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The Late Pleistocene microvertebrate fauna of the Vaskapu Cave (North Hungary) and its taphonomical, biostratigraphical and palaeoecological implications

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(with 1 figure and 2 plates)

About 60 years later than the systematic excavation in 1933 carried out by Dr. Mária Mottl and her coworkers, the Vaskapu locality in North Hungary was rediscovered by Dr. János Hír. In the following 15 years, several different field surveys were take place at the site and a rich microvertebrate assemblage were found. The aims of the present study were to review the vertebrate fauna (paying particular attention to the previously poorly studied herpetofauna) and to summarize its taphonomical, biostratigraphical and palaeoecological implications. The slightly mixed assemblage with elements of the forest as well as the grassland habitat is interpreted here as the result of a mosaic or quickly shifting environment left behind a retractive glaciation in the late Würm (namely at the time of the transition between the Pilisszántóian and Palánkian local biochronological stages around 15 000 years ago).

Introduction

The Vaskapu Cave (Fig. 1.) is a rock shelter, situated approximately 4 km NW from Felsőtárkány on the west side of the Lök Valley (Bükk Mountains, North Hungary) close to the Eger-Miskolc highway. Rich Late Pleistocene microvertebrate fauna and a few larger remains were described by KADIĆ and MOTTL (1938) and later by MOTTL (1941) from the original locality (mentioned here as Vaskapu I). In the summer of 1994 Dr. János Hír (director of the Museum of Pásztó) identified a previously unexplored fissure (mentioned here as Vaskapu II) near the original site, with a microvertebrate-rich infilling. Additional sites were numbered later with a bottom-up approach. Vaskapu VI and VII (which provided similar fauna) are most plausibly connected to the same fissure as Vaskapu II, while Vaskapu III, IV and V (which yielded a recent assemblage) are connected to an other fissure closer to the Eger-Miskolc highway. Present study aimed to make the revision of the vertebrate fauna (paying particular attention to the previously poorly studied herpetofauna) of the fossil localities, to summarize the complex taphonomic situation of the fissure system, and to draw biostratigraphical and palaeoecological consequences.

Material and Methods

KADIĆ and MOTTL (1938) described 4 layers from the Cave (Vaskapu I locality) which are the following:

- 1. reddish-brown clay with limestone fragments near the entrance of the main rock shelter
- 2. greenish-gray sandy clay (plausibly a stream sediment) with a few limestone fragments
- 3. light gray clay with limestone fragments situated above layer 2.
- 4. dark brown or black humus at the top of the sequence

The fauna originated from layer 1-3 of the original site is also discussed here, although the material (a total of about 220 kg) studied in the present article was collected during several different field surveys from 1994 to 2009 from the reddish-brown clay infilling of the approximately 15 m high fissure (with the Vaskapu II locality at the bottom and the Vaskapu VII at the top) closest to the 6 m wide and 5 m high rock shelter (namely the Vaskapu I site). This sediment is plausibly the same as layer 1 of the first

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excavation in 1933 (described by KADIĆ and MOTTL, 1938, see above). Most of the samples (approximately 180 kg) are originated from the Vaskapu II site, and additional 20 kg samples were removed from the Vaskapu VI and VII localities.

The material was washed through a 0.5 mm sieve

and in several cases was pre-treated with hydrogenperoxide to remove the high organic content. The studied fossils were emplaced to the Stratigraphical Collection of The Department of Paleontology and Geology at the Hungarian Natural History Museum.



Fig. 1. The Vaskapu Cave (Vaskapu I site) and its surrounding fissure system (with Vaskapu II – Vaskapu VII localities). *Abbreviations:* VK = Vaskapu.

The fauna

Fish

The group Osteichthyes is represented in the studied material only with 4 amphicoelous vertebral centra from the Vaskapu II site. No such remains were found from the surrounding localities so far.

