FOSSIL LAND SALAMANDERS (CAUDATA, HYNOBIIDAE) FROM THE CARPATHIAN BASIN: RELATION BETWEEN EXTINCT AND EXTANT GENERA

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Abstract. In the past few years skeletal remains of land salamanders (Caudata, Hynobiidae), coming from the fossil localities of Tardosbánya 3 (MN 12), Polgárdi 4 "Lower" (MN 13), Osztramos 1/C (MN 14), Hungary and from the Lower Pleistocene of Betfia 9/C, Romania have been reported. The osteological characters, as compared to those of recent genera, show that the European hynobiid stock belonged to the completely metamorphosed terrestrial-type land salamanders of *Hynobius*-group, the latter having a significantly wider geographic distribution during the Neogene and Quaternary. Based on the available fossil record, the genus *Parahynobius* reached the Carpathian Basin in the Late Miocene and became extinct during Lower Pleistocene times.

Keywords: Hynobiidae, fossil record, Neogene, Quaternary, Europe, morphology.

INTRODUCTION

Many salamander taxonomists have agreed that the family Hynobiidae most closely resembles the ancestral caudate. They have been placed together with the family Cryptobranchidae in the suborder Cryptobranchoidea, sharing with the latter a number of primitive characters (e.g. vomerine teeth located across the vomer, angular not fused with prearticular, spinal nerves exit from intervertebral foramina, external fertilization, chromosome number high. microchromosomes present). Based on combined molecular morphological data the land salamanders forms a monophyletic group relative to all other salamanders (Larson & Dimmick, 1993). They are differentiated from the Cryptobranchidae in having a more complete metamorphosis (Estes, 1981). Despite this a diagnosis based on the shared derived character states is not yet available for the Hynobiidae, the members of the family sharing a number of primitive character states (maxilla, septomaxilla, lacrimal, and a separate angular bone present; spinal nerves. except the atlas intervertebrally; ypsiloid cartilage, microchromosomes present), and only few derived characters could be identified (e. g. vomerine teeth located posteriorly on vomer, and their replacement proceeds from the posterior of the vomer; first hypobranchial and first ceratobranchial fused; second ceratobranchial consisted off from two elements). According to Zhao & Hu (1983, 1984) some derived states have arisen within the family. The above authors placed the hynobilds into two natural groups: Hynobius-group with the genera Hynobius, Pachypalaminus and Salamandrella, and the Ranodonthe genera Batrachuperus, Onychodactylus and Ranodon. The Pachyhynobius, described from Henan, China (Fey et al., 1983), shows some characters transitional between the above mentioned groups, lacking the premaxillary fontanelle, but having similar vomerine teeth series as those in the Ranodon-group. The hynobiids are widely distributed from Eastern into Central Asia: west through the Ural Mountains, south-west into Turkestan, Afganistan and Iran, and south to China, Korea and Japan.

THE FOSSIL RECORD

Despite of the fact that the hynobiids are among the most primitive group of amphibians, Estes (1981)

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reported that no fossil remains could be assigned to this family. Since then only few fossils, coming from the Russian Plain and from the Asiatic part of Russia have been referred to this family (e.g. Khozatsky, 1982; Chkhikvadze, 1984; Ratnikov, 1989).

In the past few years we studied a number of Neogene and Quaternary vertebrate collections, coming from the Carpathian Basin, which were extremely rich in herpetological remains. In three Neogene localities from Hungary we discovered few remains referable to Hynobiidae (Table 1). Moreover, during the excavation of the Lower Pleistocene aged fossil locality of Betfia 9/C (Bihor county, Romania) between 1995 - 1999, further material of land salamanders was found. The hynobiid remains studied in this paper belong to the following museums: Hungarian Geological Museum in Budapest (HGM), Hungary; Hungarian Natural History Museum in Budapest (HNHM), Hungary; Tării Crişurilor Museum in Oradea (MTC), Romania. Based on the above material we described recently a new hynobiid genus (Parahynobius VENCZEL, 1999) with two new species: P. betfianus VENCZEL,1999 and P. kordosi VENCZEL, 1999. Below we give the emended diagnosis of the taxa and a brief version of the original description.

Genus Parahynobius VENCZEL, 1999

Type species: Parahynobius betfianus VENCZEL, 1999

Type locality: Betfia 9/C, Bihor county, W-Romania Type horizon: Lower Pleistocene, Early Biharian (MQ1)

Distribution: Carpathian Basin (Hungary and Romania), Late Miocene (MN12) - Lower Pleistocene (MQ1)

Name derivation: from latin "para" – beside, and Hynobius – a living land salamander genus.

