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A New Dipnoan from the Middle Devonian (Givetian) of Central Russia[1]

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Abstract—A new dipnoan species, *Dipnotuberculus bagirovi* sp. nov. (Dipnoiformes, Dipnorhynchidae), is described based on an incomplete palatal part of the skull from the Upper Givetian (Middle Devonian) of the Pavlovsk (Shkurlat) quarry in the Voronezh Region of Central Russia. This is the first discovery of dipnoan material in the Middle Devonian of the Central Devonian Field of Russia and the first record of Dipnorhynchidae of this age within the Baltic paleozoogeographical Province. Distribution analysis of this family supported by general zoogeographical faunistic analysis suggests the dipnorhynchid dispersal from Gondwana to Laurussia via Armorican faunistic province.

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INTRODUCTION

The Dipnorhynchidae include the Lower Devonian East Gondwanan genera *Dipnorhynchus* Jaekel, 1927 and *Cathlorhynchus* Campbell, Barwick et Senden, 2009; the Middle Devonian (Givetian) North Gondwanan genus *Dipnotuberculus* Campbell, Barwick, Chatterton et Smithson, 2002; and the problematic Middle-Upper Devonian Laurussian, Armorican, and North Gondwanan genus *Ganorhynchus* Traquair, 1873 .The new specimen described here is referred to the dipnorhynchid lungfishes and identified as a new species of the genus *Dipnotuberculus* Campbell et al, 2002 on the basis of the following features: the palate is formed by a single plate; the dentition consists of paired marginal and intermediate and unpaired median ridges, forming symmetrically disposed obtuse, tuberous teeth separated by furrows or depressions corresponding to projecting tuberosities on mandible for occlusion and bearing traces of lifetime wear; margins of the palate have a raised rim along its posterolateral edge; the dorsal area forms an irregularly ornamented surface resulting from former lifetime contact to coarse vascular bone of the weakly ossified braincase (Campbell et al., 2002).

Geological and Geographical Setting

The new specimen originates from scree siltstones of the Vorobyevka–Yastrebovka Regional Stage (Middle Devonian, Givetian), exposed in the Pavlovsk (Shkurlat) quarry, 160 km south-southeast of the city of Voronezh, Voronezh Region, Central Russia (Fig. 1).

A distinctive feature of the Pavlovsk quarry is that it is the only known site in the Central Devonian Field of Central Russia, in which the Middle Devonian deposits are exposed to the day surface. The geological section is characterized by the presence of diverse fossil assemblages, including invertebrates, vertebrates, and

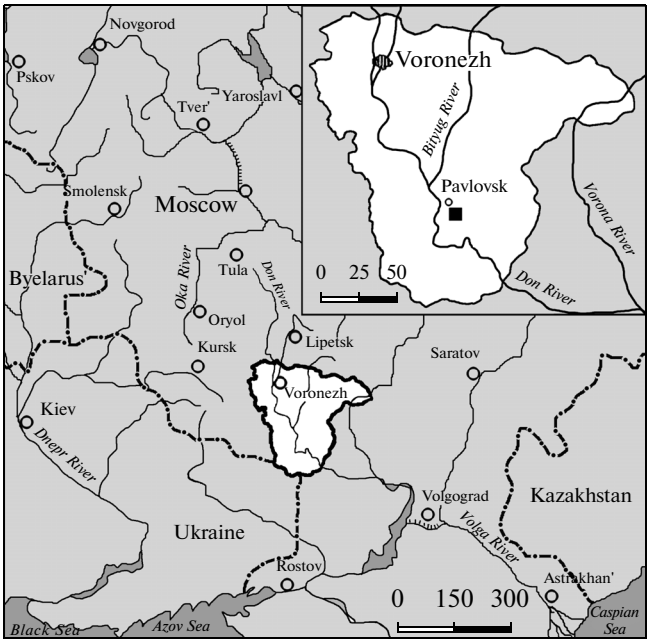

Fig. 1. Schematic map of Voronezh Region, Central Russia, showing the position of the locality (black square): Base map shows the central and southern parts of Eastern Europe.

