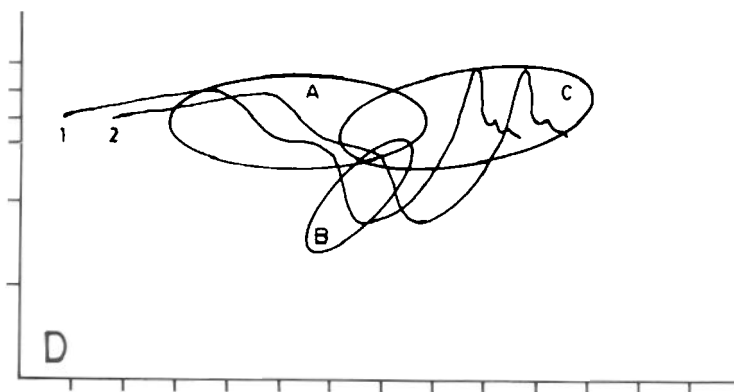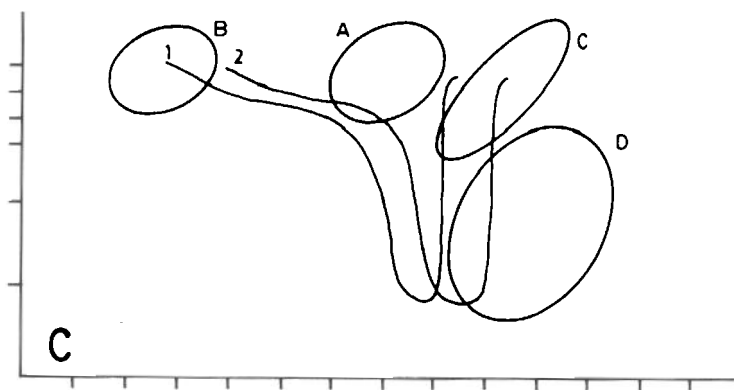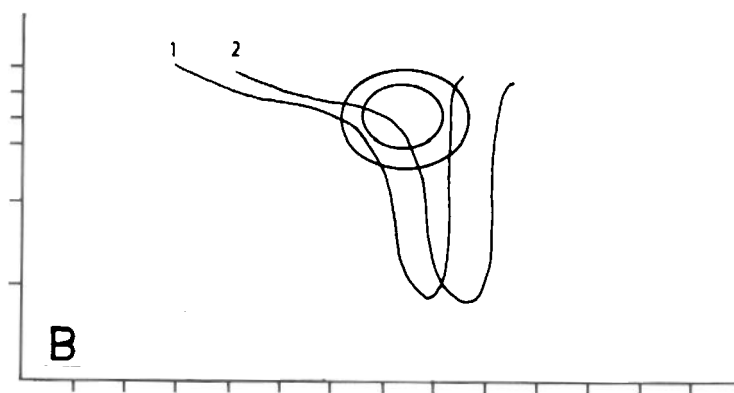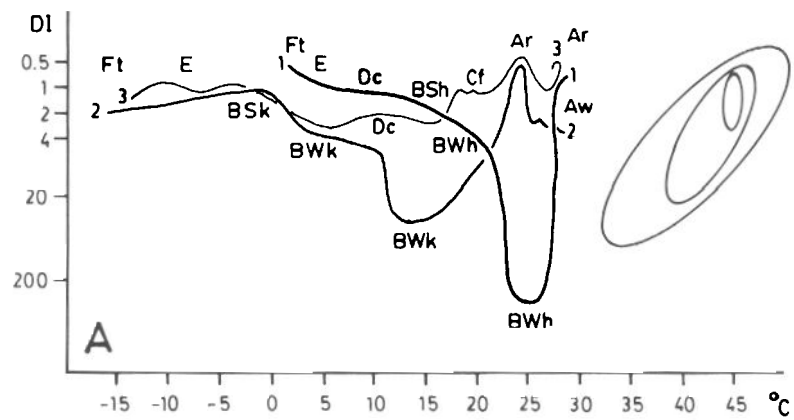# MIGRATIONS AND CLIMATE

