Research Proposal:
Biotic Change in the Terrestrial Neogene of the Old World
(NOW)

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Abstract

Several independent developments have contributed to a situation where it seems natural and necessary to address Neogene biotic change in the Old World using fossil land mammals. The global time scale has improved significantly during recent years, and intercontinental correlations have been correspondingly refined. Stable isotope data from both the deep sea and from terrestrial settings provide an increasingly precise background in terms of timing and amplitude of physical changes during the Neogene. For the problematic floating biochronology of Europe recent progress in Anatolia (the Sinap Project) offers the hope of correlations with the global chronology, which would finally make it possible to use the excellent European fossil material in work requiring precise correlation with other regions. The excellent Chinese fossil collection in Uppsala, Sweden can be tied to the Anatolian chronology, and offers a unique source of eastern Asian Neogene material of high quality. The development of several databases designed to handle and process information relating to fossil mammals and their localities provides an existing format and methodology that can be employed with minor modification for the Old World Neogene. And finally, the major Neogene faunas and taxa have been recently screened and revised, along with other relevant information, for Europe and the Eastern Mediterranean between 15 and 5 Ma ago. These and other recent developments offer the opportunity, for the first time, to investigate long-term changes and patterns over this large area without insurmountable problems of data acquisition and analysis. Ultimately the aim would be to understand the changes that shaped the terrestrial environments and biota of the Old World during the epochs leading up to the Quaternary Ice Age, but there are several immediate short-term aims as well. The main research tool would be a relational database of mammalian fossils and localities of the Neogene of the Old World (NOW), lightly adapted from the existing Evolution of Terrestrial Ecosystems (ETE) database and incorporating mainly data that already exists in easily accessible form. The database would not only be employed for the present project, but would eventually constitute one of the most powerful palaeontological research tools available anywhere. The ETE-NOW collaboration is already established and involves scientists from Europe, the United States and Japan.

Introduction: Why NOW?

The rich Tertiary mammalian faunas from Europe, China and Africa have been important for the development of palaeontology and the understanding of the phylogeny and evolutionary history of many major taxa, and are the main basis for the chronology and correlation of sediments. They have also played an essential role for understanding the broad patterns of biotic change (e.g., Janis, 1982; Bernor, 1983, 1984; Wing et al., 1992; Potts & Behrensmeyer et al., 1992; Vrba, 1992). Issues requiring a fine temporal resolution and secure stratigraphic correlations between distant regions (diversity and turnover patterns, evolutionary rates etc.) have, however, been investigated primarily in the New World, and in North America in particular, where long stratigraphic sequences are readily available and a relatively sophisticated chronology was developed at an early stage (Woodburne, 1987;

Lindsay, 1989). Study of the relationships between global physical and biotic changes similarly requires good temporal control, and has so far been restricted mostly to North America (Stucky, 1990; Prothero, 1989 It has not been possible to tackle global questions directly, and the discussion has rarely proceeded much beyond the exasperating truism that changes have been either synchronous or asynchronous, depending on which correlation is adopted. This is especially frustrating since the understanding of global physical changes during the Tertiary has improved dramatically during the past few years, and investigating the sequence and timing of corresponding changes in the terrestrial biota is becoming an increasingly desirable research objective. Advances in the Palaeogene strongly indicate that changes believed until recently to have been asynchronous, have, in fact, been globally synchronous within the limits of resolution (Prothero & Berggren, 1992), and the same is likely to hold for the Neogene.

For the terrestrial Neogene of the Old World, absence of stratigraphic control and ties to the geochronology remain a serious difficulty. The main exception are the Siwaliks of the Indian subcontinent (Barry et al. 1982, 1985, 1990; Barry & Flynn, 1990), for which good temporal control does exist throughout the Neogene in the form of a magnetic reversal stratigraphy calibrated by radiometric dates. The Indian material thus holds a key position for anchoring the mammalian biochronology for the Old World Neogene to the geochronology. Its potential in this regard is limited by two factors, however: the relatively endemic nature of its mammalian fauna and the fact that most fossil specimens represent isolated surface finds with limited environmental context. The East African (Pickford, 1986) and Spanish (Agustí, 1989) sequences also suffer from being endemic, and from a lack of continuous fossiliferous sections. Other areas have even less to offer, either because appropriate sediments are lacking or because they have not yet been studied. This emphasises the importance of Anatolia, which is both centrally placed at the junction of Europe, Asia and Africa, and has long, richly fossiliferous sequences offering excellent potential for radiometric and palaeomagnetic dating (Sickenberg, 1976). It is, however, only now that the potential of Anatolia in this regard is being realised (Kappelman et al., in review). The crucial role of the Anatolian material will be presented in more detail below.

At present virtually all studies involving Neogene mammals in Europe rely on the biochronologic system of MN (Mammalian Neogene) units (Mein, 1975, 1977, 1979, 1989). This system is based on first and last appearances of land mammals and on characteristic associations of common taxa, and each unit is tied to a type locality. More than for almost any other continent, direct ties to the geochronology are lacking. The resolution of the system is on the order of 1 Ma, and this is also its approximate precision (i.e., the boundaries of units may be shifted by about 1 Ma maximum as calibration improves, but probably not much more). Since MN units measure evolutionary time it is probable that they are of unequal length, episodes of rapid change appearing similar to units corresponding to long periods of slow change. Despite these limitations, which are generally recognised (Mein, personal communication, 1992), the MN system is by far the best chronology available for the terrestrial Neogene of Europe. If it could be calibrated by ties to the geochronology, as is already beginning to happen in central Anatolia, it would become one of the best chronologies available and an important standard for the Old World correlations. Hopefully it will eventually be augmented by additional local dated sequences and a stratigraphy based on superposition (as in North America). This, however, will require considerable time, and for the immediate future extension of a calibrated MN-system,

using all available ties to the geochronology, appears the only realistic possibility.

