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The type material of *Parahynobius betfianus*

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Abstract. *Parahynobius betfianus* Venczel, 1999 is the only hynobiid salamander known up to present from the Quaternary of Central and Western Europe. The type and referred material is briefly redescribed and reevaluated taken into consideration the new results in the molecular phylogeny of Hynobiidae. The lack of premaxillary fontanelle, due to extensive ossification of the alary process of premaxilla, may represent a synapomorphy shared with *Salamandrella* and *Hynobius*. Beside *Parahynobius*, the bicapitate transverse processes in the trunk vertebrae are also present in *Hynobius leechi*, *Onychodactylus* and *Salamandrella keyserlingii* and this condition may be considered as an intracolumnar variation. However, the presence of osseous knobs on the distal part of the transverse processes in *Parahynobius* are never present in *Salamandrella* and *Hynobius*. The fossil record of hynobiids from the Carpathian region and the palaeoenvironmental conditions from the type locality are also discussed.

Keywords. Central Europe, Extinction, Hynobiidae, Morphology, Quaternary.

Introduction

The Hynobiidae are a small group of primitive salamanders consisting of about 69 extant species assigned to nine genera (AmphibiaWeb 2018) with a mostly Asiatic distribution and in the northeastern part of European Russia (Zhang et al. 2006, Frost 2016).

The hynobiids have been regarded by many authors as the most primitive living tetrapods in retaining a suit of ancestral features: external fertilization, presence of a lacrimal bone in the skull and a separate angular in the mandible, a large number of microchromosomes (Estes 1981), and the spinal nerves, excepting the atlas, exit intervertebrally (Edwards 1976). They are grouped with the Cryptobranchidae in the suborder Cryptobranchoidea, from which differ in having a more complete metamorphosis (Estes 1981). The monophyly of Hynobiidae is supported by molecular data (Zhang et al. 2006, Pyron & Wiens 2011, Weisrock et al. 2013), or by combined molecular and morphological data (Larson & Dimmich 1993, Wiens et al. 2005). The earliest fossils related to Cryptobranchoidea are known from the Middle Jurassic - Lower Cretaceous of China consisting of well-preserved skeletons, like that of *Chunerpeton tianyiensis* from the Middle Jurassic Jiulongshan Formation (about 161 Ma) of Inner Mongolia (Gao & Shubin 2003), *Liaoxitriton zhongjiani* from the Lower Cretaceous Yixian Formation of western Liaoning (Dong & Wang 1998) and *Nuominerpeton aquilonaris* from the Lower Cretaceous Guanghua Formation of Inner Mongolia (Jia & Gao 2016). The hypothetical place of origin of this group, as indicated by the above fossils, may be in the present-day northern China (Zhang et al. 2006). In contrast to the extant fully aquatic Cryptobranchidae (giant salamanders), *Aviturus exsecratus*, known from the late Paleocene of Mongolia (Gubin 1991), exhibits adaptation to a terrestrial life-style (Vasilyan & Böhme 2012).

Contrary to giant salamanders, the fossil remains of Hynobiidae are extremely rare being unknown from the Palaeogene. The geologically oldest fossil record from Asia is an isolated vertebra, identified as *Salamandrella* sp., recorded from the early Miocene Khalagay Formation (Syromyatnikova 2014); *Salamandrella* sp. has been also reported from Malyi Kalkaman 1 (middle Miocene, western Siberia, Russia) by Vasilyan et al. (2017); *Salamandrella* sp. was reported also from the Upper Miocene of China (Vasilyan et al. 2012) and from several localities of Middle Pleistocene of European Russia (Ratnikov 2002). *Ranodon* cf. *sibiricus* (eight incomplete vertebrae, two partial humeri and a femur), is known from the late Pliocene (MN16) of Kiikbai, southern Kazakhstan (Averianov & Tjutkova 1995).

The first occurrence date (FOD) of hynobiid salamanders from the European continent may be considered the record from the latest Sarmatian/ earliest Pannonian (MN 7/8 - MN 9) of Felsőtárkány 3/10, from northern Hungary (Venczel & Hír 2013; Hír et al. 2017), consisting of eight precaudal and two caudal vertebrae that have been assigned to *Parahynobius* sp. (Venczel & Hír 2013). The remaining fossil record is much younger, as follows: late Miocene (MN 12) of Tardosbánya, Hungary (six incomplete trunk vertebrae of cf. *Parahynobius* sp.); late Miocene

(MN 13) of Polgárdi 4 “Lower”, Hungary (four trunk vertebrae and one caudal vertebra of *Parahynobius kordosi* Venczel, 1999), early Pliocene (MN 14) of Osztramos 1C, Hungary (two trunk vertebrae and one sacral vertebra of cf. *Parahynobius* sp.) and early Pleistocene of Betfia 9/C, Romania, described as *Parahynobius betfianus* Venczel, 1999 (Venczel 1999, 2000a)(see below). The record from Betfia 9/C represents the only record of Hynobiidae from the Quaternary of Central Europe (from western Europe this group has never been recorded) and therefore the last occurrence date (LOD) from this area.

The purpose of the present paper to amend the descriptions of the type material of *Parahynobius betfianus* given by Venczel (1999, 2000a) and comment on the morphological variations observed in the vertebrae and appendicular skeletal parts.

The fossil locality and taphonomy

The Betfia fossil locality is situated about nine kilometres southwest to Oradea. The fossil site Betfia 9/C is situated approximately 20 m north to Betfia pothole, at 314 m altitude, presumably close or more probably parts of the classical locality Betfia 2 (Fig. 1). It consists of sediments of a partly eroded endokarst system, grooved in early Cretaceous limestone of Barremian-Aptian age.

The micromammals coming from this locality were first published by Terzea (1988). The brecciated sediments of type ‘terra rosa’ have yielded among others: *Talpa* cf. *fossilis*, *Crocidura kornfeldi*, *Sorex* gr. *minutus*, *Petenya hungarica*, *Beremendia fissidens*, *Cricetus cricetus*, *Mimomys pusillus*, *Mimomys tornensis*, *Pliomys episcopalis*, *Allophaiomys pliocaenicus*, *Lagurus praepannonicus*, *Hypolagus brachygnathus*, *Mustella praenivalis*, *M. palerminea*, *Canis lupus mosbachensis*. In 1994 Venczel re-excavated the locality and found a rich microvertebrate fauna (named as Betfia 9/B to differentiate from that excavated by E. Terzea and T. Jurcsák) with an abundant series of *Allophaiomys* molars. However, the list of micromammals from Betfia 9/B (Hír & Venczel 1997), with few exceptions, is closely like that of Terzea (1988). In 1995 M. Venczel has found a ‘terra rossa’ layer (named as Betfia 9/C) under the brecciform sediment of 9/B. This lower layer produced a special fauna dominated by *Apodemus*, *Pliomys* and *Muscardinus* indicating a forested palaeoenvironment.

