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The Herpetofauna (Amphibia: Caudata, Anura; Reptilia: Scleroglossa) of the Upper Miocene Locality Kohfidisch (Burgenland, Austria)

by

Petra M. Tempfer*)

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Summary

Diverse groups of invertebrates and vertebrates of the Upper Miocene MN11 locality Kohfidisch (Pannonian Basin) in Burgenland, Austria, have already been published. Herein, the herpetofauna containing Amphibia and Reptilia except the Testudines is presented. It is composed of the Caudata: *Mioproteus caucasicus* (Proteidae); *Chelotriton paradoxus*, *Triturus* (*cristatus*) sp., *Triturus* (*vulgaris*) sp., and *Triturus* sp. (Salamandridae) as well as the Anura: *Bombina* cf. *bombina*, *Latonia gigantea*, *Latonia ragei*, *Latonia* sp. (Discoglossidae); *Pelobates* cf. *cultripes* (Pelobatidae); *Bufo bufo* (Bufonidae); *Hyla* sp. (Hylidae); *Rana* (*ridibunda*) sp. (Ranidae) and Anura indet. Reptilia are represented by Lacertilia: Gekkonidae indet. (Gekkonidae); *Lacerta* cf. *viridis*, *Lacerta* sp. A, *Lacerta* sp. B, *Miolacerta tenuis*, *Edlartetia sansaniensis* (Lacertidae); Scincidae indet. (Scincidae); *Anguis fragilis*, *Pseudopus pannonicus* (Anguidae); *Varanus* cf. *hofmanni* (Varanidae); Lacertilia indet. and the Serpentes: *Typhlops* cf. *grivensis* (Typhlopidae); *Elaphe kohfidischi*, *Coluber planicarinatus*, *Natrix longivertebrata* (Colubridae); *Naja romani* (Elapidae) and *Vipera burgenlandica* (Viperidae).

Compared with today's condition, the Recent distribution of the taxa or their closest relatives and especially the gekkos and skinks indicate the predominance of a dryer and warmer climate including frost-free winters during the Upper Miocene. With regard to the climate during the Upper Miocene of Austria, the herpetofaunas indicate a climatic change towards aridity and rising temperatures between the Uppermost MN9 and the MN11.

The paleoenvironment is reconstructed as a sparse and dry wood where a stagnant, shallow lake near the cave attracted the animals.

Zusammenfassung

Aus der obermiozänen MN11 Fundstelle Kohfidisch (Pannonisches Becken) im Burgenland, Österreich, sind bereits diverse Wirbellose und Wirbeltiergruppen beschrieben worden. Diese Dissertation widmet sich der Herpetofauna mit Ausnahme der Schildkröten, welche sowohl Amphibia als auch Reptilia beinhaltet. Erstere setzen sich aus den Caudata: *Mioproteus caucasicus* (Proteidae); *Chelotriton paradoxus*, *Triturus* (*cristatus*) sp., *Triturus* (*vulgaris*) sp., *Triturus* sp. und Caudata indet. (Salamandridae) und den Anura: *Bombina* cf. *bombina*, *Latonia gigantea*, *Latonia ragei*, *Latonia* sp. (Discoglossidae); *Pelobates* cf. *cultripes* (Pelobatidae); *Bufo bufo* (Bufonidae); *Hyla* sp. (Hylidae); *Rana* (*ridibunda*) sp. (Ranidae) und Anura indet. zusammen. Reptilia sind durch Lacertilia: Gekkonidae indet. (Gekkonidae); *Lacerta* cf. *viridis*, *Lacerta* sp. A, *Lacerta* sp. B, *Miolacerta tenuis*, *Edlartetia sansaniensis* (Lacertidae); Scincidae indet. (Scincidae); *Anguis fragilis*, *Pseudopus pannonicus* (Anguidae); *Varanus* cf. *hofmanni* (Varanidae); Lacertilia indet. und die Serpentes: *Typhlops* cf. *grivensis* (Typhlopidae); *Elaphe kohfidischi*, *Coluber planicarinatus*, *Natrix longivertebrata* (Colubridae); *Naja romani* (Elapidae) und *Vipera burgenlandica* (Viperidae) vertreten. Die heutige Verbreitung der vorhandenen Taxa beziehungsweise ihrer engsten Verwandten, und speziell Geckos und Skinke zeigen gegenüber heute ein trockeneres und wärmeres obermiozänes Klima mit frostfreien Wintern an. In der generellen Klimaentwicklung des Obermiozän Österreichs wird anhand der Herpetofaunen ein Wechsel zu größerer Trockenheit und höheren Temperaturen zwischen der obersten MN9 und der MN11 deutlich. Ökologischen Überlegungen zufolge befanden sich die Höhle von Kohfidisch und ihr nahe gelegener, ruhender seichter See inmitten eines lichten und trockenen Waldes.

1. Introduction

The outcrop Kohfidisch (between 284,09 m and 302 m high) in Burgenland is located 115 km south of Vienna, south of Kirchfidisch and on the western slope of the Hohensteinmais Mountain. More precisely, it is positioned

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*) Dr. Petra M. Tempfer, Naturhistorisches Museum Wien, Geologisch-Paläontologische Abteilung, Burgring 7, A-1014 Wien, Österreich

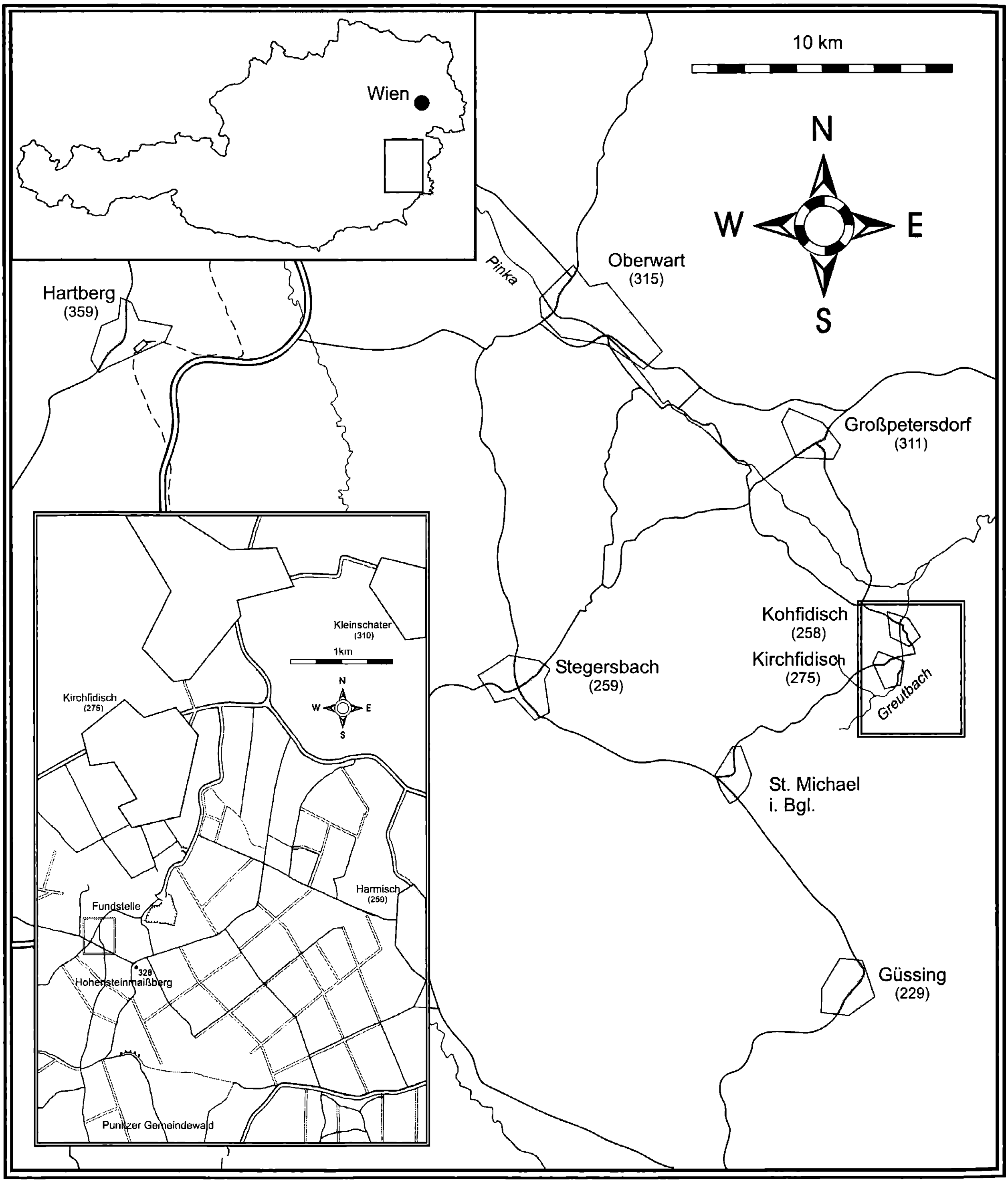


Figure 1, 2: Geographical position of the outcrop (within the rectangle) Kohfidisch in Burgenland, Austria (modified after Bachmayer & Zapfe 1969).

slightly above the road leading from Kirchfidisch to Punitz (Bachmayer & Zapfe, 1969; fig. 1, 2).

In 1955, the geologist F. Krümel of the department of Geology and Paleontology of the Natural History Museum Vienna brought some fossil remains of Kohfidisch in Burgenland, Austria, to Vienna. Shortly after his detection, he was killed in an accident in the Alps. Together with the landholder's steward S. Wölfer he ranks as the discoverer of that locality. Subsequently, F. Bachmayer and H. Zapfe of the department of Geology and Paleontology of the Natural History Museum Vienna organized each summer excavations in the Upper Miocene locality (fig. 1, 2, 3). From 1955 to 1984, they washed, sieved and sorted the material. Merely in 1958, F. Bachmayer leaded together with E. Flügel. The countess J. Palffy-Erdödy as landowner promoted the excavations and the Society of Nature and Technology (Vienna), the federal agency of monuments as well as S. Wölfer subsidized them (Bachmayer & Zapfe, 1969).

The firstly discovered sediments leading fossils belonged

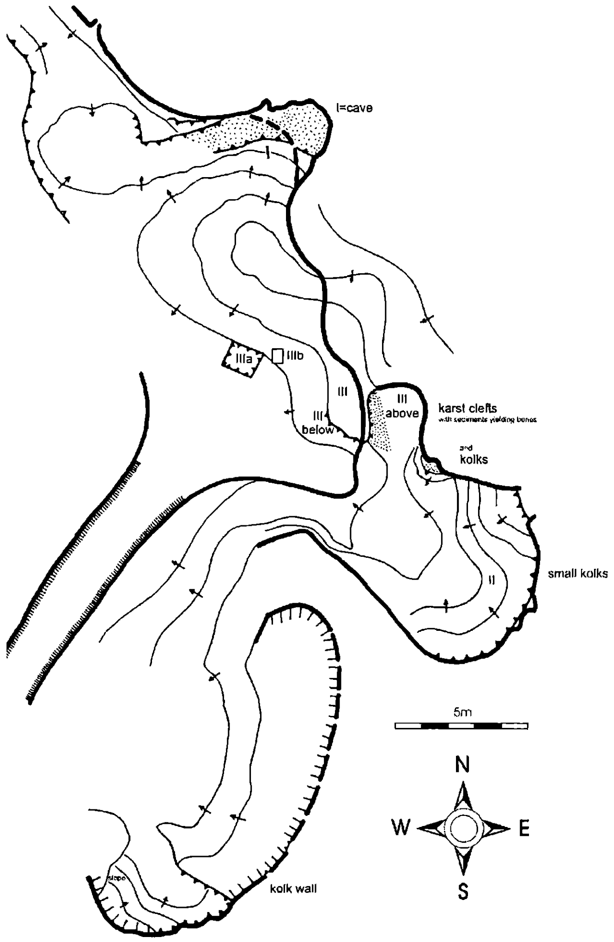


Figure 3: Detailed sketch of the outcrop-situation of Kohfidisch (modified after BACHMAYER & ZAPFE 1969).

to the cave ("Höhle" = I). After some years, the density of the fossil record got less and the excavations in the deeply dug off cave became dangerous to life. Near the cave, BACHMAYER & ZAPFE (1960) found fossil bones in a fox-earth and in the soil in front of it. Test excavations revealed kolks and fissures filled by fossil-leading clay sediments. 50 m³ soil had to be removed to expose the new outcrop. From 1960 on, kolks ("Kolke") and fissures ("Spalten" = II), and from 1961 to 1969 mainly the kolks ("Kolke" = III) situated between I and II were examined. Excavations continued in an old limepit ("alte Kalkgewinnungsstelle" = IV) in 1964. Further on, the terms "old stock" ("Altbestand"), "cm", "a", "b", "7", "9", "III below" ("III unten"), "III above" ("III oben"), "V" and "VI" exist for special outcrop-places (BACHMAYER & ZAPFE, 1969; fig. 3).

Fossils are present in the cave, fissure and kolk sediments and in the further outcrop-places (see above) of Kohfidisch. Concerning the herpetofauna, there exists no difference in the faunal composition of the diverse outcrop-places.

Some of the invertebrates and vertebrates have already been described. BACHMAYER & ZAPFE (1969) have worked on the Mollusca. M. BÖHME (pers. advice) had a look on the Teleostei, and some representatives of the Reptilia have already been described by BACHMAYER & MŁYNARSKI (1977: Lacertilia, 1983: Testudines), BACHMAYER & SZYNDLAR (1985, 1987: Serpentes) and SZYNDLAR & ZEROVA (1990: Serpentes). BACHMAYER & WILSON (1970, 1978, 1980, 1983, 1985, 1990), BACHMAYER & ZAPFE (1969, 1972), RABEDER (1989), and WEERS & MONTOYA (1996) have published the small **Mammalia**, while the large **Mammalia** are mentioned in RABEDER (1989). Proboscidea have been described by BACHMAYER & ZAPFE (1972).

A faunal list of Kohfidisch results as follows:

Mollusca:
Bivalvia:
    Dreissenidae: *Congeria neumayri* ANDRUSOV, 1897
Gastropoda:
    Carychiidae: *Carychium bertae* (HALAVÁTS, 1911)
    Planorbidae: *Planorbis (Anisus) confusus* SOOS, 1934
    Helicidae: *Tacheocampylea (Mesodontopsis) doderleini* (BRUSINA, 1897)

Teleostei:
    Teleostei indet.
Cypriniformes:
    Cyprinidae: *Tinca* sp.
    Siluridae: *Silurus* sp.
Percomorphi:
    Gobiidae: Gobiidae indet.

Reptilia:
Testudines:
    Emydidae: *Mauremys* aff. *gaudryi* (DEPÉRET, 1885)
    Testudinidae:
        Testudinidae indet.
        Testudo burgenlandica (BACHMAYER & MŁYNARSKI, 1983)
Lacertilia:
    Anguidae: *Ophisaurus pannonicus* (KORMOS, 1911)
Serpentes:
    Colubridae:
        Elaphe kohfidischi BACHMAYER & SZYNDLAR, 1985
        Coluber planicarinatus (BACHMAYER & SZYNDLAR, 1985)
        Natrix longivertebrata SZYNDLAR, 1984
    Elapidae: *Naja romani* (HOFFSTETTER, 1939)
    Viperidae: *Vipera burgenlandica* BACHMAYER & SZYNDLAR, 1987

Mammalia:
Insectivora:
    Erinaceidae:
        Schizogalerix cf. *moedlingensis* (RABEDER, 1973)
        Schizogalerix zapfei BACHMAYER & WILSON, 1970
        Lanthanotherium sp.
        Erinaceus ? sp.
    Soricidae:
        Blarinellia (="*Petenyia*") *dubia* (BACHMAYER & WILSON,1970)
        Paenelimnoecus (="*Petenyiella*") *repenningi* (BACHMAYER & WILSON, 1970)
        Anourosorex kormosi BACHMAYER & WILSON, 1970
        Neomyinae ? indet.
    Talpidae:
        Talpidae indet.
        Desmana ("*Dibolia*") *vinea* STORCH, 1978
        Desmanella cf. *crusafonti* RÜMKE, 1974
        Talpa gilothi STORCH, 1978
Chiroptera:
    Megadermidae: *Megaderma vireti* MEIN, 1964

- Rhinolophidae:
  - *Rhinolophus delphinensis* Gaillard, 1899
  - *Rhinolophus grivensis* (Deperet, 1892)
- Vespertilionidae:
  - *Myotis* cf. *boyeri* Mein, 1964
  - *Paraplecotus* sp.
  - *Myotis* sp.

Lagomorpha:
- Ochotonidae: *Prolagus* cf. *oeningensis* (König, 1825)

Rodentia:
- Sciuridae:
  - *Pliopetaurista* cf. *bressana* Mein, 1970
  - *Spermophilinus* cf. *bredai* (v. Meyer, 1848)
- Castoridae: *Chalicomys* cf. *jaegeri* Kaup, 1832
- Gliridae:
  - *Paraglirulus* cf. *lissiensis* (Hugueney & Mein, 1965)
  - *Myomimus dehmi* (de Bruijn, 1966)
  - *Vasseuromys pannonicus* (Kretzoi, 1978)
  - *Muscardinus austriacus* Bachmayer & Wilson, 1970
  - *Graphiurops austriacus* Bachmayer & Wilson, 1980
  - *Glis* cf. *minor* Kowalski, 1956
- Zapodidae: *Protozapus intermedius* Bachmayer & Wilson,1970
- Eomyidae:
  - *Keramidomys* sp.
  - *Leptodontomys* sp.
- Cricetidae:
  - *Neocricetodon* (= "*Kowalskia*") *fahlbuschi* Bachmayer & Wilson, 1970
  - *Epimeriones* cf. *austriacus* Daxner-Höck, 1972
  - *Prospalax petteri* Bachmayer & Wilson, 1970
  - *Promimomys* sp.
- Muridae:
  - *Progonomys woelferi* Bachmayer & Wilson, 1970
  - *Parapodemus lugdunensis* Schaub, 1938
- Hystricidae: *Hystrix parvae* (Kretzoi, 1951)

Perissodactyla:
- Rhinocerotidae: *Aceratherium* sp.
- Equidae: *Hipparion* sp.

Artiodactyla:
- Cervidae: Cervidae indet.
- Bovidae: Bovidae indet.

Carnivora:
- Hyaenidae: *Percrocuta eximia* (Roth & Wagner, 1854)
- *Ictitherium* sp.

Proboscidea:
- Proboscidea indet.
- Deinotheriidae: *Deinotherium giganteum* Kaup, 1829

The material described herein completes the faunal list with regard to the herpetofauna:

Amphibia:

Caudata:
- Proteidae: *Mioproteus caucasicus* Estes & Darevsky, 1978
- Salamandridae:
  - *Chelotriton paradoxus* Pomel, 1853
  - *Triturus* (*cristatus*) sp. (Laurenti, 1768)
  - *Triturus* (*vulgaris*) sp. Linnaeus, 1758
  - *Triturus* sp.

Anura:
- Anura indet.
- Discoglossidae:
  - *Bombina* cf. *bombina* (Linnaeus, 1761)
  - *Latonia gigantea* (Lartet, 1815) nov. comb. Lydekker, 1890
  - *Latonia ragei* Hossini, 1993
  - *Latonia* sp.
- Pelobatidae: *Pelobates* cf. *cultripes* (Cuvier, 1829)
- Bufonidae: *Bufo bufo* (Linnaeus, 1758)
- Hylidae: *Hyla* sp.
- Ranidae: *Rana* (*ridibunda*) sp. Pallas, 1771

Reptilia:
- Lacertilia: Lacertilia indet.
- Gekkonidae: Gekkonidae indet.
- Lacertidae:
  - *Lacerta* cf. *viridis* (Laurenti, 1768)
  - *Lacerta* sp. A
  - *Lacerta* sp. B
  - *Miolacerta tenuis* Roček, 1984
  - *Edlartetia sansaniensis* (Lartet, 1851)
- Scincidae: Scincidae indet.
- Anguidae:
  - *Anguis fragilis* Linnaeus, 1758
  - *Pseudopus pannonicus* (Kormos, 1911)
- Varanidae: *Varanus* cf. *hofmanni* Roger, 1898

Serpentes:
- Serpentes indet.
- Typhlopidae: *Typhlops* cf. *grivensis* Hoffstetter, 1946
- Colubridae:
  - *Elaphe kohfidischi* Bachmayer & Szyndlar, 1985
  - *Coluber planicarinatus* (Bachmayer & Szyndlar, 1985)
  - *Natrix longivertebrata* Szyndlar, 1984
- Elapidae: *Naja romani* (Hoffstetter, 1939)
- Viperidae: *Vipera burgenlandica* Bachmayer & Szyndlar, 1987

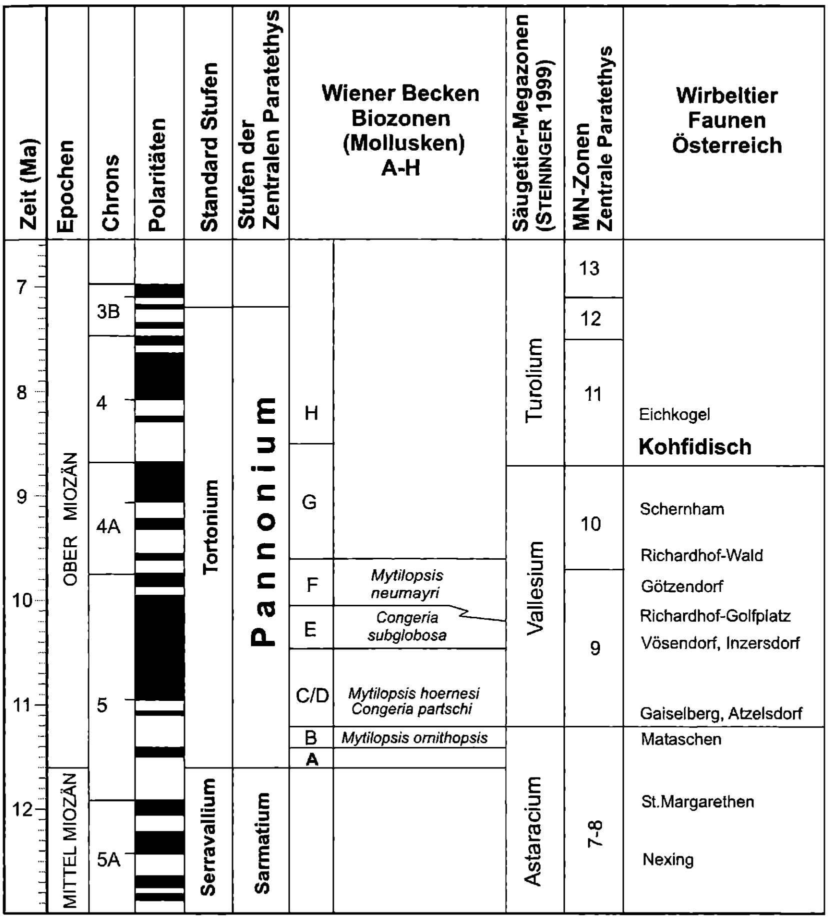
2. Geology and Stratigraphy

Kohfidisch is situated on the western slope of the Hohensteinmais Mountain (between 298 m and 302 m high) in the Pannonian Basin. The Hohensteinmais Mountain belongs to the "Südburgenländische Schwelle"

The Südburgenländische Schwelle divides the Pannonian Basin into the Styrian Basin and the Western Pannonian Basin. It extends from Mureck in Styria (SW) to Hohensteinmais Mountain-Eisenberg-Rechnitz in Burgenland (NE). Striking NE-SW or NNE respectively, it represents an emerging horst which consists of Paleozoic grey to darkgrey dolomitic limestone, dolomite and schists. The Paleozoic is transgressively covered by Neogene and Pleistocene brackish to freshwater sediments (Flügel & Heritsch, 1968; Pollak, 1962).

The clay sediments of the cave have petrographically been investigated by P. Wieden (Chemical laboratory Vienna). He discovered bentonite within the cave sediments which points to an acid volcanism after the filling of the caves and fissures (Bachmayer & Zapfe, 1969).

Stratigraphically, Bachmayer & Zapfe (1958) have firstly dated Kohfidisch as a Lower Pliocene locality founded on the existence of the "*Hipparion*-fauna" and on the constitution of the cave filling sediments. They correlated Kohfidisch with the Hungarian cave of Csákvár. In 1960, Bachmayer & Zapfe still classified the Insectivora into the



Zeit (Ma)	Epochen	Chrons	Polaritäten	Standard Stufen	Stufen der Zentralen Paratethys	Wiener Becken Biozonen (Mollusken) A-H		Säugetier-Megazonen (STEININGER 1999)	MN-Zonen Zentrale Paratethys	Wirbeltier Faunen Österreich
7	OBER MIOZÄN	3B		Tortonium	Pannonium	H		Turolium	13	
									12	
8		4							11	Eichkogel **Kohfidisch**
9		4A				G		Vallesium	10	Schernham Richardhof-Wald
10		5				F	*Mytilopsis neumayri*		9	Götzendorf Richardhof-Golfplatz
						E	*Congeria subglobosa*			Vösendorf, Inzersdorf
11						C/D	*Mytilopsis hoernesi Congeria partschi*			Gaiselberg, Atzelsdorf
						B	*Mytilopsis ornithopsis*	Astaracium	7-8	Mataschen
12	MITTEL MIOZÄN	5A		Serravallium	Sarmatium	A				St.Margarethen Nexing

Table 1: Stratigraphical correlation of Middle and Upper Miocene mammal faunas from Austria after DAXNER-HÖCK (2004).

Lower Pliocene. BACHMAYER & ZAPFE (1969) accurately discuss the geological age of the cave and fissure filling sediments of Kohfidisch. Based on the altitude of the cave, on the relative sea levels of the Lake Pannon and on the geological conditions of the surroundings, they ascertain a Lower Pliocene age of the Upper Pannonian "zone" Pannonian F after PAPP. As carnivors inhabited the caves and fissures of Kohfidisch, they must have offered dry conditions and could not have been flooded by the Lake Pannon. *Deinotherium giganteum* points to the existence of a large mainland and not an island system. According to PAPP (1951), two regional low levels of the Lake Pannon existed in the "zones" Pannonian A (Lower Pannonian) and F (Upper Pannonian) after PAPP. The top of the Hohensteinmais Mountain which is higher and younger relative to the outcrop, yields Upper Pannonian, limnic deposits with freshwater gastropods of the "zone" Pannonian G after PAPP. Further, the sediments of Kohfidisch contain small mammals indicating the Upper Pannonian and *Congeria neumayri* typical of the "zone" Pannonian F after PAPP. Therefore, BACHMAYER & ZAPFE (1969) assign the locality Kohfidisch an Upper Pannonian age of the "zone" Pannonian F after PAPP.

BACHMAYER & WILSON (1970) treat the small mammal fauna of Kohfidisch and carry out stratigraphical correlations with Austrian and Hungarian localities. They classify the Vösendorf fauna as older than the Kohfidisch one which agrees more closely with the Eichkogel fauna. The Hungarian locality Polgárdi is slightly younger as well as Csákvár whose beaver may be younger than the ones of Eichkogel.

Further investigations on the small mammal faunas of Kohfidisch and Eichkogel turned out the slightly higher age of Kohfidisch still younger than Vösendorf (BACHMAYER & WILSON 1978). As it was, the Kohfidisch fauna represents the Upper Pannonian "zone" Pannonian F, while the one of Eichkogel points to the "zone" Pannonian H.

Just MEIN (1975) and subsequently BACHMAYER & WILSON (1985) correlate the fauna of Kohfidisch with the Neogene Mammal Zone MN11. The latter compare Austrian localities of the Pannonian and clearly assign Eichkogel and Kohfidisch to MN11 and to the Upper Pannonian "zone" Pannonian H such as PAPP & STEININGER (1979) did. Götzendorf of the MN10 is correlated with the "zone" Pannonian F, and Vösendorf (MN10) with the "zone" Pannonian E.

BACHMAYER & SZYNDLAR (1985) and BACHMAYER & WILSON (1985) appealing to the West European classification shift the age of Kohfidisch from the Lower Pliocene into the Upper Miocene.

Based on the presence of well-defined species of the Muridae (*Progonomys* and the more advanced *Parapodemus*), BACHMAYER & WILSON (1990) offer to change the position in time of the Kohfidisch fauna again. As already considered before, they suggest Kohfidisch as equivalent to "zone" Pannonian F again because the land was not submerged at that time. Concerning the biostratigraphic relationships of the Vienna Basin faunas, Kohfidisch is closer to Götzendorf than to Eichkogel.

DE BRUIJN et al. (1992) revise the biochronological (MN) zonation of the continental Neogene of Europe and Western Asia. They correlate the fauna of Kohfidisch with the Uppermost MN10 and Masia del Barbo as reference locality. Cucalón (Spain), Ambérieu 1 (France) and Lefkon (Greece) are also positioned in MN10.

Based on the abundance of *Progonomys woelferi* (Muridae), RÖGL & DAXNER-HÖCK (1996) still position the fauna of Kohfidisch into the MN10 but into the "zone" Pannonian G after PAPP.

As current state, DAXNER-HÖCK (2004; Table 1) correlates the fauna of Kohfidisch with the Lower MN11 and the Uppermost "zone" Pannonian G of the Upper Miocene. After STEININGER (1999), the geochronological calibrations of the European Land Mammal Zone MN11 result in a base at 8.7 Ma, a top at 8.0 Ma and therefore in a total duration of 0.7 m.y. The chronostratigraphical correlation of the

MN11 with the Mediterranean results in the upper middle part of the Tortonian and the one of the Eastern Paratethys with the middle part of the Maeotian.

Daxner-Höck (2004; Table 1) queues the Upper Miocene, Austrian vertebrate faunas of the Vienna and the Pannonian Basin as follows: Gaiselberg, Obersulz (both: Lower MN9), Vösendorf, Inzersdorf (both: Middle MN9), Richardhof-Golfplatz (Upper MN9), Götzendorf (Uppermost MN9), Richardhof-Wald, Neusiedl a. See (both: Lower MN10), Schernham (Upper MN10), Kohfidisch, Eichkogel (both: MN11).

Kohfidisch as a locality influenced by the high and low levels of the Lake Pannon leads to general considerations about the development and correlation of the Vienna Basin with the Pannonian Basin during the Pannonian.

Rögl et al. (1993) and Rögl & Daxner-Höck (1996) document the history of the Pontian and the Pannonian in the Vienna Basin. Following Fuchs (1873), the Sarmatian/Pannonian boundary is marked by the appearance of *Congeria subglobosa* which itself is followed by the Paludina beds of the Levantinian. Hoernes (1903) correlated the *Congeria* beds of the Vienna Basin with the Pontian Stage and the freshwater beds of Moosbrunn and Eichkogel with the Levantinian. The Pannonian Stage was erected by Roth von Telegd (1879) for the *Congeria* beds and Schaffer (1927) subdivided it into the Pannonian (lower unit) and Pontian (upper unit). Friedl (1932, 1937) defined the Pontian as the unit above the one containing *Congeria subglobosa* but Lörenthey (1905) united all *Congeria* leading units between the Sarmatian and the Levantinian to the Pannonian and zonated it by molluscs.

With regard to the Pannonian of the Vienna Basin, Janoschek (1943) and Papp (1948) followed Lörenthey (1905). Papp (1948, 1951) does not believe in a possibility to correlate with the Eastern Paratethys' Maeotian and Pontian Stages. He subdivides the Pannonian s. l. into the "zones" A to H. The Upper Pannonian ("zone" Pannonian F to "zone" Pannonian H) sets in above the *Congeria subglobosa* zone and with the extinction of limnocardiids and most of the Pannonian ostracoda taxa. The "zone" Pannonian F represents the last zone leading congerias. Stevanovic (1951) correlates the upper *Congeria* beds in the Southeastern Pannonian Basin with the base of the Pontian Stage in the Dacian Basin leading *Congeria ungulacaprae* or *Paradacna abichi* (Radmanest bed). Although these species do not occur in the Vienna Basin, Papp et al. (1974) and Stevanovic (1987) adopt the zonation for the Central Paratethys. The "zone" Pannonian F leading *Congeria neumayri* and *Congeria zahalkai* in the Vienna Basin is correlated with the *Congeria ungulacaprae* zone of the Pannonian Basin. With regard to the Dacian and Euxinian Basin, the corresponding Pannonian/Pontian boundary is marked by the first emigration of limnocardiids, *Pseudoprosodacna* and *Pseudocatillus*.

Based on the occurrence of *Margaritifera* cf. *flabellatiformis* ("*Unio wetzleri*"), a limited correlation between the Vienna Basin and the Eastern Paratethys is possible. The species is present in the Maeotian of the Southern Ukraine, appears in the Pannonian Basin at the base of the Tihany formation and can be found in the Vienna Basin in the Upper Pannonian "zone" Pannonian F (Schultz 1993).

Considering the evolution of limnocardiids, Müller & Magyar (1992, 1994) correlate between the Pannonian and the Dacian Basin. The evolutionary lineage leads from *Lymnocardium decorum ponticum* to *Lymnocardium decorum decorum* and *Prosodacnomya vutskitsi*. The transition from *Lymnocardium decorum ponticum* to *Lymnocardium decorum decorum* coincides with the base of the *Congeria balatonica* zone of the Lake Balaton area just above the top of the magnetic anomaly 4A (about 8,7 Ma according to Berggren et al. 1995). A locality yielding small mammals in Tihany-Feherpart stratigraphically lies above the beds with *Lymnocardium decorum* and has been referred to MN11. *Prosodacnomya* has evolved from *Lymnocardium* between 7.0 and 7.7 Ma ago. *Prosodacnomya vutskitsi* occurs in the 6.0 to 6.4 Ma old locality Szarvas in Hungary.

The correlation of the Pontian between the Pannonian and the Dacian Basin is based on the FADs of *Prosodacnomya dainelli* and *Prosodacnomya sturi* (closely relative to *Prosodacnomya vutskitsi*). Following Andreescu (1977) and Pavnotescu & Andreescu (1978), these short-living species appear in the Lower or Middle Pontian of the Dacian Basin. Therefore, the *Congeria ungulacaprae* zone and the *Congeria balatonica* zone which are stratigraphically older correlate with the Maeotian. With regard to the Vienna Basin, that applies to the beds with *Congeria neumayri*/*Congeria zahalkai* ("zone" Pannonian F) correlative with the Maeotian as well.

By the aid of FADs and LADs of Miocene mammals, the faunas of the Vienna Basin may be correlated with MN zones (Mammal Neogene zones) after Mein (1975, 1989, 1999). The "zones" Pannonian C to F coincide with the MN9 localities. The most primitive representative of *Hipparion* appears at the base of "zone" Pannonian C (Gaiselberg; Table 1). Bernor (1993) discusses an evolutionary lineage of *Hipparion* from the base of "zone" Pannonian C to "zone" Pannonian F.

Generally, during the MN9 of the Lower Vallesian Middle Miocene genera (e. g. *Democricetodon*, *Albanensia*, *Myoglis*) still dominate the assemblage, and *Hipparion*, *Microtocricetus*, *Hylopetes*, *Eozapus*, and *Muscardinus* immigrate. In the relatively short MN10 of the Upper Vallesian, a remarkable faunal change occurs. Muridae become more prominent, *Epimeriones*, *Pliopetaurista* and *Graphiurops* occur while *Progonomys* disappears at the end of the Vallesian. The beginning of the MN11 (Lower Turolian) is marked by an extensive number of extinctions of old taxa. The faunas of MN11 and MN12 are relatively uniform and just differentiated by the species composition. *Parapodemus lugdunensis* is typical of MN11 while the appearance of *Parapodemus gaudryi* marks the MN12. The genus *Parapodemus* is replaced by the advanced murid *Apodemus* in the MN13 (Upper Turolian) when the modern cricetine *Cricetus* s. l. first appears (Daxner-Höck, 1993, 1996; Rögl & Daxner-Höck, 1996).

Daxner-Höck (1996) correlates the "zones" Pannonian A and B (Uppermost MN7/8) of the Vienna Basin with the Astaracian and the "zones" Pannonian C to G (MN9, MN10) with the Vallesian. The "zone" Pannonian H (MN11, 12, 13) belongs to the Turolian.

With regard to the stages of the Central Paratethys, the Paratethys Sea retreated during the latest Sarmatian, and the Sarmatian/Pannonian boundary coincides with the progradation of several deltaic bodies. The emerged wetlands of the Lower Pannonian ("zones" Pannonian A, B, C) were destroyed again with the beginning of the "zone" Pannonian D. The level of the Lake Pannon rose and stayed high during the "zone" Pannonian E. The corresponding sedimentary sequence is represented by pelitic deposits yielding a diverse endemic mollusc fauna in the Vienna Basin. With the "zone" Pannonian F, the final withdraw of the Lake Pannon from the Vienna Basin set in and allowed the formation of wetlands and extended floodplains. Drainage systems from the Alps and the Molasse Basin entered the Vienna Basin. Along the margin of the eastern Alps, the freshwater lakes could emerge slightly earlier than in the basin. This diachronism also concerns the small mammal faunas of the "marginal" locality Richardhof-Golfplatz and the "basinal" locality Götzendorf slightly younger than Richardhof-Golfplatz and both belonging to the "zone" Pannonian F (Harzhauser & Tempfer, 2004; Harzhauser et al., 2003; Hudáčková et al., 2000; Kováč et al., 1998).

3. Material and Methods

The whole material is stored in the department of Geology and Paleontology of the Natural History Museum Vienna. At the very beginning of this dissertation and financed by the FWF-project: P-15724-N06, we sorted the material into the following groups: seeds and fruits; Mollusca; Pisces; Amphibia; Reptilia; Aves; Insectivora; Chiroptera; Lagomorpha; Rodentia; Carnivora; Proboscidea; Perissodactyla; Artiodactyla. International specialists have already been invited for investigations about the fauna of Kohfidisch. Each part represents one more step toward a global impression of the Upper Miocene situation in and around Kohfidisch.

After having sorted the material, I described, counted and measured the herpetofaunal remains except the Testudines. For description, I made comparisons with the following fossil material:

Oberdorf, Austria, Lower Miocene (MN4); Sanchiz (1998a):
Amphibia and Reptilia: Inv. Nr.: NHMW1998z0015 – 1998z0026
Obergänserndorf and **Teiritzberg**, Austria, Lower Miocene (MN5); M. Böhme (2002b):
Amphibia and Reptilia: Inv. Nr.: NHMW2002z0013 – 2002z0027
Grund, Austria, Middle Miocene (MN5); Miklas-Tempfer (2003):
Amphibia and Reptilia: Inv. Nr.: NHMW2002z0094 – 2002z0098
Mühlbach, Austria, Middle Miocene (MN5); Miklas-Tempfer (2003):
Reptilia: Inv. Nr.: NHMW2002z0099 – 2002z0107
Sandelzhausen, Germany, Middle Miocene (MN5); M. Böhme (1999):
Chelotriton paradoxus: BSP
Ambach, Germany, Middle Miocene (MN5); Estes & Schleich (1994):
Mioproteus caucasicus: Inv. Nr.: BSP 1982 I 146-159
Hitzhofen, Germany, Middle Miocene (MN5); Estes & Schleich (1994):
Mioproteus caucasicus: Inv. Nr.: BSP 1980 I 189
Dieshof, Germany, Middle Miocene (MN5-6); Estes & Schleich (1994):
Mioproteus caucasicus: Inv. Nr.: BSP 1982 XXIII 2
Untershausen 2, Germany, Middle Miocene (MN5-6); Estes & Schleich (1994):
Mioproteus caucasicus: BSP
Oggenhof, Germany, Middle Miocene (MN6); Estes & Schleich (1994):
Mioproteus caucasicus: Inv. Nr.: BSP 1963 IX 147-152
Neudorf a. d. March (=Devinska Nová Ves), Slovakia, Middle Miocene (MN6); Herre (1955), Wettstein-Westersheimb (1955):
Amphibia: Inv. Nr.: NHMW1977/1865
Götzendorf, Austria, Upper Miocene (MN9); Miklas (2002):
Amphibia: Inv. Nr.: NHMW2000z0186 – 2000z0197
Götzendorf, Austria, Upper Miocene (MN9); Bachmayer & Młynarski (1977):
Pseudopus pannonicus (sensu Klembara 1979): NHMW

NHMW...Naturhistorisches Museum Wien
BSP........Bayerische Staatssammlung für Paläontologie

Beside the fossil comparison material for determination, I also used skeletons of Recent specimens which I prepared using Danclor (contains Natriumhypochlorit). The 1st Zoological Department of the Natural History Museum Vienna lent me specimens for preparation and skeletons. The main part of my Recent comparison material originates from the private skeleton collection leg. et prep. P. F. Keymar.

Herpetofaunal bones were measured using a Leica MZ6 microscope with a graduated dial 12mm 120. Each maxillare of members of the genus *Latonia* is measured according to Miklas (2002). The measurements of vertebrae of *Mioproteus caucasicus* follow Estes & Schleich (1994) and the ones of *Chelotriton paradoxus*, *Triturus* (*cristatus*) sp., *Triturus* (*vulgaris*) sp., *Triturus* sp. and of the Anura follow Haller-Probst & Schleich (1994). Relating to *Rana* (*ridibunda*) sp. as a member of the Anura, the specific ilia have been measured after G. Böhme & Günther (1979). According to Fejérváry-Lángh (1923), measurements of the osteodermalia of Lacertilia have been taken and vertebral measurements of the Lacertilia and Serpentes were designated by Auffenberg (1963) and Bachmayer & Szyndlar (1985).

Generally, the heterogeneity of the elements complicates statistical evaluations of the measurements. Especially the vertebrae of Anura are specialized to such a degree that their rank along the extremely short vertebral column

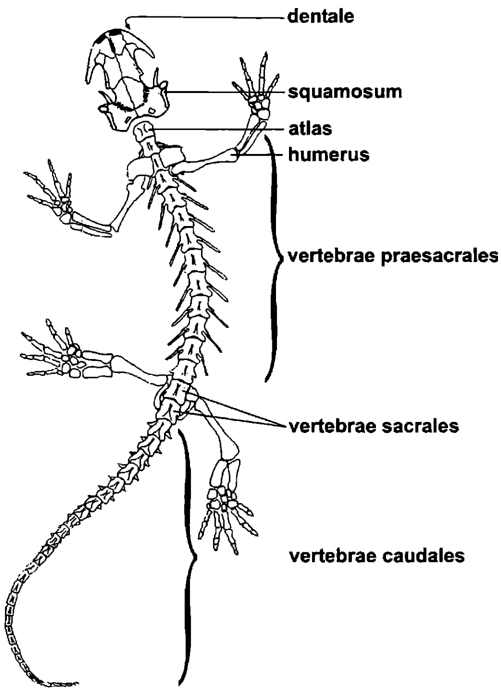


Figure 4: Terminology of the skeletal elements of the Caudata (*Triturus alpestris* in dorsal view modified after Haller-Probst & Schleich, 1994).

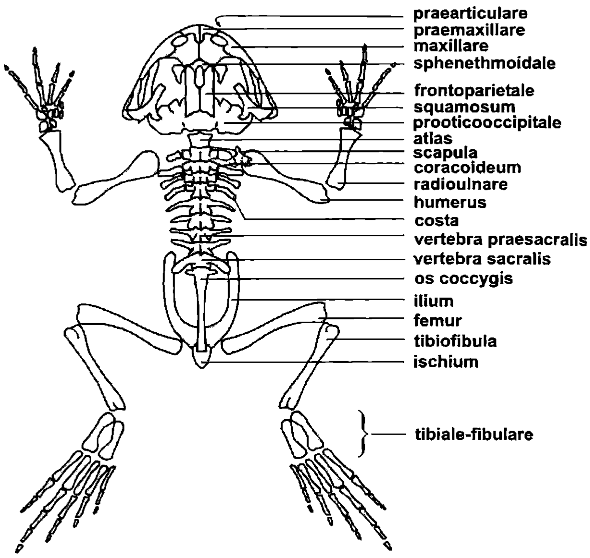
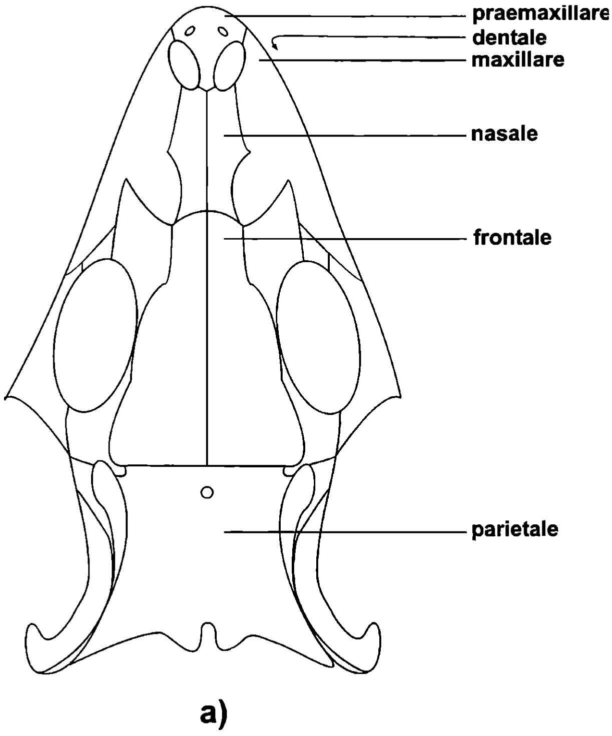


Figure 5: Terminology of the skeletal elements of the Anura.



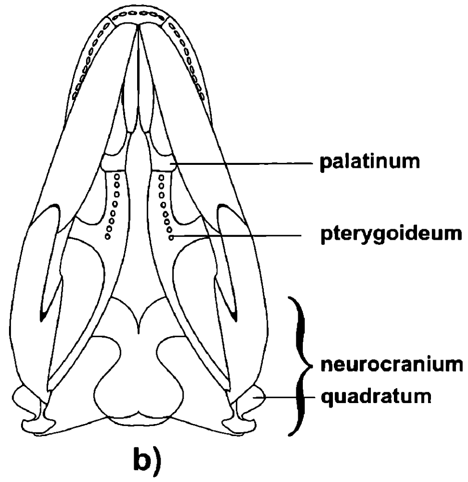


Figure 6: Terminology of the skull elements of the Scleroglossa (member of the Anguidae in dorsal (a) and in ventral (b) view).

can be identified. The vertebrae of Serpentes considerably differ within the column as well. Therefore, no further statistical tests would be adequate.

Using a JEOL 6400 scanning electron microscope of the Institute of Paleontology of the Vienna University, I took the micrographs. A. Schumacher of the Natural History Museum Vienna photographed the larger bones of *Pseudopus pannonicus*, *Varanus* cf. *hofmanni* and *Naja romani*. The skeletal anomalies were x-rayed by M. Marinelli using a Faxitron radiograph, 3mA, 50kV and the film Agfa Structurix D2.

I made the illustrations by means of a Leica drawing mirror. E. Höck prepared the computer graphics, figs. 1, 2, 3, while I constructed the others with the computer programs Corel Graphics 11 (CorelDRAW 11, Corel PHOTO-PAINT 11).

Tables and diagrams were produced by Microsoft Office 10 (Microsoft Excel).

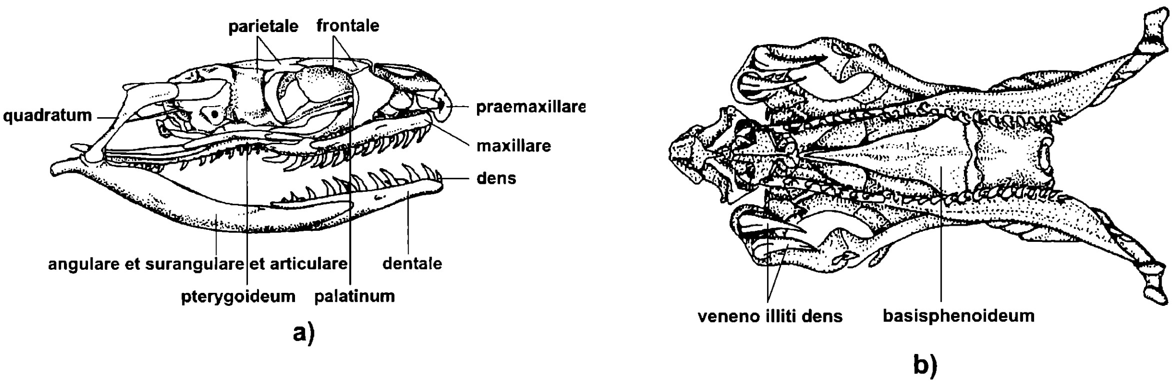


Figure 7: Terminology of the skull elements of the Serpentes (*Ptyas* sp. in lateral view (a) modified after CARROLL, 1993 and *Naja haje* in ventral view (b) modified after KAMAL et al., 1970).

3.1. Number of Individuals

Description and counting of the herpetofaunal bones resulted in the Maximum Number of Individuals (MXNI: Table 2, 3; Diagram 1, 2) of Amphibia and Reptilia (except the Testudines) of MXNI = 55.319. The MXNI corresponds to the number of identified bones. Reptilia represented by 51.959 remains (94%) are more frequent than Amphibia with 3.360 remains (6%; Diagram 5). Serpentes feature the highest Maximum Number of Individuals of MXNI = 36.076 (max: *Elaphe kohfidischi* MXNI = 13.862; min: *Typhlops* cf. *grivensis* MXNI=27) followed by the Lacertilia with maximum 15.883 remains (max: *Pseudopus pannonicus* MXNI = 11.826; min: Gekkonidae indet. MXNI = 3). Among the Amphibia, Anura with the Maximum Number of Individuals of MXNI=2998 (max: *Latonia* sp. MXNI = 815; min: *Bombina* cf. *bombina* MXNI = 5) are more frequent than Caudata with MXNI = 362 (max: *Triturus* (*cristatus*) sp. MXNI = 170; min: *Chelotriton paradoxus* MXNI = 23).

The more predicative Minimum Number of Individuals MNI = 2 013 (MNI: Tables 4, 5; Diagrams 3, 4) differs extremely from the MXNI. The MNI results from the maximum number of the most frequently present single existing bone (i. e. number of ossa coccygea) or the left or the right element respectively of the most frequently present symmetrical bone (i. e. number of left ilia). Although Reptilia are still most frequent featuring MNI = 1 259, they represent just 62% in relation to the Amphibia with MNI = 754 (38%; Diagram 5). Lacertilia dominate because MNI= 814 (max: *Lacerta* sp. A MNI = 497; min: Gekkonidae indet. MNI = 3) followed by the Anura, MNI=626 (max: *Latonia* sp. MNI = 182; min: *Bombina* cf. *bombina* MNI= 3). The Minimum Number of Individuals of Serpentes represents MNI = 445 (max: *Naja romani* MNI = 130; min: *Typhlops* cf. *grivensis* MNI = 16) and Caudata with MNI = 128 (max: *Triturus* (*cristatus*) sp. MNI=40; min: *Chelotriton paradoxus* MNI = 10) are less frequent.

With regard to the percental Minimum Number of Individuals of Amphibia and Reptilia in descending frequency (MNI (%): Table 6; Diagram 6), the lizard *Lacerta* sp. A (25%) is most frequent. It is followed by: *Latonia* sp. and *Bufo bufo* equally frequent with 9%, *Pseudopus pannonicus*, *Elaphe kohfidischi*, *Naja romani*, and *Rana* (*ridibunda*) sp. altogether featuring a relative frequency of 6%, *Pelobates* cf. *cultripes* (5%), *Anguis fragilis*, *Natrix longivertebrata*, and *Vipera burgenlandica* (altogether: 3%), *Lacerta* sp. B, *Varanus* cf. *hofmanni*, *Coluber planicarinatus*, *Triturus* (*cristatus*) sp., and *Triturus* sp. (altogether: 2%), *Edlartetia sansaniensis*, *Typhlops* cf. *grivensis*, *Mioproteus caucasicus*, *Triturus* (*vulgaris*) sp., *Latonia gigantea*, and *L. ragei* (altogether: 1%), Scincidae indet. (0.8%), *Hyla* sp. (0.7%), *Chelotriton paradoxus* (0.5%), *Miolacerta tenuis* (0.4%), *Lacerta* cf. *viridis* (0.3%), Gekkonidae indet. (0.2), and finally *Bombina* cf. *bombina* (0.1%).

Most obviously, the Minimum Number of Individuals may be influenced by taphonomy and preservation. More detailed information concerning the MNI and MNI (%) is given in chapter 6 combined with the paleoclimatic and -environmental conclusions.

3.2. Terminology

As nomenclature of the skeletal elements, the terms mainly follow BAILON (1991), HALLER-PROBST & SCHLEICH (1994): Caudata (fig. 4); BAILON (1991), KÄMPFE et al. (1966), ROČEK (1994a), SANCHIZ (1998b), SEDLÁČKOVÁ (2000): Anura (fig. 5); BAILON (1991), FEJÉRVÁRY-LÁNGH (1923), MERTENS (1942), RAUSCHER (1992), ROČEK (1984): Lacertilia (fig. 6); and BAILON (1991), CARROLL (1993), SZYNDLAR (1984): Serpentes (fig. 7). I have chosen the Latin translation because it is uniform and international.

4. Systematic Part

If not explicitly cited, the depository of the type material is taken from ESTES (1981; Caudata), SANCHIZ (1998b; Anura), ESTES (1983; Lacertilia), and RAGE (1984b; Serpentes).

4.1. Class Amphibia

Order Caudata Scopoli, 1777
Suborder Proteoidea (Noble, 1931)
emend. Edwards, 1976
Family Proteidae Hogg, 1838

Genus *Mioproteus* Estes & Darevsky, 1978

Mioproteus caucasicus Estes & Darevsky, 1978

(Plate 1: a, b; Table 2, 4, 6, 7)

Holotype: Zoological Institute, Academy of Sciences, Saint Petersburgh, Russia (former U.S.S.R.), ZIL 240; slightly damaged anterior vertebra praesacralis (Estes & Darevsky 1977).

Type locality: Maykop, valley of the Belaya River, northern Caucasus, capital of the Adyghe Republic (former U.S.S.R.).

Stratigraphical Age of the Type material: Middle Miocene (Middle Sarmatian, Bessarabian).

Range: Lower Miocene – Upper Miocene: Central and Eastern Europe, Russia.

Material: 1 dentale sin. (AO: Inv. Nr.: NHMW2004z0009/0001). 2 atlantes. 30 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0009/0002). (BM: Inv. Nr.: NHMW 2004z0009/0003).

Description:

dentale (Plate 1: a): The single left, slightly convex dentale is 5,17 mm long and 0,75 mm broad at the symphysis. The latter possesses an oval shape. Below the position of the second tooth, the Meckel's groove widely opens. No teeth are preserved.

atlas: Both atlantes lacking parts of the neural arch are fragmentary. The dorsoventrally flattened centrum, the processus odontoideus and the left or right neural arch respectively are preserved. The condyli occipitales are dorsoventrally depressed and connected. In ventral view, an anteriorly pointed and posteriorly flattened keel is present.

vertebra praesacralis (Plate 1: b; Table 7): The 30 vertebrae praesacrales represent each state of preservation. Most of them lack the neural arch, but 12 nearly complete ones are present. Their measurements are given in Table 7. The vertebrae are amphicoelous and similar to the atlas, they possess a posteriorly flattened keel from ventral aspect, which ends in two lateral basapophyses. A prominent ventral lamina is present on the processus transversi. The neural arch is flattened and the processus spinosus is deeply forked posteriorly.

Comparison: The elements correspond to the ones of *Mioproteus caucasicus* described first by Estes & Darevsky (1977). Compared with *Mioproteus caucasicus* from Götzendorf, the bones altogether are smaller in Kohfidisch. Further, the processus odontoidei of the atlantes of Kohfidisch are rounded contrary to the pointed ones of the Götzendorf specimens.

Mioproteus caucasicus of Ambach is similar to the Kohfidisch specimens concerning the well-rounded processus odontoideus. Relating to the size, it is larger and therefore resembling *Mioproteus caucasicus* from Götzendorf. The same applies to *Mioproteus caucasicus* from Dieshof, Hitzhofen, Oggenhof, and Untershausen 2.

As a second species of the genus *Mioproteus*, Estes (1984) has described *Mioproteus wezei* from the Upper Pliocene (MN16) of Poland. *Mioproteus wezei* also occurs in the Upper Pliocene of France (Bailon, 1995) and in the Lower Pleistocene of Moldavia (Averianov, 2001). The processus spinosus of its vertebra is forked more anteriorly, the interzygapophyseal ridge is curved more dorsally in the posterior region, the ventral lamina of the processus transversus is more prominent and the ventral keel is more distinct.

The Recent relative *Proteus anguineus* has the widely open Meckel's groove of the dentale in common with *Mioproteus caucasicus*. Otherwise, it possesses more fragile vertebrae. Their neural arches are narrower and the processus spinosi forked more posteriorly. Both species seem to be paedomorphic (Estes & Darevsky, 1977).

Discussion: *Mioproteus caucasicus* has been described from the Lower Miocene to the Upper Miocene of Germany (M. Böhme pers. advice; Estes & Schleich, 1994; Schleich, 1985), from the Middle Miocene of eastern Kazakhstan and the Caucasus region, Russia (Estes ,1981; Estes & Darevsky, 1977; Milner, 2000) and from the Upper Miocene of Hungary (Roček, 2004) as well as Götzendorf and Richardhof-Golfplatz in Austria (Miklas, 2002; Harzhauser & Tempfer, 2004.).

In 1977, Estes & Darevsky have described the new genus *Mioproteus* as a member of the Proteidae containing also the genera *Proteus*, *Necturus* and *Orthophyia*. Skull and tooth characteristics of *Mioproteus* as well as *Proteus* and *Necturus* point to paedomorphism. Relating to the tooth number on the vomer and calcification of the vertebrae, *Mioproteus* shows more similarities to *Necturus* than to *Proteus*, although its vertebrae are generally more calcificated and therefore more robust. Further, *Mioproteus* and *Necturus* possess a well distinct posterior processus of the vomer together with the genus *Palaeoproteus* (Batrachosauroididae, Proteoidea). The genus *Orthophyia* is probably synonymous with *Mioproteus* (Estes & Darevsky, 1977), but unfortunately the type specimen is lacking.

According to Estes & Darevsky (1977), Larsen & Guthrie (1974) and Naylor (1978), *Mioproteus* and *Necturus* belong to the family Proteidae. Hecht (1957) and Hecht & Edwards (1976) doubt the relationship between *Proteus* and *Necturus*. They explain the similarities by parallel evolution and assume a polyphyletic origin.

The suborder Proteoidea divides into the Proteidae and the Batrachosauroididae. Early members of the Batrachosauroididae (*Opisthotriton*, *Prodesmodon*) possess opisthocoelous vertebrae while the vertebrae of younger members (*Palaeoproteus*) are amphicoelous such as the ones of Proteidae. Following Estes (1975), Batrachosauroididae are more specialized than Proteidae. Contrary to that hypothesis, Naylor (1978) suggested that Proteidae arose from the Batrachosauroididae by reversion to amphicoely (Estes 1981).

Ecology and Climate – living relatives: Although *Mioproteus caucasicus* represents an extinct species, the faunal associations can be used as ecological hints. Lotic, aerial conditions are indicated by its appearance. The type material was associated with newts and frogs (ESTES & DAREVSKY, 1977) and in Ingolstadt, Germany, it has been found (SCHLEICH, 1985) among a rich stream-side fauna (DEHM, 1961). In Götzendorf, Austria, *Mioproteus caucasicus* occurs together with *Andrias scheuchzeri*, whose larvae very probably needed well-flowing, oxygenated water such as the ones of its Recent relative *A. davidianus* (HARZHAUSER & TEMPFER, 2004; MIKLAS, 2002; TEMPFER, 2004). M. BÖHME (2002a) interprets the accompanying fish fauna there as a lotic assemblage.

As living relative, *Proteus anguineus* lives subterraneously and blind. It exclusively inhabits underground streams and lakes with a temperature ranging between 5°C and 10°C. Intolerant with regard to temperature fluctuation, it does not hibernate.

Proteus anguineus is widespread in limestone cave systems along the eastern Adriatic seaboard, as far north as the Istrian region and as far south as Montenegro. Its occurrence in North-East Italy is documented as an isolated one. There is also a small introduction in the French Pyrenees (ARNOLD & OVENDEN, 2002; GASC et al., 1997). The distribution of *Proteus anguineus* is mainly restricted to the Köppen's climate type Cs and partly Cf following MÜLLER (1996; see chapters 5, 6).

Suborder Salamandroidea NOBLE, 1931
Family Salamandridae GRAY, 1825

Genus *Chelotriton* POMEL, 1853

Chelotriton paradoxus POMEL, 1853

(Plate 1: c; Table 2, 4, 6, 7)

Neotype: Muséum National d'Histoire Naturelle, Paris, France, Cod. 12; vertebra praesacralis (ESTES 1981).

Type locality: Coderet, France.

Stratigraphical Age of the Type material: Uppermost Oligocene.

Range: Lower Oligocene – Upper Miocene: Central and Western Europe.

Material: 1 squamosum dext. 3 atlantes (AO: Inv. Nr.: NHMW2004z0010/0001). 19 vertebrae praesacrales. (BM: Inv. Nr.: NHMW2004z0010/0002).

Description:

squamosum: The right squamosum is complete, 6,75 mm broad (processus zygomaticus-processus posterodorsalis) and 7,29 mm long (processus dorsalis-processus posterolateralis). Its dorsal aspect is deeply pustularly sculptered, and the ramus paroticus is prominent.

atlas (Plate 1: c): Two atlantes are nearly complete, one lacks the neural arch and the posterior part. The condyli occipitales are oval and the processus odontoideus broad with two disconnected lateral facets. A heart-shaped, pustular sculpture characterizes the posterior, dorsal part of the processus spinosus. Ventrally, many small to prominent and round to oval foramina are present.

vertebra praesacralis (Table 7): 10 of the 19 significant robust vertebrae praesacrales are preserved by their dorsal and ventral parts. The measurements are noted in Table 7. The opisthocoelous vertebrae are broad. On the ventral, porous side, a medial keel is present. Similar to the atlas, the posterior, dorsal part of the processus spinosus possesses a heart-shaped, pustular sculpture.

Comparison: The holotype of *Chelotriton paradoxus* got lost, but POMEL (1853) precisely describes its vertebrae correlating with the ones described herein. He explains the principle of the vertebral connection which results in a kind of resistant ossified dorsal carapax.

Obergänserndorf and Teiritzberg yield *Chelotriton* sp. represented by elements of the skull, maxillaria and rib-fragments. The squamosum correlates to the one of Kohfidisch concerning the shape and the pustulate sculpture. It is smaller than the squamosum of Kohfidisch but indicates a larger individual than in Oberdorf.

Compared with *Chelotriton paradoxus* from Sandelzhausen, the atlantes are similar relating to the shape of the condyli occipitales and to the disconnected lateral facets.

The material of *Chelotriton* sp. from Oberdorf is remarkably small and some processus spinosi show a sculpture based on pits and not on pustules. Perhaps it represents larval or metamorphosing specimens. The atlantes and the vertebrae praesacrales of Kohfidisch are much bigger and the pustular pattern is more distinct. The atlas differs from the one of Oberdorf relating to the shape of the condyli occipitales. The Kohfidisch specimens possess dorsoventrally compressed ones while in Oberdorf, the condyli occipitales are compressed laterally. The lateral facets on the Kohfidisch atlantes are clearly separate similar to the Oberdorf specimens.

A rather large specimen of *Chelotriton paradoxus* was present in Götzendorf. The size of not only the atlas but also of the vertebrae praesacrales ranges between the minimum and maximum measurements of the Kohfidisch specimens but below the mean. Their shape and characteristics are similar except for the lateral facets of the atlas. Contrary to the atlantes of Kohfidisch, the lateral facets contact each other on the Götzendorf atlas.

The genus *Chelotriton* includes the species *Chelotriton paradoxus*, *Chelotriton ogygius* (Lower Miocene), *Chelotriton robustus* (Middle Eocene) and *Chelotriton pliocenicus* (Pliocene). *Chelotriton ogygius* is very probably synonymous with *Chelotriton paradoxus* although no pustulate sculptured plates on the processus spinosi are known (GOLDFUSS, 1831). The sculpture pattern of *Chelotriton robustus* is composed of small pits and grooves present on broad neurapophyseal plates (WESTPHAL, 1980) while the one of *Chelotriton paradoxus* as well as of the vertebrae described herein consists of pustules on smaller plates. *Chelotriton pliocenicus* has been described by BAILON (1989). The pustulate sculpture on the processus spinosi extends more anteriorly and the oval zygapophyses are more transversally orientated. Behind the praezygapophyses a well distinct foramen is present. The ventral keel on the centrum is broader and diverges posteriorly while *Chelotriton paradoxus* possesses a rather narrow, consistent one. The Crocodile Newt *Tylototriton* occurs in the Middle Eocene of Germany (HERRE, 1935) and represents a living relative of *Chelotriton.* Contrary to *Chelotriton,* its vertebrae are smaller and the sculpture pattern of the processus spinosi is formed of pits and grooves but not of pustules. Diagnostic of *Chelotriton*, a bony lamina (the anterior zygapophyseal ridge) connects the praezygapophyses to the processus costales. Behind the processus costales, a marked notch is present in dorsal view (ESTES, 1981).

Discussion: *Chelotriton paradoxus* occurs in Western Europe from the Lower Oligocene to the Upper Miocene. Herrlingen (Lower or Middle Oligocene), Rott bei Bonn, Gaimersheim, Burgmagerbein, Weißenburg 4, Oppertshofen, Floersheim (Upper Oligocene), Weißenburg 6 (Upper Oligocene to Lower Miocene), Bissingen 1 "Wüterich", Weisenau, Grafenmühle, Wintershof-West, Erketshofen (Lower Miocene), Weißenburg 5, Dinkelscherben, and Sandelzhausen (Middle Miocene) number among the German localities. Coderet (Uppermost Oligocene) and Peublanc both in France (Lower Miocene), Rubielos de Mora and Las Plana IV-A both in Spain (Lower Miocene), La-Grive-Saint-Alban and Sansan both in France (Middle Miocene), as well as Öhningen (Upper Miocene) of Germany supplement the list of localities (ESTES, 1981; M. BÖHME, pers. advice; MILNER, 2000). MŁYNARSKI et al. (1982) have described the species from the Middle Miocene of Opole (Poland). The Upper Miocene, Hungarian localities Rudabánya (ROČEK, 2004) and Polgárdi 4 (VENCZEL, 1999a) yield *Chelotriton paradoxus* as well. In Austria, *Chelotriton* sp. occurs in Oberdorf (Lower Miocene, MN4; SANCHIZ 1998a), in Obergänserndorf and Teiritzberg (Lower Miocene, MN5; M. BÖHME, 2002b), and represented by *Chelotriton paradoxus* in Götzendorf (Upper Miocene, MN9; MIKLAS, 2002).