Amphibians

Approximately 100 anuran skeletal elements

(including cranial remains, vertebrae, limb bones, pectoral and pelvic girdles) was found in the material studied in the present paper of which 8 ilium and an angulospleniale was securely identifiable on a species level from the Vaskapu II site. Most of the other remains are attributable to the genus *Bufo* or *Rana*. The identification of the anuran remains was carried out by T. CSÉFÁN and Z. SZENTESI.

The most distinctive skeletal element of the Pleistocene anurans is the ilium. The genus *Bufo* and

Rana were identified on the basis of the ilia from the Vaskapu II locality.

The ilium of a bufonid toad usually lacking dorsal crest (or vexillum), but have a pronounced dorsal prominence (also called tuber superior). According to HOLMAN (1998) three species belong to the genus *Bufo* are detectable in the European Pleistocene record, which are *B. bufo*, *B. viridis*, and *B. calamita*.

B. calamita has a triangular dorsal prominence and a noticeable ridge and/or groove (often called calamita ridge, see Pl. 1, Fig. 2b) on the posteroventral side of the ilial shaft just anterior to the ventral acetabular expansion (or pars descendens ilii). The other species lack this ridge and/or groove. *B. bufo* has a low, rounded (or occasionally blade-like) dorsal prominence sometimes with a rough dorsal surface, while *B. viridis* has a two-lobed dorsal prominence (see Pl. 1, Fig. 5b).

All the three species were detected in the case of the Vaskapu II locality. Specimen VK2.18 (Pl. 1, Fig. 3) and VK2.19 shows typical characteristics of a *B. bufo*. VK2.20 and VK2.21 have a more pronounced tuber superior, similar to *B. calamita*, however the distinctive ridge of the latter taxon is not present, therefore these specimens were identified here as *B. bufo* as well. VK2.15 (Pl. 1, Fig. 5a,b) and VK2.16 (Pl. 1, Fig. 4) have a bilobate dorsal prominence, characteristic to *B. viridis*. VK2.17 (Pl. 1, Fig. 2a,b) is a typical *B. calamita* with triangular tuber superior and a well-developed ridge and groove on the posteroventral side of the ilial shaft just anterior to the ventral acetabular expansion.

Rana is a diverse genus usually with a pronounced dorsal crest and an elongate, compressed dorsal prominence. Specific identification could be difficult in closely related species, but the VK2.14 specimen (Pl. 1, Fig. 1) has a smooth, elongated tuber superior and a well-developed vexillum, therefore identified here as a member of the aforementioned genus. Compared with the European Pleistocene *Rana* species, it has a more pronounced and anteriorly downward sloping dorsal crest, broadly similar to *R. arvalis*. In contrast, according to HOLMAN (1998), the other common Pleistocene brown frog, namely *R. temporaria* have noticeably less-developed vexillum and a tuber superior with often not smooth but slightly roughened dorsal surface.

An additional angulospleniale (VK2.22, Pl. 1, Fig. 6) was identified in the present study as *R. temporaria*. The shaft of the bone is only moderately curved, or almost straight, and the processus coronoideus have a steep posterior surface in lateral view. In contrast, the angulospleniale of a bufonid toad (such as VK2.23 on Pl. 1, Fig. 7 and VK 2.24 on Pl. 1, Fig. 8) is obviously curved, the processus coronoideus is less prominent, while the Meckelian canal is more pronounced (BAILÓN, 1999).

Based on the above described observations, the

following anuran taxa were indentified from the Vaskapu II locality:

Bufo bufo Bufo viridis Bufo calamita Rana temporaria Rana cf. R. arvalis

Reptiles

Among the relatively few snake and lizard material studied in the present paper, postcranial elements (ribs and anteriorly concave but posteriorly convex procoelous vertebrae) were the most abundant. 13 toothbearing skeletal remains were also found from the Vaskapu II site, which were identified here as lacertids. The identification of these remains was carried out by L. M. KELLNER.