Rzebik-Kowalska (2000a, 2000b) gave the following list of insectivores (based on the material coming from all these localities: Betfia 9 A+B+C): *Sorex* cf. *subaraneus*, *S. minutus*, *S. runtonensis*, *Sorex* (*D.*) *margaritodon*, *Asoriculus gibberodon*, *Petenya hungarica*, *Beremendia fissidens*, *Crocidura kornfeldi*,



Figure 1. Location of the type locality of Betfia 9/C (marked with arrow) near the Betfia cave, Bihor County, Romania.

Crocidura cf. *obtusa*, *Sorex* sp., *Erinaceus* sp. 2, *Talpa minor*, *T. fossilis*, *T. cf. episcopalis*, *T. cf. semsey* and *Desmana thermalis*.

Kessler (1975) listed the birds identified from this locality (noted as coming from “Betfia 3” and respectively from “breccia with microfauna”): *Anas clypeata*, *Falco subbuteo*, *Perdix perdix*, ?*Otis tarda*, ?*O. lambrechtii*, *Asio* cf. *otus*, *Corvus* cf. *monedula*, *Garrulus glandarius*, *Turdus merula*, *Anthus* aff. *trivialis*.

The fossil herpetofauna of this locality complex consisted of *Parahynobius betfianus*, *Triturus* cf. *cristatus*, *Lissotriton* cf. *vulgaris*, *Bombina* cf. *bombina*, *Palaeobatrachus* (= *Pliobatrachus*) *langhae*, *Pelobates fuscus*, *Bufo bufo*, *Bufotes viridis*, *Hyla* cf. *arborea*, *Rana* cf. *dalmatina*, *R. temporaria*, *Scolecophidia* indet., *Hierophis viridiflavus*, *Coronella austriaca*, *Zamenis paralongissimus*, *Elaphe quatuorlineata*, *Telescopus* cf. *fallax*, *Natrix natrix*, *N. tessellata*, *Vipera ammodytes* and *V. berus* (Venczel 2000b, 2000c). The fauna may be correlated with the *Miomys pusillus* - *M. savini* biozone with an approximate age of 1.5-1.2 Ma.

Material and Methods

The hynobiid specimens described here originate from about 500 kg of sediment collected between 2004–2008 from the locality Betfia 9/C. The samples were dried

and screen-washed using a sieve set with the mesh size ranging between 1.2–0.8 mm. The resulting isolated skeletal remains were sorted under a binocular microscope and identified by applying standard taxonomic criteria. The digital photographs were taken at the Țării Crișurilor Museum, Oradea, using a Canon EOS digital camera equipped with a 60-mm f/2.8 macro lens. The standard anatomical orientation system is used throughout this paper; osteological terms come from Estes (1981) and Venczel (1999).

Descriptions and comments

Premaxilla (holotype). The specimen MTC. No. 19913, represents a right premaxilla that may have belonged to an adult individual. The dorsal process (alary process) is moderately high, flattened and projecting faintly dorsolaterally; the base of the process is broadened and produced into a sinuous lateral crest connected to the pars dentalis. The labial surface is faintly ornamented by rarely distributed small pits. The dorsal process displays a constriction above the lateral crest owing to a lateral sinuosity and by an incompletely closed medial foramen; the lingual surface is thickened by a bony ridge extending dorsoventrally that might have been connected to a spur like process extending to the nasal, as observed in recent hynobiids (Venczel 1999: fig. 1b, c). The pars palatina is moderately wide with its posterior margin thickened; the lateral portion is damaged. The pars dentalis is well developed; medially the ventral part is damaged, whereas laterally the distal portion is missing; the remaining part preserves the basal parts of about nine pedicellate teeth; in the intact premaxilla the inferred number of teeth could have been about 13–15.

Comments. The holotype specimen shares with some hynobiids (*Hynobius*, *Pachyhynobius* and *Salamandrella*) a moderately high premaxillary dorsal process with ossification medially and therefore the premaxillary fontanelle is closed. The studies of Zhao & Hu (1983, 1984) have shown that the presence of a premaxillary fontanelle may represent a plesiomorphic feature, reason of which they placed the hynobiids into two 'natural groups': the *Hynobius*-group (*Hynobius*, *Pachyhynobius* and *Salamandrella*) lacking a premaxillary fontanelle and the *Ranodon*-group (*Batrachuperus*, *Liua*, *Onychodactylus* and *Ranodon*) possessing a fontanelle. However, the reconstruction of the ancestral states proposed by Zhang et al. (2006), based on molecular phylogeny and Bayesian inference, suggests that the ancestral state for hynobiids is the presence of a premaxillary fontanelle. This proposal is also reinforced by the fossil record of presumed early hynobiid-like