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Abstract

Migrations, or expansions of the geographical ranges of mammals, will, if not limited by barriers, occur geologically instantaneously into areas that are favorable for the species. The geographical distribution of favorable habitat for a taxon is largely determined by climate. It is assumed that areas of high species diversity of a (higher) taxon indicate an optimal environment for this taxon. Such optima may migrate due to climatic changes. The niche of a species, or at least several aspects of this niche, may be described in terms of climatic factors, such as temperature and humidity. Climates tend to be distributed in east-west belts and the distribution of animals tends to follow this pattern. Small changes in one parameter of climate may cause great changes in the distribution of the habitat favorable for a taxon. This may cause migrations over long distances. For instance, a slight global increase in temperature may cause a species to migrate via a corridor from a tropical humid climate to a temperate humid belt. If such a temperature increase continues it may pass several thresholds and may cause several (waves of) migrations. The niche of a species is determined by a number of parameters and different species may react in very different ways to the same small climatic change. For this reason, communities do not move across the globe as units in accordance with climatic changes. Instead, communities may be broken up, one species moving north and another south, and new communities may be formed. The great amount of entries and exits that allow for a detailed biostratigraphy is probably largely due to minor changes in climate, rather than to frequent great changes in climate, the frequent breakdown of barriers, or strong competition between species.

Introduction

Understanding species migrations is of great importance to stratigraphy and paleoecology. 'Migrations' should not be seen as travelling individuals, but as a territory of a species that expands as the population grows into an 'empty area'. Similarly, a species may become extinct in a part of its territory. It would be better to speak of 'expansion' and 'contraction' of the geographical range of a species (SIMPSON 1940). By a combination of

Dl

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2
4

20

200

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Ft
E
Dc
BSh
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Ar
3
Ar
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BWk
BWh

A

-15 -10 -5 0 5 10 15 20 25 30 35 40 45 °C

1   2

B

B
1
2
A
C
D

C

A
1
2
C
B

D

Fig. 1: The niches of imaginary taxa represented as fields in temperature-humidity diagrams and sequences of climate from the Equator to the poles; DI = index of aridity (potential evapotranspiration/precipitation), T = temperature, reconstructed to sea level. Figure 1A represents real climatic curves, Figs. 1B - 1D represent imaginary curves. It is likely that the exact shape of the curves is different at different global temperatures, although the overall shape is expected to be similar if temperature differences are not too great.

Fig. 1A shows real climatic curves representing three sections from the Equator (right hand side) to the Arctic Circle (left hand side): 1) Kenya - Norway, 2) Sri Lanka - the mouth of the river Lena, Siberia and 3) Indonesia - the mouth of the river Indigirka, Siberia (data from WOLTERS-NOORDHOFF ATLASPRODUCTIES 1991). Climatic codes after TREWARTHA. The ellipses show the circumstances in which an imaginary taxon can survive (= the niche; outer ellipse), the more favorable circumstances and the optimal circumstances (inner ellipse).

Fig. 1B shows the imaginary niches of sympatric taxa A (inner ellipse) and B (outer ellipse) and two imaginary climate curves at low global temperatures (1) and at high global temperatures (2). In the first case both taxa live in the same area, but in the second case taxon B may live in both tropical and temperate climates and taxon A does not find a suitable habitat in which to live. The ellipses may also be read as indicating acceptable (outer ellipse) and favorable habitat (inner ellipse) for a taxon, expressed as biomass per km^2, or species diversity in the case of a taxon of a higher order: the second climatic curve provides optimal circumstances - a great density of biomass or space for two species in one area.

Fig. 1C shows the niches of a wet temperate adapted species (A), a cold adapted species (B), a hot humid adapted species (C) and a hot arid adapted species (D). At low global temperatures (curve 1) species A would become extinct, species C retracts to the north and species D disappears. In the case of higher global temperatures (curve 2), species B would go extinct.

Fig. 1D shows hypothetical niches of a cold adapted species (A), a dry adapted species (B) and a hot adapted species (C) and two climatic curves. At a low global temperature (1) the three taxa have distributions that do not overlap, at higher global temperatures (2) the three species have overlapping distributions.

expansion on the one hand and contraction on the other, the range of a species may shift to another place on the globe, which process might be termed translation of the geographical range.

Migration can not only be seen as the expansion of the geographical range of taxa, but also as the expansion of the environment where these taxa are able to survive. This means that the values of the parameters describing the environment in this area are within the ranges that limit the niche of this taxon. In physical terms the extension of the suitable habitat of a species may mean a shift of an isotherm, an isopach, a coast or the edge of a forest. However, not only may the limits of the acceptable conditions shift, but the place with the optimal conditions for a taxon may also move to another geographical position. Contraction is not limited by barriers and for that reason may, in certain cases, give clearer information on paleoclimate.