Lacertidae is a widespread lizard group (PIANKA & VITT 2003, BAILÓN 2004, VITT & CALDWELL 2008), of which generic and/or specific identification is problematic in many respects. There is a remarkable osteological homogeneity between the different members of the clade and in addition the intraspecific variability of each taxon is significant. The most easily recognizable, but not always diagnostic skeletal elements are the tooth-bearing maxillary, praemaxillary and dentary bones with the following main characteristics:

- 1. The teeth are pleurodont, usually have two (bicuspid), but occasionally only one (unicuspid) or even three (tricuspid) cusps, and their shafts are approximately cylindrical. The number of teeth should not always be taken into a reliable taxonomic allocation, since it depends on the age of the individual (DELFINO & BAILÓN, 2000) (see e.g. Pl. 2, Fig. 1b and 2b).
- 2. The subdental shelf, of which outline could be diagnostic in several cases extends medially below the tooth row (ESTES et al. 1988).
- The Meckelian canal is widely open medially (RAGE & BAILÓN, 2005), as in most scincomorphs (ESTES et al. 1988).
- 4. An intramandibular septum is located in the Meckelian canal between the descending inner wall of the dentary bone and the subdental shelf (ESTES et al. 1988).

VK2.1 (Pl. 2, Fig. 1a-d) is a left dentary bone with space for 19 teeth and with a broadly similar overall morphology to *L. agilis*. According to KOSMA (2004) unicuspidity is restricted to the two anteriormost teeth in the case of the most representatives of the latter species, as in the case of the VK2.1 specimen. In

contrast, the other two abundant Pleistocene European small lacertid species, Podarcis muralis and Lacerta vivipara have 1-5 and 4 anterior unicuspid teeth, respectively. The following teeth are bicuspid with a distally situated main cusp and a smaller mesial accessory cusp, while tricuspid morphology lacks in the case of the VK2.1 specimen. Teeth become more robust in the distal portion of the tooth row. The length of the tooth row is 7.2 mm. On the basis of the data presented by HOLMAN (1998), the length of the tooth raw is approximately 5-6 mm in the case of an adult L. agilis, which is a bit more than Podarcis muralis and Lacerta vivipara, but noticeably less than in the case of L. viridis. The teeth are slightly worn, but obviously striated lingually and labially, which feature is arguing against the genus Podarcis (KOSMA, 2004). The posterior border of the intramandibular septum (which is located approximately below the 5th or 6th tooth positions counted from posterior to anterior direction) is parabolic in ventromedial view (Pl. 2, Fig. 1d). Based on the aforementioned observations specimen VK2.1 is identified here as Lacerta cf. L. agilis.

VK2.4 is a smaller left dentary bone with space for 20 or 21 teeth. The length of the tooth row is 5.1 mm. The parabolic posterior border of the intramandibular septum is located under the 5^{th} or 6^{th} tooth positions counted from posterior to anterior direction. The existence or the number of anterior unicuspid teeth can not be determined, since the fragmentary nature of the specimen. In contrast to the above described VK2.1 specimen, this dentary has tricuspid teeth posteriorly. Despite the differences in the size and tooth morphology, the specimen is plausibly assignable to the same morphotype as VK2.1.

VK2.8 (Pl. 2, Fig. 2a-d) is a right dentary bone with space for 21 or 22 teeth. The teeth are striated with the striae restricted to the lingual surface of the crown which is characteristic for L. viridis according to KOSMA (2004). The adult specimens of the latter species have usually 21 to 26 tooth positions. The first 4 teeth of the VK2.8 specimen are unicuspid, while the next 3 are rather unrecognizable as a result of damage. The following teeth are bicuspid. Teeth are more or less equally robust along the entire length of the tooth row, which is 7.2 mm. The posterior border of the intramandibular septum is located below the 7th and 8th tooth positions (counted from posterior to anterior direction) and is not parabolic but sigmoid in outline with an anteriorly descending ventral edge (Pl. 2, Fig. 2d). Based on the previous observations this specimen is referred here to an other morphotype, which is plausibly closely related to L. viridis.

