News and Views

Hominoid evolution and environmental change in the Neogene of Europe: a European Science Foundation network

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The later Neogene (the period between 14 and 2·4 m.y.a.) is crucial to understanding the present state of the terrestrial ecosystems. It was during this phase that the middle Miocene subtropical forests were replaced by more open habitats that still prevail in warm–temperate areas. In the late Neogene the first climatic shifts preceding the great Pleistocene glaciations took place. Regional geological changes occurred, leading to the present physical configuration of the Old World. For the land mammals, this was a time of intense faunal interchange coupled with regional differentiation and accelerating evolution.

This dynamic background must have directly influenced hominoid evolution during the later Neogene. Around 10 m.y.a. Eurasia displayed a large variety of apes, with gracile forest-dwellers (*Dryopithecus*, *Sivapithecus*), dry-adapted forms (*Ankarapithecus*) and large robust gorilla-like forms (*Graecopithecus*), whereas almost nothing is known about African primates of this interval. In some ways the Eurasian Miocene radiation of apes parallels that observed in Africa 5 Ma later. Unlike during the Pliocene in Africa, however, deforestation and expansion of dry open-lands in Eurasia did not result in the emergence of bipedal apes, but in the extinction of generalized morphotypes and the persistence of highly specialized forms in relict areas (*Gigantopithecus*, *Pongo*). Knowledge of the ecosystems in which hominoids of the late Miocene evolved is still incomplete only occasionally has an integrated analysis of data been attempted.

In order to focus on these issues and to foster cooperation between scientists dealing with them, the scientific network ''Hominoid evolution and environmental change in the Neogene of Europe'' was approved by the European Science Foundation in 1995. One of the goals of this network is to create a database on Neogene mammals of Eurasia, that could be used for further analysis of the ecosystems where hominoids lived. The network also organizes three workshops in order to analyse different aspects of the late Neogene time and their relevance to hominoid evolution.

The first workshop was held in Sant Feliu de Guixols (Spain; organizer: J. Agustí) in October 1996 and had the topic ''The Vallesian''. The Vallesian (ca. 11–9 m.y.a.) is the period that in Western and Central Europe marks the change from equable and wooded to more open and seasonal conditions with a marked dry period. As a

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consequence of this environmental change, the mammalian community structure also changed in a dramatic way, leading to the extinction of several forest adapted forms. In particular, this event caused the extinction of the hominoid species that occurred in Europe in the earlier part of the late Miocene. Twenty-four scientists from 11 countries attended this first workshop. The majority of presentations dealt with regional mammalian successions ranging from Spain to Southern Asia: Central Spain (Van Dam *et al.*), Eastern Spain (Agustí *et al.*), France (Mein), Italy (Rook & Engesser), Central Europe (Frenzen & Storch), the Aegean area (Koufos & De Bonis), Anatolia (De Bruijn *et al.*), Eastern Europe (Nesin & Bernor) and Pakistan (Morgan). In the case of Eastern Spain, the communications presented by the Spanish team were followed by a field-trip in the Vallès-Penedès Basin to provide participants with an idea of the work recently developed in this area.

The emphasis of the first workshop was on comparison and close correlation of long sequences of large and small mammal localities. Thus, comparison among sections offering magnetostratigraphic control was a significant subject of the meeting, especially those of the Potwar Plateau (Pakistan), the Vallès-Penedès (Spain) and Sinap (Turkey). Climate and environmental evolution during the Vallesian and Turolian times was also a main topic of the workshop, developed especially by Andrews (selected localities of Western Eurasia), Van Dam and Van der Meulen (Central Spain), and Morgan (Potwar Plateau in Pakistan). Another significant topic of the workshop was the so-called ‘‘Mid-Vallesian Crisis’’, an extinction event that followed the change from the middle to the late Miocene. Results reviewed at the workshop suggested that a change similar to the Mid-Vallesian Crisis of Western Europe occurred at different times in different areas. The change was already established in the early Vallesian in the so-called Sub-Parathetyan Province (data from Maragheh by Bernor), but in Western Europe this did not take place until about 9·6 m.y.a. (data from the Vallès-Penedès by Agustí *et al.*). On the other hand, in Central Europe, several species indicating wet, forested conditions persisted well into the late Vallesian (data from Franzen & Storch). Finally, such a change was not seen in Southern Asia (Pakistan) until 8–7·2 m.y.a. (data from the Potwar Plateau by Morgan *et al.*).

