

Lower Vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin – palaeoecological, environmental and palaeoclimatical implications

by

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Abstract

Seventeen species of continental Lower Vertebrates (freshwater fishes, amphibians, reptiles) are described from the localities Obergänserndorf 2 (OG2; 023/R/B) and Teiritzberg 1 (T1; 001/D/C) and Teiritzberg 2 (T2; 001/Z/C), Upper Karpatian (MN5) of the Korneuburg Basin. This is the youngest record in Europe for two species (*Latonia ragei*, Cordylidae indet.). Based on taphonomy there is some evidence that the allochthonous assemblage of Lower Vertebrates and mammals originates from washed out and basin wards transported pellets of nocturnal birds of prey. These isotaphonomic assemblages represent different palaeoenvironments. The faunal composition of Obergänserndorf indicates an open, probably abandoned floodplain environment above the groundwater level, whereas the Teiritzberg 001/D/C-fauna points to an environment with higher groundwater levels and probably originates from a channel fill. High mean annual temperatures (above 17,0° C) and frost free winter months are indicated by crocodiles and cordylid lizards. The frequent occurrence of dry adapted taxa points to an enhanced seasonality.

Zusammenfassung

Siebzehn Arten kontinentaler Niederer Wirbeltiere (Süßwasserfische, Amphibien, Reptilien) werden von den Aufschlüssen Obergänserndorf 2 (OG2; 023/R/B) und Teiritzberg 1 (T1; 001/D/C) und Teiritzberg 2 (T2; 001/Z/C) aus dem Karpatium (MN5) des Korneuburger Beckens beschrieben. Für zwei Arten, *Latonia ragei* und Cordylidae indet., ist dies der jüngste Nachweis in Europa. Die Taphonomie der Funde läßt darauf schließen, daß die allochthone Fossilvergesellschaftung von Niederen Wirbeltieren und Säugern auf ausgewaschene und beckenwärts transportierte Gewölle nachaktiver Greifvögel zurückzuführen ist. Diese allochthonen Fossilvergesellschaftung stammen aus unterschiedlichen Palaeoenvironments. Die Fauna von Obergänserndorf weist auf eine offene, möglicherweise verlassene Altarm- oder Überschwemmungslandschaft hin,

die deutlich über dem Grundwasserspiegel lag. Hingegen weist die Fauna von Teiritzberg 001/D/C auf eine Umgebung mit hohem Grundwasserspiegel hin und ist wahrscheinlich auf die Füllung einer ehemaligen Flußrinne zurückzuführen. Hohe Jahresdurchschnittstemperaturen (über 17° C) und frostfreie Wintermonate werden durch den Nachweis von Krokodilen und Gürtelchsen belegt. Das häufige Vorkommen von an Trockenheit adaptierten Taxa macht eine verstärkte Saisonalität wahrscheinlich.

Key words

Lower Vertebrates – freshwater fishes – amphibians – reptilians – Karpatian – palaeoclimate

Schlüsselwörter

Niedere Wirbeltiere – Süßwasserfische – Amphibien – Reptilien – Karpatium – Paläoklima

1. Introduction

The fossils from Karpatian continental and marine sediments of the Korneuburg Basin fill a gap in our knowledge of Middle Miocene Lower Vertebrates of the Central Paratethys. This time interval is of special interest because around the Lower/Middle Miocene transition a palaeoclimatic change toward an enhanced seasonality is documented in the Western Paratethys area (BÖHME 2002b submitted). The timing and the dynamic of climatic and environmental changes on continental scale is important for our understanding and modeling of current and future climate trends based on high-resolution palaeoclimate records. Since more extensive spatial sampling of diverse proxy climatic records is urgently needed, the investigation of the fauna of the Korneuburg Basin broadens our knowledge of past climate variability.

The material is stored in the Natural History Museum of Vienna (Naturhistorisches Museum Wien; abbreviated as NHMW).

A detailed description of the locations is given by Sovis (1998). He uses the following numbers:

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Obergänserndorf 023/R/B = OG2
 Teiritzberg 001/D/C = T1
 Teiritzberg 001/Z/C = T2
 Teiritzberg 001/Z/C3 = T2/5
 Teiritzberg 001/Z/C4 = T2/6
 Teiritzberg 001/Z/C 120-140 = Rögl 62/83

2. Systematic Palaeontology

Teleostei
 Order Esociformes
 Family Esocidae
 Genus *Esox*

Esox sp.
 (Pl. 1, Fig. A)

Material: OG2: 1 isolated tooth (NHMW2002z0011/0001).

Description and comparison: The circular cross-section of the tooth, cutting edges on both latero-apical sides and an angle of approximately 40° between the base and the axis of the tooth are indicative of pikes.

Autecology: The Palaearctic genus *Esox* lives in standing or slow running waters. The occurrence of isolated teeth alone (without skeletal elements) is characteristic for floodplain deposits or riparian pools in the North Alpine Foreland Basin (NAFB) (BÖHME, 2000). Pikes probably enter such environments during the spawning season.

Order Cypriniformes BLEEKER, 1885
 Family Cyprinidae CUVIER, 1817
 Genus *Barbus* CUVIER & CLOQUET, 1816

Barbus (Barbus) sp.

v 1998 *Barbus* (? *Puntius*) sp. – Schultz: 303, Taf. 3, Fig. 9, 10

Material: T1: 1 tooth (NHMW1995/0062/0064); T2/5: 2 teeth (NHMW1995/0063/0008-0009); Teiritzberg, Probe Rögl 62-83: 3 tooth fragments (NHMW1995/0064/0003).

Description and comparison: These teeth show a typical *Barbus*-like morphology: slender, round in cross-section, with a concave and rough masticatory area, and a strong and hooked tip. According to MACHORDOM & DOADRIO (2001), the genus *Barbus* sensu lato can be divided in five main mitochondrial lineages, one of them *Barbus* sensu strictu (tetraploid barbels of the Palaearctic) with the subgenera *Barbus* and *Luciobarbus*. The tooth morphology of *Luciobarbus* is quite different from the teeth described here (cf. BÖHME 2002a, submitted), whereas the teeth of the subgenus *Barbus* are most similar. Taxonomical affinities to the subgenus *Puntius* (Asian diploid barbels of MACHORDOM & DOADRIO, 2001) as proposed by SCHULTZ (1998) are unlikely both for biogeographical and morphological reasons (the only available species for comparison is *B. (Puntius) gomnionotus* from Thailand).

