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The influence of Quaternary climatic development on the Central European mollusc fauna

Dietrich MANIA

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Abstract. This paper presents a brief overview of the dependence of the Central European mollusc fauna on climatic conditions and development during the Quaternary. This dependence is exemplified by the last glacial-interglacial cycle (Eem interglacial-Weichsel glacial-Holocene). From this, the basic Pleistocene molluscan faunal succession can be deduced and can be identified as far back as the Early Pleistocene. The associations of the different Middle and Late Pleistocene interglacials are qualitatively distinct through the presence of so called exotic species which currently inhabit the Mediterranean region. Their frequency decreases towards the Holocene. Thermophile, species-rich associations characterize the warm phases. Glacials are characterized by loess steppe and tundra faunas that are poor in species. During these periods, species that currently inhabit circum-polar, boreo-alpine and Central Asian areas were present in Central Europe. During the interglacial-glacial transitions, faunas of the wood steppes and tschernosem steppes appeared. The molluscan succession develops in parallel with the climatically induced successions of plants and vertebrates.

Key words: Mollusca, Quaternary, Central Europe, climate, environment, migration.

Dietrich MANIA, Ibrahimstrasse 29, D-6900 Jena, Germany.

I. INTRODUCTION

All species of molluscs present in Central Europe today have been in existence since the Early Pleistocene. Comparative studies have shown that they responded rapidly to the climatic developments of the Ice Ages. Their ecological requirements in the late Early Pleistocene already corresponds closely to those of the present. They have therefore proved to be reliable environmental and climatic indicators. Together with other faunal components, such as vegetation, ostracods and vertebrates, as well as geological and geomorphological features, molluscs can assist in a comprehensive reconstruction of paleoecological and paleoclimatic developments (LOŽEK 1964, 1965; MANIA 1973).

In this contribution I shall present the development of the Central European mollusc fauna of the Elbe-Saale region during the last Quaternary climatic cycle and an overview of molluscan faunal development during the Quaternary.

The sedimentation sequence in the basin of the former lake of Aschersleben in the northern foreland of the Harz (MANIA 1967, 1975, in press; MANIA & TOEPFER 1973) includes a nearly complete record of the last cycle (Figs 1, 2). It is complemented by the last interglacial travertine sequence of Burgtonna in Thuringia (MANIA 1978) and a more detailed record of the late glacial and Holocene sequence from the Geisel valley (Mücheln 1-5; MANIA & TOEPFER, 1971; MANIA in press; MANIA et al. 1993).

According to these studies, the cycle spans 125 000 years and including two late interglacial climatic oscillations (Burgtonna), at least 17 climatical cycles of lower order. The interglacial (1) was followed by a long early glacial beginning at about 90 000 BP and ending at about 20 000 BP. This period was subdivided by a strong stadial between 60 000 and 50 000 BP into an older (2) and a younger (3) part, each with four lesser cycles and four interstadials. During the first two interstadials (cycles 2 and 3) the climate was still cool-temperate whereas in the two following interstadials (cycles 4 and 5) it was already cooler. The climate during the stadials was already arctic. During the interstadials of the 6th to 9th cycles the climate was predominantly subarctic with relatively warm summers. At the same time aridity increased.

After this there followed the climatic maximum of the great cycle with the pleniglacial (4) from about 20 000 to 13 000 BP. At this point the temperature oscillations of the three

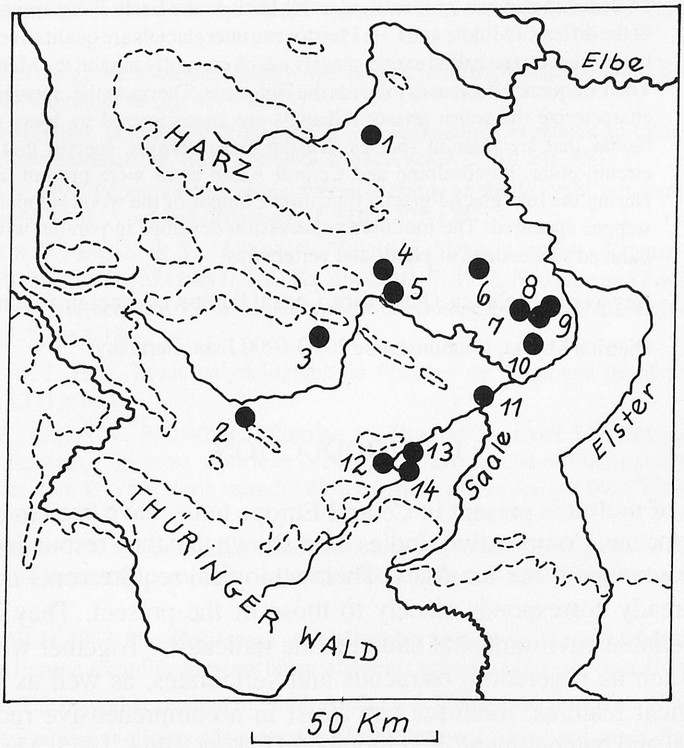

Fig. 1. The middle Elbe-Saale region. Sites described in the text are: 1 – Ascherslebener See (Aschersleben lake) in the northern Harz foreland; 2. – Burgtonna; 3 – Bilzingsleben; 4 – Edersleben-Voigtstedt near Artern; 5 – Kalbsrieth; 6 – Langenbogen; 7 – Mücheln; 8 – Krumpa; 9 – Neumark-Nord (7-9 – Geisel river valley); 10 – Borntal; 11 – Lengefeld-Bad Kösen; 12 – Ehringsdorf; 13 – Süßenborn; 14 – Taubach.

