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ORIGINAL PAPER

Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria)

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Abstract In this paper, we present the ectothermic vertebrate fauna from the late Middle Miocene locality Gratkorn (Austria). In total, 2 fish, 8 amphibian and 17 reptile taxa have been described. Among them reptiles are the most abundant group. Fish remains are very rare and comprise only small-sized cyprinids (Leuciscinae indet.) and gobiids (Gobiidae indet.). Caudates are represented by a small-sized newt (*Triturus* sp. aff. *T. vulgaris*), a salamander (*Salamandra sansaniensis*), and a crocodile newt (*Chelotriton* aff. *paradoxus*). Anurans are documented by *Rana* sp., *Pelophylax* sp., *Latonia* sp., *Bufotes* cf. *viridis*, and *Pelobates sanchizi*. The most diverse and numerous ectothermic vertebrate group are scincomorph reptiles (lizards), of which more than 30 bones belonging to six taxa (Scincidae indet., *Lacerta* s.l. sp. 1–3, *Miolacerta tenuis*, ?*Edlartetia* sp.) have been recognised. Gecko remains (Gekkonidae indet.) are rare. Anguimorphs are represented by a large monitor lizard (*Varanus* sp.) and a small-size species of *Ophisaurus spinari.* Four snake taxa are present in Gratkorn: two "small-sized colubrins" Colubrinae sp. 1 and sp. 2, a natricine (Natricinae sp.), and a cobra (*Naja* sp.). Turtles are represented by two aquatic turtles (*Clemmydopsis turnauensis, Chelydropsis murchisonae*) and two terrestrial tortoises (*Testudo* cf. *steinheimensis, Testudo* cf. *kalksburgensis*). The fauna of amphibians and reptiles of Gratkorn (layer 11b) reflects a variety of habitats, relatively sparsely vegetated floodplain with sandy soils, including short-lived ponds, streams or rivulets in the close vicinity, relatively open landscapes, with a dry, semi-arid climate (MAP 486±252 mm).

Keywords Gratkorn · Austria · Middle Miocene · Fishes · Amphibians · Reptiles · Palaeoprecipitation

Abbreviations

GPIT	Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany
UMJGP	Universalmuseum Joanneum, Graz, Austria

Introduction

The locality Gratkorn (Styria, Austria) provides unique and one of the most abundant and complete vertebrate fauna from the European late Middle Miocene (beginning late Sarmatian s.str., 12–12.2 Ma; Gross et al. 2014, this issue). The vertebrate remains, deriving from a palaeosol, include all vertebrae groups (fishes, amphibian, reptiles, birds, mammals; e.g. Prieto et al. 2010a, b, 2012; Gross et al. 2011). Among these groups, ectothermic vertebrates are of prime importance for palaeoenvironmental studies and reconstruction of climatic parameters. At Gratkorn, 27 taxa of fishes, amphibians, and reptiles have been excavated, and are presented in detail, providing a unique opportunity to view the late Middle Miocene terrestrial biota.

Materials and methods

The Gratkorn fossils are stored in the Landesmuseum Joanneum (Graz, Austria) and the Palaeontological collection of University of Tübingen (Tübingen, Germany). Most of the

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material was collected by screen-washing of the uppermost part of the palaeosol; the remaining specimens (mostly partial skeletons) were quarried. The fossils are considered to present a single individual, since they were found together in a small area, have bones of comparable size, and do not duplicate each other. The photographs were made using a digital microscope (Leica DVM5000) and digital camera (Nikon D70) of the Department of Geosciences, University Tübingen. The terminology used in the description follows Francis (1934) (Caudata), Sanchíz (1998) (Anura), Zangerl (1969) (Testudinata), Klembara (1986), Klembara et al. (2010) (Anguimorpha), Evans (2008) and Roček (1984) (Scincomorpha) and Kosma (2004) (scincomorph tooth crown morphology), and Szyndlar (1991a) (Serpentes).

Systematic palaeontology

Order Cypriniformes Bleeker, 1859
Family Cyprinidae Bonaparte, 1832
Subfamily Leuciscinae Howes, 1991

Leuciscinae indet.
Fig. 1a

Material: 1 pharyngeal tooth (UMJGP GR3-79).
Description and remarks: Teeth mesiodistally compressed, tapering apically; short, robust and with a pointed terminal hook. Grinding surface elongate and narrow. Both mesial and distal edges of the grinding surface are rough, without any denticles. Proximally, the tooth crown is wide, while tooth shaft narrows toward its base. Based on tooth morphology, we assign the studied material to subfamily Leuciscinae.

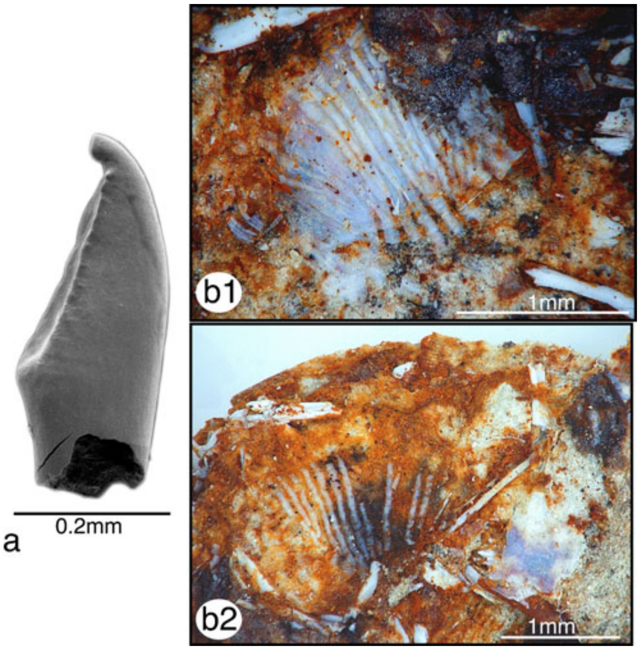


Fig. 1 Fishes from Gratkorn. **a** A pharyngeal tooth of Leuciscinae indet. (UMJGP GR3-79); **b** scale of Gobiidae indet. (GPIT/OS/00800)

Fig. 2 Amphibians from Gratkorn. **a** partial skeleton of *Chelotriton* aff. ▶ *paradoxus* (UMJGP 204.730); frontal (**a**1), rib (**a**2), and trunk vertebra (**a**3). **b**, **e** *Triturus* sp. aff. *T. vulgaris* (GPIT/AM/00724); **b** otoccipital in ventral view, **e** trunk vertebrae in dorsal (**e**1), ventral (**e**2), anterior (**e**3), lateral (**e**4), and posterior (**e**5) views. **c**, **d**, **f** *Salamandra sansaniensis* (GPIT/AM/00725); **c** right dentary in lingual view, **d** rib, **f** trunk vertebrae in dorsal (**f**1, **f**4), ventral (**f**2), lateral (**f**3), anterior (**f**5), and posterior (**f**6) views. **g** *Bufotes* cf. *viridis* (GPIT/AM/00726) right ilium from laterial view. **h**–**k** *Latonia* sp. (GPIT/AM/00727); **h** right maxilla in labial view, **i** right premaxilla in labial, **j** atlas in ventral, **k** urostyle in dorsal views. **l**, **m** *Pelobates sanchizi*; **l** partial skeleton on two (**l**1, **l**2) (UMJGP 204.692) plates, **m** frontoparietal (UMJGP 204.708) from dorsal (**m**1) and ventral (**m**2) views. **n** *Pelophylax* sp. (GPIT/AM/00731) right ilium in lateral view. **o** *Rana* sp. (GPIT/AM/00732) right ilium in lateral view

Order Gobiiformes Günther, 1880
Family Gobiidae Cuvier, 1816

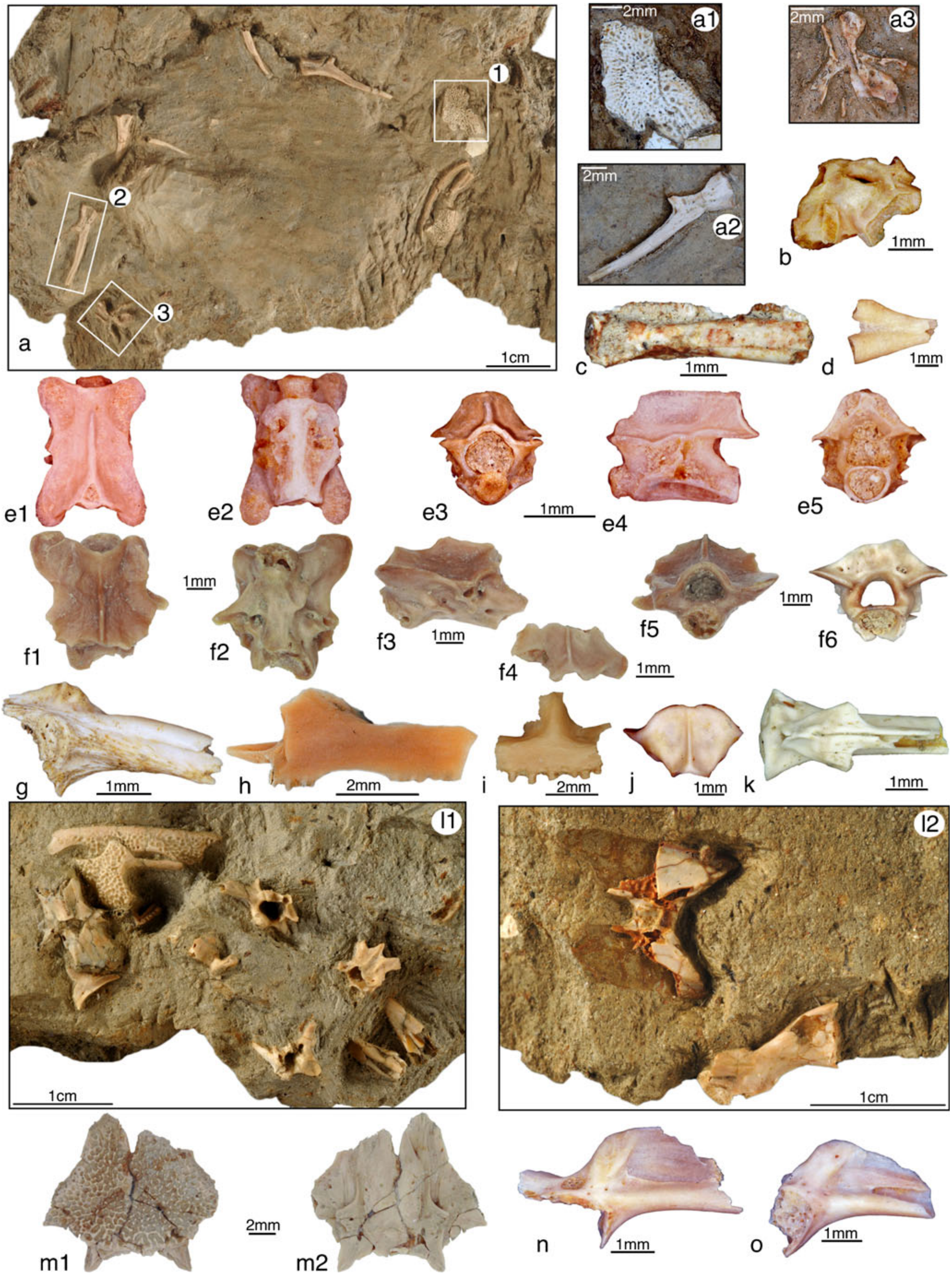
Gobiidae indet.
Fig. 1b

Material: (GPIT/OS/00800).
Description and remarks: A scale ca. 1 mm in diameter belongs to a small-sized gobiid. The ctenii, which are represented by well-developed radii, converge on the scale nuclei, but they never merge. The circulii are very fine and very dense. This scale morphology is widely distributed among gobiid fishes.

