

The Middle Pleistocene Herpetofaunas from Kärlich (Neuwied Basin, Germany)

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ABSTRACT

The Kärlich locality is well known because of the exposure of a long sequence of Quaternary deposits yielding large and small mammal remains as well as early Middle Pleistocene Palaeolithic artifacts. In addition to mammalian remains, the vertebrate record from Kärlich includes amphibians and reptiles in Kärlich units E, G, and H. The most diverse herpetofauna was recovered from level G, and contains at least seven species, including two salamanders, one anuran, and four lizards; Kärlich H yielded at least one salamander and two lizards; and Kärlich E produced a single anuran species.

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INTRODUCTION

Long continental sequences with deposits spanning a number of Quaternary glacial/interglacial cycles are rare in northwestern and central Europe north of the Alps. One of the few quarries exposing a long sequence is located near the village of Kärlich, Germany (Figure 1). The Kärlich pit is situated on the southwestern edge of the Neuwied Basin, a basin situated in the central part of the Rhineland, formed by a combination of uplift of the Rhenish Shield and subsidence of the Neuwied Basin area. The pit has been quarried since the end of the 19th century for its highly valuable Tertiary clay deposits. Overlying the Tertiary clays there are Quaternary deposits dating from the late

Early Pleistocene to the Holocene (Figure 2). These deposits include gravels of the Rhine and Moselle Rivers and an alternation of loess, loess-like, and slope deposits (Brunnacker 1968, 1971; Boenigk and Frechen 2001) and tephras (ashes, pumices), which originate from extinct volcanoes located in the neighbouring East Eifel volcanic field (Van den Bogaard and Schmincke 1990).

A number of lithological/lithostratigraphical units (oldest to youngest: Kä A - Kä J) were defined by Brunnacker (1968). The mainly coarse grained sediments of the Units Kä A, Kä Ba, and Kä Bb are covered by more fine grained sediments, representing several sedimentary cycles, referred to the Units Kä C - Kä H. Units Kä C and Kä D consist of

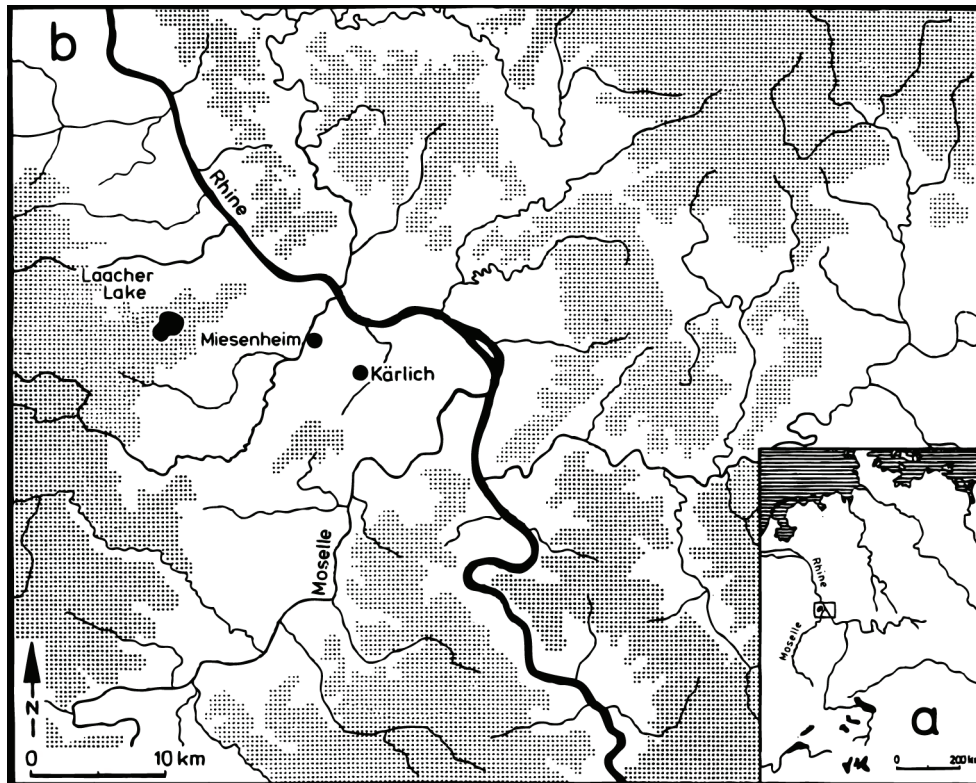


FIGURE 1. Map with the geographical position of the Kärlich (Neuwied Basin, Germany) locality. 1a. Location of the Neuwied Basin in Europe; 1b. Location of the site Kärlich in the Middle Rhine area (Germany).

alternating re-deposited gravels, flood loam deposits, sandy deposits, and slope deposits with stratified calcium concretions, representing three sedimentary cycles separated by erosional unconformities. A clear erosional unconformity forms the lower boundary of Unit Kä E, a unit with cross-bedded sands with mainly fragmented molluscs, the so-called 'Schneckensande.'

