New finds of fishes in the lower uppermost Famennian (Upper Devonian) of Central Russia and habitats of the Khovanshchinian vertebrate assemblages

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Abstract. New vertebrate finds from the Khovanshchinian Regional Stage (lower uppermost Famennian, Upper Devonian) made an important contribution to our knowledge of the composition and distribution of vertebrate assemblages in Central Russia. The remains of the latest arthrodires found for the first time in the East European Platform are described from the Voskresenskoye quarry (Lipetsk Region, Central Russia). Those occur within the deposits of the same basin, which had also been dwelled by tetrapods. The upper and uppermost Famennian non-groenlandaspidid arthrodires are known from only few localities in North America, Belgium and Poland. The separation of habitats of the tetrapod community and arthrodires in the Khovanshchinian basin may be due to local variations in the salinity level; these placoderms are possibly stenohaline marine dwellers. Environmental conditions of vertebrate communities in the Khovanshchinian Sea of the Moscow syneclise basin ranged from shallow-water brackish environment with still hydrodynamics and fast sedimentation to marine conditions with active hydrodynamics in the near-shore shallow waters. The osteolepiform genus *Eusthenodon*, recognized now from the Gorbachevo quarry (Tula Region, Central Russia), is characteristic of the Khovanshchinian vertebrate assemblage of Central Russia, but is also a marker genus of palaeotetrapod communities in Laurussia and East Gondwana.

Key words: Devonian, Khovanshchinian, Central Russia, Arthrodira, *Eusthenodon*, bivalves, ostracods, palaeoecology, vertebrate communities.

INTRODUCTION

For a long time, the Andreyevka-2 locality in the Tula Region (Central Russia) was the only source of information on vertebrates from the lower uppermost Famennian Khovanshchinian Regional Stage (RS). The Andreyevka-2 community including antiarch placoderms, acanthodians, chondrichthyans and osteichthyans, as well as tetrapods, has been discussed on repeated occasions by the first author of this paper (Lebedev 1986, 1992, 2013; Lebedev et al. 2010). Abundant remains of ostracods, bivalves, ‘serpulid worms’ (microconchs), charophyte algae and stromatolites from this section in association with vertebrates have been discussed by Alekseev et al. (1994).

In 2011, S. V. Grishin of the Geological Institute of the Russian Academy of Sciences (GIN RAS) presented a postcranial bone of an arthrodire placoderm to the Borissiak Paleontological Institute of RAS (PIN RAS). Grishin had found the bone in the Voskresenskoye quarry in the Lipetsk Region (Central Russia) (Fig. 1). He also extracted, and V. A. Aristov (GIN RAS) identified conodonts from the matrix around the specimen. Those turned out to be characteristic of the Famennian Ozerkian–Khovanshchinian interval of Central Russia. As the matrix block which yielded fossils was similar in its lithological features to the Khovanshchinian part of the section and disposed only slightly below apparently Malevkian strata in this quarry, the age of the specimens described in this paper is regarded to be Khovanshchinian rather than Ozerkian. In addition to conodonts, dental plates of juvenile lungfishes became also etched with acid from the same piece of rock. No arthrodires had been known from the Khovanshchinian vertebrate localities of Central Russia before.

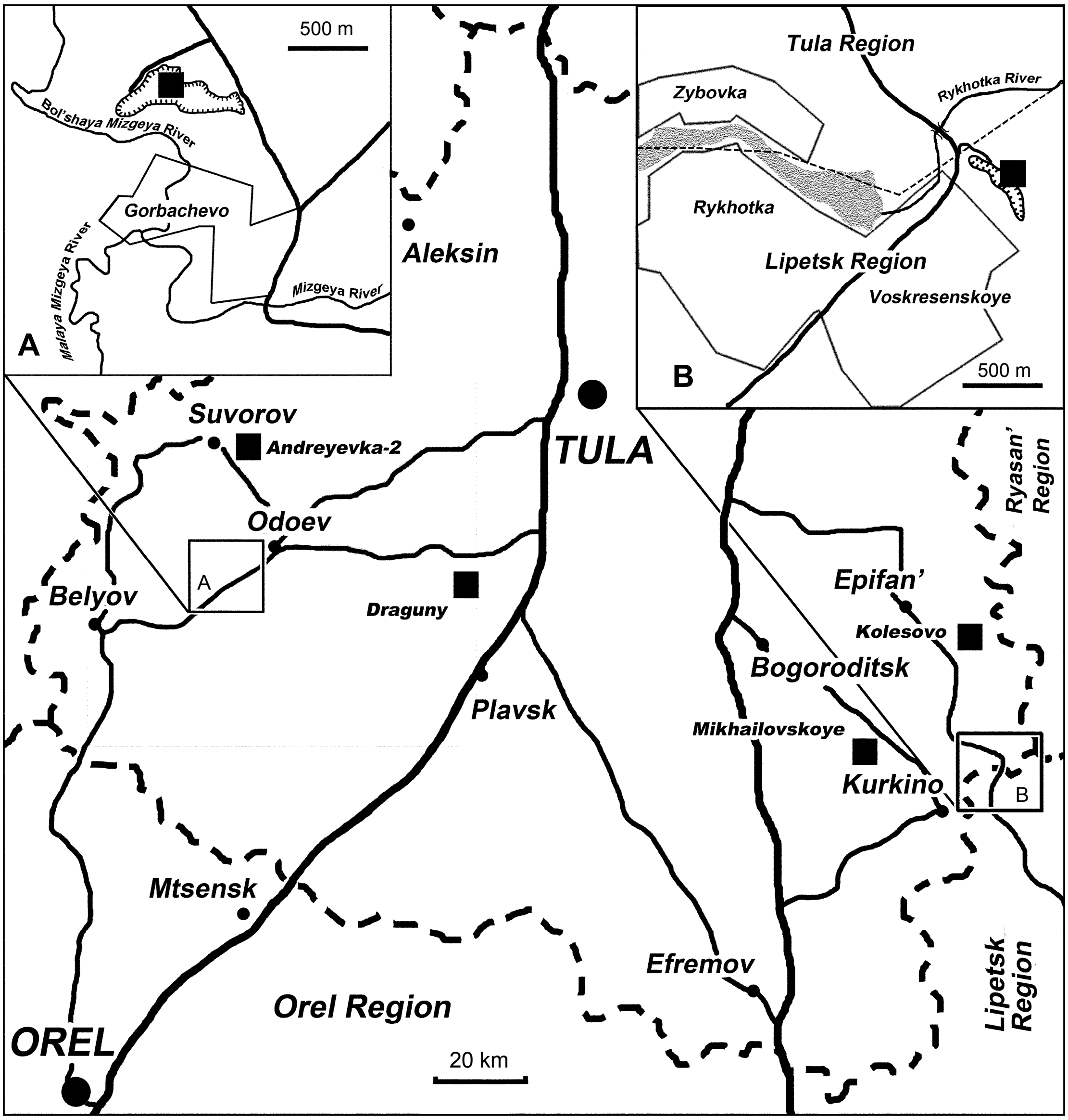

Fig. 1. Vertebrate localities of the Khovanshchinian RS (lower uppermost Famennian, Upper Devonian) in Central Russia. **A**, position of the Gorbachevo quarry; **B**, position of the Voskresenskoye quarry.

In 2013, the first author of this paper in co-operation with other staff members of the PIN RAS, A. V. Pakhnevich and S. V. Bagirov, visited some Khovanshchinian vertebrate localities in the Tula and Lipetsk regions. They found two more arthrodire specimens in the same quarry. In 2014, Yu. A. Gatovsky (Geological Faculty, Lomonosov Moscow State University) identified a conodont assemblage from the matrix of the second arthrodire specimen. More juvenile dipnoan tooth plates as well as acanthodian scales and conodonts were obtained from a new sample. During the same visit A. V. Pakhnevich found a uniquely preserved natural external mould of the ventral side of the skull of an osteolepiform sarcopterygian *Eusthenodon* sp. typical for the Famennian palaeotetrapod communities of Laurussia in the Khovanshchinian deposits of the Gorbachevo quarry in the west of the Tula Region (Fig. 1).

