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THE FIRST APPEARANCE OF *HUCHO* (SALMONIDAE) IN THE FOSSIL RECORD OF EASTERN EUROPE

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The First Appearance of *Hucho* (Salmonidae) in the Fossil Record of Eastern Europe. Kovalchuk, O. M. — Until now, fossil remains of *Hucho* Günther, 1866 are known only from the Oligocene — middle Miocene strata of Baikal Russia, and from the late Pleistocene of Germany. New specimens, now identified as *Hucho* sp., come from the late Miocene of southern Ukraine. Numerous fragments of opercular bones and jaw teeth, morphologically similar to those in the extant genus *Hucho*, were found in Kubanka 2, Cherevychnoe 3, Tretya Krucha localities and dated by the late Sarmatian — early Maeotian (10–8 Ma). These remains document the first appearance of huchen in geological past of Europe, filling in gap in distribution of this genus during the late Neogene, and throw light upon its biogeographical history.

Key words: *Hucho*, Salmonidae, Teleostei, late Miocene, Ukraine, palaeobiogeography.

Первое появление *Hucho* (Salmonidae) в палеонтологической летописи Восточной Европы. Ковальчук А. Н. — На данный момент ископаемые остатки *Hucho* Günther, 1866 известны лишь из отложений олигоцена — среднего миоцена Забайкалья, а также из позднего плейстоцена Германии. Новые образцы, идентифицированные как *Hucho* sp., получены из отложений позднего миоцена юга Украины. Многочисленные фрагменты жаберных крышек и челюстные зубы, морфологически сходные с таковыми у представителей рода *Hucho*, были обнаружены в материалах из местонахождений Кубанка 2, Черевычное 3, Третья Круча и датированы поздним сарматом — ранним мэотисом (10–8 млн л. н.). Эти остатки документируют первое появление тайменей в геологическом прошлом Европы, заполняя пробел в распространении рода на протяжении позднего неогена, и проливают свет на его биогеографическую историю.

Ключевые слова: *Hucho*, Salmonidae, Teleostei, поздний миоцен, Украина, палеобиогеография.

Introduction

The salmonid family (Salmonidae) comprises about 228 extant anadromous and freshwater fish species, belonging to 11 genera (Pauly, Froese, 2014), inhabiting temperate and subarctic regions of Eurasia and North America (Nelson, 2006). All salmonids spawn in fresh water, but in many cases, the fish spend most of their lives at sea, returning to the rivers only to reproduce. This lifecycle is described as anadromous. They are predators, feeding on small crustaceans, aquatic insects, and smaller fish (McDowell, 1998). As has been noted by many ichthyologists, the interrelationships among all members of the Salmoniformes still need much more study to improve our understanding of the evolution of this group. Current salmonids (Salmonidae) comprise three lineages, taxonomically treated as subfamilies: Coregoninae (whitefish), Thymallinae (graylings), and Salmoninae (char, trout and salmons). Generally, all three lineages are accepted to share a suite of derived traits indicating a monophyletic group (McPhail, Strouder, 1997).

Despite the molecular systematics and phylogenetic investigations of salmonids have been elaborated in the previous studies (Crespi, Fulton, 2004; Phillips et al., 2004; Shedko et al., 2012, 2013; Macqueen, Johnston, 2014), it is difficult to determine what fossil material may be important to the evolution of the group. The relationships of Salmonidae are as uncertain as those of the higher groups. Sanford (2000) gave an overview of various hypotheses of relationships among the salmonid genera, and provided an analysis of relationships based on osteological characters.

The Salmonidae first appear in the fossil record in the middle Eocene (48.6–37.2 Ma) with the fossil *Eosalmo driftwoodensis* Wilson, 1977, which was first described from fossils found at Driftwood Creek, central British Columbia. This genus shares traits found in the Salmoninae, Coregoninae and Thymallinae subfamilies. Hence, *E. driftwoodensis* is an archaic salmonid, representing an important stage in salmonid evolution (Wilson, Williams, 2010). Yakovlev (1961) pointed that fossil record of salmonids in the Europe is extremely sparse. Gorjanović-Kramberger (1891) reported fossil remains of *Salmo imigratus* from the upper Miocene deposits of Samoborska Gora (Croatia), while Anđelković (1989) stated that these remains took the lower Sarmatian stratigraphic position within the central Pannonian Basin. Bones of *Salmo* sp. are reported from the middle Pleistocene of England (Schreve et al., 2002), as well as *Salmo trutta* and *Salmo* sp. from the late Pleistocene and Holocene of Ukraine and Russia (Tichij, 1929; Shpet, 1949; Lebedev, 1960). Here I describe huchen remains from the late Miocene of Ukraine. This material represents the first appearance of *Hucho* in Southeastern Europe.