In this paper a model that may explain how small changes in global climate may cause rapid expansions and contractions over large distances and even sequences of such events will be presented. First it will be shown that expansions may be instantaneous, geologically speaking. Then in a purely theoretical model, the niche, in terms of humidity and temperature, will be compared to sequences of climates from the Equator to the Arctic Circle. Finally, this model will be applied to the geographical distributions of animals. Many of the examples used here are from the Miocene, when the climate was more stable than in the Pleistocene. The reaction of the fauna to climatic changes can be seen as if in 'slow motion'.

Rate of expansion of the geographical distribution of a species

Whereas a contraction of the geographical range of a species may obviously be instantaneous, expansion could take some time. The 'Proboscidean Datum Event' (MADDEN & VAN COUVERING 1976) appears to have taken at least 3 Ma, instead of being instantaneous (TASSY 1990). Similarly, equid dispersals that were once considered to be synchronous are now considered to be diachronous. The reason for the delay is not always obvious.

Several examples of rapid expansion are known from historical times: man introduced rabbits (*Oryctolagus cuniculus*) in Australia and the muskrat (*Ondatra zibethicus*) in Europe. The rate of migration of *Ondatra* is
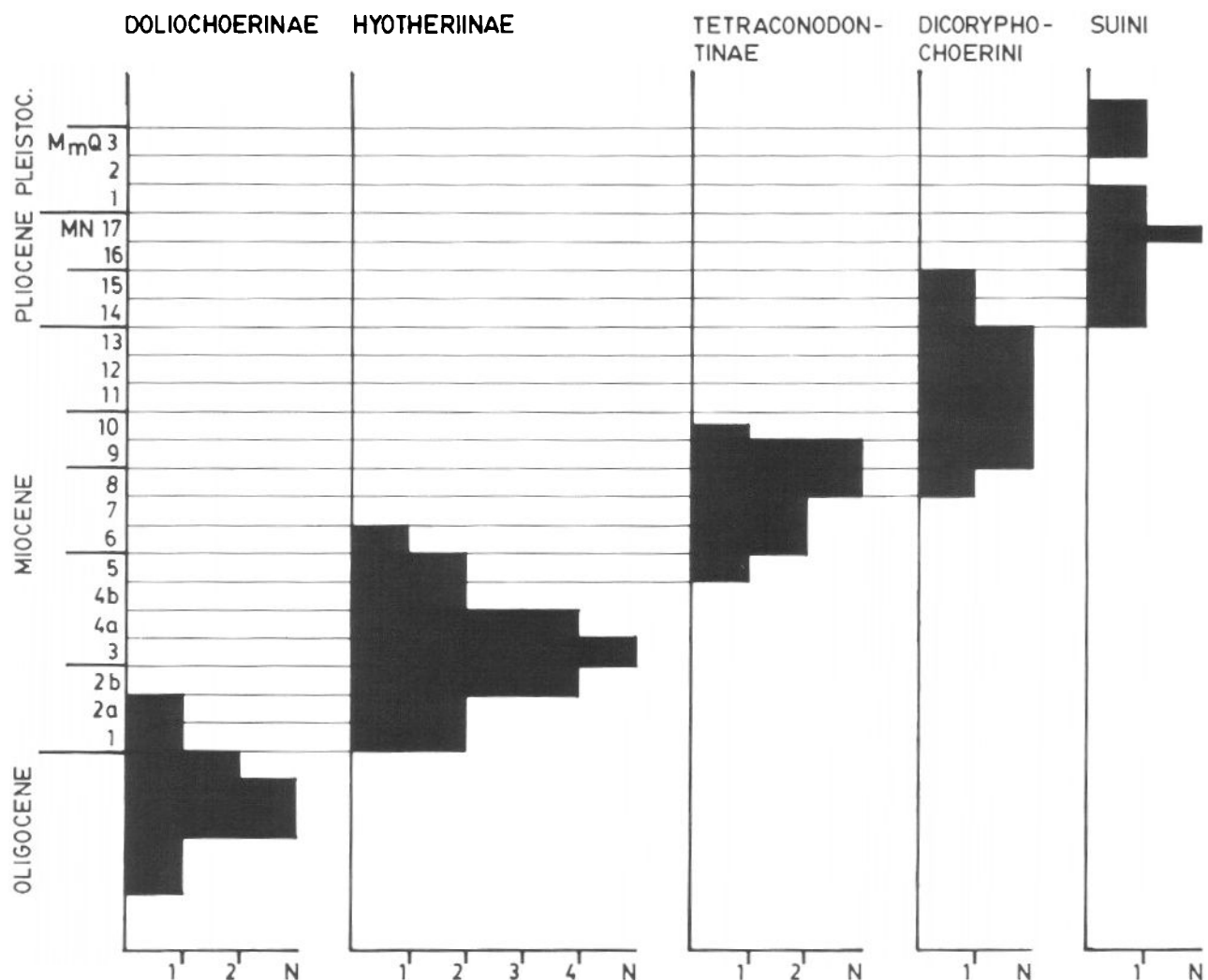
Fig. 2: The distribution of moles (*Talpa*) (diagonally hatched) and the distribution of 'red and grey soils of the deserts' (stippled) (after BURTON & BURTON 1970/71; BRIDGES 1984). The distribution of moles is limited by soil type.

