Late Pleistocene Squamate Reptiles from the Baranica Cave near Knjaževac (Eastern Serbia)

DRAGANA ĐURIĆ1, KATARINA BOGIĆEVIĆ2, DRAGANA PETROVIĆ3 & DRAŽENKO NENADIĆ2

Abstract. The Late Pleistocene layers (2–4) of the Baranica Cave near Knjaževac (Eastern Serbia) contain rich and diverse vertebrate fauna, as well as several Palaeolithic artefacts. The squamate reptile fauna contains three lizard and six ophidian (snakes) taxa (Lacerta agilis, Lacertidae indet., Anguis fragilis, Zamenis cf. longissimus, Coronella austriaca, Coronella cf. australis, cf. Natrix sp., Vipera cf. berus, Vipera sp.). This is only the second of Late Pleistocene herpetofauna described from Serbia. It consists of the forms mainly characteristic for cold and temperate semi-open regions.

Key words: squamate reptiles, snakes, Coronella, Late Pleistocene, Serbia.

Introduction

Baranica cave system comprises three small caves (Baranica I, II and III), situated in the southeastern part of Serbia, 4 km south of Knjaževac, near the state border with Bulgaria (Fig. 1). The archaeological excavation of this cave was carried out by The Faculty of Philosophy from Belgrade and the National Museum of Knjaževac from 1994 till 1997.

Not much is known about the squamate associations from Late Pleistocene in Serbia and the Central Balkans in general. This is only the second cave in Serbia which yielded Pleistocene herpetofauna that was described in detail (Smolučka pećina being the first – PAUNOVIĆ & ĐIMITRIJEVIĆ, 1990). Anuran fauna from Baranica cave has also been analyzed recently (ĐURIĆ et al., 2016) and this is the second paper dealing with the herpetofauna from this rich locality. Thus, it will give important insight into the distribution of species and it is also important for the palaeoenvironmental studies, since the amphibians and squamate reptiles are climate sensitive organisms.

During the 1995 field season, a trench was opened in Baranica I and four layers with overall thickness of 2.5 m were uncovered (Fig. 1). The uppermost layer (Layer 1) is of the Holocene age and the remaining three are of the Late Pleistocene age. Numerous remains of small vertebrates have been found in Layers 2 and 4, while only a few were found in Layer 3. For a more detailed description of the locality (see BOGIĆEVIĆ et al., 2011, 2012).

Already during the course of preliminary investigation of this cave, a multitude of small and large vertebrate remains was observed. Besides squamates, there were remains of large and small mammals (rodents, insectivores, lagomorphs and chiropterans), birds, fish,
Material and methods

Material described in this paper comes from the 1995 field season. Overall 22 sediment samples (2–3 kg each) were taken from Baranica I: six from Layer 2, one from Layer 3 (which was thought to be completely sterile) and fifteen from Layer 4. All samples were water-screened in the Laboratory of Department of Palaeontology, University of Belgrade – Faculty of Mining and Geology, on screens of 2, 1 and 0.5 mm mesh.

The Squamata remains consist of disarticulated and fragmented skeletal elements. The studied sample included 153 fragments, 102 of which representing at least nine different taxa of lizards and snakes. The lizard material includes mostly fragmented jawbones, several vertebrae and only one fragment of parietal bone. The snake remains comprise disarticulated vertebrae, primarily praesacral (trunk and a couple of cervical). A small number of the caudal vertebrae is quite damaged and couldn’t be precisely determined.

The fossil material was identified following the general criteria given by BAILON (1991), HOLMAN (1998), RATHNIKOV (2004), RAUSCHER (1992), SZYNDLAR (1984, 1991a, b), VENCZEL (2000), as well as by comparison to recent skeletons from the collections of the Natural History Museum in Belgrade. The systematic nomenclature follows SPEYBROECK et al. (2010). The measurements were taken from a small number of well-preserved snake vertebrae with a digital camera UCMOS03100KPA, by methods described in AUFENBERG (1963) and SZYNDLAR (1984). This analysis takes into consideration only centrum length (CL), centrum width (NAW) and centrum length/centrum width ratio (CL/NAW). In the drawings, the standard anatomical orientation system is used throughout this paper. The fossil material is stored in the Department of Palaeontology, University of Belgrade – Faculty of Mining and Geology.