The complete sequence of Unit Kä F is bound by erosional unconformities. It contains re-deposited gravels and sands, re-deposited loam, re-deposited loess with thin windblown sand layers at the base, real loess with molluscs, re-deposited loess, real loess, and a Bt horizon. A second soil formation, related with the one in the overlying Unit Kä G, is present in the top of Unit Kä F. The boundary between Unit F and G is obscured. Unit Kä G is rather complex; five sedimentary cycles can be observed in the most complete section. The cycles start with a weak erosional phase, followed by the deposition of fluvial deposits with colluvial sediments, and are completed (in cycles 2, 4 and 5) by soil formation at the top. The soils of Kä G cycles 4 and 5 are well developed. Scattered, isolated large mammal remains and artifacts were found in all levels of Unit Kä G. Unit Kä H, between the top of

Kä G and the base of a well-developed scoria horizon, the 'Kärlicher Brockentuff,' is complex and can be divided into nine sedimentary cycles. The sediments and the observed ice wedges indicate that deposition of these subunits took place mainly under (early, full, and late) glacial conditions alternated with deposition during interstadial and stadial phases. Evidence of interglacial conditions is present in the upper part of Unit Kä H, just beneath the early glacial colluvial sediments with interglacial molluscs at the top of this unit (Boenigk and Frechen 2001).

Paleomagnetic fluctuations are recorded in the lower part of the section. The Matuyama/Brunhes boundary with an age of about 783,000 years is located in Unit Kä Bb (Brunnacker et al. 1976). Reversed paleomagnetic signals, possibly correlative with the Jaramillo event, were recovered from the sediments of Unit Kä A (Boenigk et al. 1974; Brunnacker et al. 1976). Important changes in the heavy-mineral associations also were recognized in the Kärlich sequence (Boenigk and Frechen 2001). Unit G is dominated by brown hornblende, whereas Unit Kä H contains mainly pyroxenes (augite). The hornblende-augite boundary is located in the Dutch Pleistocene sequence at the

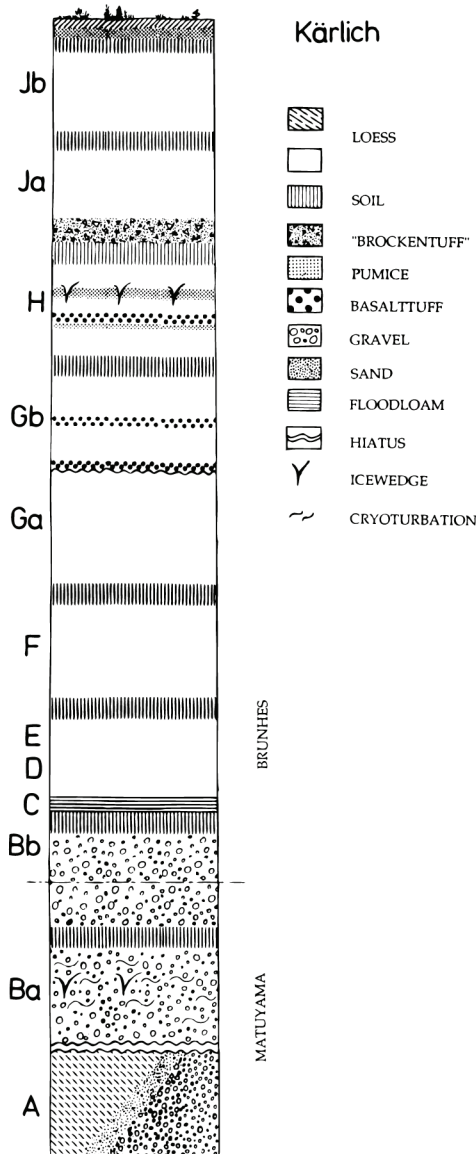


FIGURE 2. Schematic picture of the main sequence at Kärlich (Neuwied Basin, Germany).

transition of late Glacial C to Interglacial IV of the "Cromerian Complex." More detailed descriptions of the Kärlich sequence are available in Boenigk and Frechen (2001), Brunnacker (1968, 1971), and Brunnacker et al. (1969).

The paleomagnetic data and the heavy mineral associations indicate that the Kärlich main section correlates with the late Early Pleistocene (Kä A and Kä Ba) and the early Middle Pleistocene (Kä Bb - Kä G). The stratigraphic position of Kä H remains unclear.