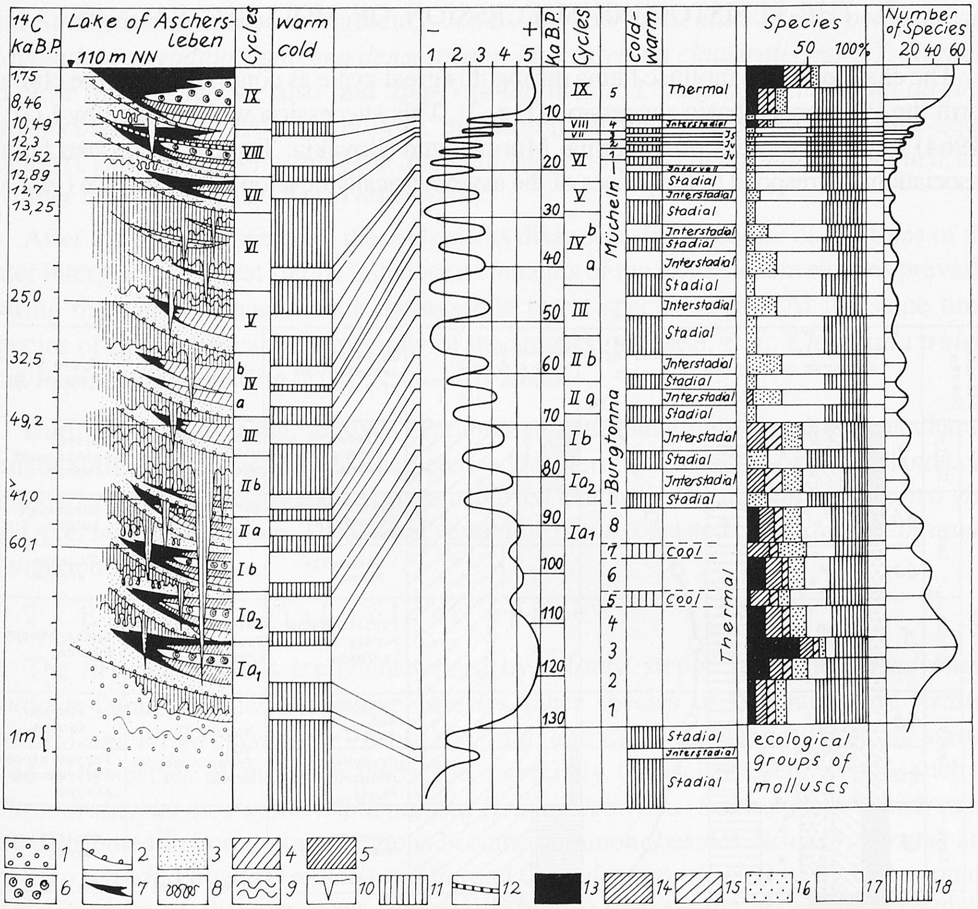

Fig. 2. The climatic cycle from the Eem interglacial to the Holocene as an example of Pleistocene climatic change and the development of the mollusc fauna. The great cycle is composed of numerous lesser cycles. They have been identified in the sediment sequences of Aschersleben lake, in the Geisel river valley (Mücheln) and in the travertine of Burgtonna. 1 – sandy gravels; 2 – denudation unconformity; 3 – sands; 4 – silts and silty gyttjas; 5 – clay gyttjas; 6 – calcareous gyttja; 7 – peats and swampy soils (Anmoor); 8 – phenomena related to gravitative processes; 9 – cryoturbations; 10 – frost cracks; 11 – solifluction soils and loess-like silts; 12 – tephra from the'Laacher See' volcano (Eifel); 13 – forest species; 14 – species of dry, open woods, forest steppe and shrublands; 15 – 'Auwald' species; 16 – steppe species; 17 – common species of the open landscape; 18 – species with differing demands on humidity and aquatic species (groups 1-10 after LOŽEK 1964). Climatic zones: 1 – extreme arctic; 2 – arctic; 3 – subarctic; 4 – boreal-cool temperate; 5 – warm temperate. Mü 1-5 – sediment sequence Mücheln 1-5.

lesser cycles 10-12 reached subarctic conditions at best. The aridity reached a maximum during this time. The late glacial (5), ending at about 8000 BP, represents the shortest phase of the great cycle and rapidly led to the interglacial climate of the Holocene (6). The late glacial includes two cycles (13 and 14). The climate was again cool-temperate during the Alleröd interstadial.

II. THE PLEISTOCENE SUCCESSION OF MOLLUSC FAUNAS

The changes in the mollusc fauna during this great cycle as conditioned by the climate form the Pleistocene basic succession (Fig. 2). This succession was outlined by LOŽEK (1964) in the sequences of Bohemia, Moravia and Slovakia. Typical molluscan faunal associations correspond to the phases of the asymmetrically developing great cycle (Fig. 3).

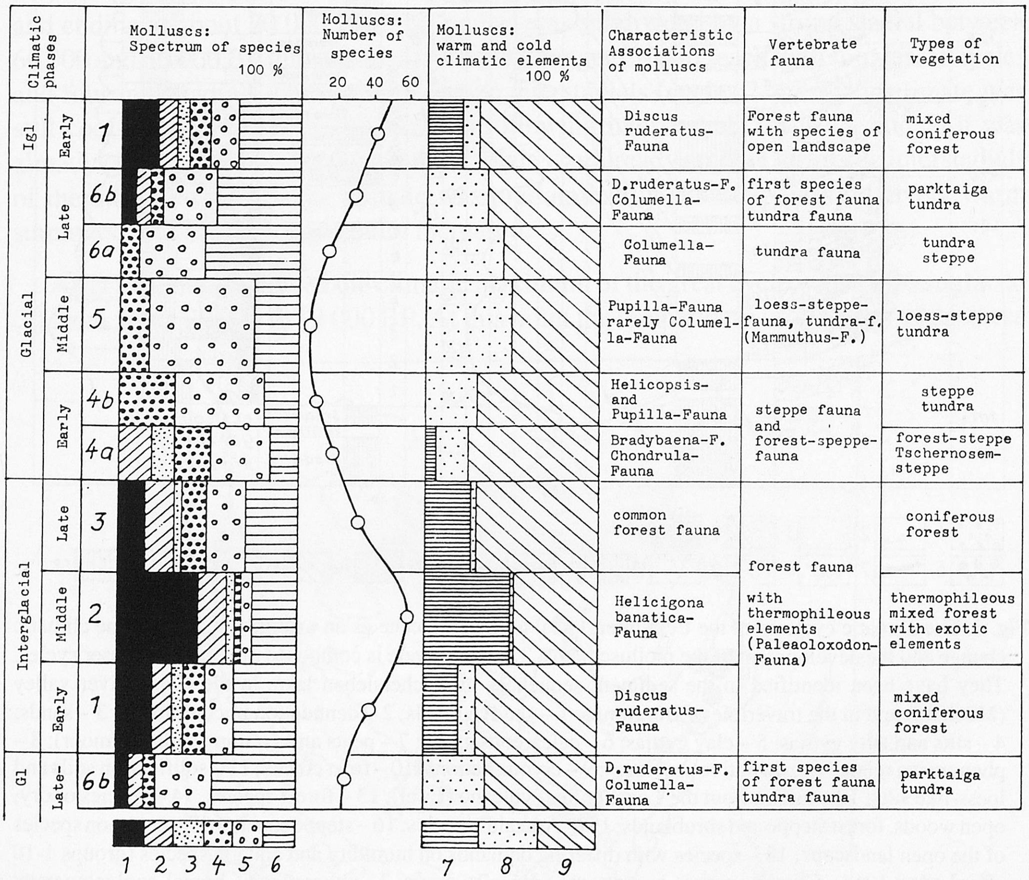

Fig. 3. Generalised course of the Pleistocene basic cycle of the Central European mollusc fauna (after LOŽEK 1964; MANIA 1973). 1 – forest fauna; 2 – species of dry, open forests, forest steppes and shrublands; 3 – 'Auwald' species; 4 – steppe species; 5 – common species of the open landscape; 6 – species with differing demands on humidity; 7 – thermophile elements; 8 – elements of a glacial environment; 9 – fauna independent of climate.

1. Interglacial

A thermophile forest fauna rich in species of the *Helicigona banatica*-fauna was present. Besides the marker species, other exotic elements currently inhabiting in Southern and Southeastern Europe are present, such as *Aegopis verticillus*, *Discus perspectivus*, *Pagodulina pagodula*, *Iphigena densestriata*, *Truncatellina claustralis*, and *T. strobeli*. In older interglacials we also find *Iphigena latestriata*, *I. tumida*, *Pseudalinda turgida*, *Mastus bielzi*, and *Cochlodina costata*. In addition, atlantic species reach the Elbe-Saale region (*Cepaea nemoralis*, *Iphigena lineolata*, the spring snail *Belgrandia germanica*, and in older interglacials also *Azeca menkeana*).

After the climatic optimum these elements disappear. In the cooler oscillations of the later interglacial a forest steppe fauna with elements of the tschernosem steppes prevails; during the warmer phases some thermophile forest species return. At the same time, species of open landscapes, especially of the steppes, increase, e. g., *Chondrula tridens* and *Pupilla triplicata* (Fig. 4).

During the interglacial, lessivés (Parabraunerden, Fahlerden) developed as characteristic soils. The vegetation was characterised by thermophile mixed oak woodland taxa. In the travertine of Burgtonna, oak trees occurred alongside *Ilex aquifolium*, *Myrica gale* and *Acer monspessulanum*. The typical vertebrate fauna consisted of an *Elephas antiquus*-fauna rich in species.

2. Early glacial, older phase

The first interstadials are characterised by a forest steppe fauna, the *Bradybaena fruticum*-fauna. Besides the marker species other species of this fauna are *Arianta arbustorum*, *Vitrea crystallina*, *Discus ruderatus* and *Clausilia pumila*. These are associated with species of the open landscape, especially the tschernosem steppe, such as *Chrondrula tridens*, *Pupilla triplicata* and *Helicopsis striata*. Some species which today are distributed in boreo-alpine regions become common (besides *Discus ruderatus* also *Vertigo genesii*, *Valvata piscinalis antiqua* and *Gyraulus acronicus*) (Fig. 5). In the aquatic fauna, species of *Pisidum* occur frequently (Fig. 6). During the younger interstadials, *Chondrula tridens* was predominant.