Order Caudata Scopoli, 1777
Family Salamandridae Goldfuss, 1820
Genus *Chelotriton* Pomel, 1853

Chelotriton aff. *paradoxus* Pomel, 1853
Fig. 2a

Material: A partial skeleton with 1 frontal, 2 trunk vertebrae, 6 ribs, and fragmentary preserved limb bones, belonging to one individual (UMJGP 204.730).
Description and remarks: The dorsal surface of the frontal displays characteristic dense, pustular and very regular dermal ossification (Fig. 2a1). The frontal is as broad as long, and the anterior border straight. The medial margin in its posterior portion inclines laterally. The frontosquamosal process is very broad, its posteromedial corner concave. The vertebrae are considerably damaged. However, they show an opistocoelous centrum. Several ribs are present (Fig. 2a, a2), showing bicapitate articulation (with distinct dorsal tuberculum and ventral capitulum) of the rib body at its proximal end. In its middle portion, the rib is constricted, but extends posteriorly forming one distinct dorsal spine. Distally, the ribs terminate in a long and gracile process. The type of sculpturing as well as morphology of the frontal from Gratkorn resembles that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from Coderet (France) (frontal type A in Böhme 2008; pl. 2, fig. 3), the type locality for *Chelotriton paradoxus*. All recovered ribs show only one distinct dorsal spine, which also agrees with observations on *Chelotriton paradoxus* from Coderet. In the material from Coderet, two-thirds of the recovered ribs have only one spine, the remaining one-third have two and more spines (Böhme 2008). Unfortunately, the comparison of ribs from Gratkorn with the Coderet material is not reliable, due to the smaller number of available vertebrae from Gratkorn. The holotype of *Ch. paradoxus* is an isolated vertebra and is not associated with any other bone. In the material from Gratkorn, only two fragmentary preserved vertebrae are present, not allowing any comparison. Despite the similarities of the Gratkorn crocodile newt with *Ch. paradoxus*, it cannot be securely referred to this species, so tentative assignment to this taxon is preferable.

Genus *Triturus* Rafinesque, 1815

Triturus sp. aff. *T. vulgaris* (Linnaeus, 1758)
Fig. 2b, e

Material: 1 right maxilla, 1 left otoccipital, 5 trunk vertebrae, and 1 femur (GPIT/AM/00724).

Description: The otoccipital is short anteroposteriorly, not massive, and broken. A distinct occipital condyle is knob-like, the fenestra ovalis is large. The facies parasphenoidalis is narrow and short (Fig. 2b). Trunk vertebrae are small, up to 2 mm in length. The vertebrae are compact and broad. They have nearly the same width along their entire length. The centrum is opistocelous and massive. In ventral view, it possesses several subcentral foramina of varying size. Weakly developed anterior and posterior alar processes are present. They both terminate on the ventral surface of the transverse processes. In anterior view, the large neural canal has a rounded outline, and is dorsoventrally slightly compressed. The neural arch is high, broad and smooth. The moderately high neural spine is thin, without ornamentation, and reaches the dorsal edge of pterygapophysis. The pre- and postgyzapophyses are oval in shape and do not project laterally. Both the weakly developed accessory alar process and posterior lamina are situated on the same level, but separated by the dorsal edge of the transverse process (Fig. 2e).

Remarks: Otoccipital morphology, e.g. general outline, narrow and short facies parasphenoidalis, resembles the species group *Triturus vulgaris*, while *T. boscai* and *T. helveticus* were available for comparison. The structure of the vertebrae strongly resembles Recent *T. vulgaris* in their small size and the high neural spine developed in the cranial part of each vertebra (Hodrová 1984; Tempfer 2004). However, because of the poor preservation of the fossil bone material, further characters cannot be observed. Therefore, we tentatively assign the remains to *Triturus vulgaris*.

Genus *Salamandra* Laurenti, 1768

Salamandra sansaniensis Lartet, 1851
Figure 2c, d, f

Material: 1 left and 1 right dentaries, 11 fragmentary to nearly completely preserved trunk vertebrae, 5 ribs (GPIT/AM/00725).

Description and remarks: Two anterior dentary fragments are slender and low. The symphysis is rounded. In lingual view, a shallow depression is located at the ventral corner. The Meckelian groove is still covered by prearticular (Fig. 2c). The vertebrae are large, robust, and dorsoventrally compressed, the neural arch is low and broad, and the centrum is opistocelous. The largest trunk vertebra is 6 mm in length, which corresponds to an animal of about 20 cm in total length (estimation based on comparison with Recent *S. salamandra*). The subcentral foramina on the ventral surface of centrum are variable in form but small in size. The anterior projection of the neural arch is long and smooth; the neural spine, which begins behind this projection, is broken but probably was not very high; it does not reach the forked posterior margin of neural arch. The pre-and postzygapophyses are rounded and massive. The bases of the prezygapophyses are broad and robust. They are laterally connected by a prominent horizontal interzygapophyseal ridge (Fig. 2f1, f3). The five recovered ribs are bicapitate, with rounded articulation surfaces; they do not possess any dorsal spines (Fig. 2d). We consider these ribs to belong to *S. sansaniensis*, since they are too large to belong to *Triturus* aff. *vulgaris* and do not possess a dorsal spine as in *Chelotriton*. The vertebral morphology, observable on the available material, agrees with *S. sansaniensis* (Rage and Hossini 2000): large-sized (5–6 mm), dorsoventrally compressed, robust and broad vertebrae, rather prominent neural arch, with strongly forked posterior margin.

Order Anura Fischer von Waldheim, 1813
Family Bufonidae Gray, 1825
Genus *Bufotes* Rafinesque, 1814

Bufotes cf. *viridis* (Laurenti, 1768)
Figure 2g

Material: 2 right ilia, 1 right, and 1 left scapulae, 1 right frontoparietal (GPIT/AM/00726).

Description and Remarks: The tuber superior is low and wide, with two tubercles. The acetabulum is distinct, and its ventroposterior corner possesses a wide and deep preacetabular fossa. A shallow longitudinal groove is present on the lateral surface of the preserved proximal portion of the iliac shaft. A moderately developed spiral groove is located behind the tuber superior. No calamita ridge is observable. The scapula is compact, and short but tall. The glenoid process bears a distinct crista supragleinoidalis. A small angular fossa is present at the junction of the body of the scapula and the processus glenoidalis. The margo anterior is provided with an extremely low keel. The presence of a low and bilobate tuber superior and a distinct preacetabular fossa on the ilium, as well as a crista supraglenoidalis and angular fossa on the scapula (Blain et al. 2010), allows assignment of the fossil remains to the *Bufotes viridis* group.

Family Alytidae Fitzinger, 1843
Genus *Latonia* Meyer, 1843

Latonia sp.
Figure 2h–k

Material: 1 left and 2 right premaxillae, 1 left and 1 right maxillae, 1 atlas, 2 vertebrae, 1 urostyle (GPIT/AM/00727).
Description and remarks: The maxilla is robust, its labial surface is smooth (Fig. 2h), and the lamina horizontalis is wide and massive. In labial view, the premaxilla surface is smooth, and the pars facialis has a triangular form with a rounded surface. In lingual view, a large hollow is present. The pars dentalis of both maxilla and premaxilla bear tooth pedicles. An atlas, belonging to a large individual, has a triangular-shaped centrum, with a well-developed crista on the ventral surface, distinct occipital fossae, and a rounded cotyle on the posterior side (Fig. 2j). The urostyle is bicotylar, and provided with a pair of transverse processes and a proximal portion of carina dorsal (Fig. 2k). The robust maxilla, with a wide and massive lamina horizontalis, the atlas with a ventral crista, and the morphology of the urostyle clearly resemble the genus *Latonia* (Roček 1994). Lack of ornamentation on the smooth labial surface of the maxilla clearly separates it from from the widespread species *L. gigantea*. *Latonia ragei* is the only species known to display a smooth maxilla (Hossini 1993), and most probably the Gratkorn specimens belong to this species. In the Miocene of Europe, there are several localities where discoglossine maxillae without ornamentation have been recorded, e.g. ?juv. *Latonia* or *Discoglossus* from Sansan, France (Rage and Hossini 2000), cf. *Discoglossus* from Rudabánya, Hungary (Roček 2005), etc. From these taxa, the Gratkorn frogs can also be distinguished by their larger size. However, due to the fragmentary preservation of the bone, we describe the fossil remains as *Latonia* sp.