The Quaternary deposits yielded both freshwater and terrestrial molluscs, (Remy and Lozek, in Brunnacker 1971; Roth 1995), paleobotanical remains (pollen and macrofossils) (Urban 1983; Bittmann 1988, 1990), and Palaeolithic artifacts (e.g., Bosinski et al. 1980; Vollbrecht 1994). Several stratified mammalian faunas, within which the *Mimomys* - *Arvicola* transition occurs, were collected from the Pleistocene sequence (Kärlich main section - Kä A - Kä H) exposed in the Kärlich pit (van Kolfschoten and Turner 1996). The older faunas Kä C - Kä F are characterized by the presence of *Mimomys savini*. The oldest representatives of the water vole, *Arvicola terrestris cantiana*, were recovered in the rich fauna from Kä G.

The Kä C fauna includes *Microtus gregaloides* and represents open environment and continental climatic conditions. The Kä E faunal assemblages is characterized by the occurrence of *Dicrostonyx* sp., indicative of an open environment and cool, glacial climatic conditions, and *Clethrionomys glareolus* and *Apodemus* sp, indicative of a more wooded environment and more temperate conditions. The presence of *Dicrostonyx* and *Spermophilus* in the Kä F fauna indicates an open environment, and *Dicrostonyx* suggests cold climatic conditions. *Clethrionomys* sp. points to the occurrence of at least locally forested areas. The composition of the Kä G assemblage indicates an environment with bodies of water, forested areas (most probably along the beds of the river), and areas with steppe vegetation outside the river valley. The relatively high percentage of *Clethrionomys glareolus*, *Apodemus sylvaticus* and *Apodemus* cf. *maastrichtiensis*, and the occurrence of *Eliomys quercinus* point to interglacial, or at least interstadial, climatic conditions during deposition of Kä G. The faunal record from Kä H is rather poor; the number of fossils remains is low, and the identified species are not very informative.

The amphibian and reptiles record from Kärlich is restricted to units Kä E, Kä G, and Kä H. The amphibians and reptiles are listed in Table 1. The stratigraphic and paleoecological conclusions that can be drawn based on their occurrence are also discussed below.

SYSTEMATIC DESCRIPTION OF THE HERPETOFAUNA FROM THE KÄRLICH MAIN SECTION

The fossil material was identified through comparisons with specimens of extant species from western and central Europe. Due to the limited comparisons, the occurrence of bufonids and lacertids restricted to other parts of Europe and

TABLE 1. The Herpetofauna of the Kärlich Middle Pleistocene Levels E, G, and H.

Species	E	G	H
<i>Triturus cristatus</i>		+	
cf. <i>Triturus vulgaris</i>		+	
<i>Triturus vulgaris</i> or <i>T. helveticus</i>			+
<i>Bufo bufo</i>		+	
<i>Bufo</i> sp. indet.	+	+	
cf. <i>Lacerta agilis</i>		+	
<i>Lacerta</i> sp. (large species)		+	
<i>Lacerta vivipara</i>		+	
cf. <i>Lacerta</i> or <i>Podarcis</i> sp. indet.			+
<i>Anguis fragilis</i>		+	+

regions such as the Near East cannot be excluded with certainty.

The fossil material is stored in the collection of the Faculty of Archeology (FdA), Leiden University, The Netherlands.

Class AMPHIBIA Linnaeus, 1758

Order CAUDATA Opperl, 1811

Family SALAMANDRIDAE Gray, 1825

The family Salamandridae has a wide distribution at present, occurring in Britain, Eurasia, north-western Africa in the Old World, and from southern Canada through the United States into northern Mexico in the New World (Frost 1985). Species that presently occur in Germany are *Salamandra salamandra*, *S. atra*, *Triturus alpestris*, *T. carnifex*, *T. cristatus*, *T. helveticus*, and *T. vulgaris* (Günther 1996). *Triturus cristatus*, *T. vulgaris*, and *T. vulgaris* or *T. helveticus* were recovered from the Pleistocene deposits at Kärlich.

Triturus cristatus (Laurenti, 1768)

Northern Crested Newt

Material. One trunk vertebra from Kä G. (FdA-Kä G nr. 8001).

Remarks. Trunk vertebrae of *Triturus cristatus* differ from those of *T. alpestris*, *T. helveticus*, *T. marmoratus*, and *T. vulgaris* in having the posterior border of the neural arch flared and continuing well behind the level of the postzygapophyses (see Holman and Stuart 1991: Figure 1a). The trunk vertebrae of *T. cristatus* further differ from those of *T. alpestris*, *T. helveticus*, and *T. vulgaris* in being larger and in having a much lower neural spine. Northern crested newts often are aquatic throughout the year, although in some situations they become terrestrial during the non-breeding season. These large newts prefer still or slowly flowing water with large amounts of aquatic vegetation (Arnold and Burton 1978). *Triturus cristatus* previously was called the 'warty newt' or the 'great

crested newt,' but the common name now is standardized as 'the northern crested newt' (Frank and Ramus 1995). *Triturus cristatus* presently occurs in the vicinity of Kärlich (Grosse and Günther 1996).

cf. *Triturus vulgaris* (Linnaeus, 1758)
Smooth Newt

Material. One trunk vertebra from Kä G. (FdA-KäG nr. 8002).

