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New materials on *Ventalepis ketleriensis* Schultze, 1980 extend the zoogeographic area of a Late Devonian vertebrate assemblage

OLEG LEBEDEV[1] and ERVĪNS LUKŠEVIČS[2]

[1] *Palaeontological Institute of Russian Academy of Sciences, 123 Profsoyuznaya Street, Moscow, 117997, Russia. E-mail: olebed@paleo.ru*
[2] *Department of Geology, University of Latvia, Raiņa Boulevard 19, Riga, LV-1586, Latvia. E-mail: ervins.luksevics@lu.lv*

ABSTRACT:

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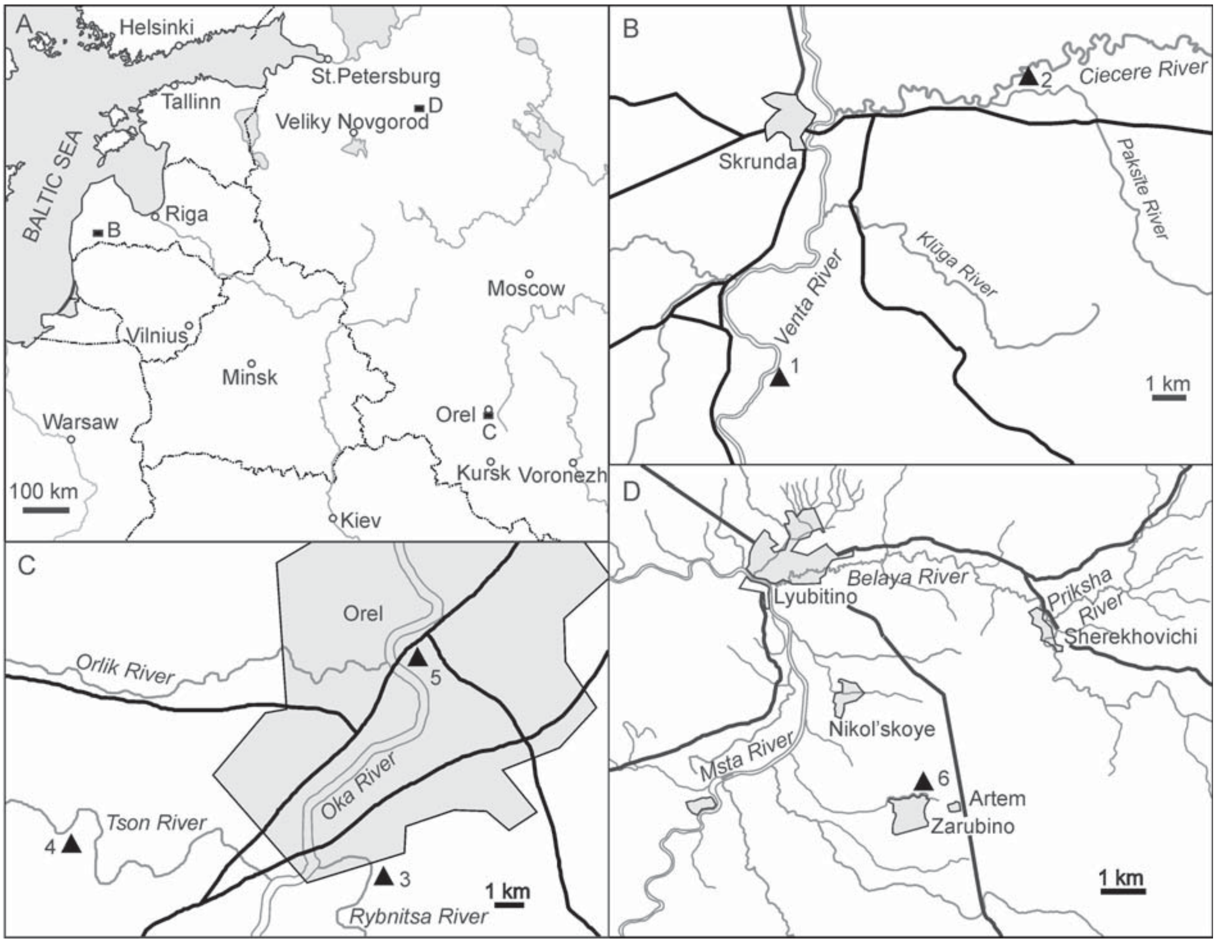
Newly collected and restudied earlier materials on an enigmatic fish *Ventalepis ketleriensis* Schultze, 1980 from the upper Famennian (*postera* – ? Lower *expansa* conodont zones) of Latvia and central and northwestern Russia support its porolepiform affinities. A new family Ventalepididae fam. nova is established for this genus upon a peculiar combination of characters, including scale structure and dermal bones ornamentation. New records extend the distribution of this genus and the Ventalepis vertebrate assemblage on the whole to a vast geographical zone along the south-eastern coast of the Old Red Sandstone continent. The habitat area of the Devonian vertebrate assemblage over such a large territory within the zoogeographical province of Baltica is established for the first time. Palaeozoogeographical analysis suggests Laurentian affinities of the Ventalepis assemblage demonstrating the major congruency to the Belgian and East Greenland ones. These and Russian localities are separated by a vast ORS continent. Presence of the dipnoan *Jarvikia* in all three locations, as well as an *Ichthyostega*-like tetrapod in the Belgian one reveals palaeozoogeographical connections, which might reflect possible dwelling not only in the near-shore continent periphery but also in the river systems of the continent itself.

Key words: Porolepiformes; *Ventalepis*; Palaeozoogeography; Famennian; Latvia; Russia.

INTRODUCTION

In 1958, a joint crew of Estonian, Latvian, Lithuanian and Russian palaeoichthyologists leaded by Dmitry Obruchev made a field trip to the western part of the Main Devonian field. In Latvia, the crew visited a locality close to the former Ketleri farm known at least since the 1930s due to the works by an outstanding German–Latvian palaeoichthyologist Walter Gross (1933, 1941, 1942). This field research provided a wide range of the upper Famennian fish remains including large peculiar scales of uncertain systematic position unknown earlier.

Material collected in 1958 was shared between the Institute of Geology, Latvia (later the collection of the Museum of Institute of Geology was donated to the Latvian Museum of Natural History, Riga), Lithuanian Institute of Geology and Geography of the Academy of Sciences of Lithuania, and then Palaeontological Institute of the Academy of Sciences of USSR (now A.A. Borissiak Palaeontological Institute of the Russian Academy of Sciences) (PIN).



Text-fig. 1. A – Map of the northern part of Eastern Europe showing the position of studied localities (black quadrangles); B – Skrunda municipality, western Latvia; C – Orel Region, Central Russia; D – eastern part of the Novgorod Region, north-west Russia. Localities, marked by black triangles: 1 – the Ketleri site; 2 – the Pavāri site; 3 – Rybnitsa quarry; 4 – the Saburovo site; 5 – the Nizhne-Shchekotikhino site; 6 – Zarubino mine

In 1977, Hans-Peter Schultze visited Vilnius and later Riga, where he examined these yet undescribed specimens as well as materials collected by L. Lyarskaya in the 1970s. Materials from the Ketleri site stored in PIN remained unstudied.

In 1980, H.-P. Schultze published a paper describing a new genus and species *Ventalepis ketleriensis* based upon the Latvian and Lithuanian collections. One of the most important points in this work is the discussion of the systematic position of the fish. Its bizarre features such as thick two-layered scales of the transitional rhomboid-cycloid type and minute denticulation over the non-overlapped surface of the scales and external side of the bones precluded its ready attribution to any sarcopterygian order. Schultze's final decision to relate the genus to the Porolepiformes was based upon the structure of the cranial bones; this assignment is supported here. Additional cranial materials we describe below definitely indicate the porolepiform affinities of this genus. A peculiar combination of characters within the order Porolepiformes makes ground for establishment of a new family for this single genus, as it can be assigned to neither of the existing families (Porolepididae and Holoptychiidae).

Until 1999, *Ventalepis* had been regarded to be endemic to western Latvia. However, during that field season one of the authors (O.L.) found new *Ventalepis ketleriensis* material in the almost coeval deposits in the Orel Region of Central Russia. That was the first find of this species in the Central Devonian field.

New field studies by one of the authors (E.L.) in the type locality during the 2014–2016 field seasons introduced some additional cranial and postcranial elements that are also described below. Restudy of the Ketleri collection at PIN yielded key specimens, including two cranial bones. These materials are important in the study of the *Ventalepis* osteology as well as of its systematic position.

In 2016, one of the authors (O.L.) discovered new material of *Ventalepis* in the upper Famennian Lnyanaya Formation (Novgorod Region of Russia) among the remains of other fishes belonging to the Latvian and Central Russian Ketleri-type vertebrate assemblages.

Special attention to this vertebrate community is due to the presence of a unique stem tetrapod *Ventastega curonica* Ahlberg, Lukševičs and Lebedev, 1994 in the Latvian localities (Ahlberg *et al.* 1994). Similarity of composition and structure of the assemblage in the Latvian, as well as central and north-western Russian localities, indicates to potential existence of *Ventastega* or another tetrapod within this community.

Faunistic analysis performed by the authors in their previous paper (Lebedev and Lukševičs 2017) suggested the genus *Ventalepis* to distinguish the Ventalepis vertebrate community. The find in the Novgorod Region made possible the extension of the zoogeographic area and its relationships with the vertebrate faunas in the adjacent regions. New finds of *Ventalepis* within the Baltica zoogeographical province raises the taxon status from the local to provincial endemic *sensu* Lebedev and Zakharenko (2010).

Institutional abbreviations: GM Geological Museum, a part of the Museum of Science and History of the University of Latvia, Riga, Latvia; LDM Latvijas Dabas Muzejs (Latvian Museum of Natural History), Riga, Latvia; LGD former Museum of Geology of the Institute of Geology of Latvia. At the beginning of 1970s collections of this museum were transferred to Latvian Museum of Natural History (LDM); LGGI Institute of Geology and Geography of the Lithuanian Academy of Sciences (Vilnius, Lithuania); PIN A.A. Borissiak Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia.

GEOGRAPHICAL DISTRIBUTION AND GEOLOGICAL SETTING

Latvian material of *Ventalepis ketleriensis* comprises specimens from the two localities in the western Latvia. The type locality is the Ketleri outcrops at the right bank of the Venta River downstream from the abandoned Ketleri farm, approximately 3 km upstream from the Lēnas village and 15 km south from the Skrunda Town. The other locality is the outcrop at the left bank of the Ciecere River close to the abandoned Pavāri farm 14 km to the east from the Skrunda Town (Text-fig. 1B). Deposits of the Upper Devonian upper Famennian Ketleri Formation (Fm) outcrop in both sites. Based on the position above the Sniķere, Švete and Žagare Formations, containing conodonts of the postera CZ (from the Švete Fm), the Ketleri Fm was correlated with the Upper postera or probably expansa CZ (Lukševičs 2001); however, sometimes this interval has been correlated with the expansa CZ (Esin *et al.* 2000).