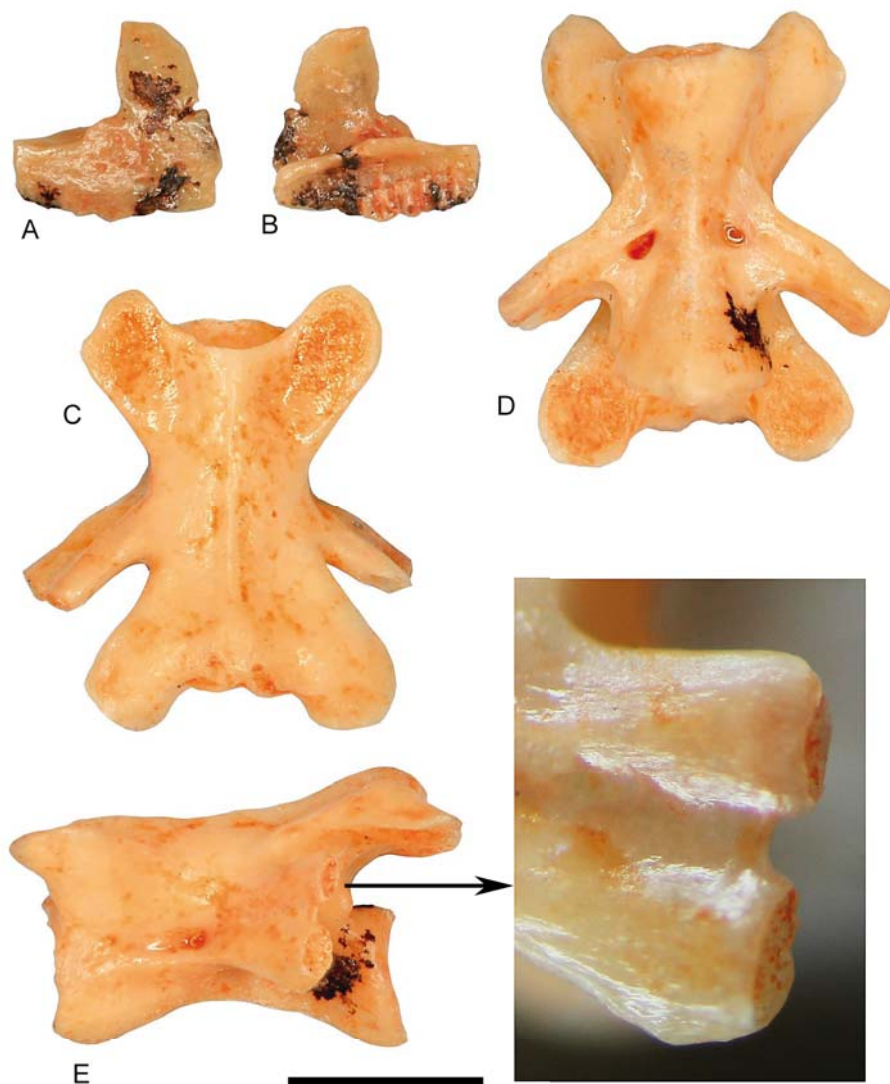


Figure 2. Type material of *Parahynobius betfianus* Venczel, 1999. A, B, holotype right premaxilla (MTC No. 19913) in anterior (A) and posteroventral (B) views. C–E, paratype middle trunk vertebra (MTC No. 19910) in ventral (C), dorsal (D) and left lateral (E) views; the arrow points to detail of the transverse process possessing a bicapitate condition. Scale = 2 mm.

fossils, like *Liaoxitriton* (Wang 2004) and *Jeholotriton* (Wang & Rose 2005), both possessing a premaxillary fontanelle.

Trunk vertebrae. The best-preserved specimen is a completely preserved middle trunk vertebra (except the distal part of the right prezygapophysis and of the right diapophysis that are missing) designated as the paratype (MTC No. 19910). The centrum is amphicoelous and moderately elongated; small and flattened anterior basapophyses are inserted near the ventrolateral side of the cotylar rim. The transverse processes, inserted near the midpoint of the centrum, are relatively long and distally widening with their distal margin distinctly bicapitate; a bony prominence is present on the dorsal margin of the diapophysis and on the ventral margin of the parapophysis near their distal end; the ventral prominence is distinctly larger. Posterior to the transverse processes there is no trace of a spinal nerve foramen. The neural arch is flattened, whereas the neural spine is reduced to a low neural ridge; the interzygapophyseal ridges are faintly developed. In dorsal view, the anterior border of the neural lamina is moderately wide and concave, whereas the prezygapophyses are oval in shape trending anterolaterally and slightly obliquely; the posterior border of the neural lamina bears the imprints of the paired hyperapophyses. In ventral view, the subcentral keel is reduced, whereas a pair of subcentral foramina are present near the base of the transverse processes. The postzygapophyses are ovaloid in shape, and their lateral sides are slightly bent ventrally and therefore the postzygapophyseal surface is concave. The centrum length of the paratype is 3.42 mm.

The remaining trunk vertebrae closely resemble the shape of the paratype specimen (Figs. 4-8). However, the sizes of most specimens are usually smaller depending on their individual age and a few damages are observed (e.g. in most specimens the transverse processes are broken off). In most specimens the insertion point of the transverse processes is near the mid-length of the centrum, but in some examples the insertion point is more posterior (Figs. 5G, H, K; 6A, C, H; 8H); the bicapitate condition of the distal part of the transverse processes is present in several better-preserved examples; in some vertebrae the transverse process is distinctly curved posteriorly (Figs. 4C, 5B, 6A, K, L). The neural ridge of few examples is nearly imperceptible (Figs. 4A, C; 5G, 6A), but in some others it is more prominent (Figs. 4E, H; 5I, J); the subcentral ridge is variably present, whereas the paired subcentral foramina of variable sizes are present in most specimens. The imprints of the hyperapophyses are well discernible, but sometimes seem confluent.

The morphology of the anterior trunk vertebrae may be differentiated from those of the middle trunk vertebrae in having a considerably shorter centrum, a relatively higher neural arch and a more prominent neural ridge (Fig. 3). In some examples the dorsal margin of the neural ridge widens posteriorly (Figs. 3C, E, K, O, P). The transverse processes are usually short, flattened anteroposteriorly

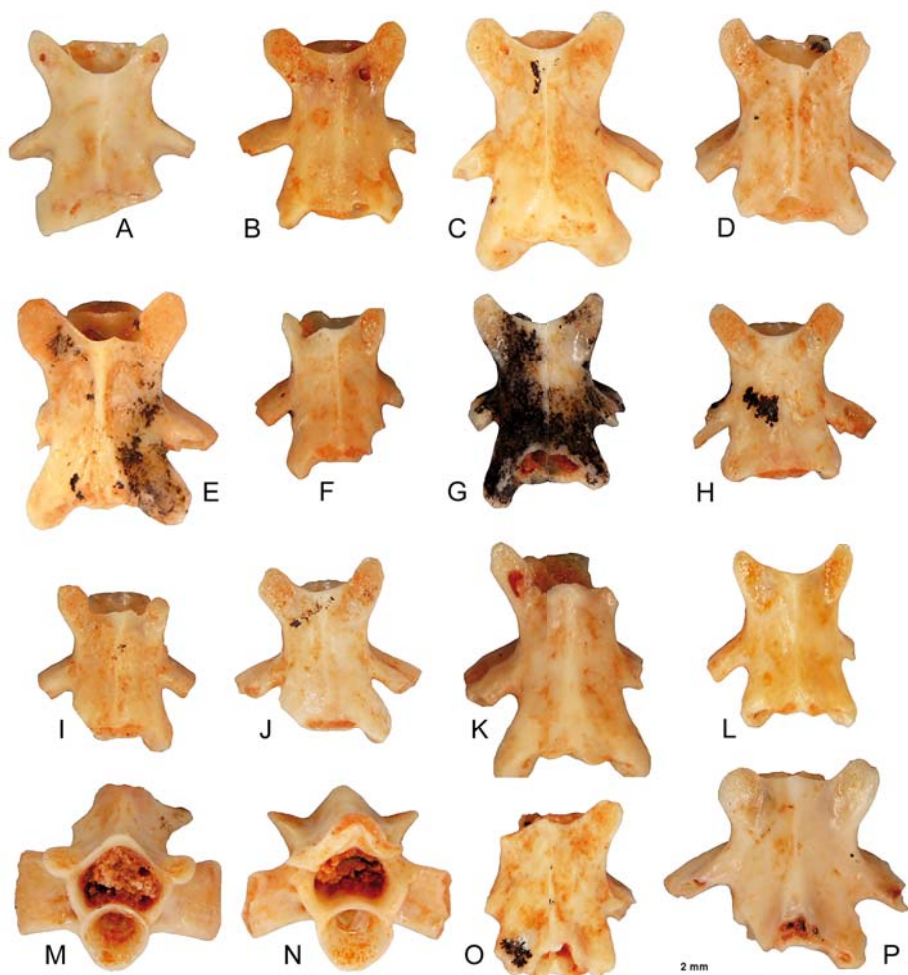


Figure 3. Anterior trunk vertebrae of *Parahynobius betfianus* (MTC No. 19911/1-15). A-L, O, P, anterior trunk vertebrae in dorsal views. M, anterior trunk vertebra in anterior view. N, anterior trunk vertebra in posterior view. Scale = 2 mm.

and high dorsoventrally and with unicapitate distal margins (in few specimens the transverse processes are distinctly bicapitate). The subcentral keel is usually reduced, whereas the subcentral foramina are extremely small or lacking. No spinal nerve foramina are observed.