The relationships between global physical changes ("climate") and the history of living organisms are, of course, highly complex. The study of these relationships is the subject matter of the recently evolved field of 'evolutionary palaeoecology', which "considers the manner in which ecological processes, including those acting over longer intervals than can be observed today, play out over spans of time relevant to the history of life on earth" (Wing et al., 1992). In concrete terms, this means a synthesis of genealogical and ecological data in the context of known physical and environmental changes. This is an ambitious programme, but not beyond the realm of the doable. It will involve considerable data accumulation under a critical protocol as well as analysis of this data in a more sophisticated theoretical framework than has been customary in traditional 'palaeoecology'. These processes are already underway in the form of the Evolution of Terrestrial Ecosystems (ETE) programme as described by Damuth (1990) and Behrensmeyer et al. (1992). Not surprisingly, the ETE is centered on the New World, in practice if not in intent.

For the Neogene of the Old World the nature and quality of the data requires a certain amount of very basic groundwork before anything in the nature of serious evolutionary palaeoecology can be attempted. On the other hand, the Old World offers an attractive, dynamic theatre for the evolutionary play: biotic provinciality was high and a multitude of physical changes took place during the past 20 Ma. The changing land and sea configurations have, partly independently of their climatic effects, determined the opportunities for interchange between bioprovinces as well as the appearance and disappearance of the bioprovinces themselves. So far the understanding of such interchange is not very satisfactory: even for the best documented case, the 'Great American Interchange' in the Plio-Pleistocene, interpretations remain more or less controversial (Simpson, 1950, 1980; Webb, 1976, 1978; Marshall et. al, 1982; Stehli & Webb, 1985; Vrba, 1992). Comparative work is probably the best strategy to advance understanding of the processes involved. Emerging results suggest that the changes seen the Neogene of in western Eurasia can be related to global physical changes (for timing) and to resultant habitat changes (for effect), as shown below (Example, pp 10-18).

The relevance of the project for Finnish and European palaeontology should also be assessed here. At present nothing comparable to NOW exists in Europe. Apart from ad hoc data compilations for individual research projects there are two European databases on fossil mammals. The first is the Utrecht database maintained by Dr. Albert van der Meulen, which comprises mainly Spanish fossil localities and is tailored towards the specific aims of micromammal biochronology. The second is the database of the Quaternary Mammal Fauna Databank of the ESF (Werdelin et al., 1992), which in fact has not yet been implemented although advanced plans exist. The latter database (QMF) has been designed to be compatible with ETE (and thus with NOW). It is limited to the Quaternary of Europe, and does not overlap with NOW in content. In general, long term research aims there is some overlap between QMF and NOW, and they should complement each other usefully.

For geology and biology students the NOW database would provide immediate hands-on access to a powerful research tool and modern research concepts, as well as to an active international research team. Even if such students would later turn to other fields than mammal palaeontology (which, after all, cannot be expected to offer very many opportunities for employment) the experience would undoubtedly be of lasting value. Such opportunities are unfortunately quite rare in Finland, and for palaeontology this would be unique even for Europe.

The Terrestrial Neogene of the Old World

The Old World witnessed several dramatic changes associated with interchange of land mammals during the Neogene, from the docking of Afro-Arabia at the beginning of the Miocene and to the drying-out of the Mediterranean at the beginning of the Pliocene. Eustatic and regional tectonic control on geography are documented in western Eurasia and northern Africa in the sediments of the Tethys and Paratethys complexes (Rögl & Steininger, 1983, 1984), with main dispersal and turnover events in the land mammal fauna corresponding to regression peaks and other physical events (e.g., Bernor, 1983; Bernor & Tobien, 1990; De Bruijn & Hussain, 1984; Haq et al., 1987; Raymo & Ruddiman, 1992; Steininger et al., 1989; Van der Meulen & Daams, 1992).

The first modern attempt to understand the biogeography of western Eurasia and the Mediterranean during the Neogene was made by Bernor (1983, 1984), who recognised six zoogeographic provinces: (1) Western and Southern European, (2) East and Central European, (3) Rumanian - Western USSR, (4) Sub-Paratethyan, (5) North African and (6) Siwaliks (Fig. 1). Bernor was able to create a coherent model relating the history of land mammals between the Middle Miocene and the

Pliocene primarily to vegetational and inferred general paleoenvironmental changes, and his model is still regarded as valid in its essentials (e.g., Potts & Behrensmeyer et al., 1992).

Bernor's success was undoubtedly due, in large part, to two factors. First, his insistence on a sound geochronologic framework as the basic requirement of synthesis, and secondly, his recognition of "palaeobiomes" without modern analogs. Between them, these allowed correlation of changes in fauna with changes in flora, and detection of diachroneity of change over large areas. Specifically, they led Bernor to recognise the Sub-Paratethyan province as the origin of the "open country woodland chronofauna" with its extremely diverse assemblage of ungulates, and the dispersal of this fauna west into Europe as well as east into the Siwalik province. This dynamic interpretation replaced older simplistic notions of abrupt and synchronous change from the Middle Miocene "forests" to the Late Miocene "savanna", spanning Eurasia from Spain to China. (It is true that Kurtén [1952] had a much more nuanced and palaeoecologically sophisticated model, but Kurtén's work seems to have had surprisingly little impact.) The detailed interpretation of the history Tethys-Paratethys seaways that emerged simultaneously with Bernor's results (Rögl & Steininger, 1983, 1984) and the detailed information on global sea-level history that has emerged since (Haq et al., 1987) offer important means of testing and tightening the biogeographic interpretations, although this has so far been attempted only for limited problems (e.g., Bernor et al., 1988).