In this paper, we describe the newly obtained vertebrate and invertebrate material. We discuss the differences in the composition of the marine communities in the Khovanshchinian basin on the territory of the present-day Tula and Lipetsk regions (Central Russia) and suggest possible reasons for these differences.

MATERIAL AND METHODS

The postcranial bones of arthrodires PIN 2921/3267 (right posterior dorsolateral, PDL) and PIN 2921/3268 (an indeterminate fragment of the arthrodire dermal plate) were prepared manually. The arthrodire right anterior lateral plate PIN 2921/3269 (AL) was extracted in pieces from the limestone block at the locality, impregnated with polyvinylbutiral consolidant and put together. Then the specimen was etched with a 10% acetic acid solution.

The bones themselves of the osteolepiform sarcopterygian *Eusthenodon* sp. PIN 2921/3270 are almost absent from the surface of the natural mould, despite its satisfactory preservation showing the ventral side of the skull. A latex cast was made from this natural mould. Macrophotography was performed using ammonium chloride whitening. Dipnoan tooth plates were photographed with the scanning electronic microscope TESCAN VEGA in the PIN RAS.

Ostracods and bivalves could not be extracted from limestone by either hyposulphite or concentrated acetic acid processing. Thus these specimens were studied on the surface of the rock broken into small blocks.

Vertebrate materials are stored in the Borissiak Paleontological Institute of the RAS (Moscow) (collection PIN 2921), bivalves in the Department of Paleontology and Stratigraphy of Kazan Federal University (Kazan). Ostracods are deposited in A. P. Karpinsky Russian Geological Research Institute (VSEGEI), St Petersburg.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Khovanshchina Beds, the topmost Devonian strata in the central part of the East European Platform, were originally recognized and described by A. S. Kozmenko in the central part of European Russia (Tula Governorate) (Kozmenko 1911). Later, in assemblage with the nether Ozerki Beds, those were included in the Zavolzhskian RS and finally, according to the decisions of the Interdepartmental Regional Stratigraphic Session in 1988, became regarded as a separate regional stage (*gorizont*) (Rzhonsnitskaya & Kulikova 1990). The deposits of the Khovanshchinian RS are spread on the East European Platform within the Moscow Syneclise and on the eastern slope of the Voronezh Anteclise. The Khovanshchinian RS conformably overlies the Ozerkian RS, but there is a hiatus between the former and the locally overlying it basal Tournaisian Kupavna Formation of the Malevkian RS (Rodionova et al. 1995). The position of the Devonian–Carboniferous boundary on the East European Platform, especially in the Moscow Syneclise, and the duration and correlation of the Hangenberg Event interval with respect to the breaks in sedimentation below the base of the Carboniferous are thoroughly discussed by Menning et al. (2006). Rzhonsnitskaya & Kulikova (1990) correlate the Khovanshchinian RS to the upper part of the *costatus* conodont Zone (CZ) which is equivalent to the lower part of the *praesulcata* CZ of the standard conodont zonation (Ziegler & Sandberg 1990). Unfortunately, Devonian conodont assemblages on the East European Platform are dominated by shallow-water taxa and thus exact and direct correlation to the standard conodont scale is not possible (Alekseev et al. 1994; Rodionova et al. 1995). Alekseev et al. (1996) placed the Khovanshchinian RS in the middle of the local *Pelekysgnathus peejayi* CZ using the palynological data as an intermediate tool. These authors demonstrated that this zone spans the Middle–Upper expansa + praesulcata CZ interval of the standard scale, thus the Khovanshchinian RS was correlated to the upper part of the *expansa* CZ.

The Voskresenskoye quarry (Fig. 1B) is located on the right bank of the Rykhotka River (right tributary of the Don River), about 100 m to the north of the Voskresenskoye village (Lipetsk Region, Dankov District). The section in the quarry includes carbonates of the Khovanshchinian RS (lower uppermost Famennian, Upper Devonian) and the Malevkian RS (Lower Tournaisian, Lower Carboniferous). The Khovanshchinian deposits are massive limestones including numerous horizons of dome-shaped stromatolites. The Malevkian deposits are argillaceous limestones intercalated by thin clay layers. Unfortunately, all specimens from the Voskresenskoye quarry are found in the talus or isolated limestone blocks stored in a heavily piled-up part of the quarry that prevents exact recognition of the fossiliferous layer in the succession.

The rock which yielded the arthrodire bones is a light grey organogenic (ostracod) limestone with inclusions of bivalves identified as '*Arca*' cf. *oreliana* de Verneuil and overfilled with ostracods *Cryptophyllus socialis* (Eichwald) dispersed on the bedding planes. Venyukov (1886, p. 161) considered the latter species to be characteristic of the Upper Famennian Dankov–Lebedyan strata (according to the present stratigraphic chart Lebedianian + Optukhovian + Plavskian RS) of the Central Devonian Field (CDF). Later these forms became known even from the Lower Frasnian (Nalivkin 1953).

The Gorbachevo quarry (Fig. 1A) is located about 1 km to the north of the Gorbachevo village on the right bank of the Bol′shaya Mizgeya River (Tula Region, Odoyev District). The quarry exposes the deposits of the Khovanshchinian RS (lower uppermost Famennian) represented by limestones and dolomites interbedded by clays. Locally the carbonates are strongly impregnated by gypsum. Stromatolites build significant parts of the section in some areas. An external mould of the *Eusthenodon* skull has been found in a block of greyish-yellow, strongly cavernous clayey limestone in the talus.

The rock samples with arthrodire bones from Voskresenskoye also include conodont elements characteristic of the Ozerkian–Khovanshchinian interval (lower uppermost Famennian) in Central Russia: *Icriodus costatus* (Thomas, 1949), *Pandorinellina humulus* (Rhodes, Austin & Druce, 1969), *Pelekysgnathus* aff. *peejayi* Druce, 1969, *Bispathodus stabilis* (Branson & Mehl, 1934) and *Acodina* sp. (identification by V. A. Aristov and Yu. A. Gatovsky). *Icriodus costatus* is known in the CDF from the Kudeyarovo Beds (the upper part of the Plavskian RS) to the Khovanshchinian RS. *Pelekysgnathus* aff. *peejayi* was also recorded in the Khovanshchinian deposits in borehole 71 (Mikhailovka, Saratov Region). All these forms inhabited shallow-water environments (Aristov 1988; Rodionova et al. 1995). The conodont assemblage may be referred to the local *Pelekysgnathus peejayi* CZ characterizing the Khovanshchinian RS (Gatovsky 2016).

RESULTS

The Khovanshchinian basin within the Moscow Syneclise was populated by foraminifers, ostracods, gastropod and bivalve molluscs, brachiopods, 'serpulid worms' (microconchs), charophytes, conodonts, as well as various fishes and early tetrapods; it is also characterized by numerous stromatolitic structures (Reutlinger 1960; Rodionova et al. 1995) (Fig. 2). Newly found vertebrate remains, as well as bivalves and ostracods occurring in association with those, are discussed below.