Tschernosem soils had developed in the drier areas; degraded tschernosems and brownsoils were common in the moister areas, along with forests and park forests. Pine birchwoods with *Picea omorica* and some thermophile species (*Corylus*, *Quercus*, *Alnus*) dominated in the park-taigas. In the open vegetational types Gramineae, Chenopodiaceae, *Helianthemum, Artemisia* and other herbs were present. In the older early glacial there is a horizon where *Lagurus lagurus* is present along with *Hystrix*. The large mammal fauna was a transitional one, including species of the *Mammuthus* fauna along with *Cervus elaphus*, *Dicerorhinus hemitoechus*, *Equus hydruntinus* and *E. mosbachensis*.

3. Early glacial, younger phase

During this time the fauna becomes poor in species, including only limited associations that could endure cold temperatures of the open landscape. The *Helicopsis striata*-fauna (with *H. striata*, *Pupilla triplicata* and *P. sterri*) preferred summer-warm steppes and the *Pupilla*-fauna increased in abundance, which is a characteristic feature of the loess steppes. Tundra species such as *Columella columella* appear. The aquatic fauna was species-poor, being composed of eurythermal unpretentious species. Boreo-alpine elements such as *Valvata piscinalis alpestris* and *Gyraulus acronicus* occur. Species of *Pisidium* are

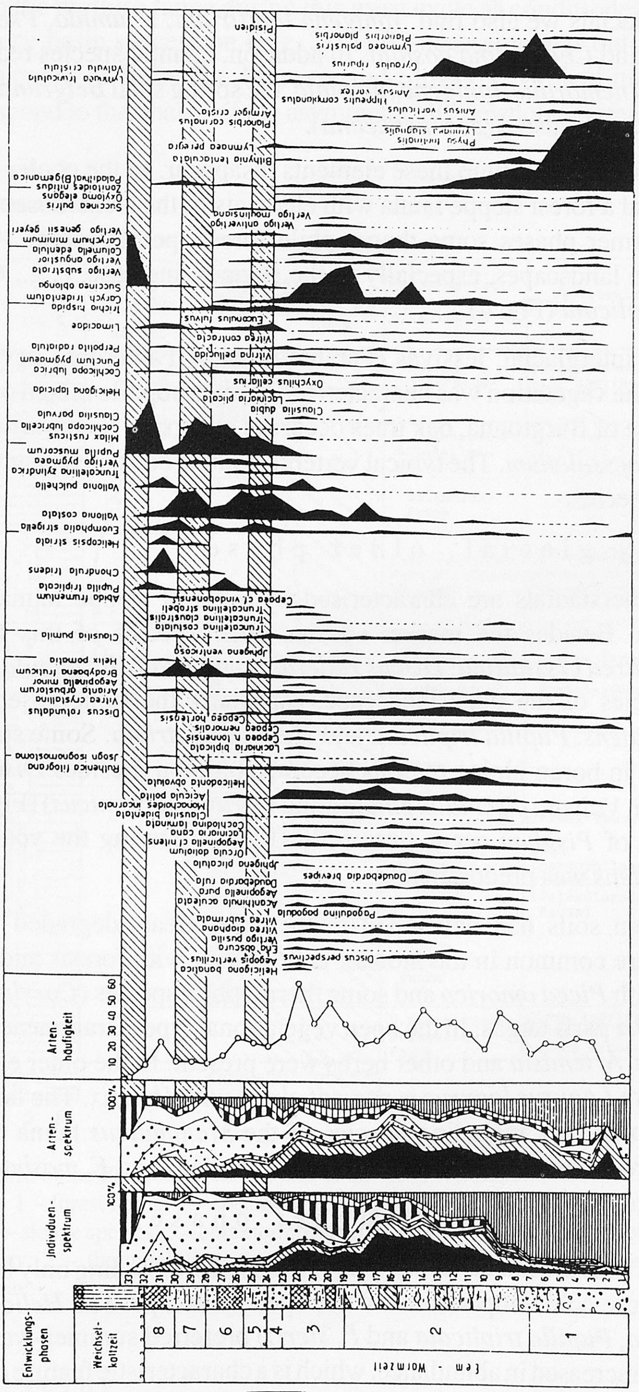

Fig. 4. Burgtonna (Thuringia). Travertine sequence and mollusc succession (after MANIA 1978). Characteristic interglacial development demonstrating late interglacial oscillations. 1 – marl with gravels; 2 – travertine sands; 3 – loose travertine; 4 – porous structured travertine; 5 – bank solid travertine; 6 – humus zone (soils and humus colluvium); 7 – alluvial travertine; 8 – loess. 1-10 ecological groups after LOŽEK 1964 (1-5 – see Fig. 3; 6 – xerothermal species; 7 – species of semi-moist habitats; 8 – species of moist habitats; 9 – swamp species; 10 – aquatic species.

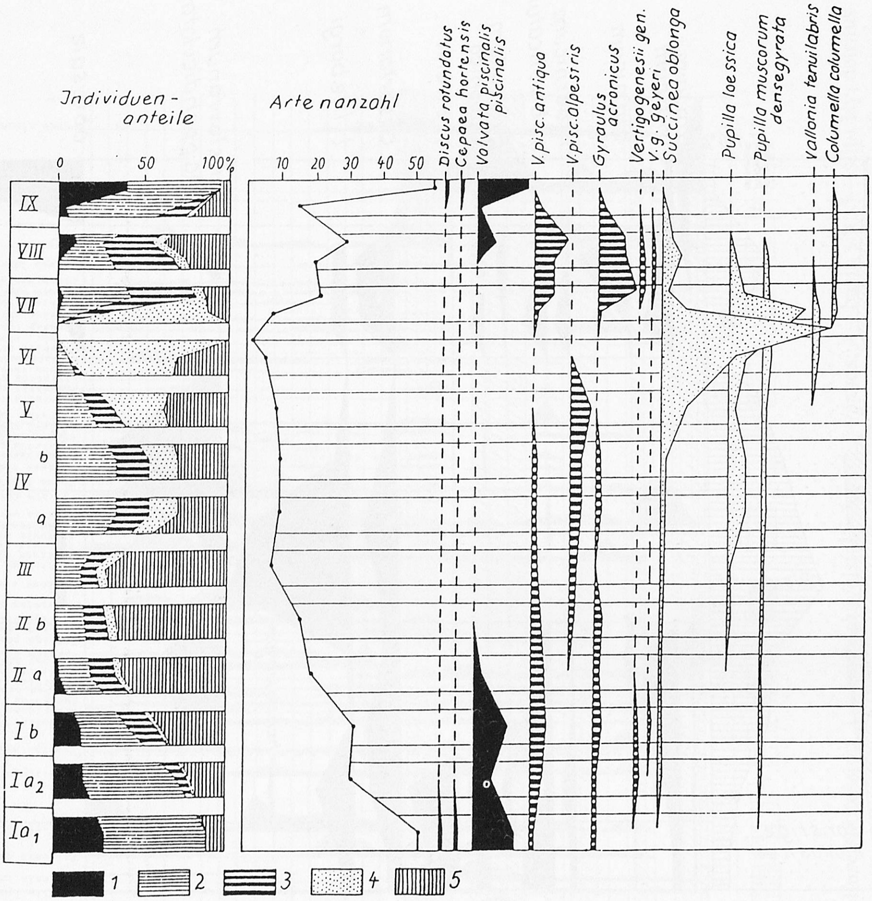

Fig. 5. Aschersleben lake. Late Quaternary mollusc succession. 1 – warm-stenothermal species; 2 – eurythermal species; 3 – boreo-alpine species; 4 – species of the loess steppe; 5 – species of *Pisidium*.

notably common (the boreo-alpine *Pisidiumlilljeborgi-stewarti-lapponica*-association, at the close of the early glacial) with *P. conventus* (Figs 5, 6).

Pseudogleys and weak loaming typify the interstadial soils. Characteristic vegetational types are grass-steppes rich in herbs, especially loess-steppes. In some isolated cases, birch, pine and willow have been found. The *Mammuthus*-fauna is typical and includes *M. primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Equus przewalskii*, *Ursus spelaeus*, *Crocuta crocuta*, *Gulo gulo*, *Canis lupus*, *Alopex lagopus*, *Vulpes vulpes* and *Lepus timidus*.

