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Original article

Late Pleistocene small mammals from the Wannenköpfe volcanoes (Neuwied Basin, western Germany) with remarks on the stratigraphic range of *Arvicola terrestris*

Petits mammifères du Pléistocène supérieur provenant des volcans de Wannenköpfe (bassin de Neuwied, Allemagne de l'Ouest) et remarques sur l'échelle stratigraphique de *Arvicola terrestris*

Позднеплейстоценовые мелкие млекопитающие вулканического района Ванненкопфе (Нойвидский бассейн, западная Германия) с обсуждением стратиграфического диапазона *Arvicola terrestris*

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Abstract

Redeposited loess sediments from a Pleistocene crater filling in the Neuwied Basin (western Germany) yielded a small mammal fauna mainly composed of arvicoline rodents. The occurrence of rare faunal elements such as *Sorex minutissimus*, *Sicista subtilis*, and a species of *Microtus (Terricola)* is remarkable. Based on the evolutionary level of *Arvicola terrestris*, the biostratigraphic age of the fossiliferous horizon is transitional between late Eemian and early Weichselian. This conclusion is partly supported by the generalized ecological requirements of a few dominant rodent species. The fauna contributes to the knowledge of this time period, which is poorly documented in western Germany. A new character of the m1 is proposed for the discrimination of *Sicista betulina* and *S. subtilis*. To avoid further confusion in the specific assignment of transitional *Arvicola* specimens from the late Middle Pleistocene to early Late Pleistocene, we propose the formal taxonomic boundary between chronospecies *A. mosbachensis* and *A. terrestris* to be shifted from SDQ value 100 to SDQ value 120.

Résumé

Les sédiments redéposés de lœss provenant du remplissage d'un cratère pléistocène dans le bassin de Neuwied (Allemagne de l'Ouest) ont livré une faune de petits mammifères principalement composée d'arvicolinés. La présence d'éléments rares tels que *Sorex minutissimus, Sicista subtilis* et une espèce de *Microtus (Terricola)* est remarquable. Basé sur le niveau d'évolution d'*Arvicola terrestris*, l'âge biostratigraphique de l'horizon fossilifère est transitoire entre le Eemien supérieur et le Weichselien inférieur. Cela est soutenu par la dominance de quelques espèces qui ont des exigences écologiques généralisées. Cette faune contribue à la connaissance de cette période de temps qui est mal documentée en Allemagne de l'Ouest. Pour la distinction des deux espèces de *Sicista, S. betulina* et *S. subtilis*, on propose un nouveau caractère dentaire de la première molaire inférieure. Pour éviter davantage de confusion dans l'attribution spécifique des spécimens d'*Arvicola* du Pléistocène moyen supérieur au Pléistocène supérieur inférieur, nous proposons de déplacer la frontière taxonomique formelle entre les chrono-espèces *A. mosbachensis* et *A. terrestris* de la valeur 100 de SDQ à la valeur 120 de SDQ.

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Резюме

Из перемытых лессовидных отложений, заполняющих кратер плейстоценового маара Ваннен в Нойвидском бассейне на западе Германии, получена фауна мелких млекопитающих, представленная в основном полевками. Интересно отметить присутствие таких редких видов как *Sorex minutissimus*, *Sicista subtilis* и *Microtus (Terricola)*. На основании эволюционного уровня *Arvicola terrestris* костеносный уровень датируется в интервале от позднего Эема до ранней Вислы. Этот вывод подтверждается преобладанием немногих видов с широкими экологическими требованиями. Новая фауна характеризует временной интервал, слабо предсЁ тавленный на западе Германии. Для диагностики двух видов мышовок, *Sicista betulina* и *S. subtilis* предлагается использовать новый признак первого нижнего коренного. Для преодоления запутанной ситуации с видовой диагностикиой переходных форм водяной полевки Arvicola конца среднего – начала позднего плейстоцена, предлагается принять за границу хронотаксонов *A. mosbachensis* и *A. terrestris* среднее значение коэффициента дифференциации эмали (SDQ) 120, вместо 100.

Keywords: Insectivores; Rodents; Enamel thickness quotient (SDQ value); Biostratigraphy; Late Eemian; Early Weichselian

Mots clés : Insectivores ; Rongeurs ; Quotient d'épaisseur de l'émail (valeur SDQ) ; Biostratigraphie ; Eemien supérieur ; Weichselien inférieur

Ключевые слова: насекомоядные; грызуны; коэффициент дифференциации эмали (SDQ); биостратиграфия; поздний эем (микулино); ранняя висла (валдай)

1. Introduction

Small mammal faunas from the Eemian/Weichselian transition, a time of important climatic change, are poorly known in Central Europe. In western Germany, the Neuwied Basin region of the East Eifel Volcanic Field with its numerous volcanoes yielded a new faunal association from that time interval.

Intensive mining of the alkalibasaltic lava since the 1970s produced large exposures in the Neuwied Basin suitable for interdisciplinary investigations. Many archaeological excavations in the Pleistocene fillings in the central crater depressions have been made since the 1980s (Bosinski et al., 1986, 1995). Besides stone tools and artefacts almost all archaeological sites yielded bones and teeth of large (e.g. Turner, 1991), as well as small mammals (Kolfschoten and Roth, 1993). The most recent and very spectacular find is a cranial calotte of a "late" Pre-Neanderthal from the early phase of the Saalian glaciation discovered at the Wannenköpfe volcanoes (Berg et al., 2000).

The Wannenköpfe volcanoes (topographical map 1:25,000 of Bassenheim no. 5610) belong to the eastern part of the NW-SE extending Wannen scoria complex, which also include the volcanoes Langenberg and Michelberg (Fig. 1). The Wannenköpfe volcanoes can be subdivided into an older western and a younger eastern field (Schmincke et al., 1990). According to 40Ar/39Ar dating, the formation of the Wannenköpfe volcanoes took place in the late Middle Pleistocene under interstadial climate conditions, most probably within oxygen isotope stage 7a or 7b (Frechen, 1995). The last eruption of the East Eifel Volcanic Field was that of the lake Laacher See, determined by a varve record from the lake Meerfelder Maar (Litt et al., 2003). This is in agreement with single crystal Ar/Ar dating (Boogard, 1995) of about 12,900 years cal BP. The Laacher See Tephra (LST) is an important stratigraphic marker horizon in Central Europe.

The Wannenköpfe volcanoes with their central crater depressions, as well as intracone depressions served as traps for aeolian sediments. The fossil-bearing horizon is located to the East of a quarry drive way at the southeastern end of the western Wannenköpfe quarry (detail of Fig. 1; 50° 21′ 50″N/07° 24′ 39″E). Scattered small mammal bones together with gastropods were enriched in a zone about 2.20–2.40 m below the Laacher See Tephra (Fig. 2). Pellet-sized bone concentrations were observed in a few places.

The profile (Fig. 2) is made up of debris-flow deposits. They consist of three zones of redeposited, compact loess without sedimentary structures. Scoria fragments are intercalated in lenses or layers. Except for the LST no in situ sediments are present. The lowest redeposited loess shows frequent pyroxene crystals. Irregularly, rounded patches of slightly darker sediment between 6 and 13 cm in height and 9–16 cm in width are occasionally encountered. They probably represent the sediment fill of a fossil burrow system. Judging from the gallery diameters, the burrows were made by a rodent in size between a small ground squirrel (*Tamias*) and a hamster (*Cricetus*) (Görner and Hackethal, 1988). At about 50 cm from the ground follows an approximately 20 cm thick layer enriched with scoria fragments of different grain size with no evident sorting. The second redeposited loess above is about 80 cm thick and is characterized by numerous scoria fragments, clay clasts, as well as gastropod and vertebrate remains. The fauna described here was discovered by I. Stritzke in 1993 when mapping for her master's thesis (Stritzke, 1994). Above this loess is an approximately 70 cm thick multilayered zone with frequent scoria fragments. Layers with larger fragments are found at the base, while smaller fragments dominate the top. The layers might originate from four or five different short-time events (e.g. heavy rains or winter storms). The third redeposited loess on top is about 130 cm thick. Only some smaller scoria fragments are visible. At some places the uppermost part of this unit is slightly darker, which could represent a poorly developed Allerød soil. The profile is covered by 30 cm of LST.