Systematic taxonomy

Class Reptilia LAURENTI, 1768
Order Squamata OPPEL, 1811
Suborder Lacertilia GÜNTER, 1867
Family Lacertidae BATSCH, 1788
Genus Lacerta LINNAEUS, 1758

Lacerta agilis LINNAEUS, 1758
(Pl. 1, Figs. 1–4)

Material: Layer 4 – one praemaxilla (BAR-H-IV/17), four maxillae (BAR-H-IV/18/1-4), six den-
and rounded teeth are preserved.

is thin and broken on both ends. The six cylindrical
medial keel tapering distally. The lamina horizontalis
face of the nasal process is provided with a prominent
somewhat narrows with a rounded tip. The inner sur-
orbitalis is rather straight and most similar to
praefrontalis was not preserved. Following margo
maxilla is smooth. The dorsal part with processus
tra exonarina (RAUSCHER, 1992). From the lingual si-
pointed) and it continues in the irregular Margo fenes-
Processus praemaxillaris is rounded (in
Dentary. The dentary is relatively short and robust.
The Meckel’s groove is widely open with a rather
thickened border. The dentition is with bicuspid tips
differing from tricuspid in
L. viridis 
number of teeth is 17 (in
Timon lepidus

Family Anguidae GRAY, 1825
Genus Anguis LINNAEUS, 1758

Anguis fragilis LINNAEUS, 1758
(Pl. 1, Fig. 6)

Material: Layer 4 – one vertebra.
Description: The single one trunk vertebra is pre-
served. This is a very small vertebra (CL < 3 mm)
slightly longer than wide. The centrum is dorsoven-
trally flattened. In lateral view, the neural spine is long
and moderately high, arises posteriorly. Left side of
neural arches and tip of neural spine is partly broken.
In ventral view, the centrum is elongated and triangu-
lar in shape. The wide flat sagittal ridge is visible
along the midline of the centrum. On the anterior half
of the centrum subcentral foramen is visible.

Suborder Serpentes LINNAEUS, 1758
Family Colubridae OPPEL, 1811
Genus Coronella LAURENTI, 1768

Coronella austriaca LAURENTI, 1768
(Pl. 2, Fig. 1)

Material: Layer 4 – three vertebrae.
Description: All three vertebrae are rather dam-
aged. On the centrum, a flattened and wide haemal
keel is clearly visible. The praeyzagapophyseal
processes are short, at least twice shorter than praey-
zagapophyseal facet. Basal portion of praeyzagapophyses
are strongly built and parapophyses longer than
diapophyses as in C. austriaca (Szyndlar, 1984,
1991a). The neural arches are moderately vaulted
while the neural spines are mostly damaged. The
haemal keel can be well expressed in posterior trunk
vertebrae of C. austriaca (Ivanov, 1997).

Coronella cf. austriaca LAURENTI, 1768
(Pl. 2, Fig. 2)

Material: Layer 4 – one vertebra.
Description: The preserved vertebra is heavily
damaged. The centrum is very short (2.55 mm), trian-
gular shaped in the ventral view, the haemal keel is
poorly developed. Although broken, the praey and
postzygapophyseal portions of vertebra keep an X-
like shape in dorsal view. The praeyzagaphyseal
processes and zygosphenal ruff are damaged which
makes precise identification difficult.
Genus *Zamenis* Wagler, 1830

*Zamenis cf. longissimus* (Laurenti, 1768)  
(Pl. 2, Fig. 3)

Material: Layer 4 – two vertebrae.  
Description: The centrum is relatively short and triangular with a spatulate haemal keel in both vertebrae. Neither of them has preserved praenzygapophyseal processes, and the praenzygapophyseal facets have oval shape. The zygosphenes are truncated, but they show an indication of three lobes. The neural spines are quite damaged, so their height could not be assessed precisely, nor is there an overhanging. These vertebrae are most similar to the species *Zamenis longissimus*, but they are too damaged for the precise identification.

