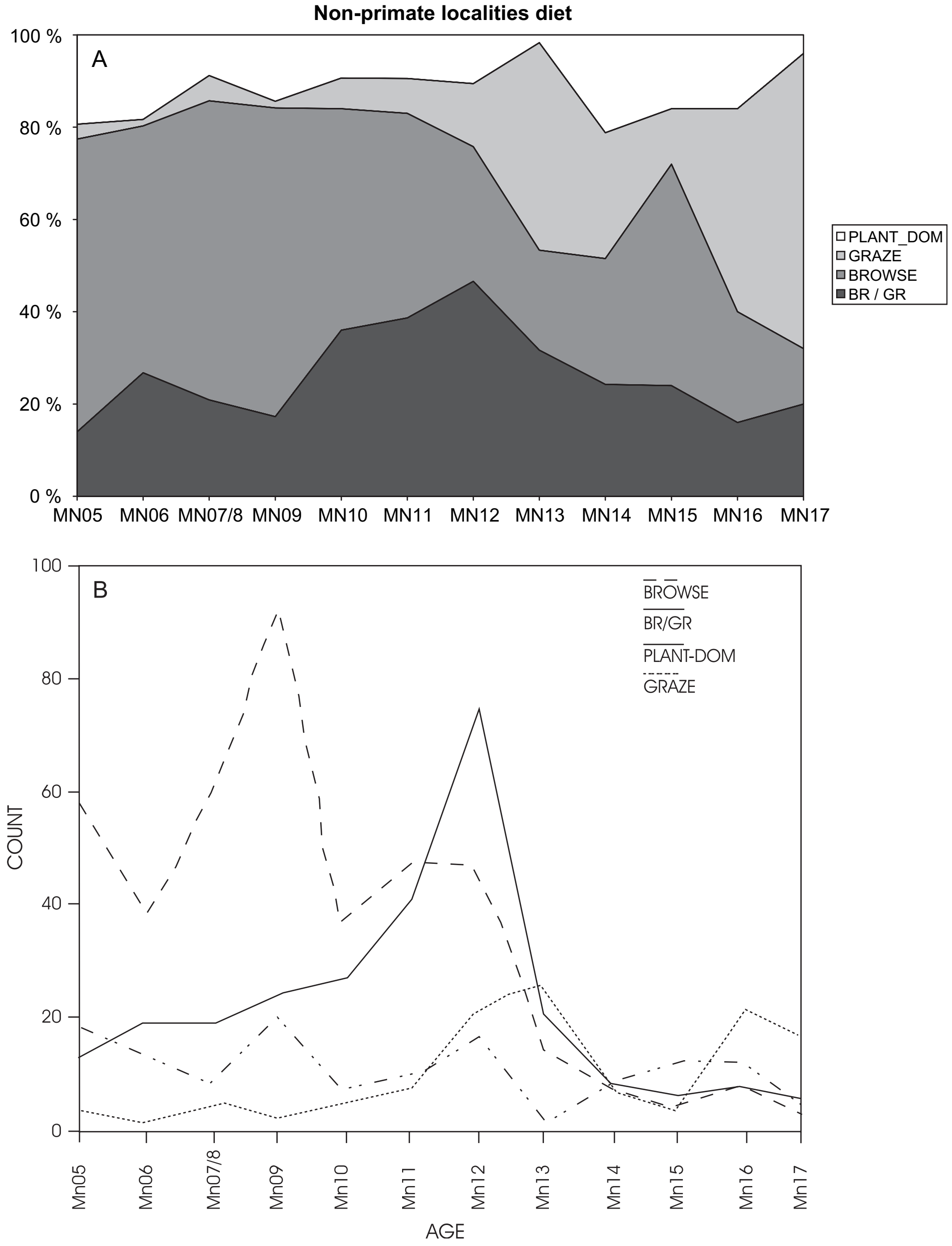

Fig. 5. a. Relative proportions of different dietary behaviours in non-primate localities. Age refers to MN-units 5b. absolute numbers of different dietary behaviours in non-primate localities. Age in the X-axel is in MN-units.

full agreement with the wide distribution of pliopithecids and hominids during the time span of MN5–MN7/8.

