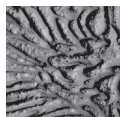


# Squamation of the Permian actinopterygian *Toyemia* Minich, 1990: evenkiid (Scanilepiformes) affinities and implications for the origin of polypteroid scales

ALEKSANDR S. BAKAEV & ILJA KOGAN



*Toyemia* Minich, 1990, is a widespread member of late Permian freshwater fossil assemblages of European Russia. The scales and lepidotrichia hemisegments of this taxon show general resemblance to the palaeoniscoid-type ‘ganoid’ scales of most Palaeozoic actinopterygians, but differ from these in some morphological features. Architecture of the vascular system is more complex: part of the canals (the wider ones) are located within the bone layer, constituting a complicated three-dimensional pattern, while the thinner canals usually lie on the border of the bone and the dentine layers (with the canal lumen usually surrounded by dentine but positioned in the basalmost part of the odontode), forming a regular network, especially in the posterior and ventral part of a scale. Whereas in most basal actinopterygians, vascular canals only occur underneath the sculptural ridges of the free field, scales of *Toyemia* possess wide, sinuous canals underneath the depressed field, opening to its surface in large pores. These and further features of the squamation (vascular canals cased in concentric layers of bone reminiscent of osteons and surrounded by numerous osteocyte lacunae; the presence of true secondary osteons; the shape of articulating elements and the general scale outline; the ornamentation of the free field, mainly consisting of concentric rolls; *etc.*) are similar to representatives of the Triassic order Scanilepiformes, especially to the family Evenkiidae, suggesting that *Toyemia* should be placed within this family. An enigmatic ‘circular structure’ of interwoven collagen fibers, first observed in *Toyemia* scales, is reminiscent of polypterid elasmodine. In several aspects, scales of *Toyemia* appear to represent the ancestral condition of the polypteroid scale. • Key words: ganoid scales, lepidotrichia, palaeohistology, Osteichthyes, Scanilepiformes, Permian, European Russia.

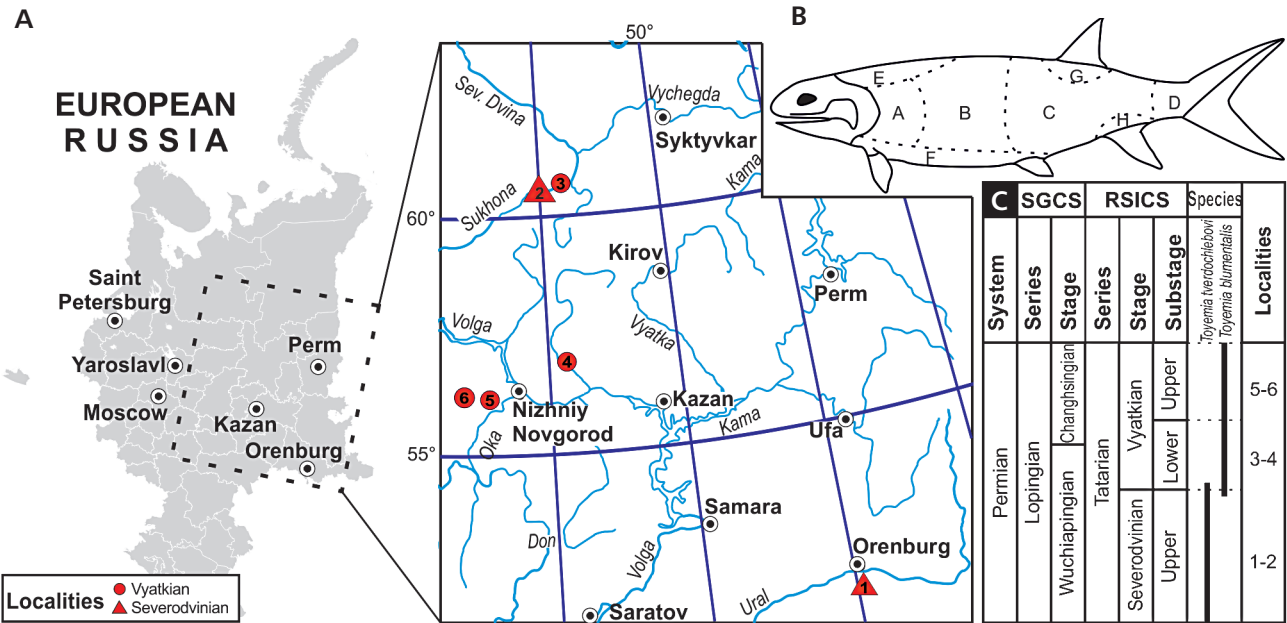
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Scales attributed to *Toyemia* Minich, 1990, frequently occur in the continental upper Permian successions of European Russia. Due to their abundance and characteristic morphology, they have been used as index fossils for biostratigraphic zonation schemes in order to define substage-level assemblage zones and even the so-called *Toyemia* superassemblage zone, slightly exceeding the duration of a stage (Esin & Mashin 1996, Minikh & Minikh 2009). The onset of this superassemblage, characterized by a high degree of endemism, coincides with the disappearance of several generalist fish forms as well as shifts in tetrapod and aquatic invertebrate communities, and has been interpreted in the context of major palaeoenvironmental changes on a regional scale (Bakaev *et al.* 2017). *Toyemia* was originally described

