

## Fish, amphibian and reptilian assemblage from the middle Miocene locality Gračanica—Bugojno palaeolake, Bosnia and Herzegovina

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### Abstract

This paper presents the first fossil fish, amphibian and reptilian fauna from Bosnia and Herzegovina Dinarides. The fauna of ectothermic vertebrates of the Bugojno palaeolake, dated to 15.2–14.0 Ma, composes of killifishes (Cyprinodontiformes indet.), a barb (Barbini indet. (aff. *Barbus*), a crocodile newt (*Chelotriton* sp.), a painted frog (*Latonia* sp.) and a crocodile (Alligatoroidea indet. [? *Diplocynodon*]). The crocodile remains are confined to the lower part of the section corresponding to the swamp deposit (unit 1). The remaining fauna, which includes fishes and amphibians, come from the upper lacustrine unit 2. A possible *Barbus* (Barbini indet. (aff. *Barbus*)) could represent one of the oldest fossil records of the genus found in Europe, which composes of skeletal elements and pharyngeal teeth. The crocodile newt (*Chelotriton* sp.) represents the first record of this group from the area. For the first time, fossil tadpoles of the genus *Latonia* are described in this paper, which, moreover, are the first record of tadpole for both the family Discoglossidae and clade of discoglossoid frogs. The crocodile remains, identified as Alligatoroidea indet., should belong to the genus *Diplocynodon*, which will be tested later on a better preserved material. The fossils, coming from the lacustrine interval, are referred to the deeper water facies. Taphonomic observations of the fossil remains suggest relatively short phase of decay of the animal bodies and their (probably quick) sedimentation in the deeper parts of the lake, with poor oxygen content.

**Keywords** Ectothermic vertebrates · Palaeobiogeography · Palaeoecology · Middle Miocene · Bosnia and Herzegovina

### Introduction

The Dinarides area, located between the Adriatic and Pannonian basins, is provided with rich record of the Neogene continental deposits filled with lake sediments (Mandic et al. 2016a). Despite this abundant record, the fossil vertebrate faunas from the continental deposits are very poorly known. Malez and Slišković (1976) have summarised the

Cainozoic vertebrate fossil record of Bosnia and Herzegovina, providing an overview on faunas of different vertebrate groups and discussing their relations with neighbouring areas. The area represents an interesting palaeobiogeographic region between Central and Southern Europe as well as Asia (Anatolia). As it has been recently documented on examples of the following: (1) insectivore and marsupial faunas of the localities Banovići, late Oligocene (van der Sar et al. 2017) and (2) large vertebrate fauna of the Gračanica locality, Bugojno palaeolake (this issue), at least the mammal faunas of the regions contain element characteristics for both European and Anatolian fossil records. Aside from the mammal remains, other vertebrate groups, such as fishes, amphibians and reptiles, have received less attention. Only remains of crocodiles and turtles have been reported from the early-middle Miocene locality Banja Luka (Malez and Slišković 1976). The present paper describes for the first time fossil fauna of fishes, amphibians and a reptile from the Neogene of Bosnia and Herzegovina and discusses relation of the ectothermic vertebrate fauna with those from neighbouring areas.

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**Table 1** Meristic and morphometric measurements of the tadpoles of *Latonina* sp. from Gračanica (Bugojno palaeolake), with indication of the ontogenetic stages. The different shades of blue indicate the younger (bright blue) to older (dark blue) tadpoles. *Dp* *Discoglossus pictus*, *Bb* *Bombina orientalis*, *Bv* *Bombina variegata*, *Xl* *Xenopus laevis*

coll. nr.	length (in mm)		number of			ontogenetic stage (Ročková, Roček, 2005)				(latest) developmental event		
	skull	body	total	vertebrae	caudal vertebrae	hyochord	ribs	<i>Dp</i>	<i>Bb</i>		<i>Bv</i>	<i>Xl</i>
MJSN GRC-100	>15,5	22	37,5	9	2	1	-	<58-66	59	56	59-60	11th vertebra begins to ossify
MJSN GRC-101	18	-	-	9	>1	1?	-	<58-66	59	56	59-60	(11th) 10th vertebra begins to ossify
MJSN GRC-102	14,8	18,2	33	9	1	missing	3	≥56-57	≥58	≥55-56	≥59-60	10th vertebra begins to ossify
MJSN GRC-103	-	-	-	-	(?)	1	3	≥56-57	≥58	≥55-56	≥59-60	10th vertebra begins to ossify
MJSN GRC-104	7,4	9	16,4	>7	-	-	0	56-57	58	55	58	neural arches of SV begin to ossify
MJSN GRC-105	14,4	>18,4	32,8	9	-	1?	3	≥55-56	≥56	≥55-56	≥57-58	according to sizes (comparable with GRC-100)
MJSN GRC-106	>7,4	13	20,4	7	-	-	1(+1)	≥56-57	≥58	≥55	≥58	neural arches of SV begin to ossify
MJSN GRC-107	-	26,3	-	9?	-	-	-	-	-	-	-	-
MJSN GRC-112	12,2	20	32,2	9?	-	-	3	-	-	-	-	-
MJSN GRC-113	11,6	13	24,6	>8	-	-	3	-	-	-	-	-
MJSN GRC-114	-	-	-	-	-	-	-	-	-	-	-	-
MJSN GRC-115	18,4	29	47,4	9	2	1	3	<58-66	59	56	59-60	11th vertebra begins to ossify

## Systematic palaeontology

Class Actinopterygii Cope, 1887  
 Clade Teleostomorpha Arratia, 2000  
 Order Cypriniformes Bleeker, 1859  
 Family Cyprinidae Rafinesque, 1815  
 Subfamily Cyprininae (Rafinesque, 1815) (sensu Yang et al. 2015)  
 Tribe Barbini Bleeker, 1859 (sensu Yang et al. 2015)

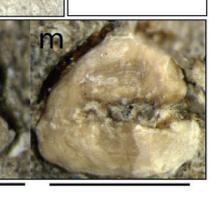
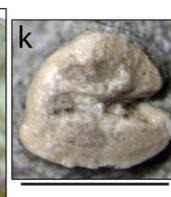
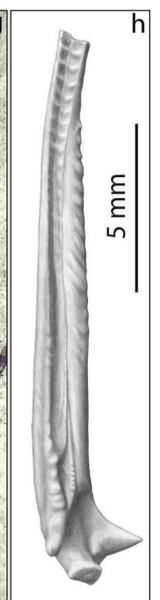
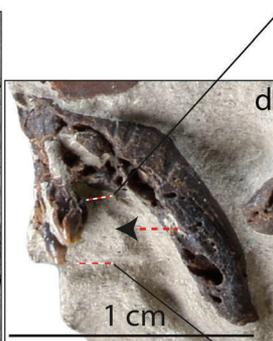
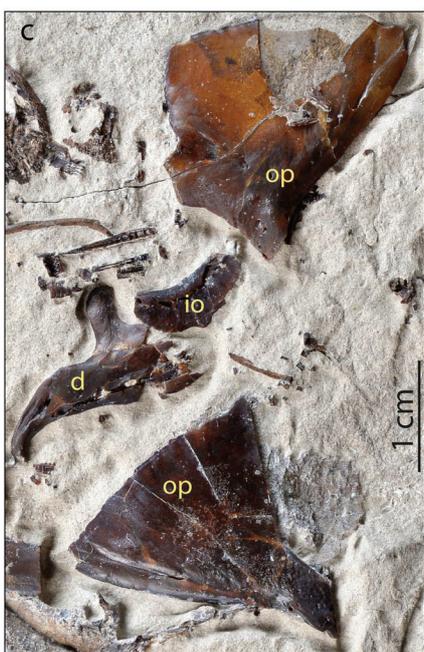
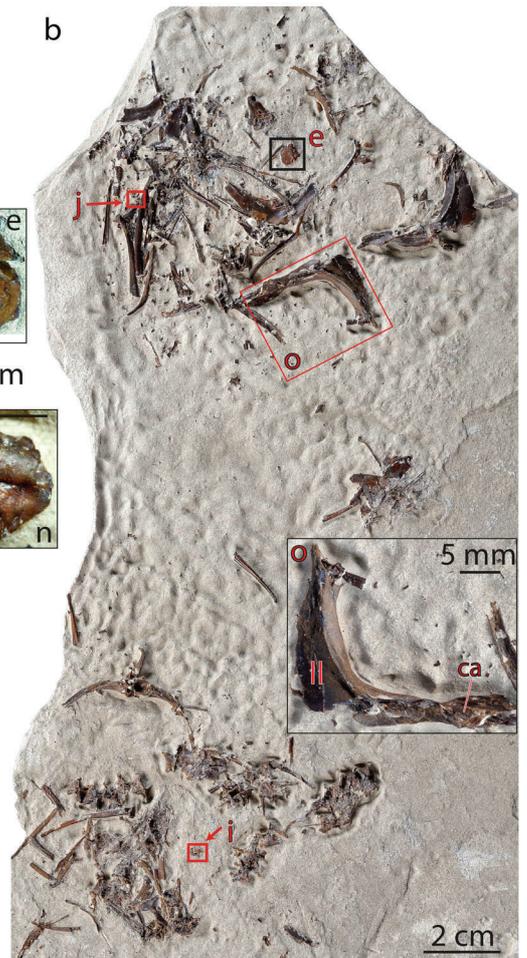
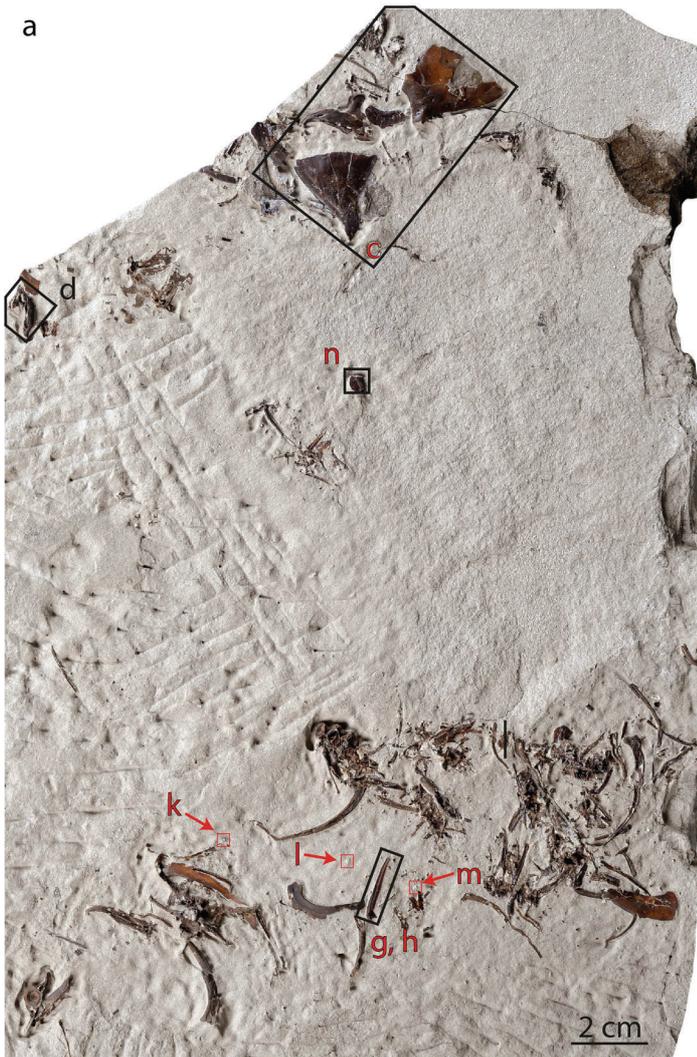
Barbini indet. (aff. *Barbus*)  
 (Figures 2 and 3)

**Material:** Two partial skeletons: MJSN GRC-70.1 (part) and GRC-70.2 (counterpart), MJSN GRC-71.1 (part) and GRC-72.2 (counterpart).