difficult to estimate, since the species was introduced at various places, but may have been up to 25 km/yr within one catchment basin (based on data given by BURGHAUSE 1988). For the red fox (*Vulpes*) the rate of expansion has been estimated as 21.5 km/yr on Baffin Island, Canada (MACPHERSON 1964 in DELANY 1982). *Nyctereutes procyonoides* expanded from the USSR to Western Europe by some 13 km/yr (calculated from data given by NOWAK 1988). The nine-banded armadillo expanded from southern Texas in the beginning of the century to Florida (HUMPHREY 1974 in DELANY 1982). This is over 16 km/yr. Although these species have a higher rate of reproduction than horses and elephants, it may be assumed that even in species with a slow rate of reproduction expansion may be very rapid, even instantaneous when seen in a geological perspective.

Niches and climate

It is possible to describe the niche of a species in terms of the ranges of a number of parameters, such as amount of sunlight (minimum in winter, average per year), temperature (average, extremes), amount of precipitation, balance precipitation-evapotranspiration, wet or dry season or the presence of certain plants or other animal species. Climates tend to be distributed in alternating dry and humid belts. These belts are east-west oriented. Near the equator temperatures are high and change little though the year, towards the poles temperatures decrease and differences between winter and summer temperatures increase. IVERSEN (1944) described the niche of plants at high latitudes by the combination of winter and summer temperatures. Here, humidity and average temperature are taken as parameters. The range of a species may contract or expand as a direct result of changes
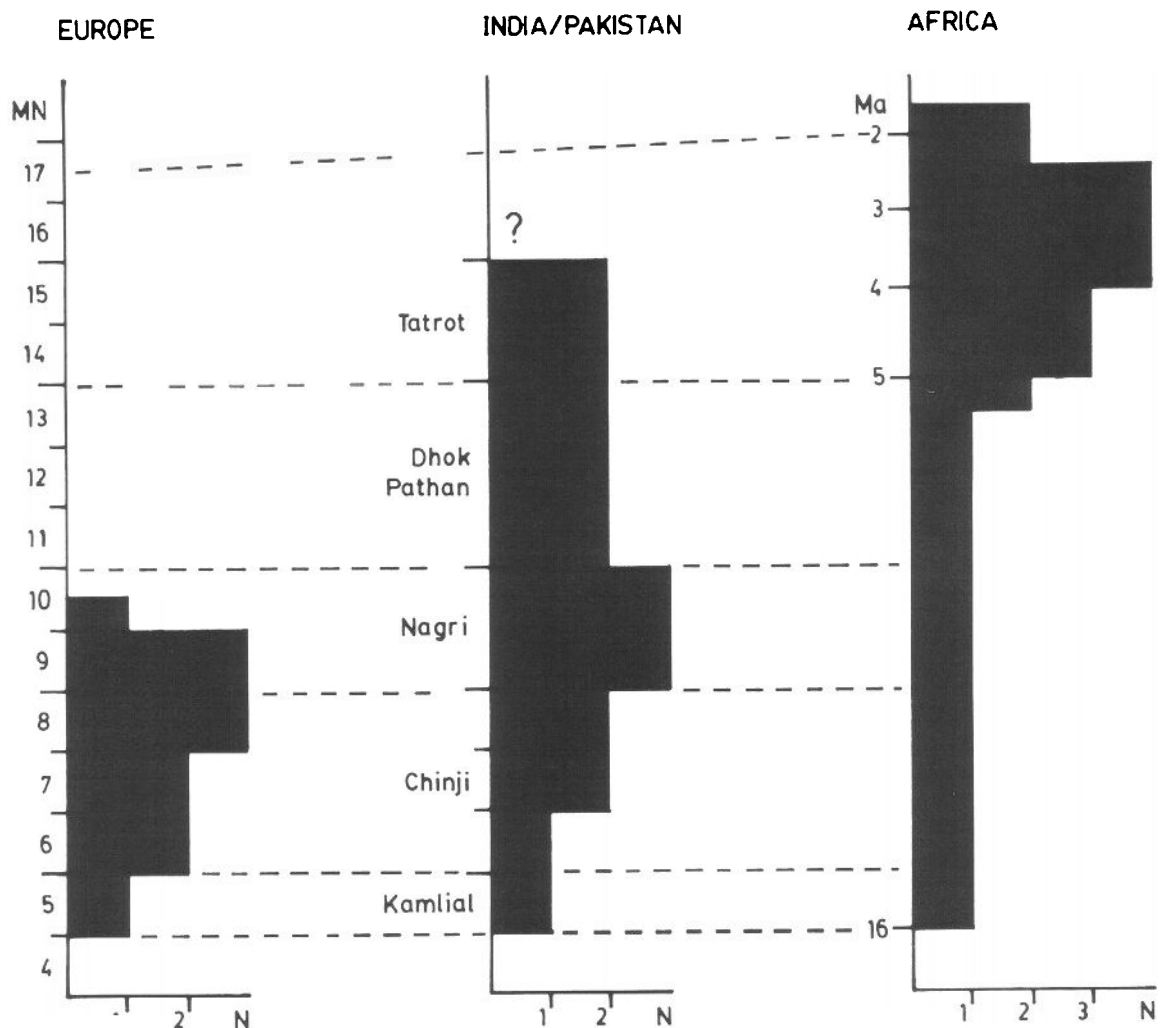
Fig. 3: Species diversity of Doliochoerinae (Tayassuidae; excluding *Taucanamo*, *Schizochoerus* and *Barberahyus*, but including *Doliochoerus* and *Palaeochoerus*), Hyotheriinae (Suidae), Tetraconodontinae (Suidae), Dicoryphochoerini (Suidae, Suinae) and Suini (Suidae, Suinae) in Europe (data from MADE in press). Species diversity is expressed as number of species per biozone.