In MN9 we have the first increase in aridity starting from Asia minor and East Europe (a pattern confirming the early observation on provinciality patterning of Western Eurasia; Fortelius et al., 1996; Bernor et al., 2004), but the general pattern is still humid and uniform with pliopithecids widespread in all central and western

Europe. This is seen in vegetation as more restricted distribution of swamp forests and lower frequencies of paleotropical elements in Forecarpathian area (Ivanov et al., 2002), and spread of dry-woodland biomass to western Europe (Van Der Burgh et al., 1993). As a whole the environments became dryer at the beginning of late Miocene (10–11 Ma ago) (Van Der Burgh et al., 1993, Ivanov et al., 2002) and according to Agusti et al. (2003) the spread of warm temperate deciduous woodlands in Europe heralded the extinction of pliopithecid and hominid primates in Europe. The spread of more open vegetation occurred approximately 1 Ma later (Agusti et al., 2003).

The spread of arid conditions from the east is really visible if we compare two localities that virtually straddle between the MN9/10 boundary: Can Llobateres (MN10 here) in Spain and Sinap (MN9 here) in Turkey. If we compare these with MN9 and MN10 localities nearby (Fig. 1), we see that Can Llobateres belongs still to the MN9 according to crown height proxy whereas Sinap is already dryer and closer to conditions present in MN10.

The Sinap locality of Turkey is especially interesting because there we have a hominid appearing in an arid assemblage. The large mammals in the Sinap are a very peculiar mix of older, more humid adapted species and newcomers that are starting to dominate the assemblages in late Miocene. According to Gentry (2003) the ruminants of Sinap are a mix of woodland adapted and more open-terrain adapted species. Bernor et al. (2003) found really diverse array of hipparions from Sinap indicating openess of habitats. The appearance of *Ankarapithecus* in this kind of assemblage could be interpreted as an expression of provinciality (sensu Bernor 1983, 1984) as environment changes in easternmost areas towards conditions that in MN 10 and MN 11 will be much more wider distributed across eastern and central Europe.

It is worthy of note that Miocene Hominidae reached their northernmost distribution during MN9. In the following time units (MN10–MN12) hominids are found in more southern and insular localities (Central Italy localities, OZF in Bernor et al., 2001). Fortelius and Hokkanen (2001) proposed that this might not be due to lack of humid conditions in the North, but rather to the lower temperatures (i.e. increase in thermal seasonality).

In MN10 the spread of arid conditions from the east continued and in MN11 the aridity contrast between east-west was particularly evident. This trend of "transgression" of arid conditions to the west continued until the beginning of MN13. One explanation for this is probably the continentalization process of Paratethys (Ramstein et al., 1997; Rögl, 1998), which started in the middle Miocene and continued to the late Miocene. It is also connected with the spread of "Pikermian biome" (sensu Bernor, 1983, 1984; Solounias et al., 1999). This process is seen in the dietary structure comparison between the primate and non-primate localities (Figs. 4 and 5). From MN11 onwards the differences between these began to grow and culminate in MN13 where the dietary structure of mammal communities was significantly different in primate and non-primate localities. The non-primate localities started to show open-habitat diet structure with more grazers and less browsers. In general the primate localities had more closed-habitat diet structure with browsers and only a few grazers.

In the primate record the dispersion of *Mesopithecus* (above) and contraction of hominids towards the more humid habitats depicts this "continentalization" process (The locality of Udabno in Georgia [Gabunia et al., 2001] being the exception). It is worth to note that even today the area of the Caucasus between greater and lesser caucasian mountain ranges acts as a refuge area for mammals. The continentalization process of Paratethys might be interpreted as disappearance (or lesser amount) of suitable humid habitats thus restricting hominids to suitable habitats at Mediterranean latitudes. The Late Tortonian (MN11 and early MN12) Central Mediterranean area retained humid climates (Griffin, 2002). Hominid occurrences documented in few sites in Greece and in insular habitats of Italy witness this. Hominids disappeared from Europe in the end of MN12, while *Mesopithecus* did not seem to suffer much. This is in good accordance with the fact that *Mesopithecus* was semiterrestrial (Szalay and

Delson, 1979; Ciochon, 1993) and therefore able to survive in more open environments. Considering that the dietary structure remains the same during the time period MN11–MN13 in primate localities, it is probable that even the "dry" localities were situated in small tree-stands close to, or within, open habitats.