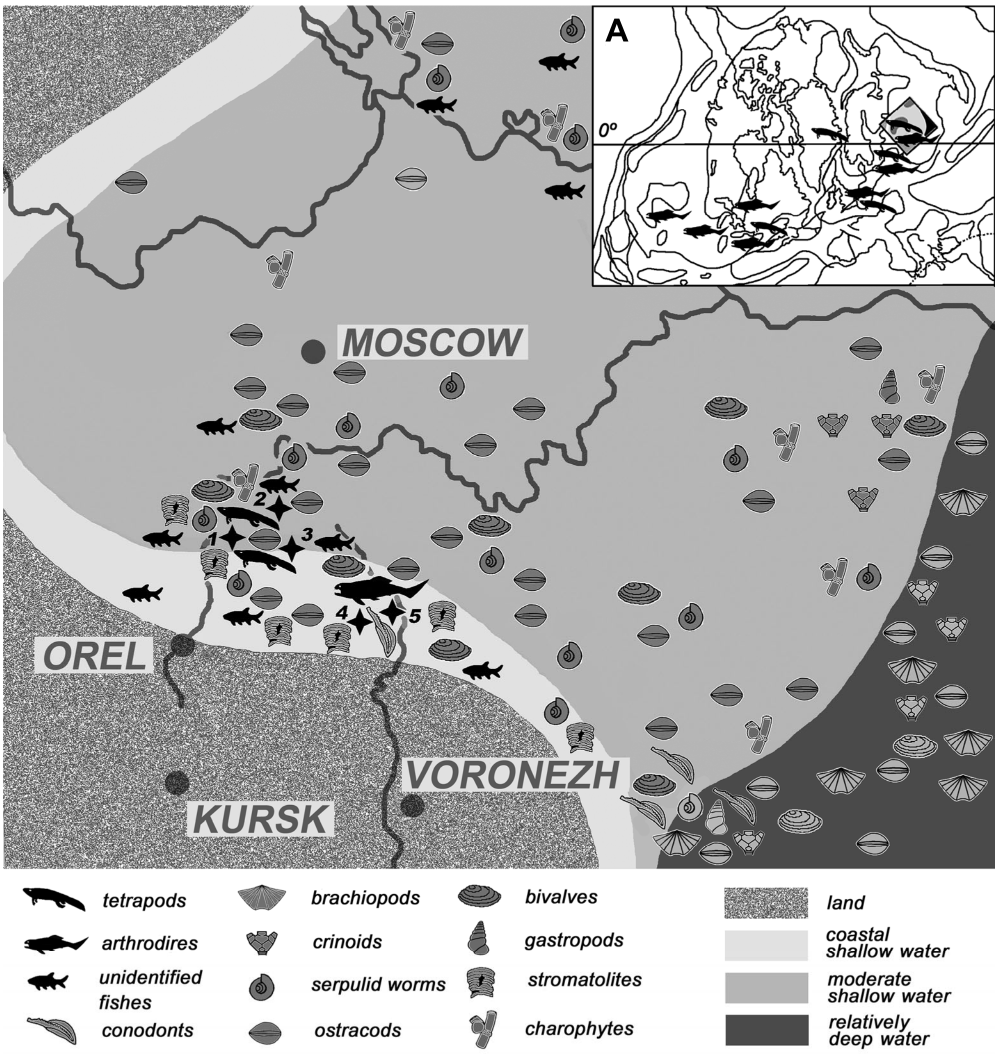

Fig. 2. Palaeobiogeographic scheme of the Khovanshchinian basin in the central part of the East European Platform. **A**, arthrodires and palaeotetrapod communities in Laurentia and Baltica palaeozoogeographic provinces. Localities: **1**, Gorbachevo quarry; **2**, Andreyevka-2; **3**, Draguny; **4**, Voskresenskoye quarry; **5**, Kolesovo quarry. Conodont data after Aristov (1988), palaeogeographic setting and data on other invertebrate groups after Makhlaev (1964). Data on the areas inhabited by tetrapods and arthrodires by the authors.

Bivalves

Bivalves are usually mentioned in the faunistic lists of the Khovanshchinian RS (for example, Makhlaev 1964; Rodionova et al. 1995), but their identifications are never listed due to poor preservation. Alekseev et al. (1994) also mentioned bivalves from two levels in the Andreyevka-2 section. These thin-walled valves are poorly visible on the rock surface and may be extracted only by chemical preparation if they are slightly silicified, but this is a rare case.

The limestone layer which yielded the arthrodiran anterior lateral plate in the Voskresenskoye quarry included isolated valves of small bivalves. The 5–10 mm long valves are placed on the bedding plane. The shell is elongated and inequilateral. The hinge line is straight and is slightly shorter than the maximum shell length. The umbo is shifted anteriorly and is located at a distance of a quarter of the length of the entire hinge line. A blunt keel runs diagonally from the umbo towards the lower and posterior margins. A slight depression running from the umbo to the lower margin gradually expands and tilts back. It forms a hardly visible notch on the lower edge. The valve surface is ornamented by thin, closely spaced, concentric dichotomizing growth lines running parallel to the shell edges. Features of external morphology correspond well enough to the diagnosis of the species '*Arca*' *oreliana* de Verneuil in Murchison et al. 1845 (p. 314, pl. XX, fig. 3). This species was described by de Verneuil from presumably Plavskian (Upper Famennian) limestones of the city of Orel and its images were published by Venyukov (1886, p. 161, pl. VIII, figs 6, 7) and Nalivkin (1947, pl. XXXIV, fig. 1). The attribution of this species to the genus *Arca* Linnaeus, 1758 cannot be accepted nowadays, but the material available does not make the revision possible.

The valves identified as '*Arca*' cf. *oreliana* de Verneuil are also mentioned from the Torchin Formation (correlating to the Khovanshchinian RS) of the Lviv–Volyn′ coal basin (Shulga 1962, p. 70). Hall (1885, pp. lvi, 516) described the bivalves *Archanodon* (*Amnigenia*) *catskillensis* (Vanuxem, 1842) from the Frasnian of the Catskill Formation in the New York State, which are very similar by their external morphology to that in '*Arca*' *oreliana* de Verneuil, but usually much larger. The latter species may turn to be conspecific to the former (or vice versa), but better preserved material is required for systematic revision.

Ostracods

The same limestone sample which includes the arthrodire bone and the mollusc valves is overfilled by ostracod shells. The ostracod assemblage is extremely monotonous taxonomically, being represented by morphotypes of *Cryptophyllus socialis* (Eichwald) described by Samoilova (1979) as *C. socialis* (Eichwald) forma *multicincta* and *C. socialis* (Eichwald) forma *chovanensis*. This species dominates (about 99%), few ?*Phlyctiscapha* cf. *pusilla* Gurevitsch, 1972 and *Sulcella* sp. specimens are also present.

These morphotypes have been described from the Khovanshchinian RS of the Ryazan Region and are also distributed in these deposits in the Moscow Syneclise and on the southern slope of the Voronezh Anteclise. Apart from that, the morphotypes *C. socialis* (Eichwald) forma *chovanensis* Samoilova and ?*Phlyctiscapha* cf. *pusilla* Gurevitsch are known, like '*Arca*' *oreliana*, in the Torchin Formation of the Lviv–Volyn′ basin (Gurevich 1972; Samoilova 1979).

Such an impoverished ostracod assemblage and concentration of micro- and macrofossils within a thin layer suggests coastal (intertidal?) sedimentary conditions in the Voskresenskoye locality.

Arthrodire placoderm fishes

The latest arthrodires from the CDF and the East European Platform, in general hitherto known ('*Dinichthys*' *makhlaevi*), were described by Obrucheva (1956) from the 'Orel–Saburovo Beds' (lower part of the Plavskian RS). Thus the material described here is the latest (youngest) record of arthrodires in this territory.

Late Famennian arthrodires belong to the families Titanichthyidae, Mylostomatidae, Selenosteidae, Dinichthyidae, Bungartiidae and Groenlandaspididae (Denison 1978). Members of the last one have been described from various localities in Laurentia and Gondwana (Janvier & Clement 2005). The fishes belonging to other families are known from Laurentia, with the exception of Polish species (Kulczycki 1957) in the margin of the Baltica palaeozoogeographic province (Lebedev et al. 2010). Laurentian non-groenlandaspidid arthrodires are known from only few localities, the most important of which is the Cleveland Shale assemblage in Ohio including a minimum of 18 genera (Carr & Jackson 2009). Separate species in common with it have also been recorded from the New York and Missouri states (USA) and Ontario province (Canada) (Denison 1978). Apart from North America and Poland, late arthrodires had been described from Belgium (Lelièvre 1982).

The major part of arthrodires are marine dwellers, but groenlandaspidid euryhalinity made possible their participation in numerous marine and non-marine vertebrate assemblages (Janvier & Clement 2005), including the Late Devonian tetrapod communities of Western Europe, eastern North America and eastern Australia (Lebedev 2004, 2013; Clack 2006). No other late arthrodires demonstrate faunistic affinities with the earliest tetrapod communities.