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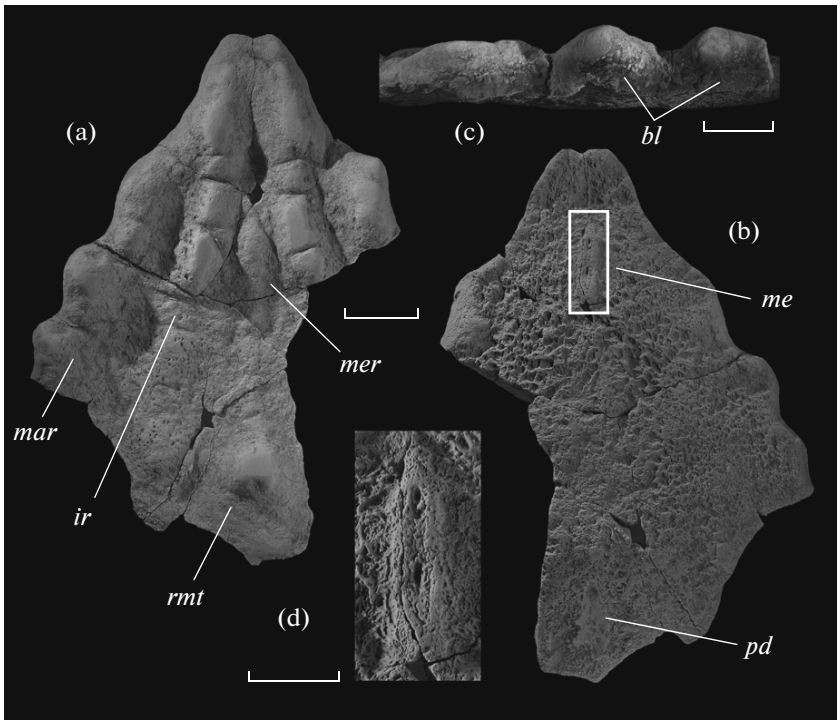

Fig. 2. *Dipnotuberculus bagirovi* sp. nov., holotype PIN, no. 5163/50, incomplete palatal skull part, Pavlovsk (Shkurlat) quarry, 160 km south-southeast of the city of Voronezh, Voronezh Region, Central Russia; Vorobyevka–Yastrebovka Regional Stage, Givetian, Middle Devonian: (a) ventral view, (b) dorsal view, (c) tuberosities of the left lateral side showing the blisters, (d) enlargement of the median elevation area in the white box at 2b. Designations: (*bl*) blisters, (*ir*) intermediate tooth row, (*mar*) marginal tooth row, (*me*) median elevation, (*mer*) median tooth row, (*pd*) posterior depression on the dorsal surface, (*rmt*) rounded medial tooth.

plants. Invertebrates include brachiopods, bivalves, crinoids, colonial and solitary corals and conodonts. Remains of flora are represented by abundant algae, higher plants, micro- and megaspores (Raskatova, 2004). This interval also yielded abundant remains of a diverse vertebrate assemblage, including psammosteids: *Psammosteus* cf. *P. praecursor* Obruchev, *Psammolepis* sp., *Schizosteus shkurlatensis* Moloshnikov (Moloshnikov, 2009); ptyctodont placoderms: *Rhynchodus* sp., "*Ptyctodus*" sp.; arthrodires: *Holonema* sp. nov., *Livosteus* sp. nov., *Eastmanosteus* cf. *E. pustulosus* (Eastman), *Actinolepis* sp.; teeth and scales of osteolepiform rhipidistians (Ivanov, 2009) and dipnoans, including a new species of the genus *Dipnotuberculus*, described below.