Autecology: Among the subgenus *Barbus*, the extant North Mediterranean lineage shows two paraphyletic ecophenotypes, a rheophilic and a fluvio-lacustrine species group (TSIGENOPOULOS et al., 1999). Both groups show a very similar tooth morphology (personal observation). Within the NAFB two species of *Barbus* (*Barbus*) are detected (personal unpublished data). One of them (*Barbus (Barbus)* sp. B) seems to be conspecific with the fossils described here. These teeth remain occur particularly in oxbow lakes or in sediments of slow running waters.

Class Amphibia
 Subclass Lissamphibia HAECKEL, 1866
 Order Allocaudata FOX & NAYLOR, 1982
 Family Albanerpetonidae FOX & NAYLOR, 1982
 Genus *Albanerpeton* ESTES & HOFSTETTER, 1976

Albanerpeton sp.
 (Pl. 1, Fig. B, C)

Material: OG2: 3 right, 2 left dentaries, 1 left maxilla (NHMW2002z0012/0001-0003); T2/3: 1 dentary fragment (NHMW2002z0012/0004); T2/6: 1 left dentary (NHMW2002z0012/0005).

Description and comparison: The presence of highly pleurodont teeth, a closed Meckelian canal and symphyseal prongs with an associated foramen on the underside of the dental symphysis are indicative for albanerpetontid jaws (GARDNER, 2000). Since praemaxilla, the most taxonomical informative element among *Albanerpeton* (GARDNER, 2000), is lacking, the taxonomic assignment to the European species *A. inexpectatum* ESTES & HOFSTETTER, 1976 and *A. nov. sp.* (undescribed species from the Lower Miocene of Bohemia) is impossible.

Autecology: Albanerpetontids are known in the European post-Mesozoic sediments since the MP21, base of the Oligocene (personal unpublished data) and represent probably Asiatic immigrants during the "grande coupure" faunal turnover. Up to now, material from 21 localities is known. The latest record is from the uppermost Middle Miocene. Nothing is known about the biology (e.g. the presence or absence of lungs) of this small animal. Nevertheless, some autecological details can be inferred from the fossil record. GARDNER (1999) stated that some cranial apomorphies of *A. inexpectatum* are related to burrowing in rocky substrate. Generally, *Albanerpeton* shows the highest abundance in fissure fillings, up to several hundred specimens in one outcrop. In some fissure fillings (e.g. Petersbuch 2) it is the most abundant vertebrate. Possibly, *Albanerpeton* represents an autochthonous inhabitant of the fissures and caves preferring the more stable microclimate therein. In basin deposits it occurs only with low abundance in relative dry or drying up environments like floodplains, riparian pools or moor deposits. Therefore these animals are regarded as dry adapted and are good indicators for a higher seasonality in the NAFB (BÖHME 2002b, submitted).

Order Caudata OPPEL, 1811
 Family Salamandridae GRAY, 1825
 Genus *Chelotriton* POMEL, 1853

***Chelotriton* sp.**
 (Pl. 1, Fig. G)

Material: OG2: 1 maxilla-fragment, 1 rib (NHMW2002z0013/0002); T1: 1 rib-fragment; T2/3: 1 parietal-fragment, 1 squamosal-fragment, 1 rib-fragment, 2 undeterminable skull fragments (NHMW2002z0013/0003); T2/5: 1 maxilla-fragment, 1 squamosal-fragment, 1 right frontal-fragment, 1 parietal-fragment, 7 undeterminable skull fragments (NHMW2002z0013/0001, 0004).

Description and comparison: All skull fragments exhibit a pustulate sculpture, typical for the crocodile newts of the genus *Chelotriton*. The rib fragments possess only one dorsal spine. Until now, *Chelotriton* sensu lato represents a mixture of different salamandrid taxa and contains probably four genera and several species (personal observation). The taxonomic most informative elements are not the vertebrae but the skull. Further investigations must evaluate the taxonomy of this interesting group.

Autecology: Like albanerpetontids, *Chelotriton* s.l. has no direct extant representative and his abundance in fissure fillings is much higher than in basin sediments. This points also to an adaptation to a drier environment with lower ground water levels.

Order Anura RAFINESQUE, 1815
 Family Discoglossidae GÜNTHER, 1858 (1845)
 Genus *Latonia* v. MEYER, 1843

***Latonia ragei* HOSSINI, 1993**
 (Pl. 1, Fig. H, I)

Material: OG2: 2 right ilia (NHMW2002z0014/0001, 0003); T1: 1 frontoparietal-fragment, 1 maxilla-fragment (NHMW2002z0014/0006); T2/5: 1 right ilium, 1 left, 2 right maxilla, 1 praemaxilla, 1 frontoparietal-fragment (NHMW2002z0014/0002, 0004); T2/6: 1 right praemaxilla (NHMW2002z0014/0005).

Description and comparison: The lack of a supraacetabular fossa, the high but less pronounced tuber superius, the vexillum (crista dorsalis ilii) which is lower than the tuber superior, the concave depression at the internal surface between the pars ascendens and descendens ilii and the dorsal less defined acetabulum characterize the ilium of the genus *Latonia*. The difference between the two *Latonia* species from the Lower and Middle Miocene, *L. ragei* and *L. gigantea*, is that in the latter species the outer surface of the posterior part of the maxilla is covered by a rugose dermal ossification (ROCEK, 1994). The well preserved left maxilla from Teiritzberg T2/5 shows no traces of such a dermal ossification and an assignment of these fossils to *Latonia ragei* seems without doubt.

In the NAFB and elsewhere outside Austria *L. ragei* is distributed in sediments from MP30 (oldest record Code-ret) to lower MN4 age (youngest record Petersbuch 2) and would be substituted by *L. gigantea* in the upper MN4 (oldest records Dolnice, Günzburg). In 1998 SANCHIZ described *L. ragei* from the upper MN4 sediments from Oberdorf (Styrian Basin, Austria), so *Latonia ragei* from the lower MN5 of the Korneuburg Basin is the stratigraphic youngest record of this species. This implies further that:

1. *Latonia ragei* and *L. gigantea* have a contemporaneous distribution in Europe during upper MN4 and lower MN5 (~17,5 to 16,6 Myr) but
2. lived not syntopically because *L. ragei* survived only at that time in the Vienna and Styrian Basin where *L. gigantea* is missing.
3. *Latonia gigantea* is probably not the phylogenetical descendent of *L. ragei* but may be an immigrant.