Land mammals, especially megaherbivores, are evidently capable of changing their environment, even drastically (Owen-Smith, 1987, 1988). They also respond to changing environments, behaviourally and, with some delay, by evolutionary changes. Both kinds of changes are potentially recorded in the fossil material, for example, in the case of grazers, as changes of dental microwear and molar crown height, respectively. The influence of grazing herbivores on the evolution of habitats has undoubtedly been a major environmental factor during the Tertiary.

A heuristic example relevant in this context is the rapid spread of grasslands in the Old World around 10-8 Ma ago, which appears to have followed rather than preceded the immigration of the hipparionine grazing horses from the New World. The timing of Himalayan uplift and the development of the Indian monsoon are of critical importance here, and may account for a separate but related event: the rapid spread of C4 grasses in tropical areas around 7 Ma ago (evidenced by a shift in the isotopic ratios of carbon and oxygen from palaeosol carbonate nodules; Prell & Kutzbach, 1992; Cerling, personal communication 1992). The C4 photosynthetic pathway is superior to the C3 [=Calvin Cycle] pathway under conditions of high solar influx and water stress, and it is thus difficult to construct a scenario for its spread that does not involve an initial phase of well-developed C3 grasslands to provide such conditions. The existence of these grasslands, undetectable by isotopic analysis, presents a hypothesis testable using terrestrial land mammals. Especially ungulates offer information of dietary adaptation in their dental morphology (review by Janis & Fortelius, 1988) as well as direct information on food selection in their dental microwear (reviews by Teaford, 1988; Walker & Teaford, 1989). Their skeletal build also incorporates information about habitual feeding posture (Zeuner, 1934; Janis, 1982) and locomotion (Kappelman, 1988), which together allow reconstruction of their habitat in general terms of vegetation structure. The resolution of this method may not be very high, but it is certainly sufficient to tell open grasslands from forested biotopes.

Fossil land mammals offer both 1) a source of independent data for investigating the nature and timing of these and other similar changes, and 2) a direct window on other, related and/or simultaneous changes in the mammal communities in different habitats and on several continents. Conversely, the evolution of land mammals in relation to such an increasingly detailed background of environmental change offers challenging opportunities for evolutionary research with an ecological perspective and a geological time scale.

An important step towards a more global analysis of the European fossil land mammals was recently taken by Bernor, Fahlbusch and Rietschel, who organised a roundtable workshop at Schloss Reisensburg (Germany) on the *Evolution of Continental Biotopes in Central Europe and the Eastern Mediterranean (15-5 Ma)* in July 1992. For this workshop specialists were invited to revise the material for all relevant taxa and for a large number of fossil localities from Poland to Iran, and to analyse temporal and biogeographic patterns. This particular area was chosen because it can be related to the history of the Paratethys complex, and the interval because major physical and faunal changes are known to have taken place then. The Neogene land mammals are diverse enough and have a sufficiently rapid turnover to allow quantitative treatment of the data. This data will form the basis of the first scientific investigation undertaken using the NOW database, a collaborative project between Fortelius, Bernor & Mittmann (Letter 1).

Research Aims

The timing thus seems right for a broad analysis of biotic change in the terrestrial Neogene of the Old World (NOW). The ultimate aim is to contribute to the global evolutionary palaeoecology of the Neogene, both by direct problem-oriented research and by creation of a powerful analytical tool available for research that cannot now be anticipated in detail. For the immediate future the research activities must be focused towards aims that are obtainable with a reasonable expenditure of time and effort, and, when obtained, are likely to result in significantly improved understanding. The ways and means to achieve this are discussed below, and a concrete example is given (pp. 10-18).

Immediate, practical aims:

- Improved calibration of the MN system using the Anatolian sequences (especially the Sinap Formation)
- Establishment of long-distance correlations from the European-Anatolian biochronology to Africa and Asia, especially India and China
- Review of taphonomic, sedimentological and other environmental data available for the main (several hundred) localities

Short-term scientific aims:

- Occurrence, magnitude and nature the main biotic changes in Europe and West Asia during the Middle and Late Miocene, using the "Schloss Reisensburg" data (collaboration between Fortelius, Bernor & Mittmann; see Letter 1)
- Correlation between occurrence of individual taxa and sediment types (and other simple sedimentological/taphonomical variables), to test previously proposed autecological hypotheses
- Inferred ecological changes in the mammal communities associated with major changes in taxonomic composition of the faunas (including floral and other environmental data according to availability)
- Calculation of quantitative parameters of diversity and turnover for different provinces and faunal similarity between them. Calculation of absolute rates of change and estimation of diachroneity of change between provinces.
- Ecological changes associated with important dispersal events, especially in relationship to questions of diachroneity (for example, the *Hipparion* event and the origin of Old World grasslands)
- The relationships between major groups with different ecological profiles (e.g., suoidea and primates versus rhinoceroses and horses)
- The relationship between carnivores and their potential prey in the Old World Neogene

Long-term scientific aims:

- (Re)defining and tracing palaeobiomes through Neogene time, including specifically the east-to-west reduction of forest habitats in Europe, and the roles in this process of the sub-Paratethyan, Siwaliks, Chinese and African provinces
- The evolution of the ungulate fauna of the Late Miocene of the Old World, and the relationship in it between grazing horses and bovids (including the relationship between the spread of C4-grasses and the radiation of grazing bovids in the latest Miocene)
- General patterns of change in terms of taxonomic diversity, habitat diversity, degree of provinciality, province size etc. in a comparative global setting (using the ETE/NOW connection)
- Relationships between taxonomic turnover and environmental change, including the "tempo and mode" of evolution and the response of co-evolved communities to various type of change

Data Acquisition

The material to be analysed is primarily the data that will be included in the database NOW. This material consists of two classes of locality data, published and unpublished, and of data pertaining to the mammalian taxa included, such as phylogenetic information, autecological attributes, body size estimates etc. 'Taxon-free' ecological information, related directly to fossil specimens rather than to their taxonomic identity, will also be included when available. The data will be stored and

analysed in to the format of the ETE database (see below).