Emended diagnosis: Medium to small sized fossil land salamanders with complete metamorphosis; body length up to 160 mm. Vertebrae are amphicoelous with neural spines reduced to median neural ridges; the vertebral centrum has small and laterally placed anterior basapophyses and no well-defined haemal keel; the transverse processes of the middle - posterior trunk vertebrae are bicipital; postsacral ribs present.

Parahynobius betfianus VENCZEL, 1999

Holotype. A right premaxilla (MTC. No. 19913)(Venczel, 1999; fig.1: A, B).

Paratype: A middle trunk vertebra (MTC. No.19910) (Venczel, 1999; fig. 1; C - F)

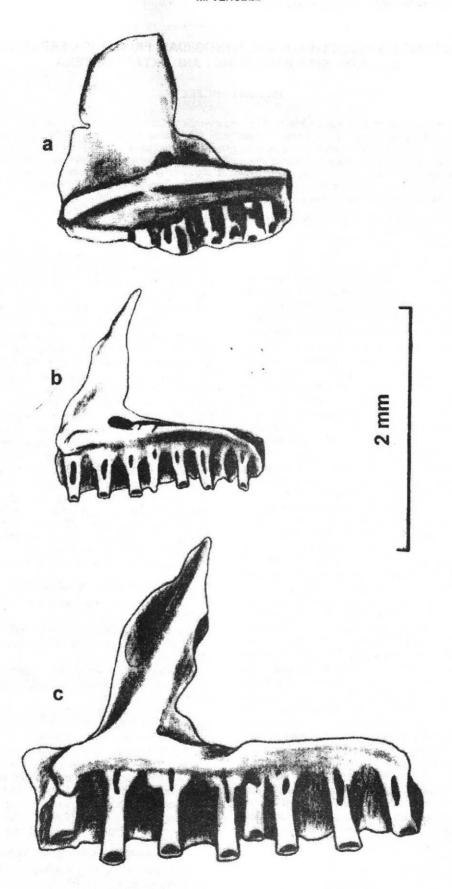


Figure 1 - Right premaxilla in hynobiids. a. Parahynobius betfianus (holotype), b. Salamandrella keyserlingii, c. Ranodon sibiricus. All in posteroventral views.

Table 1 - The fossil record of hynobiid salamanders from the Carpathian Basin

Locality	Age	Minimum number of Individuals
Betfia 9/C	Lower Pleistocene (MQ 1)	6
Osztramos 1/C	Lower Pliocene (MN 14)	2
Polgárdi 4 "Lower"	Upper Miocene (MN 13)	2
Tardosbánya 3	Upper Miocene (MN 12)	2

Type locality and type horizon. As for the genus. Name derivation: from the fossil locality Betfia, Bihor county, W-Romania.

Referred material: 110 vertebrae (MTC. No.19908, 19909, 19911, 19914, 19916, 19917, 20390) 2 scapulocorocoids (MTC: No.19912/1, 19915/1), humeri (MTC. No. 19912/2-3, 19915/2, 20391), 6 femora (MTC. No. 19907, 19912/4-5, 19915/3-5)

Emended diagnosis. Medium sized fossil land salamander species with complete metamorphosis; body length up to 160 mm. The premaxillary pars dorsalis is relatively short and wide, and there is no premaxillary fontanelle. The transverse processes of the trunk vertebrae are rather close to each other; the

prezygapophyses are not widely separated.

Description of the holotype: A completely preserved right premaxilla, except for the ventromedial margin of the pars dentalis which is broken off. In anterodorsal view the pars dentalis is slightly convex, the external surface is slightly rugose and possesses several small pits. The ventral margin is irregular with the tooth tips broken off. The lower part of the medial margin is slightly concave, while the dorsal part is irregular for attachement to the left premaxilla. The pars dorsalis is relatively wide and short (= spatulate) being somewhat narrow at its base, widened in its middle part and narrowed again at its dorsal tip. A small foramen, incompletely closed, is found near the base of the medial side of the pars dorsalis. No trace of a premaxillary fontanelle is observed. In ventral view eight tooth positions are preserved in the pars dentalis. Medially, no trace of tooth position can be observed (probably due to erosion). The pars palatina is well developed, being triangular and having its posterolateral margin thickened. Dorsolaterally to the medial margin of the lamina horizontalis, a relatively large nutritive foramen is observed. The lamina horizontalis is relatively thin, delimiting ventrally a shallow sulcus dentalis.

Parahynobius kordosi VENCZEL, 1999

Holotype. A posterior trunk vertebra (HGM. No. V. 20780) (Venczel, 1999: Fig. 3: A - D)

Type locality and type horison. Polgárdi 4 "Lower" (Hungary), Late Miocene, Pontian or Upper Turolian (MN13).