Anterior caudal vertebrae. The neural arch of the anterior caudal vertebrae is flattened and provided with unicapitate transverse processes; the rib articulating sur-

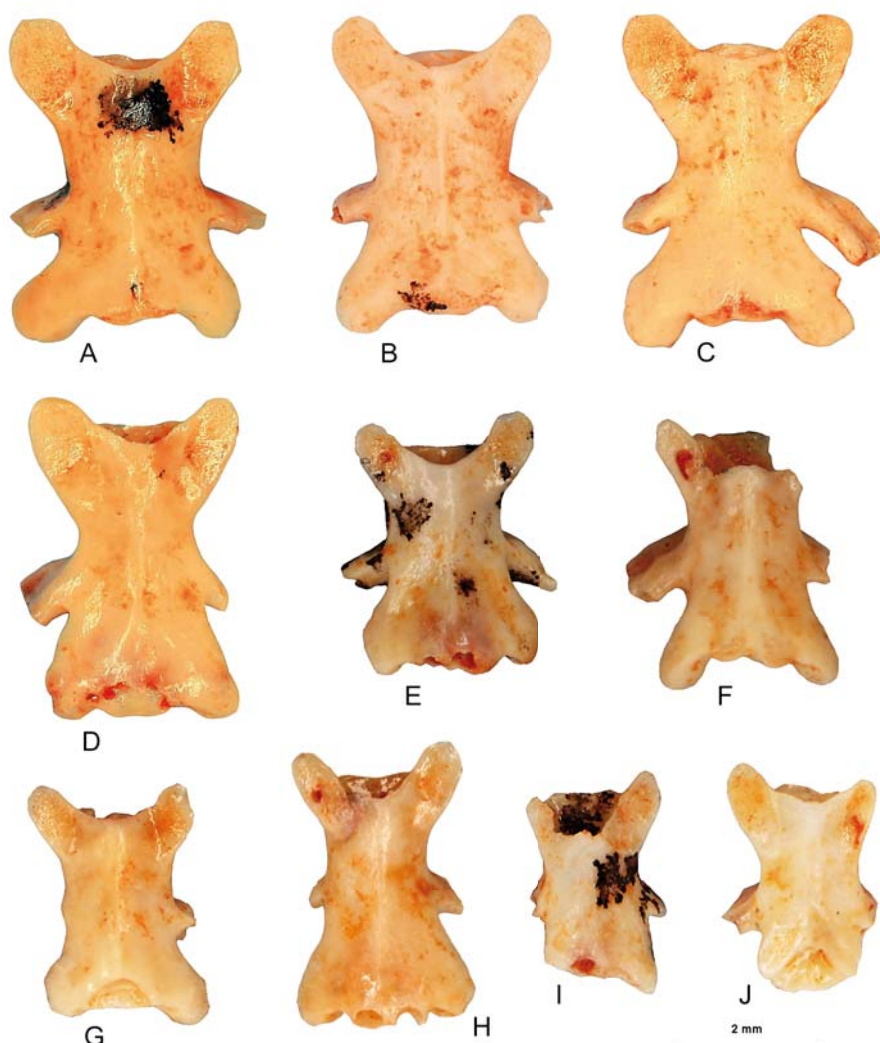


Figure 4. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19911/16-25). A-J, various sized specimens in dorsal views. Scale = 2 mm.

face is present and therefore the postsacral ribs were present (Figs 9, 10). The haemal arch is closed completely ventrally (Fig. 10D), and the haemal canal is oval in shape. The neural spine is reduced to a median neural ridge. In some specimens, the insertion surface of the hyperapophyses is prominent and distantly spaced from each other (Figs. 9A; 10I, G). There are no spinal nerve foramina present.

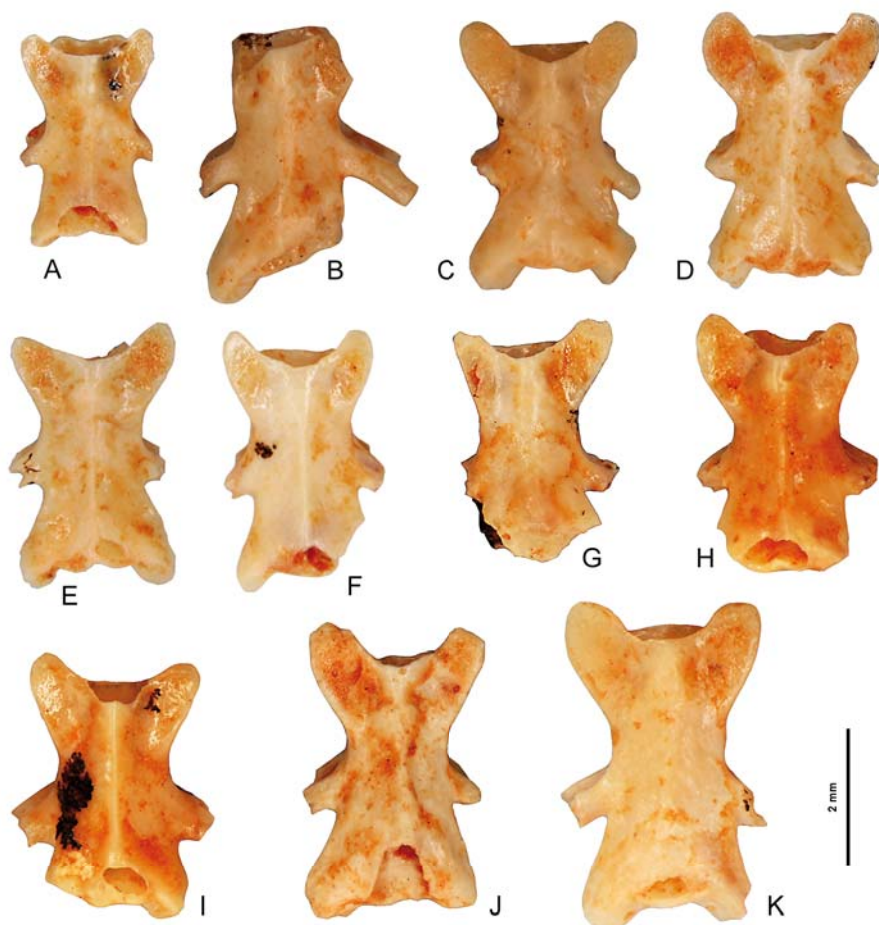


Figure 5. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19908/1-11). A-K, various sized specimens in dorsal views. Scale = 2 mm.