VK2.9 is a fragment of a left dentary bone with at least 21 tooth places of which the most are apparently bicuspid starting from the 3rd tooth position. Teeth are more or less equally robust along the entire length of the tooth row, which is 7.5 mm. The tooth crowns are

striated lingually. The posterior border of the intramandibular septum is located below the 7th and 8th tooth positions (counted from posterior to anterior direction) and similar to the VK2.8 specimen. Asides from some uncertain striation on the labial side of the tooth crown, this dentary plausibly belongs to the same morphotype as VK2.8.

Specimen VK2.6, VK2.10 and VK2.12 are dentary bones, which show lacertid characteristics, however the fragmentary preservation does not allow even generic level identification.

VK2.2 (see on Pl. 2, Fig. 3a,b), VK2.3, VK2.7 (see on Pl. 2, Fig. 4a,b), VK2.11, and VK2.13 are maxillary fragments with a broadly similar morphology with a space for a relatively reduced number of tooth positions (16 or 17). The total length of the tooth row is 6-6.5 mm. The opening of the canalis alveolaris superior is usually placed at the border of the middle and the posterior third of the dental lamina above the 6th or 7th tooth position (counted from posterior to anterior direction). According to DELFINO & BAILÓN (2000) the latter morphology is similar to the genus Podarcis. However, on the basis of KOSMA (2004), Podarcis lacks striated tooth crowns, which is clearly present in the case of the aforementioned specimens. HOLMAN (1998) stated that tricuspid teeth are absent in the case of the L. agilis maxillae, while often present in the case of L. viridis. On the basis of the tricuspid tooth morphology observed on the VK2.2 and VK2.7 specimen, this morphogroup was identified here as Lacerta cf. L. viridis.

VK2.5. is a significantly fragmentary maxillary bone, which shows lacertid characteristics, however the preservation does not allow generic level identification.

Based on the above described observations, the following reptiles were indentified from the Vaskapu II locality:

Serpentes indet. Lacerta cf. L. agilis Lacerta cf. L. viridis

Birds

Birds are mainly represented by a few praemaxillary bones, carpometacarpi and tarsometatarsi from both the Vaskapu II and Vaskapu VII sites. Based on the revision of the list presented by KADIĆ & MOTTL (1938), the following taxa can be found at the Vaskapu I site:

Lagopus albus Lagopus mutus Tetrao (or Lyrurus) tetrix Pyrrhocorax alpinus Falco tinnunculus

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Mammals

The most abundant and most frequently studied part of the material is the mammalian fauna. KADIĆ and MOTTL (1938) described small and large mammals from the Vaskapu I locality, MÉSZÁROS (1999, 2003, 2004 and 2013) paid particular attention to the shrew remains from the Vaskapu II site, while SÓRON & VIRÁG (2009) focused mainly on the rodent assemblage of the latter locality.

Based on the revised list of KADIĆ and MOTTL (1938), the data published in the above mentioned articles, and the present observations of A. VIRÁG, the following other mammalian remains can be found at the Vaskapu I, II, VI, and VII sites:

Chiroptera indet. (Vaskapu II and VII)

Talpa europaea (mentioned from the Vaskapu I locality)

Sorex alpinus (Vaskapu II and VII) (see MÉSZÁROS, 2013)

Sorex minutus (Vaskapu II and VII) (see MÉSZÁROS, 2013) Sorex araneus (Vaskapu II and VII) (see

Mészáros, 2013)

Crocidura russula (Vaskapu VII) (see MÉSZÁROS, 2013)

Crocidura suaveolens (Vaskapu II and VII)⁴

Lepus sp. (Vaskapu I and II)

Ochotona pusilla (Vaskapu I and II)

