A BIOSTRATIGRAPHYCAL BASE FOR DATING PALAEOLITHIC SITES

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Abstract: The age of Palaeolithic sites is often a matter of debate. Absolute dating is problematic for the older records with an age beyond the limit of radiocarbon dating (>50 ka) and hence, other methods have to be applied. A classical method is the use of biostratigraphical data, using knowledge of the changes in flora and fauna that are caused by the evolution, extinction and migration or dispersal of species. The Quaternary larger and smaller mammal records are subdivided into a number of biozones that form a biostratigraphical framework that is widely applied among Quaternary continental stratigraphers. The Quaternary biozonation, described in this paper, plays an important role in Palaeolithic research.

Keywords: Quaternary, Palaeolithic, mammalian biostratigraphy.

Introduction

One of the most debated questions in Palaeolithic research is the age; the age of a site, the age of the hominin dispersal into Europe or the extinction of, for instance, Neanderthals. There are different ways to solve questions about the age. Apart from physical methods such as ¹⁴C dating it is often also possible to make us of the accompanying mammal fossils. The presence of a certain species, its evolutionary stage, or (although restricted) the absence of a species, can be used for dating deposits- not absolute age-estimation but an indication of a relative age. In other words, dating in the sense of: older than, or younger than or about the same age. In other words to make use of the classical, widely used method biostratigraphy i.e. the science of dating and correlating rocks and sediments using animal and plant fossils. The fact that during the Quaternary the continental flora and fauna almost constantly changed means that biostratigraphy for dating provides a good basis for correlation of stratigraphic sequences or events at one locality to those at another locality e.g. for correlation between Eastern and Western Europe or between Europe and Asia. However, biostratigraphy is a relative dating method and must be independently calibrated with numerical dating methods before numerical ages can be assigned to biostratigraphic zones or events.

The rapid and continuous climatic changes during the Quaternary induced major changes in environmental conditions and available habitats. This is particularly the case in higher latitudes or in areas such as the western part of the North European plain, where the conditions are less diverse, in comparison to mountainous areas such as Central Italy or the Balkan Peninsula. The forest vegetation, which dominated the flora of North-western Europe during interglacial phases, disappeared during the cold stages and was replaced by the so-called Mammoth Steppe- treeless vegetation types which are "analogous but not necessarily identical in plant-composition to present-day tundra, steppe and alpine meadows" (Guthrie & Kolfschoten 2000). The climatic changes that characterise the Quaternary affected the composition of the flora and fauna in three major ways: a) the evolution of species; b) the extinction of species, and c) the dispersal or migration of species.

The evolution of species

The evolution of species is a natural phenomenon that is observed throughout geological history. Natural selection is the basis for evolution and it can take place if: a) there are more offspring than can grow to adulthood; b) there will be a struggle for survival among individuals; c) in sexually reproducing species, no two individuals are identical and variation is rampant; d) much of this variation is inheritable. From this, one can infer that in a world of stable populations where each individual must struggle to survive, those with the "best" characteristics will be more likely to survive, and those desirable traits will be passed to their offspring; and that these advantageous characteristics are inherited by following generations, becoming dominant among the population through time. This is natural selection that leads to the evolution of species that is observed in the Quaternary fossil record.

Many different species show evolutionary changes during the past 2.6 Ma. However, there are also species with a long

stratigraphical range that have hardly evolved or have not evolved at all. This applies to nearly all plant species but also to molluscs, insects, amphibians and reptiles. Among the Quaternary mammals there are species that do not show clear evolutionary changes such as the Chiroptera or bats. Another example is the Pygmy Shrew Sorex minutus, a species that only shows some fluctuations in size during the past 2.6 Ma. The Pygmy Shrew is widespread in Europe and lives under different climatic conditions. It inhabits areas with good ground cover although it is uncommon in woodland. The Pleistocene climatic and inherent environmental changes influenced the geographical distribution of the species but hardly affected the morphology of the dentition and the skeleton of the species. Therefore the fossil record of the species does not show a clear evolution. This applies also to a number of forest dwellers such as the Wood Mouse Apodemus sylvaticus, squirrels (e.g. the Red Squirrel Sciurus vulgaris) and glirids (e.g. the garden Dormouse Eliomys quercinus and the Common Dormouse Muscardinus avellanarius).