Russian material originates from two distant locations. The first one is placed on the northern slope of the Voronezh anticline in Central Russia within the "Orel-Saburovo Beds" (lower part of the Turgenevo Fm, Plavskian Regional Stage) of the upper Famennian (Rzhonsnitskaya and Kulikova 1990; Alekseev *et al.* 1996). These beds outcrop in several natural exposures in the riverbanks and minor quarries near the city of Orel (Orel Region) (Text-fig. 1C), the most important of which is the industrial Rybnitsa quarry. Its geology and correlation to the Latvian sections has been discussed recently by Lebedev and Lukševičs (2017). A single *Ventalepis* scale has also been found in the natural exposure on the bank of the Orlik River by the Maslovo village to the west of the Orel city. Alekseev *et al.* (1996) correlated the Plavskian Regional Stage (RS) to the Upper postera CZ, whilst Esin *et al.* (2000) correlated its lower part to the Lower expansa CZ.

The second site is located in the north-west of European Russia in the Lyubytino District in the east of the Novgorod Region (Text-fig. 1D). In geological terms, this locality belongs to the east of the Main Devonian field or the western wing of the Moscow syncline (Ostrometskaya and Kotlukova 1966). Specimens had been collected in the slagheap of a mine abandoned in the 1990s in the town of Zarubino. The mine quarried for the Lower Carboniferous fire clays overlaying the upper Famennian Lnyanaya Formation. The Lnyanaya Fm is divided into two subformations, the lower one being correlated to the upper Famennian Optukhovian RS and the upper to the Plavskian RS (Geological Map of USSR 1989).

Burden rock from the mine had been dumped in three slagheaps, one of which had been withdrawn from a draining horizontal gallery (drift) situated right below the productive Carboniferous horizons. The rocks in the slagheaps are represented by variegated clays (light and dark grey, pink, lilac, crimson-red, bluish-grey); clays contacting lemon-yellow marl lenses are light-yellow. There are occasional fragments of probably interrupted layers of hard, massive, vary-grained, dark grey sandstones bearing caverns on the layer top and bottom; these sandstones are occasionally laminated. Strongly ferruginated brown-crimson sandstones dominate the rock. Argillites and silts coloured in the same hue spectrum as the clays, numerous haematite concretions, pyrite crystal aggregates, and limonite oolites are also found. Numerous white-coloured fish remains are found within the pink clay on the western and southwestern slopes of the largest slagheap of three. The bones are strongly fragmented partly due to weathering and partly due to destruction by mining machine. Numerous poorly identifiable bone fragments are seen in the massive sandstone blocks. These rocks fit in the upper part of the Lnyanaya Fm by their lithological features being distinctively different from predominantly grey sand and sandstone of the lower part of the formation (Ostrometskaya and Kotlukova 1966).

Being overlain by Carboniferous deposits, the Lnyanaya Fm outcrops only in a small area. Moreover, Quaternary deposits are also wrapping over the Palaeozoic; the whole area is very densely vegetated, thus there is little hope to see a natural exposure of the layers presented in the mine slagheaps. This hampers establishment of the position of the fossiliferous layers in the section.

Sycidium charophyte gyrogonites found later after the screen-washing suggest that sedimentary conditions and, most likely, the depositional environment in this locality had been different from those in the Latvian and Central Russian ones, in which charophytes had been never found by us nor described by other authors. These remains are not helpful in age determination, being common within the upper Frasnian to upper Famennian interval on the Main Devonian field, but are often used as indicators of basin salinity different from normal marine (hypersaline or brackish) (e.g., Hecker 1983). However, some charophyte taxa (not *Sycidium*) are known from definitely marine deposits (Samoilova and Prinada 1966; Racki and Racka 1981).

Geological sections of the Latvian and central Russian localities have been published recently by Lukševičs and Zupiņš (2004) and Lebedev and Lukševičs (2017). Both Latvian and central Russian assemblages include: ?*Haplacanthus* sp., "*Devononchus*" *tenuispinus* (Gross), "*D.*" *ketleriensis* Gross, "*Cheiracanthus*" sp., "*Acanthodes*" sp. (scales), *D.* sp. (spines), *Bothriolepis ciecere* Lyarskaja, *Cryptolepis grossi* Vorobyeva, *Glyptopomus bystrowi* (Gross), ?*Glyptolepis dellei* (Gross), *Holoptychius* cf. *nobilissimus* Agassiz, *Ventalepis ketleriensis* Schultze, *Strunius* cf. *rolandi* Gross, *Orlovichthys limnatis* Krupina and "*Dipterus*" *arcanus* Krupina. Stem tetrapod *Ventastega curonica* Ahlberg *et al.* is missing from the Russian localities. On the contrary, the central Russian assemblages additionally include: "*Dinichthys*" *machlaevi* Obrucheva, *Chelyophorus verneuili* Agassiz, *Pycnacanthus fischeri* Lebedev, "*Dipterus*" *marginalis* (Agassiz), "*D.*" *pacatus* Krupina, "*D.*" *expressus* Krupina, *Grossipterus venustus* Krupina, *Chirodipterus interstitus* Krupina, *Conchodus excussus* Krupina, *Jarvikia lebedevi* Krupina and *Mimipiscis* sp. Presence of these placoderms, struniiforms, dipnoans and actinopterygians was probably due to more significant marine influence.

New material collected in the Zarubino slagheap in the Novgorod Region include numerous bones and scales of: "*Devononchus*" *tenuispinus*, *Bothriolepis* cf. *ciecere*, *?Cryptolepis grossi*, *Glyptopomus bystrowi, Holoptychius* cf. *nobilissimus*, *Ventalepis ketleriensis*, "*Dipterus*" cf. *arcanus* and Dipnoi indet. (Lebedev 2017). This list includes all taxa in the one cited above, although some of them are not found yet in Zarubino or may be missing. The bones and scales are mostly white or light grey, but sometimes pinkish and red-brownish. Unbiased sampling demonstrates dominance of antiarch armour fragments and *Holoptychius* scales. Dipnoan cranial bones are not uncommon, but only one poorly preserved tooth plate has been recovered. Osteolepiform ?*Cryptolepis* and *Glyptopomus* scales and porolepiform *Ventalepis* scales are rarer. Several unidentifiable arthrodire bone fragments have been found. "*Devononchus*" *tenuispinus* scales, shed *Ventalepis* denticles and gyrogonites of charophyte *Sycidium* cf. *paucisulcatum* Prinada, 1966 have been obtained by screen washing in the laboratory. No invertebrates are known from these layers. The vertebrate assemblage may be clearly correlated to the Latvian ones of the Ketleri age and central Russian ones of the Plavskian age.

There are some problems concerning the existing stratigraphical correlation of the Lnyanaya Fm to the Ketleri Fm of Latvia and Orel-Saburovo Beds of Central Russia. Lukševičs (2001) regarded the Lnyanaya Fm to be contemporaneous to the wide interval from the Mūri Fm below to the Sniķere and Žagarė Formations above (*trachytera* – Upper *postera* CZ) basing upon the distribution of *Bothriolepis ornata* and *Phyllolepis* sp. in the lower part of the Lnyanaya Fm and the Tērvete Fm just below the Sniķere Fm in Latvia. However, the Ketleri Fm is situated above the Žagarė Fm and correlates with the Upper *postera* – Lower *expansa* CZ. The lower part of the Plavskian RS, corresponding to the Orel-Saburovo Beds, correlates with the *Polygnathus irregularis* local CZ corresponding to the older *postera* Zone of the standard scale (Alekseev *et al.* 1996).

MATERIAL AND METHODS

Studied specimens include newly collected cranial bones: ?postorbital GM 290-210, ?gular bone 290-631, right lateral extrascapular GM 290-656, numerous scales GM 290-169 – 290-209, 290-211 – 290-255, 290-338 – 290-347, 290-359 – 290-368, 290-423, 290-425 – 290-432, 290-540 – 290-542, 290-588, 290-632 – 290-634, 290-716 – 290-745 in the GM collections. Two previously collected bones are in the collection of the PIN: postparieto-supratemporal PIN 1491/127 and a preopercular PIN 1491/128. All these are from western Latvia, Venta River near Ketleri farm, Upper Devonian, upper Famennian, Ketleri Formation. Several scales bear marks of lifetime damage.

Scales PIN 3725/678-680 come from the Orel-Saburovo Beds of the Plavsk RS (upper Famennian, Upper Devonian) exposed in the Rybnitsa quarry to the east of the Orel city, Central Russia. One more scale comes from a natural exposure on the bank of the Orlik River by the Maslovo village to the west of the Orel city.

Scale PIN 835/46, scale fragment PIN 835/47 and isolated scale denticles PIN 835/48-835/54 from Novgorod Region, Lyubytino District, was collected on the slopes of a slagheap of an abandoned mine in the town of Zarubino, Upper Devonian, upper Famennian, Lnyanaya Formation.

Material from the Ketleri locality has mostly been prepared manually by mounted needle, and the skeletal elements covered by dolomite crystals have been prepared using the airbrush. Central Russian materials were included in hard quartz sandstone with calcite cement and were prepared by combination of manual and chemical preparation with the 10% solution of acetic acid. Scales and denticles from the Zarubino mine clays had been screen-washed and after drying selected manually from the bone debris.

Skull bones nomenclature in this paper follows that used by Westoll (1938) for osteolepiforms and elpistostegalians, with modifications in terminology applied to porolepiforms.

SYSTEMATIC PALAEONTOLOGY

Dipnomorpha Ahlberg, 1991
Order Porolepiformes Jarvik, 1942
Family Ventalepididae fam. nov.

TYPE GENUS: *Ventalepis* Schultze, 1980.

DIAGNOSIS: Large porolepiforms characterised by thick rounded rhomboid scales. Straight anterodorsal and anteroventral margins form obtuse angle. Overlapped surface separated from exposed one by a shallow groove. Scales transmitting lateral line canal form a longitudinal keel along the body. Non-overlapped surface ornamented by conical denticles. Lateral line canal gives off short single branches on the scales, seismo-sensory canals on the cranial bones form multiple branching grooves.

FAMILY COMPOSITION: Monotypic family.

REMARKS. Schultze (1980) claimed that *Ventalepis* scales are transitional between cycloid, characteristic of the Holoptychiidae and rhombic, known in Porolepididae. Despite this, although questionably, this author assigned the genus to the family Holoptychiidae basing upon the structure of the cranial bones identified as “tabular” and “operculum or suboperculum”. Restudy of the scale structure demonstrates that apart from somewhat rounded outline, *Ventalepis* scales demonstrate no cycloid characters like traces of concentric growth on the visceral surface or a sector of radiating rows of horse-shoe shaped denticles on the overlapped surface (e.g. Ørvig 1957). This does not make possible further attribution of *Ventalepis* to the family Holoptychiidae.

The following features in *Ventalepis ketleriensis* scales contrast the condition observed in the members of the Holoptychiidae: a groove separating overlapped from non-overlapped surfaces externally, more deep contact area for the anterodorsally placed neighbouring scale and angled vertical ridge on the visceral surface. Those clearly suggest a special version of the rhomboid construction. General shape of the median row scale (Schultze 1980: text-fig. 10) and its overlapped anterior margin which is short, narrow, straight or slightly concave, are highly reminiscent of those in the Porolepididae porolepiforms and osteolepiforms with rhombic scales (Ørvig 1957). Transition from typically rhombic to round scale morphology with preservation of rhombic features occurs in the porolepiform genus *Heimenia* (Clément and Janvier 2004) and osteolepiforms *Marsdenichthys* (Long 1985) and *Medoevia* (Lebedev 1995). However, very special ornamentation of the non-overlapped surface precludes its attribution to the family Porolepididae, thus we erect here a new family Ventalepididae fam. nov. for this genus. Retention of archetypically rhomboid scale structure suggests early origin of these fishes, going back to before the origin of the round-scaled holoptychiids.