POMEL's collection together with the holotype of *Chelotriton paradoxus* unfortunately got lost. He characterized this salamander as a significant large, terrestrial one. After ESTES (1981), it belongs to the "group II" genera of the Salamandridae.

ESTES (1981) subdivided the family of the Salamandridae into three informal groups:

"group I" genera containing the most primitive forms such as *Salamandra* and relatives divergent in feeding specializations. Only members of this group are adapted to terrestrial food based on their special tongue type.

"group II" consists of the primitive newts *Pleurodeles* and *Tylototriton*, *Echinotriton* (since NUSSBAUM & BRODIE, 1982) and their fossil allies such as *Chelotriton.* WAKE & ÖZETI (1969) separate the two Recent genera from the group, but the classification of ESTES (1981) is based on the common presence of the frontosquamoseal arch. Further, the dermal sculpture on the skull and the processus spinosi as well as the long ribs are typical characteristics of members of "group II"

"group III" represents the most derived group with complex interrelationships. Beside others, *Archaeotriton*, *Euproctus* and *Triturus* are members of "group III"

ESTES (1981) and ROČEK (1994b; 1996) discuss the separation of the genera *Brachycormus*, *Chelotriton* and *Tylototriton.* Although differences based on the size, the sculpture pattern, the level of ossification on carpus and tarsus, and the position of the sacrum are remarkable, the occurrence of neotenic evolutionary trends in these genera complicates the classification.

Following HERRE (1950) and based on skull and vertebral characteristics, the genera *Palaeopleurodeles* and the living *Pleurodeles* (Salamandridae) represent an evolutionary level more primitive than *Tylototriton.*

ESTES (1981), ESTES & HOFFSTETTER (1976) and WESTPHAL (1980) suspect that *Tylototriton* and the European fossil genera *Chelotriton*, *Grippiella*, *Heliarchon*, *Palaeosalamandrina*, and *Tischleriella* are synonyms. In this case, *Chelotriton* would have priority over *Tylototriton.* NUSSBAUM & BRODIE (1982) point to either significant differences or the lack of diagnostic characters which would justify to synonymize these genera.

The genus *Tylototriton* has been split into *Tylototriton* and *Echinotriton* by NUSSBAUM & BRODIE (1982). Four extant species (*asperrimus*, *kweichowensis*, *taliangensis*, *verrucosus*) are retained in *Tylototriton* while two extant species (*andersoni*, *chinhaiensis*) are placed in *Echinotriton. Echinotriton* differs in a number of significant morphological and life history features from *Tylototriton. Tylototriton primigenius* NOBLE, 1928 from the Upper Miocene of Öhningen in Germany may be synonymous to *Chelotriton paradoxus.*

Ecology and Climate – living relatives: The ecological requirements of *Tylototriton* represent a valuable hint to the environment of its close relative *Chelotriton.* The terrestrial Crocodile Newt inhabits wooded hills up to 3000 m and damp biotopes with dense vegetation. Its preferred temperature ranges between 22°C and maximum 28°C. *Tylototriton* may hibernate at 15°C but if the temperature is above, it does not. On arid conditions, it keeps a dryness sleep. Its larvae require ponds or similar water bodies (OBST et al. 1984). The environment of *Tylototriton* correlates to the sedimentological situations where *Chelotriton* has been found. Its specimens have mainly been discovered in terrestrial fissure-fillings but also in the sediments of slack water (*Chelotriton robustus* of the Grube Messel near Darmstadt, Germany, Eocene; WESTPHAL, 1980 and *Chelotriton paradoxus* of Sandelzhausen, Germany, Middle Miocene; M. BÖHME, 1999), swamps (*Chelotriton* sp. of Oberdorf, Austria, Lower Miocene; SANCHIZ, 1998a) and floodplains structured by swift, oligotrophic rivulets accompanying the main channel (*Chelotriton paradoxus* of Götzendorf, Austria, Upper Miocene; HARZHAUSER & TEMPFER, 2004; MIKLAS, 2002). Very probably, it mainly lived terrestrial in wooded terrains and its larvae inhabited damp environments with slack or slowly running waters. The Recent genus *Tylototriton* inhabits North India to South-West China, North Thailand, Burma, North Vietnam, West Yunnan and the Ryukyu islands in Japan (OBST et al., 1984; STEJNEGER, 1996). According to MÜLLER (1996; see chapters 5, 6), these areas belong to the Köppen's climate types Af, Aw, BS, Cf, and Cw.

Genus *Triturus* RAFINESQUE, 1815

Triturus (*cristatus*) sp. (LAURENTI, 1768)

(Plate 1: d; Table 2, 4, 6, 7)

Recent species: *Triturus cristatus* (LAURENTI, 1768)
Range: Upper Miocene – Upper Pleistocene: Austria, Germany, Slovakia, Poland, Rumania, Hungary, England;
Holocene: most of Europe, eastwards to Caucasus and Central Asia.
Upper Miocene of Kohfidisch: FOD (= first occurrence date).
Material: 170 vertebrae praesacrales (AO: Inv.Nr.: NHMW2004z0011/0001).
(BM: Inv. Nr.: NHMW2004z0011/0002).
Description:

vertebra praesacralis (Plate 1: d; Table 7): The dorsal part of the 170 opisthocoelous vertebrae praesacrales is preserved in any case. Measurements are given in Table 7. The centra and the entire vertebrae are flattened dorsoventrally. Due to the slightly rising neural arch, they are higher posteriorly. Ventrally, two distinct lateral foramina are present where the prominent parapophyses insert. The latter are almost directly connected to the diapophyses (forming together with the parapophyses the processus transversi), just a short lamina exists. From dorsal aspect, the two very large oval praezygapophyses are orientated longitudinally but clearly introversive posteriorly. The oval postzygapophyses are orientated longitudinally as well, but introversive anteriorly. The low processus spinosus flattens and extends to posterior overtopping the centrum. Its posterior margin is slightly concave.

Triturus (*vulgaris*) sp. LINNAEUS, 1758

(Plate 1: e; Table 2, 4, 6, 7; figs. 8, 9)

Recent species: *Triturus vulgaris* LINNAEUS, 1758
Range: Middle Miocene – Pleistocene: Austria, Germany, Slovakia, Rumania, Italy, Greece, Britain;
Holocene: Europe, West Asia.
Material: 5 atlantes. 46 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0012/0001). 1 humerus ♀ sin. (AO: Inv. Nr.: NHMW2004z0012/0002).
(BM: Inv. Nr.: NHMW2004z0012/0003).
Description:

atlas: Two atlantes are complete and three atlantes consist of the centrum with the onsets of the neural arch. The centrum possesses extremely concave lateral margins, small foramina and longitudinal ridges ventrally. The roundish oval condyli occipitales are orientated to dorsoventral and the lateral facets of the broad and flat processus odontoideus are of a round shape and disconnected. From dorsal aspect, the neural arch becomes narrow posteriorly. Anteriorly, it is well rounded showing a ridge which conjoins medially to lead into a prominent, longitudinal one. Lateral to that ridge, a distinct one is present on both sides.

vertebra praesacralis (Plate 1: e; Table 7): The measurements of the 46 vertebrae praesacrales are given in Table 7. The opisthocoelous vertebrae praesacrales represent different states of preservation. In any case, the processus spinosus is present. The vertebrae and especially the centra are flattened dorsoventrally. The neural arch rises posteriorly. From ventral aspect, two relatively large foramina are present on both sides of the centrum where the parapophyses join nearly the full length of the centrum. The latter are connected to the diapophyses by a thin lamina. The praezygapophyses are ovally shaped and orientated longitudinally but slightly introversive posteriorly. That applies to the postzygapophyses as well, unless they are introversive anteriorly. The high processus spinosus forks slightly posterior the insertion of the processus transversi.

humerus ♀ (fig. 8): The left ♀ humerus is 2.65 mm long and 0.55 mm wide distally from flexor aspect. In that view, it is straight and sandglass-like shaped. Epicondylus radialis and epicondylus ulnaris split in the distal third and enclose a foramen slightly above the caput humeri. Proximally, the prominent crista ventralis is slightly convex. From lateral view, the crista paraventralis results in a long and thin, pointed processus at an angle of 59° with the humerus.

Comparison: Comparisons of the fossil elements with skeletonized material of Recent specimens resulted in the determinations given herein.

The atlantes show all characteristics typical of *Triturus vulgaris*. Contrary to an atlas of *Triturus cristatus*, the ones described herein broaden just slightly anteriorly and possess round, disconnected lateral facets on the processus odontoideus. The neural arch with a prominent processus spinosus is distinctly rounded anteriorly.

With regard to *Triturus roehrsi* from Neudorf a. d. March (= Devinska Nová Ves) and from Oberdorf, the centra of the atlantes are extremely similar to the ones of *Triturus vulgaris*. Solely the condyli occipitales are ovaler and more transversally orientated. Concerning *Triturus roehrsi* from Neudorf a. d. March, the lateral facets of the processus odontoideus are connected from ventral aspect and the neural arch is less rounded anteriorly. The latter is not preserved on the Oberdorf specimens. Taking these characteristics as well as the description of HALLER-PROBST & SCHLEICH (1994) into consideration, the atlantes have been assigned to *Triturus* (*vulgaris*) sp.

Viewing the measurements of the vertebrae praesacrales of the two species *Triturus* (*cristatus*) sp. and *Triturus* (*vulgaris*) sp. described herein, the difference relating to their size is clearly remarkable. While the mean measurements of the vertebrae praesacrales of *Triturus* (*cristatus*) sp. range between 0.97 mm and 2.63 mm, the ones of *Triturus* (*vulgaris*) sp. measure between 0.62 mm and 2.36 mm (see Table 7). The ratios yield nearly the same data. Skeletal morphological differences of the vertebrae praesacrales are clearly distinct as well. Vertebrae including the centra of *Triturus* (*cristatus*) sp. are more flattened possessing a posteriorly less rising neural arch. The ventral, lateral foramina of the centrum are larger and the thicker para- and diapophyses insert narrower. The lamina connecting the parapophyses with the diapophyses is definitively smaller and not detectable in some specimens. Dorsally, the vertebrae of *Triturus* (*cristatus*) sp. possess larger zygapophyses and a lower processus spinosus not forked posteriorly but flattened and extended. The neural arch overtops the centrum contrary to the one of *Triturus* (*vulgaris*) sp.

Contrary to *Triturus vulgaris*, *Triturus roehrsi* possesses a broad, more deeply forked crista on the lower processus spinosus of the vertebra praesacralis. Para- and diapophyses are closely connected and the diapophyses are fused to the neural arch by a bony plate. Ventrally, bony ridges lead from the parapophyses to the centrum.

The vertebrae praesacrales of members of the *Triturus cristatus* group or the *Triturus vulgaris* group respectively (see below) can hardly be distinguished. Therefore, the determinations have resulted in *Triturus* (*cristatus*) sp. and *Triturus* (*vulgaris*) sp.

Comparing the humeri of members of the genus *Triturus*, the ones of *Triturus cristatus* are larger and more vaulted to anterior possessing a shorter crista paraventralis (fig. 9). As noted by HOLMAN & STUART (1991), the humeri of *Triturus cristatus* have a more elongate crista ventralis and a thicker shaft than in *Triturus vulgaris* and *Triturus helveticus* but it is impossible to separate the humeri of the latter two species satisfactorily from one another. The humerus of *Triturus roehrsi* from Oberdorf is longer, vaulted to anterior and shows a short crista paraventralis. These characteristics remind more of *Triturus cristatus* than of *Triturus vulgaris*.

The species *Triturus vulgaris* shows sex-related differences between females and males with regard to the humerus of Recent specimens. While the crista paraventralis of females is more pointed, the one of males is blunt and directed more dorsally (fig. 8). Concerning the humerus of the Kohfidisch specimen, it correlates with a female humerus of *Triturus vulgaris* which is difficult to distinguish from *Triturus helveticus*. Therefore, it is determined as a humerus of a female *Triturus* (*vulgaris*) sp.

Figure 8: *Triturus* (*vulgaris*) sp.♀. Humerus sin. lateral view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0012/0002), scale bar equals 1 mm.

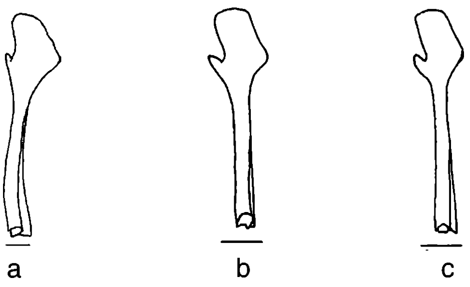


Figure 9: a: *Triturus cristatus* ♀. Humerus sin. lateral view (Recent). b: *Triturus vulgaris* ♀. Humerus sin. lateral view (Recent). c: *Triturus vulgaris* ♂. Humerus sin. lateral view (Recent), scale bar equals 1 mm.

Triturus sp.
(Table 2, 4, 6, 7)

Recent species: *Triturus cristatus* (LAURENTI 1768)
Range: Middle Miocene – Upper Pleistocene: Austria, Germany, Poland, Greece, Italy, Spain, France, Belgium, Britain;
Holocene: Europe, eastwards to Caucasus and Central Asia.
Material: 65 vertebrae praesacrales. 19 vertebrae caudales. (BM: Inv. Nr.: NHMW2004z0013/0001).
Description:

vertebra praesacralis (Table 7): The measurements (Table 7) of the 65 vertebrae praesacrales altogether give no result of "GL" because the posterior part of the neural arch is missing in each specimen. Therefore, no definitive determination of species can be given although the size and the shape of the vertebrae recall *Triturus* (*cristatus*) sp. or *Triturus* (*vulgaris*) sp. (see above).

vertebra caudalis: In either case, the opisthocoelous centra of the 19 vertebrae caudales covered by a lot of small foramina are preserved. At least parts of the neural and the hemal arch are connected. The cross section of the centrum is round. The hemal arch is as high as the neural arch and forked posteriorly as well. It inserts posterior to the cotylus while the neural arch reachs it. Oval prae- and postzygapophyses are orientated longitudinally. The para- and diapophyses represent connate laminae full of foraminae.

Comparison: The vertebrae praesacrales of *Triturus* sp. measure between 0.61 mm and 2.34 mm (see Table 7). The posterior part of their neural arch is missing. This is why no precise determination into species can be given. The size as well as the shape resemble *Triturus* (*cristatus*) sp. or *Triturus* (*vulgaris*) sp. It is improbable that a third species of *Triturus* was present in Kohfidisch.

It is difficult to identify species on the basis of vertebrae caudales of Recent members from the genus *Triturus*. Therefore, the ones described in this paper are determined as *Triturus* sp.

Discussion: Concerning *Triturus* (*cristatus*) sp., the species *Triturus cristatus* has already been described from the Upper Pliocene of Poland (SANCHIZ & MŁYNARSKI, 1979a), from the Upper Pliocene as well as the Lower Pleistocene of Slovakia (HODROVÁ, 1984, 1985; ROČEK, 1988), from the Lower Pleistocene of Rumania (VENCZEL, 1991) and as *Triturus* cf. *cristatus* from the Lower Pleistocene of Hungary (VENCZEL, 1997b), from the Middle Pleistocene of Poland (SANCHIZ & SZYNDLAR, 1984) and England (HOLMAN, 2000), and from the Upper Pleistocene of Germany (G. BÖHME, 1979) and Poland (SANCHIZ & SZYNDLAR, 1984). Therefore, Kohfidisch represents the stratigraphically oldest locality of *Triturus* (*cristatus*) sp.

The presence of *Triturus vulgaris* has been noted by M. BÖHME (1999) from the Middle Miocene of Sandelzhausen, by VENCZEL (1991) from the Lower Pleistocene of Rumania, by HOLMAN (2000) from the Middle Pleistocene of England, by G. BÖHME (1979) from the Upper Pleistocene of Pisede bei Malchin both in Germany, and by HODROVÁ

(1984, 1985) and ROČEK (1988) from the Upper Pliocene as well as the Lower Pleistocene of Slovakia. HOLMAN & STUART (1991) have described *Triturus vulgaris* from the Lower Holocene of Britain. Members of the *Triturus vulgaris* group are present in the Upper Miocene of Greece (SANCHIZ, 1977a) and the Lower Pleistocene of Italy (DELFINO & BAILON, 2000).

Triturus sp. is known perhaps from the Eocene of Belgium, England and France (MILNER, 2000), reliably from the Oligocene (MP22) of France, from the Lower Miocene of Spain (SANCHIZ, 1977 a, b), the Upper Miocene of Richardhof-Golfplatz in Austria (HARZHAUSER & TEMPFER, 2004.), the Upper Pliocene of Poland (SANCHIZ & MŁYNARSKI, 1979a), the Lower Pleistocene of Italy (VERGNAUD-GRAZZINI, 1970), and the Upper Pleistocene of Spain (SANCHIZ 1977a) and Germany (BRUNNER, 1956; PETERS, 1977). Already the Lower Eocene of France (AUGÉ et al., 1997) and the Middle Oligocene of Belgium (HECHT & HOFFSTETTER, 1962) yield cf. *Triturus*.

The postglacial distribution of the European Urodela features two origins following STEINER (1950): the area southern and southwestern of the Black sea (Pontic refuge) as well as the western and northwestern part of the Mediterranean (Ibero-African refuge). Caused by the glacial isolation, a western and an eastern line of the genus *Triturus* could evolve, namely *Triturus marmoratus* + *Triturus cristatus* ssp. or *Triturus helveticus* + *Triturus vulgaris*.

Contrary to STEINER (1950), COGALNICEANU & VENCZEL (1992) recognize three great refuges of the genus *Triturus* caused by the glaciations: the Iberian, the Apennine and the Balkan Peninsula refuge. Beside others, *Triturus boscai*, *Triturus pygmaeus*, *Triturus helveticus sequerei*, and *Triturus alpestris cyreni* in the Iberian Peninsula, *Triturus italicus*, *Triturus vulgaris meridionalis*, *Triturus carnifex*, and *Triturus alpestris inexpectatus* in the Apennine Peninsula and more than 10 species and subspecies in the Balkan Peninsula. After the glaciations, a slow invasion of northern Europe started in the Holocene. Invaders coming from the southwestern (Iberian Peninsula) and the southeastern (Balkan Peninsula) refuges were more successful. Generally, the centre of the dispersal of *Triturus* seems to be the Balkan Peninsula rather than Western Europe.

The genus *Triturus* is divided into three groups based on genetic similarities such as the "Small-Bodied" and the "Large-Bodied" species. The "Small-Bodied" group consists of *Triturus boscai*, *Triturus helveticus*, *Triturus italicus*, *Triturus montandoni*, and *Triturus vulgaris*. It is usually designated as the *Triturus vulgaris* group. The "Large-Bodied" group also called *Triturus cristatus* group contains the species *Triturus cristatus*, *Triturus carnifex*, *Triturus dobrogicus*, *Triturus karelinii*, *Triturus marmoratus*, *Triturus pygmaeus*, and *Triturus vittatus*. The *Triturus alpestris* group is composed of *Triturus alpestris* only (OBST et al., 1984).

With regard to the *Triturus cristatus* group, the several species formerly ranked as subspecies. Current studies based on molecular identifications by DNA analyses convincingly classified them as closely related but distinct species (MIKULÍČEK & PIÁLEK, 2003).

According to HALLER-PROBST & SCHLEICH (1994), osteological skull characteristics of *Triturus cristatus* separate the species from *Triturus marmoratus* and *Triturus vittatus*. An exact classification seems to be difficult mainly due to the species diversity and little interspecific anatomical differences.

Relating to the extinct species *Triturus roehrsi* from the Middle Miocene (MN6) locality Neudorf a. d. March (= Devinska Nová Ves) in Slovakia, HERRE (1955) points to its remarkable similarities in size and shape with *Triturus italicus*. ESTES (1981) as well quotes it as a member of the *Triturus vulgaris* group. After SANCHIZ (1998a), the morphology of the Oberdorf material of *Triturus roehrsi* rather points to the "Large-Bodied" group. Especially the combination of the vertebral features and the skull bones recall *Triturus vittatus*, a "Large-Bodied" species. Both *Triturus roehrsi* and *Triturus vittatus* possess a skull sculpture although the one of *Triturus roehrsi* is more distinct. It is questionable if the vertebral and skull sculpture can be considered as primitive and if *Triturus roehrsi* and *Triturus vittatus* present a sister-species relationship or just a plesiomorphic phenetic similitude.

The genus *Triturus* shows similarities with *Neurergus* (WAKE & ÖZETI, 1969). Especially *Triturus alpestris* seems to be closely related to *Neurergus kaiseri* (HERRE, 1932) although their living habits are completely different (HALLER-PROBST & SCHLEICH, 1994).

Together with *Archaeotriton*, *Euproctus*, *Koalliella*, *Notophthalmus*, *Oligosemia*, *Procynops*, and *Taricha*, the genus *Triturus* belongs to the "group III" genera of the Salamandridae. This group mainly consists of water-adapted representatives (ESTES, 1981; see Discussion about *Chelotriton paradoxus*)

Ecology and Climate – living relatives: *Triturus cristatus* represents an often fairly aquatic newt that may be encountered in water throughout the year but is usually terrestrial out of the breeding season. It prefers stagnant or slowly flowing water with good weed growth, ponds and woods and occurs up to 2000 m (ARNOLD & OVENDEN, 2002).

More terrestrial than many other species of European newts, *Triturus vulgaris* inhabits damp environments such as gardens, woods, field edges and stone piles. During the breeding season, it occurs in stagnant, often shallow water but preferentially in weedy ponds and ditches. It extends to over 1000 m and even 2000 m in southern parts of range (ARNOLD & OVENDEN, 2002).

Usually, members of the genus *Triturus* survive at a water temperature of 12°C to 20°C and an air temperature of 18°C to 22°C. 22°C must not be exceeded for a longer time period. For hibernation, they need frost free places with 4°C to 9°C such as below roots, stone piles or heaps of earth.

The geographical range of the Recent *Triturus cristatus* encloses most of Europe but not South and South West France, Iberia, South Greece, Ireland, and Mediterranean islands (ARNOLD & OVENDEN, 2002; GASC et al., 1997; GROSSENBACHER & THIESMEIER, 2003). It also occurs eastwards to the Caucasus and Central Asia. Following

Müller (1996; see chapters 5, 6), these areas belong to the Köppen's climate types B, mainly Cf, marginally Cs, Csa, Df, and Ds.

Triturus vulgaris is present in most of Europe exclusively South France, Iberia, South Italy, and most Mediterranean islands (Arnold & Ovenden, 2002). It occurs in West Asia as well and is therefore restricted to the Köppen's climate types mainly Cf and just marginally Cs, Df, and Ds (Müller, 1996; see chapters 5, 6).

Order Anura Rafinesque, 1815
Suborder Archaeobatrachia (Reig, 1958)
Infraorder Discoglossoidea Sokol, 1977
Family Discoglossidae Günther, 1859 "1858"
Subfamily Bombinatorinae Gray, 1825

Genus *Bombina* Oken, 1816

***Bombina* cf. *bombina* (Linnaeus, 1761)**

(Plate 2: a, b; Table 2, 4, 6, 8; fig. 10, 11)

Recent species: *Bombina bombina* (Linnaeus, 1761).
Range: Upper Miocene: Austria.
Upper Miocene or Pliocene – Pleistocene: Kazakhstan, Poland, Russia and Ukraine.
Material: 1 sphenethmoideum (AO: Inv. Nr.: NHMW 2004z0014/0003). 1 vertebra praesacralis. 1 os coccygis (AO: Inv. Nr.: NHMW2004z0014/0001). 1 ilium dext. (AO: Inv. Nr.: NHMW2004z0014/0002). 1 humerus ♀ dext. (BM: Inv. Nr.: NHMW2004z0014/0005).
Description:

sphenethmoideum (fig.10): In anterior aspect, the left half of the sphenethmoideum is missing. The pars tubiformis is slightly convex and the margo nasalis is continuous. A nearly trapezoidal antrum olfactorium dext. is bordered by a straight septum nasi. The dorsoventrally perpendiculary oval foramen pro nervus olfactorius is located mediolateral to the septum nasi while the foramen pro nervus ophthalmicus is situated medial to the dorsal margo nasalis.

vertebra praesacralis (Table 8): Measurements of the complete, opisthocoelous vertebra praesacralis are given in Table 8. Remarkably, the centrum is short but broad possessing a distinct condylus. The processus transversi broaden laterally and are as long as half of the centrum width. A large and round canalis neuralis characterizes the vertebra. From ventral aspect, the neural arch overtops the centrum posteriorly twice as far as the centrum length. Anterodorsally, it is carved and the processus spinosus is indistinct. Both prae- and postzygapophyses are oval sloping posterolaterally.

os coccygis (Plate 2: a): The os coccygis lacking the tips of the processus transversi is broken posteriorly. The single fossa condyloidea ossis coccygei is 0,83 mm wide. From dorsal aspect, the insertions of the processus transversi extend far posteriorly and include an angle of nearly 90° The neural arch is deeply carved. In posterior direction, the crista ossis coccygei becomes smooth.

ilium (Plate 2: b; fig. 11): The just slightly curved ala ossis ilii of this right ilium is broken anteriorly. A high and distinct, oval tuber superior is situated a little behind the anterior margin of the acetabulum. The fossa praeacetabularis exists, and the straight pars ascendens ilii rises slightly. From medial aspect, a tubercle is visible on the clearly developed pars descendens ossis ilii. The junctura ilioischiadica is figured in fig. 11.

humerus ♀: The right humerus is lacking the distal half of the eminentia capitata. The latter is round and together with the distal humerus shifted laterally. Measured from the proximal margin of the eminentia capitata to the caput humeri, the length amounts to 3.96 mm. Neither the crista medialis nor the crista lateralis are prominent. The crista ventralis is high proximally.

Comparison: The characteristics of the sphenethmoidea described herein correspond to those of Recent specimens of *Bombina bombina*. The sphenethmoideum of *Bombina variegata* is broader, the foramina pro nervus olfactorius are half-round with the straight side parallel to the septum nasi. Contrary to *Bombina bombina*, the foramina pro nervus ophthalmicus are situated more laterally. However, both European species of *Bombina* are osteologically extremely similar as adults. Keeping their variability within several individuals, the comparisons and the description of skeletal elements of Anura by G. Böhme (1977) in mind, the sphenethmoideum has been referred to *Bombina* cf. *bombina*.

Relating to the vertebral column, the vertebrae praesacrales and especially the os coccygis of *Bombina bombina* and *Bombina variegata* are remarkably similar (also see Sanchiz & Młynarski, 1979b). Just the vertebrae praesacrales show little differences such as the more distinct condylus and the neural arch overtopping the centrum farther posteriorly in *Bombina bombina*. Based on these comparisons with Recent specimens and on the determination of the remainder of the elements, the description has resulted in *Bombina* cf. *bombina*.

The ilium clearly refers to *Bombina bombina*. Typical characteristics such as noted by G. Böhme (1977), Hodrová (1985) and Sanchiz & Młynarski (1979b) are present: a high and distinct, oval tuber superior; a fossa praeacetabularis; a clearly developed pars descendens ilii showing a tubercle from medial aspect. Further, the shape of the junctura ilioischiadica (fig. 11) clearly correlates to the one of *Bombina bombina*. Yet, due to the variability present in adult members of *Bombina*, the ilia have been referred to *Bombina* cf. *bombina*.

Comparing humeri of Recent specimens of *Bombina bombina* and *Bombina variegata*, no typical species-differences could be detected (also see Sanchiz & Młynarski, 1979b). In fact, they are sex-related. While the male humeri show a clearly developed crista medialis and crista lateralis extending far proximally, the female humeri possess just short, indistinct ones (also see Sedláčková, 2000). Therefore, the humerus described in this paper has been referred to a female specimen of *Bombina* cf. *bombina*.

Discussion: *Bombina bombina* has been present from the Middle Pleistocene (Sanchiz & Szyndlar, 1984) and the Upper Pliocene of Poland (Sanchiz & Młynarski, 1979b) and the Czech Republic (HODROVÁ, 1981) to the Holocene of Germany and Poland (SANCHIZ, 1998b). In Austria, it has already been described from the Holocene locality Sommerein (MARINELLI, 2001).

Bombina cf. *bombina* or *Bombina* (*bombina*) sp. respectively is known from the Upper Miocene or Pliocene of Kazakhstan, the Upper Pliocene of Poland (HODROVÁ, 1985), and the Upper Pliocene and Pleistocene from Russia and Ukraine (SANCHIZ, 1998b). *Bombina* cf. *bombina* from Kohfidisch represents the stratigraphically reliably oldest record of the species.

The oldest known record of *Bombina* sp. dates back to the Lower Miocene of Germany (SANCHIZ & SCHLEICH, 1986). MŁYNARSKI et al. (1982) describe the genus from the Middle Miocene of Poland. In Central and Eastern Europe, it is present up to the Holocene (SANCHIZ, 1998b).

The osteological differences between *Bombina bombina* and *Bombina variegata* are few, but the characteristics of the latter can be regarded as autopomorphic (SANCHIZ & MŁYNARSKI, 1979b). The reduction of the tuber superior and the pars descendens ilii would then represent derived character-states. It is unclear, if *Bombina variegata* directly derived from *B. bombina* or both from an ancestral species. HODROVÁ (1981) and MŁYNARSKI et al. (1982) have detected ilia with "hybrid" characters between *Bombina bombina* and *Bombina variegata.* The findings date back to the Middle Miocene of Opole, Poland (MŁYNARSKI et al., 1982) and the Upper Pliocene of Ivanovce, Czech Republic and Slovakia (HODROVÁ, 1981).

Despite different molecular constitution and ecological requirements, *Bombina bombina* and *Bombina variegata* are able to produce fertil descendants today. As the recombination of the characteristics typical of the species results in numerous hybride genotypes, single characteristics can be examined for the selection value and their genetic base (MCCALLUM et al., 1998).

These days, *Bombina maxima* from West China as well as *Bombina orientalis* from North-East China and Korea represent two more Recent species of *Bombina.* Osteologically, they can be distinguished from *Bombina bombina* and *Bombina variegata* (MŁYNARSKI et al., 1982). Since recently, *Bombina pachypus* from Italy is regarded as a regular, Recent species as well.

With regard to the Recent subspecies, their classification is still discussed because of their intergradient characteristics (NÖLLERT & NÖLLERT, 1992).

Ecology and Climate – living relatives: The Fire-bellied Toad *Bombina bombina* represents a lowland animal contrary to the Yellow-bellied Toad *Bombina variegata*, which lives in more mountainous or hilly areas. It usually inhabits shallow water such as edges of rivers and streams, ponds and small pools (ARNOLD & OVENDEN, 2002). For breeding, waters should be weedy. They also like sunexposed watersides. At 5°C to 10°C, the Fire-bellied Toad hibernates below wood or in burrows.

The geographical range of *Bombina bombina* is restricted to Eastern and Central Europe as far north as Denmark, South Sweden and Russia and south to North Serbia and Turkey. It is also present in a small area of North-West Anatolia (ARNOLD & OVENDEN, 2002), which belong altogether to the Köppen's climate type Cf (MÜLLER, 1996; see chapters 5, 6).

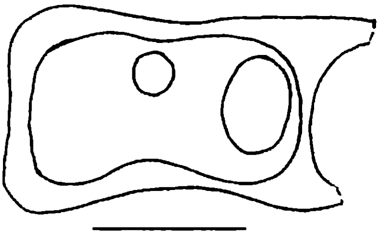


Figure 10: *Bombina* cf. *bombina.* Sphenethmoideum anterior view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0014/0003), scale bar equals 1 mm.

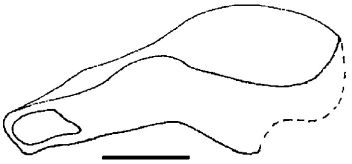


Figure 11: *Bombina* cf. *bombina.* Junctura ilioischiadica of ilium dext. (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0014/0002), scale bar equals 1 mm.

Subfamily Discoglossinae GÜNTHER, 1859 "1858"

Genus *Latonia* MEYER, 1843

Latonia gigantea (LARTET, 1815) nov. comb. LYDEKKER, 1890

(Table 2, 4, 6, 9)

Neotype: Musée National d'Histoire Naturelle, Paris, France, Sa – 23448; frontoparietale. Designated by RAGE & HOSSINI (2000) but figured in error as lectotype by ROČEK (1994).

Type locality: Sansan, France.

Stratigraphical Age of the Type material: Middle Miocene (Astaracian, MN6).

Range: Lower Miocene – Pliocene: Europe.

Material: 23 maxillaria dext. 23 maxillaria sin. (BM: Inv. Nr.: NHMW2004z0015/0001).

Description:

maxillare (Table 9): Each of the 46 fragmentary maxillaria possesses a preserved processus zygomaticomaxillaris but no complete processus palatinus. Measurements are given in Table 9. Labially, a sculpture pattern formed by parallel ridges and pustules exists mainly on the processus zygomaticomaxillaris but also beyond. The margo orbitalis is concave. Lingually, the thick lamina horizontalis covers the crista dentalis bearing many close teeth. The latter exceeds the lamina horizontalis posteriorly. Bordering the posterior medial depression, the processus pterygoideus is orientated to posteromedial.

Latonia ragei Hossini, 1993
(Table 2, 4, 6, 9)

Holotype: Univ. Claude Bernard, Villeurbanne, France, 150.800; right maxillare.
Type locality: Laugnac, France.
Stratigraphical Age of the Type material: Lower Miocene (Agenian MN2).
Range: Lower Miocene – Upper Miocene: Central Europe.
Upper Miocene of Kohfidisch: LOD (= last occurrence date).
Material: 7 maxillaria dext., 5 maxillaria sin.
(BM: Inv. Nr.: NHMW2004z0016/0001).
Description:
maxillare (Table 9): The 12 maxillaria are altogether fragmentary. The processus zygomaticomaxillaris is preserved in any case. The measurements are noted in Table 9 Its margo orbitalis is concave and the outer surface is smooth. From lingual aspect, the lamina horizontalis is thick bordering the crista dentalis with many closely spaced teeth. The tooth row exceeds the lamina horizontalis posteriorly. The processus pterygoideus is orientated to posteromedial. A posterior medial depression is present.
Comparison: After Roček (1994), *Latonia gigantea* features a dermal sculpture on the outer surface of the maxillare while *Latonia ragei* does not. Therefore, the specific maxillaria have been assigned to these species herein.
Comparisons between the maxillaria of *Latonia gigantea* und *Latonia ragei* described in this paper have shown differences concerning the size and dermal sculpture. While the mean width between the dorsal edge of the lamina horizontalis and the ventral edge of the crista dentalis (= DL; see Table 9) is remarkably identic, the processus zygomaticomaxillaris is higher in *Latonia gigantea* (= DZ; see Table 9). Further, the outer surface of the maxillare of *Latonia gigantea* bears a sculpture mainly on the processus zygomaticomaxillaris. The maxillare of *Latonia ragei* is unsculptured such as first described by Hossini (1993).
The frontoparietale of *Latonia ragei* was not known for a long time. Therefore, it was not sure if it was ornamented or not. But the description by Sanchiz (1998a) of this bone from the Lower Miocene (MN4) locality Oberdorf in Austria, has proved that the frontoparietalia of *Latonia ragei* show a dermal sculpture as well.
Comparing the maxillaria, the ones with the *Latonia ragei*-morphotype could represent an ontogenetic stage in the growth of the larger *Latonia gigantea*. Though, sculptered maxillaria in the mean size range of the *Latonia ragei*-morphotypes exist (Table 9). That eliminates the possibility of ontogenetic stages but however, this problem requires further investigations.
Hossini (1993) also discusses the difficulty of distinguishing between *Latonia ragei* and *Latonia seyfriedi*. The latter has been described by von Meyer in 1843 and the presence or absence of any sculpture on the maxillare cannot be ascertained. Nevertheless, characteristics of the scapula are different. *Latonia ragei* possesses an elongated one as well as a rather straight coracoideum while *Latonia seyfriedi* features a stout scapula and not only straight but also curved coracoidea (Hossini 1993).
After Roček (1994a), the outer surface of the maxillare of *Latonia vertaizoni* (Oligocene) does not bear any sculpture as well. Merely, characteristics of the praearticulare and the sacrum are specific. It is possible that *Latonia vertaizoni* is synonymous with *Latonia ragei*. In this case, *Latonia vertaizoni* would have priority.
Discoglossus giganteus described by Wettstein-Westersheimb (1955) from the Middle Miocene (MN6) locality Neudorf a. d. March (= Devinska Nová Ves) in Slovakia has been regarded as synonymous with *Latonia gigantea* (Sanchiz, 1998b). Wettstein-Westersheimb (1955: Tafel 2, fig. 3a) corresponds two maxillaria to the new genus and new species *Miopelobates zapfei*. The maxillaria possess the shape, the teeth and the sculpture on the outer surface reminiscent of *Latonia gigantea*. Therefore, they should be referred to *Latonia gigantea*.

Latonia sp.
(Plate 2: c, d, e; Table 2, 4, 6, 8; fig. 12)

Type species: *Latonia seyfriedi* Meyer, 1843
Type locality: Karlsruhe, Germany.
Stratigraphical Age of the Type material: Middle Miocene (Astaracian, MN7-8).
Range: Oligocene – Peistocene: Europe, North Africa.
Material: 56 fragmenta frontoparietalium. 2 prooticooccipitalia dext. 1 prooticooccipitale sin. 7 praemaxillaria dext. (AO: Inv. Nr.: NHMW2004z0017/0001). 8 praemaxillaria sin. 34 maxillaria dext. 28 maxillaria sin. 45 maxillaria indet. 33 praearticularia dext. 22 praearticularia sin. 21 atlantes. 210 vertebrae praesacrales. 52 vertebrae sacrales. 1 costae. 59 ossa coccygea. 47 ilia dext. (AO: Inv. Nr.: NHMW2004z0017/0002). 46 ilia sin. (AO: Inv. Nr.: NHMW2004z0017/0004). 3 ischia (AO: Inv. Nr.: NHMW2004z0017/0003). 17 scapulae dext. 18 scapulae sin. 24 coracoidea. 17 humeri dext. 27 humeri sin. 22 radioulnaria dext. 13 radioulnaria sin. 2 radioulnaria indet. (BM: Inv. Nr.: NHMW2004z0017/0005).
Description:
fragmentum frontoparietalis: Each of the 56 frontoparietalia is fragmentary. Their outer surface is typically sculptered, bearing ridges and pustules. In either case, the incrassatio frontoparietalis and occasionally the foramen parietale as well as the processus paraoccipitales are present.
prooticooccipitale: One right prooticooccipitale is nearly complete while one right and one left lack the crista parotica and other parts. Sulcus venae jugularis and foramen prooticum are distinct. Ending in an oval knob, the prominentia ducti semicircularis posterioris represents a robust lamina and the condylus occipitalis is trapezoid from posterior aspect. A thin horizontal lamina connects the lower end of the prominentia ducti semicircularis posterioris with the crista parotica.
praemaxillare (Plate 2: c): Two praemaxillaria are complete while 13 mostly lack the top of the pars facialis. The outer surface is unsculptured and a keel is running horizontally

on the tooth-bearing part. Due to the prominent recessus marsupiatus, the praemaxillare looks almost rectangular. From lingual aspect, the lamina horizontalis leads into a medial recessus. Together with the pars facialis, the latter encloses the pars palatina.

maxillare: 107 maxillaria altogether consist of parts of the lamina horizontalis connected to the crista dentalis with some teeth. In some cases, the processus palatinus is preserved. The lamina horizontalis is thick, and the outer surface is unsculptured.

praearticulare: In any case, the processus coronoideus and the processus paracoronoideus of the 55 praearticularia are preserved. While the first is complete in any case, the second is either complete or represented by its base. Especially the presence of two coronoid processes, the distinct recess in the bottom of the sulcus pro cartilago Meckeli at the level of the coronoid process, and the distinct depression on the posterior part of the outer surface of the bone above the crista mandibula externa are remarkable. The praearticulare as well as its sulcus pro cartilago Meckeli are s-shaped. Some praearticularia show a foramen situated posterior the processus coronoideus.

atlas: Just one atlas is complete. 20 atlantes are represented by their centra. From ventral aspect, the crista ventralis is more or less well developed. The condyli occipitales are concave, orientated to lateral dorsally and orientated to medial ventrally. In any case, they are disconnected. The canalis neuralis is inverted heart-shaped. In dorsal view, the triangular neural arch extends far posteriorly into a cusp and the processus spinosus is distinct. Postzygapophyses feature rather small and rectangular.

vertebra praesacralis (Table 8): Measurements of the 210 opisthocoelous vertebrae praesacrales are given in Table 8. They are either complete or represent only the centra or the neural arches. The complete ones show a rectangular centrum, a drop-shaped canalis neuralis and laterally broadening processus transversi. The rectangular prae- and postzygapophyses are inclined toward the centrum. From dorsal aspect, the neural arch bearing the processus spinosus extends into a cusp far posteriorly. It is carved anteriorly where the sharp carina neuralis arises.

vertebra sacralis: Among the 52 vertebrae sacrales, complete ones and ventral parts are preserved. They are diplasicoelous featuring oval condyli as well as an oval canalis neuralis. The processus transversi orientated to posterolateral broaden just slightly. In dorsal view, the rectangular praezygapophyses are inclined toward the centrum.

costa: The single rib very probably originates from one of the vertebrae V2-V4. Constricted in the middle, its cross section is oval and becomes wider at the end. Looking from proximal, the processus posterioris centers 135° while the distal end of the rib centers -135°

os coccygis: The 59 ossa coccygea are either complete or lack their distal ends or parts of the processus transversi. Their fossae condyloideae are oval and the canalis neuralis is triangular. Posteroventral to the processus transversi, the foramina for the canalis intervertebralis are present. The processus transversi are directed to posterolateral and often bear a continuous carina. The carina neuralis slightly opens distally.

ilium (Plate 2: d; fig. 12): 93 ilia represent each state of fragmentation. The junctura ilioischiadica features the shape of "3" and is illustrated in fig. 12. Connecting archlike the concave pars ascendens ilii with the vexillum, the tuber superior borders the fossula tuberis superioris. Dorsal and anterior to the acetabulum, the fossa supraacetabularis and the fossa praeacetabularis exist.

ischium (Plate 2: e): Concerning the size, the 3 ischia correlate to the ilia. They are oval while the acetabuli are half-oval. The junctura ischioiliaca shows a bulge in the dorsal third.

scapula: Either the pars acromialis or the pars glenoidalis is missing at the incomplete exemplars of the 35 scapulae. They appear short and robust. Opposite to the concave sinus interglenoidalis, the tenuitas cranialis straightly connects the pars acromialis with the pars suprascapularis.

coracoideum: The 24 coracoidea are altogether broken representing either the proximal or the distal part. While the pars glenoidalis shows a roundish cross section, the pars epicoracoidalis expands and flattens distal to the medial constriction.

humerus: Nearly each of the 31 humeri is complete just lacking the proximal part or the distal half of the usually round eminentia capitata. Approximately the distal half of the humerus is shifted to lateral. Not only the epicondylus medialis and the epicondylus lateralis but also the crista medialis and the crista lateralis are prominent. The sporadically thickened margin of the crista medialis is bent in its proximal part and arches towards the crista ventralis proximally. The less distinct crista lateralis is concave.

radioulnare: 35 radioulnaria possess the capitulum with the olecranon while 2 of them represent just the distal parts of radius and ulna. The olecranon corresponds in size to the eminentia capitata of the humerus. It is nearly round bearing a well thickened lateral margin. Typically, the collum antibrachii is just slightly narrower than the distal end of the radioulnare.

Comparison: The elements do not have characteristics typical of species, either *Latonia gigantea* or *Latonia ragei*. According to ROČEK (1994a), they are typical of genus but not of species. The maxillaria lacking the processus zygomaticomaxillaris are too fragmentary to display wether their outer surface is sculptured or not. Therefore, the determination has resulted in *Latonia* sp.

Discussion: The species *Latonia gigantea* was present from the Lower Miocene to the Upper Pliocene in Europe. Recently, it has been described from the Austrian locality Götzendorf of the Upper Miocene (MIKLAS, 2002) and is also present in Richardhof-Golfplatz, Austria, Upper Miocene (HARZHAUSER & TEMPFER, 2004).

Latonia ragei from Kohfidisch represents the stratigraphically youngest record of the species. So far, it has been described from Lower Miocene localities of France and doubtfully of Germany and Spain (SANCHIZ, 1998b) as well as from the Lower Miocene of Austria, Oberdorf (MN4; SANCHIZ, 1998a) and Obergänserndorf and Teiritzberg (MN5; M. BÖHME, 2002b). *Latonia* sp. is known from the

Oligocene to the Pleistocene of Europe (Delfino, 2002; Rage & Roček, 2003; Sanchiz, 1998b). With regard to the geographical and stratigraphical distribution of the genus in Central and South Europe, Roček (1994a) documents the expansion from West to East. While *Latonia* is present in France during the Upper Oligocene, the Lower Miocene localities Oberdorf (Sanchiz, 1998a), Obergänserndorf and Teiritzberg (Austria; M. Böhme, 2002b), and Dolnice (Czech Republik) are situated more eastern. In the Middle Miocene, *Latonia* was already present in Belomechetskaya (Russia) and still in the western localities such as Sansan, La-Grive-Saint-Alban (France), Neudorf a. d. March (= Devinska Nová Ves; Slovakia), Przeworno and Opole (Poland) as well. Upper Miocene localities such as Öhningen (Germany), Götzendorf (Austria; Miklas, 2002), Tardosbánya (Venczel, 1999b), Polgàrdy (Hungary), Suchomasty (Czech Republik; Hodrová, 1987a) and Gritsev (Ukraine) together with the Pliocene localities Kuchurgan (Ukraine), Ivanovke (Slovakia), Arondelli (Italy), Puy du Teiller, Tour de Boulade and Serrat d`en Vacquer (France) do not represent a farther eastern distribution.

Relative to *Latonia* and as members of the Discoglossinae, *Latoglossus zraus* has been described from the Upper Miocene of Oued Zra in Morocco (Hossini, 2000), and the new genus *Paralatonia* containing the single species *Paralatonia transylvanica* has been erected by Venczel & Csiki (2003) from the Upper Cretaceous of Hateg Basin in Romania.

Furthermore, Roček (1994a) notes the possible evolutionary line of the genus *Latonia*. The medium sized *Latonia vertaizoni* featuring a smooth maxillare from the Upper Oligocene probably continued as a lineage of *Latonia ragei*. At that time, the trend towards the "gigantism" had already started. A medium sized *Latonia* with sculptured maxillare appeared in the Lower Miocene, which may be considered as the earlierst record of *Latonia gigantea*. This lineage also increased in size and spread all over Europe and, questionable, North Africa rapidly. Evolutionary trends within the genus *Latonia* are represented by the fusion of the both frontoparietalia, the appearance of two coronoid processes on the praearticulare and probably of the slendering of the sacral processus transversi.

M. Böhme (2002b) states that *Latonia ragei* and *Latonia gigantea* did not live syntopically because no common records had been known at that time. The concurrent occurrence of the two species in Kohfidisch documents their syntopical life. Nevertheless, the quantity of *Latonia gigantea* was considerably higher than the one of *Latonia ragei* in Kohfidisch.

The stratigraphically youngest record of *Latonia ragei* from Kohfidisch and its syntopical occurrence with *Latonia gigantea* more likely excludes their phylogenetical interrelation. *Latonia gigantea* as possible immigrant is dicussed by M. Böhme (2002b).

The origin of the Recent genus *Discoglossus* has not been resolved yet. It is known already from the Oligocene-Miocene boundary (Sanchiz pers. advice). Cranially, the skeleton of *Discoglossus* resembles the one of a young specimen of the genus *Latonia*. Hypothetically, *Latonia* and *Discoglossus* evolved from the same ancestor. This ancestor might have come from Asia due to close morphological affinities of Cretaceous discoglossids from Central Asia with *Discoglossus* (Roček, 1994a; Roček & Nessov, 1993). More probably and due to the paleontological record of *Latonia* from Europe (see above), the group represents a truly native European one.

Ecology & Climate – living relatives: Młynarski (1976), who has described *Discoglossus giganteus* (synonymous with *Latonia gigantea*) from Przeworno in Poland, discusses the possible ecology of the species. It might have inhabited ecological niches rich in frogs serving for prey. With regard to the climate, he expects more arid than humid conditions. During the Pleistocene, its descendants migrated to the South because of the climatic degradation.

Following M. Böhme (2002b), ecological differences between *Latonia gigantea* and *Latonia ragei* are not obvious. Due to the find situations such as fissure fillings, moor areas and fluvio-lacustrine deposits, environments with azonal vegetation can be expected for *Latonia*.

Furthermore, the autecology of *Latonia* and the Recent *Discoglossus* has to be called into question (M. Böhme, 2002b). The ilia of *Latonia* feature a well developed tuber superior as well as a high vexillum which is rather similar to members of the *Rana temporaria* species group (brown frog group). Therefore, *Latonia* was very probably adapted to jumping and swimming such as brown frogs. Members of the *Rana temporaria* species group lack in Miocene and Pliocene localities where *Latonia* is abundant. They first occurred more frequently during the Pleistocene when *Latonia* became extinct because of the climatic changes (see above).

Today, members of the genus *Discoglossus* such as *Discoglossus galganoi*, *Discoglossus jeanneae*, *Discoglossus montalentii*, *Discoglossus pictus*, and *Discoglossus sardus*, are usually found in or around stagnant or running water but also in marshes and brackish water. Both prefer shallow areas in pools, streams, cisterns and river-edges (Arnold & Ovenden, 2002). Usually, the temperature may rise up to 30°C.

Discoglossus inhabits the warmest regions of Europe such as Iberia (except North East), southernmost France (Pyrénées Orientales only), Sicily, Malta, Gozo, North-East Spain, and North-West Africa (*Discoglossus pictus*) as well as Corsica, Sardinia, Giglio, Monte Cristo and Iles d'Hyères (*Discoglossus sardus*) (Arnold & Ovenden, 2002). Following Müller (1996), these areas mainly belong to the Köppen's climate types Cs and Csa (see chapters 5, 6).

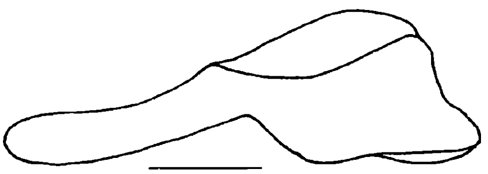


Figure 12: *Latonia* sp. Junctura ilioischiadica of ilium sin. (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0017/0004), scale bar equals 1 mm.

Suborder Mesobatrachia LAURENT, 1979
Superfamily Pelobatoidea BOLKAY, 1919
Family Pelobatidae BONAPARTE, 1850
Subfamily Pelobatinae BONAPARTE, 1850

Genus *Pelobates* WAGLER, 1830

***Pelobates* cf. *cultripes* (CUVIER, 1829)**

(Plate 2: f, g; Table 2, 4, 6, 8; fig. 13)

Recent species: *Pelobates cultripes* (CUVIER, 1829)
Range: Middle(?) Miocene – Holocene: Western Europe.
Material: 110 fragmenta frontoparietalium. 10 squamosa dext. 3 squamosa sin. (AO: Inv. Nr.: NHMW2004z0018/0001). 1 nasale dext. 5 praemaxillaria dext. 6 praemaxillaria sin. 55 maxillaria dext. 38 maxillaria sin. 10 maxillaria indet. 1 praearticulare sin. 1 atlas. 19 vertebrae praesacrales. 3 vertebrae sacrales copulatae cum ossa coccygea. 13 ilia dext. (AO: Inv. Nr.: NHMW2004z0018/0002, 0003). 10 ilia sin. 1 ischium. 1 scapula dext. 10 humeri dext. 3 humeri sin. 1 radioulnare sin. (BM: Inv. Nr.: NHMW2004z0018/0004).
Description:

fragmentum frontoparietalis: The 110 frontoparietalia are altogether fragmentary. They show a dermal sculpture formed by dense tubercles. From dorsal aspect, a prominent ridge is running down the processus paraoccipitales. In posterior view, the frontoparietale appears nearly flat and just the processus paraoccipitales are convex.

squamosum (Plate 2: f): Among the 13 squamosa, a few lack the processus posterolateralis or dorsal parts. They are sculptured dorsally by numerous tubercles similar to the sculpture of the frontoparietale. The large processus dorsalis is triangular, the processus posterodorsalis extends widely, and the ramus paroticus is blunt but distinct. As the processus zygomaticus is long, the concave margo orbitalis results in elongation as well. From ventral aspect, the fronto-squamosal bridge is present.

nasale: The right nasale is nearly complete and just the lip of the processus parachoanalis as well as the top of the processus anterius are broken. It is sculptured by numerous tubercles missing on the anterior half of the margo medialis. The processus anterius features a broad base becoming narrower. Bearing a distinct processus paraorbitalis, the margo orbitalis is half-round while the margo medialis is irregular and just slightly convex.

praemaxillare: Each of the 11 praemaxillaria lacks the processus frontalis. The outer surface of the convexe pars dentalis elongated horizontally is unsculptured. The crista lateralis is missing. From lingual aspect, the foramen at the base of the pars facialis is well developed. The praemaxillare possesses a narrow lamina horizontalis bordering the crista dentalis with 11-13 teeth which reaches the symphysis medialis. Medially, the lamina horizontalis grades into a triangular process orientated to ventromedial and not into the extended pars palatina. The lamina horizontalis and that process form an angle of nearly 90° from dorsal view. Neither the sulcus dentalis nor the recessus marsupiatus are present.

maxillare: The 93 maxillaria represent each state of preservation. Ventral to the posterodorsal vertical margin, the processus posterior elongates. Processus palatinus, processus frontalis and processus zygomaticomaxillaris are well developed. The nearly complete maxillaria are elongated and high featuring a concave margo orbitalis. Their outer surface is sculptured by numerous tubercles which may be fused to form curved or circular ridges ventrally. The sculpture is missing on a narrow ventral margin. From lingual view, the lamina horizontalis is narrow grading into the processus pterygoideus. Nearly exactly below the latter, the crista dentalis ends.

praearticulare: Lacking just the anterior tip, the left praearticulare is nearly completely preserved. It is s-shaped in dorsal view and slender. From dorsal aspect, the sulcus pro cartilago Meckeli appears shallow anteriorly. Posterior to the processus coronoideus, it opens into the extremitas spatulata. The processus coronoideus is indistinct and elongated. It features two cusps lingually, a more prominent one posteriorly and a nearly undistinguishable one medially.

atlas: The single atlas is represented by the centrum bearing the bases of the neural arch. It is short, broad, and covered by small foramina. No crista ventralis but a shallow triangular depression anterior to the condylus is present. The latter is flattened dorsoventrally. With regard to the condyli occipitales, they are disconnected and reniform.

vertebra praesacralis (Table 8): Measurements concerning the 19 vertebrae praesacrales are given in Table 8. 12 are nearly complete originating from the position V5 to V8. Further, one single neural arch and one broken centrum are preserved. The procoelous centrum of the vertebrae praesacrales is elongated and straight featuring small and round cotylus and condylus. The neural arch is elongated as well, carved anteriorly and elongated into a cusp posteriorly. An indistinct processus spinosus is present and the rectangular prae- and postzygapophyses are orientated nearly horizontally. They possess a roundish-oval canalis neuralis. As for the processus transversi, they are thin, cylindrical and cuspid pointing together with the praezygapophyses at an angle of 45° to anterior.

vertebra sacralis copulata cum os coccygis: Procoelous as well, the three vertebrae sacrales are fused to the os coccygis in any case. The latter is lacking the posterior fourth or the posterior three-fourths respectively. Just one element shows the left apophysis elongated anteriorly and posteriorly of the vertebra sacralis while the others are broken. In anterior view, the canalis neuralis is flattened-oval. The praezygapophyses are rectangular and orientated nearly horizontally. From ventral aspect, the limit between the vertebra sacralis and the os coccygis is well visible. It shows a monocondylar articulation. The processus spinosus just of one element is well-developed while it is indistinct otherwise. Laminae horizontales of the os coccygis are present on one element. They are not fused to the apophyses of the vertebra.

ilium (Plate 2: g; fig. 13): 23 ilia are present which lack the anterior part of the ala ossis ilii and in some case also parts of the pars ascendens or the pars descendens ossis ilii respectively. Remarkably, vexillum, tuber superior, fossa praeacetabularis, and fossa supraacetabularis are missing. While the pars ascendens ossis ilii is straight and pointed, the pars descendens ossis ilii is round and extends anteriorly. Together with the ala ossis ilii, it forms an angle of 90 ° approximately. Dorsally, the transition between the ala ossis ilii and the corpus ossis ilii is marked by a furrow. The junctura ilioischiadica is illustrated in fig. 13. It is nearly straight but concave ventrally from inner aspect as well as concave medially from lateral view.

<u>ischium:</u> From lateral view, the oval ischium is broken dorsally. It possesses a remarkable dilatation in the middle of the posterior symphysis opposite to the acetabulum.

<u>scapula:</u> The right scapula appears elongated. From dorsal aspect, the pars glenoidalis inclined to ventral and bearing a drop-like fossa glenoidalis is rectangular enclosing just a narrow slitted sinus interglenoidalis with the pars acromialis. The latter features a dorsal and a ventral bump on its posterior margin. While the anterior margin of the scapula is slightly concave, the posterior margin is convex.

<u>humerus:</u> Just lacking diminutive proximal parts, the 13 humeri altogether are nearly complete. They are slender but robust distally, the round eminentia capitata is positioned laterally, the epicondylus medialis distinct and nearly reaching the distal border of the eminentia capitata. The epicondylus lateralis is reduced. Opening laterally, the fossa cubitalis ventralis appears large and shallow. The crista ventralis and the crista paraventralis are robust and not sharp. Contrary to humeri of other members of the Anura, no sexual-dimorphism exists.

<u>radioulnare:</u> The left radioulnare is represented by the capitulum with the olecranon and its collum antibrachii. The olecranon is slender and the crista radialis is missing. Elongated, the collum antibrachii shows a well-distinct fossa radialis.

Comparison: The elements described herein have been compared with those of Recent specimens. In addition, according to Bailon (1991), G. Böhme (1977), and Roček (1991), they are typical at species level except for the ilium, the scapula and the radioulnare which are typical of genus. Following the description of the other elements typical of species of Kohfidisch, they have also been determined as *Pelobates* cf. *cultripes*.

As for the ischium, no descriptions typical of the species exist. Based on comparisons with material of Recent specimens, the ischium of *Pelobates* is laterally oval featuring the posterior dilatation of the symphysis. Contrary to the ischium of *Pelobates cultripes*, the one of *P. fuscus* is elongated and pointed ventrally.

The squamosa as well as the maxillare of *Pelobates* sp. from Obergänserndorf and Teiritzberg are similar in size but the latter one features a different dermal sculpture on the outer surface. It consists of ridges and pits fused circularly. As distinct and numerous tubercles as typical of the Kohfidisch specimens are missing. The margo orbitalis is straighter. Further, the maxillare of Obergänserndorf and Teiritzberg possesses a thicker lamina horizontalis. In 1982, W. Böhme et al. rediscovered the description of *Pelobates decheni* from Rott near Bonn, Germany (Uppermost Oligocene). Contrary to *Pelobates cultripes*, the general sculpture pattern consists of numerous pits separated from each other by sharp ridges. Beside, it is a species closely similar to *Pelobates cultripes* although some features on the quadratojugale, quadratum, costa, and radioulnare can be regarded as plesiomorphic. Therefore, *Pelobates cultripes* very probably represents the most conservative species among the living members of the genus (see also Roček, 1981).

As a close relative of *Pelobates*, the extinct genus *Eopelobates* differs among others in the dermal sculpture, the lack of a fronto-squamosal bridge, and the shape of the nasale (Estes, 1970a; Špinar & Roček, 1984). Further, the presence of a spinal nerve foramen on some vertebrae praesacrales (Hodrová, 1987a; Sanchiz & Młynarski, 1979b; Vergnaud-Grazzini, 1970), the lack of a neurapophysis, and reduced lateral ridges are typical of *Eopelobates*. The vertebra sacralis is never fused to the os coccygis (Venczel, 2001). Relating to the ilium, *Eopelobates* has no striation of the opposite side to the pars descendens ossis ilii and the lower part of the acetabulum in inner lateral view (Sanchiz & Młynarski, 1979b). However, the distinction of *Pelobates* from *Eopelobates* is highly questionable (see below; Rage & Roček, 2003).

Discussion: The fossil records of *Pelobates cultripes* date from the Middle Pleistocene to the Holocene (Sanchiz, 1998b) and questionably from the Middle Miocene (Bailon et al., 1988) of Western Europe. W. Böhme et al. (1982) propose to refer the specimen to *Pelobates decheni*. Extinct and featuring a combination of plesiomorphic characters, *Pelobates decheni* seems to be more primitive.

Rage & Roček (2003) have delivered the oldest record of *Pelobates* from the Lower/Middle Oligocene. Its second record dates from the Lower Miocene of Germany (Sanchiz, 1983). Following Sanchiz (1998b), *Pelobates* sp. has been described from the Miocene to the Holocene of Europe and Turkey. It is also present in the Austrian Upper Miocene locality Richardhof-Golfplatz (Harzhauser & Tempfer, 2004).

According to W. Böhme et al. (1982), *Pelobates* and the extinct genus *Eopelobates* were already well-separated in the Lower Miocene based on their coexistence in Rott near Bonn. During the Polish Pliocene, the two genera still existed parallel (Młynarski, 1961, 1977). However, reliable identification of *Pelobates* and *Eopelobates* can exclusively be based on cranial bones, especially on the frontoparietale. Therefore, their distinction is highly questionable moreover because disarticulated postcranial elements of Tertiary pelobatids have often been referred to *Eopelobates* only due to their stratigraphic occurrence (Rage & Roček, 2003).

Overall, *Pelobates cultripes*, *Pelobates fuscus* and *Pelobates syriacus* represent not only Recent and fossil species as well. Although *Pelobates varaldii* similar to *Pelobates cultripes* is considered to be a morphologically conservative species (Busack et al., 1985), no fossil record exists. On the contrary, the description of the species *Pelobates decheni* is exclusively based on fossil material.

Eclogy and Climate – living relatives: Spadefoots in general are confined to areas with sandy soil to hide during the day in almost vertical burrows dug by the aid of spades on their hind feet. *Pelobates cultripes* can often be found in large numbers on sandy coasts but also in open marshy areas by shallow water (ARNOLD & OVENDEN, 2002). If the temperature falls below 3°C to 4°C, hibernation sites are frequented.

Pelobates cultripes occurs in Iberia and West and South France. The closely related species *Pelobates varaldii* occurs in North-West Africa (ARNOLD & OVENDEN, 2002; GASC et al., 1997). Following MÜLLER (1996; see chapters 5, 6), these areas are restricted to the Köppen's climate types Cs and Csa.

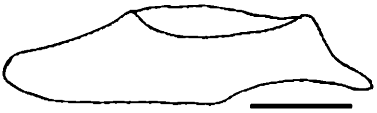


Figure 13: *Pelobates* cf. *cultripes*. Junctura ilioischiadica of ilium dext. (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0018/0003), scale bar equals 1 mm.

Suborder Neobatrachia REIG, 1958
Superfamily Hyloidea WIED, 1856
Family Bufonidae GRAY, 1825

Genus *Bufo* LAURENTI, 1768

Bufo bufo (LINNAEUS, 1758)

(Plate 3: a-d; Table 2, 4, 6, 8; fig. 14, 15)

Recent species: *Bufo bufo* (LINNAEUS, 1758)
Range: Miocene – Middle Pleistocene and Holocene: Europe, Kazakhstan, Morocco;
Holocene: Europe, North-West Africa, across the Palaearctic Asia to Japan.
Material: 3 sphenethmoidea (AO: Inv. Nr.: NHMW2004 z0019/0005). 6 praearticularia dext. 1 praearticulare sin. 4 atlantes (AO: Inv. Nr.: NHMW2004z0019/0002). 222 vertebrae praesacrales. 53 vertebrae sacrales. 13 ossa coccygea. 59 ilia dext. 59 ilia sin. (AO: Inv. Nr.: NHMW2004z0019/0003, 0006). 8 ischia (AO: Inv. Nr.: NHMW2004z0019/0004). 28 scapulae dext. 19 scapulae sin. 13 coracoidea (AO: Inv. Nr.: NHMW2004z0019 /0001). 57 humeri ♀ dext. 33 humeri ♂ dext. 58 humeri ♀ sin. 34 humeri ♂ sin. 1 humerus indet. 34 radioulnaria dext. 31 radioulnaria sin. 28 radioulnaria indet.
(BM: Inv. Nr.: NHMW2004z0019/0007).
Description:
sphenethmoideum (fig. 14): The three short and broad sphenethmoidea are well preserved. Ventrally, the pars tubiformis is slightly concave mediolongitudinally and dorsally, the insignificant "incisura semielliptica" possesses a nearly straight anterior margin. From anterior view, the margo nasalis is interrupted on the two dorsolateral corners. The kidney-like antra olfactoria feature a large and irregularly round foramen pro nervus olfactorius.
praearticulare: The 7 praearticularia altogether are broken anteriorly and posteriorly. They are slightly s-shaped in dorsal view featuring a relatively wide open sulcus pro cartilago Meckeli. Posteriorly, the extremitas spatulata is not notably wider than the remaining praearticulare. The processus coronoideus is elongated and well developed while the crista paracoronoidea is reduced anteriorly.
atlas (Plate 3: b): Just the centra of the four atlantes are preserved. They are flattened dorsoventrally and the kidney-like condyli occipitales are clearly disconnected by a slit. The cotylus expands far laterally and therefore does not project from the centrum.
vertebra praesacralis (Table 8): Complete vertebrae praesacrales which may lack the tops of the processus transversi, or just their centra are present. Their measurements are quoted in Table 8. One of the 222 vertebrae praesacrales represents the V2 while the rest belongs to V3 – V8. They are procoelous featuring a flattened centrum and a round canalis neuralis. From dorsal aspect, the neural arch is short and the equally short processus spinosus poorly developed. The latter broadens posteriorly. Prae- and postzygapophyses are oval. While the praezygapophyses diverge anterolaterally, the postzygapophyses diverge posterolaterally. Concerning the V2, it possesses processus transversi flattened dorsoventrally which broaden distally. Remarkably, the centrum is much shorter. The narrow oval praezygapophyses orientated to nearly dorsoventral are facing medioanteriorly. They are directed to anterior. The V3-V8 feature cylindrical processus transversi directed either to posterior (V3) or to lateral (V4-V8).
vertebra sacralis: 53 procoelous vertebrae sacrales are present. The distal ends of the processus transversi may be broken. The latter are flattened and amplified distally. From ventral aspect, the condyli are well separated indicating a bicondylar sacro-urostylar articulation. The canalis neuralis is oval. In dorsal view, the rectangular praezygapophyses are orientated transversally and a just slightly developed or even absent fossa dorsalis is present on the relatively short neural arch. The processus spinosus shows the shape of an inverted Y.
os coccygis: The 13 ossa coccygea either lack parts of the fossae condyloideae or their distal end. The former are large, oval and separated by a ridge. Enclosing an oval to triangular canalis neuralis, the crista dorsalis is prominent featuring a sporadically open medial groove ventrally. The foramina for the canalis intervertebralis are small.
ilium (Plate 3: c; fig. 15): Relating to the 118 ilia, they are lacking the anterior ends of the ala ossis ilii. The broad and nearly straight junctura ilioischiadica is illustrated in fig. 15. No vexillum is present. Featuring about two cusps as well as a thickened dorsal margin, the prominent tuber superior is situated dorsal to the acetabulum. The latter may be twice carved dorsally on some elements. Contrary to the well developed pars descendens ilii, the pars ascendens ilii is short and concave. The ilia do not bear any fossa praeacetabularis.
ischium (Plate 3: d): As the 8 ischia feature a straight

ventral margin from lateral aspect, they are not exactly oval-shaped. The posterior symphysis is formed by two continuously parallel margins.

scapula: The 47 scapulae represent each state of preservation. Parts of the pars acromialis, the pars suprascapularis, or the pars glenoidalis may be broken. The scapula is flat and elongated. From dorsal view, the slit-like sinus interglenoidalis is clearly visible and the drop-like fossa glenoidalis is situated on a broadly attached pars glenoidalis. The scapula is constricted medially. Therefore, the pars suprascapularis as well as the pars acromialis possessing a convex anterior margin appear broad.

coracoideum (Plate 3: a): Concerning the coracoideum, it is relatively straight due to the equally broad pars epicoracoidealis and pars glenoidalis. While the former is flattened, the latter possesses a nearly round cross section.

humerus: 196 humeri featuring a smooth surface are present. Either the broad caput humeri or the distal eminentia capitata are broken. The latter is round and dislocated laterally. The fossa cubitalis ventralis is poorly developed. While the prominent epicondylus medialis is as long as the eminentia capitata in some case, the epicondylus lateralis is insignificant. The typical sexual-dimorphism concerns the development of the diaphysis as well as of the crista medialis and the crista lateralis. In contrast to the straight diaphysis of the male humerus featuring a transversal crista medialis, the diaphysis of the female humerus is curved. This appearance is additionally supported by a concave crista medialis.

radioulnare: The 94 radioulnaria are broken distally. They feature a robust collum antibrachii nearly as broad as the radius and ulnare. The olecranon expanded mediolaterally bears a clearly thickened lateral as well as a less thickened medial margin. Proportionally smaller, the capitulum is oval and directed to medioanterior.

