

Chondrichthyan spines from the Famennian (Upper Devonian) of Russia

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ABSTRACT:

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Very rare chondrichthyan spines from the Famennian (Upper Devonian) of European Russia are referred here to ctenacanthiforms, euselachians and a chondrichthyan group of uncertain systematic position. *Ctenacanthus* Agassiz, 1837 is recorded from the lower and middle Famennian of the central and north-western parts of the area. *Sculptospina makhlaevi* Lebedev gen. et sp. nov. originates from the lower Famennian of the Lipetsk Region. The holotype of '*Ctenacanthus*' *jaekeli* Gross, 1933 and a new specimen from the upper Famennian of the South Urals are shown to belong to the same taxon, which is transferred to *Acondylacanthus* St. John and Worthen, 1875. New specimens of *Tuberospina nataliae* Lebedev, 1995 from the upper Famennian of Central Russia are described in detail. The newly presented material increases our knowledge of the composition of Famennian marine assemblages from the East European Platform. It is suggested that these assemblages may be classified as chondrichthyan-dominated and dipnoan-dominated. Hypothetically, after the end-Devonian Hangenberg extinction event, which affected numerous secondary consumers in vertebrate communities, some chondrichthyan groups could have encroached to take advantage of previously occupied ecological niches. *Ctenacanthus*, as well as *Acondylacanthus* and *Amelacanthus* survived the end-Devonian mass extinction to continue into the Carboniferous.

Key words: Chondrichthyes; Ctenacanthiformes; Euselachii; Fin spines; Famennian; Devonian; Russia.

INTRODUCTION

Skeletal elements of elasmobranch chondrichthyans occur widely in the Upper Devonian Famennian deposits. Numerous isolated spines or partially preserved skeletons with spines usually referred to ctenacanthid sharks have been described from the Famennian of North (Zangerl 1981; Maisey 1981, 1984) and South America (Janvier and Maisey 2010),

Europe (Kulczycki 1957; Derycke-Khatir 2005; Blom *et al.* 2007; Derycke *et al.* 2014; Cuny *et al.* 2015), and the Middle East and North Africa (Lehman 1977; Janvier *et al.* 1984; Derycke 1992, 2017).

In contrast, chondrichthyan macroremains are very rare in the Upper Devonian deposits of European Russia. During more than a hundred years, only a few specimens have been recovered from the Famennian of this territory by professional geologists

and palaeontologists: A.A. Krasnopolskiy in 1899, B.P. Markovskiy in 1929, E.A. Ivanova in the 1930s, V.G. Makhlayev in the 1950s, L.A. Lyarskaya in 1985 and V.N. Pazukhin in 1992, who was the first to recover a euselachian shark spine in the Urals. The spine found in 2016 by an amateur palaeontologist, A.A. Kachalkin, was kindly made available by him for this study.

Since 2011, the staff members of the E.E. Shimkevich Natural History Museum in Andreapol have investigated the exposures and collected fossils along the banks of the smaller tributaries of the Lovat River in the Andreapol and Toropets districts (Tver Region, Russia). In 2018, one of the authors of the current research (VVL) found a chondrichthyan spine in the Bilovo village section on the left bank of the Maliy Tuder River. This spine collection has remained undescribed until now.

In the Russian literature, a Devonian elasmobranch spine was first mentioned by Obruchev (1958) in his analysis of the Devonian and early Carboniferous ichthyofaunas of the USSR. He cited *Ctenacanthus* aff. *triangularis* Newberry, 1873 in the list of vertebrates from the Elelsian Regional Stage (RS; lower Famennian) of Central Russia. The same specimen was also mentioned by Obrucheva and Obrucheva (1977) in their review of vertebrate assemblages in the Central Devonian Field.

Lebedev (1995) provided a diagnosis, but illustrated only the holotype of *Tuberospina nataliae* Lebedev, 1995, and did not properly describe it. Here we revise the diagnosis and present a detailed species description based upon newly collected specimens and a micro-CT study.

This paper aims at the revision of previously published data, as well as at the description of newly presented specimens from the Famennian deposits of European Russia. Despite its scarcity, this material gives a new insight into the biodiversity of the Devonian chondrichthyans and extends the earlier known spatiotemporal distribution of chondrichthyans in the territory of the East European Platform during the Famennian. Those vertebrate communities which incorporate the chondrichthyan taxa described below will be examined as models for study of vertebrate biocenoses restructuring during the end-Devonian extinction.

MATERIAL AND METHODS

The material described in this paper is represented by isolated dorsal spines in various states of

preservation. The specimens originate from diverse carbonate rocks. The enclosing matrix was removed manually or by dissolution in 10% acetic acid. When missing parts left imprints on the matrix surface, those were filled with resin to strengthen the adjoining thin broken edges and to preserve the internal shape of the missing parts after rock dissolution.

SEM photography was carried out on Tescan VEGA-II XMU and JEOL JSM-5610 LV scanning electronic microscopes. Macrophotography was performed on specimens coated with ammonium chloride.

The internal structure of the *Tuberospina nataliae* spine fragment was reconstructed using a Bruker-microCT SkyScan 1172. The specimen was scanned at 100 kV voltage and 100 μ A current, with aluminium and copper filters for a half rotation of 180°. Images of virtual cross-sections were generated from 3D reconstructions by DataViewer, CTAn and CTvox software. The transparent mode of skeletal tissues was used for reconstruction of the canal system.

Institutional abbreviations:

GIT – Department of Geology, Tallinn University of Technology, Tallinn, Estonia;

KMA – E.E. Shimkevich Natural History Museum of the Andreapol District, Andreapol, Tver Region, Russia;

MB – Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany;

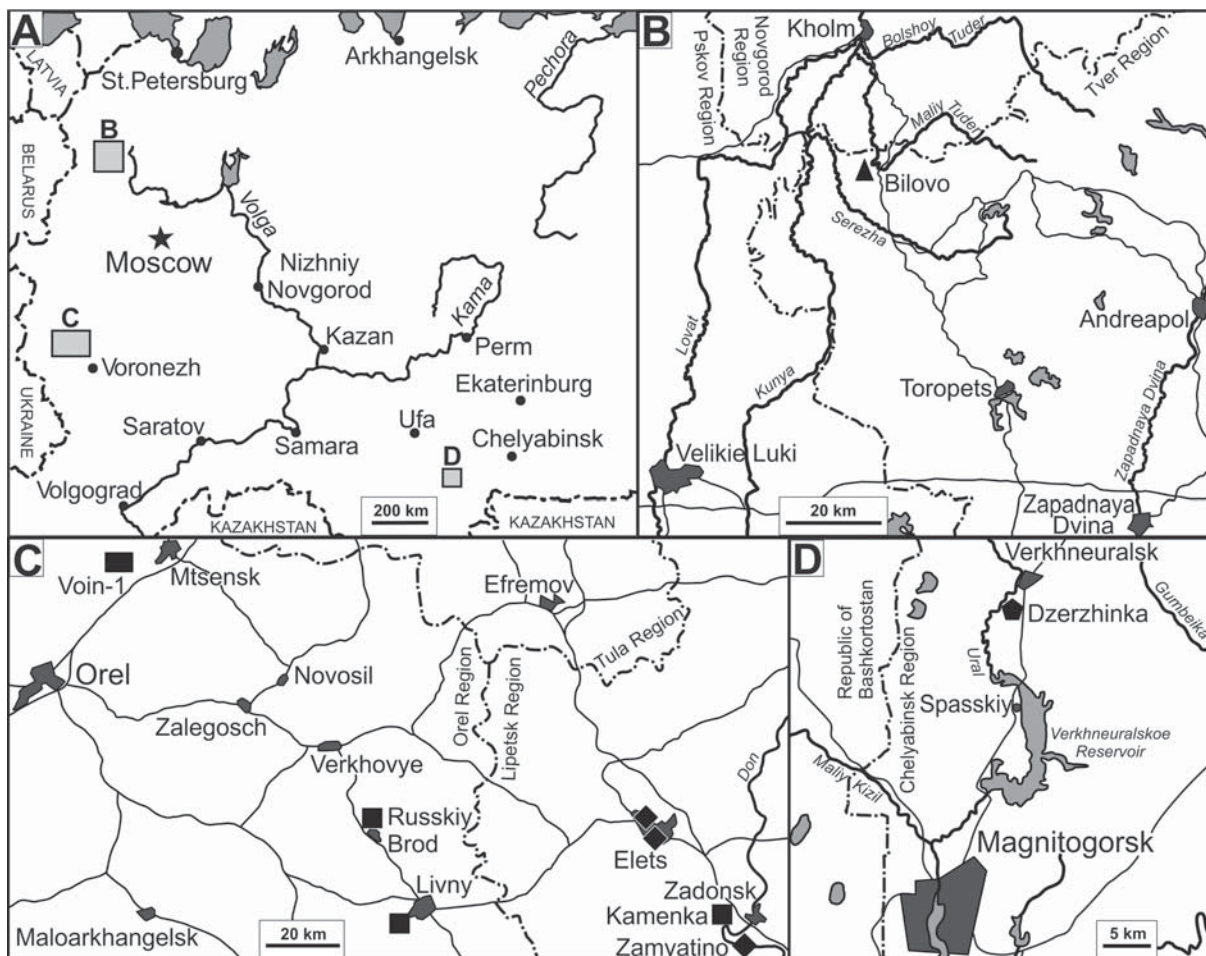
PIN RAS – A.A. Borissiak Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; the standard prefix PIN is used with the collection or specimen number;

PM SPU – Palaeontological Museum of the St. Petersburg State University, St. Petersburg, Russia.

GEOGRAPHIC DISTRIBUTION AND GEOLOGICAL SETTING

The specimens described in this paper come from the Bilovo Formation (middle Famennian) in the north-west of European Russia (Main Devonian Field) (Text-fig. 1B), the Zadonskian and Elelsian RS (lower Famennian) and the Plavskian RS (upper Famennian) in Central Russia (Central Devonian Field) (Text-fig. 1C), and from the Kushelga RS (upper Famennian) in South Urals (Text-fig. 1D).

In most of the East European Platform, the lowermost Famennian Volgogradian RS representing the lower–middle *triangularis* Conodont Zone of



Text-fig. 1. A – Sketch-map showing the position of Famennian localities with elasmobranch spines in the northern part of European Russia. B – Bilovo locality in the Tver Region. C – Localities in the Orel and Lipetsk regions of Central Russia. D – Popovskiy locality in the Chelyabinsk Region. Explanation of symbols showing the stratigraphic position of the localities: black squares – Zadonskian RS, diamonds – Eletsian RS, triangles – Lebedyanian RS, rectangles – Plavskian RS, pentagons – Kushelga RS.

the Standard Conodont Zonation (SCZ) is missing (Menning *et al.* 2006; Sobolev and Evdokimova 2008; Text-fig. 2). In the Central Devonian Field, the Famennian Zadonskian RS, represented mostly by shallow-water marine carbonates and clays, progressively and disconformably overlies the Livnian RS (Frasnian). In the south-east of the Orel Region, the Zadonskian carbonate deposits are of shallow-water marine and coastal, possibly deltaic terrigenous origin. The Zadonskian RS deposits are characterised by a rich fauna of invertebrates, including cephalopod and bivalve molluscs, brachiopods, ostracods and conodonts (Rodionova *et al.* 1995). This stage correlates to the ?upper *triangularis-crepida* interval of the SCZ (Sobolev and Evdokimova 2008). The vertebrate assemblage in that part of the section which yielded the spine identified below as cf.