Autecology: The nearest living relatives of *Latonia*, the Mediterranean *Discoglossus* species are highly endemic and according to a hypothesis of ROCEK (1994) the paedomorphic descendents of the Neogene *Latonia* (but see MAXSON & SZYMURA, 1984). Therefore, the autecology of these species can not be very helpful to interpret that of *Latonia*. Up to now, my own database comprises 75 Miocene localities with remains of *Latonia*. Ecological differences between *L. ragei* and *L. gigantea* are not obvious. Remains of *Latonia* are abundant in various types of environments which yielded an azonal vegetation, e.g. in fissure fillings, moor areas and the several kinds of fluvio-lacustrine deposits. Only in Maar lakes with surrounding zonal vegetation, this genus seems to be absent. Further, a remarkable difference between *Discoglossus* and *Latonia* is that the ilia of the latter one possess a well developed tuber superius and a high vexillum, whereas both features are lesser developed in *Discoglossus*. In this respect *Latonia* is much more like the genus *Rana*, especially the *Rana temporaria* species group (= brown frog group). Species of this group are well adapted to both swimming and jumping (in contrast to the water frogs of the *Rana ridibunda* species group) and therefore live in a very broad spectrum of environments. It is remarkable that remains of frogs with such an ecological plasticity like the *Rana temporaria* group are lacking in the European Miocene and Pliocene, except the first and only proof from the Lower Miocene Maar lake Dietrichsberg (Thuringia; BÖHME, 2001). It could be possible that *Latonia* inhabits environments during the Miocene and Pliocene which are preferred today by the *Rana temporaria* group, whereas the brown frogs lived at that time more outside of the sedimentary basins in the forests of the zonal ecosystems. During the Pliocene/Pleistocene climatic deterioration *Latonia* became extinct (or evolved in southern regions into *Discoglossus*) and species of the *Rana temporaria* group entered the former habitat of *Latonia* (various types of azonal ecosystems). This hypothesis coincides with the more frequent occurrence of the *Rana temporaria* group since the Lower Pleistocene (HOLMAN, 1998).

Family Pelobatinae BONAPARTE, 1850

Genus *Pelobates* WAGLER, 1830

***Pelobates* sp.**

(Pl. 1, Fig. D, L, M)

Material: OG2: 2 left, 4 right squamosals, 2 left, 2 right maxilla (NHMW2002z0015/0001-0003); T1: 1 left maxilla (NHMW2002z0015/0004).

Description and comparison: The broken, but already broad medial border of the Obergänserndorf squamosal (Pl. 1, Fig. D) suggests the existence of a fronto-squamosal bridge like in all extant species of *Pelobates* (see *Pelobates fuscus*, Pl. 1, Fig. F) and in *Pelobates* cf. *decheni* (Pl. 1, Fig. E) from Burtenbach 1b (NAFB, lower MN5). In *Eopelobates* PARKER, 1929 a fronto-squamosal bridge is absent (ESTES, 1970). The dermal sculpture of the maxilla is of a pit-and-ridge type (Pl. 1, Fig. M; see also BÖHME, 1999: fig. 4), whereas in *Eopelobates* it is "coarse and open" (ESTES, 1970: 305).

Autecology: Extant pelobatid frogs, or spadefoots are well adapted to a terrestrial mode of life. Two facts are interesting in this respect: the development of a spade and the exogenous induced spawning season. The possession of a spade, an enlarged praehallux, enables these animals to dig themselves in up to 1 m depth. Outside the spawning season (e.g. the dry season), they are nocturnally and live mostly subterranean. The condition of the soil is an important factor regarding the distribution of extant *Pelobates* species (HILDENHAGEN et al., 1981). They prefer sandy soils with a grain size between 0,5 and 3,0 mm (MEISSNER, 1970). The spawning season is triggered by exogenous factors, especially by precipitation ("anuran xeric breeding pattern" sensu BRIGGS; VIERTTEL & WUTTKE, in press; references herein). Both adaptations are essential for living under strong seasonal climate. It is remarkable that in Central Europe during the MN3 and MN4 (Eggenburgian to Lower Karpatian), a time with an almost tropical, especial humid climate (BÖHME 2002b, submitted), *Pelobates* remains are very scarce in contrast to the genus *Eopelobates*. From MN5 onwards (upper Karpatian/Badenian), the most common pelobatid frog is *Pelobates* coinciding with a stronger seasonality at that time (BÖHME, 2002b, submitted). The extinct genus *Eopelobates*, which lack a spade (ESTES, 1970) and probably belong to an own subfamily (Eopelobatinae SPINAR, 1972), is therefore indicative for a more humid micro- or meso-climate.

Family Ranidae GRAY, 1825

Genus *Rana* LINNAEUS, 1758

***Rana* aff. (*ridibunda*) sp.**

(Pl. 1, Fig. K)

Material: T1: 1 right ilium-fragment (NHMW2002z0016/0001).

Description and comparison: The very fragmentary right ilium shows a high, strong and well pronounced tuber superius, a high vexillum and a deep concavity between the tuber superius and the ilial shaft. All this features are characteristic for the *Rana ridibunda* species group (= green or water frogs) to which this fossil is assigned tentatively.

Autecology: Species of the *Rana ridibunda* group are highly adapted to aquatic environments and individuals move away not more than some meters from their home water body. In the NAFB, remains of green frogs are abundant and occur in all types of perennial waters (streams, oxbow lakes, flood swamps, riparian ponds, lakes; BÖHME, 2000).

Order Crocodylia GMELIN, 1788

Suborder Eusuchia HUXLEY, 1875

Family Crocodylidae CUVIER, 1807

Subfamily Alligatorinae KÄLIN, 1940

Genus *Diplocynodon* POMEL, 1847

Diplocynodon* cf. *styriacus

(Pl. 2, Fig. E)

Material: T1: 41 isolated teeth (NHMW2002z0017/0002), 1 left angular (NHMW2002z0017/0001); T2/5: 2 isolated teeth (NHMW0017/0003).

Description and comparison: The left angular from Teiritzberg shows no significant difference compared with the angular remains of *Diplocynodon styriacus* from Sandelzhausen and Appertshofen (both lower MN5; described by SCHERER, 1973, 1978, 1981 as *D. cf. bueticonensis*), except the less pronounced sculptured surface and the smaller size. The 42 mm long angular fragment points to an individual much smaller than 1 m. 80% of the teeth are smaller than 5 mm (mostly 2 - 4 mm). Most teeth, especially the big ones, are broken and show signs of corrosion. Some of the better preserved small tooth crowns were probably lost by tooth replacement. The small size of all remains and the comparatively less sculptured angular surface indicate the presence of small, possibly juvenile individuals.