Family Pelobatidae Bonaparte, 1850
Genus *Pelobates* Wagler, 1830

Pelobates sanchizi Venczel 2004
Figure 2l, m

Material: 1 frontoparietal (UMJGP 204.708), 2 right and 3 left fragments of maxilla (GPIT/AM/00728, GPIT/AM/00729, UMJGP 204.692), 1 right premaxilla (UMJGP 204.692), 1 sphenethmoid (UMJGP 204.692), 1 right and 1 left squamosals (GPIT/AM/00729, UMJGP 204.692), 1 scapula (UMJGP 204.692), 5 trunk (UMJGP 204.692) and 2 sacral vertebrae (UMJGP 204.692, UMJGP 204.731).
Description: Skull bones, i.e. frontoparietal, maxilla,and squamosal, display dermal ornamentation with prominent pit-and-ridge sculptured surfaces. The nearly complete azygous frontoparietal is convex in outline. The processus posterior superior is reduced. The posterolaterally pointed paraoccipital process is short. The squamosal-frontoparietal articulation surface is low and is nearly one-fifth of the total bone length. The facies posterior is vertical, slightly convex, and with a smooth surface. Medial to the processus, the opening of the arteriae occipitalis is visible. Beside this is a small foramen on the posteriomedial sides of both paraoccipital processes. A small lamelliform ridge projects over the foramina. The processus posterior interior is small and projects ventrolaterally. The incrassatio frontoparietalis is broad and maintains nearly the same width along its entire length, but anteriorly it narrows sharply. The tectum supraorbitale is wide and projects laterally above the pars contacta. At the junction of the processus lateralis inferior and pars contacta is the orifice of arteria orbitonasalis. Anteriorly, the arteria runs uncovered in a deep groove on the ventral surface of the tectum supraorbitalis (Fig. 2m).

In labial view, the maxilla is elongated and low in outline (Fig. 2l1). The lamina anterior is bilobate and the dorsal lobe is prominent. The flange connecting the processus zygomatico-maxillaris and processus posterior is concave. The former process projects posterodorsally and has a rounded outline. The margo orbitalis and flange between the processus frontalis and lamina anterior are concave. In lingual view, the lamina horizontalis is pronounced. The sulcus dentalis is moderately deep and broad. The depression on the posterior portion of the bone (the surface between processes pterygoideus, zygomatico-maxiallaris, and posterior) is extremely shallow. Posteriorly, the lamina dentalis terminates shortly behind the processus pterygoideus.

A well-preserved right squamosal is present. The posterolateral process is slender and long. The lamella alaris is very broad, while posteriorly it is convex and distally slightly broader than proximally. The ventral margin of the lamella alaris is concave and does not project over the base of the posterolateral process. The distal portion of the zygomatic process is broken, but it is clear that the margo orbitalis is strongly concave (Fig. 2l1).

A well-preserved scapula is seen in ventral view. It is anteroposteriorlly elongate and shallow, and slightly curved. The crista supraglenoidalis is massive and prominent, and as long as the glenoidal process. The keel on the margo anterior is broken (Fig. 2l2).

The centrum of the trunk vertebrae is elongate and cylindrical. In dorsal view, the anterior margin of the neural arch is slightly concave, while the posterior margin terminates in a spine. Three preserved sacral vertebrae are not fused with the urostyle. They display widened triangular sacral wings (Fig. 2l).

Remarks: Based on the sculpturing of the dermal bones, *Pelobates* remains from Gratkorn can be assigned to the group of fossil species of *Pelobates* including *P. decheni*, *P. sanchizi*, and *P. fahlbuschi* (Venczel 2004; Böhme 2010). These spatefoot toad remains resemble the morphology of *P. sanchizi* in the broad anterior portion of the frontoparietal: the degree of development of the tectum supraorbitale and groove of the arteria orbitonasalis; the outline of the incrassation frontoparietalis; as figured in Venczel (2004: fig. 6G), the ventral margin of the lamella alaris is concave and does not project over the base of the posterolateral process in *P. sanchizi*; and the caudal part of the bone is high and provided with a wide and pointed processus zygomatico-maxillaris (Ivanov 2008). The completely preserved maxilla from Gratkorn can be distinguished from Recent *Pelobates* species and fossil *Pelobates decheni* by the generally lower outline, bilobate anterior and posterior margins, and stronger development of processes zygomatico-maxillaris and dorsal lobe of the lamina anterior; furthermore, the flange between the processus frontalis and lamina anterior is concave, whereas in the Recent species, it is convex. Compared with *P. falbuschi* Böhme (2010; fig. 5T), the Gratkorn spadefoot has a higher and less concave margo orbitalis.

Family Ranidae Rafinesque, 1814
Genus *Pelophylax* Fitzinger, 1843

Pelophylax sp.
Figure 2n

Material: 1 right ilium (GPIT/AM/00731).

Description: The tuber superior is tall, well defined, dorsally thinning, rounded, and slightly S-shaped in outline. It is oriented more dorsally than anteriorly. The dorsal crest is very thin and high, higher even than the tuber superior. A well-developed supraacetabular fossa is located between the tuber superior and pars ascendens. The latter is high and pronounced, whereas the pars descendens is reduced.

Remarks: See below under *Rana* sp.

Genus *Rana* Linnaeus, 1758

Rana sp.
Figure 2o

Material: 1 right ilium (GPIT/AM/00732).

Description: Bone dorsally bears a robust, massive, anteriorly directed, low tuber superior. The low dorsal crest is lower than the tuber and diminishes distally, but it is intact proximally and no breakage at this portion is observable. The supraacetabular fossa is small, and the pars descendens is reduced.

Remarks: At Gratkorn, both green *Pelophylax* and brown *Rana* frogs are present. The ilia (present in the Gratkorn material) of these two groups can be separated from each other by the following: *Pelophylax* are characterised by more dorsally oriented, dorsally thin and high, S-shaped tuber superior and dorsal crest higher than tuber superior. *Rana* has a more anteriorly directed, robust, oval, low tuber superior, with a dorsal crest lower than the tuber superior (Böhme 1977; Sanchíz et al. 1993; Bailon 1999; Blain et al. 2007). It is important to note that within the brown frogs *Rana* the morphology of ilium is highly variable at the species level (*Rana temproraria* vs. *R. arvalis*), and sometimes can show similarities to green frogs, e.g. the degree of development of tuber superior in *Rana arvalis* and *Pelophylax*. However, taking into account the characters listed above. we are able to identify both green and brown frogs at Gratkorn.

Order Testudinata Linnaeus, 1758
Family Chelydridae Agassiz, 1857
Genus *Chelydropsis* Peters, 1868

Chelydropsis murchisoni (Bell, 1832)
Figure 3a

Material: 1 fragmentary left 10th peripheral (UMJGP 204.725).

Description and Remarks: The lateral and posterior sides of the peripheral are broken. The dorsal surface has a distinct scutal sulcus. The visceral side is concave and bears at its anterior third the synchondrosal pit for joints with the free ends of the rib, characteristic of the Chelydridae, the only known Miocene Eurasian genus *Chelydropsis*. Anterior to the pit, the bone is distinctly thicker than posterior to it. This as well as the asymmetric position of the pit indicates a left peripheral 10, most similar to *Ch. murchisoni* (according to the skeletons from Unterwohlbach; see Młinarski 1980a; Gaffney and Schleich 1994: fig. 1). This species is characteristic of the late Middle Miocene and is known, as well as from Unterwohlbach, from the type locality Öhningen and from Przeworno 2 (Młynarski 1984). Whether the Steinheim *Chelydropsis* (*Ch. murchisoni steaschei* Młinarski 1980b) is conspecific remains to be resolved (Gaffney and Schleich 1994).

Fig. 3 **a** Peripheral of *Chelydropsis murchisoni* (UMJGP 204.725) in medial (**a**1) and dorsal (**a**2) views. **b** *Clemmydopsis turnauensis* (UMJGP 204.057) neural plate in dorsal view. **c** *Testudo* cf. *steinheimensis* (UMJGP 204.690) and **d** *Testudo* cf. *kalksburgensis* (UMJGP 204.113) anterior portion of plastra in visceral (**d**1) and visterolateral (**d**2) views. **e** Gekkonidae gen. et sp. indet. (GPIT/RE/09224) left dentary in lingual view. **f**–**j** *Ophisaurus spinari*. **f** parietal (UMJGP 204.749) in dorsal (**f**1) and ventral (**f**2) views. **g** right dentary (GPIT/RE/09253) in lingual view, **h** left maxilla (GPIT/RE/09253) in lingual view, **i** osteoderm (UMJGP 204.728), **j** partial skeleton of one individual (UMJGP 204.728) with premaxilla (**j**1) and trunk vertebrae (**j**2)

Family Geoemydidae Theobald, 1868
Genus *Clemmydopsis* Boda, 1927

Clemmydopsis turnauensis (Mayer, 1847)
Figure 3b

Material: 1 isolate neural I (UMJPG 204.057-1); 2 fragmentary pleurals (UMJPG 204.726-1, 2).

Description and remarks: The neural plate is sub-rectangular, 8.3 mm long and narrower anteriorly (6.7 mm) than posteriorly (7.6 mm) (Fig. 3b). A median keel is poorly developed. The vertebral sulcus, which crosses the plate in the posterior half, is pointed anteriorly. According to its size and morphology, this bone can be classified as a neural 1 of the geoemydid genus *Clemmydopsis* (the two small fragmentary pleurals also fit with this determination). An elongate, sub-rectangular neural 1 with a weak medial keel and clearly anteriorly pointed vertebral 1/2 sulcus are characteristic features for the type species *C. turnauensis* (Młinarski and Schleich 1980; Schleich 1981; Gross 1994), the only Middle Miocene representative of this genus (Gross 2004).

Family Testudinidae Gray, 1825
Genus *Testudo* Linnaeus, 1758

Testudo cf. *steinheimensis* Staesche 1931
Figure 3c

Material: 1 complete anterior plastron (UMJPG 204.690) and an associated, disarticulated and partial carapace (not described here); 1 fragmentary anterior plastron (UMJPG 204.672); 2 left hyoplastra (UMJPG 204.108 and 203.661).

Description: The complete anterior part of the plastron (UMJPG 204.690) has strongly fused bone sutures and belongs to a mature specimen, whereas the plastron fragment (UMJPG 204.672) displays weakly sutured bones, which indicates an ontogenetically younger individual. The estimated plastron length of both specimens was well below 20 cm (estimation based on the regression models on Recent *Testudo* species). The shell thickness is comparatively thin (6.7–7.8 mm in the postero-medial part of the hyoplastron). The anterior margin of the epiplastron is rather rounded in both specimens. In visceral view, the epiplastron lip is very indistinct (UMJPG 204.690) or weakly (UMJPG 204.672) developed. The maximal thickness of the epiplastral lip along the suture is 15.0–15.5 mm. In ventral view, the gular sulci meet in the anterior quarter of the entoplastron. The entoplastron is longer than wide (40 mm×27 mm in 204.690 and 38 mm×33 mm in 204.672; measured from ventral). The humeral-pectoral sulcus contacts the posterior suture of the entoplastron (UMJPG 204.690), or runs immediately (1 mm) behind (UMJPG 204.672).