Ventalepis Schultze, 1980

1980. *Ventalepis* n. g.; H.-P. Schultze, p. 226.

TYPE SPECIES: *Ventalepis ketleriensis* Schultze, 1980, Upper Devonian, Famennian, Latvia.

DIAGNOSIS. As for the family.

GENERIC COMPOSITION. Monotypic genus.

Ventalepis ketleriensis Schultze, 1980
(Text-figs 2–3, 5–6)

1980. *Ventalepis ketleriensis* n. sp.; H.-P. Schultze, p. 226, figs 1–13.

HOLOTYPE: Scale LDM 57/790 (LGD 0001 in the original publication), western Latvia, Venta River near Ketleri farm, Upper Devonian, upper Famennian, Ketleri Formation.

REFERRED SPECIMENS: Praeopercular (= tabular in the original publication) LDM 57/893 (LGD 0009 in the original publication); opercular LDM 57/897 (LGD 0002 in the original publication); ?postorbital GM 290-210; right lateral extrascapular GM 290-656; postparieto-supratemporal PIN 1491/127, preopercular PIN 1491/128, scale bearing lifetime traces of damage PIN 1491/129, all from western Latvia, Venta River near Ketleri farm, Upper Devonian, upper Famennian, Ketleri Formation. Scales PIN 3725/678-680, Rybnitsa quarry, east of the Orel city; and scale PIN 3725/681 from a natural exposure on the bank of the Orlik River by the Maslovo village to the west of the Orel city, both from the Orel Region, Central Russia, Upper Devonian, upper Famennian, Orel-Saburovo Beds of the Plavsk Regional Stage; scale PIN 835/46 and scale fragment PIN 835/47, isolated denticles PIN 835/48-54 and several dozens of unnumbered specimens from a slagheap of an abandoned mine in the town of Zarubino, Lyubytino District, Novgorod Region, Upper Devonian, upper Famennian, Lnyanaya Formation.

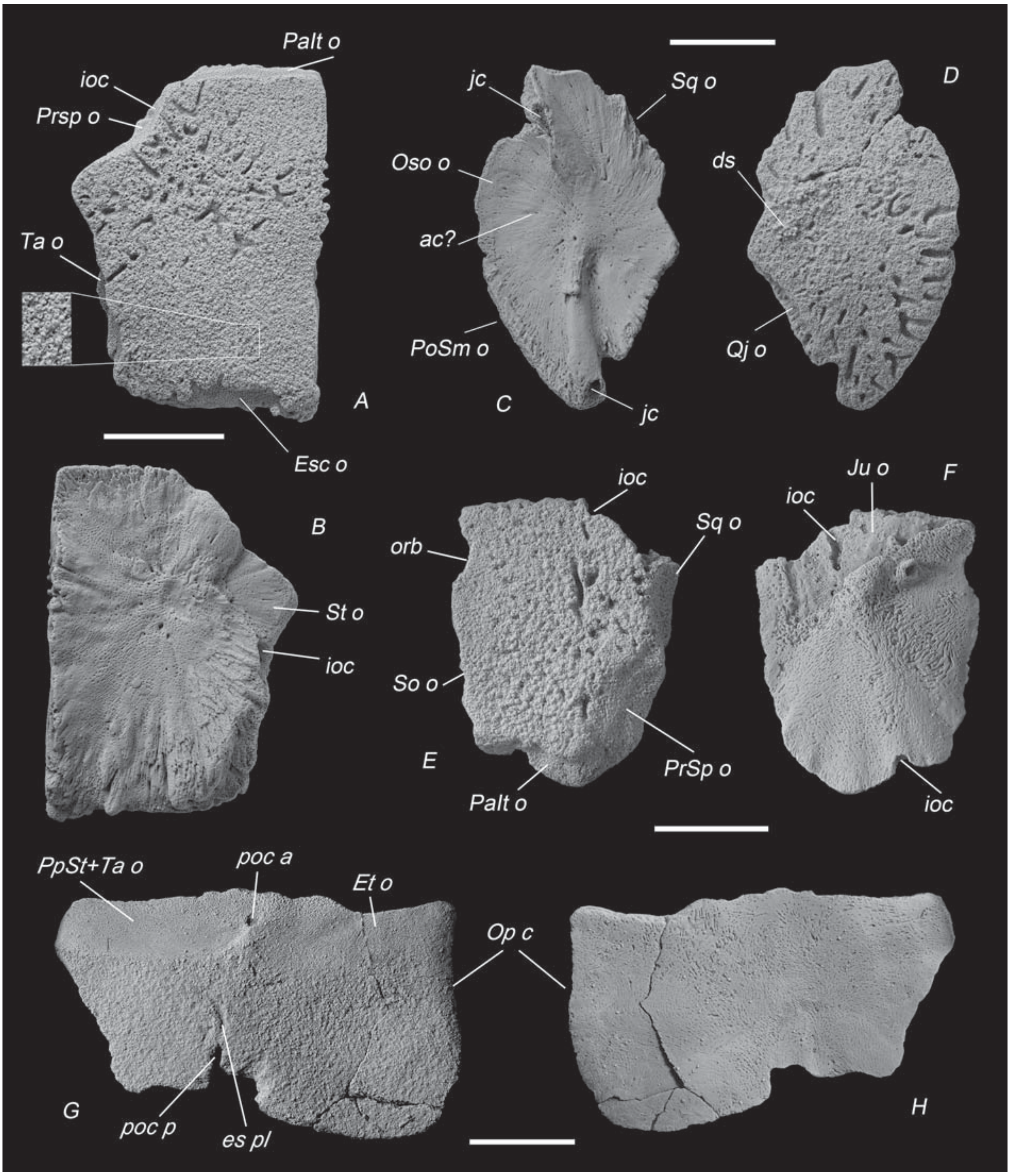
Numerous scales which we do not describe here from the Ketleri Fm are stored in the Latvian Museum of Natural History (LDM) (155 specimens from the Ketleri locality and several specimens from the Pavāri locality); in the Geological Museum (GM) of the University of Latvia (more than 100 specimens from Ketleri); in the Institute of Geology and Geography (LGGI) of the Lithuanian Academy of Sciences (Vilnius, Lithuania) and in the A.A. Borissiak Palaeontological Institute of the RAS, Moscow, Russia (PIN).

REMARKS: In the original description H.-P. Schultze (1980) provided no explanation why he regarded scales and cranial bones to belong to the same fish. However, we support his attribution upon the unique sculpturing consisting of delicate thin conical denticles, which ornament the exposed surfaces on both scales and dermal cranial bones.

DESCRIPTION

Cranial bones

The structure of the postparieto-supratemporal (*PpaSt*) (PIN 1491/127, Text-fig. 2A–B) differs from that in holoptychiids, in which the otico-occipital shield is known (*Glyptolepis*, *Holoptychius, Quebecius* and *Laccognathus*: Jarvik 1972; Cloutier and Schultze 1996; Vorobyeva 2006), in that the infraorbital seismo-sensory canal (*ioc*) enters this bone from the intertemporal by the anterolateral overlapped contact for the prespiracular (*Prsp o*). This odd construction may be interpreted by means of a suggestion that the canal occupied the extreme lateral position on the intertemporal and passed caudally via a small posterolateral process of this bone, which skirted the anterior portion of the PpaSt laterally. The opening foramen on this bone is thus situated ventrally from the anterior-most part of the contact area for the prespiracular. The latero-caudal opening of this canal is situated at approximately mid length of the lateral margin. This edge bears a prominent process separating the contact area for the prespiracular from that of the tabular (*Ta o*), like in holoptychiids. The latter area forms a smooth dorso-laterally facing surface in the posterior half and a wide rectangular area on the ventral side of this process which supposedly overlapped the anterior part of the medial margin of the tabular; these two contacts are separated by the caudal opening of canal. The straight median sutural margin bears rough ridges diverging from a point opposite the ossification centre in a fan-shaped manner. The contact surfaces for the parietointertemporal (*PaIt o*) and for the extrascapulars (*Esc o*) are straight; the former is facing antero-dorsally; the latter bears a short notch dorsally. The anterior part of the dorsal surface shows numerous pits and grooves for the external branches of the infraorbital canal but no pit-lines are distinguishable. The ventral surface demonstrates rough pits and swollen ridges



Text-fig. 2. *Ventalepis ketleriensis* Schultze, 1980. Cranial bones. A, B – postparieto-supratemporal PIN 1491/127; C, D – preopercular PIN 1491/128; E, F – ? postorbital GM 290-210; G, H – lateral extrascapular GM 290-656. A, C, E, G, externally, B, D, F, H, viscerally. All from the Ketleri locality, right bank of the Venta River, western Latvia; Upper Devonian, upper Famennian Ketleri Formation. Scale bars 1 cm. Abbreviations: *ac?* possible lateral wall of the adductor chamber; *ds* denticulated sculpturing; *Esc o* contact area for the extrascapulars; *es pl* extrascapular pit-line; *Et o* area overlapped by extratemporal; *ioc* infraorbital canal; *jc* opening for the jugular canal; *Ju o* contact area for the jugular; *Op c* opercular contact area; *orb* orbital margin; *Oso o* opercular and subopercular contact area; *PaIt o* contact area for the parieto-intertemporal; *poc a* anterior opening of the postotic canal; *poc p* posterior opening of the postotic canal; *PoSm o* contact surface for the preoperculosubmandibular; *PpaSt* postparieto-supratemporal; *PpSt+Ta o* area overlapped by postparieto-supratemporal+tabular; *PrSp o* contact area for the prespiracular; *Qj o* overlapped surface for the quadratojugal; *So o* contact area for the supraorbital; *Sq o* contact area for the squamosal; *Ta o* contact area for the tabular radiating from the ossification centre; no traces of endocranial ossifications are preserved. The minimum width at the anterior margin makes 45% of the total length and the maximum width of the PpaSt at the lateral wedge separating the contact areas for the prespiracular from that of the tabular makes 74% of the total length. These parameters differ from those observed in *Glyptolepis groenlandica* Jarvik, 1972 (30% and 52% respectively), *Holoptychius* sp. (31% and 46% respectfully), *Porolepis* (50% and 67% respectfully) (Jarvik 1972), in *Laccognathus panderi* Gross, 1941 (29% and 47% respectfully) (Gross 1930), *L. grossi* Vorobyeva, 2006 (33% and 46% respectfully) (Vorobyeva 2006) and in *L. embryi* (22% and 40% respectfully) (Downs *et al.* 2011). Thus, the otico-occipital shield in *Ventalepis* is prominent in its shortness in comparison to holoptychiids and is the closest in its proportions to that in *Porolepis*.