Posterior caudal vertebrae. The posterior caudal vertebrae are much smaller in size than the anterior caudal vertebrae and lack any transverse processes; the haemal arch is closed ventrally (Fig. 9I), and the spinal nerve foramen is lacking (Figs. 9H, I; 10K-M).

Comments. The centrum length of the trunk vertebrae is variable in length being shorter in the anterior ones (Duellman & Trueb 1986), however Jiang et al. (2018) reported that in *Batrachuperus londongensis* there is no significant change in length of the centrum along the trunk series. In most hynobiids the parapophyses

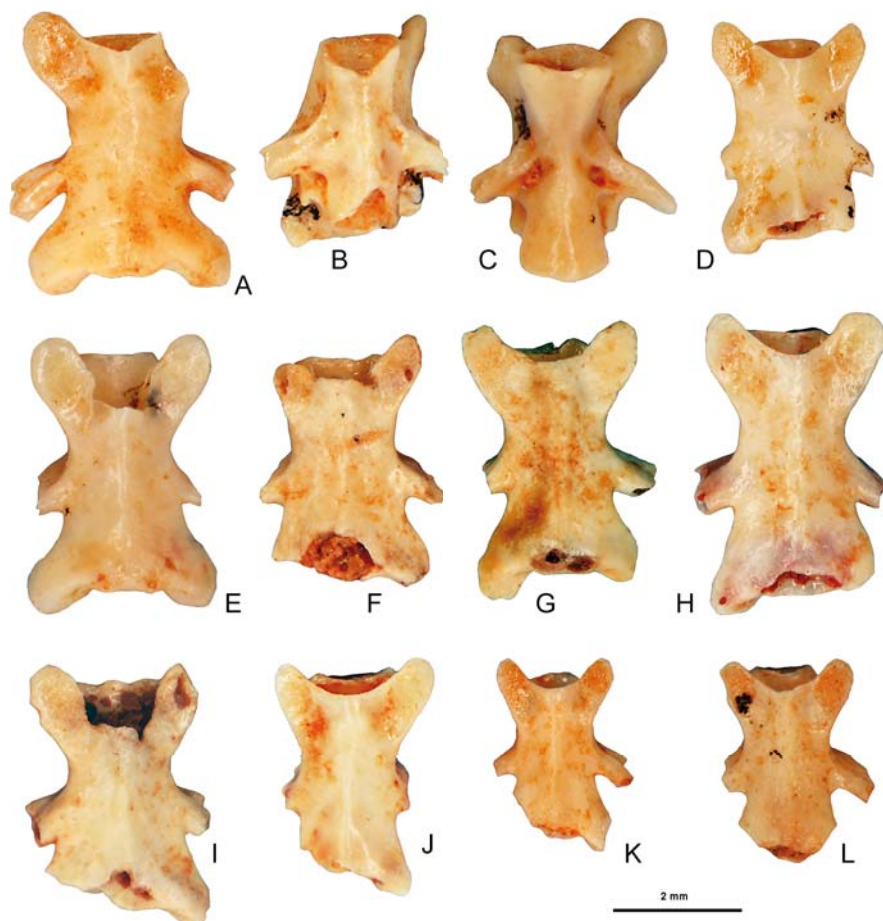


Figure 6. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19909/1-12). A, D-L, various sized specimens in dorsal views. B, C, specimens in ventral views. Scale = 2 mm.

(situated ventrally) and diapophyses (situated dorsally) in the trunk vertebrae are closely connected by a bony lamella to form unicapitate (= unicapital) transverse processes (Estes 1981). However, this condition was never explored in detail in most hynobiids (but see below). In the transverse processes of *Parahynobius betfianus* and *P. kordosi* the bicapitate condition is rather frequent (considering that in the most available specimens the transverse processes are strongly damaged) and both conditions occur at least in *P. betfianus* (Venczel 1999, 2000a). The unicapitate condition is present in *Onychodactylus*, *Ranodon* (pers. obs.) and *Batrachuperus londongensis* (Jia et Gao 2016, Jiang et al. 2018), whereas

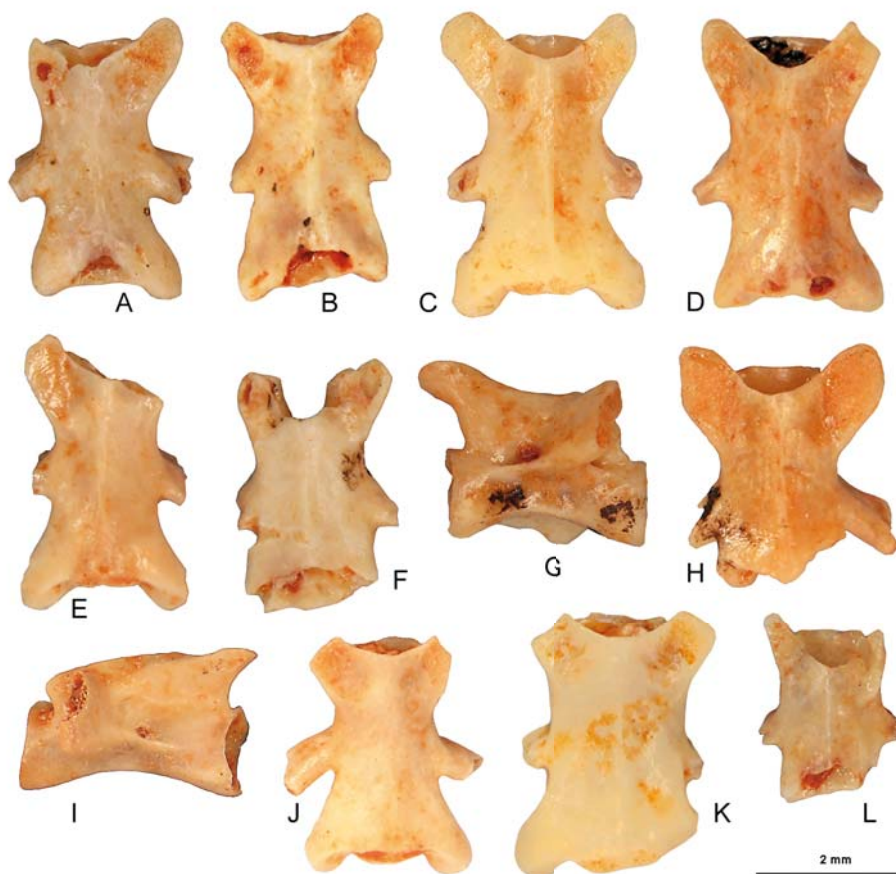


Figure 7. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19914/1-14). A-F, H, J-L various sized specimens in dorsal views. G, I, specimens in ventrolateral views. Scale = 2 mm.

in *Salamandrella keyserlingii* and some *Hynobius* (e.g. *H. leechi*) there are some trunk vertebrae with bicapitate transverse processes; the bicapitate condition is also present in *Onychodactylus* and *Ranodon* cf. *sibiricus* (Vasilyan et al. 2013 and references therein). Osseous prominences on the distal parts of transverse processes, reported in *P. betfianus*, are also present in *R. sibiricus*, but on the parapophyses only (pers. obs.), whereas these are lacking in *Onychodactylus*, *Salamandrella* (Ratnikov & Litvinchuk 2007) and *H. leechi* (pers. obs.).

