Land salamanders of the family Hynobiidae from the Neogene and Quaternary of Europe

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Abstract. A new extinct genus with two new species of land salamanders of the family Hynobiidae, from the Late Miocene of Polgárdi (MN13), Hungary (*Parahynobius kordosi* gen. n. sp. n.) and from the Lower Pleistocene of Betfia IX/C (MQ1), Romania (*Parahynobius betfianus* gen. n. sp. n.), is described. The Late Miocene locality of Tardosbánya (MN12) and the Lower Pliocene locality of Osztramos 1C (MN14), Hungary, also yielded several vertebrae, assigned with some doubt to the above genus (cf. *Parahynobius*). The new taxa belonged to the westernmost distributed stock of land salamanders of the *Hynobius*-group, which, based on the available fossil record, reached the Carpathian Basin during Late Miocene and disappeared from the area during Lower Pleistocene times. The Hynobiidae had a wider geographic distribution during the Tertiary and Quaternary compared to their present range, which is limited to Asia.

Introduction

Several phylogenetic analyses suggest that the Hynobiidae were one of the first group of urodeles to differentiate (Larsen, 1963; Edwards, 1976; Estes, 1981; Duellman and Trueb, 1986; Larson and Dimmick, 1993). Nevertheless, the fossil record of Hynobiidae is rather scarce. Estes (1981) reported that no fossil finds could be assigned to this group. Since then only a few fossil finds from the Russian Plain and from the Asiatic part of Russia can be referred to this family (e.g. Khozatsky, 1982; Chkhikvadze, 1984; Ratnikov, 1989).

Unexpectedly, while sorting some dissociated fossil vertebrate remains from Polgárdi 4 "Lower", collected in 1984 and 1985 by Prof. László Kordos and co-workers, and from Tardosbánya 3 and Osztramos 1C collected by Prof. Dénes Jánossy, several vertebrae referable to the Hynobiidae were found. Furthermore, during re-excavation of the fossil locality Betfia IX, W-Romania in 1995 (named as Betfia IX/C), additional remains of land salamanders were found. Hir and Venczel (1997) made the first report on hynobiids from Betfia IX/C.

The purpose of the present paper is to describe the above mentioned land salamander remains. The fossil materials from Polgárdi 4 "Lower" belong to the collections of the Hungarian Geological Museum in Budapest, Hungary, those from Osztramos 1C to the collection of Hungarian Natural History Museum in Budapest, while those coming from Betfia IX/C to the collection of Ţării Crişurilor Museum in Oradea, Romania. The terminology used in this paper follows Larsen (1963) for cranial bones, and Estes (1981, 1988) for the axial and appendicular skeleton. The methodology of measurements of vertebrae follows Estes and Schleich (1994).

Systematic description

Order Caudata Oppel, 1811
Suborder Cryptobranchoidea Dunn, 1922
Family Hynobiidae Cope, 1859

The family Hynobiidae consists of salamanders differentiated from the Cryptobranchidae in having a more complete metamorphosis (Estes, 1981). The members of the family share a number of primitive character states: maxilla, septomaxilla, lacrimal, and a separate angular bone present; spinal nerves (except the atlas) exit intervertebrally; ypsiloid cartilage, and microchromosomes present. Based on combined molecular and morphological data the hynobiids forms a monophyletic group relative to all other salamanders (Larson and Dimmick, 1993), 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 consisting of two elements). Some derived states have arisen within the group, for which reason Zhao and Hu (1983, 1984) placed the hynobiids into two natural groups: the *Hynobius*-group with the genera *Hynobius*, *Pachypalaminus* and *Salamandrella*, and the *Ranodon*-group with the genera *Batrachuperus*, *Liua*, *Onychodactylus* and *Ranodon*. The genus *Pachyhynobius*, described recently from Henan, China (Fei 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 into Turkestan, Afganistan and Iran).

Parahynobius *gen. n.*

Type species. *Parahynobius betfianus* sp. n.

Type locality. Betfia IX/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.

Diagnosis. As for the type-species.

Parahynobius betfianus *gen. n. sp. n.*

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

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

Type locality and type horizon. As for the genus.

Name derivation. From the fossil locality Betfia, Bihor county, W-Romania.

Referred material. 108 vertebrae (MTC. No. 19908, 19909, 19911, 19914, 19916, 19917), 2 scapulocoracoids (MTC. No. 19912/1, 19915/1), 3 humeri (MTC. No. 19912/2-3, 19915/2), 6 femora (MTC. No. 19907, 19912/4-5, 19915/3-5).