MATERIALS AND METHODS

A fragment of a lungfish palate was found by the amateur paleontologist S.V. Bagirov in the Pavlovsk quarry of the Voronezh Region, Central Russia in 2008. This collector kindly donated the specimen to the Paleoichthyology Department of the Borissiak Paleontoiogical Institute of the Russian Academy of Sciences, Moscow (PIN), where the specimen is housed and catalogued as PIN, no. 5163/50. Preparation of the specimen was carried out by mounted needle and etching in dilute acetic acid. Photographs of the specimen were taken whitened by ammonium chloride.

SYSTEMATIC PALEONTOLOGY

INFRACLASS DIPNOI MÜLLER, 1844

Order Dipnoiformes Cloutier, 1990

Family Dipnorhynchidae Berg 1940

Genus *Dipnotuberculus* Campbell, Barwick, Chatterton et Smithson, 2002

***Dipnotuberculus bagirovi* sp. nov.**

Etymology. The species is named in honor of S.V. Bagirov, who collected the specimen and donated it to the PIN.

Holotype. PIN, no. 5163/50, incomplete palatal skull part, Pavlovsk (Shkurlat) quarry, 160 km south-southeast of the city of Voronezh, Voronezh Region, Central Russia; Vorobyevka–Yastrebovka Regional Stage interval, Upper Givetian, Middle Devonian.

Diagnosis. Wide anterior corner of palatal skull part with paired tuberous teeth on each side from midline. Paired intermediate tooth rows continuing paired anterior teeth. Teeth of intermediate row elongated rostrocaudally rather than transversally.

Description (Figs. 2a–2d). The palatal fragment of PIN, no. 5163/50 belonged to a senile individual, judging from the tooth wear and width of furrows separating the tooth rows. The palate is in the shape of a sharp triangle in outline, its right and left posterolateral corners are broken off. The maximum

length of the specimen in the best preserved place is 10 cm; the maximum reconstructed width is 8 cm. The palate narrows rostrally, demonstrating symmetry in the pattern of paired and medial tooth rows. Anterior angle of the palate is about 70°. The absence of a median suture suggests complete fusion of pterygoids at the midline in the complex forming the palate. The parasphenoid contact surfaces or sutures are unrecognizable on either surfaces of the specimen.

Ventral surface (Fig. 2a). The general pattern of tooth rows arrangement is the rostrocaudal bifurcation of marginal (*mar*) and intermediate (*ir*) ones over each side of the palate from the anteriormost pair of elongated teeth over the beaklike process. The median tooth row (*mer*) wedges in between the paired intermediate branches. The lateral margins are bounded on both sides by rows of large massive obtuse teeth separated by gaps of approximately equal length. The teeth are tuberous and elongated rostrocaudally. The apices of marginal teeth slant laterally. The posteriormost tooth in the median row (*rmt*) is rounded in outline. The intermediate rows (*ir*) consist of pairs of elongated teeth forming a ridge running from the anterior tip of the palate and extending over the anterior one-third of the palate length, then fading due to heavy wear. The angle between these intermediate rows is 35°. The median tooth row runs along the midline from a poorly developed elongated anterior tooth, then fades and reaches a large mesial symmetrical tooth close to the caudal margin of the specimen. Wide shallow furrows separate the marginal rows from the intermediate ones and the latter from the median row. The furrows seem especially wide in comparison with those in the type species due to heavy wear of large posterior teeth in the intermediate rows. The posterior part of the specimen lacks a flat raised surface of the type found in *Dipnotuberculus gnathodus*. The only short edge of the palate preserved at the midline tapers caudally to the mesial tooth.

Dorsal surface of the palate (Fig. 2b) is sculptured with a meshwork of irregularly arranged pits resulting from close contact with a loose vascular endochondral bone of the ventral part of the braincase, poorly ossified during the animal's life and weathered in the burial. Anteriorly, in the midline, there is a narrow rostrocaudally elongated elevation (*me*) composed of more compact bone (Fig. 2d). Its dorsal surface has two small pits positioned one after another, the function of which is unclear. Close to the caudal margin on the midline, there is a shallow irregularly shaped depression lined with compact bone, the surface of which is pitted by small vascular canals (*pd*). This isolated area suggests close connection of unknown part of the brain cavity. Thin, slightly expressed rounded ridges, best preserved on the right side, run along the lateral margins of the palate.