Amelacanthus sp. in Gornostayevka Quarry (Orel Region) includes scales of undeterminable acanthodi-form acanthodians and chondrichthyans ‘*Cladolepis*’ sp., Ctenacanthidae indet., as well as teeth of *Protacrodus* sp., *Phoebodus* cf. *typicus* Ginter and Ivanov, 1995 and *Stethacanthus* sp., skeletal parts of dunkleosteid arthrodi- res and bothriolepid antiarchs, struniiform, osteolepiform and dipnoiform sarcopterygians, and actinopterygians (Esin *et al.* 2000; Moloshnikov 2001; Lebedev *et al.* 2010; also previously unpublished data from the collections in PIN RAS). Other elasmobranch spines of Zadonskian age (cf. *Amelacanthus* sp.) originated from the river bank exposures in Russkiy Brod (left bank of Lyubovsha River, Orel Region); *Ctenacanthus* aff. *concinus* (Newberry, 1875) was found close to Kamenka vil- lage, 10 km downstream from Zadonsk town on the

Stage and standard conodont zones		Regional stages of the EEP (after Sobolev and Evdokimova 2008)	Stratigraphic ranges of taxa
FAMENNIAN	<i>praesulcata</i>	Ziganian	<i>concinus</i> <i>Ctenacanthus aff. concinnus</i> <i>Sculptospina makhlaevi</i> <i>Ctenacanthus aff. venustus</i>
	<i>expansa</i>	Khovanschinian	
		Ozerkian	
	<i>postera</i>	Plavskian	<i>Amelacanthus sp.</i> <i>Ctenacanthus aff. concinnus</i> <i>Sculptospina makhlaevi</i> <i>Ctenacanthus aff. venustus</i> <i>Tuberospina nataliae</i>
	<i>trachytera</i>	Optukhovian	
	<i>marginifera</i>	Lebedyanian	
	<i>rhomboidea</i>	Eletsian	<i>cf. Amelacanthus sp.</i> <i>Ctenacanthus aff. concinnus</i> <i>Sculptospina makhlaevi</i> <i>Ctenacanthus aff. venustus</i> <i>Tuberospina nataliae</i>
	<i>crepida</i>	Zadonskian	
	<i>triangularis</i>	Volgogradian	

Text-fig. 2. Distribution of the taxa studied in the Famennian of the East European Platform (EEP), showing their ranges with regard to the Standard Conodont Zonation. Black thick lines refer to occurrences in the Central Devonian Field, grey thick line refers to an occurrence in the Main Devonian Field.

Don River (Lipetsk Region; Text-fig. 1B); these localities, however, yielded no other vertebrate remains.

The Eletsian RS (Text-fig. 2), represented mostly by limestones and dolomites conformably overlies the Zadonskian RS being a continuation of the same sedimentary cycle and marking the sea-level maximum (Rodionova *et al.* 1995). This stratigraphic unit correlates to the *rhomboidea*–middle *marginifera* interval of the SCZ (Sobolev and Evdokimova 2008). The Eletsian RS limestones are also rich in various marine invertebrates, such as cephalopod and bivalve molluscs, brachiopods, ostracods and conodonts. In contrast to the rich marine invertebrate assemblage, only a dipnoan tooth plate and a chondrichthyan spine previously identified as '*Ctenacanthus aff. triangularis*' (identified herein as '*Sculptospina makhlaevi* Lebedev gen. et sp. nov.') have been recorded (Esin *et al.* 2000; Lebedev *et al.* 2010) from these deposits in Central Russia. Elasmobranch spines are known from localities within Elets town itself and Lavskiy Quarry in its close suburbs (*Ctenacanthus aff. venustus* Eastman, 1902; *Ctenacanthus aff. concinnus*), as well as from the section on the right bank of the Don River, in a ravine by Zamyatino village (Lipetsk Region; Text-fig. 1C).

The incomplete spine PIN 1660/36 with a strongly abraded ornamentation on the ribs was collected by E.A. Ivanova in the 1930s. She labelled the specimen as "Voronezh Devonian". No details on the exact lo-

cality are available. This imprecise term was widely used for the Devonian outcrops of the Voronezh Governorate and later for the Voronezh Region formed in 1934. At that time this administrative unit included the contemporary Voronezh, Lipetsk, Orel and Tambov Regions of Central Russia. There are no Devonian exposures in the latter region, thus the first three limit the possible location area. In this territory, the exposed Devonian deposits range from the lower Frasnian to the upper Famennian, but, most likely, the specimen comes from the Zadonskian – Eletsian interval of the lower Famennian.

In the Central Devonian Field, the Lebedyanian RS conformably overlies the Eletsian RS (Text-fig. 2). Its dolomites and limestones are interpreted as hypersaline lagoonal deposits. Shelled worms, cephalopod, bivalve and gastropod molluscs, brachiopods, echinoderms, ostracods and conodonts are characteristic of this regional stage (Rodionova *et al.* 1995). The Lebedyanian RS correlates with the upper *marginifera* – *trachytera* SCZ (Sobolev and Evdokimova 2008). A few vertebrate taxa including ptyctodont placoderms and sarcopterygians are recorded from this interval in the Central Devonian Field (Obruchev 1958; Obrucheva and Obrucheva 1977; Esin *et al.* 2000; Lebedev *et al.* 2010).

In the eastern part of the Main Devonian Field dolomites characteristic of the Lebedyanian RS in Central Russia become replaced by intercalations of siliciclastics and limestones of nearshore marine origin forming the Bilovo Formation. This formation contains abundant remains of small sized gastropod, bivalve and cephalopod molluscs, spiriferid and rare rhynchonellid brachiopods, phyllocariids and ostracods (Sammet 1973), and rare conodonts. The Bilovo locality which yielded one of the spines we describe below (as *Ctenacanthus aff. venustus*) is situated in the north-west of the Tver Region on the left bank of Maliy Tuder River by Bilovo village (Text-fig. 1B). Apart from the Bilovo Formation itself, the uppermost part of the underlying Tuder Formation and the lower member of the Lnyanka Formation, correlated respectively to the Eletsian, Lebedyanian and Optukhovian RS, are exposed in this section (Sammet 1973; Verbitskiy *et al.* 2012). Almost the entire succession is rich in vertebrate macroremains; the assemblage includes antiarch placoderms, dunkleosteid arthrodires, porolepiform, struniiform, osteolepiform and dipnoi-form sarcopterygians (Lebedev *et al.* 2019). The layer within the Bilovo Formation which yielded the new elasmobranch spine is rich in spiriferid brachiopods characteristic of the Lebedyanian RS (Rodionova *et al.* 1995). Microremains obtained from the same sam-

ple include the charophyte algae gyragonites, fragments of phyllocarid crustaceans, scales of acanthodians, scales and teeth of struniiform sarcopterygians, fragmented actinopterygian scales and separate teeth.

No chondrichthyan remains are known yet from the succeeding Optukhovian RS. The overlying Plavskian RS (Text-fig. 2) includes the Turgenevo and Kudeyarovka Beds. Both units are composed of dolomites and dolomitic limestones. The Plavskian RS is rich in microconchs, bivalves, ostracods and conodonts (Rodionova *et al.* 1995), and correlates with the lower *expansa* Zone of the SCZ (Sobolev and Evdokimova 2008). Elasmobranch spines of *Tuberospina nataliae* originated from the Turgenevo Beds in a quarry close to Voin-1 village in the Mtsensk District (Orel Region) and Rybnitsa Quarry close to Orel (Text-fig. 1C). Apart from those, acanthodian scales, chondrichthyan teeth originally identified as '*Symmorium*' sp. (Lebedev 1995), skeletal parts of ptyctodontid placoderms, porolepiform, struniiform and dipnoiform sarcopterygians and stegotrachelid actinopterygians are known from these deposits.

An incomplete spine of an euselachian shark was found in the upper Famennian Kushelga RS in an outcrop in Dzerzhinka (Popovskiy) village, Chelyabinsk Region, South Urals (Gatovsky *et al.* 2017; Text-fig. 1D). The Kushelga RS is correlated to the *postera*–upper *expansa* zones of the SCZ (Artyushkova *et al.* 2011). These deposits comprise bioclastic limestones with abundant fossils such as brachiopods, ammonoids, bivalves, trilobites, ostracods, conodonts, and fish. Fish remains include chondrichthyan teeth, scales and a fin spine, fragments of ptyctodontid and arthrodire plates, sarcopterygian teeth, and actinopterygian teeth and scales. The chondrichthyans are represented by *Phoebodus limpidus* Ginter, 1990, *Thrinacodus* sp., *Cladodoides* sp., *Squatinactis* sp., *Jalodus australiensis* (Long, 1990), and *Protacrodus* sp.

SYSTEMATIC PALAEOLOGY

Class Chondrichthyes Huxley, 1880
 Subclass Elasmobranchii Bonaparte, 1838
 Order Ctenacanthiformes Glikman, 1964
 Family Ctenacanthidae Dean, 1909

Ctenacanthus Agassiz, 1837

Ctenacanthus aff. *venustus* Eastman, 1902
 (Text-fig. 3)

MATERIAL: Incomplete spine KMA/4958, Bilovo

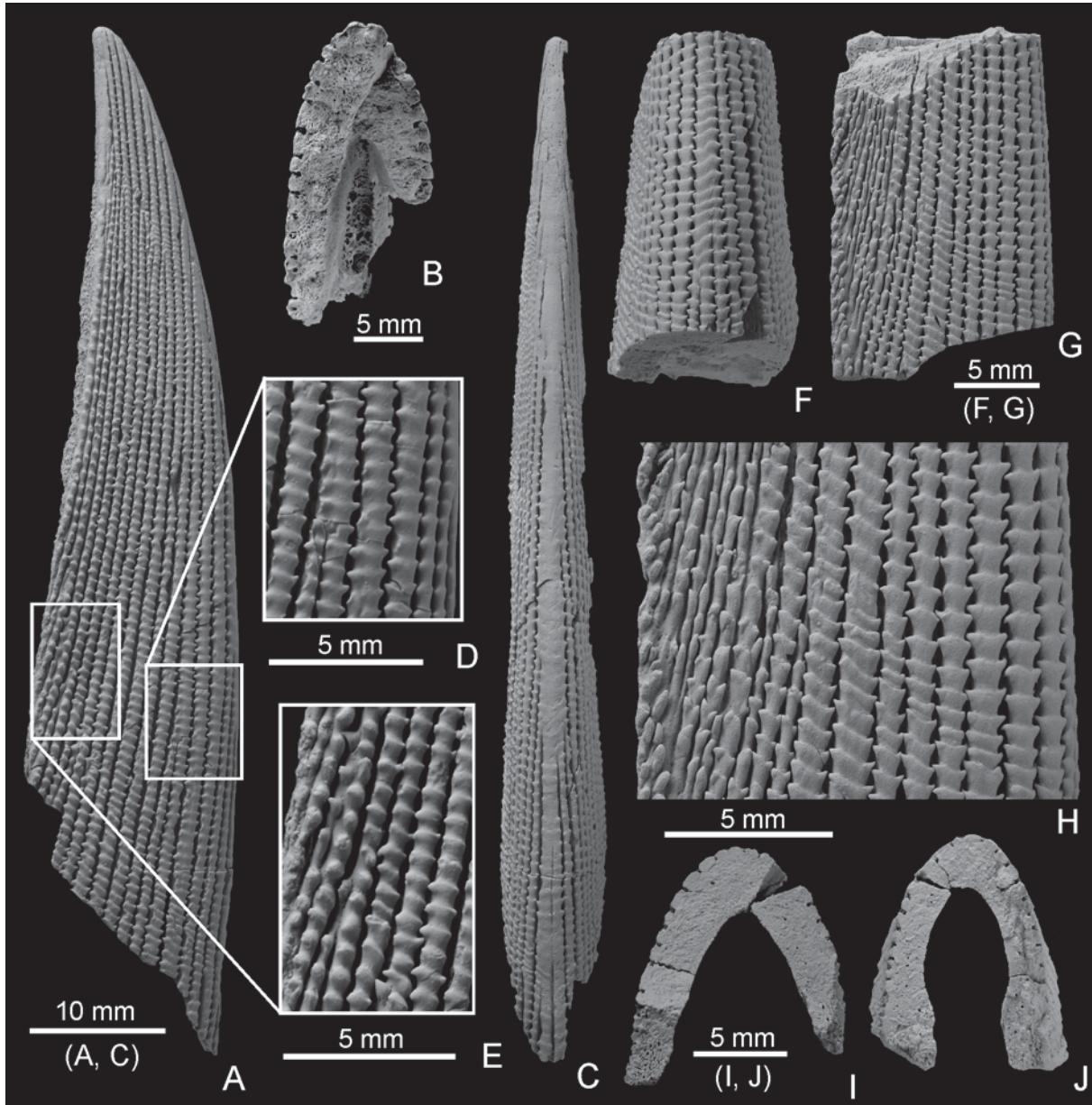
village, left bank of Maliy Tuder River, Toropets District, Tver Region, Central Russia; Bilovo Formation, Lebedyanian RS, middle Famennian, collected by V.V. Linkevich in 2018; fragment of middle part of spine GIT 779-1, Lavskiy Quarry, Elets Town, Lipetsk Region; middle substage of the Eletsian RS, lower Famennian, collected by L.A. Lyarskaya in 1985.