Autecology: *Diplocynodon styriacus* ranged from the lower MN5 (? upper MN4) to the upper MN6 and represents the last crocodile of Europe north of 37°N palaeolatitude (BÖHME, 2002b, submitted). Remains are frequently found in all types of wet environments like streams, ponds, pools, floodplains or lakes. In contrast to *Gavialosuchus* (ANTUNES, 1994), they never enter brackish or marine environments.

Supraorder Squamata OPPEL, 1811

Order Scleroglossa ESTES, QUEIROZ & GAUTHIER 1988

Infraorder Gekkota CUVIER, 1807

Family Gekkonidae GRAY, 1825

Gekkonidae indet.

(Pl. 2, Fig. F)

Material: OG2: 1 left and 1 right dentary-fragment, 1 left maxilla-fragment, 1 dentary/maxilla fragment (NHMW 2002z0018/0001, 0002).

Description and comparison: The minute and slender dentary with a closed Meckelian canal and small unicuspid teeth is indicative of gekkonids. An assignment to one of the three Miocene genera of Europe (*Gerandogekko*, *Palaeogekko*, *Phyllodactylus*) based on this fragmentary material is impossible.

Autecology: Gekkonids have only a scarce record in the European Miocene. In the literature only four localities are mentioned: Saint-Gerand-le-Puy, Steinberg/Ries, Devinska Nova Ves, La-Grive-Saint-Alban. Two localities are fissure fillings (the latter two) and two represent accumulations of bird pellets in a possible open environment. In the NAFB gekkonids are also rare and are recorded from fissure fillings, the crater wall of the ries-impact structure and from floodplain sediments. The extant gekkonids are mostly nocturnal and (except the Eublepharinae) due to adhesive pads on the digits excellent climbers on trees, walls or rocks. Like albanerpetontids, gekkonids are regarded as dry adapted and are good indicators for a higher seasonality in the NAFB (BÖHME 2002b, submitted).

Infraorder Scincomorpha CAMP, 1923
Suprafamily Lacertoidea FITZINGER, 1826
Family Lacertidae BONAPARTE, 1831
Genus *Lacerta* LINNAEUS, 1758

Lacerta sensu latu div. sp. 1

Lacerta sensu latu div. sp. 2

(Pl. 2, Fig. A-C)

Material:

Lacerta sp. 1: OG2 1 left dentary-fragment, 2 left and 1 right maxilla-fragments, 3 dentary/maxilla-fragments (NHMW2002z0019/0001, 0002); T1: 2 left dentary-fragments, some dentary/maxilla fragments (NHMW2002z0019/0003).

Lacerta sp. 2: OG2: 3 left and 1 right dentary-fragments, 1 left maxilla-fragment, 9 dentary/maxilla-fragments (NHMW2002z0020/0001-0003); T2/3: 1 left dentary-fragment (NHMW2002z0020/0004).

Description and comparison: The remains of lacertids are too fragmentary for a detailed examination. Nevertheless, two size categories and two types of tooth morphology can be distinguished. The most frequent tooth morphology, which belongs to a smaller sized species (*Lacerta* sp. 2), is characterized by a slender but strong and dominant middle cusp and a tendency to tricuspid teeth on the posterior dentary positions. Tricuspid teeth are

characteristic for the genus *Miolacerta* which is known until now only from Dolnice (ROCEK, 1984) and Sandelzhausen (BÖHME, 1999a). But tricuspid teeth occur frequently in the family Lacertidae and are not indicative enough for a taxonomic assignment. The second tooth morphology, which belongs to a larger species (*Lacerta* sp. 1), is characterized by a simple bicuspid tooth with a broad and blunt middle cusp and without any signs of tricuspidity, similar to *Lacerta* sp. from Dolnice (ROCEK, 1984, MN4b) and *L. poncenatensis* from Poncenat (MÜLLER, 1996, MN2b).

Autecology: Members of the exclusively Old World family Lacertidae are diurnally. They lived in various types of habitats, but show the highest diversity in seasonal climates. Without a more detailed taxonomical and phylogenetical analysis of the Tertiary lacertids a specific autecology is impossible to give.

Suprafamily Scincoidea OPPEL, 1811

Family Scincidae GRAY, 1825

Scincidae indet.

(Pl. 2, Fig. D)

Material: OG2: 2 left frontals, 2 left, 2 right dentaries, 14 dentary/maxilla fragments (NHMW2002z0021/0001, 0002); T1: 4 dentary/maxilla fragments (NHMW2002z0021/0003).

Description and comparison: The dorsal side of both left frontal fragments is covered with a tiny dermal sculpture. The facet for attachment of the prefrontal is deep (deeper than in *Eumeces*) suggesting a more robust connection for both bones. The Meckelian canal is very narrow and partly covered by the medially orientated crista ventralis. The paired frontal and the narrow Meckelian canal are indicative for scincids.

Autecology: Skinks are mostly diurnal and live in a variety of habitats (SPAWLS et al., 2002). In the NAFB Scincidae are frequently found in floodplain deposits. But like for the Lacertidae a more detailed taxonomical and phylogenetical analysis is needed to give evidence of their detailed autecology.

Suprafamily Cordyloidea FITZINGER, 1826

Family Cordylidae GRAY, 1837

Cordylidae indet.

(Pl. 2, Fig. G-P)

Material: OG2: 1 left, 2 right dentaries, 3 maxilla fragments, 6 dermal ossifications (NHMW2002z0022/0001-0008).

Description and comparison: It is difficult to differentiate disarticulated skeleton remains of cordylids from

scincids in the fossil record. In the present material the maxilla and the dermal ossifications are most informative. The outer surface of the maxilla fragment behind the fenestra exonaria is thickened and sculptured (Pl. 2, Fig. I, K). Between the sculptured area and the crista dentalis a smooth stripe is developed pierced in the upper part by two foramina. At the posterior wall of the fenestra exonaria, the foramen of the canalis nervi alveolaris superioris lies within a depression (Pl. 2, Fig. K). This posterior wall passes into the outer surface of the maxilla by an indistinct ridge. The blunt to allusively unicuspid teeth are striated on the labial side. All these features are typical for the fossil genus *Palaeocordylus* and except the striated labial tooth side also for the extant genera *Pseudocordylus*, *Tracheloptychus* and *Cordylus* (ROCEK, 1984). My investigations on three extant *Cordylus* species (*C. cataphractus*, *C. cordylus*, *C. polygonus*) suggest that most similarities, especially in respect to the morphology of the fenestra exonaria, exist with *C. cordylus*.