Diagnosis. Medium sized fossil land salamanders with complete metamorphosis, with body length up to 140-160 mm. The premaxillary pars dorsalis is relatively short and wide, and there is no premaxillary fontanelle; 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 are variable in shape, some are bicipital.

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 (fig. 1: A, B). 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. The external surface is smooth with a nearly imperceptible concavity extending dorsoventrally. The medial margin is emarginated at the base of the pars dorsalis, while at the base of the lateral margin a short and shallow groove extends ventromedially. In medial or lateral view the pars dorsalis is flattened dorsoventrally, while in ventral view it is slightly convex (due to the fact that the stem is somewhat thickened in the middle). 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 positions 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.

Description of the paratype (fig. 1: C-F). A completely preserved middle trunk vertebra, except for the anterolateral part of the left prezygapophysis and the distal end of the right diapophysis. The centrum is amphicoelous, and it is provided with short and wide anterior basapophyses on the ventrolateral side of the cotyle rim. The neural arch is flattened and of moderate length. The transverse processes are closely appressed but are distinctly bicipital. The dorsal margin of the diapopysis and the ventral side of the parapophysis near their distal end bear a prominence. The rib articulating surface is somewhat smaller in the diapophysis (having an elongated shape) than in the parapophysis (having an oval shape). The neural spine is reduced to a low keel. No spinal nerve exit can be observed. In ventral view the basapophyses are very short and flattened dorsoventrally (the right one is broken off and is situated laterally to the midline of the centrum). The subcentral keel is reduced, visible only at the level of the subcentral foramina. The latter structures are oval in shape, and the right one is about twice as large than the left one. Anteriorly and posteriorly to the subcentral foramina, two slanting ridges of low height run to the subcentral keel. The ventral laminae are moderately developed anteriorly and posteriorly to the parapophyses. The latter structures are projected posterolaterally and are slightly bent posteriorly. The postzygapophyses are ovaloid in shape, and their lateral sides are slightly bent ventrally. In dorsal view the anterior border of the neural