Spermophilus (formerly Citellus) rufescens

(mentioned from the Vaskapu I locality)

Glis glis (Vaskapu I, II, and VII)

Apodemus cf. sylvaticus (Vaskapu I, II, and VII)

- Cricetus cricetus (Vaskapu I and II)
- *Myodes* (formerly *Clethrionomys*) glareolus (Vaskapu I, II, and VII)
- Arvicola terrestris (Vaskapu I, II, and VII)
- Microtus arvalis-agrestis gr. (Vaskapu I, II, and VII)
- *Microtus (Alexandromys) oeconomus* (mentioned from the Vaskapu I locality)
- *Microtus (Stenocranius) gregalis* (Vaskapu I, II, and VII)
- *Chionomys* (formerly *Microtus*) *nivalis* (mentioned from the Vaskapu I locality)
- Canis lupus (mentioned from the Vaskapu I locality)
- *Vulpes vulpes* (mentioned from the Vaskapu I locality)
- Ursus arctos (mentioned from the Vaskapu I locality)
- Martes martes (mentioned from the Vaskapu I locality)
- Mustela erminea (mentioned from the Vaskapu I locality)

Mustela nivalis (mentioned from the Vaskapu I locality)

Rangifer tarandus (Vaskapu I; represented by a molar at Vaskapu VI?)

Rupicapra rupicapra (Vaskapu I; represented by a molar at Vaskapu VII?)

Bison priscus (mentioned from the Vaskapu I locality).

Taphonomy of the Vaskapu localities

The fauna most likely represent a mixture of a contemporaneous but more or less mosaic environment (forest and grassland within a small area) or could also be the result of a repeated redeposition of successively changing habitats. The remains were transported to the Vaskapu site by water (probably by a stream) from the original biocoenoses. It is possible, that layer 2 of Vaskapu I represent the sediment of the aforementioned stream. Nevertheless, the smaller or occasionally greater limestone fragments embedded in the clayey layers are indicative for some gravitational movement.

Similar or the same material was washed later from the plateau at top of the Vaskapu VII locality into the fissure system by the spring snowmelt and the repeated rainfalls. This model is in agreement with the results of the taphonomic study carried out by SÓRON & VIRÁG (2009), according to which splitting and flaking resulting from weathering and drying of the bones are common modifications at the locality. The material under the influence of gravity as well as the infiltrating water moved downwards in the fissure system (i.e. towards Vaskapu II locality). During the latter transportation the remains were further damaged and size selective processes occurred.

It is in agreement with the fact that the material is more fragmented and contains less relatively long (more than 10 mm) bones at the Vaskapu II site compared with the Vaskapu VII locality. It is also in agreement with the observations of SÓRON & VIRÁG (2009), according to which the most common fractures of the limb bones are perpendicular to the main axis of the bone and the broken surface is smooth or stepped, which means that the damage occurred after the loss of the collagen fibers (i.e. the remains were most likely at least partly mineralized at that time). The abundance of bone fragments, isolated molars and empty alveolar spaces suggest a relatively significant transportation of the material.

Although the Vaskapu II locality has a natural

sediment refill from the fissure system situated above the site, it was almost deserted due to the repeated sediment extraction from 1994 to 2009. As the airspace of the cavity gradually increased it became more often inhabited by recent faunal elements. As a consequence, the sediment collected in 2009 contains some recent remains as well, but those bones obviously differ from the fossil ones which are more fragmented and have darker (yellow or yellowishbrown) colour.