Lateral surface (Fig. 2c). The dorsal edge of the lateral margin is ornamented by small dentine blisters (*bl*), the surface of which is shiny possibly because of enameloid coating. The blisters are generally rounded but irregularly shaped, closely spaced; their tops are flattened. Blisters provide material for marginal growth of the dental plate (Campbell and Barwick, 1985; Campbell et al., 2002).

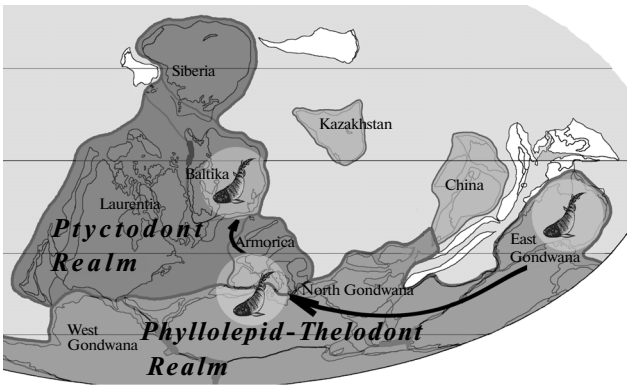

Fig. 3. Global paleozoogeographical regionalization during the Givetian and migration of the Dipnorhynchidae (redrawn from Lebedev and Zakharenko, 2010, modified). Base map after Golonka (2007), modified.

Comparison and remarks. Comparison of the palate of the new form with that of *Dipnotuberculus gnathodus* (Campbell et al. 2002, Fig. 3) shows their distinction despite general similarity.

Similarities include general resemblance of the palate shape and structure. These unpaired plates bear separate tuberous teeth ("tuberosities", Campbell et al., 2002) set in rostrocaudally directed unpaired median, paired marginal, and intermediate rows. The dorsal surface of the palate contacted poorly ossified braincase, which resulted in preservation of ornament formed due to contact to a coarse poorly ossified endochondral bone. The accretion areas of the new dental material are marked by small dentine blisters concentrated at the lateral margins of the palatal plate.

Distinctions in the palatal structure of these two species concern the structure of the anterior corner, including the shape of the median tuberosity and arrangement of the tooth rows. In *Dipnotuberculus gnathodus* (Campbell et al., 2002, text-Fig. 3a), the anterior tooth is a high, elongated bulb bearing no trace of the median groove, while, in the new species, the corner itself is wider and the tooth is paired (Fig. 2a). The paired intermediate tooth rows of the new species continue the anterior tooth, while, in the type species, they rather wedge in between the median and marginal rows. The teeth of the intermediate row are elongated rostrocaudally rather than transversally, as in *Dipnotuberculus gnathodus*.

DISCUSSION

Paleozoogeographical Considerations

Campbell et al. (2009) briefly discussed the distribution of Early Devonian dipnorhynchids, concluding