Fortunately, there are a large number of species that clearly have evolved even in such a relative short period as the Quaternary. The evolution is in some cases rather rapid, in others rather slow, and not all the evolutionary changes occur in the same period of time. Some species mainly evolved during the Early Pleistocene whereas others show clear changes during a later phase of the Quaternary. Remarkably many mammalian species e.g. mammoths, rhinoceros, and different voles, show comparable evolutionary changes. A general feature in the evolution is:

the increase in the height of the crown of the (pre)molars,
the increase of complexity of the enamel pattern of the (pre)molars.

Both features are related to the adaptation to more abrasive nutrition. The deterioration of climate led to the reduction of woodland vegetation and an expansion of a more open habitat with a dominance of grasses. For many herbivores this implies a change to more abrasive food.

Change in size is another feature that can be observed in a number of Quaternary species. Pleistocene wolverines of the genus *Gulo* show a remarkable increase in size during the Middle Pleistocene (Kolfschoten 2001). The same, though less extensive, can be seen in wolves (Bonifay 1971). Horses, on the other hand, increased in size during the early part of the Middle Pleistocene but reduced in size from the later part of the Middle Pleistocene onwards. Changes in size are generally not unidirectional and are therefore not a good feature for biostratigraphical purposes. Therefore changes in size can only be used in combination with other data.

Mammoth evolution

Among the species that show clear evolution during the Quaternary and are, hence, biostratigraphically relevant, are the mammoths belonging to the lineage *Mammuthus rumanus* - *Mammuthus meridionalis* - *Mammuthus trogontherii* - *Mammuthus primigenius*. Mammoth evolution began in Africa and during the late Pliocene mammoths migrated to Eurasia.

The late Pliocene and Pleistocene fossil record indicates that the Eurasian mammoth underwent very significant changes: a shortening and heightening of the cranium and mandible, an increase in the relative height of the molars, an increase in the number of plates and thinning of the dental enamel (Lister *et al.* 2005). The earliest representatives of the European mammoth *Mammuthus rumanus* from the interval 3.5-2.5 Ma are characterised by upper M³ molars with 8-10 plates, a hypsodonty index (i.e. the height of the crow divided by the width x 100) of about 120 and an average thickness of the enamel of about 3.8 mm. The upper M³ of the most advanced representative of the mammoth lineage *Mammuthus primigenius* has 20-28 plates, an average hypsodonty index of about 200 and enamel with a thickness that ranges between 1.0 and 2.5 mm with an mean of about 1.6 mm.

Previously it was assumed that the transformation within the Mammuthus rumanus - Mammuthus meridionalis -Mammuthus trogontherii - Mammuthus primigenius lineage was gradual and more or less simultaneous across the species' range. However, recent investigations of the geographical variation across the whole of northern Eurasia indicated a more complex model (Lister et al. 2005). The transition between Mammuthus rumanus and Mammuthus meridionalis is still poorly known; the number of late Pliocene fossil remains is too limited. The Early - and early Middle Pleistocene Mammuthus meridionalis is better known. The species was widely dispersed in Eurasia and migrated to America during the Early Pleistocene. The European fossil record indicates that the species hardly evolved despite the fact that it occurred in the region for almost 2 Ma. In eastern Asia, probably in China, however, Mammuthus meridionalis evolved into Mammuthuis trogontherii in the interval 2.0-2.5 Ma. Mammuthus trogontherii expanded its original range and spread to NE Siberia by 1.2 Ma and towards Europe around 1 Ma. In NE Siberia Mammuthus trogontherii began a transformation into Mammuthus primigenius as early as 700 ka. The European population of Mammuthus trogontherii also hardly evolved and only shows a reduction of size in the interval between 1 Ma and 200 ka. Mammuthus primigenius, with its origin in NE Siberia, invaded Europe during the late Middle Pleistocene about 200 ka ago.

The evolution of voles

Rodents are well represented in the present-day fauna; nearly 40% of all living mammalian species are rodents. They represent a huge variety of animals including for example beavers, squirrels, marmots, hamsters, rats, mice, voles, lemmings, dormice and porcupines. Voles are a rather recent branch of diminutive grazers in rodent evolutionary history. They arose from the hamster lineage during the late Pliocene and have been very successful in Quaternary, with about 100 extant species. The evolution of the voles shows radiations leading to a number of different lineages. All these lineages show in principle the same type of evolution.