Scapulocoracoid. Both specimens are fragmentary lacking most part of the scapular blade (Figs. 11A, B). The procoracoid foramen is present, whereas on the lat-

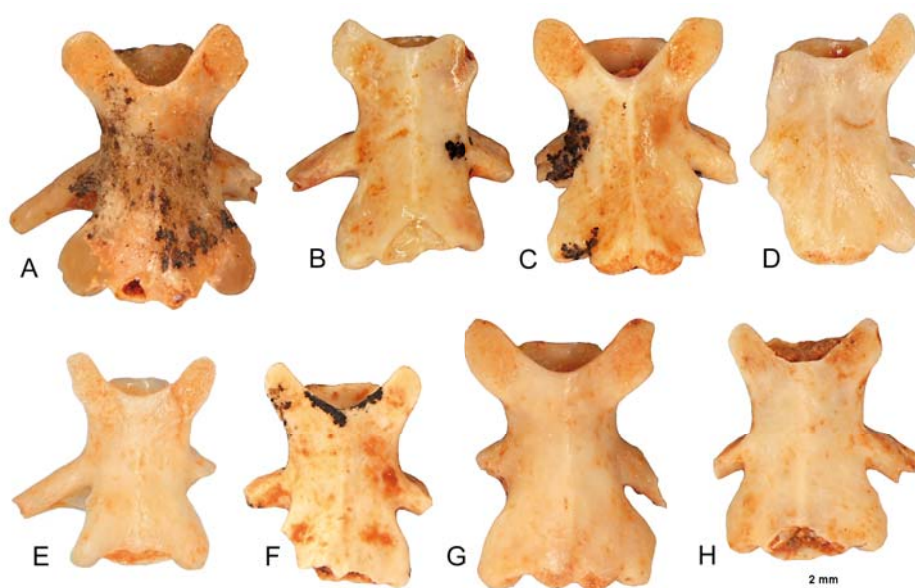


Figure 8. Trunk vertebrae of *Parahynobius betfianus* (MTC No. 19916/1-8). A-H, various sized specimens in dorsal views. Scale = 2 mm.

eral surface of the scapular blade, starting from the margin of the glenoid cavity, a prominent ridge is present.

Comments. In *Ranodon sibiricus* and *Onychodactylus japonicus* the scapular blade is without a sharp crest, whereas in *Salamandrella keyserlingii* there is a prominent ridge as it has been also reported in *Batrachuperus londongensis* (Jian et al. 2018).

Humerus. The bone is almost straight, when viewed laterally or medially. The humeral head is rounded and well ossified in the larger (i.e. older) specimens (Fig. 11 F-H), whereas it remains flat (i.e. unossified) in the smaller examples (Fig. 11D, E). The ventral crest is extremely prominent and short, connected to the humeral head. The dorsal crest is triangular and of low height in the smaller specimens (Fig. 11D, H), whereas it is more strongly developed in the largest specimen (Fig. 11F, G) with a more prominent proximal projection, continued with a sinuous distal part extending approximately one third of the humeral length. The distal end of the humerus is well ossified in one of the specimens (Fig. 11C), whereas it remains unossified in a smaller example (Fig. 11D, E) with discernible facets for the radial and ulnar condyles; the fossa cubitalis ventralis is well defined. In one of the speci-

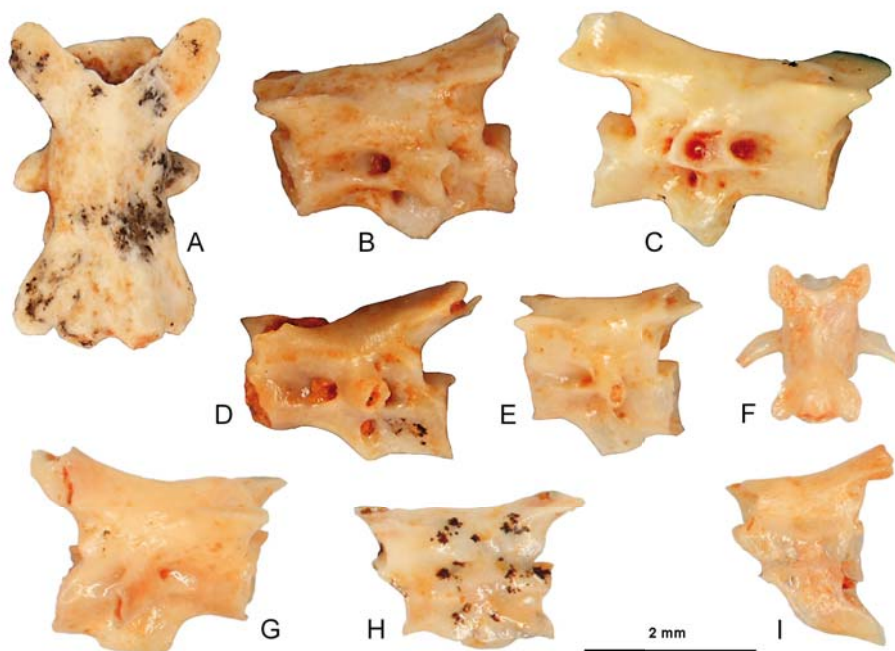


Figure 9. Caudal vertebrae of *Parahynobius betfianus* (MTC No. 19917/1-9). A, F, various sized anterior caudal vertebrae in dorsal (A, F) and lateral (B-E, G) views. H, I, posterior caudal vertebrae in lateral views. Scale = 2 mm.

mens (Fig. 11H), a fracture line is observed on the humeral stem that was healed up likely during the life of that individual.

Comments. The dorsal humeral crest has a triangular or even knob-like projection in *Batrachuperus londongensis* (Jiang et al. 2018) and *B. persicus* (AmphibiaTree. 2004), comparable to *Parahynobius betfianus*. The dorsal humeral crest is relatively short in *Ranodon shihi*, *R. tsinpaensis* (Zhao & Zhiang 1985) and in the fossil *R. cf. sibiricus* (Averianov & Tjutkova 1995: fig.4: 1b-d). In *Salamandrella keyserlingii* and *S. tridactyla* the dorsal humeral crest appears as a faint triangular projection (Ratnikov 2015), whereas in *Onychodactylus japonicus* it is undeveloped (Ratnikov 2015, AmphibiaTree. 2004).