Remarks: The plastron morphology closely resembles *Testudo steinheimensis* from Steinheim (Staesche 1931) by the rounded epiplastron, the weak epiplastral lip (thickness 17.5 mm), the anteriorly shifted course of the gular sulci, and the contact of the humeral-pectoral sulcus with the posterior suture of the entoplastron. The Steinheim type (which is about 25 % larger than the Gratkorn specimens) differs, however, in having an entoplastron that is as long as wide (45 mm×45 mm, measured from ventral). *Testudo antiqua* differs by a stronger and more excavated epiplastral lip (Corsini et al. 2013).

Testudo cf. *kalksburgensis* Toula, 1896
Figure 3d–d2

Material: 1 fragmentary anterior plastron (UMJPG 204.113) and an associated, disarticulated and partial carapace (not described here).

Description: Dimensions and the weak sutures indicate a large (projected plastron length over 24 cm; estimation based on the regression models on Recent *Testudo* species), but immature individual. In comparison to *T.* cf. *steinheimensis*, this tortoise is thick-shelled (10.2 mm in the postero-medial part of the hyoplastron) and exhibits a distinct visceral excavation on the epiplastron with a high and robust epiplastral lip (thickness along the suture 23 mm). The lip is pronounced and extends to the anterior suture of the entoplastron. The anterior margin of the epiplastron is blunted, showing a straight margin between the visceral gular sulci. The entroplastron is as long as wide (48 mm×48 mm; measured from ventral) and the ventral gular sulci meet in the anterior quarter of the entoplastron. The humeral-pectoral sulcus contacts the posterior suture of the entoplastron.

Remarks: UMJPG 204.113 differs from the Gratkorn *Testudo* cf. *steinheimensis* in the thicker shell, the excavated epiplastron with a robust and high epiplastral lip extending to the anterior suture of the entoplastron, and the straight anterior margin of the epiplastron. These characters clearly indicate a second tortoise species at Gratkorn, which resembles *Testudo* cf. *kalksburgensis* described by Staesche (1931) from Steinheim. It differs from the only known Steinheim specimen by the contact of the humeral-pectoral sulcus with the posterior suture of the entoplastron (sulcus 4 mm behind the suture in the Steinheim specimen; Staesche 1931). In a recent publication, Corsini et al. (2013) redescribe the topotype population of the late Middle Miocene *Testudo antiqua* Bronn, 1831 from Hohenheven, Germany. The authors found “significant overlap within and between species in the states of many supposedly diagnostic characters …, so much so that it is difficult to correctly diagnose a single fossil individual to species level”, illustrating the morpho-species dilemma within European fossil tortoises. The chosen taxonomic allocation of the Gratkorn tortoises therefore reflects the supposed systematic proximity of both taxa to the

Steinheim tortoises, rather than it following an unambiguous taxonomic concept, which is still lacking for *Testudo* sensu lato.

Order Squamata Oppel, 1811
Infraorder Gekkota Cuvier, 1817
Family Gekkonidae Gray, 1825

Gekkonidae gen. et sp. indet.
Figure 3e

Material: 1 left dentary (GPIT/RE/09224).

Description and remarks: The middle portion of a left dentary (3 mm in length) is present. The bone is slender and its anterior tips show medial curvature. The labial side bears three small labial foramina, arranged in a straight line. In lingual view, the Meckelian canal is closed but opens posteriorly. The lamina horizontalis is tall, due to which the subdental gutter is deep and broad. The dental lamina bears unicuspid pleurodont teeth and their cups display slight striation. This morphology (fused Meckelian canal, unicuspid pleurodont teeth) is widely considered to be characteristic for family Gekkonidae (Rage and Bailon 2005; Venczel 2007).

Infraorder Anguimorpha Fürbringer, 1900
Family Anguidae Gray, 1825
Genus *Ophisaurus* Daudin, 1803

Ophisaurus spinari Klembara 1979
Figure 3f–j

Material: A partial skeleton including 1 premaxilla, 1 quadrate, 5 trunk and 2 sacral vertebrae, osteoderms (UMJGP 204.728), 4 parietals (UMJGP 204.037, 204.137, 204.749, 204.750), 1 left maxilla (UMJGP 204.032), osteoderms (UMJGP 204.130, 204.728), 1 palatine, 1 left maxilla, 1 right dentary, 32 trunk vertebrae (GPIT/RE/09253), numerous osteoderms (UMJGP 204.122–204.124, 204.128, 204.129, GPIT/RE/09252, GPIT/RE/09253).

Description: The dorsal surface of the parietal is sculptured, but the shields are not well pronounced; sulci separating the epidermal scales from each other are very shallow or nearly invisible (Fig. 3f1–2). The parietal foramen is small and located posteriorly on the interparietal shield. The supratemporal process is curved posterolaterally, anteriorly is broad, posteriorly it narrows sharply, the parietal fossa is reduced. The carina arcuata projects dorsally over the bases of the supratemporal process. In ventral view, the cranial vault is deep and smooth.

The posterior portion of a dentary is preserved, the Meckelian groove is narrow and shallow, but exposes ventrally (Fig. 3g). The infra-Meckelian lip is low. The ventral margin of the bone is represented by a crista splenialis, posteriorly it terminates in a distinct pointed spina splenialis. The premaxilla is broad; the maxillary process is long and low, and the nasal process elongate and narrow (Fig. 3j1). The maxilla is a thin-walled bone, and the facial process is low. In ventral view, the supradental shelf is broad, posteriorly it is pierced by a foramen for maxillary division of the fifth cranial nerve (Fig. 3h). Teeth on the maxilla and dentary are subpleurodont, sharp, and posteriorly curved. In lingual view, the tooth cusps show lateral ridges. The labial surfaces of both bones are smooth, bearing only small labial foramina.

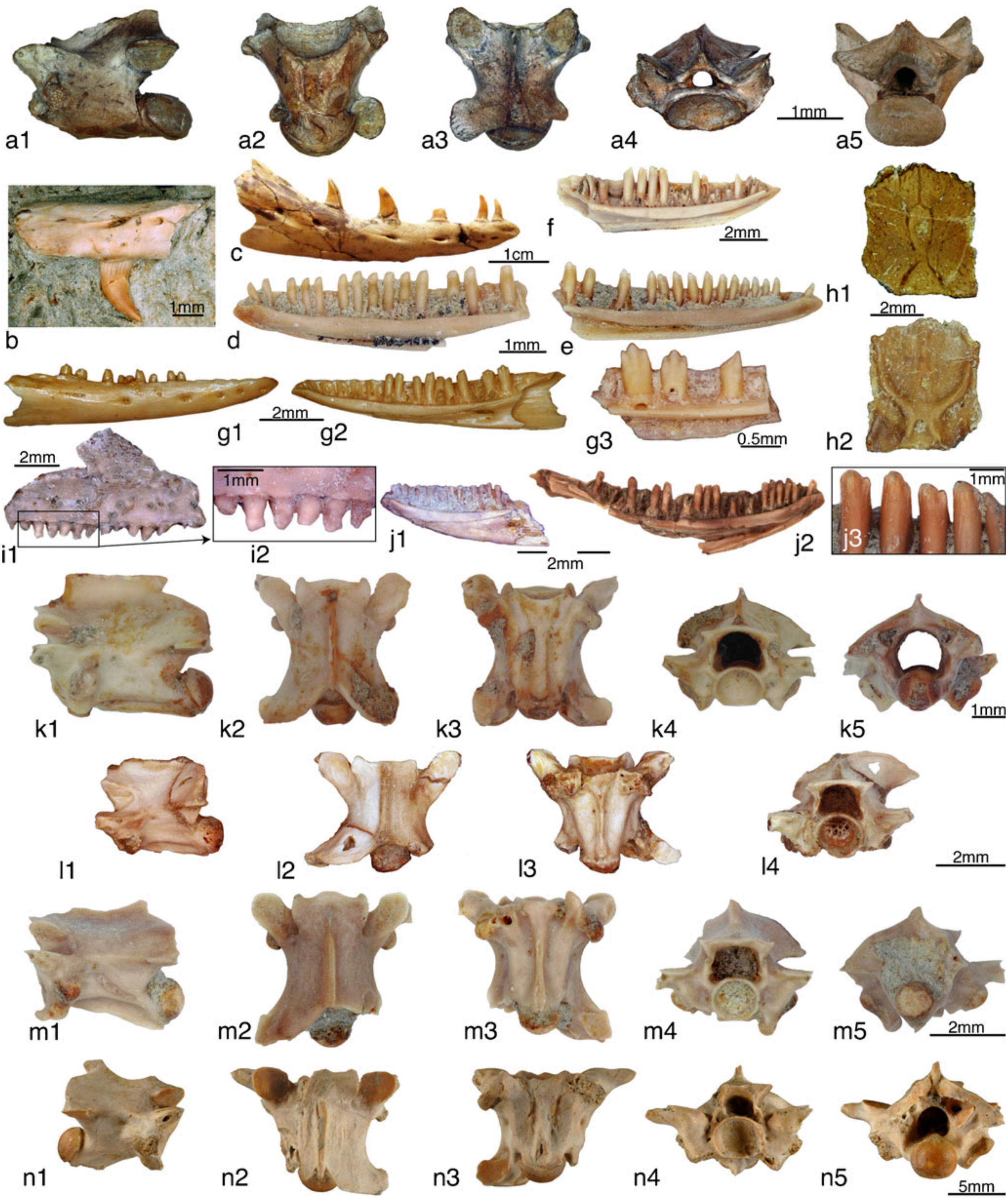
The centra of compact vertebrae are triangular in shape (Fig. 3j2). The ventral surface is mostly flat and anterolateral portions are slightly concave; it bears a pair of small subcentral foramina. The neural spine is high and long. The postzygapophyses are projected laterally, the prezygapophyses laterodorsally and bent anteriorly.