Osteolepiform fishes

Separate skeletal elements of the tristichopterid osteolepiform *Eusthenodon* are known from the three Khovanshchinian localities in the Tula Region of Central Russia (Fig. 1): Andreyevka-2 (Lebedev 1992, 2013; Alekseev et al. 1994), Mikhailovskoye quarry and Draguny section. A bone imprint identified as ?*Eusthenodon* sp. by its dermal ornament was found by Yu. V. Gatovsky in the Kolesovo quarry, Tula Region (Fig. 1). The natural mould of the ventral side of the skull, shoulder girdle and squamation of *Eusthenodon* sp. (PIN 2921/3270) from the Gorbachevo quarry shows the skeletal elements in articulation; this preservation type is unique for Central Russia. This find enlarges the geographic area of vertebrate communities in the Khovanshchinian basin of the Moscow Syneclise.

The genus *Eusthenodon* represented by *E. wangsjoei* Jarvik, 1952 was described from the Upper Famennian of East Greenland as a member of the tetrapod vertebrate community (Jarvik 1952; Blom et al. 2007). *Eusthenodon* is also known from the Upper Famennian Duncannon Member of the Catskill Formation in Pennsylvania, which also yielded fish and tetrapod remains (Elliot et al. 2000), and from the Australian fish locality of Grenfell, contemporaneous to that from which the tetrapod *Metaxygnathus* is known (Johanson & Ritchie 2000). Blieck et al. (2007) dated the Duncannon Member of the Catskill Formation as the *trachytera*–middle *expansa* CZ interval. Young & Turner (2000) placed the Australian locality with *Eusthenodon gavini* Johanson & Ritchie, 2000 in a wide *postera*–*praesulcata* CZ interval. *Eusthenodon* has also been preliminarily identified from the uppermost Famennian Witpoort Formation of South Africa (Anderson et al. 1999; Gess & Coates 2015). Thus, all *Eusthenodon* material fits within the interval from the middle part of the late Famennian to the latest Famennian.

The genus *Eusthenodon* is a member of the palaeotetrapod communities in Laurentia, Baltic and East Greenland as a high-rank consumer; it is also their good indicator (Lebedev 2013). Only the *Sinostega* palaeotetrapod community, which existed in the North China faunistic province, lacks this genus; however, there are some yet undescribed sarcopterygians mentioned by Zhu et al. (2002).

Dipnoan fishes

The tooth plates are morphologically similar to those described by Krupina & Reisz (1999) as *Andreyevichthys epitomus* Krupina, 1987. They have been found in association with both the first and the second arthrodire specimen in the Voskresenskoye quarry, which suggests the abundance of these animals in the basin. The new material may be identified only as cf. *Andreyevichthys* sp., because the tooth plates belong to an earlier growth stage than those described by the two authors and, in addition, the preservation is worse than that of the original material. Yu. V. Gatovsky (pers. comm. 2015) also recovered juvenile dipnoan tooth plates from the Khovanshchinian interval in the Kolesovo quarry in the east of the Tula Region (Fig. 1).

Juvenile dipnoan tooth plates of *Andreyevichthys* sp. have been described from the sublittoral deposits of the Chaffee Group (late *postera* CZ) of Colorado by Ginter (2001, fig. 7A–C). Anderson et al. (1994) figured a dipnoan parasphenoid bone from the uppermost Famennian Witpoort Formation of South Africa, which is similar morphologically to that described as *Andreyevichthys epitomus* Krupina, 1987. The South African evidence is a good indication of the potential presence of *Andreyevichthys* in the Witpoort vertebrate community. All these records suggest a wide, but still poorly studied palaeozoogeographic distribution of *Andreyevichthys*-like dipnoans.

Acanthodian fishes

Apart from the dipnoan tooth plates, small acanthodian scales with deep bases and rhomboid smooth crowns were found in etched limestone residues from the Voskresenskoye quarry. Scales of this type, usually identified as ‘*Acanthodes*’ sp., are not uncommon in the Devonian and Carboniferous assemblages of fish microremains. Scales of this type are characteristic not only of various genera, but of families belonging to the order Acanthodiformes; their features do not permit a precise identification. However, these scales are evidence of the presence of small acanthodians in the vertebrate community.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI McCoy, 1848
Order ARTHRODIRA Woodward, 1891

Arthrodira gen. et sp. indet.
Figure 3A, B, D

Locality. Lipetsk Region, Central Russia, right bank of the Rykhotka River (right tributary of the Don River), a local quarry approximately 100 m north of the Voskresenskoye village.

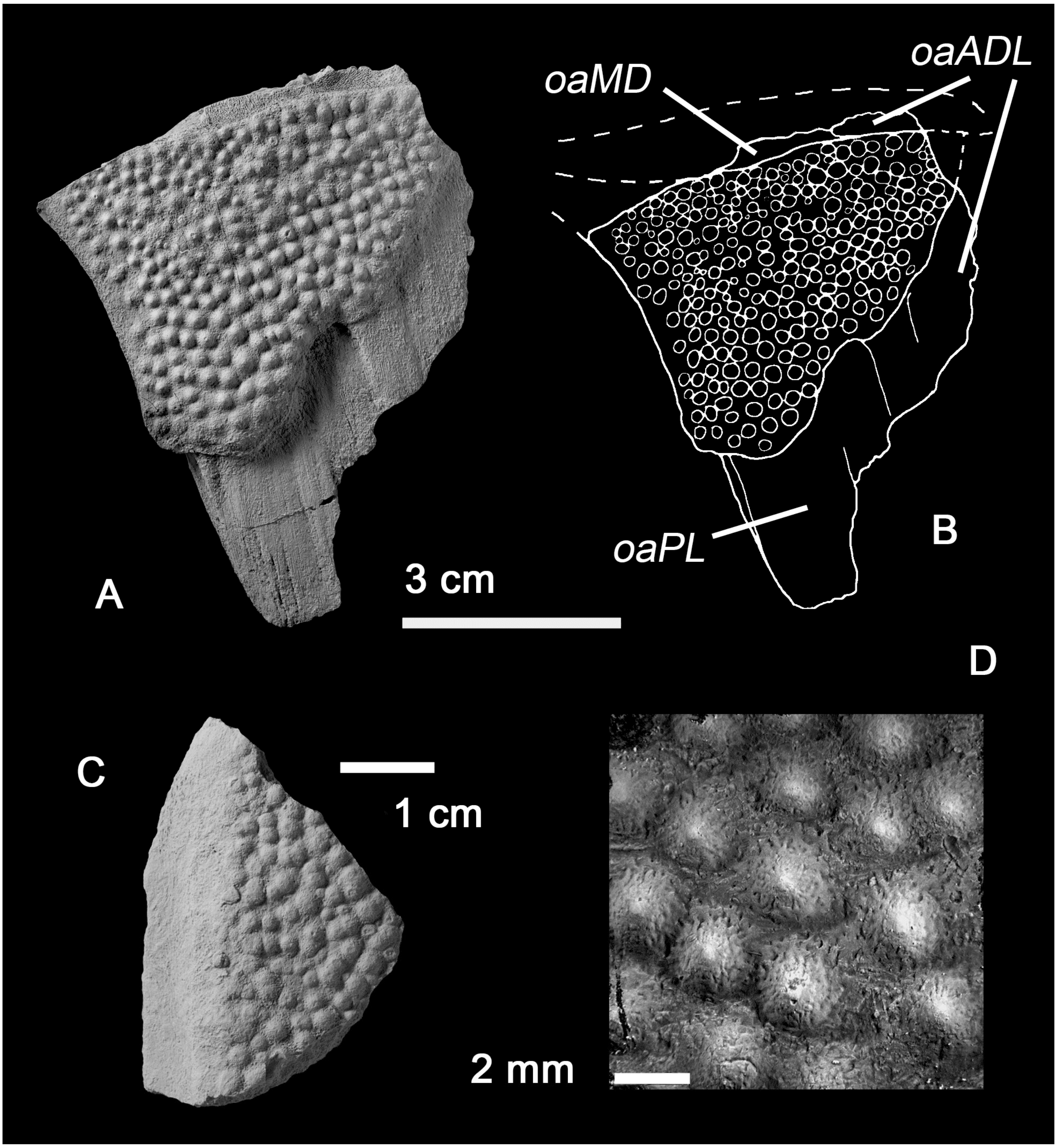

Fig. 3. Arthrodira gen. et sp. indet. Lipetsk Region, Central Russia, right bank of the Rykhotka River (right tributary of the Don River), a local quarry approximately 100 m north of the Voskresenskoye village. **A, D**, right posterior dorsolateral plate PIN 2921/3267; **B**, schematic drawing of the same view in A; **C**, bone fragment PIN 2921/3268; **D**, a fragment of dermal sculpture in PIN 2921/3267. Abbreviations: *oaADL*, overlap area for the anterior dorsolateral; *oaMD*, overlap area for the mediodorsal; *oaPL*, the main overlap area for the posterior lateral plate.