The dermal ossifications referred to cordylids (Pl. 2, Fig. M-P) are small (up to 3 mm), subangular to rounded, nearly smooth and pierced by plentiful foramina of different size. Only one osteoderm shows an indistinct transverse ridge, but no spiny specimen was found. Such osteoderm morphology is reported from the articulated, Upper Oligocene cordilyd "*Lacerta*" *rottensis* (BÖHME & LANG, 1991: fig. 3) and similar dermal ossifications exist in extant cordylids (Pl. 2, Fig. ??; RICHTER, 1994: fig. 31). In "*Lacerta*" *rottensis* spiny osteoderms are lacking and the dermal ossification is restricted to the caudal region as in the extant *Pseudocordylus*. This can probably be assumed also for the Miocene cordylids, because spiny osteoderms are lacking in all cordylid bearing localities (besides Obergänserndorf, Dolnice, and Petersbuch 2) and the above described osteoderm type is very rare. The restriction of the dermal ossification to the caudal region can be interpreted as an adaptation to crevice dwelling (BÖHME & LANG, 1991).

Autecology: Extant cordylids (Cordylinae + Gerrhosaurinae) are restricted to tropical and subtropical regions in Africa, south of the Sahel Zone and Madagascar. They can be regarded as thermophilous and for this reason their fossil distribution is very useful for palaeoclimatic reconstructions (see below; BÖHME, 2002b submitted). Most species lived in rocky environments (SPAWLS et al., 2002). Up to the present knowledge, cordylids never enter the NAFB.

Suprafamily Amphisbaenia GRAY, 1844
Family Amphisbaenidae GRAY, 1865

Amphisbaenidae indet.
(Pl. 1, Fig. N)

Material: OG2: 2 left dentaries, 1 praemaxillary (NHMW2002z0023/0001, 0002); T1: 2 right dentaries (NHMW2002z0023/0003).

Description and comparison: The amphisbaenid material is too fragmentary in preservation for an assignment to one of the two Neogene genera *Blanus* WAGLER, 1830 and *Palaeoblanus* SCHLEICH, 1988. Some fragments show features of one of the two genera. The dentary on Pl. 2, Fig. N shows blunt and short teeth typical for *Palaeoblanus*, whereas the teeth of the second dentary from OG2 are more elongated and pointed like in *Blanus*. Furthermore, the position of the labial foramina is different on each specimen indicating that possibly more than one taxon occurs in the sediments of the Korneuburg Basin.

Autecology: Extant amphisbaenids are burrowing, subterranean animals. Despite their relative frequent occurrence, their fossil record is only poorly understood. Previous studies (BÖHME, 1999b) indicate that *Palaeoblanus* and *Blanus* are contemporaneous during MN3 to MN5, whereas unpublished data suggest a much longer coexistence lasting from the Upper Oligocene (MP30) to the lower Middle Miocene (MN5). The records from the NAFB are mostly from floodplain sediments (palaeosoils) and in some cases from fissure fillings. Except for the more frequent occurrence, their distribution is quite similar to gekkonids.

Supraorder Anguimorpha FÜRBRINGER, 1900
Suprafamily Anguioidea FITZINGER, 1826
Family Anguidae GRAY, 1825
Genus *Ophisaurus* DAUDIN, 1803

***Ophisaurus* aff. *fejfari* KLEMBARA, 1979**
(Pl. 1, Fig. O)

Material: OG2: 2 isolated teeth, 1 right dentary fragment (NHMW2002z0024/0001); T1: 1 maxilla-fragment (NHMW2002z0024/0002).

Description and comparison: The tooth of the maxilla fragment is strong, caniniform and bent posterior. Such teeth are typical for the genus *Ophisaurus*. At the anterior side of the tooth a sharp cutting edge is developed. The Miocene species of *Ophisaurus* (*O. spinari*, *O. fejfari*, *O. (? Anguis) robustus*) are based on the morphology of parietals (KLEMBARA, 1981). Studies on Central European anguids have shown that sharp anterior cutting edges occur on maxilla and dental teeth associated with *O. fejfari* parietals, whereas teeth associated with *O. spinari* parietals lack such a sharp cutting edge (personal observations; *O. (? Anguis) robustus* is only known from the type locality). The maxilla fragment therefore can be tentatively assigned to *Ophisaurus fejfari*. Other *Ophisaurus* remains (especially from layer OG2) with a much poorer preservation are named as *Ophisaurus* sp. in table 1.

Autecology: Both Miocene *Ophisaurus* species are described from one locality (Dolnice, KLEMBARA, 1981). My investigations show that the abundance of both species is dependent on the sedimentary environment. Whereas *O. fejfari* is abundant in fissure fillings (e.g. Pe-

tersbuch 2), *O. spinari* is found mainly in fluvio-lacustrine basin sediments (e.g. Sandelzhausen, BÖHME, 1999a). That implies that *Ophisaurus feffari* is, in contrast to *O. spinari*, more adapted to environments of low ground water level.

Genus *Pseudopus* MERREM, 1820

***Pseudopus* aff. *fraasi* (HILGENDORF, 1883)**

(Pl. 1, Fig. P)

Material: OG2: 1 left, 1 right dentary-fragment, 2 dentary/maxilla-fragments (NHMW2002z0025/0001, 0002).

Description and comparison: Members of the genus *Pseudopus* are characterized by blunt and strong, amblyodont teeth (KLEMBARA, 1981). The dentition is closed spaced. From the Obergänserndorf material only the last dentary teeth is small and spherical, the anterior ones are larger and post-like. The Upper Miocene species *P. pannonicus* differ from the Lower/Middle Miocene species *P. fraasi* (possibly synonym to *P. moguntinus* BOETTGER, 1875) by its larger size and the spherical morphology of more than one posterior tooth.

Autecology: The only extant member of the genus (*P. apodus*) lives in South-East Europe and West Asia in open, rocky environments. The diet composition of these diurnal animals mainly consists of land snails and beetles (ENGELMANN et al., 1993). In the fossil record of Southern Germany *Pseudopus* is of very frequent occurrence and of higher abundance in the karst fissure fillings than in the NAFB.

Anguidae indet.

Material: numerous osteoscutes from the layers OG2 (NHMW2002z0026/0001), T1 (NHMW2002z0026/0002), T2/3 (NHMW2002z0026/0003), T2/5 (NHMW2002z0026/0004), 001/Z/D (NHMW2002z0026/0005) and 001/Z/250-280 (NHMW2002z0026/0006).

Description and comparison: The osteoscutes show the typical anguid morphology. A distinction of the more than six Miocene anguid species of the genera *Ophisaurus* and *Pseudopus* based on osteoscutes is impossible.

Order Testudines BATSCH, 1788

**Testudines indet.
Testudinarum ovum**

Material: OG2: 2 plate fragments (NHMW2002z0027/0001), 1 egg shell fragment (NHMW2002z0027/0002).