Comparison: Except for the atlas, lacking the neural arch, as well as the coracoideum typical of the genus *Bufo* and except for the ischium and the radioulnare, the elements described herein correspond to those of *Bufo bufo*. Based on comparisons with material of Recent specimens and additionally following BAILON (1986, 1991), G. BÖHME (1977), and SANCHIZ (1977b), the elements have been referred to *Bufo bufo*.

Concerning the ischium, members of the genus *Bufo* share the straight ventral margin from lateral aspect. The radioulnare which is nearly straight laterally and whose olecranon expands to mediolateral is characteristic of *Bufo*. Comparing *Bufo bufo* with *Bufo viridis*, the radioulnare of the former is even straighter in lateral view. The margin of its olecranon is thickened not only laterally but also medially while the one of *Bufo viridis* is thickened only laterally. After SANCHIZ (1977b), the fossa radii is more developed in *Bufo viridis*. Following comparisons with Recent material and keeping the distinct determination of the other elements in mind, the description of the atlas, the ischium, the coracoideum, and the radioulnare has resulted in *Bufo bufo*.

Bufo bufo from the Lower Holocene to Holocene locality Sommerein in Austria (MARINELLI, 2001) is represented by sphenethmoidea, scapulae, sacra, ossa coccygea, ilia, and humeri which altogether are noticeably larger. The bigger size is also typical of material of Recent specimens.

Discussion: The oldest records of *Bufo bufo* date from the Middle Miocene (MN6) of Neudorf a. d. March (= Devinska Nová Ves) in Slovakia (HODROVÁ, 1980) and from the Upper Miocene (MN12) of Spain (SANCHIZ, 1977b). The former description is rather controversal because HODROVÁ (1988) partly assigned these remains to *Bufo* cf. *viridis* and subsequently ŠPINAR et al. (1993) to *Bufo priscus*. HODROVÁ (1987a) has described *Bufo* cf. *bufo* from the Upper Miocene of Slovakia. Generally, the species is present in Europe from the Middle Miocene to the Holocene such as furthermore in the Lower Pliocene of Hungary (VENCZEL, 1997a, 2001), from the Upper Pliocene of Slovakia (HODROVÁ, 1981, 1985), of Poland (MŁYNARSKI, 1977; MŁYNARSKI & SZYNDLAR, 1989; MŁYNARSKI et al., 1984), of Hungary (BOLKAY, 1913), and of Sicily (VERGNAUD-GRAZZINI, 1970). During the Lower Pleistocene it was present in Italy (DELFINO & BAILON, 2000), and PAUNOVIČ (1984) has recorded it from the Upper Pleistocene of Slovenia. BAILON & AOURAGHE (2002) have described *Bufo bufo* from the Upper Pleistocene of Morocco, where the species appears from the Middle Pleistocene to Holocene (SANCHIZ, 1998b). The Austrian Lower Holocene yields *Bufo bufo* such as noted by MARINELLI (2001).

According to RAGE (2003a), *Bufo* sp. was present as early as the Palaeocene in Europe. It has also been described from the Lower Miocene (BAILON & HOSSINI, 1990; SANCHIZ, 1977a, 1977b) to the Holocene. In South America, *Bufo* sp. was present during the Middle Palaeocene and the Oligocene, in Japan during the Pleistocene, and in West Asia during the Miocene and the Pliocene (SANCHIZ, 1998b) and doubtfully in the Oligocene (RAGE, 2003a). While in North Africa *Bufo* sp. appears in the Miocene and in the Upper Pleistocene, in East Africa it is present just during the Lower Pleistocene. In North America, *Bufo* sp. has doubtfully been described from the Oligocene and from the Miocene to the Holocene (RAGE, 2003a).

As extinct species, *Bufo priscus* has been described from the Middle Miocene Bonanza site of Neudorf a. d. March (= Devinska Nová Ves) in Slovakia by ŠPINAR et al. (1993). Due to characters of the skull and partly of the postcranial skeleton, they range the species in the “more primitive narrow-headed” toads according to MARTIN (1972) who remarks two lineages within the genus *Bufo*. The “wide-headed” toads were more advanced and the “narrow-headed” toads adapted to life on highlands more primitive. They might have divided already at the end of the Mesozoic era.

The three European Recent species *Bufo bufo*, *Bufo calamita* and *Bufo viridis* can be traced back until the Upper Miocene (MN12). SANCHIZ (1977b) reviewed the family of the Bufonidae in Europe and has recorded *Bufo viridis* from the Middle Miocene and *Bufo calamita* as well as *Bufo bufo* from the Upper Miocene of Spain. *Bufo* aff. *viridis* has been described from the Lower Miocene of Spain (ALFÉREZ DELGADO & BREA LOPEZ, 1981) and France (BAILON & HOSSINI, 1990). SANCHIZ (1977b) concludes that the family of the Bufonidae may represent an Asiatic immigrant which appears in the Oligo-Miocene boundary. Coming from South America via the West coast of North America to Alaska, the toads entered Asia. From there, they settled Eurasia and Africa (see also TIHEN, 1972).

Following MARTIN (1972), the toads originate from South America but immigrated into Europe via West Africa when South America and Africa were still connected. Though, the fossil record of toads is too young to support this hypothesis.

ŠPINAR et al. (1993) discuss the origin of toads and their migration and explain the small number of occurrences of toads in older Tertiary assemblages than Eocene ones. On the one hand, their terrestrial way of living causes taphonomic disadvantages compared with aquatic animals. On the other hand, their origin was very probably late and their migration considerable. They may have settled Eurasia and Africa coming from South America via North America from the Upper Miocene onwards. Australia as well as the neighbouring islands could not be invaded due to the separation of South America and Antarctica in the Upper Cretaceous.

It is remarkable that the genus *Bufo* is absent in Austria until the Uppermost Miocene. In the Lower Miocene localities Oberdorf (MN4; M. BÖHME, 2002b) and Obergänserndorf and Teiritzberg (MN5; SANCHIZ, 1998a), *Latonia* predominates according to the Minimum Number of Individuals (MNI). Also, the Upper Miocene, Austrian locality Götzendorf (MN9; MIKLAS, 2002) yields quantitatively predominant specimens of *Latonia* while *Bufo* is still missing. During the MN11 of Kohfidisch, *Bufo* appears nearly as frequent as *Latonia* (see chapter 6). The family of the Bufonidae established rapidly in Austria during the Upper Miocene.

Taphonomy probably explains the rarity or absence of bufonids in some fossil assemblages. Usually, *Bufo* is not predated by birds but by some members of the Carnivora. Therefore, it is expected to be more abundant in karstic fillings, and its true "absence" in other taphocoenotic conditions can hardly be detected.

Ecology and Climate – living relatives: *Bufo bufo* can be found in a wide variety of often fairly dry habitats today. It represents a mainly nocturnal toad which is hidden by day usually in one particular spot (ARNOLD & OVENDEN, 2002). Since hibernation is even possible at a temperature of only 1°C, *Bufo bufo* prefers burrows or damp leafage.

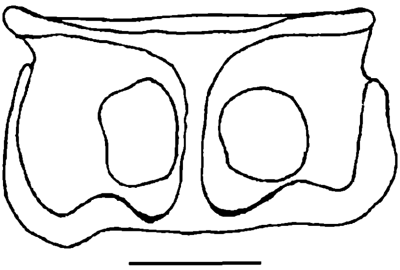


Figure 14: *Bufo bufo*. Sphenethmoideum anterior view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0019/0005), scale bar equals 1mm.

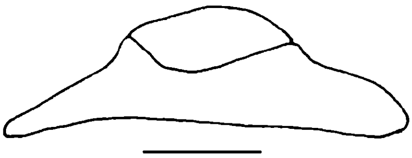


Figure 15: *Bufo bufo*. Junctura ilioischiadica of ilium sin. (Kohfidisch Inv. Nr.: NHMW2004z0019/0006), scale bar equals 1 mm.

The species is spread over most of Europe except Ireland, Corsica, Sardinia, the Balearics, Malta, Crete, and some other smaller islands. It also inhabits North-West Africa and across the Palaearctic Asia to Japan (ARNOLD & OVENDEN, 2002). Determining the climate, *Bufo bufo* is climatically relatively insensible. Following MÜLLER (1996; see chapters 5, 6), its appearance is mainly restricted to the Köppen's climate types BSk, Cf, Cs, Df, and Dw.

Family Hylidae GRAY, 1825 (1815)

Subfamily Hylinae Gray, 1825 (1815)

Genus *Hyla* LAURENTI, 1768

Hyla sp.

(Plate 3: e-g; Table 2, 4, 6, 8; fig. 16)

Recent species: *Hyla arborea* (LINNAEUS, 1758)

Range: Miocene, Middle and Upper Pleistocene: North America;

Lower Miocene – Holocene: Central and Eastern Europe;

Upper Pleistocene – Holocene: Japan;

Holocene: much of the tropical and temperate world except parts of South Asia and most of Africa.

Material: 2 maxillaria dext. 1 vertebra praesacralis (AO: Inv. Nr.: NHMW2004z0020/0001). 8 ilia dext. (AO: Inv. Nr.: NHMW2004z0020/0004). 8 ilia sin. (AO: Inv. Nr.: NHMW2004z0020/0002). 1 ischium (AO: Inv. Nr.: NHMW2004z0020/0003). 4 humeri dext. 2 humeri sin. (BM: Inv. Nr.: NHMW2004z0020/0005).

Description:

maxillare: The two right maxillaria represent anterior parts lacking the very anterior and posterior ends. They are robust and their dorsal and ventral margin just slightly diverge posteriorly. From labial aspect, a groove orientated longitudinally is present. Viewing from lingual, the thin lamina horizontalis situated medially is missing anteriorly and thickened posteriorly. The crista dentalis bearing numerous, closely attached pleurodont teeth, does not reach the anterior border of the maxillare. The two maxillaria described herein possess the ending of the crista dentalis and a part of the remaining toothless maxillare.

vertebra praesacralis (Plate 3: e; Table 8): One vertebra praesacralis is represented by its centrum broken posteriorly and the neural arch lacking the left praezygapophysis. The processus transversi are broken. Its measurements are given in Table 8. The procoelous centrum is flattened and the canalis neuralis oval. Viewing from dorsal, the neural arch lacks any processus spinosus. Postzygapophyses are distinctly isolated, longish-oval, and orientated to posterolateral. Due to the insertions of the processus transversi, they seem to be directed to anterior.

ilium (Plate 3: f; fig. 16): The proximal part of the 16 ilia is complete in nearly either case while the distal ala ossis ilii is broken. The straight and narrow junctura ilioischiadica is charted in fig. 16. Ala and corpus ossis ilii join broadly and a vexillum is missing. Situated exactly above the anterior margin of the acetabulum, the distinct tuber superior is vaulted and protrudes laterally. As the latter is higher or lower on the specific ilia, the short pars ascendens ilii appears either concave or straight. The pars descendens ilii expands ventrolaterally.

ischium (Plate 3: g): Just one ischium is present. From lateral aspect, it is longish-oval and typically carved posteriorly two times: above and below the dorsal dilatation of the posterior symphysis visible from posterior view. Below that dilatation, a second, smaller one is present.

humerus: One humerus is broken distally while the others lack the caput humeri. The round eminentia capitata is shifted to lateral and the diaphysis and crista ventralis are straight. Crista lateralis and crista medialis as well as epicondylus lateralis and epicondylus medialis are similarly well developed. The latter does not reach the proximal border of the eminentia capitata. Opening laterally, the fossa cubitalis ventralis is distinct.

Comparison:

The vertebrae praesacrales and the ilia of Kohfidisch correspond to the definitions of Bailon (1991) and G. Böhme (1977) of the genus *Hyla*. Holman (1992) distinguished between the ilia of *Hyla arborea* and *Hyla meridionalis* by means of Recent material. The differences are based on the dorsal prominence/protuberance complex. With regard to the ilia described herein, the development of this complex varies between *Hyla arborea* and *Hyla meridionalis*.

Humeri have not as often been recorded as vertebrae and ilia, but the descriptions of e.g. Delfino & Bailon (2000) and Paunovič (1984) correlate to *Hyla* sp. of Kohfidisch.

Based on comparisons with Recent members of the genus *Hyla*, the maxillaria as well as the ischium have been determined. The tooth-bearing maxillare lacking any sculpture on the outer surface, differs from the one of *Latonia ragei* in its increased tenderness, from the ones of *Bombina* and *Rana* in its increased robustness. Furthermore, the maxillare is equally thick dorsal and ventral to the lamina horizontalis, while in *Bombina* and *Rana* it is narrower dorsally. *Hyla* possesses more teeth arranged more closely.

With regard to the ischium, the posterior symphysis is typically dilated two times different to *Pelobates* where just one dilatation is present and also different from members of the Discoglossidae, *Bufo* and *Rana* which feature no dilatation. Due to these considerations, the elements have been referred to *Hyla* sp.

Discussion: First records of *Hyla* sp. in Europe date from the Lower Miocene (MN4) of Oberdorf in Austria (Sanchiz, 1998a) and of Dolnice in Slovakia (Hodrová, 1987b). The genus is present up to the Holocene in Europe (Delfino & Bailon, 2000; Hodrová, 1988; Młynarski & Szyndlar, 1989; Sanchiz 1981; Sanchiz & Młynarski, 1979b; Sanchiz & Szyndlar, 1984; Venczel, 1997a; Vergnaud-Grazzini, 1970), from Upper Pleistocene to Holocene in Japan, and in Miocene and Middle and Upper Pleistocene in North America (Sanchiz, 1998b). A second, Austrian record of *Hyla* sp. dates from the Upper Miocene (MN9) of Richardhof-Golfplatz (Harzhauser & Tempfer, 2004)

Sanchiz & Roček (1996) give an overview of the anuran fossil record and consider *Hyla* together with *Bufo*, *Bombina*, and perhaps *Pelobates* as immigrants from Asia. They explain the major change for European faunas with the "Grande Coupure" or "Stehlin faunistic turnover" at the Eocene-Oligocene boundary. With regard to the paleogeography, the Turgai Straits disappeared providing the connection between Europe and Asia. The origin of the family of the Hylidae may be located in Gondwana.

Two species of the Hylidae in Europe are represented by *Hyla arborea* and *Hyla meridionalis*. The total number of European species currently recognized might be higher than two, because some formerly considered subspecies have been raised to full species status (i.e. *Hyla sarda*). Engelmann et al. (1985) expect a restriction of the two species to areas southern the Pyrenees during the Wolstonian Glacial Age. In the Ipswichian Interglacial Age they might have invaded South France and England via the eastern route around the Pyrenees (Holman, 1992).

Ecology and Climate – living relatives: The two European species of the Hylidae, *Hyla arborea* and *Hyla meridionalis*, represent climbing frogs usually found in trees or other vegetation, and only rarely coming to the ground. Therefore, they prefer areas with bushes, trees, or red-beds ponds or cisterns (Arnold & Ovenden, 2002). They hibernate in decomposing stumps, below leaves or in burrows. Hylidae represent a large and successful group distributed over much of the tropical and temperate world except parts of South Asia and most of Africa. *Hyla arborea* occurs in most of Europe except the North and the Balearic Islands, South France and much of South and East Iberia. It is also found in Asia Minor and southern Ukraine east to the Caspian Sea. *Hyla meridionalis* as second European representative of the Hylidae is restricted to South Iberia, North-East Spain, North-West Italy (Liguria), South France, the Balearic Islands and also to North-West Africa, the Canaries and Madeira (Arnold & Ovenden, 2002). Following Müller (1996; see chapters 5, 6), the distribution of the European members of the Hylidae comprises the

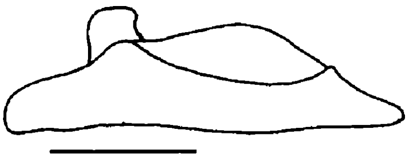


Figure 16: *Hyla* sp. Junctura ilioischiadica of ilium dext. (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0020/0004), scale bar equals 1 mm.

Köppen's climate types mainly Cf, Cs and Csa.

Superfamily Ranoidea GRAY, 1825
Family Ranidae GRAY, 1825
Subfamily Raninae GRAY, 1825

Genus *Rana* LINNAEUS, 1758

Rana (*ridibunda*) sp. PALLAS, 1771

(Plate 3: h, i; ; Table 2, 4, 6, 9; fig. 17, 18)

Recent species: *Rana ridibunda* PALLAS, 1771

Range: Lower Oligocene – Upper Pleistocene: Europe, Turkey, Morocco;

Holocene: Europe, Israel.

Material: 1 frontoparietale dext. (AO: Inv. Nr.: NHMW 2004z0021/0003). 8 praemaxillaria dext. 5 praemaxillaria sin. 1 praemaxillare indet. 35 maxillaria dext. 31 maxillaria sin. 14 maxillaria indet. 6 praearticularia dext. 6 praearticularia sin. 1 atlas. 65 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0021/0001). 4 vertebrae praesacrales copulatae cum vertebrae sacrales. 32 vertebrae sacrales. 11 ossa coccygea. 19 ilia dext. (AO: Inv. Nr.: NHMW2004z0021/0002). 16 ilia sin. (AO: Inv. Nr.: NHMW2004z0021/0004, 0005). 18 ischia. 11 coracoidea. 35 humeri ♀ dext. 28 humeri ♂ dext. 22 humeri ♀ sin. 28 humeri ♂ sin. 15 radioulnaria dext. 11 radioulnaria sin. 4 radioulnaria indet.

(BM: Inv. Nr.: NHMW2004z0021/0006).

Description:

frontoparietale (fig. 17): The single right frontoparietale is robust, and the pars frontalis slender, long, and clearly separated from the pars parietalis. The margo sagittalis is straight. In dorsal view, the top of the processus prooticalis is missing while the processus occipitalis features a right angled triangle. The linea medialis is prominently developed and between the curved linea occipitalis and the linea prooticalis, the "dens frontoparietalis ridibundae" (ridibunda tooth) is present. It is irregularely oval.

praemaxillare: 14 praemaxillaria are present which either lack the top of the pars facialis or anterior and posterior parts. One praemaxillare is complete. About 10 teeth are present on nearly the whole length, and the pars facialis inclined to lateral is slender. The prominent lamina horizontalis meets together with the pars palatina in a processus projecting mediolingually and right angularly. The recessus marsupiatus is round.

maxillare: Due to their fragility, none of the 80 maxillaria is completely preserved. From lingual aspect, the thin lamina horizontalis broadens anteriorly. Neither a processus palatinus nor a prominent processus zygomaticomaxillaris is present. The latter represents a dilatation of the maxillare. The slender processus frontalis in inclined to anterior and the processus posterioris is present.

praearticulare: The processus coronoideus is present on each of the just slightly s-shaped 12 praearticularia which may lack the anterior part and/or the posterior end of the extremitas spatulata. The processus coronoideus meeting into the indistinct processus paracoronoideus appears large and elongated anteroposteriorly. It possesses numerous small ridges orientated rectangularly to the stem of the praearticulare. Viewing from dorsal, the broad canalis pro cartilago Meckeli is visible.

atlas: One single atlas is represented by its centrum and the bases of the neural arch. It is flattened dorsoventrally, the condyli occipitales are kidney-like and fused. Typically, the oval posterior condylus projects from the centrum.

vertebra praesacralis (Plate 3: h; Table 9): Among the 65 vertebrae praesacrales, procoelous (V2-V7) and amphicoelous (V8) ones are present. The neural arch and/or the processus transversi are broken. The measurements are noted in Table 9. The centrum is flattened dorsoventrally, the canalis neuralis open-oval, and the neural arch short. Viewing from dorsal, the latter bears an indistinct processus spinosus which ends in a short cusp posteriorly. Prae- and postzygapophyses are roundish and the processus transversi just slightly flattened dorsoventrally.

vertebra praesacralis copulata cum vertebram sacralis: 4 vertebrae praesacrales (V8) typically fused with the vertebrae sacrales are nearly completely preserved. The processus transversi are broken. From ventral aspect, the fusion between the V8 and the vertebra sacralis is indicated by a ridge. Viewing from dorsal, the post- or praezygapophyses respectively of the two vertebrae are fused leaving open a slit between the neural arches. The canalis neuralis of the V8 is triangular while the one of the vertebra sacralis is flat-oval.

vertebra sacralis: 32 vertebrae sacrales are present which either are complete or lack the ends of the processus transversi or the neural arches. The flattened centra possess a single condylus anteriorly and two well-separated ones posteriorly. The canalis neuralis is flat-oval, the praezygapophyses are round. From dorsal view, the short neural arch shows a distinct processus spinosus and a continuous, transverse ridge leading into the posterior margin of the processus transversi. Typically, the cylindrical, robust processus transversi stay equally slender from proximal to distal. They form an angle of 50° posteriorly.

os coccygis: Each of the 11 ossa coccygea is broken posteriorly. The roundish-oval fossae condyloideae are well separated, the crista dorsalis as well as the canalis neuralis are high, and the intervertebral canal just hardly visible. No processus transversi are present.

ilium (Plate 3: i; fig. 18): Relating to the 35 ilia, each state of preservation is represented. Typically, the vexillum is high, the laterally flattened tuber superior situated closely anterior the round acetabulum is prominent and longish-oval, and the corpus ossis ilii is short. A fossa supraacetabularis is always present and the preacetabular zone is small. Contrary to the short pars descendens ossis ilii, the concave pars ascendens ossis ilii ends in a cusp. The junctura ilioischiadica broader ventrally and featuring a high vexillum is shown in fig. 18a. With regard to the angle α of the pars ascendens ossis ilii in the sense of BÖHME & GÜNTHER (1979), it measures less than 55° (43°-52°; Table 9, fig. 18b). Medially, the tuberculum medium is present.

ischium: The 18 ischia are completely preserved. Viewing from lateral, they are longish-oval featuring a nearly straight dorsal margin orientated to posterodorsal.

coracoideum: 11 coracoidea are either complete or represented by their pars epicoracoidealis which is remarkably flattened and extends laterally. They appear compact and robust, and their margo anterior is semicircular. The pars glenoidalis is round.

humerus: 113 humeri are present which may lack their proximal ends. The slender and straight humeri possess a prominent crista ventralis as well as a round eminentia capitata lying on the same axis with the diaphysis. The epicondylus medialis may overtop the eminentia capitata. Well delimited, the fossa cubitalis ventralis is distinct. Relating to the sexual-dimorphism, the male humeri feature well developed cristae mediales and cristae laterales with thickened margins and orientated to mesial.

radioulnare: The 30 radioulnaria featuring a narrow collum antibrachii altogether broaden distally. The crista radii is missing while the fossa radialis is present. With regard to the olecranon, it is large, round and expanded dorsolaterally. The capitulum is oval.

Comparison: The frontoparietale and the ilium correspond to *Rana ridibunda* described by G. Böhme (1977), G. Böhme & Günther (1979), Hodrová (1987b), and Sanchiz et al. (1993). The shape of the frontoparietale, the development of the lineae as well as the presence of the "dens frontoparietalis ridibundae" represent *Rana ridibunda*-like characteristics. Especially the ilium can definitely be referred to *Rana ridibunda*. The position of the tuber superior flattened laterally and situated closely anterior to the acetabulum, the small preacetabular zone, the presence of the tuberculum medium, and mainly the amplitude of the angle α of the pars ascendens ossis ilii are characteristic of *Rana ridibunda*.

With regard to the humerus, the male humerus serves for the differentiation between Green Frogs and Brown Frogs (Bailon, 1991). The male humeri described herein show a thickened crista medialis orientated to mesial and typical of Green Frogs such as *Rana ridibunda*.

Except for the atlas and the ischia, the elements are typical of *Rana* sp. such as described by Bailon (1991), G. Böhme (1977), G. Böhme & Günther (1979), and identified by comparisons with Recent material.

Relating to the atlas, the condylus projecting posteriorly and the fused condyli occipitales represent typical characteristics of members of the genus *Rana*. Members of the Discoglossidae, *Pelobates*, *Bufo*, and *Hyla* possess disconnected condyli occipitales which are rounder in *Pelobates* and *Hyla*. The posterior condylus of *Bufo* extends more laterally and does not project.

Ischia usually are not appropriate for descriptions, but the laterally longish-oval ischium of *Rana* features a characteristically straight dorsal margin which is orientated to posterodorsal. This shape correlates with the elongated pars ascendens ilii of the ilium.

The characteristics of the frontoparietale and of each ilium are typical of the species *Rana ridibunda* so defined by Böhme & Günther (1979). As current state, the features used by the authors are no longer valid since *Rana ridibunda* as known by them at that time is different now and split into several species. It is impossible today to reconstruct if the skeletons they studied were those of *Rana ridibunda* as understood today (Rage, pers. advice). Therefore, and due to the determination of the other elements as *Rana*, the description has resulted in *Rana* (*ridibunda*) sp.

Compared with *Rana* (*ridibunda*) sp. from Oberdorf, with *Rana* aff. (*ridibunda*) sp. from Obergänserndorf and Teiritzberg, with *Rana* cf. *ridibunda* from Götzendorf, and with *Rana ridibunda* from the Austrian Lower Holocene to Holocene locality Windener Bärenhöhle (Marinelli, 2001), a difference in size is remarkable. While the material of the Miocene localities corresponds in size, the remains of the Windener Bärenhöhle are conspicuously larger as are the elements of Recent specimens.

Discussion: *Rana ridibunda* was present in the Middle Pleistocene of Spain (Sanchiz, 1977a) and France (*Rana esculenta* or *Rana ridibunda*, Rage, 1969), and in the Upper Pleistocene of Spain (Bailon, 1986). A member of the *Rana ridibunda* species group has been described from the Lower Oligocene of Germany (Sanchiz et al., 1993).

The determination *Rana* (*ridibunda*) sp. comprises the fossil waterfrogs of the European Cenozoic. They appear from the Lower Oligocene to the Holocene in Europe, in the Miocene of Turkey, in the Holocene of Israel, and questionably in the Upper Eocene of France (Rage, 1984a) and in the Pliocene of Kazakhstan. In Morocco, it is present in the Middle and Upper Pleistocene (Sanchiz, 1998b).

With regard to the Austrian record, Sanchiz (1998a) has described *Rana* (*ridibunda*) sp. from the Lower Miocene of Oberdorf, and M. Böhme (2002b) *Rana* aff. (*ridibunda*) sp. from the Lower Miocene localities Obergänserndorf and Teiritzberg. *Rana* cf. *ridibunda* appears in the Upper Miocene of Götzendorf (Miklas, 2002), and *Rana* sp. is present in the Upper Miocene locality Richardhof-Golfplatz (Harzhauser & Tempfer, 2004). *Rana ridibunda* appears in the Lower Holocene to Holocene Windener Bärenhöhle (Marinelli, 2001).

The oldest record of a possible representant of the Ranidae or at least the ancestry of this family dates from the Middle Jurassic of France (Seiffert, 1969). Following Rage (1984a), this determination as a member of the Ranidae is not correct. The Upper Cretaceous of Sudan (Sanchiz, 1998b) and the Paleocene and Eocene of France (Estes et al., 1967; Rage, 1984a; Rage & Vergnaud-Grazzini, 1978; Sanchiz, 1983) yield members of the Ranidae. The paleobiogeographic history of the family with special regard to the drastic turnover of terrestrial faunas after the "Grande Coupure" at the Eocene-Oligocene boundary is discussed by Rage (1984a). Europe was isolated from North America since the Lower Eocene and from Asia until the "Grand Coupure" when the Turgai Straits disappeared. But if the latter did not represent an absolute barrier for the Ranidae, they might have invaded Europe from Asia or from Africa via Asia during the end of the Mesozoic or during the Lower Tertiary. Either Europe represents the possible center of the origin of the Ranidae (if their European Upper Eocene record is autochthonous), or the family immigrated from Asia (if their European Upper Eocene record is allochthonous). Savage (1973) and Laurent

(1975) consider Africa as the center of their origin. Following Sanchiz (pers. advice), the European, Paleocene remains assigned to the Ranidae are not convincing. More probably, the group has immigrated into Europe during the Upper Eocene.

Immunological data taken by Uzzell (1982) indicate a separation between the western palearctic Green Frog and eastern palearctic Green Frog at the "Grande Coupure" Therefore, the water frogs may have invaded Europe from Asia at the latest Eocene (Sanchiz et al., 1993).

In Europe, three main kinds of Green Frogs exist today such as the Marsh Frog *Rana ridibunda*, the Pool Frog *Rana lessonae* and their hybrid *Rana* synkl. *esculenta*, the Edible Frog. *Rana lessonae* appears in Europe from Lower Pleistocene to Holocene and *Rana* synkl. *esculenta* is present in the Middle Miocene of France (Rage & Hossini, 2000), in the Upper Miocene of Hungary (Venczel, 1997a, 1999), in the Lower Pliocene of Hungary (Venczel, 2001), and in the Lower Pleistocene of Germany (G. Böhme & Günther, 1979) and Italy (Delfino & Bailon, 2000). Their relationships have still not been fully worked out. *Rana* synkl. *esculenta* seems to exist in at least three forms: one often breeds successfully with *Rana ridibunda* and another with *Rana lessonae*. The others which are triploid, are able to breed together and the results of such unions are mainly *Rana* synkl. *esculenta* although *Rana ridibunda* and *Rana lessonae* are produced as well (Arnold & Ovenden, 2002; Tunner, 1996, 1997, 2000).

Further hybrids within the Ranidae are represented by *Rana* synkl. *grafi* and *Rana* synkl. *hispanica*. The former probably originates from hybridisation between *Rana perezi* and *Rana* synkl. *esculenta* carrying chromosomes of *Rana ridibunda*. *Rana* synkl. *hispanica* may have arisen through hybridisation of *Rana bergeri* with either *Rana ridibunda* or *Rana* synkl. *esculenta* (Arnold & Ovenden, 2002).

These three species first appear in common in the Lower Pleistocene fissure-filling-system Pisede bei Malchin, Germany (G. Böhme, 1979; G. Böhme & Günther, 1979). G. Böhme (1983) documents the paleontological record of hybridisation between *Rana ridibunda*, *Rana lessonae* and *Rana* synkl. *esculenta*. The distinct osteological difference of the frontoparietale of these three species already emerged in the Lower Pleistocene of Pisede contradicts the hypothesis of e. g. Engelmann & Kabisch (1973) and Tunner (1970). They assume the hybridisation after the Pleistocene boulder period when the species could merge. The recently recorded range of *Rana* synkl. *esculenta* from the Middle Miocene to the Holocene (Rage & Hossini, 2000; see above) proves that the differentiation into the three species happened much earlier.

Ecology and Climate – living relatives: *Rana ridibunda* represents a very aquatic Green Frog which usually lives gregarious and diurnal. It inhabits all types of sunexposed waters such as small ponds, ditches and streams. Especially flood plains with side rivers and oxbow lakes are prefered. If its habitats overlap with *Rana lessonae* and *Rana* synkl. *esculenta*, it retreats to lakes and rivers (Arnold & Ovenden, 2002; Grillitsch, 1990). For hibernation, the Marsh Frog burrows into the ground of water which demands for a depth of up to 3-4 m because it must not freeze during the winter. Occasionally, riparian fissures and caves are occupied (Günther, 1990).

A very interesting aspect concerning the hibernation of water frogs is mentioned by Lutschinger (1988). Especially *Rana ridibunda* hibernates under water while *Rana lessonae* rests on land and the behaviour of *Rana* synkl. *esculenta* varies between the two. Their behaviour may be explained by their different ability to tolerate the low oxygen tension on the ground of the water. Although *Rana ridibunda* features the smallest oxygen affinity, the bonding capacity rises with falling temperature due to the temperature-affected blood oxygenation. *Rana ridibunda* and *Rana* synkl. *esculenta* "buy" the advantageous temperature with the risk of suffocation. Juvenile frogs generally are able to tolerate suboptimal conditions better due to their better oxygen affinity.

With regard to the geographical range of Recent *Rana ridibunda*, the Marsh Frog occurs in Central and Eastern Europe including the Balkan peninsula except much of Albania and Greece. Outside the Rhine area scattered colonies in France may represent introductions as well as ones in South England. It is also present east to Central Asia (Arnold & Ovenden, 2002). These areas belong to the Köppen's climate types Cf and Cs (Müller, 1996; see chapters 5, 6).

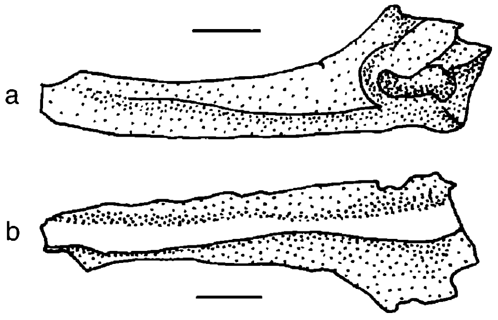


Figure 17: *Rana* (*ridibunda*) sp. Frontoparietale dext. dorsal (a) and ventral (b) view (Kohfidisch "III unten"; Inv. Nr.: NHM-W2004z0021/0003), scale bar equals 1 mm.

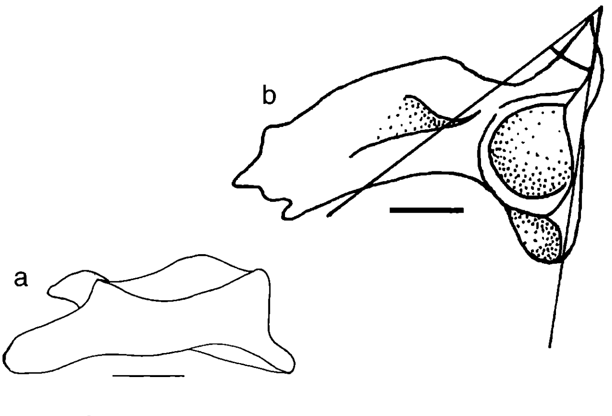


Figure 18: a) *Rana* (*ridibunda*) sp. Junctura ilioischiadica of ilium dext. (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0021/0004). b) *Rana* (*ridibunda*) sp. Ilium sin. lateral view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0021/0005), scale bar equals 1 mm.

Anura indet.

(Table 2, 4)

Material: 2 praemaxillaria sin. 182 maxillaria indet. 1 praearticulare indet. 2 atlantes. 23 vertebrae praesacrales. 1 vertebra sacralis. 1 os coccygeus. 3 ilia dext. 2 ilia sin. 4 ischia. 5 coracoidea. 2 humeri dext. 2 humeri sin. 30 radioulnaria indet. 50 femora indet. 167 tibiofibulae indet. 125 tibiale-fibularia indet.
(BM: Inv. Nr.: NHMW2004z0022/0001).

Description and Comparison: The 602 elements are too fragmentary to give any more precise determination. They do not indicate the presence of another taxon of the Anura than the ones described herein. Therefore, the remains are referred to Anura indet.

4.2. Class Reptilia

Superorder Squamata Oppel, 1811
Order Scleroglossa Estes, Queiroz & Gauthier, 1988
Suborder Lacertilia Owen, 1842
Infraorder Gekkota Cuvier, 1807
Family Gekkonidae Gray, 1825

Gekkonidae indet.

(Plate 4: a; Table 2, 3, 4, 5, 6, 10)

Range: Lower Cretaceous: Mongolia;
Palaeocene: South America;
Lower Eocene – Holocene: Europe, Africa, Madagascar;
Holocene: warmer parts of the world between 50°N and 50°S latitude.

Material: 2 dentalia sin. 1 vertebra caudalis (AO: Inv. Nr.: NHMW2004z0023/0001).
(BM: Inv. Nr.: NHMW2004z0023/0002).

Description:

dentale: Two fragmentary left dentalia are present which originate from the anterior or from the posterior part respectively. The numerous pleurodont, slender, cylindric, unicuspid teeth are closely spaced and are not striated lingually. The fragment of the anterior part possesses a closed Meckel's groove. Due to damage, it sporadically opens out ventrally. Originating from the posterior part, the second fragment features the incisura splenialis in lingual view which opens at half height. From labial aspect, the dentale is smooth with a medial row of numerous roundish to oval foramina.

vertebra caudalis (Plate 4: a; Table 10): The single vertebra caudalis features broken processus transversi as well as a broken right postzygapophysis. Its measurements are given in Table 10. From ventral view, the amphicoelous centrum with foraminae subcentrales is overtopped by the posterior neural arch. The insertion of the processus transversi slightly orientated to posterior looks as if divided by a groove. Viewing from lateral, the centrum is concave ventromedially. The oval prae-and postzygapophyses are orientated longitudinally and rise laterally. The canalis neuralis is high-triangular. Neither a zygantrum nor a zygosphene are present. In dorsal aspect, the sharp-edged processus spinosus leads into a posterior processus whose cusp is broken.

Comparison: The dentalia and the vertebra caudalis described herein feature characteristics typical of the family of the Gekkonidae such as described by Bailon (1991), Estes et al. (1988) and Hoffstetter (1946a). An assignment to a more definite level is not possible because the elements are too fragmentary or not diagnostic respectively. Comparisons with vertebrae caudales of Recent (*Cyrtodactylus*, *Hemidactylus*, *Phyllodactylus*, *Tarentola*) and fossil (*Gerandogekko*) specimens of Europe display a differentiation between Hemidactylus and other members of the Gekkonidae. The prae-and postzygapophyses of *Hemidactylus* are more orientated to lateral, the centrum is more concav ventromedially from lateral view, and the bases of the processus transversi do not appear divided as clearly. As the complete material of fossil and Recent Gekkonidae has not been studied, the determination has resulted in Gekkonidae indet.

Compared with the dentalia of Gekkonidae indet. from Obergänserndorf and Teiritzberg, the ones of Kohfidisch correlate in shape and size.

Discussion: The oldest record of a member of the Gekkonidae dates from the Lower Cretaceous of Mongolia (Alifanov, 1989). They are present in Europe since the Lower Eocene of France (Augé et al., 1997). In the Upper Eocene, Gekkonidae occur in France (Hoffstetter, 1946a; Augé, 1986; Rage, 1988a) and England (Milner et al., 1982). They have been described from the Lower Miocene of France (Hoffstetter, 1946a) and Austria (M. Böhme, 2002b), while during the Middle Miocene, they are present in Slovakia (Estes, 1969a), in Germany (Schleich, 1987) and in Morocco (Rage, 1976). The Pliocene of France (Bailon, 1989, 1991) and Sardinia (Pecorini et al., 1974), as well as the Upper Pliocene of Morocco (Bailon, 2000) yield Gekkonidae. During the Pleistocene, they still occurred in France (Bailon, 1991). Records from South America date from the Palaeocene (Estes, 1970b), and in Madagascar, they are restricted to the Pleistocene and Holocene (Estes, 1983).

During the Miocene in Europe, three genera exist such as the extinct *Gerandogekko* (Hoffstetter, 1946a) and *Palaeogekko* (Schleich, 1987), and the Recent *Phyllodactylus* (Estes, 1969a). With regard to *Gerandogekko*, Hoffstetter (1946a) and Estes (1969a) doubt wether the genus is valid. Hoffstetter (1946a) remarks osteological similarities to modern geckos and Estes (1969a) to the Recent *Phyllodactylus*.

Following Rage & Augé (1993), the family of the Gekkonidae invaded western Europe from Asia at the outset of the Eocene. Due to the Eocene/Oligocene "Grande Coupure", many species of the Scleroglossa died out but at the family level the composition of the fauna was less concerned. At the beginning of the Oligocene, immigrants increased the fauna.

Ecology and Climate – living relatives: The Recent members of the Gekkonidae represent small, plump lizards which are basically nocturnal, but especially in temperate regions such as Europe also active by day. Some are good climbers with the aid of claws and adhesive pads on the toes covered by hairlike structures. Some geckos prefer underfoot habitats. The European species *Tarentola mauritanica*, *Hemidactylus turcicus*, *Phyllodactylus europaeus*, and *Cyrtodactylus kotschyi* inhabit warm and dry areas. They can be found on dry stone walls and tree boles. *Cyrtodactylus kotschyi* climbs less and less high than its European relatives due to the lack of adhesive pads (ARNOLD & OVENDEN, 2002). Members of the Gekkonidae prefer temperatures between 20°C and 30°C and may rest during the winter at 20°C.

Geckos are distributed with about 650 species throughout the warmer parts of the world between 50°N and 50°S latitude. Just four species reach Europe. *Tarentola mauritanica* occurs in the Mediterranean area including islands, from Iberia east to Ionian islands, neighbouring parts of the mainland, Crete, Canaries, and North Africa. *Hemidactylus turcicus* also inhabits the Mediterranean coastal area including islands, North Africa, South-West Asia east to India, and North and Central America. The Range of *Phyllodactylus europaeus* is largely confined to islands in the Tyrrhenian area such as Corsica and Sardinia, islands off the coast of South-East France and North-West Italy. It also occurs on islands off the coast of North Tunisia. Finally, *Cyrtodactylus kotschyi* is present in the South and East Balkans north to Albania, Central and East Greece, Macedonia, South and East Bulgaria, Turkey, the Ionian and many Aegean islands including Crete, the South crimea and South-East Italy. It also inhabits the Asiatic Turkey to Israel, and Cyprus (ARNOLD & OVENDEN, 2002). According to MÜLLER (1996; see chapters 5, 6), this range comprises the Köppen's climate type Cs.

Infraorder Scincomorpha CAMP, 1923
Superfamily Lacertoidea BONAPARTE, 1831
Family Lacertidae BONAPARTE, 1831

Genus *Lacerta* LINNAEUS, 1758

Lacerta cf. *viridis* (LAURENTI, 1768)

(Table 2, 3, 4, 5, 6; fig. 19)

Recent species: *Lacerta viridis* (LAURENTI, 1768)

Range: Upper Miocene – Upper Pleistocene: Austria, Slovenia, Hungary, Rumania, Poland, Italy, Sicily, Monaco, France.

Holocene: Central and Southern Europe, Asia Minor, South-West Russia.

Upper Miocene of Kohfidisch: FOD (=first occurrence date).

Material: 4 parietalia (AO: Inv. Nr.: NHMW2004 z0024/0001). 1 neurocranium. 5 quadrata dext. 3 quadrata sin.

(BM: Inv. Nr.: NHMW2004z0024/0002).

Description:

<u>parietale (fig. 19):</u> The processus exoccipitales as well as the cornua frontales dext. et sin. of the most complete parietale are broken. The three remaining parietalia represent central parts. Its outer surface is sculptured by many round pits becoming longish peripherally and especially anteriorly. The facies dorsalis is trapezoid. Contrary to the spiky sutura frontalis, the margo supraoccipitalis is smooth. The round foramen parietale situated centrally is enclosed by a pentagon featuring the shortest side posteriorly and three angles anteriorly. Totalling five grooves representing the limits of the scales lead from each angle to the periphery. From ventral aspect, the sulcus medialis enclosed by a v-shaped crista is peaked. Two oval openings of the crista are situated anterior to the foramen parietale. The smooth and weak cristae cranii parietales dext. et sin. border the roughly furrowed facies semilunares dext. et sin.

<u>neurocranium:</u> The robust neurocranium consists of the basioccipitale, the parabasisphenoideum, the exoccipitalia, the supraoccipitale, as well as the two prootica.

Viewing from ventral, the basioccipitale features a distinct condylus occipitalis medialis saddle-like posteriorly and a clear margo occipitalis medialis. Anterior to the latter, the facies ventralis is depressed roundly. Two further oval depressions are present bilaterally. From the lateral margo basisphenoideus, two ridges lead to the condylus occipitalis medialis forming a triangular enclosing a forth depression. The roundish sinus laterales dext. et sin. feature a bulging margin and the margo basisphenoideus is relatively straight. From posterior view, the processus basioccipitales are orientated to lateroventral.

The processus basipterygoidei dext. et sin. of the basisphenoideum are broken. From ventral aspect, the processus parasphenoideus is carved anteriorly, and two converging ridges lead to the isthmus basiocciput-sphenoidalis enclosing a deep depression. From anterodorsal aspect, the sella turcica features two basic and horizontally oval foramina, two medial, closer arranged and vertically oval foramina, as well as two laterodorsal, transversally oval foramina. The sella turcica includes the pituitary in the fossa hypophysialis.

From posterior view, the exoccipitalia correspond to the condylus occipitalis medialis of the basioccipitale. Three foramina arranged triangularly are present on each contact such as the medial foramen hypoglossum and the lateral foramen vaguum and foramen glossopharyngeum forming the fossa jugularis. Relating to the supraoccipitale, the left processus paraoccipitalis is broken at its base and the right one lacks its distal top. Nevertheless, the right processus paraoccipitalis clarifies an elongation and a distal broadening. Its surface is inclined posteriorly and from posterior view, it is orientated nearly horizontally and just slightly to dorsal. The anterior crista supraoccipitalis is very high. Posteriorly, it leads into a low but sharp crista which divides the supraoccipitale medially.

The prootica are clearly separated from the supraoccipitale by a ridge. They feature a prominent crista prootica orientated to posterolateral. The fenestrum ovalis is separated from the fenestrum rotundum by a ridge arising posteriorly.

<u>quadratum:</u> Eight completely preserved quadrata are present. From anterior and posterior view, the crista tympani is nearly parallel to the crista pterygoidea. The

quadratum is slightly curved laterally. Viewing from anterior, the depressed facies anterior is bordered by the laterodorsal thickened, bulging crista tympani and the bulging crista pterygoidea leading into the saddle-like condylus mandibularis. Mediodorsal to the latter, a round and distinct foramen is present. From posterior aspect, the vertical and straight crista pterygoidea extremely dilates ventrally and less dorsally. Three quadrata feature a medial, small foramen on the crista pterygoidea and dorsal to the condylus mandibularis. The incisura pterygoidea is straight. The epiphysis columnaria merges inconspicuously in the condylus cephalicus which protrudes medially. In the dorsal fourth, the facies posterior is honeycombs-like sculptured.

Comparison: The parietalia and the quadrata correspond clearly to *Lacerta viridis* such as described by RAUSCHER (1992) and based on comparisons with Recent material.

With regard to the neurocranium, the description as *Lacerta viridis* refers to comparisons with the neurocrania of Recent specimens. The basioccipitale features a more distinct condylus occipitalis medialis and a clearer margo occipitalis medialis than characterized by RAUSCHER (1992). The parabasisphenoideum is typically deeply depressed between two converging ridges leading from the processus parasphenoideus to the isthmus basiocciput-sphenoidalis.

According to BAILON (1991), the long processus paraoccipitales, the high crista supraoccipitalis, and the processus basioccipitales orientated to lateral of the neurocranium are typical of members of the Lacertidae.

Keeping the discrepancy in the determination of even Recent species within the Lacertidae in mind, the elements are referred to *Lacerta* cf. *viridis*.

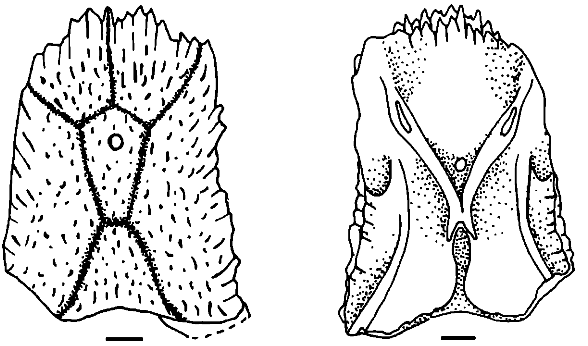


Figure 19: *Lacerta* cf. *viridis*. Parietale dorsal (a) and ventral (b) view (Kohfidisch; Inv. Nr. NHMW2004z0024/0001), scale bars equal 1 mm.

Lacerta sp. A

(Plate 4: b-d, f-h; Table 2, 3, 4, 5, 6, 10; fig. 20)

Material: 13 osteodermalia. 17 osteodermalia supraoculares. 136 fragmenta frontalium. 1 pterygoideum dext. (AO: Inv. Nr.: NHMW2004z0025/0001). 1 pterygoideum sin. 3 quadrata dext. 5 quadrata sin. 60 praemaxillaria (AO: Inv. Nr.: NHMW2004z0025/0002). 403 maxillaria dext. 322 maxillaria sin. 99 maxillaria indet. 208 dentalia dext. 236 dentalia sin. (AO: Inv. Nr.: NHMW2004z0025/0003). 1 atlas (AO: Inv. Nr.: NHMW2004z0025/0007). 2 epistrophei. 7 vertebrae cervicales (AO: Inv. Nr.: NHMW2004z0025/0004). 319 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0025/0005). 2 vertebrae sacrales. 96 vertebrae caudales anteriores. 165 vertebrae caudales AO: Inv. Nr.: NHMW2004z0025/0006). 2 ilia dext. 5 ilia sin. 6 humeri dext. 4 humeri sin.
(BM: Inv. Nr.: NHMW2004z0025/0008).

Description:

osteodermale: The 13 osteodermalia are rectangular and divided into two areas dorsally. The exaulted one third rests unsculptured while two thirds are covered by a fine sculpture. A longitudinal, transversale ridge is visible in some case. From ventral aspect, small foramina are present.

osteodermale supraocularis: 17 complete osteodermalia supraoculares are present. They are triangular, vaulted dorsally and sculptured by many fine pits. Ventrally, a triangular depression is present.

fragmentum frontalis: The 136 fragments of the frontale are too unspecific to describe them more precisely. If they are relatively well preserved, the anterior part which would provide more detailed information is missing. Dorsally, they are sculptured by small pits and grooves. The sulcus interfacialis posterior is present in any case. From ventral view, the crista cranii frontalis following the margo praefrontalis and the margo postfrontorbitalis is slightly curved and bears 3-4 oval posterior foramina.

pterygoideum (Plate 4: b): Both elements represent the central part of the y-shaped pterygoideum. The bases of the processus palatinus, processus transversus, processus basisphenoideus, and the processus quadratus are present. Four monocuspid dentes pterygoidei on the processus palatinus are orientated to medial. Viewing from ventral, the triangular sulcus pterygoideus is bordered by the crista transversa ventralis. Dorsally, the crista transversa dorsalis rises highly. Contrary to the just slightly developed longish-oval incisura cristae columellaris, the oval fossa columella deeply impresses.

quadratum: Eight fragmentary quadrata are represented by the straight crista pterygoidea bearing the condylus cephalicus. From posterior aspect, the crista pterygoidea extremely broadens ventrally and less dorsally.

praemaxillare (Plate 4: c): The 60 praemaxillaria are either completely preserved or lack parts of the processus nasalis, the processus maxillaris, or the processus palatinus. The processus nasalis features the shape of a rhomboid. The dorsal half of its outer surface is sculptured by small pits or grooves. Due to that sculpture, the dorsolateral margins irregularly taper. Bearing triangular and well-developed processus palatini orientated to posterior, the processus maxillaris is relatively short. From lingual aspect, the processus nasalis possesses a continuous, medial ridge orientated to dorsoventral. On half level, ridges directed to laterodorsal meet in the medial one. If observable, the number of the pleurodont, monocuspid teeth varies between 9 and 11.

maxillare: 824 maxillaria represent each state of fragmentation. The processus zygomaticus is short and high and, if observable, the processus praefrontalis is not present. From labial view, the facies buccalis is sculptured by small pits and grooves. Ventral to the sculptured part and dorsal to the crista dentalis, a row of serial oval to roundish foramina is present. Viewing from dorsal, the undulating lamina horizontalis features a triangular and large orificium canalis nervi alveolaris superioris. From lingual aspect, a crista borders the anterior margin of the concave facies interna. About 20 pleurodont, bicuspid and robust teeth orientated to mediolateral are present.

dentale (Plate 4: d): The 444 dentalia are robust, long and variably fragmentary. The symphysis is irregularly drop-like. From labial aspect, oval to roundish foramina occur on the anterior half. A distinct groove parallel to the posterior crista dentalis meets in the processus coronoideus. Viewing from lingual, the open sulcus meckeli broadens posteriorly. The undulating lamina horizontalis thinning out posteriorly borders the crista dentalis which bears pleurodont and robust, anterior monocuspid (about 6), medial bicuspid, and posterior tricuspid (about 3) teeth. If preserved, not only the processus coronoideus, but also the sinus supraangularis are well-developed.

atlas (fig. 20): The atlas of the Lacertidae consists of two parts. The element described herein represents the left part containing one half of the centrum and one half of the neural arch. The latter lacks its dorsal end. Viewing from anterior, it is vaulted laterally. The centrum is irregularly oval and the neural arch extremely thin. From lateral aspect, the oval centrum is separated from the bigger oval neural arch by a thin constriction. Concerning the neural arch, a blunt processus projects posteriorly. Its dorsal margin represents a sharp edge running arcuately from dorsal to posterior and enclosing a posterior depression. On the medial, very spot of the processus, the oval postzygapophysis is present. The centrum features a blunt and robust processus orientated to lateral and situated slightly posteriorly. Dorsal to that processus, a triangular depression is present. Three irregularly oval articular surfaces of the centrum represent one condylus occipitalis, one condylus articulating with the epistropheus and the third, ventral condylus connected to the intercentrum.

epistropheus: The centra of the two epistrophei are preserved. From ventral aspect, they are triangular: anteriorly, the broad and blunt dens epistrophei inserts to the whole width while posteriorly, a distinct, round condylus is present. A well-developed ventral keel leads to an anterior processus which arises from a broad base. Its top inclined to posterior is flattened laterally.

vertebra cervicalis (Plate 4: f): Seven vertebrae cervicales are nearly complete. They are procoelous featuring a short centrum and a short neural arch situated far posteriorly. While the condylus is erectly oval, the cotylus looks flattened dorsoventrally. A sharp ventral keel is present. The elongated and narrow, oval synapophysis is orientated to posterodorsal-anteroventral. Prae- and postzygapophyses are longish-oval and directed to anteroposterior. From anterior aspect, the canalis neuralis is widely open. Viewing from dorsal, the sharp processus spinosus dilates posteriorly ending in a short cusp.

vertebra praesacralis (Plate 4: g; Table 10): Featuring each state of fragmentation, the 319 procoelous vertebrae praesacrales possess a remarkably longer centrum and a longer neural arch than the vertebrae cervicales. Their measurements are given in Table 10. Contrary to the vertebrae cervicales, condylus and cotylus are flattened dorsoventrally, the ventral keel is less distinct and flat, and the synapophyses are broader. Prae- and postzygapophyses are equally longish-oval orientated longitudinally, and the sharp processus spinosus dilates posteriorly ending in a short cusp.

vertebra sacralis: Two separated vertebrae sacrales are present. Both represent the second vertebra sacralis. While one is completely preseved, the other one lacks the distal part of the right processus transversus. The cotylus is round, the condylus flattened dorsoventrally. From ventral aspect, no ventral keel is present. Inserting with a broad base, the processus transversi slightly flattened dorsoventrally constrict medially and dilate again distally. They are imperceptibly orientated to anterior. Their top features an anterior, oval and large articular surface for the connection to the processus transversus of the first vertebra sacralis. Prae- and postzygapophyses arise laterally. Contrary to the small and longish-oval praezygapophyses, the oval postzygapophyses are larger. The distinct processus spinosus dilates posteriorly ending in a cusp.

vertebra caudalis anterioris (Plate 4: h): 96 vertebrae caudales anteriores mainly preserved by their procoelous centra feature either complete or just the bases of the processus transversi. While the cotylus is round, the condylus is flattened dorsoventrally, and the ventral keel is prominent but rounded. The processus transversi orientated to anterior insert broadly and are flattened dorsoventrally. They feature parallel anterior and posterior margins fusing roundly at the tip. The roundish-oval prae- and postzygapophyses slightly rise laterally. The latter are orientated to lateral. Relating to the well-developed processus spinosus, it dilates posteriorly to lead into an elongated, round posterior cusp overtopping the postzygapophyses.

vertebra caudalis: The 165 procoelous vertebrae caudales represent anterior and posterior parts. The former feature condyli flattened dorsoventrally, a well-developed, rounded ventral keel, and the undulating plane of fracture passing across the reduced processus transversus flattened dorsoventrally and orientated to lateral. The oval praezygapophyses are directed to anteroposterior, and a distinct processus spinosus is present. Relating to the bigger posterior part, the conylus is round, and the ventral keel slightly divides posteriorly ending in two lateral cusps anterior to the cotyle. The undulating plane of fracture passes across the processus transversi flattened dorsoventrally and orientated to posterolateral which may be broken. The roundish-oval postzygapophyses incline to lateral and a cuneiform processus spinosus rises posterodorsally. After ETHERIDGE (1967), this kind of autotomy occurring in members of the genus *Lacerta* is characterized by the divergence of the anterior and posterior parts of the split processus.

ilium: The posterior parts of the 7 ilia are preserved. The large and oval acetabulum, the long axis of which, in lateral view, is directed to posterodorsal/anteroventral, forms an anterior acute angle. Anteroventral to the acetabulum, a distinct foramen is present. With regard to the tuber superior, it is long, slender and orientated to posterior. The ala ossis ilii as well as the pars descendens ossis ilii are robus, broad and flattened laterally.

humerus: 9 humeri represent proximal parts, while one fragmentary humerus consists of the distal part. From dorsal view, the former are rectangular, dilated and orientated to medial. Their margins represent ossified ridges for musculature and the crista delto-pectoralis includes an obtuse angle with the proximal humerus. Viewing from ventral, the proximal part is strongly concave. With regard to the single distal remain, the epicondylus radialis is flattened laterally while the epicondylus ulnaris is vaulted. Contrary to the massif entepicondylus, the ectepicondylus is reduced merging into the crista ectepicondylaris. The foramen ectepicondylaris is present.

Comparison: With regard to the fragmenta frontalium, the pterygoidea, the quadrata, the praemaxillaria, the maxillaria, as well as the dentalia, the elements are too fragmentary lacking diagnostic parts to refer them to *Lacerta viridis*, although the present characteristics correspond to the species according to RAUSCHER (1992) and based on comparisons with Recent material. The osteodermalia, the osteodermalia supraoculares, the vertebrae, ilia, and humeri feature characteristics typical of members of the Lacertidae but are not indicative for a more detailed information. Their determination follows BAILON (1991), BARBADILLO & SANZ (1983: vertebrae), ETHERIDGE (1967: vertebrae caudales), and LÉCURU (1969: humeri). Atlas, epistropheus, and vertebrae caudales anteriores have not been described yet and their determination is based on comparisons with Recent members of the Lacertidae.

Due to their big size, the elements have been referred to *Lacerta* sp. A, the bigger species of the Lacertidae present in Kohfidisch.

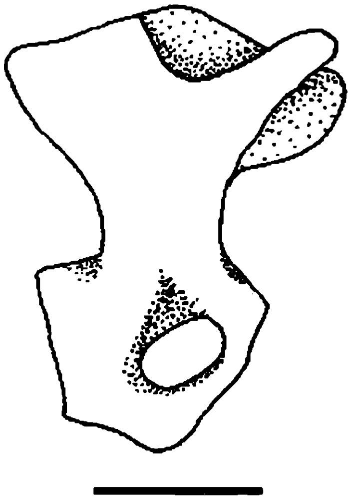


Figure 20: *Lacerta* sp. A. Left half of atlas (Kohfidisch; Inv. Nr.: NHMW2004z0025/0007), scale bar equals 1 mm.

Lacerta sp. B

(Plate 4: e; Table 2, 3, 4, 5, 6, 10)

Material: 2 praemaxillaria. 12 maxillaria dext. 9 maxillaria sin. 16 dentalia dext. 22 dentalia sin. (AO: Inv. Nr.: NHMW2004z0026/0001). 8 vertebrae praesacrales. 2 vertebrae caudales.

(BM: Inv. Nr.: NHMW2004z0026/0002).

Description: The praemaxillaria, the maxillaria and the dentalia (Plate 4: e) altogether represent very fragmentary elements mainly consisting of the lamina horizontalis bearing monocuspid (praemaxillare, anterior teeth of the dentale) and bicuspid (maxillare, posterior teeth of the dentale) teeth. Specific parts are missing. The remaining characteristics correspond to the ones described as *Lacerta* sp. A but differ in their smaller size. The measurements of the vertebrae praesacrales are listed in Table 10. Together with the vertebrae caudales, they are morphologically similar to the vertebrae of *Lacerta* sp. A but smaller.

Comparison: Based on the observable characteristics of the elements typical of members of the Lacertidae (RAUSCHER, 1992: praemaxillaria, maxillaria, dentalia; BARBADILLO & SANZ, 1983: vertebrae; ETHERIDGE, 1967: vertebrae caudales) and on comparisons with Recent material, their description has resulted in *Lacerta* sp. B. This second non-described species of the Lacertidae differs from *Lacerta* sp. A just in its smaller size. Therefore, it might represent juvenile specimens of *Lacerta* sp. A. Moreover, large and smaller-sized species of the Lacertidae usually coexist in a single habitat today (ARNOLD & OVENDEN, 2002). With regard to the fragmentariness of the elements and the habits of Recent relatives, a more detailed determination than *Lacerta* sp. A and *Lacerta* sp. B is not possible.

The maxillaria and dentalia of *Lacerta* sp. 1 and *Lacerta* sp. 2 from Obergänserndorf and Teiritzberg correlate in size, shape and tooth morphology to *Lacerta* sp. A and *Lacerta* sp. B of Kohfidisch. These elements are too fragmentary for detailed examination as well.

Discussion: *Lacerta viridis* appears in the Upper Pliocene to the Middle Pleistocene of Hungary, in the Upper Pliocene to the Pleistocene of Sicily, in the Plio-/Pleistocene of Austria (RAUSCHER, 1992), in the Lower Pleistocene of Rumania, in the Upper Pleistocene of Italy, in the Upper Pleistocene of Slovenia (PAUNOVIĆ, 1984), in the Pleistocene of Monaco, as well as in the Holocene of Middle and Southern Europe and Asia Minor (ESTES, 1983).

So far, *Lacerta* cf. *viridis* has been described from the Upper Pliocene of Poland (MŁYNARSKI, 1964; MŁYNARSKI et al., 1984), from the Lower Pleistocene of Hungary (KRETZOI, 1956) and from the Middle Pleistocene and Holocene of France (BAILON, 1991). Thus, *Lacerta* cf. *viridis* from the Upper Miocene of Kohfidisch represents the oldest record.

The oldest fossil determined as *Lacerta* s. l. dates from the Middle Oligocene and the Upper Oligocene (*Lacerta filholi*) of France (AUGÉ, 1986, 1988). *Lacerta* sp. appears in the Lower Miocene of France (HOFFSTETTER, 1955) and Austria (BÖHME, 2002b), in the Middle Miocene of Germany (BÖHME, 1999), in the Middle and Upper Miocene of Austria (MI-

KLAS-TEMPFER, 2003; HARZHAUSER & TEMPFER, 2004), and in the Lower Pliocene of Austria (PAPP & THENIUS, 1954) and Poland (MŁYNARSKI, 1956, 1962). The Plio-/Pleistocene of Austria as well, bears *Lacerta* sp. (RAUSCHER, 1992). Further, *Lacerta* sp. has been described from the Upper Pliocene to the Holocene of Germany, Poland, France, Spain, Greece, Italy, Slovenia, Menorca, and Malta (ESTES, 1983).

Probably, the lacertid lizards inherited from the Cretaceous appeared in Europe during the Palaeocene/Eocene. Ascertained, they are present in the Lower Eocene of Belgium (AUGÉ, 1990; RAGE & AUGÉ, 1993). Not only the Palaeocene, but also the Eocene herpetofaunas of Europe implying the Lacertidae display a Laurasian pattern (RAGE, 1997).