Material. An almost completely preserved posterior dorsolateral plate (PDL) PIN 2921/3267, a fragment of the skull or armour bone PIN 2921/3268.

Description. The right PDL PIN 2921/3267 is triangle-shaped; its flatness may be due to the large size of the fish or its deep body. The plate misses the posterodorsal part including the dorsal part of the external plate and the larger part of the area overlapped by the mediodorsal plate (MD) (*oaMD*). The preserved area of the lateral surface demonstrates well-defined surfaces overlapped by the posterior lateral plate (PL) (*oaPL*) and anterior dorsolateral plate (ADL) (*oaADL*). The MD contact surface is strongly damaged; the contact surface for the ADL process anteriorly from it is more depressed due to double overlapping of plates in this area. The posterior armour margin is slightly concave; its external lamina overhangs a longitudinally directed furrow which possibly housed a thin dorsal process of the PL. The main area overlapped by the PL (*oaPL*) shows a sinusoid notch along the ventral margin of the external surface of PDL. The posterior part of the area forms a wide, flat process. The short surface overlapped by the ADL (*oaADL*) is equal in length to that occupied by the PL.

The non-overlapped external surface is ornamented by rounded, compact tubercles (Fig. 3D). Those are more or less evenly distributed and are set apart at the distance comparable to the tubercle diameter. The size of tubercles increases towards the centre of the bone, where they are set chaotically, whilst towards the margins of the sculptured area their distribution tends to be more organized. There are no traces of the sensory canal (main lateral line). The visceral side of the bone is featureless and ornamented only by dorsoventrally directed striations formed during bone growth.

The bone fragment PIN 2921/3268 (Fig. 3C) bears no characters enabling its morphological identification. The external side of the fragment demonstrates an overlapped surface. Only the tuberculated dermal ornament links this specimen to the PDL; however, this sculpturing differs in more closely spaced tubercles, which locally fuse with their edges and even partly overlap each other. These tubercles differ in size; both large and small ones may be set close to each other. However, the dermal ornament of the skull and armour of arthrodires may be very variable within the same individual, so it is not possible to confirm or deny the connection between PIN 2921/3268 and PIN 2921/3267. In the former bone the thickness exceeds that in the latter approximately 1.5 times.

Comments. The establishment of the systematic position of arthrodires on the basis of isolated skeletal elements, especially postcranial ones, is rather complicated and only rarely secure. We made an attempt to overcome this problem by the examination of those late Famennian genera in which tuberculated dermal ornament is known: dinichthyids, selenosteids, groenlandaspidids and several arthrodires of uncertain taxonomic position. The postcranial skeletal elements are described in only few of those. However, characters seen in our specimens are insufficient to relate them to one or another taxon; it is also probable that they belong to a new genus. For these reasons we describe PIN 2921/3267 and PIN 2921/3268 as Arthrodira gen. et sp. indet.

Suborder PACHYOSTEOMORPHI Stensiö, 1944
Superfamily DUNKLEOSTEOIDEA Vézina, 1990
Family ?DUNKLEOSTEIDAE Stensiö, 1963

?*Dunkleosteidae* gen. et sp. indet.
Figure 4A–D

Locality. Lipetsk Region, Central Russia, right bank of the Rykhotka River (right tributary of the Don River), a local quarry approximately 100 m north of the Voskresenskoye village.

Material. The right anterior lateral plate (AL) PIN 2921/3269.

Description. The postcranial right anterior lateral plate (AL) PIN 2921/3269 is strongly abraded *post mortem* from the lateral surface and to a lesser extent from the visceral one in such a manner that all thin edges are completely destroyed and better preserved areas are seen in the thickest parts. Small patches of only slightly damaged superficial bone layers (*orn*) are observed medioventrally and mediodorsally. This type of wear resulted in that the successive bone layers became exposed forming a concentric pattern. The anteroventral process (*avw*) is broken off to the postbranchial thickening (*thpbe*) and the contact area for the interlateral bone reconstructed here (*oaIL*) is not preserved. The posterior margin of the obstentic process (*pro*) bears two shallow notches, the posterodorsal and posteroventral one. A deep but short notch in the middle of the posterodorsal margin had possibly been overlapped by the ventral process of the anterior dorsolateral plate (*oaADL*). The preserved margin which contacted the pectoral fin (*pemb*) is straight. The anterior margin of the dorsal lamina is almost completely eroded; the postbranchial embayment (*pbe*) is shallow.

On the visceral surface the area contacting the ADL (*cfADL*) shaped as a rounded triangle is expanding ventrally to the two thirds of the bone depth. Only a small part of the postbranchial lamina (*pbla*) is preserved. Two massive ridges form the base of the anteroventral process.

Comments. The shape of this bone definitely demonstrates the open nature of the pectoral fenestra. This AL structure is characteristic of arthrodires belonging to the suborder Pachyosteomorphi Stensiö, 1944. The ventral part of the AL is strongly reduced within this taxon in Titanichthyidae, Mylostomatidae, Bungartiidae,