DESCRIPTION: The incomplete specimen KMA/4958 is an apical half of a spine with missing posterior face except the apically and incompletely preserved left side (Text-fig. 3A–E). The anterior edge is moderately arched apically, becoming straighter in the basal direction. The outline of the preserved part of the posterior face is only slightly concave. The apical part of the spine including the anterior rib is slightly worn and polished, most likely during life time. Instead of a regular row of basally directed denticles on the preserved posterolateral edge typical of *Ctenacanthus*, there are only few worn tubercles closer to the apical part of the spine; the more basal portion does not seem to bear any.

The dorsal fin spine fragment GIT 779-1 (Text-fig. 3F–J) is a mid-spine portion including the apical part of the portion occupied by a posterior opening. At this level lateral faces are sculptured by more than 22 closely spaced fine longitudinal ribs. The specimen lacks the posterolateral margin from the left side.

The width of the cross-section in KMA/4958 is half the depth of the spine (Text-fig. 3B), and in GIT 779-1 it is at least 0.7 of its depth (Text-fig. 3I, J). In both specimens the lateral faces are slightly convex. The ornament ribs are much wider than the intercostal grooves, and even partly close these sulci from both sides (Text-fig. 3I, J).

The anterior (median) rib is wider than the first adjoining ribs of the lateral sides of the spine and is similarly ornamented (Text-fig. 3C, F). The ribs originate in the anterior sector adjacent to the rib on the anterior edge and in the posterior sector between that and the posterior edge of the lateral face. In the anterior sector ribs bifurcate from the more anterior one in the basal direction, whilst the posterior sector has thinner costae originating from the posterior-most wide rib of the anterior sector (Text-fig. 3E). In the anterior margin and the anterior sector ribs are sculptured by pectinate tubercles, arising one from another; consecutive tubercles are only slightly separated from each other in the basal part of each by a shallow transverse or oblique groove. Each tubercle in the middle part of the spine widens forming symmetric or asymmetric oblique barbs jutting out into the intercostal grooves on both sides from the rib.

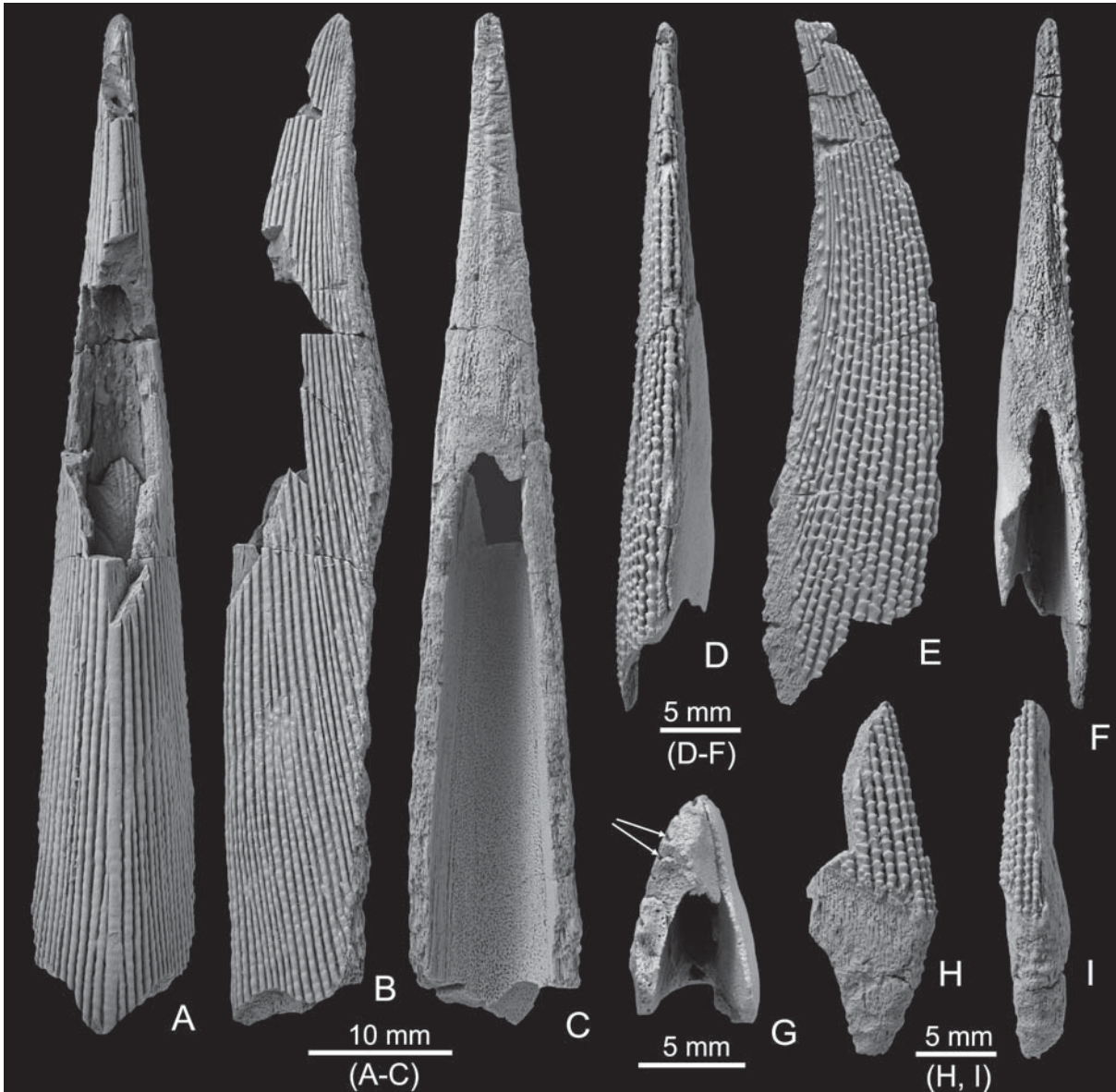


Text-fig. 3. Dorsal spines of *Ctenacanthus* aff. *venustus* Eastman, 1902. A–E – KMA/4958, Bilovo village, left bank of Maliy Tuder River, Toropets District, Tver Region, Central Russia; Bilovo Formation, Lebedyanian RS, middle Famennian; A – right lateral view, B – transverse section of broken basal part, C – anterior view, D – sculpture in anterior part of lateral face, enlarged, E – sculpture in posterior part of lateral face, enlarged. F–J – GIT 779-1, Lavskiy Quarry, Elets Town, Lipetsk Region; middle substage of the Eletsian RS, lower Famennian; F – anterior view, G – right lateral view, H – sculpture of lateral face, enlarged, I, J – cross-sections: I – basal, J – apical.

Barbs of adjacent ribs almost touch each other or interlock fitting into free spaces. Apically the sculpturing elements become narrower and the barbs shorten without contacting the barbs of adjacent ribs, and show no interlocking (Text-fig. 3A). Posterior parts of both lateral margins bear up to 10 much thinner, sometimes intercalating costae sculptured by similar,

but much narrower tubercles, or, closer to the posterior margin, by double or single barbed tubercles directed apically (Text-fig. 3E, H).

REMARKS: The described spines are similar to those of *Ctenacanthus venustus* (Eastman 1902; Maisey 1981; Derycke 1992; Lebedev 2001) but differ



Text-fig. 4. Dorsal spines of *Ctenacanthus* aff. *concinnus* (Newberry, 1875). A–C – PIN 1660/36, unknown locality and undetermined age, labelled as the “Voronezh Devonian”, Central Russia; A – anterior view, B – left lateral view, C – posterior view. D–G – PIN 2657/369, Elets Town, Lipetsk Region, Central Russia; middle substage of the Eletsian RS, lower Famennian; D – anterior view, E – right lateral view, F – posterior view; G – basal view of broken surface, right side restored with plastic. H, I – PIN 2657/368, Kamenka village, 10 km downstream from Zadonsk town, Don River, Lipetsk Region, Central Russia; Zadonskian RS, lower Famennian; H – right lateral view, I – anterior view. Arrows in G point to intercostal grooves.

in having wider pectinated tubercles with symmetric or asymmetric barbs overlapping the intercostal grooves. The spines from Central Russia also resemble those of *Ctenacanthus denticulatus* McCoy, 1855 (McCoy 1855; Maisey 1981) by having wide pectinated tubercles with short barbs but are distinguished by the wider and more incurved spine itself, as well as having fewer ribs on the lateral surfaces.

Ctenacanthus aff. *concinnus* (Newberry, 1875)
 (Text-fig. 4)

MATERIAL: Incomplete spine PIN 2657/369, Elets Town, Lipetsk Region, Central Russia; middle substage of the Eletsian RS, lower Famennian, collected by A.A. Krasnopolsky in 1899; spine fragment PIN 2657/368, Lipetsk Region, Don River, Kamenka

village, 10 km downstream from Zadonsk town; Zadonskian RS, lower Famennian, collected by V.G. Makhlayev in 1950; incomplete spine with strongly abraded sculpturing tubercles on the ribs of the lateral faces, PIN 1660/36, originating from an unknown locality and labelled as “Voronezh Devonian”, collected by E.A. Ivanova in the 1930s.

DESCRIPTION: Three specimens in various states of preservation are described under this heading, the most complete of those is PIN 1660/36 (Text-fig. 4A–C), although superficially its sculpturing is worn most of all. The incomplete specimen PIN 2657/369 is an apical half of the spine with basal part missing and left face partially preserved (Text-fig. 4D–G). The fragmentary specimen PIN 2657/368 bears a well-preserved ornament on its anterior and right lateral faces, making possible its grouping with the two other specimens (Text-fig. 4H, I).

The anterior margin of specimens PIN 1660/36 and PIN 2657/369 is arched (Text-fig. 4A, B, D, E); the lateral faces are slightly convex. The apical part of the posterior face is slightly concave, but in the basal direction it gradually turns convex (Text-fig. 4C, F). The posterolateral edge from the right side in specimen PIN 2657/369 bears a row of basally directed tubercles typical of *Ctenacanthus*, on the left edge tubercles are abraded. The width of the cross-section is not less than 0.5 smaller than at least half its depth (Text-fig. 4G).

The width of the anterior rib is the same or slightly more than that of the adjoining lateral ones bifurcating basally. Lateral faces bear 10 wider anteriorly and 5 narrower longitudinal ribs opposite to the level of the apical end of the posterior opening (Text-fig. 4B, E). The posterior sector is sculptured by thinner ribs added by insertion rather than bifurcation. The ornament ribs are about twice as wider as the intercostal grooves (Text-fig. 4G).

In all three specimens, but especially in PIN 2657/369 (Text-fig. 4D, E) and PIN 2657/368 (Text-fig. 4H, I), the anterior rib and those of the anterior sector are sculptured by narrow pectinate tubercles. These tubercles are generally similar in shape to those in the specimens of *Ctenacanthus* aff. *venustus* described above, arising one from another, but the barbs on the sides of the tubercles are shorter, mostly asymmetric and only rarely jut out into intercostal grooves. In the apical direction the tubercles become narrower and the barbs shorten. Posterior sectors of both lateral faces bear up to 6 intercalating costae being much thinner than those in the anterior sector, and sculptured by single tubercles directed apically.