The first change that can be observed is an increase in height of the crown. The brachiodont molars developed into hypsodont molars with high enamel-free areas or dentine tracts. The increase of crown height led to a delay in the formation of

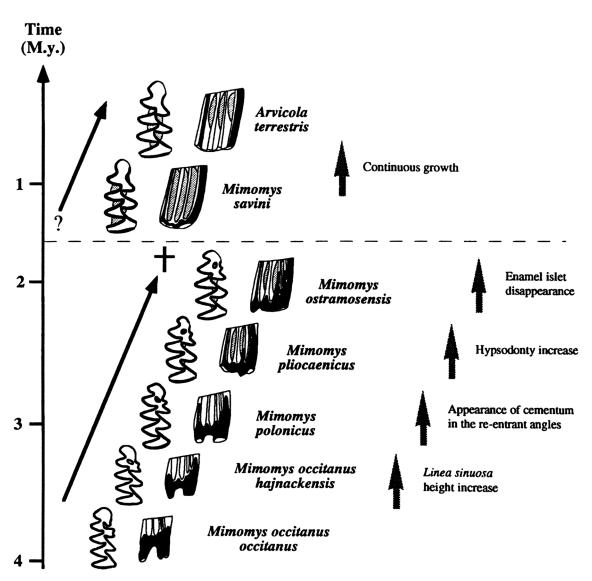


Figure 1. Phyletic gradualism in the *Mimomys occitanus – M. ostramosensis* lineage, showing the major evolutionary trends: increased hypsodonty related to a higher linea sinuosa; appearance of cementum in the re-entrant angles, and disappearance of the enamel islet. Continuous only occurs between *Mimomys savini* and Arvicola terrestris *cantiana*. From: Neraudeau *et al.* 1995.

roots, an evolutionary trend that finally results in voles that have molars without roots (fig. 1). A second feature that can be observed in the evolution of voles is the development of crown cement in a number of the lineages, crown cement that occurs in the re-entrant angles of the hypsodont molars. In addition, different lineages show an increase in the length of the posterior upper molar (M^3) and the anterior lower molar (M_1), an increase that parallels the increase of complexity of the posterior (M^3) or anterior (M_1) lobe of both molars.

Another general feature that can be observed in different lineages is change in the differentiation of the thickness of the enamel. The occlusal surface of the molars of voles shows a number of dentine fields covered with enamel at the outer side. The anterior enamel edge of the salient angles of the lower molars is concave and the posterior convex. The concave edges first occlude during the longitudinal movement of mastication; they are the so-called leading edges. The convex edges are the trailing edges. In a large number of living species the enamel of the trailing edges is much thinner than that of the leading edges. The opposite can be observed in many more primitive species. The transition from having trailing edges that are thicker to one in which the leading edges are relatively thicker is called the evolution in the differentiation in the thickness of the enamel.

The evolutionary changes described above did not occur simultaneously in the different lineages or within the lineages in the same region. The evolution of voles is a complicated story, studied by a large number of palaeontologists. Because of the geographically wide range of the species, their often dominant occurrence in the Quaternary fossil record and the extremely quick evolution that can be observed in a number of lineages, voles are extremely important for Quaternary continental stratigraphy. In particular for Eurasia the *Mimomys savini - Arvicola terrestris* lineage is important for the subdivision of the Middle and Late Pleistocene. *Mimomys savini*, a vole with rooted molars, is the ancestor of the living

water vole *Arvicola terrestris*. The species occurred in European faunas during the late Early and the early Middle Pleistocene. The transition of populations of water voles with rooted molars to populations with more hypsodont, unrooted molars referred to the genus *Arvicola* (fig. 2), took place during the first half of the Middle Pleistocene. This transition seems to be well established since populations with a small percentage of rooted molars are known from several localities in Germany, Italy, the Czech Republic and Russia. The genus *Arvicola* clearly shows a gradual evolution in the differentiation in the thickness of the enamel since its appearance during the early Middle Pleistocene. Enamel differentiation appears to be an important marker to indicate the evolutionary stage of *Arvicola* and hence the relative age of the fossil record.