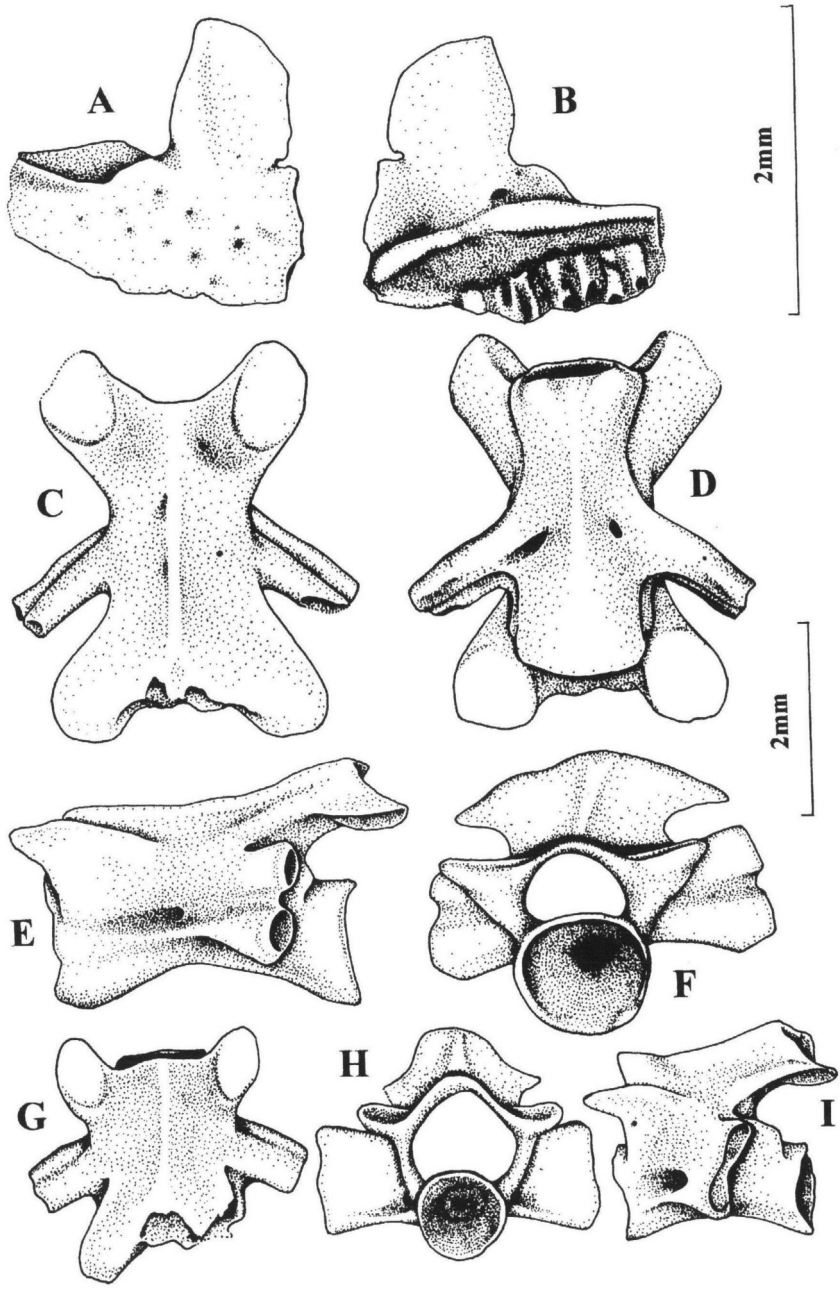

Figure 1. *Parahynobius betfianus* gen. n. sp. n. A, B: right premaxilla (holotype). C-F: trunk vertebra (paratype), G-I: anterior trunk vertebra. A — anterodorsal view, B — posteroventral view, C, G — dorsal views (anterior on top), D — ventral view, E, I — left lateral views, F, H — anterior views.

lamina is concave, while the prezygapophyses of elongated oval shape are oriented anterolaterally and slightly obliquely. The neural spine is reduced to a median neural ridge. The posterior border of the neural lamina is notched centrally, bearing in each side an imprint of a tendinous ligament insertion. The interzygapophyseal ridges are reduced in the vicinity of the transverse processes. The latter are oriented posterolaterally and are inserted only slightly posteriorly to the midpoint of the centrum. In anterior view the cotyle is circular, while the neural canal is of a rounded triangular shape. The posterior lamina is convex dorsally. The transverse processes are connected by a bony lamella except near their tips. The prominence in the ventral side of the parapophysis is distinctly larger than that in the dorsal side of the diapophysis. In posterior view the cotyle is somewhat teardrop shaped, while the postzygapophyses are nearly horizontal. The centrum length is 3.42 mm, the median width between postzygapophyses is 3.22 mm, while the median height equals 2.74 mm.

Description of the referred material. The anterior trunk vertebrae (fig. 1: G-I) have considerably shorter centra and higher neural arch than those of the middle trunk vertebrae. The neural spine is reduced to a keel, but it is more prominent than in the middle trunk vertebrae. The transverse processes are usually unicipital with a relatively large articular surface (= dumb-bell shaped), but in a few specimens the transverse processes are distinctly bicipital. The subcentral keel is reduced, while the subcentral foramina are extremely small or lacking. No spinal nerve exit is observed. The anterior caudal vertebrae (fig. 2: A, B) are provided with unicipital transverse processes, while the posterior ones (fig. 2: C) lack any transverse processes. No foramina for spinal nerve exit are present. In the anterior caudal vertebrae the rib articular surface is clearly observed. The haemal arch is closed from below and the haemal canal is ovaloid. The neural spine is reduced to a median neural ridge. In well-preserved specimens, a posterodorsally oriented area for paired ligament insertion can be observed on the posterior border of the neural lamina. The centrum length in eight measured trunk vertebrae ranges between 3.06-3.38 mm, the median width between postzygapophyses ranges between 2.47-3.08 mm, while the median height ranges between 2.44-2.73 mm.

Scapulocoracoid (fig. 2: D). The bone is very fragmentary. The procoracoid foramen is present, while on the lateral surface of the scapula, beginning from the margin of the glenoid cavity, a distinct ridge is observed.

Humerus (fig. 2: E, F). The bone is almost straight, when viewed laterally or medially. The proximal articular surface is well ossified. The ventral crest is extremely prominent and short, abruptly ended distally, proximally reaching the head of the bone. The head is oval. The dorsal surface is provided with a sharp crista of low height, running below the head, approximately one third of the length of the humerus. The distal end is also well ossified and considerably widened, the dorsal surface being flat or slightly convex, while on the ventral side a well-defined fossa cubitalis ventralis is observed. The ectepicondyle is considerably larger then the entepicondyle. The caput humeri is oval in shape.