Remarks. The trunk vertebrae of *Triturus vulgaris* may be distinguished from those of *T. helveticus* on the basis of having a deeper and less broadly U-shaped notch in the posterior border of the neural arch (Holman and Stuart 1991, figures 1b and 1c). This notch also tends to be deeper in *T. vulgaris* than in *T. alpestris*, but there is some overlap in this character. Nevertheless, *T. alpestris*, a medium-sized salamander, has larger vertebrae than the smaller species, *T. vulgaris*. The smooth newt presently occurs in the Kärlich area (Buschendorf and Günther 1996), spends more time on land than most other species of European newts, and lives in a variety of damp terrestrial habitats. It breeds in shallow, still water with ample vegetation.

Triturus vulgaris (Linnaeus, 1758) or *T. helveticus* (Razoumowsky, 1789)

Smooth Newt or Palmate Newt

Material. A fragmentary vertebra from Kä H. (FdA-KäH nr. 8001).

Remarks. This small vertebrae represents either a smooth newt or a palmate newt, but the bone is not complete enough to be identified to the specific level. Both forms occur at or near the Kärlich area today (Buschendorf and Günther 1996; Schlüppmann et al. 1996).

Order ANURA Rafinesque, 1815

Family BUFONIDAE Gray, 1825

The family Bufonidae is cosmopolitan in distribution except for Australia, Madagascar, and isolated oceanic islands (Frost 1985). Species that presently occur in Germany are *Bufo bufo*, *B. calamita*, and *B. viridis* (Günther 1996). *Bufo bufo* and *Bufo* sp. indet. were found in the Pleistocene at Kärlich.

Bufo bufo (Linnaeus, 1758)

Common European Toad

Material. One right distal humerus of a male individual from KäG, (FdA-KäG nr. 8003) (Figure 3).

Remarks. The humerus is identified as a male on the basis of its enlarged mesial crest (Bailón 1986). The fossil humerus may be separated from those of male specimens of the two other European

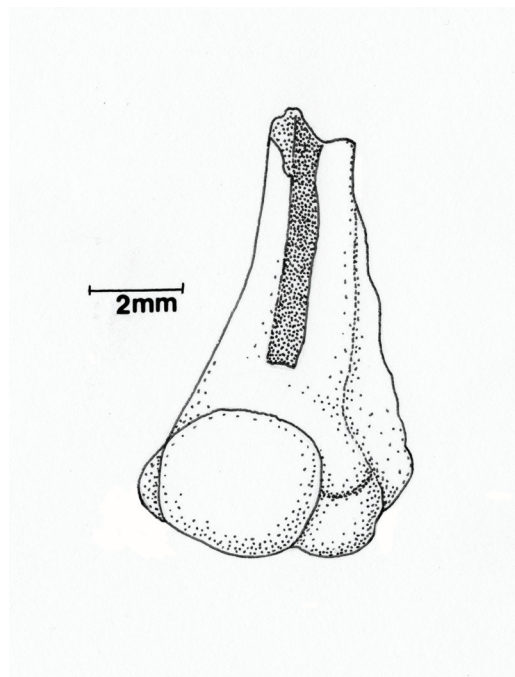


FIGURE 3. Right distal humerus of a male individual (ventral view) of *Bufo bufo* from Kä G. (FdA-KäG nr. 8003).

toads (*Bufo calamita* Laurenti and *B. viridis* Laurenti) because the shaft is more robust and less curved, the distal condyle is wider, the radial epicondyle is more distally swollen, and the mesial crest is shorter and wider (see Bailón 1986, figure 4).

Bufo bufo occurs in the Kärlich area today (Günther and Geiger 1996). The common European toad is the most widespread of the three European toad species and occurs in a large variety of habitats, some being rather dry. In southern Europe, *Bufo bufo* may reach a very large size (Arnold and Burton 1978). *Bufo bufo* previously was called the 'common toad,' but its vernacular name was recently standardized as the 'common European toad' (Frank and Ramus 1995).

Bufo sp. indet.

Material. A damaged right distal humerus of an immature individual (FdA-KäG nr. 8004) and a damaged right scapula (FdA-KäG nr. 8005) from Kä G. A fragmentary scapula of a juvenile individual (FdA-KäE nr. 8001) from E.