as a member of Gonatodidae Gardiner, 1967, although similarities with the scanilepiform *Evenkia* Berg, 1941 have equally been pointed out (Minikh & Minikh 1990). *Toyemia* is reconstructed as a medium-sized predator of freshwater habitats (Minikh & Minikh 2009, Romano *et al.* 2016).

For a better understanding of the palaeobiology and interrelationships of this both ecologically and stratigraphically significant taxon, we are conducting a comprehensive morphological study based on new and rediscovered, previously undescribed material. In this contribution, we present new morphological and histological data on the squamation of *Toyemia* and the evenkiids *Evenkia* and *Oshia* Sytchevskaya, 1999, and discuss their possible phylogenetic implications.



**Figure 1.** Geographic and stratigraphic distribution of *Toyemia* Minich, 1990, and a general scheme of the topological variability of scales according to body areas. A – map of European Russia with *Toyemia* finding localities: 1 – Donguz-6; 2 – Mikulino-3; 3 – Klimovo-1; 4 – Galibikha; 5 – Gorokhovets; 6 – Bykovka (see Table 1 for details). B – generalized basal actinopterygian with typical body areas A–H according to Esin (1990). C – stratigraphic scale showing the stratigraphic position of the finding localities and the range of *T. tverdochlebovi* Minich, 1990 and *T. blumentalis* A. Minich, 2009. Abbreviations: SCCS – Standard Global Chronostratigraphic Scale; RSICS – Russian Standard Interregional Chronostratigraphic Scale.

Geological setting

Extensive middle and upper Permian deposits cover the eastern part of the East European Platform, from the Barents Sea in the north to the Caspian Depression in the south. Best outcrops are found along the banks of the large rivers: Ural, Volga, Severnaya Dvina and their tributaries (Fig. 1). During late Permian, the East European Platform was located somewhat north to the equator, in a semiarid palaeoclimatic zone.

Large amounts of terrigenous red-bed sediments accumulated during late Permian in present-day European Russia, forming up to 1500 m thick units of mainly fluvial and lacustrine origin (Tverdokhlebov *et al.* 2005). They are mainly composed of subhorizontally bedded red, reddish-yellow, or reddish-brownish-yellow mudstones, siltstones and fine-grained muddy sandstones, deposited on floodplains. Lenses of cross-bedded alluvial sandstones and conglomerates, indicating river channels, frequently occur within these deposits. Rare carbonates, represented by grey or purple-grey limestones and marls, document shallow lacustrine conditions (Tverdokhlebov *et al.* 2005, Arefiev *et al.* 2015).

Fish remains usually occur in the grey limestone units and in the sandstone lenses, while fossils are less frequent in the red-bed mudstones.

