

***Latonia gigantea* (Lartet, 1851) remains and other herpetological observations from the middle Pleistocene Esztramos 6 locality (Aggtelek–Rudabánya Mountains, North Hungary)**

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Abstract – The fossil material of Esztramos 6 palaeovertebrate locality has been revised in this study with special regard to its herpetofauna. Result of this study has shown the presence of the species *Latonia gigantea* and the fauna list of the locality has been expanded by amphibian, reptilian, and mammalian taxa. Considering differences of the mammalian fauna the Esztramos 6 lower and upper sites are probably not coeval, however their palaeoenvironment shows similarities. With 23 figures and 1 table.

Key words – Alytidae, Esztramos, herpetofauna, *Latonia gigantea*, middle Pleistocene, palaeoecology

INTRODUCTION

Genus *Latonia* has been described by MEYER (1843) based on an articulated skeleton. They are the most common fossil anurans in Europe. Their earliest record is known from the late Oligocene (FRIANT 1944), they became rare in the Pleistocene but survived to the present day (*Latonia nigriventer*) in a single known area in the eastern Mediterranean Hula Valley, Israel (BITON *et al.* 2013). The species *Latonia gigantea* was first described by LARTET (1851) as *Rana gigantea* and later LYDEKKER (1890) changed this to the currently valid name. This taxon has been placed by various authors to 7 genera and 18 species (e.g. ROČEK 1994; RAGE 1998; SYROMYATNIKOVA & ROČEK 2018). *Latonia gigantea* was one of the most common frog species from the Miocene of Europe (see Table 1).

The species is also detected from the middle Miocene (e.g. BERNOR *et al.* 2004; VENCZEL 2004; ROČEK 2005; VENCZEL & HÍR 2015), the upper Pliocene (VENCZEL 2001) and in this study, from the middle Pleistocene of Hungary (see Table 1).

Palaeovertebrate localities of the Esztramos Hill (in former studies as Osztramos which form is incorrect; e.g. JÁNOSSY 1973, 1974, 1986; JÁNOSSY &

Table 1. Occurrences of the species *Latonia gigantea* (Lartet, 1851) in the European palaeovertebrate localities

geological age	locality	references
middle Pleistocene	Esztramos 6, Hungary	this study
upper Pliocene (Villanyian)	Arondelli, Italy	VERGNAUD-GRAZZINI 1970; ROČEK 1994
Pliocene (Ruscinian, MN15)	Ivanovce, Slovakia	ŠPINAR 1978; ROČEK 1994
	Kuchurgan, Ukraine	CHKHIVADZE 1981; ROČEK 1994
	Sète, France	BAILON 1991
lower Pliocene (MN 14)	Esztramos 1, Hungary	VENCZEL 2001
upper Miocene (MN 13)	Polgárdi 2, 4, 5, Hungary	BOLKAY 1913; VENCZEL 1997; VENCZEL & CSIKI 2002
upper Miocene (MN 12)	Tardosbánya, Hungary	VENCZEL 1999; VENCZEL & CSIKI 2002
upper Miocene (Vallesian, MN 9)	Götzendorf, Austria	MIKLAS 2002
	Rudabánya, Hungary	BERNOR <i>et al.</i> 2004, ROČEK 2005
	Vallès-Penedès	VILLA <i>et al.</i> 2017.
upper Miocene (Sarmatian, MN 7–8)	Felsőtárkány “Güdör-kert”, Hungary	HÍR <i>et al.</i> 2001
	Gritsev, Ukraine	CHKHIVADZE 1981; ROČEK 1994; SYROMYATNIKOVA & ROČEK 2018
	Opole, Poland	MLYNARSKY 1984; MLYNARS- KY <i>et al.</i> 1984; ROČEK 1994
upper Miocen (Turolian, MN 13)	Polgárdi, Hungary	BOLKAY 1913; ROČEK 1994
upper middle Miocene (MN7+8)	Tauț, Romania	VENCZEL & ȘTIUCĂ 2008
middle Miocene (MN6 and MN7/8)	Subpietră, Romania	VENCZEL <i>et al.</i> 2005.; VENCZEL 2007; HÍR & VENCZEL 2005
middle Miocene (late Badenian, MN 6)	Mátraszőlős 1–2, Hungary	GÁL <i>et al.</i> 2000; VENCZEL 2004; VENCZEL & CSIKI 2002
middle Miocene (Badenian)	Przeworno II, Poland	MLYNARSKY 1984; ROČEK 1994
middle Miocene (MN 7/8)	Felsőtárkány-Felnémet 2/3	VENCZEL 2004; VENCZEL & CSIKI 2002