**Description:** Partial skeletons of two individuals are deformed and disarticulated. The bones are lightly (GRC-71) (Fig. 3) and more strongly (GRC-70) scattered (Fig. 2). Among the bone remains of the specimen GRC-70, at least seven otoliths of killifishes (Cyprinodontiformes indet., see below) and several vertebrae of small-sized fishes (?Cyprinodontiformes indet.) are scattered as well. These finds suggest that the barbs could be piscivorous and prey on killifishes.

The opercle is trapezoid in shape. The anterior and ventral margins of the opercles are slightly convex, whereas the posterior and dorsal margins are concave. The supraglenoidal process is well pronounced but it is rather short. The process is pierced by a dorsoventrally running praeopercular sensory canal. In lateral view, a distinct narrow groove, corresponding to a secondary branch of the praeopercular sensory canal, runs parallel to the anterior margin of the bone (Figs. 2c and 3c). The praeopercle is narrow (Fig. 3c). The dorsal lamina is moderately developed. The maxilla is broad at its mid portion. The dental process is narrow and short, and it terminated with an extension. The dentary shows a long mental process. The symphysis is bent ventromedially (Figs. 2c and 3c). The dorsal process of the dentary is high and bent slightly posteriorly. The openings of the sensory canal are located parallel and close to the ventral margin of the bone. Several infraorbital bones are present (Fig. 2c, e, m). They are pierced by a large infraorbital canal.

The pharyngeal bone is preserved by its thick and elongated anterior branch and a part of the tooth bearing plate. Three pharyngeal teeth are present on the plate, two of them are located next to each other (Fig. 2f), suggesting the presence of at least two tooth rows on the pharyngeal bone. Besides these teeth, two further pharyngeal teeth are found on the slabs with the fossil specimen (Fig. 2h, i). The tooth is cylindrical and terminate with a small hook. The latter projects over the grinding surface and forms either right or obtuse angle to the tooth axis. The grinding surface has a concave surface and the form of an ellipse. The ventral portion of the grinding surface is wider than the dorsal one. The edge surrounding the grinding surface is slightly raised (Fig. 2f).



◀ **Fig. 2** Barbini indet. (aff. *Barbus*) (MJSN GRC-70) from Gračanica (Bugojno palaeolake). General overview of **a** part (MJSN GRC-70.1) and **b** counterpart (MJSN GRC-70.2). The black frames indicate the location of the zoomed in parts of the body. (**c**) Opercles, a dentary and an infraorbital bone. **d** pharyngeal bone with teeth. **e, n** Infraorbital bone (lacrymal?). **f** Pharyngeal teeth. **g** The photograph of the last unbranched ray of the dorsal fin and **h** its drawing. **i, j** Isolated pharyngeal teeth from different parts of the body. **k-m** Otoliths of cyprinodontoform fishes. **o** Cleitrum. *ca* coracoid ala; *d* dentary; *io* an infraorbital bone; *ll* lateral lamina; *op* opercle. The scale bars, where not indicated, equal 1 mm

The cleitrum is L-shaped. Both its rami form an obtuse angle. The coracoid ala is located in the cranial part of the horizontal ramus. The lateral lamina is moderately pronounced. It is round in outline (Fig. 2n). The rays of the pectoral fin are strongly disarticulated and laying over the skull bones. The ventral fin measures 30 mm and consists of one unbranched and seven branched rays (V I 7) (Fig. 3d). The anal fin is at least 36 mm long and consists of two unbranched and six and half branched rays (A II 6 ½) (Fig. 3f). The dorsal fin measures at least 37 mm and consists of three unbranched and at least seven branched rays (D III 7) (Fig. 3e). Whether the last branched ray of the dorsal fin (numbered as 10 in Fig. 3e) represents the last one, cannot be stated with confidence since its size has rather large size than typically found in barbini. The posterior margin of the third unbranched dorsal fin ray is serrated by small (nearly invisible) posteroventrally directed denticles (Fig. 2g). The denticles are present only at the dorsal two-third of the ray. The vertebrae are preserved on GRC-70, but they are strongly disarticulated. They have an amphicoelous centrum.

**Remarks:** Both fish specimens share similar morphology of the dentary, opercle and serration of the last unbranched ray of the dorsal fin, thus they can be considered to belong to one species. The combination of the following characters allows to assign the described remains to the Cyprininae (sensu Kottelat and Freyhof 2007), which includes *Aulopyge*, *Luciobarbus* and *Barbus* genera: (1) at least seven branched rays in the dorsal fin; (2) last unbranched ray of the dorsal fin posteriorly serrated; (3) last unbranched ray of the anal fin posteriorly not serrated; (4) pharyngeal teeth arranged at least in two rows (Kottelat and Freyhof 2007). From these genera, the studied fossil barb can be distinguished by a higher number of the unbranched/branched rays in the anal fin (III 6 ½ in studied material vs. II 5 in *Aulopyge* (Bănărescu 1999), III 5 in both *Barbus* and *Luciobarbus* (Bănărescu and Herzig-Straschil 1995)). A comparable number of the branched rays in the anal fin have been documented in few genera e.g. *Cyprinion* (Bănărescu and Herzig-Straschil 1995), which, in any case, can be excluded from the consideration, since it has a much higher number (15–16) of the branched rays in the dorsal fin (Bănărescu and Herzig-Straschil 1995) as well as the characteristic morphology of the pharyngeal dentition (Vasileiadou et al. 2017). The fossil remains show hooked pharyngeal teeth, resembling the morphology typical for the genus *Barbus* (Böhme 2002) (Kottelat and Freyhof 2007). The early

Miocene species “*Barbus*” *bohemicus* shows comparable amount of anal (III 7/II 9) and dorsal (II–III 7/II 9) fin rays (Obrhelová 1967) as well as teeth with rather similar morphology (Obrhelová 1990).

Numerous early to middle Miocene localities in Europe provided fossil remains of the genus *Barbus* (Böhme and Ilg 2003). Only few of them have been described or illustrated, making the comparison of the Bosnian *Barbus* with a limited number of fossils e.g. Lesvos Island, Greece and Steinheim, Germany. The Gračanica (Bugojno palaeolake) barbini differs from the Greece fossils (Vasileiadou et al. 2017) by significantly slender and gracile pharyngeal teeth and grinding surface of teeth. The herein described fossil can be distinguished from the middle Miocene species from Steinheim, Germany *Barbus steinheimensis* (Gaudant 1989) by the following: (1) the reduced serration of the last unbranched ray of the dorsal fin (vs. well pronounced in *Barbus steinheimensis*) and (2) (ventrally) closed and smooth grinding surface of the pharyngeal teeth (vs. ventrally open and rough grinding surface in *Barbus steinheimensis*).

Taking into account the listed similarities and differences, it seems more probable that the described fish remains belong to a form (new genus) closely resembling the true barbs *Barbus*. This, however, cannot be identified due to the lack of comprehensive osteological studies of the genus *Barbus* and its relatives (*Luciobarbus*, *Augolype*, etc.) and the lack of revision of the earlier described fossil forms. Thus, an open nomenclature is preferable at this stage.

Order Cyprinodontiformes Berg, 1940

Cyprinodontiformes indet.  
(Figure 2j–l)

**Material:** six otoliths: MJSN GRC-70.

**Description and remarks:** The general morphology and dimensions of the otoliths, the shape of the rostrum and antirostrum (Fig. 2j–l) allow assigning the available otoliths to the order Cyprinodontiformes (Reichenbacher and Weidmann 1992; Reichenbacher and Kowalke 2009). These otoliths together with skeletal remains of the groups from the locality Gračanica (Bugojno palaeolake) will be published elsewhere.