that, during this time, Gondwanan dipnorhynchids evolved in isolation within this area. Subsequent history of the group is not known in East Gondwana and their migration to North Gondwana during the Givetian was the major event (Campbell et al., 2002). During the Frasnian, the questionable dipnorhinchid *Ganorhinchus* reached Armorica (Gross, 1965) and Laurussia (France: Cloutier and Candilier, 1995; Pennsylvania, USA: Newberry, 1890; Voronezh Region, Russia: Krupina, 2004). The only find of this genus was described by Krupina (1979) also from the Famennian of Transcaucasus. Only now the true dipnorhynchid Dipnotuberculus also became known from the Givetian of Laurussia (Fig. 3). Further zoogeographical study requires the analysis of accompanying vertebrate assemblages. Possibly associated with *Dipnotuberculus* is the only local Moroccan endemic arthrodire *Maideria* (Leliévre, 1995) of approximately the same age and known in geographical proximity from the Djbel Issoumour locality (Campbell et al., 2002). Comparison of assemblages is thus possible only on a higher, provincial scale. Apart from these two genera, the north Gondwanan list includes the endemic arthrodire *Hollardosteus*, polydemic thelodont *Turinia,* chondrichthyan *Antarctilamna*, acanthodian *Cheiracanthoides*, and cosmopolitan chondrichthyans *Phoebodus* and *Omalodus* (Lebedev and Zakharenko, 2010). Polydemic *Turinia* demonstrates connection with East Gondwana and Western Yunnan; *Antarctilamna* is distributed within Gondwana, except for its western part, and questionably known from Spain. *Cheiracanthoides* is known from North and East Gondwana, but also described from Germany. The distribution of *Phoebodus* and *Omalodus* is almost identical and includes Laurentia, Baltica, Armorica, and Siberia within the Ptyctodont Realm. *Phoebodus* is also known from both East and North Gondwana in the Phyllolepid–Thelodont Realm, but *Omalodus* has not been found in Australia (Lebedev and Zakharenko, 2010).

Thus, the prevailing connection of a large part of the assemblage suggests East Gondwanan affinity, that is, agrees with the previously proposed origin of dipnorhynchids. The second but no less important direction of dispersal is Armorican; this also supports the Gondwanan–Laurussian trend of dipnorhynchid spreading during the Givetian–Frasnian (Fig. 3).

The faunal list of the Central Devonian Field, a part of the Baltica Province, includes a different set of vertebrates: the most numerous group comprises local and provincial endemics: the acanthodians *Miniioracanthus, Ptychodictyon, Rhadinacanthus* and the placoderm *Actinolepis*; didemics include the agnathan *Psammolepis*, acanthodians *Diplacanthus* and *Acanthodes; Cheiracanthus* and *Holonema* are polydemic (Lukševičs et al., 2010). Recently obtained information adds to this list the provincial endemic agnathans *Psammosteus* and *Schizosteus*, arthrodire *Livosteus*, and the didemic porolepiform *Laccognathus.* Polydemics include the placoderms "*Rhynchodus*", "*Ptyctodus*," and Eastmanosteus (Ivanov, 2009; Moloshnikov, 2009). Cosmopolitans are not known.

The number of polydemics is restricted, suggesting that this fauna is relatively isolated. *Holonema* occurs in the Ptyctodont Realm: apart from Baltica it is described from Laurentia (Spitsbergen, Scotland, Boulonnais, North America) and Siberia (Altai, Russia) (Denison, 1978). Indication that it is present in the Givetian of North Gondwana by Lebedev and Zakharenko (2010) is erroneous (Lebedev, 2013, pers. comm.). *Cheiracanthus*, despite its polydemic status, is limited to Baltica, Laurentia, and Kolyma (Valiukevičius, 1988), but this data is useless, only indicating a wider distribution of the genus rather than only the Ptyctodont Realm, as the last province is not assigned to any of two major Givetian biochores. The same refers to the distribution of *Eastmanosteus*, showing its connection with South China (Zhu, 2000). Only "*Rhynchodus*" and "*Ptyctodus*" definitely indicate the Armorican affinity (Lebedev and Zakharenko, 2010). Of the North Gondwanan and Baltican faunal lists, only *Dipnotuberculus* is shared by the two assemblages. Nevertheless, both faunas are indirectly connected with each other via the Armorican Province. This supports the hypothesis of the dipnorhynchid dispersal from Gondwana to Laurussia through Armorica.

CONCLUSIONS

The new dipnoan *Dipnotuberculus bagirovi* sp. nov. increases the composition of the Middle Devonian vertebrate assemblage from the Pavlovsk quarry and Russian Plate. This is the first record of dipnorhynchid dipnoans in the Givetian of Central Russia and Baltica Zoogeographical Province in general.

Distribution analysis of this family supported by general zoogeographical faunal analysis suggests the dipnorhynchid dispersal from Gondwana to Laurussia via the Armorican faunistic Province.

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