Materials and Methods

Fossil remains of *Toyemia* investigated herein come from six upper Permian localities of European Russia (Fig. 1A, C, Tab. 1): 1 – Donguz-6 and 2 – Mikulino-3 (upper Severodvinian, Wuchiapingian); 3 – Klimovo-1 and 4 – Galibikha (lower Vyatkian, Wuchiapingian?); 5 – Gorokhovets and 6 – Bykovka (upper Vyatkian, Changhsingian?). They are housed in the PIN under collection numbers 5652, 5674, 5676, 5787 and 5788. Additional evidence for the distribution of scales and the attribution of lepidotrichia segments is derived from previously undescribed articulated specimens without collection numbers, recently rediscovered in the PIN collections (Bakaev & Kogan, unpublished data).

We extend the investigation to the squamation of *Evenkia* from the Early Triassic of Siberia and *Oshia* from the mid-Triassic of Central Asia, the two scanilepiforms of geographically closest occurrence to *Toyemia* (Sytychevskaya 1999), which constitute the Evenkiidae Selezneva, 1985. Morphology and histology of scales of *Evenkia eunotoptera* Berg, 1941 has been addressed in the Ph.D. thesis of V.N. Yakovlev (1973), while scales of *Oshia ferganica* Sytychevskaya, 1999 were studied in the BSc thesis of F. Franeck (2013). Both descriptions remained unpublished, so our contribution represents the first detailed



**Table 1.** Stratigraphy, facies and fossil assemblages of the finding localities of the material used for this study.

No.	Locality	Location	Stratigraphy	Lithology	Fossil assemblage
1	Donguz-6	right bank of Donguz river, 3 km SE of Donguz village, Orenburg Region, Russia	Malaya Kinel' Formation, Upper Severodvinian Substage, Severodvinian Stage, Tatarian Series; Wuchiapingian Stage, Lopingian Series, late Permian	reddish-brown claystone, pale-grey limestone	bony fishes, tetrapods
2	Mikulino-3	right bank of Sukhona river, close to E-margin of Poldarsa settlement, opposite Nikulino village, Vologda Region, Russia	Purtovino Member, Poldarsa Formation, Putyatian Stage, Upper Severodvinian Substage, Severodvinian Stage, Tatarian Series; Wuchiapingian Stage, Lopingian Series, late Permian	brown-yellow, yellow-green, cherryred, mottled, friable claystone	bony fishes, tetrapods, bivalves, plants
3	Klimovo-1	left bank of Sukhona river opposite Klimovo village, Vologda Region, Russia	Rovdino Member, Salaryovo Formation, Bykovian Stage, Lower Vyatkian Substage, Vyatkian Stage, Tatarian Series; Wuchiapingian (?) Stage, Lopingian Series, late Permian	sandstone, clayey sandstone with interbeds of silts and clays	bony fishes, tetrapods
4	Galibikha	right bank of Vetluga river near Vetluga village, 7.5 km WNW of Sukhoborka village, Nizhny Novgorod Region, Russia	Zamoshnikovo Member, Vyatka Formation, Bykovian Stage, Lower Vyatkian Substage, Vyatkian Stage, Tatarian Series; Wuchiapingian (?) Stage, Lopingian Series, late Permian	mottled clays, marls and limestones	bony fishes, ostracods
5	Gorokhovets	ravine on the right bank of Klyazma river, on the NW outskirts of Gorokhovets town, on the edge of Gorodishchi village, Vladimir Region, Russia	Gorokhovets Member, Obnora Formation, Nefyodovian Stage, Upper Vyatkian Substage, Vyatkian Stage, Tatarian Series; Changsingian (?) Stage, Lopingian Series, late Permian	brown-yellow sandstones	bony fishes, tetrapods
6	Bykovka	sand quarry on the NE outskirts of Vyazniki town, Vladimir Region, Russia	Zhukov Member, Vokhma Formation, Zhukovian Stage, Upper Vyatkian Substage, Vyatkian Stage, Tatarian Series; Changsingian (?) Stage, Lopingian Series, late Permian	yellow polymictic sandstones and conglomerates	bony fishes, tetrapods
7	Anakit	right bank of Nizhnyaya Tunguska river, between Anakit and Khuntukun river mouths, Evenkiysky District, Krasnoyarsk Region, Russia	Eksa beds, Bugarikta Formation, Dvuroginsky Stage, Induan/Olenekian Stage, Early Triassic	greenish-brown, thinly laminated limestone	bony fishes, tetrapods, conchostracans, ostracods, insects, plants
8	Madygen	Urochishche Dzhaylyauchо ("northern Madygen"), ca. 30 km NW of Samarkandyk, Batken Region, Kyrgyzstan	Madygen Formation, Ladinian–Carnian Stage, Middle–Late Triassic	grey and brown siltstones	bony and cartilaginous fishes, tetrapods, various invertebrates, plants