The Microtus (Allophaiomys) - Microtus (Microtus) lineage is important for the biozonation of the later part of the Early Pleistocene. The molars of that well-known lineage already lack roots. They first of all show changes in the differentiation of the thickness of the enamel and later, near the end of the Early Pleistocene, there was a huge radiation that led to a number of different lineages such as the Microtus (Stenocranius) hintoni – M. (St.) gregaloides - M. (St.) gregalis lineage. For the early part of the Quaternary one of the important lineages is the Mimomys occitanus - Mimomys hajnackensis – Mimomys polonicus – Mimomys pliocaenicus – Mimomys ostramosensis lineage (Neraudeau et al. 1995).

Extinction

The extinction of species is also biostratigraphically important. Several examples demonstrate the global or local extinction of species. Well known are the Late Pleistocene – early Holocene extinctions of mainly larger mammals that can be observed in almost every continent. In Eurasia, species such as *Ursus spelaeus, Mammuthus primigenius, Coelodonta antiquitatis, Equus hydruntinus* and *Megaloceros giganteus* disappeared at the end of the Late Pleistocene or the beginning of the Holocene. Extinction in the smaller mammal fauna of Eurasia can be observed in Middle Pleistocene faunas. Species such as *Drepanosorex savini, Talpa minor* and *Trogontherium cuvieri* are relicts from the Early Pleistocene that became extinct during the Middle Pleistocene.

Extinction is often preceded by a strong reduction of the geographical range of a species and a retreat to a refugial area. The Late Pleistocene European rhinoceros species *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus* show a progressive southward contraction of their geographical range preceding their extinction before the Late Glacial Maximum (Stuart 1993; Stuart *et al.* 2004; Stuart 2005).

Migration and dispersal of species

The migration of mammal species is certainly the major factor in the changes of composition of the Quaternary faunas in a specific region. These migrations are primarily caused by the alternation of the available habitats due to the changes

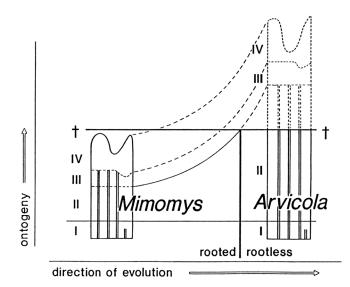


Figure 2. Model of the evolutionary transition from rooted molars in *Mimomys* to unrooted molars in *Arvicola* in terms of the heterochronous shift of ontogenetic phases I-IV Koenigswald W. von & Kolfschoten T. van (1996).

in climate and environment (Kolfschoten 1995). Eurasian cold stage faunas from the last and penultimate glacial period are characteristic and rather well known; species such as *Dicrostonyx gulielmi*, *Lemmus lemmus*, *Mammuthus primigenius*, *Coelodonta antiquitatis* and *Rangifer tarandus* expanded their range southwards and occur together with species which prefer a more steppic environment such as ground squirrels (*Spermophilus undulates*) and hamsters (*Cricetulus migratorius* and *Cricetus cricetus*) that expanded their geographical range north- and westwards.

A rise in temperature led to more distinct steppic conditions in the lower latitudes. These steppic conditions resulted in the increase of the relative number of steppe elements. Lemmings and other cold stage indicators withdrew northwards and species such as the steppe lemming *Lagurus lagurus* migrated westward and invaded Northwestern Europe. A rise in temperature was followed in certain areas such as the North European plain by an increase of oceanic influences. That resulted in a climate, which induced a re-establishment of forests with thermophilous broad-leaved and coniferous trees and the return of forest dwellers such as glirids (*Eliomys quercinus, Muscardinus avellanarius*), wild boar (*Sus scrofa*), and cervids (*Cervus (Dama) dama* and *Capreolus capreolus*) (Kolfschoten 1992).

This general picture of alternating species, more or less the same species that "come and go", is applicable to the late Middle and Late Pleistocene and may also be applicable to the earlier cold stages. However, one can distinguish a migration of species that is more or less independent of, and not only the result of climatic change. The contemporary migration of a number of species characterizes the so-called major dispersal events. In addition there are also incidental immigrations of single species. The woolly rhinoceros *Coelodonta antiquitatis*, for example, had its origin in Asia and invaded Europe during the Middle Pleistocene, together with other cold stage