Biostratigraphical and palaeoecological conclusions

According to BÖHME (1996) the development of the herpetofauna reflects the major phases of the Central European climatic cycles during the Pleistocene epoch:

- 1. *Rana temporaria* tends to be the only species present in ice-free areas during full cold stages.
- 2. *Bufo bufo, Rana arvalis,* and *Vipera berus* are early pioneers during the latter part of a cold stage.
- 3. Rana dalmatina, Rana lessonae, Triturus cristatus, Triturus vulgaris, Anguis fragilis, Lacerta agilis, Coronella austriaca, and Natrix natrix appears mainly during the early part of a warm stage.
- 4. Salamandra salamandra, Bombina bombina, Hyla arborea, Pelobates fuscus, Rana ridibunda, Lacerta viridis, Elaphe longissima, and Emys orbicularis are typical species of a climatic optimum.
- 5. *Bufo calamita* and *Bufo viridis* appear during the latter part of a warm stage.
- 6. *Rana temporaria, Bufo viridis, Lacerta vivipara and Vipera berus* are characteristic taxa of an outgoing warm stage and a developing cold stage.

Based on the observations of HOLMAN (1998), the model seems broadly applicable to the northern part of the continent as well, especially for e.g. *Rana temporaria, Hyla arborea, Elaphe longissima,* and *Emys orbicularis.* RAGE & ROČEK (2003) also stated that *Rana* is often the only genus present in the herpetofauna during the glaciation periods, while *Bufo* is more often associated with interglacial conditions.

In the case of the Vaskapu fauna, the occurrence of *Bufo bufo*, *Rana arvalis* and *Lacerta agilis* suggest phase 2 or 3 (i.e. postglacial and developing interglacial) of BÖHME (1996) which is in agreement with the mammalian fauna (described below). In contrast, *Bufo viridis*, *Bufo calamita*, and *Lacerta viridis* could suggest even warmer climate, however it is important to take into account the following considerations:

The fact that the herpetological species compared with the homoiotherms lack complex physiological mechanisms which are able to regulate the body temperature often led to the assumption that the amphibians and reptiles have greater sensitivity to temperature changes, therefore these taxa are much better indicators of local thermal conditions than are birds and mammals. HOLMAN (1998) stated, that some European herpetological species are indeed restricted to relatively warm habitats, but on the contrary, several taxa (e.g. *Rana arvalis, Rana temporaria, Lacerta vivipara* and *Vipera berus*) have very broad ranges and are able to exist in warm as well as significantly cold environments, therefore the ability to draw palaeoecological consequences on the basis of the herpetofauna is limited.

The mammalian material from the Vaskapu I site and the surrounding fissure system (including the Vaskapu II, VI and VII localities) is similar to the Late Würm faunas of Hungary (e.g. Pilisszántó I Rock Shelter, Bivak Cave, Peskő Cave, Jankovich Cave, Remetehegy Rock Shelter and Remete Cave) (see JÁNOSSY et al., 1957 and JÁNOSSY, 1986 for details). The aforementioned localities belong to the Pilisszántóian substage of the local biochronological system, which is characterised by the abundance of reindeers (Rangifer tarandus) as well as arctic-alpine vole species (such as M. gregalis and C. nivalis) and the occurrence of the arctic lemming (Dicrostonyx torquatus). Ptarmigans (such as L. albus and L. mutus) were dominant among the birds, and Rana mehelyi⁴ was dominant among the amphibians. However, in the case of the material studied in the present article the absence of the collared lemmings (genus *Dicrostonyx*) and the abundance (but obviously not dominance) of the forest elements, as well as the relatively rich herpetofauna (without Rana mehelyi) suggest a slightly younger date and a slightly warmer and more humid climate (i.e. the locality shows a transition to the Palánkian substage).

The same conclusions can be drawn from the shrew fauna. The exclusive occurrence of the genus *Sorex* within the shrew fauna is marking a cold episode, however the sporadic presence of genus *Crocidura* (see MÉSZÁROS 2013 for details) suggest slightly warmer climate.