Remarks: The anguine fossil remains can be separated from genus *Pseudopus* by small size and general bone and tooth morphology. The lack of facies muscularis and postfoveal crista on the parietal is characteristic for *Ophisaurus* and excludes the genus *Anguis* (Klembara 1981) from the comparison. The anterior branch of the parietal cranial crest is anterolaterally curved—a characteristic feature of *O. spinari* (contrary to *O. fejfari* with straight anterior branch of the crest) (Klembara 1981, p. 126). The parietal from Gratkorn morphologically also resembles *Ophisaurus spinari* in the form of the supratemporal process, carina arcuata, dorsal ornamentation, etc. (Klembara 1979, 1981, 1986). The ventral margin of the bone is represented by a crista splenialis, posteriorly it terminates by a distinct pointed spina splenialis. This morphology is observable in *Ophisaurus* cf. *spinari* described from Dolnice, Czech Republic (Roček 1984). Osteoderms, originating from different parts of the body, show morphology characteristic for *Ophisaurus* (Klembara 1979, 1981, 1986). They are small and thin, and the shape varies from square to rectangular; distal corners are rounded. The gliding surface is narrow and smooth and situated on the anterior margins. The ornamented surface is large. The median ridge extends along the entire bone and is most prominent in its central part (Fig. 3i).

Family Varanidae Merrem, 1820
Genus *Varanus* Merrem, 1820

Varanus sp.
Figure 4a–c

Material: 1 right dentary (UMJGP 210.905), 1 fragmentary left maxilla (GPIT/RE/09236), 5 trunk (UMJGP 203.732, 204.733, 203.457, GPIT/RE/09261), and 3 caudal vertebrae (UMJGP 203.457), 5 ribs (UMJGP 203.457).



Description and remarks: Both maxilla and dentary are seen in labial view (Fig. 4b, c). Teeth both on maxilla and dentary are subpleurodent, conical, posteriorly curved, and labiolingally compressed. The anterior and posterior margins are serrated; the tooth base is broad and is provided with a low rounded flange. Above the flange, the tooth surface displays numerous

◀ **Fig. 4** **a**–**c** *Varanus* sp. **a** trunk vertebra (UMJGP 203.457) in lateral (**a**1), ventral (**a**2), dorsal (**a**3), anterior (**a**4), and posterior (**a**5) views. **b** maxilla (GPIT/RE/09236) and **c** dentary (UMJGP 210.905) in labial view. Dentaries of **d** *Lacerta* sp. 1 (UMJGP 204.133), **e** *Lacerta* sp. 2 (GPIT/RE/09230), and **f** *Lacerta* sp. 3 (UMJGP 204.107) in lingual views. **g** *Miolacerta tenuis* right dentary (UMJGP 204.031) in labial (**g**1) and lingual (**g**2) views and fragmentary left dentary with teeth (UMJGP 204.106) (**g**3). **h** Lacertidae incertae cedis parietal in dorsal (**h**1) and ventral (**h**2) views. **i** *Edlartetia* sp. (UMJGP 204.752) Right maxilla (**i**1) and teeth row (**i**2) in labial view. **j** Scincidae gen. et sp. indet. Right (GPIT/RE/09266) and left dentary (UMJGP 204.748) from lingual views (**j**1, **j**2) and tooth crowns (GPIT/RE/09265) (**j**3). Trunk vertebra of **k** Colubrinae sp. 1 (GPIT/RE/09257), **l** Colubrinae sp. 2 (GPIT/RE/09258), **m** Natricinae sp. (GPIT/RE/09256), and **n** *Naja* sp. (GPIT/RE/09255) in lateral (**m**1, **n**1), dorsal (**m**2, **n**2), ventral (**m**3, **n**3), anterior (**m**4, **n**4), and posterior (**m**5, **n**5) views

vertical striae. The dentary is elongate, and posteriorly it is thrice as high as anteriorly at the first tooth position. Five teeth are preserved on the dentary. Six moderately large, slightly elongated labial foramina are situated in a line running parallel to the bone anterior margin. The anterior part of a left maxilla with a single tooth is preserved. In dorsolabial view, the palatal facet is convex. The vertebrae are compact. In ventral view, the procelous centrum has a flat surface and it is triangular in shape, anteriorly less than twice as broad as posteriorly (Fig. 4a). The cotyle and condyle are depressed, their axis have marked obliquity. The condyle displays well-developed precondylar constriction. The neural arch is low anteriorly, and gradually increases in height. The anterior part of its surface possesses pores and small striae. Posteriorly, the surface is provided with pronounced and larger striae. The pre- and postzygapophyses are slightly elongated and oblique. A moderately developed lateral ridge projects posteromedially from the posterolateral corner of the prezygapophyses to the longitudinal axe of the neural arch. In posterior view, the neural canal is round, whereas in anterior view, it is arched dorsally and flat ventrally. The neural spine is broken, but extends along the entire length of the neural arch. The fossil remains with present skeletal elements and preservation can be identified at best to the generic level. The bone material from Gratkorn can be separated from the varanid genus *Saniwa*, which went extinct in Europe by the end of the Eocene (Rage 2012), by better developed precondylar constriction, smaller zygosphene. The material can be assigned to the genus *Varanus* based on dentition, general morphology of vertebra, dentary and maxilla, as well as the presence of a lateral ridge and striation on the neural arch, and precondylar constriction (Smith et al. 2008; Delfino et al. 2013).

Infraorder Scincomorpha Camp, 1923
Family Lacertidae Gray, 1825
Genus *Lacerta* sensu lato Linnaeus, 1758

Lacerta s.l. sp. 1
Figure 4d

Material: 7 (1 left and 6 right) dentaries (UMJGP 204.131, 2014.133, GPIT/RE/09226–GPIT/RE/09229, GPIT/RE/09260).
Description: The dentary is low and elongate. The largest dentary is at least 6.5 mm in length and belongs to a medium-sized species. It possesses at least 19 (UMJGP 204.131) bicuspid, posteriorly directed teeth. The Meckelian groove is narrow, exposed ventrally, as well as slightly lingually. The lamina horizontalis is slightly curved and massive; it is thick in its middle portion. In lingual view, the narrow and short articulation facet for the splenial is present at the most posterior part of the lamina horizontalis. The symphysis is large and mostly directed medially. The crista ventralis is very low, and projects slightly below the lamina horizontalis. Its dorsal margin bears a narrow articulation facet for the splenial. Behind the symphysis, the crista ventralis begins with a concave margin. In labial view, seven labial foramina are observable. In dorsal view, a thin and shallow sulcus dentalis is visible.

Lacerta s.l. sp. 2
Figure 4e

Material: 2 left dentaries (GPIT/RE/09230, GPIT/RE/09231).
Description: Dentaries of this medium-sized lizard (the largest dentary is more than 5.7 mm long) are moderately high, the symphysis is elongated and moderately broad, and directed more lingually. The pars dentalis bears 19–21 bicuspid teeth. In lingual view, the Meckelian groove is ventrolingually open, while anteriorly it is narrow and broadens gradually posteriorly. The lamina horizontalis is relatively straight; the anterior half has the same height while it narrows posteriorly. In lingual view, at the last tooth positions, the articulation facet for the splenial is extremely reduced and is present as a narrow strip. In labial view, the bone bears 5–6 labial foramina.

Lacerta s.l. sp. 3
Figure 4f

Material: 1 left dentary (UMJGP 204.107).
Description: The large dentary, belonging to a large species (dentary length more than 9.3 mm) is tall and displays at least 19 large bicuspid teeth. The Meckelian groove is well developed, high, and ventrolingually open. The lamina horizontalis is curved; it is high at its central part, but the anterior and posterior portions are narrower. As can be seen on the preserved bone, the Meckelian groove is as high as the lamina horizontalis behind the symphysis and extends posteriorly in the ventral direction. In dorsal view, the sulcus dentalis is narrow and shallow. Five labial foramina are present on the labial surface.
Comparison: Lacertid remains are very difficult to identify at the species and generic level based only on isolated bones

(mainly dentaries). This diverse “*Lacerta* sensu lato” group is anatomically generalised and displays very few morphologic characters at the species and even generic level (Böhme 2010). However, three distinct *Lacerta* s.l. species, with biscuspid teeth on denateries, can be recognised in the fossil material from Gratkorn. They are clearly distinguished from each other by the size and general outline of the bone, as well as tooth morphology. *Lacerta* sp. 1 and *Lacerta* sp. 2 are similar in dentary and tooth sizes, but can be separated from each other by narrow shallow (*L.* sp. 1) and moderately tall (*L.* sp. 2) dentaries, as well as by the morphology of symphysis (massive in *L.* sp. 1, slender in *L.* sp. 2). *Lacerta* sp. 3 can be clearly separated from these two species by the large and tall dentary, large teeth, and a well-developed and the widest Meckelian groove. The Meckelian groove is correspondingly extremely reduced or moderately developed in *L.* sp. 1 and *L.* sp. 2. Any further comparison with other known lizards from a similar age remains impossible, due to the lack of a detailed revision of the group.

Lacerta s.l. sp.

Material: fragmentary preserved 20 left and 17 right dentaries, 16 left and 18 right maxillae, 3 premaxillae, 5 jaw bones (GPIT/RE/09235), 2 left (UMJGP 204.134, 204.147) and 1 right (UMJGP 204.131) dentaries, 2 left (UMJGP 204.132, 204.136) and 1 right (UMJGP 204.135) maxillae.
Remarks: All bones are fragmentary and represent individuals of all size groups. The jaw bones possess bicuspid teeth similar to those found in three *Lacerta* sensu lato species described above. Any further taxonomic allocation is impossible due to poor preservation. However, we took into account this material for the estimation of the minimal number of individuals of scincomorphs.

Genus *Miolacerta* Roček 1984

Miolacerta tenuis Roček 1984
Figure 4g

Material: 8 (4 left and 4 right) fragmentary or completely preserved dentaries (UMJGP 204.106, 204.031, GPIT/RE/09232−/09234, GPIT/RE/09262, GPIT/RE/09263).
Description and remarks: the best preserved dentary possesses 23 pleurodont teeth. Teeth of the most completely preserved dentary (UMJGP 204.031) are bicuspid anteriorly and tricuspid posteriorly. Tricuspid teeth have two, small, equally developed accessory cusps; the central cusp is massive and high. The symphysis is not robust, and projects dorsolingually. In lingual view, the lamina horizontalis is well developed and curved. It is thin behind the symphysis, while at the 8th tooth position it extends and reaches its maximal height. Posteriorly, it narrows, and its termination is represented as a thin plate, at the level of the last tooth. In lingual view, the articulation facet for the coronoid is observable only at the most posterior portion as a narrow strip. The Meckelian groove is not very large. Its most anterior part is open ventrally, while posteriorly it exposes ventrolingually. In labial view, the bone is smooth, and 6–8 labial foramina are present. In dorsal view, the lamina horizontalis is broad and slightly concave, forming a distinct sulcus dentalis. The weakly developed longitudinal edge on the roof of Meckelian groove is present behind the last tooth, where the lamina horizontalis is absent. In labial view, the facet for coronoid attachment is absent. The splenial preserved on UMJGP 204.031 is anteriorly elongated, and its posterior margin is concave. A large (anterior inferior alveolar foramen) and small (anterior mylohyoid foramen) foramina are present on a slender splenial.

