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The Miocene Herpetofaunas of Grund (Caudata; Chelonii, Sauria, Serpentes) and Mühlbach am Manhartsberg (Chelonii, Sauria, Amphisbaenia, Serpentes), Lower Austria

by PETRA MARIA MIKLAS-TEMPFER[1]

(With 14 text-figures and 4 plates)

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Abstract

The herpetofaunas of the two Middle Miocene localities Grund (near Hollabrunn, Lower Austria; MN5) and Mühlbach am Manhartsberg (near Maissau, Lower Austria; MN5) are presented. While that of Grund is composed of Amphibia: *Salamandra sansaniensis* (Salamandridae) and Reptilia: *Testudo* sp. (Testudinidae); *Ptychogaster grundensis* (Bataguridae); Anguidae indet.; *Elaphe kohfidischi* (Colubridae) as well as *Naja romani* (Elapidae), the herpetofauna of Mühlbach consists of Reptilia only, such as Chelonii indet., cf. *Mauremys* sp. (Emydidae); cf. *Lacerta* sp. (Lacertidae); *Ophisaurus* sp., cf. *Ophisaurus* sp. (Anguidae); *Blanus antiquus*, cf. *Blanus* cf. *antiquus* (Amphisbaenidae); Colubrinae indet. and Natricinae indet. (Colubridae). The sedimentology and most of the fossil groups indicate marine conditions, whereas the herpetofaunas of both localities most probably belong to the fauna-association of the hinterland. In Grund, the environment was dry and woody, whereas in Mühlbach more humid conditions are indicated.

Zusammenfassung

Die Herpetofaunen der beiden mittelmiozänen Fundstellen Grund (bei Hollabrunn, Niederösterreich; MN5) und Mühlbach am Manhartsberg (bei Maissau, Niederösterreich; MN5) werden vorgestellt. Während jener von Grund sowohl Amphibia: *Salamandra sansaniensis* (Salamandridae) als auch Reptilia: *Testudo* sp. (Testudinidae); *Ptychogaster grundensis* (Bataguridae); Anguidae indet.; *Elaphe kohfidischi* (Colubridae) sowie *Naja romani* (Elapidae) angehören, finden sich in der Herpetofauna von Mühlbach ausschließlich die Reptilia Chelonii indet., cf. *Mauremys* sp. (Emydidae); cf. *Lacerta* sp. (Lacertidae); *Ophisaurus* sp., cf. *Ophisaurus* sp. (Anguidae); *Blanus antiquus*, cf. *Blanus* cf. *antiquus* (Amphisbaenidae); Colubrinae indet. und Natricinae indet. (Colubridae). Da die Sedimentologie der Fundstellen und die vorhandenen anderen zoologischen Taxa vorwiegend marine Bedingungen anzeigen, dürften die Herpetofaunen dem jeweiligen Hinterland entstammen. In Grund lag ein trockener, waldreicher Lebensraum vor, während in Mühlbach feuchtere Bedingungen vorherrschend waren.

Introduction

The localities Grund near Hollabrunn, Lower Austria, and Mühlbach at the Manhartsberg near Maissau, Lower Austria, can both be correlated with the Mammal Zone MN 5 of the Lower Lagenidae Zone (DAXNER-HÖCK 2003). RÖGL & SPEZZAFERRI (2003) have

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[1] Mag. Petra Maria MIKLAS-TEMPFER, Naturhistorisches Museum Wien, Burgring 7, A-1014 Wien. – e-mail: petra.tempfer@nhm-wien.ac.at

pointed out an absolute age of about 15.1 ma. The two localities belong to the upper part of the Grund beds ("Obere Grunder Schichten") in the Alpine Molasse Basin (Fig. 1).

In **Grund**, the deposits of the Grund-Formation represent channel-fillings. Sandy sediments and pelite clusts containing the terrestrial elements alternate. During short, high energetic sedimentation the sands were deposited, whereas the pelites originate from low energetic, quiet sedimentation. This situation in Grund is comparable with a gently sloping shore where terrestrial elements also assembled; these were then mixed up with the marine elements during short-term storm events (Roetzel et al. 1999). More detailed information concerning the geological situation is given by Roetzel & Pervesler (in press). The Institut für Paläontologie der Universität Wien and the Geol.-Pal. Abteilung des Naturhistorischen Museums Wien have organized the excavations in Grund in 1998 and 1999. Part of the material originates from the collection of A. Kroh. The herpetofauna is composed as follows:

Grund:

Amphibia:

Caudata:
Salamandridae: *Salamandra sansaniensis*

Reptilia:

Chelonii:
Testudinidae: *Testudo* sp.
Bataguridae: *Ptychogaster grundensis*

Sauria:
Anguidae: Anguidae indet.

Serpentes:
Colubridae: *Elaphe kohfidischi*
Elapidae: *Naja romani*

From an ecological point of view, the herpetofauna in Grund indicates very dry conditions and a dense vegetation.

The sediments of **Mühlbach am Manhartsberg** belong to the Gaindorf-Formation, which replaces the Grund-Formation to the west (Roetzel et al. 1999). Within pelite-rich sediments, layers of middle and fine marine sands contain not only deep-water foraminifera among other marine elements, but also amphibians, reptiles and small mammals. The latter most probably were transported into sublittoral marine areas during storm events (Roetzel 2003). In 1996, G. Daxner-Höck of the Geol.-Pal. Abteilung des Naturhistorischen Museums Wien conducted a dig in Mühlbach am Manhartsberg. The herpetofauna is composed as follows:

Mühlbach am Manhartsberg:

Reptilia:

Chelonii: Chelonii indet.
Emydidae: cf. *Mauremys* sp.

Sauria:
Lacertidae: cf. *Lacerta* sp.
Anguidae: *Ophisaurus* sp.
cf. *Ophisaurus* sp.

Amphisbaenia:
Amphisbaenidae: *Blanus antiquus*
cf. *Blanus* cf. *antiquus*

Serpentes:
Colubrida: Colubrinae indet.
Natricinae indet.

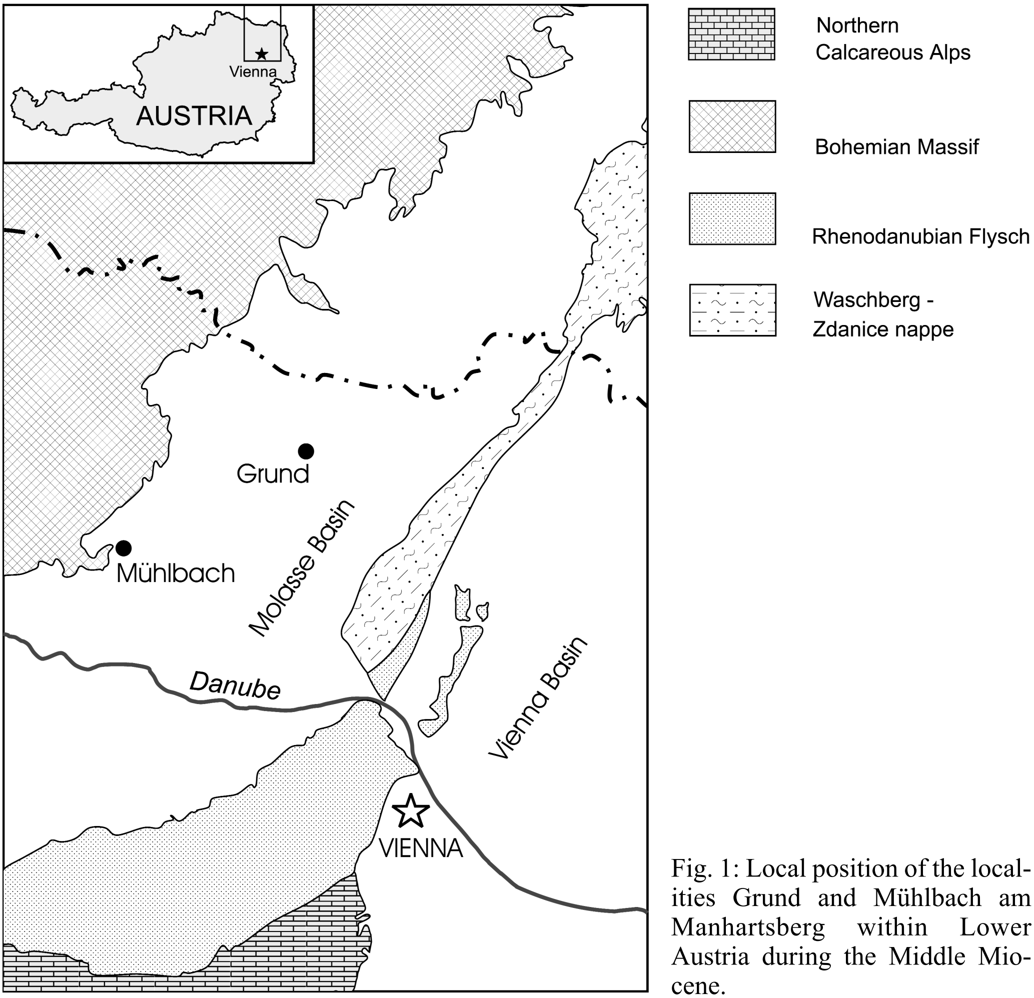

Fig. 1: Local position of the localities Grund and Mühlbach am Manhartsberg within Lower Austria during the Middle Miocene.

Ecologically, the herpetofauna of Mühlbach am Manhartsberg points to a moist area such as a small standing water or a slowly flowing river within a woody, mainly dry environment.

The fossil material is deposited in the Geol.-Pal. Abteilung des Naturhistorischen Museums Wien except for one fragment of a carapace, which is part of the collection of the Institut für Paläontologie der Universität Wien.

Methods

Bones and fragments were measured using a Leica MZ 6 microscope with a graduated dial 12mm : 120 with reticule. A drawing mirrow was connected to the same microscope to make the illustrations. The photographs were taken with a Nikon COOLPIX 990 digital camera connected to a WILD M420 microscope.

Systematic Part

Grund

Class Amphibia
Order Caudata Oppel, 1811
Suborder Salamandroidea Noble, 1931
Family Salamandridae Gray, 1825
Salamandra Laurenti, 1768

***Salamandra sansaniensis* Lartet, 1851** (Fig. 2; Plate 1: A, B)

Locality and Stratigraphy: Grund (GRU-B1-1), Lower Austria; sand of the Grund Formation (Roetzel et al. 1999), Lower Badenian, MN5.

Material: 1 trunk vertebra (GRU-B1-1: Inv. Nr.: NHMW2002z0094/0000)

Description: This single trunk vertebra lacking parts of the processus transversi is broken anterodorsally as well as laterally. Due to mechanical influences, it seems to be compressed slightly dorsoventrally. Its measurements are as follows: GL=7.52 mm; PB=5.9 mm; WL=5.2 mm; WH=1.3 mm (sensu Haller-Probst & Schleich 1994). The very broad, flat and opisthocoelous vertebra most probably originates from the posterior region because the posterior border of the neural arch shows prominent projections. The preserved posterior neural spine is flat but clearly developed. The pre- and postzygapophyses are round and the dorsoventrally flattened condyle bears a pit in the middle. Ventrally, two big foramina are present at the base of the processus transversi.

Comparison: The identification of this vertebra as *Salamandra sansaniensis* is based on the descriptions given by Estes & Hoffstetter (1976) from the Middle Miocene locality La Grive-Saint Alban in France. The unusually very broad shape resembles *Salamandra broilii* as described by Herre (1955) from the Upper Miocene locality Neudorf an der March (CZ), but Estes (1981) has referred this taxon to *S. sansaniensis* because the vertebral measurements fall within the range of variation seen in the holotype. Moreover, the vertebrae of *Salamandra sansaniensis* of the Lower Miocene of Oberdorf near Graz (Sanchiz 1998), the second Austrian locality where this species has already been described, are narrower than the one presented in this paper. It is much broader and larger than the vertebra of a recent living species of the genus *Salamandra* such as *S. salamandra.*

Discussion: The stratigraphic range of *Salamandra sansaniensis* spans from the Upper Eocene (Rage 1988a) to the Upper Miocene of Europe (Estes 1981). Widespread in Europe during the Tertiary, *Salamandra sansaniensis* most probably represents the ancestor of the living species *S. salamandra* and *S. atra* (Estes & Hoffstetter 1976). The recent distribution of *Salamandra salamandra* is Europe west of the Caucasus, whereas *S. atra* is restricted to the Alps and alpine regions of the Western Balkan Peninsula up to Albania. The glacial period can by no means be considered a reason for the extinction of *S. sansaniensis* and the speciation resulting in both *S. salamandra* and *S. atra* because SANCHIZ & MLYNARSKY (1979) have described *Salamandra salamandra* from a Pliocene Polish locality. SANCHIZ (1998) mentions close similarities between *Salamandra sansaniensis* and the living form *S. infraimmaculata* (MARTENS, 1885) from Turkey, Lebanon and Israel.