Only a few publications deal with small mammals from the Neuwied basin. They document faunas from the early Middle Pleistocene to almost the Pleistocene/Holocene boundary. Kolfschoten and Turner (1996) described the oldest small mammal material from the Kärlich B–F sites. They also worked on the younger sites of Miesenheim 1 and Kärlich G, which represent the Middle Pleistocene (Kolfschoten, 1990;

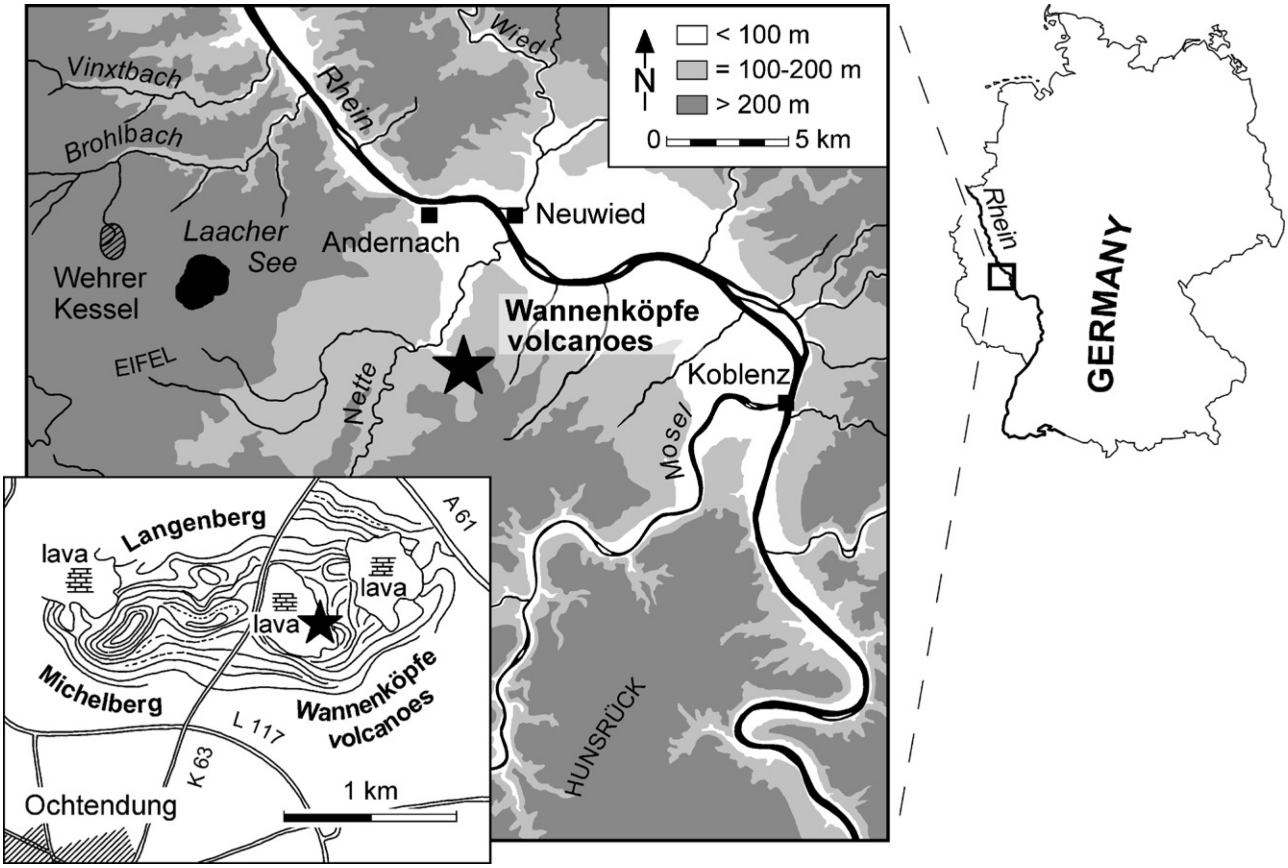

Fig. 1. Map showing the location of the Wannenköpfe volcanoes (star) in the Neuwied Basin west of the town of Koblenz. The star in the detail indicates more precisely the fossil site within the lava quarry.

Fig. 1. Carte de localisation des volcans de Wannenköpfe (étoile) dans le bassin de Neuwied à l'ouest de la ville de Koblenz. L'étoile dans la carte détaillée indique plus précisément le gisement fossilifère dans la carrière de lave.

Kolfschoten and Turner, 1996). The transition to the late Middle Pleistocene is marked by the localities Kärlich H and Kärlich-Seeufer (Kolfschoten, 1990; Kolfschoten and Turner, 1996). Kolfschoten (1990) and Kolfschoten and Roth (1993) studied several late Middle Pleistocene volcano sites in the Neuwied basin; Plaidter Hummerich A, Schweinskopf-Karmelenberg, Wannen, and Tönnchesberg 1. Small mammals are also known from Late Pleistocene faunas of Andernach-Martinsberg (Rabenstein, 1988), Gönnersdorf (Malec, 1978), Kettig (Kalthoff, 1998), Michelberg (Boecker et al., 1972), Plaidter Hummerich B–F, and Tönnchesberg 2 (Kolfschoten and Roth, 1993).

The purpose of the present study is to increase the knowledge of Pleistocene mammalian faunal successions of the low mountain range of western Germany in general and of the Neuwied Basin in particular. The small mammal fauna described here is much richer in taxa and specimens and different in composition compared to the Wannen fauna described by Kolfschoten and Roth (1993). The composition of our fauna is also different from those of the other localities mentioned above. It represents a time slice poorly known in the area of operation and is therefore of particular interest.

We refer to our fauna as "Wannenköpfe-West" to distinguish it from the Wannen fauna described by Kolfschoten and Roth (1993).

2. Materials and methods

Sediment samples were taken from the fossiliferous horizon from spots with frequent bone fragments. Overall, 250 kg of sediment was screen washed, most of it with a minimum mesh-width of 1 mm. For testing, a mesh of 0.5 mm was used for 30 kg but no improvement of the faunal list could be achieved. Eight hundred identified teeth were included in this study. The larger bones and the tooth and atlas of a large bovid were also recovered directly from the fossiliferous horizon.

Almost all fossils from Wannenköpfe-West are isolated bones and teeth, mainly of rodents. It is generally assumed that small mammal enrichments originate from accumulated pellets of avian predators (Andrews, 1990). The material is fairly well preserved, with partly dissolved bones and teeth.

The faunal list of the mammals is based exclusively on teeth, which were assigned by their characteristic occlusal patterns. Tooth dimensions are given in length x width in mm. For the talpids we used the terminology of Rümke (1985), for the arvicolines Meulen (1973) (Fig. 3), for the murine Storch (1987), and for the soricids Reumer (1984). The data on distribution and ecology were taken from Niethammer and Krapp (1978, 1982a, 1990) and Mitchell-Jones et al. (1999). The taxonomy follows Wilson and Reeder (2005) and Jaarola et al. (2004) for the arvicoline subgenera.

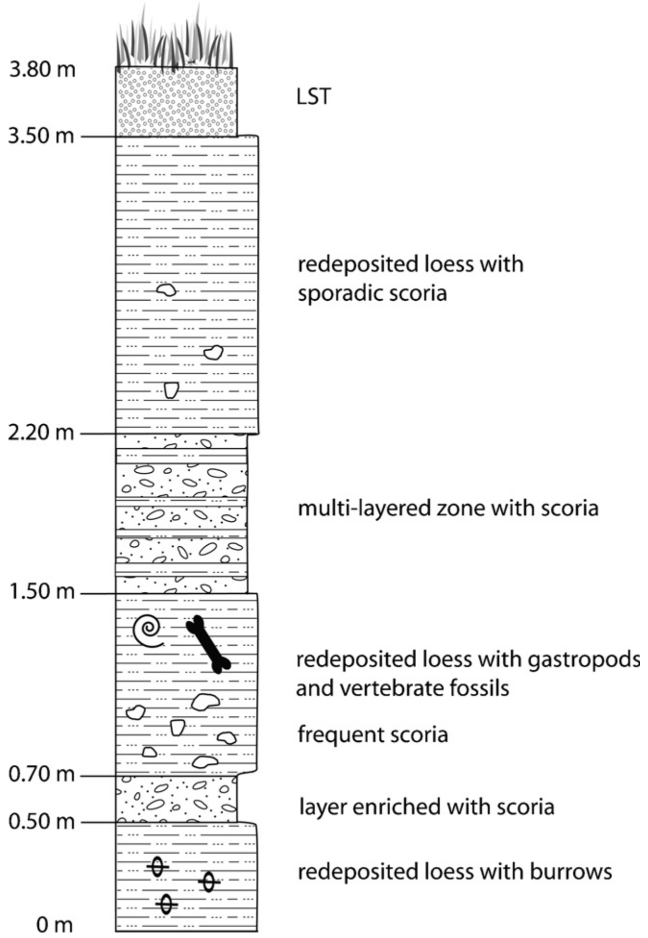

Fig. 2. Section of the Pleistocene loessic debris-flow deposits at the fossil site of Wannenköpfe-West. LST, Laacher See Tephra.

Fig. 2. Coupe géologique des dépôts de type écoulement de débris lœssique du gisement fossilifère de Wannenköpfe-West. LST, Tephra du Laacher See.