Material and methods

The fish material described here was recovered in the same microvertebrate sample obtained from dry screening as the small mammalian faunas previously described (Topachevsky et al., 2000; Sinitsa, 2005, 2011). It is derived from three late Miocene localities in southern Ukraine (fig. 1). Their age was established based on the small mammals (Nesin, Nadachowski, 2001) and is consistent with biostratigraphic dates derived from the accompanying fauna.

Fig. 1. Localities of the late Miocene huchen remains in Ukraine: 1 — Kubanka 2; 2 — Cherevychnoe 3; 3 — Tretya Krucha.

The material under study is recently housed in the Paleontological Museum of the National Museum of Natural History (NMNHU-P), National Academy of Sciences of Ukraine (collection No. 41, 45). It includes forty small fragments of opercular bones (NMNHU-P 41/3746–3785) from the Kubanka 2, two isolated jaw teeth and sixteen operculars (NMNHU-P 45/5699–5716) from the Cherevychnoe 3, as well as four near-complete opercular bones (NMNHU-P 41/3079–3082) from the Tretya Krucha locality. Comparative material is from the Zoological Museum (NMNHU-Z). Isolated bones were identified based on comparisons with extinct and modern taxa. Determination of elements was accomplished using diagnostic features. The taxonomic hierarchy follows Nelson (2006), and correlation of the Eastern Paratethys stages with European Mammal Neogene Zones follows Topachevsky et al. (1997), Nesin and Nadachowski (2001). The specimens were measured using a digital caliper with 0.1 mm precision. Bone terminology follows Sytchevskaya (1989) and Lepiksaar (1994).

Geological setting

All three studied localities are situated at the south of Ukraine, in the Odesa Region (fig. 1). Kubanka 2 site is located on the left bank of the Kuyalnik estuary, in 400 m eastwards from the eponymous village. Greenish-gray sandy loams with clays contain numerous remains of small mammals and freshwater fishes (Sinitsa, 2011; Kovalchuk, 2012). Geological age of this locality responds to the late Sarmatian (Kovalchuk, 2015), first half of the middle Turolian, MN 11 (Sinitsa, 2011). Multilayered Cherevychnoe locality was previously described in detail (Topachevsky et al., 2000). The bones of mammals, as well as accompanying freshwater fish remains are located in the thickness of alluvial sands and grits above the contact zone with the Sarmatian limestones in the coastal bluffs of the eastern shore of the Khadzibei estuary, in three km northwards from the Cherevychnoe village and in 20 km from Odesa (fig. 1). Age of the lower fosilliferous horizon (Cherevychnoe 3) is based on the small mammal and responds to the early Maeotian, MN 12 (Nesin, Nadachowski, 2001). Tretya Krucha locality includes the numerous remains of vertebrates, dated by the early middle Maeotian (MN 12). It was discovered in 2002 in a coastal slope of the Kuyalnik estuary (fig.1), between the Kubanka and Krasnoselka villages, Odesa Region. The bones of freshwater fishes, amphibians, reptiles, birds, as well as small mammals are located in alluvial layer of gravels having a thickness of about 2 m, which lies on sandy loams with *Mactra* sp. (Sinitsa, 2005). It can be assumed based on the preservation of bone remains that they were transported by the water flow on a short distance and later deposited near the site of the death of animals (Kovalchuk, 2015).

Systematic paleontology

Subdivision TELEOSTEI Müller, 1846
Order SALMONIFORMES Bleeker, 1859
Family SALMONIDAE Cuvier, 1816
Hucho Günther, 1866
Type species: *Hucho hucho* (Linnaeus, 1758)

***Hucho* sp.**

Description. The opercular bone (fig. 2, 3, *a, a*$_1$) is high, dorsally narrowed and ventrally expanded. The maximum width at the straight ventral edge is about 1.2–1.3 of the bone height. Oval articular facet (*fovea articularis*) is slightly elongated. From its upper part the dorsal edge of the bone is curved dorsocaudally and breaks off vertically. There is a noticeable bulge in the articular part of the bone. The anterior opercular edge is almost vertical, extends slightly forward below the ventral edge of articular facet and forms a shallow ventral caudal incurvity. The ventral border of the opercular is somewhat convex and longer than the dorsal border, while the upper part of the posterior border is gently concave. Posterior ventral angle is straight, anterior ventral angle is about 80°. The outer surface of