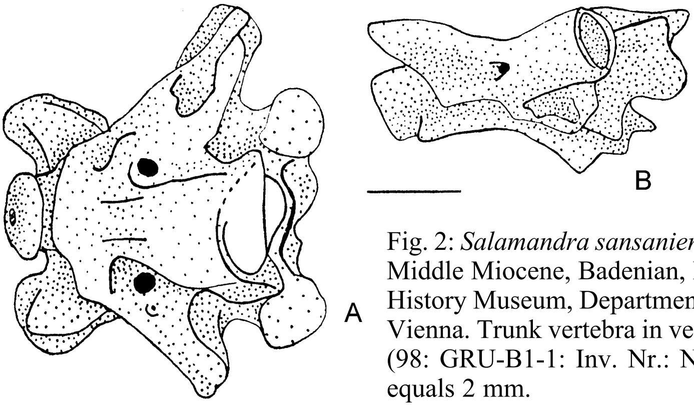

Fig. 2: *Salamandra sansaniensis* from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in ventral (A) and in lateral (B) view (98: GRU-B1-1: Inv. Nr.: NHMW2002z0094/0000). Scale equals 2 mm.

Class Reptilia

Order Chelonii BRONGNIART, 1800

Suborder Cryptodira COPE, 1868

Superfamily Testudinoidea BATSCH, 1788

Family Testudinidae GRAY 1822

Testudo LINNAEUS 1758

***Testudo* sp.** (Fig. 3)

Locality and Stratigraphy: Grund, Lower Austria; sand of the Grund Formation (ROETZEL et al. 1999), Lower Badenian, MN5.

Material: 1 element of carapace (Coll. Inst. f. Pal. Uni Wien, Inv. Nr.: IPUW3127)

Description: Viewed from lateral, this left peripheral VIII is 3.8 cm high and 1.4 cm wide dorsally respectively 1.9 cm wide ventrally. A slightly inclined groove dividing the marginialia VII and VIII extends from the posterior part of the dorsal border to the ventral, more anterior border.

In anterior view, the greatest width measures 0.9 cm, while from posterior it measures 1.3 cm.

From the ventral perspective, the element is triangular, directing the vertex cranially. The material is spongeous.

Comparison: The spongeous consistency of the carapace is suggestive of a tortoise. The peripheral is thick, forming together with the others a massive border as is typical for adult specimens of *Testudo*. Characteristically, the groove dividing the marginalia is very well visible. Based on a comparison with carapaces of recent living species of the genus *Testudo,* this carapace element has been attributed to *Testudo* sp.

Discussion: Finding a carapace element of *Testudo* sp. in Grund supplements the humerus described by BACHMAYER & SCHAFFER (1959) from the same locality. *Testudo* appears in the Eocene of Eurasia. The recent distribution also includes North Africa from Morocco to Egypt. *Testudo* is divided by MLYNARSKY (1976) into three groups: 1. "*Graeca-antiqua*"- 2. "*Kalksburgensis*"- and 3. "*Pyrenaica-stehlini*"-group. On the other hand, SCHLEICH (1981) distinguishes four groups within South Germany: 1. "*antiqua*"- 2. "*graeca-hermanni*"- 3. "*kalksburgensis*"- and the "*promarginata*"-complex. Both MLYNARSKY (1976) and SCHLEICH (1981) refer to characteristics concerning the carapace and plastron elements. LAPPARENT DE BROIN (2001) differentiates between the *Testudo* sensu stricto-group containing living species and the *Testudo* sensu lato-group consisting of fossil species as well. The fossil genus *Paleotestudo* has been set up by LAPPARENT DE BROIN (2000), who limited its occurrence to MN5-MN6 (LAPPARENT DE BROIN 2001). Characteristically, *Paleotestudo* shows a straight lateral border of the carapace, a broad lip of the epiplastron, a short, immovable posterior lobe of the plastron as well as the fossa entoplastralis extending below the lip of the gulare.

During the Tertiary, three genera can be distinguished among the tortoises. *Manouria* and *Geochelone* as giant tortoises and the smaller species of *Testudo* which are considered to lead to the recent living Mediterranean tortoise species. Fossil members of these three genera are present in Austria (GEMEL & RAUSCHER 2000).

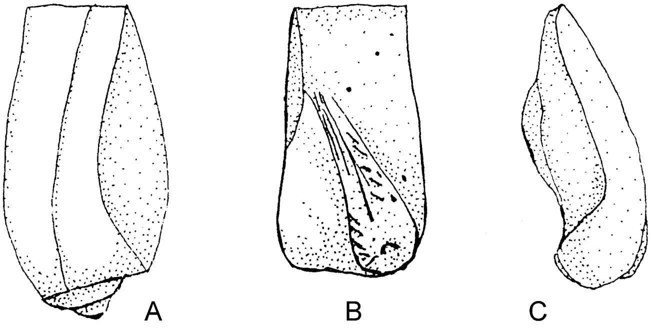

Fig. 3: *Testudo* sp. from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Left peripheral VIII in lateral external (A), in lateral internal (B) and in anterior (C) view (Coll. Inst. f. Pal. Uni Wien, Inv. Nr.: IPUW3127). Original size.

Family Bataguridae MC. DOWELL, 1964

Subfamily Ptychogasterinae DE STEFANO, 1916

Ptychogaster POMEL, 1847

***Ptychogaster grundensis* BACHMAYER & SCHAFFER, 1959** (Plate 1: C, D)

Locality and Stratigraphy: Grund (GRU-Kroh; GRU-B1-3), Lower Austria; sand of the Grund Formation (ROETZEL et al. 1999), Lower Badenian, MN5.

Material: 3 fragments of carapace (GRU-Kroh: Inv. Nr.: NHMW2002z0095/0001; GRU-B1-3: Inv. Nr.: NHMW2002z0095/0002, Inv. Nr.: NHMW2002z0095/0003)

Description: All 3 carapace fragments are peripheralia. One dorsally broken, left peripheral V (Inv. Nr.: NHMW2002z0095/0001) is vaulted at an angle of 45°. In lateral view, it is 1.1 cm wide and 1.8 cm long dorsally and 1.5 cm wide and 7 mm long ventrally. The lateral edge of the anterior half is very sharp, becoming smoother posteriorly. The straight dorsoventrally directed groove marks the separation of the marginalia IV and V.

The left peripheral IX (Inv. Nr.: NHMW2002z0095/0002) is 2.2 cm long and 9 mm wide anteriorly, and 7 mm wide posteriorly. Viewed from an anterior perspective, the triangular sectional area encloses an angle of 20° laterally. In posterior view, this angle measures 45°. The anterior half shows a laterally projecting bulge where the peripheral is 1.1 cm wide. The slight groove separating the marginalia VIII and IX originates in the posterior base of the bulge and is directed rectangular to the inner border.

The smallest remain of *Ptychogaster grundensis* is the right peripheral VII (Inv. Nr.: NHMW2002z0095/0003). Just as the left peripheral V, it is vaulted at an angle of 45°. Viewed from lateral, it is 1 cm wide and1.2 cm long dorsally. Its ventral measurements are much smaller, namely 4 mm wide and 4.5 mm long. The lateral edge is smooth and the carapace is thickest there. The groove dividing the marginalia VI and VII extends parallel to the anterior border.

Comparison: General characteristics of the genus *Ptychogaster* are, among others, the highly vaulted carapace, the complete suture strongly fixing the bone elements of the carapace, and the edge appearing on special peripheralia. While the anterior part of the plastron is firmly connected to the carapace, the posterior part is movable at the boundary hyo-hypoplastron. According to BACHMAYER & SCHAFFER (1959), who described *Ptychogaster grundensis* for the first time, this species strongly resembles *P. emydoides*, *P. reinachi* and *P. buechelbergensis*. All these species are bigger than *Ptychogaster grundensis*. BACHMAYER & SCHAFFER (1959) further point to differences concerning the outline and the transverse section of the carapace as well as the front boundary of the plastron. Direct comparisons of the carapace fragments described in this paper with the holotype of *Ptychogaster grundensis* have exclusively yielded correspondences. Therefore, the description has resulted in *Ptychogaster grundensis*.

Discussion: In general, the genus *Ptychogaster* appears in Central and Western Europe from the Upper Eocene to the Upper Miocene (LAPPARENT DE BROIN 2001). The holotype of *Ptychogaster grundensis* has been described by BACHMAYER & SCHAFFER (1959) from Grund, where it has been found together with *Trionyx vindobonensis* and the humerus of a giant tortoise *Testudo* sp. (BACHMAYER & SCHAFFER 1959; THENIUS 1953). A second fossil remain of *Ptychogaster* in Austria originates from the Teiritzberg in the Korneuburgian Basin, Lower Austria, MN5; it is described as *Ptychogaster* (*Temnoclemmys*) sp. by GEMEL (2002). GEMEL (2002) regards the high mobility of the posterior plastron of *Ptychogaster* to be the result of the highly vaulted carapace, which guarantees stability. Therefore, the inguinal buttresses can be reduced although the axillar supports are still very strong. The terrapins of today have both reduced inguinal buttresses as well as reduced axillar supports.

Order Sauria McCartney, 1802
Suborder Lacertilia Owen, 1842
Infraorder Anguimorpha Furbinger, 1900
Superfamily Anguioidea Fitzinger, 1826
Family Anguidae Gray, 1825

Anguidae indet. (Fig. 4; Plate 1: E, F, G)

Locality and Stratigraphy: Grund (GRU-F-11), Lower Austria; sand of the Grund Formation (Roetzel et al. 1999), Lower Badenian, MN5.

Material: 1 caudal vertebra (GRU-F-11: Inv. Nr.: NHMW2002z0096/0000)

Description: The single caudal vertebra measures: CL=3.68 mm; PO-PO=2.56 mm; NAW=1.84 mm; CTH=0.78 mm; CTW=1.47 mm; CL/NAW=2 (sensu Bachmayer & Szyndlar 1985). The processus spinosus, the processus transversi, the haemal arch as well as the anterior part are broken. The fracture plane passes through the possibly single or doubled processus transversi. Ventrally, two increasing ridges extend from anterior to the two bases of the haemal arch, where they are highest. They enclose the sulcus medialis. The cotyle is flattened dorsoventrally and the articular surfaces of the postzygapophyses are semicircular. This caudal vertebra most probably originates from the more posterior part of the tail because of the sulcus medialis, the absence of blood-vessel-foramina, its very long centrum in relation to its width, as well as the round outline in sectional view (see Féjerváry-Lángh 1923).

Comparison: Within the Lacertoidea, the caudal vertebrae of the various families can be distinguished based on the position of the fracture plane as well as some characteristics of the haemal arch. As the caudal vertebra described herein is broken anteriorly, the fracture plane seems to pass through either a single pair or two pairs of the processus transversi. In some Xantusiidae and Cordylidae, the fracture plane divides the single pair of processes. Teiidae, some Iguanidae and Anguidae share the characteristic of a fracture plane extending either through two pairs of processes or anterior a single one (Etheridge 1967).

The family Anguidae possesses pediculate caudal haemal arches on the centra. A diagnostic characteristic of the Subfamily Anguinae is the well forward haemal arch fused to the centrum (Camp 1923; Meszoely 1970). Due to the high ventral ridges bearing the haemal arch and to the position of the fracture plane, the caudal vertebra of Grund has been described as Anguidae indet.

Discussion: The oldest remains of Anguidae date from the Upper Cretaceous to the Paleocene of North America. In Europe, they first appear in the Middle Eocene (Estes 1983). Today, the family Anguidae represents a lizard group distributed mainly in America but also in the Old World (Arnold & Burton 1978). Etheridge (1967) has examined the evolution of caudal vertebrae types in lizards. Except for the first few caudal vertebrae, the primitive caudal sequence is considered to be autotomic with single pairs of processus transversi anterior to the fracture planes. Today, Iguanidae, Gekkonidae and Pygopodidae share these primitive characteristics. The other lizard families have differently modified caudal sequences. For instance, the Scincidae and the Anguidae are characterized by the basal separation and distal convergence of the anterior and posterior parts of the split transverse processes.

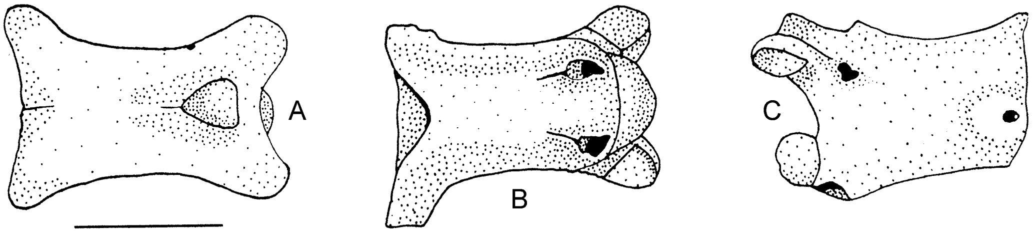

Fig. 4: Anguidae indet. from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Caudal vertebra in dorsal (A), in ventral (B) and in lateral (C) view (99: GRU-F-11: Inv. Nr.: NHMW2002z0096/0000). Scale equals 2 mm.