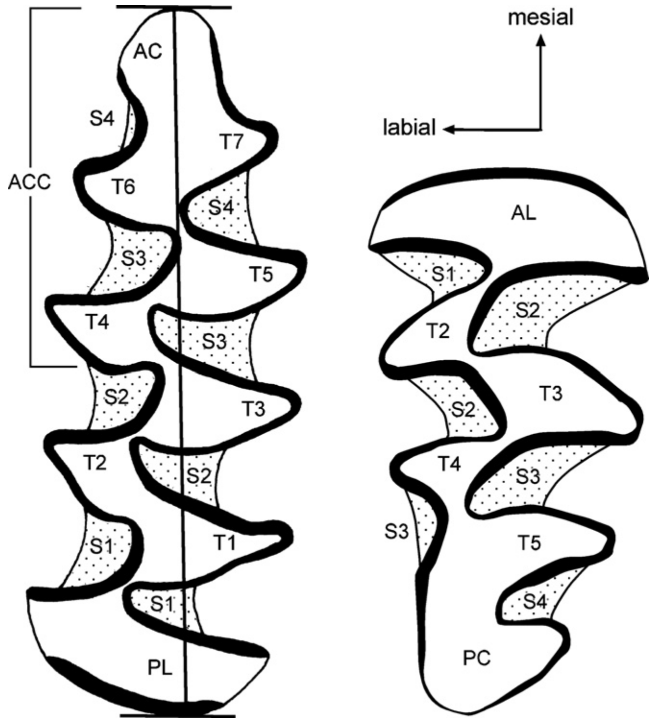

Fig. 3. Terminology of m1 (left) and M3 (right) in arvicolines (example *Microtus arvalis*). The maximum length of the m1 is indicated. AC, anterior cap; ACC, anteroconid complex; AL, anterior lobe; PC, posterior cap; PL, posterior lobe; S, syncline; T, triangle. After Meulen (1973).

Fig. 3. Terminologie de la m1 (gauche) et de la M3 (droite) chez les arvicolinés (exemple *Microtus arvalis*). La longueur maximum de la m1 est indiquée. AC, bonde antérieure ; ACC, complexe de l'antéroconide ; AL, lobe antérieur ; PC, bonde postérieure ; PL, lobe postérieur ; S, synclinal ; T, triangle. Selon Meulen (1973).

Comparative material of recent taxa were used from the collections of the Geological Institute of the Russian Academy of Sciences (GIN), the Institute of Palaeontology, Bonn University (IPB), the Swedish Museum of Natural History (NRM), the Forschungsinstitut Senckenberg (SMF), the Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), and the Zoological Museum of Moscow State University (ZMMU).

The fossil material described in this paper is stored in the collections of the Institute of Palaeontology, Bonn University, under the inventory numbers IPB Wa 1–37.

3. Results

3.1. General comments on the fauna of Wannenköpfe-West

The most abundant species in the material is *Microtus arvalis*. It comprises more than 90% of all dental remains and most likely of postcranial elements as well. Remains of juvenile individuals are common among *M. arvalis*. The second most abundant form in this material is *Arvicola terrestris* with about 5% of the remains. All other species of rodents and insectivores are represented by very few or single specimens. Large mammals are documented by two weasel teeth (Wa 6 and 7) of different size, a left lower molar (m3) and an atlas of a large bovid, most probably *Bos* or *Bison* (Wa 27).

Amphibians, reptiles, and birds represent lower vertebrates. Most of the remains belong to anurans from which we have postcranials, as well as upper and lower jaw fragments. Squamates are nearly exclusively documented by jaw remains. There are only few bird remains. The fossiliferous horizon was quite rich in $CaCO_3$, so that molluscs were preserved (Table 1).

Table 1
Frequency of land snails from Wannenköpfe-West
Tableau 1
Fréquence des gastropodes terrestres de Wannenköpfe-West

Clausiliidae (large)	3	?*Trichia* sp.	12
Clausiliidae (small)	ca. 7	?*Monachoides* sp.	4
Cochlicopa lubricella	1	Limacidae (two sp.)	1 + 3
Azeca goodalli	1	*Vertigo* sp.	3
Ena montana	3	*Lauria* vel *Pupilla*	77
Euconulus fulvus	2	*Succinea* sp.	2
Helicinae indet.	2	*Vallonia pulchella*	152

This preliminary list of the land snails was kindly made out by Dr. R. Hutterer (ZFMK).

3.2. Systematic palaeontology

Order SORICOMORPHA Gregory, 1910
Family SORICIDAE Fischer, 1814
Genus ***Sorex*** Linnaeus, 1758
Sorex araneus Linnaeus, 1758 vel *Sorex coronatus* Millet, 1828

Material and dimensions: fragment of mandible dext. with a2–m2 (m1: 1.38 × 0.82; m2: 1.14 × 0.73); fragment of mandible sin. with a 2-m1 (m1: 1.54 × 0.85); i sin. ($L = 3.89$); toothless fragment of mandible dext. Wa 2a–d.

Description: in all three mandibles, the processes and articular facets are missing. The toothless mandible shows the alveoli for m2 and m3. Teeth of Wa 2a are heavily worn. Teeth of Wa 2b are moderately worn and the jaw is anteriorly broken off. The mental foramen is situated below the protoconid of the m1. The isolated incisor is tricuspulate and only slightly worn. All teeth have pigmented cusps.

Comments: the mandibles and the incisor belong to a larger representative of the genus *Sorex* within the European *araneus*-species group. The three involved species *S. araneus* (Common shrew), *S. coronatus* (Millet's shrew), and *S. granarius* (Spanish shrew) show only minor differences in morphology and karyotype, a sign of their more or less recent speciation (Hausser, 1985). Because of its smaller dimensions, the Spanish shrew is not likely represented. Unfortunately, the specimens of Wannenköpfe-West are so poorly preserved that a distinction between *S. araneus* and *S. coronatus* is difficult. The mental foramen is situated below the protoconid of the m1 as Hausser et al. (1990) describe it for *S. araneus*. Although the lengths of the m1 and m2 of Wa 2a are below average for *S. araneus*, we assign the jaw to *S.* ex gr. *araneus* because the molars and the mandibular ramus are still clearly stronger than those of the Pygmy shrew *S. minutus*.

S. araneus is known from the Holsteinian Interglacial and *S. coronatus* is thought to be identifiable from the Middle Pleistocene (Hausser et al., 1990). From this time onwards, soricids of the *araneus*-group are frequent and continuous in the Pleistocene faunal record. In the Neuwied Basin, they occur in late Saalian times at Plaidter Hummerich A, in Eemian times at Tönchesberg II 11–18, and in the Weichselian at Plaidter Hummerich D1 (Kolfschoten and Roth, 1993). In Late Pleistocene sites like Gönnersdorf, Andernach-Martinsberg or Kettig the *S. araneus*-group is always present (Malec, 1978; Rabenstein, 1988; Kalthoff, 1998).

Sorex minutus Linnaeus, 1766

Material and dimensions: small fragment of maxilla dext. with P4 (1.15 × 1.24). Wa 3.

Description: the tooth is moderately worn; the hypoconal flange is short. The tips are pigmented.

Comments: the right P4 is intermediate in size between the larger *S.* ex. gr. *araneus* and the smaller *S. minutissimus*. The dimensions are in accordance with Plio-/Pleistocene and recent material of the Pygmy shrew *S. minutus* from Poland (Rzebik-Kowalska, 1991) and with recent material from Germany, Switzerland, Hungary, and Norway. However, the tooth is at the lower size range of this species.

Pygmy shrews are recorded from the Early Pliocene mammal zone MN 14 (Rzebik-Kowalska, 1998). *S. minutus* is a common faunal element in Middle and Late Pleistocene faunas but is not abundant. In the Neuwied Basin it is known from the Middle Pleistocene Kärlich G (Kolfschoten, 1990), the somewhat younger fauna of Plaidter Hummerich A (Kolfschoten and Roth, 1993), and in Late Pleistocene sediments from Gönnersdorf, Andernach-Martinsberg and Kettig (Malec, 1978; Rabenstein, 1988; Kalthoff, 1998). There is a slight increase in size noticeable from the Ruscinian onwards in *S. minutus* (Reumer, 1984).

Sorex minutissimus Zimmermann, 1780 Fig. 4a and b

Material and dimensions: mandible sin. ($H = 3.23$; $L = 3.18$; HC = 1.17; LUV = 0.58; LLF = 0.88) with m1–m2 (m1: 1.01 × 0.62; m2: 1.04 × 0.61). Wa 4.

Description: the mandible contains m1 and m2, while the incisor and the angular process are broken off. The mandible shows the following characteristics indicative of this species: very small size, mental foramen below transition of trigonid to talonid of m1, concave form of mandible below m1 and m2, condylar process compact with broad interarticular area. The coronoid process is slender and somewhat pointed but not obviously bent anteriorly. The tips of teeth are pigmented.

Comments: the dimensions from the mandible and the individual teeth match well with the data given by Koenigswald (1973) for *S. minutissimus* from the Middle Pleistocene Husarenhof 4 locality (southern Germany), by Rzebik-Kowalska (1991) for Plio-/Pleistocene material from Poland, by Reiner (1994/1995) for a Late Pleistocene cave in Austria, by Sulkava (1990) for recent specimens from Sweden and Finland, and with the size of a recent Siberian specimen (IPB). Fossil occurrences of *S. minutissimus* are also known from Middle and Late Pleistocene sites in France (Heim de Balzac, 1940; Jammot, 1974, 1989), the Middle Pleistocene of Bulgaria (Popov, 1989), the Late Pleistocene of England (Rzebik-Kowalska, 1968), southern Germany (Brunner, 1953; Hahn and Koenigswald, 1977), and of the Neuwied Basin (Gönnersdorf: Malec, 1978).