Here we present an alternative interpretation of the bone identified as a tabular by Schultze (1980) as a preopercular. Our suggestion is based upon the morphology of a very well preserved new specimen PIN 1491/128 identical to the specimen LDM 57/893 (LGD 0009 in the original publication) described by this author (1980, text-fig. 12). These specimens are compared here to the morphologically similar isolated preopercular of *Laccognathus grossi* (PIN 3547/47). The setting of the homologous element is seen in the complete *L. grossi* skull PIN 3547/6 (Vorobyeva 2006, text-fig. 1, on the right side).

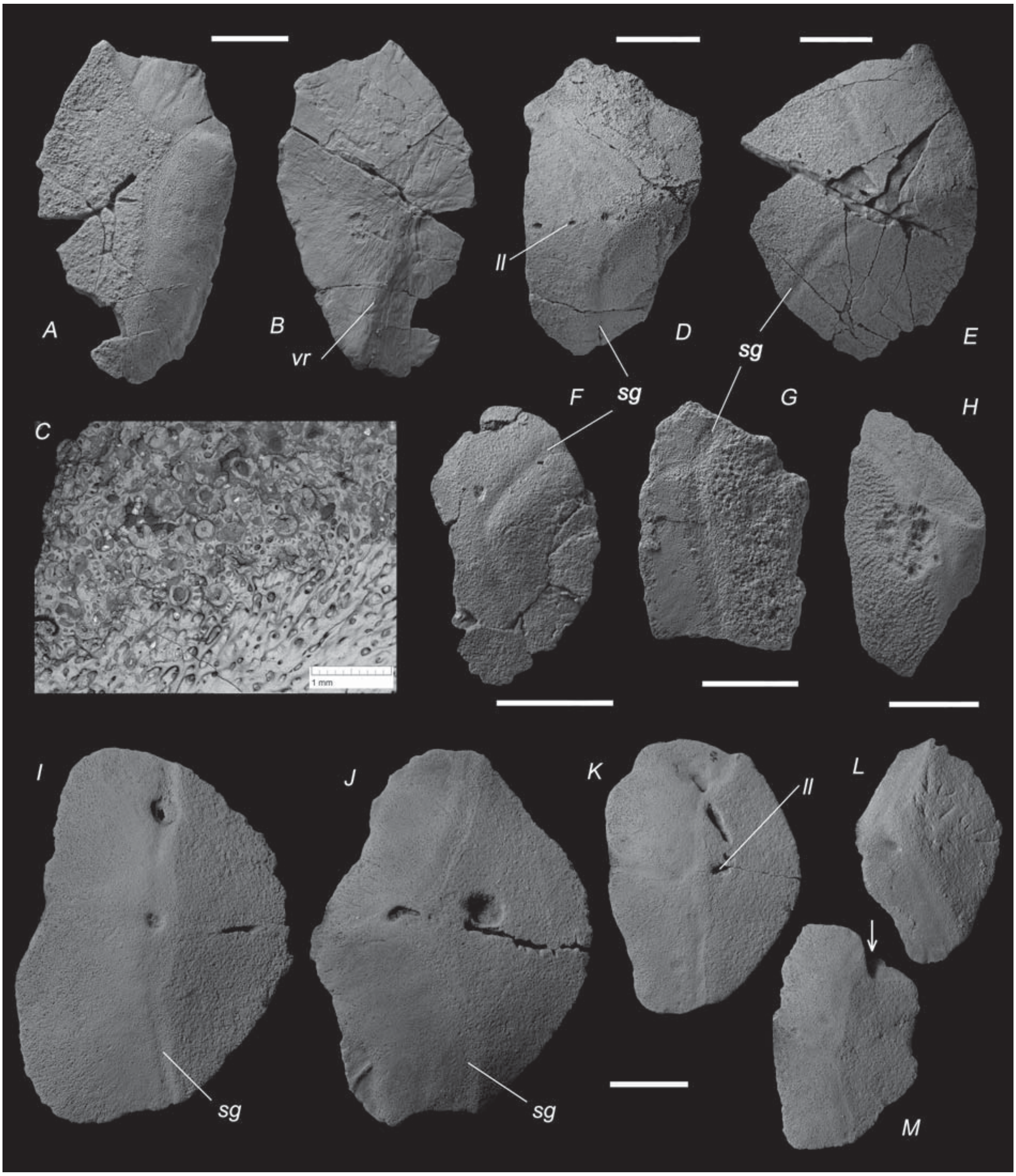
The preopercular PIN 1491/128 (Text-fig. 2C–D) is roughly rhomboid; the posterior margin contacting the opercular series is convex and rounded. The dorsal half of this margin tapers forming an overlapping edge to the opercular and subopercular (*Oso o*), but the ventral one forms a blunt contact surface for the preoperculosubmandibular (*PoSm o*). The anteroventral margin of the bone bears a narrow overlapped surface for the quadratojugal (*Qj o*). The antero-dorsal edge of the bone overlapping the squamosal (*Sq o*) shows short oblique ridges for connective tissues but the margin itself is mostly damaged and the type of connection to the squamosal is unclear. The jugular canal (*jc*) enters the bone through a foramen on the anterodorsal tip of the swollen S-shaped ridge running by the visceral surface and leaves the bone through the similar structure ventrally. The qudratojugal contact area is separated from the ventral point of this ridge by a small notch, the function of which is unclear. The posterior sector of the visceral surface is occupied by an elongated depression possibly marking the postero-dorsal part of lateral wall of the adductor chamber (*ac*?). On the external surface a small patch of original denticulated sculpturing (*ds*) is preserved in PIN 1491/128 in the middle of the bone close to the anterior margin.

Specimen GM 290-210 (Text-fig. 2E–F) is provisionally and cautiously identified here as a postorbital of unusual *gestalt*. The orbital margin (*orb*) occupies a very short part of the anterior edge of the bone, whilst the contact area for the supraorbital (*So o*) is unusually long. The infraorbital canal (*ioc*) passes through the bone along its longitudinal axis. The overlapped area for the prespiracular (*PrSp o*) is longer and wider than that for the squamosal (*Sq o*). The external surface bears pores and grooves of the superficial branches of the seismo-sensory canal. The visceral surface bears a triangular-shaped depression adjoining the orbital margin; the jugular (*Ju o*) contact forms a pocket-like depressed area separated from the rest of the surface by a sharply defined crest.

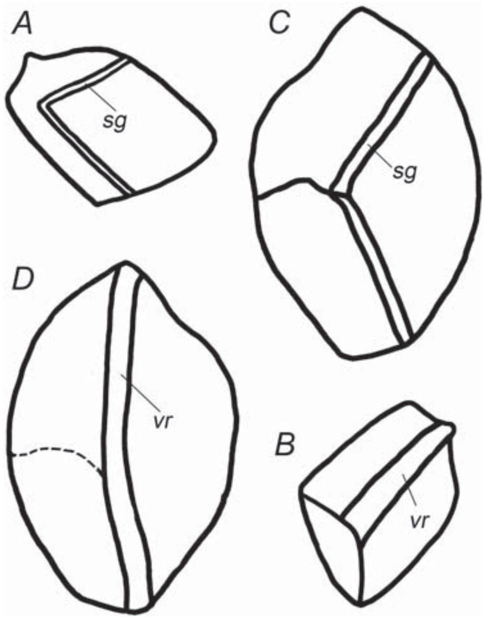
Specimen GM 290-656 (Text-fig. 2G–H) in its gross morphology is close to the lateral extrascapular bone in other porolepiforms (*Holoptychius* and *Glyptolepis*: Jarvik 1972; *Laccognathus*: Vorobyeva 2006) by shape and arrangement of contact surfaces, but differs in the absence of the occipital commissure canal. In contrast to other porolepiforms, GM 290-656 is also approximately twice wider than longer. The anterior opening of the postotic canal (*poc a*) is situated on the lateral margin of the area overlapped by the postparieto-supratemporal and tabular; the posterior one (*poc p*) approximately in the medial third of the posterior margin of the bone. A short curved extrascapular pit-line (*es pl*) is placed slightly anteriorly from this opening. The anterior margin is clearly subdivided into two overlapped areas: for the postparieto-supratemporal+tabular (*PpSt+Ta o*) medially and extratemporal (*Et o*) laterally. The lateral margin presumably contacting the opercular (*Op c*) is thickened, the others are thin. The visceral surface of the bone is rather smooth and featureless, but demonstrates pores and tiny grooves possibly following its multidirectional growth.

Scales

A thorough description of scale morphology and histology was provided by Schultze (1980). New material from Central Russia (specimens PIN 3725/678-681) and Novgorod Region (PIN 835/46-47) does not differ much from that described from Latvia (Text-fig. 3). However, we are highlighting here several characters, which had not received enough attention previously. A keel-like swollen ridge on the visceral surface stretching dorsal to ventral (*vr*, Text-fig. 3B)



Text-fig. 3. *Ventalepis ketleriensis* Schultze, 1980, scales. A-C – PIN 3725/678, C, an enlargement of the boundary between the overlapped and exposed surfaces in A showing bases of broken denticles; D – PIN 3725/679, E, PIN 3725/680. A-E – Rybnitsa quarry in the vicinity of the city of Orel, Orel Region, Central Russia; Orel-Saburovo Beds, lower part of the Turgenevo Formation, Plavskian Regional Stage, upper Famennian; F – PIN 3725/681, natural exposure on the bank of the Orlik River by the Maslovo village to the west of the Orel city, same age as A-E; G – PIN 835/46, slagheap of an abandoned mine in the town of Zarubino, Lyubytino District, Novgorod Region, northwestern Russia, Upper Devonian, upper Famennian, Lnyanaya Formation; H – PIN 1491/129; I – GM 290-183; J – GM 290-345; K – GM 290-430; L – GM 290-741, scales showing lifetime and post-mortem damage traces; M – GM 290-224, scale with folded free surface; Ketleri locality, right bank of the Venta River, western Latvia; Upper Devonian, upper Famennian Ketleri Formation. Scale bars 1 cm, except in the SEM photo. Abbreviations: *ll* superficial pores of the lateral line canal branches; *sg* groove separating the exposed surface from the overlapped one; *vr* visceral ridge



Text-fig. 4. Diagrammatic representation of scale structure in "osteolepidids" (A, B) and *Ventalepis ketleriensis* Schultze, 1980 (C, D) illustrating similarities in their structure. A, C, externally, B, D, viscerally. Abbreviations: *sg* groove separating the overlapped surface from the exposed one; *vr* keel-like ridge on the visceral surface. Not to scale

consists of dorsal and ventral parts usually shallowing towards the centre of the scale and growing more massive towards the margins. This keel may be homologous to those present in "osteolepidid" sarcopterygians and numerous early actinopterygians (Text-fig. 4A–D), however *Ventalepis* scales miss a characteristic connecting "peg". In "osteolepidid" sarcopterygians and in *Ventalepis* the area overlapped by dorso-rostrally placed scales is separated from the exposed surface by a shallow groove (*sg*). Of four more or less complete scales from the Orel Region, two scales belong to a lateral line canal row. There are no examples of scales with an open groove for the canal as illustrated by Schultze (1980, text-fig. 1a); material described here demonstrates typical perforation by single widely spaced pores transmitting the branches of the canal (*ll*, Text-fig. 3D).