The published locality data will be extracted from the literature according to a set of priority rules that maximise quality as well as temporal and geographic coverage. Basically, localities will be included when they have two or more of the following attributes: a recently revised faunal list, a geochronologic age, a biochronologic age, environmental information (taphonomy, sediment, isotope ratio, other), a local stratigraphy, some unusual and/or important taxon, or no substitute available for the time and place in question. An important source of data and references to primary sources will be the recent critical compilation of Lindsay et al. (1989). The database of the Schloss Reisensburg workshop on the *Evolution of Continental Biotopes in Central Europe and the Eastern Mediterranean (15-5 Ma)* mentioned in the introduction will be published soon and is already available for internal use to develop NOW (Letter 1). This material will make up a major portion of the NOW database during its initial stages and form the essential nucleus of high-quality data that will used for screening data from published sources for errors and anomalies. The "Schloss Reisensburg" data is also important because it incorporates palaeobotanical localities in the same stratigraphic framework.

The unpublished data consists primarily of the 100+ central Anatolian localities of the Sinap Project, which cover approximately the past 15 Ma. The stratigraphic and environmental information associated with these localities is currently being developed by a large team of specialists, and information is already available for several of the most important ones. The Sinap localities will not only provide a means of tying the European biochronology to the global geochronology through magnetic reversal stratigraphy and radiometric dates (Kappelman et al., in review), but will also constitute an important source of directly associated data on environmental and faunal change.

Another source of (partly) unpublished locality data is the Lagrelius Collection of Chinese fossil mammals in Uppsala, Sweden. The number and nature of localities ('single quarry'; Bernor et al., 1990) is similar to those of the Sinap project, but unfortunately stratigraphic and environmental data is largely lacking. The fossil material, on the other hand, is of superb quality, with numerous complete skulls and sets of associated skeletal elements. The material is mainly late Miocene in age, and offers such striking similarities to the Anatolian material that the establishment of biochronological ties between the two must be relatively easy (preliminary studies by Fortelius and Watabe in 1992; Letter 2). This is especially interesting in view of the fact that the geographically intermediate Siwaliks appear to have a rather different fauna, and offers an intriguing and promising subject of study. Some locality data for the Lagrelius collection has been published (Zdansky, 1923; Kurtén, 1952; Bernor et al., 1990), some exists in the form of sediment samples in the collection itself, and some appears to be under study in China (Qiu, 1989; Bernor & Flynn, personal communication 1992). At any rate, the Uppsala material offers an important complement to the Sinap collection, and its proximity to Helsinki is a very fortunate circumstance for the NOW project. Access to the material and working space at Uppsala are available for this project (Letter 3).

The autecological and other information tied to the identification will be generated by the methods and standards developed for the ETE. Body mass estimates will be produced from all available elements according to the methodology developed by Fortelius & Kappelman (in press). All such information will be critically examined for inter-population variability, and morphologically different populations (vicariant taxa and 'avatars') will be distinguished. 'Taxon free' information (Damuth et al.,

1992), especially dental microwear and stable isotope ratio data, will be among the first to be included in the database after the initial phases of data screening and "quasi-quantitative" analysis have been completed.

The NOW database: Characteristics and implementation

Several relational databases have recently been designed explicitly for the analysis of vertebrate fossil material and associated information (Damuth, 1990; Graham & Lundelius, 1990; Blum, 1991; Werdelin et al. 1992). The most sophisticated of these is the Evolution of Terrestrial Ecosystems (ETE) database, designed and maintained by the 'ETE Consortium' (see Behrensmeyer et al., 1992). The copyright for the ETE database design and software is owned by John Damuth (Santa Barbara), who will allow the cloning and necessary modifications of it for NOW (Letter 4). It is already possible to access the ETE database remotely from Helsinki over Internet, and preliminary sessions have been run during the autumn of 1992, showing that direct interaction will be feasible. The establishment of an Ethernet local computer network in the Helsinki geology building in January 1993 has improved conditions significantly.

Implementation of NOW is already underway using the commercial database designer Clarion. The ETE files and fields are recreated here based on the ETE structure as documented in Damuth (1990) and lookup table files provided by John Damuth. Required software will be written by Mikael Fortelius with professional assistance by the Database Manager of the Finnish Museum of Natural History, Mr. Michael Haldin (Letter 5). The NOW database will effectively be a clone of the ETE database, and local software will be written such that it emulates the ETE interface and uses identical import and export (ASCII) formats. The transfer of data will therefore be straightforward and the pooling of records easy. For the first phase of research described in this proposal much of the NOW database will remain empty, however. Most Old World data is very incomplete, and the short-term aims of the project have been chosen accordingly.

Input of data into the database will start with the Sinap localities and proceed quickly to extracting data from the literature. As soon as some data has been entered trial analyses will be run to ensure that the database is functioning appropriately. The compilation, screening and input of published data will be a very time-consuming part of the project, and a research assistant would be needed for this purpose, at least during the first two years of the project.

The analyses to be run on the data will center on diversity, turnover and provinciality, which will be studied in the context of phylogeny, biogeography, and timing of known physical changes, global and regional. The programming potential of the database will allow easy calculation of a great number of parameters and their graphic representation, and methods will undoubtedly evolve as the database begins to function. Even simple analysis does produce meaningful patterns beyond the obvious and expected when previous synthesis has been as limited as it has in this case (see Example below). Even if NOW achieves nothing more than this, for most groups and most of the Old World, it will have advanced present understanding very significantly. It is assumed here that NOW will achieve considerably more than that.