Femur (fig. 2: G, H). The bone is slightly sigmoidal, with ossified epiphyses. The head of the bone is thickened and rounded, provided with a deep ventral depression. The trochanter possesses a relatively thin and rounded spurlike process, and lacks a well-defined crista trochanterica. The distal part of the bone is widened and flattened dorsoventrally.

Comparison and comments. The relatively large pars palatina of the premaxilla suggest that *Parahynobius* gen. n. belonged to the completely metamorphosed terrestrial-type hynobiids. The pars dorsalis of the premaxilla in *Parahynobius betfianus* gen. n. sp. n. is inserted somewhat similarly to those of the genera of the *Hynobius*-group (namely *Hynobius*, *Pachypalaminus* and *Salamandrella*). In the genera of the *Ranodon*-group (namely *Batrachuperus*, *Liua*, *Ranodon* and *Onychodactylus*), there is a premaxillary fontanelle (a derived condition) between the relatively short and tapering partes dorsales, inserted somewhat laterally to the medial margin of pars dentalis. The pars dorsalis in the former group is attached syndesmotically to its counterpart for its whole length (fused with true synostosis in *H. nebulosus*) and consequently there is no premaxillary fontanelle. In

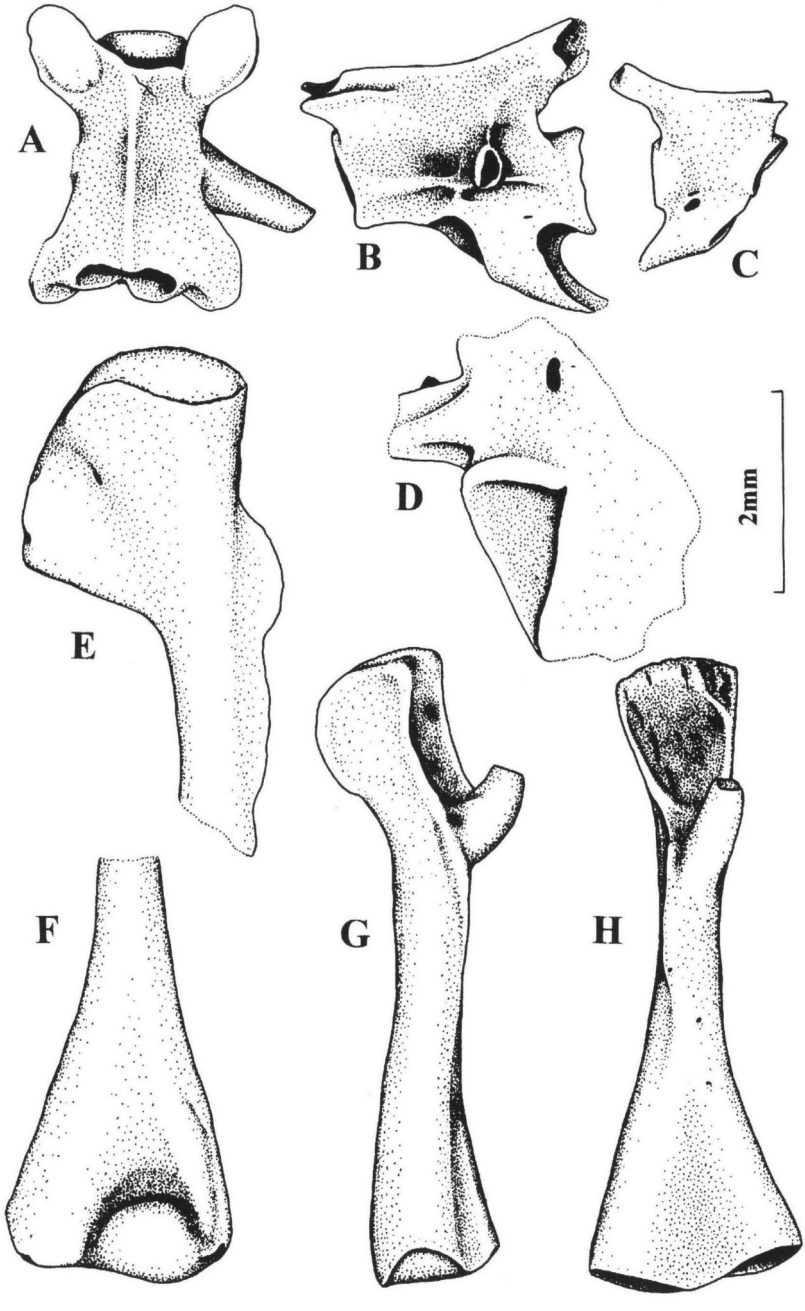

Figure 2. *Parahynobius betfianus* gen. n. sp. n. A, B: anterior caudal vertebrae, C: posterior caudal vertebra, D: fragmentary scapulocoracoid E: proximal fragment of humerus, F: distal fragment of humerus, G, H: femur. A, E — dorsal views, B, C, G — lateral views, D — ventrolateral view, F, H — ventral views.

this respect *Parahynobius* gen. n. shares a primitive condition with that of the *Hynobius*-group. In the latter group the slightly thickened lateral side of the pars dorsalis is gradually tapering, surrounded by the nasal bone, unlike in *Parahynobius betfianus* gen. n. sp. n. in which the pars dorsalis is distinctly wider and shorter, a primitive feature comparable with that observed in cryptobranchids and dicamptodontids. However, several vertebral characters (e.g. spinal nerves exit intravertebrally in the caudal vertebrae, basapophyses if present are projecting and situated closer to midline, better defined neural spine) prevent further association