Groups of related animals replace each other in Europe. Each group consists of similar animals, differing mainly in size.

in these parameters (for instance, an animal does not tolerate high temperatures) or through their effects on other species of animals or plants (the distribution of prey species, preferred plants for food, etc.).

In Fig. 1, climates and niches are indicated as temperature-humidity curves or fields. In Fig. 1A, the ellipses indicate the niche or acceptable circumstances for an imaginary species (outer ellipse), and the good and optimum circumstances (inner ellipse); the three undulating curves represent combinations of temperature and humidity for three different sections from the Equator to the Arctic Circle. In the three following examples the climatic curves are imaginary: it is not my intention to show a model of climatic changes, but to illustrate how species might react to a change in the climatic curve. For this reason, it is irrelevant exactly how the shape of the climatic curves changes.

Fig. 1B shows the acceptable circumstances of sympatric taxa A and B. Both ellipses intersect with climatic curve 2. This indicates that the niches for these taxa exist at the intersection. If we imagine a global cooling (forgetting any complications of evapotranspiration or precipitation or change in the shape of the curve), we arrive at the situation given by line 1. Ellipse A no longer intersects line 1 and ellipse B intersects it in two places: the habitat of species A has disappeared and the species will go extinct and species B now has two smaller

EUROPE INDIA/PAKISTAN AFRICA

Fig. 4: Species diversity of Tetraconodontinae in Europe (data from MADE 1988, in press), the Indian Subcontinent (PICKFORD 1988; personal observations) and Africa (PICKFORD 1989).
The optimum as well as the range of the Tetraconodontinae shifted to the south.

areas with favorable conditions. If a climatic 'bridge' allows species A to cross to the tropics it will do so. It is possible that the 'bridge' or 'corridor' is in existence and that the actual change in climate triggers the expansion, or that a local change creates a 'corridor' and triggers the expansion. An immigration may be the reflection of a local change elsewhere. A minor change in temperature might cause the expansion of a species in a narrow but long east-west belt, thus causing expansion over thousands of kilometers (in an east-west direction). It is also easy to imagine how a slow but continuous change in temperature might cause this type of migration to be repeated by different species, each with a different 'threshold-temperature'.