Family Natricidae Bonaparte, 1840  
Genus *Natrix* Laurenti, 1768

cf. *Natrix* sp.  
(Pl. 2, Fig. 4)

Material: Layer 4 – one vertebra.  
Description: An incomplete haemapophysis is developed with an indication of sygmoidity (sigmoid shape). The subcentral ridge that runs to the condyle is quite similar to the genus *Natrix*. Other features are rather damaged for the determination of species.

Family Viperidae Oppel, 1811  
Genus *Vipera* Garisiault, 1764

*Vipera cf. berus* (Linnaeus, 1758)  
(Pl. 2, Figs. 5–6)

Material: Layer 2 – two vertebrae; Layer 3 – one vertebra; Layer 4 – 36 praesacral vertebrae.  
Description: The centra of vertebrae are cylindrical and elongated. The neural arch is distinctly flattened. The neural spine and hypapophyses are more or less damaged in most vertebrae. The best preserved hypapophyses is short and projected backward beyond the cotyle (Szyndlar, 1984). The centrum length/width ratio (n=31) is between 1.53–2.29 (mean±SD=1,89±0,18). Although badly preserved, these vertebrae retain characteristics of small viperid from ‘*berus* group’ – cylindrical, elongated centra, distinctly flattened neural arch and very low neural spine.

*Vipera* sp.  
(Pl. 2, Figs. 7–8)

Material: Layer 2 – two vertebrae; Layer 4 – 16 fragmented vertebrae.  
Description: All the vertebrae are more or less damaged. Generally, they have a moderately long, almost cylindrical centrum. Many of them possess only the base of the hypapophyses or a damaged part that projects straight like in the living *Vipera ammodytes* (Szyndlar, 1984). On the best preserved vertebra (Pl. 2, Figs. 7, 8) parapophyses are directed anteriorly and downward, which is characteristic of Viperidae. In all the vertebrae neural arch is depressed, but neural spine is mostly damaged. The fragments have only some diagnostic features (parapophyses directed anteriorly, straight hypapophyses) that connect them to the genus *Vipera*.

Taphonomy

The small vertebrate remains located in the entrance part of Baranica I, are very abundant. The small mammals are relatively well preserved while the Squamates are heavily damaged but without traces of water transport. They are probably prey remains, although it is not yet clear which predator is responsible for their accumulation (Bogicević et al., 2011). For squamate reptiles, the potential predators are most commonly small carnivores and diurnal birds of prey (Blain et al., 2008), but since that kind of predators break bones and dissolve them with their gastric juices (Andrews, 1988) and such traces are not visible in the bones from Baranica, we could suggest they were the owls’ prey or the remains of animals that used the cave as a shelter and died in situ.

Comparison with the recent squamate fauna of the southeastern Serbia

The composition of the squamate fauna of Baranica bears much similarity to the recent fauna of the area. From the 13 recent Sámatas species that could be found in the wider vicinity of Knjaževac (Tomović et al., 2014) five are present in Baranica (Table 1). All ophidian taxa live today in the vicinity of Knjaževac. Southeastern Serbia is today characterized by the quite rich and distinct reptile fauna and presence of Mediterranean species (Tomović et al., 2014), and this was obviously also the case in MIS 3, when Layer 4 was formed. Modern reptile fauna in Serbia is not so rich as in some other Balkan countries, and after its composition and diversity it is most similar to the fauna in Romania (Tomović et al., 2014). Today in the area of Knjaževac, temperate-continental climate dominates, with an average annual temperature of 10,2°C, hot and dry summers and cold winters (Miopenović, 2010).

Palaeoclimatological reconstructions on the basis of herpetofauna

The remains of herpetofauna have been lately much used for the reconstruction of the palaeoenvironment
Because of the small number of remains from Baranica and the lack of comparative fauna from the vicinity, a detailed palaeoecological analysis is not possible yet, but some preliminary results could be drawn by comparison with recent fauna.

A small number of snakes and lizards have been found in Layer 2 (Table 2) among them *Vipera cf. berus* and *Lacerta agilis*, which can tolerate very low temperatures. This layer, according to dating (DIMITRIJEVIĆ, 2011), was formed during LGM (Last Glacial Maximum), so the poor herpetofauna is expected. Layer 3 is otherwise poor in vertebrate remains, so only one sample has been taken from it during excavation, and only one vertebra has been found in it, also ascribed to “berus” group. Thus most of our conclusions on palaeoenvironment refer to Layer 4.