The Least shrew is always a rare species in fossil, as well as in recent faunas. Today, *S. minutissimus* occurs from Scandinavia to western Russia and outside Europe from Siberia, Mongolia, to Japan. However, in Holocene times it still could be found in Central Europe (e.g. Schaefer, 1975). The presence of *S. minutissimus* is indicative of tundra and taiga environments where its ecological requirements are diverse. Therefore, *S. minutissimus* is an excellent indicator for boreal conditions (Rzebik-Kowalska, 1995).

Family TALPIDAE Fischer, 1814
Genus ***Talpa*** Linnaeus, 1758
Talpa europaea Linnaeus, 1758

Material and dimensions: fragment of mandible dext. with p3–p4; two m1 sin. (2.46 × 1.36; 2.12 × 1.18); P1 sin.; small fragment of maxilla sin. with M1 (2.68 × 1.54); M2 dext. (2.38 × 2.08). Wa 1a–f.

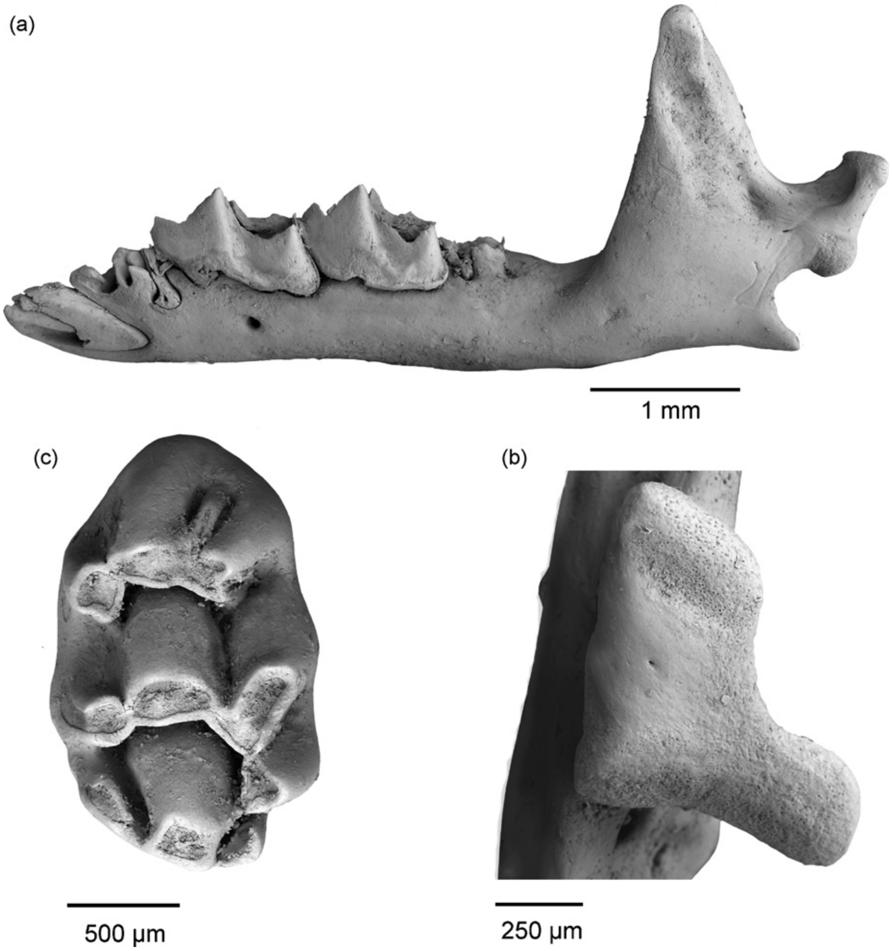

Fig. 4. *Sorex minutissimus* and *Apodemus sylvaticus* from the Late Pleistocene of Wannenköpfe-West. **a, b**. *Sorex minutissimus* (IPB Wa 4). (**a**) left mandible with m1–m2, labial view. (**b**) detail of the condyle process, view from posterior. (**c**) *Apodemus sylvaticus* (IPB Wa 9a). Left M1, occlusal view.

Fig. 4. *Sorex minutissimus* et *Apodemus sylvaticus* du Pléistocène supérieur de Wannenköpfe-West. **a**, **b**. *Sorex minutissimus* (IPB Wa 4). (**a**) mandibule gauche avec m1–m2, vue labiale. (**b**) détail du Processus condylaris, vue postérieure. (**c**) *Apodemus sylvaticus* (IPB Wa 9a). M1 gauche, vue occlusale.

Description: the three premolars are two-rooted and only slightly worn. The metaconid and parastylid of the P4 are well expressed. One of the m1 (Wa 1b) is fairly worn. Likewise are both upper molars, which have three main roots and one central small auxiliary root. The paracone of the M1 is partially damaged.

Comments: there is a considerable size variation in the species of the genus *Talpa* that can make a species determination difficult (Koenigswald, 1985). In Middle and Late Pleistocene times two talpid species may occur sympatrically. However, some authors think that a broad size spectrum in one fauna may be related to sexual dimorphism (Boecker et al., 1972; Malec, 1978). This opinion is rejected by others (Storch, 1973).

The preserved teeth belong to at least two individuals (two m1). The dimensions fit well with data given by Ziegler (1995) for late Middle Pleistocene moles from southern Germany and for data of recent *T. europaea*. An assignment to the Late Pleistocene Giant mole *T. e. magna* cannot be determined by the given material. This subspecies is mostly identified by humeri, which are not preserved in the Wannenköpfe-West material. The Middle Pleistocene mole *T. minor* is smaller than the species from this assemblage.

Moles in the size of *T. europaea* are known from the Late Pliocene (Niethammer, 1990). Their characteristic humeri are especially common in Middle and Late Pleistocene associations. In the Neuwied Basin moles occur, for example, in the Plaidter Hummerich A (late Saalian) and D1 (early Weichselian), and in the Eemian of Tönnchesberg II 11–18 (Kolfschoten and Roth, 1993). In Late Pleistocene localities such as Michelberg, Gönnersdorf, or Kettig (Boecker et al., 1972; Malec, 1978; Kalthoff, 1998) specimens of *T. europaea* surpassing the size of recent moles were described.

Order RODENTIA Bowdich, 1821
Family DIPODIDAE Fischer de Waldheim, 1817
*Genus **Sicista*** Gray, 1827
Sicista subtilis (Pallas, 1773)
Fig. 5c

Material and dimensions: m1 sin. (1.11 × 0.88). Wa 8.

Description: the molar is notably worn, with two roots.

Comments: the two European species of *Sicista*, the steppe dwelling Southern birch mouse *S. subtilis* and the forest dwelling Northern birch mouse *S. betulina*, can be distinguished on the basis of dimensions and the relative complexity

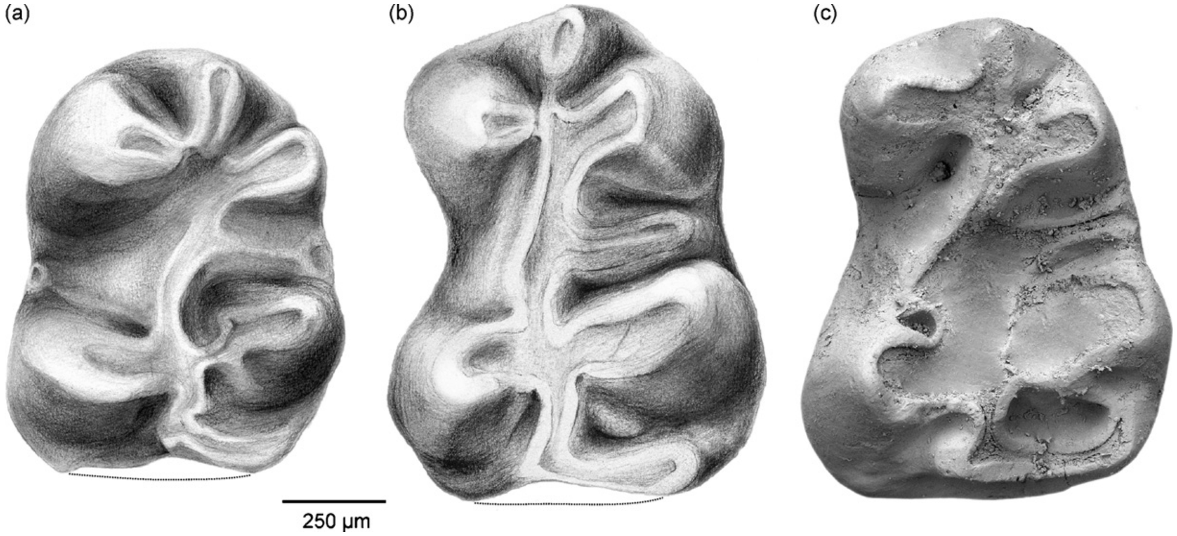

Fig. 5. Left m1 of European *Sicista* species. (**a**) Recent *Sicista betulina* (NRM A 561358). (**b**) Recent *Sicista subtilis* (NRM A 592319). (**c**) *Sicista subtilis* from the Late Pleistocene of Wannenköpfe-West (IPB Wa 8). All in occlusal view. **a**, **b**, drawings. **c**, SEM image. Note the distinct shallow concavity on the labial side of both *Sicista subtilis*.