Methodological Example: "Der Untergang des Abendlandes"

It may be illustrative to review the methods used for the analyses carried out for the 1992 Schloss Reisensburg workshop *Evolution of Continental Biotopes in Central Europe and the Eastern Mediterranean (15-5 Ma)*. Selected extracts from our manuscript (86 ms pages!) on the Suoidea (Fortelius et al., in review) are given below as an example of the kind of data that is now available for western Eurasia, and the kind of analysis that they allow. It should be noted that different groups have different histories: for example, primates show a pattern similar to that seen in the suoidea, while rhinoceroses and horses show a pattern that is practically a mirror image of it. By using the whole fauna a much more sophisticated and informative interpretation will become possible. Herewith, the Suoidea:

The good stratigraphic and paleogeographic record of the Paratethys realm (Thenius, 1959; Rögl and Steininger, 1983, 1984; Bernor et al. 1988; Steininger et al. 1989; Zapfe et al., in press; Bernor et al., in press), and the rich terrestrial fossil record found around its margins, provide the opportunity to study fossil land mammal and paleofloral assemblages in relationship to a background of changing land-sea configurations. The Eastern Mediterranean - Southwest Asian area is

FIGURE 8. Biochronologic range chart of the taxa included in this chapter. WE=Western Europe, CE=Central Europe, SE E=Southeast Europe, SW A=Southwest Asia. A star indicates a lineage of more than one taxon.

richer yet in diverse continental vertebrates which are often associated with observable stratigraphic units and volcanic debris suitable for radioisotopic analysis.

The intensity of recent study on later Neogene paleontology, stratigraphy and geochronology represents a rich data base for us to tap in our effort to synthesize the evolutionary history of middle and late Miocene terrestrial mammals.

The Suoidea constitute a relatively common and diverse group, ecologically as well as taxonomically, which underwent moments of rapid turnover during the Middle and Late Miocene. They are sufficiently well known to allow judicious use of the published literature in the few places where one of us has not been able to study original specimens. We summarize data on the geographic and temporal distribution of this group and reconstruct patterns of change in species diversity, turnover and extinction.

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Being largely adapted to subtropical and warm temperate forests and woodlands, the later Neogene Suoidea are sensitive indicators of environmental change which would appear to have been progressive, albeit episodic. Roughly speaking, the time considered here includes two "desiccation" episodes in Europe, the Paratethys Middle Badenian (= Serravallian Stage; Middle Miocene) Salinity Crisis the paleo-Mediterranean/Paratethyan Messinian (latest Miocene) "Salinity Crisis". The former corresponds with the origin of the Eurasian "Listriodon mammal fauna" with numerous African and Western Asian elements (Thenius, 1979;

FIGURE 9. Biogeographic range chart for the taxa included in this chapter. WE=Western Europe, CE=Central Europe, SE E=Southeast Europe, SW A=Southwest Asia.

Bernor, 1983; De Bruijn and Hussain, 1984). The latter marks the maximum extension of so-called "Pontian" open country woodlands, and directly precedes the basal Pliocene's sharp shift to cooler temperate forests (Bernor et al., 1979; Bernor, 1983, 1984). The interval considered here also marks some major shifts in environments including early Astaracian (MN 6), early Vallesian (MN9), the "Mid-Vallesian Crisis" (MN 9/10) and the medial Turolian (MN 12).

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     Species distributions reveal three geographic groupings (Fig. 9): western, eastern and "cosmopolitan" (we use these terms only with reference to the study area and interval). Of the 14 taxa found in Central Europe during MN 6-13, 11 are also found in Western Europe, but only 7 are known from Southwest Asia. Conversely, of the 16 taxa known from Southwest Asia during the entire interval, only 7 are known from Central and 6 from Western Europe. It would also seem that the "cosmopolitan" group (including <u>Schizochoerus</u>, <u>Listriodon</u>, <u>Conohyus</u>, <u>Propotamochoerus</u> and <u>Hippopotamodon</u>- <u>Microstonyx</u>) has an Asiatic origin, while the western group (<u>Taucanamo</u> <u>grandaevum</u>, <u>Hyotherium</u> and <u>Parachleuastochoerus</u>) seems autochthonous within the study period. Within our spatio-temporal limits <u>Albanohyus</u> also behaves like a western taxon, but it may be related to African forms and its plausible broader geographic distribution is an interesting aspect which should be further investigated.

     The faunal similarity of regions can be roughly quantified (although not tested statistically, for a large number of reasons) using Simpson's Index of Faunal Resemblance (Table 1). The overall diversity is very low, and the index consequently gives a very coarse indication of the patterns, but it definitely does provide a convenient descriptive handle. The main results as they appear in Fig. 10 are easily summarized (we discuss their reliability together for all these analyses): 1) Southeast Europe shows complete (100%) similarity to Southwest Asia (in terms

FIGURE 10. Graphic representation of Simpson's Index of Faunal Resemblance, showing high resemblance between Central and Western Europe as well as the highly similar resemblance trends of these regions with respect to Southwest Asia. See text for discussion. WE=Western Europe, CE=Central Europe, SE E=Southeast Europe, SW A=Southwest Asia.

of Simpson's Index!) for all the MN units that it can be calculated. 2) Western and Central Europe are very similar throughout the interval (index 80-100%), except for a somewhat dubious drop to 50% in MN 10 caused by the appearance in Western Europe of <u>Schizochoerus</u> and the (uncertain) disappearance there of <u>Propotamochoerus palaeochoerus</u>. 3) Western and Central Europe behave as a block towards Southwest Asia throughout the interval. The index ranges from 33 to 67% except for an episode of "total resemblance" (index 100%) in MN 11, caused by the presence of <u>Microstonyx</u> alone over the entire area. 4) The general trend from MN 6 to MN 11 is one of increasing similarity between Europe and Southwest Asia, but the trend is reversed at the end due to the appearance in Western and Central Europe of <u>Propotamochoerus provincialis</u> and of "<u>Postpotamochoerus</u>" <u>hyotheroides</u> at Samos (here treated as part of Anatolia).