Order Serpentes LINNAEUS, 1758

Suborder Alethinophidia NOPCSA, 1923

Superfamily Colubroidea OPPEL, 1811

Family Colubridae OPPEL, 1811

Subfamily Colubrinae OPPEL, 1811

Genus *Elaphe* FITZINGER, 1833

***Elaphe kohfidischi* BACHMAYER & SZYNDLAR, 1985** (Fig. 5; Plate 2: A, B, C)

Locality and Stratigraphy: Grund (GRU-Kroh; GRU-B1-1; GRU-F-11), Lower Austria; sand of the Grund Formation (ROETZEL et al. 1999), Lower Badenian, MN5.

Material: 3 trunk vertebrae (GRU-Kroh: Inv.Nr.: NHMW2002z0097/0001; GRU-B1-1: Inv. Nr.: NHMW2002z0097/0002; GRU-F-11: Inv. Nr.: NHMW2002z0097/0003); 1 caudal vertebra (GRU-Kroh: Inv. Nr.: NHMW2002z0097/0004)

Description: Two of the trunk vertebrae are nearly the same size. The first (Inv. Nr.: NHMW2002z0097/0001) lacks the right prezygapophysis and measures as follows: PR-PO(L)= 5.42 mm; CL=4.72 mm; PO-PO=6.42 mm; NAW=3.23 mm; ZW=3.21 mm; CTH=1.92 mm; CTW=2.32 mm; CL/NAW=1.46. The neural spine, the right prezygapophysis, the left postzygapophysis as well as the posterior part of the centrum are broken on the second trunk vertebra (Inv. Nr.: NHMW2002z0097/0002), which measures: PR(L)-PO(R)=5.68 mm; NAW=3.44 mm; ZW=3.44 mm; CTH=2.42 mm; CTW=2.32 mm. The third trunk vertebra (Inv. Nr.: NHMW2002z0097/0003) consists of the centrum with the right rest of the neural arch and the right pre- and postzygapophyses. Its measurements are the smallest, namely: PR-PO(R)=5.57 mm; CL=4.48 mm; NAW=3.16 mm; CTH=1.68 mm; CTW=1.9 mm; CL/NAW=1.42. The single caudal vertebra represents the centrum with its two hemapophyses, the left prezygapophysis and a broken, left pleurapophysis. Just one measurement: CL=3.68 mm, can be taken (measurements sensu BACHMAYER & SZYNDLAR 1985).

All three trunk vertebrae share the following characters: In lateral view, the neural spine is rather thin and low. (Just one vertebra: Inv. Nr.: NHMW2002z0097/0001 bears a complete neural spine.) The interzygapophyseal ridges are well visible but not sharp; they are smoothest in the middle. The small lateral foramen is located directly below these ridges. The parapophysis is somewhat smaller than the diapophysis and both are distinct. Posterior to the parapophysis, the subcentral ridge rises, extending posteriorly very straight and then flattening at the base of the condyle.

In dorsal view, the prezygapophyseal processes are directed anterolaterally and the prezygapophyseal articular facets are oval. The zygosphene is concave, showing two lateral lobes.

Ventrally, the haemal keel is well developed, possessing a characteristic "step" behind the cotylar rim (see SZYNDLAR 1991b). While the subcentral grooves are relatively deep anteriorly, they become shallower posteriorly. The small subcentral foramina are located directly beside the haemal keel. The postzygapophyseal articular facets are oval, but aligned more laterally.

From the cranial perspective, the haemal keel reaches the round cotyle with two lateral tubercles. The paracotylar foramina are doubled and located in very deep depressions. The prezygapophyses rise slightly, the vaulted neural arch is low and the zygosphenal roof straight.

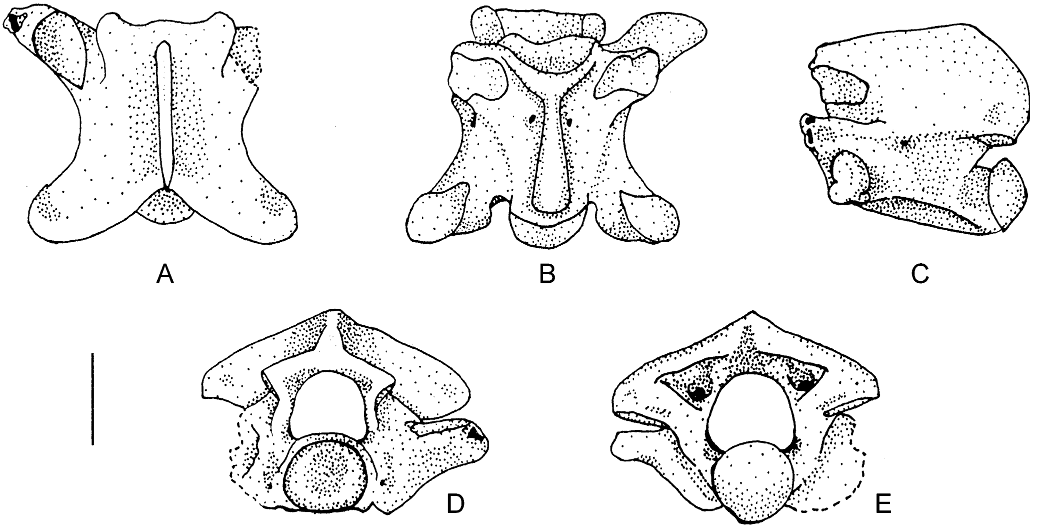

Fig. 5: *Elaphe kohfidischi* from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in dorsal (A), in ventral (B), in lateral (C), in cranial (D) and in caudal (E) view (GRU-Kroh: Inv. Nr.: NHMW2002z0097/0001). Scale equals 2 mm.

Comparison: The shape of all the vertebrae resembles that described by BACHMAYER & SZYNDLAR (1985) as the holotype respectively as the caudal vertebra of *Elaphe kohfidischi*, but they are slightly smaller. "Colubrine" vertebrae lack hypapophyses throughout the postcervical precaudal region of the column. The vertebrae described herein refer to the "small sized colubrines" whose total length rarely exceeds 100 cm (see SZYNDLAR 1991a). According to BACHMAYER & SZYNDLAR (1985), the vertebrae of *Elaphe kohfidischi* are closest to those of the living *E. longissima* and extinct *E. paralongissima,* but actually are more similar to *Coluber caspius* in elongation, morphology of the haemal keel and the concave zygosphene.

Discussion: The first colubrid snake determined for Europe is *Coluber cadurci* from the Middle Oligocene (HOLMAN 1977). The genus *Elaphe* appears in the Upper Miocene of Austria, Poland, Hungary, Greece, Romania and USSR (SZYNDLAR 1991b).

The three species *Elaphe longissima*, *E. paralongissima* and *E. kohfidischi* represent an interesting example of evolutionary differentiation. Although they originate from geographically close territories, these three species are clearly distinct. Today, *Elaphe longissima* inhabits Southern & Central Europe while *E. paralongissima* appears solely in the type locality in Southern Poland (Upper Pliocene). *Elaphe kohfidischi* is known from the type locality Kohfidisch in Austria (Upper Miocene) as well as doubtfully from the Ukraine (Upper Miocene). Probably related forms originate from nearby areas such as *Elaphe kormosi* from Hungary (Uppermost Miocene) (BACHMAYER & SZYNDLAR 1985).

Family Elapidae BOIE, 1827

Genus *Naja* LAURENTI, 1768

***Naja romani* HOFSTETTER 1939** (Fig. 6; Plate 2: D)

Locality and Stratigraphy: Grund (GRU-Kroh; GRU-B1-1; GRU-F-11), Lower Austria; sand of the Grund Formation (ROETZEL et al. 1999), Lower Badenian, MN5.

Material: 3 trunk vertebrae (GRU-F-11: Inv. Nr.: NHMW2002z0098/0001; GRU-B1-1: Inv. Nr.: NHMW2002z0098/0002; GRU-F-11: Inv. Nr.: NHMW2002z0098/0003); 2 fragments of vertebrae (GRU-F-11: Inv. Nr.: NHMW2002z0098/0003; GRU-Kroh: Inv. Nr.: NHMW2002z0098/0004)

Description: The three trunk vertebrae are relatively complete, all consisting of an entire centrum and either each or just some of the zygapophyses. Their measurements (sensu BACHMAYER & SZYNDLAR 1985) are as follows: PR-PO(R)=9.76 mm; CL=8.56 mm; NAW=6.24 mm; ZW=5.28 mm; CTH=3.84 mm; CTW=4.24 mm; CL/NAW=1.37 (Inv. Nr.: NHMW2002z0098/0001), PR(L)-PO(R)=6.64 mm; CL=6.88 mm; NAW=3.68 mm; ZW=3.84 mm; CTH=2 mm; CTW=3.21 mm; CL/NAW=1.87 (Inv. Nr.: NHMW2002z0098/0003) and CL=8.41 mm; NAW=7.22 mm; ZW=4.64 mm; CTH=4.42 mm; CTW=5.23 mm; CL/NAW=1.16 (Inv. Nr.: NHMW2002z0098/0002). Two fragments of vertebrae just allow a single measurement in each case, namely ZW=5.92 mm (Inv. Nr.: NHMW2002z0098/0003) respectively CTH=3.52 mm (Inv. Nr.: NHMW2002z0098/0004). The first one represents the posterior part of the neural arch, whereas the latter consists of the left pre- and postzygapophyses as well as the left half of the centrum.

The three relatively complete vertebrae show wide centra that become remarkably broad anteriorly. In lateral view, a low neural spine, prominent interzygapophyseal ridges as well as distinct lateral foramina are recognizable. Para- and diapophyses are not divided and the parapophyseal processes are directed anteriorly. From dorsal, the zygosphenal lip is either concave (Inv. Nr.: NHMW2002z0098/0001) or straight (Inv. Nr.: NHMW2002z0098/0003). In ventral view, the subcentral ridges and grooves are less prominent and the subcentral foramina small. From the cranial perspective, the neural arch is broadly vaulted and the neural canal is wide with short lateral sinuses. The paracotylar foramina are located in deep depressions.

Comparison: The vertebrae of cobras found in European fossil sites share the typical distinctive marks compared with e.g. large-sized colubrine snakes: hypapophyses throughout the precloacal region of the column and very low neural spines. More precise determinations can be given based on characters of the skull bones (SZYNDLAR 1991b). BACHMAYER & SZYNDLAR (1985), SZYNDLAR & ZEROVA (1990) as well as SZYNDLAR (1991b) give detailed descriptions of the trunk vertebrae of *Naja romani* which correspond to those presented in this paper. Nevertheless, the latter are smaller than the Kohfidisch material described by BACHMAYER & SZYNDLAR (1985) but similar-sized to those from the same locality examined later by SZYNDLAR & ZEROVA (1990). They mention the relatively longer centra, the wider neural canals and the distinctly crenate zygosphenal roofs present in smaller vertebrae. Therefore, the characteristics of the vertebrae described herein point to *Naja romani.*

Discussion: The fossil *Naja romani* in general resemble the living poisonous snake *Naja naja,* which today occurs in Asia and Africa (SZYNDLAR 1991b).

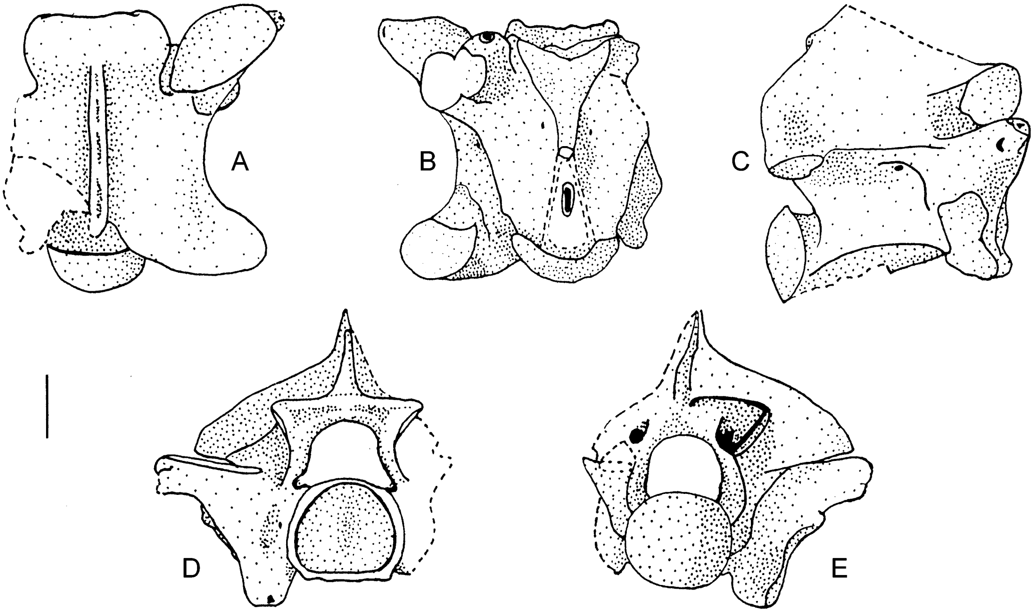

Fig. 6: *Naja romani* from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in dorsal (A), in ventral (B), in lateral (C), in cranial (D) and in caudal (E) view (99: GRU-F-11: Inv. Nr.: NHMW2002z0098/0001). Scale equals 2 mm.