Fig. 5. m1 gauche d'espèce européenne de *Sicista*. (**a**) *Sicista betulina* récente (NRM A 561358). (**b**) *Sicista subtilis* récente (NRM A 592319). (**c**) *Sicista subtilis* du Pléistocène supérieur de Wannenköpfe-West (IPB Wa 8). Toutes en vue occlusale. **a**, **b**, dessins. **c**, image SEM. Il est à noter la concavité peu profonde mais distincte du côté labial des m1 des deux *Sicista subtilis*.

of the molars (Pucek, 1982). In the extant fauna of southern Eastern Europe, each of the widespread sicistine species has its partly sympatric chromosome sibling species (Pavlinov et al., 2002). It is, respectively, *S. strandi* for the Northern birch mouse, and *S. severtzovi* for the Southern birch mouse. Diagnostic morphological features are currently unknown. *S. subtilis* is the larger species, with a somewhat simpler molar morphology than *S. betulina* (Pucek, 1982; Storch, 1994). The occlusal outline of lower first molar of Wannenköpfe-West clearly converges anteriorly and there is a distinct shallow concavity where the ectoflexid reaches the lateral margin of the tooth (Fig. 5c). This is a well-expressed difference from *S. betulina*, which shows a more oval and rounded outline (Fig. 5a). It might be an additional and easily visible character for distinguishing the two European birch mouse species. This feature was consistent in 26 specimens available in the collections of NRM and SMF. It should be verified with more material of *Sicista*. However, the problem is the rareness of this genus in museum collections, as well as in the fossil record.

Dimensions of the *Sicista* molar from Wannenköpfe-West fit the size range of recent *S. subtilis* from Romania (Pucek, 1982; SMF: own measurements) and from the Ural mountains (NRM: own measurements). It is larger than Latest Pleistocene and recent *S. betulina* reported by Storch (1994), even though these specimens surpass Pucek's (1982) measurements of *S. betulina*, especially in width. There are no accessory ridges observable such as those figured by Storch (1994: Fig. 8) for Latest Pleistocene Northern birch mice. Due to its size and overall morphology, we can reliably assign the sicistine molar of Wannenköpfe-West to the Southern birch mouse, *S. subtilis*.

Kolfschoten (1990) reported remains of *S. betulina* from the late Cromerian of Miesenheim I and of *S. subtilis* from the Saalian of Maastricht-Belvedère 3B and Plaidter Hummerich I. Later Kolfschoten and Roth (1993) and Kolfschoten and Turner (1996) considered the material from the Saale loess of Miesenheim I and of Plaidter Hummerich I as *Sicista* sp.

Family CRICETIDAE Fischer, 1817
Genus ***Arvicola*** Lacépède, 1799
Arvicola terrestris (Linnaeus, 1758)

Material and dimensions: fragmentary mandible dext. with m1–3, fragmentary mandible dext. with m1–2, seven m1, five m2, four m3, six M1, 10 M2, 11 M3, and fragments of molars. Wa 10–12. For dimensions see Table 2.

Description: the first lower molars have the characteristic morphology of the anteroconid complex with anterior cap and triangles T4 and T5 broadly confluent. The third upper molars show the typical hook-shaped posterior cap with a deep second lingual syncline (S3). The molars have more or less uniformly thick enamel. The enamel thickness quotient (Schmelzband-Differenzierungs-Quotient, SDQ, see Heinrich, 1982, 1990) of the first lower molars is 98.3 with a range of 83–115 ($n = 9$).

Comments: there is a well-documented evolutionary process in water voles from the middle latitudes of Eurasia:

Table 2
Dimensions of the molars of *Arvicola terrestris* from Wannenköpfe-West
Tableau 2
Dimensions des molaires de *Arvicola terrestris* de Wannenköpfe-West

	Length			Width		
	n	Range	Mean	*n*	Range	Mean
m1	9	3.67–4.07	3.87	9	1.40–1.67	1.58
m2	7	2.20–2.50	2.38	7	1.40–1.53	1.47
m3	4	2.07–2.33	2.25	4	1.13–1.27	1.22
M1	6	3.20–3.60	3.35	6	1.80–2.00	1.88
M2	10	2.27–2.60	2.48	10	1.33–1.67	1.55
M3	11	2.20–2.80	2.45	11	1.20–1.47	1.33

the shift of the enamel band thickness in the triangles of the molars from the so-called *Mimomys* pattern, with thicker posterior enamel walls to an *Arvicola* pattern with thicker anterior walls (Heinrich, 1978, 1982, 1987, 1990; Markova, 1980; Zazhigin, 1980; Agadjanian, 1983; Martin, 1987; Kolfschoten, 1990, 1992; Rekovets, 1990; Koenigswald and Kolfschoten, 1996; Koenigswald and Heinrich, 1999). This shift of the enamel band thickness is quantified by the SDQ with a general trend from higher values in the Middle Pleistocene to lower values in the Late Pleistocene and Holocene. Various species names have been proposed for the transitional form of *Arvicola* with uniformly thick enamel (SDQ approximately 100) from the late Middle and the early Late Pleistocene, such as *A. chosaricus* Alexandrova, 1976 and *A. hunasensis* Carls, 1986. More often, the name *A. cantianus/terrestris* is used for these forms (e.g. Heinrich, 1982; Kolfschoten, 1985; Koenigswald and Heinrich, 1999). However, Röttger (1987) and Kolfschoten (1990) demonstrated a notable archaism of enamel thickness pattern in modern populations of *A. terrestris* from Southern Europe and Asia Minor, comparable with that in the early Middle Pleistocene *A. cantianus*. On the basis of these results for recent *Arvicola*, the sudden shift to higher SDQ values at the beginning of the Eemian was interpreted by Kolfschoten (1990, 1992) and Koenigswald and Kolfschoten (1996) as at least one immigration event of a more primitive *Arvicola* from southern Europe.

The traditional use of an SDQ value of ±100 as a character to distinguish the Middle Pleistocene, more primitive *Arvicola* from more advanced Late Pleistocene *Arvicola*, thus causes taxonomic problems on the species level. Clearly, an SDQ value of 100 cannot be used to distinguish the Middle Pleistocene transitional forms of *Arvicola* (*A. cantianus/terrestris*) from the Late Pleistocene and extant *A. terrestris*. One solution to the problem, published by Kolfschoten (1990, 1992) was to assign all fossil *Arvicola* finds to subspecies of *A. terrestris*. On the other hand, Maul et al. (2000) proposed that all Middle Pleistocene *Arvicola* molars with SDQ values of more than 100 should be referred to *A. mosbachensis*. Maul et al. (2000) restrict the species *A. cantianus* only to the fragmentary (and therefore not diagnostic) type material. On the basis of published SDQ values of different Central European localities there is a clear distinction between *Arvicola* from the older Middle Pleistocene and those from the younger Middle Pleistocene (Fig. 6).

In our opinion, though being a common practice, the distinction of a species boundary using an SDQ index is arbitrary and has a questionable biological meaning.

A. mosbachensis and *A. terrestris* are considered to be members of a phyletic series and thus should have been merged into a single species, namely *A. terrestris*. We would not like to go into discussion on what kind of speciation, cladogenetic or anagenetic, is more ‘‘real’’. There are arguments for both approaches and probably both are real. However, strict coordination of taxonomy with the current concept of the cladogenetic pattern bears a potential taxonomic instability. In case of water voles, the lumping of all fossils and recent voles into one species contradicts the existence of at least two separate extant species of the genus *Arvicola*, that is, an evidence of at least one cladogenetic event within *Arvicola*. These are *A. terrestris* (SDQ values 65.7–134.4; Röttger, 1987) with a huge Eurasian range and a SW European species, *A. sapidus* showing more primitive values of SDQ near 100 (SDQ values 119.7–120.8; Röttger, 1987). This ‘‘Middle Pleistocene’’ appearance of the SW European form together with its more ancestral karyotype ($2n = 40$) shows that *A. terrestris* is a derived form (with more advanced chromosome number, $2n = 36$), which split off the main lineage at an unknown time in the Pleistocene. There is an opinion that *A. sapidus* was present in most Eurasian faunas prior to Late Pleistocene, whereas the chromosome speciation and a wide spread of *A. terrestris* occurred in Late Pleistocene (Agadjanian, 2001). Although there is no sound data on the time of *sapidus–terrestris* divergence, the proposed scenario is quite plausible. Rekovets and Nadachowski (1995) also assumed a quite complex phylogenetic history of the genus *Arvicola*. However, only further molecular phylogenetic studies, including possible advances of molecular palaeontology, together with refinement of traditional morphological diagnostics would elucidate the phyletic structure of Pleistocene water voles. In this situation, we prefer to follow the traditional taxonomy with two chronospecies of *Arvicola*, *A. mosbachensis* for early Middle Pleistocene and *A. terrestris* for later part of Pleistocene. Regardless of the model used, it should be remembered that the shift of the SDQ during the Middle and Late Pleistocene is a stratigraphically powerful tool. As mentioned above, an SDQ index of 100 is not appropriate to the discrimination of more primitive from more advanced *A. terrestris*, whereas a clear distinction is given by the use of an SDQ index of 120 (Fig. 6). The 120-value has already been proposed by Kolfschoten (1990) and Steensma and Kolfschoten (1997) as a subspecies boundary between their *A. terrestris cantiana* and the younger intermediate populations. Using the 120-value means that the shift from more primitive *A. mosbachensis* to more advanced *A. terrestris* falls within the Middle Pleistocene (Fig. 6).