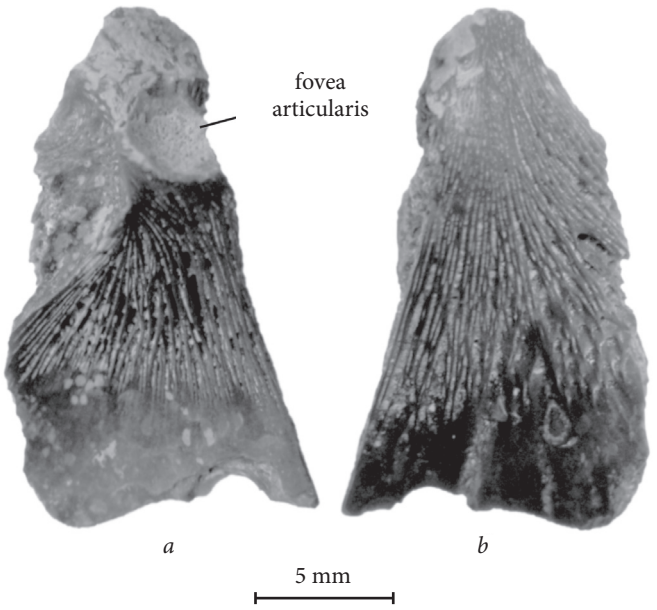

Fig. 2. Left opercular bone of *Hucho* sp., NMNHU-P 41/3079, Tretya Krucha: *a* — medial view; *b* — lateral view. Scale bar 5 mm.

the bone is sculptured by weak radial grooves directing ventrocaudally from the articular facet area. There are numerous shallow furrows at the inner surface of the opercular bone diverging radially from the articular facet and reaching in a length of about 2–2.5 of its height. Measurements are presented in the table 1. Elongated jaw canine teeth (fig. 3, *b, c*) are conical, with slightly curved crowns, rounded thickened bases and sharpened tops. Height of the teeth is 7.0 and 5.0 mm, diameter of the crowns — 2.6 and 2.1 mm, respectively.

Comparison. Presented bones are the most similar in morphology with those in representatives of the genus *Hucho* Günther, 1866. *Hucho* sp. from the late Miocene of Ukraine, in comparison to extant *Hucho hucho* and *H. taimen*, is characterized by smaller, slightly higher and narrower opercular bones. Specimens from Kubanka 2 and Cherevychnoe 3 have most as twice shorter articular process and significantly smaller diameter of the articular facet. Described opercular bones are comparable in size and completely similar to those in *Hucho* sp. from the late Oligocene — middle Miocene of Russia (Sytchevskaya, 1989) except the presence of well-visible weak radial grooves at the inner surface. Although jaw teeth are similar to those of *Hucho*, I only tentatively identify them as belonging to this genus because of the significant resemblance of teeth in salmonid taxa and the lack of reliable diagnostic features for this kind of remains.

Table 1. Measurements of opercular bones of *Hucho* sp. from the late Miocene of Ukraine: AAH — articular axis height; OW — opercular width; LAP — length of articular process; DAF — diameter of articular facet

Locality	n	AAH, mm	OW, mm	LAP, mm	DAF, mm
Tretya Krucha	4	18.1–26.0	13.6–21.2	4.6–8.1	1.9–3.6
Cherevichnoe 3	16	15.3–23.7	11.4–19.1	4.1–4.6	1.9–3.2
Kubanka 2	40	13.8–19.4	11.5–15.0	3.1–3.7	1.8–2.4