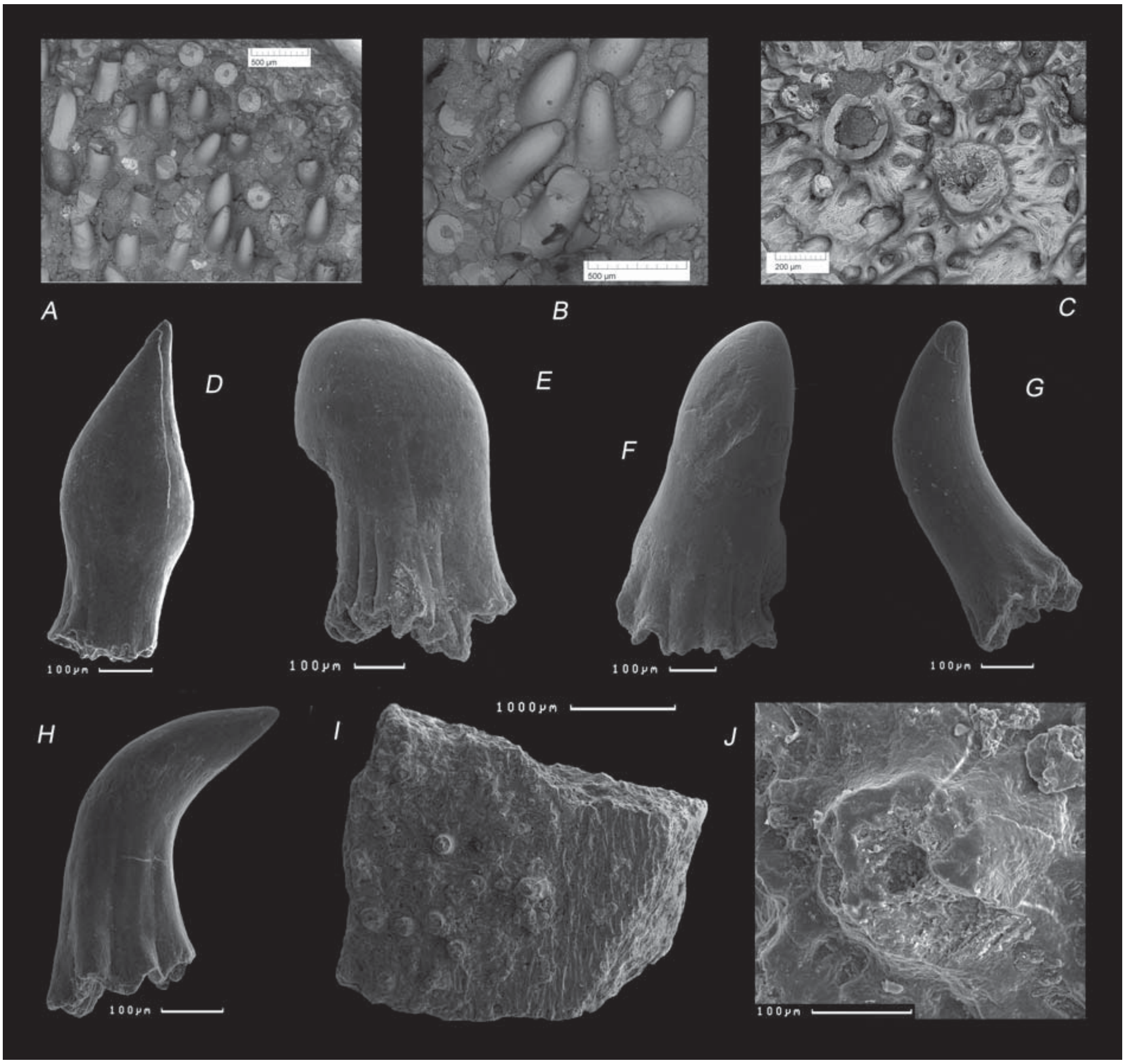
Scale height being larger than its length suggests that the fish was deep-bodied.

Some scales from Ketleri (Text-fig. 3H–K) show various pathologies on the outer surface, usually represented by a single rounded pit or rarely several closely spaced pits on the external surface. Scale PIN 1491/129 bears a rounded group of small pits on the boundary between the free and overlapped surfaces externally. Similar rounded pits and pit groups had been interpreted by Lukševičs *et al.* (2009) as lifetime traces of trematode larvae (metacercaria), branchiuran and copepod crustaceans, or leeches. The attachment of adult females of extant lernaeid copepods to the integument of fish induces an intense inflammatory response and the tissue around the anchor of a parasite turns into a granuloma or necrotic lesion (Paperna 1996). The visceral surface of the scales does not show any traces of damage or its healing, thus parasite activity was only superficial. Chaotically oriented short narrow scratches on the free surface of the scale GM 290-741 (Text-fig. 3L) could be the post-mortem damages. The free surface of the scale GM 290-224 (Text-fig. 3M) shows unusual pocket-like folding along the margin overlapping caudally situated scale, two round pits on the overlapped surface and two small pits on the free surface, which possibly are the traces left by predator teeth.

Denticles of the dermal ornamentation

As far as the Russian material has been cleaned of the hardly cemented sandstone by acid preparation, scale surfaces show minute details of the surface structure. Specimen PIN 3725/678 demonstrates a field of numerous tiny denticles like those described by Schultze (1980, text-fig. 2a1–a2). Most of them on the free surface are broken off, but a large group close to the posterior margin of the scale is intact (Text-fig. 5A–C). Denticle bases are situated close to each other; the distance between those rarely exceeds a half of their diameter or may be less than that (Text-fig. 5C). When cusps are unbroken, their tips form a uniform field composed of loosely set apices arched caudally (Text-fig. 5A–B). Denticles form wide stump-like structures at their bases consisting of radially directed massive outgrowths of well-seen bony fibers. These outgrowing processes may encircle or bypass large nutrient foramina. The denticles contain simple, rather wide conical pulp cavities.

Denticle crown shape varies from simple high conical and sharply pointed to massive and blunt (Text-figs 5D–H and 6), all of them rounded in cross-section. Some cusps are bulb-shaped with a deep well expressed neck and high pointed apex (Text-fig. 5D). All denticles demonstrate strong but simple folding at the base. The distal circular zone of these vertical folding bears microornamentation consisting of minute pits; this zone may probably fix the adherence of epidermis to the cusps, which stand free out of the skin. One of the specimens (PIN 835/54) unusually demonstrates two belts of microsculpture

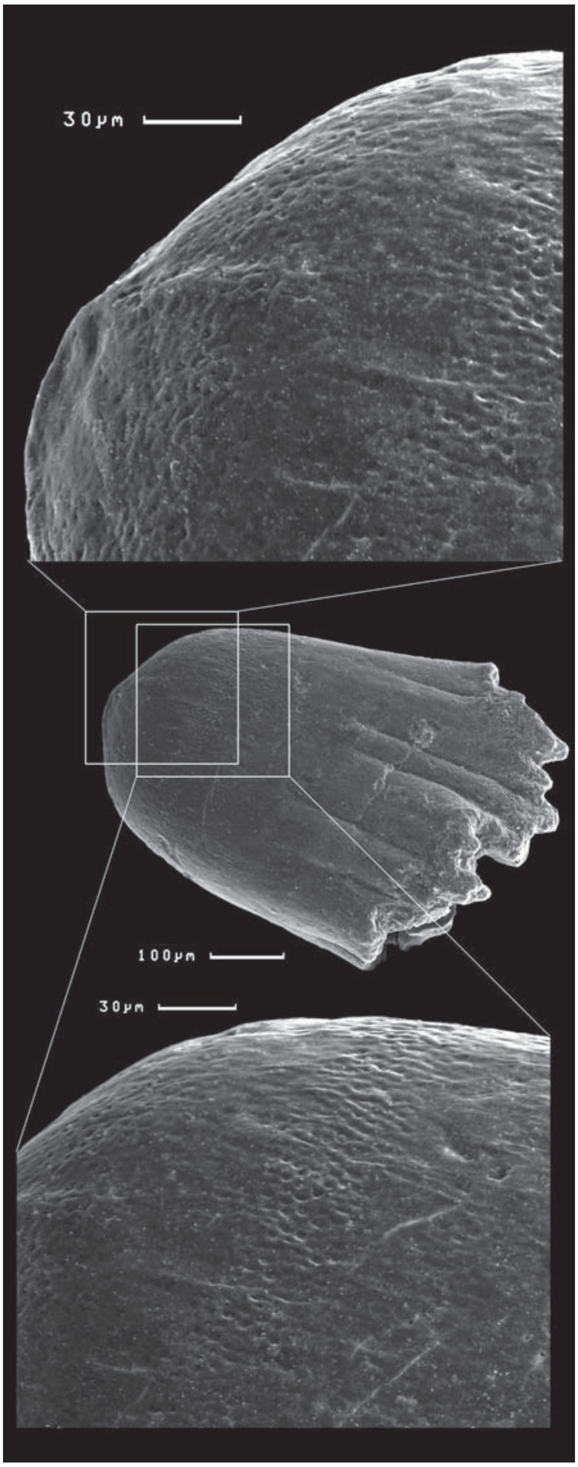


Text-fig. 5. *Ventalepis ketleriensis* Schultze, 1980, denticles on scales. A, B – intact denticles preserved in an area on the scale PIN 3725/678; C – denticle bases in the same specimen; D-H – isolated denticles: PIN 835/52 (D), PIN 835/48 (E), PIN 835/50 (F), PIN 835/49 (G), PIN 835/51 (H); I – scale fragment; J – an enlargement showing denticle base in the same specimen. A-C – Rybnitsa quarry in the vicinity of the city of Orel, Orel Region, Central Russia; "Orel-Saburovo Beds", lower part of the Turgenevo Formation, Plavskian Regional Stage, upper Famennian; D-J – slagheap of an abandoned mine in the town of Zarubino, Lyubytino District, Novgorod Region, northwestern Russia, Upper Devonian, upper Famennian, Lnyanaya Formation. Scale bars as indicated on the figures

of this kind, one situated in the distal third of the denticle height and another encircling the apical-most tip of the cusp (Text-fig. 6).

Absence or presence of enameloid layer on the cusp surface was neither rejected nor supported by Schultze (1980). In some of our specimens (PIN 835/49-51), in which the surface is slightly damaged, one can observe a thin superficial layer on the breakage surfaces (Text-fig. 5G–H); this layer might consist of enameloid.

As already noted by Schultze (1980), no other osteichthyan fish show this kind of sculpturing. Denticles on *Ventalepis* scales demonstrate the most primitive condition for all other types of dermal denticles. By their conical shape, simple dentine folding at the base and simple conical pulp cavity they strongly resemble



Text-fig. 6. *Ventalepis ketleriensis* Schultze, 1980. Distal micro-ornamentation forming circular zones on the denticles of scale ornamentation. Specimen PIN 835/54, showing enlargements of the apical part of the isolated denticle. Slagheap of an abandoned mine in the town of Zarubino, Lyubytino District, Novgorod Region, north-western Russia, Upper Devonian, upper Famennian, Lnyanaya Formation

marginal teeth in the jaws or shagreen denticles on the dermal bones and platelets of the orobranchial cavity. This primitive condition is especially surprising to see in the late porolepiform fish.