with *Dicamptodon*, and with the related Paleocene-Upper Miocene fossil European dicamptodontid genera (*Bargmannia*, *Geyeriella*, *Wolterstorfiella*) (Estes, 1981). Due to the fact that the material of *Geyeriella* and *Wolterstorfiella* (including types) are lost, closer comparison with *Parahynobius* gen. n. is rather difficult (e.g. presence or absence of spinal nerve foramina has never been considered). In consequence only *Bargmannia* can be definitively placed in the Dicamptodontidae (Estes, 1981), while the taxonomic status of *Geyeriella* and *Wolterstorfiella* on the basis of the above mentioned morphological characters remains unsolved.

The vertebrae of *Parahynobius betfianus* gen. n. sp. n. resemble those of other hynobiids (e.g. spinal nerves exit intervertebrally, presence of postsacral ribs, reduced neural spine, a.o.), their size being slightly larger than those of the *Hynobius*-group. The shape of the zygapophyses and the anterior margin of neural lamina, as well as the morphology and position of the transverse processes approaches the condition observed in *Hynobius* (fig. 4: A-B).

Parahynobius kordosi *sp. n.*

Holotype. A posterior trunk vertebra (HGM. No.V. 20780) (fig. 3: A-D).

Type locality and type horizon. 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) and one caudal vertebra (HGM. No. V. 20782).

Diagnosis. Land salamanders resembling *P. betfianus* but having smaller absolute size and more widely separated transverse processes of the trunk vertebrae, 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 and it is provided with two small tubercles on the anteroventral side of the cotyle. The neural arch is flattened and is relatively short. The transverse processes 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 articular surface of the parapophysis is oval, while that of the diapophysis is somewhat elongated. In ventral view the centrum lacks the subcentral keel, the right subcentral foramen is extremely small, while the left one is relatively large. The ventral laminae are moderately developed anteriorly and posteriorly to the parapophyses. The postzygapophyses are elongated and slightly oriented ventrolaterally. In dorsal view 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