Most of the species, such as *Lacerta agilis*, *Coronella austriaca*, *Zamenis cf. longissimus*, indicate the presence of relatively drier open regions of steppe and forest-steppe type, covered with sparse vegetation (RATNIKOV, 1996). *Natrix natrix* and *Anguis fragilis* inhabit also forests (humid, wooded (broad-leaved or mixed) and/or shrubby) and grass areas with much greater moisture. *Vipera berus* prefers relatively cold and moist habitats in the plain regions, like swamps and bogs (BRUNO & MAUGERI, 1992; BLAIN & VILLA, 2006).

RATNIKOV (1996, 2016) made a table in which the distribution of several amphibians, snakes and lizard species in different habitats had been presented (Table 3). Most of the determined taxa currently have relatively broad ecological niches. None of the herpetofaunal species present in the Baranica Cave lives in tundra. All of them occur in mixed and deciduous forest and in forest-steppe, especially in the latter, where all the mentioned species are rather common (*Vipera berus*, common in forest-tundra, is among rare remains which were found in “cold” Layer 2).

**Distribution of squamate remains in Late Pleistocene of the central Balkans**

Very similar squamate fauna in Serbia is known only from Smolučka cave (PAUNOVIĆ & DIMITRIJEVIĆ, 1990). In Baranica, *Lacerta viridis* and *Ophisaurus apodus* were not found (present in Smolučka).

**Comparison with other proxies**

Unlike rodents, in which the composition of fauna in Layers 2 and 4 is rather similar, squamate fauna is...
much more diverse in Layer 4. For Layer 2 the conclusions for rodents and squamates are the same – they indicate a cold period and an open environment, while squamate fauna from Layer 4 indicates much warmer climate and more closed environment than that of rodents. Anuran fauna is not rich enough (5 taxa), and in most cases it cannot be identified to the species level, so it cannot be useful, but it is also richer in Layer 4 and it corresponds to drier, steppe habitats (Đurić et al., 2016). There are some data on large fauna and pollen grains which come from Baranica II (Argant & Dimitrijević, 2007; Dimitrijević, 2011), but their exact age is not known, so they could not be directly compared to these results.

Stratigraphical distribution of the species

The squamate fauna from Baranica is composed exclusively of extant genera and species, so it could not be used for stratigraphical purposes. Representatives of herpetofauna, in general, are not good stratigraphical indicators in Quaternary, but the composition of the fauna, its diversity could help in determination of stratigraphic age of fauna (Holman, 1993). Based on the herpetofaunal associations, glacial or interglacial conditions could be inferred (Ratnikov, 2016).

On the basis of herpetofauna from the central Europe, Böhme (1996) has formed 6 groups that are characteristic for the specific part of glacial cycles, where the species *Rana temporaria* is characteristic of the coldest period, and *Emys orbicularis* and *Zamenis longissimus* of the warmest period. Of course, the fauna from the Balkan Peninsula differs from the central European one, because it lived under the conditions of somewhat warmer climate on which glacial cooling had less impact than in the latter area. Based on this and other localities, our aim in the future will be to establish how much of the distribution of the Late Pleistocene herpetofauna in the Balkans follows the Böhme’s scheme and what are the differences, if any. In that manner, herpetofauna could be useful in the determination of to which glacial cycle certain Pleistocene layers belong.

Conclusion

In Late Pleistocene deposits of the Baranica cave at least 9 taxa of squamates have been found: *Lacerta agilis*, Lacertidae indet., *Anguis fragilis*, *Zamenis cf. longissimus*, *Coronella australica*, *Coronella cf. austriaca*, cf. *Natrix sp.*, *Vipera cf. berus*, *Vipera sp.*, Serpentes indet. Results of palaeoenvironmental analyses indicate that association from Layer 4 lives in somewhat warmer period compared to Layer 2, with more forests and forest-steppe environment, while Layer 2 contains only colder elements (*Vipera berus*). Presence of *L. agilis* and *V. berus*, which are the most cold-tolerant species in recent fauna, indicates a cold and temperate climate of Baranica surroundings. However, today these two species are part of the herpetofauna of Serbia in fragmented range which is probably a consequence of the anthropogenic influence (Tomović et al., 2014). Presence of the thermophilic species related to warmer periods of glacial (Böhme, 1996) such as *Zamenis longissimus*, *Coronella australica* brings to a conclusion that the climate was similar to the one occurring today. Considering that Serbian recent herpetofauna has predominantly Eastern-Mediterranean and South-European characteristics (Tomović et al., 2014), future studies of Pleistocene squamates of Serbia have yet to give a more precise picture of the climatic changes during the Pleistocene. These conclusions are mostly in compliance with data obtained by the analysis of rodent and anuran fauna.