Description: The eggshell-fragment is 4 x 2 mm in size and 0,8 mm thick. The typical shell structures of turtles, a thick membrana testacea and a palisade layer consisting

of spherulitic aragonite crystals (SCHLEICH & KÄSTLE, 1988), are well visible under the light microscope. The two plate fragments are too fragmentary for a detailed analysis.

	OG2	T1	T2/3	T2/5	T2/6
<i>Barbus</i> sp.		X (1)		X (1)	
<i>Esox</i> sp.	X (1)				
<i>Albanerpeton</i> sp.	X (3)		X (1)		X (1)
<i>Chelotriton</i> sp.	X (1)	X (1)	X (1)	X (1)	
<i>Rana</i> aff. (<i>ridibunda</i>) sp.		X (1)			
<i>Latonia ragei</i>	X (2)	X (1)		X (2)	X (1)
<i>Pelobates</i> sp.	X (4)	X (1)			
Amphisbaenidae indet.	X (2)	X (2)			
Gekkonidae indet.	X (1)				
<i>Lacerta</i> sp.1	X (2)	X (2)			
<i>Lacerta</i> sp. 2	X (3)		X (1)		
Cordylidae indet.	X (2)				
Scincidae indet.	X (2)	X (1)			
<i>Ophisaurus</i> aff. <i>feffari</i>	X (1)	X (1)			
<i>Pseudopus</i> aff. <i>fraasi</i>	X (1)				
Anguidae indet.	X	X	X (1)	X (1)	
<i>Diplocynodon</i> sp.		X		X	
Testudines indet.	X				
Total MNI					
Lower Vertebrates	25	11	4	5	2
mammals	223	158			
all vertebrates	248	169			
% mammals	89,92	93,49			
% Lower Vertebrates	10,08	6,51			
% fish	4	9			
% amphibian	40	36			
% reptile	56	55			

Tab. 1: Taxa of Lower Vertebrates from the Obergänserndorf and Teiritzberg 1 and 2 localities.

The minimal number of individuals (MNI) is given in brackets for each taxon of Lower Vertebrates. The MNI for mammals (mostly Rodentia, but also Marsupialia, Insectivora, Chiroptera, Lagomorpha, Carnivora and Artiodactylia) are summed up from the literature (RADEBER, 1998; BOON-KRISTKOIZ, 1998; DAXNER-HÖCK, 1998; RÖSSNER, 1998). For T2 samples mammal data were not available.

3. Biostratigraphy

The use of Lower Vertebrates for biostratigraphy is limited by their low evolutionary rates and based only on migration events (=first appearance date, FAD) or regional extinction events (=last occurrence date, LOD). Most of the taxa recorded from Obergänserndorf and Teiritzberg have a wide temporal distribution in the Lower and Middle Miocene. Nevertheless, the coexistence of *Barbus* (*Barbus*) sp., *Latonia ragei* and *Pelobates* sp. points to a Karpatian age. *Barbus* (*B.*) sp. has its FAD in the upper MN4 of the NAFB, *Latonia ragei* its LOD also in the upper MN4 of the Styrian Basin, and *Pelobates* reaches higher abundancies from the MN5 onwards. This corresponds with the mammal based biostratigraphic dating to the lowermost MN5 (DAXNER-HÖCK, 1998). Two species have their LAD in Europe at the locality Obergänserndorf 2: Cordylidae indet. and *Latonia ragei* (see above for possible explanations).

4. Taphonomy

Taphonomy is of great importance in comparative palaeoecology, mainly due to identification of isotaphonomic assemblages (WING et al., 1992). The vertebrate assemblages described here are deposited in different palaeoenvironmental settings varying from nearshore deposits (Teiritzberg 1) to brackish (Teiritzberg 2) and freshwater (Obergänserndorf) environments (for more information see SOVIS, 1998; DAXNER-HÖCK, 1998).

Some of the allochthonous bone material, especially of the amphibians, show a high degree of breakage, while other (e.g. reptile jaws) are of better preservation but complete bones are missing totally. Indication of weathering or digestion was not found. Obviously, predation and transport were the most important taphonomic processes to generate the faunal composition. To evaluate the most likely group of predators (mammalian predators, diurnal birds of prey, nocturnal birds of prey) the relative abundance of mammals and non-mammals (Lower Vertebrates, bird remains are lacking) is given in Tab. 1. The minimal number of individuals (MNI) is given for each Lower Vertebrate taxon. The highest amount is counted in OG2 (MNI = 25) followed by T1 (MNI = 11) and the T2 samples. This comparatively low amount of Lower Vertebrates is contrasted by the high abundance of mammal individuals in OG2 (MNI=223) and T1 (MNI=158). The relative abundance of mammals is in OG2 89,92 % and in T1 93,49 %. This faunal composition corresponds well with the diet composition of extant European nocturnal birds of prey (Tab. 2). Except for *Bubo bubo*, the diet of all Striginae and Tytoninae species contains mostly small mammals ranging from 85% - 98% of the whole vertebrate prey. The diet composition of diurnal birds of prey contains a high percentage of birds but also of Lower Vertebrates (UTTENDÖRFER, 1930) whereas mammal predators can show both strategies, mostly specialized on small mammals (ANDREWS, 1990) but also with a dominant portion of Lower Vertebrates (HEINRICH et al., 1983). But in contrast to birds, mammals crushed the bones of their prey by their shearing teeth and thus produce the highest measure of breakage among the three predatory groups (ANDREWS, 1990). Additionally, the bone destruction by digestion is greater in diurnal birds of prey and mammals than in nocturnal birds of prey (ANDREWS, 1990).

Both subfamilies of owls are present in the European Middle Miocene (Tytoninae since the Middle Eocene, Striginae since the Lower Miocene; FEDUCCIA, 1999), wherefore it seems possible that the vertebrate assemblages of Obergänserndorf and Teiritzberg represent washed out owl pellets which were transported and buried allochthonous.