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Diversity shows the same basic pattern for all areas: high in the early Astaracian, declining to a low in the late Vallesian and early Turolian (Figs. 8 and 11). The diversity curves for Western and Central Europe are quite similar (Fig. 11), even though the individual taxa are partly different. The main difference in

FIGURE 11. Species diversity and absolute turnover between MN 6 and MN 12/13 for the different regions. See text for discussion. Diversity is the number of species or lineages recognised for that MN unit and region. Absolute turnover is the total number of entries and exits of species or lineages for the MN unit and region. WE=Western Europe, CE=Central Europe, SE E=Southeast Europe, SW A=Southwest Asia.

pattern is that there is little change from MN 6 to MN 9 in Central Europe, whereas a marked increase to an all-time high in MN 7/8 and MN 9 is seen in Western Europe. In both regions there is a dramatic decrease from MN 9 to MN 10, after which diversity stays low everywhere. For Southwest Asia the most dramatic change is the drop from MN 6 to MN 7/8, while the drop from MN 9 to MN 10 is virtually absent there.

The total number of entries and exits per MN unit ("Absolute Turnover") shows distinct peaks at MN 6 and MN 9, the latter being much more distinct for Europe than Asia (Fig. 11). The high value for Southwest Asia in MN 6 is partly artificial, due to the absence of data for MN 5 which results in all taxa present being counted as "entries". From MN 10 onwards the pattern is roughly similar between Western Europe, Southeast Europe and Southwest Asia, with a minimum at MN 11. Central Europe appears to be out of phase with the other regions, with a rising trend from MN 10 to MN 12/13. Closer scrutiny reveals that the rhythmic pattern is mainly due to extinctions, the pattern of entries being similar but more noisy (see also Werdelin & Solounias, this volume). A comparison with Simpson's index (Fig. 10, Table 1) shows that similarity between Southwest Asia and Western-Central Europe decreased after each turnover event (MN 6, MN 9 and MN 12).

Since the number of turnover events is generally highly correlated with diversity (in this case, r=0.76; P<0.001) two relative parameters were also

FIGURE 12. Relative turnover and probability of extinction between MN 6 and MN 13 for the different regions. See text for discussion. Relative turnover is absolute turnover divided by diversity. Probability of extinction is the number of extinctions divided by an estimate of the number of taxa at risk (see under Methods). WE=Western Europe, CE=Central Europe, SE E=Southeast Europe, SW A=Southwest Asia.

calculated: "Relative Turnover" (absolute turnover divided by diversity) and Van Valen's (1984) diversity independent Probability of Extinction. Relative Turnover (Fig. 12) shows a sinking trend from MN 6 to MN 11, with a marked rise to MN 12/13. The MN 9 peak is relatively weakly indicated for Western and Central Europe and not at all for Southwest Asia, and Central Europe again appears out of phase with the other regions, with a minimum at MN 10 rather than MN 11. The very high values for Southeast Europe in MN 9 and MN 12/13 may be due to lack of material. The MN 9 value simply represents the entry and exit in that interval of the only taxon present (Schizochoerus), while the MN 12/13 value represents the dubious entry of one and exit of both species of Microstonyx in MN 12.

Probability of Extinction (Fig. 12) also peaks at MN 6 and MN 9, but the highest values are now seen in MN 12/13. The curve for Central Europe is now strikingly different from the others, lacking a peak at MN 9 and being instead uniformly high from MN 7/8 to MN 11. Although the diversity is too low for any great confidence, this could indicate that different controls operated on extinction in Central Europe than in the Tethys-Paratethys realm.

How reliably these patterns reflect reality is difficult to assess. They are certainly affected by various factors reflecting the incomplete nature of the data that could be referred to collectively as sampling error, and the sample sizes are well below the minima needed for statistical significance (e.g., Koch, 1987). Sampling error is primarily present at two levels: 1) within the composite faunal lists based on several localities from a given region and time interval, and 2) among these composite faunal lists. The effects are compounded at the second level, which unfortunately is the most relevant to our analyses. In practice, however, the problems boil down to relatively simple specific issues that lend themselves to critical discussion.

For example, the MN 6 turnover peak for Southwest Asia might be inflated by poor sampling of MN7/8 as well as by the artificial "entries" due to lack of data for MN 5. Conohyus is known from later deposits in Europe and the Siwaliks, and might have been present in between as well, while "Gen. nov. cf. Taucanamo" may have given rise to Schizochoerus, in which case its exit is an artifact of taxonomy. The exits of Taucanamo, the Bunolistriodon latidens-lineage and Kubanochoerus (2 taxa) are most probably genuine, however, as is the entry of Listriodon, since they concern the entire area. The fact that all three Anatolian MN 6 localities have a rich suoid fauna while all the four Anatolian MN 7/8 localities have yielded material only of Listriodon but not of any other taxon present in MN 6 also indicates that sampling error is not the main explanation of this pattern. Even a conservative interpretation of the evidence therefore suggests that this event was significantly stronger in Southwest Asia than in Europe.

The somewhat arbitrary decision to terminate the range of Propotamochoerus palaeochoerus with MN 9 in Western Europe emphasizes the MN 9 turnover peak there, but it is only one of six changes recorded so the effect is relatively small (extending its range would strengthen the pattern of diachronous east-to-west change that our analysis suggests, an effect we wished to avoid). The difference in turnover patterns (especially probability of extinction) between Central Europe and the other regions is affected by many samples and also appears unlikely to be a pure artifact, especially given the highly congruent rhythm exhibited by all the other regions, including the poorly sampled Southeast Europe.