Class Amphibia Linnaeus, 1758

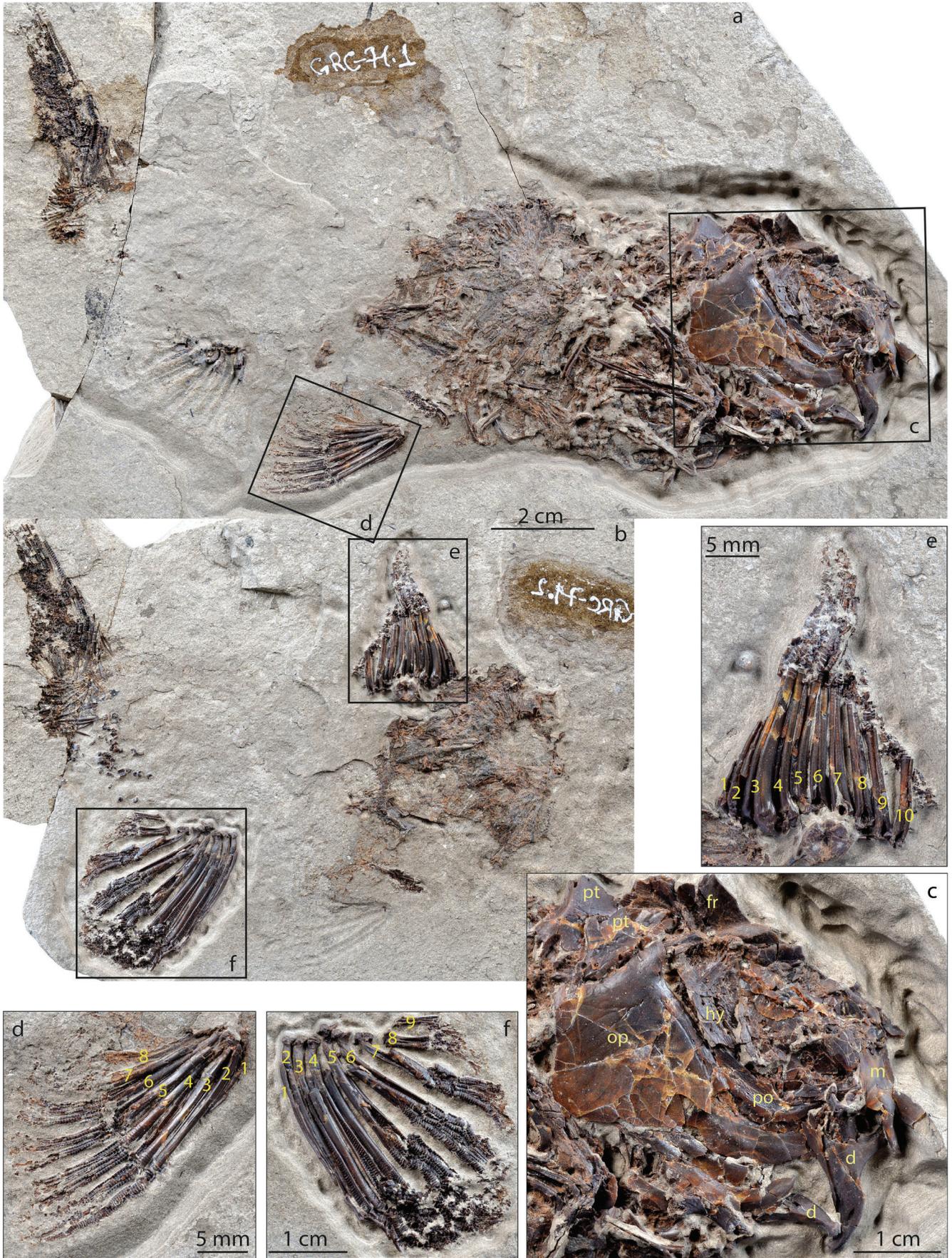
Order Caudata Scopoli, 1777

Family Salamandridae Goldfuss, 1820

Genus *Chelotriton* Pomel, 1853

*Chelotriton* sp.  
(Figures 4 and 5)

**Material:** Three partial bodies: MJSN GRC-072.1 (part) and GRC-072.2 (counterpart); GRC-109.1 (part) and GRC-109.2



◀ **Fig. 3** Barbini indet. (aff. *Barbus*) (MJSN GRC-71) from Gračanica (Bugojno palaeolake). General overview of **a** part (MJSN GRC-70.1) and **b** mirrored view of counterpart (MJSN GRC-70.2). The black frames indicate the location of the zoomed in parts of the body. **c** Head. **d, e, f**, Dorsal, ventral, and anal fins correspondingly. *d*, dentary; *f*, frontal; *hy*, hyomandibular; *op*, opercle; *po*, praeopercle; *pt*, pterygoid

(counterpart); GRC-111; 26 additional individuals will be described elsewhere.

**Description:** The studied specimens are not complete. The bones are slightly displaced, suggesting post-mortem decay before final fossilisation. The preserved part of the largest individual is 19 cm long. Its snout-vent length, measured from the tip of the snout until the posterior end of the second sacrocaudal vertebra, is 15 cm. The skull outline appears to be parabolic (MJSN GRC-109) (Fig. 4b), which can be confirmed by the dentary outline of the specimen MJSN GRC-72 (Fig. 5c).

The dorsal surface of several skull bones (dentary, maxillae, nasal, frontal, squamosal) is covered by dermal ornamentation consisting of dense pustules and rather deep pits (Fig. 5). Other skull bones are either exposed by their ventral surface or their remnants are strongly damaged, which does not allow their identification. The dentaries are linguolabially compressed. The medial surface of the symphysis is convex, the pars dentalis possesses traces of the dental pedicles (Fig. 5c, d). The maxilla is an elongated bone, the traces of a broken off process are visible on the second half of the maxilla, corresponding, most probably, to the posteromedial process. The pars dentalis possesses the traces of the dental pedicles. The length of the pars dentalis is about half of the entire bone length and is located in the anterior portion of the bone (Fig. 5c). The anterior margin of the bone is concave and possesses dorsal and ventral processes.

The nasals (Fig. 5c, d) have rounded outline. Their dorsal surface is covered with pustular ornamentation. In ventral view, the bone has a concave surface. The articulation surface with maxilla is well-developed (Fig. 5c). The frontals are about triangular in shape. Anteriorly, the frontal, where the prefrontal articulates with the bone, is narrow. Posteriorly, in the area of the orbital cavity, the frontal broadens. The frontosquamosal process is narrow and projects posterolaterally. The posterior margin of the bone is strongly concave. In dorsal view, the roof of the braincase has nearly the same width along the entire bone length. The parietals are exposed from the ventral surfaces, the roof of braincase is flat and rectangle-shaped. The bone possesses a posterolaterally directed squamosal process. The squamosal is present by its posterolateral portion. It is broad and possesses a robust and curved frontal process (Fig. 5c).

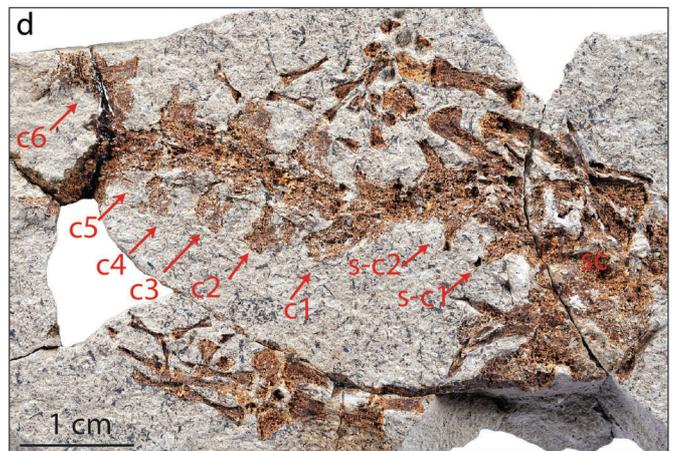
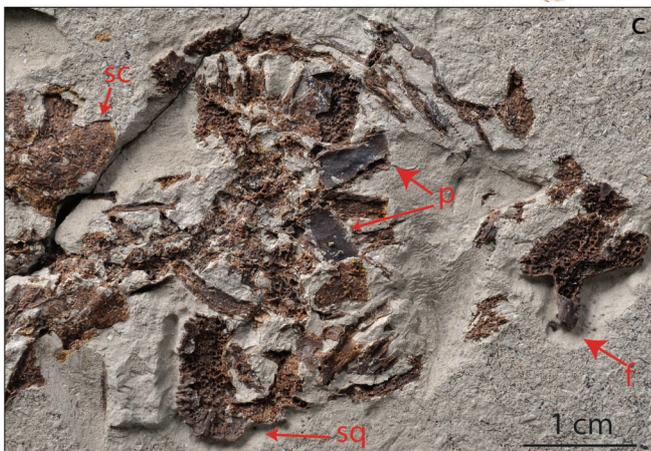
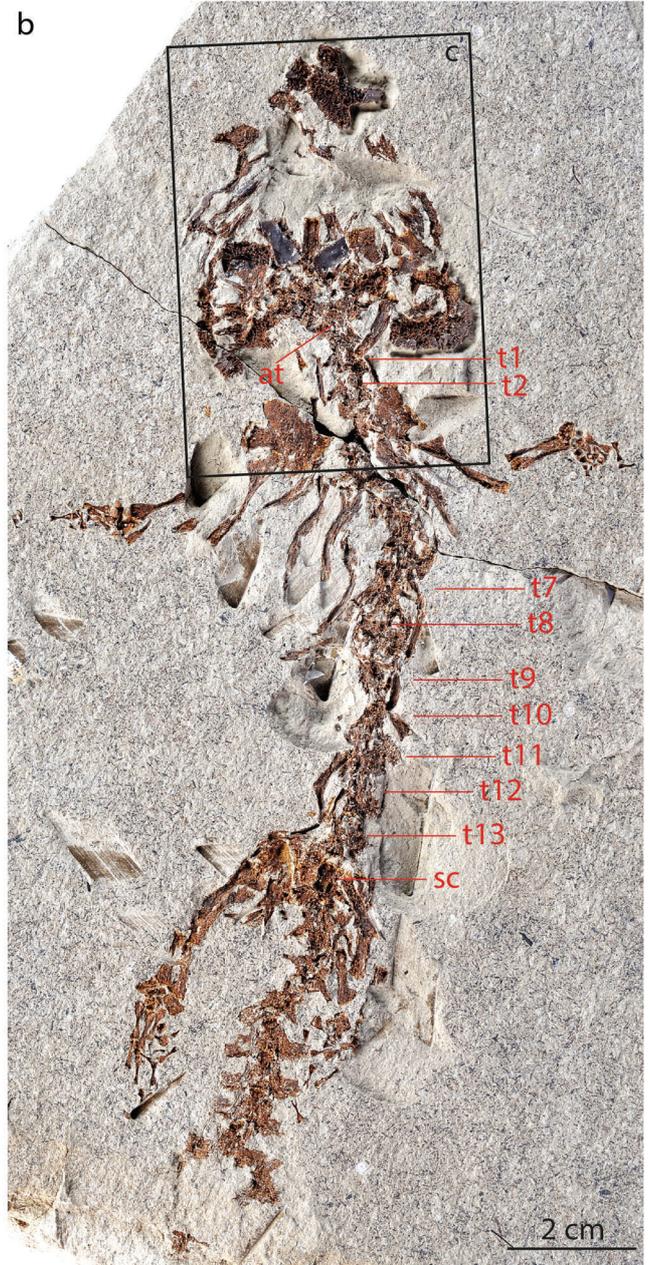
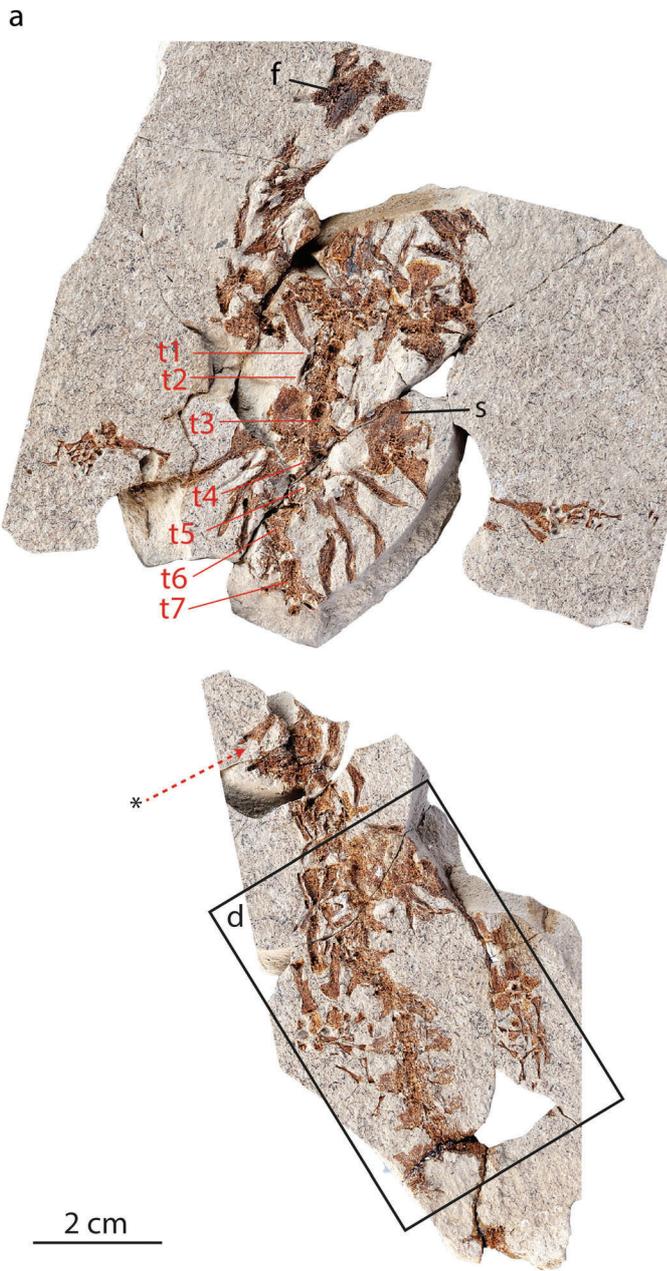
The vertebral column consists of the atlas, 13 trunk and one sacral vertebra with opisthocoelous centrum, two sacrocaudal vertebrae and six preserved caudal vertebrae, representing the anterior portion of the tail (MJSN GRC-109). The sacrocaudal vertebrae are those which do not possess haemapophyses and