account on the squamation of these taxa. The scale cover of *Evenkia* could not be investigated in great detail because the material at our disposal is restricted to the type series housed in the PIN, which consists of articulated skeletons with overlapping scales. More abundant material was available of *Oshia*, collected during several field seasons by FG researchers and prepared mechanically or by acid dissolving of the rock. Scales of *Evenkia eunotoptera* (PIN collections No. 1876, 3852) come from the Anakit locality [Evenkiysky District, Krasnoyarsk Region, Russia; Early Triassic (Induan), Dvuroginsky Regional Stage, Bugarikta

Fm.]. Remains of *Oshia ferganica* (PIN collection No. 3267; FG collection No. 596/III) were recovered from the Madygen locality [Batken Region, Fergana Valley, Kyrgyzstan; Middle–Late Triassic (Ladinian–Carnian), Madygen Fm.; Table 1].

Scanning electron micrographs were made in the PIN Analytic Instrument Department on Cambridge CamScan 4 electron microscopes with LINK-860, TESCAN VEGA-II XMU and TESCAN VEGA-III XMU microanalyzers, without or with gold or gold-palladium coating. Thin sections have been prepared in the TU BAF Geological

Institute and were studied at TU BAF under a ZEISS AxioLab.A1.

Study of the vascular system was conducted by photographing scales immersed in a fluid (anise oil in this case). This method has been extensively used previously when studying internal structures of chondrichthyan microremains (e.g. Ivanov 2005). The material has been photographed at the PIN Analytic Instrument Department using a Leica MZ16 microscope with a camera mounted. Image stacks have been created using the software Helicon Remote 3.2.7 and processed in Helicon Focus 7.6.1 Pro + Portable.

Scales are described following the algorithm proposed by Esin (1990) in order to subdivide the squamation into areas of sufficiently similar morphology (Fig. 1B). This scheme, introduced on the example of the eurynotoidiform *Eurynotoides costatus* (Eichwald 1860) (= *Amblypterina costata* sensu Esin, *partim*), has been successfully used for describing the scale cover of the basal osteichthyans *Ligulalepis* (Burrow 1994), *Psarolepis* (Qu *et al.* 2013b), *Guiyu* (Cui *et al.* 2019), *Andreolepis* (Chen *et al.* 2012), *Sparalepis* (Choo *et al.* 2017) and the actinopterygians *Moythomasia* (Trinajstić 1999a, b), *Mimipiscis* (Trinajstić 1999b, Choo 2011), *Donnrosenia* (Long *et al.* 2008), *Gogosardina* (Choo *et al.* 2009), *Burguklia* (Bakaev & Kogan 2020) and *Isadia* (Bakaev & Bulanov 2021). Generalities emerging from this range of descriptions ensure a higher confidence for our interpretation of the topological variability in the material studied.