In Fig. 1C a similar case is given for species A, living in a humid temperate climate, species B, living in a polar climate, species C, living in the hot tropics and species D living in the dry tropics. Due to global cooling species A and D become extinct and species C contracts to the north. Species B may survive in a cold climate, but contracts in case of global warming. A small global climatic change might trigger major extensions and contractions of the ranges of different taxa in different places of the world. Mammoth, musk ox and lemming have niches comparable to species B.

In Fig. 1D the niches of three taxa with different habitats (cold, wet hot and dry hot) are indicated, as well as two imaginary climatic curves. In one case the ranges of the three species overlap, in the other case they occur in three regions with different climates (cold-wet, dry and hot-wet). In a similar way a 'community' may split up due to global warming. GRAHAM (1990) cites a case where *Dicrostonyx* (now living in the cold north), *Sorex*

fumeus (now living in the wet east) and *Spermophilus tridecemlineatus* (now living in the dry center of North America) occurred together in the late Pleistocene. An increase in the difference between summer and winter temperatures was considered to be the reason for breaking up the community, but an alternative explanation may be that a change in temperature-humidity characteristics of the environment is the cause. Although it is likely that global warming will cause the climatic curve to not only change its position, but also its shape, the real point here is that a change in this curve may have very different effects on the distributions of different species.

Climatic belts and corridors

Climates tend to be distributed in east-west belts, but at some places a climate may occur that is atypical for that latitude. Such an area may act as a 'corridor' for animals to cross climate belts that would otherwise be difficult or impossible for these particular species to cross. An example is the Cf climate in China (climatic code of TREWARTHA; RILEY & SPOLTON 1983, fig. 111). It is caused by the trade winds, bringing humid air from the oceans. In the center and west of Eurasia and Africa dryer climates prevail at this latitude.

Moles (*Talpa*) live mainly on earthworms, but also on insect larvae and other animals living in the soil. Earthworms are very sensitive to characteristics of the soil and in general prefer humid, slightly acid soils with abundant organic matter and not too high temperatures (lethal temperatures vary between 25° and 40°C for different species) (EDWARDS & LOFTY 1977). The distribution of such soil types is dependent on climate and for that reason moles are found mainly in climates that are wet all year round and not in arid climates. Moles seem to be restricted by soil type (Fig. 2). As *Talpa* never entered the Middle East, Africa and large parts of India it seems likely that such soil types always restricted *Talpa*. However, the subtropical humid climate of China made a corridor of suitable soils for *Talpa* to spread to the south.