Table 1. (continued)

geological age	locality	references
middle Miocene (lower Badenian)	Sámsonháza 3, Hungary	HÍR <i>et al.</i> 1998; VENCZEL 2004
middle Miocene (Astaracian, MN 6)	Devínska Nova Ves, Slovakia	WETTSTEIN-WESTERSHEIMB 1955; ROČEK 1994; SYROMYATNIKOVA & ROČEK 2018
	La Grive St. Alban, France	HOSSINI 1993; ROČEK 1994
	Sansan, France	ROČEK 1994; RAGE & HOSSINI 2000; SYROMYATNIKOVA & ROČEK 2018; SYROMYATNIKOVA <i>et al.</i> 2019
lower-middle Miocene (MN 6)	Litke, Hungary	VENCZEL & HÍR 2015
lower-middle Miocene (lower Badenian, MN 5)	Untereichen-Altenstadt	PRIETO <i>et al.</i> 2009
lower-middle Miocene (Tchokrakian)	Belomechetskaya, Russia	CHKHIVADZE 1981; ROČEK 1994
lower-middle Miocene (MN 4)	Sandelzhausen, Germany	BÖHME 2010
lower Miocene (Orleanian, MN4)	Dolnice, Czech Republik	ŠPINAR 1975; HODROVÁ 1987; ROČEK 1994
lower Miocene (Burdigalian-Aquitania)	Przeworno I, Poland	MLYNARSKY 1976; MLYNARSKY 1984; ROČEK 1994

KORDOS 1977; VENCZEL 2001; SZENTESI 2019) have been unearthed by mining activities. Previous studies mentioned 15 fossiliferous sites on the Esztramos Hill discovered between 1956 and 1973 (JÁNOSSY 1973, 1974, 1986; JÁNOSSY & KORDOS 1977; VENCZEL 2001; KORDOS 2008). Material from these sites was investigated by Dénes Jánossy and his colleagues from the Hungarian Natural History Museum, Budapest. Later more sporadic cavities have been discovered which had been filled with vertebrate remains containing red clay but these have not been described yet (KORDOS 2008). Currently 27 sites identified by numbers and 2 identified by names (Osztramos 3 alatti békás = under Osztramos 3 with frogs, and Cseppkőbarlang = Dripstone Cave) are known from the Esztramos Hill (SZENTESI 2019). Based on the palaeovertebrate remains from the first 14 localities the fossil sites of Esztramos are of lower Pliocene and Middle Pleistocene ages (e.g. JÁNOSSY 1974, 1986; JÁNOSSY & KORDOS 1977; KORDOS 2008).

GEOLOGY, MATERIAL AND METHODS

The Esztramos Hill is situated between Tornaszentandrás and Bódvarákó (at northern latitude 49° 30'), in the Upper Bódva Basin which is located in the Rudabánya Hills, North Hungary (Fig. 1). It emerges out from the low-