REMARKS: The spines described herein are similar to those in *Ctenacanthus compressus* Newberry, 1889 and *C. clarki* Newberry, 1889 (Newberry 1889; Maisey 1981; Derycke 1992), but differ by having a narrower ornamented part, fewer costae and asymmetric barbs on the tubercles. Williams (2001) mentioned that spines of these two species belong to the same taxon and *C. clarki* should be considered a junior synonym of *C. compressus*. However, he did not describe the material in detail and this problem remained unresolved, although Ginter (2010) regarded *C. compressus* as a junior synonym of *Ctenacanthus concinnus* based upon similarities in tooth morphology. Here we formally accept his point of view with reservation. In any case, the ctenacanthid material from the Cleveland Shale needs a revision.

Family indet.

Genus *Sculptospina* Lebedev gen. nov.

TYPE SPECIES: *Sculptospina makhlaevi* Lebedev gen. et sp. nov.

ETYMOLOGY: From *sculptus* (Latin, sculptured) and *spinus* (Latin, spine).

DIAGNOSIS: Elasmobranch *Ctenacanthus*-type dorsal spines, slender, gradually tapering apically, slightly arched anteriorly. Strong median swelling on almost straight posterior face. Up to 20 longitudinal ribs ornamented by rounded pectinated tubercles lined along ribs and additional drop-shaped tubercles fused from both sides of each rib on lateral faces. Cross-section depth 1.4 larger than width.

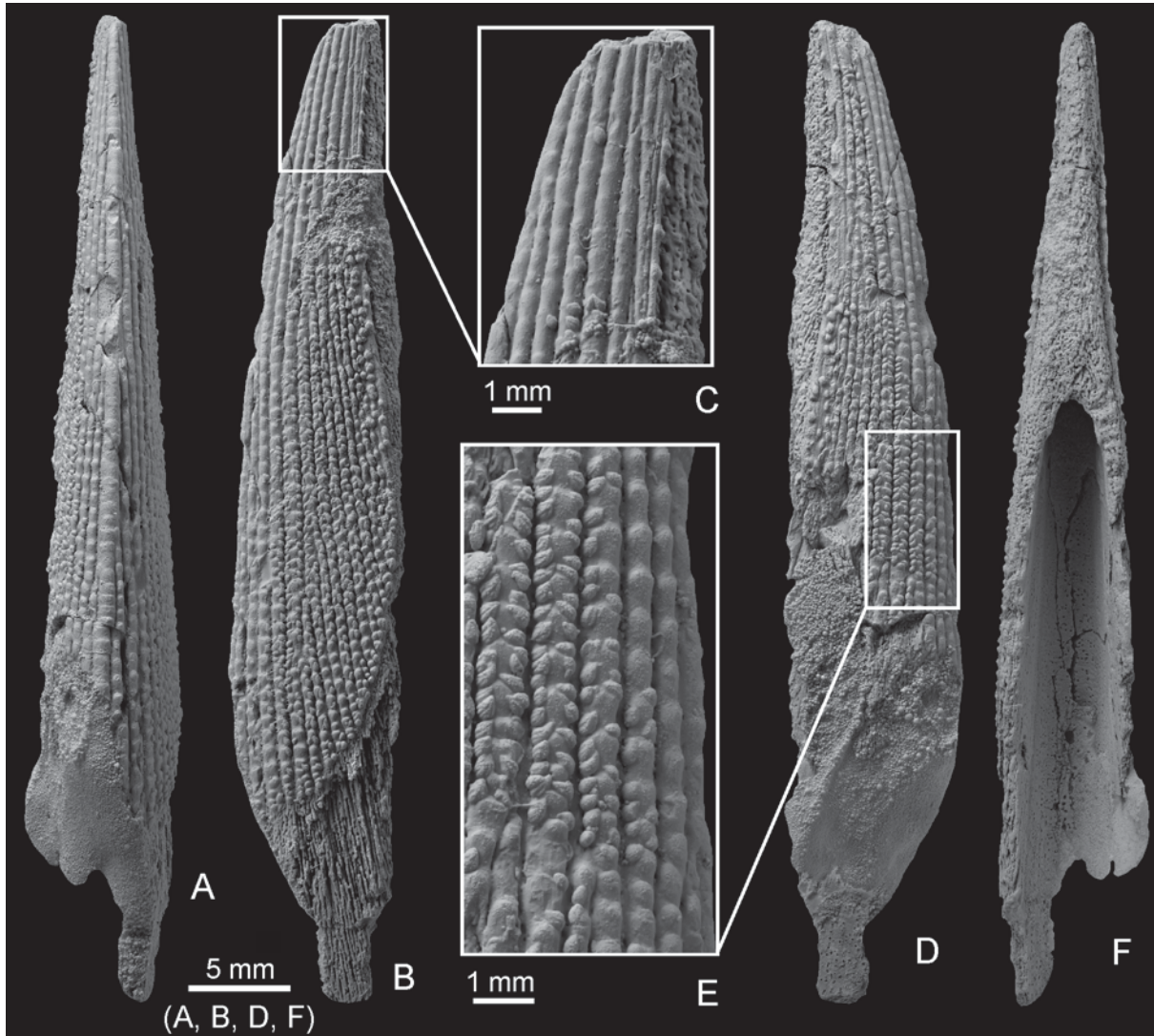
OCCURRENCE: Eletsian RS, lower Famennian, Upper Devonian; Lipetsk Region, Central Russia.

Sculptospina makhlaevi Lebedev gen. et sp. nov.
(Text-fig. 5)

ETYMOLOGY: Named after the prominent geologist Vasilij G. Makhlaev, who found the holotype and many other important vertebrate remains in the Devonian of Central Russia.

HOLOTYPE: Dorsal fin spine PIN 2266/70, collected by V.G. Makhlaev in the 1950s.

TYPE LOCALITY: Right bank of Don River, in a ravine by Zamyatino village, Lipetsk Region, Russia.



Text-fig. 5. Holotype of *Sculptospina makhlaevi* Lebedev gen. et sp. nov., PIN 2266/70, dorsal spine, right bank of Don River, ravine by Zamyatino village, Lipetsk Region, Central Russia; Eletsian RS, lower Famennian. A – anterior view, B – left lateral view, C – enlargement of sculpture near the spine apex in left lateral view, D – right lateral view, E – enlargement of sculpture near the boundary between the projecting and inserted portions of the spine in right lateral view, F – posterior view.

TYPE HORIZON: Eletsian RS, lower Famennian, Upper Devonian.

DIAGNOSIS: As for the genus.

MATERIAL EXAMINED: Only the holotype.

DESCRIPTION: Holotype and only specimen PIN 2266/70 is incompletely preserved with the inserted portion mostly missing, being only partly preserved on the left side. The anterior edge is slightly arched apically and almost straight closer to the basal end (Text-fig. 5A, B, D). The posterior face bears a mas-

sive semi-circular (in cross-section) median swelling, which strongly stands out in the lateral view and runs from the apex, basally becoming even more prominent. Posterolateral margins each bear a row of low, poorly preserved denticles (Text-fig. 5B, C, F). The posterior opening extends closer to the apex than the mid-length of the ornamented part of lateral faces. The ornamented/non-ornamented boundary is traced from the basal part of the anterior edge backwards and apically so that the inserted portion extends to the basal part at the posterolateral margin. Lateral faces are ornamented by up to 20 longitudinal ribs counting along the boundary between the

ornamented/non-ornamented areas. Wider costae of the anterior sector bifurcate from the anterior rib, whilst thin posterior ones diverge from wide posterior costae of the anterior sector. Rounded pectinate tubercles are lined along the costae. Additional drop-shaped tubercles sculptured by bifurcating ridges are fused additionally from both sides of each rib irrelevant of the position of the main tubercles (Text-fig. 5B, D, E). The additional tubercles are located irregularly on the lateral surfaces. On the right side these almost reach the spine apex, but from the left side in this area they are missing (Text-fig. 5B–E). Cross-section depth is 1.4 larger than width.

REMARKS: Originally D.V. Obruchev identified the specimen in a label in the 1950s as *Ctenacanthus* aff. *triangularis*. The spine of the new taxon resembles that in the heslerodid *Avonacanthus* Maisey, 2010 in the shape of the boundary between ornamented and non-ornamented parts, outline of the cross-section, and length and position of the notch of the posterior opening (Khabakov 1928; Maisey 2010).

OCCURRENCE: As for the genus.

Cohort Euselachii Hay, 1902
Order and Family indet.

Genus *Acondylacanthus* St. John and Worthen, 1875

TYPE SPECIES: *Acondylacanthus gracilis* St. John and Worthen, 1875, Kinderhookian, Mississippian, Carboniferous; Burlington, Iowa, USA.

Acondylacanthus jaekeli (Gross, 1933)
(Text-fig. 6)

1933. *Ctenacanthus jaekeli* sp. nov.; Gross, p. 64, pl. 11, fig. 9.

HOLOTYPE: Dorsal fin spine MB.f.206, Bad Wildungen, Hesse, Germany; Adorfer Limestones, *Manticoceras* Beds, upper Frasnian, Upper Devonian.

MATERIAL: Apart from the holotype, spine fragment PM SPU 58-1, Dzerzhinka (Popovskiy) village, 5 km south from Verkhneuralsk town, Chelyabinsk Region, South Urals; Kushelga RS, upper Famennian, Upper Devonian, collected by V.N. Pazukhin in 1992.

DIAGNOSIS: Incurved, slender, moderately sized

dorsal spines compressed laterally, with 9–10 costae basally and up to 4 costae apically on lateral face, with two rows of numerous ornamented, closely spaced and hook shaped posterolateral denticles.

DESCRIPTION: The spine PM SPU 58-1 is moderately sized, slender, recurved, and partly falcate in lateral view, moderately compressed laterally in cross-section, especially in the acuminate apical part (Text-fig. 6A–C). The anterior face is acuminate and bears a thin rib. The lateral face is slightly convex, bears 9–10 costae basally and up to 4 costae apically (Text-fig. 6A–E). In cross section costae are semilunar, their surface is slightly wavy. The costae are wider than intercostal grooves. The non-ornamented basal part of the spine is rather short.

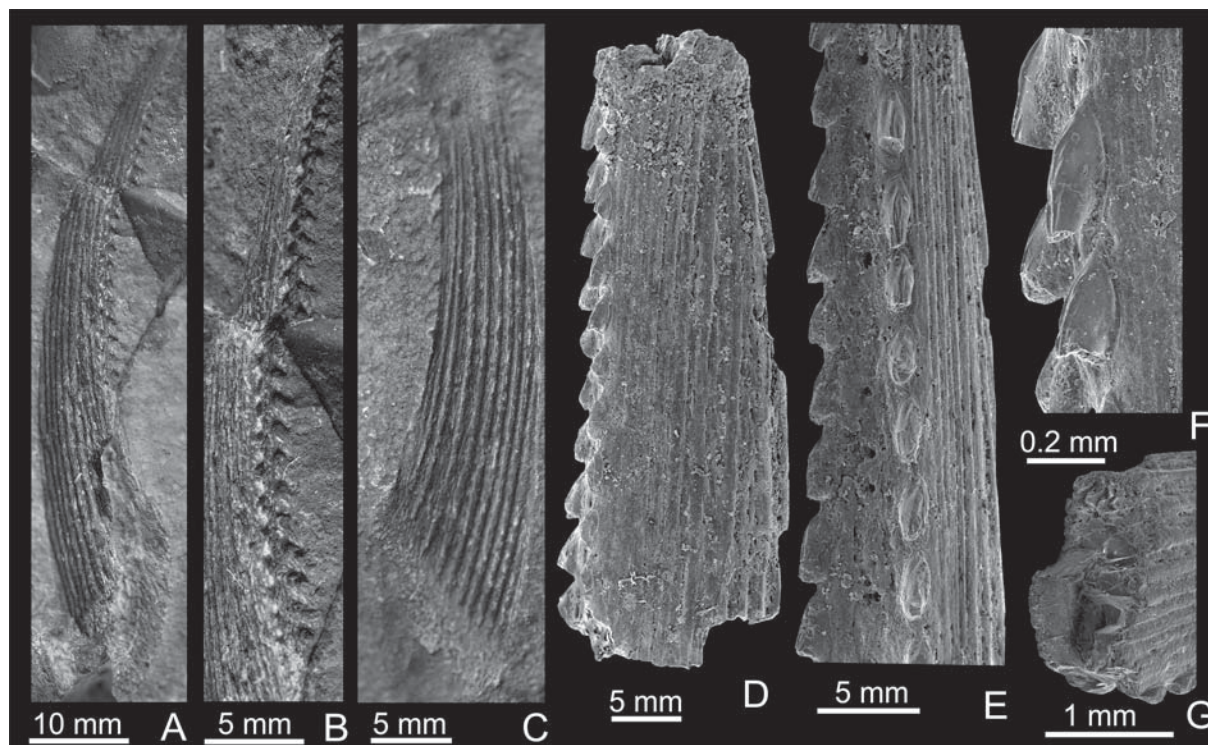
The posterior face of the spine is concave and bears two rows of numerous posterolateral denticles (Text-fig. 6A, B, D–F) reaching the posterior opening. The rows are placed on the marginal ribs separated by a shallow groove. The denticles are hook-shaped, acuminate, compressed laterally. Denticles in the left and right row are placed asymmetrically closely spaced in a row, the distance between them is much less than the length of the denticle base.