Femur. The bone is slightly sigmoidal, with well ossified epiphyses in the larger specimens (Fig. 12A, B, E), whereas it remains cartilaginous in the smaller examples (Fig. 12C, D). The head of the bone is thickened and rounded, provided with a deep ventral depression. The femoral trochanter possesses a relatively thin and

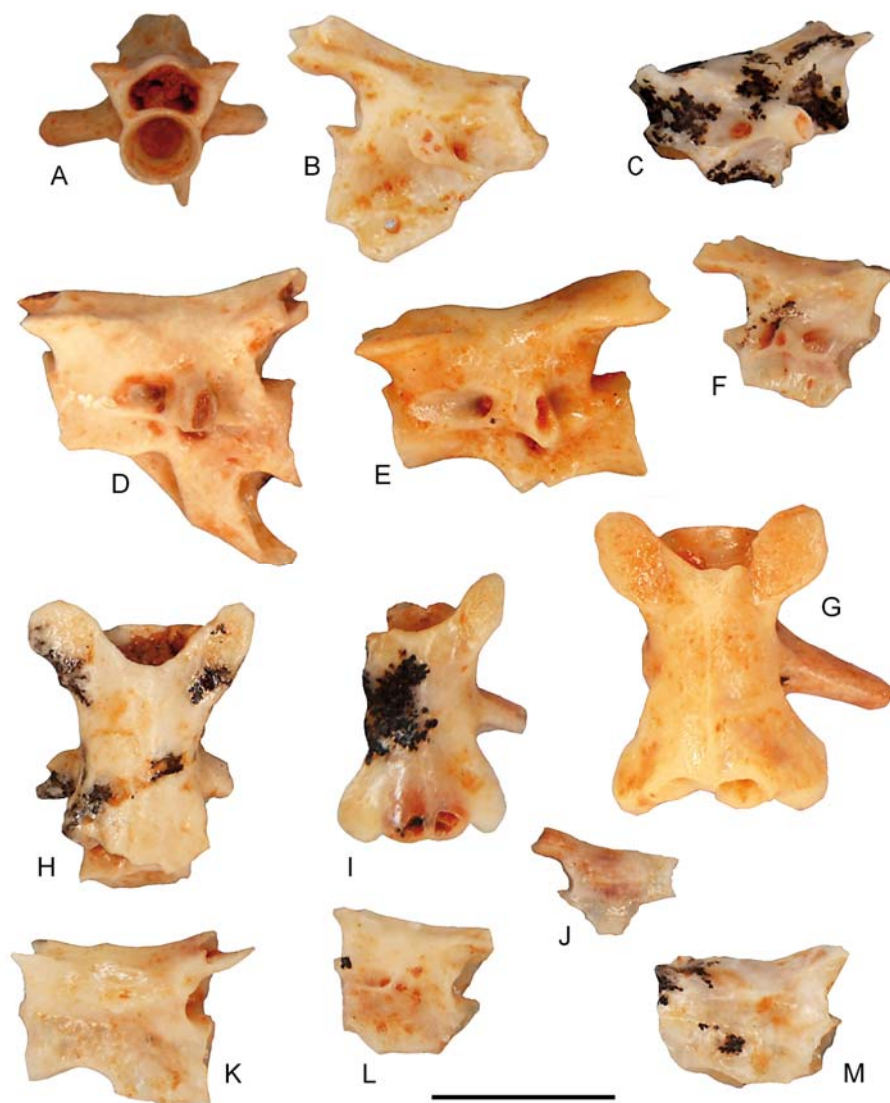


Figure 10. Caudal vertebrae of *Parahynobius betfianus* (MTC No. 19911/26-38). A-G, various sized anterior caudal vertebrae in anterior (A), lateral (B-F) and dorsal (H-G) views.

J-M, various sized posterior caudal vertebrae in lateral views. Scale = 2 mm.

rounded spur-like process connected to a short and sharp crista trochanterica; the latter is lacking in the smaller specimens (Fig. 12C, D). The distal part of the bone is widened and flattened dorsoventrally.