Remarks. Unfortunately the humerus is too damaged to identify to the specific level. We used characters given by Hallock et al. (1990) to distinguish the scapula of *Bufo* from *Rana* and other European anurans. The authors state that "scapulae of *Bufo*

may be separated from those of *Rana* on the basis that *Bufo* lacks the ridge on the dorsomedial side of the scapula that occurs in *Rana*. Moreover, the ventral end of the scapula is more deeply notched in *Bufo* than it is in *Rana*."

Class REPTILIA Laurenti, 1768

Order SAURIA McCartney, 1802

Family LACERTIDAE Bonaparte, 1831

The Lacertidae is a widespread Old World lizard group that occurs in Europe, Africa, and much of Asia (Estes 1983). The six species that occur in Germany today are *Lacerta agilis*, *L. bilineata*, *L. horvathi*, *L. viridis*, *L. vivipara*, and *Podarcis muralis* (Günther 1996). Cf. *Lacerta agilis*, *Lacerta* sp. (large species), *L. vivipara*, and *Lacerta* or *Podarcis* species have been identified in the Pleistocene record of Kärlich.

cf. *Lacerta agilis* Linnaeus, 1758

Sand Lizard

Material. One essentially complete right dentary (FdA-KäG nr. 8006), one partial left dentary (FdA-KäG nr. 8007)(Figure 4), and one partial maxilla (FdA-KäG nr. 8008) from Kä G.

Remarks. The right dentary has 21 teeth and alveolar spaces, and the tooth row is 5.6 mm in length. The dentary differs from the large *Lacerta* species *L. lepida* and *L. viridis* in being smaller (much smaller than in a modern adult *L. lepida* specimen Michigan State University (MSU I643) which has a tooth row 22.0 mm long), by having fewer dentary teeth (many fewer than in two modern *L. lepida* (MSU I643, and Museo Nacional de Ciencias Naturales, Madrid (MNCN) I6506) which, respectively, have 27 and 28 dentary teeth, and by lacking tricuspid teeth in the dentary (tricuspid teeth are present in *L. lepida* and *L. viridis*).

The right dentary differs from the small Lacertidae species, *L. vivipara* and *Podarcis muralis* in being larger (tooth row usually less than 5.0 mm in *L. vivipara* and *P. muralis*), in having all of the dentary teeth more swollen and robust, in having the anterior teeth less pointed and posteriorly curved, and in having the Meckelian groove with its borders more robust. The less complete dentary agrees with the right dentary in all of the characters above.

The partial maxilla has only unicuspid and bicuspid teeth present as in *L. agilis* and *P. muralis*, but differs from *P. muralis* in having larger and more robust teeth. The teeth fossils appear identical to those in modern adult specimens of *L. agilis* from MNCN and National Museum of Natural History Leiden (NMNH). At present, *Lacerta agilis*

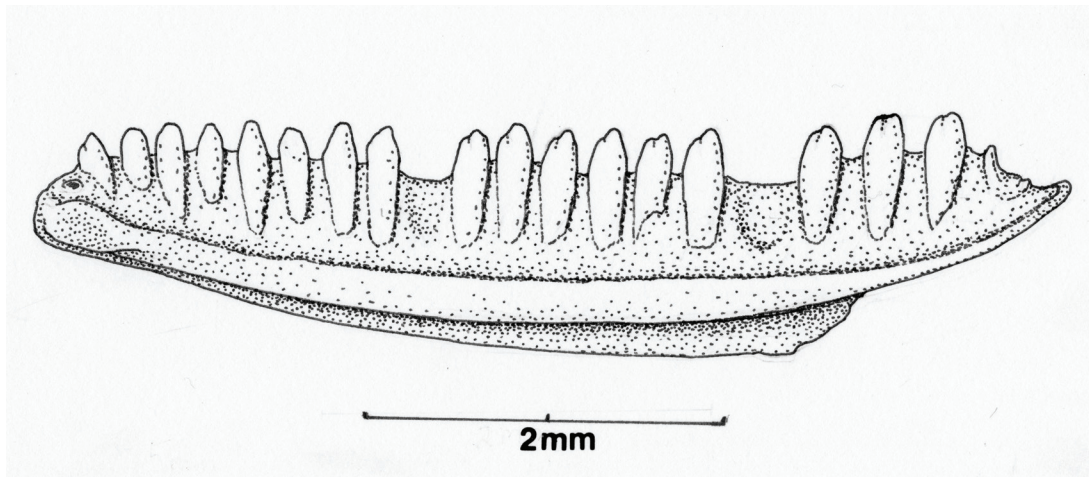


FIGURE 4. Right dentary (lingual view) of *Lacerta agilis* from Kä G. (FdA-KäG nr. 8007).

occurs throughout most of Germany, including the Kärlich area (Ebling et al. 1996). The sand lizard lives throughout its range in rather dry habitats, i.e., in areas with sandy, well-drained soils. In England and northern Europe, it is usually found on coastal sand dunes with some plant cover or in sandy heathland (Arnold and Burton 1978).