The fragment from the middle part of spine demonstrates well-preserved ornamentation of posterolateral denticles (Text-fig. 6E, F). They bear long medial and short lateral cristae. The external surface of the denticles is stronger ornamented than the internal one. Each denticle is surrounded by a narrow groove. A row of foramina opens in a groove between the denticle rows. The large central canal is located posteriorly, closer to this groove (Text-fig. 6G).

REMARKS: Gross (1933) described the holotype specimen as *Ctenacanthus jaekeli*. Later this species was referred to the acanthodian *Homacanthus* Agassiz, 1845 by Denison (1979). Maisey (1984) mentioned that the type specimen was lost, but in fact the holotype MB.f.206 is housed in the Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany.

Acondylacanthus jaekeli differs from other species of this genus in having shorter but recurved spines, and numerous ornamented posterolateral denticles closely spaced in a row. *Acondylacanthus aequicostatus* St. John and Worthen, 1875 is rather similar to this species but differs by being longer, more straight and compressed laterally in the ornamented part of the spine, with smooth and smaller posterolateral denticles sparsely located in the rows (St. John and Worthen 1875; Maisey 1983).

Maisey (1984) questionably referred to *Acondyla-*



Text-fig. 6. Dorsal fin spines of *Acondylacanthus jaekeli* (Gross, 1933). A–C – holotype MB.f.206 (A, B – part and C – counter-part); Bad Wildungen, Hesse, Germany; Adorfer Limestones, *Manticoceras* Beds, upper Frasnian; A – left lateral view, B – enlargement of posterior denticles, oblique posterior view, C – left lateral view. D–G – PM SPU 58-1, Dzerzhinka village, Chelyabinsk Region, South Urals; Kushelga RS, upper Famennian; D – right lateral view, E – oblique posterior view, F – enlargement of posterior denticles, G – basal view of broken surface.

canthus some forms originally referred to *Ctenacanthus*: ‘*C.* *browni* Branson, 1916; ‘*C.* *keokuk* St. John and Worthen, 1875; ‘*C.* *obscuracostatus* Branson, 1916 and ‘*Ctenacanthus*’ sp. described by Kulczycki (1957).

In his original description, Gross (1933) noted the similarities between *A. jaekeli* and *Tristychius* Agassiz, 1837 described earlier by Traquair (1894) as *Euphyacanthus*. However, these euselachians have short spines with only few costae on the lateral surface and narrow posterolateral denticles very sparsely located in the rows. Zangerl (1981) referred the genus *Acondylacanthus* to *Ctenacanthoidea incertae sedis*. We do not support this attribution, as *Acondylacanthus* spines resemble those in such late Palaeozoic hybodontoid euselachians as *Tristychius*, *Onychoselache* Dick, 1978, *Hamiltonichthys* Maisey, 1989 and *Gansuselache* Wang, Zhang, Zhu and Zhao, 2009 (Stock 1883; Dick 1978; Maisey 1989; Coates and Gess 2007; Wang *et al.* 2009) by their recurvature and lateral compression with ornamentation by wide costae, a short non-ornamented basal part, concave posterior face and two rows of posterolateral

denticles. The morphology of *Acondylacanthus* fin spines suggests their attribution to euselachians without further specification of their systematic position.

The fish assemblage from the upper Frasnian Adorfer Limestones of Bad Wildungen includes the only euselachian *Protacrodus vetustus* Jaekel, 1921 (Gross 1938). *Protacrodus* teeth are also present in the chondrichthyan assemblage of the upper Famennian Kushelga RS in the South Urals. It is not impossible that the *Acondylacanthus jaekeli* spine, and the jaws with dentition and a part of squamation assigned to *Protacrodus vetustus* might belong to the same taxon.

Other species of the genus *Acondylacanthus* were earlier known only from the lower Carboniferous of the British Isles (McCoy 1855; Davis 1883), as well as the Mississippian and Pennsylvanian of the USA (St. John and Worthen 1875; Maisey 1983, 1984; Itano *et al.* 2003). Thus, the specimen described by Gross (1933) and the newly introduced material are the first Devonian records of this genus.

OCCURRENCE: Upper Devonian, upper Frasnian of Germany; upper Famennian of Russia, South Urals.

Cohort and Order indet.

Genus *Amelacanthus* Maisey, 1982

cf. *Amelacanthus* sp.
(Text-fig. 7)

MATERIAL: Incomplete dorsal spine PIN 2266/69, Gornostayevka Quarry, Orel Region, Central Russia; collected by A. Kachalkin, 2016; dorsal spine fragment PIN 2266/68, Russkiy Brod, left bank of Lyubovsha River, Orel Region, Central Russia, collected by B.P. Markovsky, 1929; both from the Zadonskian RS, lower Famennian.

DESCRIPTION: Specimen PIN 2266/69 is slender and moderately bent, incomplete basally and strongly abraded on the lateral sides (Text-fig. 7A–C). Both the anterior and posterior faces are curved to a larger extent closer to the apex. As well as in this specimen, in PIN 2266/68 the posterior face is slightly concave apically, but a massive median ridge semi-circular in cross-section and jutting out in the lateral view arises in the basal direction, then becomes more and more prominent closer to the base (Text-fig. 7C, H). Posterolateral margins are mostly worn, but several denticles are still visible on the left side of specimen PIN 2266/69 (Text-fig. 7C, D).

The width of the anterior rib is slightly more than that of the adjoining apical ones; lateral ridges diverge from it in the basal direction (Text-fig. 7A, F). Lateral faces bear 8–9 wider ribs in the anterior sector and 8 or more narrower ribs in the posterior sector in specimen PIN 2266/69 (not clear because of the wear; Text-fig. 7B) and 9 wider ribs in the anterior sector and 4–5 narrower longitudinal ribs in the anterior sector in specimen PIN 2266/68 (Text-fig. 7G). Intercostal grooves are narrow; ribs are more than twice wider than those. Thinner ribs in the posterior sector add by insertion and/or bifurcation to the wider ones in the anterior sector. The longitudinal vascular canal is located closer to the anterior edge (Text-fig. 7E).

Fin spines of most known *Amelacanthus* species bear ribs coated by an enameloid layer (Maisey 1982). The external surfaces of the spines described above are abraded, thus providing no possibility of examining the superficial tissue. This being the only specimen, it is not possible to prepare cross-sections, but a thin compact external layer, though of uncertain histological structure, can still be traced on the broken surface in the basal part of the spine.

REMARKS: The general morphology and ornamen-

tation makes possible a tentative assignment of these incomplete and superficially strongly worn specimens to the genus *Amelacanthus*, but there is no possibility of assigning them to any species of this genus.

Most of all the spines described here resemble those in *Amelacanthus laevis* Davis, 1883 and *A. plicatus* Davis, 1883, but differ in the smaller number of lateral ribs (Davis 1883; Maisey 1982). In *Amelacanthus sulcatus* (Agassiz, 1837) and *A. americanus* Maisey, 1983 the spines bear considerably wider ribs (Maisey 1982, 1983). Maisey (1982) noticed that the spines of *Amelacanthus* and *Eunemacanthus* St. John and Worthen, 1883 are similar to those in fossil and recent neoselachians but their relationships remain controversial.

Genus *Tuberospina* Lebedev, 1995

TYPE SPECIES: *Tuberospina nataliae* Lebedev, 1995.

DIAGNOSIS (amended after Lebedev 1995): Chondrichthyan fin spines slightly curved caudally in their apical part, almost straight in the middle, inserted portion forming a turn at an obtuse angle to the exposed part of spine. About 20 costae on lateral faces, anterior rib equal in width. Pore rows in intercostal grooves interconnected by transverse sulci. Ornamenting tubercles set over longitudinal ribs apically, form transverse rows basally, oval or drop-shaped, basally their dentine caps surrounded by narrow rims. Cross-section depth 1.6 larger than width. Several straight longitudinal vascular canals run parallel to the long axis of the spine.

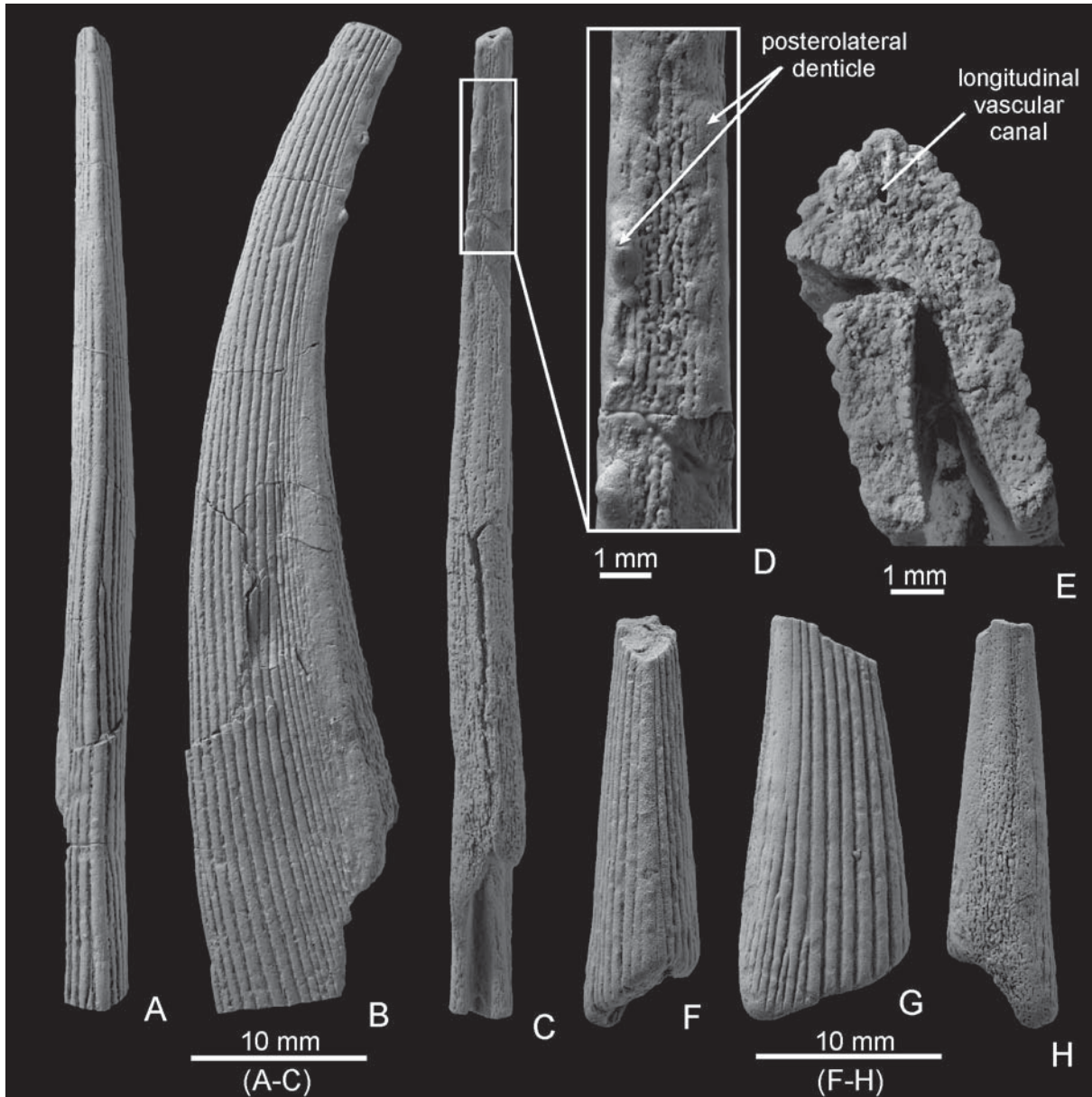
OCCURRENCE: Plavskian RS, upper Famennian, Upper Devonian; Orel Region, Central Russia.