The second workshop took place in April 1997 in Certosa di Pontignano (Siena, Italy; organizer: L. Rook) and was devoted to the ‘‘Climatic and Environmental Change in the Neogene of Europe’’. Twenty-five scientists from 11 countries and different palaeoenvironmental disciplines had the rare opportunity to experience a real interfacing of data from the terrestrial ecosystems, the shallow marine realm and the deep sea. A first set of contributions dealt with the palaeogeographic evolution of the Tethys area and its effects on faunal distributions and climate evolution. Rögl presented a summary of the evolution of this area from the early Tertiary to the late Miocene. Plate tectonic movements during the Tertiary closed down the Tethys ocean with the northward movement of the African and Indian continents. The Tethys ocean vanished, leaving as relics the Mediterranean sea at its western end and the Paratethys sea. These were connected at times, and they were also connected to the Arctic ocean through the Turgai Strait in western Siberia, preventing faunal interchange between Europe and Asia. With the contact between the Arabian plate and the Anatolian plate, land bridges formed between Africa and Eurasia opened and closed throughout the middle Miocene, beginning about 19 m.y.a. No hominoid primates are known this early in Europe, but of particular significance to hominoid migrations was the end-Burdigalian regression of the sea at around

16 m.y.a., because this coincides with the earliest evidence of hominoids in Central Europe.

A second set of contributions was devoted to the analysis of the sedimentary record in terms of paleoclimatic reconstruction (Krstic; Benvenuti, Papini and Testa; Meulenkamp, Zachjariasse, Hilgen, Langereis and the European Union network ''Miocene Marine Archives Reading''-MIOMAR-co-workers). Krstic pointed out the remarkable influence of the lake system established in the Western part of the Balkan Peninsula in modelling the local climate of the area during the Middle Miocene (some 15 m.y.a.). Benvenuti *et al.* found that lignite seams in Baccinello (Tuscany) testify to subtropical humid conditions in the Tortonian, whereas semi-arid conditions were established during the Messinian. In Greece, the results presented by Meulenkamp and the co-workers of the MIOMAR projects indicate that it is possible also in alluvial fan and lake systems to recognize the influence of orbital forcing. Insolation variations due to precessional cyclicity were recognized in the sequence of alternating marls and lignites of the Ptolemais section. High insolation resulted in the extension of humid and open lake conditions (marls), which alternated with periods of low insolation and arid conditions resulting in the development of swamps and lignites.

Contributions to climate modelling during the late Neogene were provided by DeMenocal & Brown, and by O'Brien. According to DeMenocal & Brown, marine records of African climatic variability document a shift toward prolonged and seasonally more arid conditions after 2·8 m.y.a. This is linked to cold North Atlantic sea-surface temperatures associated with onset of Arctic ice sheets. Major changes in African faunas coincide with this climatic change suggesting that some speciation events might have been climatically mediated. O'Brien demonstrated that a large proportion (79%) of African woody plant species richness is accounted for by two aspects of climate, annual rainfall and an optimized function of energy (minimum monthly potential evapotranspiration). These two measures can predict variations in plant species richness, whereas temperature is only weakly related to diversity changes and its addition to the model fails to increase its resolving power. The addition of topographic variation, on the other hand, does increase the resolution of the model to 82%, so that this is an important additional factor.

The palaeobotanical approach included both the point of view of macrofloral remains (Kovar-Eder) and the palynological analysis (Suc, Bertini, Clauzon and Suballyova). Analysis of database on fossil plants compiled by Kovar-Eder has identified several patterns of plant association in the Neogene of Europe. Laurel forests with many palaeotropical species were present in the early Miocene (and earlier) but disappeared during the middle Miocene in central Europe, although they persisted for longer in Southeast Europe (for example in Greece). Deciduous taxa invaded Europe gradually during the middle Miocene, with replacement of tropical to subtropical plant associations by more temperate taxa by the end of the Miocene. On the other hand, pollen records contributed by Suc *et al.* show that in the earliest Miocene significant differences between Central Europe and the Mediterranean already existed, the latter region being characterized by a mosaic organization of dry open landscapes adjacent to humid forests. In the mid-upper Miocene times, the most important event seems to be the disappearance of the *Avicennia* mangrove from the North Mediterranean shorelines. At the same time, the *Taxodium* and *Sequoia* humid subtropical forests were replaced by deciduous mesophytic forests by the Pliocene, and after 3·5 m.y.a. much of the northern Mediterranean coastal area changed to steppic associations dominated by *Artemisia*.