By MN13 the situation changes and the Mediterranean latitudes with Spain and Turkey experience arid conditions. This pattern of aridity in southern latitudes drives the distribution of *Mesopithecus* northwards to Central Europe and to Central Italy, with exception of localities in Sicily and Greece, which are at the margin of the humid area. The humidity might be due to their closeness to a large water-body. Surprisingly, the evaporitic Messinian had also strong rainfall associated with it (Griffin, 2002). It can be argued that during the final drawdown of the Mediterranean sea, the substantially dried Mediterranean Basin would be the focus of a low-pressure cell during the summertime (Ramstein et al., 1997; Griffin, 2002). This low-pressure would affect the whole Mediterranean area and bring summer rains to the area, thus increasing seasonality in precipitation. Whether this was the case is doubtful, but we wish to point out this possibility in this context. It has been demonstrated that this happened during the continentalisation process of Paratethys (Ramstein et al., 1997). In the humidity maps we can see the late remains of the central Paratethyan area in Central Europe, where there is a concentration of primate localities. The pattern of primate occurrences also seems to affect the later distribution of Cercopithecoidae as a whole during the period of MN14–MN16. The main distribution range of Cercopithecoidae is more northern than before MN13. Only in MN17 is the main area of occurrence back in the Mediterranean.

After the Messinian "crisis" (latest MN13) the conditions in Europe seem to have became more homogenous in terms of humidity, with less "arid" areas. This might have been the result of lessening seasonality, changes in soil moisture and/or change in overall precipitation values in Europe (ie. return of humid conditions to Europe [Griffin, 2002]). The early Pliocene (MN14–MN15) vegetation of Western Europe and Northwestern Mediterranean was subtropical. At the time Southwest Mediterranean was dominated by arid-semiarid vegetation (Suc et al., 1995). In the dietary comparison we can see this as lessening of differences between primate and non-primate localities. Both locality sets are similar in MN14–MN15 with lesser amount of grazers and rise in browsers in MN15. The climate started to grow cooler in the early Pliocene, and in the early–middle Pliocene transition (between MN15–MN16) the temperatures dropped considerably. This is interpreted by Suc et al. (1992, 1995) as an increase in thermal seasonality in the Mediterranean. In MN16 the frequency of grazers begins to rise in non-primate localities whereas in primate localities the rise is in MN17. This suggests that the primates remained in the closed habitats of central and western Europe, while the increased seasonality started to affect eastern Mediterranean and Iberian peninsula. This is also seen in the mean hypsodonty values: the differences between primate and non-primate localities are significant during this period. This time the mean hypsodonty value of primate localities plummets while the value of non-primate localities rises. The phenomenon might be interpreted as reaction to seasonality. The primates moved to the preferred habitat areas, while non-primate communities adapted to the changing environment more rapidly. In MN17 we see the cooling effect of the coming ice age already pressing the primates to new habitats and there is almost no difference between the dietary structures of primate and non-primate localities.

All these trends in primate communities are also connected to the actual dynamics in the primate record. *Dolichopithecus* continues to co-occur with *Mesopithecus* in MN15 in the mid-humid area of southern France (Perpignan) but also in very humid central European site of Wölfersheim (Germany). The increase in thermal seasonality (Suc et al., 1992, 1995) coincidences with the disappearance of *Dolichopithecus* in the end of MN15.

Paradolichopithecus (a large-sized baboon-like cercopithecoid) is found in semi-humid habitats in MN15. In MN16 it is found also in more arid habitats. This occurrence heralds a shift in ecologic preferences, or change forced by environmental change. *Paradolichopithecus* is even more terrestrial than *Mesopithecus* (Szalay and Delson, 1979, Van der Geer and Sondaar, 2002), which might suggest that *Paradolichopithecus* prefers humid and closed localities, but is also able to survive in more arid and open localities. It also seems that *Paradolichopithecus* was able to persist in cooler temperatures than *Mesopithecus*, that disappears from the European record in the end of MN16.