5. Palaeoenvironment

5.1. Obergänserndorf 2

The most remarkable feature of the Obergänserndorf 2 Lower Vertebrate assemblage is the abundance of burrowing animals (*Albanerpeton* sp., *Pelobates* sp., *Amphisbaenidae* indet.) which represent 36% of the total indi-

Nocturnal birds of prey	Total vertebrates	% mammals	% birds	Lower Vertebrates (fish/amphibian/reptile)
<i>Asio otus</i> (Long-eared owl, Waldohreule)	20640	98,15	1,62	0,23 2/98/0
<i>Asio flammeus</i> (Short-eared owl, Sumpfohreule)	1786	97,82	2,13	0,05 0/100/0
<i>Strix aluco</i> (Tawny owl, Waldkauz)	3559	85,50	8,60	5,90 11/88/1
<i>Athene noctua</i> (Little owl, Steinkauz)	1505	88,24	9,97	1,79 0/92/8
<i>Tyto alba guttata</i> (Barn owl, Schleiereule)	47640	97,50	2,08	0,42 0/100/0
<i>Bubo bubo</i> (Eagle owl, Uhu)	334	64,37	33,83	1,80 0/100/0

Tab. 2: Comparison of diets of Central European nocturnal birds of prey (after UTTENDÖRFER, 1930). The German and English names of the species are given in brackets.

dual content. This high portion of subterranean species indicate the presence of a suitable soil substrate above the groundwater level. Derived from the preferred substrate of *Pelobates* (the most abundant species) sandy soils with a grain size from 0,5 to 3,0 mm can be presumed. The presence of turtle eggshells also points to the same direction. A lower groundwater level and a dryer environment can also be inferred from the occurrence of three species of *Lacerta*, the Gekkonidae, *Ophisaurus* aff. *feffari* and *Pseudopus* aff. *fraasi*. The latter three taxa are a typical association of the karst plateaus in Southern Germany. The presence of one isolated pike tooth argues in favour for a floodplain environment. The remaining amphibian species have a wide ecological range (*Latonia ragei*) or are indistinct at the genus level (*Chelotriton* sp.). It is remarkable that arboreal reptiles like the big *Chamaeleo* species and as well as the aquatic reptiles like crocodiles are lacking.

Summarizing, the Lower Vertebrates of Obergänserndorf indicate an open, probably abandoned floodplain environment above the groundwater level. Since most of the vertebrate assemblage probably originated from owl pellets (excluding the pike and the turtle eggshell) and the fossil bearing layer is a small sandy channel (DAXNER-HÖCK, 1998), the fossils were possibly washed away during heavy rainfalls and buried into distal fans.

5.2. Teiritzberg 1

The principal faunal composition of T1 is similar to OG2 with the following important exceptions: *Pelobates* is not dominant, the absence of the pike, *Albanerpeton*,

gekkonids, cordilyds, *Pseudopus*, and turtles, and the presence of a barb, waterfrogs, and crocodils. The portion on burrowing animals remains high (27%) but lower than in OG2. Obviously, the local environment was wetter in terms of the groundwater level. The only freshwater fish, *Barbus* (*Barbus*) sp. is possibly conspecific with *Barbus* (*B.*) sp. B from the NAFB, where it is indicative for oxbow lakes or slow running rivers. It is further important that in the NAFB the co-occurrence of *Rana*, *Latonina*, *Pelobates* and *Diplocynodon* is common in fluvial assemblages (channel fills).

Therefore we can conclude that the terrestrial Lower Vertebrate assemblage of Teiritzberg 1 points to an environment with higher groundwater level and probably originates from a channel fill. These sediments were resedimentated afterwards and finally deposited in a nearshore environment.

5.3. Teiritzberg 2

From the different Teiritzberg 2 samples only three (T2/3, T/25, T2/6) yielded terrestrial Lower Vertebrates. The material is scarce and not suitable for a bed by bed comparison. But putting the data from all samples together, there is only an insignificant difference to T1, except for the very few or absent remains of terrestrial reptiles. Furthermore, it may be possible that the faunal content is more selective due to a wider sediment transport, but this is rather speculative.

6. Palaeoclimate

Using Lower Vertebrates for palaeoclimatological studies can be an important approach because of their close physiological dependence on temperature and humidity. But in practise especially the interpretation as temperature indicators is restricted, because in most cases only the lower limit of temperature within the geographical distribution of their closest extant relatives is useful.

The Lower/Middle Miocene palaeoclimate evolution of Central Europe was recently stressed by BÖHME (2002b submitted). This investigation is based on the temporal distribution of thermophilic and dry adapted Lower Vertebrates as well as using additional palaeobotanical and palaeopedological proxies. The results indicate a Miocene climatic optimum ranging from the Eggenburgian to the Middle Badenian (20,0 Myr - 13,5 Myr). This optimum peaked at 18,0 Myr to 16,5 Myr (Ottangian, Karpatian) with a mean annual temperature (MAT) of 22°C and a high humidity. The Lower and Middle Badenian is characterized by probably unchanged temperatures but a remarkable seasonality with two major excursions at the lowermost Lower Badenian (16,3 to ~15,7 Myr) and at the Lower/Middle Badenian transition (14,7 to ~14,5 Myr). The Miocene climatic optimum ends abruptly between 14,0 and 13,5 Myr with a drop of the MAT of probably more than 7°C to around 14,8 to 15,7°C. New results implicate that these climatic variations are probably orbital forced.

From the thermophilic Lower Vertebrates used by BÖHME (2002b submitted) two taxa are present in the sediments of the Korneuburg Basin: the crocodile *Diplocynodon* (Alligatoridae) and the cordilyd lizards (Cordylidae). The range of the MAT in the distribution area of their extant relatives is: 15,7 to 27,2°C for Alligatoridae and 17,0 to 30,1°C for Cordylidae (all temperature data from HALLER-PROBST 1997). The minimal cold month temperature (CMT) for the Alligatoridae is -1,7°C and for Cordylidae 3,0°C respectively. We can conclude that the data from the Korneuburg basin point to a MAT of more than 17,0°C and frost free winter months with more than 3,0°C. This agrees with the multiproxy data from BÖHME (2002b submitted) for the Karpatian of ~22°C MAT and more than 8,0°C CMT.

The analysis of the evolution of humidity in the NAFB was based on a composite section ranging from the Ottangian (upper MN4) to the Middle/Upper Badenian (upper MN6) and used relative abundances of dry adapted taxa assuming their immigration during more seasonal climate stages. Until now it is not possible to quantify the humidity changes. Therefore it is difficult to compare one locality (or two of the same age) from another basin with this relative humidity curve of the NAFB.

Generally, two of the dry adapted taxa used in BÖHME (2002b submitted) are present in the Korneuburg Basin: *Albanerpeton* sp. and Gekkonidae indet.. Additionally, the occurrence of *Ophisaurus* aff. *feffari* and *Pseudopus* aff. *fraasi* which have a dominant distribution in the surrounding karst plateaus of the NAFB and the dominance of the spade foot (*Pelobates* sp.) also point to a seasonal regional climate during the deposition of Upper Karpatian sediments in the Korneuburg Basin. In contrast, the time equivalent mammal faunal unit in the NAFB, the OSM 1 (reference locality Langenmoosen, see DAXNER-HÖCK, 1998) precedes the first remarkable seasonality phase at OSM 3 to 5 by approximately 300 kyr. For a better understanding of this difference and for a usage of a kind of climatostratigraphy (correlation of climatic events) we need longer sections with good faunal records.