Ecology and Climate – living relatives: Not only habitats in and around dense bushy vegetation with good exposure to sun, such as open woods, wood and field edges, hedgerows, and bramble thickets, but also damp environments and highland areas up to 1800 m represent living spaces of *Lacerta viridis*. If bushes are present, heath areas may be inhabited as well. Members of the species hunt and climb in dense vegetation but come out to bask in the morning and in the evening (ARNOLD & OVENDEN, 2002). They hibernate in burrows. *Lacerta viridis* occurs in much of the southern half of Europe, extending north to most of France, the Channel Islands, West and South Switzerland, South and East Austria, parts of the Czech Republik and Slovakia and South Ukraine including the Dneiper Valley. Isolated populations are present in the Rhine Valley. It extends south to North Spain, Sicily and North and Central Greece. The species lacks in many Mediterranean islands, but is present on Euboa, Thasos, Samothrace, Skiathos, Corfu, and Elba (ARNOLD & OVENDEN, 2002). This area of distribution is restricted to the Köppen's climate types Cf, Cs, and Df (following MÜLLER, 1996; see chapters 5, 6).

Genus *Miolacerta* ROČEK, 1984

Miolacerta tenuis ROČEK, 1984

(Plate 5: a; Table 2, 3, 4, 5, 6)

Holotype: Charles University, Department of Palaeontology, Prague, Czech Republik, DP FNSP 3785; section of the left dentale with 14 anterior tooth positions (ROČEK, 1984).

Type locality: Dolnice, Czech Republik.

Stratigraphical Age of the Type material: Lower Miocene (Ottnangian, Orleanian, MN4).

Range: Lower Miocene: Czech Republik; Middle Miocene: Germany; Upper Miocene: Austria.

Upper Miocene of Kohfidisch: LOD (= last occurrence date).

Material: 2 maxillare sin. 3 dentalia dext. (AO: Inv. Nr.: NHMW2004z0027/0001). 1 dentale indet.

(BM: Inv. Nr.: NHMW2004z0027/0002).

Description:

maxillare: The two maxillaria are fragmentary. They are 5.04 mm or 2.5 mm respectively long representing the middle parts of the elements and consist of three tricuspid teeth declined to anterior and the lamina horizontalis. Slightly dorsal to the latter, the maxillare is broken. The orificium canalis nervi alveolaris superioris is present on each maxillare.

dentale (Plate 5: a): Three right dentalia are represented by their anterior parts while one remain consists of two tricuspid teeth and the adjacent lamina horizontalis of a dentale. The most complete dentale is 2.92 mm long, elongated and shows a rectangular symphysis. The massive lamina horizontalis reaches one third of the bone height at the level of the most probably 4th to the 12th tooth positions. Anteriorly, it starts as a thin cusp which becomes continuously wide and leads into a plate posteriorly. Exposed ventromedially, the sulcus meckeli opens well anteriorly. Relating to the dentition, the most probably 3rd, the 5th, and the 7th to the 10th tooth are preserved. They attach pleurodontly overtopping the crista dentalis with more than one third of their entire height, and they are slender, cylindrical and slightly convex lingually. While the 3rd and the 5th tooth possess simply rounded cusps, the 7th to the 10th ones are tricuspid. From labial aspect, a regular row of four foramina pro ramis nervi alveolaris inferioris is present.

The two other anterior remains of the dentalia consist of three teeth and the massive lamina horizontalis adjoining to a sulcus meckeli opened ventromedially. While one remain contains three tricuspid teeth, the second one possesses an anterior monocuspid and two posterior tricuspid teeth. They are 3 mm or 2.75 mm long respectively.

Comparison: The tricuspid teeth of the maxillaria as well as the dentition and the characteristics of the dentalia are typical of *Miolacerta tenuis* such as described by ROČEK (1984). Although dentalia with tricuspid teeth also occur in other members of the Lacertidae, the dentalia described herein feature more and more distinct tricuspid teeth as well as a general morphology justifying their description as *Miolacerta tenuis*.

Discussion: The genus *Miolacerta* and the species *Miolacerta tenuis* have been described by ROČEK (1984) from the Lower Miocene locality Dolnice in Bohemia, Czech Republik. M. BÖHME (1999) mentions the species in her faunal list of Sandelzhausen, Middle Miocene, Germany. Finally and according to M. BÖHME (2002b), *Lacerta* sp. 2 from Obergänserndorf and Teiritzberg, Lower Miocene, Austria, features similarities to *Miolacerta* but unfortunately is represented by too fragmentary and therefore unspecific remains. Concluding, the record of *Miolacerta tenuis* from Kohfidisch represents the third and simultaneously the stratigraphically youngest one.

?Lacertidae BONAPARTE, 1831

Genus *Edlartetia* AUGÉ & RAGE, 2000

Edlartetia sansaniensis (LARTET, 1851)

(Plate 5: b; Table 2, 3, 4, 5, 6)

Neotype: Musée National d'Histoire Naturelle, Paris, France, Sa 23595; right, incomplete dentale (AUGÉ & RAGE, 2000).

Type locality: Sansan, Gers, France.
Stratigraphical Age of the Type material: Middle Miocene (Astaracian, MN6).
Range: Middle Miocene: France; Upper Miocene: Austria.
Upper Miocene of Kohfidisch: LOD (= last occurrence date).
Material: 9 maxillaria dext. 3 maxillaria sin. 12 dentalia dext. (AO: Inv. Nr.: NHMW2004z0028/0001). 12 dentalia sin. (BM: Inv. Nr.: NHMW2004z0028/0002).
Description:
maxillare: 12 maxillaria are present which are altogether fragmentary. The outer surface is smooth. The typical teeth are pleurodont, slender, closely attached, and irregularly orientated. Apart from the most frequent ventrally broken teeth, monocuspid and bicuspid teeth exist. The latter mostly show a dilatation shortly before the two cusps which are unequally prominent. From lingual view, the cavities for the tooth replacement are straight dorsoventrally and rather narrow. Some teeth feature that slit up to slightly dorsal the cusps. The lamina horizontalis results in a bulge lingually. Viewing from labial, numerous foramina are present. While the ventral row consists of regularly arranged foramina, an irregular second and third dorsal row follow.
dentale (Plate 5: b): The 24 slender dentalia lack their posterior part and few of them also their anterior or ventral part. The ventral margin is just slightly arched ventrally. Together with the crista dentalis, the lamina horizontalis is marginally arched ventrally as well. The sulcus meckeli opens ventral at the symphysis and widens regularly from anterior to posterior. From labial aspect, a row of relatively large, oval foramina is present. The distance that separates them increases posteriorly. With regard to the teeth, they are pleurodont, cylindric and irregularly inclined. Similarly to the teeth of the maxillare, the bicuspid ones feature a dilatation shortly ventral to the two cusps. One cusp is prominent. Formed like a slit, the cavities for the tooth replacement reach up to slightly ventral to the cusps.
Comparison: Following Augé & Rage (2000), the ventral margin of the dentale that slightly arches ventrally as well as the bicuspid teeth featuring the typical dilatation are characteristic of *Edlartetia sansaniensis*. They point to a high similarity to the dentale of *Miolacerta tenuis*, sharing the slenderness, the small size, the general shape, and the shape of the lamina horizontalis. But contrary to *Edlartetia sansaniensis*, the teeth of *Miolacerta tenuis* are typically tricuspid. Generally, the latter does not feature any facet for the attachment of the coronoid on the outer surface of the dentale, which unfortunately is not observable in the material described herein.
The material from Sansan, the type locality, does not include maxillaria, but the dentition including the irregularly inclined teeth, the dilatation dorsal the two cusps, and the slit-like cavities for the tooth replacement reaching up to slightly dorsal to the cusps is similar to the teeth of the dentale. Keeping these considerations in mind, the description of the maxillaria and the dentalia has resulted in *Edlartetia sansaniensis*.

Discussion: Augé & Rage (2000) have erected the new genus *Edlartetia* for the reception of the species *Lacerta sansaniensis* Lartet, 1851 of Sansan in France, Middle Miocene. They designated a neotype from this locality. *Lacerta sansaniensis* was just shortly described and not figured. Gervais (1859) refers a specimen from Sansan to *Lacerta sansaniensis* whereupon Estes (1983) declares *L. sansaniensis* as *nomen dubium*. The record of *Edlartetia sansaniensis* from the Upper Miocene of Kohfidisch represents the stratigraphically youngest one and the second locality only in which the species is known.
The tooth morphology of *Edlartetia sansaniensis* correlates more with the Teiidae than with the Lacertidae although the teeth of the Teiidae typically possess a deposit of cementum at their base and the dentale is more arched ventrally. Teiidae have never been recorded from Europe but from America and Asia. As during the Miocene, mammals and snakes changed between North America and Europe, the attribution of *Edlartetia sansaniensis* to the family of the Teiidae is possible (Augé & Rage, 2000).
Furthermore, Augé & Rage (2000) point to similarities of the tooth morphology between *Edlartetia sansaniensis* and a member of the Anguinae of the type locality Sansan. Due to these incertitudes, they call the definite attribution of the species to the family of the Lacertidae into question.

Superfamily Scincoidea Gray, 1825
Family Scincidae Gray, 1825

Scincidae indet.

(Plate 5: c; Table 2, 3, 4, 5, 6, 10)

Range: Upper Cretaceous and Upper Eocene – Holocene: U.S.A.
Lower Miocene – Middle Pleistocene: Austria, Germany, Czech Republic, Ukraine, France, Spain, Morocco;
Holocene: South Europe, South-East Asia, Africa, America, Australia.
Material: 7 maxillaria dext. 5 maxillaria sin. 1 dentale dext. (AO: Inv. Nr.: NHMW2004z0029/0001). 2 dentalia sin. 3 vertebrae praesacrales.
(BM: Inv. Nr.: NHMW2004z0029/0002).
Description:
maxillare: The 12 fragmentary maxillaria are represented by the crista dentalis, teeth, the lamina horizontalis, and the broken dorsal part. The lamina horizontalis emerges two times forming an edge. The most prominent one is situated at the level of the 2nd to 3rd tooth positions, where the large orificium canalis nervi alveolaris superioris is present. The smaller edge is formed at the level of the 4th tooth position. Viewing from labial, the large and oval foramina pro ramis nervi alveolaris superioris are longitudinally orientated. The processus zygomaticus is elongated, triangular, pointed, and slightly bent to labial. Concerning the pleurodont teeth, they are cylindrical, massive, blunt, and closely attached. Their tips are compressed labiolingually featuring a fine vertical striation. In general, they are monocuspid although just a few of them feature an indistinct, underdeveloped and very small anterior cusp.

dentale (Plate 5: c): Three dentalia are present. One of the two left dentalia broken anteriorly and posteriorly lacks the ventral part. The right dentale is the most complete one although the very anterior end as well as the posterior part are missing. The ventral margin is straight and arises directly at the symphysis. Typically, the rounded lamina horizontalis is flat and low. It thins out posteriorly and carries a medial thin slit which might be the contact between the dentale and the spleniale. With regard to the sulcus meckeli, it forms a slit exposed ventrally with parallel margins farther to the 8th tooth position. At the position of the very large and oval orificium canalis nervi alveolaris inferioris elongated anteroposteriorly, the sulcus meckeli opens widely but remarkably shallowly. At that position as well, the dentale broadens posteriorly. The pleurodont and monocuspid teeth are cylindrical, massive, blunt, and closely spaced. Their tips are compressed labiolingually and feature a fine vertical striation. While the anterior teeth are inclined anteriorly, the posterior ones erect vertically.

vertebra praesacralis (Table 10): One of the three vertebrae praesacrales is complete, one lacks its condylus, and one features a broken posterior neural arch. Relating to their measurements, see Table 10. The centrum is procoelous, flattened dorsoventrally and elongated, possessing a well distinct condylus. It broadens anteriorly and features a smooth ventral surface. The pseudozygosphene (sensu HOFFSTETTER & GASC, 1969) is visible on each vertebra while the pseudozygantrum is reduced. From anterior aspect, the canalis neuralis is high. Viewing from dorsal, the neural arch is deeply carved anteriorly featuring a sharp processus spinosus which overtops the postzygapophyses posteriorly with a blunt cusp serving for an interzygapophyseal articulation. With regard to the prae- and postzygapophyses, they are longish-oval and orientated longitudinally.

Comparison: The characteristics of the maxillaria refer to a member of the Scincidae based on comparisons with maxillaria of Recent specimens and on BAILON (1991) and ROČEK (1984). The dentalia correlate with the ones described by AUGÉ & RAGE (2000) and BAILON (1991) as Scincidae indet. and with Recent material of members of the family. Therefore, their determination has resulted in Scincidae indet.

Comparisons with dentalia of Recent members of the Scincidae have shown affinities of the dentalia described herein to *Chalcides*. Those closely attached, massive teeth and mainly the development of the sulcus meckeli and the shape, position and large size of the orificium canalis nervi alveolaris inferioris point to the living *Chalcides*. *Eumeces*, another living scincid, features a sulcus meckeli more continuously open from anterior to posterior contrary to *Chalcides*, where the sulcus meckeli represents a slit up to the 12th tooth position and opens abruptly at the position of the orificium canalis nervi alveolaris inferioris. The lamina horizontalis of the living *Mabuya* is more raised posteriorly and more distinct, bordering a deeper sulcus meckeli which just opens at the 15th tooth position, and the orificium canalis nervi alveolaris inferioris is smaller. The sulcus meckeli of the Recent species *Ablepharus* is closed. Due to the lack of specimens of more Recent genera of the Scincidae, a more precise determination than Scincidae indet. is not possible.

The maxillaria and dentalia of Scincidae indet. of Obergänserndorf and Teiritzberg feature a tooth morphology and size similar to the ones of Kohfidisch. Though, the teeth of the dentalia are not as closely spaced and unfortunately, none of the ventral parts of the dentalia is preserved to inform about the development of the sulcus meckeli. Therefore, comparisons with regard to possibly different genera are insufficient.

Due to the lack of the processus transversi and the anterior broadening of the centrum flattened dorsoventrally, the vertebrae represent vertebrae praesacrales. Their characteristics are typical of members of the Scincidae following BAILON (1991), ESTES et al. (1988), and personal observations on material of Recent specimens. Especially the interzygapophyseal articulation point formed by the processus spinosus overtopping the postzygapophyses is typical of Scincidae. Keeping these considerations in mind, the description has resulted in Scincidae indet.

Discussion: The oldest records of a member of the Scincidae doubtfully date from the Upper Cretaceous and unquestionably from the Middle Oligocene of North America (ESTES, 1969b; ESTES, 1983). In the U.S., the family of the Scincidae is present from the Middle Oligocene to the Holocene (ESTES 1983). M. BÖHME (2002b) has described Scincidae indet. from Obergänserndorf and Teiritzberg in Austria, ROČEK (1984) a member of the cf. Family Scincidae from the Lower Miocene of Dolnice in the Czech Republic, and SCHLEICH (1985) cf. *Mabuya* from Germany as the three oldest records of the family from the Lower Miocene of Europe. The Upper Miocene and the Lower Pleistocene of the Ukraine yield members of the Scincidae (DAREVSKY & TSHUMAKOV, 1962; ZEROVA, 1987). In France, Scincidae occur in the Middle Miocene (AUGÉ & RAGE, 2000) and in the Middle Pleistocene to the Holocene (BAILON, 1991), while in Spain, they are present in the Upper Pliocene (BAILON, 1991) and the Pleistocene (BARBADILLO, 1989).

Scincidae are closely related to Xantusiidae and especially to the Cordylidae with regard to the morphology of the dentale and the vertebrae (ESTES, 1983; PRESCH, 1988). ESTES et al. (1988) regard Scincidae and Cordylidae as sister groups within the Superfamily Scincoidea. AUGÉ & RAGE (2000) point to the deficiency of the generalized similarities between the families. They mention the common presence of the pseudozygosphene and pseudozygantrum on vertebrae of Scincidae, some Cordylidae, and some Lacertidae and suggest further comparisons between the families.

Following RAGE (1997), the family of the Scincidae invaded Europe during the Miocene either from Asia or from Africa. Exchanges of terrestrial forms between Europe and Asia were no longer hindered by marine barriers from the Lower Miocene onwards, after the Eurasian and Afro-Arabian plates had collided by the Oligocene-Miocene transition. Due to the Messinian event, when the Mediterranean largely dried up, a terrestrial connection occurred between Europe and Africa on the site of Gibraltar during the Upper Miocene.

Ecology and Climate – living relatives: Members of the European Scincidae represent ground-dwelling lizards with small or even totally reduced limbs. They are diurnal, often rather secretive animals feeding on a wide variety of invertebrates (Arnold & Ovenden, 2002). *Chalcides* in detail prefers dry habitats often in lowlands but may also occur on damp meadows (Obst et al., 1984). The optimal temperature of a skink ranges between 25°C and 30°C. The Scincidae preferentially inhabit South-East Asia, Australia and Africa (Obst et al., 1984), but also America and Europe. Merely five of the about 700 extant species occur in Europe which belong to the genera *Ablepharus*, *Chalcides* and *Ophiomorus*. *Chalcides* is found in South France, Iberia, Malta, Elba, Sardinia, Sicily, Italy, Greece, Euboa, Crete, North and North-East Africa, and South-West Asia (Arnold & Ovenden, 2002). That area of distribution belongs to the Köppen's climate type Cs (Müller, 1996; see chapters 5, 6).

Infraorder Anguimorpha Fürbringer, 1900
Superfamily Anguioidea Gray, 1825
Family Anguidae Gray, 1825
Subfamily Anguinae Gray, 1825

Genus *Anguis* Linnaeus, 1758

Anguis fragilis Linnaeus, 1758

(Plate 5: d-h; Table 2, 3, 4, 5, 6, 11; fig. 21)

Recent species: *Anguis fragilis* Linnaeus, 1758
Range: Upper Miocene – Upper Pleistocene: Austria, Hungary, Poland, Rumania, France, Spain;
Holocene: Europe north to Finland, east to the Caucasus and Iran, south to North-West Africa.
Upper Miocene of Kohfidisch: FOD (= first occurrence date).

Material: 842 osteodermalia. 1 quadratum dext. (AO: Inv. Nr.: NHMW2004z0030/0006). 2 maxillaria dext. 11 maxillaria sin. 11 dentalia dext. 14 dentalia sin. (AO: Inv. Nr.: NHMW2004z0030/0001). 1 vertebra cervicalis (AO: Inv. Nr.: NHMW2004z0030/0002). 554 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0030/0003). 5 vertebrae sacrales. 253 vertebrae caudales (AO: Inv. Nr.: NHMW2004z0030/0004, 0005).
(BM: Inv. Nr.: NHMW2004z0030/0007).

Description:

osteodermale: 842 osteodermalia altogether are oval to rectangular. One third of the outer surface is smooth, while two thirds are covered by a fine sculpture of pits, bulges, and grooves. Lateral and medial osteodermalia bear a median ridge. The inner surface features two medial rows of 2-3 foramina each. Measurements of the ossicula dermalia dorsalia medialia are given in Table 11.

quadratum (fig. 21): The single right quadratum is complete. From posterior aspect, it is 2.31 mm long, and the condylus mandibularis is 0.92 mm broad. The vertical, thin crista tympani runs parallel to the irregularely thickened crista pterygoidea in the medial section. The latter broadens funnel-shaped ventrally, and the condylus cephalicus extremely bends posteriorly. Viewing from anterior, the straight crista pterygoidea features a medial foramen. Epiphysis columnaria and condylus cephalicus are separated by a shallow recess.

maxillare: The 13 maxillaria are either completely or just medially preserved. Their general shape remarkably features a prominent, roundish to nearly quadratic dorsal part lacking any processus praefrontalis and incisura nasalis. Its anterior margin possesses a broad but flat lingual bulge. The cuspid processus zygomaticus is more elongated than the divided and pointed processus praemaxillaris enclosing a deep excavatio nasalis. The margo fenestra exonarina is sickle-shaped. Typically, the thin and lamella-like lamina horizontalis bulged marginally becomes concave medially. The posterior expansion of the lamina horizontalis bears the lentiform orificium canalis nervi alveolaris superioris. Viewing from labial, the round and distinct foramina pro ramis nervi alveolaris superioris range regularly in a row. Relating to the monocuspid teeth, they are widely spaced, shallowly pleurodont, pointed, and curved posteriorly. Completely preserved maxillaria feature 10-11 teeth or tooth positions respectively.

dentale (Plate 5: d): 25 dentalia are present. They are complete, broken posteriorly, or represented by a part of the lamina horizontalis with two or more teeth. The dentalia are slender featuring an irregularly drop-like symphysis. The more prominent and triangular processus coronoideus, the less distinct processus supraangularis, as well as the relatively shortest processus angularis are altogether pointed. Both incisura coronoidea and sinus supraangularis represent cuneiform slits. With regard to the sulcus meckeli, it opens just ventrally on the anterior half. With the beginning of the posterior half, the lamina horizontalis rises abruptly and the sulcus meckeli opens widely. The former features a cusp orientated to posterior at the position of the last but one tooth which encloses the foramen alveolaris anterioris inferioris. From labial aspect, oval foramina pro ramis nervi alveolaris inferioris elongated anteroposteriorly are situated in a medial row. The pleurodont, monocuspid teeth are widely spaced featuring pointed cusps curved to posterior. The height of the posterior ones is reduced. 11 teeth or tooth positions are present on completely preserved dentalia.

vertebra cervicalis (Plate 5: e): The single procoelous vertebra cervicalis is nearly completely preserved. Just the hypapophysis is broken. The short centrum flattened dorsoventrally and widened anteriorly features a sharp ventral keel meeting the broadly inserted hypapophysis. Viewing from anterior, the canalis neuralis is roundish, and the neural arch rises highly. It bears a processus spinosus forming a posterior, high and blunt cusp. Prae- and postzygapophyses are oval and slightly orientated to anterolateral or posterolateral respectively. The longish-oval synapophyses stick out posterolaterally.

vertebra praesacralis (Plate 5: f; Table 11): The larger part of the 554 vertebrae praesacrales is completely preserved.

Their measurements are noted in Table 11. The typically elongated and straight centrum is flattened dorsoventrally. The margines laterales are nearly straight posteriorly and diverge in their anterior half. Two medioventral foramina subcentrales are present. Viewing from lateral, the longish-oval synapophyses are slightly orientated to anteroventral/ posterodorsal. From posterior view, the canalis neuralis is round. From dorsal aspect, the neural arch is remarkably concave laterally. It bears a relatively sharp processus spinosus which ends as a posterior high and blunt cusp. The latter does not overtop the postzygapophyses and serves for an interzygapophyseal articulation. Prae- and postzygapophyses are large, roundish-oval, and inclined to dorsolateral.

vertebra sacralis: 5 vertebrae sacrales are present lacking the distal ends of the processus transversi. They are procoelous featuring a centrum flattened dorsoventrally. The enlarged processus transversi flattened dorsoventrally are divided by a ventral foramen at their base, orientated to posterior and inclined to ventral. From posterior view, the canalis neuralis is round. Viewing from dorsal, the neural arch possesses a processus spinosus leading into a blunt posterior cusp. The prae- and postzygapophyses are roundish-oval orientated to anterolateral or posterolateral respectively and inclined to dorsolateral. One sacrum features the broken bases of the presumed hemapophysis.

vertebra caudalis (Plate 5: g, h): The larger part of the 253 vertebrae caudales is nearly completely preserved just missing the ventral part of the hemapophysis. The fragmentary ones lack their anterior or their posterior parts or the ends of the processus transversi respectively. The centrum flattened dorsoventrally is elongated. Typically, it bears a posterior hemapophysis. Viewing from posterior, the canalis neuralis is round. From dorsal aspect, the neural arch is elongated as well. It features a processus spinosus leading into a posterior blunt cusp which does not overtop the postzygapophyses. The prae- and postzygapophyses are roundish-oval and orientated to anterolateral or posterolateral respectively. With regard to the processus transversi, they are flattened dorsoventrally, horizontal and orientated to anterior. Ventrally, a distinct slit marks the plane of fracture and divides the processus transversus. The anterior part representing just one fourth of the vertebra caudalis bears the much smaller and pointed processus transversi orientated to lateral. ETHERIDGE (1967) specifies this kind of autotomy with the basal separation and distal convergence of the anterior and posterior parts of the split processus.

Comparison: The determination especially of the osteodermalia and the quadratum but also of the other elements is based on comparisons with material of Recent specimens of *Anguis fragilis*. Maxillaria and dentalia correlate to the ones described by RAUSCHER (1992) as *Anguis fragilis*. The vertebrae point to *Anguis fragilis* such as characterized by BAILON (1991).

BAILON (1991) as well has observed the fact of broken bases of the probable hemapophysis on one vertebra shaped as a vertebra sacralis of *Anguis fragilis* (La Combe Grenal in France, Upper Pleistocene). He considered the vertebra as the first vertebra caudalis. As none of the Recent material of *Anguis fragilis* I have studied features a first vertebra caudalis developed that way and due to the typically sacral shape of the centrum and the processus transversi, I account the existence of a hemapophysis on the vertebra sacralis and not on the first vertebra caudalis.

No parietale of *Anguis* is present in the Kohfidisch material which would distinguish *Anguis fragilis* from the extinct *Anguis robustus* (Lower Miocene) described by KLEMBARA (1979). The other elements of the latter are not known. KLEMBARA (1981) himself points to serious similarities of *Anguis robustus* to *Ophisaurus*. *Anguis stammeri* (Upper Pleistocene) possesses more robust teeth, *Anguis acutidentatus* (Middle Miocene) and *Anguis lemanensis* (Upper Oligocene) represent *nomina dubia* (ESTES, 1983). *Anguis polgardiensis* of the Upper Miocene (BOLKAY, 1913) is listed as a synonym of the extant *Pseudopus apodus* (sensu KLEMBARA, 1979) by ESTES (1983).

The Recent situation of *Anguis* features two extant species both in Europe namely *Anguis fragilis* and *Anguis cephallonicus*. *Anguis fragilis* contains the two subspecies *Anguis fragilis fragilis* and *Anguis fragilis colchicus* continuously merging by hybridization. *Anguis cephallonicus* includes the formerly so called subspecies *Anguis fragilis peloponnesiacus* and *Anguis fragilis* var. *cephallonica*. The differentiation between the two species is based on the development of the external ear opening (DELY, 1981; GRILLITSCH & CABELA, 1990), on morphometric data (GRILLITSCH & CABELA, 1990), and on proteinelectrophoretic analysis (MAYER et al., 1991).

Due to the indistinct situation of extinct members of *Anguis* and because the second extant species *Anguis cephallonicus* is endemic to the Peloponnesus where it originated and to the southern Ionian Islands (CABELA, 1997), the description has resulted in *Anguis fragilis*.

Discussion: *Anguis fragilis* is known from the Lower Pliocene of Hungary (VENCZEL, 2001), from the Middle and the Upper Pliocene of France and Spain (BAILON, 1991), from the Lower Pleistocene of Poland (SZYNDLAR, 1981) and Rumania (BOLKAY, 1913), and from the Middle and the Upper Pleistocene of France (BAILON, 1991) and Spain (SANCHIZ, 1980). In Austria, RAUSCHER (1992) has described *Anguis fragilis* from the Plio-Pleistocene locality Bad Deutsch-Altenburg. The Upper Miocene record of *Anguis fragilis* from Kohfidisch represents the stratigraphically oldest one.

The Lower and Upper Pliocene of Poland (MŁYNARSKI, 1962, 1964; MŁYNARSKI et al., 1984) yields *Anguis* cf. *fragilis* as well as the Lower and Middle Pleistocene of France (CLOT et al., 1976) and Poland (MŁYNARSKI, 1977).

The oldest record of cf. *Anguis* in Europe dates from the Lower Eocene of France (AUGÉ et al., 1997). Therefore, the Upper Oligocene origin of the lineage of *Anguis* so expected by KLEMBARA (1981) has to be older.

Following RAGE (1997), the Anguidae dating from the Upper Cretaceous were probably of Laurasian origin and display affinities with those known from North America. Palaeocene localities from Europe lack Anguidae which may very probably be an artefact of fossilization because although Europe was isolated from North America and due to the Turgai Straits still from Asia during the Eocene, Anguidae are back in the Eocene European fossil record.

Ecology and Climate – living relatives: *Anguis fragilis* prefers well vegetated habitats with extensive ground cover and rather damp situations. It occurs in pastures, glades in woods, in lush scrub-land, on heaths, hedge-banks, and railway embankments. *Anguis fragilis* represents an usually slow-moving and secretive animal which may occasionally bask openly in sun but normally lies beneath sun-warmed objects such as stones or beneath vegetation (Arnold & Ovenden, 2002). It hibernates in frost-protected places together with other reptiles and amphibians.

The Recent distribution of *Anguis fragilis* extends almost over the whole mainland of Europe except South Iberia, South Greece, most Mediterranean islands, Ireland, or the extreme north. It occurs east to West Siberia, Caucasus, North Asiatic Turkey and North-West Iran. (Arnold & Ovenden, 2002). Following Müller (1996; see chapters 5, 6), this distribution belongs to the Köppen's climate types Cf, Cs, and Df.

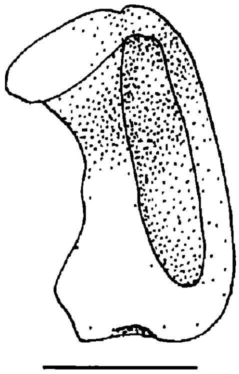


Figure 21: *Anguis fragilis*. Quadratum dext. posterior view (Kohfidisch "I" ; Inv. Nr. NHMW2004z0030/0006).

Genus *Pseudopus* Merrem, 1820

Pseudopus pannonicus **(Kormos, 1911)**

(Plate 6: a-h, 7: a-d; Table 2, 3, 4, 5, 6, 11)

Synonyms:

1977 *Ophisaurus pannonicus*. – Bachmayer & Młynarski, p. 289, Tafel 1: Figs. 3, 5, 7; Tafel 2: Figs. 12 – 14; Tafel 4: fig. 23.

Neotype: Hungarian Geological Institute, Budapest, Hungary; mandibulare.

Type locality: Polgardi 2, Hungary.

Stratigraphical Age of the Type material: Upper Miocene (Turolian, MN13).

Range: Upper Miocene – Pleistocene: Austria, Czech Republic, Hungary, Poland, Rumania, South-West Russia.

Material: 11276 osteodermalia (AO: Inv. Nr.: NHMW 2004z0031/0008). 4 frontalia dext. 6 frontalia sin. 34 parietalia et fragmenta parietalium (AO: Inv. Nr.: NHMW2004z0031/0001). 1 palatinum dext. (AO: Inv. Nr.: NHMW2004z0031/0002). 1 palatinum sin. 3 pterygoidea dext. 4 pterygoidea sin. 5 praemaxillaria (AO: Inv. Nr.: NHMW2004z0031/0003). 7 maxillaria dext. 15 maxillaria sin. (AO: Inv. Nr.: NHMW2004z 0031/0004). 13 maxillaria indet. 17 dentalia dext. (AO: Inv. Nr.: NHMW2004z0031/0005). 14 dentalia sin.140 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0031/0006). 3 vertebrae sacrales. 283 vertebrae caudales (AO: Inv. Nr.: NHMW2004z0031/0007).

(BM: Inv. Nr.: NHMW2004z0031/0009).

Description:

osteodermale (Plate 7: d): 11276 osteodermalia are recorded. Information about the size of the ossicula dermalia dorsalia medialia is given in Table 11. Each development of the ossicula dermalia medialia (trapezoidal), the ossicula dermalia lateralia (rectangular), the ossicula dermalia dorsalia of the side groove (oval), as well as the ossicula dermalia ventralia of the side groove (longish-oval) is present. The osteodermalia are robust and thick. At about two thirds of their outer surface feature a bulging dermal sculpture with pits which may be divided by a median keel extended on the non-sculptured third. The inner surface is slightly undulated and possesses 2-5 foramina arranged squared or triangular respectively.

frontale: Four right and six left fragmentary but robust and thick frontalia are present. Three frontalia feature the anterior part lacking the end of the processus descendens medialis, five remains represent the posterior part, and two medial pieces are preserved. The single anterior part possesses a margo nasalis anterior orientated to posterolateral and a margo nasalis posterior. While the sutura medialis is straight, the margo praefrontalis together with the margo postfrontorbitalis are slightly concave. From dorsal view, the frontale features a dermal sculpture similar to the one of the osteodermalia and composed of thick tubercles and small pits. Peripherally, the ridges become more parallel and are directed to lateral. Just the lobus parietalis lacks that sculpture. Viewing from ventral, the irregularly high crista cranii features ridges and furrows. Thin and indistinct, parallel ridges on the facies sphenoidalis are directed to lateral.

parietale et fragmentum parietalis (Plate 6: a, b): The 34 parietalia et fragmenta parietalium feature each state of preservation. 9 elements are nearly completely preserved. The parietalia are unpaired, very robust, thick, and broad. Viewing from dorsal, they possess a typical, nearly quadratic table with a thick, dermal sculpture consisting of pits and tubercles. Peripherally, the tubercles become parallel ridges orientated to radial. The field of dermal sculpture bears a medial, round and distinct foramen parietale. The latter is situated shortly anterior to the crosspoint of the sulci interparietales and the sulci occipitales. The processus fronto-postfrontales and the areae frontales are not sculptured but covered by thin and close, parallel ridges. The bases of the long and pointed processus parotici are very broad and separated by a half-round margo supraoccipitalis. Their common base is unsculptured as well. Ventrally, the rami posteriores cristae cranii parietalis are distinct and high but rounded contrary to the sharp and higher rami anteriores cristae cranii parietalis. The latter are highest at the position of the lateral constriction of the parietale where the processus parotici insert. The crista postfovealis is low but still well-developed enclosing the half-oval fossa parietalis.

palatinum (Plate 6: c): The processus jugalomaxillaris, the processus maxillaris, the processus vomerinus, as well as the posterior end of the processus pterygoideus are broken on the two remains of palatina. The elements are robust and thick. Dorsally, three well-developed, roundish to oval foramina mediales are arranged in a row orientated to anteromedial/posterolateral. From ventral aspect, three rows of massive, blunt dentes palatini are present. The outer row features the biggest teeth while the medial row consists of smaller but more teeth. Containing just two to three moderately big teeth, the inner row is the shortest. Altogether, 17-18 dentes palatini exist. The area pterygoidea is steep, and the sulcus palatinus represents a shallow depression.

pterygoideum: One of the 7 pterygoidea is nearly completely preserved. Just the anterior ends of the processus palatinus and the processus transversus are missing. The element is Y-shaped and 2,62 mm long measured from its most anterior to its most posterior points. The other remains feature broken processus quadrati, processus transversi, and/or processus palatini. The elongated processus quadratus is flattened laterally. Dorsally, two round foramina are well-developed. One is situated at the constriction between the processus quadratus and the two anterior processus, and the second is located more anteriorly. From ventral aspect, the processus basisphenoideus forming an angle of about 45° with the processus quadratus ends in a blunt cusp. While the processus transversus is triangular from anterior view, the expanded processus palatinus is flattened dorsoventrally. The latter bears the large area palatina elongated anteroposteriorly which features about 6 tooth rows with blunt and conical dentes pterygoidei. The inner two rows contain the most numerous teeth (~ 20 each). Altogether, about 60 teeth are present. The tuberculum contracoronoideum is indistinct and blunt. Not only the crista transversa ventralis but also the crista transversa dorsalis are well-developed.

praemaxillare (Plate 6: d): One of the five praemaxillaria is completely preserved. The others consist of the broken crista dentalis with teeth and the ventral rest of the processus nasalis. The praemaxillare represents an extremely massive element. With regard to the processus nasalis, its ventral, triangular cross section becomes flattened dorsoventrally in its dorsal section. It is hyperbola-like shaped. Viewing from labial, an indistinct dermal sculpture consisting of very shallow, large grooves is observable on the dorsal third. From lingual aspect, parallel ridges orientated to dorsoventral are present on the dorsal part. The triangular spatium interosseum processus nasalis opens dorsally. The two lobes of the spinae praemaxillares are orientated to lateral. About 5-6 pleurodont and monocuspid teeth are present which are altogether massive, long and blunt. They dilate ventrally, may feature striated cusps, and are arranged with interspace.

maxillare (Plate 6: e, f): The 35 maxillaria feature each state of preservation. Five of them are nearly complete. Viewing from labial, the high processus praefrontalis is nearly rectangular except for the dorsal margin arising posteriorly. A dermal sculpture, the "crusta calcarea" sensu FEJÉRVÁRY-LÁNGH (1923) consisting of ridges and grooves, is present on the posterior triangle of the rectangular processus praefrontalis. The anterior and the posterior oval foramina maxillaria pro ramis nervi alveolaris superioris are elongated anteroposteriorly. In between, they are round. While the processus praemaxillaris exterior is well-developed, long and cusp-like, the processus praemaxillaris interior is reduced. At their base, they are separated by the triangular impressio internasalis. The processus zygomaticus is elongated. From lingual view, one of the processus nasales features fine ridges orientated to posterodorsal. While the anterior lamina horizontalis is concave, the posterior one is convex. The pleurodont, monocuspid, amblyodont, and closely spaced teeth become bigger medially. Their bases broaden medially as well. About 16 teeth are present, the 10th is the biggest one.

dentale (Plate 6: g, h): Due to their robustness, 12 of the 31 dentalia are completely preserved. The dorsal processus supraangularis represents the most distinct one, and the narrow sinus supraangularis incises it deeply. The kidney-like symphysis opens to the sucus meckeli which opens ventrolingually as far as the 8th tooth position. At the 9th tooth position, the lamina horizontalis rises steeply and the sulcus meckeli opens widely. The spina splenialis of the lamina horizontalis is located below the 9th tooth position and the orificium canalis nervi alveolaris inferioris opens deeply below the 12th tooth position approximately which may vary. The orificium canalis nervi alveolaris inferioris represents the apex of a triangular depression within the sulcus meckeli. The depression features weak, curved grooves orientated longitudinally. From labial aspect, 6-7 foramina pro ramis nervi alveolaris inferioris are present. With regard to the teeth, they are pleurodont, monocuspid, blunt, and closely spaced. Their cusps dilate and may be striated. The anterior teeth are narrower, they enlarge medially and grow smaller posteriorly.

vertebra praesacralis (Plate 7: a, b; Table 11): The 140 vertebrae praesacrales are either complete or fragmentary. Their measurements are listed in Table 11. The procoelous centrum is flattened dorsoventrally and triangular pointing to posterior except for the vertebrae V11-V15 which possess parallel lateral margins of the centrum. Vertebrae V6-V10 feature a ventral, median keel, and the vertebrae V30-V49 possess two parallel, lateral and longitudinal grooves. Ventrally, two small foramina subcentrales located in the anterior half are present on some vertebrae. From anterior aspect, the canalis neuralis is half-round to triangular and flat. Viewing from dorsal, the neural arch features a median constriction. Anteriorly, the distinct and sharp processus spinosus forms a triangular processus from lateral view which becomes concave more posteriorly. The posterior half of the processus spinosus rises highly and becomes rhomboid-shaped and inclined to posterior ("epiphysis processus spinosi" sensu FEJÉRVÁRY-LÁNGH, 1923). The rectangular praezygapophyses are orientated to lateral while the rectangular postzygapophyses are directed to posterolateral. Both rise laterally. Relating to the synapophyses, they are oval and orientated to anteroventral/posterodorsal.

vertebra sacralis: One vertebra sacralis lacks the lateral ends of the processus transversi. The two others are represented by the centrum and the right processus transversus lacking its very end. Compared to the other vertebrae, the vertebrae sacrales are extremely massive. Cotyle and condyle are roundish-oval. The centrum features a relatively broad and distinct median keel ("margo inferior centri" sensu FEJÉRVÁRY-LÁNGH, 1923) accompanied by the two lateral, kidney-like sulci gemelli inferiores which contain a total of three round foramina. The bases of the processus transversi insert broadly on the whole length of the centrum. The preserved processus transversi are flattened dorsoventrally and orientated to posterior. From anterior aspect, the canalis neuralis is flat half-round. Viewing from dorsal, the neural arch appears constricted medially, short and massive. The rectangular prae- and postzygapophyses are orientated to dorsolateral. The processus spinosus forms a posterior cusp whose end is broken ("epiphysis processus spinosi" sensu FEJÉRVÁRY-LÁNGH, 1923).

vertebra caudalis (Plate 7: c): 283 vertebrae caudales are present which are either complete or feature each state of fragmentation. Just one hemapophysis is closed ventrally. The others altogether are broken at their base. The elongated centrum is flattened dorsoventrally possessing slightly concave lateral margins. The two distinct, longitudinal cristae inferiores are separated by the sulcus medialis enclosing numerous, small and round foramina. Posteriorly, the former pass between the bases of the hemapophyses. From anterior view, the canalis neuralis is flat-oval. Viewing from dorsal, the processus spinosus ends as a posterior, high and slender cusp ("epiphysis processus spinosi" sensu FEJÉRVÁRY-LÁNGH, 1923) which overtops the oval-rectangular postzygapophyses orientated to dorsolateral. Anteriorly, the rectangular praezygapophyses orientated to anterolateral and inclined to dorsolateral represent the continuation of a boomerang-like depression. The posterior top of this depression is marked by a cuspid pike. The slender processus transversi flattened dorsoventrally insert far anteriorly. Ventrally as well as dorsally, they feature a narrow, transversal slit at their base as division. They are cusp-like and orientated to anterior. A plane of fracture is absent. After ETHERIDGE (1967), no plane of fracture is present in *Pseudopus apodus* (sensu KLEMBARA, 1979), the closest, extant relative to *Pseudopus pannonicus*. Its tail does not appear to be fragile.

Comparison: The osteodermalia, the frontalia, the parietalia, the palatina, the pterygoidea, the praemaxillaria, the maxillaria, the dentalia, and the vertebrae described herein correspond to the ones determined as *Pseudopus pannonicus* ("*Ophisaurus*" *pannonicus*) by FEJÉRVÁRY-LÁNGH (1923).

The osteodermalia as well as the vertebrae praesacrales of Kohfidisch are sized similarly to the ones described by FEJÉRVÁRY-LÁNGH (1923) from the Upper Miocene (MN13) locality Polgárdi 3 in Hungary. This applies to *Pseudopus pannonicus* of Götzendorf, too.

As an additional extinct species of *Pseudopus*, *Pseudopus moguntinus* differs from *Pseudopus pannonicus* in its smaller size. Although the skull elements are relatively similarly sized, the postcranial elements and especially the osteodermalia and the vertebrae of *Pseudopus pannonicus* are remarkably more massive and bigger. Osteodermalia as thick as the ones of *Pseudopus pannonicus* just appear in this species only representing the biggest Glass Lizard which ever existed.

Pseudopus laurillardi, the third extinct representative of *Pseudopus*, is smaller than *Pseudopus pannonicus* and even than *Pseudopus moguntinus*. As diagnostic difference to *Pseudopus pannonicus* and *Pseudopus apodus*, the processus praefrontalis of its parietale is larger developed. While *Pseudopus laurillardi* reached a presumptive length of 100 cm (AUGÉ & RAGE, 2000), *Pseudopus moguntinus* one of 140 cm, and the extant representative *Pseudopus apodus* actually measures up to 120 cm, *Pseudopus pannonicus* supposably was even 200 cm long (FEJÉRVÁRY-LÁNGH, 1923).

Keeping these considerations in mind, the determination of the elements has resulted in *Pseudopus pannonicus*.

Discussion: The oldest remains of *Pseudopus pannonicus* so far dated from the Upper Miocene of Austria (Vösendorf, MN9: PAPP & THENIUS, 1954; Richardhof-Golfplatz, MN9: HARZHAUSER & TEMPFER, 2004; Götzendorf, MN9: BACHMAYER & MŁYNARSKI, 1977; Eichkogel, MN11: THENIUS, 1952) and the Ukraine (ESTES, 1983). Therefore, *Pseudopus pannonicus* of Kohfidisch ranks among the oldest records. It has been described from the Upper Miocene (FEJÉRVÁRY-LÁNGH, 1923) and the Pliocene of Hungary (VENCZEL, 2001), Czech Republic (FEJFAR, 1961), Poland (MŁYNARSKI, 1960, 1962, 1964; MŁYNARSKI et al., 1984), and France (BAILON, 1991). The Plio-Pleistocene of Austria (Bad Deutsch-Altenburg: RAUSCHER, 1992), and the Pleistocene of Hungary (KRETZOI, 1956), Poland (MŁYNARSKI, 1962), Rumania (ESTES, 1983), and France (BAILON, 1991) yield the species.

During the European Tertiary, three different species of the genus *Pseudopus* existed:

- *Pseudopus moguntinus* (BOETTGER, 1875) (synonymous with *Ophisaurus moguntinus* BOETTGER, 1875, *Propseudopus fraasi* HILGENDORF, 1883 and *Ophisaurus ulmensis* GERHARDT, 1903) known from the Upper Oligocene till the Upper Miocene of Germany, Poland (Middle Miocene, Upper Miocene: MŁYNARSKI, 1984; Middle Miocene: MŁYNARSKI et al., 1984), Czech Republic, and France (KLEMBARA, 1981),
- *Pseudopus laurillardi* (LARTET, 1851) (synonymous with *Anguis* ? *laurillardi* LARTET, 1851 and *Ophisaurus* ? *laurillardi, nomen dubium* (ESTES, 1983)) from the Middle Miocene (MN6) of Sansan in France (AUGÉ & RAGE, 2000) and
- *Pseudopus pannonicus* (KORMOS, 1911) (synonymous with *Ophisaurus pannonicus* KORMOS, 1911). The latter is younger ranging from the Upper Miocene up to the Pleistocene.

The species *Pseudopus moguntinus* is regarded as characteristic of the older localities. Following FEJÉRVÁRY-LÁNGH (1923) and MŁYNARSKI (1962), the series *Pseudopus moguntinus - Pseudopus pannonicus Pseudopus apodus* might be a phyletic one.

MŁYNARSKI et al. (1984) also suggest *Pseudopus pannonicus* as ancestor to *Pseudopus apodus.* The only significant difference of size could have resulted from fluctuating climatic conditions in particular stages of the Plio-Pleistocene. Moreover, they point to the possibility of the synonymy of the two species but also know about insufficient evidences.

As the single difference between the following three species is represented by their different size, I would synonymize *Pseudopus moguntinus* and *Pseudopus pannonicus* with *Pseudopus apodus* such as ESTES (1983) and MŁYNARSKI et al. (1984) proposed. The increasing paleontological record of the extinct representatives will give more information about their relation.

Pseudopus laurillardi cannot be osteologically discriminated from *Pseudopus moguntinus.* If the two species became synonymous, the term *Pseudopus laurillardi* would have priority to *Pseudopus moguntinus* (AUGÉ & RAGE, 2000).

KLEMBARA (1979, 1981) noted the difference between the two taxa *Pseudopus* and *Ophisaurus* (s. str.) based on very evident characteristics ("anguis-signs") on the parietale. The "anguis-signs" consist of a group of characteristics in the posterior part of the ventral parietale and of the fossa parietalis in particular. Together with *Ophisaurus*, members of the genus *Anguis* possess the "anguis-sign" which is absent at *Pseudopus.* Furthermore, the typical shape of the teeth distinguishes *Pseudopus* from *Ophisaurus.* While members of the genus *Pseudopus* typically possess robust, amblyodont (sensu FEJÉRVÁRY-LÁNGH, 1923) and closely spaced teeth, *Ophisaurus* features conical teeth curved to posterior. Finally, very reduced but present hind limbs are characteristic of *Pseudopus* and not of *Ophisaurus.* KLEMBARA (1979) resurrected the genus *Pseudopus* for the reception of the species *Ophisaurus apodus*, *Ophisaurus pannonicus* and *Ophisaurus moguntinus.*

KLEMBARA (1979) points out the existence of the two genera *Ophisaurus* and *Pseudopus* as two different evolution 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 the more gracile members of the genus *Ophisaurus* crossing the Bering Strait reached America. The oldest representative, *Ophisaurus canadensis*, dates from the Upper Miocene of Canada.

In contrast, SULLIVAN (1987) states the geographical restriction of the two taxa *Ophisaurus* and *Parophisaurus* (s. str.) to the New World different from fossil and recent "anguine" taxa assigned to *Ophisaurus* from various regions of the Old World. 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. SULLIVAN et al. (1999) affirm the restriction of the genus *Ophisaurus* to North America. They refer the Old World fossil lizards previously described as *Ophisaurus* to the either *Ophisauriscus-Anguis* or *Pseudopus* lineages.

Ecology and Climate – living relatives: As Recent relative, *Pseudopus apodus* (*Ophisaurus apodus*) needs habitats with dense vegetation not only in valleys but also in wooded hills and mountains up to 2100 m. It prefers spinose crevices, vineyards, and gardens with the opportunity to hide in burrows or stone piles. The European Glass Lizard represents a diurnal animal often active after rain which prefers a temperature ranging between 20°C and 26°C. For hibernation, it rests deeply burrowed into the soil (PETZOLD, 1971).

Following ARNOLD & OVENDEN (2002), *Pseudopus apodus* (*Ophisaurus apodus*) is restricted to the Balkans as far north as North-West Croatia, North Greece, South Macedonia and South and East Bulgaria. It also inhabits the Crimea, the Caucasus, and parts of South-West and Central Asia. That area of distribution mainly belongs to the Köppen's climate type Cs (MÜLLER, 1996; see chapters 5, 6).

Superfamily Varanoidea GRAY, 1827
Family Varanidae GRAY, 1827

Genus *Varanus* MERREM, 1820

Varanus cf. *hofmanni* ROGER, 1898

(Plate 7: e-g, 8: a-e; Table 2, 3, 4, 5, 6, 11)

Holotype: Bayerische Staatssammlung für Paläontologie und Historische Geologie(?), München, Germany; vertebrae.

Type locality: Statzling (Dinotheriensande), Germany.

Stratigraphical Age of the Type material: Middle Miocene (Astaracian, MN6).

Range: Middle – Upper Miocene: Austria, Germany, France, Spain.

Material: 2 dentalia dext. (AO: Inv. Nr.: NHMW 2004 z0032/0003). 4 dentalia sin. 5 dentes (AO: Inv. Nr.: NHMW2004z0032/0001, 0002). 3 vertebrae cervicales (AO: Inv.Nr.: NHMW2004z0032/0005). 38 vertebrae praesacrales (AO: Inv.Nr.: NHMW2004 z0032/0004). 26 vertebrae caudales (AO: Inv. Nr.: NHMW 2004z0032/0006).

(BM: Inv. Nr.: NHMW2004z0032/0007).

Description:

dentale (Plate 7: e-g): 4 dentalia are represented by one tooth and the adjoining piece of the ventral dentale. One right and one left dentale are more complete featuring one complete and one broken tooth. The most complete dentale is 11 mm high measured from the dorsal to the ventral margin. Its tooth lacking just the cusp measures 8 mm height. It represents the posterior part where the lamina horizontalis rises dorsally and the sulcus meckeli opens more widely. In the anterior part, it opens ventrally. Concerning the lamina horizontalis, it expands as a relatively sharp lamella orientated to ventrolingual and concave dorsally. Anterior to its rising part, it is convex lingually from dorsal view while the rising lamina horizontalis is concave. A sulcus dentalis does not exist. Viewing from labial, rather small and longish-oval foramina pro ramis nervi alveolaris inferioris are situated in a slit-like depression. The subpleurodont teeth are conical, inclined to posterior and flattened labiolingually featuring a sharp leading and trailing edge. Some edges are slightly serrate. Their dilated bases are distinctly striated (due to plicidentine, BULLET, 1942) while the teeth themselves feature closer and shallower stripes. About three deep furrows (two labial and one lingual furrow) may be present. A small, medial foramen marks each tooth base ventrally. From anterior aspect, the teeth are slightly inclined to lingual.

vertebra cervicalis (Plate 8: c, d): While one vertebra cervicalis is complete, one lacks only the posterior neural arch. One remain represents the posterior neural arch. The procoelous centrum is more elongated and more flattened dorsoventrally than the one of a vertebra praesacralis. It is distinctly constricted anterior to the condylus. From ventral view, two foramina subcentrales located anteriorly are present which are not arranged in a transversal line but irregularly. The massive hypapophysis becomes high and drop-like in the posterior half. It possesses two lateral epiphyses on its posterior lobes. Viewing from lateral, the posterior part of the hypapophysis is rhomboid-shaped and inclined to posterior. The parapophyses are orientated to anteromedial/posterolateral from ventral aspect, and the diapophyses to anteroventral/posterodorsal from lateral view. They strongly project laterally. Looking from anterior, the canalis neuralis is regularly triangular. From dorsal view, the elongated neural arch is constricted medially bearing a sharp processus spinosus which rises highly in the posterior two thirds. Laterally viewed, the risen processus spinosus is rhomboid-shaped and inclined to posterior. It does not overtop the postzygapophyses. Viewing from posterior, a medial, vertical, and thin ridge marks the risen and thickened posterior aspect of the processus spinosus. The latter, together with the praezygapophyses, are longish-oval and well-inclined to dorsal.

vertebra praesacralis (Plate 8: a, b; Table 11): 38 vertebrae praesacrales are present which altogether are nearly complete due to their high robustness. The neural arch may be broken. Their measurements are given in Table 11. The procoelous centrum is shorter than the one of a vertebra cervicalis, triangular with concave lateral margins, and flattened dorsoventrally. A distinct constriction anterior to the condylus is present. The two indistinct foramina subcentrales situated anteriorly are arranged in a transversal line. From lateral view, the synapophyses are orientated to anteroventral/posterodorsal. Viewing from anterior, the triangular canalis neuralis is more flattened than the one of a vertebra cervicalis. From dorsal aspect, the neural arch is constricted in the posterior half. Similar to a vertebra cervicalis, the processus spinosus rises highly posteriorly and is rhomboid-shaped from lateral view. The risen processus spinosus is inclined to posterior, does not overtop the postzygapophyses and lacks the posterior ridge present at a vertebra cervicalis. Prae- and postzygapophyses are oval, orientated to anterolateral or posterolateral respectively, and inclined to dorsal. An essential characteristic is present on the dorsal neural arch: The praezygapophyses grade into the well-developed, triangular pars tectiformis the apex of which reaches the posterior fourth of the processus spinosus.

vertebra caudalis (Plate 8: e): Each of the 26 vertebrae caudales features broken hemapophyses as well as broken processus transversi. The procoelous centrum is completely preserved in either case, and 11 remains possess the neural arch. The centrum is elongated and broader than the one of a vertebra cervicalis. Its lateral margins are concave. While the cotyle is roundish-oval, the condyle is more flattened dorsoventrally. Viewing from ventral, two parallel ridges pass from the cotyle to the bases of the hemapophyses located posteriorly and inclined to posterior. The insertions of the processus transversi flattened dorsoventrally and slightly inclined to ventral are situated more anteriorly. From anterior aspect, the triangular canalis neuralis is flattened. Looking from dorsal, the elongated neural arch is constricted posteriorly. While the praezygapophyses are oval and orientated to anterolateral, the postzygapophyses are nearly round. Both are inclined to dorsal. The processus spinosus extremely rises and elongates in the posterior half. A spine flattened laterally, inclined to posterior and as long as the vertebra caudalis overtops the centrum. Similar to a vertebra praesacralis, the praezygapophyses pass into a distinct, triangular depression the apex of which leads into the processus spinosus. The vertebrae caudales of Varanidae never have planes of fracture (ETHERIDGE, 1967).

Comparison: The dentalia and the dentes are typical of a member of the Varanidae based on comparisons with material of Recent representatives as well as published by BULLET (1942), ESTES et al. (1988), MERTENS (1942), and RIEPPEL & LABHARDT (1979).

With regard to the vertebrae cervicales and the vertebrae caudales, they correspond to the ones of Recent members of the Varanidae and to the definition given by HOFFSTETTER & GACS (1969).

ROGER (1898), as primary describer, discusses the vertebrae praesacrales of *Varanus hofmanni* and figures them in a following publication (ROGER, 1900). HOFFSTETTER (1969) declares the triangular and deep depression of the neural arch as characteristic of *Varanus hofmanni*.

Due to the characteristics of the vertebrae praesacrales typical of *Varanus hofmanni*, but considering ZEROVA & CKHIKVADZE (1986), who correlated the typical characteristics of *Varanus hofmanni* with *Varanus tyrasiensis*, *Varanus pronini*, *Varanus semjonovi*, and *Varanus lungui* of the Ukraine I was not able to study, the description of the elements has resulted in *Varanus* cf. *hofmanni*.

The vertebra praesacralis determined by HOFFSTETTER (1969) as *Varanus* cf. *hofmanni*, is sized similarly as the largest vertebrae of Kohfidisch. Following HOFFSTETTER (1969), the expected total length (with tail) of the animal ranges between 1 m and 1.60 m. *Varanus hofmanni* of Kohfidisch might have been similarly long.

Comparisons with the skeleton of the Recent *Varanus prasinus* which is arboreal have generally pointed out more slenderness and a smaller size of the Recent relative. The dentale is more slender, less massive, and the lamina horizontalis less expanded ventrolingually. The teeth seem to insert more subpleurodontally. They are similarly shaped but weak, smaller, and less curved to posterior. *Varanus prasinus* feeds on insects and small mammals. Due to the similarly shaped teeth of the Recent species and *Varanus* cf. *hofmanni*, the prey of the latter might correlate. Merely, *Varanus* cf. *hofmanni* was very probably able to feed on larger mammals, because of its bigger size and the robustness of its teeth.

The vertebrae of the Recent *Varanus prasinus* are more gracile and do not feature the distinct triangular depression of the neural arch. The processus spinosus inserts farther anteriorly at the level of the cotyle (also see HOOIJER, 1972). In the elements described herein, it inserts slightly posterior the cotyle. The examined specimen of *Varanus prasinus* featured a body length (without tail) of 26 cm. The elements of *Varanus* cf. *hofmanni* are twice as big approximately. Therefore, the probable body length without tail of the fossil species results in 52 cm and in 1 m to 1.60 m with tail.

Discussion: *Varanus hofmanni* first described by ROGER (1898) and figured by ROGER (1900) dates from the Middle Miocene of Stätzling in Germany. In 1969, HOFFSTETTER reported the oldest record of *Varanus* in Europe, that is *Varanus* cf. *hofmanni* of the Lower Miocene of Artenay in France. Further, he describes *Varanus* cf. *hofmanni* from the Middle Miocene of France and the Upper Miocene of Spain. Thus, *Varanus* cf. *hofmanni* of Kohfidisch ranks among the youngest records of the species.

The oldest record of *Varanus* sp. dates from the Lower Miocene of Kenya (CLOS, 1995) and Namibia (RAGE, 2003b), and the oldest members of the Varanidae have been described from the Upper Cretaceous of America (*Palaeosaniwa canadensis*; ESTES, 1983) and Mongolia (*Telmasaurus grangeri*; BORSUK-BIALYNICKA, 1991). Following NORRELL et al. (1992), the Varanidae arose in Laurasia and subsequently dispersed to Africa and Australia.

Today, the family of the Varanidae just includes the two genera *Varanus* and *Lanthanotus* (PREGILL et al., 1986) contrary to the fossil representatives belonging to the genera *Varanus*, *Iberovaranus*, *Megalania*, *Palaeosaniwa*, *Saniwa*, and *Telmasaurus*. The relations and taxonomy of Recent members of the Varanidae are still discussed. Based not only on molecularbiological methods including protein-, DNA-, and chromosome-analyses, but also on morphological and behavioural studies, different theories of the systematics of the Varanidae summarized by BENNET (1996) exist.

Ecology and Climate – living relatives: Recent members of the Varanidae have captured nearly each kind of habitat. They are present not only in sandy deserts, gramineous steppes and savannahs, but also in tropical rainforests. Even rivers, lakes, and estuaries may be inhabitat. Following their special living spaces, the Monitor Lizards can be divided into four groups with smooth transitions consisting of aquatic, terrestrial, saxicolous and/or arboreal representatives. The different way of life reflects in different morphological structures as regards the tail and the scales (EIDENMÜLLER, 1997).

Monitor Lizards occur in the tropical and subtropical climes of Africa, Asia Minor, South and South-East Asia, Australia, as well as the Indo-Australian island world. In Australia, they are most prevalent (EIDENMÜLLER, 1997). Following MÜLLER (1996; see chapters 5, 6), that area of distribution mainly belongs to the Köppen's climate types Af, Aw, BS, BSh, BWh, Cf, Cs, Csa, and Cw.

Lacertilia indet.

(Table 2, 3)

Material: 8 maxillaria indet. 6 dentalia indet. 11 ungues. (BM: Inv. Nr.: NHMW2004z0033/0001).

Description and Comparison: The highly fragmentary 8 maxillaria as well as 6 dentalia either do not bear any teeth or only broken ones. Typical characteristics for a more detailed determination than Lacertilia indet. are missing. The 11 ungues allow the correlation with Lacertilia indet. because in general, they are not indicative of a more precise declaration.

Suborder Serpentes LINNAEUS, 1758
Infraorder Scolecophidia DUMÉRIL & BIBRON, 1844
Family Typhlopidae GRAY, 1825

Genus *Typhlops* OPPEL, 1811

Typhlops cf. *grivensis* HOFFSTETTER, 1946

(Plate 9: a; Table 2, 3, 4, 5, 6, 12 ; fig. 22)

Syntype: *Typhlops grivensis* HOFFSTETTER, 1946
Muséum National d'Histoire Naturelle, Paris, France, n° LGA 53, 54, 55 ; three vertebrae praesacrales.
Type locality: La-Grive-Saint-Alban, Isère, France.

Stratigraphical Age of the Type material: Middle Miocene (Astaracian).

Range: Middle Miocene – Upper Miocene: France, Austria.

Upper Miocene of Kohfidisch: LOD (= last occurrence date).

Material: 27 vertebrae praesacrales (AO: Inv. Nr.: NHMW 2004z0034/0001). 4 vertebrae caudales copulatae (=1 "os coccygis"; AO: Inv. Nr.: NHMW2004z0034/0002). (BM: Inv. Nr.: NHMW2004z0034/0003).

Description:

vertebra praesacralis (Plate 9: a; Table 12): Each centrum of the 27 vertebrae praesacrales is preserved. One vertebra praesacralis is complete, 23 elements are just slightly damaged, and three single centra are present. With regard to the measurements, they are given in Table 12. The procoelous centrum is flattened dorsoventrally and twice as wide as high. It features parallel lateral margins. No haemal keel is present. While the cotylus faces slightly ventrally, the condylus is orientated to dorsal. Ventrally, two foramina, a single lateral or a single medial one, may be present in the anterior half (serving for branches of the vertebral artery;

Mookerjee & Das, 1933). Their size differs even on the same centrum. The rounded synapophyses orientated to anteroventral/posterodorsal and separated from the centrum by a deep groove may be kidney-like (concave anteriorly). In anterior view, the canalis neuralis is half-oval. Viewing from dorsal, the neural arch lacks any processus spinosus, just two vertebrae feature an indistinct shallow ridge typical of the anterior part of the vertebral column (Hoffstetter, 1946b). Zygantrum and zygosphene are clearly developed and oval-shaped. The latter is trilobate from above. The longish-oval prae- and postzygapophyses either extend longitudinally or are orientated to anterolateral or posterolateral respectively. A long praezygapophyseal process is present. The prae- and postzygapophyses of the anterior vertebrae praesacrales featuring an indistinct shallow ridge on the neural arch are rounder.

vertebrae caudales copulatae ("os coccygis"; fig. 22): The single "os coccygis" consists of 4 vertebrae caudales. It is 1.21 mm long, 0.5 mm high and 0.46 mm wide in cross section, slightly depressed laterally and indistinctly curved ventrally. Reduced centra, processus transversi and open haemal arches are present. The canalis neuralis is half-oval from anterior view. A terminal foramen passes into a posterior, narrow slit which extends mediodorsally. At the position of the terminal foramen, Recent representatives feature a prick maximally as long as the os coccygis.

Comparison: The vertebrae praesacrales feature characteristics typical of *Typhlops grivensis* first described by Hoffstetter (1946b) from France. *Typhlops grivensis* differs from the second fossil species, *Typhlops cariei*, in its flatter and more elongated shape (Hoffstetter, 1946b). The author points to morphological similarities with the Recent species *Typhlops diardi* and *Typhlops braminus* but distinguishes *Typhlops grivensis* by its smaller size. He appreciates the grave morphological similarities between the vertebrae of members of the Typhlopidae and therefore justifies his description also with the fossil age and the geographical position.

Compared with a skeleton of the Recent species *Typhlops vermicularis*, the vertebrae praesacrales of *T. grivensis* feature a condylus which faces more dorsally. Therefore, it appears more waved in lateral view. Additionally, the neural arch rises higher posteriorly. The size of the vertebrae is similar. As the prepared specimen of *Typhlops vermicularis* featured a total length of 185 mm, a similar length can be expected for the fossil species.

The fused vertebrae caudales reminiscent of the os coccygis of frogs correlate to the ones of the Recent Typhlopidae discussed by List (1966) and observed personally. Keeping the description of Hoffstetter (1946b) in mind, accounting the affiliation of the os coccygis to Recent members of the family but considering the existence of about 165 species I have not been able to study, the elements have been referred to *Typhlops* cf. *grivensis*.

Discussion: *Typhlops grivensis* first described by Hoffstetter (1946b) is known from the Middle Miocene type locality La-Grive-Saint-Alban in France only. Its record from Kohfidisch represents the youngest one. As second fossil representative of the Typhlopidae, *Typhlops cariei* originates from the Subrecent locality La-Mare-aux-Songes in Mauritius. As well, it has been described by Hoffstetter (1946b) from the type locality only. Rage (1984b) calls their membership to the family of the Typhlopidae into question based on the homogeneous morphology of the vertebrae of Scolecophidia but List (1966) presented clear osteological differences between Typhlopidae and Leptotyphlopidae, the two families of the Scolecophidia. Mc. Dowell (1967) deals with those osteological comparisons of List (1966).

The oldest representative of the Scolecophidia originates from the Upper Palaeocene of Morocco (Gheerbrant et al., 1993). Subsequently, they occur in the Lower Eocene of Belgium (Godinot et al., 1978), in the Upper Eocene of France (Rage, 1974), in the Middle Miocene of Hungary (Hír et al., 2001), in the Lower Miocene of the Czech Republic (Szyndlar, 1987), in the Lower Pleistocene of Rumania (Venczel, 1997c, 2000a), and in the Pleistocene of Greece, Spain, France, Ukraine, Africa, and Asia (Bailon, 1991).

According to Bailon (1991), fossil members of the Scolecophidia reacted sensitively to climatic changes. They are present from the Lower Eocene to the Pliocene in Europe and might have yielded to the climatic changes of the Pleistocene to South-East Europe where they still exist. As the fossil record of the Pliocene is restricted to localities of Western Europe (France, Spain), Bailon (1991) assumed a climatic difference between Western and Central Europe during that period. Though, in Lower Pleistocene the Scolecophidia are still present in the South-East of Central Europe (Ivanov et al., 2000).