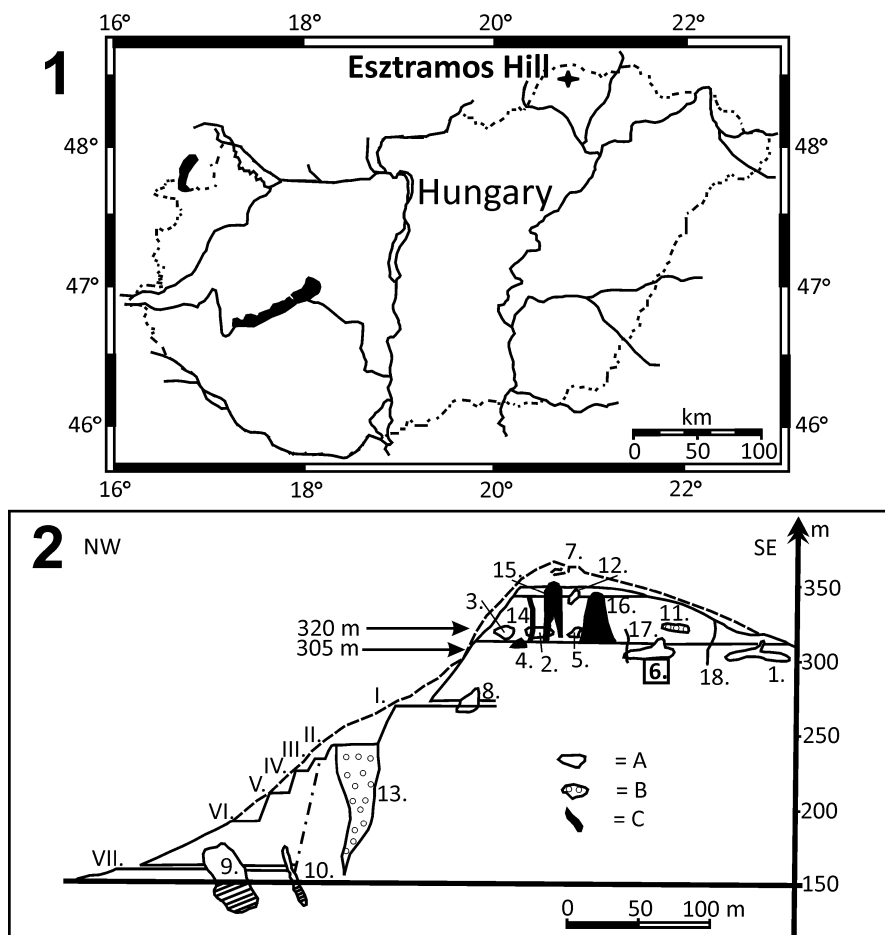


Fig. 1. Map showing the geographic location of the Esztramos Hill

Fig. 2. Sketchy cross section of the Esztramos Hill with sites (modified after KORDOS 2008): A = caves; B = fossil caves; C = fissures; 1 = Esztramos cave; 2 = Upper number 2 cave; 3 = Upper number 3 cave; 4 = Upper number 4 cave; 5 = Upper number 5 cave; 6 = Upper number 6 cave; 7 = Cave under the peak; 8 = Cave of level 1; 9 = Rákóczi cave number 1 part; 10 = Rákóczi cave number 2 part; 11 = Fossil cave of the vertebrate locality number 2; 12 = Fossil cave of the number 3 vertebrate locality; 13 = Fossil cave without number; 14 = Vertebrate locality number 14; 15 = Vertebrate locality number 1; 16 = Middle Pleistocene fissure; 17 = Fissure of vertebrate locality number 8; 18 = Vertebrate locality number 7

land like an island, as the last member of the Rudabánya Hills. The hill mainly consists of moderately metamorphosed middle Triassic limestones (Steinalm and Szentjánoshegy Limestone Formations) (BALOGH & PANTÓ 1949; PANTÓ 1956; KRETZOI 1956; JÁNOSSY 1986; KORDOS 1973, 1974). Ruddle and mine were mined on the Esztramos from the middle Ages to the early 1950s, which unearthed the recently known (or meanwhile destroyed) palaeovertebrate sites (JÁNOSSY & KORDOS 1977; KORDOS 2008). These sites are situated in karst cavities and caves (with stalactites) which are located in two levels (at altitudes of 320 and 305 m) in the hill. These cavities were formed due to the dissolution of limestone, probably during the Pliocene period (KORDOS 2008).

The studied material from Esztramos 6 has been originally collected as a fossiliferous deposit by Dénes Jánossy in 1969 from a small karst cavity (1 m × 1 m) at the southern side of part XI of the limestone quarry in Esztramos Hill, 15 m from Esztramos 3. These deposits were different from other dark red materials on the hill; its colour was yellow-red, significantly lighter than those from the other cavities and caves. Jánossy divided this site into two parts: a lower and an upper phase (JÁNOSSY & KORDOS 1977) for an unknown reason which has not been described anywhere but was only revealed during the examination of this restudied material.

This sediment contained seeds of hackberry (*Celtis* sp.) besides plenty of bat bones and some other small mammal remains (JÁNOSSY & KORDOS 1977). The age of Esztramos 6 has been determined as an older phase of the middle Pleistocene based on the presence of *Allocricetus bursae* and the small *Glis* sp. (JÁNOSSY & KORDOS 1977).

The *Latonia gigantea* fossils described herein were selected by the author from the previously screen-washed material collected by Dénes Jánossy in 1969.

SYSTEMATIC PALAEOONTOLOGY

Phylum Vertebrata Linnaeus, 1758
Class Amphibia Linnaeus, 1758
Subclass Lissamphibia Haeckel, 1866
Order Anura Fischer, 1813
Family Alytidae Fitzinger, 1843
Genus *Latonia* Meyer, 1803

Latonia gigantea (Lartet, 1851)

Referred material – **Esztramos 6 lower**: Right maxilla (VER 2019.109.); frontoparietal (VER 2019.110.); right prooticooccipital (VER 2019.111.); right angulosplenic (VER 2019.112.); 3 vertebrae (VER 2019.113.1–3.); urostyl (VER

2019.114.); 2 right (VER 2019.115.1–2.) and 1 left ilia (VER 2019.115.3.); right humerus (VER 2019.116.); calcaneum (VER 2019.117.).

Esztramos 6 upper: Left humerus (VER 2019.108.).

TAPHONOMICAL OBSERVATIONS

The here described specimens are all isolated but almost complete or identifiable. These anuran fossils show smooth (frontoparietal) to strongly eroded (e.g. calcaneus) red or reddish-brown surfaces. Some bones have patchily coatings of manganese oxides which probably originate from mobilized soluble manganese compounds transported by artesian water which attributable to the nature of the cave site.

Description – Maxilla. The labial surface of this specimen (VER 2019.109.) is covered by secondary sculpture. Sculpture is formed of prominent tubercles which stay dispersed (mainly posteriorly) or usually constitute different rows (mainly anteriorly) (Fig. 4). The most prominent tubercles are in the area of processus zygomaticomaxillaris. Between the anterior and posterior ornamentation, the labial surface is relatively smooth especially on the ventral part of bone.