FIGURE 13. Distribution of size classes 1-4 (less than 20 kg, 21-80 kg, 81-200 kg and 200- 1000 kg). The width of the column indicates the number of taxa in that size class for the MN unit for region. Note increase in mean size accompanied by decrease in diversity, proceeding time-transgressively from east to west. WE=Western Europe, CE=Central Europe, SE E=Southeast Europe, SW A=Southwest Asia.

Probably the most difficult pattern to interpret is that of the Turolian. The suoid material is extremely limited for the end of the interval, and unlikely to give a reliable picture of the distribution of the taxa that have been recorded. Taken literally the evidence suggests that regional differentiation increased greatly in MN 12/13, following the (apparent?) regional extinction of Microstonyx outside Central Europe, when Propotamochoerus provincialis appeared in Western and Central Europe and "Postpotamochoerus" hyotheroides in Southwest Asia. However, as discussed above P. provincialis appears closely related to Chinese and African taxa, and its absence from the eastern part of the study area may well be a sampling artifact. On the other hand it seems likely that Sus arvernensis entered Sardinia in MN 13, even though the oldest finds are from MN 14 in Spain, so the late Turolian diversity was probably greater than recorded by our data (sampling error operating in the opposite direction). The change in MN 12/13 may appear more radical than it really was, but there is no denying the contrast to MN 11, when only Microstonyx is recorded in relatively rich material from the entire study area.

It may therefore be concluded that although some details are undoubtedly spurious the main pattern appears quite robustly founded. This impression is further supported by the paleoecological review that follows here.

....

To summarize, the fossil Class 1 taxa were probably forest forms. Class 2 contains a mixture of forms but would seem to be predominantly composed of forms that did not inhabit open environments. Class 3 is an ecologically heterogeneous group with the majority of taxa exhibiting open habitat associations. Class 4 contains forms from woodland-grassland mosaic habitats and (later on) forms more definitely associated with open woodlands. The pattern seen in Fig. 13 thus strongly suggests that the increase in mean size and concomitant loss of taxonomic and ecological diversity was associated with a loss of environmental diversity, involving especially the reduction of forest habitats.

....

The timing of evolution and extinction events is suggestively synchronous with physical changes. The initial sharp drop in suoid diversity (and extinction peak) during MN 6 occurs closely coincident with the Serravallian regression (= Paratethyan "Badenian Salinity Crisis" sensu Rögl and Steininger, 1984), and directly following the last extension of Indomalayan tropical currents into Central Europe. This regressive phase further corresponds to active Alpine orogeny and a series of closely spaced global sea lowering events at 16.5, 15.5 and 13.5 Ma (Haq et al., 1987; Bernor and Tobien, 1990) and the rapid shift in the oceanic oxygen isotope record, indicating an episode of rapid Antarctic glaciation (re: Raymo and Ruddiman, 1992; Van der Meulen and Daams, 1992).

Scattered data from other vertebrate groups reinforce the pattern seen in the suoid fauna. In MN 6 there were still crocodiles in Central Europe (Scherer, 1981) while in France the last record is MN 5 (Antunes and Ginsburg, 1989). Flamingoes are abundant in MN 6, but in MN 7 they become rare as ducks become more abundant (Hesse, personal communication). Tragulid diversity decreased in Central Europe from 4 species in MN 5-6 to 1 species in MN 7-12. Van der Meulen and Daams (1992) interpreted the change in Spanish rodent faunal composition as

evidence for decreasing temperature during MN 6, with particularly sharp temperature declines documented at the beginning and end of the interval.

The second extinction peak, during MN 9, has less obvious physical correlates but might relate to a significant global environmental event. There is a global cooling spike recorded in the oceanic oxygen record at 11.5 Ma, and the culmination of the European Serravallian regression occurs at 10.5 Ma (depending on the calibration of the MN units). The "Hipparion Datum" now appears to correlate with this latter event (Swisher, this volume). It may be that the global cooling spike, closely followed by the terminal Serravallian event, and aggravated by continued Alpine orogeny, had the effect of driving terrestrial environments progressively further toward seasonal open country environments (sensu Bernor, 1983; Bernor et al., 1988, 1990). Fossil floras from the Eastern Mediterranean and Spain both indicate a decrease in temperature at this time, with marked fluctuations in humidity (Benda, 1971; Benda and Meulenkamp 1990; Baltuille et al., 1992). In Spain, the Boselaphini were the dominant bovids during the Aragonian and Early Vallesian, but after MN 9 nearly all species of this group were replaced by bovines (Alcalà et al., 1989). Hominoid primates became rare or disappeared after MN 9 in Europe and Southwest Asia. The crocodiles, too, appear to have become extinct in the Tagus Basin and Algarve at this time (Antunes and Ginsburg, 1989).

The final extinction peak occurred during MN 12/13, and may well correspond to the terminal Miocene Paratethys and Mediterranean regression (ca. 7-5 Ma; re: Zapfe et al., in press). If so, it may be significant that Central Europe, displaced geographically from the Mediterranean, and continuing to support a viable lake system, is the only region where Microstonyx is definitely known not have become locally extinct until MN 13.

The provinciality of the study area would appear to be strongly affected by the Central and Eastern Paratethys system. During the Astaracian, when diversity is high, Simpson's Index of Faunal Resemblance reveals that suoid species are segregated into an eastern and a western province (Fig. 10). A bottleneck passage through the alpine foredeep (Austria-Germany) may have been episodically operational, but clearly did not result in increased faunal similarity, since the differentiation was greatest in MN 8. It is interesting in this context that the extinction pattern found for Central Europe differs from that of the three other regions, but the species-level reasons for the difference do not lend themselves to simple explanation, and in any case a handful of species is a poor data base for deciphering the timing of distant biogeographic connections. It is certainly probable that Central Europe differed climatically from the more southern regions of the Tethys-Paratethys realm, and different environmental controls may have operated there, even if the composition of the fauna was quite similar to that of adjacent regions.