Ecology and Climate – living relatives: Recent representatives of the Typhlopidae are small (usually under 30 cm, sometimes to over 70 cm) and slender featuring an inconspicuous head with reduced eyes. They are secretive burrowers mainly in barren areas even fairly close to sea. The single European species, *Typhlops vermicularis*, prefers dry, open habitats without dense and high vegetation such as grassy fields and slopes with scattered stones. Their favourite food is composed of small invertebrates, especially ants and their larvae (Arnold & Ovenden, 2002). A deepest temperature of about -20°C is tolerated (Grillitsch & Grillitsch, 1993). During winter, *Typhlops vermicularis* may rest for 2-6 months (Engelmann et al., 1985).

Today, members of the Typhlopidae occur on all continents where they inhabit tropical and subtropical climes. In Europe, the single species *Typhlops vermicularis* lives in the South Balkan extending north to Dugi Otok (island) in Croatia, South-West Montenegro, West Albania, Central Macedonia, South Bulgaria, Turkey, and on a few Greek islands. Its further geographical distribution ranges between South-West Asia, the Caucasus and North-East Egypt (Arnold & Ovenden, 2002; Grillitsch & Grillitsch, 1993). Following Müller (1996; see chapters 5, 6), the area of circulation of the Recent Typhlopidae is restricted to the Köppen's climate types A, B, C. *Typhlops vermicularis* occurs in the Köppen's climate type Csa of Europe.

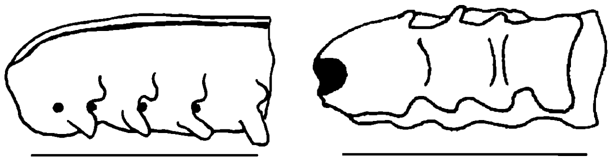


Figure 22: *Typhlops* cf. *grivensis*. Vertebrae caudales copulatae ("os coccygis") lateral (a) and ventral (b) view (Kohfidisch "cm"; Inv. Nr.: NHMW2004z0034/0002), scale bar equals 1 mm.

Infraorder Alethinophidia Nopcsa, 1923
Superfamily Colubroidea Oppel, 1811
Family Colubridae Oppel, 1811
Subfamily Colubrinae Oppel, 1811

Genus *Elaphe* Fitzinger, 1833

***Elaphe kohfidischi* Bachmayer & Szyndlar, 1985**
(Plate 9: b; Table 2, 3, 4, 5, 6, 12;
fig. 23, 24, 25, 26, 36)

Holotype: Natural History Museum Vienna, department of Geology and Paleontology, Austria, Inv. No. 1984/96; mid-trunk vertebra (Bachmayer & Szyndlar, 1985).
Type locality: Kohfidisch, Austria.
Stratigraphical Age of the Type material: Upper Miocene (Turolian, MN11).
Range: Middle Miocene – Upper Miocene Austria, ?Ukraine.
Material: 1 palatinum dext. (AO: Inv. Nr.: NHMW 2004z0035/0002). 5 palatina sin. 3 pterygoidea dext. 6 pterygoidea sin. 6 parabasisphenoidea. 2 quadrata dext. (AO: Inv. Nr.: NHMW2004z0035/0003). 2 quadrata sin. 21 maxillaria dext. 11 maxillaria sin. 18 maxillaria indet. 12 dentalia dext. 13 dentalia sin. 17 articularia dext. (AO: Inv. Nr.: NHMW2004z0035/0004). 18 articularia sin. 11 axis (AO: Inv. Nr.: NHMW2004z0035/0005). 374 vertebrae cervicales. 13315 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0035/0001, 0006, 0007). 27 vertebrae caudales.
(BM: Inv. Nr.: NHMW2004z0035/0008).
Description:
palatinum (fig. 23): One of the 6 palatina is nearly complete just lacking its teeth. Viewing from lateral, the nearly half-oval processus vomeris rises slightly more steeply anteriorly than posteriorly. Just the process of the triangular processus choanalis is vaulted to medial. The posterior margin of the relatively short triangular processus maxillaris includes an angle of nearly 90° with the tooth row. It is orientated to posteroventral parallel to the ventral branch of the posterior processus whose dorsal branch is about twice as long as the ventral one. From dorsal aspect, the palatinum continuously broadens in anterior direction.
pterygoideum: None of the 9 pterygoidea is complete. They feature a thick and distinctly bulging lateral margin which possesses a nearly rectangular processus ectopterygoideus with thickened outer corners. From dorsal view, the distinct, lateral groove for the ectopterygoid overtops the processus ectopterygoideus anteriorly.The teeth are robust and curved to posterior.
parabasisphenoideum: A detailed description of the basisphenoideum of *Elaphe kohfidischi* from Kohfidisch is given in Bachmayer & Szyndlar (1987:26; Plate 1: Figs. 1, 2; fig. 1:1-4).
quadratum (fig. 24): The 4 quadrata are either complete or nearly complete. They are robust but slender. The trochlea quadrati is nearly as narrow as the ventral half of the quadratum, and the oval processus stapedialis is positioned in the middle of the anterior margin. The convex crista dorsalis rises slightly posteriorly and passes into a discoidal processus orientated to posteromedial. From lateral aspect, the sharp crista quadrati is straight.
maxillare: A detailed description of the maxillare of *Elaphe kohfidischi* from Kohfidisch is given in Bachmayer & Szyndlar (1987:28; fig. 1:7, 8).
dentale: A detailed description of the dentale of *Elaphe kohfidischi* from Kohfidisch is given in Bachmayer & Szyndlar (1987:28; fig. 1:9, 10).
articulare (fig. 25): The posterior half of the 35 articularia is preserved in any case, the anterior half may be broken. From dorsal aspect, the bone is slightly s-shaped. The constriction of the trochlea leaves blank just a thin lateral margin of the bone beneath. Lentiform, the fossa mandibularis opens widely and the anterior foramen therein is longish-oval.The distinct foramen supraangularis is situated closely anterior to the rise of the crista medialis. Viewing from lateral, the crista lateralis is nearly straight while the crista medialis highly arches.
axis (fig. 26): A detailed description of the axis of *Elaphe kohfidischi* from Kohfidisch is given in Bachmayer & Szyndlar (1985:81, 82; fig. 1:12-14).
vertebra cervicalis: A detailed description of the vertebra cervicalis of *Elaphe kohfidischi* from Kohfidisch is given in Bachmayer & Szyndlar (1985:82; fig. 1:15).
vertebra praesacralis (Plate 9: b, 11: a, b; Table 12): A detailed description of the vertebra praesacralis of *Elaphe kohfidischi* (Holotype) from Kohfidisch is given in Bachmayer & Szyndlar (1985: pp. 80, 81, 82; Plate 1: Figs. 1-3; fig. 1:1-16). The measurements of the vertebrae praesacrales examined herein are noted in Table 12.
vertebra caudalis: A detailed description of the vertebra caudalis of *Elaphe kohfidischi* from Kohfidisch is given in Bachmayer & Szyndlar (1985: p. 82; fig. 1:16).
Comparison: With regard to the parabasisphenoidea, maxillaria and dentalia, they correlate to the ones described by Bachmayer & Szyndlar (1987) from the type material of *Elaphe kohfidischi*. The parabasisphenoideum of *Elaphe praelongissima* from the Late Miocene (MN13) locality Polgárdi in Hungary (Venczel, 1994, 1998) possesses a smaller frontal step and lacks the frontal crest. The characteristics of the axis and the remaining vertebrae are typical of *Elaphe kohfidischi* so described by Bachmayer & Szyndlar (1985).

The palatinum neither of *Coluber planicarinatus* nor of *Natrix longivertebrata* both members of the Colubridae has been described from the type material. Recent members of the Natricinae possess a palatinum more elongated featuring a dorsal branch of the posterior processus about five times longer than the ventral one. The dorsal branch of the posterior processus described herein is about twice as long as the ventral one. While the processus vomeris of Recent members of the Natricinae is rectangular and extremely elongated, the one of the Kohfidisch material is short and half-oval. Its short and triangular processus choanalis only slightly vaults medially in the Kohfidisch material. The one of members of the Natricinae is strongly elongated and arched to anteromedial. Contrary to the relatively short triangular processus maxillaris whose posterior margin is at an angle of nearly 90° with the tooth row in the palatina described herein, the one of members of the Natricinae is slender, elongated, directed to posteroventral, and at a much smaller angle with the tooth row. From dorsal aspect, the palatinum of the Kohfidisch material continuously broadens in anterior direction while the more slender one of Natricinae slightly broadens and narrows again from posterior to anterior. Further, the teeth of Natricinae are more slender and more curved to posterior. The general characteristics of the palatina described herein correlate to the ones of Recent Colubrinae.

Based on these comparisons, the palatina belong to a member of the Colubrinae of Kohfidisch. The number of bones of *Coluber planicarinatus* represents only 1% with regard to *Elaphe kohfidischi*. The former comprises vertebrae praesacrales and only one cranial bone. Totalling, the great number of 6 palatina has been found. Therefore, they have been referred to *Elaphe kohfidischi*.

The pterygoideum described herein differs from the one of *Natrix longivertebrata* already described by SZYNDLAR (1984) and from the ones of Recent members of the Natricinae. Generally, it correlates to the one of Recent Colubrinae. It is rectangular featuring thickened outer corners. The processus ectopterygoideus of the pterygoidea of Natricinae are flatter and half-oval but also possess thickened outer corners. Viewing from dorsal, the lateral groove for the ectopterygoid is developed more broadly in members of the Natricinae. Although the latter has a straighter tooth row, the pterygoideum is more vaulted to lateral in the posterior portion. Teeth of Natricinae are more slender.

The second member of the Colubrinae of Kohfidisch, *Coluber planicarinatus*, is represented by a much smaller number of bones. The great number of 9 pterygoidea, which differ from the ones of *Natrix longivertebrata* (see above), has been counted in Kohfidisch. Thus, their determination has resulted in *Elaphe kohfidischi*.

Comparing the quadratum of *Elaphe kohfidischi* with the ones of the Recent species *Elaphe longissima* and *Coluber gemonensis*, the extinct species has a narrower trochlea quadrati. From anterior aspect, the processus stapedialis is positioned more anteriorly, and the crista dorsalis is straight but not arched outward. Viewing from lateral, the crista quadrati is orientated more to posterior than to lateral.

Natrix longivertebrata, as another member of the Colubridae in Kohfidisch, features a quadratum more constricted medially contrary to the more slender quadratum of *Elaphe kohfidischi*. Both cristae quadrati run straight in lateral view, but still differ: while the crista quadrati of *Elaphe kohfidischi* is sharp, the one of *Natrix longivertebrata* is blunt.

Quadrata of *Elaphe kohfidischi* and *Coluber planicarinatus*, both Colubrinae of Kohfidisch, have been unknown. The determination of the 4 quadrata has resulted in *Elaphe kohfidischi* because of the proved great record of the species in Kohfidisch and based on the comparisons mentioned above.

The articulare of *Elaphe kohfidischi* has not been described from the type material. Compared with the articularia of the Recent relatives *Elaphe longissima* and *Coluber gemonensis* both members of the Colubrinae, the one of *Elaphe kohfidischi* possesses a narrower trochlea, a less highly arched crista medialis as well as a more rounded margin of the crista lateralis.

Contrary to the articulare of *Natrix longivertebrata*, a further member of the Colubridae described by articularia from Kohfidisch, the one of *Elaphe kohfidischi* features a less constricted trochlea leaving blank a thinner lateral margin of the bone beneath which does not stay visible lateral the narrower fossa mandibularis. The foramen supraangularis is situated farther posteriorly, closely anterior to the rise of the crista medialis. Finally, the crista lateralis of *Natrix longivertebrata* is parallel to the lowly arched crista medialis while the one of *Elaphe kohfidischi* possesses a straight crista lateralis and a more highly arched crista medialis.

Based on these comparisons and due to the well-documented existence of *Elaphe kohfidischi* contrary to *Coluber planicarinatus* in Kohfidisch, the great number of 35 articularia has been referred to the species.

Discussion: In 1985, BACHMAYER & SZYNDLAR have first described *Elaphe kohfidischi* from the type locality Kohfidisch, and in 1987, a second contribution to the species followed. Doubtfully, cf. *Elaphe kohfidischi* is present in another Upper Miocene locality namely Cherevichnoie in the Ukraine (SZYNDLAR & ZEROVA, 1992). MIKLAS-TEMPFER (2003) has afforded the oldest record of *Elaphe kohfidischi* from the Middle Miocene locality Grund in Austria.

Elaphe kormosi of the Uppermost Miocene locality Polgárdi in Hungary first described by BOLKAY (1913) and the Lower Pliocene of Osztramos 1 (VENCZEL, 2001) probably represents a form closely related to *Elaphe kohfidischi* (BACHMAYER & SZYNDLAR, 1985). Following BACHMAYER & SZYNDLAR (1985), the three species *Elaphe longissima*, *Elaphe paralongissima*, and *Elaphe kohfidischi* clearly demonstrate evolutionary differentiation. Although they originate from geographically close territories, they definitely represent distinct species. *Elaphe longissima* occurs in the Uppermost Miocene and inhabits Southern and Central Europe today. The extinct species *Elaphe paralongissima* is known from its Polish Upper Pliocene type locality and the Lower Pleistocene of Hungary (VENCZEL, 1998). In the opinion of SZYNDLAR (1991a), the elongation of the vertebrae of *Elaphe kohfidischi*, the morphology of the haemal keel, as well as the concave zygosphene are reminiscent of the living *Coluber caspius*.

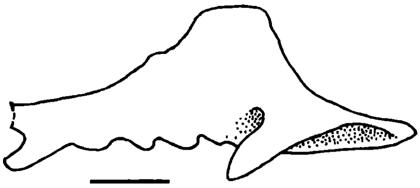


Figure 23: *Elaphe kohfidischi.* Palatinum dext. lateral view (Kohfidisch; Inv. Nr.: NHMW2004z0035/0002), scale bar equals 1 mm.

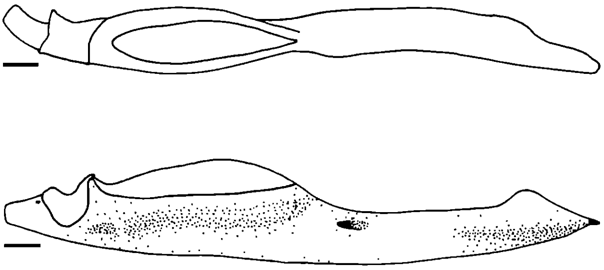


Figure 25: *Elaphe kohfidischi.* Articulare dext. dorsal (a) and lateral (b) view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0035/0004), scale bar equals 1 mm.

The oldest fossil record of the latter dates from the Uppermost Miocene of Hungary.

Elaphe kormosi and *Elaphe praelongissima* undoubtedly represented two distinct lineages. While the former was related to *Elaphe kohfidischi*, the latter belonged to a hypothetical lineage leading to the extant *Elaphe longissima* (VENCZEL, 1994).

During the Plio- and Pleistocene of Austria, further representatives of the genus *Elaphe* occurred. *Elaphe quatuorlineata* and *Elaphe longissima* have been described by RABEDER (1974) from the Plio- Pleistocene of Bad Deutsch-Altenburg and *Elaphe longissima* is present in the Middle Pleistocene of St. Margarethen (RABEDER, 1977).

The oldest member of the genus *Elaphe* dates from the Upper Miocene (MN9) of Gritsev in the Ukraine. During the Upper Miocene, it occurs in Austria, Hungary, Poland, Romania, Greece, and the Ukraine (SZYNDLAR, 1991b).

Ecology and Climate – living relatives: Recent members of the genus *Elaphe* represent very adept climbers, and especially *E. longissima* closely related to *Elaphe kohfidischi* even ascends vertical tree trunks. It is found up to 1800 m in some areas and prefers dry habitats such as sunny woods, shrubby vegetation, old walls, ruins, and hay stacks. If heat becomes excessive, *Elaphe longissima* retreats (ARNOLD & OVENDEN, 2002). The proper temperature ranges between 20°C and 28°C in the daytime and between 18°C and 22°C during the night. *Elaphe longissima* may rest at a temperature between 5°C and 12°C for 4-5 months in winter.

Following ARNOLD & OVENDEN (2002), *Elaphe longissima* occurs in France except the North, in West and South Swizerland, in South and East Austria, in the South-East Czech Republic, Slovakia, South-East Poland, Ukraine,

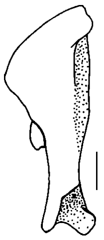


Figure 24: *Elaphe kohfidischi.* Quadratum dext. medial view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0035/0003), scale bar equals 1 mm.

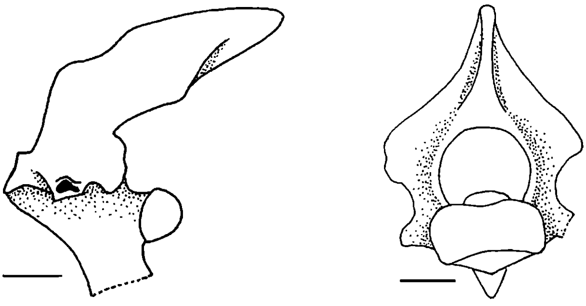


Figure 26: *Elaphe kohfidischi.* Axis lateral (a) and anterior (b) view (Kohfidisch "II"; Inv. Nr.: NHMW2004z0035/0005), scale bar equals 1 mm.

and south to North-West Spain, Central Italy and South Greece (although absent from the Aegean islands). It is also present in a few isolated localities in Germany near Heidelberg and ones in the North-West Czech Republic. Possibly, its distribution expands to West Sardinia. Outside Europe, it occurs in Turkey, the Caucasus and North Iran. This distribution belongs to the KÖPPEN's climate types Cf, Cs, Csa, Df, and Ds (MÜLLER, 1996; see chapters 5, 6).

Genus *Coluber* LINNAEUS, 1758

Coluber planicarinatus (BACHMAYER & SZYNDLAR, 1985)

(Plate 9: c; Table 2, 3, 4, 5, 6, 13)

Synonyms:

1985 *Nanus planicarinatus* sp. nov. — BACHMAYER & SZYNDLAR, p. 84, fig. 1:17-22 ; pl. 1: Figs. 4-6.

Holotype: Natural History Museum Vienna, department of Geology and Paleontology, Austria, Inv. No. 1984/97; trunk vertebra (BACHMAYER & SZYNDLAR, 1985).

Type locality: Kohfidisch, Austria.

Stratigraphical Age of the Type material: Upper Miocene (Turolian, MN11).

Range: Upper Miocene: Austria.

Material: 1 parabasisphenoideum. 154 vertebrae praesacrales (AO: Inv.Nr.: NHMW2004z0036/0001).
(BM: Inv. Nr.: NHMW2004z0036/0002).

Description:

parabasisphenoideum: A detailed description of the parabasisphenoideum of *Coluber planicarinatus* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1987: p. 29; Plate 1:

Figs. 3, 4; fig. 2).

vertebra praesacralis (Plate 9: c; Table 13): A detailed description of the vertebra praesacralis of *Coluber planicarinatus* (Holotype) from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985: pp. 84, 86; Plate 1: Figs. 4-6; fig. 1: 17-22). The measurements of the vertebrae praesacrales examined herein are noted in Table 13.

Comparison: The parabasisphenoideum shows characteristics typical of *Coluber planicarinatus* described by BACHMAYER & SZYNDLAR (1987) from Kohfidisch. The vertebrae praesacrales as well refer to *Coluber planicarinatus* characterized by BACHMAYER & SZYNDLAR (1985). Therefore, the description of the elements has resulted in this species.

Discussion: The species *Coluber planicarinatus* has been known so far from the type locality Kohfidisch only. In 1985, BACHMAYER & SZYNDLAR described the new extinct genus and species *Nanus planicarinatus* and based the creation of the fossil distinct genus *Nanus* on the peculiar morphology of the vertebrae praesacrales. The subsequent discovery of a parabasisphenoideum in 1987 caused the removal of the fossil to the genus *Coluber*. The parabasisphenoideum closely resembles the ones of the Recent *Coluber najadum-Coluber rubriceps* group (BACHMAYER & SZYNDLAR, 1987).

The presence of Colubrinae is common in the Austrian fossil record. Even the Austrian Middle Miocene localities Mühlbach (MIKLAS-TEMPFER, 2003; DAXNER-HÖCK et al., 2004)

and Grund (MIKLAS-TEMPFER, 2003) yield Colubrinae. During the Upper Miocene (MN9) of Austria, Colubrinae indet. are present in Götzendorf and Richardhof-Golfplatz (HARZHAUSER & TEMPFER, 2004). The Plio-/Pleistocene of Bad Deutsch-Altenburg yields a rich snake fauna consisting of diverse representatives of the Colubrinae. *Coluber gemonensis*, *Coluber jugularis*, *Coluber viridiflavus*, *Coluber* sp., and *Coronella* sp. have been described by RABEDER (1974) and mentioned by MAIS & RABEDER (1984). *Coluber viridiflavus* and *Coluber gemonensis* are present in the Middle Pleistocene locality St. Margarethen (RABEDER, 1977).

Coluber cadurci ranging between the Lower Oligocene and the Upper Oligocene of France represents the oldest member of the genus *Coluber* (RAGE, 1988b).

The subfamily Colubrinae is divided into

1. diurnal, terrestrial snakes prefering dry and sunny habitats;
2. nocturnal, terrestrial snakes in dry habitats;
3. climbing snakes hunting at dawn and inhabiting damp environments such as woods;
4. nocturnal, burrowing, terrestrial snakes in dry habitats with different kinds of substrata.

While members of the genus *Coluber* belong to the 1st group, the species of *Elaphe* represent members of the 3rd group (OBST et al., 1984).

Ecology and Climate – living relatives: After BACHMAYER & SZYNDLAR (1987), *Coluber planicarinatus* is suggestive of the Recent *Coluber najadum - Coluber rubriceps* group. *Coluber najadum* represents a diurnal and mainly terrestrial snake inhabiting dry and often stony environments usually with bushes and some dense, grassy vegetation for climbing. It is also found in open areas in woods, by overgrown walls, stony banks, and path edges (ARNOLD & OVENDEN, 2002). It may rest at a temperature above 0°C during the winter months.

Coluber najadum is mainly distributed in the South Balkans from mainland Greece north to coastal Croatia, Macedonia and extreme South Bulgaria. Absent from many Aegean islands, it is found on the ones that lie close to Asiatic Turkey. It inhabits the Caucasus region and South-West Asia. Following MÜLLER (1996; see chapters 5, 6), these areas belong to the Köppen's climate types Cf, Cs, and Csa.

Subfamily Natricinae BONAPARTE, 1838

Genus *Natrix* LAURENTI, 1768

Natrix longivertebrata SZYNDLAR, 1984

(Plate 9: d; Table 2, 3, 4, 5, 6, 13; fig. 27, 28, 29, 30)

Holotype: Institute of Systematic and Experimental Zoology of the Polish Academy of Sciences in Cracow, Poland, Inv. No. RK I-10000; mid-trunk vertebra (SZYNDLAR, 1984).

Type locality: Rębielice Królewskie I, Poland.

Stratigraphical Age of the Type material: Upper Pliocene (MN16).

Range: Upper Miocene – Lower Pleistocene: Austria, Hungary, Poland, Moldavia, France.

Material: 1 parabasisphenoideum (AO: Inv.Nr.: NHMW 2004z0037/0002). 1 quadratum dext. (AO: Inv.Nr.: NHMW2004z0037/0003). 2 maxillaria dext. 2 maxillaria sin. 1 dentale dext. 2 dentalia sin. (AO: Inv.Nr.: NHMW2004z0037/0004). 4 articularia dext. 6 articularia sin. (AO: Inv.Nr.: NHMW2004z0037/0005). 1 vertebra cervicalis. 1407 vertebrae praesacrales (AO: Inv.Nr.: NHMW2004z0037/0001). 51 vertebrae caudales.

(BM: Inv. Nr.: NHMW2004z0037/0006).

Description:

parabasisphenoideum (fig. 27): One nearly complete parabasisphenoideum is present. The processus basipterygoidei as well as the top of the processus parasphenoideus are broken. It is triangular and relatively short. From ventral aspect, the cristae pterygoideae situated far posteriorly are strongly inclined backward. Their anterior branches converge but do not fuse. A crista parabasisphenoidea is missing. The anterior orifice of the Vidian canal is present anterior to the posterior branches of the cristae pterygoideae while the posterior orifice is situated near the posterior border of the bone and accompanied by the foramen cerebralis. In dorsal view, the pituitary fossa appears relatively round. The crista frontalis is distinct and thickened posteriorly. Posterior to the postero-lateral corners of the pituitary fossa, the posterior foramina for the nervus abducentes are present.

quadratum (fig. 28): The single, robust quadratum is broken dorsally. The ventral half appears constricted because the trochlea quadrati as well as the dorsal half broaden distinctly. The oval processus stapedialis is situated in the middle of the extremely concave anterior margin. Viewing from lateral, the quadratum features a straight but blunt crista quadrati.

maxillare: 4 posterior fragments of maxillaria preserving the processus ectopterygoideus are present. The latter is trapezoidal, orientated to anteroventral and features a medial margin directed to anteromedial. One left maxillare demonstrates that it is typically opisthomegadontic. The last, prominent, much longer, and sharp tooth is preserved.

dentale (fig. 29): The three dentalia lack their posterior parts. Two anterior halves are completely preserved. The Meckel's groove opens below the 4th tooth position. It represents a thin slit opening laterally and widening just slightly but continuously posteriorly. The lamina horizontalis rises and inclines in dorsolingual direction at the processus angularis. Viewing from labial, the dentalia feature an oval, large and distinct foramen mentalis, which is situated below the 7th tooth position on the two anterior halves. The incisura articularis opens high dorsally.

articulare (fig. 30): 10 articularia are present which collectively document the complete posterior half. The anterior half may be broken. Viewing from dorsal, the extremely constricted trochlea leaves blank a relatively thick lateral margin of the bone beneath which, also lateral to the fossa mandibularis, stays visible. The latter is lentiform and opens narrowly. Anteriorly, within the fossa mandibularis, a large oval foramen is present. The foramen supraangularis is situated in the middle of the anterior, narrow half of the bone. From lateral aspect, the slightly undulated crista lateralis is parallel to the lowly arched crista medialis.

vertebra cervicalis: A detailed description of the vertebra cervicalis of *Natrix longivertebrata* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985: p. 88; fig. 2: 6, 7).

vertebra praesacralis (Plate 9: d; Table 13): A detailed description of the vertebra praesacralis of *Natrix longivertebrata* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985: pp. 87, 89; fig. 2: 1-5). The measurements of the vertebrae praesacrales examined herein are noted in Table 13.

vertebra caudalis: The 51 vertebrae caudales can be divided into more anterior and more posterior ones. Their general shape resembles the one of the vertebrae praesacrales. They become longer and smaller as one proceeds posteriorly. All of them feature pleurapophyses flattened dorsoventrally which are rectangular in dorsal view, long, and directed to lateral in the more anterior caudal region. The more posterior vertebrae caudales possess shorter and lenticular pleurapophyses directed to anterior. With regard to the bifurcated haemapophysis, its orientation passes from posterior to ventral in the course of the caudal region.

Comparison: SZYNDLAR (1984) has precisely described parabasisphenoidea, a quadratum, maxillaria, articularia, and vertebrae caudales from the Polish type material of *Natrix longivertebrata*. Their characteristics match the ones of the Kohfidisch material. Therefore, the elements are referred to *Natrix longivertebrata.*

The articulare of *Natrix* aff. *longivertebrata* described by RAGE & SZYNDLAR (1986) from the French Middle Miocene shows a lower medial flange of the fossa mandibularis and a more thickened upper border of the lateral flange.

At *Natrix* cf. *longivertebrata* of the Upper Miocene, Hungarian locality Polgárdi (VENCZEL, 1994), the higher medial flange of the articulare rises steeper posteriorly.

The presence of *Natrix longivertebrata* in Kohfidisch is based on the description of vertebrae cervicales and vertebrae praesacrales (BACHMAYER & SZYNDLAR, 1985) similar to the vertebrae examined herein.

The dentale of *Natrix longivertebrata* is unknown from the type material. Contrary to *Natrix natrix*, the Meckel's groove opens farther anteriorly (below the 4th tooth position and not below the 8th tooth position approximately), the incisura articularis is positioned farther dorsally, and the teeth are longer and more robust.

At *Natrix* cf. *longivertebrata* of the Upper Miocene, Hungarian locality Polgárdi (VENCZEL, 1994), the Meckel's groove of the dentale opens below the 8th tooth position which reminds of *Natrix natrix.*

Comparing the dentalia of *Natrix longivertebrata* and *Elaphe kohfidischi*, both members of the Colubridae represented by dentalia in Kohfidisch, the one of *Natrix longivertebrata* is more slender, and the Meckel's groove as well as the incisura articularis open more narrowly. From lingual view, the lamina horizontalis is more undulated and does not rise straight and continuously. The teeth of *Natrix longivertebrata* are more slender while the ones of *Elaphe kohfidischi* have a broader base and a significant sharp bend in the middle.

Based on the comparisons with extant and extinct material, the characteristics of the elements described herein are typical of *Natrix longivertebrata* and therefore referred to the species.

Discussion: SZYNDLAR (1984) has first based *Natrix longivertebrata* on a vertebra praesacralis from the Polish Upper Pliocene (MN16) locality Rębielice Królewskie I in Poland. Up to now, *Natrix longivertebrata* has additionally been known from the Upper Miocene of Hungary (VENCZEL, 1994, 1998), from the Middle Pliocene and Upper Pliocene of Moldavia (REDKOZUBOV, 1987) and from the Lower Pleistocene of Osztramos in Hungary (VENCZEL, 2001).

Natrix cf. *longivertebrata* has been described from the Upper Miocene of Cherevichnoie in the Ukraine and Polgárdi in Hungary (VENCZEL, 1994), from the Middle Pliocene of Węze 1, and the Upper Pliocene of Rębielice Królewskie 2 both in Poland (SZYNDLAR, 1991b). Following RAGE & SZYNDLAR (1986), *Natrix* aff. *longivertebrata* is present in the Middle Miocene of France.

Natrix aff. *longivertebrata* occurs in the Middle Miocene of France, and *Natrix longivertebrata* in the Upper Miocene of Austria. In Poland, the species is not present before the Upper Pliocene. About 10 million years separate the stratigraphical level of the French from the Polish localities, but no specific distinction between the forms are observed. Rage & Szyndlar (1986) expect an important, perhaps the longest evolutionary stasis quite unusual among snakes.

After Szyndlar (1991b), most cranial bones of *Natrix longivertebrata* are identical to those of the living species *Natrix natrix* except the compound bone and especially the basisphenoideum. Szyndlar (1991c) demonstrates that the living species *Natrix natrix* most probably represents the direct descendant of the Neogene species *Natrix longivertebrata*. While some skull characters remain invariant, a gradual modification of two basicranial morphological patterns exists. The basisphenoideum reflects an "ancient" (primitive) and a "modern" (derived) morphological pattern. The most important difference beside others lies in the course of the Vidian canals and the location of accompanying structures. Further, the position and separation of the foramen nervi trigemini of the prooticum feature the evolutionary *Natrix longivertebrata-Natrix natrix* lineage. The foramen for the re-entry of the cid branch of the trigeminal nerve may be located either inside the V_2 recess or separately below the V_2 recess (primitive). While in living or subfossil specimens of *Natrix natrix* both conditions are equally represented, fossil members display exclusively the latter condition. In Middle Pleistocene specimens of *Natrix natrix* of St. Margarethen in Austria (Rabeder, 1977), the foramen nervi trigemini is always divided into a large dorsal opening and a smaller ventral one which may be present in Recent snakes.

Concluding, the only taxonomically significant difference observed in the skulls of the *Natrix longivertebrata-Natrix natrix* lineage is restricted to the posterior braincase. In the Middle Miocene, the "ancient" condition of the basisphenoideum was fixed but was almost entirely replaced by the "modern" pattern around the Pliocene/Pleistocene boundary. The transformation of the older condition of the prooticum into the more Recent one seems to be a younger occurrence. However, the ophidian species inhabiting Europe since the Lower Miocene do not differ significantly from their living relatives. The genera are clearly referable to extant ones. Therefore, the origin of modern genera of advanced snakes may have taken place long before the Paleogene/Neogene boundary (Szyndlar, 1991c).

The oldest member of the genus *Natrix* is *Natrix mlynarskii* from the Lower Oligocene of France. Placed in the genus *Coluber* but combining characteristics of both modern "natricines" and "colubrines", the oldest known European representatives of the family Colubridae appeared in West Europe in the Lower Oligocene (Rage, 1988b). As 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). Following Ivanov (2000, 2001) and Ivanov et al. (2000), just primitive members of the Colubroidea were present in Europe since the Eocene, and Colubridae might have immigrated into Central Europe areas probably across the Mazury-Mazowsze continental bridge in the Lower Oligocene. Subsequently, they penetrated into Western Europe across the Rhine Graben in several waves of dispersal. 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 (Ivanov, 2000, 2001; Ivanov et al., 2000; Szyndlar, 1998). Most obviously, the Boidae were displaced by the Colubridae in Europe (Ivanov, 2000, 2001; Ivanov et al., 2000; 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.

With regard to the Austrian Miocene, Natricinae indet. are present in the Middle Miocene of Mühlbach (Miklas-Tempfer, 2003) and in the Upper Miocene (MN9) of Richardhof-Golfplatz (Harzhauser & Tempfer, 2004). The Plio- Pleistocene of Austria yields *Natrix natrix* in the locality Bad Deutsch-Altenburg (Rabeder, 1974; Mais & Rabeder, 1984). The same species is part of the vertebrate fauna dominated by snakes from the Middle Pleistocene fissure filling St. Margarethen in Burgenland (Rabeder, 1977).

Ecology and Climate – living relatives: *Natrix natrix*, the presumed closest Recent relative to *Natrix longivertebrata*, inhabits damp places and usually prefers water in its more southern occurrences where it may reach altitudes of 2400 m. In North Europe, *Natrix natrix* is more a lowland animal but may sometimes also be found in quite dry woods, hedgrows, and meadows. It swims well and hunts in water (Arnold & Ovenden, 2002). Slipping in autumn, the juvenile representatives of *Natrix natrix* hibernate in warmer places such as in compost.

The Grass Snake is distributed nearly allover Europe north to South Norway and Sweden (as far north as 67°N), South Finland, and Russia. It is absent in some islands such as Ireland, the Balearics, Malta, Crete, and some Cyclades.

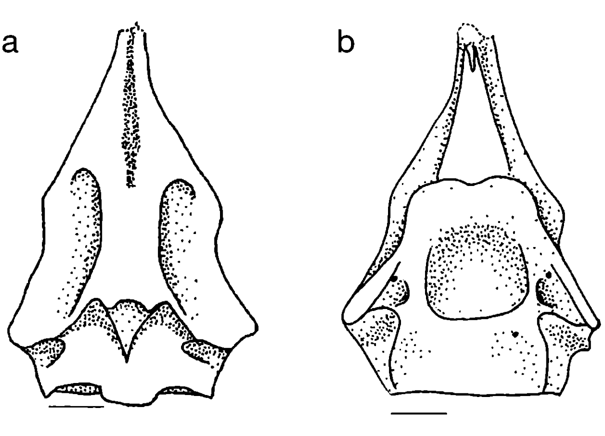


Figure 27: *Natrix longivertebrata*. Parabasisphenoideum dorsal (a) and ventral (b) view (Kohfidisch "III unten"; Inv.Nr.: NHMW-2004z0037/0002), scale bar equals 1 mm.

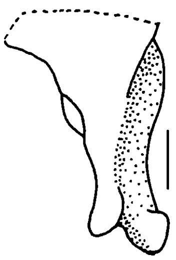


Figure 28: *Natrix longivertebrata.* Quadratum dext. medial view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0037/0003), scale bar equals 1 mm.

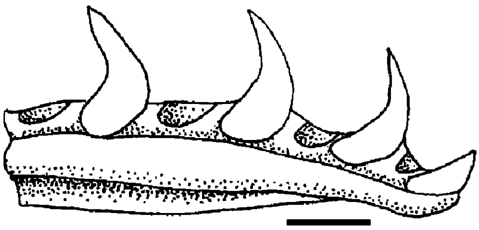


Figure 29: *Natrix longivertebrata.* Dentale sin. lingual view (Kohfidisch "III"; Inv. Nr.: NHMW2004z0037/0004), scale bar equals 1 mm.

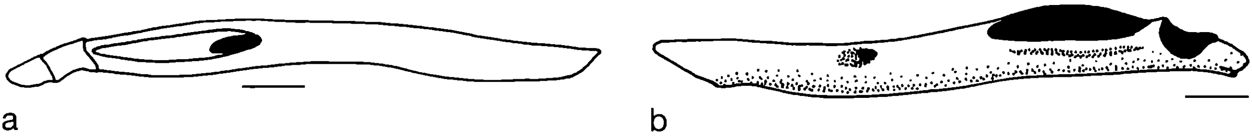


Figure 30: *Natrix longivertebrata.* Articulare sin. dorsal (a) and lateral (b) view (Kohfidisch "III unten"; Inv. Nr.: NHM-W2004z0037/0005), scale bar equals 1 mm.

Natrix natrix also occurs in North-West Africa and Asia east to Lake Baikal (ARNOLD & OVENDEN, 2002). Its distribution is restricted to the Köppen's climate types Cf, Cs, Csa, and Df (MÜLLER, 1996; see chapters 5, 6).

Family Elapidae BOIE, 1827

Genus *Naja* LAURENTI, 1768

Naja romani (HOFFSTETTER, 1939)

(Plate 9: e, 10: a-e; Table 2, 3, 4, 5, 6, 14;
fig. 31, 32, 33, 34, 37)

Synonyms:

1985 *Naja austriaca* sp. nov. – BACHMAYER & SZYNDLAR, p. 88, Text-figs. 3-5; pl. 1: Figs. 4–6 ; pl. 2: Figs. 10–13.

Holotype: Université Claude-Bernard, Département des Sciences de la Terre, Lyon, France, n° FSL 92856; rather complete skeleton.

Type locality: La Grive-Saint Alban, Isère, France.

Stratigraphical Age of the Type material: Middle Miocene (Astaracian, MN7-8).

Range: Lower Miocene – Upper Miocene: Austria, France.

Material: 10 palatina dext. 5 palatina sin. 3 pterygoidea dext. 4 pterygoidea sin. 1 parietale sin. 2 parabasisphenoidea. 2 prootica. 7 quadrata dext. 2 quadrata sin. 27 maxillaria dext. 19 maxillaria sin. 44 maxillaria indet. 3 maxillaria dext. et veneno illiti dentes (AO: Inv.Nr.: NHMW2004z0038/0001). 5 maxillaria sin. et veneno illiti dentes. 57 veneno illiti dentes (AO: Inv.Nr.: NHMW2004z0038/0004, 0005). 35 dentalia dext. 23 dentalia sin. 4 articularia dext. 7 articularia sin. 8 axis (AO: Inv.Nr.: NHMW2004z0038/0006). 45 vertebrae cervicales. 6227 vertebrae praesacrales (AO: Inv. Nr.: NHMW2004z0038/0002). 118 vertebrae caudales. 481 costae (AO: Inv.Nr.: NHMW2004z0038/0003, 0007, 0008). (BM: Inv.Nr.: NHMW2004z0038/0009).

Description:

palatinum: A detailed description of the palatinum of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1987:32; fig. 4:7, 8) and SZYNDLAR & ZEROVA (1990:57).

pterygoideum: A detailed description of the pterygoideum of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985:90; fig. 4:1, 2).

parietale: A detailed description of the parietale of *Naja romani* from Kohfidisch is given in SZYNDLAR & ZEROVA (1990:57; fig. 2: D).

parabasisphenoideum: A detailed description of the basisphenoideum of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985:89; Plate 1: Figs. 7, 8; fig. 3) and SZYNDLAR & ZEROVA (1990:56; fig. 1).

prooticum: A detailed description of the prooticum of *Naja romani* from Kohfidisch is given in SZYNDLAR & ZEROVA (1990:56; fig. 2: A, B).

quadratum: A detailed description of the quadratum of *Naja romani* from Kohfidisch is given in SZYNDLAR & ZEROVA (1990:57; fig. 2: G).

maxillare: A detailed description of the maxillare of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985: p. 90; fig. 4:7-10) and SZYNDLAR & ZEROVA (1990:57).

maxillare et veneno illiti dens (Plate 9: e ; fig. 31, 32): A detailed description of the maxillare et veneno illiti dens of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985:90; fig. 4:7-10). See also comparison.

dentale: A detailed description of the dentale of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985: p. 90; fig. 4:3, 4) and in BACHMAYER & SZYNDLAR (1987:31; fig. 4:5, 6).

articulare: A detailed description of the articulare of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYND-

LAR (1987:31; fig. 4:1-4).

axis (fig. 34): A detailed description of the axis of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985:90; fig. 5:7, 8). See also comparison.

vertebra cervicalis : A detailed description of the vertebra cervicalis of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985:90, 91; fig. 5:9).

vertebra praesacralis (Plate 10: a-d; Table 14): A detailed description of the vertebra praesacralis of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985: pp. 91, 92; fig. 5: 1-5) and SZYNDLAR & ZEROVA (1990: p. 58; fig. 3: A-C). The measurements of the vertebrae praesacrales examined herein, are noted in Table 14.

vertebra caudalis : A detailed description of the vertebra caudalis of *Naja romani* from Kohfidisch is given in BACHMAYER & SZYNDLAR (1985:94; fig. 5:10).

costa (Plate 10: e): A detailed description of the costa of *Naja romani* from Kohfidisch is given in SZYNDLAR & ZEROVA (1990:57; fig. 2:E, F).

Comparison: The pterygoidea, the parabasisphenoidea, the maxillaria, the dentalia, the vertebrae cervicales, the vertebrae praesacrales, and the vertebrae caudales correlate to those already described by BACHMAYER & SZYNDLAR (1985) as *Naja austriaca*, i. e. *Naja romani* from Kohfidisch. Beside again dentalia, BACHMAYER & SZYNDLAR (1987) have found palatina and articularia of *Naja romani*. Their characteristics correspond to those of the material examined herein. Palatina, parabasisphenoidea, maxillaria, and vertebrae praesacrales of *Naja romani* from Kohfidisch are also described by SZYNDLAR & ZEROVA (1990). For the first time, they define a parietale, prootica, quadrata, and costae of the Kohfidisch material similar to the one examined in this paper. Therefore, the elements are referred to *Naja romani*.

BACHMAYER & SZYNDLAR (1985) have already described the maxillare et veneno illiti dens of *Naja romani* from Kohfidisch. The material described herein also contains one maxillare et veneno illiti dens of the replacement series (fig. 32). After JACKSON (2002), teeth of snakes are replaced continuously throughout life. The replacement teeth are not attached to the dentigerous bone during their development. When they replace the functional tooth, their basal end establishes an attachment to the rim of the shallow alveolus. With regard to members of the Elapidae, the discharge orifice in replacement fangs has the same size as in functional fangs. No sign of any infolding of an open groove of the venom canal exists. Fangs of the replacement series just differ in size from the functional fang. These characteristics correlate to the "brick chimney" hypothesis of fang development.

BOGERT (1943) distinguishes between spitting and nonspitting cobras by the size and the shape of the venom discharge orifice of the veneno illiti dens. Likewise, WÜSTER & THORPE (1992a) examine the difference of the fang structure in the Asiatic species of *Naja* with regard to the ability to spit. Especially males demonstrate, if they belong to the group of spitting or nonspitting cobras. Independent from the length of the fang, spitting cobras have smaller, more rounded venom discharge orifices than nonspitting cobras (fig. 33). The fangs of the extinct species *Naja romani* clearly show a long and broad venom discharge orifice (fig. 31). Therefore, *Naja romani* very probably belonged to the group of nonspitting cobras such as the Recent species *Naja naja* and *Naja oxiana*.

With regard to the axis, a single one has already been described from Kohfidisch by BACHMAYER & SZYNDLAR (1985). The authors characterize the axis by a flattened processus odontoideus and a short intercentrum III (hypapophysis) not protruding outside the condyle neck. One of the 8 axis described herein is well preserved lacking only its neural arch and the processus transversi (fig. 34). Oval, broad and elongated, the lateral, anterior condyli are orientated to anterolateral. Their ventral lobe is broad-oval as well. Contrary to the single axis already described by BACHMAYER & SZYNDLAR (1985) from Kohfidisch, they form a blunt and broad processus odontoideus (which represents the centrum of the atlas) straightly directed to anterior. The blunt and long intercentrum III (hypapophysis) flattened laterally protrudes out of the condyle neck and is directed to posteroventral.

Axis of Recent species of the genus *Naja* resemble the ones of Kohfidisch described herein. Beside its characteristic size, the processus odontoideus straightly directed forward distinguishes the axis from members of the Colubridae and Viperidae which altogether possess a processus odontoideus directed slightly to dorsal.

Examining accurately the axis already mentioned by BACHMAYER & SZYNDLAR (1985) from Kohfidisch, the so-described "flattened" processus odontoideus as well as the "short" intercentrum III (hypapophysis) are broken. Therefore, the determination of the axis described in this paper has resulted in *Naja romani* although its processus odontoideus and centrum are relatively long.

Discussion: Originating from the Middle Miocene of La-Grive-Saint-Alban in France, the extinct species *Palaeonaja romani* was first described by HOFFSTETTER (1939). The genus *Palaeonaja* was referred to the synonym of the living genus *Naja* by SZYNDLAR & RAGE (1990). With regard to the remains of Kohfidisch, BACHMAYER & SZYNDLAR (1985) described them as the new extinct species *Naja austriaca*. SZYNDLAR & ZEROVA (1990) synonymized *Naja austriaca* with *Naja romani* based on special skull bone features. After BACHMAYER & SZYNDLAR (1985), big similarities between *Naja romani* and the living cobra *Naja naja* exist. Comparing the fang structure of *Naja romani* and *Naja naja*, both belong to the nonspitting cobras (see above) which confirms their close resemblance. Formerly, the Asiatic cobras altogether were assigned to the single species *Naja naja* split into diverse subspecies. WÜSTER & THORPE (1989, 1990, 1991, 1992b) have shown that the Asiatic cobra complex comprises a total of at least eight separate species with numerous areas of sympatry between species pairs. Their investigations are based on multivariate analyses of a large number of morphological characters. However, the similarities shown by BACHMAYER & SZYNDLAR (1985) in fact refer to *Naja romani* and the species *Naja naja* and not to another one of the former subspecies of *N. naja*.

Naja romani from the Lower Miocene of Petersbuch 2 in southern Germany (SZYNDLAR & SCHLEICH, 1993) represents the oldest record of the species. In Austria, it was present already during the Middle Miocene of Grund (MIKLAS-TEMPFER, 2003). The Upper Miocene locality Gritsev of the Ukraine yields *Naja romani* as well (SZYNDLAR & ZEROVA, 1990). IVANOV (2000) has described *Naja* cf. *romani* and *Naja* sp. from the Lower/Middle Miocene site Vieux Collonges in France. *Naja* sp. is present in the Middle Miocene of Sandelzhausen in Germany (M. BÖHME, 1999) and in several other localities in Europe up to the Pliocene.

Following IVANOV (2000, 2001), small representatives of the family Elapidae such as *Micrurus* and *Maticora* most probably appeared in Europe somewhat earlier than the larger ones. The small morphotype Elapidae A reported from the Lower Miocene (MN3) locality Merkur in Czech Republic may represent the oldest record of the family. Members of the genus *Naja* immigrated from Asia and some Elapidae in general perhaps also from Africa (IVANOV et al., 2000). During the Quaternary, Elapidae disappeared in Europe due to the deterioration of climate (IVANOV, 2001). Living members of the genus *Naja* represent two separate phyletic lineages inhabiting either Africa or Asia. Both living and fossil African or Asiatic representatives of the genus may be differentiated from each other by a set of characters of the basisphenoideum and of other skull bone elements. Following SZYNDLAR & ZEROVA (1990) and SZYNDLAR & RAGE (1990), *Naja romani* representing an old evolutionary branch of the genus *Naja* clearly belongs to the Asiatic lineage although SZYNDLAR & SCHLEICH (1993) point to considerable differences from its living Asiatic relatives with regard to the morphology of the hypapophysis in the posterior trunk vertebrae.

Ecology and Climate – living relatives: Members of the genus *Naja*, the poisonous cobra, 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). Flat country with high grass and scattered groves of trees represents an optimum habitat. When alarmed, the cobra typically flattens its neck (BROWN, 1979). The Asiatic cobras may rest for 3-4 months in winter.

The Asiatic cobra *Naja naja*, close relative of *Naja romani*, inhabits India today and is therefore restricted to the Köppen's climate types Af, Aw, BS, BW, Cs, and Cw (MÜLLER, 1996; see chapters 5, 6).

Family Viperidae OPPEL, 1811

Subfamily Viperinae OPPEL, 1811

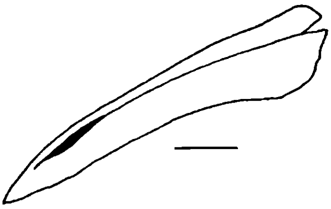


Figure 31: *Naja romani*. Veneno illiti dens (Kohfidisch; Inv. Nr.: NHMW2004z0038/0004), scale bar equals 1 mm.

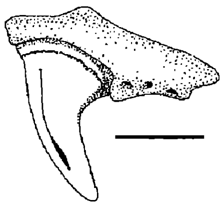


Figure 32: *Naja romani*. Veneno illiti dens (of replacement series) of maxillare dext. lateral view (Kohfidisch; Inv. Nr.: NHMW2004z0038/0005), scale bar equals 1 mm.

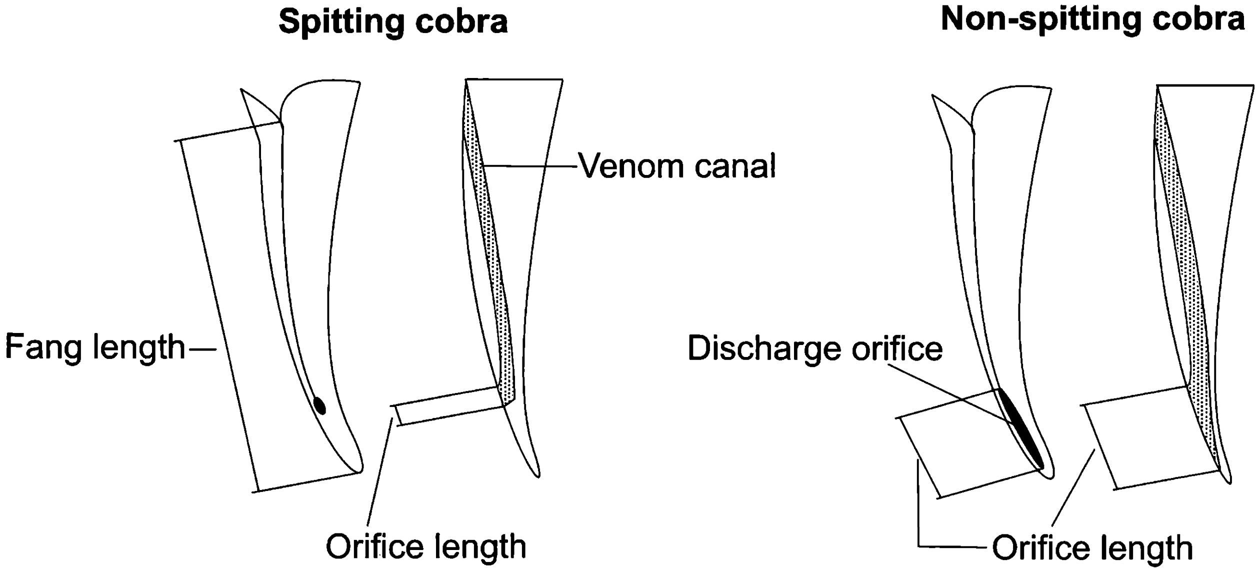


Figure 33: Fang structure in Asiatic spitting and nonspitting cobras: frontolateral view and longitudinal section (modified after WÜSTER & THORPE, 1992a).

Genus *Vipera* Laurenti, 1768

Vipera burgenlandica Bachmayer & Szyndlar, 1987

(Plate 10: f, g; Table 2, 3, 4, 5, 6, 14; fig. 35)

Synonyms:

1985 *Vipera* sp. (= *Daboia* sp.) — Bachmayer & Szyndlar, p. 96, fig. 6.

1993 *Macrovipera*? *burgenlandica* — Rage [in:] Golay et al., p. 273.

Holotype: Natural History Museum Vienna, department of Geology and Paleontology, Austria, Inv.No. 1986/3; basisphenoideum (Bachmayer & Szyndlar, 1987).
Typelocality: Kohfidisch, Austria.
Stratigraphical Age of the Type material: Upper Miocene (Turolian, MN11).
Range: Upper Miocene: Austria.
Material: 10 veneno illiti dentes (AO: Inv.Nr.: NHMW 2004z0039/0001, 0003). 7 dentalia dext. 8 dentalia sin. 3 dentalia indet. 3 articularia dext. 1 articulare sin. 1 vertebra cervicalis. 1159 vertebrae praesacrales (AO: Inv.Nr.: NHMW2004z0039/0002). 1 vertebra caudalis.
(BM: Inv. Nr.: NHMW2004z0039/0004).
Description:
veneno illiti dens (Plate 10: f; fig. 35): 10 exemplars of either complete or nearly complete veneno illiti dentes are present. They are slender and equally curved to posterior. The venomous canal is closed and opens basally as an entrance orifice for the venom duct. Apically, that canal opens as a slit for discharging the venom. The suture connecting the entrance orifice with the discharge orifice is almost invisible on the anterior surface of the tooth.
dentale: A detailed description of the dentale of *Vipera burgenlandica* from Kohfidisch is given in Bachmayer & Szyndlar (1987:35; fig. 5:7, 8).
articulare: A detailed description of the articulare of *Vipera burgenlandica* from Kohfidisch is given in Bachmayer & Szyndlar (1987: p. 35; fig. 5:4-6).
vertebra cervicalis : A detailed description of the vertebra cervicalis of *Vipera burgenlandica* from Kohfidisch is given in Bachmayer & Szyndlar (1985:96; fig. 6:7).
vertebra praesacralis (Plate 10: g; Table 14): A detailed description of the vertebra praesacralis of *Vipera burgenlandica* from Kohfidisch is given in Bachmayer & Szyndlar (1985:96; fig. 6:1-6, 8) and Bachmayer & Szyndlar (1987:35-37; fig. 6:1-8). The measurements of the vertebrae praesacrales examined herein, are noted in Table 14.
vertebra caudalis : One vertebra caudalis is nearly completely preserved. The vertebra originates from the anterior part of the caudal region because it is broad, short, and nearly as large as the mean of the size of the vertebrae praesacrales. Although the pleurapophyses are broken, their bases flattened dorsoventrally are directed to anteroventral. The bifurcated haemapophysis is orientated to ventrolateral. From ventral aspect, two foramina are present closely anterior to the bases of the haemapophysis. The distinct subcentral grooves run between the cotyle and the pleurapophyses. The postzygapophyses are round. Viewing from dorsal, the oval praezygapophyses are directed to anterolateral. The neural arch strongly constricted medially forms a distinct and relatively high processus spinosus. It is longer than high and just slightly overhanging posteriorly. Anteriorly, the anterior margin of the zygosphene is trilobate. From posterior view, the lateral margins of the neural arch are distinctly concave.
Comparison: Bachmayer & Szyndlar (1985) already described the vertebrae cervicales as well as the vertebrae praesacrales of *Vipera burgenlandica* from Kohfidisch as *Vipera* sp. In 1987, Bachmayer & Szyndlar created the new species *Vipera burgenlandica* also with regard to the material formely referred to *Vipera* sp. based on dentalia, articularia and vertebrae praesacrales.
Comparing the veneno illiti dentes of the two venomous snakes of Kohfidisch, i.e. *Naja romani* and *Vipera burgenlandica*, the general difference between Elapidae and Viperidae is clear. Both species have a basal entrance orifice connecting the venom duct with the tooth canal and a discharge orifice apically (Jackson, 2002). The latter is narrower in *Vipera burgenlandica*, which generally possesses a more slender veneno illiti dens. The robust veneno illiti dens of *Naja romani* bends sharply to posterior in the middle. As distinct difference between members of the Elapidae and the Viperidae, the former possess a visible suture along the anterior surface of the fang connecting the entrance orifice with the discharge orifice (Jackson, 2002).
The so-called proteroglyph Elapidae have small, fixed front fangs. When they bite, they hang on and chew to envenomate the prey. Contrary, the solenoglyph members of the Viperidae possess movable front fangs folded back into the mouth until they are needed.
Based on these differentiations, the determination of the veneno illiti dentes has resulted in *Vipera burgenlandica*.
The vertebra caudalis features characteristics typical of members of the Viperidae such as observed on Recent material and published by Bailon (1991). As no more species of the Viperidae seems to be present in Kohfidisch, the vertebra caudalis has been referred to *Vipera burgenlandica*.
Discussion: Based on the holotype parabasisphenoideum, Bachmayer & Szyndlar (1987) have defined the new species *Vipera burgenlandica* from Kohfidisch. Formerly, Bachmayer & Szyndlar (1985) had referred vertebrae praecaudales together with one basioccipitale from Kohfidisch to *Vipera* sp. Following Bachmayer & Szyndlar (1987), *Vipera burgenlandica* belongs to the large-sized members of the genus *Vipera* namely the so-called “oriental vipers”. Bones of the lower jaw are almost identical in all “oriental vipers” and the remaining bones except the parabasisphenoideum of *Vipera burgenlandica* differ little from those of other members of the group. *Vipera burgenlandica* closely resembles the species *Macrovipera lebetina*, *Vipera palaestinae* and *Montivipera xanthina* but not *Daboia russelii* (sensu Nilson et al., 1999), altogether living large-sized vipers.
The old genus *Vipera* is an assemblage of at least five dif-

ferent lineages. The lineages exhibit their own ecological adaptions and taxa with similar reproductive systems are further united by similar adaptions to climate and habitats (NILSON & ANDRÉN, 1997). Formerly, OBST (1983) related the large-sized "oriental vipers" to the genus *Daboia* which was not universally followed. HERRMANN et al. (1992) used albumin immunology and blood serum electrophoresis to examine the phylogeny of Eurasian viperines. They found out that *Vipera russelii* occupied an isolated position. This is why they proposed the revalidation of *Daboia* GRAY, 1842 as a monotypic genus with *Daboia russelii* as the only species. *Vipera lebetina* and related species were assigned to the revalidated genus *Macrovipera* REUSS, 1927. NILSON et al. (1999) created the new subgenus *Montivipera* to separate the *Vipera xanthina* group from other members of *Vipera*. It differs morphologically, genetically, serologically, and ecologically and therefore represents an evolutionary clade of its own. The phylogenetic position of *Vipera palaestinae* still remains unsolved but it is definitely excluded from the *xanthina* complex, i. e. from *Montivipera* by NILSON et al. (1999).

In 1993, RAGE placed *Vipera burgenlandica* so described by BACHMAYER & SZYNDLAR (1987) in the genus *Macrovipera* with reservation which refers to closer similarities of the fossil species to the *Macrovipera lebetina* group than to *Vipera palaestinae* or *Montivipera xanthina*.

The Miocene, Hungarian species *Vipera gedulyi* as well as *Vipera antiqua* from the Lower Miocene of Dolnice in the Czech Republic (SZYNDLAR, 1987) represent distinct species well differentiated from *Vipera burgenlandica* (BACHMAYER & SZYNDLAR, 1987). However, the maxillare of *Vipera burgenlandica* is similar to the one of *Vipera gedulyi* following SZYNDLAR (1991b). After VENCZEL (1994), corresponding characteristics of cranial bones and vertebrae connect *Vipera burgenlandica* with *Vipera gedulyi* similar to *Macrovipera lebetina*. VENCZEL (1994) doubts the opinion of NILSON et al. (1999) who classifies *Vipera burgenlandica* and *Vipera gedulyi* together with *Vipera maghrebiana* from the Middle Miocene of Morocco as members of the *Vipera ammodytes* lineage while *Vipera meotica* from the Upper Miocene locality Cherevichnoie of the Ukraine (SZYNDLAR & ZEROVA, 1992) shows similarities to *Vipera aspis*.

Together with *Vipera antiqua*, *Vipera platyspondyla* has been found in the Lower Miocene locality Dolnice in the Czech Republic (SZYNDLAR & SCHLEICH, 1993). ZEROVA (1992) has described *Vipera ukrainica* from the Ukraine. After NILSON et al. (1999), these fossil species belong to the *Vipera xanthina* complex. SZYNDLAR & RAGE (2002) update the fossil record of the true vipers.

In Austria, the extant species *Vipera berus* occurs in the Middle Pleistocene of St. Margarethen in Burgenland (RABEDER, 1977). Today, it is still present in the Austrian Alps. The oldest members of the Viperidae originate from the Lowermost Miocene of France (RAGE & AUGE, 1993) and Germany (SZYNDLAR & RAGE, 1999). KINKELIN (1892) first described *Provipera boettgeri* from the Lowermost Miocene of Germany. In 1896, KINKELIN referred the species to the Crotalinae. Following RAGE (1997), the Eurasian and Afro-Arabian plates collided during the Miocene and viperid snakes appeared in Europe. Exchanges of terrestrial forms between Europe and Asia were no longer hindered by marine barriers.

Viperidae represent an especially variable group. While some members are small and relatively innocuous (e.g. *Vipera berus*, *Vipera ursinii*), others are extremely dangerous such as *Macrovipera lebetina* and *Daboia russelii* (BROWN, 1979).

Ecology and Climate – living relatives: Recent vipers showing close similarities to *Vipera burgenlandica* are represented by *Macrovipera lebetina*, *Vipera palaestinae* and *Montivipera xanthina* (sensu NILSON et al., 1999; BACHMAYER & SZYNDLAR, 1987). The ecological preferences of *Macrovipera*? *burgenlandica* would differ from those of *Montivipera*. While *Montivipera* inhabits rocky habitats at higher altitudes and mostly in temperate areas with a pronounced hibernation period, *Macrovipera* prefers deserts, semi-deserts and steppe habitats (NILSON et al., 1999). The preferred temperature ranges from 25°C to 30°C during the day, and from 17°C to 20°C during the night.

Macrovipera lebetina is distributed on Cyprus and the Cyclades Islands through the Caucasus and Middle East to Kashmir mainly belonging to the Köppen's climate types Cf and Csa (MÜLLER, 1996; see chapters 5, 6). *Montivipera xanthina* occurs in the Caucasus Mountains, in North-West Iran, West Turkey, and south to Israel and Jordan (BROWN, 1979). This area mainly belongs to the Köppen's climate types BS, Cf, Csa, and peripherally to Ds (MÜLLER, 1996; see chapters 5, 6).

Serpentes indet.
(Table 2, 3, 4, 5)

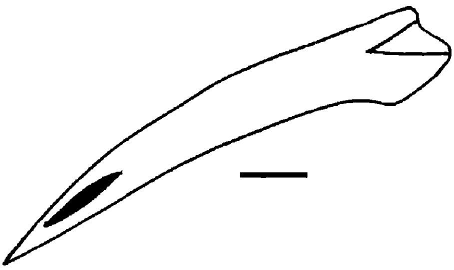


Figure 35: *Vipera burgenlandica*. Veneno illiti dens (Kohfidisch "Altbestand"; Inv. Nr.: NHMW2004z0039/0003), scale bar equals 1 mm.

Material: 19 fragmenta capitis. 1 praemaxillare. 1 quadratum. 16 fragmenta maxillarium indet. 67 fragmenta dentalia indet. 3 dentes. 5 atlantes. 59 vertebrae cervicales. 6016 vertebrae praesacrales. 5925 vertebrae caudales. 4 vertebrae caudales coniunctae. 107 costae.
(BM: Inv. Nr.: NHMW2004z0040/0001).

Description and Comparison: The 12169 elements are fairly fragmentary but the presence of another taxon of the Serpentes than the ones described herein is not indicated.

They are referred to Serpentes indet.

4.3. Skeletal Anomalies of the described Material

Examining the herpetofaunal material of Kohfidisch, two skeletal anomalies could be detected.

Two vertebrae praesacrales (Kohfidisch "Altbestand"; Inv.Nr.: NHMW2004z0035/0007) of *Elaphe kohfidischi* are fused. Their neural arch is broken. The anterior vertebra seems to be slipped into the more posterior one. Its praezygapophyses are separated by a thin slit from the ones of the posterior vertebra. The size of the fused vertebrae is remarkably reduced. Beside that fusion and reflecting on the X-ray photograph (fig 36), the vertebrae show no more anomalies. Very probably, they may be fused from birth on.

The material of *Naja romani* contains a costa (Kohfidisch; Inv.Nr.: NHMW2004z0038/0008) united after fracture. The X-ray photograph (fig. 37) shows a thickened area slightly distal from the caput costae consisting of a bone structure typical of consolidated fractures (Marinelli, pers. advice).

4.4. Paleontological Aspect – an excerpt

Viewing the stratigraphical range (Table 15, 16) and the possible evolutionary trends within the species, the herpetofauna of Kohfidisch essentially supplements the current state of the paleontological record, also in regard to the FODs (= first occurrence dates) and LODs (= last occurrence dates). Among the present taxa, *Triturus (cristatus)* sp., *Bombina* cf. *bombina*, *Lacerta* cf. *viridis*, and *Anguis fragilis* show their FODs, and *Latonia ragei*, *Miolacerta tenuis*, *Edlartetia sansaniensis*, and *Typhlops* cf. *grivensis* their LODs in Kohfidisch. The snakes *Vipera burgenlandica* and *Coluber planicarinatus* have only been described from Kohfidisch as their type locality. As well, Kohfidisch is the type locality of *Elaphe kohfidischi*.

As a member of the Caudata, *Mioproteus caucasicus* stratigraphically ranges from the Lower Miocene to the Upper Miocene of Central and Eastern Europe as well as the Ukraine. In Austria, it is also present in the Upper Miocene localities Richardhof-Golfplatz (MN9; Harzhauser & Tempfer, 2004) and Götzendorf (Uppermost MN9; Miklas, 2002). Therefore, its record from the Upper Miocene locality Kohfidisch numbers among the youngest ones.

The occurrence of *Chelotriton paradoxus*, which is present from the Lower Oligocene to the Upper Miocene in Western Europe, is not unusual in Kohfidisch. In Austria, *Chelotriton paradoxus* existed in Götzendorf (Upper Miocene, Uppermost MN9; Miklas, 2002). The older species *Chelotriton robustus* of the Middle Eocene of Germany can clearly be distinguished from *Chelotriton paradoxus* by the density of tuberculation on the vertebrae (Westphal, 1980). As well, *Chelotriton pliocenicus* of the French Upper Pliocene represents a species well distinct from the others (Bailon, 1989). If these three representatives are part of an evolutionary lineage within *Chelotriton* requires further investigations.