Lingually, the slender and long pterygoid process projects posteromedially (Fig. 3). The posterior depression is shallow and limited anteriorly by a transversal bony ridge at the level of the pterygoid process. The processus palatinus, p. frontalis and p. zygomaticomaxillaris are relatively low, but the latter one is a bit taller. The fossa maxillaris is deep, the prominent lamina horizontalis widens posteriorly and conveys lingually. The tooth row extends posteriorly to the posterior end of pterygoid process. The teeth are broken and not preserved along the entire length of the bone. The bone is curved labiolingually.

Frontoparietal – The dorsal surface is broad on this fused bone, which is covered with a dense secondary sculpture (VER 2019.110.). The posterior part is mostly covered with unique tubercles, whereas anteriorly, the tubercles are united and form ridges which extend mainly anterolaterally. The paraoccipital processes are well-developed, between these the zigzag edged margo occipitalis is situated with broad contacting surface posteriorly.

The ventral surface exhibits the roughly circular, well-defined posterior frontoparietal incassation with a rim and a less defined, elongated (elliptical) anterior incassation. This latter structure is bordered laterally by prominent bony laminae which diverge posteriorly, and represent the pars contacta. The pars contacta extends ventrolaterally; the rounded foramen parietale is situated anteriorly from the frontoparietal incassation. The well-developed margo prootica is rounded lateroventrally. The contacting surfaces between the frontoparietal and sphenethmoid and respectively the frontoparietal and prooticooccipital are

strongly striated with lateroventrally projecting grooves. The anterolateral end of the anterior horns is damaged.

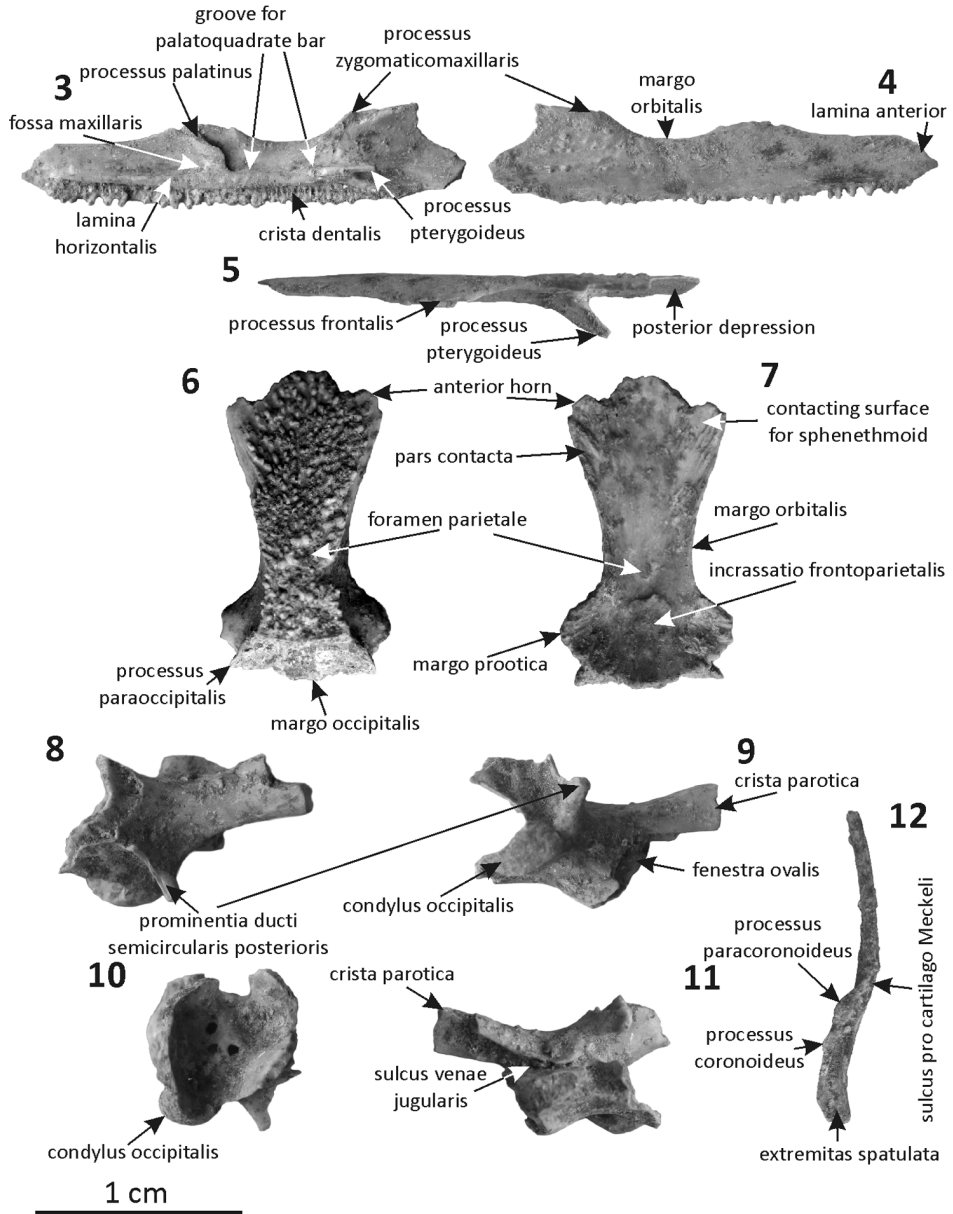
Prooticooccipital – The dorsal part of the bone (VER 2019.111., Figs 8–11) is slender and widening towards the crista parotica. The crista is V-shaped, with its shorter anterior branch, and longer posterior branch. The contact area for the frontoparietal is indented and strongly striated, separated with deep, irregularly situated furrows or grooves. The prominentia ducti semicircularis posterioris is prominent as an extensive thin lamina (Fig. 8), which is terminated by a knob; its dorsal end is broken. The thin horizontal lamina runs from the lower and from the latter mentioned structure towards the crista parotica. On the anterior surface of the bone there is a rather prominent elevation which is devoid of periost. Its ventral margin is adjoined by the ramus pterygoidei. Immediately dorsally from this elevation there is a horizontal groove (sulcus venae jugularis) which is not roofed. The well-developed condylus occipitalis has a slightly curved drop shape.