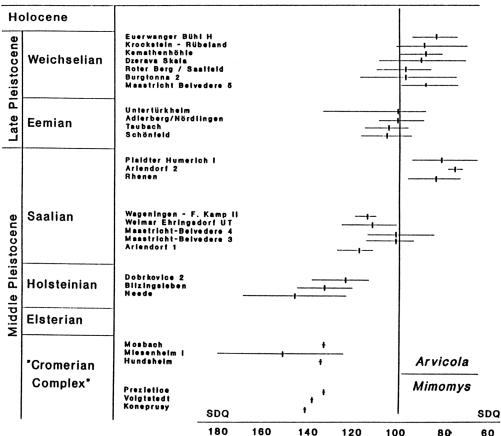
faunal elements. Since its appearance, the species became a permanent element of the European cold stage faunas. The straight-tusk elephant *Elephas (P.) antiquus* invaded North Western Europe for the first time during the early Middle Pleistocene and occurred during every subsequent interglacial period until the Holocene. *Hippopotamus amphibius* also invaded Europe during the early Middle Pleistocene, most probably during the same warm phase in which *Elephas (P.) antiquus* appeared. However, *Hippopotamus* did not return until the Late Pleistocene (Eemian), after its withdrawal at the end of the early Middle Pleistocene.

Another aspect is the migration and dispersal at subspecies level: the migration and dispersal of populations to areas which were inhabited by the same species. Tracing these migrations demands significant morphological differences between the "new" population and the "old" one, as is the case between the Late Saalian and Eemian *Arvicola terrestris* populations of Northwestern Europe. The gradual change in differentiation of the enamel (fig. 3) was interrupted and showed an important fluctuation at the Saalian-Eemian transition. An explanation of this feature is the invasion of less derived populations. *Arvicola terrestris* disappeared from the northern areas which were covered by inland ice and along the edge of the inland ice shield during the Late Saalian. The

of less advanced populations which survived in areas located more to the south- (east). The presence of more primitive features in southern populations during the Pleistocene is very plausible since it has been demonstrated that the living *Arvicola* populations also show a strong morphological cline in the development of the enamel differentiation. In this aspect the southern populations are much more primitive than the northern populations (Kolfschoten 1992).

Biostratigraphical subdivision of the Quaternary

The changes in the Quaternary mammalian fossil record described above form the basis for a biostratigraphical subdivision of the Quaternary (fig. 4). The extensive and well investigated Quaternary mammalian fossil record allows us to divide the record into clusters and to establish a biostratigraphical subdivision or zonation of the Quaternary period. Each biostratigraphical unit or biozone is characterised by a distinct faunal assemblage. A number of mammal biozonations have been established by different authors. However, many of these zonations are not defined in accordance with the official guide to stratigraphic nomenclature, and the terminology used by some authors is confusing. Furthermore, the application of several biozonations is geographically restricted. Two different biozonations are widely used in Quaternary biostratigraphy: the first one is based on the changes in the Eurasian larger



Populations from Central and Northwestern Europe

Figure 3. The range and mean of the enamel thickness quotient (SDQ) of a number of Middle and Late Pleistocene populations of *Arvicola* from Central and Northwestern Europe. From: Koenigswald W. von & Kolfschoten T. van (1996).

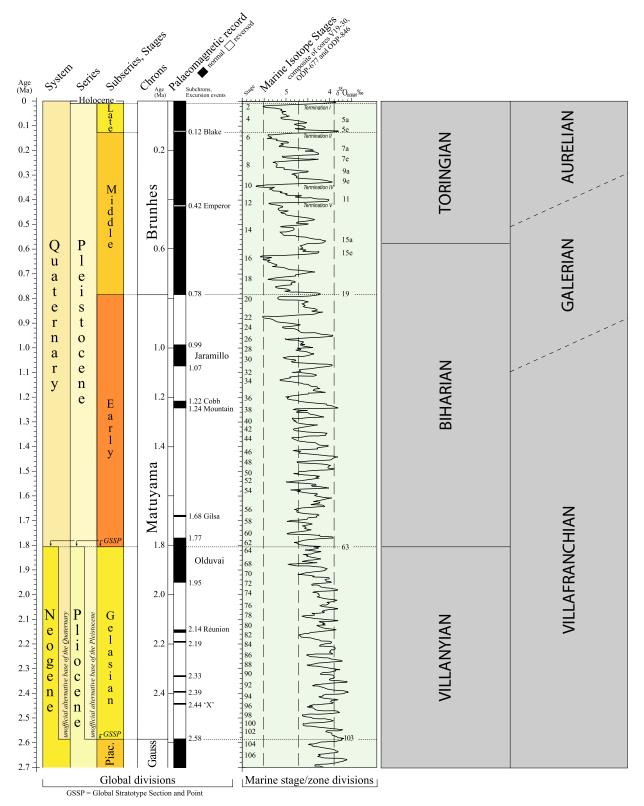


Figure 4. A correlation of chronostratigraphical subdivisions of geological time, spanning the last 2.7 million years with the applied biozonations.