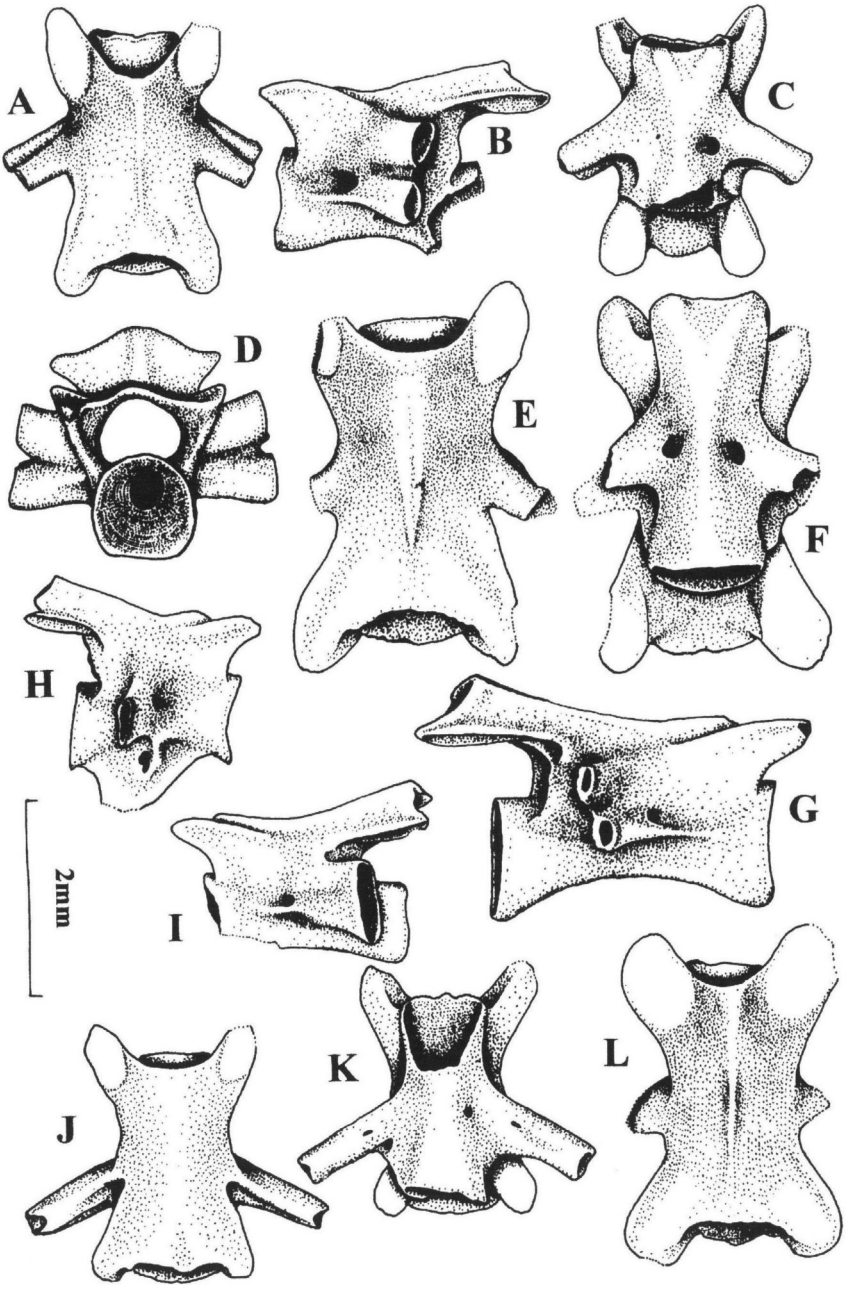

Figure 3. *Parahynobius kordosi* sp. n. (A-H) and cf. *Parahynobius* (I-L). A-D: trunk vertebra (holotype). E-G: trunk vertebra, H: caudal vertebra, I-K: sacral vertebra, L: trunk vertebra. A, E, J, L — dorsal views (anterior on top), B, G, H, I — lateral views, C, F, K — ventral views, D — anterior view.

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 are comparatively short, oriented posterolaterally, and inserted at the midpoint of the centrum. In anterior view, the cotyle is rounded, while the neural canal is of rounded triangular shape. The posterior portion of the neural lamina is somewhat upraised. In posterior view the cotyle is broken off, while the postzygapophyses are oriented slightly ventrolaterally.

Description of the referred material. Three trunk vertebrae (fig. 3: E-G) are relatively larger than the holotype, the length of the centrum ranging from 2.52 mm to 3.15 mm. All the referred specimens are provided with flattened neural arch and amphicoelous centra and with a reduced subcentral keel. The anterior basapophyses are lacking, or are reduced to paired tubercles situated on the ventrolateral margin of the cotyle rim. The subcentral foramina are variable in shape and size. The neural spine is reduced to a median neural ridge. The transverse processes (preserved only in a single specimen) are distinctly bicipital. The pre- and postzygapophyses are elongated, except the largest specimen in which it is oval. The neural lamina is projected far posteriorly to the level of the vertebral centrum. The cotyle is rounded, while the neural canal is of rounded triangular shape. The single caudal vertebra is relatively well preserved (except the ventral margin of the haemal arch and the left transverse process, which are broken off). The transverse process is unicipital, with a distinct articular surface for a postsacral rib. There is no trace of an intravertebral nerve exit.