Angulosplenial – The slightly eroded angulosplenial (VER 2019.112., Fig. 12) is bearing two coronoid processes (p. coronioideus and p. paracoronioideus), having a distinct recess in the bottom of the sulcus for the Meckel's cartilage (= sulcus pro cartilage Meckeli) at the level of the coronoid process and having a distinct depression on the posterior part of the outer surface of the bone above the crista mandibulae externa.

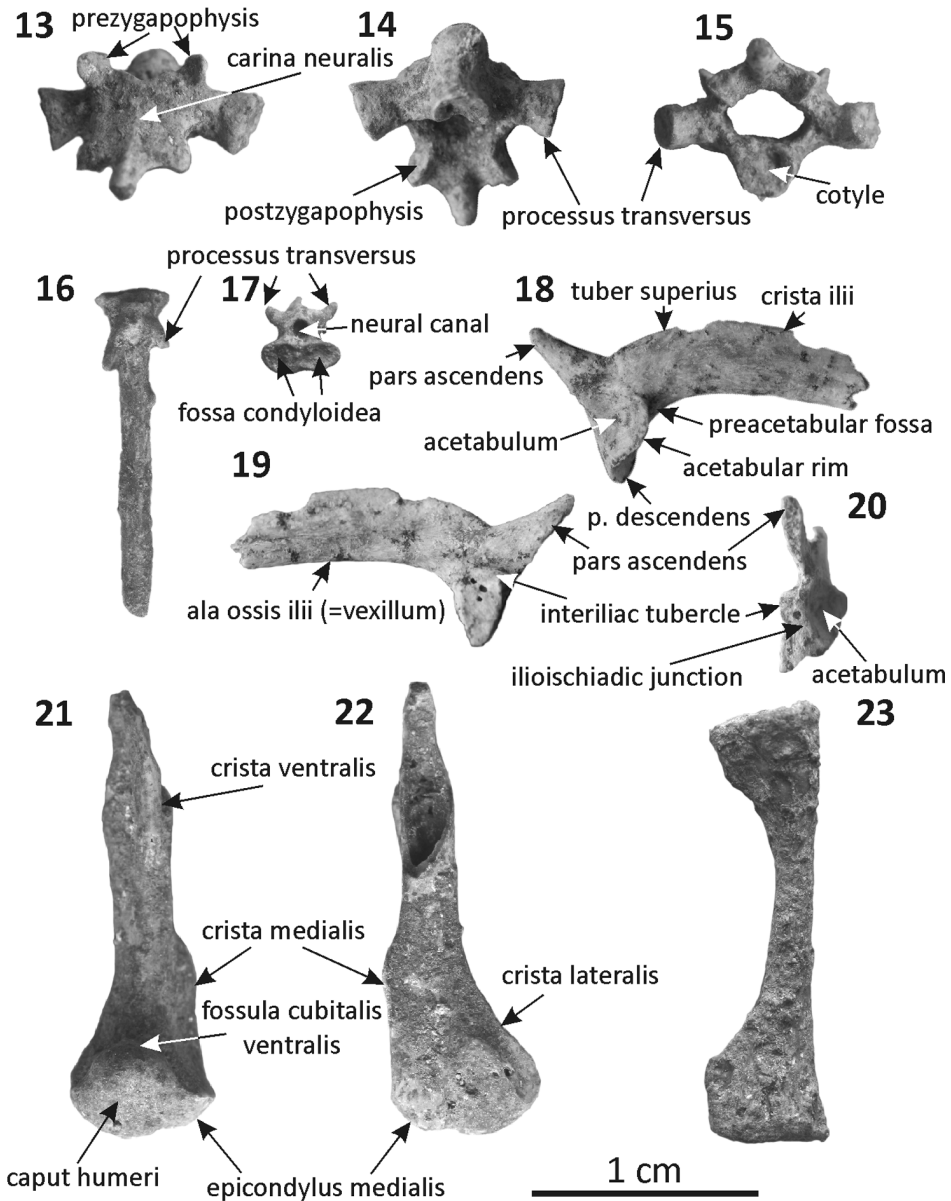
Presacral vertebrae – One (VER 2019.113.1.) of the three vertebrae is almost completely preserved (Figs 13–15). This opisthocoelous vertebra has a cylindrical centrum, provided with well-developed interzygapophyseal ridges, a low neural ridge with relatively long spinal process and a massive, and laterally oriented cylindrical processus transversus.