4. Pleniglacial

During this phase the mollusc fauna was composed of the resistant, species-poor, loess fauna, the so called *Pupilla*-fauna (5-10 species, sometimes only one species). Important species are *Pupilla muscorum*, *P. m. densegyrata*, *P. loessica*, *Succinea oblonga* and

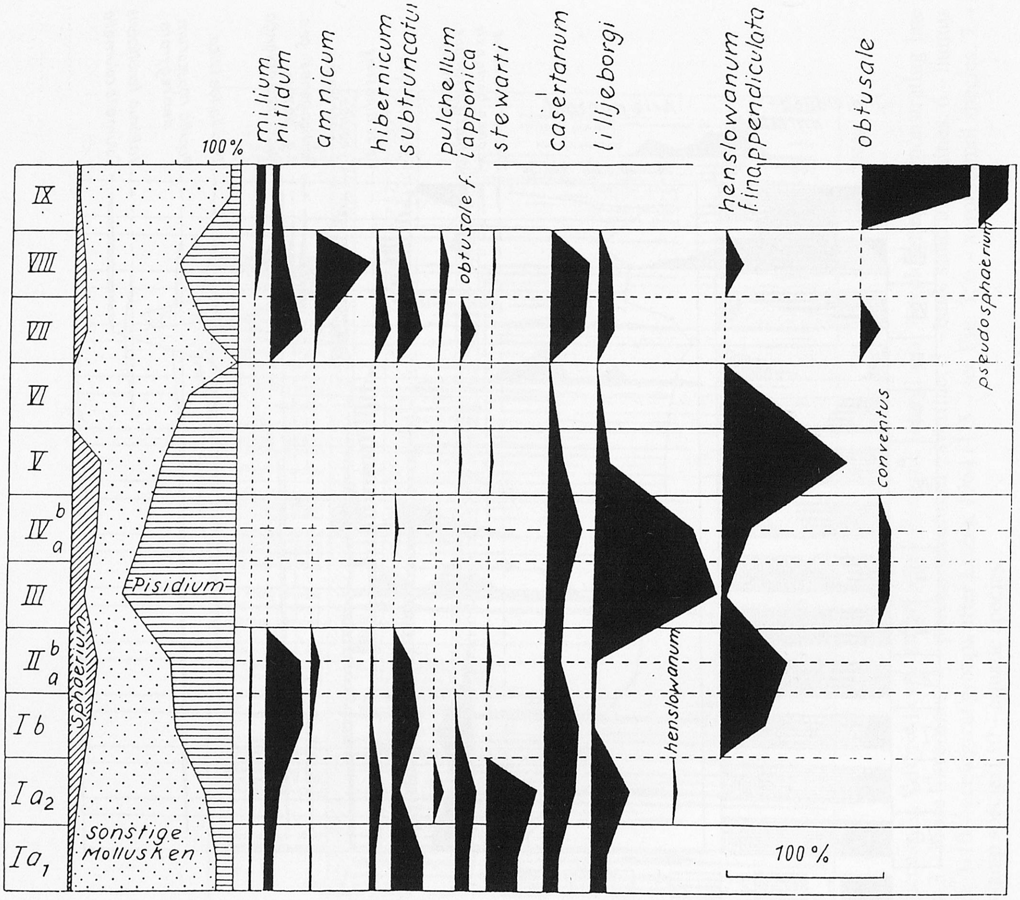

Fig. 6. Aschersleben lake. Late Quaternary succession of the *Sphaerium-Pisidium* associations.

Trichia hispida. In addition, accessory eurythermal species occur in some places with a favourable microclimate. A conspicuous continental element is the north Asian *Vallonia tenuilabris* (Fig. 5). *Columella columella* occurs in the lowland tundras. Some eurythermal aquatic species, especially species of *Pisidium*, lived in the seasonal waters of the arctic-subarctic summer.

Loess steppes and lowland tundras rich in herbs and grass associated with dwarf shrubs dominated. As can be seen from pollen analyses, some trees, such as *Betula*, *Pinus* and *Salix* appear, though they constitute less than 5% of the pollen counts. More than 50% of the pollen belong to Gramineae. The *Mammuthus*-fauna is composed of arctic representatives (*Ovibos moschatus*, *Saiga tatarica*; *Bison* disappears).

5. Late glacial

The *Pupilla*-fauna is gradually replaced by a *Columella*-fauna of the moister tundra (Fig. 7). *Vallonia tenuilabris* is characteristic of the fauna of the dry steppes. Numerous

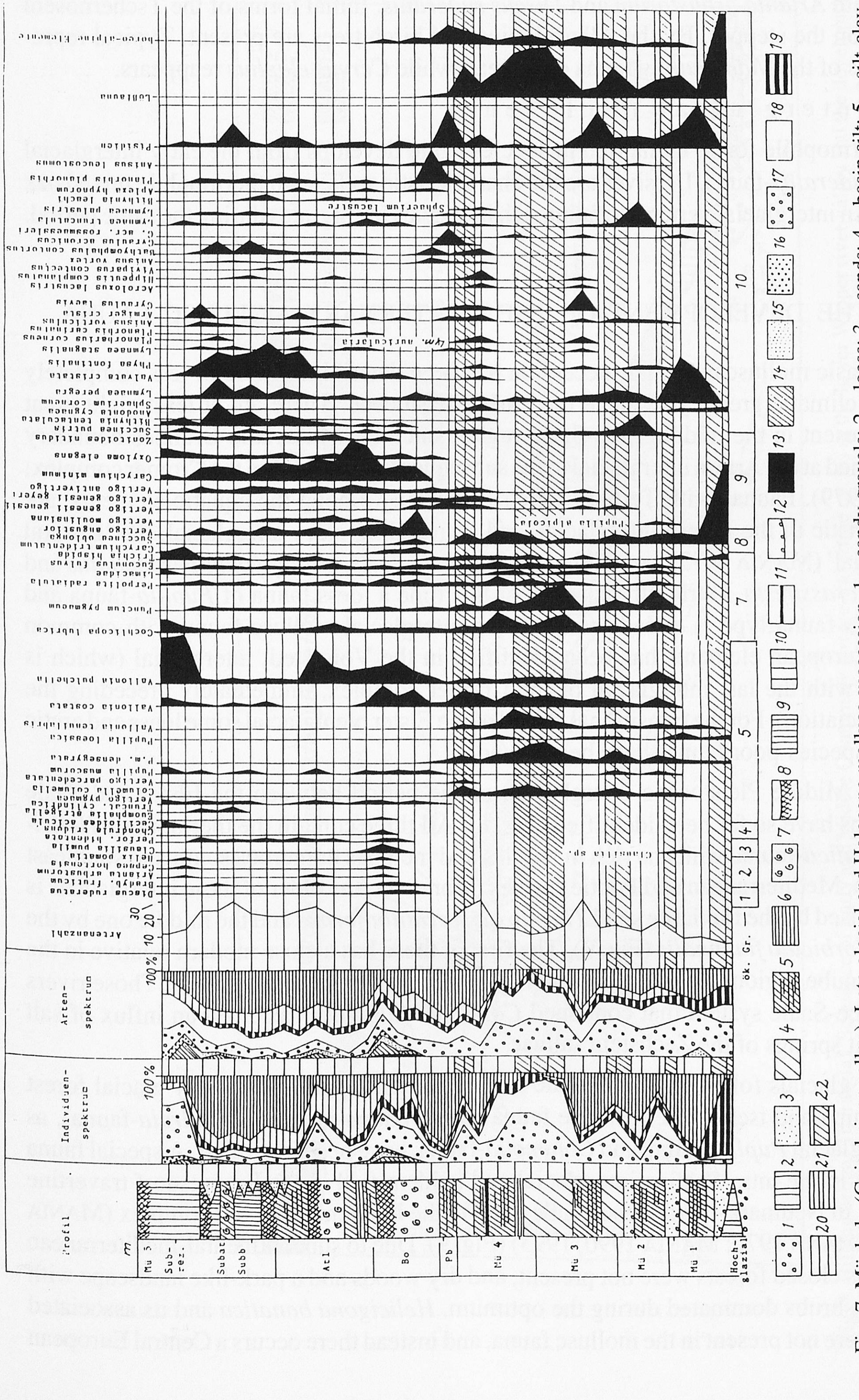

Fig. 7. Mücheln (Geisel river valley). Late glacial and Holocene mollusc succession. 1 – sandy gravels; 2 – loess; 3 – sands; 4 basin silt; 5 – silt-clay, detritus gyttjas; 6 – peats of the low-lying moor; 7 – calcareous gyttjas, gyttja limestone; 8 – swampy soils (Anmoor); 9 – older humus loam ('Auelehm'); 10 – younger loam ('Auelehm'); 11 – tephra from 'Laacher See' volcano; 12 – denudation unconformity; 13 – ecological group 1; 14 – group 2; 15 – group 3; 16 – group 4; 17 – group 5; 18 – group 7; 19 – group 8; 20 – group 9; 21 – group 10 (see Figure 4); 2 –. cold phases.