Taxonomic and ecologic diversity decreased, and the uniformity between regions increased from MN 6 until MN 11. The main mechanism behind the faunal unification was replacement of the taxonomically and ecologically diverse suoid fauna by considerably less diverse eastern immigrants (Schizochoerus, Hippopotamodon-Microstonyx and Propotamochoerus). This replacement occurred during the Astaracian in Southwest Asia and the Vallesian in Europe, where the last native taxa are found in Spain. In Southwest Asia, there appears to be a gap between the local MN 6 extinction and the appearance of Propotamochoerus and Hippopotamodon in MN 8. If this is not a sampling artifact it would strengthen the impression that no direct interaction was involved between the two groups. The

extinction peaks at MN 6 and MN 9 both decreased faunal uniformity, and the less rhythmic immigration pattern seems to have been mainly responsible for increased uniformity in most of the area during most of the time. We correlate the early Turolian uniformity of Western Eurasian suoid faunas with the expansion of open country woodlands reported by Bernor (1983) and Bernor et al. (1990). This phase came to an end with the extinctions in MN 12/13, and was followed by a less uniform, though still extremely sparse suoid fauna.

A mirror image of the suoid pattern is seen for the hipparionine horses (Bernor, Fortelius, Koufos and Woodburne this volume), while the pattern for primates is more similar to that of the suoids (Andrews et al., this volume). It is entirely plausible, of course, that taxa from more continental regions should be ecologically preadapted to the increasingly dry and open habitats that developed in Europe during the Vallesian and Turolian. It is unlikely that much competition was involved, since there is little ecological overlap between the natives and the invaders. Suoid succession would appear to be related to rapid shifts in the originally diverse local habitats, which precipitated the extinction of native forms and their replacement by immigrants from more uniform, open environments.

Schedule 1993-1996

First year:

- Implementation of the NOW database
- Input of the Sinap project and "Schloss Reisensburg" data
- Input of key data not included in the preceding (from the literature)
- Trial runs on this material to ensure that the database is functioning properly
- Beginning of analyses of "Schloss Reisensburg" data

Second year:

- Development of NOW software to allow the analyses required by the research aims
- Continued compilation, screening and input of data from the literature
- Study and revision of the Uppsala collection and establishment of biochronological ties between China and Anatolia.
- Completion of "Schloss Reisensburg" analyses, preparation of manuscript
- First publications (method and design issues, preliminary results)

Third year:

- Continued compilation, screening and input of data; updating of the database (these activities will, of course, continue as long as the database exists)
- Main analyses (for short-term scientific aims)

- First summarising publications (collaboration with Bernor, Damuth, Kappelman, Mittmann, Viranta, Watabe and others)

Beyond:

- Pooling of data from other databases (especially ETE, QMF and a palaeofloral database currently nearing completion (=publication of data) in Vienna)
- Incorporation of "taxon-free" data and other more sophisticated palaeoecological information (the ETE approach)
- Addressing general and global research questions (long term scientific aims)

Annotated Budget

1. Research assistant (forskningsbiträde) for compiling, screening and entering data from the literature and other sources and for practical maintaining of the database.

Even though much data already exists in accessible form it is still a fact that the creation and maintenance of a database requires a great deal of practical work. For Mikael Fortelius to do this alone would mean either considerable delays or alternatively a period of low scientific output. For this position a reasonable familiarity with the subject matter is necessary, and the palaeontology graduate student Suvi Viranta would be a very suitable selection. The NOW database is intimately related to Viranta's PhD research programme concerning the evolution and palaeoecology of mammalian carnivores (Appendix 5).

In the future NOW will allow students easy access to one of the most powerful palaeontological research tools available anywhere, which is not irrelevant in a country virtually lacking fossil collections. Such students might also be employed as research assistants during their research projects, which would be of benefit to them as well as to the database.

- salary for research assistant, per month: 8,600 (FIM)

Annual total: 103,200

2. Computer for the database

The database should reside in its own computer. This would minimise the risk of accidents, protect the system from viruses etc., and would allow remote collaborators straightforward access to the database over Internet. A minimum choice for the first stage would be a PC with a 486 processor and at least 200 MB of hard disk memory.

Considering the presently strained financial situation it should be noted that purchase of a 200 MB hard disk for existing hardware would allow creation and initial development of the database using extant hardware, albeit under less than optimal conditions.

None of this hardware could possibly be purchased by the Geological Museum, which has recently had its funding reduced very drastically.

- computer   20,000

        or alternatively (minimum requirement):

- 200 MB hard disk   6,000

3. Travel funds for visiting the Lagrelius collection in Uppsala

The Lagrelius collection is one of the best collections of Miocene Chinese land mammals. It has been relatively little used and it offers an important proximal source of high-quality material for NOW. The Lagrelius collection is of critical importance for the establishing of biochronological ties between Anatolia and China. During the second and third year it would be important to spend substantial time in Uppsala working on this collection

- 3 trips annually: 2,000

- cheep lodgings in Uppsala, 30 days annually: 3,000

- per diem (30 x 320):   9,600

Annual total: 14,600

4. Laboratory costs (photography, replication etc.)

Preparation of photographs and casts will be necessary for confirming identifications of critical specimens. Availability of these is a basic requirement for achieving and maintaining a high quality of taxonomic data, which in turn is crucial

for the scientific value of the entire undertaking. See also Letter 3.

<u>Annual total:</u>   <u>5.000</u>

Breakdown of costs by category and year:

	Year 1	Year 2	Year 3	Years 1-3 (rounded)
salary	103,200	103,200	103,200	310,000
expenses	5,000	5,000	5,000	15,000
travel		14,600	14,600	29,000
equipment	20,000 (6,000)			20,000 (6,000)
totals (rounded)	128,000 (114,000)	123,000	123,000	374,000 (360,000)

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