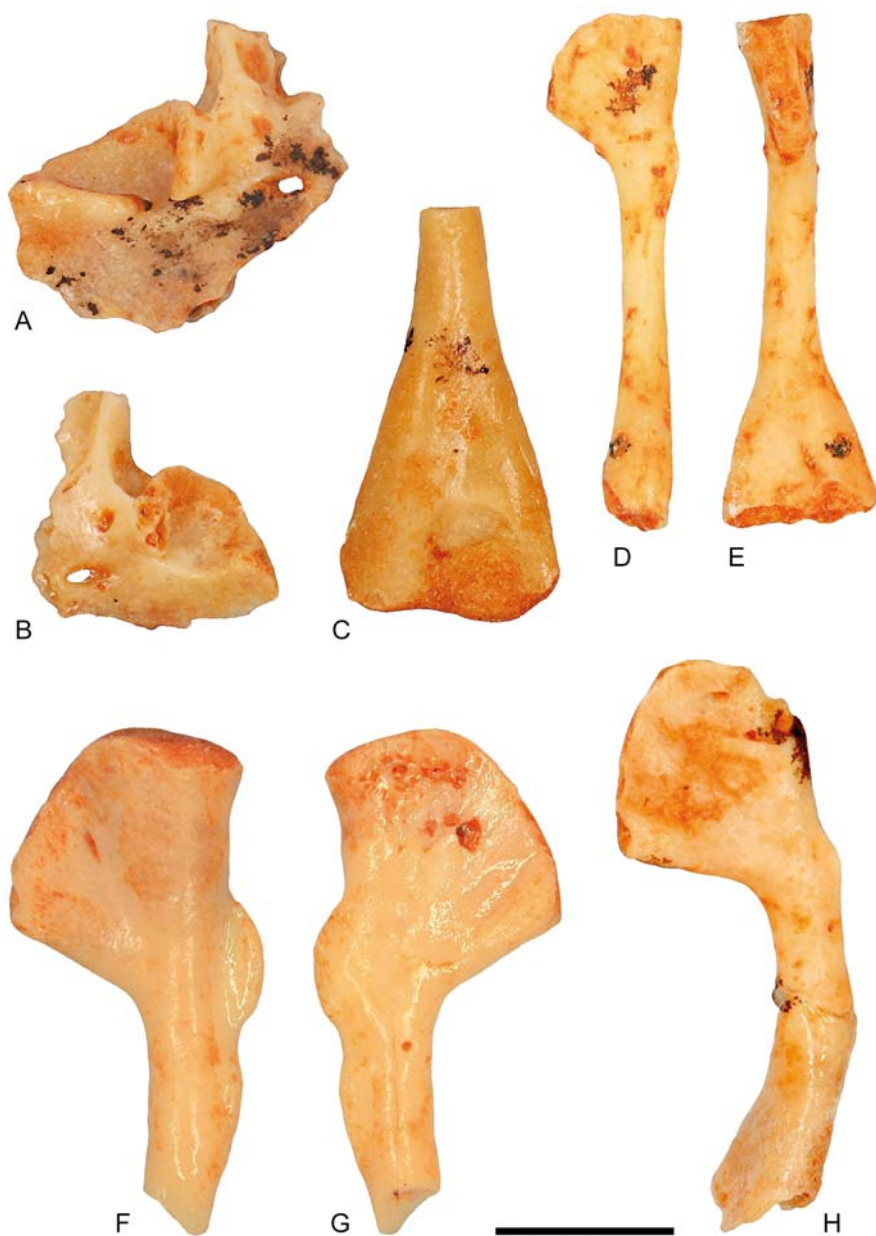


Figure 11. Scapulocoracoid and humerus of *Parahynobius betfianus*. A, fragmentary scapulocoracoid (MTC No. 19912/1) in lateral view. B, fragmentary scapulocoracoid (MTC No. 19915/1) in lateral view. C, distal humeral fragment (MTC No. 19915/2) in ventral view. D, E, humerus (MTC No. 19912/3) in lateral (D) and ventral (E) view. F, G, proximal humeral fragment (MTC No. 19912/2) in lateral views. H, proximal humeral fragment (MTC No. 20391) with healed up marks. Scale = 2 mm.

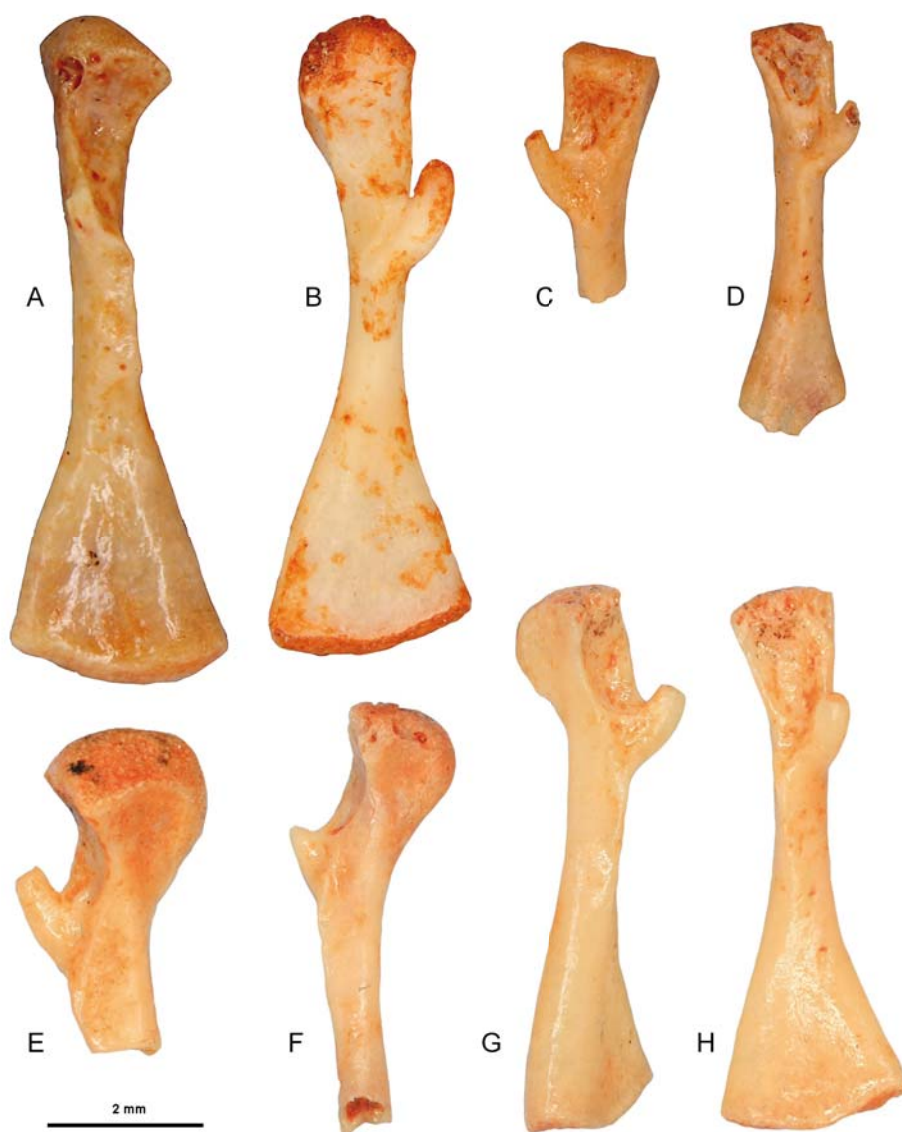


Figure 12. Femur of *Parahynobius betfianus*. A, B, G, H, various sized specimens (MTC No. 19907/1, 19907/2 and 19915/3) in ventral (A, B, H) and lateral (G) views. C-F, proximal femoral fragments (MTC No. 19912/4, 19912/5, 19915/4, 19915/5) in ventral (C, D) and lateral (E, F) views. Scale = 2 mm).

Comments. In *Salamandrella keyserlingii* and *Ranodon sibiricus* the crista trochanterica is faintly developed as a small triangular projection below and medial

to the femoral trochanter (pers. obs.), whereas in *Batrachuperus londongensis* it is relatively long extending from the femoral trochanter distally into the tibial condyle (Jiang et al. 2018).

Concluding remarks

The hynobiid material from Betfia 9/C is unique because it represents the single fossil record from the Quaternary of Europe. The isolated skeletal parts (premaxilla, vertebrae, scapulocoracoids, humeri and femora) most likely have belonged to a single species, and the variations observed, especially those on the trunk vertebrae (e.g. presence of unicapitate or bicapitate transverse processes, subcentral foramina, subcentral keels, height of neural crest, a.o.) may be considered intra-specific variations. In fact, the combined presence of unicapitate and bicapitate transverse processes is not unique (i.e. autapomorphic) to *Parahynobius betfianus*, since it has been observed in other hynobiid genera (e.g. *Hynobius*, *Onychodactylus* and *Salamandrella*).

The fossil material from Betfia 9/C may represent an attritional assemblage that may have belonged to at least seven or even more individuals (estimation based on the number of femoral examples) of various size. In spite of the fact that the material is fragmentary rarely were documented deformed bones (except the fracture observed on a single partial humerus).

If the assumption of Zhang et al. (2006) on the character evolution of the hynobiids is correct, then *Parahynobius* may have belonged to the pond-type hynobiids sharing the breeding places with newts (*Triturus* and *Lissotriton*) and with the palaeobatrachid frog *Palaeobatrachus langhae*, a permanent water dweller. Both the climatic and ecologic changes may have contributed to the extinction of *Parahynobius betfianus* and *Palaeobatrachus langhae*.

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