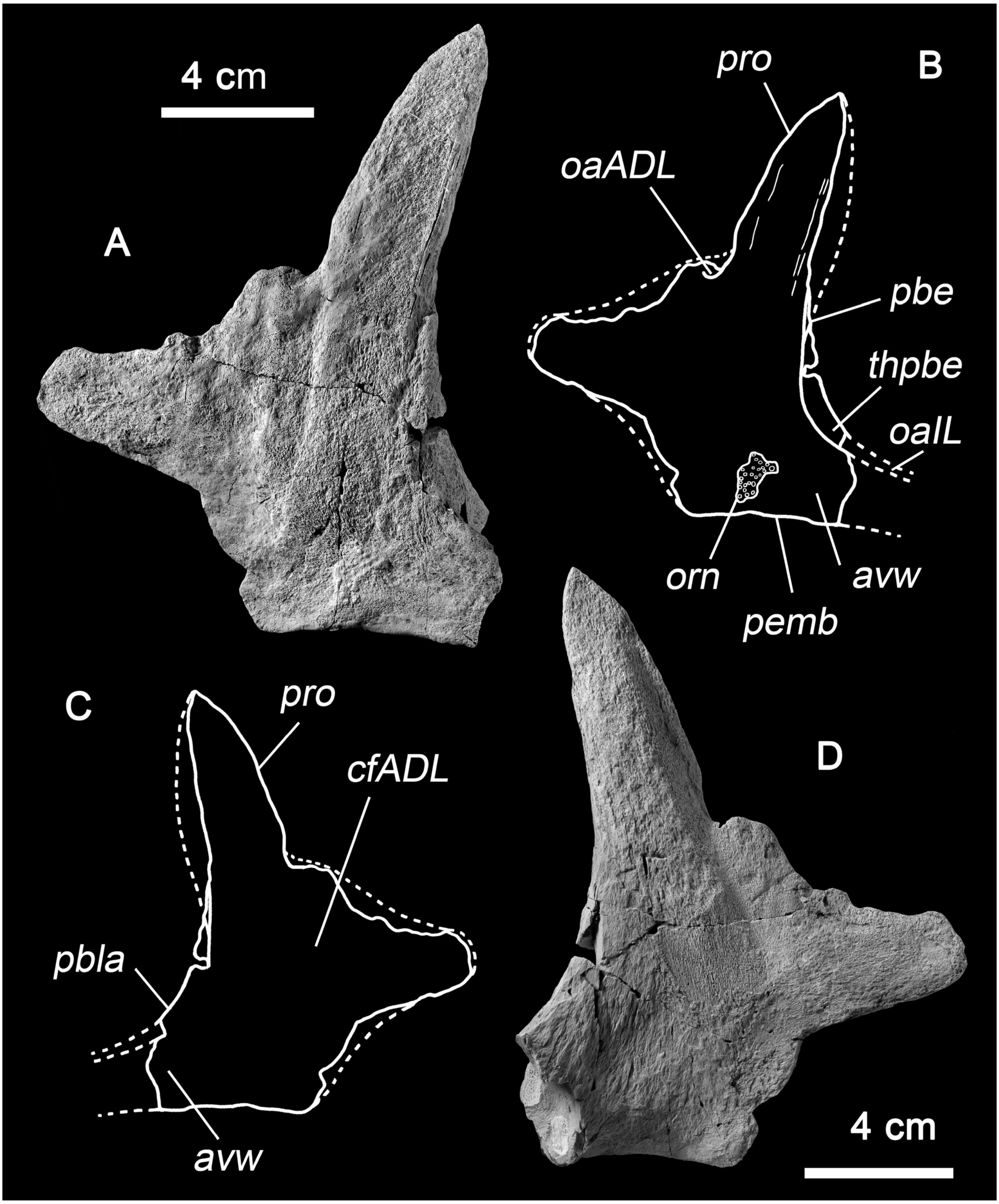

Fig. 4. ?Dunkleosteidae gen. et sp. indet., PIN 2921/3269, anterolateral plate of the thoracic armour (AL). Lipetsk Region, Central Russia, right bank of the Rykhotka River (right tributary of the Don River), a local quarry approximately 100 m north of the Voskresenskoye village. **A**, lateral view; **B**, interpretative drawing of the lateral view; **C**, interpretative drawing of the visceral view; **D**, visceral view. Abbreviations: *avw*, anteroventral process; *cfADL*, contact face for the anterior dorsolateral plate; *oaADL*, overlap surface for the anterior dorsolateral plate; *oaIL*, reconstructed position of the overlap surface for the interlateral plate; *orn*, an area showing preserved dermal sculpturing; *pbe*, postbranchial embayment; *pbla*, postbranchial lamina; *pemb*, the margin adjoining the pectoral fin; *pro*, obstentic process; *thpbe*, postbranchial thickening of the anteroventral process.

Leiosteidae, Trematosteidae and Selenosteidae. In the families Dunkleosteidae and Dinichthyidae, the ventral part is massive and wide. It bears contact surfaces for the interlateral and spinal plates and demonstrates a well-expressed dorsal lobe. The anterior lateral plate (AL) PIN 2921/3269 shows the closest affinity to *Dunkleosteus terrelli* (Newberry, 1873), thus it is identified as belonging to the family Dunkleosteidae.

Class SARCOPTERYGII Romer, 1955
Family TRISTICHOPTERIDAE Cope, 1889
Genus *Eusthenodon* Jarvik, 1952

Eusthenodon sp.
Figure 5

Locality. Tula Region, Central Russia, right bank of the Bolʹshaya Mizgeya River, a local quarry approximately 1 km north of the Gorbachevo village.

Material. A natural external mould of the ventral side of the skull PIN 2921/3270.

Description. The matrix block presents a natural external mould of the ventral side of the skull including mandibles, submandibular plates, lateral and median gulars, part of the shoulder girdle, a fragment of the pectoral fin and squamation of the anterior part of the body. The left side is better preserved than the right one. Some scale imprints still bear bony matter.

The lower jaws are rotated laterally due to *post mortem* dorsoventral compression of the skull and a small gap is seen between their symphysial parts. The preserved part of the left mandible (*md*) is observed from the symphysis to the submandibulo-branchiostegal element (*Smb1-Rbr*). Four submandibular elements are visible (*Smb2–Smb5*). The second element carries a pit line (*plSmb2*). The left lateral gular (*GuL*) is preserved

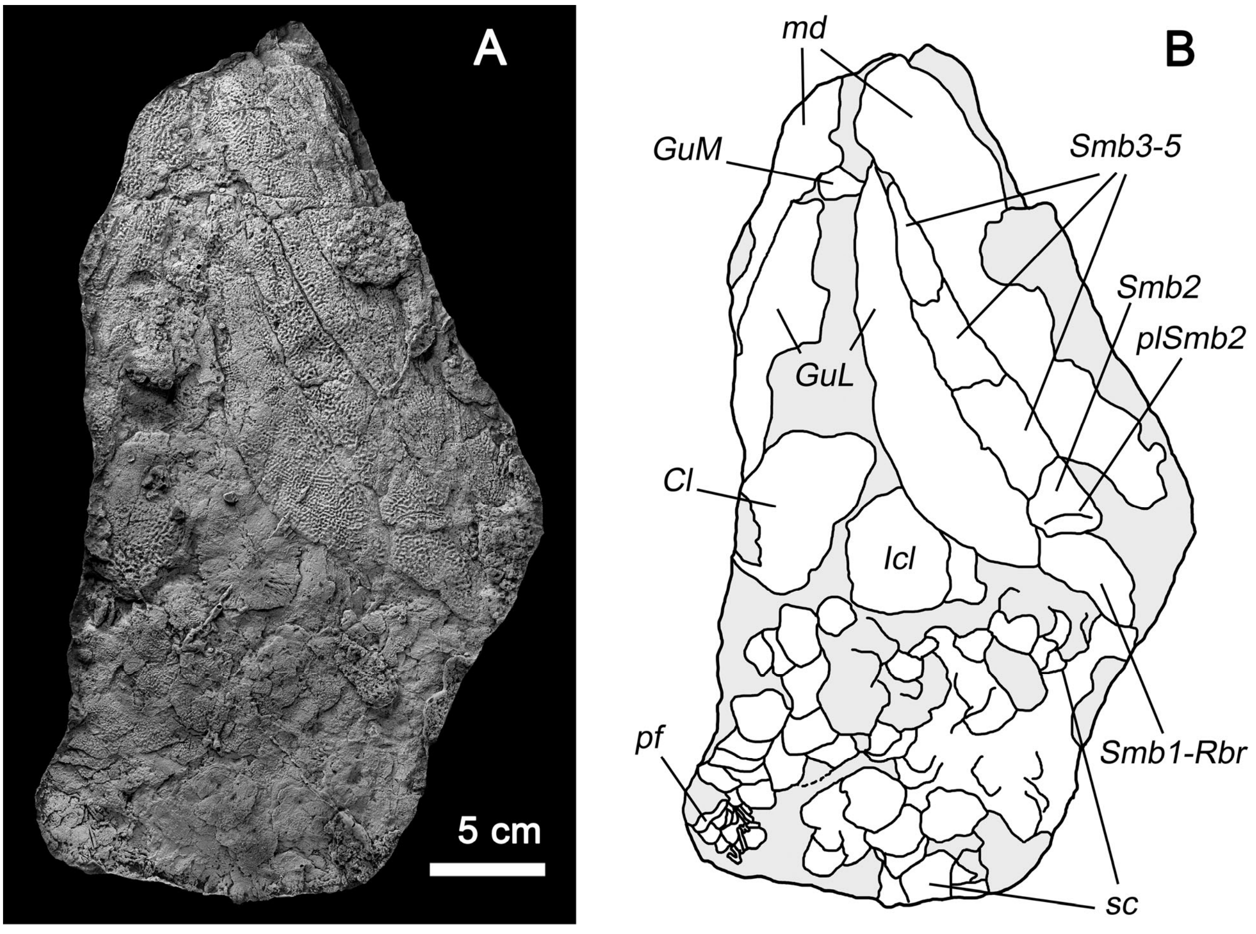

Fig. 5. Ventral side of the skull, shoulder girdle and squamation of *Eusthenodon* sp., PIN 2921/3270. Tula Region, Central Russia, right bank of the Bolʹshaya Mizgeya River, a local quarry approximately 1 km northwards from the Gorbachevo village. **A**, latex rubber cast; **B**, schematic explanatory drawing. Abbreviations: *Cl*, clavicle; *GuL*, lateral gular; *GuM*, median gular; *Icl*, interclavicle; *md*, mandible; *pf*, pectoral fin; *plSmb2*, pit line on submandibular 2; *Smb1-Rbr*, submandibulo-branchiostegal element; *sc*, scale; *Smb2, Smb3-5*, submandibulars.

almost completely, and only its rostral part cannot be traced. Its maximum width to its length makes approximately 1:4.5, which is almost the same as in the type species *Eusthenodon waengsjoei* Jarvik, 1952 (Jarvik 1952). The visible part of the median gular element (*GuM*) is rounded rather than longitudinally elongated, but possibly its posterior part is overlapped by matrix. Mesially the lateral gulars as well as the mandibles are separated by a wide gap due to *post mortem* deformation. The ventral side of the interclavicle (*Icl*) demonstrates a median ridge marking the boundary between the opposing clavicles and thin straight crests running from it towards the lateral margins of the bone in a fan-shaped manner. These crests mark the ligament attachment to the clavicles. The horizontal plate of the clavicle is seen only from the right side. The pectoral fin (*pf*) is marked by a concentration of small scales and several small bony rays. The posterior third of the specimen shows numerous poorly preserved imprints of rounded scales of various sizes (*sc*).