Anchitherium and the Tapiridae never entered India or Africa and cervids not before the Pleistocene. Barriers have been proposed to explain this. *Anchitherium* and cervids were found in the Middle Miocene (MN 5/6; MN zonation of MEIN 1990) of Pasalar, Turkey (FORSTÉN 1990; GENTRY 1990). Other elements of this and other faunas of the region indicate that connections with India, Africa and Europe must have existed (MADE & HUSSAIN 1992). From the Middle Miocene onwards, these connections must have been present, as is indicated by the distribution of fossil and recent species. Like recent *Talpa*, Miocene tapirs, *Anchitherium* and cervids are found in South China. This suggests the same explanation as for the moles: a dry or semi-dry climate prevented these animals from moving into the Middle East, India and Africa, but a humid climate allowed them to move south in China. This suggests a long persistence of a general climatic pattern and a high age for the 'Chinese migration corridor'.
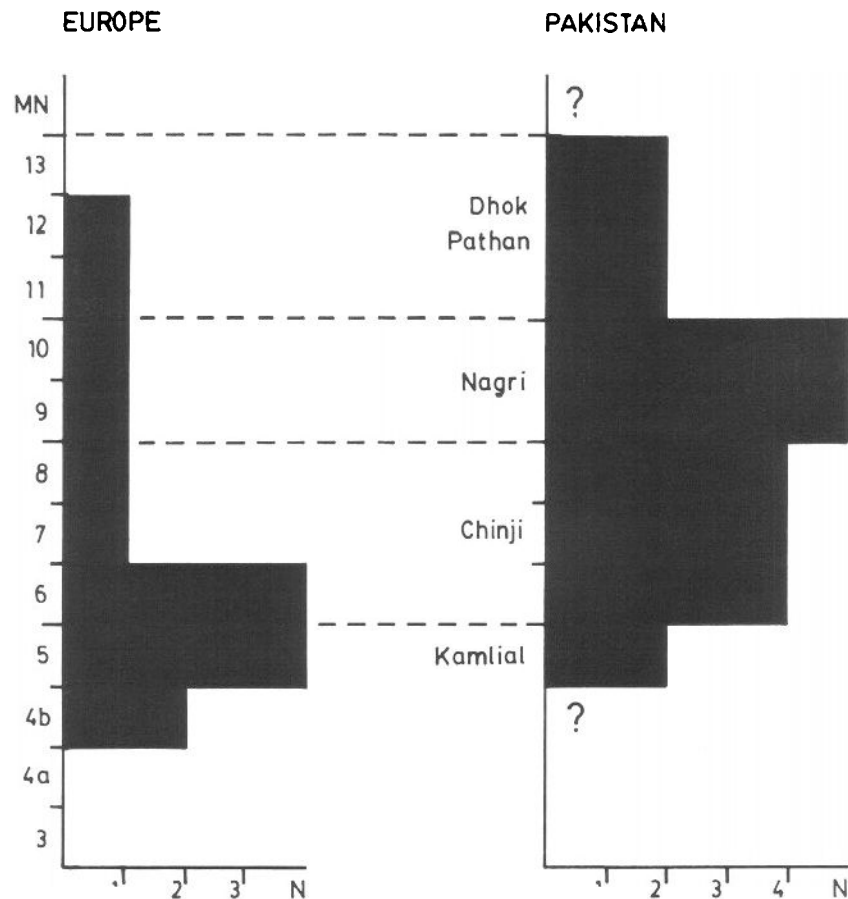
Tapirs and *Nyctereutes* disappeared from Europe during the Pleistocene due to deterioration of the climate. Tapirs lived in China till the Middle Pleistocene (XUE & ZHANG 1991). *Nyctereutes* still lives in China and would probably have migrated into Europe again if it were not prevented by the E climate of Central Asia, which it would have to cross. *Nyctereutes* lives in China in Dc and Cf climates, and when it was introduced by man in a Dc climate in western Russia it expanded rapidly (NOWAK 1988).

Migration of optima

If the range of a taxon expands, the geographical range of its potential habitat widens. However, this is not the same as the optimal habitat. High biomass per square kilometer or high species diversity reflect optimal conditions for a taxon. There are many cases of sympatric congeneric species, both fossil and recent. In many cases, the only known or main difference between those species is size (MADE 1990a). It is likely that such species compete, wherefore either the position or migration of the range of the higher order taxon, or its optimum, may give better information on the environment than the ranges of the individual species.

Whereas in the earlier examples humidity had an important role, the following examples will show a gradual southward translation of optima during a period of cooling. This suggests that suoids, tragulids and anthracotheres mainly reacted to temperature.

In Europe, the Suoidea (peccaries, Tayassuidae, and pigs, Suidae), was represented by groups of related species replacing each other over time (Fig. 3). In several cases, when a group of suoids was replaced by another group, the replaced group moved south, or persisted in the south, like the Tetraconodontinae (Fig. 4) and the Dicoryphochoerini (even individual lineages of this tribe contracted to the south: MADE 1990b).

33

EUROPE   PAKISTAN

MN   ?

13
                          Dhok
12   Pathan

11

10
                          Nagri
9

8

7   Chinji

6

5   Kamlial

4b   ?

4a

3

      1 2 3 N   1 2 3 4 N

Fig. 5: Species diversity of Tragulidae in Europe (data from FAHLBUSCH 1985) and Pakistan. The species diversity for Pakistan is based on material from the lower Manchar Formation, Sind (Kamlial equivalent strata; HGSP collection) and material from the Chinji, Nagri and Dhok Pathan Formations (collection IVAU). The species diversity is expressed as the number of species per unit, MN zones for Europe (MEIN 1990) and for Pakistan formations or subdivision of formations.
The optimum as well as the range of the Tragulidae shifted to the south.