The presence of *Triturus cristatus* (*Triturus* (*cristatus*) sp. described herein) in Kohfidisch shifts its FOD into the Miocene. Previously, the oldest record of the species

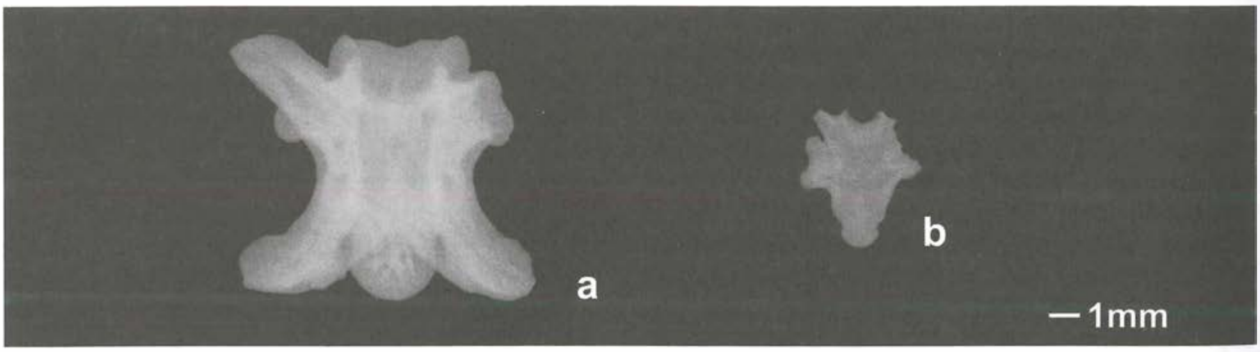


Figure 36: *Elaphe kohfidischi*. Skeletal anomaly (b) of a vertebra preasacralis in comparison to an intact (a) one (Kohfidisch "Altbestand"; Inv.Nr.: NHMW2004z0035/0006, 0007). X-rayed by 50 kV, 0.50 min.

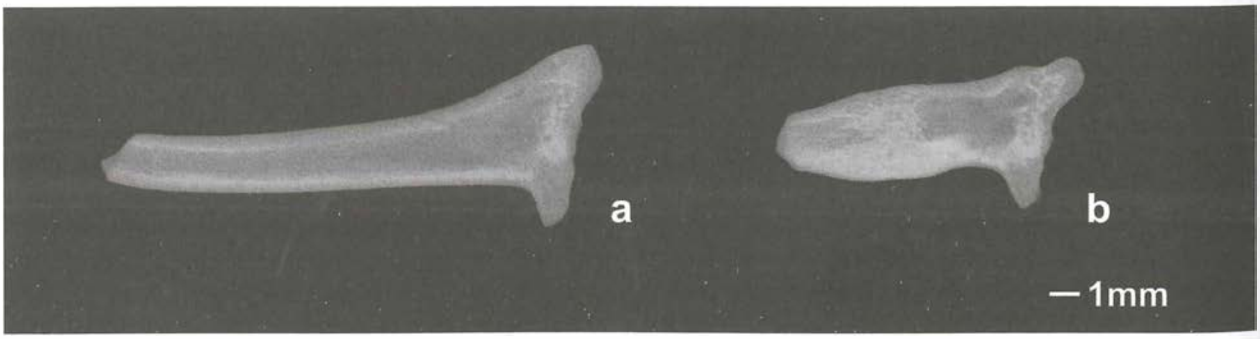


Figure 37: *Naja romani*. Skeletal anomaly (b) of a costa in comparison to an intact (a) one (Kohfidisch; Inv.Nr.: NHMW2004z0038 / 0007, 0008). X-rayed by 50 kV, 1.20 min.

dated back to the Upper Pliocene. As current state, *Triturus cristatus* occurs from the Upper Miocene to the Upper Pleistocene in Austria, Germany, Slovakia, Hungary, and Poland. Today, it inhabits most of Europe, eastwards to the Caucasus and Central Asia.

Triturus vulgaris (*Triturus* (*vulgaris*) sp. described herein) is present from the Middle Miocene to the Pleistocene in Austria, Germany, Slovakia, Italy, Greece, and Britain. The Recent species *Triturus vulgaris* inhabits Europe and West Asia. The two species belong to different groups based on genetic similarities within the genus *Triturus*. While *Triturus cristatus* represents a member of the "Large-Bodied" species group, *Triturus vulgaris* numbers among the "Small-Bodied" species group. *Triturus roehrsi*, an extinct representative of the Lower Miocene to the Upper Miocene of Austria, Slovakia and Hungary, cannot be considered to be the ancestor of one of the two species because its affiliation to the special group is still unclear. While Estes (1981) classifies it into the "Small-Bodied" group, Sanchiz (1998a) observes more similarities to the "Large-Bodied" group.

As a member of the Anura, *Bombina bombina* (*Bombina* cf. *bombina* described herein) has been known from the Upper Pliocene of Poland and the Czech Republic to the Holocene of Austria, Germany and Poland. Regarding the Austrian record, it has been described from the Holocene locality Sommerein by Marinelli (2001). Today, it occurs in Central and Eastern Europe. *Bombina* cf. *bombina* is known from the Upper Miocene or Pliocene of Kazakhstan, the Upper Pliocene of Poland, and the Upper Pliocene and Pleistocene of Russia and Ukraine. The presence of *Bombina* cf. *bombina* in Kohfidisch represents its stratigraphically reliably oldest record. It is unclear, if *Bombina variegata* from the Central European Upper Pleistocene and Holocene directly derived from *Bombina bombina* or both from an ancestral species (Sanchiz & Młynarski, 1979b). Following McCallum et al. (1998), they are able to produce together fertil descendants these days.

Latonia gigantea present from the Lower Miocene to the Pliocene in Europe and *Latonia ragei* just known from the Lower Miocene of Austria, Germany, France, and Spain until now, both occur in Kohfidisch. *Latonia gigantea* has been described from the Austrian locality Götzendorf of the Upper Miocene (Uppermost MN9; Miklas 2002) and is also present in Richardhof-Golfplatz, Austria, Upper Miocene (MN9; Harzhauser & Tempfer, 2004). *Latonia ragei* shows its LOD in the Upper Miocene of Kohfidisch. It has just been described from the Lower Miocene. In Austria, it was present in Oberdorf (MN4; Sanchiz, 1998a) and in Obergänserndorf and Teiritzberg (MN5; M. Böhme, 2002b). The syntopical record of the two species throws a new light on the hypothesis of Roček (1994a) who discusses the possible evolutionary line of the genus *Latonia*: As a lineage, the medium sized *Latonia vertaizoni* of the Upper Oligocene continued as *Latonia ragei* and, following the trend of "gigantism", a medium sized *Latonia gigantea* evolved in the Lower Miocene. The latter increased in size and spread all over Europe, perhaps even to North Africa. Although *Latonia ragei* existed longer than suspected, the quantity of *Latonia gigantea* in Kohfidisch is disproportionately higher. The larger and therefore more robust species *Latonia gigantea* may have displaced *Latonia ragei*.

The oldest questionable record of *Pelobates cultripes* (*Pelobates* cf. *cultripes* described herein) dates back to the Middle Miocene of France. Confidently, it occurs in the Middle Pleistocene to the Holocene of Western Europe. *Pelobates* cf. *cultripes* of Kohfidisch raises the number of the questionable, old records. Extinct and featuring a combination of plesiomorphic characters, *Pelobates decheni* of the Oligocene-Miocene boundary of Germany represents the more primitive form to *Pelobates cultripes* (W. Böhme et al., 1982).

Bufo bufo existed from the Miocene to the Middle Pleistocene and Holocene in Europe, Kazakhstan and Morocco. The Austrian Lower Holocene yields *Bufo bufo* such as noted by Marinelli (2001). Today, it inhabits Europe, North-West Africa and across the Palaearctic Asia to Japan. Its occurrence in the Upper Miocene of Kohfidisch does not appear unexpected.

Present from the Lower Oligocene to the Upper Pleistocene in Europe, Turkey and Morocco, the existence of *Rana* (*ridibunda*) sp. in Kohfidisch is not unusual. With regard to the Austrian record, Sanchiz (1998a) has described *Rana* (*ridibunda*) sp. from the Lower Miocene of Oberdorf (MN4), and M. Böhme (2002b) *Rana* aff. (*ridibunda*) sp. from the Lower Miocene localities Obergänserndorf and Teiritzberg (MN5). *Rana* cf. *ridibunda* appears in the Upper Miocene of Götzendorf (Uppermost MN9; Miklas, 2002). *Rana ridibunda* is present in the Lower Holocene to Holocene Windener Bärenhöhle (Marinelli, 2001).The species can be found in Europe and Israel these days. The determination as *Rana* (*ridibunda*) sp. comprises the fossil waterfrogs of the European Cenozoic (Sanchiz, 1998b).

Among the Reptilia, the lizard *Lacerta* cf. *viridis* shows its FOD in Kohfidisch. Rauscher (1992) has described *Lacerta viridis* from the Plio-/Pleistocene of Bad Deutsch-Altenburg in Austria. In all, the fossil record of the species *Lacerta viridis* and *Lacerta* cf. *viridis* dated from the Upper Pliocene to the Upper Pleistocene of Austria, Slovenia, Hungary, Rumania, Poland, Italy, Sicily, Monaco, and France. Today, it inhabits Central and Southern Europe, Asia Minor and South-West Russia.

Miolacerta tenuis was known from the Lower Miocene of Czech Republik and the Middle Miocene of Germany. The third record in all of this extinct species in Kohfidisch represents its LOD.

Edlartetia sansaniensis, just described from the Middle Miocene of France till now, shows its LOD in the Upper Miocene of Kohfidisch. The definite attribution of the species to the family of the Lacertidae is called into question by Augé & Rage (2000), because the tooth morphology features similarities to the Teiidae as well as to a member of the Anguinae.

The presence of *Anguis fragilis* in Kohfidisch represents its FOD. *Anguis fragilis* also existed in the Plio-Pleistocene locality Bad Deutsch-Altenburg of Austria (Rauscher, 1992). Beside Kohfidisch, it occurred from the Lower

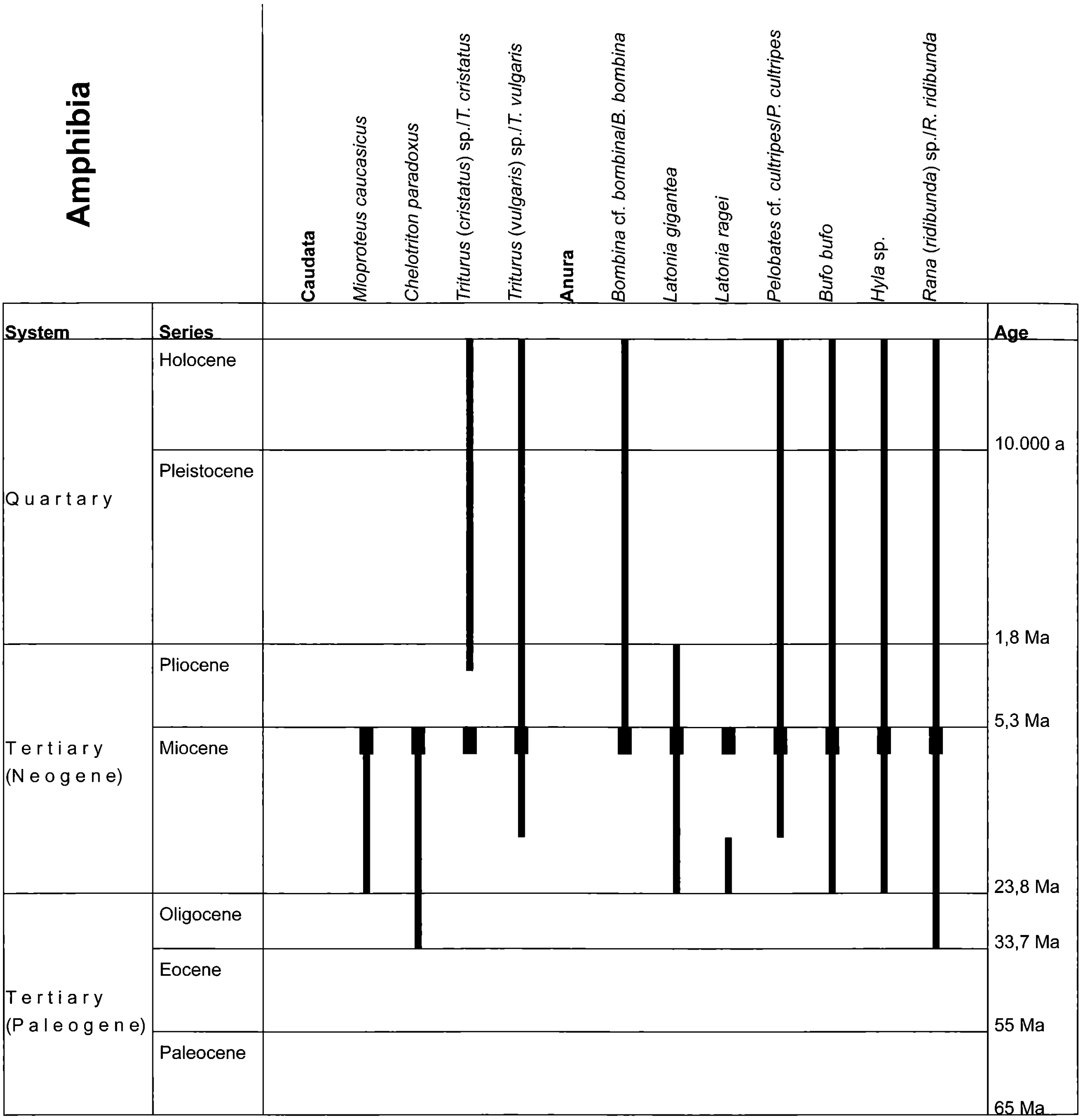


Table 15: Stratigraphical range: Amphibia of Kohfidisch.

Pliocene to the Upper Pleistocene of Austria, Hungary, Poland, Rumania, France, and Spain up to now. The species is distributed from Europe north to Finland, east to the Caucasus and Iran and south to North-West Africa these days.

Pseudopus pannonicus is known from the Upper Miocene to the Pleistocene of Austria, Czech Republic, Hungary, Poland, Rumania, and South-West Russia. More precisely, the oldest remains of *Pseudopus pannonicus* date from the Upper Miocene of Austria (Vösendorf, MN9: Papp & Thenius, 1954; Richardhof-Golfplatz, MN9: Harzhauser & Tempfer, 2004; Götzendorf, Uppermost MN9: Bachmayer & Młynarski, 1977; Eichkogel, MN11: Thenius, 1952) and the Ukraine (Estes, 1983). Therefore, *Pseudopus pannonicus* of Kohfidisch ranks among the oldest records. The Plio-/Pleistocene of Austria (Bad Deutsch-Altenburg: Rauscher, 1992) yields the species as well. *Pseudopus pannonicus* differs just in its bigger size from the extinct species *Pseudopus moguntinus* (Upper Oligocene to Upper Miocene) and the extant representative *Pseudopus apodus*. *Pseudopus laurillardi* (Middle Miocene, MN6, of Sansan in France) represents the smallest Glass Lizard at all and shows osteological dignostic differences to *Pseudopus pannonicus* and *Pseudopus apodus*. Fejérváry-Lángh (1923) suspects the series *Pseudopus moguntinus* – *Pseudopus pannonicus* – *Pseudopus apodus* to be a phyletic one. Due to insufficient discrimination, I would synonymize the three species such as Estes (1983) and Młynarski et al. (1984) proposed. The record of *Varanus* cf. *hofmanni* of Kohfidisch ranks among the youngest

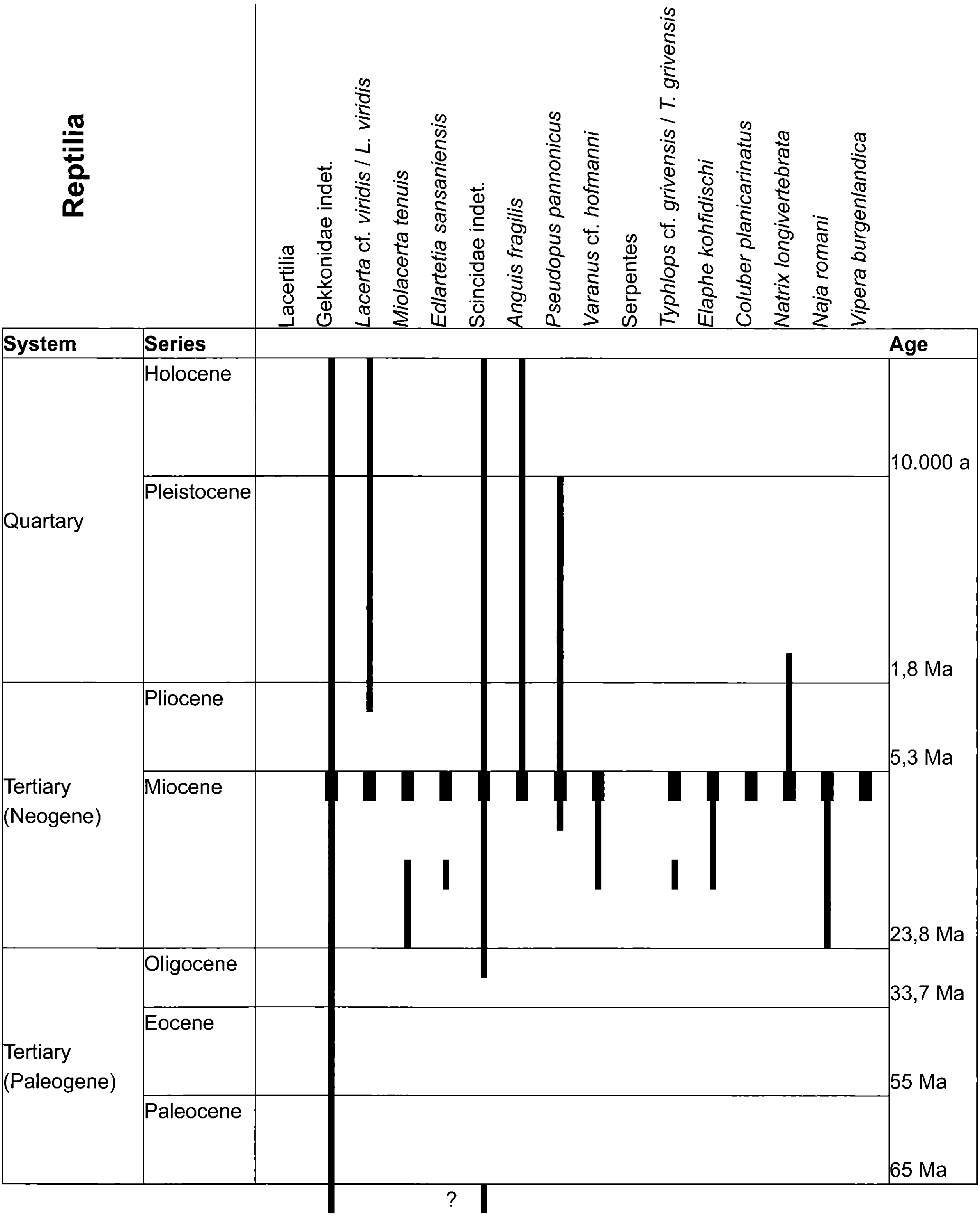


Table 16: Stratigraphical range: Reptilia of Kohfidisch.

ones of the species. Thus, *Varanus hofmanni* and *Varanus* cf. *hofmanni* have been described from the Middle to the Upper Miocene of Austria, Germany, France, and Spain. The relations and the taxonomy even of Recent members of the Varanidae are discussed (Bennet, 1996).

The snake *Typhlops grivensis* was known from the Middle Miocene type locality La-Grive-Saint-Alban in France only. *Typhlops* cf. *grivensis* of Kohfidisch represents the second record and simultaneously the LOD of the species. Kohfidisch represents the type locality of *Elaphe kohfidischi* described by Bachmayer & Szyndlar (1985). Miklas-Tempfer (2003) has afforded the oldest record of *Elaphe kohfidischi* from the Middle Miocene locality Grund (MN5) in Austria. Altogether, it ranges from the

Middle Miocene to the Upper Miocene of Austria. Cf. *Elaphe kohfidischi* is questionably present in the Upper Miocene of the Ukraine. Evolutionary differentiation is visible at the three species *Elaphe longissima – Elaphe paralongissima – Elaphe kohfidischi.* The extant species *Elaphe longissima* inhabiting South and Central Europe these days occurs in the Uppermost Miocene of Polgárdy in Hungary. *Elaphe kormosi* of the same locality is probably closely related to *Elaphe longissima. Elaphe paralongissima* has been described from the Upper Pliocene locality Węze II in South Poland (Szyndlar, 1984) and is also present in the Lower Pleistocene of Hungary and Romania (Venczel, 2000b). Although the three species of *Elaphe* originate from geographically close territories, they are clearly distinct (Bachmayer & Szyndlar, 1985).

Coluber planicarinatus is known so far from the Upper Miocene type locality Kohfidisch only. The parabasisphenoideum closely resembles the ones of the Recent *Coluber najadum- Coluber rubriceps* group (Bachmayer & Szyndlar, 1987).

With regard to Austria, *Natrix longivertebrata* is present in Kohfidisch only. In all, it is distributed from the Upper Miocene to the Lower Pleistocene of Austria, Hungary, Poland, Moldavia, and France. *Natrix longivertebrata* shows an important, perhaps the longest evolutionary stasis quite unusual among snakes (Rage & Szyndlar, 1986). Most cranial bones except the compound bone and especially the parabasisphenoideum are identical to those of the living species *Natrix natrix* (Szyndlar, 1991b). The latter most probably represents the direct descendant of the Neogene species *Natrix longivertebrata* (Szyndlar, 1991c).

The distribution of *Naja romani* ranges from the Lower Miocene to the Upper Miocene of Austria and France. Beside Kohfidisch, the Austrian locality Grund of the Middle Miocene (MN5) yields *Naja romani* (Miklas-Tempfer, 2003). It closely resembles the living species *Naja naja* (Bachmayer & Szyndlar, 1985). Due to their fang structure, both belong to the nonspitting cobras. Following Wüster & Thorpe (1989, 1990, 1991, 1992b), the Recent Asiatic cobra complex comprises a total of at least eight separate species with numerous areas of sympatry between species pairs. Their investigations are based on multivariate analyses of a large number of morphological characters.

As the last member of the snakes, *Vipera burgenlandica* has been described from its Upper Miocene type locality Kohfidisch only. It belongs to the large-sized members of the genus *Vipera*, the so-called "oriental vipers" *Vipera burgenlandica* closely resembles the species *Macrovipera lebetina*, *Vipera palaestinae* and *Montivipera xanthina* but not *Daboia russelii* (sensu Nilson et al., 1999) altogether living large-sized vipers (Bachmayer & Szyndlar, 1987).

5. Köppen's Climate Classification

The Köppen climate system (Köppen, 1923; Köppen & Geiger, 1930-39) represents one of the most clearly arranged classifications. Besides, e.g. Troll & Paffen (1964) have constructed a more detailed climate classification concentrating on vegetation and daily/seasonal differences. I have chosen Köppen's climate classification as the more suitable one to make paleoclimatic conclusions by means of vertebrates.

Köppen's climate formulas are easy to impress. Five major climate types are based on the annual and monthly averages of temperature and precipitation. Each type is designated by a capital letter (Strahler & Strahler, 1984):

A	Moist Tropical Climates are known for their high temperatures all year round and for their large amount of rain all year round.
B	Dry Climates are characterized by little rain and a very high daily temperature range. Two subgroups, **S** - semiarid or steppe, and **W** - arid or desert, are used with the **B** climates.
C	In Humid Middle Latitude Climates land/water differences play a large part. These climates have warm, dry summers and cool, wet winters.
D	Continental Climates can be found in the interior regions of large land masses. Total precipitation is not very high and seasonal temperatures vary widely.
E	Cold Climates describe this climate type perfectly. These climates are part of areas where permanent ice and tundra are present. Only about four months of the year have above freezing temperatures.

Further subgroups are designated by a second, lower case letter which distinguishes specific seasonal characteristics of temperature and precipitation.

f	Moist with adequate precipitation in all months and no dry season. This letter usually accompanies the **A**, **C**, and **D** climates.
m	Rainforest climate in spite of short, dry season in monsoon type cycle. This letter only applies to **A** climates.
s	There is a dry season in the summer of the respective hemisphere (high-sun season).
w	There is a dry season in the winter of the respective hemisphere (low-sun season).

To further denote variations in climate, a third letter was added to the code.

a	Hot summers where the warmest month is over 22°C (72°F). These can be found in **C** and **D** climates.
b	Warm summer with the warmest month below 22°C (72°F). These can also be found in **C** and **D** climates.
c	Cool, short summers with less than four months over 10°C (50°F) in the **C** and **D** climates.
d	Very cold winters with the coldest month below -38°C (-36°F) in the **D** climate only.
h	Dry-hot with a mean annual temperature over 18°C (64°F) in **B** climates only.
k	Dry-cold with a mean annual temperature under 18°C (64°F) in **B** climates only.

Taxa (%)	**Köppen's climate types**																	
	A	Af	Aw	B	BS	BSh	BSk	BW	BWh	C	Cf	Cs	Csa	Cw	D	Df	Ds	Dw
Lacerta sp. A (25)																		
Latonia sp. (9) / *Discoglossus*																		
Bufo bufo (9)				x			x			x	x	x			x	x		x
Pseudopus pannonicus (6) / *Pseudopus apodus*										x		x						
Elaphe kohfidischi / *Elaphe longissima* (6)										x	x	x	x		x	x	x	
Naja romani (6) / *Naja naja*	x	x	x	x	x			x		x		x		x				
Rana (*ridibunda*) sp. (6) / *Rana ridibunda*										x	x	x						
Pelobates cf. *cultripes* (5) / *Pelobates cultripes*										x		x	x					
Anguis fragilis (3)										x	x	x			x	x		
Natrix longivertebrata (3) / *Natrix natrix*										x	x	x	x		x	x		
Vipera burgenlandica (3) / *Macrovipera lebetina*										x	x		x					
Montivipera xanthina				x	x					x	x		x		x		x	
Lacerta sp. B (2)																		
Varanus cf. *hofmanni* (2) / Varanidae	x	x	x	x	x	x			x	x	x	x	x	x				
Coluber planicarinatus (2) / *Coluber najadum*										x	x	x	x					
Triturus (*cristatus*) sp. (2) / *Triturus cristatus*				x						x	x	x	x		x	x	x	
Triturus sp. (2)																		
Edlartetia sansaniensis (1)																		
Typhlops cf. *grivensis* (1) / Typhlopidae	x			x						x								
Typhlops vermicularis										x			x					
Mioproteus caucasicus (1) / *Proteus anguineus*										x	x		x					
Triturus (vulgaris) sp. (1)/Triturus vulgaris										x	x	x			x	x	x	
Latonia gigantea (1)																		
Latonia ragei (1)																		
Scincidae indet. (0.8)																		
Hyla sp. (0.7) / Hylidae																		
Chelotriton paradoxus (0.5) / *Tylototriton*	x	x	x	x	x					x	x			x				
Miolacerta tenuis (0.4)																		
Lacerta cf. *viridis* (0.3) / *Lacerta viridis*										x	x	x			x	x		
Gekkonidae indet. (0.2)																		
Bombina cf. *bombina* (0.1) / *Bombina bombina*										x	x							

Table 17: Köppen's climate types (following MÜLLER, 1996) set in relation to Amphibia and Reptilia of Kohfidisch (MN11) or their closest relatives.

6. Paleoclimatic and -environmental Conclusions, with special remarks on the climatic changes during the Upper Miocene of Austria

Which climate predominated in the Upper Miocene MN11 of Kohfidisch and therefore influenced the flora and fauna? Amphibia and Reptilia and their Recent closest relatives can help approaching a climatic reconstruction.

The Köppen's climate types (see chapter 5) of Eurasia are set in relation to the Amphibia and Reptilia of Kohfidisch or their living, closest relatives respectively which are listed in the percentual, descending frequency of the Minimum Number of Individuals (Table 17).

Generally, each taxon without exception occurs in the Köppen's climate type **C** which designates humid Middle Latitude Climates where land/water differences play a large part. These climates have warm, dry summers and cool, wet winters. The more frequent taxa require the Köppen's climate types **Cf** and **Cs**. East Austria and Kohfidisch in particular belong to the Köppen' s climate type Cf today as Europe except the Iberian Peninsula and the Mediterranean Area where Cs predominates. Therefore, it is not unusual to find Amphibia and Reptilia of that climate in the Upper Miocene of Kohfidisch. Nevertheless, the more frequent taxa remarkably prefer Cs. Less frequently, **Csa** and **Cw** are represented climate types. Csa can be found in Turkey and Afghanistan today, while Cw is present in North India and South China.

The next less frequently inhabited Köppen's climate type is represented by **D** which designates Continental Climates found in the interior regions of large land masses. Total precipitation is not very high and seasonal temperatures vary widely. **Df** is more preferred than **Ds** and **Dw**. While

Taxa (%)	**Köppen's climate types**																		
	A	Af	Aw	B	BS	BSh	BSk	BW	BWh	C	Cf	Cs	Csa	Cw	D	Df	Ds	Dw	E
Latonia gigantea (44) / *Discoglossus*										X		X	X						
Mioproteus caucasicus (31) / *Proteus anguineus*										X	X		X						
Rana cf. *ridibunda* (9) / *Rana ridibunda*										X	X	X							
Andrias scheuchzeri (4) / *Andrias*				X	X		X			X	X			X	X	X			X
Pliobatrachus cf. *langhae* (3)																			
Chelotriton paradoxus (2) / *Tylototriton*	X	X	X	X	X					X	X			X					
Pseudopus pannonicus (2) / *Pseudopus apodus*										X		X							
Triturus roehrsi (1) / *Triturus vulgaris*										X	X	X			X	X	X		
Trionyx sp. (1)																			
Testudo sp. (1)																			
Scleroglossa indet. (1)																			
Colubridae indet. (1)																			

Table 18: Köppen's climate types (following Müller, 1996) set in relation to Amphibia and Reptilia of Götzendorf (Uppermost MN9) or their closest relatives (range of distribution taken from Arnold & Ovenden, 2002; Obst et al., 1984).

Taxa (%)	**Köppen's climate types**																	
	A	Af	Aw	B	BS	BSh	BSk	BW	BWh	C	Cf	Cs	Csa	Cw	D	Df	Ds	Dw
Latonia gigantea (25) / *Discoglossus*										X		X	X					
Lacerta sp. (19)																		
Rana sp. (17)																		
Hyla cf. *arborea* (8) / *Hyla arborea*										X	X	X	X		X		X	
Albanerpeton inexpectatum (6)																		
Pseudopus pannonicus (6) / *Pseudopus apodus*										X		X						
Natricinae indet. (5)																		
Mioproteus caucasicus (4) / *Proteus anguineus*										X	X		X					
Pelobates sp. (4)																		
Triturus sp. (3)																		
Colubrinae indet. (3)																		

Table 19: Köppen's climate types (following Müller, 1996) set in relation to Amphibia and Reptilia of Richardhof-Golfplatz (Upper MN9) or their closest relatives (range of distribution taken from Arnold & Ovenden, 2002).

Df is typical of North Asia, Ds occurs in East Turkey and West Iran. Dw is present in East Asia. The third frequent species *Bufo bufo* occurs among others in the climate types Df and Dw, and the fifth most frequent taxon *Elaphe longissima* inhabits the climate types Df and Ds.

Nearly equally frequently, **A** and **B** are present. The former characterizes moist Tropical Climates known for their high temperatures all year round and for their large amount of rain throughout the year. The climate type **B** typifies a dry one featuring little rain and a very high daily temperature range. Two subgroups, **s** - semiarid or steppe, and **w** - arid or desert, are used with the **B** climates. **Af** is typical of Indonesia, Malaysia, South-West Thailand, and Sri Lanka. **Aw** is present in East India and Thailand. The sixth most frequent species, *Naja naja*, can be found in these climate types at present. The Varanidae and *Tylototriton*, a relative of *Chelotriton*, are typical of Af and Aw. However, the taxa do not represent limiting factors with regard to a Tropical climate. Additionally, they occur in other climate types such as *Naja naja* in Cs and Cw.

Climate **Bs** is typical of Central Iran and Irak east to Central India. The climate type **Bsh** occurs as a narrow zone in North-, Central-, and South Africa. **Bsk** is present as a relatively narrow zone extending from West to East in Central Asia. In Saudi Arabia, Iran and Pakistan, the climate type **Bw** can be found, while **Bwh** is widely distributed in North Africa and just little in East and South Africa. *Bufo bufo* as third frequent species also inhabits the climate type Bsk, *Naja naja* occurs in Bs and Bw. Remarkably, the climatically insensible family of the Varanidae has adapted to the climate types Bs, Bsh and Bwh.

Concluding, the mostly preferred Köppen's climate type Cs designates humid Middle Latitude Climates where land/water differences play a large part with warm and dry summers, cool, wet winters and a dry season in the summer of the respective hemisphere (high-sun season).

Amphibia	Caudata	Albanerpeton inexpectatum	Andrias scheuchzeri	Mioproteus caucasicus	Chelotriton paradoxus	Triturus (cristatus) sp.	Triturus (vulgaris) sp.	Triturus roehrsi	Triturus sp.	Anura	Bombina cf. bombina	Latonia gigantea	Latonia ragei	Latonia sp.	Pliobatrachus cf. langhae	Pelobates cf. cultripes	Pelobates sp.	Bufo bufo	Hyla sp.	Rana cf. ridibunda/R. (ridibunda) sp.	Rana sp.
Richardhof-Golfplatz; MN9	x	x		x					x	x		x					x		x		x
Götzendorf; MN9	x		x	x	x			x		x		x			x					x	x
Kohfidisch; MN11	x			x	x	x	x		x	x	x	x	x	x		x		x	x	x	

Reptilia	Testudines	Trionyx sp.	Mauremys aff. gaudryi	Testudo burgenlandica	Testudo sp.	Testudinidae indet.	Lacertilia	Gekkonidae indet.	Lacerta cf. viridis	Lacerta sp.	Miolacerta tenuis	Edlartetia sansaniensis	Scincidae indet.	Anguis fragilis	Pseudopus pannonicus	Varanus cf. hofmanni	Lacertilia indet.	Serpentes	Typhlops cf. grivensis	Elaphe kohfidischi	Coluber planicarinatus	Colubrinae indet.	Natrix longivertebrata	Natricinae indet.	Colubridae indet.	Naja romani	Vipera burgenlandica
Richardhof-Golfplatz; MN9							x			x					x			x				x		x			
Götzendorf; MN9	x	x			x		x								x		x	x							x		
Kohfidisch; MN11	x		x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x			x	x

Table 20: Presence of herpetofaunal taxa in the Upper Miocene, Austrian localities Richardhof-Golfplatz (Upper MN9), Götzendorf (Uppermost MN9) and Kohfidisch (MN11).

The subgroup Csa includes hot summers where the warmest month is over 22°C. Contrary to Cs, today's climate type Cf of Kohfidisch has no dry season but adequate precipitation in all months. It designates a moist climate. Summing up, the climate in Kohfidisch was drier during the Upper Miocene than today. Occurring on the Iberian Peninsula and the Mediterranean Area, Cs is most probably typical of more southern regions today than during the Upper Miocene.

Concerning the temperature, a higher minimum mean day temperature than today during the active phase of the year is indicated. *Discoglossus* as close relative to the second frequent species *Latonia* sp. inhabits the warmest regions of Europe and tolerates temperatures up to even 30°C. *Pseudopus apodus* needs a temperature of 20°C to 26°C, and the preferred temperature of *Elaphe longissima* ranges between 20°C and 28°C. During the day, *Macrovipera lebetina* is active at a temperature from 22°C to 30°C and *Montivipera xanthina* at a temperature from 25°C to 30°C. Although little frequent but representing limiting factors, the Scincidae need a temperature ranging between 25°C and 30°C, and the living genus *Tylototriton* prefers 22°C to 28°C. Regions inhabited by Recent Gekkonidae are characterized by a temperature between 20°C and 30°C. In Austria, the mean day temperature during the year except winter months ranges between 4.7°C and 19.9°C (Müller, 1996). Some of the Amphibia and Reptilia of the Upper Miocene of Kohfidisch tolerate this temperature. The more predicative taxa which are unable to survive at such low temperatures indicate a warmer climate than today.

For hibernation, frost free places are needed. The majority of the Amphibia and Reptilia may hibernate during winter months at a temperature above 0°C. Protected under stones and leaves, *Bufo bufo* tolerates a temperature of 1°C, *Pseudopus apodus* rests deeply burrowed in the soil for hibernation. The fifth most frequent taxon *Elaphe longissima* needs a temperature between 5°C and 12°C during winter. *Rana ridibunda* hibernates at the bottom of waterbodies where it does not freeze. The temperature for hibernation of *Pelobates cultripes* ranges between 3°C and 4°C. *Anguis fragilis* as well needs frost protected places in winter. As limiting factors, *Tylototriton* hibernates at a temperature of 15°C, and the Gekkonidae require 20°C for hibernation. Representing a remarkable exception, *Typhlops vermicularis* even survives at a minimum temperature of about -20°C. Summarizing and based among others on the presence of *Tylototriton* and the Gekkonidae, frost-free winters are indicated in Kohfidisch during the Upper Miocene.

Reconstructing the climatic evolution of the Miocene in Austria, the herpetofauna of Kohfidisch points to remarkably dry conditions during the MN11 of the Upper Miocene. Two main migration events of thermophilic ectotherms at ~20.0 Ma and ~18.0 Ma (Lower Miocene) indicate the beginning of the Miocene Climatic Optimum in Central Europe (M. Böhme, 2003). With regard to the late Lower Miocene (~18.0 Ma), subtropical climate with a minimum mean annual temperature of 17°C and frost-free winters implying a minimum cold month temperature from 3°C to 8°C predominated (M. Böhme, 2002b). Hofmann et al. (2002) and Meller (1998) as well predicted a subtropical climate of the late Lower Miocene with a minimum mean annual temperature of 14°C based on palynomorphs, fruits and seeds. Following M. Böhme (2003), the Central European climax of the Miocene climatic optimum during the Eggenburgian and Karpatian (Lower Miocene) was accompanied by high humidity.

The Early Badenian of the Middle Miocene is characterized by probably unchanged temperatures but a seasonality in precipitation with dry periods up to six months. Two major seasonal phases are indicated by an immigration of dry adapted taxa. During the Early/Middle Badenian transition, a climatic cooling possibly with frost periods occurred which led to the extinction of thermophilic groups such as alligators, chameleons and giant turtles. The mean annual temperature dropped to temperatures around 14.8°C and 15.7°C. A more distinct climatic zonation began.

Beside Kohfidisch, the Upper Miocene of Austria yields further herpetofaunally interesting localities. They represent additional links for a climatic reconstruction. The locality Sandberg near Götzendorf (henceforth "Götzendorf") belongs to the Uppermost MN9 (Table 1; Daxner-Höck, 2004; Rögl et al., 1993). It is situated in the vicinity of Mannersdorf am Leithagebirge in Lower Austria. Miklas (2002) describes the amphibian fauna and Harzhauser & Tempfer (2004) discuss the Late Pannonian wetland ecology based on the results obtained in Götzendorf. The herpetofauna of Götzendorf (Table 20) or their closest relatives are set in relation to the Köppen's climate types (Table 18).

Richardhof-Golfplatz is positioned close to the western margin of the southern Vienna Basin near Mödling, vicinity Gumpoldskirchen in Lower Austria. Slightly older than Götzendorf, the locality belongs to the Upper MN9 (Daxner-Höck, 2004; Table 1). Its herpetofauna is given in Harzhauser & Tempfer (2004) referring to the Late Pannonian wetland ecology (Table 20). The affiliation of the described species or their closest Recent relatives is given in Table 19.

Unfortunately, the fauna of the locality Richardhof-Golfplatz nearly solely consists of genera or subfamilies and not of species. Therefore, a comparison with Kohfidisch is not possible. Comparing Kohfidisch with the Uppermost MN9 of Götzendorf, the tendency towards dryer conditions is indicated in the MN11 of Kohfidisch. The climatic change towards aridity must have taken place between the Uppermost MN9 and the MN11.

With regard to the temperature, the species or their close living relatives of the Uppermost MN9 locality Götzendorf preferred lower temperatures than in the MN11 locality Kohfidisch. *Discoglossus* as close relative to the most frequent species *Latonia gigantea* tolerates temperatures up to 30°C. *Proteus anguineus* inhabits lakes between 5°C and 10°C. The third most frequent species *Rana ridibunda* lives at temperatures around 20°C, and *Tylototriton* prefers 22°C to 28°C. *Pseudopus apodus* needs 20°C to 26°C, while members of the genus *Triturus* tolerate temperatures from 18°C to 22°C. In all, the climatic change between the Uppermost MN9 and the MN11 should also have influenced the temperature rising in the MN11.

In conclusion, the tendency towards aridity of the Upper MN11 represents a climatic change during the Upper Miocene compared with the Uppermost MN9 of Götzendorf. Very probably, the climate of the Middle Miocene Early Badenian (MN5), during which a seasonality in precipitation with dry periods up to six months (following M. Böhme, 2003) existed, was interrupted by more humid conditions. They predominated in the Uppermost MN9 and changed towards aridity again during the MN11. Additionally, rising temperatures with above all frost-free winters of the MN11 may represent a warming climate in contrast to the climatic cooling (following M. Böhme, 2003) from the Early/Middle Badenian transition (MN5/MN6) on. Between the Uppermost MN9 and the MN11, a climatic change took place.

Fortelius et al. (2002) observe a similar climatic change during the Miocene. They study the fossil teeth of terrestrial plant-eating mammals and their trend to hypsodonty connected with aridity. During the Lower Miocene (24 to 15 Ma), humidity predominates, but increasing hypsodonty including slightly more aridity is indicated in the later part of the interval (later than 18 Ma ago). The Middle Miocene (15 to 11 Ma) shows only little more evidence of increasing aridity. A strong contrast between western and eastern Europe develops. Hypsodont faunas begin to evolve in northern China and Eastern Europe. The earlier Upper Miocene (11 to 8 Ma) features a major strengthening of the hypsodonty in the present-day Mediterranean region and in East-Central Asia. Iberia still remains an area of predominantly low hypsodonty. The pattern changes drastically in the later Upper Miocene (8 to 5 Ma). High hypsodonty predominates all over Europe except parts of Eastern Europe. In East Asia, hypsodonty levels remain moderate and in North China, humidity increases. During the Lower Pliocene (5 to 2 Ma), Europe reverts to lower hypsodonty similar to today's conditions. Increasing humidity after the terminal Miocene is also indicated by non-mammalian evidence.

The extraordinarily rich herpetofauna of Kohfidisch is suitable for a detailed and global paleoenvironmental reconstruction. The outcrop-situation indicates the presence of a cave, fissures and kolks. Within the cave sediments, bentonite has been discovered (P. Wieden; Chemical laboratory Vienna) pointing to an acid volcanism which may have caused the development of the cave. Due to the cooling of the volcanic sediments, fissures may have evolved. Just one profile eastern to the outcrop Kohfidisch and above the quarry ("Steinbruch") exists where fossils are present in clay sediments (Bachmayer & Zapfe, 1969). The sediments are not stratified. Therefore, they do not indicate a permanent water body but however a stagnant, damp environment.

Amphibia and Reptilia of Kohfidisch have been investigated by means of their or their living relatives' ecological requirements (see chapter 4.: Systematic Part). Their order in the text refers to their percentual, descending frequency with regard to the Minimum Number of Individuals (Table 6). They divide into three groups: indicators of dryness alternate with inhabitants of ponds and shallow waters. The third group is represented by both dryness and humidity adapted animals. Homogeneously, the herpetofauna of Kohfidisch prefers a well vegetated ground-cover and open woods with shrubby vegetation. Spinose crevices as well as stone piles offer opportunities to hide.

Mainly members of the Reptilia (%)/Recent relatives of Kohfidisch need dry habitats such as *Elaphe kohfidischi* (6)/*Elaphe longissima* additionally prefering sunny woods with bushy vegetation for climbing. *Naja romani* (6)/*Naja naja* and *Coluber planicarinatus* (2)/*Coluber najadum* inhabit dry places offering vegetation and crevices. Both mainly occur in open areas in woods with scattered groves of trees. As burrower in barren areas, *Typhlops* cf. *grivensis* (1) / *Typhlops vermicularis* occurs in dry and open habitats with slopes and scattered stones.

Not only Amphibia (%)/Recent relatives but also Reptilia (%)/Recent relatives of Kohfidisch represent inhabitants of ponds, stagnant or slowly flowing, shallow waters. Although presumably insensible concerning its ecology, *Latonia* sp. (9) has more often been found in fluviolacustrine deposits. The aquatic species *Rana* (*ridibunda*) sp. (6) / *Rana ridibunda* inhabits sunexposed waters such as small ponds, ditches or streams, and *Pelobates* cf. *cultripes* (5) / *Pelobates cultripes* can be found on sandy coasts near shallow water where it burrows itself into the soil. As representative of the Reptilia, *Anguis fragilis* (3) prefers rather damp, well vegetated environments offering an extensive ground-cover. The aquatic newts *Triturus* (*cristatus*) sp. (2) / *Triturus cristatus* and *Triturus* (*vulgaris*) sp. (1) / *Triturus vulgaris* need stagnant or slowly flowing, shallow water such as ponds for breeding which have a good submerged vegetation. *Mioproteus caucasicus* (1) most probably represented an aerial olm contrary to its living relative *Proteus anguineus*. Due to its fauna assotiation, lotic conditions are indicated. As climbing frog on bushes and trees, *Hyla* sp. (0.7) / *Hyla arborea*; *Hyla meridionalis* inhabits ponds surrounded by low vegetation. The mainly terrestrial living *Chelotriton paradoxus* (0.5) / *Tylototriton* prefers wooded terrains. Its larvae need slowly running water such as ponds or similar water bodies. Therefore, the newt inhabits damp environments with dense vegetation. The lizard *Lacerta* cf. *viridis* (0.3) / *Lacerta viridis* lives in open woods offering bushy vegetation and sunexposed places. Also damp environments are inhabited. Finally, *Bombina* cf. *bombina* (0.1)/*Bombina bombina* as well indicates the existence of shallow water and ponds for breeding. It likes sunexposed watersides.

Indicators of both damp and dry conditions are represented by *Natrix burgenlandica* (3) / *Natrix natrix* and the Scincidae indet. (0.8). Swimming well and hunting in water, the former inhabits damp places near water bodies but may also be found in quite dry woods. The latter represent ground-dwelling lizards which occur in dry habitats as well as in damp meadows.

Summing up, the paleoenvironment of the Upper Miocene locality Kohfidisch is reconstructed. The cave, the fissures and kolks were situated in a sparse, dry wood with a dense and bushy ground-cover. As a water body with good weed growth requiring insolation is indicated, no, or not exclusively a cave-lake existed. More probably, a non-permanent, stagnant, shallow pond near the cave with sunexposed watersides for warming up offered the opportunity to breed, swim and hunt.

A similar environment is required by the terrapin and turtles described by BACHMAYER & MŁYNARSKI (1983). *Mauremys* aff. *gaudryi*/*Mauremys* is typical of stagnant water bodies or slowly flowing rivers with a dense vegetation (DECKERT et al., 1991). The herbivorous turtle *Testudo burgenlandica*/Testudinidae lives 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,S 2001).

Fishes as indicators of limno-fluvial ecosystems are represented among others by the Cypriniformes *Tinca* sp. and *Silurus* sp. (M. BÖHME, pers. advice). *Tinca tinca*, the former's Recent relative, occurs in shallow lakes and slow rivers with dense ground-vegetation. The European species *Silurus glanis* inhabits mainly warm lakes and slowly running waters.

The sparse wood and the water body offered ideal living conditions for diverse small mammals. Especially the large flying squirrel *Pliopetaurista* cf. *bressana* (RABEDER, 1989) needs a stepped light wood for gliding. Large mammals frequently visited the shallow lake for drinking. Unfortunately, they easily fell victim to their predators which retreated into the cave with their prey. Birds brought pellets containing bones of Lower vertebrates into the cave. Hyaenidae (RABEDER, 1989) frequented it and fed on the carrion.

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8. References

ALFÉREZ DELGADO, F. & BREA LÓPEZ, P., 1981. Estudio preliminar de los restos de Peces, Anfibios y Reptiles del yacimiento mioceno de Córcoles (Guadalajara). — Bol. R. Soc. Española Hist. Nat. (Geol.), **79**:5–20, Madrid.

Alifanov, V.R., 1989. The oldest gecko (Lacertilia, Gekkonidae) from the early Cretaceous of Mongolia. — Palaeont. Journ, **23**:128–131, Moskva.

Andreescu, I., 1977. Systématique de Lymnocardiidés prosodacniformes. Sous-famille Prosodacninae. — Mem. Inst. Géol. Géoph., **26**:1–74, Bucarest.

Arnold, E.N. & Ovenden, D., 2002. A Field Guide to the Reptiles and Amphibians of Britain and Europe. — 288 pp., London (HarperCollinsPublishers).

Auffenberg, W., 1963. The fossil snakes of Florida. — Tulane Stud. Zool., **10**/3:131–216, New Orleans.

Augé, M., 1986. Les Lacertiliens (Reptilia, Squamata) de l'Eocene supérieur et de l'Oligocene ouest europeens. — Thèse 3ᵉ. Cycle, **VII** :218 pp., Paris.

Augé, M., 1988. Une nouvelle espèce de Lacertidae (Sauria, Lacertilia) de l'Oligocène français *Lacerta filholi*. – Place de cette espèce dans l'histoire des Lacertidae de l'Eocene superieur au Miocéne inferieur. — N. Jb. Geol. Paläont. Mh., **8**:464–478, Stuttgart.

Augé, M., 1990. La faune de lézards et d'amphisbaenes (Reptilia, Squamata) du gisement de Dormaal (Belgique, Eocène inférieur). — Bull. Inst. Roy. Sci. Nat. Belg., Sci. Terre, **60**:161–173, Bruxelles.

Augé, M. & Rage, J., 2000. Les Squamates (Reptilia) du Miocène moyen de Sansan. — [in:] L. Ginsburg (ed.): La faune miocène de Sansan et son environnement. — Mém. Mus. natn. Hist. Nat., **183**:263–313, Paris.

Augé, M., Duffaud, S., Lapparent de Broin, F. de, Rage, J.-C. & Vasse, D., 1997. Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin Parisien): une herpétofaune de référence pour l'Eocene inférieur. — Géol. France, **1**:23–33, Paris.

Averianov, A.O., 2001. New record of proteid salamanders (Amphibia, Caudata) from the Pliocene of Ukraine and lower Pleistocene of Moldavia. — Vést. zool., **35**/1:43–46, Kiev.

Bachmayer, F. & Młynarski, M., 1977. Bemerkungen über die fossilen *Ophisaurus*-Reste (Reptilia, Anguinae) von Österreich und Polen. — Österr. Akad. Wissensch., Math.-naturw. Kl., Abt. I, **186**/6-10:285–299, Wien.

Bachmayer, F. & Młynarski, M., 1983. Die Fauna der pontischen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich)-Schildkröten (Emydidae und Testudinidae). — Ann. Naturhist. Mus.Wien, **85**/A: 107–128, Wien.

Bachmayer, F. & Szyndlar, Z., 1985. Ophidians (Reptilia: Serpentes) from the Kohfidisch Fissures of Burgenland, Austria. Die Fauna der pontischen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich): Schlangen (Reptilia: Serpentes). — Ann. Naturhist. Mus.Wien, **87**/A:79–100, Wien.

Bachmayer, F. & Szyndlar, Z., 1987. A second contribution to the ophidian fauna (Reptilia: Serpentes) of Kohfidisch, Austria. Zweiter Beitrag zur Schlangenfauna (Reptilia: Serpentes) von Kohfidisch (Burgenland, Österreich). — Ann. Naturhist. Mus.Wien, **88**/A:25–39, Wien.

Bachmayer, F. & Wilson, R.W., 1970. Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). Small Mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch Fissures of Burgenland, Austria.— Ann. Naturhist. Mus.Wien, **74**:533–587, Wien.

Bachmayer, F. & Wilson, R.W., 1978. A second Contribution to the Small Mammal Fauna of Kohfidisch, Austria. Zweiter Beitrag zur Kleinsäugerfauna von Kohfidisch (Burgenland, Österreich). — Ann. Naturhist. Mus.Wien, **81**:129–161, Wien.

Bachmayer, F. & Wilson, R.W., 1980. A Third Contribution to the Fossil Small Mammal Fauna of Kohfidisch (Burgenland), Austria. — Ann. Naturhist. Mus.Wien, **83**:351–386, Wien.

Bachmayer, F. & Wilson, R.W., 1983. Tertiary Gliridae (Dormice) of Austria. — Ann. Naturhist. Mus. Wien, **85**/A:129–134, Wien.

Bachmayer, F. & Wilson, R.W., 1985. Environmental significance and stratigraphic position of some mammal faunas in the Neogene of eastern Austria. Ökologische Bedeutung und stratigraphische Stellung einiger Säugetier-Faunen im Neogen von Ost-Österreich. — Ann. Naturhist. Mus. Wien, **87**/A:101–114, Wien.

Bachmayer, F. & R. W. Wilson, R.W., 1990. Two additions to the Kohfidisch (Burgenland) fauna of Eastern Austria. — Ann. Naturhist. Mus. Wien, **91**/A:1–5, Wien.

Bachmayer, F. & Zapfe, H., 1958. Eine Höhle vor 10 Millionen Jahren – Die Ausgrabung einer vorzeitlichen Tierwelt. — Veröffentlichungen aus dem Naturhistorischen Museum, **1**:6–9, Wien.

Bachmayer, F. & Zapfe, H., 1960. Paläontologische Ausgrabungen des Naturhistorischen Museums-Erschließung einer neuen Fundstelle. — Veröffentlichungen aus dem Naturhistorischen Museum, **3**:21–23, Wien.

Bachmayer, F. & Zapfe, H.,1969. Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). — Ann. Naturhist. Mus. Wien, **73**:123–139, Wien.

Bachmayer, F. & Zapfe, H., 1972. Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). Proboscidea. — Ann. Naturhist. Mus.Wien, **76**:19–27, Wien.

Bailon, S., 1986. Los anfibios y los reptiles del yacimiento de Cueva-Horá (Darro, Granada). — Antrop. y Paleoecol. Humana, **4**:131–155, Granada.

Bailon, S., 1989. Les Amphibiens et les Reptiles du Pliocène superieur de Balaruc II (Herault, France). — Palaeovertebrata, **19**/1:7–28, Montpellier.

Bailon, S., 1991. Amphibiens et reptiles du Pliocene et du Quaternaire de France et d'Espagne: mise en place et evolution des faunes. — 499 pp., Ph. D. thesis, Univ. Paris VII.

Bailon, S., 1995. Présence de *Mioproteus wezei* (Amphibia, Proteidae) dans le Pliocène supérieur (MN 16) d'Europe de l'Ouest. — N. Jb. Geol. Pal. Monatsh., **1**:1–8, Stuttgart.

Bailon, S., 2000. Amphibiens et reptiles du Pliocène terminal d'Ahl al Oughlam (Casablanca, Maroc). — Geodiversitas, **22**/4:539–558, Paris.

Bailon, S. & Aouraghe, H., 2002. Amphibiens, chéloniens et squamates du Pléistocène supérieur d'El Harhoura 1 (Témara, Maroc). — Geodiversitas, **24**/4:821–830, Paris.

Bailon, S. & Hossini, S., 1990. Les plus anciens Bufonidae (Amphibia, Anura) d'Europe les espèce du Miocene français. — Ann. Paleont. (Vert.-Invert.), **76**/2:121–132, Paris.

Bailon, S., Bour, R. & Rage, J.-C., 1988. Quand les espèce de l'herpétofaune française sont-elles apparues? — Bull. Soc. Herp. Fr., **45**:1–8, Paris.

Barbadillo, L.J., 1989. Las Reptilia (Sauria y Amphisbaenia) de los yacimientos Plio-Pleistocenicos de la cuenca de Guadix-Baza (Sudeste espanol). — [in:] Alberdi, M.T. & Bonadonna, F.B. (eds.): Geologia y Paleontologia de la cuenca de Guadix-Baza. Trabajos sobre Neogeno-Cuaternario, **11**:15–165, Madrid.

Barbadillo, L.J. & Sanz, J.L., 1983. Análisis osteometrico de las Regiones Sacra y Presacra de la Columna vertebral en los Lagartos Ibericos *Lacera viridis* Laurenti, *Lacerta lepida* Daudin y *Lacerta schreiberi* Bedriaga. — Amphibia-Reptilia, **4**:215–239, Leiden.

Bennet, D., 1996. Warane der Welt. Welt der Warane. — 383 pp., Frankfurt am Main (Edition Chimaira).

Berggren, W.A., Kent, D.V., Swisher III, C.C. & Aubrey, M.P., 1995. A revised Cenozoic geochronology and chronostratigraphy. — [in:] Berggren, W.A., Kent, D.V. & Hardenbol, J. (eds.): Geochronology, Time Scales and Global Stratigraphic Correlations: A Unified Temporal Framework for an Historical Geology. — Soc. Econom. Pal. Min. Sp. Publ., **54**:129–212, Tulsa.

Bernor, R.L., 1993. *„Hipparion"* von Götzendorf *Hippotherium* cf. *primigenium*. — [in:] Rögl, F. et al.: Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). — Jb. Geol. B.-A., **136**/2:514, Wien.

Bogert, C.M., 1943. Dentitional phenomena in cobras and other elapids, with notes on adaptive modification of fangs. — Bull. Am. Mus. Nat. Hist., **81**:285–360, New York.

Böhme, G., 1977. Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. — Wissenschaftliche Zeitschrift Humboldt-Univ. Berlin, Math.-Nat. Reihe, **26**/3:283–300, Berlin.

Böhme, G., 1979. Die jungquartäre Amphibienfauna aus dem fossilen Tierbautensystem von Pisede bei Malchin. — Ph. D. thesis, Humboldt Univ., Berlin.

Böhme, G., 1983. Paläontologische Beläge für die Bastardierung bei Raniden (Amphibia, Salientia). — Schriftenr. geol. Wiss., **19-20**:31–37, Berlin.

Böhme, G. & Günther, R., 1979. Osteological studies in the European Water Frogs *Rana ridibunda*, *Rana lessonae* and *Rana "esculenta"* (Anura, Ranidae). — Mitt. Zool. Mus. Berlin, **55**/1:203–215, Berlin.

Böhme, M., 1999. Die miozäne Fossil-Lagerstätte Sandelzhausen. 1b. Fisch- und Herpetofauna - Erste Ergebnisse. — N. Jb. Geol. Pal., Abh., **214**/3:487–495, Stuttgart.

Böhme, M., 2002a. Freshwater fishes from the Pannonian of the Vienna Basin with special reference to the locality Sandberg near Götzendorf, Lower Austria. — Cour. Forsch.-Inst. Senckenberg, **237**:151–173, Frankfurt a. M.

Böhme, M., 2002b. Lower Vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin-palaeoecological, environmental and palaeoclimatical implications. — [in:] Sovis, W. & Schmid, B. (eds.): Das Karpat des Korneuburger Beckens Teil 2. — Beitr. Paläont., **27**:339–353, Wien.

Böhme, M., 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. — Palaeogeography, Palaeoclimatology, Palaeoecology, **195**/3-4:389–401.

Böhme, W., Roček, Z. & Spinar, Z.V., 1982. On *Pelobates decheni* Troschel, 1861, and *Zaphrissa eurypelis* Cope, 1866 (Amphibia: Salientia: Pelobatidae) from the Early Miocene of Rott near Bonn, West Germany. — Journ. Verteb. Paleont., **2**/1:1–7, Lawrence.

Bolkay, S.J., 1913. Additions to the fossil Herpetology of Hungary from the Pannonian and Praeglacial Period. — Mitt. Jahrb. Königl. Ungar. Geol. Reichsanst., **21**/7:217–230, Budapest.

Borsuk-Bialynicka, M., 1991. Cretaceous lizard occurrences in Mongolia. — Cretaceous Res., **12**:607–608, London.

Broin, F. de, Buffetaut, E., Koeniguer, J.C., Rage, J.C., Russell, D.E., Taquet, P., Vergnaud-Grazzini, C. & Wenz, S., 1974. La faune de Vertébrés continentaux du gisement d`In Beceten (Sénonien du Niger). — C. R. Acad. Sci. Paris D, **279**:469–472, Paris.

Brown, R.B., 1979. Poisonous Snakes of the World. A manual for use by U. S. amphibious forces. Department of the Navy bureau of Medicine and Surgery. — 212 pp., Washington, D. C. (United States Government Printing Office).

Brunner, G., 1956. Nachtrag zur Kleinen Teufelshöhle bei Pottenstein (Oberfranken). Ein Übergang von der letzten interglazialen Riß-Würm-Warmfauna zur Würm-I-Kaltfauna. — N. Jb. Geol. Pal., Monatsh., **1956**:75–100, Stuttgart.

Bullet, P., 1942. Beiträge zur Kenntnis des Gebisses von *Varanus salvator* Laur. — Viertel. Naturf. Gesell. Zürich, **87**:139–192, Zürich.

Busack, S.D., Maxson, L.R. & Wilson, M.A., 1985. *Pelobates varaldii* (Anura: Pelobatidae): a morphologically conservative species. — Copeia, **1985**:107–112, Carbondale.

Buskirk, J.R., Keller, C. & Andreu, A.C., 2001. *Testudo graeca* Linnaeus, 1758 - Maurische Landschildkröte. — [in:] Fritz, U. (ed.): Handbuch der Reptilien und Amphibien Europas Band 3/IIIA - Schildkröten (Testudines) I (Bataguridae, Testudinidae, Emydidae). — p. 125–178, Wiebelsheim (Aula-Verlag).

Cabela, A., 1997 *Anguis cephallonicus* Werner, 1894. — [in:] Gasc, J.-P. (ed.): Atlas of Amphibians and

Reptiles in Europe. — Soc. Europ. Herp., p. 194–195, Paris.

Cadle, J.E., 1988. Phyletic relationships among advanced snakes. A molecular perspective. – University of California Publications in Zoology, **119**:1–77. – Berkeley.

Carroll, R.L., 1993. Paläontologie und Evolution der Wirbeltiere. – 684 pp. – Stuttgart; New York (Georg Thieme Verlag).

Cheylan, M., 2001. *Testudo hermanni* Gmelin, 1789 Griechische Landschildkröte. – [in:] Fritz, U. (ed.): Handbuch der Reptilien und Amphibien Europas Band 3/IIIA - Schildkröten (Testudines) I (Bataguridae, Testudinidae, Emydidae). – p. 179 – 289. – Wiebelsheim (Aula-Verlag).

Clos, L.M., 1995. A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. — Journ. Vert. Paleont., **15**/2:254–267, Lawrence.

Clot, A., Chaline, J., Jammot, D., Mourer-Chauviré, C. & Rage, J.C., 1976. Les poches ossifères du Pléistocène moyen et inférieur de Montoussé (Hautes-Pyrénées). — Bull. Soc. d'Hist. Nat. de Toulouse, **112**/1-2:1–16, Toulouse.

Cogalniceanu, D. & Venczel, M., 1992. The evolution of the genus *Triturus* (Amphibia, Urodela). Zoogeographical and behavioural data. — Rev. Roum. Biol.–Biol. Anim., **37**/1:57–65, Bucarest.

Darevsky, I. & Tshumakov, I., 1962. A new Pleistocene species of the lizard *Ablepharus* from the Rudny Altai. – Pal. Zurnal, **1**:127–130, Moskva.

Daxner-Höck, G., 1993. Fossilführung: Mammalia: Rodentia. – [in:] Rögl, F. et al.: Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). — Jb. Geol. B.-A., **136**/2:510–511, Wien.

Daxner-Höck, G., 1996. Faunenwandel im Obermiozän und Korrelation der MN-„Zonen" mit den Biozonen des Pannons der Zentralen Paratethys. — Beitr. Paläont., **21**:1–9, Wien.

Daxner-Höck, G., 2004. *Pseudocollimys steiningeri* nov. gen. nov. spec. (Cricetidae, Rodentia, Mammalia) aus dem Ober-Miozän der Molassezone Oberösterreichs. — Cour. Forsch.-Inst. Senckenberg, **246**:1–13, Frankfurt a. M.

Daxner-Höck, G., Miklas-Tempfer, P.M., Göhlich, U., Huttunen, K., Kazár, E., Nagel, D., Roessner, G. E., Schultz, O. & Ziegler, R., 2004. Marine and terrestrial vertebrates from the Middle Miocene of Grund (Lower Austria). — Geologica Carpathica, **55**/2:191–197, Bratislava.

De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P. & Morales, J., 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. — Newsl. Stratigr., **26**/2/3:65–118, Stuttgart.

Deckert, K., Deckert, G., Freytag, G.E., Günther, K., Peters, G. & Sterba, G., 1991. Fische, Lurche, Kriechtiere., 724 pp. — [in:] Die große farbige Enzyklopädie Urania Tierreich., Leipzig; Jena; Berlin (Urania-Verlag).

Delfino, M., 2002. Erpetofaune italiane del Neogene e del Quaternario. — 382 pp., Ph. D. thesis, Univ. Modena e Reggio Emilia.

Delfino, M. & Bailon, S., 2000. Early Pleistocene Herpetofauna from Cava dell'Erba and Cava Pirro (Apulia, Southern Italy). — Herp. Journ, **10**:95–110, London.

Dely, O.G., 1981. *Anguis fragilis* Linnaeus 1758-Blindschleiche. — [in:] Böhme, W. (ed.): Handbuch der Reptilien und Amphibien Europas. Band 1. Echsen I., p. 241–258, Wiesbaden (Akademische Verlagsgesellschaft).

Dehm, R., 1961. Über neue tertiäre Spaltenfüllungen des süddeutschen Jura- und Muschelkalk-Gebietes. — Mitt. Bayer. Staatss. (Pal., Histor. Geol.), **1**:27–56, München.

Eidenmüller, B., 1997. Warane; Lebensweise, Pflege, Zucht. – 157 pp., Offenbach (Verlag Herpeton).

Engelmann, W. E. & Kabisch, K., 1973. Neue Erkenntnisse zum Artcharakter unserer einheimischen Wasserfrösche. — Aquarien u. Terrarien, **1**:16–19, Leipzig, Jena, Berlin.

Engelmann, W.E.F., Jürgen, G.R. & Obst, F.J., 1985. Lurche und Kriechtiere Europas., 420 pp., Stuttgart (Verlag F. Enke).