Supraorder DIPNOI Müller, 1845
Family FLEURANTIIDAE Berg, 1940
Genus *Andreyevichthys* Krupina, 1987

cf. *Andreyevichthys* sp.
Figure 6

Locality. Lipetsk Region, Central Russia, right bank of the Rykhotka River (right tributary of the Don River), a local quarry approximately 100 m north of the Voskresenskoye village.

Material. Pterygoid and prearticular tooth plates from juvenile individuals PIN 2921/3281–3284.

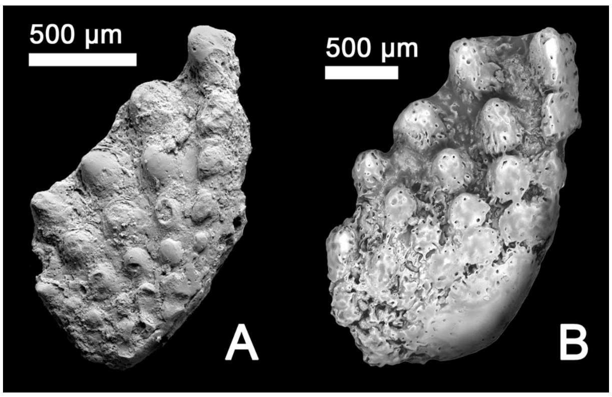

Fig. 6. Prearticular tooth plates of the juvenile dipnoan fishes cf. *Andreyevichthys* sp. Lipetsk Region, Central Russia, right bank of the Rykhotka River (right tributary of the Don River), a local quarry approximately 100 m north of the Voskresenskoye village. **A**, PIN 2921/3281; **B**, PIN 2921/3284, occlusal view.

Description. In most specimens thin edges are broken off; prearticular plates are separated from their bony bases and in the pterygoid ones the thin bony layer is not formed yet into a complete bone. Both pterygoid (PIN 2921/3282) and prearticular tooth plates (PIN 2921/3281and 2921/3284) bear 5 or 6 rows of conical, laterally compressed denticles, and their compression tends to increase from the posterior row towards the mesial one. The number of denticles varies from 2–3 in the posterior to 5 in the mesial row. The angle between the mesial and posterior rows is about 110°. Lifetime wear of the plate apex may be observed only in the largest specimen PIN 2921/3284.

DISCUSSION

Palaeoecology

Depth and hydrodynamics

The Khovanshchinian basin occupied the central and eastern part of the East European Platform. Sedimentation occurred in shallow-water conditions. This is supported by the wide distribution of clastic carbonate material, oolites, stromatolites and vertical branching channels (burrows or 'rhizoid' structures), sometimes even at a distance from reconstructed sea shores. Sands and clays had been deposited in a narrow coastal area which adjoined Voronezh Island; limestones and dolomites dominated in other regions (Makhlaev 1964) (Fig. 2). Strong abrasion of the arthrodire specimen PIN 2921/3269 from Voskresenskoye as well as pebbling of ostracods valves, position of some shells inside the others and concentration of fossils within a thin layer suggest that the sedimentation of this particular layer occurred in the extremely shallow-water conditions with active hydrodynamics, probably intertidally.

On the contrary, the limestone layer, which yielded the *Eusthenodon* skull from the Gorbachevo quarry, formed in calm hydrodynamic conditions. Sedimentation had been fast as the skull, shoulder girdle and scales are preserved almost in life position rather than have been separated by scavengers or wave action. An intermediate hydrodynamic situation is reconstructed in the Andreyevka-2 locality, in which almost all skeletal elements are disassociated but still demonstrate perfect preservation without traces of mechanic wear.

Salinity

Two opposing viewpoints concern the salinity level in the Khovanshchinian Sea. The first opinion suggests high salinity based on the wide distribution of dolomites (Makhlaev 1964). The stromatolites which are widely distributed in the Khovanshchinian strata have until recently also been regarded as indicative of an increased salinity level. Recent stromatolites, which occur in Shark Bay (Western Australia), where the amount of salt dissolved in water attains 70‰, are used as an example (Burns et al. 2004). The opposing opinion favours somewhat brackish water in the Khovanshchinian Sea based on the wide distribution of charophytes (Samoilova 1954). Naumova (1953) suggested a rise in the atmospheric humidity level during this time based on the composition of the spore assemblages; an increase in precipitation might result in general decrease in the salinity level. Local decrease in salinity might also result from shoal waters and islands, which hampered water mixing (Makhlaev 1964).

Rodionova et al. (1995) reconstructed near-shore marine conditions with an almost normal marine salinity level in the southern part of the basin, which adjoined the northern shore of Voronezh Island. The salinity might fluctuate due to drainage from land as well as input of marine water from the open-sea basin in the southeast. The conodonts in Voskresenskoye also suggest marine salinity level.

To solve these contradictions in the Andreyevka-2 locality, Lebedev (1992) suggested a model of inconstant fluctuating salinity as both charophytes and stromatolites are abundant in its deposits (Alekseev et al. 1994). However, it has become known in the last decades that recent cyanobacterial assemblages may exist in basins with a wide spectrum of salinity, from significantly low to strongly increased values (e.g., Breitbart et al. 2009). Thus there is no more argument for increased salinity based on the presence of stromatolites. The decreased salinity in the Khovanshchinian basin may be accepted; that agrees well with the existence of amphibians (e.g., *Tulerpeton curtum* Lebedev, 1984) in the Khovanshchinian biota, which do not or hardly tolerate salt-water habitats. The palaeobiogeographic scheme (Fig. 2) demonstrates the distribution of stromatolites within the coastal area of Voronezh Island, which largely coincides with the main area of tetrapod finds. Quiet hydrodynamics prevented coarse-grained terrigenous sedimentation with the exception of clays in the areas inhabited by vertebrate communities. This might also explain predominantly carbonate rather than terrigenous sedimentation in brackish-water environments.

Certain controversy exists between various data on the habitat of bivalves. Thin-walled bivalves are found in the brackish-water Andreyevka-2 locality and presumably more marine deposits in the Voskresenskoye locality. The bivalves in the Andreyevka-2 locality might support the hypothesis of brackish-water conditions, whilst the existence of these bivalves is less explicable in the marine deposits of the Voskresenskoye locality. This fact may suggest that these bivalves had been euryhaline.

The ostracod assemblage including *Aparchites globulus* Posner, *Aparchitellina* sp., *Bykovites nativus* Tschigova, *Evlanella sokolovi* Tschigova, *Glyptolichwinella* cf. spiralis (Jones & Kirkby), *Healdianella punctata* Posner and *Carbonita* sp. from the Andreyevka-2 locality (Alekseev et al. 1994) does not include species in common with those from the Voskresenskoye locality. Most likely, this dissimilarity is due to significant differences in the habitats of these assemblages, very likely to salinity and depth. The ostracods *Cryptophyllus* dwelled in shallow-water marine conditions in the open-shelf and closed-shelf facies. The practically monotaxic ostracod association in the Voskresenskoye locality suggests rather unfavourable conditions within a shallow-water semi-closed shelf area with possibly hampered water circulation and unstable salinity. The presence of *Phlyctiscapha* and *Sulcella* in this association does not contradict this assumption.

We suggest that the coastal (intertidal?) conditions were characterized by sharp fluctuations of environmental conditions in the Voskresenskoye locality, as indicated by the impoverished ostracod assemblage in contrast to the ostracod assemblage in the Andreyevka-2 locality, in which the environmental conditions were much more stable. This difference influenced the diversity of all animal communities, both invertebrate and vertebrate. Environmental instability might impoverish communities by eliminating taxa with high demands on stable environments, whereas stable settings favoured the increase in diversity.