DISCUSSION

Distribution of Ventalepis vertebrate community within the Baltica zoogeographical province

The similarity of the Latvian vertebrate fauna from Ketleri and the central Russian localities from the Orel Region had been discussed for a long time (Lebedev and Lukševičs 1996). Despite evident resemblances (Table 1) faunistic exchanges between these two assemblages had been thought to occur indirectly along the southern coast of the Polish-Belarus Peninsula (despite an arrow indicating direct connection across the Latvian Isthmus in Lebedev *et al.* 2010, text-fig. 4). However, as it became evident recently, the tectonic Latvian Saddle separating the upper Famennian deposits of the Baltic Devonian basin and the Central Devonian Field of Russia (and interpreted in this paper as an isthmus) arose later during the Hercynian orogeny; thus after this event the Famennian sediments on the saddle became eroded and these deposits became separated by a field of older, Frasnian deposits. This upgrade of knowledge made possible establishment of a direct palaeogeographic connection of the Moscow and Baltic syneclise basins and, correspondingly, explained the faunistic entity in a simple way. The newly found Zarubino assemblage placed halfway between the two known earlier supports the idea on the distribution of the Ventalepis assemblage in a vast coastal territory of the eastern margin of the Old Red Sandstone continent.

Recently Beznosov *et al.* (2012, 2013, 2018) described new vertebrate assemblages from the Pokayama Formation in North Timan (Table 1). The assemblage from the middle part of the Pokayama Formation includes *Bothriolepis ciecere* Lyarskaya, *B*. sp., "*Devononchus*" *tenuispinus* Gross, cf. *Dunkleosteus* sp., *Holoptychius* sp., *Dipterus* sp. 1, *Dipterus* sp. 2 and Chirodipteridae gen. indet. The composition of this assemblage matches those from the Ketleri Formation of Latvia, the Orel-Saburovo Beds of Central Russia and the upper part of the Lnyanaya Formation of north-western Russia. Althought no *Ventalepis* remains are yet known from the Pokayama Formation, this assemblage includes highly characteristic antiarch species *B. ciecere* and an acanthodian "*Devononchus*" *tenuispinus* that suggests its palaeozoogeographic connection

Vertebrates		Western Latvia (lower expansa CZ) (Lebedev and Lukševičs 2016)	Orel Region, Central Russia (upper postera CZ) (Lebedev and Lukševičs 2016)	Volyn, Ukraine (Zapadny Bug Formation, ?trachytera – lower postera CZ) (Plax 2011)	Zarubino (Novgorod Region, NW Russia)	Pokayama, North Timan (trachytera–postera CZ) (Beznosov *et al.* 2012, 2013, 2018)
Acanthodians		?*Haplacanthus* sp., *Devononchus* sp., "*D.*" *tenuispinus*, "*D.*" *ketleriensis*, "*Cheiracanthus*" sp., "*Acanthodes*" sp.	*Haplacanthus* sp., *Devononchus* sp., "*D.*" *tenuispinus*, "*D.*" *ketleriensis*, "*Cheiracanthus*" sp., "*Acanthodes*" sp.	cf. *Haplacanthus*, *Devononchus* sp., "*D.*" *ketleriensis*, cf. *Cheiracanthus*, *Acanthodes* sp.	"*Devononchus*" *tenuispinus*	"*Devononchus*" *tenuispinus*
Placodermi	Antiarchi	*Bothriolepis ciecere*	*Bothriolepis ciecere*	*Bothriolepis* sp.	*Bothriolepis* cf. *ciecere*	*Bothriolepis ciecere, B.* sp.
	Arthrodira		"*Dinichthys*" *machlaevi*, Pachyosteina gen. ind.	*Dinichthyidae* gen. ind.	Pachyosteina gen. ind.	*cf. Dunkleosteus*
	Ptyctodonti		*Chelyophorus verneuili*	*Chelyophorus* sp., *Ptyctodontida* gen. indet.		
Sarcopterygii	Osteolepiformes	*Cryptolepis grossi*, *Glyptopomus bystrowi*, Tristichopteridae ind.	*Cryptolepis grossi*, *Glyptopomus bystrowi*	?*Platycephalichthys* sp., Osteolepididae gen. ind.	*Cryptolepis grossi, Glyptopomus bystrowi*	
	Porolepiformes	?*Glyptolepis dellei*, *Holoptychius* cf. *nobilissimus*, *Ventalepis ketleriensis*	?*Glyptolepis dellei*, *Holoptychius* cf. *nobilissimus, Ventalepis ketleriensis*	?*Glyptolepis dellei*, *Holoptychius* sp., Sarcopterygii ind. (?*Ventalepis ketleriensis*)	?*Glyptolepis dellei, Holoptychius* cf. *nobilissimus*, *Ventalepis ketleriensis*	*Holoptychius* sp.
	Struniiformes	*Strunius* sp.	*Strunius* cf. *rolandi*, *Pycnacanthus fischeri*	*Strunius* cf. *rolandi*		
	Dipnoi	*Orlovichthys limnatis*, "*Dipterus*" *arcanus*	*Orlovichthys limnatis*, "*Dipterus" arcanus*, "*D.*" *marginalis*,"*D.*" *pacatus*, "*D.*" *expressus*, *Grossipterus venustus*, *Chirodipterus interstitus, Conchodus excussus*, *Jarvikia lebedevi*	*Dipterus* sp., Dipnoi ind.	"*Dipterus*" cf. *arcanus*, Dipnoi indet.	"*Dipterus*" sp. 1 and 2, *Chirodipteridae* gen. indet.
Tetrapoda		*Ventastega curonica*, Tetrapoda indet.				
Actinopterygii		Actinopterygii ind.	*Mimipiscis* sp.	Actinopterygii ind.		

Table 1. Late Famennian vertebrate assemblages of the Baltica Province

to those mentioned above. This suggests newly recognized extension of the habitat area of the community to the northeast from the western and central part of the East European Platform.

Plax (2011) published, among other materials on the Devonian fishes, the primary identifications of vertebrate remains from the upper part of the Zapadny Bug Formation (Volyn monocline, Ukraine), obtained from the boreholes. His list of taxa includes: Dinichthyidae gen. indet., *Bothriolepis* sp., *Chelyophorus* sp., Ptyctodontida gen. indet., *Orodus* sp., Chondrichthyes indet., cf. *Haplacanthus*, *Devononchus* sp., "*Devononchus*" *ketleriensis* Gross, cf. *Cheiracanthus*, *Acanthodes* sp., *Holoptychius* sp., ?*Glyptolepis dellei* (Gross), *Strunius* cf. *rolandi* (Gross), ?*Platycephalichthys* sp., Osteolepididae gen. indet., Sarcopterygii indet., *Dipterus* sp., Dipnoi indet., Actinopterygii indet. Plax correlated these deposits to the Švete-Žagare interval (= Spārnene-Piemare in modern nomenclature (trachytera – lower postera conodont zones) by the composition of the vertebrate assemblage. His illustration of a scale fragment on pl. III, fig. 7 (identified by this author as Sarcopterygii ? indet.), shows clearly a small scale fragment sculptured by characteristic *Ventalepis* denticles.

Faunistic analysis applied to these data (Table 1) demonstrates significant affinity of assemblages from the Latvian, central and north-western Russian, Ukrainian and Timan localities especially by presence of *Holoptychius* sp. (?*H. nobilissimus*), *Bothriolepis ciecere,* "*Devononchus*" *tenuispinus* and "*D.*" *ketleriensis*. These fishes are highly characteristic of the Ventalepis assemblage and form its basal structure. A set of acanthodian and sarcopterygian species make the Latvian and central Russian assemblages very close. The sarcopterygian cluster in Zarubino is also very close to those. On the other hand, the pachyosteine arthrodires are unknown from Ketleri in contrast to the other areas despite huge amount of collections accumulated for many years. The Central Russian localities differ from the others except Volyn by a significant variety of dipnoan taxa as well as abundant struniiforms and ptyctodont placoderms. Apart from vertebrates, a limited set of invertebrate taxa including bivalve and cephalopod molluscs, crustaceans and conodonts is presented here. These differences are interpreted here as resulting from the maximum marine influence to the Central Russian area. Tetrapods have been found until now only in the Latvian localities; their occurrence in Central Russian and Novgorod Region ones may be shown up in future. The composition of the Volyn assemblage in general, as well as *Ventalepis* scale record in combination with "*Devononchus*" *ketleriensis* scales make us suggest the pervasion of the Ventalepis community to the west not only by the strait north of the Polish-Belarus Island, but also to the south from it, demonstrating direct connection of the Central Devonian field basin to west Ukraine.

Thus, the Ventalepis vertebrate assemblage occupied a vast territory in the East European platform being confined to the coastal-marine territories and coastal lowlands periodically invaded by sea as shown on the palaeogeographic and facial maps created by Vinogradov and Nalivkin (1960) and Ziegler (1988).

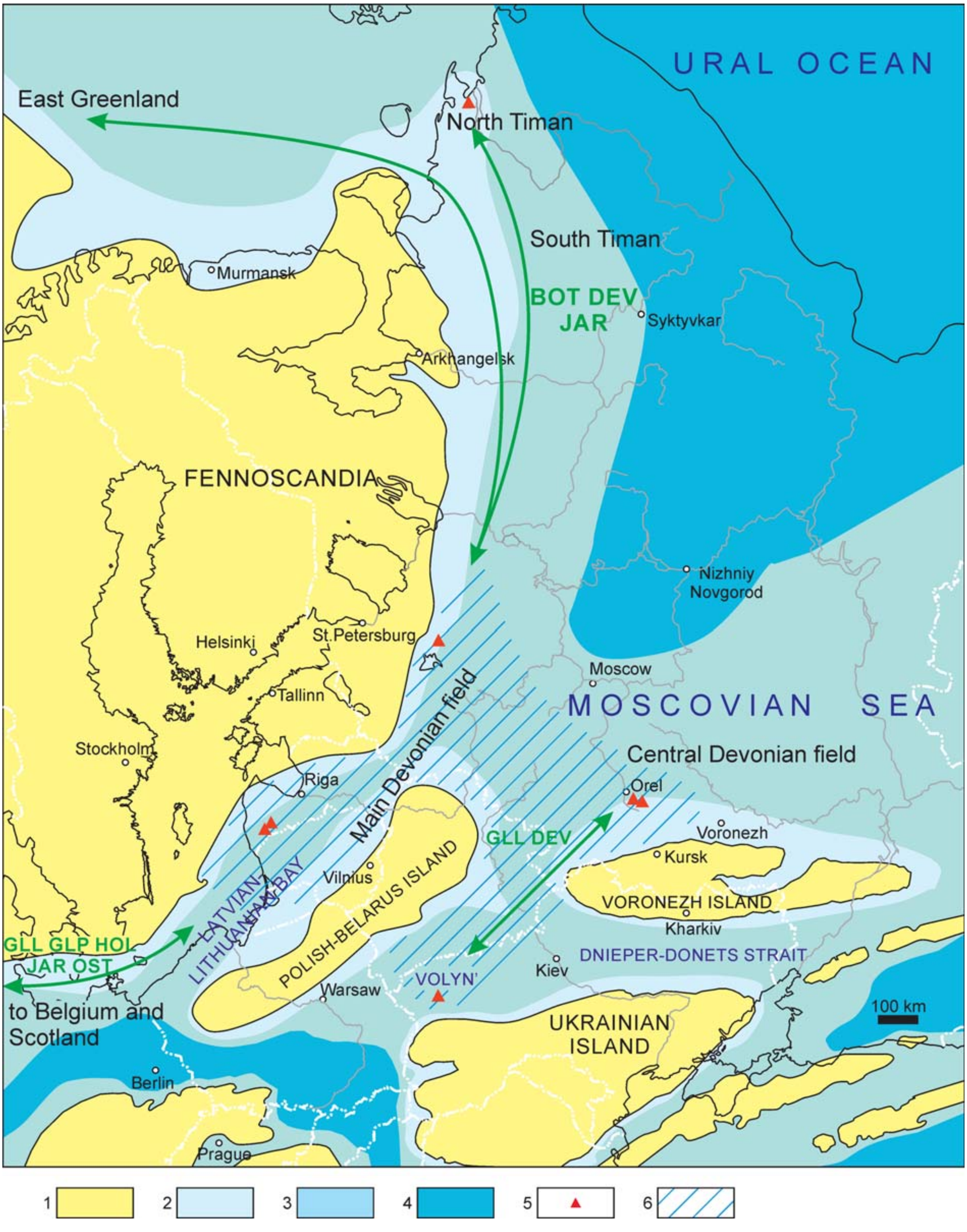
Zoogeographical connections of Ventalepis vertebrate community to the adjoining provinces