accessory elements are present. These are above all boreo-alpine forms, comparable to those of the early glacial. During the Alleröd, the fauna again resembles a forest steppe fauna, with *Arianta arbustorum* and *Discus ruderatus*. Initial forms of the Tschernosem develop on the steppes. By the Alleröd, pine and birch trees are present. Typical representatives of the M*ammuthus*-fauna disappear, while *Cervus elaphus* reappears.

6. Interglacial (Holocene)

A thermophile forest fauna rich in species again develops from the early interglacial *Discus ruderatus*-fauna. Lessivés are the characteristic soils, with thermophile mixed oak woods. An interglacial vertebrate fauna rich in species immigrates during the same period.

III. THE DEVELOPMENT OF THE QUATERNARY MOLLUSC FAUNA

The basic molluscan faunal succession has been determined more or less completely for each climatic great cycle since the Early Pleistocene. There are at least eight great cycles present in the middle Elbe-Saale region since the Matuyama-Brunhes boundary (determined at the Artern interglacial to the subsequent glacial within the Cromer complex; CEPEK 1979). Faunas with Tertiary relicts, especially among the aquatic elements, are characteristic of the Artern interglacial, and a preceding older interglacial, the 'Borntal interglacial' (MANIA 1973), containing *Fagotia acicularis*, *Lithoglyphus pyramidatus* and *Bithynia crassitesta*. During the glacials of this time a loess fauna of *Pupilla*-fauna and *Columella*-fauna type is already present. An interglacial mollusc fauna with common middle European elements has been identified in the Voigtstedt interglacial (which is identical with the last interglacial of the Cromer complex, immediately preceding the Elster glaciation). For the transitional period of the Elster pleniglacial some loess and arctic aquatic, species-poor faunas have been found.

Three Middle Pleistocene interglacials of the period between the Elster and Saale glaciations have so far been identified (Fig. 8). All three contain the thermophile *Helicigona banatica*-fauna, which is rich in species and includes numerous south and southeast European, Mediterranean and Pontic species. Moreover, the older of these interglacials is characterised by the fluviatile snail *Theodoxus serratiliniformis* and the middle one by the mussel *Corbicula fluminalis* (Fig. 9). The first of these has a close modern relative in the lower Danube region, the latter lived in high salinity river systems of Asia. Those rivers of the Elbe-Saale system that contained *Corbicula fluminalis* received an influx of salt due to salt springs of the Zechstein salinar.

In the glacials following the Middle Pleistocene interglacials an early glacial forest steppe fauna and tschernosem steppe fauna (*Bradybaena*-fauna, *Chrondrula*-fauna), as well as a glacial *Pupilla*-fauna and *Columella*-fauna, have been identified. A special fauna is present in the intra-Saalian interglacial and is identified in the Erhingsdorf travertine (Fig. 10), in Neumark-Nord/Geisel valley and in the Langenbogen soil complex (MANIA & ALTERMANN 1970; MANIA 1990, 1993) (Fig. 9). Due to subcontinental-mediterranean conditions closed forests were not present, and dry woods and a park-like landscape with plenty of shrubs dominated during the optimum. *Helicigona banatica* and its associated species were not present in the mollusc fauna, and instead there occurs a Central European

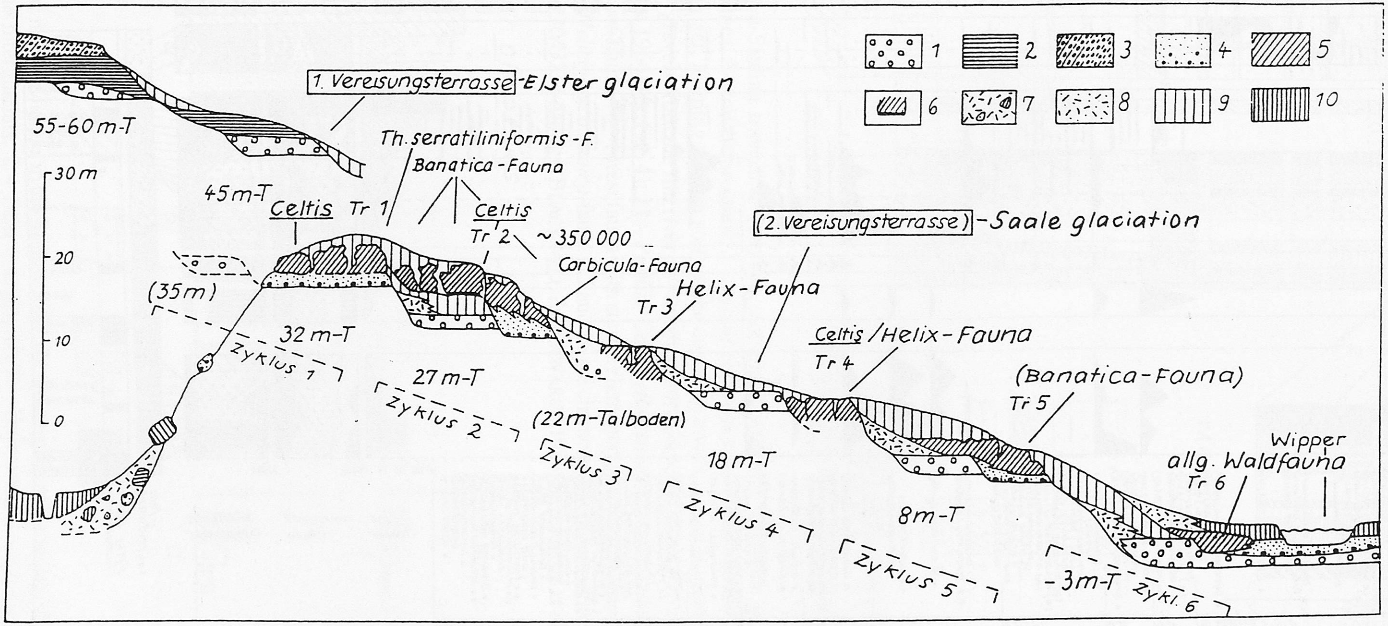

Fig. 8. Bilzingsleben (Thuringia). Sequence of Early and Middle Quaternary terrace-travertine cycles in the lower Wipper river valley and the development of the interglacial mollusc fauna. 1 – gravels; 2 – glaci-limnic deposits; 3 – ground moraine (boulder clay) of the Elster glaciation; 4 – interglacial fluviatile sediments (gravelly sands); 5 – travertine sequences; 6 – Lower Palaeolithic find horizon from the 'Steinrinne' near Bilzingsleben; 7 – solifluction and soil debris; 8 – humus colluvium; 9 – loess; 10 – 'Auelehm'; T – terrace; Tr – travertine sequence; Tr 1-3 – Middle Pleistocene interglacials; Tr 4 – Intra-Saalian interglacial; Tr 5 – Eem interglacial; Tr 6 – Holocene.