Khovanshchinian vertebrate communities in the southern part of the Moscow syneclise

Vertebrate remains are not uncommon in the Khovanshchinian of the Moscow syneclise (Rodionova et al. 1995), nevertheless vertebrates are recorded rarely in the literature. Apart from the Andreyevka-2, Voskresenskoye and Gorbachevo localities, Khovanshchinian vertebrates are known from the Draguny (S. V. Tikhomirov 1947 collection, PIN 2921) and Mikhailovskoye quarries (O. A. Lebedev 1994 collection, PIN 2921) (Fig. 1). Table 1 presents vertebrate and invertebrate faunistic lists of these sites in the Tula and Lipetsk regions of Central Russia. Invertebrate assemblages are more or less studied only in the Andreyevka-2 and Voskresenskoye sites.

To the southeast of the Andreyevka-2 locality, the community composition becomes more and more impoverished. No chondrichthyans have been recorded in Draguny and no antiarchs, actinopterygians and tetrapods are known further to the east in Mikhailovskoye.

Table 1. Fossil remains in the Khovanshchinian assemblages of the Tula and Lipetsk regions of Central Russia. Data in the Andreyevka-2 locality from Alekseev et al. (1994)

	Localities and assemblages				
	Gorbachevo	Andreyevka-2	Draguny	Mikhailovskoye	Voskresenskoye
Conodonti	–	–	–	–	*Pandorinellina humulus*, *Icriodus costatus*, *Pelekysgnathus* aff. *peejayi*, *Bispathodus stabilis*; *Acodina* sp.
Ostracoda	–	*Aparchites globulus*, *Aparchitellina* sp., *Bykovites nativus*, *Evlanella sokolovi*, *Glyptolichwinella* cf. *spiralis*, *Healdianella punctata*, *Carbonita* sp.	–	–	*Cryptophyllus socialis* f. *multicincta*, *C. socialis* f. *chovanensis*, ?*Phlyctiscapha* cf. *pusilla*, *Sulcella* sp.
Bivalvia	–	indet.	–	–	ʻ*Arca*ʼ *oreliana*
Gastropoda	–	–	–	–	Gastropoda indet.
Vermes	–	*Serpula vipera*	–	–	–
Charophyta	–	*Quasiumbella* sp.	–	–	–
Stromatolithi	+	+	–	–	+
Chondrichthyes	–	?Eugeneodontiformes	–	–	–
Arthrodira	–	–	–	–	Arthrodira gen. et sp. indet.
Antiarchi	–	*Remigolepis armata*	*Remigolepis armata*	–	–
Acanthodei	–	*Devononchus tenuispinus*, ʻ*D.*ʼ *laevis*, ʻ*Cheiracanthus*ʼ *longicostatus*, ʻ*Acanthodes*ʼ sp.	ʻ*Cheiracanthus*ʼ sp. ʻ*Acanthodes*ʼ sp.	ʻ*Cheiracanthus*ʼ sp. ʻ*Acanthodes*ʼ sp.	ʻ*Acanthodes*ʼ sp.
Porolepiformes	–	*Holoptychius* sp.	–	*Holoptychius* sp.	–
Osteolepiformes	*Eusthenodon* sp.	*Eusthenodon* sp. nov. Osteolepiformes gen. nov.	Osteolepiformes gen. ind. *Eusthenodon* sp. nov.	*Eusthenodon* sp. nov. Osteolepiformes gen. nov.	–
Struniiformes	–	*Strunius* sp.	*Strunius* sp.	*Strunius* sp.	–
Dipnoi	–	*Andreyevichthys epitomus*	*Andreyevichthys epitomus*	*Andreyevichthys epitomus*	cf. *Andreyevichthys* sp.
Actinopterygii	–	*Moythomasia* sp.	*Moythomasia* sp.	–	–
Tetrapoda	–	*Tulerpeton curtum* Tetrapoda indet.	Tetrapoda indet.	–	–

– Fossil remains absent or currently unknown; + fossil remains known but currently unidentified.

Eusthenodon-bearing sediments of Gorbachevo did not yield additional vertebrate material. Only juvenile dipnoan tooth plates and presumably *Eusthenodon* bones have been recovered from the easternmost Kolesovo quarry according to preliminary information. Finally, no vertebrates typical for the Andreyevka-2 locality, except for some dipnoans and acanthodians are known in the Voskresenskoye locality, which is most distant from the Andreyevka-2 locality. The presence of a conodont association and a poor ostracod assemblage in Voskresenskoye contrasts with the rich ostracod complex in the Andreyevka-2 locality. Such a faunistic gradient may follow the environmental one and result from changes in hydrodynamics and water salinity, probably through changes in the composition of primary invertebrate consumers. Differences in both environmental and faunistic conditions might have led to the separation of coastal marine vertebrate biocoenosis from the brackish-water one within the same basin. The placoderms of the Voskresenskoye locality might have entered a separate community of their own from the tetrapod one of the Andreyevka-2 locality and have been stenohaline, possibly depending on a food type missing from the latter. This peculiarity contrasts with the habitat of the Laurentian and Gondwanan Groelandaspididae, which had probably been euryhaline (Janvier & Clement 2005).

CONCLUSIONS

New arthrodire remains are the first record of these fishes in the Khovanshchinian basin of Central Russia, as well as in the uppermost Famennian of the East European Platform in general. At the same time this is the latest evidence of arthrodires in that basin.

The osteolepiform genus *Eusthenodon* is a characteristic marker of the Khovanshchinian vertebrate community as well as of other palaeotetrapod communities in Laurussia and East Gondwana.

Environmental conditions for the vertebrate associations change from hydrodynamically quiet, brackish, shallow-water conditions with fast sedimentation to shallow-water near-shore conditions with active hydrodynamics demonstrating salinity close to normal marine in the Khovanshchinian basin of the Moscow syneclise. The faunistic composition changes within the present Tula and Lipetsk regions of Central Russia. The impoverishment of the ostracod association takes place in parallel with the appearance of a conodont assemblage. At the same time a rich vertebrate assemblage becomes substituted by an impoverished arthrodire–dipnoan–acanthodian association. The separation of arthrodires into the community of their own from the tetrapod one might be due to their stenohaline habits and dependence on a food type missing in the basin part of the Andreyevka-2 locality.

For the first time in the world, non-groenlandaspidid arthrodires were recorded within the same basin where tetrapods dwelled.

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Uued kalaleiud Kesk-Venemaa Ülem-Famenne'ist (Ülem-Devon) ja Hovanštšina ea selgroogsete koosluste elukeskkonnad

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Uued kalaleiud Hovanštšina lademest (Ülem-Famenne'i algus, Ülem-Devon) annavad olulise lisa vertebraatide koosluse ja leviku tundmisele Kesk-Venemaal. Esmakordselt on Ida-Euroopa platvormilt leitud hiliste artrodiiride kivistisi Voskressenskoje paemurrust Lipetski rajoonis. Sama basseini kivimitest on leitud ka tetrapoodide jäänuseid. Hilis-Famenne'i mittegroenlandiidseid artrodiire on seni leitud vaid vähestest paljanditest Põhja-Ameerikas, Belgias ja Poolas. Tetrapoodide ja artodiiride biotoopide erinevad areaalid võivad olla põhjustatud Hovanštšina basseini vete soolsuse piirkondlikest erinevustest. Plakodermid olid tõenäoliselt stenohaliinsed mereloomad. Selle mereala elutingimused ulatusid nõrgalt magestunud madala- ja vaikseveelisest, kuid kiire sedimentatsiooniga keskkonnast kuni normaalse soolsuse ning aktiivse dünaamikaga rannalähedase madalmere oludeni. Gorbatševost (Tula rajoon, Kesk-Venemaa) leitud osteolepiformne perekond *Eusthenodon* on selle piirkonna Hovanštšina lademe selgroogsete koosluse iseloomulik vorm, aga samuti on ta Laurussia ja Ida-Gondvana paleotetrapoodide koosluse markeeriv liige.