The stratigraphic position of *Arvicola* from Wannenköpfe-West can be evaluated using SDQ values (Fig. 6). SDQ values around 100 are characteristic for latest Eemian and earliest Weichselian localities (Koenigswald and Heinrich, 1999). However, such values were also recognized by Koenigswald and Kolfschoten (1996) for the late Middle Pleistocene (Saalian) of Maastricht-Belvedère 3 and 4 (Fig. 6).

In the late Middle Pleistocene to early Weichselian of the Neuwied Basin, *Arvicola* finds were reported from Ariendorf, Plaidter Hummerich, Schweinskopf, Tönnchesberg, and Wannen. But this taxon is generally not very frequent and represented by only one to a maximum of 19 specimens (Kolfschoten and Roth, 1993; Koenigswald and Heinrich, 1999).

Genus ***Microtus*** Schrank, 1798

Microtus (Microtus) arvalis (Pallas, 1778)

Material and dimensions: 74 m1, 101 M1, 73 M2, 110 M3, about 330 m2–3, and molar fragments, two edentulous mandible fragments sin. Length of m1: 2.4–3.1; mean: 2.63; $n = 74$. Wa 13–19.

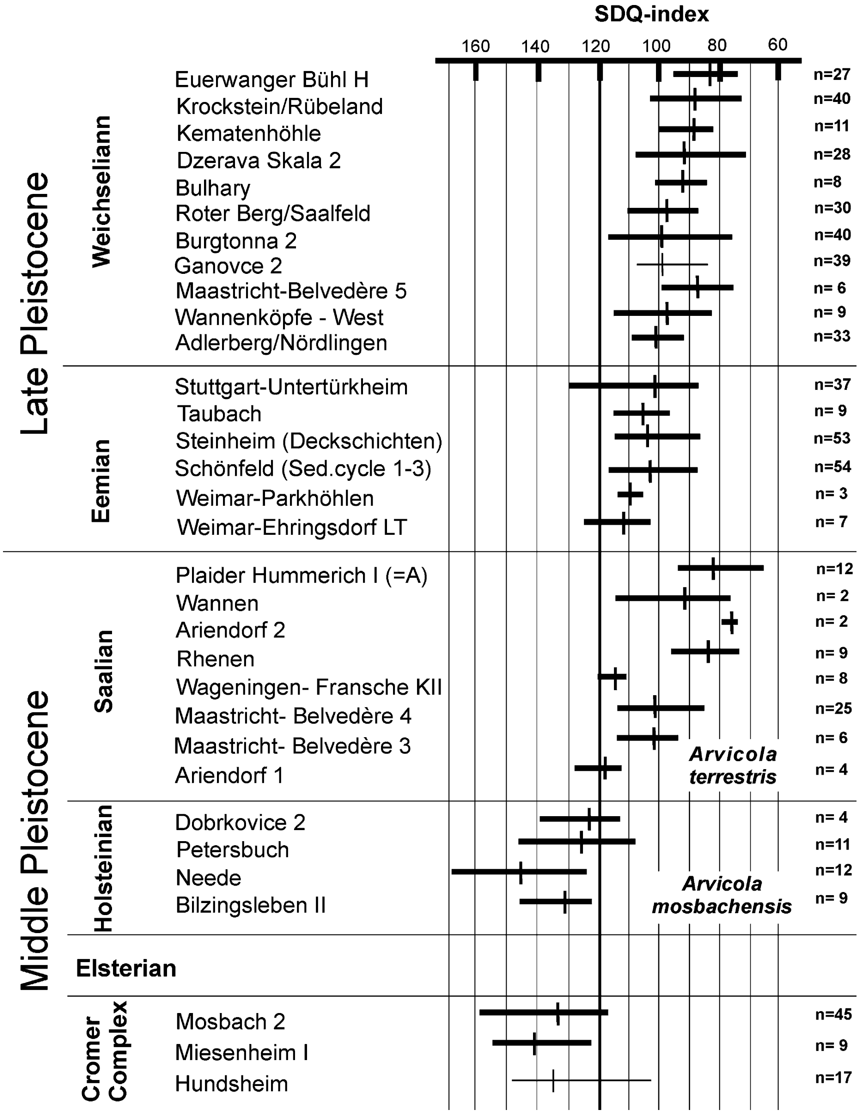

Fig. 6. Enamel thickness quotient (SDQ) values of Middle and Late Pleistocene *Arvicola* from Central Europe. An SDQ value of 120 (instead of 100) is proposed as formal boundary between chronospecies *A. mosbachensis* and *A. terrestris*. The stratigraphic assignment and the SDQ values have been taken from Kolfschoten (1990, 2001), Heinrich (1991), Kolfschoten and Roth (1993), Kahlke (1995), Koenigswald and Kolfschoten (1996), and Koenigswald and Heinrich (1999). The thin-lined SDQ values of Hundsheim and Gánovce 2 had to be estimated from Koenigswald and Heinrich (1999: Fig. 4).

Fig. 6. Valeurs du quotient d'épaisseur de l'émail (SDQ) d'*Arvicola* du Pléistocène Moyen et Supérieur d'Europe Centrale. Une valeur de SDQ de 120 est proposée comme frontière formelle entre les chrono-espèces *A. mosbachensis* et *A. terrestris*. Le classement stratigraphique et les valeurs de SDQ sont repris de Kolfschoten (1990, 2001), Kolfschoten et Roth (1993), Kahlke (1995), Koenigswald et Kolfschoten (1996) et Koenigswald et Heinrich (1999). Les valeurs en lignes fines de SDQ de Hundsheim et Gánovce 2 devraient être estimées à partir de Koenigswald et Heinrich (1999 : Fig. 4).

Description: 74 m1s can be attributed to the *arvalis/agrestris*-species group. All show three lingual and two labial anticlines. The morphology of the anteroconid complex is variable and shows three main morphotypes, following Reiner (1994/1995). The most abundant morphotype (68%) features a broadly confluent anterior cap and confluent T6 and T7 (“arvalis”). Much less numerous (6%) is the morphotype with a distinct separated T6 (“extratriangulatus”). Relatively rare (2.5%) is the morphotype with an anterior cap distinctly separated from the broadly confluent T6 and T7 (“maskii”). The anteroconid complex has an average relative length (A/L *sensu* van der Meulen, 1973) of 54% with a range 50–58% ($n = 74$).

The M3 has a typical structure with an anterior lobe, three triangles (T2–T4), and a posterior cap of varying complexity. The naming of the morphotypes follows Niethammer and Krapp (1982b). The most common M3 morphotype (63%) has three well-developed lingual synclines S2-4 (“basic form”). The second most abundant morphotype (30%) shows a distinct development of a fourth lingual syncline S5 (“type 3/5”). The third morphotype with a poorly developed third lingual syncline S4 (“transition to simplex”), is more rare (8%).

Comments: there are four arguments for the assignment of this material to *Microtus arvalis*:

- In the m1 the *arvalis*-morphotype is dominant (68%). According to Reiner (1994/1995), the “basic” morphotype is generally most abundant within the species.

- The dimensions of the m1 from Wannenköpfe-West fit well with measurements taken from recent *M. arvalis* from the Rhineland (mean = 2.60; *n* = 20) but are smaller than recent *M. agrestis* from Switzerland (mean = 2.98; *n* = 20; Niethammer and Krapp, 1982b). When both species occur sympatrically *M. arvalis* is usually smaller.
- The m1s generally have more symmetrical lingual and labial triangles. Nadachowski (1984) introduced an index relating the width of T4–T5 (LT4/LT5 in Nadachowski, 1984). Values lower than 65 can clearly show the asymmetry of lingual and labial triangles typical for *M. agrestis*. On the average our material shows a much more symmetrical pattern of triangles arguing for an "*arvalis*", rather than an "*agrestis*" morphology.
- Only six M1s and three M2s show tiny additional posterior triangles (exsul-loop, agrestis-loop), and much less developed than in typical *M. agrestis*.

Chromosomal studies of the last decade revealed a strong genetic heterogeneity of the European common vole, *M. arvalis* (Malygin, 1983). The former ubiquitous species turned out to be a complex of sibling species. One of the two widespread cryptic species of the group, 46-chromosome *M. arvalis* occurs throughout West and Central Europe and also in some eastern parts of the continent. The second species, the 54-chromosome *M. rossiaemeridionalis*, is distributed in Eastern and South-eastern Europe.

The first results of multivariate morphometric techniques applied to the lower m1 of the two species provide reliable discrimination in extant and fossil material from Eastern Europe (Markova, 2003; Markova et al., 2003). According to these studies, *M. arvalis* has generally more asymmetrical lingual and labial triangles and less complicated anteroconid complex morphotypes than *M. rossiaemeridionalis*. As both species could possibly be present in the western part of Germany due to recurrent migration, E. Markova kindly checked a reference sample of molars from Wannenköpfe-West. The preliminary study revealed that only *M. arvalis* is present (E. Markova, written communication, 2004).