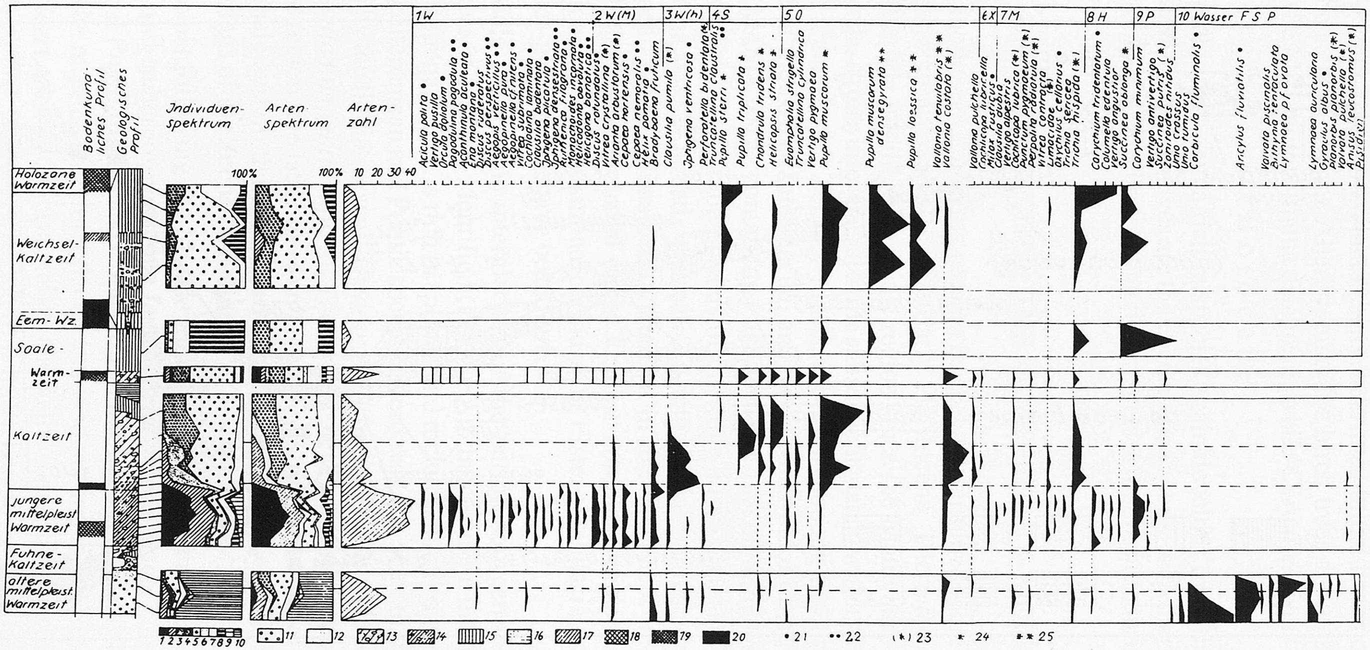

Fig. 9. Lengefeld-Bad Kösen (middle Saale river valley). Mollusc sequences of the Middle and Late Quaternary. 1-10 – ecological groups after LOŽEK 1964 (see Figure 4); 11 – gravels; 12 – fluviatile sand; 13 – limestone slope debris mixed with loess; 14 – loamy slope debris; 15 – loess; 16 – basin silt (glaci-limnic sediments of the Saale glaciation); 17 – brown soils; 18 – lessivés deriving from the Middle Pleistocene (Rudelsburger soil) and from the intra-Saalian interglacial (Langenbogen soil containing *Celtis*); 19 – Para-brown soil from the Eem interglacial (Naumburger soil); 20 – humus zone; 21 – common interglacial species; 22 – thermophile species; 23 – species also occurring in loess; 24 – loess species; 25 – characteristic species of the loess; W(h) – moist forest species; M – mesophile species; S – steppe species; O – common species of the open landscape; X – xerothermous species; H – hygrophile species; P – swamp species; F – river species; S – species of stagnant water; W – forest species.

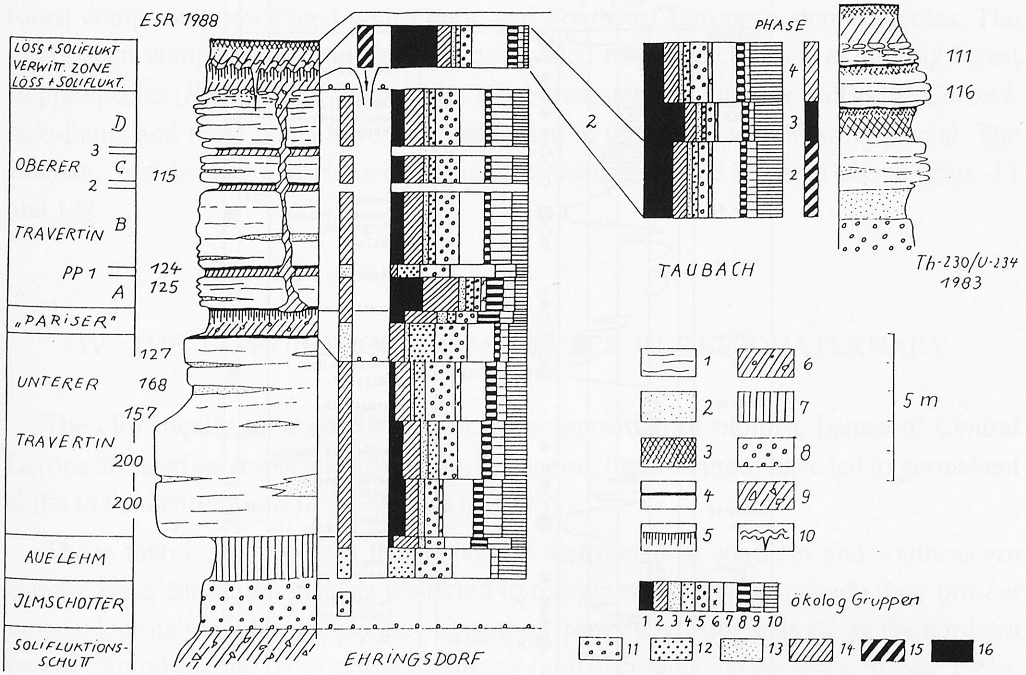

Fig. 10. Ehringsdorf. Intra-Saalian travertine complex, compared with the travertine of Taubach (Eem interglacial). 1 – travertines; 2 – travertine sands; 3 – humus colluvium; 4 – humus zones; 5 – rendzina and Tschernosem on the Pariser, loaming (brown soil) in the covering layers; 6 – colluvium originating from the slope; 7 – loess; 8 – gravels from the Ilm river; 9 – solifluction debris; 10 – frost structures. Ecological groups: 1-10 after LOŽEK 1964 (see Fig. 4); 11 – *Pupilla-Columella*-fauna; 12 – *Chrondrula tridens*-fauna; 13 – *Bradybaena fruticum*-fauna; 14 – forest fauna with steppe elements; 15 – *Pagodulina pagodula-Discus perspectivus*-fauna; 16 – *Helicigona banatica*-fauna (15 and 16 are characteristic phases of the Eem interglacial fauna). ESR datings, Th230/U234 datings (BLACKWELL & SCHWARCZ 1986; SCHWARCZ et al. 1988).

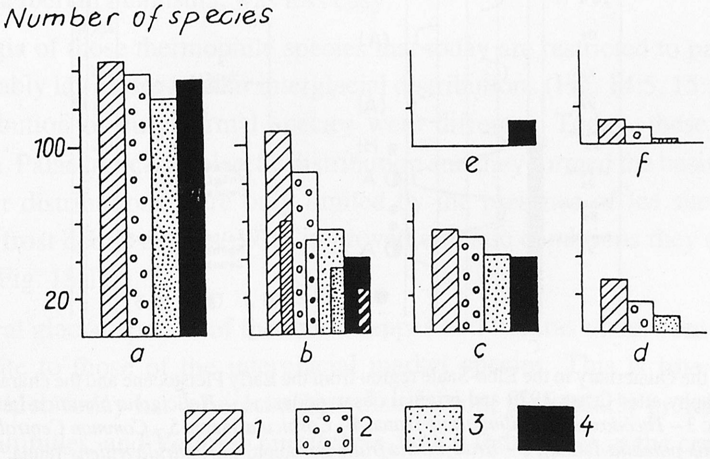

Fig. 11. Comparison of the mollusc faunas in the Middle and Late Quaternary of the middle Elbe-Saale region. 1 – Middle Pleistocene interglacials; 2 – Eem interglacial; 3 – Holocene; 4 – Recent; a – total no. of determined species; b – absolute and average frequency of species, density in habitat; c – proportion of forest fauna in habitat; d – proportion of exotic species to total no. of species; e – proportion of characteristic species of cultivated lands; f – proportion of exotic species to total no. of forest fauna species.