Naja romani was first described by HOFSTETTER (1939) from the French Middle Miocene as a member of the extinct genus *Palaeonaja,* which SZYNDLAR & RAGE (1990) set synonymous with the living genus *Naja*. The two Upper Miocene localities Gritsev of the Ukrainian SSR (SZYNDLAR & ZEROVA 1990) as well as Kohfidisch, Austria (BACHMAYER & MLYNARSKY 1985) also bear *Naja romani*. In Kohfidisch, this taxon was firstly described as a new extinct species, *Naja austriaca* (BACHMAYER & SZYNDLAR 1985); it was then synonymized with *N. romani* by SZYNDLAR & ZEROVA (1990) based on special skull bone features.

African and Asiatic members of the genus *Naja* can be differentiated by a set of characters of the basisphenoid. *Naja romani* clearly belongs to the Asiatic lineage (SZYNDLAR & ZEROVA 1990).

Mühlbach am Manhartsberg

Class Reptilia

Order Chelonii BRONGNIART, 1800

Chelonii indet. (Fig. 7: A, B; Plate 2: E)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ1; MÜ2), Lower Austria, brownish silt of the Gaindorf Formation (ROETZEL this volume), Lower Badenian, MN5.

Material: 4 fragments of carapace (MÜ2: Inv. Nr.: NHMW2002z0099/0001; MÜ2: Inv. Nr.: NHMW2002z0099/0003; MÜ1: Inv. Nr.: NHMW2002z0099/0004); 218 fragments of eggshells (MÜ2: Inv. Nr.: NHMW2002z0099/0002; MÜ2: Inv. Nr.: NHMW2002z0099/0005)

Description: One fragment of carapace including the left peripheralia, probably X and XI (Inv. Nr.: NHMW2002z0099/0001), one fragmentary peripheral (Inv. Nr.: NHMW2002z0099/0004) and two fragmentary pleuralia (Inv. Nr.: NHMW2002z0099/ 0003; NHMW2002z0099/ 0004), all of them are of a spongeous consistency. The piece of the left peripheralia, probably X and XI, is 41 mm long , 23 mm wide and their dorsal and ventral surfaces are at an angle of approximately 15° posteriorly and 43° anteriorly. The fragmentary peripheral is 33 mm long, 14 mm wide and its dorsal and ventral surfaces are at an angle of approximately 36° respectively 43°. The fragmentary pleuralia (length: 29 mm/20.5 mm; width: 18 mm/14.5 mm) provide an anteroposteriorly grooved slight sculpture. The first one (Inv. Nr.: NHMW2002z0099/0003) more likely originates from the peripheral region, showing one straight groove as a boundary between two costalia, and the second one (Inv. Nr.: NHMW2002z0099/0004) features the point of attachment of the rib on the ventral surface.

The fragments of eggshells are approximately 3 mm long and 0.5 mm thick. They are nearly flat and sculptured on the inner surface where they possess pustules with openings.

Comparison: Due to the spongeous consistency, the 4 fragments of the carapace most probably belong to the Testudinidae, tortoises, whose living representatives all share this characteristic. However, the fossilisation process as well as the taphonomy could also be responsible for this feature. Therefore, the determination has resulted in Chelonii indet.

The determination of the eggshells is based on comparisons with the ones of recent living reptiles. Lizards and snakes have leathern eggshells. Gekko eggs are round, very small and therefore with a small radius of curvature. The eggs of the Chelonii show pores, those of terrapins are longish with a wide radius of curvature on the long side and rather thin. Tortoises possess rounder eggs comparably thick with pustules and openings of the same size and position as present in the fossil eggshells described herein. The sculpture on the inner surface is similar although the one of the fossil eggs is deeper cleft showing distincter pustules. This could very probably be the result of fossilisation. Comparing the SEM photographed section of the fossil eggshells with ones of *Testudo* (see SCHLEICH & KÄSTLE 1988), the correspondence is remarkable. Detailed information on eggshells of recent living reptiles concerning e. g. the layers of the shell, the porosity and the sculpture is given, among others, by SCHLEICH & KÄSTLE (1988), by BAJPAI et al. (1998), EWERT (1985), KOHRING (1996), MIKHAILOV (1997), MILLER (1985), MITRUS (1997) and MOLL (1979). Due to the scarcity of the material and the differences concerning the sculpture, the fossil eggshells are referred to Chelonii indet.

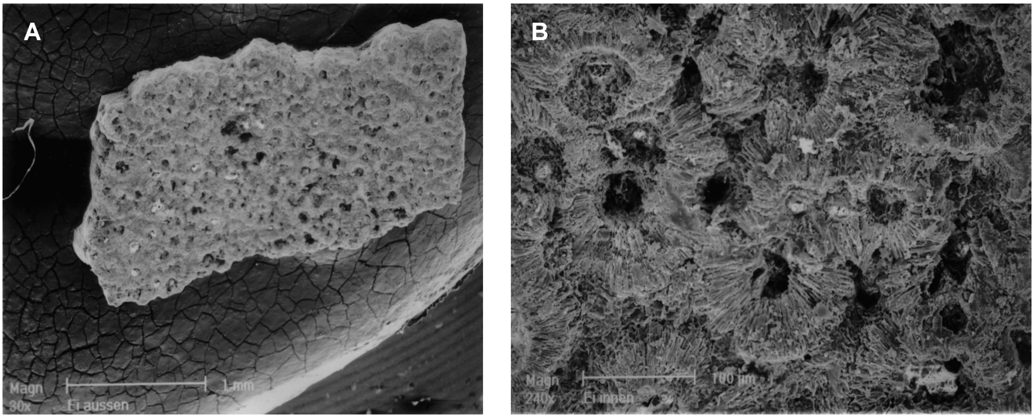

Fig. 7: Chelonii indet. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Fragment of eggshell in internal view (A and B) (MÜ2: Inv. Nr.: NHMW2002z0099/0002).

Suborder Cryptodira COPE, 1870

Superfamily Testudinoidea BAUR, 1893

Family Emydidae GRAY, 1825

Subfam. Batagurinae GRAY, 1870 emend. MCDOWELL, 1964

Mauremys GRAY, 1869

cf. *Mauremys* sp. (Plate 3: A, B)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ1), Lower Austria, brownish silt of the Gaindorf Formation (ROETZEL this volume), Lower Badenian, MN5.

Material: 1 fragment of carapace (MÜ1: Inv. Nr.: NHMW2002z0100/0000)

Description: This terrapin from Mühlbach is represented by one right pleural I. It is 24 mm long and 25 mm wide and of a very compact consistency. The vertebralia I and II are separated from the costal I by a posteriorly concave and anteriorly convex groove. On the ventral surface the point of attachment of the rib is well recognizable.

Comparison: The compact consistency of the carapace is typical of the terrapins (GEMEL pers. comm.). Besides, Emydidae possess hexagonal neuralia (MLYNARSKY 1976), which are recognizable in the shape of the pleural I described herein. Comparisons with recent material have shown that in *Mauremys* the vertebral I is wider than in *Emys orbicularis,* as is indicated by the groove on the carapace fragment described herein. Moreover, the position of the attachment point of the rib and the shape of the pleural I resemble those of *Mauremys*. A more precise determination than cf. *Mauremys* sp. is not possible because of the polymorphism of *Mauremys* and the scarcity of the material.

Discussion: The three genera *Testudo, Manouria* and *Geochelone* of the Testudinidae appear in the Tertiary and are known as fossil forms from Austria (GEMEL & RAUSCHER 2000) (see discussion of *Testudo* sp. from Grund in this paper).

With regard to the Emydidae, the Batagurinae inhabited Central Europe before *Emys orbicularis* advanced (GEMEL & RAUSCHER 2000). The stratigraphic range of *Mauremys* spans from the Oligocene to the Holocene of Asia, Europe and North Africa (MLYNARSKY 1976). Its recent distribution is restricted to Iberia, the South Balkan Peninsula, North-West Africa and South-West Asia (ARNOLD & BURTON 1978).

In Central and Eastern Europe, *Mauremys* is very common during the Miocene, especially the Upper Miocene. Some species have been described from the Austrian Middle Miocene, including *Mauremys sarmatica* from the "Türkenschanze", Vienna, and *Mauremys* or *Chinemys pygolopha* from Stein a. d. Donau, Lower Austria (GLAESSNER 1926, 1933). *Mauremys ukoi* from Gramatneusiedl, Lower Austria (BACHMAYER 1957), as well as *Mauremys* aff. *gaudryi* from Kohfidisch, Burgenland (BACHMAYER & MLYNARSKY 1983), date from the Austrian Upper Miocene.

The taphonomic questions related to the *Ocadia – Mauremys – Palaeochelys* – complex within the Batagurinae remain to be solved. The genus *Ocadia* can be distinguished from *Mauremys* solely by the development of the inguinal buttresses. They are connected to the pleuralia V and VI in *Ocadia,* whereas in *Mauremys* the pleural V is merely involved in this structure (MLYNARSKY 1976). According to MLYNARSKY (1976), *Ocadia* is synonymous with *Palaeochelys*, but as the holotype of *Palaeochelys* is lost, it is not clear which pleuralia are involved in the inguinal buttresses (BÖHME 1999c). LAPPARENT DE BROIN (1977) points out that the metric data of the plastron distinguish *Mauremys* from *Palaeochelys* and that *Ocadia* is apparently not present in Europe during the Tertiary.

Order Sauria Mc Cartney, 1802

Suborder Lacertilia Owen, 1842

Infraorder Scincomorpha Camp, 1923

Superfamily Lacertoidea Fitzinger, 1826

Family Lacertidae Bonaparte, 1831

Lacerta Linnaeus, 1758

cf. *Lacerta* sp. (Fig. 8; Plate 3: C, D)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ1; MÜ2), Lower Austria, brownish silt of the Gaindorf Formation (Roetzel this volume), Lower Badenian, MN5.

Material: 2 right dentaries (MÜ2: Inv. Nr.: NHMW2002z0101/0001; MÜ1: Inv. Nr.: NHMW2002z0101/0002)

Description: The first right dentary (Inv. Nr.: NHMW2002z0101/0001) is 3.4 mm long and 1.8 mm wide (measured without teeth). It is broken posteriorly after the position of the 7th tooth and only the first 3 teeth containing an incomplete 1st tooth remain. Its sulcus dentalis is developed moderately. The margin of the crista dentalis is wavy, the lamina horizontalis regularly thick, the irregularly rounded symphysis reaches the 3rd tooth and the Meckel´s groove is open. Labially, 2 relatively widely opened foramina with an elliptic border exist. The first is located below the 3rd tooth and near the crista ventralis. The 2nd foramen below the position of the 6th tooth is situated at middle height between the crista dorsalis and the crista ventralis.

The second right dentary (Inv. Nr.: NHMW2002z0101/0002) lacks both the anterior and the posterior end; it is 3 mm long and 1.6 mm wide (measured without teeth). There are 3 incomplete teeth. While the 1st and the 2nd tooth on this dentary only reach the margin of the crista dentalis, the 4th tooth is longer. The crista dentalis has an irregularly wavy shape and the sulcus dentalis is developed moderately. The Meckel´s groove is open. Labially, 3 foramina with elliptic borders are present. The first is located below the 2nd tooth, and the 2nd foramen can be found below the space between the 2nd and the 3rd tooth and a bit nearer to the crista ventralis than the other foramina. The 3rd foramen is positioned below the 4th tooth, exactly in the middle of the crista dorsalis and the crista ventralis.

Comparison: The family Lacertidae characteristically has pleurodont, cylindrical and bicuspid teeth as well as a widely open Meckel´s groove (Estes 1983). Only the back teeth, however, are bicuspid and the first teeth do not show the typical humps. The posterior teeth of *Pseudomecetes* are pillar-like and enlarged, and the molariform teeth of *Dracaenosaurus* are even larger (Estes 1983). Unfortunately, the back teeth of the two dentaries described herein are either missing (1st dentary) or broken (2nd dentary). This makes it impossible to determine whether they are bicuspid or not. According to Rauscher (1992) the dentaries in the genus *Lacerta* are characterized by an irregularly wavy crista dentalis, a rounded symphysis dissimilar to the pointed one in the living genus *Podarcis* and labial foramina with an elliptic border. The characteristics of the remaining fragments of the dentaries described herein correspond with those mentioned by Rauscher (1992). The first dentary (Inv.Nr.: NHMW2002z0101/0001) strongly resembles in size, shape and development of the foramina that of the living species *Lacerta viridis*. Considering the incompleteness of the two dentaries, the material is referred to cf. *Lacerta* sp.