mammal faunal community and the second one is based on the evolution in the smaller mammal assemblages. The coexistence of two different biozonations, one for the larger and one for the smaller mammalian record, is purely historical and is the result of specialisation within the community of mammalian palaeontologists.

Larger mammal biozonation

The widely adapted larger mammal biozonation is mainly based on the Italian fossil record and was established by Azzaroli and co-workers (Azzaroli *et al.* 1988). The Quaternary larger mammal faunas are divided into three main units: Villafranchian faunas, Galerian faunas and Aurelian faunas. The term Aurelian, indicating "modern mammal association" whereas the Galerian faunas are "becoming modern in appearance" (Sardella et al. 1998) is not often used. The Villafranchian is divided into an early, middle and late Villafranchian with the transitions marked by major events. The "Leptobos" event, indicating the appearance of species of the genus Leptobos in the Italian mammal faunas, marks the beginning of the Villafranchian. The first occurrence of Mammuthus meridionalis and Equus, the socalled elephant-Equus event, marks the transition of the early to middle Villafranchian and the appearance of Canis etruscus, the "Wolf" event, the middle to late Villafranchian transition. The "end-Villafranchian" dispersal event was originally described as a total faunal turnover, with massive extinctions and replacements marking the transition to the Galerian. However, it appears that the original definition of the boundary between the Villafranchian and the Galerian is unsatisfactory since the duration of the total faunal turnover took altogether about 0.5 Ma.

The Villafranchian starts well before the Quaternary with the oldest Villafranchian faunas having an age of about 3.3 Ma. The elephant-*Equus* event has an age of 2.8 - 2.9 Ma and the "Wolf" event an age of 2.2 - 2.3 Ma. The stratigraphical position and age of the Villafranchian – Galerian transition is still problematic. Some authors put the transition at an age of about 1.1 - 1.2 Ma, whereas others put the beginning of the Galerian close to the Brunhes/Matuyama boundary with an age of 0.78 Ma.

Smaller mammal biozonation

The smaller mammal biozonation that is widely used as a standard for the Early and Middle Pleistocene of Eurasia, is mainly a modified version of the Hungarian biozonation established by Kretzoi (1965). In this subdivision, three biozones are recognized for the Pleistocene period in the literature often erroneously referred to as "stages": Villányian, Biharian and Toringian. The Villányian faunas can be recognized by the dominance of voles of the genus Mimomys and the absence (or the occurrence in only a very low percentage) of voles of the genus Microtus. The Biharian faunas are characterised by a dominance of Microtus co-occurring with Mimomys. The Biharian biozone is also divided into two substages: Lower and Upper Biharian. The disappearance of the subgenus Microtus (Allophaiomys) marks the transition from the Lower to the Upper Biharian. The Toringian biozone can be recognized by the Arvicola - Microtus assemblages. Mimomys is missing in Toringian faunas.

The numerical ages of boundaries of the biozones and hence, the age ranges of the biozones is still a matter of debate. The Villányian started well before the beginning of the Quaternary at about 3.6 - 3.7 Ma ago. One of the most important abrupt changes in the smaller mammalian fauna took place during the transition of the Villányian to the Biharian biozone. Until recently the major faunal "turnover", in particular the reconstruction of the vole community, and the expansion of rootless voles characterised by the appearance of *Microtus (Allophaiomys)* (a group of voles, easily recognisable and well

represented in the fossil record of the Northern Hemisphere), was dated just after the Olduvai Event. This transition formed one of the strong 'continental' arguments to put the Plio-Pleistocene boundary near the top of the Olduvai. New data, however, indicate that the age of this faunal "turnover" is questionable. Tesakov (2004) argues that this faunal 'turnover' took place long before the Olduvai Event and he dates the transition between 2.1 and 2.2 Ma. The transition between the Lower and the Upper Biharian is rather well dated with most authors agreeing that Microtus (Allophaiomys) disappeared during or just before the Jaramillo palaeomagnetic Subchron. The Biharian – Toringian transition is studied in great detail because the age of this transition is very important for dating the earliest Palaeolithic sites in Europe. The first occurrence of the genus Arvicola, marks the beginning of the Toringian, dates around 0.5 Ma ago (Kolfschoten 1992; Koenigswald and Kolfschoten 1996).