Tuberospina nataliae Lebedev, 1995
(Text-figs 8, 9)

1995. *Tuberospina nataliae* gen. et sp. nov.; Lebedev, p. 362, pl. 1, figs 3a–c.

HOLOTYPE: Imperfect fin spine PIN 3725/536, from the now infilled quarry close to Voin-1 village, Mtsensk District, Orel Region, Central Russia; Turgenevo Beds, Plavskian RS, upper Famennian, Upper Devonian, collected by N.I. Krupina in 1980.

MATERIAL: Apart from the holotype, three incompletely preserved spines: PIN 3725/537 and PIN 3725/538 from the same locality and stratum, also



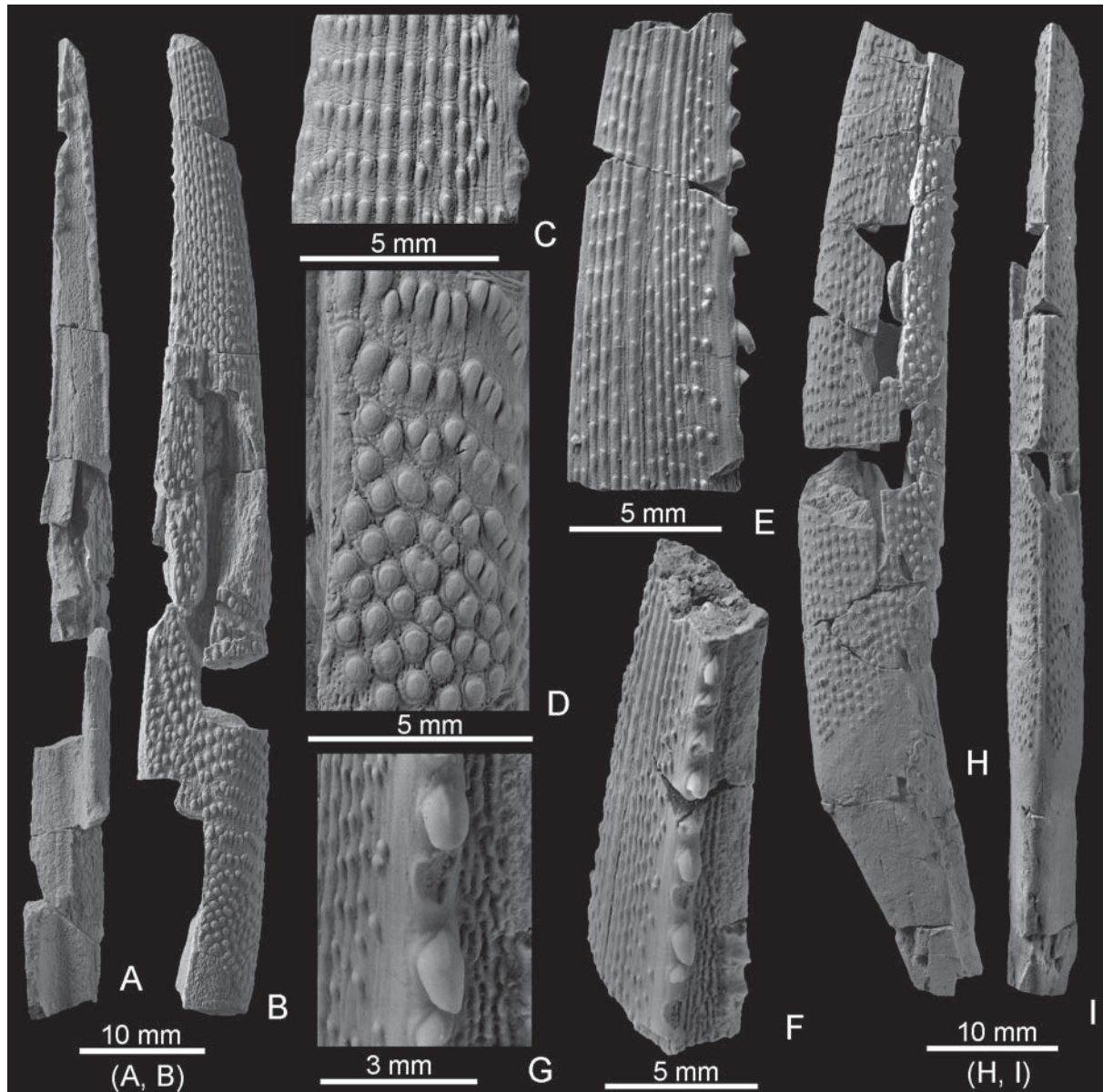
Text-fig. 7. Incomplete dorsal spines of cf. *Amelacanthus* sp. from the Orel Region, Central Russia, Zadonskian RS, lower Famennian. A–E – PIN 2266/69, Gornostayevka Quarry; A – anterior view, B – left lateral view, C – posterior view, D – apical part of posterior face showing posterolateral denticles, E – basal view of broken surface. F–H – PIN 2266/68, Russkiy Brod, left bank of Lyubovsha River; F – anterior view, G – right lateral view, H – posterior view.

collected by N.I. Krupina in 1980, and PIN 3725/682 from the Rybnitsa Quarry in the same region and stratum, collected by the first author (OL) in 2013.

DESCRIPTION: The holotype PIN 3725/536 (Text-fig. 8A–D) and the specimen PIN 3725/537 (Text-fig. 8H, I) are incompletely preserved; in the former most of the basal and in the latter the apical parts are

missing. A spine fragment from the apical part, PIN 3725/538 (Text-fig. 8E–G), shows better preserved posterolateral denticles. Specimen PIN 3725/682 (Text-fig. 9) is a completely preserved inserted portion also showing a small part of the base of the exposed portion of the spine.

The spines are medium-sized, symmetric and slender, slightly curved in the posterior direction in

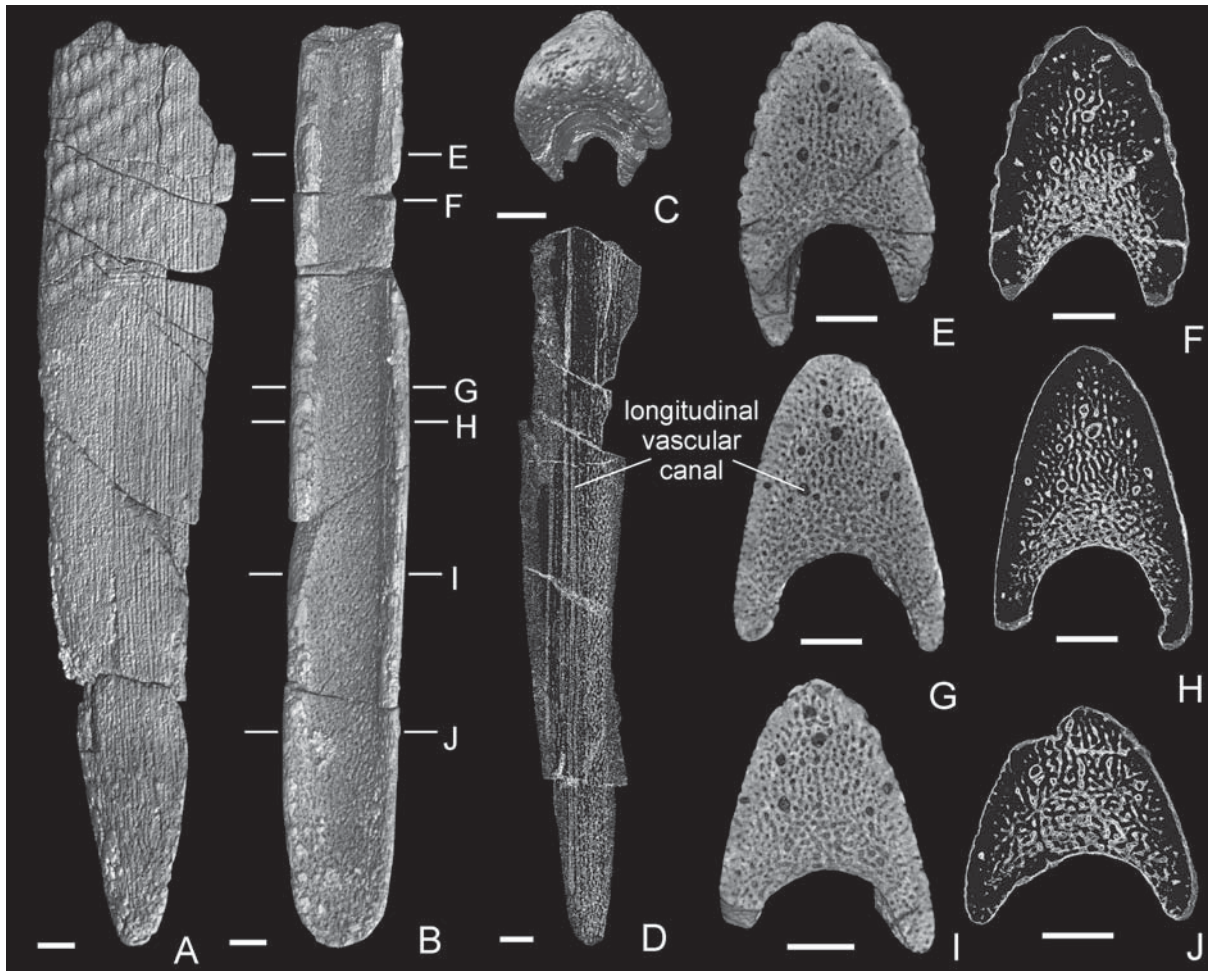


Text-fig. 8. Dorsal fin spines of *Tuberospina nataliae* Lebedev, 1995 from a currently closed-down and infilled quarry close to Voin-1 village, Mtsensk District, Orel Region, Central Russia; Turgenevo Beds, Plavskian RS, upper Famennian. A–D – holotype PIN 3725/536, A – posterior view, B – right lateral view, C – ornamentation close to apical part of spine on left lateral face, D – ornamentation close to inserted part of spine on right lateral face. E–G – PIN 3725/538, E – left lateral view, F – left posterolateral view, G – enlargement of left posterolateral view to show the shape of posterolateral denticles. H–I – PIN 3725/537, H – left lateral view, I – anterior view.

the apical portion; in the middle both the anterior and posterior faces are almost straight, but the inserted portion sharply bends posteriorly again, forming a turn at an obtuse angle (Text-fig. 8B, H). The inserted non-ornamented basal part is short; its length might be estimated as not more than a third of the total spine length. The lateral surface of the ornamented part is slightly convex, but that of the non-ornamented part is

flat with slightly incurved posterolateral edges (Text-fig. 9G, H). The posterior opening, on the contrary, is very long; its length is about a half of the spine length.

The anterior margin is formed by a thin low rib equal in width to those of the adjoining costae on the lateral faces (Text-fig. 8H, I). Lateral faces bear about 20 longitudinal ribs (Text-fig. 8B, C, E, H). New costae add by insertion from the basal part of the spine.



Text-fig. 9. Microtomographic images of spine fragment of *Tuberospina nataliae* Lebedev, 1995, PIN 3725/682, Rybnitsa Quarry, Orel Region, Central Russia; Turgenovo Beds, Plavskian RS, upper Famennian. A – left lateral view, B – posterior view with positions of virtual cross-sections, C – basal view, D – virtual sagittal cross-section, E–J – virtual transversal cross-sections. Scale-bars equal to 1 mm.