The faunal approach to climate evolution was considered both from the side of the ‘‘invertebrate’’ and vertebrate associations. According to data presented by Rosen, most coral reefs (and their associated z-corals) occur in the Mediterranean area in three major high sea-level phases, corresponding to the early (Aquitanian), middle (Langhian-Serravalian) and late Miocene (Tortonian-early Messinian). The z-coral pattern suggests predominantly warmer temperatures through the early and middle Miocene, but a sharp decline started in the early late Miocene (Tortonian), continuing throughout the remaining Neogene. According to continental molluscs (data by Esu), the early Miocene was characterized by the dominance of genera of Oligocene and earliest Miocene origin, whereas most of these elements are lacking in subsequent (middle Miocene and younger) associations. A significant turnover took place at the Mio-Pliocene boundary, with several genera becoming extinct and new ones making their first appearance—the second most important change in the Neogene.

Small mammals were the topic of the contributions by Reumer (Insectivores), Alvarez, Daams, van der Meulen and Pelaez (rodents from Central Spain) and Agustí (rodents from Eastern Spain). Shrews (Soricidae, Insectivora) are among the most sensitive mammals to climatic shifts, because of their very small size and accordingly high surface/volume ratio. Three main periods of faunal turnover, corresponding to humid and warm conditions, characterize the Neogene history of shrews: the early Miocene (19–20 m.y.a.), the early-late Miocene (Vallesian; 9–11 m.y.a.), and the latest Miocene to Pliocene (6 and 2·5 m.y.a.). Climatic deterioration at around 2·7–2·3 m.y.a. finally caused a severe reduction of the European shrew fauna. Among rodents, the analysis of the Calatayud-Daroca succession developed by Alvarez *et al.* also suggests, as for the shrews, that species diversity is more related to relative humidity than to temperature. Quantitative analysis of the rodent succession in the Vallès-Penedès Basin by Agustí *et al.* allows the recognition of an alternation of dry and humid phases during the Miocene and early Pliocene. Early Miocene localities indicate forested, humid conditions, similar to those recorded in the early Miocene of Central Europe. Increasingly dry conditions are recorded across the late early and middle Miocene (early middle Aragonian), but a return to more humid conditions is observed in the late Aragonian (Serravallian) times. The middle/late Miocene boundary coincides with a relatively dry period, followed again by a humid peak in the early Vallesian (early Tortonian), coinciding with the maximum abundance of hominoid remains in Western Europe.

Contributions dealing with large mammal associations were those of Solounias, Plavcan, Witmer and Quade, de Bonis and Koufos, Kordos, and Bernor. After a detailed analysis based on a variety of sources (dental and postcranial ecomorphology of bovids, palynology, isotopes), Solounias *et al.* concluded that the main habitat of the Pikermian mammals was not a savanna (‘‘the savanna myth’’) but evergreen woodland similar to today’s mixed monsoon forest and grassland glades of north Central India. With the drying up of Africa, large mammals with lucky exaptations migrated into Africa from the Pikermian bioprovince. A similar topic was developed by de Bonis and Koufos, who found in Greek faunas evidence of a trend towards drier conditions in the late Miocene. On the other hand, the disappearance of hominoids and other forest elements in the Pannonian Basin at 9–7 m.y.a. was attributed by Kordos to the regression of this large lake, rather than to a general climatic trend. Finally, Bernor discussed the patterns of hominoid immigration, dispersal and extinction. The first appearance of hominoids is documented at around 15 m.y.a.: *Griphopithecus* at Engelswies and *Pliopithecus* at Neudorf-Spalte in Slovakia, both immigrations from Africa. *Griphopithecus* occurred at about the same time in Turkey, and *Pliopithecus* dispersed rapidly into Western Europe, and later as far east as China. There are no records of *Griphopithecus* younger than 14 m.y.a, whereas *Pliopithecus* persisted in Europe until about 9·6 m.y.a. At around 12 m.y.a., another dispersal from Africa led to the first appearance in Europe of *Dryopithecus*. The record of this genus also persists until about 9·6 m.y.a., but possible derivatives of this lineage persisted in the Tyrrhenian areas as *Oreopithecus* (8 m.y.a. in Italy) and the eastern Mediterranean region as *Lufengpithecus* (8 m.y.a. in China), *Graecopithecus* (9·0 m.y.a. in Greece) and *Ankarapithecus* (10–9·5 m.y.a. in Turkey). The persistence of hominoids in Southeast Europe well into the late Miocene is consistent with the evidence of the flora and fauna (above) for persistence of warmer and wetter conditions in this region.