Lacerta sp. (large species)

Material. Six partial maxillae (all with teeth) (FdA-KäG nr. 8009 - 8014) (Figure 5), and one vertebra (FdA-KäG nr. 8015) from Kä G.

Remarks. These six maxillae represent a large species of *Lacerta*. They bear teeth that are the same size and appear identical to those of an adult *Lacerta viridis* from the Natural History Museum Naturalis, Leiden with a skull length of 23.2 mm and are larger than those of an adult *L. agilis* from the NMNH with a skull length of 19.0 mm. The maxillae further differ from those of *L. agilis* in having tricuspid teeth present on the maxillary (Figure 5.1, 5.2, and 5.3); tricuspid teeth are lacking in adult *L. agilis*. On the other hand, these teeth are much smaller than those of an adult *L. lepida* from the MSU collection, a specimen that also lacks tricuspid maxillary teeth. The vertebra has a centrum length of 3.3 mm, and, thus, is larger than those in available *L. agilis* specimens, but still much smaller than those of *L. lepida*. Specific identification of the large *Lacerta* awaits more fossil and modern comparative material.

Lacerta vivipara Jaquin, 1787
 Viviparous Lizard

Material. Two left (FdA-KäG nr. 8016 - 8017) (Figure 6.1) and four right partial dentaries (FdA-KäG nr. 8018 - 8021) (Figure 6.2); two left (FdA-KäG nr.

8022 - 8023) and two right maxillae (FdA-KäG nr. 8024 - 8025); and one maxillary fragment (FdA-KäG nr. 8026), all bearing teeth, from Kä G.

Remarks. The dentaries differ strongly from *L. agilis*, *L. lepida*, and *L. viridis* in being smaller (much smaller than in *L. lepida* and *L. viridis*), having the teeth much more gracile, with the anterior teeth more pointed and usually more posteriorly curved, and with the borders of the Meckelian groove much less swollen and robust. The dentaries differ from *P. muralis* in having several tricuspid teeth in each of the dentary bones, whereas *P. muralis* has all of its teeth in the maxillary and the dentary bones unicuspid or bicuspid.

The maxillae also are smaller and their teeth much more gracile than in *L. agilis*, *L. lepida*, and *L. viridis*. The maxillae further differ from *L. agilis* and *P. muralis* in bearing tricuspid teeth. All of these elements seem identical to those in four modern adult MSU *Lacerta vivipara* skeletal specimens.

Lacerta vivipara occurs in the Kärlich area today (Günther and Völkl 1996a). At present it is a ground-dwelling lizard that is found in many kinds of open situations such as heathlands, open woods, and grasslands.

cf. *Lacerta* or *Podarcis* sp. indet.
 Small Lacertid species

Material. A small, fragmentary vertebra from Kä H (FdA-KäH nr. 8002).

Remarks. This triangular-shaped lizard vertebra represents either *Podarcis* or one of the small species of *Lacerta*, such as *L. vivipara*.

Family ANGUIDAE Gray, 1825

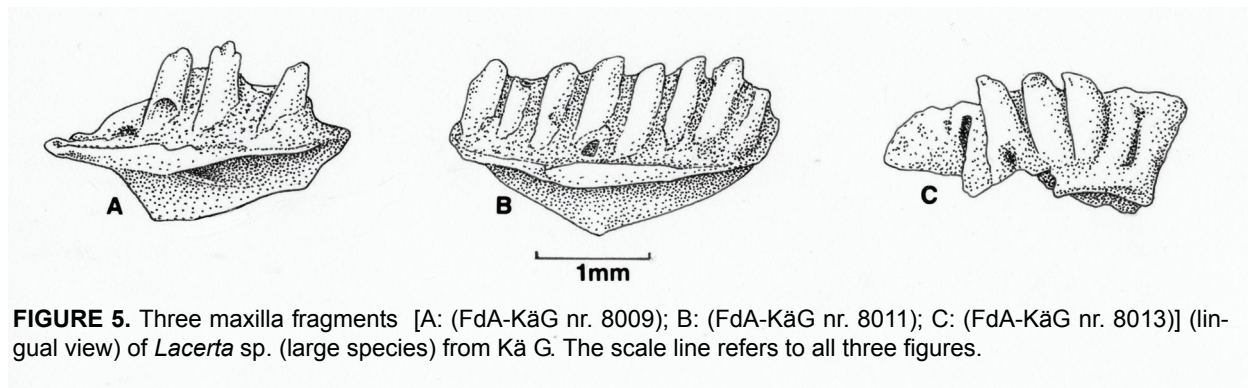


FIGURE 5. Three maxilla fragments [A: (FdA-KäG nr. 8009); B: (FdA-KäG nr. 8011); C: (FdA-KäG nr. 8013)] (lingual view) of *Lacerta* sp. (large species) from Kä G. The scale line refers to all three figures.