Urostyle – The tips of posteriorly extended transverse processes are broken (VER 2019.114., Figs 16–17); in anterior view these processes slightly curve dorsally. The fossa condyloidea is elliptical dorsoventrally and the neural canal is cylindrical anteriorly. The crista dorsalis is relatively tall anteriorly and it becomes lower posteriorly and almost disappears by the posterior end of the bone.

Ilium – On the best preserved specimen (VER 2019.115.1.) the acetabulum is large and rounded with prominent acetabular rim anteroventrally projecting laterally (Figs 18–20). On the small preacetabular region a small fossa is present. The pars ascendens is prominent, extends strongly posterodorsally, but the pars descendens is extremely small. The tuber superius (= tuber superior and dorsal protuberance) is well-defined without a lateral projection. Anteriorly, under the dorsal protuberance a fossula tuberis superioris is present. The crista ilii (= iliac crest) is rather high, the ala ossis ilii (= vexillum) is concave anteroventrally.



Figs 3–12. Cranial bones and lower jaw of *Latonia gigantea* from the Esztramos 6 lower site. – **Figs 3–5.** Right maxilla (VER 2019.109.) in lingual (3), labial (4) and dorsal (5) views; – **Figs 6–7.** Frontoparietal (VER 2019.110.) in dorsal (6) and ventral (7) views; – **Figs 8–11.** Right prooticoccipitale (VER 2019.111.) in dorsal (8), posterior (9), medial (10) and anterior (11) views; – **Fig. 12.** Right angulosplenial (VER 2019.112.) in dorsal view



Figs 13–23. Postcranial bones of *Latonia gigantea* from the Esztramos 6 lower site. – **Figs 13–15.** Vertebra (VER 2019.113.1.) in dorsal (13), ventral (14) and posterior (15) views; – **Figs 16–17.** Urostyl (VER 2019.114.) in dorsal (16) and anterior (17) views; – **Figs 18–20.** Right ilium (VER 2019.115.1.) in lateral (18), medial (19) and posterior (20) views; – **Figs 21–22.** Right humerus (VER 2019.116.) in ventral (21) and dorsal (22) views; – **Fig. 23.** Calcaneum (VER 2019.117.) in lateral view

Posteriorly, the ilioischadic junction is wide ventrally with a well-developed interiliac tubercle and significantly narrower dorsally.

Humerus – The humerus (VER 2019.116., Figs 21–22) is having laterally placed caput humeri with larger epicondylus medialis, which continues dorsally with a well-developed crista medialis. The epicondylus lateralis is smaller, continued dorsally in a less prominent crista lateralis having a concave shape, when viewed ventrally or dorsally. The bone has a well-developed crista ventralis, which is damaged proximally. The left humerus (VER 2019.108., not figured) is significantly smaller, about half of the other (VER 2019.116.) therefore it does not belong to the same frog even if it turns out that the two sites are of the same age.

Calcaneum – This eroded bone (VER 2019.117.) is robust with stout epiphyses (Fig. 23). Its lateral edge is slightly S-shaped, and medially concave.

Remarks – The fused and strongly sculptured frontoparietal, the frontoparietal incrustation consisting of two parts (elongated anterior and circular posterior); two coronoid processes on angulosplenic, distinct recess on bottom of sulcus pro cartilago Meckeli at level of processus coronoideus; processus pterygoideus maxillae slender and long, present a large depression on the inner posterior part of the maxilla; on prooticooccipital, prominentia ducti semicircularis running out with prominent ridge; the contacting surfaces between frontoparietal and sphenethmoid and frontoparietal and prooticooccipital are distinctly and irregularly striated; the prominent crista ventralis on humerus, the laterally shifted caput humeri; the thin crista ossis ilii with sharp edge which declined dorsomedially, upper margin of acetabulum terminates posteriorly with marked and nearly pointed elevation; the calcaneum is not fused with astragalus: these detected characters on this frog material are typical for the genus *Latonia* (ROČEK 1994, SYROMYATNIKOVA *et al.* 2019).

The sculpture on frontoparietal consists of small, irregularly and densely scattered tubercles on its posterior part, and tubercles which fuse usually into irregular ridges extending anteriorly on its anterior part; the labially sculptured processus zygomaticomaxillaris of the maxilla suggests these remains belong to *Latonia gigantea* (ROČEK 1994).