are located posteriorly from the sacral vertebra. The first caudal vertebra is the first which is provided with a haemapophysis (Fig. 4d). The neural spine and haemapophysis of the first caudal vertebra are very high (up to 12 mm of the total height). The ribs are large, a dorsal spine is observable on a posterior rib (Fig. 4a). The poor preservation does not allow to make any further observation on them. The scapulocoracoid is composed of a large semi-circular coracoid plate and a short and robust scapular part (Fig. 4c). The carpal and metatarsal elements are well ossified (Fig. 4b).

**Remarks:** The taxonomy of the genus *Chelotriton* is rather problematic. As it has been already mentioned, the genus *Chelotriton* should be considered as a basket taxon (Böhme 2008). So far, salamander skull bones and vertebrae possessing a dermal ornamentation composed of dense, pustular and very regular dermal ossification have been commonly referred to the genus *Chelotriton*. Recently, Schoch et al. (2015) treated the genus *Chelotriton* as having only one species *Chelotriton paradoxus*. The following features characterising *Chelotriton*, listed in Schoch et al. (2015), can be observed in the studied specimens from Gračanica (Bugojno palaeolake) (the numbering follows Schoch et al. (2015)): (1) skull outline parabolic, (5) maxilla with posteromedial process nearing/suturing pterygoid, (7) ossified carpal and tarsal elements, (8) epipleural processes on trunk ribs.

Remains of the Gračanica crocodile newts differ from the following fossil forms by a larger body size (snout-vent length of 16 cm), and thinner squamosal process of the frontal: *Chelotriton* aff. *paradoxus* of Gratkorn, middle Miocene, 12.75 Ma (Böhme and Vasilyan 2014), the figured skulls of *Chelotriton paradoxus* from Enspel, late Oligocene, 24.74–24.84 Ma and Randeck Maar, middle Miocene, 16.4–17.25 (Roček and Wuttke 2010; Schoch et al. 2015), *Chelotriton* sp. from Coderet, late Oligocene, 24 Ma (type locality of *Chelotriton paradoxus*) (Böhme 2008), *Chelotriton* sp. types I and II from Mokrá-Western Quarry, 2/2003 Reptile Joint, early Miocene, 17–17.8 Ma (Ivanov 2008). The form of the nasal, frontal and parietal of the Gračanica *Chelotriton* significantly differ from those of two forms of *Chelotriton* described from Mokrá-Western Quarry: the Czech *Chelotriton* has smaller and reduced frontals, the parietals have a rectangular shape, whereas the nasals have a trapezoidal shape (Ivanov 2008).

As it has been already shown on specimens of *Chelotriton* from the Randeck Maar and Enspel localities in Germany (Schoch et al. 2015), these salamanders are characterised by high morphological and osteological variabilities. It is possible that the observed differences between Gračanica (Bugojno palaeolake) and other European forms, especially with the material from the similar age locality Randeck Maar, could represent intraspecific morphological variability. Unfortunately, this cannot be documented or even studied considering the current state-of-art of the genus *Chelotriton*, due to the lack of comprehensive



◀ **Fig. 4** *Chelotriton* sp. (MJSN GRC-109) from Gračanica (Bugojno palaeolake). **a, b** Counterpart (MJSN GRC-109.2) and part (MJSN GRC-109.1) of the specimen correspondingly. The black frames indicate the location of the zoomed in parts of the body. **c** Zoomed in view of the head of the MJSN GRC-109.1. **d** Zoomed in view of the caudal portion of the body of the MJSN GRC-109.2. The asterisk indicates the epipleural process of the rib. *a* atlas; *c1–c6*, caudal vertebrae first to sixth; *f* frontal; *s* scapulocoracoid; *sc* sacral vertebra; *s-c1–s-c2*, sacrocaudal vertebra first to second; *sq* squamosal; *t1–t13*, trunk vertebrae first to thirteen

studies treating on one hand the osteology of the genus and on another hand the osteology of the recent salamander genera *Tylotriton* and *Echinotriton*, showing close phylogenetic relationship with *Chelotriton*. Nevertheless, investigation of fossils by means of CT scan, which is intended for Gračanica (Bugojno palaeolake) material, supposedly can provide better data on osteology of the species. Considering this, an open nomenclature for the Bosnian fossils *Chelotriton* is preferred at this point.

Order Anura Fischer, 1813  
Family Alytidae Fitzinger, 1843  
Genus *Latonia* Meyer, 1843

*Latonia* sp.  
(Figures 6–8)

**Material of larvae:** 12 tadpoles: MJSN GRC-100–GRC-115.

**Material of adults:** One partial skeleton: MJSN GRC-097.

**Description of larvae:** The available tadpole remains represent different developmental stages. They can be assigned to at least three ontogenetic stages (NF 57–58, 58 and 59–60 sensu Ročková and Roček (2005), Table 1). Tadpoles with transitional ontogenetic stages are also present in the material, which could not be clarified due to their poor preservation. The “body length”, which has only been measured on the available ossified remains, ranges from 16.4–47.4 mm.

Among skull bones, only the parasphenoid and frontoparietals show an adequate preservation. The parasphenoid has a T-shape and shows a long pars medialis and short lateral processes. The posterior process is better developed in larger individuals (Fig. 8e, f), whereas in smaller ones it cannot be clearly distinguished (Fig. 8a). In both small (MJSN GRC-106) and large (MJSN GRC-105) individuals, the bone shows a moderately broad pars medialis (processus cultriformis). It has nearly the same width along its entire length, only at its mid portion it extends laterally. In dorsal view, a distinct but rather shallow longitudinal depression runs parallel to the bone axis (Fig. 8a). This corresponds to the ventrally observable longitudinal eminentia ventralis (Fig. 8b, f). On both sides of the eminentia ventralis, at the anterior half of the pars medialis, the bone surface is concave. Both longitudinal depression (on the dorsal surface) (MJSN GRC-102) and eminentia ventralis (on the ventral surface) (MJSN GRC-115) are reduced in larger individuals.

In ventral view, the lateral processes display concave surface for the articulation with prooticoccipital (Fig. 5d).

The frontoparietals are always paired in tadpoles before metamorphosis (Figs. 6, 7, 8). The bone is rather thick and well ossified in the larger individuals (Fig. 8e, f). Their cranial ends project anterolaterally (Fig. 7a, b). The dorsal surface of the bone possesses anteroposteriorly elongated pits of various sizes (Fig. 8a, c, e). The lateral margin of the frontoparietals are rounded and deflected dorsally. In ventral view, a well-developed frontoparietal incassation is observable (Fig. 8c, f). The tadpoles show, depending on the preservation, up to nine vertebrae. The 2nd to 4th vertebrae possess well-developed transverse processes and ribs. One caudal vertebra can be recognised on the specimen MJSN GRC-115. Two caudal vertebrae are observable on the MJSN GRC-100 and GRC-115, representing the largest individuals within the available material (Figs. 7h, i, j and 8g). The ossified elongate single element, corresponding to the ossified portion of the hypochord, is observable in six individuals. Among them the largest hypochord (5.5 mm) is the one of the specimen MJSN GRC-100.

**Remarks on larvae:** All studied tadpoles are uniform both as regards their appearance and osteology; thus, they can be considered to belong to the same taxon. They can be clearly separated from palaeobatrachids, because the latter family is characterised in the late praemetamorphic stage by the following: (1) five rib pairs on the 1st–5th vertebrae (vs. three pairs in the Gračanica (Bugojno palaeolake) material); (2) fused frontoparietals (vs. not fused (paired) frontoparietals in the Gračanica material); and (3) a gracile lanceolate-shaped pars medialis without lateral processes (vs. rather broad and robust pars medialis with lateral extensions in the Gračanica (Bugojno palaeolake) material) of the parasphenoid (Roček 2003).