Tricuspid teeth are also known in other lacertids (Kosma 2004); however, the combination of this tooth morphology and the general bone morphology allows us to assign the fossil bones to *Miolacerta tenuis* (Roček 1984).

Lacertidae incertae sedis
Figure 4h

Material: 1 parietal (UMJGP 204.750).
Description and remarks: This bone belongs to a medium-sized lizard. The bone width at the most anterior part is 4.1 mm. It is slightly longer than wide (length/width=4.9/4.1 mm). In dorsal view, the parietal displays sculptured surface with six distinct (paired frontoparietal and parietal, unpaired interparietal and occipital) scales. The parietal scales are elongated and widen posteriorly, the lateral margin is concave. The frontoparietal scales have the form of an isosceles triangle, whereas the occipital scale is an equilateral triangle. The supraoccipital margin of the bone is straight. The interparietal scale is drop-shaped and is pierced by the parietal foramen in its centre (Fig. 4h1). In ventral view, the cranial vault is deep and smooth. The crista crania parietalis increases in height posteriorly. The cristae are curved and form a round posterior wall of the cranial vault. Near the depression, along the longitudinal axis of the parietal, runs a posteriorly expending central ridge. On the posterior portion of the ridge, the parietal foramen is located. Posteriorly, the crista crania parietalis continues into the crista juxtafovealis, which terminates before reaching the posterior margin. The ventrolateral ridge is reduced (Fig. 4h2). The morphology of the parietal is common among lacertids (Rauscher 1992), resembling especially *Podarcis muralis* (see Rauscher 1992; pl. 25, fig. 3) and *Lacerta viridis* (see Rauscher 1992; pl. 26, fig. 3). However, the lack of available studies on the parietal of lacertid lizards do not permit taxonomic identification of the material. Most probably, this parietal belongs to one of three *Lacerta* sensu lato species, described above based on jaw material. However, since the bone was found isolated,

assignment of the bone to one of those species is very difficult. So, we consider this bone as a lacertid of uncertain taxonomic placement.

? Lacertidae
Genus *Edlartetia* Augé and Rage 2000

Edlartetia sp.
Figure 4i

Material: 1 right (UMJGP 204.752) and 1 left (GPIT/RE/09225) maxillae.

Description and remarks: The fragmentary preserved maxilla is triangular in outline. In labial view, the base of the maxilla is smooth. Its surface is pierced by a row of labial foramina, as well as irregularly arranged small foramina. The upper portion is triangular and displays rugose ornamentation due to fused osteoderms. In lingual view, the lamina horizontalis is thin to moderately developed (Fig. 4i1). The maxilla possesses pleurodont, irregularly oriented, apically tapering teeth with broad, round bases. The tooth crowns are slightly pointed, more or less triangular or drop-shaped, and there is a constriction before the crown (Fig. 4i2). The dentition found in these maxillae is characteristic of the genus *Edlartetia* (Augé and Rage 2000). This genus has a scarce fossil record, known only from seven or eight late Early Miocene–early Late Miocene European localities (Böhme and Ilg 2003). Here, they are represented mainly by dentaries, e.g. Sansan, Sandelshausen, etc. So far, only the Late Miocene Austrian locality Kohfidisch has yielded both dentary and maxilla of *Edlartetia* (Tempfer 2004). Unfortunately, fragmentary preservation of maxilla from Kohfidisch makes the direct comparison of Gratkorn material difficult.

Family Scincidae Gray, 1825

Scincidae gen. et sp. indet.
Figure 4j

Material: 4 (3 left and 1 right) dentaries (UMJGP 204.748, GPIT/RE/09264–GPIT/RE/09266), 2 (right and left) maxillae (UMJGP 204.039, GPIT/RE/09267).

Description and remarks: Skinks from Gratkorn belong to a large species; the largest dentary is 16.2 mm in length. The dentaries are massive and robust, posteriorly deep and anteriorly shallow. The Meckelian groove is lingually open (Fig. 4j2). The symphysis is dorsolingually directed, the most anterior part of the Meckelian groove enters slightly into the symphysis. The lamina horizontalis is high, strongly curved, its anterior tip extends ventrally and forms an inflection at the 5–6 dental position. In lingual view, the medial exposure of the splenial facet at the lamina horizontalis occurs at the 14–15 dental position and gradually increases in height. The crista ventralis (infra-Meckelian lip; sensu Smith 2009), directly after symphyses, is slightly concave, where, most probably, attaches the anterior tip of the spenial. The crista ventralis displays an articulation facet for the splenial, which is high posteriorly. The longitudinal edge on the roof of Meckelian groove is moderately developed; its ventral margin runs horizontally. In labial view, the bone surface is smooth; 6–7 labial foramina are arranged in a horizontal row. The splenial covers the Meckelian groove entirely until its most anterior tip (Fig. 4j1). The dental lamina bears pleurdont, cylindirical, posteriorly curved teeth. The most completely preserved dentary possesses 26 teeth (Fig. 4j3). The anterior teeth are unicuspid, whereas the posterior are bicuspid, with a well-developed mesial cusp. The lingual surface of the crowns show striations, which are less pronounced posteriorly. The cuspis lingualis is narrow, and the antrum intercristatum is moderately wide, but narrows apically, resulting in a merger of the cuspis labialis and lingualis with a carina intercuspidalis. Dental morphology indicates strong affiliation of the dentaries to the family Scincidae (Kosma 2004). Scincidae gen. et sp. indet. from Gratkorn can differ from three skink species recorded in Sandelzhausen (see Böhme 2010; fig. 9G-I), in the strongly developed Meckelian groove, the larger and more robust teeth, and the tall lamina horizontalis, which is dorsally inflected at its anterior portion.

Infraorder Serpentes Linnaeus, 1758
Family Colubridae Oppel, 1811
Subfamily Colubrinae Oppel, 1811
«small-sized colubrines»

Colubrinae sp. 1
Figure 4k

Material: 3 trunk vertebrae on a plate (UMJGP 204.041) and 3 isolated trunk vertebrae (GPIT/RE/09257).

Description: The vertebrae are relatively small, the length of the largest one being 4.5 mm. In lateral view, the neural spine is low and is five times as longer as high. The cranial margin of the spine is vertical; the posterior base is oblique and overhangs the neural arch. The neural arch rises posteriorly. The interzygapophyseal ridges are weakly pronounced. Both dia- and parapophyses are small, knoblike. The epizygapophyseal spine is not well developed. In ventral view, the centrum has the form of an elongated triangle, with a length:width ratio of 1.25:1. The haemal keel is well preserved, expanding close to the cotyle. The base of cotyle is provided by small subcotylar tubercles. The subcentral grooves are moderately deep. The zygosphene is trilobate, with small lateral lobes and a broad median one. In posterior and anterior views, the cotyle and condyle are rounded, whereas the neural canal is rectangular and rounded. The pre- and postzygapophyses have a rounded, elongated form. The short prezygapophyseal processes are gracile at their bases.

Remarks: see Discussion of Colubrinae sp. 2.

Colubrinae sp. 2
Figure 4l

Material: 2 trunk vertebrae (GPIT/RE/09258).

Description: The vertebrae are small and compact, the largest vertebrae 3.8 mm in length. In ventral view, the centrum has the form of an equilateral triangle, and a length:width ratio of nearly 1:1. The subcentral grooves are deep and broad. In lateral view, the neural arch increases slightly in height posteriorly. The interzygapophyseal ridges are pronounced. The epizygapophyseal spine is nearly invisible. The haemal keel is high and thin, expanding close to the cotyle. The zygosphene is bilobed, and the lateral lobes are large. The cotyle and condyle are rounded, and the neural canal is rectangular anteriorly and rounded posteriorly. The pre- and postzygapophyses are oval. The prezygapophyseal processes are massive at their bases.

Comparison: The vertebrae of the two snake taxa described above are assigned to “small-sized colubrines” based on the following features: (1) The centrum is provided with a distinct haemal keel, which does not possess hypapophyses; (2) The centrum length is less than 5 mm (Szyndlar 1991a). However, two distinct species can be distinguished Colubrinae sp. 1 and Colubrinae sp. 2. Colubrinae sp. 1 shows: (1) a longer vertebrae; (2) a taller neural arch; (3) a gracile prezygapophyseal process; (4) a trilobed zygosphene; and (5) a lower neural spine and shallower subcentral grooves. Colubrinae sp. 2 has: (1) shorter, compact vertebrae; (2) a lower neural arch; (3) a massive prezygapophyseal process; (4) a bilobate zygosphene; and (5) a higher neural keel and deeper subcentral grooves.

Subfamily Natricinae Bonaparte, 1838

Natricinae sp.
Figure 4m

Material: 2 trunk vertebrae (GPIT/RE/09256).

Description and Remarks: Both small-sized vertebrae have an elongate centrum, with a length:width ratio of 1.44:1. The haemal keel is prominent and the base of the broken haemapophysis is visible. The subcentral grooves are strong. The subcentral ridge is strongly developed. The cotyle and condyle are rounded. The subcotylar tubercles are small. Anteriorly oriented para(dia)pophyseal processes are short and small, and the paradiapophyses are rounded and knoblike in lateral view, while in ventral and dorsal view they have a hook-shaped form. The zygosphene is trilobate. The neural canal has a nearly rectangular form, while the neural arch is high and posteriorly vaulted. The neural spine is low. The pre- and postzygapophyses have nearly the same length. Their articulation facets are oval, and the prezygapophyseal process is slightly longer than the prezygapophyseal articulation facet. A combination of features—posteriorly vaulted neural arch, presence of haemapophysis, shorter para(dia)pophyseal process—allow identification of the vertebrae as Natricinae sp. (Szyndlar 1991b; Ivanov 2000).