Tragulidae entered Europe in MN 4b (Early Miocene) and immediately attained a high species diversity (Fig. 5). After MN 6 (Middle Miocene) species diversity dropped from 4 to 1. In Pakistan no drop in species diversity occurred during 'Chinji-time' (Middle Miocene). Later, in 'Nagri-time' (Late Miocene), species diversity increased. After MN 12 (near the end of the Miocene) tragulids disappeared from Europe, but lived on in Pakistan and China. The living species are found in Africa and southern India (both 1 species) and Southeast Asia (2 congeneric sympatric species). The MN 6 drop in species diversity in Europe is accompanied by the replacement of flamingos (tropical) by ducks (temperate) as dominant birds (HESSE pers. comm.) and by a very strong decline in the abundance or even total disappearance of crocodiles (depending on latitude; TELLES ANTUNES & GINSBURG 1989; SCHERER 1981). The MN 12 contraction is accompanied by similar contractions for deinotheres and chalicotheres to the south. Last citations in Europe for the tragulids: Samos and Kerassia; for the deinotheres: Samos, Pikermi and Kerassia; and for the chalicotheres: Pikermi and Samos (SOLOUNIAS 1981 and material from Kerassia presently stored in the IVAU = Instituut voor Aardwetenschappen, Utrecht). Plio-Pleistocene citations exist for chalicotheres and deinotheres in Africa (MAGLIO 1978), chalicotheres and tragulids in China (XUE & ZHANG 1991) and Dorcatherium in Sangiran, Indonesia (IVAU collection).

In the Paleogene, anthracotheres were represented in Europe by several species. At the end of the Oligocene the family disappeared, but made a short come-back in MN 3 and 4 (Early Miocene) with 1 species. In Pakistan, species diversity was still up to 5 in 'Kamlial-time' (latest Early Miocene, approximately MN 5), but declined to

2 in 'Chinji-time', after which species diversity remained 1 till at least 2.56 My ago (STEENSMA & HUSSAIN 1992; IVAU & HGSP collections - HGSP = Howard-Geological Survey of Pakistan).

In these examples, geographical ranges as well as optima of species diversity of taxa were translated to the south. This recalls Matthew's theory that centers of evolution were in the north and that younger taxa tend to push older taxa to the south (MATTHEW 1915, cited by SIMPSON 1940). But MATTHEW's theory does not explain why individual species or species abundance optima of higher taxa move to the south over the course of several million years, especially not as we have seen that expansion may be very rapid. Other old Eurasian taxa did not move south in the same period as anthracotheres, tragulids and suids did. For instance, moles and beavers have an Oligocene origin, but never contracted to the south. The Tertiary shows an overall temperature decline and it may well be that anthracotheres, tragulids, suids, chalicotheres and deinotheres contracted to the south mainly or partially due to a temperature decline, whereas the distribution of moles, *Anchitherium*, tapirs and cervids was more dependent on humidity (probably through soil type, vegetation, prey species etc.).

Discussion

Areas of distribution of recent taxa are extensive, despite mountain ranges, rivers etc. This suggests that these often are not effective physical barriers. Most of the physical barriers take time to form or break down, save for sea barriers in particular settings. An extensive land-mass with only a few real barriers cannot explain the frequent migrations of very different types of animals in geological time. The breakdown of physical barriers is not likely to be the motor for the many expansions (entries) that help to distinguish the different biozones of a detailed biozonation and certainly does not explain contractions (exits), such as those mentioned in the preceding examples.

The model presented here, in which a combination of east-west oriented climatic belts and global climatic changes cause the habitats of species to expand or contract, has one particularly interesting point. It shows that a small global change may cause species to 'jump over' from one climatic belt to another in an instant, geologically speaking. This would explain long distance migrations caused by minor climatic changes that are not reflected in the fauna as a whole. A slow, continuous change might cause other species to follow later on, when their 'threshold-value' is reached, so that continued small changes may lead to a number of separate migration events, each over great distances. The model also explains why a species appears suddenly over a very extensive area instead of expanding slowly following the slow change in a certain parameter of the climate. It would also explain the presence of 'tropical' taxa in Europe, without assuming that there was a continuous tropical climate from Europe to the Equator (see PICKFORD 1990).

The translation of optima of suids, tragulids and anthracotheres shows that the idea of a slow global cooling superimposed on a relatively stable pattern of humidity as the motor of migrations during the Neogene is possible. During the Quaternary, rapid climatic changes caused an even more complex pattern of migrations. The examples of moles, tapirs, *Anchitherium* and cervids show that elements of a general pattern of climatic belts (and corridors) may have been acting for a longer period, although the exact characteristics and positions of these belts were not constant, nor, at higher latitudes, the number of climate or vegetation belts.

Acknowledgements

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