The subfamily Anguinae is a Holarctic group that is widespread in the United States and Mexico and is represented by both limb-bearing and limbless species. In Europe, however, there are only two monotypic genera, *Anguis fragilis*, and *Ophisaurus apodus*, both of which are limbless. Only one species, *Anguis fragilis*, presently occurs in Germany, and that species was found in the Pleistocene of the Kärlich locality.

Anguis fragilis Linnaeus, 1758
Slow Worm

Material. One hundred and twelve trunk vertebrae, 21 caudal vertebrae, and five osteoscutes from Kä G. Nine trunk vertebrae are from Kä H (FdA-KäH nr. 8003-8011).

Remarks. Trunk vertebrae, caudal vertebrae, and osteoscutes of *Anguis fragilis* are all characteristic, and can only be confused with those of *Ophisaurus apodus*, a very much larger form. Holman (1998) gives characters that distinguish the vertebrae of the two species. The trunk vertebrae are particu-

larly diagnostic, being quadrangular in shape, having very large prezygapophyseal and postzygapophyseal articular surfaces, and with the ventral surface of the centrum very flat and smooth. The caudal vertebrae have conspicuous fracture planes in them and the tails of slow worms are easily broken, allowing the animals to escape from predators that seize them behind the anal region.

The limbless slow worm lizard prefers habitats that are well covered with vegetation and other ground cover, and prefers somewhat damper environs than the previous lizard species. The species occurs in the Kärlich area today (Günther and Völkl 1996b).

DISCUSSION AND CONCLUSIONS

The only level with a diverse herpetofauna is Kä G, which yielded at least seven species, including two salamanders, one anuran, and four lizards (Table 1). Kä H yielded at least one salamander

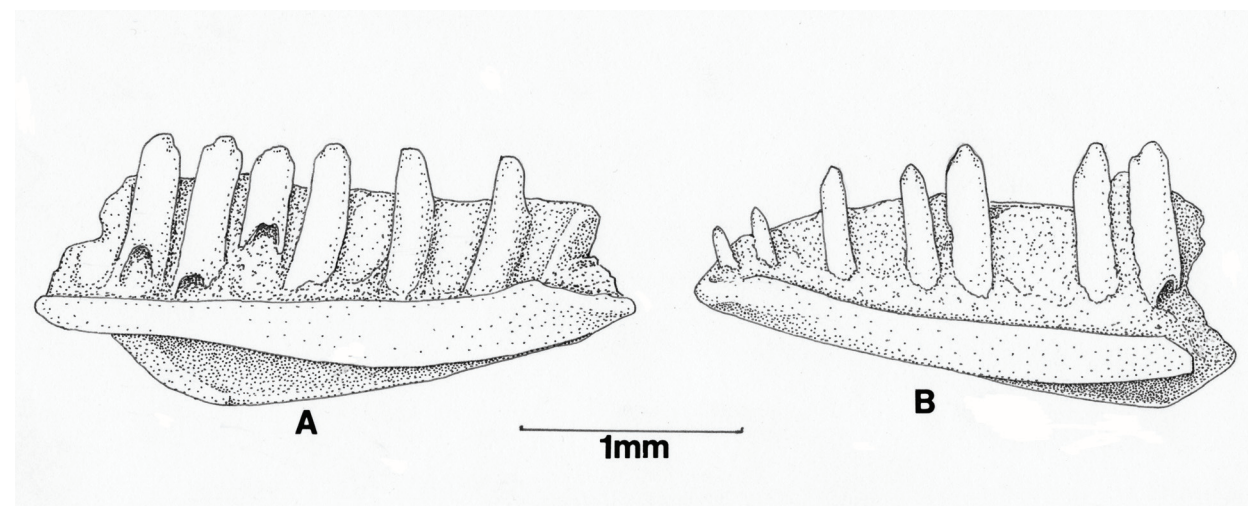


FIGURE 6. Left (A) (FdA-KäG nr. 8016) and right (B) (FdA-KäG nr. 8018) partial dentaries (lingual view) of *Lacerta vivipara* from KäG. The scale line refers to both figures.

anuran species. The fossil material has been referred to extant species that occur in the area today.