Intercostal grooves are equal in width or narrower than the ribs. The bottoms of intercostal grooves bear small pores arranged in lines along the costae, in the middle part of the spine interconnected by vascular furrows running between occasionally formed transverse rows of tubercles (Text-fig. 8C, D). In the apical part, the ornament of the lateral sides consists of ribs sculptured by flattened, vertically elongated drop-shaped or ovoid tubercles (Text-fig. 8B, C, E). Towards the base the ribs gradually fade and ornamenting tubercles start forming transverse rows oriented obliquely to the anterior rib. Closer to the basal boundary between the ornamented and the inserted portions, tubercles are set very close to each other sometimes contacting with each other (Text-fig. 8B, D). In this zone their dentine caps are surrounded by narrow rims.

Posterolateral margins bear rows of hook-shaped denticles bent basally and bearing a thin crest on their apical surfaces (Text-fig. 8F, G). Posterior face is slightly concave apically, gradually turning flat in the basal direction (Text-figs 8A, F, 9B). Cross-section depth is 1.6 larger than width.

Micro-CT scanning of the basal portion of spine PIN 3725/682 demonstrates a highly vascularized inner structure (Text-fig. 9). The ornamented part is composed of a compact outer layer showing few tiny canals. The hypermineralized layer, possibly enameloid, is traced in the ornamenting tubercles (Text-fig. 9E). The inner part of the spine is spongy and contains a dense network of small sinuous vascular canals (Text-fig. 9E–J). Several straight longitudinal vascular canals run along the long axis of the spine (Text-fig. 9D). They are located in the central part

of the cross-section closer to the anterior edge (Text-fig. 9E–J) and slightly widen in the basal direction. The network of sinuous vascular canals occupies the interior almost completely (Text-fig. 9I, J).

REMARKS: The spines of *Tuberospina* are similar to those in *Batacanthus* St. John and Worthen, 1875 and *Geisacanthus* St. John and Worthen, 1875 in general shape, ornamentation composed of rounded tubercles, shape and position of posterior denticles, but differ in the outline of cross-section, concave posterior surface of the distal part, and gradual change of ornamentation from the apical to the basal parts. The spines of a neoselachian *Nemacanthus* Agassiz, 1837 from the Permian–Triassic interval (Koot *et al.* 2013; Böttcher 2015) resemble *Tuberospina* spines very much in their general shape and type of ornamenting tubercles, but differ in the proportion of ornamented/non-ornamented parts and uniform distribution of equidimensional tubercles.

OCCURRENCE: As for genus.

DISCUSSION

Fossil record of the Devonian chondrichthyan spines

One of the major problems concerning studies of systematics in Palaeozoic chondrichthyans is incompleteness of preservation due to the delicate nature of the cartilaginous skeleton in these fishes. Normally post-mortem decay results in separation of sturdy exoskeletal elements: teeth, spines and scales during burial. Identification of these separately found elements inevitably leads to their assignment to different taxa. One of the best recent examples of the finding of a complete shark skeleton making possible taxonomic linkage between teeth and fin spines was presented by Frey *et al.* (2019a) in the same individual of *Phoebodus saidselachus* Frey, Coates, Ginter, Hairapetian, Rücklin, Jerjen and Klug, 2019. This research demonstrated the association of spines of the ‘*Ctenacanthus*’-design with quite typical *Phoebodus* dentition (Frey *et al.* 2019b). Thus, in the future, material currently referred to, for example, the genus *Ctenacanthus* might potentially be reassigned to other shark genera.

Paradoxically, from the Middle–Upper Devonian material of 55 known chondrichthyan genera in total (Lebedev and Zakharenko 2010, supplementary material), only 8 are known from fin spines (or, as

an exception, from complete skeletons), whereas all others from isolated teeth or scales. Of those, only *Ctenacanthus*, *Phoebodus* St. John and Worthen, 1875, *Acondylacanthus* and *Antarctilamna* Young, 1982 are known from their pre-Famennian records (Zangerl 1981; Young 1982; Frey *et al.* 2019a), whereas others arose only during the Famennian (*Cladoselache* Dean, 1894; Zangerl 1981; *Tuberospina*: Lebedev 1995; *Tamiobatis* Eastman, 1897; Williams 1998; *Plesioselachus* Anderson, Long, Gess and Hiller, 1999; Anderson *et al.* 1999; Gess and Coates 2015).

Apart from the material described above from European Russia and Germany, the occurrence of chondrichthyan fin spines in the Famennian of Europe is scarce. Small spine fragments identified as *Ctenacanthus?* sp. were recorded in the upper Famennian of Dinant, Belgium (Derycke-Khatir 2005; Derycke *et al.* 2014). Kulczycki (1957) ascribed to chondrichthyans three specimens resembling fin spines from the lower and upper Famennian of the Holy Cross Mountains, Poland: *Ctenacanthus* sp., *Sentacanthus zelichowskiae* Kulczycki, 1957, and *Alienacanthus malkowskii* Kulczycki, 1957. The last one was attributed to an arthodiran inferognathal by Szrek (2020). A fin spine resembling that of *Ctenacanthus angulatus* Newberry and Worthen, 1866 was found in the Devonian–Carboniferous boundary beds of East Greenland (Blom *et al.* 2007; Cuny *et al.* 2015).

The only record of a chondrichthyan spine in the Asian part of Russia is a spine fragment identified as *Xenacanthimorpha* indet. from the uppermost Famennian Podonino Formation of Yaya River, Kuznetsk Basin, Siberia, Russia (Ivanov and Rodina 2010). Earlier, Obruchev (1941) reported the imprints of a spine determined as *Ctenacanthus?* sp. from the Famennian Tuba Formation of Lake Bilyo, Minusa Region, Siberia, Russia. However, restudy of that specimen shows that this is the imprint of an antiarch plate from the pectoral appendage.

Numerous isolated spines are known from the upper and uppermost Famennian of North America. Valid *Ctenacanthus* species from North America based on fin spines include *Ctenacanthus triangularis* from the Waverly Series of Pennsylvania, *Ctenacanthus compressus* from the Cleveland Shale of Ohio, and *Ctenacanthus angustus* Newberry, 1889 from the Berea Sandstone of Ohio (Maisey 1984). A partly preserved skeleton of a ctenacanthiform *Tamiobatis vetustus* Eastman, 1897 from the Cleveland Shale of Ohio demonstrates a fin spine resembling those in some *Ctenacanthus* species (Williams 1998). A spine fragment of *Ctenacanthus* cf. *venustus* was reported

from the Percha Formation (Upper Devonian) of south-central New Mexico, USA (Ivanov and Lucas 2019). *Ctenacanthus* sp. was cited in a list of vertebrate taxa from the Catskill Formation of Red Hill, Pennsylvania, USA (Daeschler and Cressler 2011).

The Gondwanan Famennian records are also diverse. Spines of *Ctenacanthus clarki*, *Ctenacanthus venustus* (Derycke 1992, 2017), and *Ctenacanthus* sp. resembling *C. denticulatus* (Lehman 1977) were reported from the upper Famennian of Tafilalt, south-eastern Morocco. The skeletal remains of *Phoebodus saidselachus* were found in the middle Famennian of the Maïder Region, Morocco (Frey *et al.* 2019a). The skeletal parts including fin spines of *Plesioselachus macracanthus* Anderson, Long, Gess and Hiller, 1999 and *Antarctilamna ultima* Gess and Coates, 2015 are known from the uppermost Famennian Witpoort Formation of South Africa (Anderson *et al.* 1999; Gess and Coates 2015). A well-preserved fin spine of *Ctenacanthus* cf. *crenulatus* McCoy, 1855 was described by Janvier *et al.* (1984) in the Devonian–Carboniferous boundary beds (Yığınlı Formation) of Turkey. Ctenacanthid spines originate from the upper Famennian part of the Colpacucho Formation of Bolivia (Janvier and Maisey 2010).

Thus, during the Famennian, the genus *Ctenacanthus* was globally distributed. This might reflect wide environmental adaptations of these fishes, including to eurybiontic pelagic and shallow-water habitats. Apart from *Phoebodus*, other elasmobranch genera known to us by spines are much more limited in their distribution.

Dominant groups in Famennian vertebrate assemblages

Very few attempts have been made to examine the structure of Devonian vertebrate communities and classify them. The pioneering work by Schultze and Cloutier (1996) compared the Escuminac Formation ichthyofauna with other late Givetian/early Frasnian ichthyofaunas using a clustering technique in order to identify the palaeoenvironments and palaeobiogeography of localities. Ecological ordination analysis was used by Sallan and Coates (2010) to study the impact of the Hangenberg extinction event on early vertebrate evolution. These have been obtained from general databases of Devonian vertebrate occurrences. Lebedev and Zakharenko (2010) applied palaeobiogeographic methods to study the distribution of vertebrates to establish zoochoria and interprovincial faunistic exchanges during the Middle–Upper Devonian.

Here we suggest an ecological approach to the classification of Devonian vertebrate faunas based upon their systematic and trophic composition using a limited dataset relevant to our study of Famennian chondrichthyan spines.

Widely spread geographically on the EEP, the localities which yielded the chondrichthyan fin spines described above present a wide spectrum of environments and their gnathostome inhabitants. Palaeogeographically, the sites which are selected by us by the occurrence of spine material span from the south-eastern shores of the Fennoscandian continent (Main Devonian Field), to the southern part of the Moscovian Sea, north of Voronezh Island (Central Devonian Field), to the shelf of the Ural Sea on the platform margin (South Urals). The environments and sedimentary conditions in these locations ranged (Sammet 1973; Rodionova *et al.* 1995; Artyushkova *et al.* 2011) from various types of brackish-water with strong marine influence (Orel-Saburovo Beds of the Plavskian RS and Zadonskian RS in the Central Devonian Field; Bilovo Formation of the Lebedyanian RS in the Main Devonian Field), and normally marine offshore (Eletsian RS in the Central Devonian Field; Kushelga RS in South Urals), to hypersaline, lagoonal, possibly semi-enclosed basins (Lebedyanian RS in the Central Devonian Field; Turgenevo Beds of the Plavskian RS in the Central Devonian Field).

Fresh water flowing into the sea brought significant amounts of nutritive plant matter into nearshore ecotopes (Algeo and Scheckler 1998). This served as food for both invertebrate and vertebrate primary consumers. The primary and secondary vertebrate consumers which had fed upon consumer invertebrates defined the major features of the assemblage composition, being most diverse or most abundant. The secondary diversification of predators most probably resulted from the variety of secondary consumers.

Large numbers of individuals in the community belonging to the same species signals abundant food resources of the same type taken by these consumers. In contrast, differentiated secondary consumers belonging to the same systematic group most likely fed on diversified types of food as demonstrated by the variable structure of their feeding apparatuses, for example in dipnoans (Lebedev *et al.* 2019).

Of all the assemblages studied the most diverse in vertebrate taxa are the Plavskian (Orel-Saburovo; 27 species), the Zadonskian (14) and the Bilovo (13). Numerous Plavskian (Orel-Saburovo) outcrops expose various facies of deltaic origin which are likely

to yield a mixture of vertebrate skeletal remains of nearshore marine, truly deltaic brackish and freshwater origin (Lebedev and Lukševičs 2017, 2018). This might explain their unusually high diversity.

The vertebrate assemblage composition varied strongly during the Devonian (Schultze and Cloutier 1996; Sallan and Coates 2010, supplementary material; Lebedev *et al.* 2010) in terms of the type and number of different consumers. Some communities are dominated by antiarchs, others by arthrodires, dipnoans, chondrichthyans or even acanthodians. In some cases it is difficult to judge whether the predominant group, for example arthrodires in the Cleveland Shale assemblage (Carr and Jackson 2008; Sallan and Coates 2010), consists of only tertiary (predatory) or all types of consumers. These cases require a special study of the structures of feeding apparatuses. Noteworthy, the predatory tertiary sarcopterygian consumers very seldom count more than two species within the same order, though in total, the porolepiforms, struniiforms, osteolepiforms, rhizodontiforms and actinistians, or at least some of these groups may compose an important part of the total number of species in the community.