Estes, R., 1969a. Die Fauna der miozänen Spaltenfüllung von Neudorf an der March (CSSR) Reptilia (Lacertilia). — Sitzungsber. Österr. Akad. Wissensch., Math.-naturw. Kl.:77–82, Wien.

Estes, R., 1969b. A scincoid lizard from the Cretaceous and Paleocene of Montana. — Mus. Comp. Zool. Harvard Univ., **331**:1–9, Cambridge.

Estes, R., 1970a. New fossil pelobatid frogs and a review of the genus *Pelobates*. — Bull. Mus. Comp. Zool., **139**/6:293–339, Cambridge.

Estes, R., 1970b. Origin of the recent North American lower Vertebrate fauna: an inquiry into the fossil record. – Forma et Functio, **3**:139– 63, Braunschweig.

Estes, R. (1975): Lower Vertebrates from the Fort Union Formation, Late Paleocene, Big Horn Basin, Wyoming. — Herpetologica, **31**/4:365–385, Austin.

Estes, R., 1981. Caudata. — [in:] Wellnhofer, P. (ed.): Encyclopedia of Paleoherpetology. Part 2., 115 pp., Stuttgart; New York (Gustav Fischer).

Estes, R., 1983. Sauria terrestria, Amphisbaenia. — [in:] Wellnhofer, P. (ed.): Encyclopedia of Paleoherpetology. Part 10 A., 249 pp., Stuttgart; New York (Gustav Fischer).

Estes, R., 1984. Fish, amphibians and reptiles from the Etudanna formation, Miocene of South Australia. — Austral. Zoologist, **21**/ 4:335–343, Mosman.

Estes, R. & Darevsky. I., 1977. Fossil amphibians from the Miocene of the North Caucasus, U.S.S.R. — Journ. Palaeont. Soc. India, **20**:164–169, Lucknow.

Estes, R. & Schleich, H.H., 1994. New Material of *Mioproteus caucasicus* Estes & Darevsky from South German Localities (Amphibia: Caudata: Proteidae). — Courier Forsch.-Inst. Senckenberg, **173**:7–21, Frankfurt a. M.

Estes, R., Hecht, M. & Hoffstetter, R., 1967. Paleocene Amphibians from Cernay, France. — Amer. Mus. Nov., **2295**:1–25, New York.

Estes, R., Queiroz de, K. & Gauthier, J., 1988. Phylogenetic relationships within Squamata. — [in:] Estes, R. & Pregill, G. (eds.): The Phylogenetic Relationships of the Lizard Families. — p. 119–281, Palo Alto (Stanford Univ. Press).

Etheridge, R., 1967. Lizard caudal vertebrae. — Copeia, **1967**/4:699–721, Carbondale.

Fejérváry-Lángh, A., 1923. Beiträge zu einer Monographie der fossilen Ophisaurier. — Pal. Hung., **I**/7:123–220, Budapest.

Fejfar, O., 1961. Die Plio-Pleistozänen Wirbeltierfaunen von Hajnáćna and Ivanovce (Slowakei), C.S.R. — N. Jb. Geol. Pal., Abh., **3**:257–273, Stuttgart.

Flügel, H. & Heritsch, H., 1968. Das Steirische Tertiär-Becken. — [in:] Lotze, F. (ed.): Sammlung Geologischer Führer. Band **47**. — 196 pp., Berlin, Stuttgart (Gebrüder Borntraeger).

Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z. & Zhou, L., 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. — Evol. Ecol. Res., **4**:1005–1016, Tucson.

Friedl, K., 1932. Ueber die Gliederung der pannonischen Sedimente des Wiener Beckens. — Mitt. Geol. Ges. Wien, **24**/1931:1–27, Wien.

Friedl, K., 1937. Der Steinberg-Dom bei Zistersdorf und sein Ölfeld. — Mitt. Geol. Ges. Wien, **29**/1936:21–290, Wien.

Fuchs, Th., 1873. Erläuterungen zur geologischen Karte der Umgebung Wiens. — 44 pp., Wien (k. k. Geol. Reichsanst.).

Gasc, J.P., Cabela, A., Crnobrnja-Isalovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H., Oliveira, M.E., Sofiadinou, T.S., Veith, M. & A. Zuiderwijk, A., 1997. Atlas of Amphibians and reptiles in Europe. — Soc. Europ. Herp. & Mus. Nat. Hist. Nat., 496 pp., Paris.

Gervais, P.,1859. Zoologie et Paléontologie française, 2^{nde} édit. — Paris (A. Bertrand).

Gheerbrant, E., Cappetta, H., Feist, M., Jaeger, J.-J., Sudre, J., Vianey-Liaud, M. & Sigé, B., 1993. La succession de faunes de vertébrés d'âge paléocène supérieur et éocène inférieur dans le bassin d'Ouarzazate, Maroc. Contexte géologique, portée biostratigraphique et paléogéographique. — Newsl. Strat., **28**/1:33–58, Berlin.

Godinot, M. F., de Broin, F., Buffetaut, E., Rage, J.C. & Russell, A., 1978. Dormaal une des plus anciennes faunes éocènes d'Europe. - C.R. Acad. Sci. Paris, **287**:1273–1276, Paris.

Golay, P., Smith, H.M., Broadley, D.G., McCarthy, C., Rage, J.-C., Schätti, B. & Toriba, M., 1993. Endoglyphs and Other Major Venomous Snakes of the World. A Checklist. — 478 pp., Geneva (Azemiops SA).

Goldfuss, G., 1831. Beiträge zur Kenntnis verschiedener Reptilien der Vorwelt. — Nova Acta Acad. Leop.-Carol., **15**:61–128, Halle/Saale.

Grillitsch, H., 1990. Seefrosch *Rana ridibunda* Pallas, 1771. — [in:] Tiedemann, F., Cabela, A., Grillitsch, H. & Kollar, R. (eds.): Lurche und Kriechtiere Wiens. — p. 102–107, Wien (J & V Edition Wien).

Grillitsch, H. & Cabela, A., 1990. Zum systematischen Status der Blindschleichen (Squamata: Anguidae) der Peloponnes und der südlichen Ionischen Inseln (Griechenland). — Herpetozoa, **2**(3/4):131–153, Wien.

Grillitsch, H. & Grillisch, B., 1993. *Typhlops vermicularis* Merrem, 1820 - Wurmschlange oder Blödauge. — [in:] Böhme, W. (ed.): Handbuch der Reptilien und Amphibien Europas. Schlangen (Serpentes) I. (Typhlopidae, Boidae, Colubridae 1: Colubrinae). — p. 15–32, Wiesbaden (Aula-Verlag).

Grossenbacher, K. & Thiesmeier, B., 2003. Handbuch der Reptilien und Amphibien Europas. — p. 407–753, Wiebelsheim (Aula-Verlag).

Günther, R., 1990. Die Wasserfrösche Europas. — 288 pp., Wittenberg Lutherstadt (A. Ziemsen Verlag; Neue Brehm-Bücherei 600).

Haller-Probst, M. & Schleich, H.H., 1994. Vergleichende osteologische Untersuchungen an einigen Urodelen Eurasiens (Amphibia: Urodela, Salamandridae, Proteidae). — Cour. Forsch.-Inst. Senckenberg, **173**:23–77, Frankfurt a. M.

Harzhauser, M. & Tempfer, P.M., 2004. Late Pannonian Wetland Ecology of the Vienna Basin based on Molluscs and Lower Vertebrate Assemblages (Late Miocene, MN 9, Austria). — Cour. Forsch.-Inst. Senckenberg, **246**:55–68, Frankfurt a. M.

Harzhauser, M., Kovar-Eder, J., Nehyba, S., Ströbitzer-Hermann, M., Schwarz, J., Wójcicki, J. & Zorn, I., 2003. An Early Pannonian (Late Miocene) transgression in the Northern Vienna Basin. The paleoecological feedback. — Geologica Carpathica, **54**:41–52, Bratislava.

Hecht, M.K., 1957. A case of parallel evolution in the salamanders. — Proc. Zool. Soc. Bengal, Mookerjee Mem. Vol., **1957**:283–292, Calcutta.

Hecht, M.K. & Edwards, J., 1976. The determination of parallel or monophyletic relationships: the proteid salamanders - a test case. — American Naturalist, **110**:653–677, Chicago.

Hecht, M. K. & Hoffstetter, R., 1962. Note préliminaire sur les Amphibiens et les Squamates du Landénien superieur et du Tongrien de Belgique. — Bull. Inst. Roy. Science. Nat. Belg., **38/39**:1–30, Bruxelles.

Herre, W., 1932. Zur Anatomie von *Neurergus crocatus* Cope. — Zool. Anz., **100** (11/12):317–326, Leipzig.

Herre, W., 1935. Die Schwanzlurche der mitteleocänen (oberlutetischen) Braunkohle des Geiseltales und die Phylogenie der Urodelen unter Einschluß der fossilen Formen. — Zoologica, **33**:1–85, Stuttgart.

Herre, W., 1950. Neue Tatsachen zur Stammesgeschichte der Schwanzlurche. — Zool. Jahrb., Abt. Syst., **78**:217–236, Stuttgart.

HERRE, W., 1955. Die Fauna der miozänen Spaltenfüllung von Neudorf a. d. March (ČSR.). Amphibia (Urodela). — Sitzungsber. Österr. Akad. Wissensch., Math.-naturw. Kl., Abt. 1, **164**/10:783–803, Wien.

HERRMANN, H.-W., JOGER, U. & NILSON, G., 1992. Phylogeny and systematics of viperine snakes. III: Resurrection of the genus *Macrovipera* (REUSS, 1927) as suggested by biochemical evidence. — Amphibia-Reptilia, **13**/4:375–392, Leiden.

HÍR, J., KÓKAY, J., VENCZEL, M., GÁL, E. & KESSLER, E., 2001. Elözetes beszámoló a felsötárkányi "Güdörkert" n. öslénytani lelöhelykomplex újravizsgálatáról. — F. Hist. Nat. Mus. Matr., **25**:41–64, Gyöngyös.

HODROVÁ, M., 1980. A toad from the Middle Miocene at Devinska Nová Ves near Bratislava. — Věst. Ústř. Úst. Geol., **55**/5:311–316, Praha.

HODROVÁ, M., 1981. Plio- Pleistocene frog fauna from Hajnáčka and Ivanovce, Czechoslovakia. — Věst. Ústř. Úst. Geol., **56**/4:215–224, Praha.

HODROVÁ, M., 1984. Salamandridae of the Upper Pliocene Ivanovce locality (Czechoslovakia). — Acta Univ. Carol. Geol., **4**:331–352, Praha.

HODROVÁ, M., 1985. Amphibia of Pliocene and Pleistocene Vceláre localities (Slovakia). — Casopis pro mineralogii a geologii, **30**/2:145–161, Praha.

HODROVÁ, M., 1987a. Amphibians from the Miocene sediments of the Bohemian Karst. — Casopis pro mineralogii a geologii, **32**/4:345–356, Praha.

HODROVÁ, M., 1987b. Lower Miocene Frogs from the Dolnice locality in the Cheb basin (Czechoslovakia). — Acta Univ. Carol. Geol., **2**:97–115, Praha.

HODROVÁ, M., 1988. Miocene frog fauna from the locality Devinska Nová Ves-Bonanza. — Věst. Ústř. Úst. Geol., **63**/5:305–316, Praha.

HOERNES, R., 1903. Bau und Bild der Ebenen Österreichs. - [in:] DIENER, C., HOERNES, R., SUESS, F.E. & UHLIG, V.: Bau und Bild Österreichs, **I-VI**:917–1110, Wien (F. Tempsky).

HOFMANN, CH.-CH., ZETTER, R. & DRAXLER, I., 2002. Pollen- und Sporenvergesellschaftungen aus dem Karpatium des Korneuburger Beckens (Niederösterreich). — Beitr. Paläont., **27**:17–43, Wien.

HOFFSTETTER, R., 1939. Contribution à l'étude des Elapidae actuels et fossiles et de l'ostéologie des Ophidiens. — Arch. Mus. Hist. Nat. Lyon, **15**:1–78, Lyon.

HOFFSTETTER, R., 1946a. Sur les Gekkonidae fossiles. — Bull. Mus. Nat. Hist. Nat., **2**/18:195–203, Paris.

HOFFSTETTER, R., 1946b. Les Typhlopidae fossiles. — Bull. Mus. Nat. Hist. Nat., **2**/18:309–315, Paris.

HOFFSTETTER, R.,1955. Squamates de type moderne. — [in:] PIVETAU, J. (ed.): Traité de Paleo, **5**:606–662, Paris.

HOFFSTETTER, R., 1969. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. — Bull. Mus. Nat. Hist. Nat., **40**:1051–1064, Paris.

HOFFSTETTER, R. & GASC, J.P., 1969. Vertebrae and ribs of modern reptiles. — [in:] GANS, C. (ed.): Biology of the Reptilia, **1**:201–310, London, New York (Academic Press).

HOLMAN, J.A., 1992. *Hyla meridionalis* from the Late Pleistocene (last interglacial age: Ipswichian) of Britain. — British Herpet. Soc. Bull., **41**:12–14, London.

HOLMAN, J.A., 2000. New herpetological records from the Middle Pleistocene Boxgrove Hominid Site, England. — Cranium, **17**/2:112–120, Heerenberg.

HOLMAN, J.A. & STUART, A.J., 1991. Amphibians of the Whitemoor Channel Early Flandrian Site near Bosley, East Chesire; with remarks on the fossil distribution of *Bufo calamita* in Britain. — Herp. Journ., **1**:568–573, London.

HOOIJER, D., 1972. *Varanus* (Reptilia, Sauria) from the Pleistocene of Timor. — Zool. Mededel., **47**:445–449, Leiden.

HOSSINI, S., 1993. A new species of *Latonia* (Anura, Discoglossidae) from the lower Miocene of France. — Amphibia-Reptilia, **14**:237–245, Leiden.

HUDÁČKOVÁ, N., HOLCOVÁ, K., ZLINSKÁ, A., KOVÁČ, M. & NAGYMAROSY, A., 2000. Paleoecology and eustasy: Miocene 3rd order cycles of relative sea-level changes in the Western Carpathian-North Pannonian basins. — Slovak. Geol. Mag., **6**/2-3:95–100, Bratislava.

IVANOV, M., 2000. Snakes of the lower/middle Miocene transition at Vieux Collonges (Rhône, France), with comments on the colonisation of western Europe by colubroids. — Geodiversitas, **22**/4:559–588, Paris.

IVANOV, M., 2001. Changes in the composition of the European snake fauna during the Early Miocene and at the Early/Middle Miocene transition. — Pal. Z., **74**/4:563–573, Stuttgart.

IVANOV, M., RAGE, J.C., SZYNDLAR, Z. & VENCZEL, M., 2000. Histoire et origine géographique des faunes de serpents en Europe. — Bull. Soc. Herp. Fr., **96**:15–24, Paris.

JACKSON, K., 2002. How Tubular Venom-Conducting Fangs Are Formed. — Morph. Journ., **252**:291–297, Philadelphia.

JANOSCHEK, R., 1943. Das Pannon des Inneralpinen Wiener Beckens. — Mitt. Reichsamt Bodenforsch., Zweigstelle Wien, **6**:45–61, Wien.

KAMAL, A.M., MAMMOUDA, H.G. & MOKHTAR, F.M., 1970. The development of the osteocranium of the Egyptian cobra. — Acta Zool., **51**:1–17, 19–30, 31–42, Stockholm.

KÄMPFE, L., KITTEL, R. & KLAPPERSTÜCK, J., 1966. Leitfaden der Anatomie der Wirbeltiere. — 322 pp., Jena (Gustav Fischer Vlg.).

KINKELIN, F., 1892. Ein fossiler Giftzahn. — Zool. Anz., **15**:93–94, Jena.

KINKELIN, F., 1896. Ein fossiler Giftzahn aus den untermiocänen Hydrobienschichten von Hessler bei Mosbach-Biebrich. — Abh. Senck. Natur. Ges., **20**:36–40, Frankfurt a. M.

KLEMBARA, J., 1979. Neue Funde der Gattungen *Ophisaurus* und *Anguis* (Squamata, Reptilia) aus dem Untermiozän Westböhmens (SSR). — Věst. Ústř. Úst. Geol., **54**/3:163–169, Praha.

KLEMBARA, J., 1981. Beitrag zur Kenntnis der Subfamilie

Anguinae (Reptilia, Anguidae). — Acta Univ. Carol. Geol., **2**:121–168, Praha.

Klembara, J., 1986. Neue Funde der Gattungen *Pseudopus* und *Anguis* (Reptilia, Anguinae) aus drei pliopleistozänen mitteleuropäischen Lokalitäten. — Geol. Carpathica, **37**/1:91–106, Bratislava.

Köppen, W., 1923. Die Klimate der Erde. Grundriß der Klimakunde. — 369 pp., Berlin u. Leipzig (de Gruyter).

Köppen, W. & Geiger, R., 1930-39. Handbuch der Klimatologie. — 5 vols., Berlin (Gebrüder Bornträger).

Kováč, M., Baráth, I., Kováčová-Slamková, M., Pipík, R., Hlavatý, I. & Hudáčková, N., 1998. Late Miocene paleoenvironments and sequence stratigraphy: Northern Vienna Basin. — Geol. Carpathica, **49**/6:445–458, Bratislava.

Kretzoi, M., 1956. Die altpleistozänen Wirbeltier-Faunen des Villányer Gebirges. — Geol. Hungarica. Ser. Pal., **27**:1–264, Budapest.

Kümel, F., 1957. Der Süßwasseropal der Csatherberge im Burgenland. Zur Geologie, Paläobotanik und Geochemie seltener Quellabsätze. — Jb. Geol. B.-A., **100**:1–66, Wien.

Larsen, J. & Guthrie, D., 1974. Parallelism in the Proteidae Reconsidered. — Copeia, **1974**, **3**:635–643, Carbondale.

Laurent, R.F., 1975. La distribution des Amphibiens et les translations continentales. — Mém. Mus. nat. Hist. nat., A/**88**:176–191, Paris.

Lécuru, S., 1969. Étude morphologique de l'humerus des lacertiliens. — Ann. Sci. Nat. Zool., **12**/XI:515–558, Paris.

List, J.C., 1966. Comparative osteology of the snake families Typhlopidae and Leptotyphlopidae. — Illinois Biol. Monogr., **36**:1–112, Urbana and London (The University of Illinois Press).

Lörenthey, I., 1905. Adatok a Balaton-melléki pannóniai korú rétegek faunájához és sztratigráfiai helyzetéhez. — A Balaton Tudományos Tanúlmányozásának Eredményei, **4**/3:1–215, Budapest.

Lutschinger, G., 1988. Zur Überwinterung der Wasserfrösche in den Donau- und Marchauen (Ostösterreich). — [in:] Günther, R. & Klewen, R. (ed.): Beiträge zur Biologie und Bibliographie (1960-1987) der europäischen Wasserfrösche. — Jb. Feldherp., **1**:153–160, Duisburg.

Mais, K. & Rabeder, G., 1984. Das große Höhlensystem im Pfaffenberg bei Bad Deutsch-Altenburg (Niederösterreich) und seine fossilen Faunen. — Die Höhle (Festschrift H. Trimmel), **35**/3, 4:213–230, Wien.

Marinelli, M., 2001. Amphibienfaunen aus jungpleistozänen und holozänen Fundstellen Österreichs inklusive Knochenatlas der aufgefundenen Anurenarten. — Beitr. Paläont., **26**:97–110, Wien.

Martin, R.F., 1972. Evidence from Osteology. — [in:] Blair, W.F. (ed.): Evolution in the Genus *Bufo*. — p. 37–70, Austin and London (Univ. Texas Press).

Mayer, W., Grillitsch, H. & Cabela, A., 1991. Proteinelektrophoretische Untersuchungen zur Systematik der südgriechischen Blindschleichen (Squamata: Anguidae: *Anguis*). — Herpetozoa, **4**(3/4):157–165, Wien.

McCallum, C.J., Nürnberger, B., N.H. Barton & Szymura, J.M., 1998. Habitat preference in the *Bombina* hybrid zone in Croatia. — Evolution, **52**:227–239, Lawrence.

McDowell, S.B., 1967. Osteology of the Typhlopidae and Leptotyphlopidae: a critical review. — Copeia, **1967**/3:686–692, Carbondale.

Mein, P., 1975. Résultats du Groupe de travail des Vertébrés. - Report on activity of the R.C.M.N.S. Working Groups (1971-1975):78–81, Bratislava (SAV).

Mein, P., 1989. Updating of MN Zones. — [in:] Lindsay, E.H., Fahlbusch, V. & Mein, P. (eds.): European Neogene Mammal Chronology. — NATO ASI Series, (A) **180**:73–90, New York (Plenum).

Mein, P., 1999. European Miocene Mammal Biochronology. — [in:] Rössner, G. & Heissig, K. (eds.): The Miocene land mammals of Europe. — p. 25–38, München (Dr. Friedrich Pfeil).

Meller, B., 1998. Karpo-Taphocoenosen aus dem Karpat des Korneuburger Beckens (Unter-Miozän; Niederösterreich) – ein Beitrag zur Vegetationsrekonstruktion. — Beitr. Paläont., **23**:85–121, Wien.

Mertens, R., 1942. Die Familie der Warane (Varanidae). Zweiter Teil: Der Schädel. — Abh. senckenberg.-naturforsch. Ges., **465**:117–234, Frankfurt a. M.

Meyer, H.v., 1843. Summarische Übersicht der fossilen Wirbelthiere des Mainzer Tertiär-Beckens, mit besonderer Rücksicht auf Weissenau. — N. Jb. Min. Geogn. Geol. Petrefaktenkunde:379–410, Stuttgart.

Miklas, P.M., 2002. Die Amphibienfauna (Amphibia: Caudata, Anura) der obermiozänen Fundstelle Götzendorf an der Leitha (südliches Wiener Becken, Niederösterreich). — Ann. Naturhist. Mus. Wien, **103**/A:161–211, Wien.

Miklas-Tempfer, P.M., 2003. The Miocene Herpetofaunas of Grund (Caudata; Chelonii, Sauria, Serpentes) and Mühlbach am Manhartsberg (Chelonii, Sauria, Amphisbaenia, Serpentes), Lower Austria. — Ann. Naturhist. Mus. Wien, **104**/A:195–235, Wien.

Mikulíček, P. & Piálek, J., 2003. Molecular identification of three crested newt species (*Triturus cristatus* superspecies) by RAPD markers. — Amphibia-Reptilia, **24**:201–207, Leiden.

Milner, A.R., 2000. Mesozoic and Tertiary Caudata and Albanerpetontidae. — [in:] Heatwole, H. & R. L. Carrol (eds.): Amphibian Biology. Volume 4: Palaeontology. The Evolutionary History of Amphibians. — p. 1412–1444, Chipping Norton (Surrey Beatty & Sons).

Milner, A.C., Milner, A.R. & Estes, R., 1982. Amphibians and Squamates from the Upper Eocene of Hordle Cliff, Hampshire-a preliminary report. — Tertiary Res., **4**/1:149–154, Leiden.

Młynarski, M., 1956. Lizards from the Pliocene of Poland. Study on the Tertiary bone-breccia from Wéze near Dzialoszyn in Poland. Part IV. — Acta Pal. Polonica,

1:135–152, Warszawa.

Młynarski, M., 1960. Pliocene amphibians and reptiles from Rebielice Królewski (Poland). — Acta Zool. Cracov., **5**:131–153, Kraków.

Młynarski, M., 1961. Amphibians from the Pliocene of Poland. — Acta Pal. Polonica, **6**:261–281, Warszawa.

Młynarski, M., 1962. Notes on the amphibian and reptilian fauna of the Polish Pliocene and Early Pleistocene. — Acta Zool. Cracov., **7**:177–194, Kraków.

Młynarski, M., 1964. Die jungpliozäne Reptilienfauna von Rebielice Królewskie, Polen. — Senck. Biologica, **45**:325–347, Frankfurt a. M.

Młynarski, M., 1976. *Discoglossus giganteus* Wettstein-Westerheim, 1955 (Discoglossidae, Anura) from the Miocene of Przeworno in Silesia (Poland). — Acta Zool. Cracov., **21**:1–12, Kraków.

Młynarski, M., 1977. New notes on the amphibian and reptilian fauna of the Polish Pliocene and Pleistocene. — Acta Zool. Cracov., **22**:13–36, Kraków.

Młynarski, M., 1984. Notes on the amphisbaenian and reptilian Fauna of the Polish Miocene. — Acta Zool. Cracov., **27**/8:127–148, Kraków.

Młynarski, M. & Szyndlar, Z., 1989. Plazy I gady Amphibia and Reptilia. — Polia Quat., **59-60**:69–87, Kraków.

Młynarski, M., Szyndlar, Z., Estes, R. & Sanchiz, B., 1982. Lower vertebrate fauna from the Miocene of Opole (Poland). — Estudios geol., **38**:103–119, Madrid.

Młynarski, M., Szyndlar, Z., Estes, R. & Sanchiz, B., 1984. Amphibians and Reptiles from the Pliocene locality of Weze II near Dzialoszyn (Poland). — Acta Pal. Polonica, **29**/3-4:209–226, Warszawa.

Mookerjee, H.K & Das, G.M., 1933. On the peculiar apertures on the vertebral centra of *Typhlops braminus*. — Proc. Zool. Soc. Lond., **IV**:283, London.

Müller, M.J.,1996. Handbuch ausgewählter Klimastationen der Erde. — [in:] Richter, G. (ed.): Forschungsstelle Bodenerosion der Universität Trier Mertesdorf (Ruwertal), 5. Heft:400 pp., Trier.

Müller, P. & Magyar, I., 1992. Continuous record of the evolution of lacustrine cardiid bivalves in the late Miocene Pannonian lake. — Acta Pal. Polonica, **36**:353–372, Warszawa.

Müller, P. & Magyar, I., 1994. Stratigraphic significance of Upper Miocene lacustrine cardiid *Prosodacnomya* (Kötcse section, Pannonian Basin, Hungary). — Földtani Közlöny, **122**/1992:1–38, Budapest.

Naylor, B., 1978. The systematics of fossil and recent salamanders (Amphibia: Caudata), with special reference to the vertebral colum and trunk musculature. — Ph. D. thesis, Univ. Alberta.

Nilson, G. & Andrén, C., 1997. Evolution, systematics and biogeography of Palaearctic vipers. — [in:] Thorpe, R.S., Wüster, W. & Malhotra, A. (eds.): Venomous snakes: Ecology, evolution and snakebite. - Symp. zool. Soc. Lond., **70**:31–42, Oxford (Oxford University Press).

Nilson, G., Tuniyev, B., Andrén, C., Orlov, N., Joger, U. & Herrmann, H.-W., 1999. Taxonomic Position of the *Vipera xanthina* Complex. — Kaupia, **8**:99–102, Darmstadt.

Nöllert, A. & Nöllert, C., 1992. Die Amphibien Europas. — 382 pp., Stuttgart (Franck-Kosmos Verlags-GmbH & Co).

Norell, M.A., McKenna, M.C. & Novacek, M.J., 1992. *Estesia mongoliensis*, a new fossil varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia. — Amer. Mus. Nov., **3045**:1–24, New York.

Obst, F.J., 1983. Zur Kenntnis der Schlangengattung *Vipera* (Reptilia, Serpentes, Viperidae). — Zool. Abh., **38**:229–235, Dresden.

Obst, F.J., Richter, K. & Jacob, U., 1984. Lexikon der Terraristik. — 466 pp., Leipzig (Edition Leipzig).

Papp, A., 1948. Fauna und Gliederung der Congerienschichten des Pannon im Wiener Becken. — Anz. Österr. Akad. Wissensch., Math.-naturw. Kl., **85**/1948: 123–134, Wien.

Papp, A.,1951. Das Pannon des Wiener Beckens. — Mitt. Geol. Ges. Wien, **39-41**:99–193, Wien.

Papp, A. & Steininger, F., 1979. Die Äquivalente des Tortonian und Messinian in der zentralen Paratethys. — Verh. Geol. B.-A., **1979**/H. **2**:161–170, Wien.

Papp, A. & Thenius, E., 1954. Vösendorf - ein Lebensbild aus dem Pannon des Wiener Beckens. Ein Beitrag zur Geologie und Paläontologie der unterpliozänen Congerienschichten des südlichen Wiener Beckens. — Mitt. Geol. Ges. Wien, **46**:1–109, Wien.

Papp, A., Marinescu, Fl. & Senes, J., 1974. M_5-Sarmatien (sensu E. Suess 1866). Die sarmatische Schichtengruppe und ihr Stratotypus. — Serie Chronostratigraphie und Neostratotypen, **4**:1–707, Bratislava: SAV.

Paunovič, M., 1984. Fische, Amphibien und Reptilien aus oberpleistozänen Ablagerungen von Sandalja bei Pula (Istrien, Kroatien). — Palaeont. Jugosl. akad., **31**:5–44, Zagreb.

Pavnotescu, V. & Andreescu, I., 1978. Asupra unor Prosodacnine din Pontianul de la Boteni (Jud. Arges). — Stud. Cerc. Geol. Geof., Ser. Geol., **23**:143–155, Bucuresti.

Pecorini, G., Rage, J.C. & Thaler, L., 1974. La formation continentale de Capo Mannu, sa faune de vertébrés pliocènes et la question du Messinien en Sardaigne. — Rend. Sem. Fac. Sci. Univ. Cagliari:305–319, Cagliari.

Peters, G., 1977. Die Reptilien aus dem fossilen Tierbautensystem von Pisede bei Malchin. Teil I: Analyse des Fundgutes. — Wiss. Zeitschr. Humboldt Univ. Berlin (Math.-Nat. R.), **26**:307–320, Berlin.

Petzold, H.G., 1971. Blindschleiche und Scheltopusik. — 102 pp., Wittenberg Lutherstadt (A. Ziemsen Verlag; Neue Brehm-Bücherei 448).

Petzold, H.G., 1973. Giftnattern und Seeschlangen. — [in:] Grizmeks Tierleben. Band VI Kriechtiere. — p. 424–450, Zürich (Kindler).

Pollak, W., 1962. Untersuchungen über Schichtfolge, Bau und tektonische Stellung des österreichischen Anteils der Eisenberggruppe im südlichen Burgenland. — 108 pp., Ph. D. thesis, Univ. Wien.

Pomel, A., 1853. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique superieur de la Loire, et surtout dans la vallée de son affluent principal, l'Allier. — 193 pp., Paris.

Pregill, G., Gauthier, J.A. & Greene, H.W., 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. — Transact. San Diego Soc. Nat. Hist., **21**/11:167–202, San Diego.

Presch, W., 1988. Phylogenetic relationships of the Scincomorpha. — [in:] Estes, R. & Pregill, G. (eds.): The Phylogenetic Relationships of the Lizard Families. — p. 472–492, Palo Alto (Stanford Univ. Press).

Rabeder, G., 1974. Fossile Schlangenreste aus den Höhlenfüllungen des Pfaffenberges bei Bad Deutsch-Altenburg (NÖ). — Die Höhle, **25**/4:145–149, Wien.

Rabeder, G., 1977. Wirbeltierreste aus einer mittelpleistozänen Spaltenfüllung im Leithakalk von St. Margarethen im Burgenland. — Beitr. Paläont., **3**:79–103, Wien.

Rabeder, G., 1989. Die Säugetiere des Pontien in Österreich und Ungarn. — [in:] Malez, M. & Stevanovic, P. (eds.): Chronostratigraphie und Neostratotypen. Pliozän Pl_1. Pontien. — p. 821–836, Zagreb-Beograd (JAZU & SANU).

Rage, J.C.,1969. Les amphibiens et les reptiles découverts sur le sol de la cabane acheuléenne du Lazaret. — Mém. Soc. préhist. Fr., **7**:107–110, Paris.

Rage, J.C., 1974. Les serpents des Phosphorites du Quercy. — Palaeovertebrata, **6**:274–303, Montpellier.

Rage, J.C., 1976. Les Squamates du Miocène de Beni Mellal, Maroc. — Géologie méditerranéenne, Tome **III**/2 :57–70, Marseille.

Rage, J.C., 1984a. Are the Ranidae (Anura, Amphibia) known prior to the Oligocene? — Amphibia-Reptilia, **5**:281–288, Leiden.

Rage, J.C., 1984b. Serpentes. — [in:] Wellnhofer, P. (ed.): Encyclopedia of Paleoherpetology. Part 11. — 80 pp., Stuttgart; New York (Gustav Fischer).

Rage, J.C., 1988a. Le gisement du Bretou (Phosphorites du Quercy, Tarn – et – Garonne, France) et sa faune de vertebres de l'Eocène superieur I. Amphibiens et Reptiles. — Palaeontographica Abt. A, **205**/1–6:3–27, Stuttgart.

Rage, J.C., 1988b. The oldest known colubrid snakes. The state of the art. — [in:] Szyndlar, Z. (ed.): Festschrift for Maryan Młynarski. — Acta Zool. Cracov., **31**/13:457–474, Kraków.

Rage, J.C., 1997. Palaeobiological and Palaeogeographical background of the European Herpetofauna. – [in:] Gasc et al. (eds.): Atlas of Amphibians and Reptiles in Europe. Introduction: Paleobiology and Paleogeography. Chapter 3. — Soc. Europ. Herp. & Mus. nat. Hist. natl. (JEGB/ SPN), 496 pp., Paris.

Rage, J.C., 2003a. Oldest Bufonidae (Amphibia, Anura) from the Old World: a bufonid from the Paleocene of France. — Journ. Vert. Paleont., **23**/2:462–463, Lawrence.

Rage, J.C., 2003b. Squamate reptiles from the early Miocene of Arrisdrift (Namibia). — [in:] Pickford, M. & Senut, B. (eds.): Geology and Palaeobiology of the Central and Southern Namib., Vol. **2**: Palaeontology of the Orange River Valley, Namibia:43–50, Windhoeck: Memoir of the Geological Survey of Namibia, 19 (Ministry of Mines and Energy).

Rage, J.C. & Auge, M., 1993. Squamates from the Cainozoic of the Western part of Europe. A Review. — Revue de Paléobiologie, **7**:199–216, Genève.

Rage, J.C. & Hossini, S., 2000. Les Amphibiens du Miocène moyen de Sansan. — [in:] Ginsburg, L. (ed.): La faune miocène de Sansan et son environnement. — Mém. Mus. natn. Hist. nat., **183**:177–217, Paris.

Rage, J.-C. & Roček, Z., 2003. Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. — Amphibia-Reptilia, **24**/2:133–177, Leiden.

Rage, J.C. & Szyndlar, Z., 1986. *Natrix longivertebrata* from the European Neogene, a snake with one of the longest known stratigraphic ranges. — N. Jb. Geol. Pal., Monatsh., **1**:56–65, Stuttgart.

Rage, J.C. & Vergnaud-Grazzini, C., 1978. La poche à phosphate de Ste-Néboule (Lot) et sa faune de Vertébrés du Ludien supérieur. 2. Amphibiens. Etude préliminaire. — Palaeovertebrata, **8**:175–179, Montpellier.

Rauscher, K.L., 1992. Die Echsen (Lacertilia, Reptilia) aus dem Plio- Pleistozän von Bad Deutsch-Altenburg, Niederösterreich. — Beitr. Paläont., **17**:81–177, Wien.

Redkozubov, O.I., 1987. Novye svedeniya o zmeyakh pliotsena Moldavii (New data on snakes of the Pliocene of Moldavia). — Izv. Akad. Nauk Moldav. SSR, Ser. biol. Khim. Nauk, **1987**:71, Chisinau.

Rieppel, O. & Labhardt, L., 1979. Mandibular mechanics in *Varanus niloticus* (Reptilia: Lacertilia). — Herpetologica, **35**/2:158–163, Austin.

Roček, Z., 1981. Cranial anatomy of frogs of the family Pelobatidae Stanius, 1856, with outlines of their phylogeny and systematics. — Acta Univ. Carol. Biol., 1980/**3**:1–164, Praha.

Roček, Z., 1984. Lizards (Reptilia: Sauria) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia). — Rozpr. Českosl. Akad. Věd; Řada matem. A přiro. Věd, Ročnik, **94**/1:1–69, Praha.

Roček, Z., 1988. List of fossil amphibians of Czechoslovakia. — Acta Zool. Cracov., **31**/19:513–540, Kraków.

Roček, Z., 1994a. Taxonomy and distribution of Tertiary discoglossid (Anura) of the genus *Latonia* v. Meyer, 1843. — Geobios, **27**/6:717–751, Villeurbanne.

Roček, Z., 1994b. A review of the fossil Caudata of Europe. — Abh. Ber. Naturk., **17**:51–56, Magdeburg.

Roček, Z., 1996. The salamander *Brachycormus noachicus* from the Oligocene of Europe, and the role of neoteny in the evolution of salamanders. — Palaeontology, **39**/2:477–495, London.

Roček, Z., 2004. Invertebrate Fauna. Amphibians. — [in:]

Bernor, R.L., Kordos, L., Rook, L., Agusti, J., Andrews, P., Armour-Chelu, M., Begun, D.R., Cameron, D.W., Damuth, J., Daxner-Höck, G., De Bonis, L., Fejfar, O., Fassaha, N., Fortelius, M., Franzen, J., Gasparik, M., Gentry, A., Heissig, K., Hernyak, G., Kaiser, T., Koufos, G.D., Krolopp, E., Jánossy, D., Llenas, M., Meszáros, L., Müller, P., Renne, P., Roček, Z., Sen, S., Scott, R., Szyndlar, Z., Topál, G., Ungar, P.S., Utescher, T., Van Dam, J.A., Werdelin, L., Ziegler, R.: Recent Advances on Multidisciplinary Research at Rudabánya, Late Miocene (MN9), Hungary: a compendium. — Palaeontographica Italica, **89** (2002):8–9, Pisa.

Roček, Z. & Nessov, L.A., 1993. Cretaceous anurans from central Asia. — Palaeontographica, Abt. A, **226**:1–54, Stuttgart.

Roger, O., 1898. Wirbelthierreste aus dem Dinotheriensande. II. Teil. — Bericht Naturwiss. Ver. Schwaben u. Neuburg in Augsburg, **33**:385–396, Augsburg.

Roger, O., 1900. Wirbelthierreste aus dem Dinotheriensande. III. Teil. — Bericht Naturwiss. Ver. Schwaben u. Neuburg in Augsburg, **34**:53–70, Augsburg.

Rögl, F. & Daxner-Höck, G.,1996. Late Miocene Paratethys Correlations. — [in:] Bernor, R.L. & Fahlbusch, V. & Mittmann, W. (eds.): Later Neogene European biotic evolution and stratigraphic correlation, **1**/3:47–55, New York (Columbia Press).

Rögl, F., Zapfe, H., Bernor, R., Brzobohaty, R., Daxner-Höck, G., Draxler, I., Fejfar, O., Gaudant, J., Herrmann, P., Rabeder, G., Schultz, O. & Zetter, R., 1993. Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). — Jb. Geol. B.-A., **136**/2:503–526, Wien.

Roth von Telegd, L., 1879. Geologische Skizze des Kroisbach-Ruster Bergzuges und des nördlichen Theiles des Leitha-Gebirges. — Földt. Közl., **9**:99–114 (ung.), 139–150 (deutsch), Budapest.

Sanchiz, F.B., 1977a. Anfibios Cenozoicos de Europa. — COL-PA, **32**:7–9, Madrid.

Sanchiz, F.B., 1977b. La familia Bufonidae (Amphibia, Anura) en el Terciario Europeo. — Trabajos Neógeno-Cuaternario, c.s.s.c., **8**:75–111, Madrid.

Sanchiz, F.B., 1980. Anfibios fósiles de la Cueva de la Paloma (Pleistoceno terminal, Asturias). — [in:] Hoyos, M. et al. (eds.): La Cueva de la Paloma (Soto de las Regueras, Asturias). Excavaciones arqueológicas en Espana. — p. 103–108, Madrid.

Sanchiz, F.B., 1981. Registro fósil y antiguedad de la Familia Hylidae (Amphibia, Anura) en Europe. — Anais II Cong. Latino-americano Paleont., Porto-Alegre: 757–764, Porto-Alegre.

Sanchiz, F.B., 1983. The fossil record of living European amphibians. - Amphibia-Reptilia, **5**/2:198, Leiden.

Sanchiz, F.B., 1998a. Vertebrates from the Early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria): 2. Amphibia. — Ann. Naturhist. Mus. Wien, **99A**:13–29, Wien.

Sanchiz, F.B. (1998b): Salientia. — [in:] Wellnhofer, P. (ed.): Encyclopedia of Paleoherpetology. Part 4. — 276 pp., München (Dr. Friedrich Pfeil).

Sanchiz, F.B. & Młynarski, M.,1979a. Pliocene Salamandrids (Amphibia, Caudata) from Poland. — Acta Zool. Cracov., **24**/4:175–188, Kraków.

Sanchiz, F.B. & Młynarski, M., 1979b. Remarks on the fossil Anurans from the Polish Neogene. -- Acta Zool. Cracov., **24**/3:153–174, Kraków.

Sanchiz, B. & Roček, Z., 1996. An overview of the anuran fossil record. — [in:] Tinsley, R.C. & Kobel, H.R. (eds.): The Biology of *Xenopus*. — p. 317–328, Oxford (Clarendon Press).

Sanchiz, F.B. & Schleich, H.H., 1986. Erstnachweis der Gattung *Bombina* (Amphibia: Anura) im Untermiozän Deutschlands. — Mitt. Bayer. Staatss. (Pal., Histor. Geol.), **26**:41–44, München.

Sanchiz, F.B. & Szyndlar, Z., 1984. Pleistocene amphibian fauna from Kozi Grzbiet in the Holy Cross Mts. — Acta Geol. Polonica, **34**/1-2:51–62, Warszawa.

Sanchiz, F.B., Esteban, M. & Schleich, H.H., 1993. Water Frogs (Ranidae) from the Oligocene of Germany. — J. Herpetol., **27**/4:486–489, Athens (Ohio).

Savage, J.M., 1973. The geographic distribution of frogs: patterns and predictions. — [in:] Vial, J.L. (ed.): Evolutionary Biology of the Anurans. — p. 351–445, Kansas City.

Schaffer, F.X., 1927. Geologische Geschichte und Bau der Umgebung Wiens. — 112 pp., Leipzig-Wien (F. Deuticke).

Schleich, H.H., 1985. Zur Verbreitung tertiärer und quartärer Reptilien und Amphibien. I. Süddeutschland. — Münchner Geowiss. Abh. (A), **4**:67–149, München.

Schleich, H.H., 1987. Neue Reptilienfunde aus dem Tertiär Deutschlands. 7. Erstnachweis von Geckos aus dem Mittelmiozän Süddeutschlands: *Palaeogekko risgoviensis* nov. gen., nov. spec. (Reptilia, Sauria, Gekkonidae). — Mitt. Bayer. Staatss. (Pal., Histor. Geol.), **27**:67–93, München.

Schultz, O., 1993. Fossilführung: Mollusca. — [in:] Rögl, F. et al.: Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). — Jb. Geol. B.-A., **136**/2:509, Wien.

Sedláčková, L., 2000. Comparison of skeletal development in two closely related species, *Bombina bombina* and *B. variegata*. — Ph. D. thesis, Masaryk Univ., Brno.

Seiffert, J., 1969. Sternaelement (Omosternum) eines mitteljurassischen Anuren von SE-Aveyron/Südfrankreich. — Z. f. Zool. Syst. u. Evolut. Forsch., **7**:145–153, Hamburg.

Špinar, Z.V. & Roček, Z., 1984. The discovery of the impression of the ventral side of *Eopelobates anthracinus* Parker, 1929 holotype. — Amphibia-Reptilia, **5**:87–95, Leiden.

Špinar, Z.V., Klembara, J. & Meszáros, S., 1993. A new toad from the Miocene at Devinska Nová Ves (Slovakia). — Západne Karpaty, séria paleontologia, **17**:135–160, Bratislava.

Steiner, H., 1950. Die Differenzierung der paläarktischen

Salamandrinen während des Pleistozäns. — Rev. Suisse Zool., **57**:590–603, Zürich.

STEININGER, F., 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene „European Land Mammal Mega - Zones (ELMMZ)“ and the Miocene „Mammal - Zones (MN - Zones)“ — [in:] RÖSSNER, G. & HEISSIG, K. (eds.): The Miocene land mammals of Europe. — p. 9–24, München (Dr. Friedrich Pfeil).

STEJNEGER, L., 1996. Herpetology of Japan. — 577 pp., Society for the Study of Amphibians and Reptiles.

STEVANOVIC, P.M., 1951. Pontische Stufe im engeren Sinne – Obere Congerienschichten Serbiens und der angrenzenden Gebiete. — Serb. Akad. Wiss. Math.-naturw. Kl., ser. 2 (Sonderausgabe), **187**:1–361, Beograd.

STEVANOVIC, P.M., 1987. Delimination and correlation of the Pontian and the Messinian stages on the basis of malacofauna. — Ann. Inst. Geol. Publ. Hung., **70**:363–370, Budapest.

STRAHLER, A.N. & Strahler, A.H., 1984. Elements of Physical Geography. — 538 pp., New York (Wiley & Sons).

SULLIVAN, R.M., 1987. *Parophisaurus pawneensis* (GILMORE, 1928) new genus of anguid lizard from the middle Oligocene of North America. — J. Herpetol., **21**/2:115–133, Athens, Ohio.

SULLIVAN, R.M., KELLER, T. & HABERSETZER, J., 1999. Middle Eocene (Geiseltalian) anguid lizards from Geiseltal and Messel, Germany. I. *Ophisauriscus quadrupes* KUHN 1940. — [in:] SCHAAL, S. & HABERSETZER, J. (eds.): Current Geological and Paleontological Research in the Messel Formation. — Cour. Forsch.-Inst. Senckenberg, **216**:97–129, Frankfurt a. M.

SZYNDLAR, Z., 1981. Early Pleistocene reptile fauna from Kozi Grzbiet in the Holy Cross Mts. — Acta Geol. Polonica, **31**/1-2:80–101, Warszawa.

SZYNDLAR, Z.,1984. Fossil snakes from Poland. — Acta Zool. Cracov., **28**/1:1–156, Kraków.

SZYNDLAR, Z., 1987. Snakes from the Lower Miocene locality of Dolnice (Czechoslovakia). — Journ. Vert. Paleont., **7**/1:55–71, Lawrence.

SZYNDLAR, Z., 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. — Estudios geol., **47**:103–126, Madrid.

SZYNDLAR, Z., 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. — Estudios geol., **47**:237–266, Madrid.

SZYNDLAR, Z., 1991c. Ancestry of the Grass Snake (*Natrix natrix*): Paleontological Evidence. — Herp. Journ., **25**/4:412–418, London.

SZYNDLAR, Z., 1998. Vertebrates from the Early Miocene lignit deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria) 3. Reptilia 2: Serpentes. — Ann. Naturhist. Mus. Wien, **99**/A:31–38, Wien.

SZYNDLAR, Z. & RAGE, J.C., 1990. West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): interrelationships among extinct and extant species. — Amphibia-Reptilia, **11**:385–400, Leiden.

SZYNDLAR, Z. & RAGE, J.C., 1999. Oldest fossil vipers (Serpentes: Viperidae) from the Old World. — Kaupia, Darmstätter Beitr. Naturgesch., **8**:9–20, Darmstadt.

SZYNDLAR, Z. & RAGE, J.-C., 2002. Fossil record of the true vipers. — [in:] SCHUETT, G.W., HÖGGREN, M., DOUGLAS, M.E. & GREENE, H.W. (eds.): Biology of the vipers: 419 – 444. — Eagle Mountain, Utah (Eagle Mountain Publishing).

SZYNDLAR, Z. & SCHLEICH, H.H., 1993. Description of Miocene snakes from Petersbuch 2 with comments on the Lower and Middle Miocene ophidian faunas of Southern Germany. — Stuttgarter Beiträge zur Naturkunde, B/**192**:1–47, Stuttgart.

SZYNDLAR, Z. & ZEROVA, G.A., 1990. Neogene Cobras of the Genus *Naja* (Serpentes: Elapidae) of East Europe [Neogene Kobras der Gattung *Naja* (Serpentes: Elapidae) aus Osteuropa]. — Ann. Naturhist. Mus. Wien, **91**/A:53–61, Wien.

SZYNDLAR, Z. & ZEROVA, G.A., 1992. Miocene snake fauna from Cherevichnoie (Ukraine, USSR), with description of a new species of *Vipera*. — N. Jb. Geol. Pal., Abh., **184**/1:87–99, Stuttgart.

TEEGE, M.-J., 1957. Studien zur Entwicklung und Gestalt der Urodelenwirbel. — Zeitschr. wiss. Zool., **160**:95–163, Leipzig.

TEMPFER, P.M., 2004. *Andrias scheuchzeri* (Caudata: Cryptobranchidae) aus der obermiozänen (MN 7-8) Fundstelle Mataschen/Steiermark. *Andrias scheuchzeri* (Caudata: Cryptobranchidae) from the Upper Miocene (MN 7-8) locality Mataschen/Steiermark. — Joannea Geol. Pal., **5**:257–268, Graz.

THENIUS, E., 1952. Über das Vorkommen von *Ophisaurus* (Anguidae, Rept.) im Pannon von Niederösterreich. — Anz. Österr. Akad. Wiss., **11**:177–180, Wien.

TIHEN, J.A., 1972. The Fossil Record. — [in:] BLAIR, W.F. (ed.): Evolution in the Genus *Bufo*. — p. 8–13, Austin and London (Univ. Texas Press).

TROLL, C. & PAFFEN, K.H., 1964. Die Jahreszeitenklimate der Erde. (Summary: The seasonal climates of the Earth). — Erdkunde, **18**:1–28, Bonn.

TUNNER, H.G., 1970. Das Serumeiweißbild einheimischer Wasserfrösche und der Hybridcharakter von *Rana esculenta*. — Verhandlungsber. Dt. zool. Ges., **64**:352–358, Stuttgart.

TUNNER, G.H., 1996. Der Teichfrosch *Rana esculenta* - Ein evolutionsbiologisch einzigartiger Froschlurch. — Stapfia **47**, zugleich Kataloge des O.Ö. Landesmuseums N. F., **107**:87–102, Linz.

TUNNER, G.H., 1997. Warum ist der Teichfrosch noch nicht aus der heimischen Fauna verschwunden? — Symp. F. Vivaristik:71–76, Lindabrunn.

TUNNER, G.H. (2000): Evidence for genomic imprinting in unisexual triploid hybrid frogs. — Amphibia-Reptilia, **21**:135–141, Leiden.

UZZELL, T., 1982. Immunological relationship of Western Palearctic water frogs (Salientia: Ranidae). — Amphibia-Reptilia, **3**:135–143, Leiden.

VENCZEL, M., 1991. New contributions to the herpetofauna of Subpiatrã (Bihor County, Romania). — Nymphaea,

21:81–88, Oradea.

VENCZEL, M., 1994. Late miocene snake from Polgárdi (Hungary). — Acta Zool. Cracov., **37**/1:1–29, Kraków.

VENCZEL, M., 1997a. Late Miocene anurans from Polgárdi (Hungary). — [in:] BÖHME, W., BISCHOFF, W. & ZIEGLER, T. (ed.): Herpetologica Bonnensis:383–389, Bonn.

VENCZEL, M., 1997b. Amphibians and Reptiles from the lower pleistocene of Osztramos (Hungary). — Nymphaea, **23-25**:77–88, Oradea.

VENCZEL, M., 1997c. Un grup nou de ofidieni pentru fauna paleoherpetologica a României. — Nymphaea, **23-25**:89–92, Oradea.

VENCZEL, M., 1998. Late Miocene snakes (Reptilia: Serpentes) from Polgárdi (Hungary): a second contribution. — Acta Zool. Cracov., **41**:1–22, Kraków.

VENCZEL, M., 1999a. Land salamanders of the family Hynobiidae from the Neogene and Quaternary of Europe. — Amphibia-Reptilia, **20**:401–412, Leiden.

VENCZEL, M., 1999b. Anurans from the late Miocene of Tardosbánya (Hungary). — Nymphaea, **XXVII**:82–90, Oradea.

VENCZEL, M., 2000a. Quaternary snakes from Bihor (Romania). — 142 pp., Oradea (Tarii Crisurilor Museum).

VENCZEL, M., 2000b. The Genus *Elaphe* in the Carpathian Basin: Fossil Record. — Nymphaea, **28**:65–82, Oradea.

VENCZEL, M., 2001. Anurans and squamates from the Lower Pliocene (MN14) Osztramos 1 locality (Northern Hungary). — Fragmenta Palaeontologica Hungarica, **19**:79–90, Budapest.

VENCZEL, M. & CSIKI, Z., 2003. New frogs from the latest Cretaceous of Hateg Basin, Romania. — Acta Palaeontol. Pol., **48**/4:609–616, Warszawa.

VERGNAUD-GRAZZINI, C., 1970. Les amphibiens du gisement d'Arondelli. - Palaeont. Ital., **66**:47–65, Pisa.

WAKE, D. & ÖZETI, N., 1969. Evolutionary Relationships in the Family Salamandridae. — Copeia **1969/1**:124–137, Carbondale.

WEERS VAN, D.J. & MONTOYA, P., 1996. Taxonomy and Stratigraphic record of the oldest European porcupine *Hystrix parvae* (KRETZOI, 1951). — Proc. Kon. Ned. Akad. v. Wetensch., **99**/1-2:131–141, Amsterdam.

WELCH, K., 1988. Snakes of the Orient. A checklist. — 192 pp., Malabar, Florida (Krieger Publishing).

WESTPHAL, F., 1980. *Chelotriton robustus* n. sp., ein Salamandride aus dem Eozän der Grube Messel bei Darmstadt. — Senckenbergiana Lethaea, **60**/4-6:475–487, Frankfurt a. Main.

WETTSTEIN-WESTERSHEIMB, O., 1955. Die Fauna der miozänen Spaltenfüllung Neudorf a. d. March (CSR) Amphibia (Anura) et Reptilia, Amphibia (Froschlurche). — Sitzungsber. Österr. Akad. Wissensch. math.-naturw. Kl., Abt. 1, **164**/10:801–815, Wien.

WÜSTER, W. & THORPE, R.S., 1989. Population affinities of the Asiatic cobra (*Naja naja*) species complex in Southeast Asia: Reliability and random resampling. — Biol. J. Linn. Soc., **36**:391–409, London.

WÜSTER, W. & THORPE, R.S., 1990. Systematics and biogeography of the Asiatic cobra (*Naja naja*) species complex in the Philippine Islands. — [in:] PETERS, G. & HUTTERER, R. (eds.): Vertebrates in the Tropics. — p. 333–344, Bonn (Museum A. Koenig).

WÜSTER, W. & THORPE, R.S., 1991. Asiatic cobras: Systematics and snakebite. — Experientia, **47**:205–209, Basel.

WÜSTER, W. & THORPE, R.S., 1992a. Dentitional phenommena in cobras revisited: spitting and fang structure in the Asiatic species of *Naja* (Serpentes: Elapidae). — Herpetologica, **48**/4:424–434, Austin.

WÜSTER, W. & THORPE, R.S., 1992b. Asiatic cobras. Population systematics of the *Naja naja* species complex (Serpentes: Elapidae) in India and Central Asia. — Herpetologica, **48**:69–85, Austin.

ZEROVA, G.A., 1987. Lézards et serpents des gisements du Miocène superieur au Pléistocène inférieur d'Ukraine. — [in:] SKOMOROVSKAIA, E.I. (ed.): Sur quelques groupes de vertébrés du Cénozoïque supérieur d'Ukraine. — Institut Zoologii Akademii Nauk Ukrainskoy S.S.R.:12–18.

ZEROVA, G.A., 1992. *Vipera* (*Daboia*) *ukrainica* - a new viper (Serpentes; Viperidae) from the Middle Sarmatian (Upper Miocene) of the Ukraine. — N. Jahrb. Geol. Paläont. Abh., **184**/2:235–249, Stuttgart.

ZEROVA, G.A. & CKHIKVADZE, V.M., 1986. Neogene Varanids of the URSS. — [in:] ROČEK, Z. (ed.): Studies in Herpetology. — p. 689–694, Prague.

APPENDIX

Taxa	o. Ang.	Altb.	cm	a	b	7	9	I	II	III	III unten	III oben	IV	V	VI	total
Amphibia	451	149	31	—	—	—	—	163	64	393	1714	330	64	1	—	**3360**
Reptilia	14156	2141	434	50	24	9	28	3073	1195	8760	12635	9006	384	2	62	**51959**
Amph. et Rept.	14607	2290	465	50	24	9	28	3236	1259	9153	14349	9336	448	3	62	
Amphibia																**3360**
Caudata																**362**
Mioproteus caucasicus	7	4						2	1	4	7	8				33
Chelotriton paradoxus	8	2						5		2	3	3				23
Triturus (*cristatus*) sp.	45	6	5					11	2	12	62	22	4	1		170
Triturus (*vulgaris*) sp.	16	1						7		6	21		1			52
Triturus sp.	11	3	1					7	1	9	40	11	1			84
Anura																**2998**
Bombina cf. *bombina*		1									4					5
Latonia gigantea	11	1						2		3	27	2				46
Latonia ragei	2							2		2	4	2				12
Latonia sp.	115	39	2					33	7	106	445	49	19			815
Pelobates cf. *cultripes*	42	10	3					6	5	31	161	37	6			301
Bufo bufo	85	43	7					37	28	80	360	101	23			764
Hyla sp.	1	2						2	1	1	14	3	2			26
Rana (*ridibunda*) sp.	45	9	3					18	8	29	279	28	8			427
Anura indet.	63	28	10					31	10	109	287	64				602

Table 2: Maximum Number of Individuals (MXNI) of Kohfidisch: Amphibia and Reptilia.

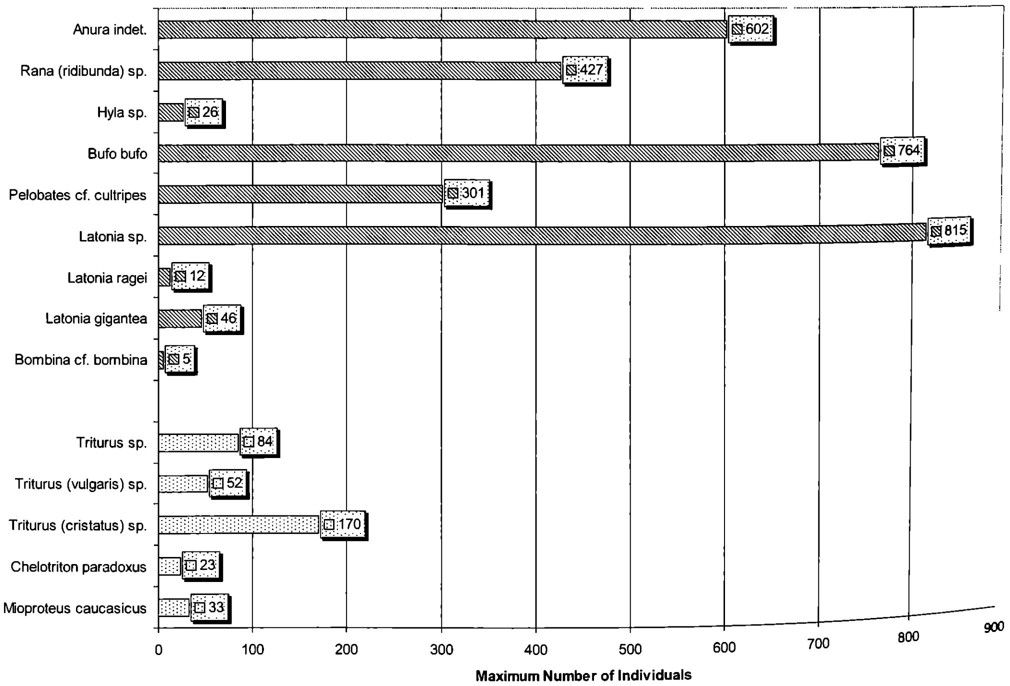

Diagram 1: Maximum Number of Individuals (MXNI) of Kohfidisch: Amphibia.

Taxa	o. Ang.	Altb.	cm	a	b	7	9	I	II	III	III unten	III oben	IV	V	VI	total
Reptilia																**51959**
Lacertilia																**15883**
Gekkonidae indet.										3						3
Lacerta cf. *viridis*	6		1					1		1	2	2				13
Lacerta sp. A	687	63	34					291	96	187	531	209	15			2113
Lacerta sp. B	18		16					9		10	12	6				71
Miolacerta tenuis	2		1					1			1	1				6
Edlartetia sansaniensis	15							5			12	4				36
Scincidae indet.	10								1	2	2	3				18
Anguis fragilis	257	53	69					34	35	117	937	164	28			1694
Pseudopus pannonicus	5177	321	6	4	3	1		931	192	790	2582	1725	32		62	11826
Varanus cf. *hofmanni*	12	1						19	9	14	15	8				78
Lacertilia indet.	6	1	1							1	13	3				25
Serpentes																**36076**
Typhlops cf. *grivensis*	5	1	4					3	1	1	10	2				27
Elaphe kohfidischi	2232	700	73			1		429	222	3395	3977	2673	159	1		13862
Coluber planicarinatus	33	2	3					10	9	29	33	35	1			155
Natrix longivertebrata	278	44	3					51	21	330	451	273	27			1478
Naja romani	2939	280	113	37	21	6	22	806	189	954	687	1055	29			7138
Vipera burgenlandica	234	71	6	2				54	44	344	282	147	9			1193
Serpentes indet.	2245	604	104	7		1	6	429	376	2580	3088	2698	84	1		12223

Table 3: Maximum Number of Individuals (MXNI) of Kohfidisch: Reptilia.

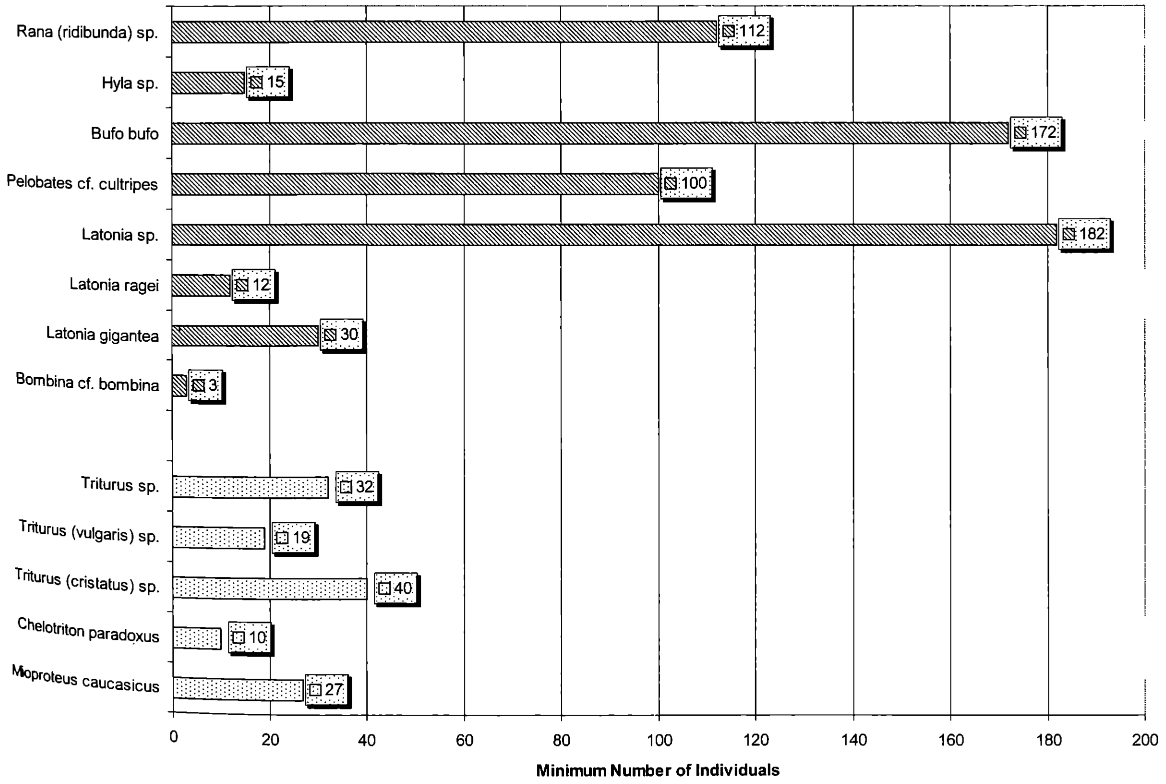

Diagram 2: Maximum Number of Individuals (MXNI) of Kohfidisch: Reptilia.

Taxa	o. Ang.	Altb.	cm	a	b	7	9	I	II	III	III unten	III oben	IV	V	VI	total
Amphibia	128	29	9	/	/	/	/	48	24	101	290	109	15	1	/	**754**
Reptilia	331	18	28	3	2	3	1	146	65	195	264	187	14	1	1	**1259**
Amph. et Rept.	459	47	37	3	2	3	1	194	89	296	554	296	29	2	1	**2013**
Amphibia																**754**
Caudata																**128**
Mioproteus caucasicus	6	1						2	1	4	6	7				27
Chelotriton paradoxus	2	1						1		2	2	2				10
Triturus (*cristatus*) sp.	8	1	2					2	1	5	11	8	1	1		40
Triturus (*vulgaris*) sp.	5							1		5	7		1			19
Triturus sp.	7	1	1					1	2	4	8	7	1			32
Anura																**626**
Bombina cf. *bombina*		1									2					3
Latonia gigantea	6	1						1		3	17	2				30
Latonia ragei	2							2		2	4	2				12
Latonia sp.	48	4	1					13	3	32	63	16	2			182
Pelobates cf. *cultripes*	15	4	1					3	2	18	41	14	2			100
Bufo bufo	15	11	2					13	8	17	69	33	4			172
Hyla sp.	1	2						2	1		6	2	1			15
Rana (*ridibunda*) sp.	13	2	2					7	6	9	54	16	3			112

Table 4: Minimum Number of Individuals (MNI) of Kohfidisch: Amphibia and Reptilia.