The co-occurrence of the faunal elements of the

⁴ *Rana mehelyi* differs from *Rana temporaria* only in its larger size and it is presently often synonymized with the latter (see e.g. HOLMAN, 1998).

forest habitat (e.g. *Glis glis, Apodemus sylvaticusflavicollis* gr., *Myodes glareolus*) and the open environment (e.g. *Microtus arvalis-agrestis* gr.) could be explained by a mosaic or quickly shifting environment left behind a retractive glaciation. The presence (but not abundance in the case of the Vaskapu site) of the *Rangifer tarandus* indicates that the boundary zone of the taiga and the tundra was still close to the locality at that time.

Similar postglacial fauna was mentioned by BÁCSKAY & KORDOS (1984) from layers 9-6 of the Jankovich Cave, which are transitional between the older *Dicrostonyx* and *M. gregalis* dominated

sediments of the Würm-3 glaciation (layer 11-10) and the younger Holocene deposits with *Apodemus* as well as abundant lizard and snake material (layer 5-1). PAZONYI (2006, in press) dated layer 7 and 8 of the Jankovich Cave to approximately 12000 uncal B.P. (which is ca. 13-15000 cal B.P.). According to her, the age of the Bivak Cave (which is close to a glacial fauna with even *Dicrostonyx*) is slightly older (approximately 15000 uncal B.P., which means ca. 19000 cal B.P.). Although the age estimation of the locality remains uncertain without an exact radiocarbon date, the above mentioned observations suggest a 15-14 kya age for the Vaskapu locality.

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Plate 1 - Frogs

- 1. Rana cf. R. arvalis (VK2.14) left ilium in lateral view from the Vaskapu II site.
- 2. *Bufo calamita* (VK2.17) left ilium (a) in lateral view from the Vaskapu II site. The characteristic calamita ridge is shown in ventral view (b).
- 3. Bufo bufo (VK2.18) left ilium in lateral view from the Vaskapu II site.
- 4. Bufo viridis (VK2.16) left ilium in lateral view from the Vaskapu II site.
- 5. *Bufo viridis* (VK2.15) right ilium fragment (a) in lateral view from the Vaskapu II site. The bilobate dorsal prominence is shown in lateral view (b).
- 6. Rana temporaria (VK2.22) right angulospleniale in lateral view from the Vaskapu II site.
- 7. Bufo sp. (VK2.23) right angulospleniale in lateral view from the Vaskapu II site.
- 8. Bufo sp. (VK2.24) right angulospleniale in lateral view from the Vaskapu II site.

Abbreviations:

- $\mathbf{a} = acetabulum$
- **cr** = calamita ridge and/or groove
- dae = dorsal acetabular expansion or pars ascendens ilii
- dc = dorsal crest or vexillum
- **dp** = dorsal prominence or tuber superior
- **is** = ilial shaft
- Mc = Meckelian canal
- **paf** = preacetabular fossa
- **pc** = processus coronoideus
- $\mathbf{saf} =$ supraacetabular fossa
- vae = ventral acetabular expansion or pars descendens illi







Plate 2

Lizards

- 1. *Lacerta* cf. *L. agilis* (VK2.1.) left dentale in lateral (a) and in medial view (b,c) from the Vaskapu II site. The posterior border of the intramandibular septum is shown in ventromedial view (d).
- 2. *Lacerta* cf. *L. viridis* (VK2.8.) right dentale in lateral (a) and in medial view (b,c) from the Vaskapu II site. The posterior border of the intramandibular septum is shown in ventromedial view (d).
- 3. Lacerta cf. L. viridis (VK2.2.) right maxilla in medial (a) and in lateral (b) view from the Vaskapu II site.

4. Lacerta cf. L. viridis (VK2.7.) right maxilla in medial (a) and in lateral (b) view from the Vaskapu II site.

Abbreviations:

ac = accessory cusp
dl = dental lamina
is = intramandibular septum
mc = main cusp
Mc = Meckelian canal
ocas = opening of the canalis alveolaris superior
pis = posterior border of the intramandibular septum
rp = resorption pit
sds = subdental shelf
uni = unicuspid tooth