Additional biozonations

The biozonations described above are mainly used by Eurasian continental biostratigraphers, often next to regional zonations applicable in the area of investigation. There is no elaborated widely applicable biozonation of the continental floral record despite the fact that the impact of Quaternary climate changes on the floral composition in most regions is huge and the stratigraphical range of many species is very fragmented and/or restricted. Floral species hardly show any evolution during the Quaternary and also the number of extinctions is restricted. On the other hand, they are very valuable for identifying climate changes through changes in species composition.

In the marine realm there are a number of micropalaeontological zonations (Gibbard and Kolfschoten 2004; Lourens *et al.* 2004). Biozonations have been established for the fossil record of different microfossils: planktonic foraminifera, calcareous nannofossils, diatoms, radiolaria and dinoflagellates. The planktonic foraminifera biozonation and the calcareous nannoplankton biozonation are the major tools for subdividing marine sediments. The application of the other fossils is generally restricted to areas with specific conditions.

The application in Palaeolithic research

A biozonation dividing the Quaternary in periods of 0.5 Ma or even more is of restricted utility in Palaeolithic research. This is in particular the case for early Quaternary deposits. The use of biostratigraphy is less relevant in younger deposits because the biozonation is too coarse for the detailed information one is looking for. The stratigraphical setting of Middle and Late Pleistocene strata in many cases allows correlation to regional stages such as the widely adapted North West European Stages. Furthermore, there is a tendency to use the Marine Isotope Stages as a timescale for continental finds, in spite of the very restricted number of direct correlations between continental and marine zonations.

Using mammalian biozonation to indicate the age of Palaeolithic sites results only in very rough indication.

The statement that the Palaeolithic remains from Dmanisi (Georgia) have a Villafranchian age based on the larger mammal remains suggests there we are dealing with very old finds. The fact is that the mammalian biozonation of the Quaternary is too coarse for Palaeolithic research. To get more detailed information, one should use our knowledge of the fauna evolution within the different zones. The late Biharian faunas can put in a biostratigraphical order using our knowledge about the evolutionary tread in the *Microtus (Stenocranius) hintoni/Microtus (Stenocranius) gregaloides/ Microtus (Stenocranius) gregalis* lineage (Kolfschoten & Markova 2005).

The Biharian – Toringian transition plays a role in the "short chronology" debate. Roebroeks and van Kolfschoten (1994) launched the short chronology hypothesis and argued that all the undisputed Palaeolithic sites in Europe have a Toringian age, i.e. the related mammalian faunas are characterised by the occurrence of voles of the genus *Arvicola* and the absence of *Mimomys savini*. Shortly after, Palaeolithic remains (including human remains) were discovered in a "*Mimomys*" context in Atapuerca (Spain). The occurrence of *Mimomys*

and representatives of the *Microtus (microtus)* guild indicate a late Biharian age. The number of Biharian Palaeolithic sites is however, restricted.

To put the European Toringian Palaeolithic in the right stratigraphical order The evolutionary changes in the genus Arvicola during the past 500 Ka, observed in many different areas in Europe and by different authors, is used. The Arvicola molars from Maastricht-Belvédère and Schöningen 13-11-4 differ in the relative thickness of the enamel and hence differ in ages. The Arvicola molars indicate that the remains from Schöningen 13-11-4 are older than the main Maastricht-Belvédère fauna (M-B 4). The evolution level of the Arvicola molars is one of the most important age indicator. Other factors eg. the occurrence or absence of species (smaller as well as larger mammal species) are taken into account to determine the (relative) age of a site. Palaeolithic researchers in Europa use a more detailed "biozonation". There is no problem to apply this detailed "biozonation" in a geographically restricted area. For long distance correlation of sites one should be aware of the fact that geographical gradients might play an important role.

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