Another feature characterising the community is the composition of the group below the most numerous one. For example, in the Cleveland Shale assemblage (Carr and Jackson 2008) the group second in richness represents chondrichthyan fishes counting 13 species. This suggests a mostly pelagic origin of the oryctocenosis, though condensed on the bottom. An opposite situation is shown by the late Famennian Tafilalt assemblage of Morocco, in which numerous chondrichthyan species dominate over slightly less numerous arthrodires (Sallan and Coates 2010, supplementary material; Derycke 2017).

Analysis of the community dominants might give a tool to subdivide the known oryctocenoses into several groups. Such classification stresses similarities and difference between the grouped complexes, thus making a 'manual' rather than computed study possible. For the time being, the presence of chondrichthyan-, antiarch-, arthrodire-, phyllolepid- and dipnoan-dominated assemblages may be noticed within the Famennian faunas based upon the information presented by Sallan and Coates (2010, supplementary material), all of them being primary and/or secondary consumers.

Here we aim at making a limited analysis of only those Famennian assemblages which yielded the elasmobranch taxa described above. Those fall into two groups: (1) chondrichthyan-dominated and (2) dipnoan-dominated. This separation is based upon cal-

culating the maximum number of taxa belonging to the same phylum. We keep in mind that data on the number of species in the list is far from being complete, but even preliminary information seems to be representative.

Chondrichthyan-dominated assemblages

This group includes epicontinental Zadonskian (at least 7 taxa) and Eletsian assemblages (at least 3 taxa), and possibly the Kushelga assemblage of the island arc shelf (at least 6 taxa).

The Zadonskian RS section in Gornostayevka Quarry consists of two successions, a lower sandy deltaic one (Moloshnikov 2001: layers 1–8) and an upper clayey–carbonaceous shallow marine one (layers 9–10). Other Zadonskian RS localities which have yielded chondrichthyan spines correlate to the upper part of the section. The faunistic composition of the upper part differs from that of the lower one (Moloshnikov 2001; Lebedev 2004) in the absence of antiarchs, porolepiforms and osteolepiforms, instead representing chondrichthyans *Ctenacanthus* aff. *concinus*, cf. *Amelacanthus* sp., '*Cladolepis*' sp., *Phoebodus* cf. *typicus*, *Stethacanthus* sp., Ctenacanthidae indet. and *Protacrodus* sp. The dipnoans *Conchodus* sp., *Holodipterus* sp., *Dipterus* sp. and the actinopterygian *Moythomasia* sp. are found through the whole section. Antiarch remains were found only at the base of this part of the section. It is unclear whether tetrapods, acanthodians and ptyctodonts are present in this succession.

Younger Eletsian RS deposits are regarded as being of normal marine origin (Rodionova *et al.* 1995). These yielded the following spine-based chondrichthyan taxa: *Ctenacanthus* aff. *venustus*, *Ctenacanthus* aff. *concinus*, *Sculptospina makhlaevi* Lebedev gen. et sp. nov., as well as extremely rare ptyctodont and dipnoan remains, but no acanthodians, antiarchs, arthrodires, porolepiforms, osteolepiforms, struniiforms or actinopterygians.

The more deep-water Kushelga RS vertebrate complex included chondrichthyans *Phoebodus limpidus*, *Thrinacodus* sp., *Cladodoides* sp., *Squatinactis* sp., *Jalodus australiensis* and *Protacrodus* sp. Arthrodires, ptyctodontids, acanthodians, sarcopterygians and actinopterygians were also a part of the community. No antiarchs and dipnoans are known within this assemblage.

Thus, all three assemblages grouped here into the chondrichthyan-dominated type are characterised not only by the prevalence of this group in the number of taxa, but also by the absence of at least antiarchs and

porolepiforms from the community. This may be due to the absence of food resources for these primary consumers and, consequently, of nutrition for the predators feeding on them (?porolepiforms). On the contrary, food resources for chondrichthyan species should have been enough as shown by their diversity. Ctenacanthiforms, symmoriiforms and phoebodontiforms are characteristic of these assemblages. The epicontinental nearshore Zadonskian RS assemblage includes also at least three various dipnoans, two of those durophagous. This might reflect the abundance of diverse prey, suitable for sharks (crustaceans?) and hard-shelled for dipnoans.

Dipnoan-dominated assemblages

These assemblages include the epicontinental Lebedyanian Central Devonian Field assemblage (at least 3 taxa), the Lebedyanian Main Devonian Field (Bilovo) assemblage (at least 3 taxa), as well as the Plavskian RS assemblage (at least 10 taxa). The Plavskian RS assemblage demonstrates an unusually high number of various dipnoans comprising 10 species (Lebedev and Lukševičs 2018). Despite only one cited dipnoan record, *Dipterus* sp., in the Lebedyanian RS assemblage in the Central Devonian Field (Obruceva and Obruceva 1977; Esin *et al.* 2000; Lebedev *et al.* 2010) and, apart from *Anchidipterus dariae* Krupina in Lebedev *et al.*, 2019 in the Bilovo Lebedyanian RS assemblage in the Main Devonian Field (Lebedev *et al.* 2019), there are not less than two or three other dipnoan species in each of these two communities (work in progress). This exceeds the amount of all other species in other than dipnoan high-rank systematic categories taken separately.

Several localities in the Central Devonian Field belonging to the Lebedyanian RS are suggested to have been formed within a semi-closed marine basin with an increased salinity level that resulted in impoverishment of its biota (Rodionova *et al.* 1995). The vertebrate complex presents abundant ptyctodonts (*Chelyophorus verneuili* Agassiz, 1844), at least three dipnoan species (previously united as *Dipterus* sp.) and exclusively rare *Holoptychius* sp. scales (Obrucev 1958; Obruceva and Obruceva 1977; Esin *et al.* 2000; Lebedev *et al.* 2010). So far, no acanthodian, antiarch, or osteolepiform remains are known from these strata.

In contrast to this limited set of taxa, an almost contemporaneous community of the Bilovo locality formed in nearshore marine conditions (Sammet 1973) represents abundant acanthodians *Acanthodes* sp. and ?*Devononchus* sp., antiarchs *Bothriolepis heck-*

eri Lukševičs, 2001, dipnoans *Anchidipterus dariae* and Dipteridae indet., osteolepiforms *Megapomus heckeri* Vorobyeva, 1977, struniiforms *Struniiformes* indet., but only a few porolepiforms *Holoptychius* sp., arthrodires *Dunkleosteoida* indet., ptyctodonts, chondrichthyans *Ctenacanthus* aff. *venustus* and actinopterygians *Actinopterygii* indet. In contrast to the Lebedyanian RS community of the Central Devonian Field, this complex is much poorer in ptyctodont remains, but demonstrates a set of acanthodian, arthrodire and antiarch placoderm, osteolepiform and struniiform sarcopterygian, as well as actinopterygian taxa unknown from the former.

The Plavskian RS localities belonging to the Turgenevo Beds level fall in two large groups: those formed in the so called 'Orel-Saburovo facies' of deltaic origin and Turgenevo Beds proper of shallow-water marine, locally hypersaline origin. The faunal difference between these two groups is significant, although both yielded *Tuberospina nataliae* spines. Both are rich in ptyctodonts, dipnoans, osteolepiforms and struniiforms. Apart from *Tuberospina*, only teeth originally identified as '*Symmorium*' sp. had been found in lagoonal deposits of this age (Lebedev 1995). Antiarchs, arthrodires, porolepiforms, actinopterygians are either missing or extremely rare in the latter facies. On the contrary, the deltaic facies contains about 5–6 acanthodian species, numerous skeletal parts of the antiarch *Bothriolepis* Eichwald, 1840, a pachyosteomorph arthrodire, osteolepiform and porolepiform sarcopterygians, and an outstanding set of ten dipnoan species (Lebedev and Lukševičs 2017, 2018). As far as *Tuberospina* spines are known from both facies, the total species count from both facies is applied. The abundance of dipnoan species might be explained by the wide spectrum of environmental conditions in this nearshore area and the abundance of various plant and invertebrate food sources.

Chondrichthyan-dominated communities and the end-Devonian extinction

The Hangenberg event at the end of the Famennian is known to have resulted in a mass extinction, which affected numerous vertebrate taxa (Sallan and Coates 2010; Friedman and Sallan 2012). This loss caused the destruction of vertebrate communities based upon secondary consumers. Apart from complete extermination of antiarch, ptyctodont, phyllolepid and arthrodire placoderms, several Devonian dipnoan families also vanished from the record. The structure of the dipnoan-dominated assemblages became strongly reduced, which resulted in the restructuring of near-

shore vertebrate biocenoses at the beginning of the Carboniferous. The drastic changes of the number of dipnoan taxa and transition to other than Devonian lineages was examined by Lloyd *et al.* (2012).

Chondrichthyan-dominated assemblages turned out to be more stable after the D/C extinction, although the losses were also significant at a generic level. The number of chondrichthyan genera had grown starting from the Viséan, after the decrease needed for recovery during the Tournaisian. At that time, major chondrichthyan groups which arose during the Late Devonian or even during the Givetian (Symmoriiformes, Ctenacanthiformes, Phoebodontiformes, Squatinactiformes, Hybodontiformes, Orodontiformes, Helodontiformes, Cochliodontiformes, Copodontiformes, Psammodontiformes) underwent a burst of radiation.

The Devonian pelagic *Phoebodus–Thrinacodus* and more shallow-water *Protacrodus* assemblages (Ginter 2001) did not suffer as much as the non-chondrichthyan ones. This resulted in the migration (and/or adaptation) of some groups of shelf and pelagic chondrichthyans into shallow nearshore habitats, in which food resources became available after the destruction of dipnoan-, acanthodian- or antiarch-dominated communities. Apart from this source, as exemplified by our data, the previously existing – but suppressed during the Devonian – chondrichthyan members of the dipnoan communities (such as symmoriiforms and ctenacanthiforms in the Lebedyanian RS community) profited from newly available resources and invaded these communities to conquer previously occupied ecological niches.

Of all the Famennian elasmobranch genera known from spines, only *Ctenacanthus*, *Acondylacanthus* and *Amelacanthus* survived the end-Devonian global extinction. On the contrary, putative demersal chondrichthyans, including orodontiforms, helodontiforms, cochliodontiforms and psammodontiforms, which arose during the Famennian (Zangerl 1981; Stahl 1999), not only continued further, but significantly diversified and became abundant in Carboniferous marine habitats.

CONCLUSIONS

The chondrichthyan spines described from the Famennian of European Russia, referred to ctenacanthiforms, euselachians and some groups of uncertain systematic position demonstrate the high taxonomic diversity of these fishes in this area. The genus *Ctenacanthus* is recorded from the lower and middle

Famennian of the Central and Main Devonian fields. The new genus and species *Sculptospina makhlaevi* Lebedev gen. et sp. nov. originated from the lower Famennian of the Central Devonian Field. The holotype of '*Ctenacanthus*' *jaekeli* Gross, 1933 and a new specimen from the upper Famennian of the South Urals are shown to belong to the same species of the genus *Acondylacanthus* St. John and Worthen, 1875.

The studied Famennian vertebrate assemblages fall into chondrichthyan-dominated and dipnoan-dominated types characterised by the prevalence of these groups over the others in the total number of taxa. After the end-Devonian Hangenberg extinction event, which decimated secondary consumers in the vertebrate communities, some chondrichthyan groups migrated into these to take advantage of the previously occupied ecological niches.

During the Famennian, *Ctenacanthus* was a widely distributed taxon. *Ctenacanthus*, *Acondylacanthus* and possibly *Amelacanthus* survived the Hangenberg extinction event and widely radiated during the early Carboniferous.

Chondrichthyan taxa of the Palaeozoic ctenacanthiforms and euselachians which are based on isolated fin spines require a revision focusing on their ornamentation details, histological structure and vascularization system. Specimens presented by holomorphic skeletons need a detailed redescription of their fin spines; the *Phoebodus* skeleton with a ctenacanthid-type spine ornamentation demonstrates the necessity of revising the ctenacanthid taxa represented by isolated fin spines only.

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