The *M. arvalis/agrestris* species group is present in Central Europe from the older Middle Pleistocene onwards. In the late Middle Pleistocene and especially in the Late and Latest Pleistocene, *M. arvalis/agrestris* is a very common faunal element in glacial and stadial, as well as in interglacial and interstadial faunas (Ziegler, 1995; Koenigswald and Heinrich, 1999). In the Neuwied Basin, *M. arvalis/agrestris* has been reported by Kolfschoten and Roth (1993) from their Wannen fauna, as well as from other neighboring faunas of late Middle and early Late Pleistocene age.

Microtus (Terricola) cf. *multiplex* (Fatio, 1905) Fig. 7.

Material and dimensions: two m1 sin. Length: 2.53, 2.87. Wa 20–21.

Description: the two first lower molars display the characteristic confluent triangles T4 and T5 found in *Terricola* and some other arvicoline taxa (Fig. 7a, b). The anterior cap of the anteroconid complex is rounded in one specimen and has a poorly developed labial anticline in the other one. The relative length of the anteroconid complex is 54% in both specimens. The smaller specimen shows juvenile morphology (Fig. 7a). The enamel microstructure in the triangles of both m1 shows inner lamellar and outer radial enamel on the leading edge (Fig. 7c). The lamellar enamel continues to some extent on the trailing edge. Most parts of the trailing edge only consist of radial enamel, but a short segment of outer tangential enamel is present towards the triangle apex (Fig. 7c, d). This tangential enamel is somewhat better developed in the anterior triangles than in the posterior ones, and it is also present in the posterior lobe.

Comments: the overall morphology, especially the shape of confluent T4-5 of the first lower molars resembles the modern Alpine pine vole *M. multiplex* and that of the closely related Common pine vole *M. subterraneus*. Today, both species occasionally coexist in the Alps where *M. multiplex* is generally larger than *M. subterraneus* (Table 3).

Though the fossil material is very limited, we tentatively assign the two molars to *M. multiplex* since the length of the adult molar exceeds even the largest molars of a recent sample of *M. subterraneus* from Bonn, Germany (Niethammer, 1982). We can exclude a primitive morphotype of *M. arvalis*, as tangential enamel is totally reduced in this species (Koenigswald, 1980).

Only a few arvicoline teeth with confluent T4-5 have been described from the Late Pleistocene. The difficulty in determining the species from isolated molars can be seen in

Table 3
Dimensions of m1 from Recent and fossil *Microtus multiplex* and *Microtus subterraneus*
Tableau 3
Dimensions des m1 de *Microtus multiplex* et *Microtus subterraneus* fossiles et récents

Taxon	*n* (m1)	Range	Mean
M. multiplex (Recent; Reiner, 1994/1995)	295	–	2.62
M. multiplex Monte Baldo (Recent; Krapp, 1982)	25	2.50–3.00	2.78
M. multiplex (Recent; Brunet-Lecomte et al., 1993)	166	–	2.60
M. cf. *multiplex* Große Badlhöhle (Late Pleistocene; Reiner, 1994/1995)	14	–	2.51
M. multiplex vuillemeyi Gigny (Late Pleistocene; Brunet-Lecomte et al., 1993)	121	–	2.64
M. cf. *multiplex* Wannenköpfe-West, this paper	1	–	2.87
M. subterraneus Bonn (Recent; Niethammer, 1982)	25	2.44–2.72	2.43
M. subterraneus (Recent; Reiner, 1994/1995)	310	–	2.48
M. subterraneus (Recent; Brunet-Lecomte et al., 1993)	226	–	2.49
M. subterraneus Genkingen (Late Pleistocene; Ziegler, 1995)	9	2.44–2.74	2.52

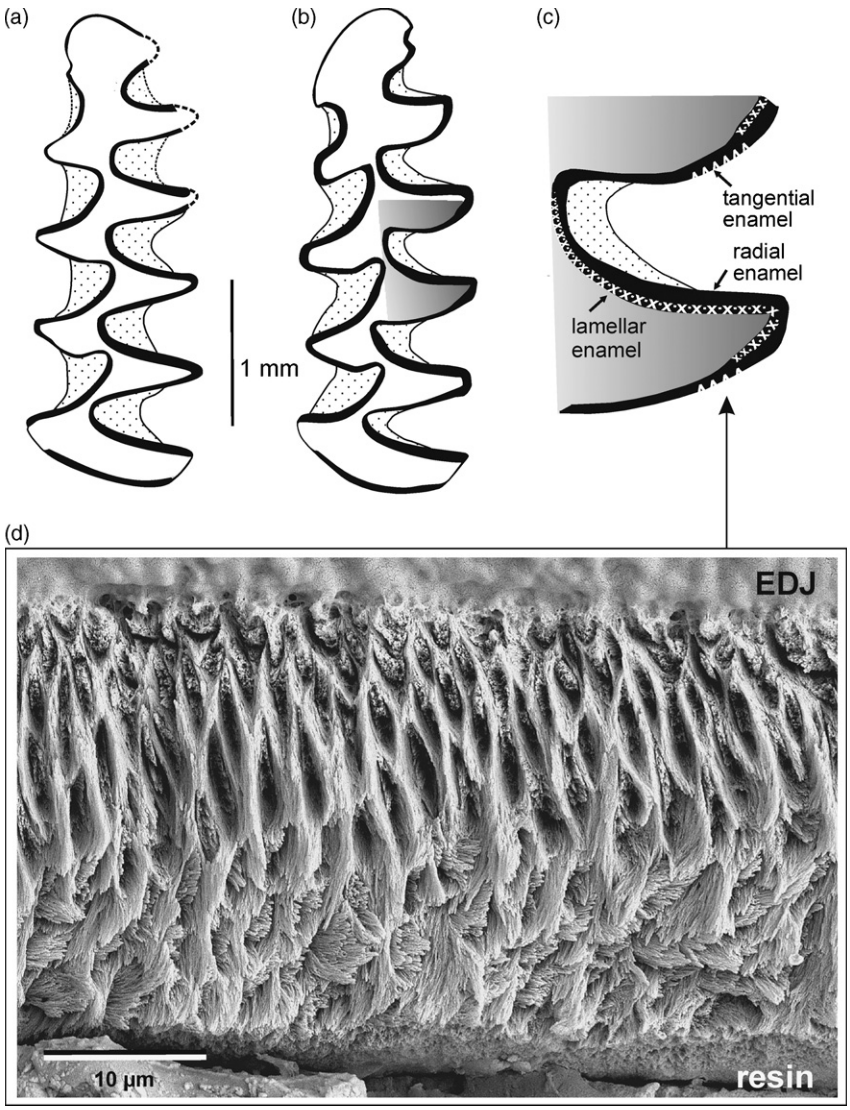

Fig. 7. *Microtus* cf. *multiplex* from the Late Pleistocene of Wannenköpfe-West. (**a**) left m1 with juvenile morphology (IPB Wa 20). (**b**) left m1 of an adult individual (Wa 21). (**c**) cut out with the enamel types present in leading and trailing edges of the triangles. (**d**) SEM image showing a part of the trailing edge indicated by the arrow. In the lower half of the enamel band the persisting tangential enamel is well visible. EDJ, enamel dentine junction.

Fig. 7. *Microtus* cf. *multiplex* du Pléistocène supérieur de Wannenköpfe-West. (**a**) m1 gauche de morphologie juvénile (IPB Wa 20). (**b**) m1 gauche, individu adulte (Wa 21). (**c**) agrandissement du secteur grisé montrant la répartition des types d'émail des côtés antérieurs et postérieurs des triangles. (**d**) image SEM montrant une partie du côté arrière indiquée par la flèche. Dans la partie inférieure de la bande d'émail, l'émail tangentiel persistant est apparent. EDJ, limite émail – dentine.

the examples of Genkingen and Große Badlhöhle: although the m1s from both localities are about the same mean size (Table 3) the former were assigned by Ziegler (1995) to *M. subterraneus*, while the latter were attributed by Reiner (1994/1995) to *M.* cf. *multiplex*. The earliest known record of *M. multiplex* is from the late Middle Pleistocene French site Lazaret (Alpes-Maritimes) (Brunet-Lecomte et al., 1993).

Microtus (Pallasiinus) oeconomus (Pallas, 1776)

Material and dimensions: two m1 sin., two m1 dext. (Wa 22). Length: 2.2, 2.3, 2.3 (for the juvenile specimens).

Description: the four molars available show the typical *oeconomus* tooth pattern with two anticlines at the lingual and labial side, as well as a labially flattened anterior cap. Only one molar belongs to an adult animal but is slightly damaged. The other specimens show juvenile morphology with gracile anticlines, uninterrupted dentine tracts, and a notably deep anterolingual fold in the anterior cap of the anteroconid complex.

The anteroconid complex of all four specimens shows the "*oeconomus*" morphotype (Angermann, 1984). The adult specimen and two of the juvenile teeth show the "oec$_2$" variety but only the worn tooth can be attributed to the "brachyratticeps" variety *sensu* Rabeder (1981). The third juvenile m1 features the "oec$_3$" variety with an additional labial anticline.

Comments: *M. oeconomus* is represented by limited material. Three m1s show the "oec$_2$" variety that is also dominant in the recent area of distribution of the species (Angermann, 1984). The "oec$_3$" variety is relatively rare in recent populations but also known in the fossil record (Angermann, 1984).