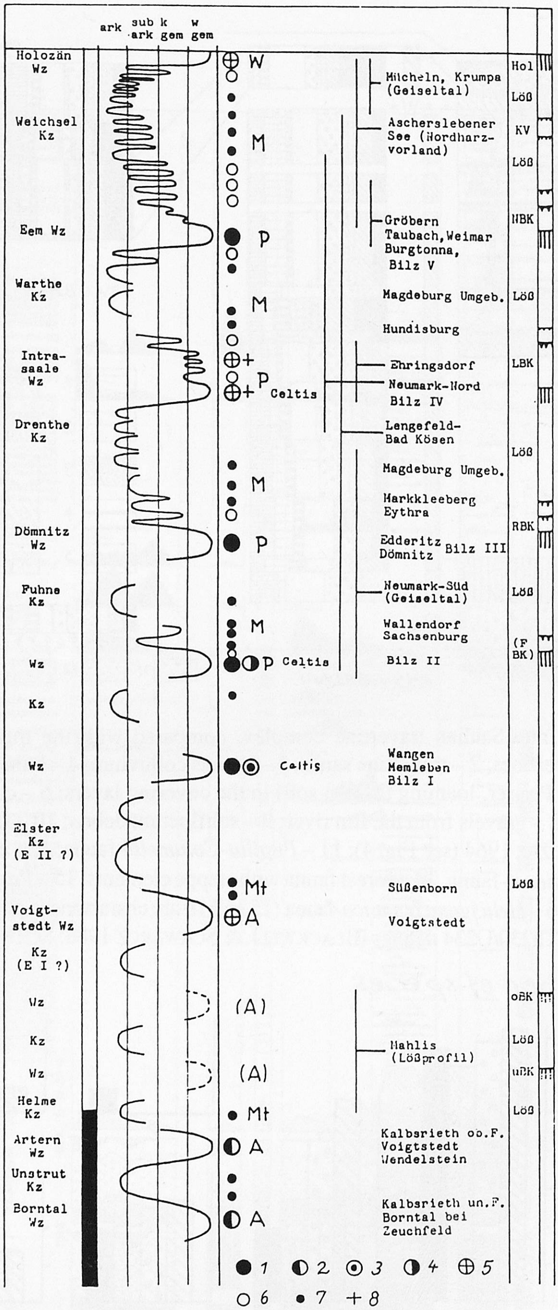

Fig. 12. Course of the Quaternary in the Elbe-Saale region from the Early Pleistocene and the characteristic mollusc faunas (stratigraphy after CEPEK 1979 and original observations). 1 – *Helicigona banatica*-fauna; 2 – *Fagotia acicularis*-fauna; 3 – *Theodoxus serratiliniformis*-fauna; 4 – *Corbicula*-fauna; 5 – *Common Central European forest* fauna (e. g., *Helix pomatia*-fauna); 6 – *Bradybaena fruticum*-fauna, *Chrondrula tridens*-fauna; 7 – *Pupilla*- and *Columella*-fauna; 8 – *Pontic steppe elements. Vertebrate fauna*: A – *Archidiskon*-fauna; Mt – *Mammuthus trogontherii*-fauna; P – *Elephas antiquus*-fauna; M – *Mammuthus*-fauna; W – Holocene forest fauna. Palaeo-soils: uBK, oBK – lower and upper soil complex of Mahlis (pseudo-gleys); FBK, RBK, LBK, NBK – Freyburg, Rudelsburg, Langenbogen and Naumburg soil complexes with lessivés and humus zones (Tschernosems, degraded Tschernosems); Kv – 'Kösener Verlehmungszone', Kösen loaming zone; Hol – Holocene soils. Climatic phases: arctic, subarctic, cold-temperate, warm-temperate; Wz – interglacial; Kz – glacial; unF – Kalbsrieth lower sequence; obF – Kalbsrieth upper sequence.

forest component associated with Pontic and Southeast European steppe species. The interglacial complex of Ehringsdorf is subdivided by a cooler phase exhibiting forest steppe species (*Bradybaena*-fauna) (Fig. 10). Forest steppe faunas, as well as the *Chrondrula*-fauna and loess fauna have been identified in the subsequent Warthe glacial. The Eemian, Weichselian and Holocene fauna has been described in detail above (Figs. 11 and 12).

IV. THE DISTRIBUTION OF MOLLUSCS IN THE QUATERNARY

The climatically induced changes in the composition of mollusc faunas of Central Europe affected each species differently. In general, these changes have led to permanent shifts in the distributions of the species (Fig. 13).

Those thermophile species that today are distributed in southern and southeastern Europe were during the glacials restricted to refugia which lay far outside their present ranges. During the interglacials they expanded from these refugia as far as the northern part of Central Europe. The northwesternmost limit of *Helicigona banatica, Mastus bielzi, Discus perspectivus* and *Pagodulina pagodula* lies in the northern Harz foreland and of *Aegopis verticillus* in the Rhine region (Fig. 14:1-4).

A similar distributional shift between northwest and southeast can be demonstrated for many other thermophile species of Central Europe (Fig. 14:5). This is above all due to the fact that geographic factors rendered a migration to and from southeastern Europe as far as Asia Minor relatively easy, whereas a shift of atlantic species to southwestern Europe, especially the Iberian Peninsula, was less easy.

The refugia of those thermophile species that today are restricted to parts of Central Europe probably lay closer to their interglacial distributions (Fig. 14:5, 15:2-4). Changes in the distribution of eurythermal species were different. Today, these have a large Eurosiberian, Palaearctic or Holarctic distribution and they formed the basis of the glacial faunas. Their distributions were only limited by the presence of ice sheets, mountain glaciers and frost debris deserts. With improved climatic conditions they expanded into these areas (Fig. 15:1).

The typical glacial species of the loess steppes and tundras underwent distributional shifts opposite to those of the interglacial marker species. This is true of *Columella columella*, which today has a boreo-alpine distribution, particularly in northern Eurasia and in high altitudes, and *Vallonia tenuilabris*, which today lives in the continental, cold winter mountain steppes of northern Central Asia. During the glacials, these species were distributed in the areas that were not ice-covered and during the interglacials they migrated back to their boreal, continental, circum-polar and high-alpine habitats along with their corresponding vegetational and climatic belts (Fig. 15:5-6).