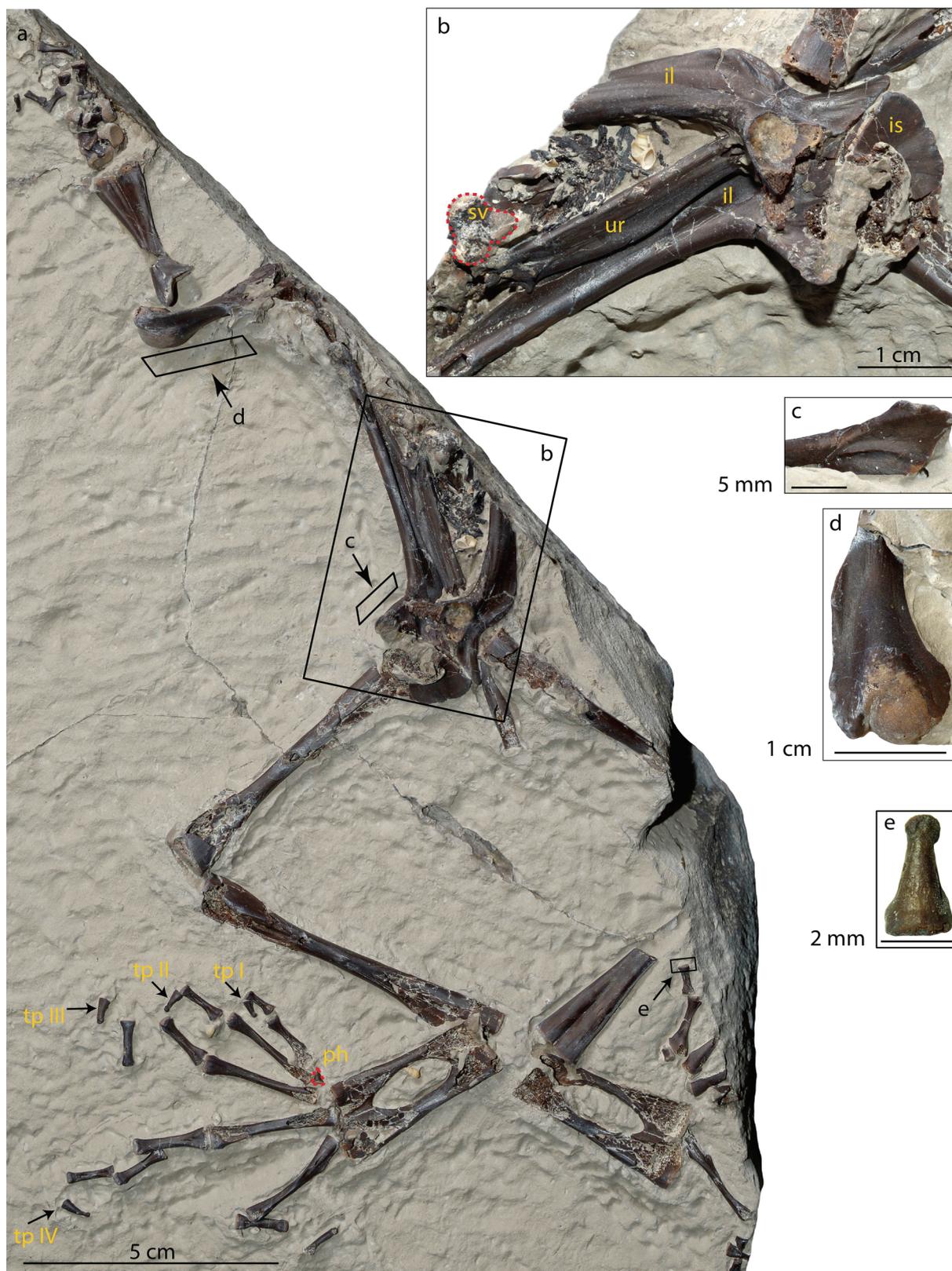
The frontoparietals with rough dorsal surface indicate that adults of this frog taxon had ornamented frontoparietals. Therefore, further comparisons can be confined to the families Alytidae (genus *Latonia*) and Pelobatidae, which have ornamented frontoparietals and are present in the fossil record of Europe. The genus *Thaumastosaurus* can be excluded from the comparison since it disappeared from Europe at the Eo-Oligocene boundary (Vasilyan 2018).

The comparison with the family Pelobatidae shows that the most important character of the genera *Pelobates* and *Eopelobates*, the presence of the tripartite composition of the frontoparietal, cannot be observed in the available material (Roček and Wuttke 2010). The third unpaired element of the frontoparietal is not developed in the Gračanica (Bugojno palaeolake) material. Further characteristic features, such as a rounded small process on the posterior margin of the bone (present in all Pelobatidae) and a distinct keel on the medial process of the parasphenoid (present in fossil species *Pelobates decheni* and the genus *Eopelobates*) (Roček 1981; Špinar and Roček 1984; Roček and Wuttke 2010), also cannot be found in the material.



**Fig. 5** *Chelotriton* sp. from Gračanica (Bugojno palaeolake). **a** Counterpart (MJSN GRC-072.2) and **b** part (MJSN GRC-072.1). The black frames indicate the location of the zoomed in parts of the body. **c**, **d** Zoomed in views of the head of the specimen MJSN GRC-072.2 and

GRC-072.1 correspondingly. **e** MJSN GRC-111. *d* dentary; *f.d* right frontal; *f.s* left frontal; *m* maxilla; *n* nasal; *p* parietal; *ps* parasphenoid; *tv* trunk vertebra



**Fig. 6** *Latonia* sp. (MJSN GRC-097) from Gračanica (Bugojno palaeolake). **a** The general overview of the specimen. Zoomed views of **b** the pubic girdle region, **c** ventral surface of the corpus ossis ilii of the ilium, **d** posterior surface of the humerus and **e** terminal phalange V, *il*,

*is* ischium; *ph* prehallux (outlined by a dashed red line) ; *sv* sacral vertebra; *tp I*, terminal phalange I; *tp II*, terminal phalange II; *tp III*, terminal phalange III; *tp IV*, terminal phalange IV; *tp V*, terminal phalange V (the original position is outlined in red); *ur* urostyle

The comparison with alytids, especially with the genus *Latonia*, is difficult, due to the absence of any tadpole remains in the fossil record of both genus and family, as well as the lack of any information on the ossification pattern during the development of the recent species *Latonia nigriventer*.

Nevertheless, several characters that suggest relationships of the tadpoles to *Latonia* or Alytidae can be listed as the following: (1) the morphology of the parasphenoid (Biton et al. 2016), only the eminentia ventralis (observable in the Gračanica (Bugojno palaeolake) material) is missing in the recent species and (2) the presence of the adult individuals of the genus (*Latonia* sp.) in the locality, which is so far the only anuran known from Gračanica. The laterally directed cranial ends of the frontoparietals, observable on the studied material, can be considered as a further character suggesting the assignment of the tadpoles to *Latonia* and/or its sister genera. In both Recent (Biton et al. 2016) and fossil (Roček 1994) species of *Latonia* as well as in *Discoglossus sardus* (Púgener and Maglia 1997), the cranial ends of the frontoparietals are laterally deflected.

Taking into account the abovementioned, the tadpoles could be assigned rather to the genus *Latonia* than any other known group e.g. Palaeobatrachidae, Pelobatidae. However, due to lack of studies on the ontogenetic development of both recent and fossil representatives of the genus *Latonia*, any direct comparison and a secure taxonomic assignment of the tadpole material is not possible. Even if the data on the recent species would be available, the comparison could be difficult, since the body sizes of the recent species is significantly smaller than that of the fossil forms. The tadpoles available from Gračanica, Bugojno palaeolake, have definitively larger sizes (snout-vent length) up to 47 mm, which clearly exceed the body size of a young adult of the recent *Latonia nigriventer* (SVL = 31 mm) (Biton et al. 2016).

**Description of adults:** The only individual of *Latonia* sp. is represented by a well-preserved partial skeleton, in which the main part of the vertebral column, pectoral girdle, left forelimb and head are missing (Fig. 6).

**Forelimb:** The preserved portion of the forelimb is represented by phalanges, metacarpals, carpals, radioulna and humerus. The ventral surfaces of the phalanges bear well-developed cristae. The terminal phalanx is rather short, has a shape of an elongated triangle and possesses a round bulb. The carpal elements are represented by well-ossified ulnare and, possibly, radiale, which lay over each other. The radioulna possesses a rather deep longitudinal sulcus; the capitulum and collum are distinct. The humerus is partially exposed. It displays a moderately developed medial crest at its medial edge, terminating ventrally by a medial epicondyle. The humeral caput is large and located slightly laterally from the bone axis (Fig. 6d).

**Vertebral column:** The sacral vertebra shows one anterior and two posterior condyles. The urostyle is long (62.7 mm) and bears a high dorsal crest. The right transverse process of

**Fig. 7** Tadpoles of *Latonia* sp. from the Gračanica (Bugojno palaeolake). **a** MJSN GRC-104.2 (counterpart), **b** MJSN GRC-104.1 (part), **c** MJSN GRC-106, **d** MJSN GRC-105.2 (counterpart), **e** MJSN GRC-105.1 (part), **f** MJSN GRC-103.2 (counterpart), **g** MJSN GRC-105.1 (part), **h** MJSN GRC-100.2 (counterpart), **i** MJSN GRC-102.2 (counterpart), **j** MJSN GRC-115. The black frames outline bones figures in Fig. 8 as following: **e**–Fig. 8a, **d**–Fig. 8b, **e**–Fig. 8c, **h**–Fig. 8d, **i**–Fig. 8e, **j** (upper)–Fig. 8f, **j** (lower)–Fig. 8g. *hc* hypochorda. The scale bars equal to 5 mm

the urostyle, visible on the specimen, is posteriorly inclined (Fig. 6b).

**Ilium:** The ilium is long and gracile. It measures 76 mm in length. In lateral view, the pars ascendens is well prominent, at its anterior base a large supraacetabular fossa is visible. The tuber superior is relatively high but not well pronounced. The lateral surface of the tuber is highly irregular, displaying marked ridges. The dorsal crest sharply descends anteriorly from the tuber superior and reaches the anterior tip of the iliac shaft (Fig. 6b). At the posterior corner of the dorsal crest, between the tuber superior and iliac shaft, a small tubercular fossa pierces the bone surface. The pars descendens is extremely reduced, only its most posterior portion extends ventrally. The acetabulum has a rounded anterior margin. Its posterior margin extends dorsally and ventrally. The ventral surface of the corpus ossis ilii is broad and possesses a longitudinal crest (Fig. 6c). The medial surface of the pars acetabularis bears a posteriorly expanding interiliac groove (Fig. 6b).

**Hind limb:** The femur and tibiofibula are long, measuring 60 mm and 63 mm, respectively. In the middle of the tibiofibula, a nutrition foramen is visible. The astragalus and calcaneus are massive, fused together by leaving sutures (Fig. 6a). The phalanges are long. The phalangeal formula is 3-3-4-5-4 (digits I–V, respectively). At the base of the digit I, one element of the prehallux is preserved. The ventral surfaces of the phalanges, besides the metatarsals, possess paired longitudinal crests at their proximal and distal ends, serving for attachments of muscle tendons. All terminal phalanges are slender and long and possess rounded bulbs at their distal tips. The terminal phalanges of the first and fifth digits are more robust than those of other digits. They become slender from the second to the fourth phalanges (Fig. 6a).