Macaca is a genus that includes species that have both arboreal and terrestrial capabilities, and it seems to be able to survive in a variety of habitats even though they prefer humid ones. It also is able to withstand cooler temperatures. This is in good accordance with its wide occurrence and persistence in time. Today some species of *Macaca* can even live in habitats with snow and some in intense heat (Nowak, 1999).

During MN17 there is a dramatic change: no humid habitat occurs in Europe, apart from the Tyrrhenian area. In MN17 *Macaca* apparently shifts its habitat preferences and with *Paradolicopithecus* it survives evidently by adapting to dryer (and cooler) environments. MN17 represents the setting of open spaces in European environments and the definition of the ecological opportunities for the dispersal in Europe of a new primate coming from Africa, the genus *Homo*, as recorded in the Georgian site of Dmanisi (Gabunia et al., 2000; Vekua et al., 2002). After MN17, *Homo* and *Macaca* were the only primates occurring in Europe, suggesting their adaptation to more arid (and cooler) environments.

Conclusions

We have plotted the occurrences of Neogene primates on paleoprecipitation maps in order to see how primate localities are distributed in this context. The pliopithecids and hominids are found only at humid habitats whereas Cercopithecids would appear to have had a more complex habitat selection. When the environments started to change towards more open habitats, hominids and cercopithecids retreated to areas where humid conditions remained, while pliopithecids disappeared. The differences in primate and non-primate localities are strongest during times of large environmental change, when primates are found in their preferred habitats and non-primate localities show quicker adaptation to the changing conditions. Primates seem to have been adept at tracking their habitats geographically.

The contrast between primate versus non-primate localities appears from the beginning of MN10 onwards, and is highest during MN13 and MN16. The dietary comparison suggests that the primates are able to track their preferred habitats, humid and closed ones. They do not seem to occur in grasslands, even if the conditions are dry. They probably hang to locally more humid pockets, away from open habitats. Based on our results it seems that during the late Neogene in Europe not only hominids prefer the forest habitat, but also most of the Cercopithecoidea. The difference seems to be that during the Neogene in Europe hominids are not able to cope well outside humid and closed habitats, and in the end of MN12 they disappear from Europe. The cercopithecoids seem to have been able to adapt to the more open and dry environments. Our results also show that the primates seem to be able to track their preferred habitat well, and because of this there are significant differences between primate and non-primate communities in times of change. During the Neogene the most significant changes that increased the differences between primate and non-primate localities were the spread of dry conditions to Europe, the drying of the Mediterranean and the increase in seasonality during the latest Neogene. The increase in seasonality is also connected to the large scale climatic changes that started the development towards Quaternary glaciations. The exception to general habitat preference seems to be the case for *Macaca* and *Paradolichopithecus* which seem to be able to shift their habitat preferences.

The fossil record of cercopithecoids and the one of apes shows quite different patterns. Apes are limited to the European Middle Miocene and early Late Miocene, while cercopithecoids are widespread, ranging from the late Miocene to Plio-Pleistocene with an increasing number of taxa. They are a part of the evolutionary radiation that in the Old World produced differentiation in the living monkeys. This "turnover" in primate composition of Neogene fauna reflects climatic changes over Europe (as well as in all the Old World) and not just competition between monkeys and apes in a stable environment.

In respect to our knowledge of the biogeography of living Old World monkeys, the fossil record shows how both colobines (*Mesopithecus* and *Dolicopithecus*) and cercopithecines (*Macaca* and *Paradolicopithecus*) ranged over much of Europe during the last six million years. Interestingly, the observed pattern of tracking the humid conditions remains even while the last Neogene primate species are more terrestrial than the previous ones.

Macaca first occurred quite early in the fossil record of cercopithecine and has a tendency to occupy even relatively arid habitats. It has a wide range of habitat preferences and can occupy a variety of environmental conditions surviving in Europe for great part of the Quaternary. In the latest Neogene, when the humid habitats virtually disappeared, two new large sized genera occurred in Europe: the baboon-like *Paradolichopithecus* (first occurring in MN15) and *Homo* (first occurring at the latest Pliocene, in late MN17). *Paradolicopithecus* disappears from Europe at the end of the Pliocene, while *Homo*, together with *Macaca*, remained to characterize European assemblages during Quaternary (and Holocene), both well adapted to a changing world.

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