Discussion: The oldest *Lacerta* sp. has been described from the Lower Miocene locality Allier, France (HOFFSTETTER 1955), and the Middle Miocene of Sandelzhausen, Germany (BÖHME 1999b). Its stratigraphic range throughout Europe reaches up to the Holocene. In Austria, PAPP & THENIUS (1954) found *Lacerta* sp. in the Upper Miocene locality Vösendorf, whereas RAUSCHER (1992) described it from the Plio-Pleistocene locality Bad Deutsch-Altenburg. Therefore, Mühlbach belongs to the oldest localities of cf. *Lacerta* sp.

The living species *Lacerta viridis* is known from the Upper Pliocene up to the Pleistocene (ESTES 1983). In the Holocene it occurs in Central and Southern Europe and in Asia Minor. Stratigraphically, it seems unusual to find *Lacerta viridis* in Middle Miocene deposits. Lacertidae are relatively common in the Cenozoic of Europe, with a recent distribution in Europe, Africa and much of Asia (ESTES 1983). They represent a very characteristic element in the European herpetofauna, including 75% of all lizard species of this area (ARNOLD & BURTON 1978).

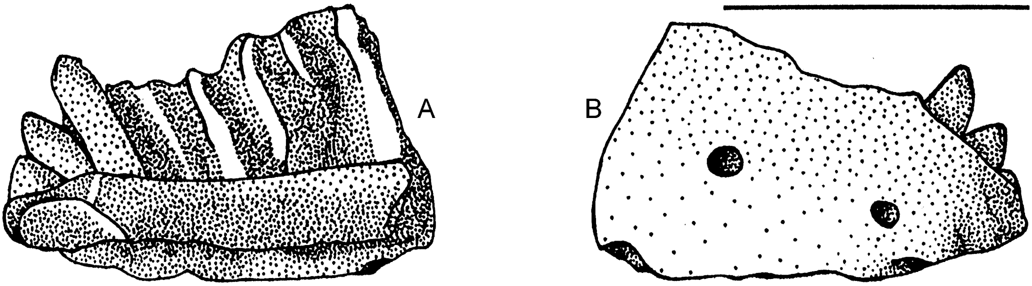

Fig. 8: cf. *Lacerta* sp. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Right dentary in internal (A) and in external (B) view (MÜ2: Inv. Nr.: NHMW2002z0101/0001). Scale equals 2 mm.

Infraorder Anguimorpha FURBINGER, 1900

Superfamily Anguioidea FITZINGER, 1826

Family Anguidae GRAY, 1825

Subfamily Anguinae GRAY, 1825

Ophisaurus DAUDIN, 1803

***Ophisaurus* sp.** (Fig. 9; Plate 3: E, F)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ1), Lower Austria, brownish silt of the Gaindorf Formation (ROETZEL this volume), Lower Badenian, MN5.

Material: 1 right maxillary (MÜ1: Inv. Nr.: NHMW2002z0102/0000)

Description: The right maxillary, which is 1.9 mm long and 1.1 mm wide (measured without teeth), is broken anteriorly, posteriorly and dorsally. It is weakly vaulted inwards and shows two conical, slightly recurved and pointed teeth with two cutting edges on each tooth: One is located in the middle of the anterior facet, and one slightly laterally on the posterior facet. The crista dentalis is irregularly wavy. Labially, two elliptic foramina are connected by a slight groove. One is situated above the 1st tooth and the other above the space between the 2nd and the position of the 3rd tooth of this maxillary fragment.

Comparison: The teeth of the genus *Ophisaurus* of the Old World are pointed and recurved, distinguishing them from the robust, pile-like teeth of *Pseudopus* (Klembara 1979). The cutting edges on the teeth of the maxillary described herein are characteristic for *Ophisaurus,* while *Pseudopus* possesses amblydont/durophagous teeth. Compared with those in the genus *Anguis* the teeth are straighter and more robust. The dentary is therefore determined as belonging to *Ophisaurus* sp.

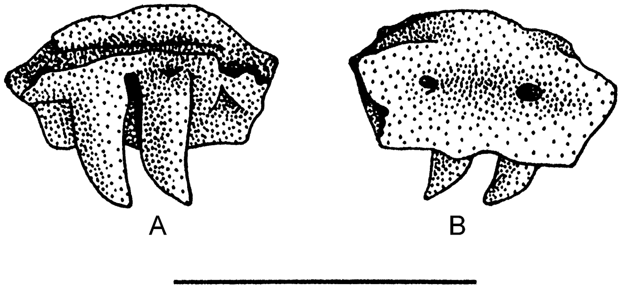

Fig. 9: *Ophisaurus* sp. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Right maxillary in internal (A) and in external (B) view (MÜ1: Inv. Nr.: NHMW2002z0102/0000). Scale equals 2 mm.

cf. ***Ophisaurus*** **sp.** (Fig. 10; Plate 3: G, H)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ2), Lower Austria, brownish silt of the Gaindorf Formation (Roetzel this volume), Lower Badenian, MN5.

Material: 3 osteoderms (MÜ2: Inv. Nr.: NHMW2002z0103/0001; NHMW2002z0103/0002)

Description: The three osteoderms are longer than wide and composed of one ossiculum dermale caudale ventrale laterale, dext. (Inv. Nr.: NHMW2002z0103/0001), which is 2.6 mm long and 1.8 mm wide, as well as of two ossicula dermales dorsales laterales, dext. (Inv. Nr.: NHMW2002z0103/0002). One of the latter is 1.9 mm long and 1.4 mm wide and the second is only slightly longer than wide, with a length of 1.6 mm and a width of 1.3 mm. They are asymmetric and in external view show two zones: the sculptured surface and the smooth margin covering the cranial and the left lateral margin. The sculpture consists of irregular radial grooves, ridges and bulges. The ossiculum dermale caudale ventrale laterale is divided into two halves by a medial keel which thins out cranially, ending in a point.

Comparison: The osteoderms described herein are thickened and subangular like those of the genus *Ophisaurus* or *Pseudopus*. They are more fragile and thinner than in

Pseudopus pannonicus. Moreover, the living species *Pseudopus apodus* shares the characteristic of thinner and more fragile osteoderms than *Pseudopus pannonicus* with the extinct species *Pseudopus moguntinus* (FEJÉRVARY-LANGH 1923; MLYNARSKY 1984; MLYNARSKY et al. 1984; THENIUS 1952). Members of the genus *Anguis* have thin and more rounded osteoderms. Although it is very difficult to find diagnostic differences for osteoderms of *Ophisaurus* and *Pseudopus*, the determination of the Mühlbach material as cf. *Ophisaurus* sp. is supported by the description of the maxillary of *Ophisaurus* sp. as representative of the Anguinae.

Discussion: Anguinae are present in Europe from the Middle Eocene up to the Holocene. The genus *Ophisaurus* appears in the Middle Eocene of Germany (Geiseltal): *Ophisaurus hallensis* shows slightly primitive characteristics on the parietal. *Ophisaurus voigti* is described based solely on osteoderm sculpture (KUHN 1940). SULLIVAN et al. (1999) consider these two taxa synonymous with *Ophisauriscus quadrupes* (KUHN, 1940) from the Middle Eocene of Germany (Geiseltal). *Ophisaurus picteti* from the Upper Eocene of Switzerland has been described by HOFFSTETTER (1942) as a species three times larger than *O. hallensis*. Both *Ophisaurus fejfari* and *O. spinari* date from the Lower Miocene of Dolnice, Western Bohemia (KLEMBARA 1979). They have been described based on the specific characteristics of the parietals, although, among other remains, osteoderms and maxillaries had also been found. While *O. acuminatus* appears in the Upper Miocene of Germany (JÖRG 1965), *O. canadensis* as well as *O. ventralis* of the Upper Miocene are the first representatives of the genus *Ophisaurus* in America (HOLMAN 1970). *Ophisaurus ventralis* ranges until the Holocene. The Middle Pliocene – Holocene species *O. compressus* and the Upper Pliocene – Holocene *O. attenuatus* are restricted to North America (ESTES 1983). The genus *Ophisaurus* in America today is represented by *O. compressus* in South Carolina, Georgia and Florida, and as *O. attenuatus* in the Mississippi plains north from Chicago and south to Lousiana with a western extension to Nebraska and Texas. Finally, *O. ventralis* ranges from Virginia through the Carolinas, via Georgia, Florida, Lousiana along river beds to Oklahoma and Missouri. *Ophisaurus koellikeri* is the only representative in North Africa; *O. harti* occurs in South China, while *Ophisaurus gracilis* is discribed from Northeast India and Burma to Southwest China and Vietnam. *Ophisaurus buettikoferi* can be found in Borneo, while *O. wegneri* occurs in Sumatra (PETZOLD 1971). MC CONKEY (1954) restricts the starting point of diversification for the three genera with lateral folds within the Anguidae (*Ophisaurus*, *Abronia* and *Gerrhonotus*) to North America.

KLEMBARA (1979) points out the existence of the two genera *Ophisaurus* and *Pseudopus* as two different evolutionary lines in nearly the same area (Western and Central Europe) during the Lower Miocene. They spread eastwards from Europe to Asia, where *Pseudopus* stayed while *Ophisaurus* crossed the Bering Strait and reached America. The oldest representative, *O. canadensis*, dates from the Upper Miocene of Canada. Following SULLIVAN et al. (1999), in contrast, the two taxa *Ophisaurus* and *Parophisaurus* (s. str.) were geographically restricted to the New World and differed from fossil and recent "anguine" taxa assigned to *Ophisaurus* from various regions of the Old World. Accordingly, both *Ophisaurus* and *Parophisaurus* of the New World represent a clade distinct from the Old World "ophisaur" *Ophisaurus-Anguis* and *Pseudopus* "species groups" or clades.

KLEMBARA (1979) noted the difference between the two taxa *Pseudopus* and *Ophisaurus* (s. str.) based on very evident characteristics ("anguis-signs") on the parietal. He resurrected the genus *Pseudopus* for the reception of the species *Ophisaurus apodus*, *O. pannonicus* and *O. moguntinus*.

During the European Tertiary and Quaternary, two different species of the genus *Pseudopus* were dominant: *Pseudopus moguntinus* sensu KLEMBARA, 1979 (*Ophisaurus moguntinus* BOETTGER, 1875, synonymous with *Propseudopus fraasi* HILGENDORF, 1883, and *Ophisaurus ulmensis* GERHARDT, 1903), known from the Upper Oligocene to the Upper Miocene of Germany and Poland (ESTES 1983), such as *Pseudopus* cf. *moguntinus* sensu KLEMBARA, 1979 from the Middle Miocene locality Opole (MLYNARSKY et al. 1982). Therefore, *Pseudopus moguntinus* is regarded as characteristic of the older localities, whereas *P. pannonicus* sensu KLEMBARA, 1979 (*Ophisaurus pannonicus* KORMOS, 1911) is younger, having been found from the Upper Miocene up to the Pleistocene. Austrian localities are Kohfidisch (Upper Miocene; BACHMAYER & MLYNARSKY 1977), Eichkogel bei Mödling (Upper Miocene; PAPP & THENIUS 1954) and Bad Deutsch-Altenburg (Plio-Pleistozän; RAUSCHER 1992). The series *Pseudopus moguntinus* - *Pseudopus pannonicus* - *Pseudopus apodus* might be a phyletic one (MLYNARSKY 1962).

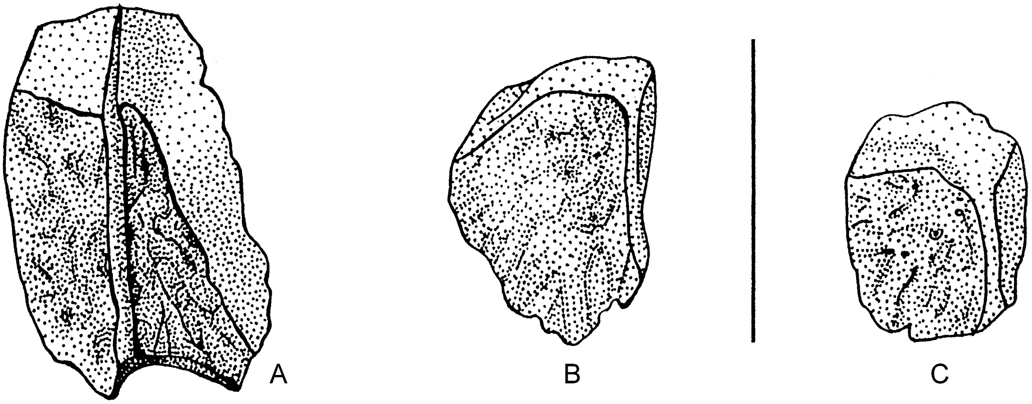

Fig. 10: cf. *Ophisaurus* sp. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Ossiculum dermale caudale ventrale laterale, dext. (A) (MÜ2: Inv. Nr.: NHMW2002z0103/0001). Ossiculum dermale dorsale laterale, dext. (B) (MÜ2: Inv. Nr.: NHMW2002z0103/0002). Ossiculum dermale dorsale laterale, dext. (C) (MÜ2: Inv. Nr.: NHMW2002z0103/0002). Scale equals 2 mm.