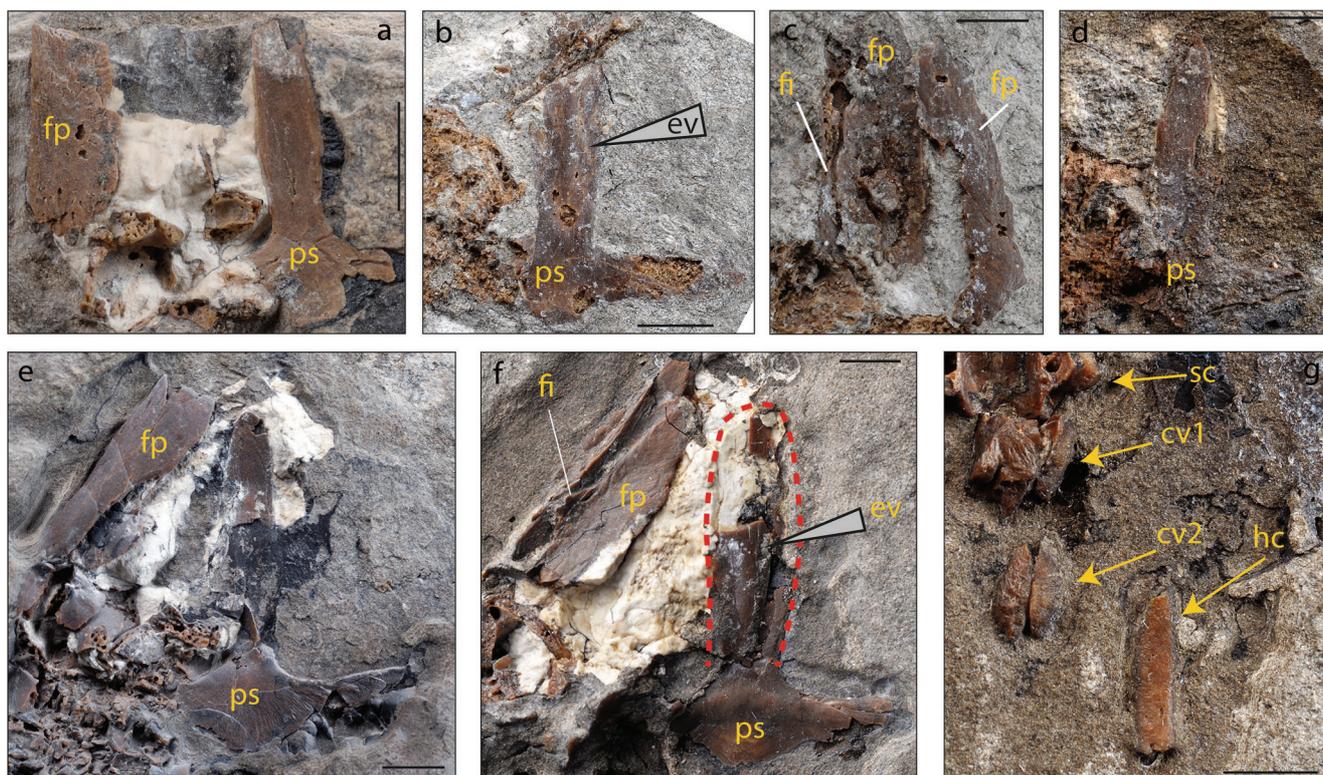
**Remarks on adult individuals:** This frog skeleton can be attributed to the genus *Latonia* based on the following characters: (1) overall large size; (2) asymmetric position of the caput of the humerus; (3) less pronounced dorsal tubercle of the ilium, well-developed pars ascendens and reduced pars descendens; and (4) presence of the posteriorly expanding interiliac groove on the medial surface of the acetabular portion (Roček 1994). Further identification is impossible, due to the lack of the skull bone, important for species identification.

Order Crocodylia Gmelin, 1789

Clade Eusuchia Huxley, 1875

Superfamily Alligatoidea Gray, 1844





**Fig. 8** Zoomed in views of tadpoles of *Latonia* sp. from the Gračanica (Bugojno palaeolake) outlined by black frames in the Fig. 7. **a** MJSN GRC-106, **b** MJSN GRC-105.2 (counterpart), **c** MJSN GRC-105.1 (part), **d** MJSN GRC-100.2 (counterpart), **e** MJSN GRC-102.2

(counterpart), **f** and **g** MJSN GRC-115. *cv1*, first caudal vertebra; *cv2*, 2nd caudal vertebra; *ev* eminentia ventralis; *fp* frontoparietal; *fi* frontoparietal incassation; *hc* hypochochorda; *ps* parasphenoid; *sc* sacral vertebra. The scale bars equal to 2.5 mm

Alligatoroidea indet. [?*Diplocynodon*]  
(Figures 9 and 10)

**Material:** One incomplete specimen: GRC-121.

**Description:** The studied specimen represents a disarticulated partial skeleton of an individual, coming from the lower coaly part of the Gračanica section (Bugojno palaeolake) (unit 1). The fossil bones were found on the surface and its certain stratigraphic position cannot be determined. The fossil bones are embedded in the coaly-clay and lie over the thin layers of the limestone, which are frequently appearing in the coaly package of the section.

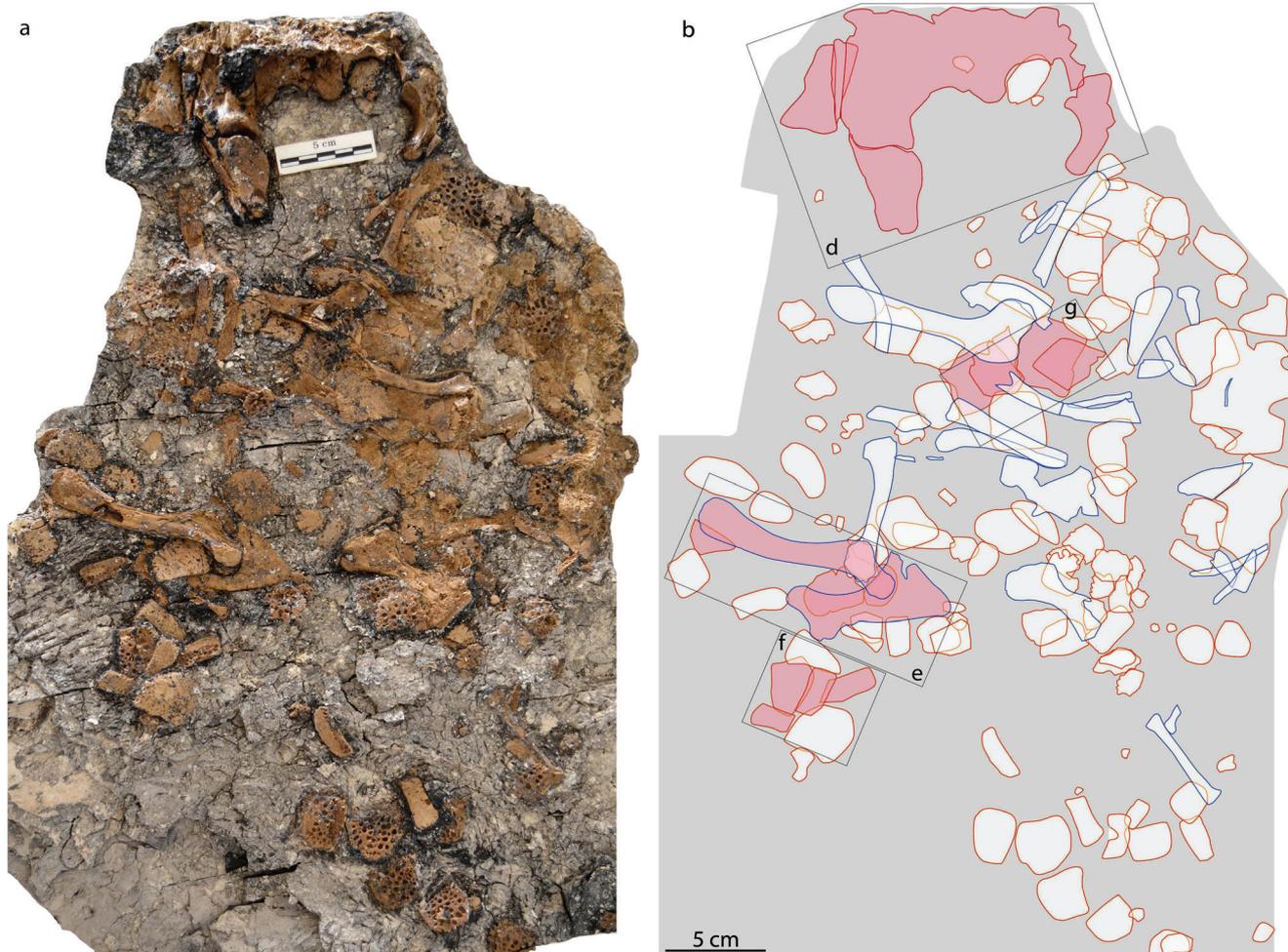
The specimen includes the posterior portion of the skull, some elements of the forelimb and pectoral girdle, damaged vertebrae and osteoderms (Figs. 9 and 10). The surangular, angular, posterior preserved portion of the skull table and osteoderms show an ornamentation typical for crocodiles, which consists of a network of well-pronounced and deep pits (Fig. 10). The angular reaches nearly the posterior end of the articular. The most posterior portion of the surangular is broken off. Due to the presence of the broad dorsal articulation surface of the angular, a surangular-angular contact along their entire posterior portions can be suggested (Fig. 10a). On the quadrate, the foramen aerum is located rather far from the medial margin of the bone. The same foramen of the articular is located on the

posterior rim of the glenoid fossa (Fig. 10a). The only preserved tooth is linguolabially compressed and shows a crown-root construction. Both its anterior and posterior margins possess sharp cutting edges (Fig. 10f). Distally, the scapula shows a narrow deltoid crest (Fig. 10c).

**Remarks:** Due to the fragmentary preservation of the specimen, its taxonomic identification is rather difficult. The location of the foramina aera in the quadrate and articular suggests its affiliation to Alligatoroidea (Brochu Brochu 1999; Díaz Aráez et al. 2017). Bipartite ventral osteoderms are present in several crocodyliforms, including *Diplocynodon* (Brochu et al. 2012). Since this genus is well known from numerous middle Miocene localities of Europe (e.g. Martin and Gross 2011), probable assignment of Gračanica (Bugojno palaeolake) crocodile remains to this genus can be suggested. This will be tested on further available material from this locality.