Lebedev *et al.* (2010) analysed the zoogeographical composition and structure of the upper Famennian community from the Ketleri Fm and Orel-Saburovo Beds (Plavskian Regional Stage). On the generic level this analysis revealed the dominance of the local (*Ventastega*, *Holodipterus*, *Grossipterus*, *Chirodipterus*, *Conchodus*) and provincial (*Devononchus*, *Chelyophorus*, *Cryptolepis*, *Ventalepis, Orlovichthys*) upper Famennian endemics in this fauna, thus showing its relative isolation. The local and provincial endemics (for the exception of the acanthodian *Devononchus*) as well as cosmopolitans are not useful for the analysis of the zoogeographic connections between adjoining provinces, thus the members of these groups are not regarded here. The acanthodian genus *Devononchus* is currently known only from the territory of the Baltica zoogeographical province and thus had been regarded by Lebedev and Lukševičs (2017) as a provincial endemic. However, personal observation made by Lebedev in 2013 of the spine specimen provisionally identified as Chondrichthyes indet. by Blom *et al.* (2007, text-fig. 3) suggests it to be rather a *Devononchus* acanthodian spine, but this possibility should be supported or rejected by future study. A patch of disarticulated spines appearing to be "from an acanthodid similar to the Frasnian *Homalacanthus* Russell, 1952" found in the Britta Dal Formation (Blom *et al.* 2007) is also waiting for elaboration of identification.

Polydemics include *Holoptychius* and *Dipterus*, and only *Bothriolepis*, "*Acanthodes*" and *Mimia* are cosmopolitan for the Famennian. The polydemic *Holoptychius* is known from Laurentia (Greenland, Scotland, Belgium, France: Jarvik 1972; Cloutier and Candilier 1995), East Gondwana (Australia: Johanson and Ritchie 2000) and Siberia (Kuznetsk Basin: Ivanov and Rodina 2004), being especially abundant in the Greenland and French-Belgian associations.

The cosmopolitan antiarch *Bothriolepis* is one of the most frequent elements in the Famennian faunas, being known from Laurentia, Siberia, East Gondwana and South Africa (Lebedev *et al.* 2010). However, on the species level this antiarch fish shows close affinities with Laurentia. *B. ciecere* from Latvia and Central Russia is morphologically rather close to *B. nielseni* from Greenland; there are no species of *Bothriolepis* from Scotland similar to *B. ciecere*. Recently *B. ciecere* has been reported also from the Famennian Pokayama Fm of North Timan (Beznosov *et al.* 2013).

Discussion of the members of the quasiendemic/didemic and polydemic groups makes possible to follow the palaeozoogeographic connections of this fauna. Didemics include fewer taxa than the endemics: *Glyptopomus*, *Glyptolepis*, *Strunius* and *Jarvikia*. Original inclusion of "*Dinichthys*" in this group (Lebedev *et al.* 2010: "*Dinichthys*" *makhlaevi* O. Obrucheva) is uncertain, as it is currently impossible to attribute the specimens united under this conditional generic name to any definite genus of the family Dunkleosteidae. Apart from the Baltica Province the didemic osteolepiform genus *Glyptopomus* is known from Scotland, Pennsylvania and Belgium (Lebedev and Lukševičs 2017). The Famennian *Glyptolepis*, known mostly from the Middle Devonian, is also recorded from the upper Famennian of Belgium (Cloutier and Candilier 1995). The struniiform genus *Strunius* was reported from Colorado, U.S.A. (Ginter 2001), but is likely to be spread much wider; it is usually represented by isolated minute dental elements and is only rarely described. Thus, all didemics show Laurentian affinities, demonstrating the major congruency to the Belgian and East Greenland assemblages.



Text-fig. 7. Distribution of the Ventalepis assemblage within the Baltica Province during the Late Famennian and possible faunistic interchanges (green arrows). Based upon paleogeographic reconstruction of the Earth for the Late Devonian by Ronald Blakey (Deep Time Maps™). Legend: 1 – land; 2 – land-sea transitional zone; 3 – shallow sea; 4 – deep sea; 5 – the studied vertebrate localities; 6 – habitat area of the Ventalepis assemblage. Abbreviations by the arrows indicate vertebrate taxa: BOT – *Bothriolepis ciecere*; DEV – *Devononchus*; GLL – *Glyptolepis*; GLP – *Glyptopomus*; HOL – *Holoptychius*; JAR – *Jarvikia*; OST – "Osteolepididae"

To the west from the Baltic Devonian basin, a band of the Old Red Sandstone continent shoreline passed through the Island of Gotland, Jutland Peninsula and further to Belgium, northern France and British Isles (Ford and Golonka 2003). Thus, a theoretical zoogeographic connection of the Baltica province to these areas in Western Europe is not improbable and finds its palaeogeographical support. During the Late Famennian (trachytera-middle expansa CZ interval) the Belgian Namur–Dinant Basin was a shallow-water siliciclastic shelf; the facies in the Strud area yielded fossil vertebrates belonging to continental, fluvial vertebrate assemblages (Denayer *et al.* 2016). Some genera in the Belgian Strud assemblage (Olive *et al.* 2015) are in common with those from the Ventalepis assemblage: a porolepiform *Holoptychius* and a dipnoan *Jarvikia*. The cosmine-covered 'Osteolepididae' might turn to be related to *Cryptolepis* known from the Latvian and Russian localities. An unnamed ichthyostegid from Strud might also be related to a second tetrapod from the Latvian Ketleri locality with future studies.

The northern faunistic exchange could physically occur through a narrow stripe of lowland and basins running to the north-west (in modern geographic orientation of the continents) along the shoreline and by the lowlands of the south-east coast of Fennoscandia towards Timan, further to the north to the easternmost point of the Scandinavian Caledonian Mountains towards East Greenland along the Barents Sea shelf.

Vertebrates composing the upper Famennian Aina Dal and Britta Dal assemblages are known from the East Greenland intramontane basins (Blom *et al.* 2007). As it is demonstrated above, these formations yielded the remains of several vertebrate taxa common with those of the Ventalepis assemblage. The faunal exchanges might occur along the coastal margins and through the fresh-water river channels opening into the sea; it is not improbable that euryhaline vertebrates might migrate by these routes. Further study should explore the interconnections of the Devonian continental and coastal marine faunas and support or reject this hypothesis.

The key dipnoan genus *Jarvikia* originally described from East Greenland (Lehman 1959; Blom *et al.* 2007) is a characteristic member of the Aina-Dal–Britta Dal vertebrate tetrapod community. Later Krupina (1999) described another species of this fish, a member of the Ventalepis assemblage from the Orel-Saburovo Beds of the Rybnitsa quarry in Central Russia. The same genus had been also recognised from Strud (Clement and Boisvert 2006). Presence of this didemic genus (*sensu* Lebedev *et al.* 2010) and an *Ichthyostega*-like tetrapod in such distant locations separated by a vast ORS continent makes us suggest their possible dwelling in the river systems and near-shore periphery of this land mass and occasional burial events in its marginal sedimentary basins. Unfortunately, the corresponding sediments of the mid-continent are not preserved to prove this hypothesis.

CONCLUSION

The porolepiform affinities of an enigmatic fish *Ventalepis ketleriensis* are supported by newly described specimens; a new family Ventalepididae fam. nova is established upon a peculiar combination of characters, including scale structure and dermal bones ornamentation.

New materials found in the central and north-western localities of Russia extend the distribution of this genus and the Ventalepis vertebrate assemblage, characteristic of the upper Famennian (*postera* – ? Lower *expansa* conodont zones interval) of the East European platform, from two isolated locations to a vast geographical zone along the southeastern coast of the Old Red Sandstone continent. *Holoptychius* sp. (?*H. nobilissimus*), *Bothriolepis ciecere* and "*Devononchus*" *tenuispinus* form the basal structure of the Ventalepis assemblage. Establishment of the habitat area of the Devonian vertebrate assemblage over such a large territory is the first case within the zoogeographical province of Baltica.

Palaeozoogeographical analysis suggests Laurentian affinities of the Ventalepis assemblage demonstrating the major congruency to the Belgian and East Greenland ones.

Presence of the dipnoan *Jarvikia* in such distant locations as East Greenland, Belgian and Russian localities, separated by a vast ORS continent, as well as an *Ichthyostega*-like tetrapod in the Belgian one makes us suggest their possible dwelling in the river systems and near-shore periphery of the ORS and occasional burial events in its marginal sedimentary basins.

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REFERENCES

Ahlberg, P.E., Lukševičs, E. and Lebedev, O. 1994. The first tetrapod finds from the Devonian (upper Famennian) of Latvia. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **343**, 303–328.

Alekseev, A.S., Kononova, L.I., Nikishin, A.M. 1996. The Devonian and Carboniferous of the Moscow Syneclise (Russian platform) and sea-level changes. *Tectonophysics*, **268**, 149–168.

Beznosov, P.A., Chuprov, V.S. and Lukševičs, E. 2012. The Volonga River section of the Pokayama Formation (Upper Devonian, North Timan). In: Zhamoyda, A.I. (Ed.), Palaeozoic of Russia: Regional Stratigraphy, Palaeontology, Geo- and Bioevents, September 24–28, 2012, Sankt-Peterburg. Proceedings of the 3d All-Russian Meeting, pp. 40–41. St. Petersburg. [In Russian]

Beznosov, P., Mantsurova, V. and Lukševičs, E. 2013. Vertebrate and Miospore Assemblages from the Famennian of North Timan (Upper Devonian, Russia). In: Rocha, R., Pais, J., Kullberg, J.C. and Finney, S. (Eds), STRATI 2013. First International Congress on Stratigraphy "At the Cutting Edge of Stratigraphy", pp. 469–473. Lisbon.