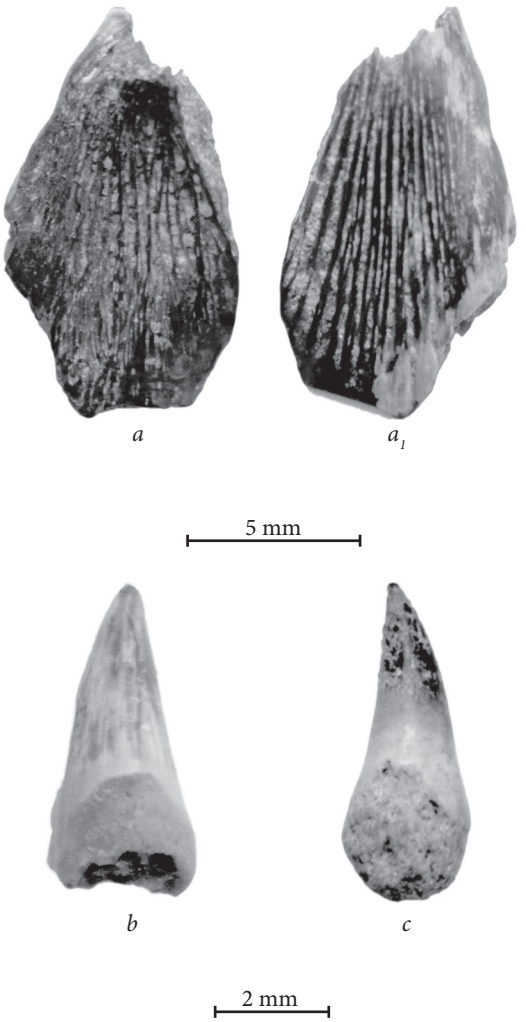

Fig. 3. Remains of *Hucho* sp. from the late Miocene localities of southern Ukraine: *a*, a_1 — fragment of left opercular bone, NMNHU-P 41/3746, Kubanka 2 (*a*— medial view; a_1— lateral view). Scale bar 5 mm; *b*, *c* — isolated jaw teeth, NMNHU-P 45/5699–5700, Cherevychnoe 3. Scale bar 2 mm.

Discussion

The genus *Hucho* Günther, 1866 is primarily Asian. It consists of five extant taxa (Pauly, Froese, 2014) including two species (Danube salmon *Hucho hucho* and Siberian taimen *Hucho taimen* Pallas, 1773) which are native to Europe (Nelson, 2006; Movchan, 2011). Other species are endemic for China (*Hucho bleekeri* Kimura, 1934) and North Korea (*Hucho ishikawae* Mori, 1928). *Hucho perryi* (Brevoort, 1856) is spread in the Northwest Pacific and is phylogeneticaly unrelated to the other *Hucho* species. This species is categorized into a separate genus *Parahucho* (Shedko et al., 1996).

The earliest representatives of the genus so far known (identified as *Hucho* sp.) appeared in the fossil record in the Oligocene — middle Miocene (between 21.2–13.2 Ma) of Russia, in the Dshilindy locality at the Vitim plateau (Sytchevskaya, 1989). Remains of the extant *Hucho hucho* along with *Salmo trutta* are reported from the late Pleistocene (27.0–43.0 kya) of Hohle Fels near Schelklingen in Germany (Böhme, Ilg, 2003; Conard et al., 2013).

Evolutionary history of the other species of the genus *Hucho* is still unknown (Holčik, 1982). There is a big gap between the existence of the first representatives of this genus in Asia, and their appearance in the fossil record in Europe. This gap is partially filled with findings of the huchen remains in the late Miocene of Ukraine. Obtained data are congruent with the hypothesis that divergence of salmonid lineages on the generic level occurred within 42–20 Ma, and further species diversification took place during the last 12 Ma (Shedko et al., 2013). Extant European huchen species have appeared ca. 1.9–1.6 Ma, in the early Pleistocene (Marić et al., 2014).

Conclusions

The genus *Hucho* Günther, 1866 has originated likely in the Eastern Asia at the end of Oligocene (ca. 22 Ma). This may be suggested due to discovery of the oldest known huchen fossils, as well as their present significant species diversity in this region. These fish were spread in water bodies of Asia and Siberia during the early Miocene and later, presumably at the end of the middle — early late Miocene, they first appeared in Europe. Given the ecological features of huchens (anadromous character of migrations and tolerance to water salinity — see Holčik, 1990; McCormick, 1994), the latitudinal settlement of this genus could be due to the existence a great marine basin (Paratethys) in the Miocene of Eurasia. Disappearance of this basin (gradual drying and the formation of the Aral-Ponto-Caspian complex with high water salinity) led ultimately to the fragmentation of the once wide range of the genus *Hucho* in the Pliocene. Modern European huchen species emerged most likely in the early Pleistocene. The endemic character of one of them (*Hucho hucho*) may be due to transformations of river network in Eastern Europe after the last glaciation.

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