### Palaeobiogeographic, environmental and taphonomic considerations

The fossil fauna of ectothermic vertebrates of Gračanica, Bugojno palaeolake contains five taxa. Four of them are as follows: (1) small-sized killifishes Cyprinodontiformes indet.;



**Fig. 9** Alligatoroid crocodile from Gračanica (Bugojno palaeolake). **a** General overview of the specimen MJSN GRC-121 and **b** its drawing, with indications of the further (separately) figured elements (outline filled

in pink) **d**–Fig. 10a and b, **e**–Fig. 10c, **f**–Fig. 10d, **g**–Fig. 10e. The red outlined elements correspond to the skull, blue ones to axial and appendicular skeleton, orange ones to osteoderms

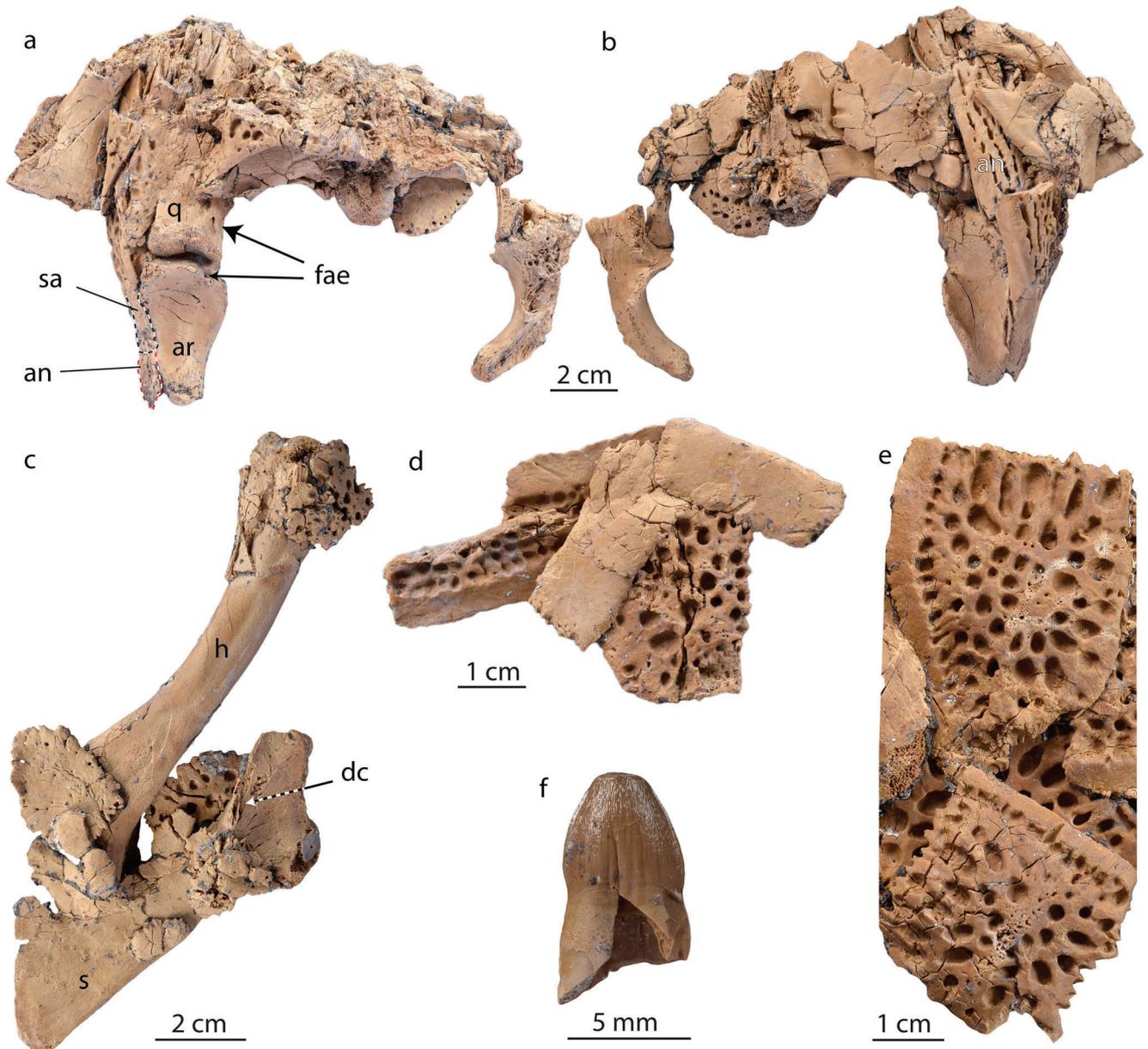
(2) medium-sized barb *Barbini* indet. (aff. *Barbus*); (3) crocodile newts *Chelotriton* sp. of different sizes; and (4) tadpoles of various sizes and a large-sized adult of *Latonia* sp., are found from the unit 2. The fifth taxon (5) an alligatoroid crocodile (? *Diplocynodon*) has been recovered from the unit 1.

All fossils from the unit 2 with certain stratigraphic position come from two intervals (24–26 m and 30.5–31.5 m) representing rather deep-water environment. The different degree of disarticulation of fish, salamander and frog skeletons suggests different degree of post-mortem decay of the animals. Fish remains are the most disarticulated, whereas in *Chelotriton* sp. and *Latonia* sp. (tadpoles and adult), the bones of the skeleton are intact or only slightly decomposed. These observations suggest a relatively short phase of decay of the animal bodies and their (probably quick) sedimentation in the deeper parts of the lake. Weak decomposition of skeletons could be also caused by the low oxygen content of the water in the deeper parts of the lake. The lamination in the fossiliferous layers of the marl (Mandic et al. in prep., this issue) and higher level of

the biogenic magnetite in these layers (Chang et al. 2014) suggest low oxygen content during its deposition.

*Barbini* indet. (aff. *Barbus*) from Gračanica, Bugojno palaeolake, is an interesting find of the group. This shows that during the Miocene, Europe has been populated by unique barbin forms, present on the continent before the arrival of the recent groups.

*Chelotriton* sp., as mentioned earlier (Böhme 2008), should be considered as a basket taxon, to which all fossil salamander forms, which show characteristic dermal ossification on skull bone and vertebrae, have been referred. The genus *Chelotriton* has a long fossil record in Europe, the oldest ones are known from the middle Eocene localities Geiseltal by *Chelotriton weigelti* (Herre Herre 1935) and Messel by *Chelotriton robustus* (Westphal 1980), both from Germany. During the Oligocene and Miocene, *Chelotriton* is common in Central and Western Europe and has been referred to the species *Chelotriton paradoxus* (e.g. Böhme and Ilg 2003; Roček and Wuttke 2010; Schoch et al. 2015). So far, the genus was



**Fig. 10** Skull of MJSN GRC-121 in **a** dorsal and **b** ventral views. **c** Scapula, humerus and some osteoderms. **d**, **e** Different morphotypes of the osteoderms. The dotted line on **a** outlines the posterior tip of the

surangular. **f** Tooth. *an* angular; *ar* articular; *fae* foramina aera; *dc* deltoic crest; *q* quadrate; *h* humerus; *s* scapula; *sa* surangular

unknown from the Dinarides area as well as the entire Balkan Peninsula. Thus, *Chelotriton* sp. from Gračanica (Bugojno palaeolake) represents its first occurrence in the Dinarides area and Balkan Peninsula. Interestingly, the Bosnian *Chelotriton*, compared with other fossil forms of the genus, has the largest body size (the snout-vent length of 16 cm). All salamander fossils in this sample represent either medium-sized or large (in total 29 specimens) animals. Surprisingly, no juvenile forms have been found. Also, whether the adults were aquatic, terrestrial or amphibious cannot be stated with confidence. Taking into consideration the presence of the ossified carpal and metatarsal elements in adults, their rather terrestrial or amphibious

lifestyle, as in recent genera *Tylostotriton* and *Echinotriton*, can be assumed.

The genus *Latonia* has been already reported from the Miocene deposits of the area (Đurić and Radosavljević 2014; Đurić 2017). This frog is well known in the European Neogene fossil record. The tadpole remains from the locality, referred to *Latonia*, represent not only the first record of *Latonia* tadpoles, but also of discoglossid and of discoglossoid frogs. Finds of tadpoles of different sizes and an adult in the sediments of the Gračanica (Bugojno) palaeolake suggest that *Latonia* was represented here by an autochthonous population. In addition to this, considering the large sizes of tadpoles, it can be assumed that the larval development of the frog was confined to the open

lake with well-oxygenized and rich in detritus nearshore shallow environment, where the life of large-sized tadpoles could be possible.

Fossil crocodiles (*Crocodylus* sp.) have been already reported from the Miocene locality Banja Luka (names also Banjaluka) in northern Bosnia and Herzegovina (Malez and Slišković 1976). Due to the lack of figures or description of this finding, it cannot be compared with the Gračanica (Bugojno palaeolake) material and its taxonomic identification cannot be verified. The crocodylian record from the neighbouring area of Serbia has been summarised in Jovanović et al. (2002), where *Crocodylia* indet. has been mentioned from three early Miocene localities (Shaft Dubrava - Aleksinac, Village Kraljevo, Jankova Klisura) and two middle Miocene localities (Popovac and Village Žitni potok). The middle Miocene locality Popovac, slightly younger (14.61–14.16 Ma, Sant et al. 2017) than Gračanica, provided three further crocodile taxa *Crocodylus moraviensis*, *Alligatorinae* indet. and *Tomistoma eggenburgensis* (Jovanović et al. 2002). However, these fossil species have never been revised considering the recent knowledge of the European fossil record of crocodiles. The revision of the Austrian Miocene crocodiles (Martin and Gross 2011) has referred them to the genus *Diplocynodon*, which was the most widely distributed crocodile in Europe during the Miocene. Probably, the Gračanica (Bugojno palaeolake) crocodile could belong to this genus as well.

The assemblage of ectothermic vertebrate of the Gračanica locality, Bugojno palaeolake, is represented by five taxa of fishes, amphibians and reptile, which include the following: (1) the first fossil tadpoles of the genus *Latonia*, as well as of discoglossid family and of discoglossoid frogs, and (2) the largest ever known crocodile newt *Chelotriton*, which in the same time is the first occurrence of the genus in the area and Balkan Peninsula. The ectothermic vertebrate assemblage is represented by taxa widely known in the middle Miocene of Europe. The study of further available material and excavation of more fossils will provide the full picture of the fauna of ectothermic vertebrates and will allow their better systematic assignment at the specific level.

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## Compliance with ethical standards

**Conflict of interest** The author declares that he has no conflict of interest.

## References

- Arratia, G. (2000). New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the ‘pholidophoriforms’. *Paläontologische Zeitschrift*, 74, 113–143. <https://doi.org/10.1007/BF02987957>.
- Bănărescu, P. M. (1999). *The freshwater fishes of Europe*. AULA-Verlag, Wiebelsheim.
- Bănărescu, P. M., Herzig-Straschil, B. (1995). A revision of the species of the Cyprinion macrostomus-group (Pisces: Cyprinidae). *Annalen des Naturhistorisches Museum Wien B*, 97, 411–420.
- Berg, L. S. (1940). Classification of fishes, both recent and fossil. *Proceedings of the Institute of Zoology*, 5, 85–517.
- Biton, R., Boistel, R., Rabinovich, R., Gafny, S., Brumfeld, V., & Bailon, S. (2016). Osteological observations on the Alytid Anura *Latonia nigriventer* with comments on functional morphology, biogeography, and evolutionary history. *Journal of Morphology*, 277, 1131–1145. <https://doi.org/10.1002/jmor.20562>.
- Bleeker, P. (1859). Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensis, Tasmanicisque. *Neerlandense*, 6, 1–276.
- Böhme, M. (2002). Freshwater fishes from the Pannonian of the Vienna Basin with special reference to the locality Sandberg near Götzendorf, Lower Austria. *Courier Forschungsinstitut Senckenberg*, 237, 151–173.
- Böhme, M. (2008). Ectothermic vertebrates (Teleostei, Allocaudata, Urodela, Anura, Testudines, Choristodera, Crocodylia, Squamata) from the Upper Oligocene of Oberleichtersbach (Northern Bavaria, Germany). *Courier Forschungsinstitut Senckenberg*, 260, 161–183.
- Böhme, M., & Ilg, A. (2003). fosFARbase. Available at [www.wahre-staerke.com](http://www.wahre-staerke.com). Accessed 1 December 2015.
- Böhme, M., & Vasilyan, D. (2014). Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). In M. Böhme, M. Gross, J. Prieto (Eds.) *The Sarmatian vertebrate locality Gratkorn, Styrian Basin. Palaeobiodiversity and Palaeoenvironments*, 94(1), 21–40.
- Brochu, C. A. (1999). Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Journal of Vertebrate Paleontology*, 19, 9–100. <https://doi.org/10.1080/02724634.1999.10011201>.
- Brochu, C. A., Parris, D. C., Grandstaff, B. S., Denton, R. K., & Gallagher, W. B. (2012). A new species of *Borealosuchus* (Crocodyliformes, Eusuchia) from the Late Cretaceous–early Paleogene of New Jersey. *Journal of Vertebrate Paleontology*, 32, 105–116. <https://doi.org/10.1080/02724634.2012.633585>.