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Plate 1

Fig. A: *Esox* sp.

OG2; isolated tooth (NHMW 001)

Fig. B, C: *Albanerpeton* sp.

OG2

B right dentary-fragment (NHMW 002)

C left maxilla (NHMW 003)

Fig. D, L, M: *Pelobates* sp.

OG2

D right squamosal-fragment (NHMW 017)

L left maxilla-fragment lingual view (NHMW 018)

M left maxilla-fragment labial view (NHMW 018)

Fig. E: *Pelobates* cf. *decheni*

Burtenbach 1b, NAFB; left squamosal (Coll. BSP)

Fig. F: *Pelobates fuscus*

recent; left squamosal (BSP 1982 X 2275)

Fig. G: *Chelotriton* sp.

T2/5; right frontal-fragment (NHMW 007)

Fig. H, I: *Latonia ragei*

H right ilium, OG2 (NHMW 011)

I left maxilla-fragment labial view, T2/5 (NHMW 012)

Fig. K: *Rana* aff. (*ridibunda*) sp.

T1; right ilium-fragment (NHMW 021)

Fig. N: *Amphisbaenidae* indet.

OG2; left dentary-fragment (NHMW 045)

Fig. O: *Ophisaurus* aff. *fejfari*

T1; maxilla-fragment (NHMW 048)

Fig. P: *Pseudopus* aff. *fraasi*

OG2; left dentary-fragment (NHMW 050)

Fig. B, C, Fig. D-F and Fig. L, M at the same scale

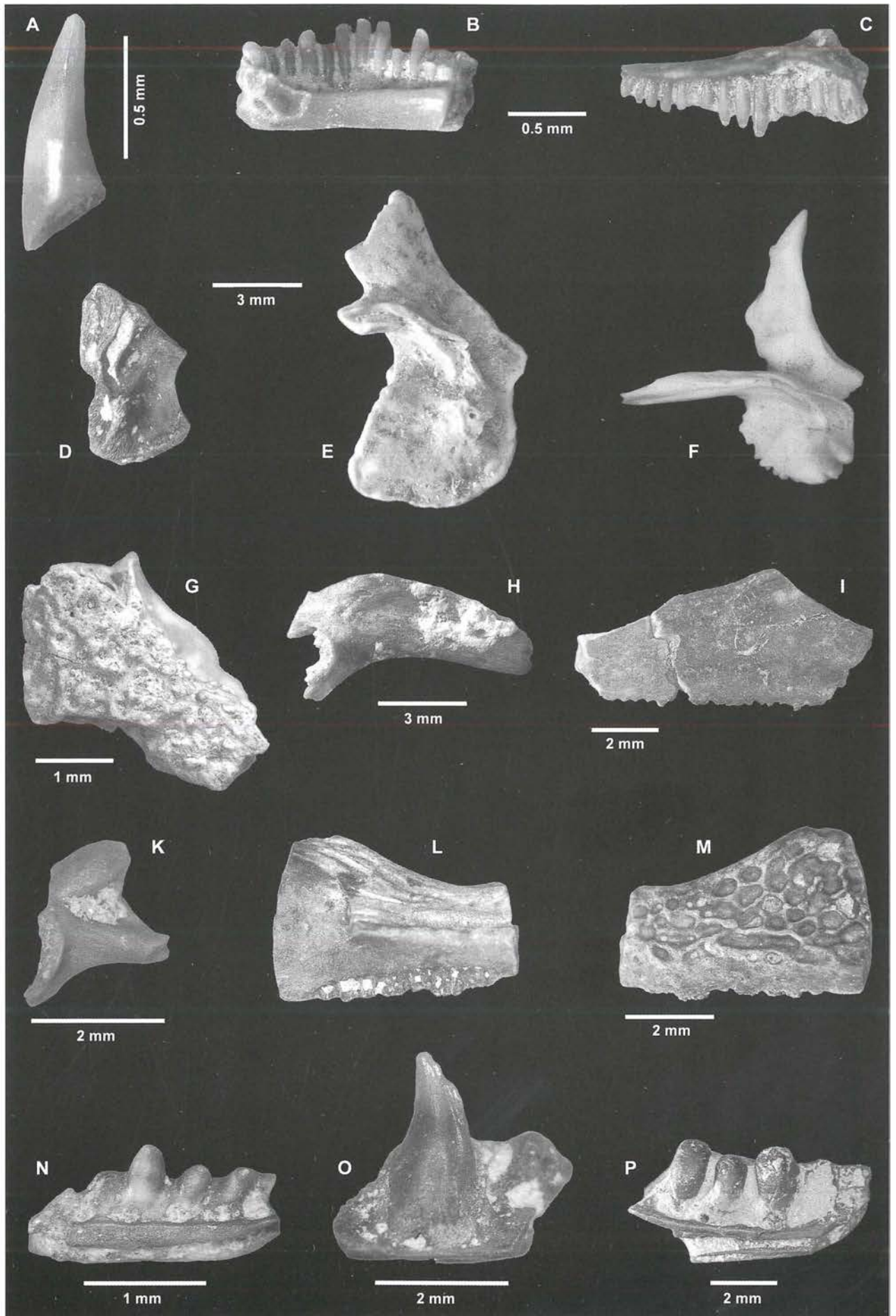


Plate 2**Fig. A: *Lacerta* sp. 1**

OG2; jaw-fragment (NHMW 027)

Fig. B, C: *Lacerta* sp. 2

OG2

B right dentary-fragment (NHMW 028),

C jaw-fragment (NHMW 029)

Fig. D: Scincidae indet.

OG2; left dentary-fragment (NHMW 034)

Fig. E: *Diplocynodon* sp.,

T1; left angular (NHMW 022)

Fig. F: Gekkonidae indet.

OG2; right dentary-fragment (NHMW 025)

Fig. G-P: Cordylidae indet.

OG2

G right dentary-fragment (NHMW 037)

H left dentary-fragment (NHMW 038)

I left maxilla-fragment in lateral view (NHMW 039)

K left maxilla-fragment in anterolateral view (NHMW 039)

L maxilla-fragment, labial tooth side (NHMW 039)

M-P: osteoscutes (NHMW 040-043)

Fig. A-C, F the same scale