Scale morphology is described using the terminology of Schultze (1966), with modifications by Esin (1990), Burrow (1994), Qu *et al.* (2013b), Bakaev & Kogan (2020) and Bakaev & Bulanov (2021). We use the following terms for different elements of scale ornamentation: prominent positive linear structures, triangular or rounded-triangular in cross-section and separated by deep negative structures, are termed ‘ridges’; flattened linear elements, rounded in cross-section and separated by shallow negative elements, are referred to as ‘rolls’; deep, elongate negative relief elements, free of ganoine, separating ridges, are called ‘grooves’ when they are longer and ‘furrows’ when they are shorter; shallow elongate depressions separating rolls are defined here as ‘cannelures’. Scale ultrastructure is described following the terminology of Märss (2006), and the terminology for histological descriptions is adapted from Francillon-Vieillot *et al.* (1990), Sire *et al.* (2009), Qu *et al.* (2013a, b, 2015, 2017), Mondéjar-Fernández (2018) and Mondéjar-Fernández & Meunier (2021). Since the homology of individual elements of the actinopterygian and the sarcopterygian pore-canal system is not clear (see Discussion), we use for these elements a terminology modified from Aldinger (1937), based on the topological interrelationship of the elements. Thus, we call all canals forming horizontal network horizontal canals. Canals

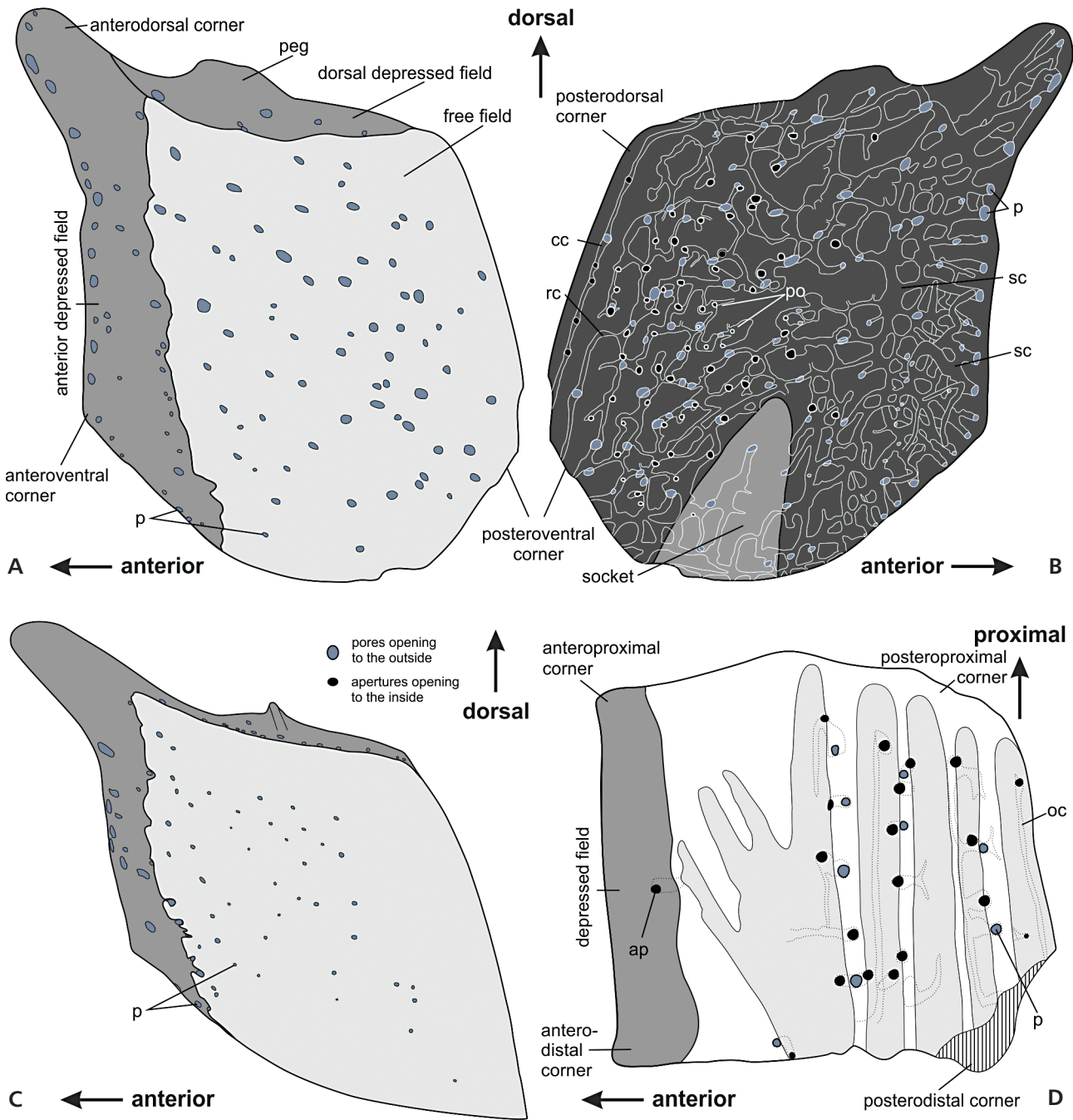
branching from the horizontal network in the upper (crown of the scale) direction are called ascending canals; those branching off in lower direction (base of the scale) are called descending canals. Canal openings to the outer surface of the scale are termed pores, those along the posterior and ventral margin of the free field are termed lateral pores, and openings to the inner surface of the scale are termed apertures.