- Chang, L., Roberts, A. P., Winklhofer, M., Heslop, D., Dekkers, M. J., Krijgsman, W., Fitz Gerald, J. D., & Smith, P. (2014). Magnetic detection and characterization of biogenic magnetic minerals: a comparison of ferromagnetic resonance and first-order reversal curve diagrams. *Journal of Geophysical Research: Solid Earth*, 119, 6136–6158. <https://doi.org/10.1002/2014JB011213>.
- Cope, E. D. (1887). Zittel's manual of palaeontology. *American Naturalist*, 21, 427–448.
- Díaz Aráez, J. L., Delfino, M., Luján, A. H., Fortuny, J., Bernardini, F., & Alba, D. M. (2017). New remains of *Diplocynodon* (Crocodylia: Diplocynodontidae) from the Early Miocene of the Iberian Peninsula. *Comptes Rendus Palevol*, 16, 12–26. <https://doi.org/10.1016/j.crpv.2015.11.003>.
- Đurić, D. (2017). The Early Miocene herpetofauna (Amphibia and Squamata) from Sibnica, Serbia. In Z. Marcović, & M. Miličević (Eds.), *Life on the shore geological and paleontological research in the Neogene of Sibnica and vicinity (Levač basin, Central Serbia)* (pp. 57–61). Belgrad: DMD.
- Đurić, D., & Radosavljević, D. (2014). Fossil herpetofauna studies in Serbia and its significance. In Z. Stevanović, & V. Cvetković, V. (Eds.) XVI Serbian Geological Congress: Proceedings. Sprint, Belgrad, pp 176–178.
- Fischer, G. (1813). Zoognosia. *Tabulis Synopticis Illustrata*, in Usum Prælectionum Academicæ Imperialis Medico-Chirurgicæ Mosquensis Edita, 3rd edn., vol 1. Typis Nicolai Sergeidis Vsevolozsky, Moscow.
- Fitzinger, L. (1843). *Systema Reptilium*. Fasciculus Primus. Braumüller et Seidel, Wien.
- Gaudant, J. (1989). Nouvelles observations Sur l'ichthyofaune miocène de Steinheim am Albuch (Wurtemberg, Allemagne). In *Stuttgarter Beiträge Naturkunde Serie B*, 151, 1–33.
- Gmelin, J. F. (1789). *Regnum animal. Caroli a Linne Systema Naturae per regna tri naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Beer, Leipzig.
- Goldfuss, G. A. (1820). *Handbuch der Zoologie*, Bd. 2. J. L. Schrag, Nürnberg.
- Gray, J. E. (1844). *Catalogue of tortoises, crocodilians, and amphibaenians in the collection of the British Museum*. British Museum. London: Natural History.
- Herre, W. (1935). Die Schwanzlurche der mitteleocänen (oberlutetischen) Braunkohle des Geiseltales und die Phylogenie der Urodelen unter Einschluß der fossilen Formen. *Zoologica - Original-Abhandlungen aus dem Gesamtgebiete der Zoologie*, 87, 1–85.
- Huxley, T. H. (1875). On *Stagonolepis robertsoni*, and on the evolution of the Crocodylia. *Quaternary Journal of Geological Society*, 31, 423–438.
- Ivanov, M. (2008). Early Miocene amphibians (Caudata, Salientia) from the Mokrá-Western Quarry (Czech Republic) with comments on the evolution of Early Miocene amphibian assemblages in Central Europe. *Geobios*, 41, 465–492.
- Jovanović, M., Đurić, D., & Marković, Z. (2002). Tertiary reptiles of the central part of the Balkan peninsula. *Biota*, 3, 67–75.
- Kottelat, M., & Freyhof, J. (2007). *Handbook of European freshwater fishes*, Bd. 13. Berlin: Publications Kottelat.
- Linnaeus, C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, Editio decima, reformata. Stockholm, L. Salvii.
- Malez, M., & Slišković, T. (1976). Statost nekih naslaga ugljena u tercijaru Bosne i Hercegovine na osnovi nalaza vertebrata. *Geoloski Glasnik Sarajevo*, 21, 39–56.
- Mandic, O., Pavelić, D., Kovačić, M., Sant, K., Andrić, N., & Hrvaatović, H. (Eds.). (2016a). *Field Trip Guidebook- lake - basin - evolution*. Zagreb: Croatian Geological Society.
- Mandic, O., Göhlich, U. B., Krijgsman, W., de Leeuw, A., & Hrvaatović, H. (2016b). Lake Bugojno - three lacustrine cycles. In O. Mandic, D. Pavelić, M. Kovačić, K. Sant, N. Andrić, & H. Hrvaatović (Eds.), *Field trip guidebook- lake - basin - evolution* (pp. 64–68). Zagreb: Croatian Geological Society.
- Martin, J. E., & Gross, M. (2011). Taxonomic clarification of *Diplocynodon* Pomel, 1847 (Crocodylia) from the Miocene of Styria, Austria. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 261, 177–193.
- Meyer, H. von (1843). Mittheilung an Professor Bronn gerichtet. *Neues Jahrbuch für Geologie und Paläontologie, Geognasie, Geologie und Petrefactenkunde*, 579–590.
- Obrhelová, N. (1967). Cyrinoidei (Pisces) aus dem hangenden des miozänen Braunkohlenflötzes Nordböhmens. *Palaeontographica A*, 126, 141–179.
- Obrhelová, N. (1971). Vergleichende Osteologie der Gattung *Leuciscus* (Pisces) aus tertiären Schichten der nördlichen und westlichen ČSSR. *Paläontologische Abhandlungen (A)*, 4, 550–660.
- Obrhelová, N. (1990). Fische des Nordböhmisches Braunkohlenbeckens. *Acta musei nationalis Pragae*, 46(1–2), 1–35.
- Pomel A (1853). Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire. J. B. Baillières, Paris.
- Pügener, L.-A., & Maglia, A. M. (1997). Osteology and skeletal development of *Discoglossus sardus* (Anura: Discoglossidae). *Journal of Morphology*, 233, 267–286.
- Rafinesque, C. S. (1815). *Analyse de Nature, ou Tableau de l'Universe et des Corps Organisés*. Jean Barravecchia, Palermo.
- Reichenbacher, B., & Kowalke, T. (2009). Neogene and present-day zoogeography of killifishes (*Aphanius* and *Aphanolebias*) in the Mediterranean and Paratethys areas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 281, 43–56. <https://doi.org/10.1016/j.palaeo.2009.07.008>.
- Reichenbacher, B., & Weidmann, M. (1992). Fisch-Otolithen aus der oligo-/miozänen Molasse der West-Schweiz und der Haute-Savoie (Frankreich). *Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)*, 184, 1–83.
- Roček, Z. (1981). Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Universitatis Carolinae - Biologica*, 1980, 1–164.
- Roček, Z. (1994). Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonina* V. Meyer, 1843. *Geobios*, 27, 717–751.
- Roček, Z. (2003). Larval development in Oligocene palaeobatrachid frogs. *Acta Palaeontologica Polonica*, 48, 595–607.
- Roček, Z., & Wuttke, M. (2010). Amphibia of Enspel (Late Oligocene, Germany). *Palaeobiodiversity and Palaeoenvironments*, 90, 321–340. <https://doi.org/10.1007/s12549-010-0042-0>.
- Ročková, H., & Roček, Z. (2005). Development of the pelvis and posterior part of the vertebral column in the Anura. *Journal of Anatomy*, 206, 17–35. <https://doi.org/10.1111/j.0021-8782.2005.00366.x>.
- Sant, K., Mandić, O., Rundić, L., Kuiper, K. F., & Krijgsman, W. (2017). Age and evolution of the Serbian Lake System: integrated results from Middle Miocene Lake Popovac. *Newsletters on Stratigraphy*, 51, 117–143. <https://doi.org/10.1127/nos/2016/0360>.
- Sar, F. N., van der Glabbeek, R., van Wessels, W., Marković, Z., & Bruijn, H., de (2017). Insectivores and marsupials from the upper Oligocene of Banovići (Bosnia and Herzegovina). *Journal of Vertebrate Paleontology*, 37, e1368529. <https://doi.org/10.1080/02724634.2017.1368529>.
- Schoch, R. R., Poschmann, M., & Kupfer, A. (2015). The salamandrid *Chelotriton paradoxus* from Enspel and Randeck Maars (Oligocene–Miocene, Germany). *Palaeobiodiversity and Palaeoenvironments*, 95, 77–86. <https://doi.org/10.1007/s12549-014-0182-8>.
- Scopoli, G. A. (1777). Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, characteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Apud Wolfgangum Gerle, Prague.

- Špinar, Z. V., & Roček, Z. (1984). The discovery of the impression of the ventral side of *Eopelobates anthracinus* Parker, 1929 holotype. *Amphibia-Reptilia*, 5, 87–95.
- Vasileiadou, K., Böhme, M., Neubauer, T. A., Georgalis, G. L., Syrides, G. E., Papadopoulou, L., & Zouros, N. (2017). Early Miocene gastropod and ectothermic vertebrate remains from the Lesvos Petrified Forest (Greece). *Paläontologische Zeitschrift*, 91, 541–564. <https://doi.org/10.1007/s12542-017-0352-x>.
- Vasilyan, D. (2018). Eocene Western European endemic genus *Thaumastosaurus*: new insights into the question “Are the Ranidae known prior to the Oligocene?”. *PeerJ*, 6, e5511. <https://doi.org/10.7717/peerj.5511>.
- Westphal, F. (1980). *Chelotriton robustus* n. sp., ein Salamandride aus dem Eozän der Grube Messei bei Darmstadt. *Senckenbergiana lethaea*, 60, 475–487.
- Yang, L., Sado, T., Vincent Hirt, M., Pasco-Viel, E., Arunachalam, M., Li, J., Wang, X., Freyhof, J., Saitoh, K., Simons, A. M., Miya, M., He, S., & Mayden, R. L. (2015). Phylogeny and polyploidy: resolving the classification of cyprinine fishes (Teleostei: Cypriniformes). *Molecular Phylogenetics and Evolution*, 85, 97–116. <https://doi.org/10.1016/j.ympev.2015.01.014>.