Order Amphisbaenia GRAY, 1844

Family Amphisbaenidae GRAY, 1865

Blanus WAGLER, 1830

***Blanus antiquus* SCHLEICH, 1985** (Fig. 11; Plate 3: I)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ1), Lower Austria, brownish silt of the Gaindorf Formation (Roetzel this volume), Lower Badenian, MN5.

Material: 1 right maxillary (MÜ1: Inv. Nr.: NHMW2002z0104/0000)

Description: The right, dorsally broken maxillary has a total length of 1.6 mm and a width of 0.8 mm (measured without teeth) and is missing the 1st tooth. The remaining pleurodont teeth are robust with slightly curved cusps. The first, absent tooth is followed by the longest one, and the 3rd , 4th and 5th teeth continuously decrease in size. Labially, a foramen broken dorsally is present above the space between the 2nd and the 3rd tooth.

Comparison: The pleurodont dentition shown by the right maxillary typically appears in the family Amphisbaenidae (Gans 1980). The maxillary perfectly resembles that of *Blanus antiquus* described by Schleich (1985) from the locus typicus Goldberg. The characteristics are the size and the shape of the teeth as well as the position of the labial foramen. Compared with *Palaeoblanus,* the jaw described herein is more robust and the teeth are conical and more differentiated. The number of the teeth (max. 5) is higher than in the recent *Blanus cinereus* (Schleich 1985). The teeth are more strongly curved in *B. cinereus* and more slender in *B. strauchi*. This justifies determining the maxillary as *Blanus antiquus*.

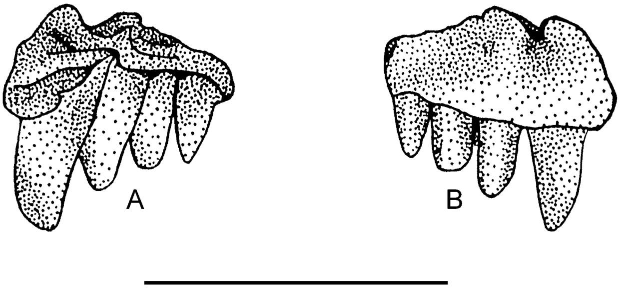

Fig. 11: *Blanus antiquus* from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Right maxillary in internal (A) and in external (B) view (MÜ1: Inv. Nr.: NHMW2002z0104/0000). Scale equals 2 mm.

cf. *Blanus* cf. *antiquus* Schleich, 1985 (Fig. 12; Plate 3: J, K)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ2), Lower Austria, brownish silt of the Gaindorf Formation (Roetzel this volume), Lower Badenian, MN5.

Material: 1 trunk vertebra (MÜ2: Inv. Nr.: NHMW2002z0105/0000)

Description: The procoelous trunk vertebra with the following measurements: PR - PR (width between outer edges of praezygapophyseal articular surface) = 1 mm and a total length of 1.2 mm, is broken posteroventrally; the condyle is missing. The cotyle is ventrally flattened and the praezygapophyses are at an angle of 65° with the vertical. Neither a zygosphene nor a neural spine can be distinguished.

Comparison: The dorsal vertebrae of the order Amphisbaenia are usually flattened and lack the zygosphene. The ventrally flattened centrum of the dorsal vertebrae is typical for the family Amphisbaenidae. The neural spine is lacking, which is distinctive to the family Rhineuridae. According to ESTES (1993) the vertebrae of Amphisbaenidae are not a diagnostic feature for the genus, as also confirmed by AUGÉ & RAGE (2000). Comparing the vertebra described in this paper with vertebrae of other representatives of the family Amphisbaenidae yields no diagnostic difference. However, it most probably belongs to the same species of the Amphisbaenidae represented by the right maxillary, leading to the determination as cf. *Blanus* cf. *antiquus*.

Discussion: In Europe, the oldest Amphisbaenia inc. sedis date from the Lower Eocene of Dormaal (HECHT & HOFFSTETTER 1962), but after ESTES (1983) these specimens are referred to the family Amphisbaenidae. *Blanus antiquus* was first described by SCHLEICH (1985) from the Middle Miocene of South Germany, followed by the description of the genus *Palaeoblanus* with *Palaeoblanus tobieni* as species from the Lower Miocene of Germany (SCHLEICH 1988). At the Lower Miocene locality Stubersheim (South Germany), M. BÖHME (1999a) has found the first contemporary record of both *Palaeoblanus tobieni* and *Blanus antiquus*. The stratigraphic range of the genus *Palaeoblanus* spans from MP27 to MN5 in Central Europe, whereas *Blanus antiquus* appears from MN3 to the upper MN6 in Central and Western Europe (M. BÖHME 1999a). Therefore, *Blanus antiquus* from the Middle Miocene locality Mühlbach is located within its stratigraphic range.

ESTES (1983) only refers the monotypic genus *Omoiotyphlops* DE ROCHEBRUNE 1884 to the family Amphisbaenidae, but mentions the close resemblance of this genus to the living *Blanus*, represented by the two species *B. cinereus* and *B. strauchi* in Europe. While *B. cinereus* inhabits the Southern Iberian Peninsula, *B. strauchi* is widespread in Turkey, the Dodekanese Islands, Cyprus and the Near East. *Blanus cinereus* was split by BUSACK (1988) into *B. mettetali* and *B. tingitanus* based on electrophoresis and morphological characters.

According to ESTES (1983) the order Amphisbaenia either intervenes between Sauria and Serpentes or represents a seperate systematic unit, whereas SCHWENCK (1988) regards it as a sistergroup of the Teiidae and Gymnophthalmidae within the Scincomorpha.

The recent Amphisbaenia are ground dwellers in moist to semiarid soils (SCHLEICH 1988).

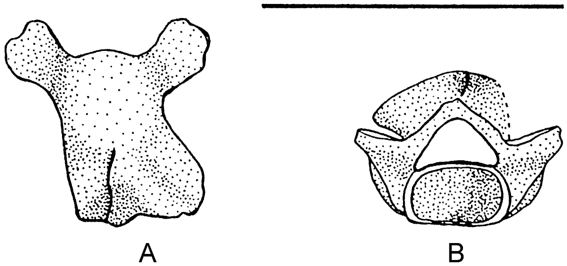

Fig. 12: cf. *Blanus* cf. *antiquus* from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in dorsal (A) and in cranial (B) view (MÜ2: Inv. Nr.: NHMW2002z0105/0000). Scale equals 2 mm.

Order Serpentes LINNAEUS, 1758

Suborder Alethinophidia NOPCSA, 1923

Superfamily Colubroidea OPPEL, 1811

Family Colubridae OPPEL, 1811

Subfamily Colubrinae OPPEL, 1811

Colubrinae indet. (Fig. 13; Plate 4: A, B, C)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ1), Lower Austria, brownish silt of the Gaindorf Formation (ROETZEL this volume), Lower Badenian, MN5.

Material: 3 trunk vertebra (MÜ1: Inv. Nr.: NHMW2002z0106/0001; Inv. Nr.: NHMW2002z0106/0002)

Description: The metric measurements (sensu BACHMAYER & SZYNDLAR 1985) of the trunk vertebra (Inv. Nr.: NHMW2002z0106/0001) are as follows: CL=3.7 mm; NAW=2.6 mm; CL/NAW= 1.4. Only this single vertebra, which lacks the prae- and postzygapophyses as well as posterodorsal parts, can be taken for measurements. The other two vertebrae consist of the condyle with a remnant of the centrum showing the haemal keel. The neural spine of the trunk vertebra is partly broken off, but is approximately two times longer than high in lateral view. The interzygapophyseal ridges are slightly developed and the lateral foramina, which are located directly below these ridges, are distinct. The laterally directed para- and diapophyses are the same size and are not divided. A nearly imperceptibly dorsally curved subcentral keel originates from there. Viewed from dorsal, the lateral lobes of the zygosphene are more developed than the medial tubercle. From the ventral aspect, the haemal keel, which is shoulder-shaped caudally, and the subcentral grooves are distinct. The subcentral foramina are very small and directly adjoin the haemal keel. From cranial view, the neural canal is rounded with well-developed lateral sinuses. Although a dorsal part of the cotyle is absent, it seems to be slightly flattened dorsoventrally. A well-developed paracotylar foramen is present on each side of the cotyle.

Comparison: The presence of a haemal keel (and not of a hypapophysis) on trunk vertebrae is characteristic of the Colubrinae (RAGE 1984; SZYNDLAR 1991a). The vertebra resembles that of the genus *Coluber* because the para- and diapophyses are not clearly divided. In the living genus *Coronella,* the neural arch is much more flattened and the haemal keel is usually weakly developed (SZYNDLAR 1991a). Because of the incompleteness and scarcity of the fossil material, the vertebrae could not be determined more precisely than Colubrinae indet.

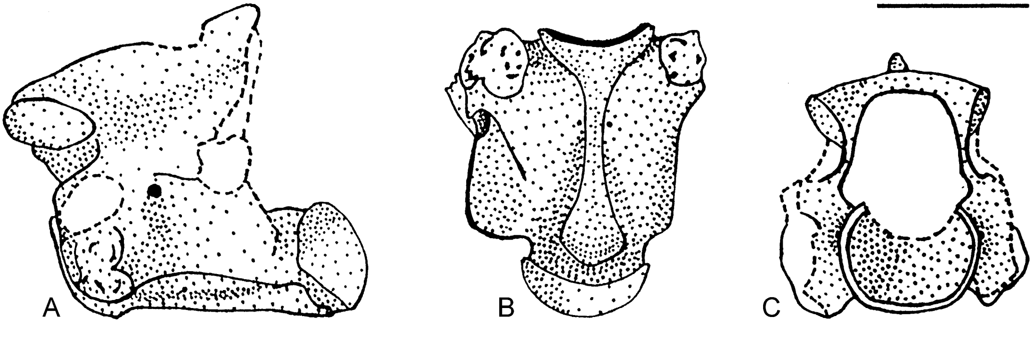

Fig. 13: Colubrinae indet. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in left lateral (A), in ventral (B) and in cranial (C) view (MÜ1: Inv. Nr.: NHMW2002z0106/0001). Scale equals 2 mm.

Subfamily Natricinae BONAPARTE, 1838

Natricinae indet. (Fig. 14)

Locality and Stratigraphy: Mühlbach am Manhartsberg (MÜ1), Lower Austria, brownish silt of the Gaindorf Formation (ROETZEL this volume), Lower Badenian, MN5.

Material: 1 trunk vertebra (MÜ1: Inv. Nr.: NHMW2002z0107/0000)

Description: The measurements (sensu BACHMAYER & SZYNDLAR 1985) of the trunk vertebra are as follows: CL=2.9 mm; NAW=1.3 mm; CL/NAW=2.2. Only the centrum with the right praezygapophysis and the right posterior neural arch is present. Laterally viewed, the para- and diapophyses are well divided and the parapophyseal process is directed anteriorly. The interzygapophyseal ridges are well developed but not sharp, the lateral foramen is situated in a shallow depression and the subcentral ridge is distinct and straight. The straight hypapophysis is slightly directed posteroventrally, showing a rounded caudal tip.Viewed from the dorsal aspect, the preserved right praezygapophyseal articular surface is oval, beyond which the pointed praezygapophyseal process overtops somewhat. In ventral view, the subcentral foramina close to the base of the hypapophysis are very small and situated in well-developed subcentral grooves. From the cranial view, the preserved right paracotylar foramen is situated in a deep depression. The centrum is circular.

Comparison: Based on the measurements, the shape and the presence of the hypapophysis as well as the lateral foramen situated in a shallow depression, this vertebra is suggestive of a natricine snake (SZYNDLAR 1991b). The centrum is much longer and the parapophyseal processes are shorter than in the Viperidae (SZYNDLAR 1984, 1988). Shorter centra and weaker subcentral ridges are typical for Elapidae (SZYNDLAR 1991b). IVANOV (2000) points out the close similarity between Natricinae and some representatives of the family Elapidae in the Neogene. The only distinguishing character he mentions are the relatively high neural spines in Natricinae. The small dimension of the vertebra described herein as well as the length of the hypapophysis resemble the genus *Neonatrix*. Unlike *Natrix mlynarskii* (RAGE 1988b), the subcentral ridges are straight and not arched dorsally. Unfortunately, the fragmentary vertebra lacks the neural spine and the postzygapophyses. The determination Natricinae indet. is probably accurate.