Unlike most workers (Qu *et al.* 2013b), we refer to vertical and horizontal sections not in relation to the point of view, but following the anatomic directions along the fish body. This means that vertical sections are oriented parallel to the dorsoventral scale rows, and horizontal sections parallel to the horizontal rows.

Among the basic morphological elements of a rhombic ganoid scale, there are: four margins termed anterior, posterior, dorsal and ventral, four corners between them termed anterodorsal, anteroventral, posteroventral and posterodorsal, further the lateral or outside, consisting of a free field covered by the ganoine layers and a depressed field along the anterior and often the dorsal margin, overlapped in life by preceding scales, and a median or inside, carrying elements for scale-to-scale articulation and the connection to the dermis (Figs 2A–C, 3).

We include lepidotrichial elements in our study on the squamation. Lepidotrichia, the name-giving structure of actinopterygians, consist of left-right pairs of usually segmented, anteroposteriorly arcuate bony hemitrichia with connective tissue in between (Geerlink & Videler 1987). It is well-established that hemisegments of fin rays are homologs of scales and may possibly be derived from those (see Zylberberg *et al.* 2016 and references therein). Morphologically, they resemble scales in being generally rectangular to square-shaped in outline, with anterior, posterior, distal and proximal margins and even traces of articulating elements on their joint surfaces (Zylberberg & Meunier 2013), as well as, sometimes, a narrow depressed field along the anterior margin overlapped by hemisegments of the preceding ray and even denticles along the posterior margin (Fig. 2D; Esin 1995). Hemisegments consist of the same tissue types as scales (bone, dentine and ganoine) and have a well-developed vascular system (although simplified when compared to flank scales). Similar to flank scales, horizontal canals underlie sculptural ridges. On the inside, the hemisegments bear a pronounced keel (often shifted posteriorly), to which numerous Sharpey’s fibers attach (Fig. 4; Zylberberg & Meunier 2013, Zylberberg *et al.* 2016).

The ligament between hemisegments of successive lepidotrichia is partly mineralised. Hemisegments of successive rays are also connected to each other by distinct protrusions (apophyses) on the anterior margin that fit into small depressions on the posterior margin (Zylberberg & Meunier 2013, Zylberberg *et al.* 2016).



**Figure 2.** General morphology of scales and fin ray segments of *Toyemia* Minich, 1990. • A, B, D – *Toyemia tverdochlebovi* Minich, 1990; A – sketch of an area B scale of a juvenile specimen (based on PIN 5788/58), seen from outside (crown view); B – same scale, seen from inside (base view), with indication of the vascular system; D – lepidotrich hemisegment (based on PIN 5788/60), seen from outside, with indication of the vascular system. • C – *Toyemia blumentalis* A. Minich, 2009, sketch of an area C scale of a juvenile specimen (based on PIN 5787/10, mirrored), seen from outside. Abbreviations: ap – apertures; cc – concentric canals; oc – underlying canals; p – pores; rc – radial canals; sc – sinuously widened canals.