Palaeoecological considerations

If we assume that extant Pleistocene amphibians and reptiles had similar ecological preferences and tolerances as they do today, herpetological assemblages can be useful to reconstruct the general habitats or even the biotopes present during the time of the deposition of the bones.

The fossils assemblage from Kä G is the only assemblage that is extensive enough from which to draw ecological conclusions. The presence of the amphibians *Triturus cristatus*, *Triturus vulgaris* and *Bufo bufo* indicate that a still-water habitat such as a marsh or pond had to be present near the site for these animals to breed. The presence of *Anguis fragilis* suggests that low vegetation and ground cover must have been present; and the lizards, especially *Lacerta agilis*, indicate that a relatively dry, at least somewhat sandy habitat, must have been available. These conclusions are supported by the paleoenvironmental reconstruction based on the accompanying mammalian assemblage. The mammalian fossil record indicates the alternation of forested areas with forest dwellers such as *Eliomys quercinus* and *Apodemus sylvaticus* alternated with areas with a prevailing steppic environment in which hamsters such as *Cricetus cricetus* and *Cricetus major* occurred. The semi-aquatic water vole, *Arvicola terrestris cantianus*, indicates the occurrence of slow moving, calm water.

The fact that all of the amphibians and reptiles of the Kärlich localities almost certainly represent extant forms is consistent with previous studies of Pleistocene amphibians and reptiles in Britain, Europe, and North America (see citations in Holman 1991, 1995, 1998). The stability of Pleistocene herpetofaunas during and at the end of the Pleistocene is a subject of considerable discussion today (e.g., Holman 1991, 1995, 1998). This is because the mammalian fauna, and (to a somewhat lesser extent) the avifauna, suffered much familial, generic, and specific extinction during the same time interval. These extinctions in the endothermic fauna were extensively discussed in the past two decades (e.g., Martin and Klein 1984). Holman (1991) posed the questions "What attributes have allowed the herpetofauna to survive the stresses that have caused dramatic extinctions in other classes during the Pleistocene." Beside other suggestions, such as the possible advantages of

being ectothermic rather than endothermic, some paleontological evidence has suggested the possibility that amphibians and reptiles might not have been as dependent upon the large endothermic species (mammalian megafauna) that became extinct during the Pleistocene as were certain predators, scavengers, or commensals (Holman 1991). For instance, at the famous Rancho La Brea Late Pleistocene site in California, scavenging or commensal birds and dung beetles became extinct along with the mammalian megafauna, but all of the amphibians and reptiles at Rancho La Brea survived into the present (Holman 1995). On the other hand, in Australia, the gigantic monitor lizard *Megalania* and the huge snake *Wonambi* (Murray 1984) were top predators and became extinct during the Pleistocene, presumably because the many large marsupials that they preyed upon died out during the epoch. Oddly, few suggestions have been made in Britain, Europe, or North America about the possible ecological relationships of amphibians and reptiles to the large extinct mammals.

We might suggest here that it is possible that the small, ectothermic amphibians and reptiles of Europe (and elsewhere) were a not significant enough part of the food web of the large mammalian herbivores, predators, and scavengers to have been highly influenced by the disappearance of these mammals.

Stratigraphic comments

Based on the evolutionary stasis of most of the Pleistocene herpetofauna (Holman 1995, 1998), one might doubt the usefulness of Pleistocene amphibians and reptiles in Pleistocene stratigraphic studies. Nevertheless, in England certain Pleistocene herpetological species with limited tolerances to cold temperatures (e.g., *Hyla arborea*, *Hyla meridionalis*, *Emys orbicularis*, and *Elaphe longissima*) are characteristically associated with temperate interglacial stages (e.g., Holman 1992, 1993; Ashton et al. 1994). On the other hand, amphibians and reptiles with broad tolerances to climatic conditions (*Bufo bufo*, *Rana temporaria*, and *Lacerta vivipara*) are the only British amphibians and reptiles (with one exception) to be found in cold, glacial stage faunas (e.g., Holman 1993, 1995). Therefore, in a broad sense, amphibian and reptile faunas are stratigraphically important, at least in indicating whether deposits represent temperate interglacial or cold glacial stages. In the Kä G fauna, for instance, the common European toad (*Bufo bufo*) and the viviparous lizard (*Lacerta*

vivipara) have broad climatic tolerances and could be representative of either glacial or interglacial stages. On the other hand, the large *Lacerta* species, perhaps representing the green lizard (*Lacerta viridis*), could be indicative of a temperate stage of the Pleistocene (Böhme 1996). The fact that all the fossil remains from the Kärlich deposits have been referred to amphibians and reptiles that occur in the vicinity at present would indicate that the climate during Kä G time was rather similar to what it is in modern times, a conclusion supported by the extensive smaller mammal fauna.

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