Comparison and comments. Based on the available material *Parahynobius kordosi* sp. n. closely resembles *P. betfianus* sp. n., but differs from the latter by its smaller absolute size and in a few details of the vertebral characters. All the specimens from Polgárdi 4 "Lower" are distinctly smaller than those coming from Betfia. The neural arch is projected far behind the posterior border of the vertebral centrum and probably related to this, the zygapophyses are more elongated than those of *P. betfianus* sp. n. The distal portion of the transverse processes of *P. kordosi* sp. n. are distinctly divergent and distinctly bicipital (a primitive feature, not seen in other hynobiids), while the anterior margins of the neural lamina resemble some dicamptodontids (Estes, 1988), rather than those of other hynobiids (fig. 4). Both members of the genus *Parahynobius* gen. n. possessed postsacral ribs (ancestral character for salamanders), present in all living members of the family Hynobiidae. Ma (1964) reported that *Salamandrella keyserlingii* lacks postsacral ribs (cited also by Zhao and Hu, 1984). However, I have observed vestigial ribs in at least the first 3-4 postsacral vertebrae in several specimens of *S. keyserlingii*.

cf. Parahynobius

Material. Tardosbánya 3, Hungary, Late Miocene (MN 12): 6 fragmentary trunk vertebrae (HNHM. No. V. 98. 11, No. 98. 12, No. 98. 13); Osztramos 1C, Hungary, Lower Pliocene, Ruscinian (MN14): 2 trunk vertebrae, 1 sacral vertebra (HNHM. No. V. 98. 10/1-3).

Description. The centrum of the trunk vertebrae (lacking prominent basapophyses) from Tardosbánya are relatively well preserved, but in all the specimens the transverse processes and various portions of neural lamina are broken off. The vertebrae coming from Osztramos 1C are well preserved except the anterior margin of the cotyle, and the transverse processes, which are broken off (preserved only in a single specimen). The vertebral characters resemble those coming from Polgárdi 4 "Lower" (fig. 3: L), except the sacral vertebra from Osztramos 1C (fig. 3: I-K), in which the transverse processes are distinctly unicipital, with a relatively large articular surface. The subcentral foramina are small (present in two specimens only), and the prezygapophyses elongated, while the postzygapophyses are oval in shape. The basapophyses, preserved only in the largest specimen coming from Osztramos 1C, are short, wide and situated on the ventrolateral side of the cotyle rim. The centrum length of the largest trunk vertebra is 2.48 mm, while that of the sacral vertebra is 2.08 mm.