It differs from *Latonia ragei* in sculptured maxilla (HOSSINI 1993, Fig. 1A₁; ROČEK 1994, Fig. 9A); and the shape of processus coronoideus on the prearticular (HOSSINI 1993, Fig. 1A₂; ROČEK 1994, Fig. 13B–E). It differs from *L. vertazoni* in more concave margo orbitalis, a significantly deeper fossa maxillaris, the shape of the processus pterygoideus, and the posterior depression (ROČEK 1994, Fig. 9C); and in the more prominent processus coronoideus (ROČEK 1994, Fig. 12F, K).

PALAEOECOLOGICAL AND PALAEOBIOGEOGRAPHICAL NOTES

The revision of the material previously studied and screen-washed by Jánosy in 1969 from Esztramos 6 (JÁNOSSY & KORDOS 1977) provides new insights into the fauna. According to JÁNOSSY & KORDOS (1977) this is an insignificant site however they mentioned the presence of bats (Chiroptera, only mentioned in the text), anuran amphibians (Anura), and snakes (Ophidia). The faunal list of Esztramos 6 has been expanded with an urodela taxon, 8 anuran taxa; presence of anguid lizards (Anguidae indet.) has been verified; two species of colubrid (Colubridae) snakes has been identified thanks to this study. The mammalian faunal list has also been expanded by demonstrating the presence of mice (Muridae indet.).

The revised faunal list of the middle Pleistocene Esztramos 6 locality is the following (the lower and the upper parts are listed separately):

Esztramos 6 lower site

Amphibia

Triturus cf. *cristatus* (Laurenti, 1768)

Bombina cf. *variegata* Linnaeus, 1758

Latonia gigantea (Lartet, 1851)

Pelobates fuscus (Laurenti, 1768)

Bufo cf. *viridis* (Laurenti, 1768)

Hyla arborea (Linnaeus, 1758)

Rana temporaria Linnaeus, 1758

Pelophylax esculentus group

Anura indet.

Reptilia

Anguidae indet.

Hierophis cf. *gemonensis* (Laurenti, 1768)

Natrix tessellata Laurenti, 1768

Natrix sp.

Colubridae indet.

Mammalia

Sorex araneus group

Glis sp. (small)

Muridae indet.

Allocricetus bursae Schaub, 1930

Chiroptera indet.

Esztramos 6 upper site**Amphibia***Latonia gigantea* (Lartet, 1851)*Pelobates fuscus* (Laurenti, 1768)cf. *Pelophylax* sp.**Mammalia**

Arvicolinae indet.

Chiroptera indet.

These faunal lists show significant difference between the faunas of the two parts of Esztramos 6. The lower site is richer in taxa than the upper. Among amphibians, the northern crested newt is only detected in the material of the lower site, similarly to the yellow-bellied frog (*Bombina variegata*), the green toad (*Bufo viridis*), the European tree frog (*Hyla arborea*), and the common frog (*Rana temporaria*). Reptilians have not been found in the fossil material of the upper site of Esztramos 6. The mammalian fauna is also more diverse in the lower site. Chiropterans were not processed from the locality.

JÁNOSSY & KORDOS (1977) interpreted the two parts as one site, which is incorrect because the fauna of the upper part is poorer, so the rich material of the lower site could not get there and the marker mammal fossils are missing from the upper site. The biostratigraphically important fossils, *Allocricetus bursae* and the small *Glis* species which suggested a middle Pleistocene age (any older phase in this period) have been unearthed only from the upper site of Esztramos 6, so the correct biostratigraphic position of Esztramos 6 upper is unknown.

The palaeoecological and the palaeobiogeographical importance of the mammal fauna of Esztramos 6 was not evaluated by JÁNOSSY & KORDOS (1977).

However, the stratigraphic relationship of the two sites is unknown, so it might be worth examining the ecology of the three anuran taxa which are present in both the lower and upper sites. Among these, *Latonia gigantea* cannot be used as a palaeoenvironmental indicator because based on its fossil record this species was highly adapted to various habitats near marshes, lakes, and along rivers (e.g. GÁL *et al.* 2000; HÍR *et al.* 2001; MIKLAS 2002; BERNOR *et al.* 2004; ROČEK 2005; VENCZEL & HÍR 2015). The spadefoot toad (*Pelobates fuscus*) shows a distinct preference for open areas with no, sparse or low vegetation, such as orpines, mosses or Graminae, for not very dense heather (e.g. EGGERT 2002), and it avoids the bushy areas (THIRION *et al.* 2002). This nocturnal species prefers the sandy-loam textured soils for digging itself (CARISIO *et al.* 2014). The fossils of the *Pelophylax esculentus* group (assuming that the fossils identified as *Pelophylax* sp. in the upper site really belong to it) have also been unearthed from both sites. This group contains two species (*Pelophylax lessonae* and *P. ridibundus*) and their

hybrid (*P. esculentus* kl.). These species inhabit small ponds and marshes with aquatic vegetation. Their terrestrial habitats are represented by meadows and broad-leaved forests (DUGUET & MELKI 2003). These frogs require a relatively long period of summer warmth (e.g. BLAIN & VILLA 2006).