M. oeconomus is a quite common element in late Middle Pleistocene "younger *Arvicola-cantianus*-faunas", as well as in the Younger and Late Pleistocene *A. terrestris*-faunas of

Central Europe (Koenigswald and Heinrich, 1999). In the Neuwied Basin, *M. oeconomus* is known from the middle Middle Pleistocene locality Miesenheim I (Kolfschoten and Turner, 1996). It is regularly present in late Middle to Late Pleistocene faunas of this area but absent in the late Middle Pleistocene Wannenköpfe fauna (Kolfschoten and Roth, 1993; Kalthoff, 1998; Koenigswald and Heinrich, 1999).

Family MURIDAE Illiger, 1811
Genus ***Apodemus*** Kaup, 1829
Apodemus (Sylvaemus) sylvaticus (Linnaeus, 1758) Fig. 4c

Material and dimensions: M1 sin. (1.91 × 1.22); tiny antero-labial fragment of m2. Wa 9a + b.

Description: the M1 of a smaller *Apodemus* species has a rather complex pattern with all cusps present (t1–t12). Additionally, there is a prestyle between t2 and t3, and t3 shows a strong posterior spur. The cusps t4 and t7 are not connected. The molar has four main roots. The fragment of the m2 shows the protoconid, the labial anteroconid, and the c3.

Comments: in the transition Middle to Late Pleistocene of Central Europe there are two *Apodemus* species known: *A. sylvaticus* and *A. maastrichtiensis* (Koenigswald and Heinrich, 1999). We can exclude the latter species because of its smaller size (Kolfschoten, 1985). Compared to recent material from the Rhineland, the length of the M1 slightly exceeds dimensions of *A. sylvaticus* (Niethammer, 1978). The M1 from Wannenköpfe-West fits the data given by Storch and Lütt (1989) for extant *A. sylvaticus* from Kleinwalsertal (Austria). The morphology of the M1 is similar to that of modern *A. sylvaticus*. However, the presence of an extant sibling species, the Lesser Wood mouse *A. uralensis*, in Central and Eastern Europe, leaves open the question of possible migration of this species to the west of the continent during the Pleistocene.

As a successor of the Pliocene *A. atavus*, *A. sylvaticus* is present in Central Europe throughout the warmer periods of the Pleistocene (Niethammer, 1978). From the Middle Pleistocene of the Neuwied Basin *A. sylvaticus* is known from Miesenheim I and Kärlich G (Koenigswald and Heinrich, 1999). Little material that is similar to *A. sylvaticus* in morphology and size was reported from the Middle Pleistocene of Tönnchesberg 2 and Plaidter Hummerich D1, D2, and E (Kolfschoten and Roth, 1993). For the Latest Pleistocene of the Neuwied Basin, *A. sylvaticus* is so far only identified from Michelberg (Boecker et al., 1972).

4. Discussion

4.1. Taphonomy

During sampling in the section we observed an irregular distribution of the fossils in the weathered surface of the loessic sediment. Circular aggregations of bones and teeth stuck close together were observed. This geometry suggests the distribution of the pellets of diurnal and/or nocturnal avian predators. A high percentage of the bones and teeth were affected by digestion as they are damaged and partly dissolved. The dominance of isolated teeth and the almost complete lack of jaws argue for a middle-sized raptor. The composition of the fauna with the strong predominance of only one species indicates that the pellets might come from only one individual bird of prey. The absence of strictly aquatic animals also indicates the scatological rather than fluviatile origin of the small mammal association.

4.2. Ecology

The Wannenköpfe-West fauna represents several biotopes. *A. terrestris* and *Microtus oeconomus* indicate intrazonal aquatic and semiaquatic habitats. *M. arvalis* shows the presence of grasslands and meadows, which also suit *M.* cf. *multiplex*. *Apodemus* is most likely associated with forested biotopes. *Talpa* lives in soils in forests and meadows, and *Sorex araneus/coronatus* and *S. minutus* are associated with the upper soil layers in forested or meadow biotopes. More open habitats are indicated by *S. minutissimus* and *S. subtilis*. The association most likely argues for a rather open grassland landscape with meadows along water basins and with restricted wooded areas.

In number of remains, the representatives of meadow and semiaquatic biotopes are by far predominant in the Wannenköpfe-West fauna. Forms that indicate forest and steppe conditions are very rare. Animals that are usually present in steppe faunas, such as *Spermophilus*, Cricetini, and *Lagurus*, were not found. The same can be said about such woodland indicators as *Clethrionomys* and glirids. *S. minutissimus* is the only representative of cold tundra conditions, whereas other typical boreal elements, such as lemmings, are completely absent. Thus, the studied fauna shows extremely few forms of both cold–dry and humid–warm conditions, and most taxa are generalized in their ecological preferences. This fact together with the predominance of few arvicoline species suggests transitional climatic conditions either from cold to warm or from warm to cold.

In contrast to the Wannenköpfe-West fauna (Table 4), the Middle Pleistocene small mammal faunas of the Neuwied Basin Tönnchesberg I, Schweinskopf-Karmelenberg, and Wannen include dry–cold adapted taxa (*Spermophilus undulatus*, *Cricetulus migratorius*, *Dicrostonyx gulielmi*, *Lagurus lagurus*, *Microtus gregalis*), which indicate an open steppe environment (Kolfschoten and Roth, 1993). The record of large mammals like mammoth, reindeer, and woolly rhinoceros supports this (Turner, 1991). The latest Saalian fauna of Plaidter Hummerich A (with *Sicista*) most resembles the composition of our new Wannenköpfe-West fauna. Mammals of the beginning of the last glacial period are represented in the Plaidter Hummerich faunal layers C–F. Here, warmer adapted forms like *Clethrionomys glareolus*, *Apodemus*, and *Glis glis*, as well as *Capreolus capreolus* and *Dama dama* among the large mammals can be found together with the above-mentioned rodents indicative of cold and dry climate.

4.3. Biostratigraphy

The dating of the Wannenköpfe-West fauna can be approached by the combination of the evolutionary level of *A.*

Table 4
Faunal list of Wannenköpfe-West (gastropods determined by R. Hutterer, ZFMK)
Tableau 4
Liste faunique de Wannenköpfe-West (gastropodes déterminés par R. Hutterer, ZFMK)

INVERTEBRATA		
GASTROPODA		
Stylommatophora		
	Clausiliidae	gen. et sp. indet. (large)
		gen. et sp. indet. (small)
	Cochlicopidae	*Cochlicopa lubricella*
		Azeca goodalli
	Enidae	*Ena montana*
	Helicarionidae	*Euconulus fulvus*
	Helicidae	Helicinae indet.
	Hygromiidae	?*Trichia* sp.
		?*Monachoides* sp.
	Limacidae	Limacidae indet.
	Pupillidae	*Vertigo* sp.
		Lauria sp. vel *Pupilla* sp.
	Succineidae	*Succinea* sp.
	Valloniidae	*Vallonia pulcella*
VERTEBRATA		
AMPHIBIA	Anura indet. (div. sp.)	
REPTILIA		
Squamata		
	Lacertidae	*Lacerta* sp.
	Squamata indet.	
AVES	Aves indet.	
MAMMALIA		
Soricomorpha		
	Soricidae	*Sorex* ex gr. *araneus*
		Sorex minutus
		Sorex minutissimus
	Talpidae	*Talpa europaea*
Rodentia		
	Sicistinae	*Sicista subtilis*
	Arvicolinae	*Arvicola terrestris*
		Microtus arvalis
		Microtus cf. *multiplex*
		Microtus oeconomus
	Murinae	*Apodemus sylvaticus*
Carnivora		*Mustela nivalis*
		Mustelidae indet.
Artiodactyla		*Bos* vel *Bison* (large)

terrestris with the ecological character of the faunal association. *A. terrestris* with an average SDQ value slightly below 100 argues either for (1) a Saalian age equivalent to the level of Maastricht-Belvedère 4 or (2) for an age equivalent to the transition from late Eemian to early Weichselian. The faunal association lacks, with the exception of *S. minutissimus*, other species indicative of boreal and steppe conditions such as lemmings or *Microtus gregalis*. Small mammals requiring temperate or even warm climatic conditions are rare (*Apodemus*) or absent (e.g. *Clethrionomys glareolus*). As discussed above, the faunal association has a transitional character. Therefore, an age correlation with Maastricht-Belvedère 4 can be excluded because this locality shows no transitional but a truly interglacial faunal association (Kolfschoten, 1985, 2001). The combined results lead to a transitional late Eemian/early Weichselian age for the Wannenköpfe-West fauna (Fig. 6).

Comparable *Arvicola* as in Wannenköpfe-West are known from the late Eemian of Adlerberg/Nördlingen and Stuttgart-Untertürkheim, and from the early Weichselian of Gánovce 2, Burgtonna 2, and Roter Berg/Saalfeld (Heinrich, 1990: Figs. 5 and 7; Koenigswald and Kolfschoten, 1996: Fig. 7; Koenigswald and Heinrich, 1999: Fig. 4). The Wannenköpfe-West fauna is younger than the late Saalian Wannen fauna described by Kolfschoten and Roth (1993).

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