Beznosov, P.A., Snigirevsky, S.M., Naugolnykh, S.V. and Lukševičs, E. 2018. The Upper Devonian delta plain deposits of North Timan. *Vestnik Instituta Geologii Komi Nauchnogo Tsentra UB RAS*, **1**, 25–44.

Blom, H., Clack, J.A., Ahlberg, P.E. and Friedman, M. 2007. Devonian vertebrates from East Greenland: a review of faunal composition and distribution. *Geodiversitas*, **29**, 119–141.

Clément, G. and Boisvert, C.A. 2006. Lohest's true and false 'Devonian amphibians': evidence for the rhynchodipterid lungfish *Soederberghia* in the Famennian of Belgium. *Journal of Vertebrate Paleontology*, **26**, 276–283.

Clément, G. and Janvier, P. 2004. *Powichthys spitsbergensis* sp. nov., a new member of the Dipnomorpha (Sarcopterygii, lobe-finned fishes) from the Lower Devonian of Spitsbergen, with remarks on basal dipnomorph anatomy. *Fossils and Strata*, **50**, 92–112.

Cloutier, R. and Candilier, A.M. 1995. Palaeozoic vertebrates of northern France and Belgium: Part III. Sarcopterygii (Devonian to Carboniferous). In: Lelièvre, H., Wenz, S., Blieck, A. and Cloutier, R. (Eds), Premiers vertébrés et vertébrés inferiéurs. *Geobios, Mémoire special*, **19**, 335–341.

Cloutier, R. and Schultze, H.-P. 1996. Porolepiform fishes (Sarcopterygii). Devonian fishes and plants of Miguasha, Quebec, Canada. In: Schultze, H.-P. and Cloutier, R. (Eds), Devonian Fishes and Plants of Miguasha, Quebec, Canada, pp. 248–270. Verlag Dr. F. Pfeil; Munchen.

Denayer, J., Prestianni, C., Gueriau, P., Olive, S. and Clement, G. 2016. Stratigraphy and depositional environments of the Late Famennian (Late Devonian) of Southern Belgium and characterization of the Strud locality. *Geological Magazine*, **153**, 112–127.

Downs, J.P., Daeschler, E.B., Jenkins, F.A., Shubin, N.H. 2011. A new species of *Laccognathus* (Sarcopterygii, Porolepiformes) from the Late Devonian of Ellesmere Island, Nunavut, Canada. *Journal of Vertebrate Paleontology*, **31**, 981–996.

Esin, D., Ginter, M., Ivanov, A., Lebedev, O., Lukševičs, E., Avkhimovich, V., Golubtsov, V. and Petukhova, L. 2000. Vertebrate correlation of the Upper Devonian and Lower Carboniferous on the East European Platform. In: Blieck, A. and Turner, S. (Eds), Palaeozoic Vertebrate Biochronology and Global Marine-Non-Marine Correlation. Final Report of IGCP 328 (1991–1996). *Courier Forschungsinstitut Senckenberg*, **223**, 341–359.

Ford, D. and Golonka, J. 2003. Phanerozoic paleogeography, paleoenvironment and lithofacies maps of the circum-Atlantic margins. *Marine and petroleum geology*, **20**, 249–285.

Geological Map of USSR. Scale 1: 1000000 (new series). Explanatory Note. Sheet O-(35), 36 – Leningrad. 1989. pp. 3–212. VSEGEI; Leningrad. [In Russian]

Ginter, M. 2001. Chondrichthyan biofacies in the Late Permian of Utah and Nevada. *Journal of Vertebrate Paleontology*, **21**, 714–729.

Gross, W. 1930. Die Fische des Mittleren Old Red Süd-Livlands. *Geologische und Paläontologische Abhandlungen*, **18**, 123–155.

Gross, W. 1933. Die fische des baltischen Devons. *Palaeontographica*, **79**, 1–74.

Gross, W. 1941. Über den Unterkiefer einiger devonischer Crossopterygier. *Abhandlungen der Preußischen Akademie der Wissenschaften*, **7**, 1–51.

Gross, W. 1942. Die Fischfaunen des baltischen Devons und ihre biostratigraphische Bedeutung. *Korrespondenzblatt des Naturforscher-Vereins zu Riga*, **64**, 373–436.

Hecker, R.F. 1983. Taphonomic and ecological peciliarities of the fauna and flora of the Main Devonian Field. *Trudy Paleontologicheskogo instituta AN SSSR*, **190**, 3–141. [In Russian]

Ivanov A. and Rodina, O. 2004. A new omalodontid-like shark from the Late Devonian (Famennian) of western Siberia, Russia. *Fossils and Strata*, **50**, 82–91.

Jarvik, E. 1972. Middle and Upper Devonian Porolepiformes from East Greenland with special references to *Glyptolepis groenlandica* n. sp. *Meddelelser om Grønland*, **187**, 1–295.

Johanson, Z. and Ritchie, A. 2000. Rhipidistians (Sarcopterygii) from the Hunter Siltstone (Late Famennian) near Grenfell, NSW, Australia. *Mitteilungen aus dem Museum für Naturkunde in Berlin*, **3**, 111–136.

Krupina, N.I. 1999. A new dipnoan from the Upper Devonian locality Rybnitsa in Oryol Region. *Paleontological Journal*, **33**, 627–629.

Lebedev, O.A. 1995. Morphology of a new osteolepidid fish from Russia. In: Arsenault, M., Lelièvre, H. and Janvier, Ph. (Eds), Études sur les Vertébrés inferiéurs. VIIth International Symposium, Parc de Miguasha, Québec. *Bulletin du Muséum National d'Histoire naturelle, section C (Sciences de la Terre: Paléontologie, Minéralogie, Géologie)*, **17**, 287–341.

Lebedev, O.A. 2013. Origin and evolution of tetrapod vertebrate communities (Devonian–Early Carboniferous). In: Rozhnov, S.V. (Ed.), Problems of biosphere evolution, pp. 206–229. Moscow. [In Russian]

Lebedev, O.A. 2017. Ventalepis vertebrate palaeotetrapod assemblage (Upper Devonian, upper Famennian) on the Main and Central Devonian Fields. In: Alekseev, A.S. (Ed.), PALEOSTRAT-2017. Annual meeting (scientific conference) of the Palaeontology section of the Moscow Naturalists' Society and the Moscow Branch of the Palaeontological Society of Russia affiliated to PIN RAS. Moscow, January 30 – February 1, 2017. Abstracts volume, pp. 38–39. Moscow. [In Russian]

Lebedev, O. A. and Lukševičs, E. 1996. Attempted correlation of the upper part of the Famennian deposits of Baltic and Central Russia by vertebrates. In: Meidla, T., Puura, I., Nemliher, J., Raukas, A. and Saarse, L. (Eds), The Third Baltic Stratigraphical Conference. Abstracts, Field Guide. pp. 35–36. Tartu.

Lebedev, O.A. and Lukševičs, E. 2017. *Glyptopomus bystrowi* (Gross, 1941), an "osteolepidid" tetrapodomorph from the upper Famennian (Upper Devonian) of Latvia and Central Russia. *Palaeobiodiversity and Palaeoenvironments*, **97**, 615–632.

Lebedev, O.A., Lukševičs, E. and Zakharenko, G.V. 2010. Palaeozoogeographical connections of the Devonian vertebrate communities of the Baltica Province. Part II. Late Devonian. *Palaeoworld*, **19**, 108–128.

Lebedev, O.A. and Zakharenko, G.V. 2010. Global vertebrate-based palaeozoogeographical subdivision for the Givetian–Famennian (Middle–Late Devonian): Endemism-cosmopolitanism spectrum as an indicator of interprovincial faunal exchanges. *Palaeoworld*, **19**, 186–205.

Lehman, J.-P. 1959. Les dipneustes du Dévonien supérieur du Groenland. *Meddelelser om Grønland*, **160**, 1–58.

Long, J.A. 1985. The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa*, **9**, 1–22.

Lukševičs, E. 2001. Bothriolepid antiarchs (Vertebrata, Placodermi) from the Devonian of the north-western part of the East European Platform. *Geodiversitas*, **23**, 489–609.

Lukševičs, E., Lebedev, O., Mark-Kurik, E. and Karatajūtė-Talimaa, V. 2009. The earliest evidence of host-parasite interactions in vertebrates. *Acta Zoologica*, **90**, 335–343.

Lukševičs, E. and Zupiņš, I. 2004. Sedimentology, fauna, and taphonomy of the Pavāri site, Late Devonian of Latvia. *Acta Universitatis Latviensis, Series Earth and Environmental Sciences*, **679**, 99–119.

Olive, S., Clément, G., Daeschler, E.B. and Dupret, V. 2015. Characterization of the placoderm (Gnathostomata) assemblage from the tetrapod-bearing locality of Strud (Belgium, upper Famennian). *Palaeontology*, **58**, 981–1002.

Ørvig, T. 1957. Remarks on the vertebrate fauna of the Lower Upper Devonian of Escuminac Bay, P.Q., Canada, with special reference to the Porolepiform Crossopterygians. *Arkiv for Zoologi*, **10**, 367–426.

Ostrometskaya, E. and Kotlukova, I. 1966. New data on the Lower Carboniferous and Upper Devonian deposits from middle flow of the Msta River. *Materialy po geologii i poleznym iskopaemym severo-zapada RSFSR*, **5**, 24–29. [In Russian]

Paperna, I. 1996. Parasites, infections and diseases of fishes in Africa: an update. *CIFA Technical Papers – CIFA/T31*. 232 p. FAO, Rome.

Plax, D.P. 2011. Devonian ichthyofauna of the Volyn Monocline. *Litasfera*, **35**, 12–21.

Racki, G. and Racka, M. 1981. Ecology of the Devonian charophyte algae from the Holy Cross Mts. *Acta Geologica Polonica*, **31**, 213–222.

Rzhonsnitskaya, M.A. and Kulikova, V.F. (Eds). 1990. Decisions of Interdepartmental Regional Stratigraphic Session (IRSS) on the Upper and Middle Palaeozoic of the Russian Platform with Regional Stratigraphic Charts. Devonian System (Leningrad, 1988), pp. 3–60. VNIGRI; Leningrad. [In Russian]

Samoilova, R.B., Prinada, V.D. 1966. On the studies of trochiliscids. *Trudy Geologicheskogo Instituta, Akademiya Nauk SSSR*, **143**, 201–212. [In Russian]

Schultze, H.-P. 1980. Crossopterygier-Schuppen aus dem obersten Oberdevon Lettlands (Osteichthyes, Pisces). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **4**, 215–228.

Vinogradov, A.P. and Nalivkin, V.D. (Eds). 1960. Atlas of the lithological-palaeogeographical maps of the Russian Platform and its geosynclinal rim. Part 1. Late Precambrian and Palaeozoic, maps 17–23. Gosgeolizdat; Moscow–Leningrad. [In Russian]

Vorobyeva, E.I. 2006. A new species of *Laccognathus* (Porolepiform Crossopterygii) from the Devonian of Latvia. *Paleontological Journal*, **40**, 312–322.

Westoll, T.S. 1938. Ancestry of the Tetrapods. *Nature*, **141**, 127–128.

Ziegler, P.A. 1988. Evolution of the Arctic – North Atlantic and the western Tethys. *American Association of Petroleum Geologists Memoirs*, **43**, 164–196.

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