Table 1 Amphibians and reptiles from Gratkorn, supposed minimal number of individuals (*MNI*), ecophysiological groups, and calculation details for the estimation of palaeoprecipitation (according to Böhme et al. 2006)

Taxon	MNI	Ecophysiologic group	Index
Triturus sp. aff. *T. vulgaris*	1	Peri-aquatic	0.3918
Chelotriton aff. *paradoxus*	1	Peri-aquatic	0.3918
Salamandra sansaniensis	1	Peri-aquatic	0.3918
Latonia sp.	2	Peri-aquatic	0.3918
Pelobates sanchizi	3	Fossorial	0.0917
Bufotes cf. *viridis*	2	Heliophil	0
Pelophylax sp.	1	Semi-aquatic	0.513
Rana sp.	1	Peri-aquatic	0.3918
Clemmydopsis turnauensis	1	Full aquatic	1
Chelydropsis murchisonae	1	Full aquatic	1
Testudo cf. *steinheimensis*	4	Heliophil	0
Testudo cf. *kalksburgensis*	1	Heliophil	0
Gekkonidae gen. et sp. indet.	1	Heliophil	0
Lacerta s.l. sp. 1	6	Heliophil	0
Lacerta s.l. sp. 2	2	Heliophil	0
Lacerta s.l. sp. 3	1	Heliophil	0
Lacerta s.l. sp.[a]	22	–	–
Miolacerta tenuis	4	Heliophil	0
Edlartetia sp.	1	Heliophil	0
Scincidae gen. et sp. indet.	3	Heliophil	0
Ophisaurus spinari	4	Heliophil	0
Varanus sp.	2	Heliophil	0
ecophysiologic index			0.21732
mean annual precipitation (in mm)		486	
95 % prediction interval (in mm)		252	

[a] *Lacerta* s.l. sp. is included in the table to indicate the minimal number of individual (*MNI*); they are not relevant for the palaeoprecipitation reconstruction

Family Elapidae Boié, 1827

Genus *Naja* Laurenti, 1768

Naja sp.
Figure 4n

Table 2 Sarmatian herpetofaunal assemblages from the Central Paratethys, according to Venczel and Hir (2013) (*FT3/2* Felsőtárkányi 3/2, *FT2* Felsőtárkányi 2, *FT1* Felsőtárkányi 1, *FF2/3* Felsőtárkányi-Felnemed 2/3), Venczel and Ştiucă (2008) (*TT* Tauţ), present study (*GRK* Gratkorn), Hír et al. (2001) *TSD* Tăşad

Taxon	Localities						
	FT3/2	FT2	FT1	FF2/3	TT	GRK	TSD
Age (Ma)	11.9	11.95	12	12.05	12.1	12.15	12.45
Salamandrina sp.			X				
Salamandra cf. *sansaniensis*						X	
Chelotriton (aff.) *paradoxus*					X	X	
Triturus cf. *roehrsi*	X	X	X				
Triturus sp. aff. *T. vulgaris*						X	
Triturus cf. *marmoratus*					X		
Triturus sp.					X		
Carpatotriton sp.					X		
Latonia gigantea	X	X	X	X	X		
Latonia sp.						X	
Palaeobatrachus (cf.) *hiri*				X	X		
Hyla (cf.) *arborea*		X	X	X	X		
Bufo (cf.) *viridis*		X			X	X	
Pelophylax sp.	X	X		X	X	X	
Rana sp.						X	
Pelobates cf. *sanchizi*	X	X	X	X		X	
Pelobates sp.					X		
Emydidae indet.		X	X	X	X		
Chelydropsis murchisoni						X	
Clemmydopsis turnauensis						X	
Testudo cf. *steinheimensis*						X	
Testudo cf. *kalksburgensis*						X	
Blanus cf. *gracilis*					X		
Agamidae indet.							X
Gekkonidae indet.		X	X		X	X	
Edlartetia sansaniensis						X	
Lacerta sp.	X		X	X	X		X
Lacerta s.l. sp. 1						X	
Lacerta s.l. sp. 2						X	
Lacerta s.l. sp. 3						X	
Lacertidae indet. sp. 1	X	X	X	X			
Lacertidae indet. sp. 2			X		X		
Miolacerta cf. *tenuis*						X	
Chalcides cf. *ocellatus*				X			
Chalcides sp.			X				
Scincidae indet.		X				X	
Varanus sp.						X	
Pseudopus sp.	X			X			X
Anguis cf. *fragilis*	X	X	X	X			
Ophisaurus (cf.) *spinari*	X	X	X	X		X	
Ophisaurus sp.					X		X
Scolecophidia indet.		X	X	X	X		X
Albaneryx cf. *volynicus*		X					
Natrix cf. *rudabanyaensis*	X	X			X		
Natrix sp.			X				
Natricinae sp.						X	

Table 2 (continued)

Taxon	Localities						
	FT3/2	FT2	FT1	FF2/3	TT	GRK	TSD
‚Coluber‘ pouchetii	X						
Coronella miocaenica					X		
Hierophis cf. *hungaricus*				X	X		
Zamenis sp.			X				
Colubrinae sp. 1						X	
Colubrinae sp. 2						X	
Colubridae indet. 1		X					
Colubridae indet. 2			X				
Colubridae indet.							X
Macrovipera sp.					X		
Vipera sp. 1 (gr. *berus*)		X	X				
Vipera sp. 2 (gr. *aspis*)				X			
Viperidae indet.	X	X	X	X			
Elapidae indet.	X	X					
Naja sp.						X	

Material: 2 trunk vertebrae (UMJGP 203.430 and GPIT/RE/09255).

Description: The largest vertebra of an elapid snake from Gratkorn has a centrum length of 10.4 mm. In ventral view, the centrum is broad and triangular, with a length:width ratio of 1:1. At the posterior end of the centrum, the base of a broken hypapophysis is present. The cotyle and condyle are large and rounded, and the

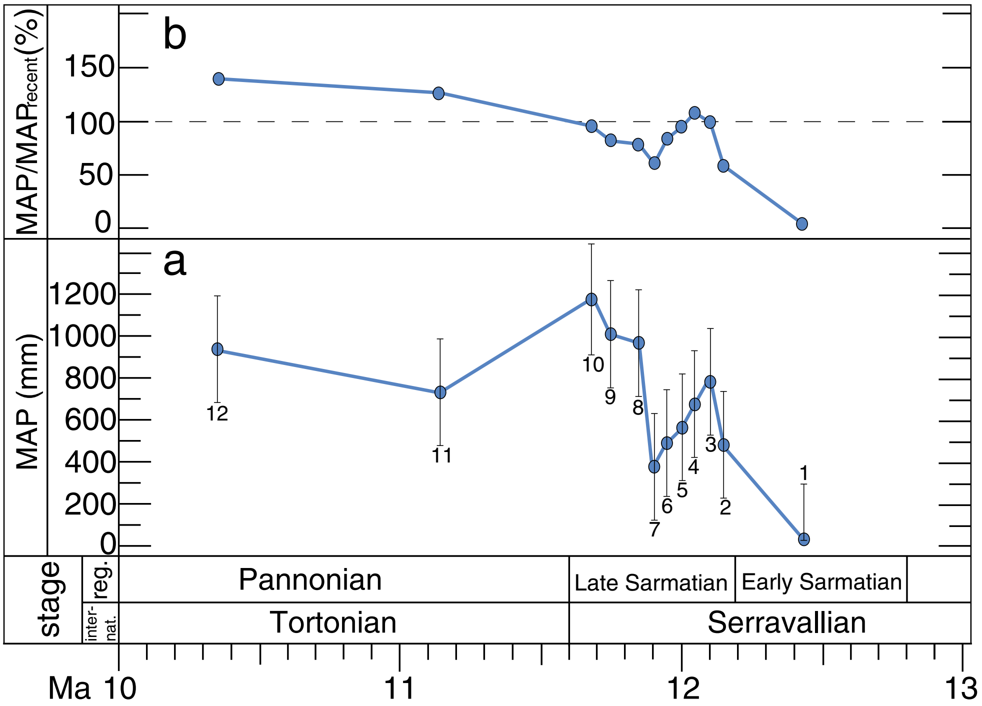


Fig. 5 Precipitation in Central Europe during the late and early Sarmatian s.str. and early Pannonian (early Tortonian–late Serravallian) estimated by bioclimatic analysis of herpetofaunas (Böhme et al. 2006). **a** absolute values of mean annual precipitation (MAP), **b** ratio of MAP to recent precipitation value, *dashed line* (100 %) means no changes relative to recent. Localities: *1* Tăşad, *2* Gratkorn, *3* Tauţ, *4* Felsőtárkányi-Felnemed 2/3, *5* Felsőtárkányi 1, *6* Felsőtárkányi 2, *7* Felsőtárkányi 3/2, *8* Hammerschmiede 1, *9* Hammerschmiede 2, *10* Hammerschmiede 3, *11* Felsőtárkányi 3/10, *12* Vösendorf. Stratigraphic arrangement of localities according to Prieto et al. (2014, this issue). Precipitation values according to Böhme et al. 2008 (for localities 1, 8–10, 12) and corrected after Venczel and Ştiucă 2008 (locality 3), Venczel and Hir 2013 (localities 4–7, 11)

subcotylar tubercles are small. The anteriorly deepening subcentral grooves are wide. Below the weakly developed interzygapophyseal ridges, in depressions, are distinct lateral foramina. The articulation facets of the pre- and postzygapophyses are rounded or slightly oval. The postzygapophyses are slightly longer than the prezagapophyses. In anterior view, the bases of prezygapophyses are wide and are provided with paracotylar foramina. The neural arch is vaulted and posteriorly increases slightly. The neural spine is broken and anteriorly terminates behind the trilobate zygosphene. The neural canal is rounded. The parapophyses are damaged; however, based on orientation of the preserved base, they were probably anteriorly directed.

Remarks: The vertebrae of a large cobra can be assigned to the genus *Naja* based on presence of hypapophysis in trunk vertebra, sharing large colubrins morphology; anteriorly directed parapophyseal process; vaulted neural arch; trilobate zygosphene; lack of an epizygapophyseal spine; and large dimensions and low length/width ratio of the centrum (Szyndlar 1991b; Ivanov 2000). Identification of vertebrae at the specific level is difficult, because of its fragmentary preservation.