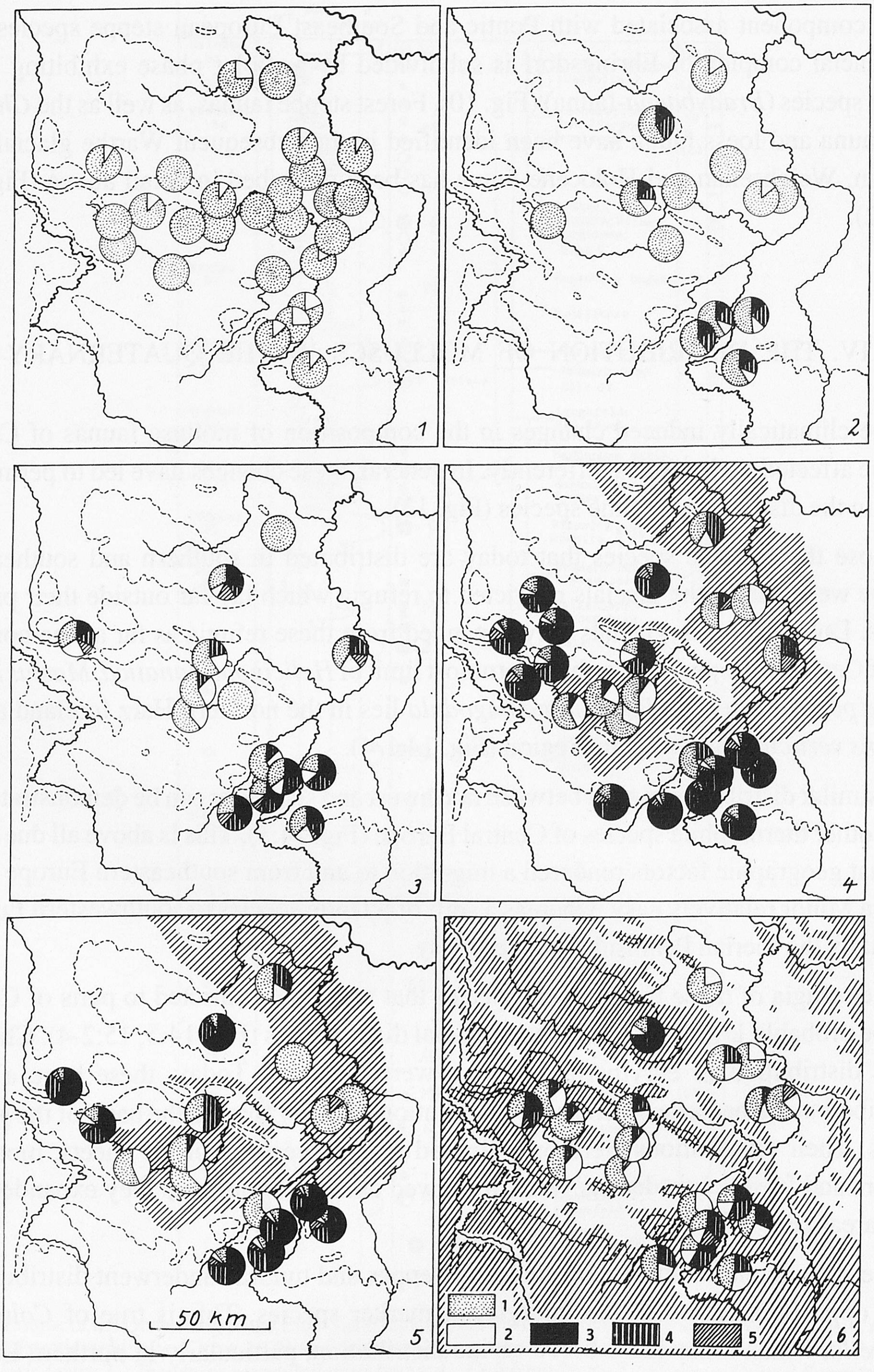

Fig. 13. The Weichselian and Holocene mollusc succession in a geographic framework (middle Elbe-Saale region). 1 – species of the open landscape; 2 – genuine steppe species; 3 – genuine forest species; 4 – forest steppe species; 5 – 'Auewald' species; Map 1 – Pleniglacial; 2 – Late Glacial (Alleröd); 3 – Boreal; 4 – Atlantikum (hatched: distribution of Tschernosem and degraded Tschernosem); 5 – Subboreal, with anthropogenic influence; 6 – Subrecent, landscape anthropogenically altered (hatched: distribution of the early historical forest).

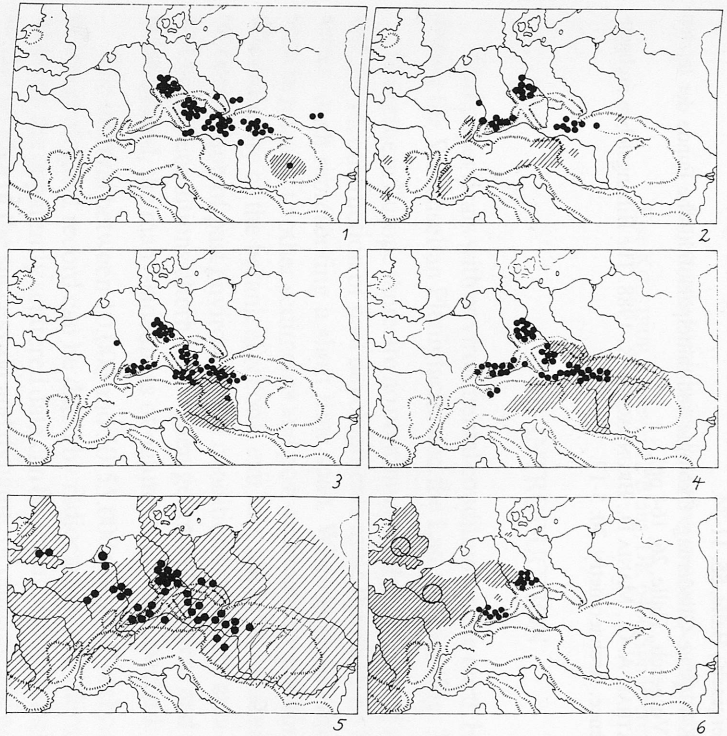

Fig. 14. Distribution of interglacial forest species in the Middle and Late Pleistocene of Central Europe. Hatched: recent areal extent; Dotted: Pleistocene sites; 1 – *Helicigona banatica* (south Carpathian); 2 – *Pagodulina pagodula* (alpine); 3 – *Aegopis verticillus* (east alpine); 4 – *Discus perspectivus* (Balkan-Carpathian-east alpine); 5 – *Cochlodina laminata* (European); 6 – *Azeka menkeana* (Western European-Atlantic).

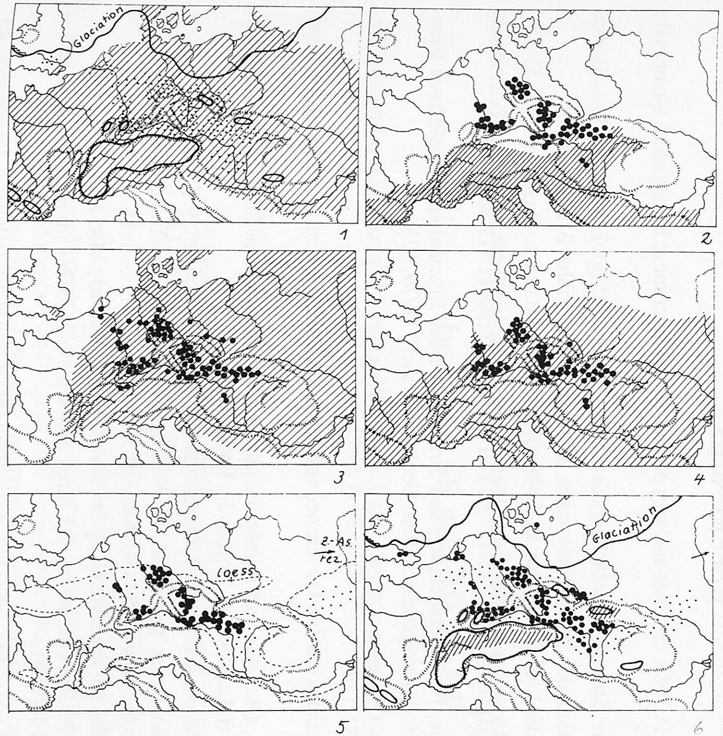

Fig. 15. Distribution of interglacial/glacial and glacial species in the Middle and Late Pleistocene of Central Europe. Hatched: recent areal extent; dotted: Pleistocene sites; 1 – *Succinea oblonga* (Eurosiberian), occurring in interglacials and glacials, typical loess species; 2 – *Pupilla triplicata* (meridional), appearing in sub-continental phases of the interglacials and in warmer phases of the glacials; 3 – *Bradybaena fruticum* (European), species of open forest and forest steppe, appearing during the interglacials and in warmer phases of the glacials; 4 – *Chrondrula tridens* (Ponto-meridional), steppe species appearing in sub-continental phases of the interglacials and in warmer phases of the glacials; 5 – *Vallonia tenuilabris* (north Central Asian), species of the glacial loess steppes, pleniglacial phases; 6 – *Columella columella* (boreo-alpine), species of the tundra, occurring during pleni- and late glacial phases.

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