Discussion: The oldest known European representatives of the family Colubridae appeared in West Europe in the Early Oligocene, while the New World colubrids can be dated back to the Middle Oligocene. The division of the family Colubridae into "colubrines" and "natricines" must have taken place earlier than the beginning of the Oligocene. The Colubridae most probably originated as early as the Cretaceous/Tertiary transition (CADLE 1988; SZYNDLAR 1991b). At the end of the Lower Miocene, numerous modern taxa coming from several coeval (in particular French and German) localities spread over Europe. Distinct radiations of the natricine Colubridae and Elapidae took place at this time (SZYNDLAR 1998). Most obviously, the Boidae were displaced by the Colubridae (SZYNDLAR & RAGE 1990).

SZYNDLAR (1991a) suggested replacing the terms used so far by ophidian paleontologists for the subfamilies Colubrinae and Natricinae by the informal forms "colubrines" and "natricines". In his opinion, the criteria used to separate these two subfamilies, such as the absence or presence of hypapophyses on postcervical thoracic vertebrae, is inconsistent with the snake systematics accepted by neoherpetologists.

Beside Mühlbach, some other European Middle Miocene localities where Colubridae have already been described are La Grive (RAGE & SZYNDLAR 1986), Sandelzhausen (SZYNDLAR & BÖHME 1993), Przeworno and Opole II (SZYNDLAR 1984, 1991a, 1991b), Dêvinská Nová Ves (IVANOV 1998) as well as the Lower/Middle Miocene locality Vieux Collonges (IVANOV 2000).

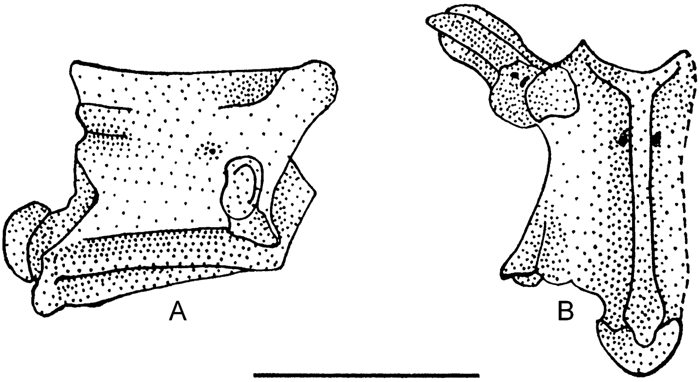

Fig. 14: Natricinae indet. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in lateral (A) and in ventral (B) view (MÜ1: Inv. Nr.: NHMW2002z0107/0000). Scale equals 2 mm.

Paleoecological conclusions

Grund and Mühlbach were characterized by different paleoecological situations. While the herpetofauna of Grund points to a dry and wooded paleoenvironment, Mühlbach was more humid. HARZHAUSER et al. (2003) precisely discuss the paleoecology of the section Mühlbach and DAXNER-HÖCK et al. (in press) the one of Grund.

The descending frequency of the specimens relating to the Minimal Number of Individuals is as follows in Grund: *Ptychogaster grundensis* (33%); *Elaphe kohfidischi* (25%); *Testudo* sp. (17%); *Naja romani* (10%); *Salamandra sansaniensis* (8%); Anguidae indet. (7%).

After MLYNARSKY (1976), the members of the fossil genus *Ptychogaster* were terrestrial-aquatic animals inhabiting bushland and woods near water bodies. GEMEL (2002) confirms this opinion, mentioning the high vaulted carapax as indicating a terrestrial way of life. In his opinion, some species were probably semiaquatic.

A living relative of *Elaphe kohfidischi* is the Aesculapian snake, *Elaphe longissima*. As a member of the Colubrinae it prefers dry and wooded environments even without permanent water nearby. The Aesculapian snake is able to climb well on trees and bushes and hunts for small mammals, birds and lizards (BÖHME 1993).

Today, the herbivorous Testudinidae live in a dry environment. Not only areas with dense vegetation but also meagre meadows are inhabited (for *Testudo graeca:* BUSKIRK et al. 2001; for *Testudo hermanni*: CHEYLAN 2001).

Members of the genus *Naja*, a poisonous snake, are restricted to tropical areas today, where they inhabit dry places. Hunting for small mammals, birds, reptiles, amphibians and insects during the night, they spend the day resting hidden in the vegetation and crevices (PETZOLD 1973; WELCH 1988).

Only one vertebra was found of *Salamandra sansaniensis*, a fossil member of the Amphibia. The occurrence of this single amphibian among reptiles could perhaps be the result of night-active predatory birds. A living relative is *Salamandra salamandra*, which prefers hilly or mountainous, wooded sites up to 2000 m but occurs in great number from 700 m to 800 m in the Alps. This terrestrial salamander needs damp environments with bushes and deciduous forests, but also inhabits semiarid environments in Southern Europe (DIESENER & REICHHOLF 1996).

The ecological requirements of today´s Anguidae span from dry (e. g. *Pseudopus apodus*) to moist (e. g. *Anguis fragilis*), and the determination Anguidae indet. is too vague to give more precise information.

In summary, and keeping the relative frequency of the specimens based on the MNI in mind, the herpetofauna of Grund points to a mainly dry and wooded paleoenvironment.

Contrary to Grund, the herpetofauna in Mühlbach indicates moist conditions. The descending frequency of the specimens based on the Minimal Number of Individuals is: Chelonii indet. (25%); *Lacerta* sp. (17%); *Ophisaurus* sp. (17%); *Blanus* cf. *antiquus* (17%); *Mauremys* sp. (8%); Colubrinae indet. (8%); Natricinae indet. (8%).

Concerning the place of depositing eggs by Chelonii, tortoises dig a hole in dry and not compact soil to lay up to 12 eggs into it. Terrapins prefer a moist ground near waters for digging the hole. They put up to 16 eggs into it (ARNOLD & BURTON 1978).

Today´s Lacertidae can be found in dense vegetation but also in very dry, sun-exposed areas, mainly on stone walls. Their range of activity differs from species to species, but could extend to more than 1 ha in the larger ones (ARNOLD & BURTON 1978).

Ophisaurus clearly prefers a wooded environment with dense vegetation. The genus prefers more or less damp conditions with the opportunity to hide in damp crevices (PETZOLD 1971).

As a member of the Amphisbaenidae, which today mainly inhabit tropical and subtropical but also temperate areas (DECKERT et al. 1991), *Blanus* cf. *antiquus* most probably also burrowed in the soil. It therefore required soft and sandy grounds (SALVADOR 1981).

The indicator for the greater humidity in Mühlbach is the *Mauremys* - Natricinae complex. Today, terrapins of the genus *Mauremys* inhabit standing water bodies or slowly flowing rivers with a dense vegetation (DECKERT et al. 1991).

Finally, the Natricinae represent a snake group which can be distinguished from an ecological point of view. They are able to swim, hunting for amphibians and fish mainly in standing but also in slowly flowing water. Some specimens even inhabit brackish milieus such as marsh meadows along the coast or river deltas.

Altogether, the herpetofauna of Mühlbach points to damper conditions than present in Grund. Perhaps a small standing water was present or a slowly flowing river passed by: here, *Blanus* led a subterranean existence and burrowed into the riparian sandy ground, while *Mauremys* and the member of the Natricinae actively populated the water body.

With the exception of the single vertebra of *Salamandra sansaniensis* in Grund, amphibians are remarkably missing. This could also be the result of a taphonomic selection because only a few of the more robust fossil reptile remains are present and even these are very fragmentary and broken. This is supported by the sedimentological situations, the storm events in Grund causing the mixture of marine and terrestrian elements and the layers containing the vertebrates within marine layers in Mühlbach (ROETZEL this volume). The herpetofaunas therefore do not appear to be autochthonous.

More probably, the very dry conditions at Grund were prohibitive for amphibians, which need permanent water nearby. Contrary to Grund, Mühlbach seems to have offered a habitat more suitable and damp enough for amphibians, which also served as a food resource for *Mauremys* and the Natricinae. Inadequate taphonomic conditions are the most probable explanation for their absence.

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Plates

Plate 1

Grund

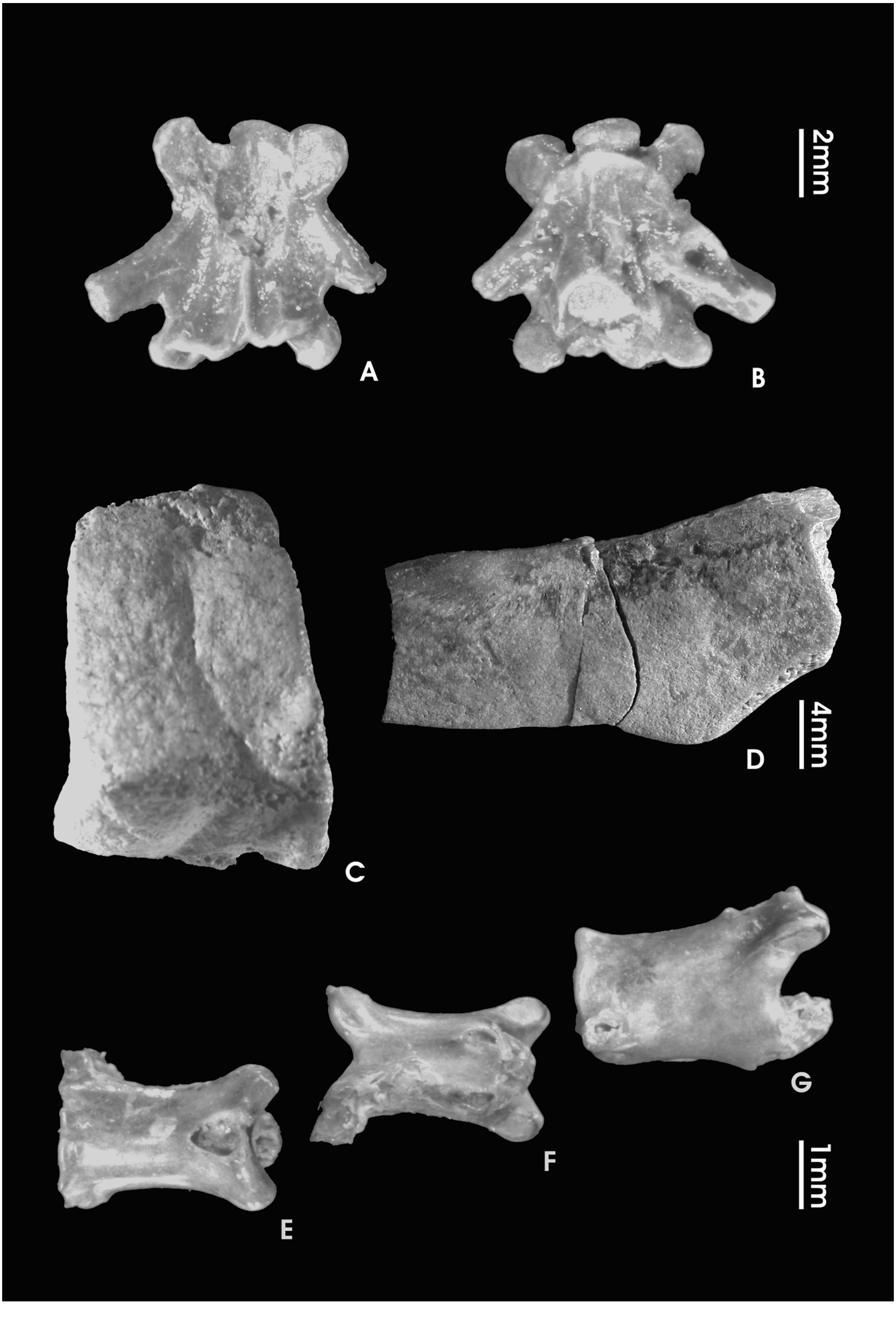
Amphibia:

Fig. A, B: ***Salamandra sansaniensis*** from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in dorsal (A) and in ventral (B) view (98: GRU-B1-11: Inv. Nr.: NHMW2002z0094/0000).

Reptilia:

Fig. C, D: ***Ptychogaster grundensis*** from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Left peripheral V in lateral (C) view (98: GRU-B1-3: Inv. Nr.: NHMW2002z0095/0001). Left peripheral IX in ventral (D) view (GRU-Kroh: Inv. Nr.: NHMW2002z0095/0002).

Fig. E, F, G: **Anguidae indet**. from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Caudal vertebra in dorsal (E), in ventral (F) and in lateral (G) view (99: GRU-F-11: Inv. Nr.: NHMW2002z0096/0000).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C
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G
F
E
1mm

Plate 2

Grund

Fig. A, B, C: ***Elaphe kohfidischi*** from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in ventral (A), in lateral (B) and in caudal (C) view (GRU-Kroh: Inv. Nr.: NHMW2002z097/0001).

Fig. D: ***Naja romani*** from Grund, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in lateral (D) view (99: GRU-F-11: Inv. Nr.: NHMW2002z0098/0001).

Mühlbach amManhartsberg

Fig. E: **Chelonii indet.** from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Left peripheralia probably X and XI in dorsal (E) view (MÜ2: Inv. Nr.: NHMW2002z0099/0001).