Palaeoenvironmental implications

Gratkorn represents the most diverse and well-documented late Middle Miocene (Sarmatian s.str.) ectotherm assemblage. Overall, 27 ectothermic vertebrate taxa belonging to fishes, amphibians and reptiles have been recorded from Gratkorn. The amphibian and reptile assemblage contains a quite diverse (25 taxa), but not very abundant (minimally 65 individuals), fauna (Table 1), which shows ecological adaptations to various environments. Small-sized cyprinids (Leuciscinae indet.) and gobiids (Gobiidae indet.) have been found only in the overlaying lacustrine pelites of the Peterstal member.

All herpetofaunal elements have been found in the upper part of paleosol, the main fossiliferous horizon in Gratkorn (Gratkorn Formation, layer 11b; Gross et al. 2014, this issue). The caudates are represented by single individuals of a small-sized newt *Triturus* sp. aff. *T. vulgaris*, a salamander species *Salamandra sansaniensis*, and a crocodile newt *Chelotriton* aff. *paradoxus*. Among anurans, five taxa can be recognised: brown and green frogs (*Rana* sp., *Pelophylax* sp.), a painted frog *Latonia* sp., a fossorial spadefoot toad *Pelobates sanchizi*, and a green toad *Bufotes* cf. *viridis*. The amphibian fauna indicates variety of environments at Gratkorn. *Salamandra sansaniensis* suggests the presence of at least seasonal streams or rivulets in the close vicinity, since this group has rheophilic larvae requiring richly oxygenated water for larval development (Duellman and Trueb 1994). The spadefoot toad *Pelobates sanchizi*—an important fossil for landscape reconstruction—is the most common amphibian with at least three individuals. Spadefoots favour open landscapes with sandy soils and have a fossorial lifestyle (Böhme 2010). Green toads, similar to burrowing spadefoots, are more adapted to a terrestrial mode of life. Green toads (*Bufotes viridis* species group) prefer open habitats, inhabiting even deserts and semi-deserts (Kuzmin 1995). Salamanders *Triturus* sp. aff. *T. vulgaris,* and frogs *Latonia* sp., *Rana* sp., live in water only during reproduction and spend the remainder of their lives near bodies of water or can survive the drying out of the water body in the mud (Böhme et al. 2006; Biton et al. 2013). So, their presence alludes to the presence of at least periodic water bodies, like small short-lived ponds, swamp habitats, etc. Even the green frog *Pelophylax* sp., which usually lives in permanent water bodies, can survive the drying out of aquatic habitats in the mud (Kuzmin 1995). Amphibians needing long-term permanent water-bodies, like *Andrias*, *Mioproteus*, or *Palaeobatrachus*, are lacking.

Two tortoises species (*Testudo* cf. *steinheimensis* and *T.* cf. *kalksburgensis*), adapted to dry and open environments, are found in associated shells, so they can be regarded as local resident species. Contrary to the tortoises, both fully aquatic turtles, *Clemmydopsis turnauensis* and *Chelydropsis murchisoni*, are represented by a very few isolated fragments.

The remaining reptile groups (gekkotan, scincomorph and anguimorph lizards), representing 57 % of all herpetofaunal individuals, are dwellers of dry open areas. These lizards exploit a more open and dry environment, where the sunlight reaches the ground, and they are mainly independent of the existence of water bodies (Böhme et al. 2006). While only one individual gecko (Gekkonidae indet.) has been recorded, the scincomorph reptiles are the most diverse and abundant ectothermic vertebrate group at Gratkorn. At least 39 individuals belonging to at least six taxa (Scincidae indet., *Lacerta* s.l. sp. 1–3, *Miolacerta tenuis*, ?*Edlartetia* sp.) are recognised, suggesting dominance of the open environments at Gratkorn.

The largest reptile of Gratkorn herpetofauna, the large monitor lizard (*Varanus* sp.) (MNI=2), one of the scavengers of the Gratkorn biome, reaches about 1.5 m (the body length estimation is based on the regressive model of Conrad et al. 2012) in total length. The second anguimorph, a small-size species of *Ophisaurus spinari* (glass lizard), is represented by at least four individuals. This lizard we interpreted as fossorial, taking into account its smaller size than the Recent *Anguis fragilis* (Böhme 2010) and the fossorial life-style of Recent small-sized species of *Ophisaurus* (McConkey 1954). Interestingly, *Ophisaurus spinari* (UMJGP 204.728) as well as both of the *Pelobates sanchizi* (UMJGP 204.692) are represented by associated skeletons (Figs. 2l, 3j). Probably, those indviduals are buried in situ, maybe in their own burrows in the sandy soil, similar to the holotype individual of the cricetid "*Cricetodon*" *fandli*, showing the same taphonomy (Prieto et al. 2010a).

The snake material recorded so far (about 12 trunk vertebrae) is rather scarce, including four taxa, namely a large-sized cobra (*Naja* sp.), two small-sized colubrines (Colubrinae sp. 1 and 2) and a natricine (Natricinae sp.).

In conclusion, the environment of Gratkorn (layer 11b), based on herpetofaunal assemblage, can be reconstructed as a relatively sparsely vegetated floodplain with sandy soils and probably only a seasonal flowing river regime.

The abundant herpetofaunal record allows reconstruction of the palaeoprecipition for the Gratkorn locality, using methods of ecophysiological groups outlined in Böhme et al. (2006). For the estimation of the palaeoprecipitation value, 21 relevant amphibians and reptiles (excluding the non-fossorial snakes) are used for this analysis and grouped into five ecophysiological groups (Table 1). Using equation (6) in Böhme et al. (2006), the ecophysiological index for the community, calculated from the relative frequency of the each group, converts into mean annual precipitation value. The estimated MAP for Gratkorn is 486± 252 mm (Table 1). The present precipitation value of the area is 840 mm (climate station Graz-Thalerhof, Müller and Hennings 2000). So, late Middle Miocene MAP amounts to 58 % of the present precipitation value, characterising a semi-arid and significantly drier climate than the present day.

Furthermore, the absence of thermophilic reptiles, like giant tortoises, cordylids, chamaeleonids, or crocodiles, indicates a cooler climate than during the Miocene climate optimum, with a mean annual temperature (MAT) not exceeding 15 °C. Apparently, *Varanus* sp. is the most thermophilic taxa of the Gratkorn fauna. Among thermophilic ectothermic vertebrates of the Early and Middle Miocene which went extinct in Europe after the Miocene climate optimum, only monitor lizards survived the Middle Miocene cooling (Böhme 2003). Taking into account the temperature requirements of the recent varanids, the occurrence of *Varanus* sp. proposes a MAT not less than 14.8 °C (Böhme 2003). Thus, a subtropical thermal regime with MAT around 15 °C can be supposed for Gratkorn, which agrees with data of Tóth et al. (2010) derived from isotopic analysis of rodent teeth from Felsötarkany.

Sarmatian fauna and Sarmatian climate

During recent years, significant progress has been made in the knowledge of Sarmatian s.str. herpetofauna from the Central Paratethys. Many abundant assemblages have been described in detail (Venczel and Ştiucă 2008; Hír et al. 2001; Venczel and Hir 2013), enabling a detailed comparison of the Gratkorn assemblage with the early Sarmatian (Tăşad, Mohrensternia-zone, ca. 12.45 Ma; Hír et al. 2001) and late Sarmatian assemblages (Tauţ, Felsőtárkányi section, late Sarmatian, ca. 12.1–11.9 Ma; Venczel and Ştiucă 2008; Venczel and Hir 2013; the relative stratigraphic positions follows Prieto et al. 2014, this issue).

Within this comparatively short stratigraphic period of about 500 kya, more than 50 species of amphibians and reptiles, belonging to 23 families, are known from seven localities (Table 2). Several taxa or species (groups) seem to be common in this time period, like *Triturus roersi*, *Pelobates* cf. *sanchizi*, *Pelophylax* sp., *Bufotes* cf. *viridis*, *Hyla* cf. *arborea*, *Latonia gigantea*, Scolecophidia, Gekkonidae, *Anguis* cf. *fragilis*, and *Ophisaurus* cf. *spinari*. Furthermore, Lacertidae display a high diversity of up to five local species.

In spite of this taxonomic richness, several families and genera, known from earlier (Badenian) and/or later (Pannonian) regional stages, are absent during this part of the Sarmatian s.str., e.g. Cryptobranchidae, Hynobiidae, Proteidae, *Eopelobates*, *Bombina*, and *Pelodytes*, as well as Trionychidae, *Mauremys*, *Ptychogaster*, giant tortoises, and crocodiles. Since these are mostly large-bodied forms with robust ossifications (except some amphibians), a taphonomic bias seems unlikely to explain the lack of the majority of groups. Interestingly, all these taxa are to different degrees related to humid environments or the presence of perennial standing or flowing water, especially cryptobranchids (Böhme et al. 2012), proteids (*Mioproteus*; Böhme 2010), crocodiles (Markwick 1998), trionychids (Obst 1986), and *Mauremys* (Keller and Busack 2001). While crocodiles were already extinct in the Sarmatian s.str. due to climatic cooling (Böhme 2003) and Hynobiidae have their first appearance at the Sarmatian–Pannonian boundary of Felsőtárkányi 3/10 (Venczel and Hir 2013), the lack of remaining taxa may possibly be attributed to the scarcity of perennial freshwater during the Sarmatian s.str. This explanation became likely given the reconstructed Sarmatian s.str. humidity. The entire regional stage is characterised by precipitation well below or at present-day values (Fig. 5; see also Böhme et al. 2008, 2011). This is especially significant for the early Sarmatian and the larger part of the late Sarmatian. At the beginning of the late Sarmatian (Tauţ, Felsőtárkányi-Felnemed 2/3, Felsőtárkányi 1), a significant increase in humidity is observed, reaching present-day values. This increase has already started at Gratkorn, which is in agreement with the estimated humidity trend based on sedimentological criteria in the clay-pit of Gratkorn, indicating significant precipitation increase from the layer 7 to layers 11a and 11b and finally to the hanging wall pelites (Gross et al. 2014, this issue). However, even under elevated precipitation values during the mid-Sarmatian humidity peak (e.g. 550–800 mm MAP; Fig. 5), the much warmer than today Sarmatian temperatures will result in increased aridity (high evaporation significantly exceeding precipitation).

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