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Херпетофауне може значајно допринети препозна¬
вању смена глацијалних – интерглацијалних кли¬
матских услова (HOLMAN, 1993; RATNIKOV, 2016).
На основу херпетофауне централне Европе, ВО¬
ЊМЕ (1996) је направио модел од 6 група веза¬
них за специфичне климатске промене током
gлацијалних циклуса. Према овом моделу Rana
temporaria је карактеристична за најхладнији
период, док су у најтоплијем периоду, између
осталих, присутни Emys orbicularis и Zamenis lon¬
gissimus. С обзиром на разлике Балкана у односу
на централну Европу, остаје да се види да ли је
овај модел одржив и да ли ће га састав херпето¬
фауне касног плеистокена Балкана подржати.

Палеоеколошком анализом установили смо да је
херпето асоцијација слоја 4 формирана у нешто
tоплијем периоду са више шума и шумо-степа, док
слој 2 садржи само хладне елементе као што је
Vipera berus. Присуство L. agilis и V. berus, које су у
савременој фауни карактеристичне као врсте изра¬
zито толерантне на ниске температуре, указује да је
околина Баранице била под утицајем хладне и
умерене климе. Такође се мора узeti у обзир да су
ове врсте и данас широко распрострањене у Срби¬
ји, али у доста фрагментисаним ареалима, што мо¬
же бити последица антропогеног утицаја (ТОМОВИЋ
et al., 2014). Присуство врста као што су Zamenis
longissimus, Coronella austriaca, које се према
ВОЊМЕ (1996) појављују у топлијим фазама квар¬
tарних циклуса, научи нас на закључак да је клима
била сличнија данашњој. С обзиром да данашња
херпетофауна Србије има већином источно-медин¬
tерански и јужно-европски карактер (ТОМОВИЋ et al.,
2014), будућа истраживања плеистоценских ска¬
mата Србије доприносе бојем сагледавању кли¬
mатских промена током плеистокена.

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PLATE 1

Figs. 1–3. *Lacerta agilis*,
1. praemaxilla (BAR-H-IV/17),
2. right maxilla (BAR-H-IV/18),
3. right dentary (BAR-H-IV/26): a – labial, b – lingual.

Fig. 4. *Lacerta agilis*, parietal (BAR-H-IV/21): a – dorsal, b – ventral view.

Fig. 5. Lacertidae indet., left dentary (BAR-H-IV/28); a – labial, b – lingual view.

Fig. 6. *Anguis fragilis*, vertebra (BAR-H-IV/31): a – dorsal, b – ventral, c – lateral view.

Scale bar 1mm.
PLATE 2

Fig. 1. *Coronella austriaca*, trunk vertebra (BAR-H-IV/34-3): a - dorsal, b – ventral view.

Fig. 2. *Coronella* cf. *austriaca*, trunk vertebra (BAR-H-IV/32): ventral view.

Fig. 3. *Zamenis* cf. *longissimus*, trunk vertebra (BAR-H-IV/33-1): a - dorsal, b – ventral view.

Fig. 4. cf. *Natrix* sp., trunk vertebra (BAR-H-IV/35): lateral view.

Fig. 5. *Vipera* cf. *berus*, praesacral vertebra (BAR-H-IV/39-6, BAR-H-IV/39-23): a - dorsal, b – lateral view.

Fig. 6. *Vipera* cf. *berus*, praesacral vertebra (BAR-H-IV/39-23): lateral view

Figs. 7–8. *Vipera* sp., praesacral vertebra (BAR-H-IV/41-9 BAR-H-IV/41-3): lateral view.

Scale bar 1 mm.