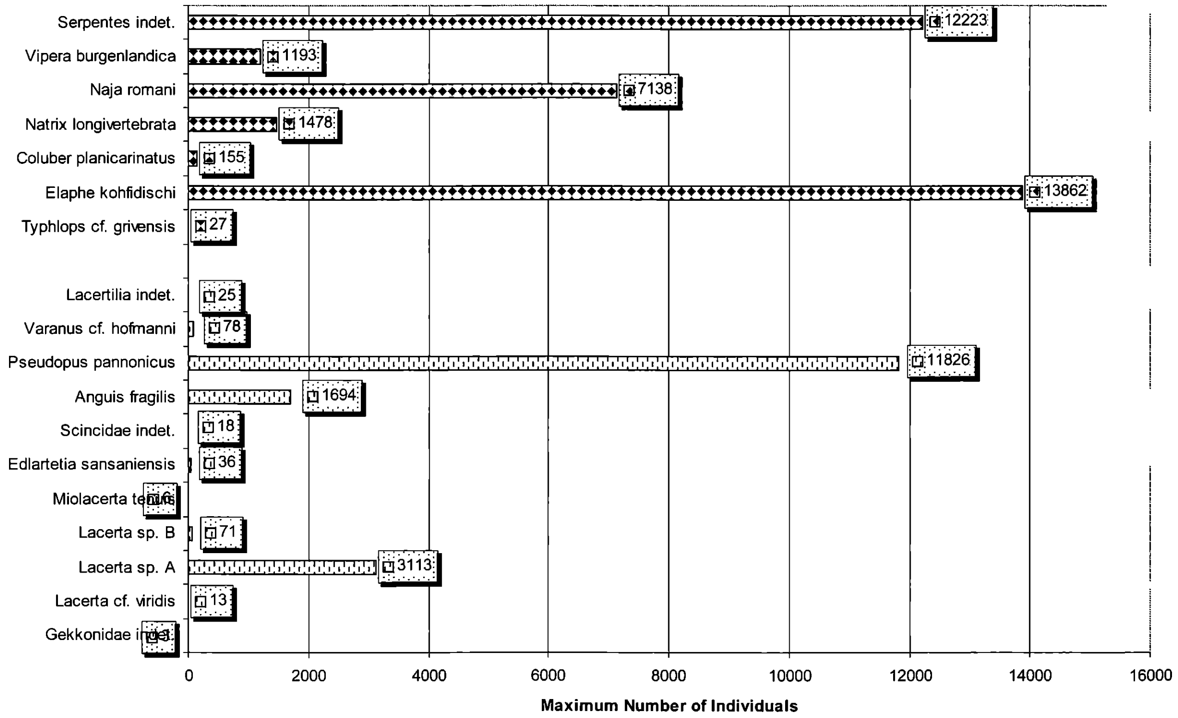

Diagram 3: Minimum Number of Individuals (MNI) of Kohfidisch: Amphibia.

Taxa	o. Ang.	Altb.	cm	a	b	7	9	I	II	III	III unten	III oben	IV	V	VI	total
Reptilia																**1259**
Lacertilia																**814**
Gekkonidae indet.										3						3
Lacerta cf. *viridis*	3							1		1		1				6
Lacerta sp. A	159	5	8					75	30	52	106	60	2			497
Lacerta sp. B	11		3					6		10	9	5				44
Miolacerta tenuis	3		1					1			1	1				7
Edlartetia sansaniensis	8							4			11	3				26
Scincidae indet.	8								1	2	2	3				16
Anguis fragilis	14	1	2					5	4	12	13	14	2			67
Pseudopus pannonicus	37	2	1	1	1	1		10	6	16	16	18	1		1	111
Varanus cf. *hofmanni*	8	1						3	3	11	6	5				37
Serpentes																**445**
Typhlops cf. *grivensis*	3	1	2					3	1	1	4	1				16
Elaphe kohfidischi	17	3	2			1		10	5	30	32	20	2	1		123
Coluber planicarinatus	7	1	1					2	2	8	9	8	1			39
Natrix longivertebrata	11	1	2					5	3	13	18	15	1			69
Naja romani	30	2	5	1	1	1	1	15	7	22	22	19	4			130
Vipera burgenlandica	12	1	1	1				7	3	14	14	14	1			68

Table 5: Minimum Number of Individuals (MNI) of Kohfidisch: Reptilia.

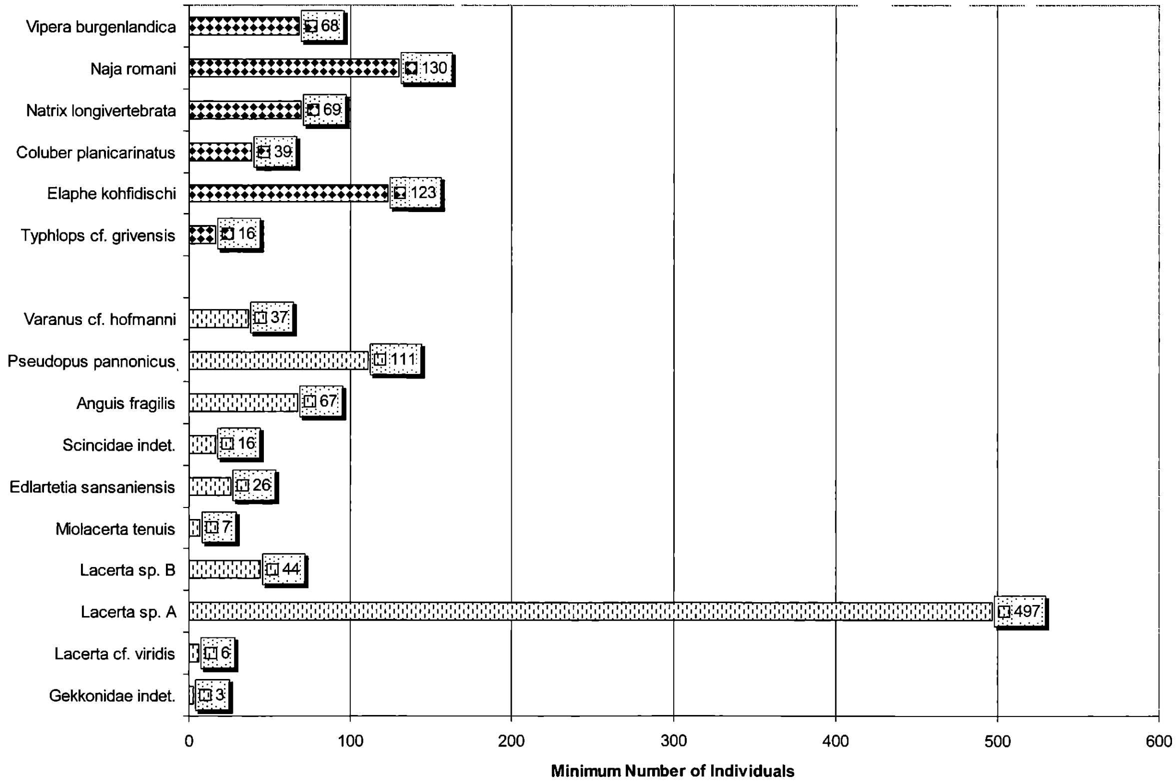

Diagram 4: Minimum Number of Individuals (MNI) of Kohfidisch: Reptilia.

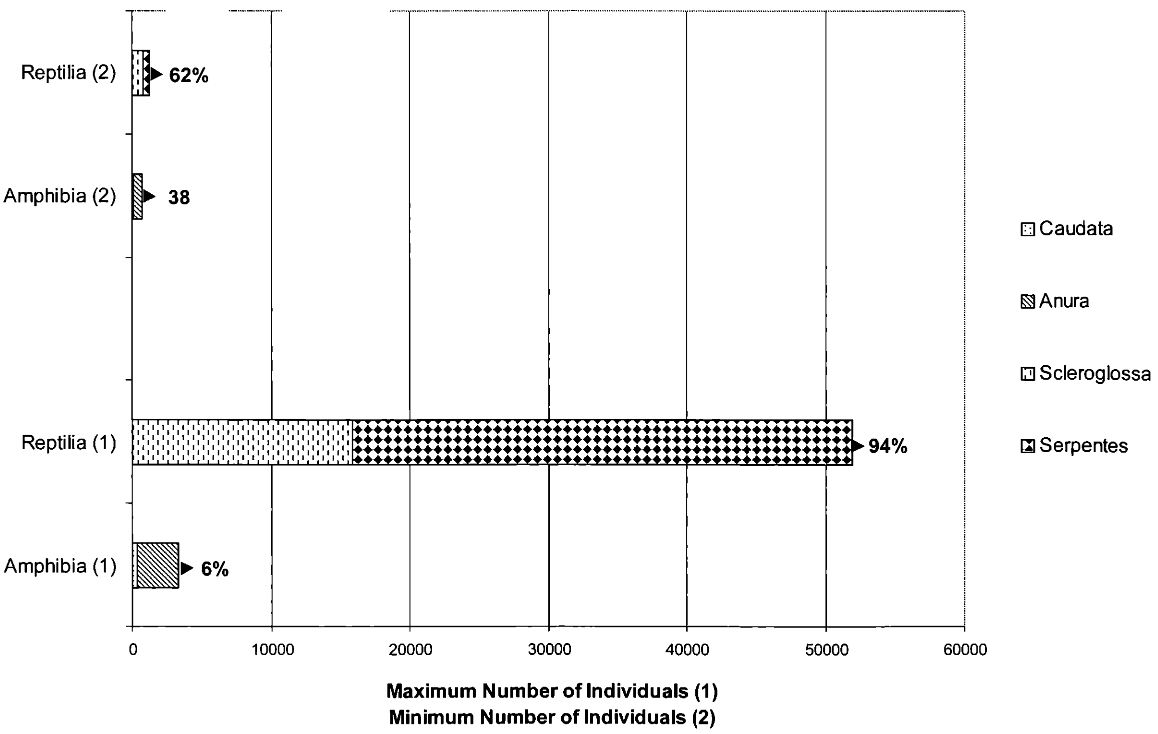

Diagram 5: Maximum Number of Indivuduals and Minimum Number of Individuals of Kohfidisch: Amphibia and Reptilia.

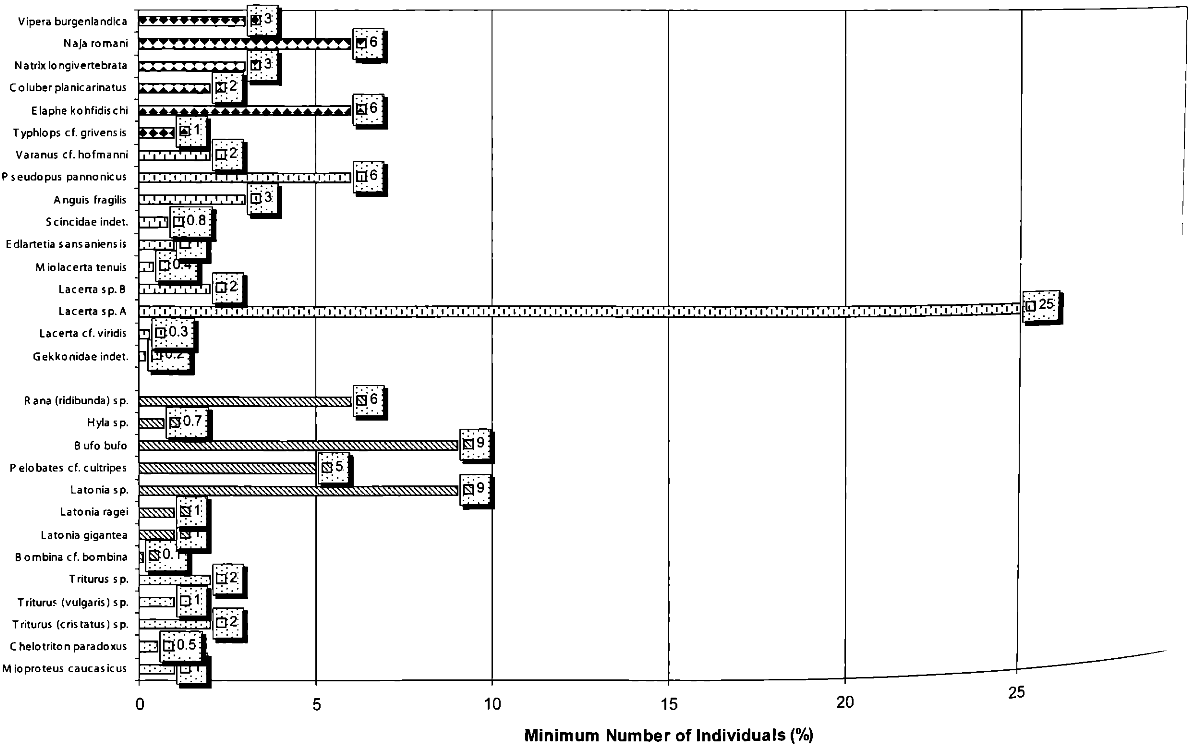

Diagram 6: Percental Minimum Number of Individuals (MNI (%)) of Kohfidisch in descending frequency: Amphibia and Reptilia.

Taxa	MNI
Lacerta sp. A	25
Latonia sp.	9
Bufo bufo	9
Pseudopus pannonicus	6
Elaphe kohfidischi	6
Naja romani	6
Rana (*ridibunda*) sp.	6
Pelobates cf. *cultripes*	5
Anguis fragilis	3
Natrix longivertebrata	3
Vipera burgenlandica	3
Lacerta sp. B	2
Varanus cf. *hofmanni*	2
Coluber planicarinatus	2
Triturus (*cristatus*) sp.	2
Triturus sp.	2
Edlartetia sansaniensis	1
Typhlops cf. grivensis	1
Mioproteus caucasicus	1
Triturus (*vulgaris*) sp.	1
Latonia gigantea	1
Latonia ragei	1
Scincidae indet.	0.8
Hyla sp.	0.7
Chelotriton paradoxus	0.5
Miolacerta tenuis	0.4
Lacerta cf. *viridis*	0.3
Gekkonidae indet.	0.2
Bombina cf. *bombina*	0.1

Table 6: Percental Minimum Number of Individuals (MNI (%)) of Kohfidisch in descending frequency: Amphibia and Reptilia.

		CL	MH	CL/MH	MPW	CL/MPW		
Mioproteus caucasicus	n	26	19	16	12	12		
	min	2.29	1.29	1.09	3.18	0.95		
	max	4.83	3.5	1.54	3.96	1.05		
	mean	3.45	2.63	1.23	3.64	0.98		
	stdev	0.575	0.702	0.139	0.331	0.047		
		KH	WL	WH	PB	GL	GL/PB	WL/WH
Chelotriton paradoxus	n	18	16	16	9	12	9	16
	min	2.25	2.63	1.08	3.17	3.83	0.88	2.21
	max	3.54	5.71	2.04	4.96	6.5	1.45	4.29
	mean	2.82	4.04	1.43	3.86	5.16	1.27	3.01
	stdev	0.358	0.996	0.24	0.646	0.923	0.2	0.667
***Triturus* (*cristatus*) sp.**	n	33	35	33	27	24	24	33
	min	1	1.63	0.38	1.21	1.75	1.32	2.62
	max	1.87	2.96	1.12	2.17	3.38	1.75	5.45
	mean	1.32	2.29	0.97	1.68	2.63	1.51	3.85
	stdev	0.162	0.397	0.102	0.253	0.421	0.12	0.644
***Triturus* (*vulgaris*) sp.**	n	32	30	30	28	26	26	30
	min	1	1.42	0.46	1.33	1.88	1.41	2.9
	max	1.38	2.61	0.75	2.04	3	1.75	4.1
	mean	1.18	2.12	0.62	1.62	2.36	1.52	3.54
	stdev	0.134	0.511	0.11	0.253	0.487	0.147	0.363
***Triturus* sp.**	n	35	38	37	24	—	—	37
	min	0.88	1.25	0.42	1.13	—	—	2.67
	max	1.58	3.42	0.79	2.25	—	—	4.98
	mean	1.25	2.34	0.61	1.66	—	—	3.87
	stdev	0.176	0.562	0.661	0.462	—	—	0.637

Table 7: Measurements (in mm) of the vertebrae praesacrales of *Mioproteus caucasicus* according to ESTES & SCHLEICH (1994) and of *helotriton paradoxus*, *Triturus* (*cristatus*) sp., *Triturus* (*vulgaris*) sp. and *Triturus* sp. following HALLER-PROBST & SCHLEICH (1994).

		KH	WL	WH	PB	GL	GL/PB	WL/WH
Bombina* cf. *bombina	n	1	1	1	1	1	1	1
		1.23	1.19	0.34	2.09	1.45	0.69	3.5
***Latonia* sp.**	n	44	56	55	46	44	44	55
	min	2.08	1.75	0.75	1.54	2.63	1.02	1.4
	max	3.79	3.96	2.25	4.38	4.38	1.71	3.73
	mean	2.7	2.88	1.39	2.81	3.58	1.38	2.33
	stdev	0.746	0.547	0.363	0.926	0.934	0.293	0.641
Pelobates* cf. *cultripes	n	11	14	12	14	14	14	12
	min	2.72	1.83	0.85	3.19	2.55	0.79	2.15
	max	3.7	4.26	1.57	4.89	4.43	0.96	3.07
	mean	3.15	3.25	1.16	4.17	3.62	0.87	2.71
	stdev	0.339	0.907	0.241	0.628	0.613	0.066	0.289
Bufo bufo	n	39	43	43	39	40	39	43
	min	2	2.26	0.68	2.72	2.26	0.79	2.19
	max	3.53	3.53	1.11	4.47	3.79	0.93	3.57
	mean	2.52	2.75	0.95	3.34	2.8	0.86	2.93
	stdev	0.497	0.388	0.14	0.528	0.464	0.042	0.395
***Hyla* sp.**	n	1	1	1	1	1	1	1
		2.29	—	1.17	3.5	—	—	—

Table 8: Measurements (in mm) of the vertebrae praesacrales of *Bombina* cf. *bombina, Latonia* sp., *Pelobates* cf. *cultripes*, *Bufo bufo* and *Hyla* sp. according to HALLER-PROBST & SCHLEICH (1994).

vertebrae:

Rana (*ridibunda*) sp.	KH	WL	WH	PB	GL	GL/PB	WL/WH
n	35	34	35	34	34	34	34
min	1.46	1.21	0.33	2.58	1.54	0.61	2.32
max	1.88	1.46	0.54	2.92	2.56	0.86	3.67
mean	1.74	1.33	0.48	2.78	1.87	0.67	2.86
stdev	0.165	0.116	0.087	0.167	0.432	0.126	0.574

ilia:

Rana (*ridibunda*) sp.	a-a	b-b	c-c	d-d	e-e	α
n	18	17	14	15	19	15
min	0.21	1.17	2.58	1.17	0.83	43,5°
max	0.75	2.17	7.58	3.71	3.08	51,5°
mean	0.37	1.69	4.01	1.95	1.62	48,9°
stdev	0.185	0.327	2.391	1.006	0.841	3.229

maxillaria:

Latonia gigantea	DL	DZ	*Latonia ragei*	DL	DZ
n	28	13	n	12	12
min	1.04	1.33	min	0.79	1.57
max	1.92	5.04	max	2.08	3.06
mean	1.44	3.28	mean	1.44	2.38
stdev	0.345	1.384	stdev	0.302	0.535

Table 9: Measurements (in mm) of the vertebrae praesacrales (following HALLER-PROBST & SCHLEICH, 1994) and ilia (according to G. BÖHME & GÜNTHER, 1979) of *Rana* (*ridibunda*) sp. Comparative measurements (in mm) of the maxillaria (after MIKLAS, 2002) between *Latonia gigantea* and *Latonia ragei*.

		CL	CTH	CTW	NAW	PO-PO	PR-PO	PR-PR
Gekkonidae indet.	n	1	1	1	1	1	1	1
		1.79	0.55	0.98	1.32	1.74	2.38	—
***Lacerta* sp. A**	n	42	42	42	41	37	38	38
	min	2.63	0.83	1.13	2.08	2.54	2.79	2.33
	max	3.79	1.13	1.58	2.71	3.54	3.79	3.42
	mean	3.19	1.01	1.36	2.49	2.87	3.32	2.93
	stdev	0.366	0.081	0.149	0.203	0.365	0.324	0.376
***Lacerta* sp. B**	n	7	7	7	7	1	1	—
	min	1.45	0.38	0.64	0.98	1.23	2.04	—
	max	1.91	0.85	1.19	1.7			—
	mean	1.67	0.61	0.91	1.17			—
	stdev	0.17	0.195	0.21	0.251			—
Scincidae indet.	n	2	3	3	3	1	1	3
		4.09	0.98	1.4	1.66	2.72	4.55	2.68
			1.06	1.87	1.83			3.11
		4.47	1.15	1.7	1.74			2.89

Table 10: Measurements (in mm) of the vertebra caudalis of Gekkonidae indet. and the vertebrae praesacrales of *Lacerta* sp. A, *Lacerta* sp. B and Scincidae indet. following Auffenberg (1963).

vertebrae:		CL	CTH	CTW	NAW	PO-PO	PR-PO	PR-PR
Anguis fragilis	n	40	41	41	41	41	41	41
	min	2.46	0.54	0.92	1.75	2.06	2.58	2.33
	max	3.92	1.21	2.21	3.83	4.67	4.42	4.54
	mean	2.76	0.74	1.45	2.41	2.76	3.11	2.91
	stdev	0.436	0.233	0.394	0.669	0.813	0.613	0.745
Pseudopus pannonicus	n	44	45	45	45	45	45	45
	min	6.23	2.13	4.06	6.12	6.52	6.14	7.02
	max	10.32	3.82	7.31	10.13	13.02	11.14	13.08
	mean	8.62	2.81	5.29	8.35	9.91	8.82	10.21
	stdev	1.015	0.486	0.808	1.223	1.686	1.326	1.591
Varanus cf. *hofmanni*	n	26	27	27	27	23	24	25
	min	8.01	3.02	4.59	5.1	8.32	10.04	9.25
	max	16.74	7.52	12	16.21	19.18	21.55	20.54
	mean	12.87	4.19	8.12	9.54	17.83	15.83	13.54
	stdev	3.096	0.828	3.229	3.278	1.137	1.368	3.295

ossicula dermalia dorsalia medialia:

		length	width	thickness
Anguis fragilis	n	42	43	43
	min	1.42	1.58	0.21
	max	2.88	3.79	0.67
	mean	2.19	2.76	0.35
	stdev	0.579	0.832	0.149
Pseudopus pannonicus	n	50	50	50
	min	4.01	5.23	1
	max	8.89	9.11	1.83
	mean	6.19	7.01	1.46
	stdev	0.743	1.299	0.271

Table 11: Measurements (in mm) of the vertebrae praesacrales (following Auffenberg, 1963) of *Anguis fragilis*, *Pseudopus pannonicus*, and *Varanus* cf. *hofmanni*. Comparative measurements of the osteodermalia (after Fejérváry-Lángh, 1923) between *Anguis fragilis* and *Pseudopus pannonicus*.

Typhlops cf. *grivensis*

	CL	CTH	CTW	NAW	ZW	PO-PO	PR-PO	PR-PR
n	27	27	27	27	25	22	22	24
min	1.11	0.26	0.51	0.68	0.72	1.12	1.15	1.06
max	2.04	0.64	1.06	1.02	0.81	1.66	1.71	1.7
mean	1.47	0.4	0.69	0.84	0.75	1.42	1.55	1.43
stdev	0.209	0.082	0.113	0.076	0.043	0.141	0.145	0.135
	CL/NAW	PO-PO/NAW	CTW/CTH	ZW/NAW	PR-PR/PR-PO	CL/ZW	PR-PR/NAW	
n	27	22	27	25	22	25	24	
min	1.37	1.32	1.36	0.73	0.84	1.18	1.18	
max	2.32	1.89	2.5	0.97	1.04	1.35	1.98	
mean	1.75	1.72	1.74	0.88	0.91	1.31	1.74	
stdev	0.216	0.149	0.261	0.106	0.054	0.083	0.233	

Elaphe kohfidischi

	CL	CTH	CTW	NAW	ZW	PO-PO	PR-PO	PR-PR
n	37	37	37	37	35	37	37	37
min	2.3	0.94	1.19	1.74	1.62	3	2.94	3.32
max	8.68	3.19	3.28	6.49	4.47	10.62	9.06	10.83
mean	4.58	1.66	1.82	3.07	2.69	5.12	4.78	5.37
stdev	1.994	0.798	0.712	1.193	0.974	2.046	1.954	2.183
	CL/NAW	PO-PO/NAW	CTW/CTH	ZW/NAW	PR-PR/PR-PO	CL/ZW	PR-PR/NAW	
n	37	37	37	35	37	35	37	
min	0.85	0.14	0.9	0.47	1	1.08	0.96	
max	1.71	2.03	1.36	1.12	1.31	2.14	1.95	
mean	1.49	1.6	1.14	0.88	1.12	1.7	1.75	
stdev	0.219	0.455	0.127	0.153	0.081	0.25	0.216	

Table 12: Measurements (in mm) of the vertebrae praesacrales of *Typhlops* cf. *grivensis* and *Elaphe kohfidischi* according to AUFFENBERG (1963).

Coluber planicarinatus

	CL	CTH	CTW	NAW	ZW	PO-PO	PR-PO	PR-PR
n	34	34	34	34	32	32	32	32
min	3.4	0.94	1.36	2	1.74	3.57	3.57	3.83
max	4.68	1.74	1.87	2.94	2.55	5.24	4.98	5.88
mean	3.84	1.32	1.56	2.32	2.12	4.26	3.94	4.27
stdev	0.321	0.197	0.116	0.269	0.246	0.393	0.342	0.45
	CL/NAW	PO-PO/NAW	CTW/CTH	ZW/NAW	PR-PR/PR-PO	CL/ZW	PR-PR/NAW	
n	34	32	34	32	32	32	32	
min	1.53	1.67	1.06	0.86	0.96	1.49	1.58	
max	1.82	2.04	1.59	1.14	1.28	2.05	2.11	
mean	1.67	1.88	1.2	0.93	1.09	1.81	1.89	
stdev	0.092	0.137	0.141	0.081	0.085	0.164	0.164	

Natrix longivertebrata

	CL	CTH	CTW	NAW	ZW	PO-PO	PR-PO	PR-PR
n	36	36	36	36	35	36	34	34
min	2.68	0.85	1.11	1.62	1.62	2.94	3.02	3.06
max	5.32	1.7	2.09	2.89	2.77	5.7	5.7	5.23
mean	3.96	1.32	1.42	2.36	2.13	4.26	4.22	4.22
stdev	0.743	0.242	0.277	0.382	0.299	0.696	0.791	0.706
	CL/NAW	PO-PO/NAW	CTW/CTH	ZW/NAW	PR-PR/PR-PO	CL/ZW	PR-PR/NAW	
n	36	36	36	35	34	35	34	
min	1.51	1.62	0.8	0.79	0.86	1.49	1.54	
max	1.96	2.08	1.35	1.08	1.1	2.16	2.21	
mean	1.68	1.81	1.09	0.93	1	1.83	1.81	
stdev	0.139	0.117	0.116	0.085	0.067	0.196	0.181	

Table 13: Measurements (in mm) of the vertebrae praesacrales of *Coluber planicarinatus* and *Natrix longivertebrata* according to AUFFENBERG (1963).

Naja romani

	CL	CTH	CTW	NAW	ZW	PO-PO	PR-PO	PR-PR
n	40	40	40	40	40	40	40	40
min	6.82	2.99	3.12	3.96	4.09	8.56	8.01	9.12
max	12.1	5.92	6.34	13.19	8.98	18.13	15.09	18.92
mean	9.82	4.52	4.71	8.94	6.27	13.56	11.39	13.94
stdev	1.564	0.753	0.781	2.405	1.191	2.681	1.991	2.796
	CL/NAW	PO-PO/NAW	CTW/CTH	ZW/NAW	PR-PR/PR-PO	CL/ZW	PR-PR/NAW	
n	40	40	40	40	40	40	40	
min	0.91	1.32	0.87	0.56	0.85	1.28	1.37	
max	1.72	2.26	1.25	1.23	1.4	2.12	2.39	
mean	1.14	1.56	1.05	0.73	1.22	1.58	1.6	
stdev	0.199	0.206	0.111	0.139	0.12	0.198	0.225	

Vipera burgenlandica

	CL	CTH	CTW	NAW	ZW	PO-PO	PR-PO	PR-PR
n	40	39	39	40	39	40	40	40
min	3.74	1.45	1.49	2.31	2.11	4.55	3.96	4.26
max	8.1	3.5	4.98	5.92	5.08	10.09	9.88	11.8
mean	6.05	2.6	3.21	4.14	3.56	7.69	6.78	8.09
stdev	1.388	0.615	0.954	0.922	0.758	1.767	1.578	2.048
	CL/NAW	PO-PO/NAW	CTW/CTH	ZW/NAW	PR-PR/PR-PO	CL/ZW	PR-PR/NAW	
n	40	40	39	39	40	39	40	
min	1.28	1.54	1.03	0.69	1.03	1.46	1.62	
max	1.63	2.17	1.53	0.99	1.49	2.03	2.41	
mean	1.46	1.86	1.22	0.85	1.19	1.73	1.95	
stdev	0.107	0.175	0.131	0.086	0.104	0.147	0.182	

Table 14: Measurements (in mm) of the vertebrae praesacrales of *Naja romani* and *Vipera burgenlandica* according to Auffenberg (1963).

PLATE 1

Mioproteus caucasicus

Fig. a dentale sin. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0009/0001).

Fig. b vertebra praesacralis dorsal view (Kohfidisch "III oben"; Inv. Nr.: NHMW2004z0009/0002).

Chelotriton paradoxus

Fig. c atlas cranial view (Kohfidisch; Inv. Nr.: NHMW2004z0010/0001).

***Triturus (cristatus)* sp.**

Fig. d vertebra praesacralis dorsal view (Kohfidisch; Inv. Nr.: NHMW2004z0011/0001).

***Triturus* (*vulgaris*) sp.**

Fig. e vertebra praesacralis dorsal view (Kohfidisch; Inv. Nr.: NHMW2004z0012/0001).

PLATE 1

PLATE 2

Bombina* cf. *bombina

Fig. a os coccygis dorsal view (Kohfidisch "Altbestand"; Inv. Nr.: NHMW2004z0014/0001).

Fig. b ilium dext. lateral view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0014/0002).

***Latonia* sp.**

Fig. c praemaxillare dext. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0017/0001).

Fig. d ilium dext. lateral view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0017/0002).

Fig. e ischium caudal view (Kohfidisch „III unten"; Inv. Nr.: NHMW2004z0017/0003).

Pelobates* cf. *cultripes

Fig. f squamosum sin. dorsal view (Kohfidisch „III oben"; Inv. Nr.: NHMW2004z0018/0001).

Fig. g ilium dext. lateral view (Kohfidisch „III unten"; Inv. Nr.: NHMW2004z0018/0002).

PLATE 2

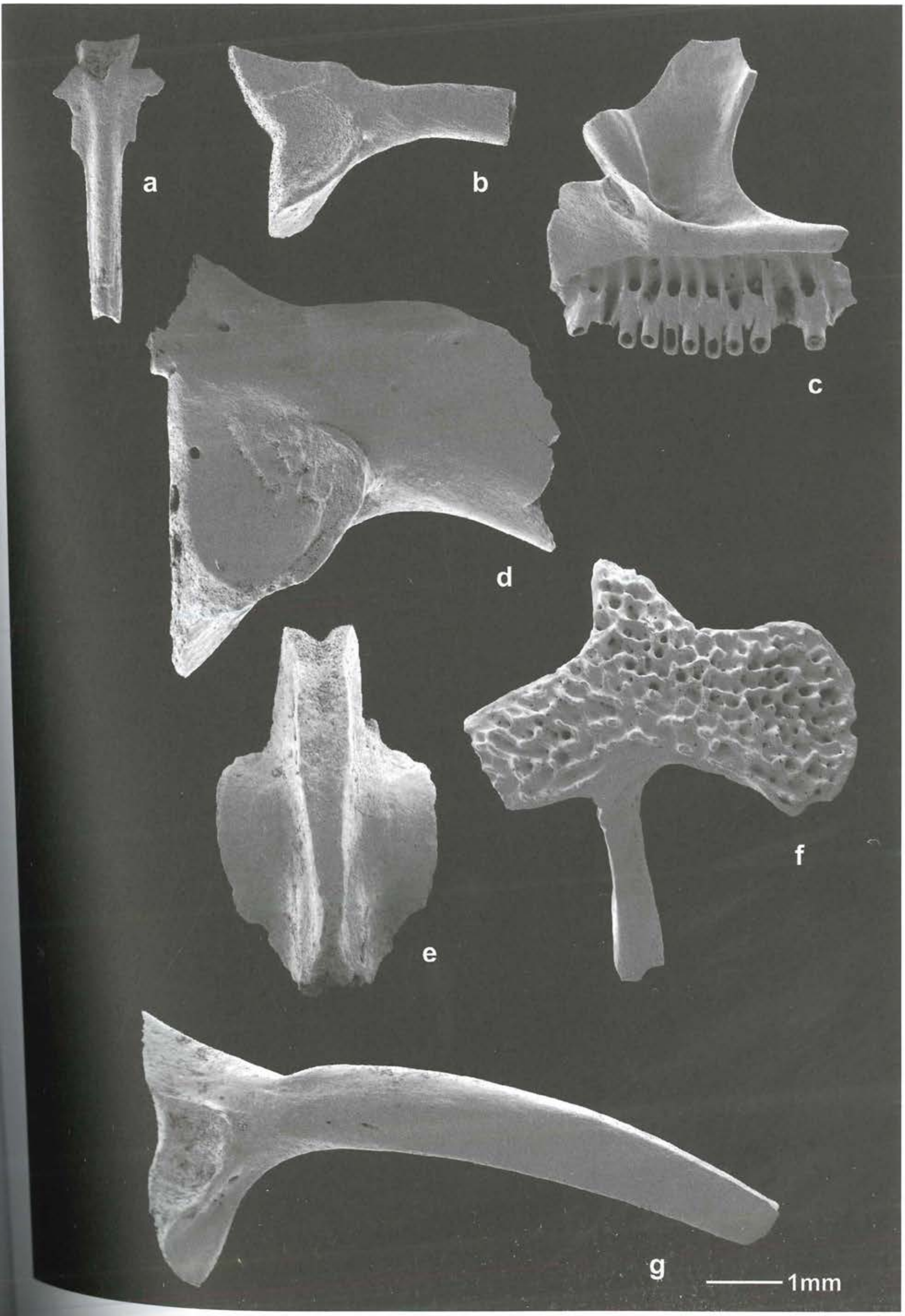

PLATE 3

Bufo bufo

Fig. a	coracoideum (Kohfidisch “III unten”; Inv. Nr.: NHMW2004z0019/0001).
Fig. b	atlas ventral view (Kohfidisch “III unten”; Inv. Nr.: NHMW2004z0019/0002).
Fig. c	ilium sin. lateral view (Kohfidisch “Altbestand”; Inv. Nr.: NHMW2004z0019/0003).
Fig. d	ischium lateral view (Kohfidisch “III”; Inv. Nr.: NHMW2004z0019/0004).

***Hyla* sp.**

Fig. e	vertebra praesacralis dorsal view (Kohfidisch „III unten“; Inv. Nr.: NHMW2004z0020/0001).
Fig. f	ilium sin. lateral view (Kohfidisch “III unten”; Inv. Nr.: NHMW2004z0020/0002).
Fig. g	ischium caudal view (Kohfidisch “III unten”; Inv. Nr.: NHMW2004z0020/0003).

***Rana* (*ridibunda*) sp.**

Fig. h	amphicoelous vertebra praesacralis (V8) ventrocaudal view (Kohfidisch “III”; Inv. Nr.: NHMW2004z0021 /0001).
Fig. i	ilium dext. lateral view (Kohfidisch “III unten”; Inv. Nr.: NHMW2004z0021/0002).

PLATE 3

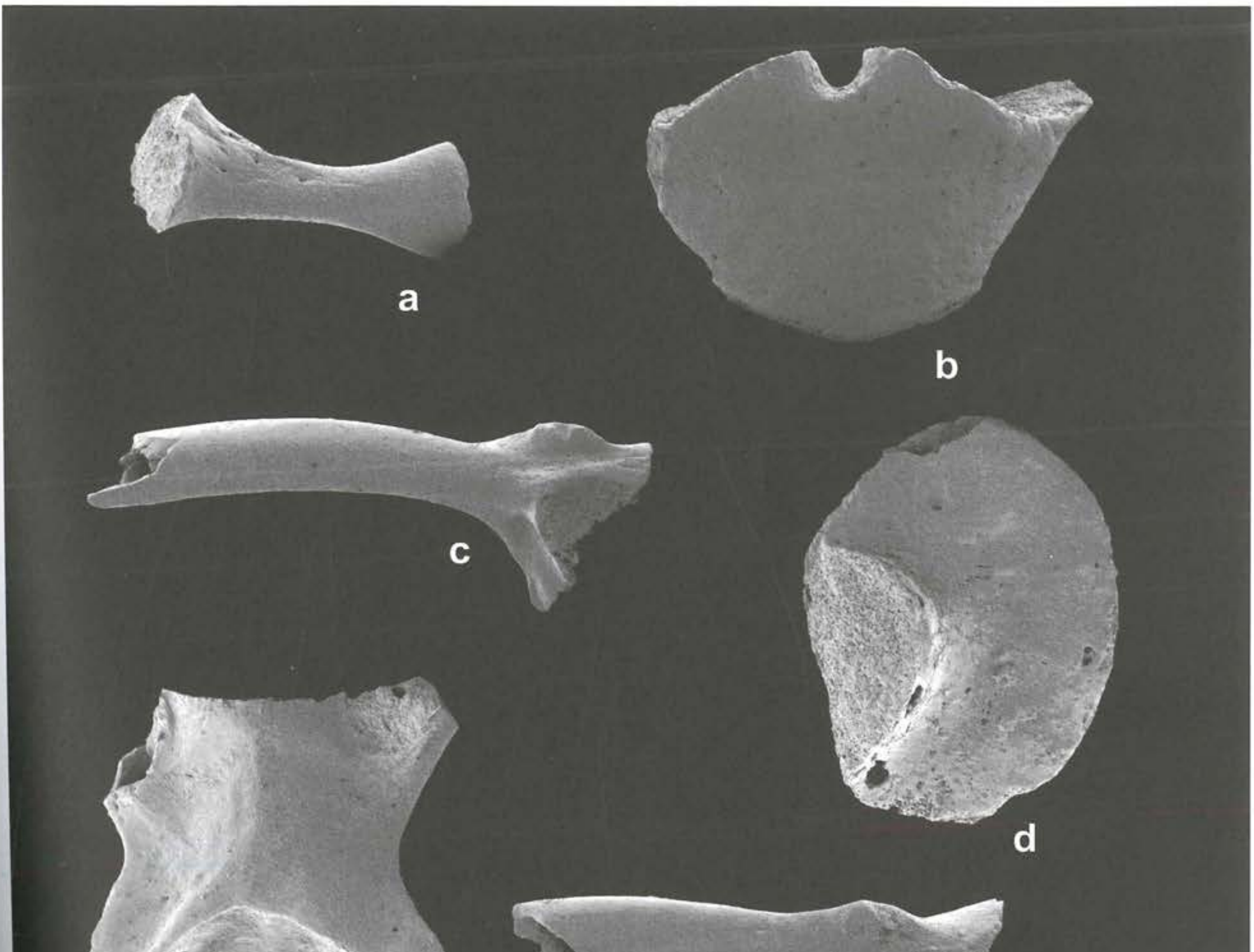

PLATE 4

Gekkonidae indet.

Fig. a vertebra caudalis ventral view (Kohfidisch “III”; Inv. Nr.: NHMW2004z0023/0001).

Lacerta sp. A.

Fig. b pterygoideum dext. ventral view (Kohfidisch “III unten”; Inv. Nr.: NHMW2004z0025/0001).

Fig. c praemaxillare lingual view (Kohfidisch “III unten”; Inv. Nr.: NHMW2004z0025/0002).

Fig. d dentale sin. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0025/0003).

Fig. f vertebra cervicalis ventral view (Kohfidisch “III oben”; Inv. Nr.: NHMW2004z0025/0004).

Fig. g vertebra praesacralis ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0025/0005).

Fig. h vertebra caudalis anterioris ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0025/0006).

Lacerta sp. B.

Fig. e dentale sin. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0026/0001).

PLATE 4

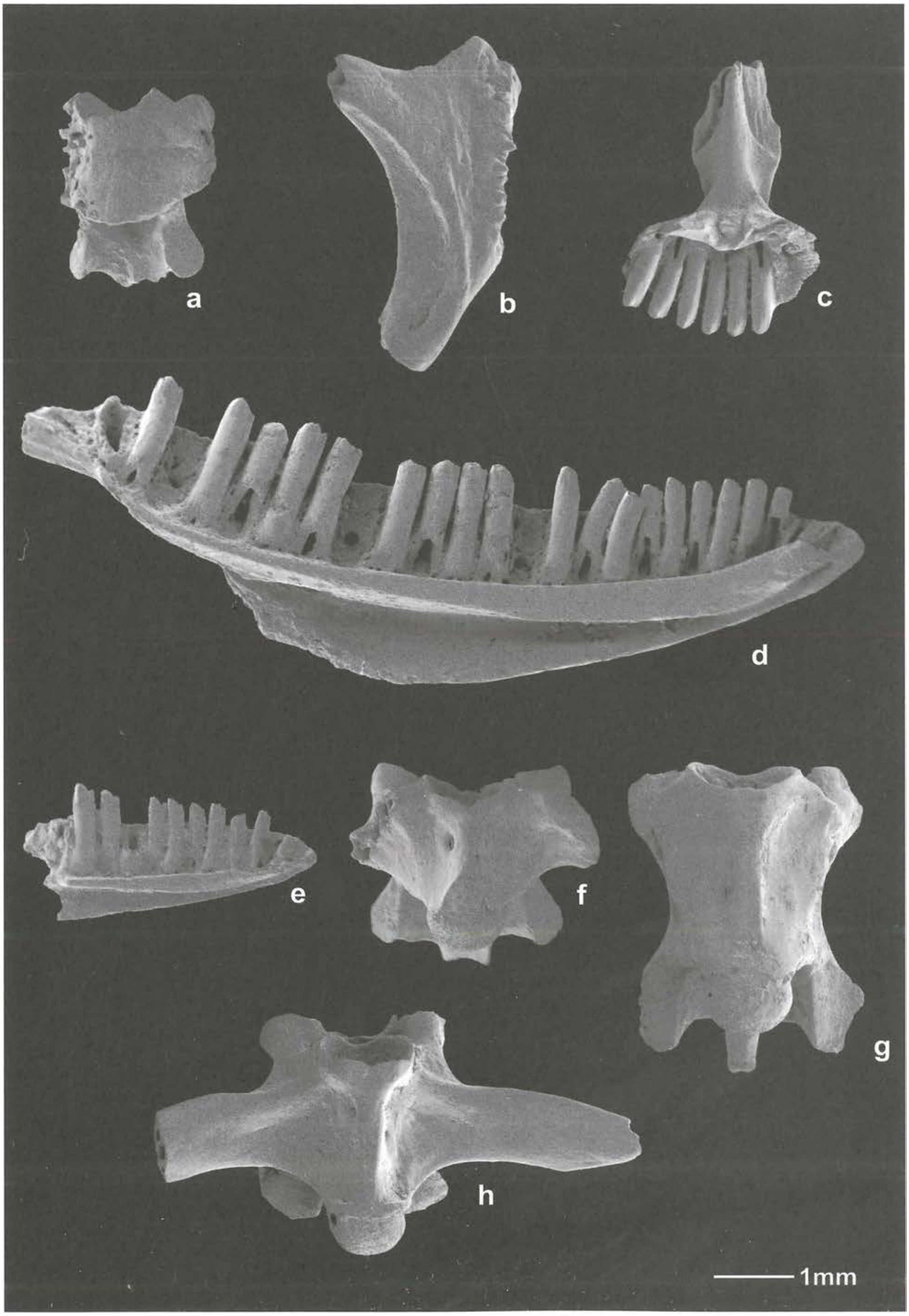

PLATE 5

Miolacerta tenuis

Fig. a dentale dext. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0027/0001).

Edlartetia sansaniensis

Fig. b dentale dext. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0028/0001).

Scincidae indet.

Fig. c dentale dext. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0029/0001).

Anguis fragilis.

Fig. d dentale sin. lingual view (Kohfidisch „Altbestand“; Inv. Nr.: NHMW2004z0030/0001).

Fig. e vertebra cervicalis ventral view (Kohfidisch “Altbestand”; Inv. Nr.: NHMW2004z0030/0002).

Fig. f vertebrae praesacrales ventral view (Kohfidisch “Altbestand”; Inv. Nr.: NHMW2004z0030/0003).

Fig. g vertebra caudalis ventral view (Kohfidisch “Altbestand”; Inv. Nr.: NHMW2004z0030/0004).

Fig. h vertebra caudalis (anterior part) anterior view (Kohfidisch “IV”; Inv. Nr.: NHMW2004z0030/0005).

PLATE 5

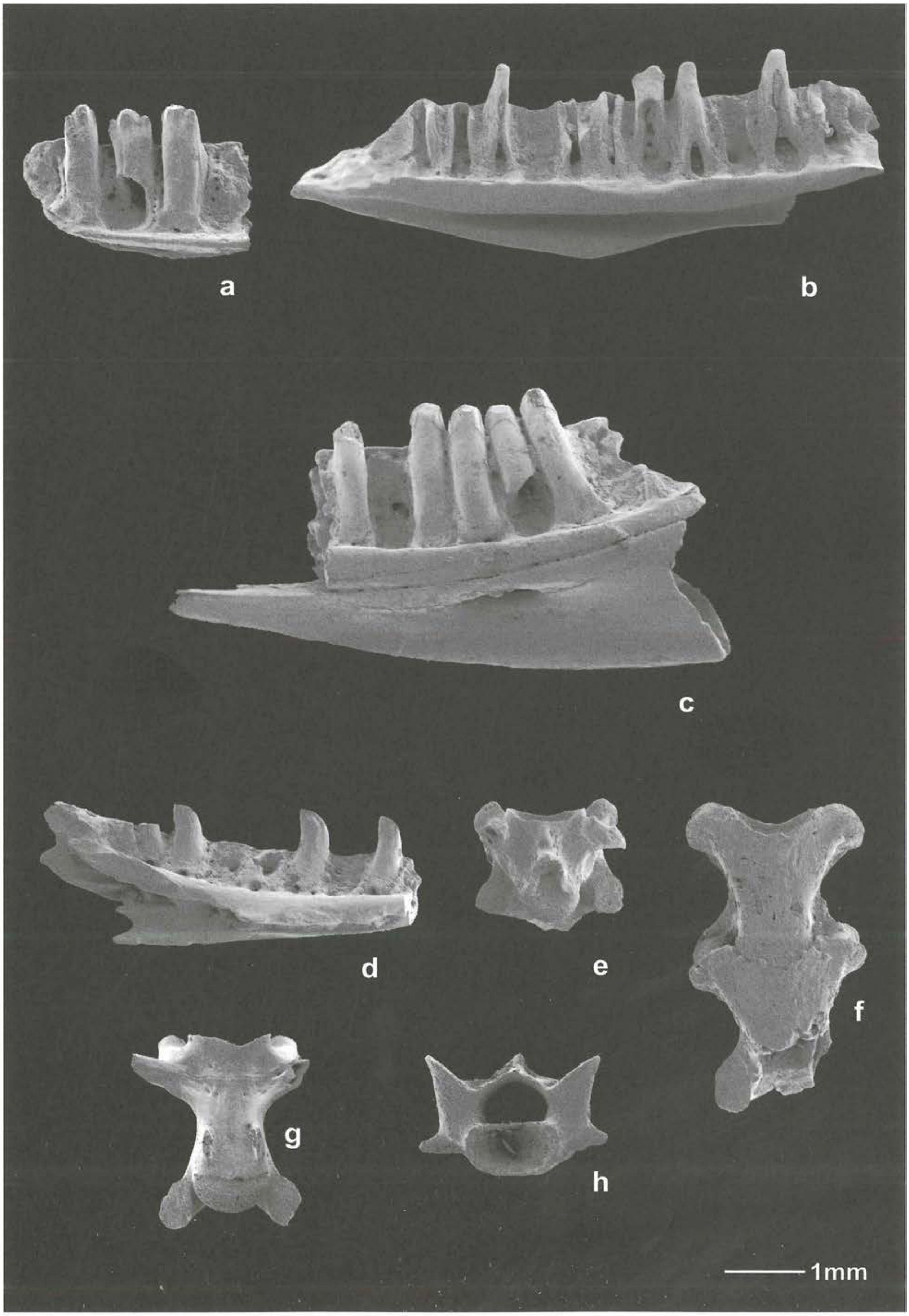

PLATE 6

Pseudopus pannonicus

Fig. a parietale dorsal view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0001).

Fig. b parietale ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0001).

Fig. c palatinum dext. ventral view (Kohfidisch "III"; Inv. Nr.: NHMW2004z0031/0002).

Fig. d praemaxillare lingual view (Kohfidisch "II"; Inv. Nr.: NHMW2004z0031/0003).

Fig. e maxillare sin. labial view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0004).

Fig. f maxillare sin. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0004).

Fig. g dentale dext. labial view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0005).

Fig. h dentale dext. lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0005).

PLATE 6

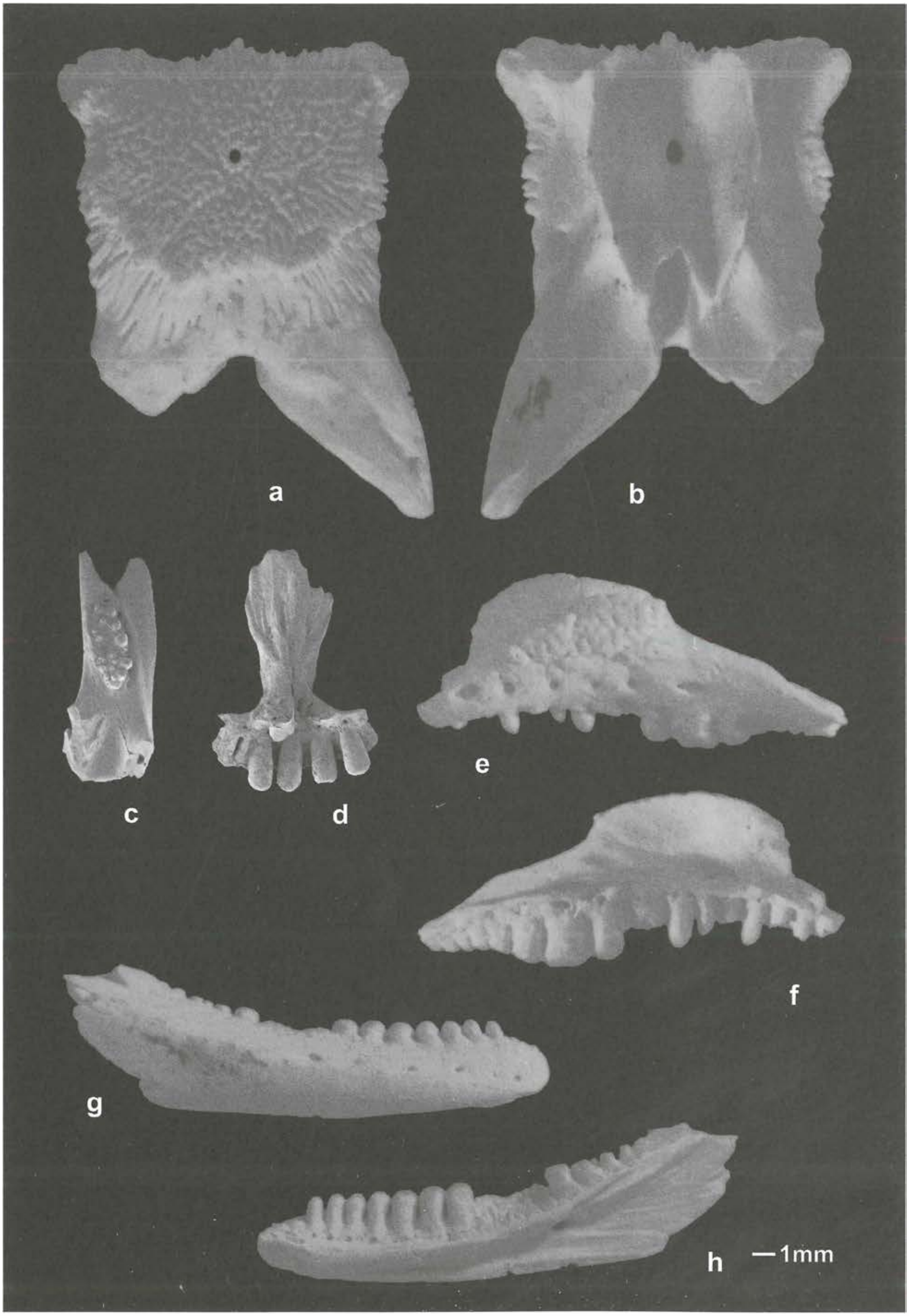

PLATE 7

Pseudopus pannonicus

Fig. a	vertebra praesacralis ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0006).
Fig. b	vertebra praesacralis dorsal view (Kohfidisch; Inv. Nr.: NHMW2004z0031/0006).
Fig. c	vertebra caudalis ventral view (Kohfidisch "III oben"; Inv. Nr.: NHMW2004z0031/0007).
Fig. d	osteodermale (ossiculum dermale caudale dorsale mediale) outer view (Kohfidisch "III unten"; Inv. Nr.: NHMW2004z0031/0008).

Varanus* cf. *hofmanni

Fig. e	dens lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0032/0001).
Fig. f	dens lingual view (Kohfidisch; Inv. Nr.: NHMW2004z0032/0002).
Fig. g	dentale dext. lingual view (Kohfidisch "I"; Inv. Nr.: NHMW2004z0032/0003).

PLATE 7

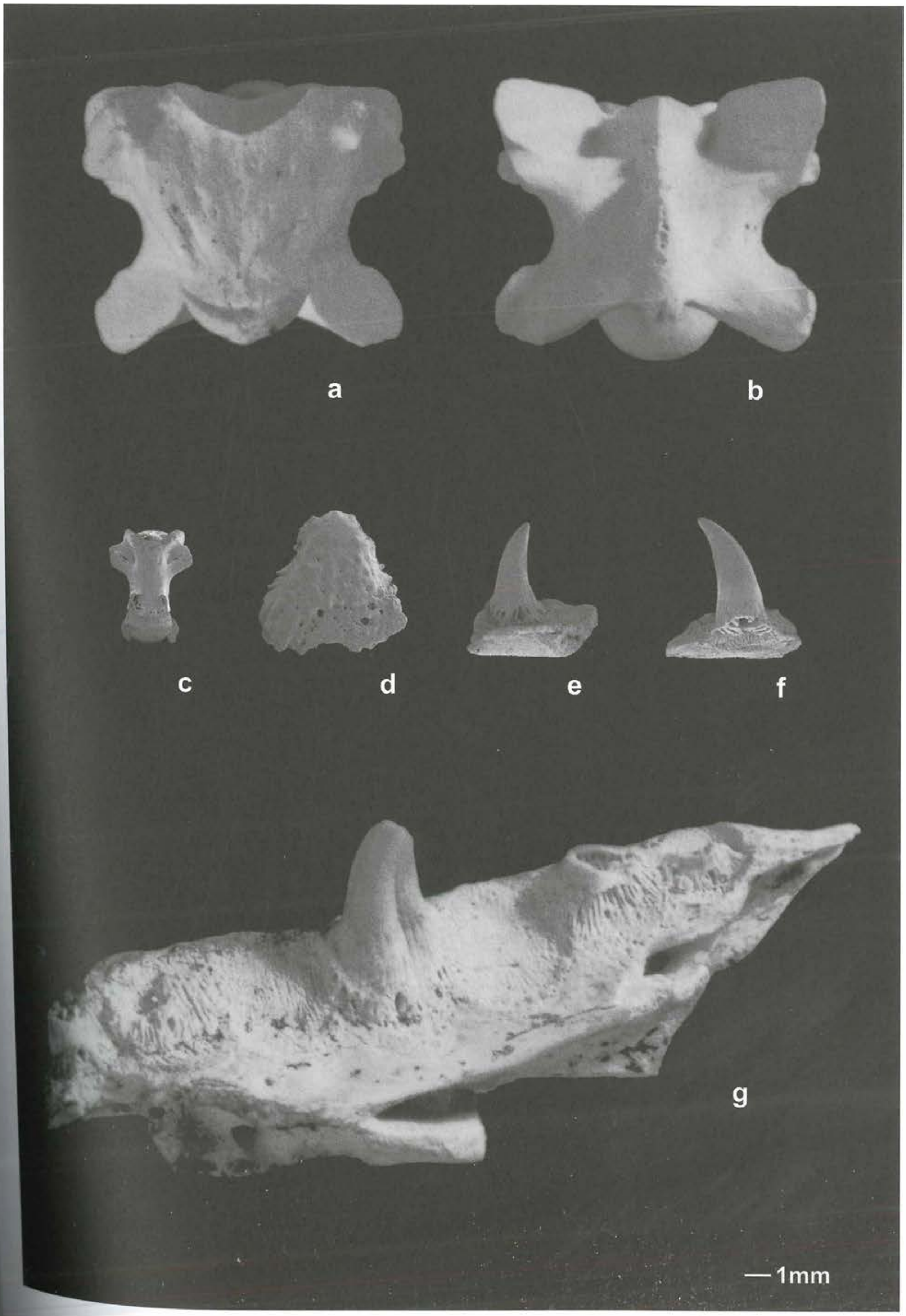

PLATE 8

Varanus cf. *hofmanni*

Fig. a vertebra praesacralis ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0032/0004).

Fig. b vertebra praesacralis dorsal view (Kohfidisch; Inv. Nr.: NHMW2004z0032/0004).

Fig. c vertebra cervicalis ventral view (Kohfidisch "I"; Inv. Nr.: NHMW2004z0032/0005).

Fig. d vertebra cervicalis dorsal view (Kohfidisch "I"; Inv. Nr.: NHMW2004z0032/0005).

Fig. e vertebra caudalis lateral view (Kohfidisch; Inv. Nr.: NHMW2004z0032/0006).

PLATE 8

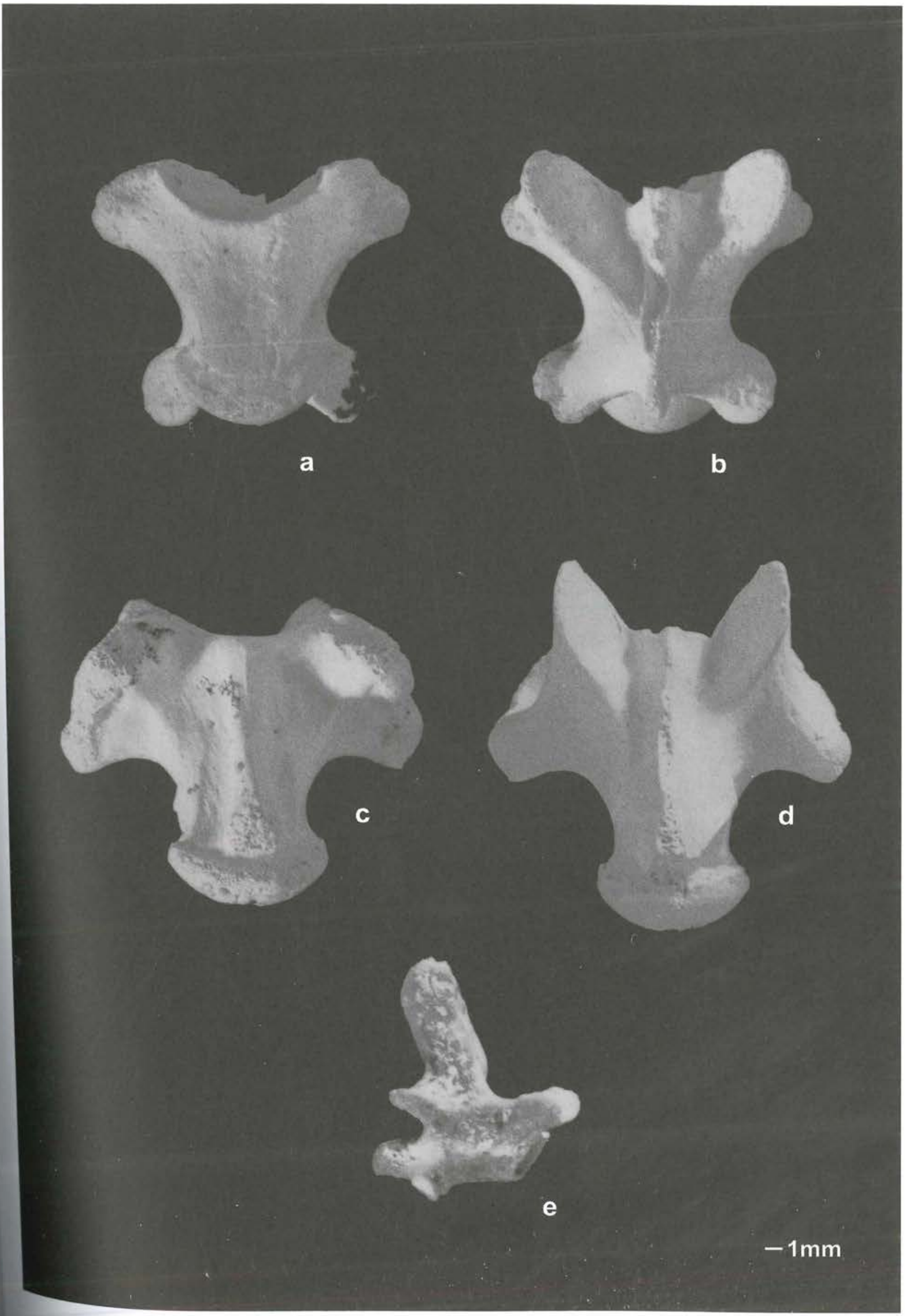

PLATE 9

Typhlops **cf.** *grivensis*

Fig. a vertebra praesacralis ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0034/0001).

Elaphe kohfidischi

Fig. b vertebra praesacralis ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0035/0001).

Coluber planicarinatus

Fig. c vertebra praesacralis ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0036/0001).

Natrix longivertebrata

Fig. d vertebra praesacralis ventral view (Kohfidisch; Inv. Nr.: NHMW2004z0037/0001).

Naja romani

Fig. e maxillare dext. et veneno illiti dens anterior view (Kohfidisch; Inv. Nr.: NHMW2004z0038/0001).

PLATE 9

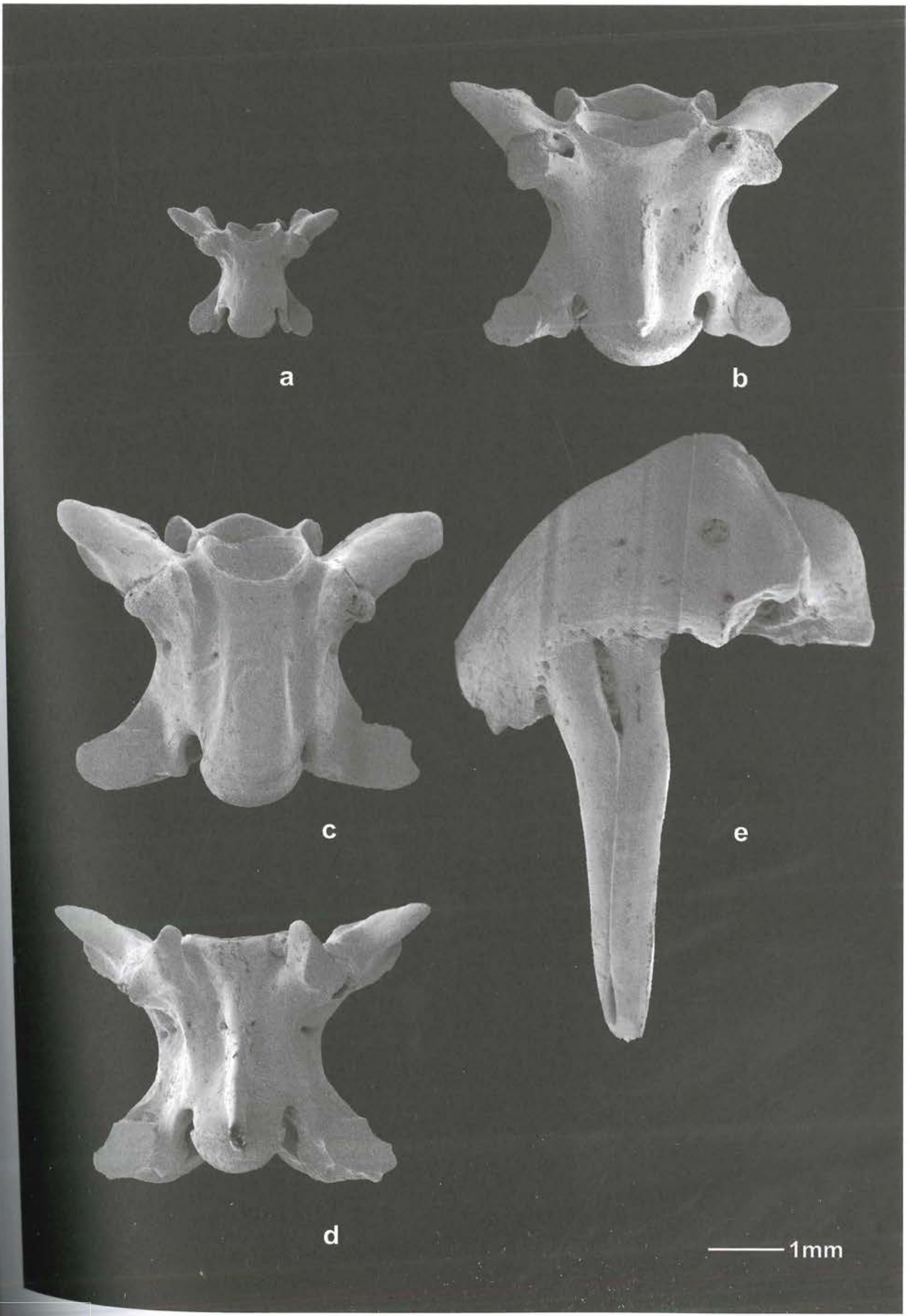

PLATE 10

Naja romani

Fig. a vertebra praesacralis ventral view (Kohfidisch "I"; Inv. Nr.: NHMW2004z0038/0002).

Fig. b vertebra praesacralis dorsal view (Kohfidisch "I"; Inv. Nr.: NHMW2004z0038/0002).

Fig. c vertebra praesacralis anterior view (Kohfidisch "I"; Inv. Nr.: NHMW2004z0038/0002).

Fig. d vertebra praesacralis posterior view (Kohfidisch "I"; Inv. Nr.: NHMW2004z0038/0002).

Fig. e costa (Kohfidisch; Inv. Nr.: NHMW2004z0038/0003).

Vipera burgenlandica

Fig. f veneno illiti dens (Kohfidisch „III oben"; Inv. Nr.: NHMW2004z0039/0001).

Fig. g vertebra praesacralis lateral view (Kohfidisch; Inv. Nr.: NHMW2004z0039/0002).

PLATE 10