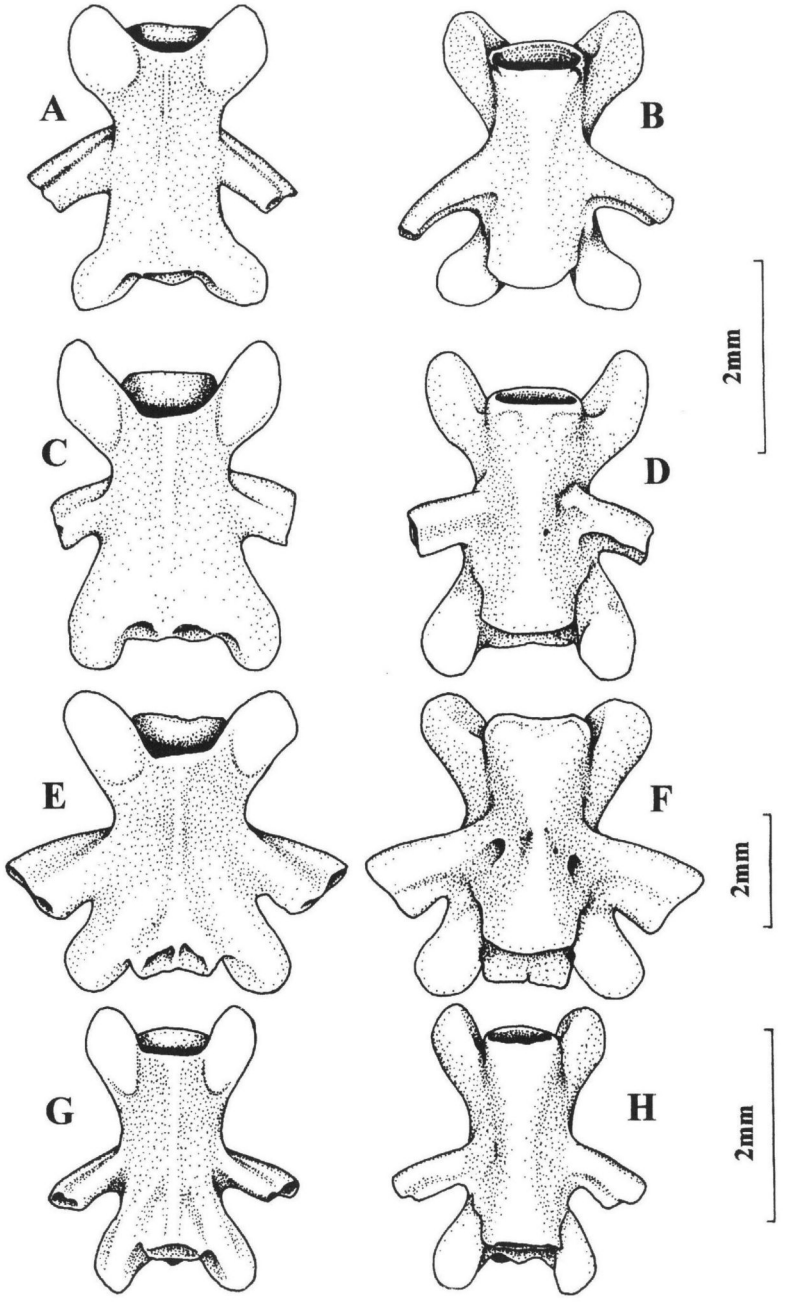

Figure 4. Trunk vertebrae of recent hynobiids. A, B: *Hynobius leechii*, C, D: *Onychodactylus fischeri*, E, F: *Ranodon sibiricus*, G, H: *Salamandrella keyserlingii*. A, C, E, G — dorsal views (anterior on top), B, D, F, H — ventral views.

Comments. The vertebrae seem to be closer in size and shape (and even considering their geological age) to those of *Parahynobius kordosi* sp. n. coming from Polgárdi 4 "Lower" (e.g. shape and size of basapophyses, median neural ridge, lack of subcentral keel, shape of pre- and postzygapophyses). The lack of any sacral vertebra from Tardosbánya, Polgárdi and Betfia means that direct comparison of the homologous bones and a more detailed systematic analysis of fossils on the basis of the available material is actually impossible. In consequence their assignment to the genus *Parahynobius* cannot be fully demonstrated.

Concluding remarks

The above-described fossils form the westernmost distributed stock of land salamanders of the family Hynobiidae. They are the first records of this taxon from the territory of Central Europe. They apparently had a rather limited biostratigraphic range in Europe. Based on the available data, the first appearance of the group was during Late Miocene times (MN12), a period characterized by fluctuating climatic conditions with evident vegetational and faunistic changes, ending in the well known Messinian event (Rögl and Steininger, 1983). The paleoenvironmental conditions of the hynobiids in the studied fossil localities were rather different: the Tardosbánya 3 and Polgardi 4 "Lower" faunal assemblage lived amid subtropical climatic conditions, with the increasing dominance of xeric vegetation. The herpetofauna included snakes dominated by small colubrids (*Coluber*, *Elaphe*, *Coronella*, *Telescopus*) (Venczel, 1994, 1998), few species of anurans, dominated by *Pelobates* and *Rana* (Venczel, 1997), as well as salamandrids (e.g. *Chelotriton paradoxus* and *Triturus* sp.; pers. obs.); the vertebrate fauna of Osztramos 1C locality lived amid wet subtropical climatic conditions and the hynobiids occurred sympatrically with *Triturus*, *Mioproteus*, *Latonia* and *Rana* (pers. obs.); the fauna from Betfia IX/C lived amid temperate climatic conditions and the small mammals were dominated by *Allophaiomys pliocaenicus*, together with species preferring forests (Hir and Venczel, 1997, 1998a, 1998b). Also present in the Betfia IX/C assemblage are: two members of the genus *Triturus*, a few anurans that were dominated by *Rana*, the lizards dominated by *Lacerta*, and the snakes, by *Natrix* (Hir and Venczel, 1997).

We can presume that the extinction of the European hynobiids was caused among other causes by the worsening climatic conditions during the Lower Pleistocene.

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