Name derivation. Species name dedicated to prof. László Kordos, director of the Hungarian Geological Museum in Budapest, Hungary.

Referred material. Three trunk vertebrae (HGM, No. V. 20781), one caudal vertebra (HGM. No. V. 20782)

Emended diagnosis. Land salamander species differing from the type-species by its smaller size, by less closely spaced transverse processes of the trunk vertebrae, and by more widely separated and elongated prezygapophyses.

Description of the holotype. A completely preserved posterior trunk vertebra, except the anterior portion of the right prezygapophysis and the posterior margin of the centrum. The centrum is amphicoelous, provided with two small tubercles on the anteroventral side of the cotyle. The neural arch is flattened and is relatively short. The transverse processes (= rib bearers) are distinctly bicipital and divergent near their distal end, without a bony lamella between them. The parapophysis is slightly curved downward and is somewhat thicker than the diapophysis, while the latter is slightly curved upward. The centrum lacks the subcentral keel; the ventral laminae are moderately developed anteriorly and posteriorly to the parapophyses. The postzygapophyses are elongated and slightly oriented ventrolaterally. The anterior border of the neural lamina is distinctly concave. The prezygapophyses are elongated and slightly inclined medially, having a nearly straight medial margin. The median neural ridge runs from the anterior margin of the neural arch to its posterior border, where a single imprint of ligament insertion can be observed. The interzygapophyseal ridges are reduced in the vicinity of transverse processes. The latter comparatively short, oriented posterolaterally, and inserted at the midpoint of the centrum.

The hynobiid remains coming from Tardosbánya 3 and Osztramos 1C, Hungary were described as cf. Parahynobius (Venczel, 1999).

COMPARISONS

The premaxilla. Material: one specimen (holotype) from Betfia 9/C (MTC. No. 19913) (fig. 1a). The insertion of pars dorsalis differs in the Hynobius-group (fig. 1b) and Ranodon-group (fig. 1c), in the former being situated at the level of the 1.- 4. premaxillary teeth, while in the latter at the level of the 3.- 6. premaxillary teeth. Due to the above character in the members of the Hynobius-group the premaxillary fontanelle is lacking, while in the members of the Ranodon-group there is a well defined premaxillary fontanelle (a derived condition). The salamander from Betfia, were provided with wider and shorter pars dorsalis when compared to the above groups, while the premaxillary fontanelle, similarly to those of the Hynobius-group, were lacking.

The vertebrae. Material: 110 vertebrae from Betfia 9/C; 4 trunk and a caudal vertebra from Polgárdi 4 "Lower" (HGM. No. 20780 – 20782); 6 trunk vertebrae from Tardosbánya 3 (HNHM. No. V. 98.11 - 98.13); 2

trunk vertebrae, 1 sacral vertebra, 1 caudal vertebra from Osztramos 1/C (HNHM. No. V. 98.10). The morphology of the vertebrae resembles that of other hynobiids (e.g the centrum is amphicoelous, provided with short and wide anterior basapophyses; the spinal nerves exit intervertebrally; postsacral ribs are present; the neural spine is reduced to a median neural ridge; a. o.). The transverse processes of the Hynobiidae are unicipital (a derived condition), with their distal end (articular surface for ribs) enlarged (= dumb-bell shaped). However Parahynobius, differs from the other hynobiids by retaining a bicipital condition in the transverse processes of trunk vertebrae (ancestral character for salamanders). The body size of the two natural groups of Hynobiidae established by Zhao & Hu (1983, 1984) differ from each other: the members of the Ranodon-group sometimes exceeding 200 mm, while those of the Hynobius-group never exceeding 130 mm. The size of the genus Parahynobius could reach (estimated on the basis of measurements made on trunk vertebrae) up to 160 mm.

The appendicular skeleton. The appendicular skeletal remains (scapulocoracoid, humerus, femur)

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mostly are similar with those of other hynobiid genera, and only variations of ontogenic nature could be observed.

CONCLUSIONS

Based on the available data the hynobiid salamanders apparently had a rather limited biostratigraphic range in Central Europe, they appeared in the Carpathian Basin during Upper Miocene times, period in which the family reached its largest distribution in Eurasia.

The newly described land salamander genus (Parahynobius) belonged to the Hynobius-group of genera, differing from these by its larger size, by the morphology of the premaxilla and by the retention of bicipital condition in the transverse processes of trunk vertebrae.

The hynobiids survived in the Carpathian Basin up to the Quaternary, their extinction being caused among others by the worsening climatic conditions during Lower Pleistocene times.

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