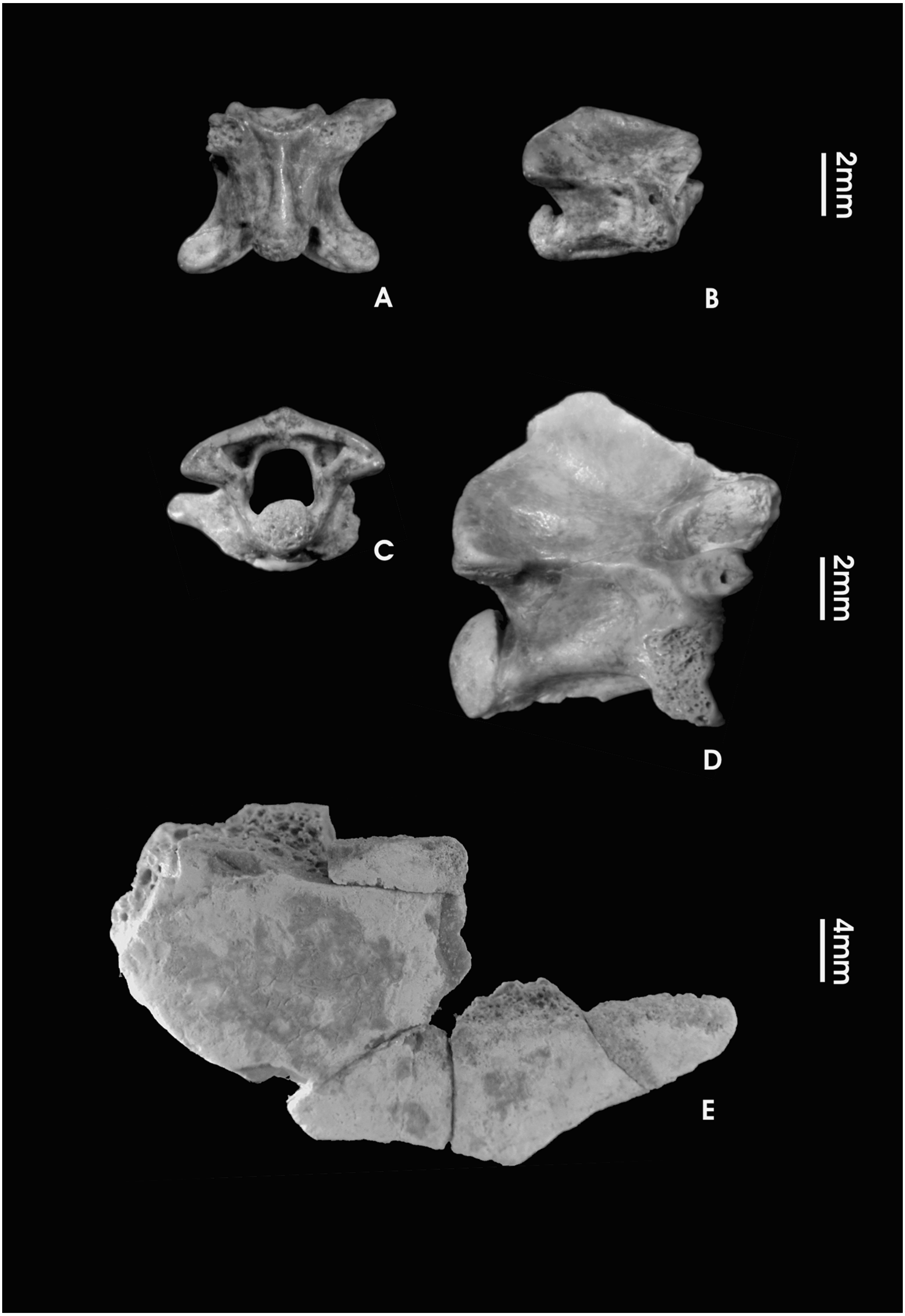
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Plate 3

Mühlbach amManhartsberg

Fig. A, B: **cf. *Mauremys* sp.** from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Right pleural I in ventral (A) and in dorsal (B) view (MÜ1: Inv. Nr.: NHMW2002z0100/0000).

Fig. C, D: **cf. *Lacerta* sp**. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Right dentary in external (C) and in internal (D) view (MÜ2: Inv. Nr.: NHMW2002z0101/0001).

Fig. E, F: ***Ophisaurus* sp**. from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Right maxillary in external (E) and in internal (F) view (MÜ1: Inv. Nr.: NHMW2002z0102/0000).

Fig. G, H: **cf. *Ophisaurus* sp.** from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Ossiculum dermale caudale ventrale laterale dext. in dorsal (G) view (MÜ2: Inv. Nr.: NHMW2002z0103/0001). Ossiculum dermale dorsale laterale dext. in dorsal (H) view (MÜ2: Inv. Nr.: NHMW2002z0103/0002).

Fig. I: ***Blanus antiquus.*** from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Right maxillary in external (I) view (MÜ1: Inv. Nr.: NHMW2002z0104/0000).

Fig. J, K: **cf. *Blanus* cf. *antiquus.*** from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in dorsal (J) and in cranial (K) view (MÜ2: Inv. Nr.: NHMW2002z0105/0000).

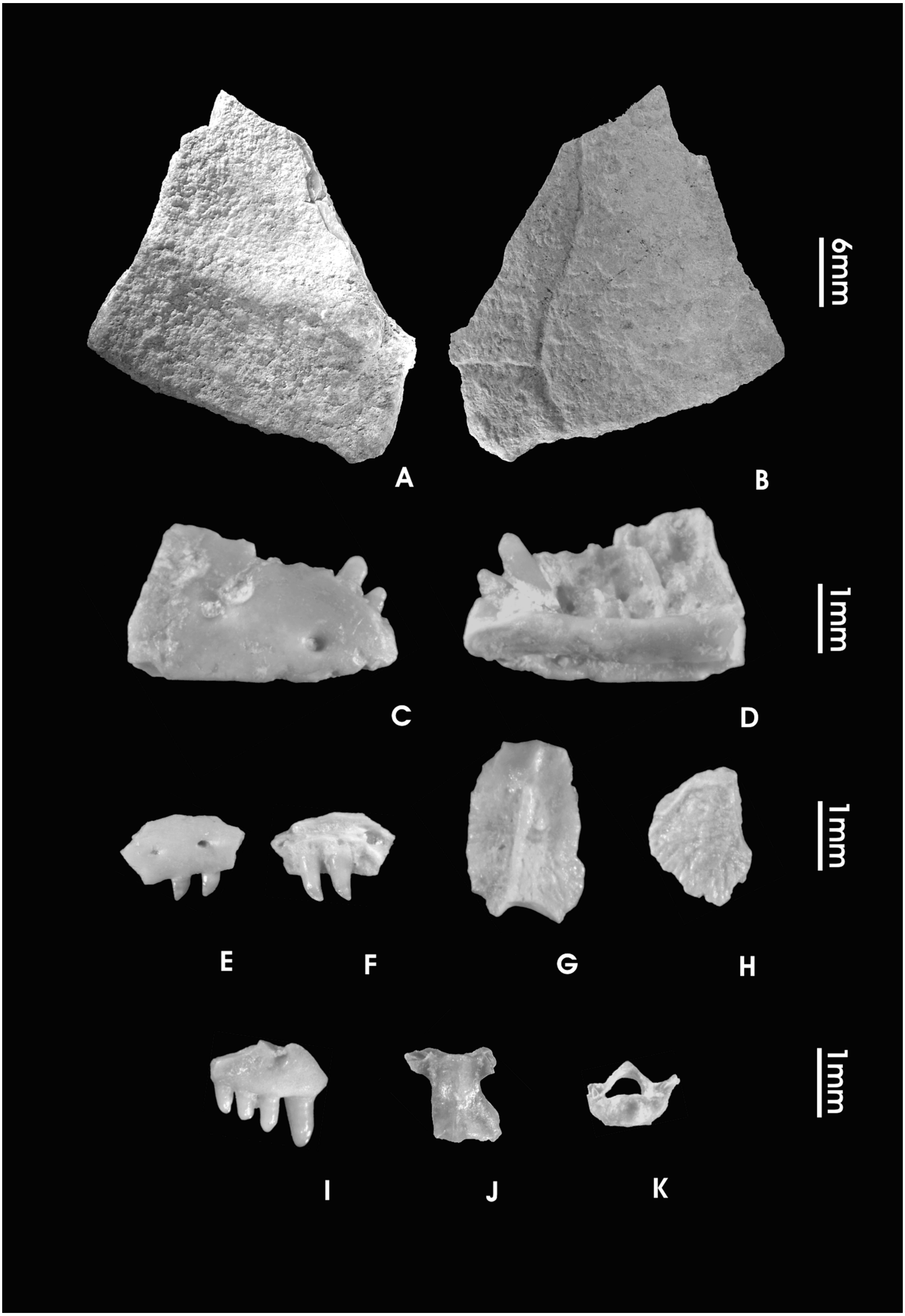
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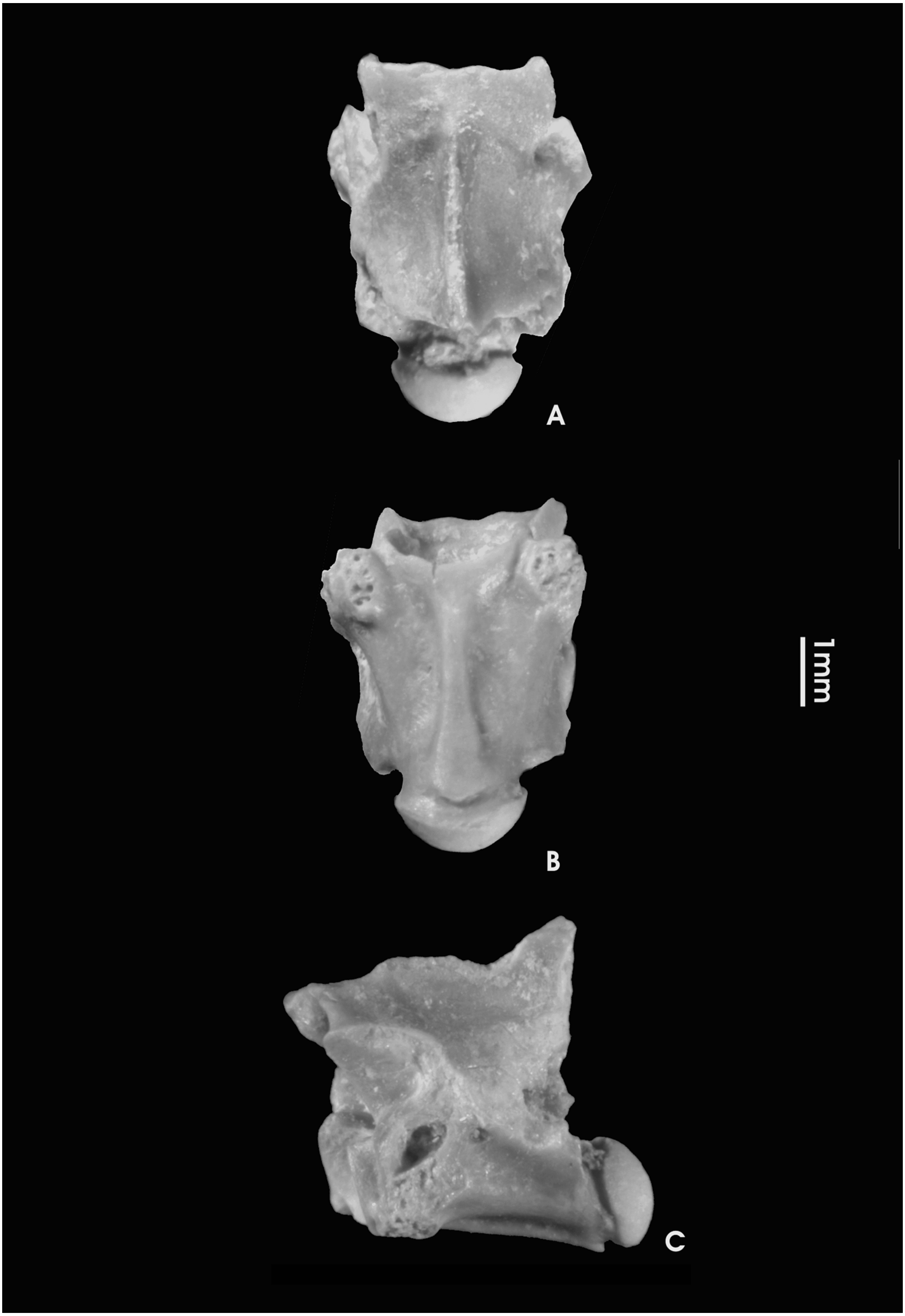
Plate 4

Mühlbach amManhartsberg

Fig. A, B, C: **Colubrinae indet.** from Mühlbach am Manhartsberg, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna. Trunk vertebra in dorsal (A), in ventral (B) and in lateral (C) view (MÜ1: Inv. Nr.: NHMW2002z0106/0001).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