Beyond that, the Esztramos 6 upper site does not contain any other herpeto-elements. The aforementioned palaeoecological conditions suggest that the palaeoenvironment of this site was mainly open areas with sparse terrestrial vegetation, ponds, marshes and aquatic vegetation probably with isolated forests. The presence of arvicolinid (Arvicolinae indet.) remains suggests also similar conditions. The bat fossils indicate only the presence of karstic holes at the time of deposition.

The herpetofauna of Esztramos 6 lower site is much richer, in addition to the aforementioned frog species it contains salamandrid, lizard, and snake remains. The northern crested newt (*Triturus cristatus*) lives in ponds where the substrate of organic muds is rich in macroinvertebrates; there are aquatic macrophytes (except for aquatic mosses and *Lemna* sp.); the soils are humus-rich; and the terrestrial habitat can be various (DENOËL 2004; MIRÓ *et al.* 2016). The yellow-bellied toads (*Bombina variegata*) can be found in various aquatic habitats except in great rivers and lakes. They are very frequent in brooks, ponds and puddles, and in their vicinity. The yellow-bellied toads are more opportunistic amphibians which colonize the available aquatic habitats at not too low elevations (DENOËL 2004). The presence of the burrowing green toad (*Bufo viridis*), similarly to spadefoot toad, suggests sandy or loose soils with few stones. BÖHME *et al.* (2006) suggest that the green toad prefers an open environment which means that they burry themselves or hide in the daytime because they are active nocturnal animals. The European tree frogs (*Hyla arborea*) mainly live on trees or shrubs thus they are classified as arboreal animals (e.g. BÖHME *et al.* 2006). The presence of the common frog (*Rana temporaria*) suggests humid, wooded (broad-leaved or mixed), and/or shrubby areas connected together (e.g. BLAIN & VILLA 2006).

Among reptiles known from the locality, anguid lizards (Anguidae indet.) prefer various habitats, ranging from arid to tropical habitats. However, these habitat preferences cannot be used for palaeoecology in this case. The typical habitats of the Balkan whip snake (*Hierophis gemonensis*) are stony areas, scree, scrub, and open woodland. It is active in the daytime, a ground dwelling species; occasionally it is in low vegetation (e.g. ARNOLD & OVENDEN 2002). Dice snakes (*Natrix tessellata*) occur more in water (in rivers or lakes) in their capture zone or very close to the water body in their buffer zone. They occur to a similar extent in grasslands and forests (ŽAGAR *et al.* 2011).

The composition of the herpetofauna (including the above discussed *Pelobates fuscus* and *Pelophylax esculentus* group) reveals that the palaeoenvironment around the Esztramos 6 lower was represented by a mosaic of habitats: from

the open and dry to partially-closed, closed and wet forest and some water bodies. The predation by owls likely played a role in the accumulation of small vertebrates. The nocturnal birds such as the Eagle Owls (*Bubo bubo*), prey on *Hyla arborea* and *Pelobates fuscus*; or the Barn Owls (*Tyto alba*) also capture amphibians though not in significant quantities, because both commonly feed on small mammals (e.g. SZÉP *et al.* 2017). Consequently, the size of their hunting grounds needs to be considered in the study of the palaeoenvironment. The size of the hunting ground of *Bubo bubo* is varying between 0.1–2.53 km radius (PÉREZ-GARCÍA *et al.* 2011), while in the case of the Barn Owl it represents an area of about 2 km radius (e.g. SZÉP *et al.* 2017) which may be changed by geomorphology and the degree of plant covering. These data suggest that the bone accumulation at the Esztramos 6 upper locality did not originate farther than some km. This palaeo-vertebrate fauna has its origin in a relatively small area and it represents only a small sample of the former wildlife around the depositional place.

The presence of bats (Chiroptera) suggests that these sites were closed karstic holes where these animals could rest. Chiropterans are not identified in this material so they are not used in the reconstruction of the palaeoenvironment.

CONCLUSIONS

The middle Pleistocene age of the Esztramos 6 lower site is proven, but the age of the Esztramos 6 upper site is uncertain because it contains different and unidentified small mammals.

The faunal lists of Esztramos 6 lower and upper are completed with some newt, frog, lizard, snake, and small mammal taxa.

The presence of *Latonia gigantea* in the middle Pleistocene of the Esztramos 6 locality is confirmed by cranial and postcranial bones described in this study.

The herpetofauna, which is significantly richer in fossils and species in the Esztramos 6 lower than in the upper site, indicates a mosaic of palaeoenvironments where the presence of permanent water source was dominant in both sites. However, this condition is less pronounced in the Esztramos 6 upper site.

The presence of bats suggests that these sites were karstic holes or small caves during the time of accumulation of the fossil bones. The taxonomic revision and the palaeoecological interpretation of bats would contribute to a more precise explanation of these palaeovertebrate sites.

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