Despite their similarity in both histology and morphology, body scales and fin ray segments are formed by different systems: body scales (except the ganoin cover) form within the mesoderm, while fin rays form within the ectodermal fin fold (Zylberberg *et al.* 2016). The

lepidotrichia mineralise proximodistally and terminate in unmineralized actinotrichia. Lepidotrichia are more similar to body scales than to fulcræ; fin ray segments of teleosts, finally, represent modified paired hemitrichia of ‘ganoid fishes’.

*Institutional abbreviations.* – PIN – Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; FG – Geological Institute, TU Bergakademie Freiberg, Freiberg, Germany.

## Systematic palaeontology

Subclass Actinopterygii Cope, 1887 *sensu* Goodrich (1930)  
Order Scanilepiformes Sytchevskaya, 1999  
Family Evenkiidae Selezneva, 1985

### Genus *Toyemia* Minich, 1990 in Minikh & Minikh (1990)

*Type species.* – *Toyemia tverdochlebovi* Minich, 1990.

*Diagnosis (emended).* – Caudal peduncle short. Skull roofing bones ornamented with long, widely spaced ridges. Scales rectangular, with a well-developed, rounded, strongly bent anteriorly anterodorsal corner. Anteroventral corner slightly pointed and usually directed anteriorly. Posterior scale margin smooth or wavy, without serrations. Peg with a pointed tip, bearing a prominent vertical crest along its midline. Posterior part of the free field ornamented with concentric rolls, flattened-roundish in cross-section (more distinct in the ventral portion), separated by shallow cannelures. Numerous small pores occurring in the cannelures concentrically follow the growth lines of the scales. Vascular system consisting of horizontal canals forming a regular network in the posterior and ventral part of the free field and a complex three-dimensional meshwork in the anterodorsal part of the free field and underneath the depressed field, where it opens to the surface through large pores. Lepidotrichia segments ornamented with characteristic vertical ridges, rounded or rounded-triangular in cross-section, separated by wide grooves. Ridges replaced by a continuous, smooth, pore-bearing ganoine field in the posterior part of the segments.

### *Toyemia tverdochlebovi* Minich, 1990 in Minikh & Minikh (1990)

Figures 2A, B, D; 3; 4; 5

1990 *Toyemia tverdochlebovi* Minich; Minikh & Minikh, p. 98, pl. 6, figs 1–4.

2009 *Toyemia tverdochlebovi* Minich. – Minikh & Minikh, p. 79, text-fig. 9, pl. 21, pl. 22, figs 1–4; pl. 23, figs 1–4.

*Material.* – Isolated scales, PIN collection nos. 5652, 5788.

*Description.* – Area A (Fig. 3A): Scales rectangular, 1.5–2 times higher than long. Anterior margin slightly concave. Anterodorsal corner well-developed, with a rounded

tip, distinctly curved anteriorly. Anteroventral corner slightly pointed, often directed anteriorly. Dorsal margin slightly concave at the level of the peg. Ventral margin slightly convex at the level of the socket. Posterior margin smooth, without denticles. Posterodorsal corner rounded, posteroventral corner pointed. Anterior depressed field occupies about  $\frac{1}{4}$  of scale length. Peg and socket triangular. Peg with a pointed tip and a prominent vertical crest along the midline. The crest has a smooth, flattened edge. Bone surface on both sides of the crest porous (indicating attachment area of collagen fibers from the stratum compactum). Socket deep. The keel is flattened, placed slightly anterior to the peg and socket.

The anterior margin of the free field is continuous, dissected by short, narrow furrows, initially pointing ventrally but smoothly turning caudally. Ridges forming between these furrows rounded in cross-section, sometimes reaching the middle of the free field. Sculpture in the posterior part of the ganoine field consisting of concentric, flattened rolls (especially distinct in the ventral part) separated by shallow cannelures. Numerous small pores located in the cannelures concentrically follow growth zones of the scale. Numerous, chaotically distributed apertures are found posterior to the keel.

Area B (Fig. 3B): Rhombic scales with height equal to or slightly exceeding the length. Free field nearly smooth, concentric flattened rolls rather indistinct, furrows dissecting the free field much shorter than in area A. Other characters equal to area A.

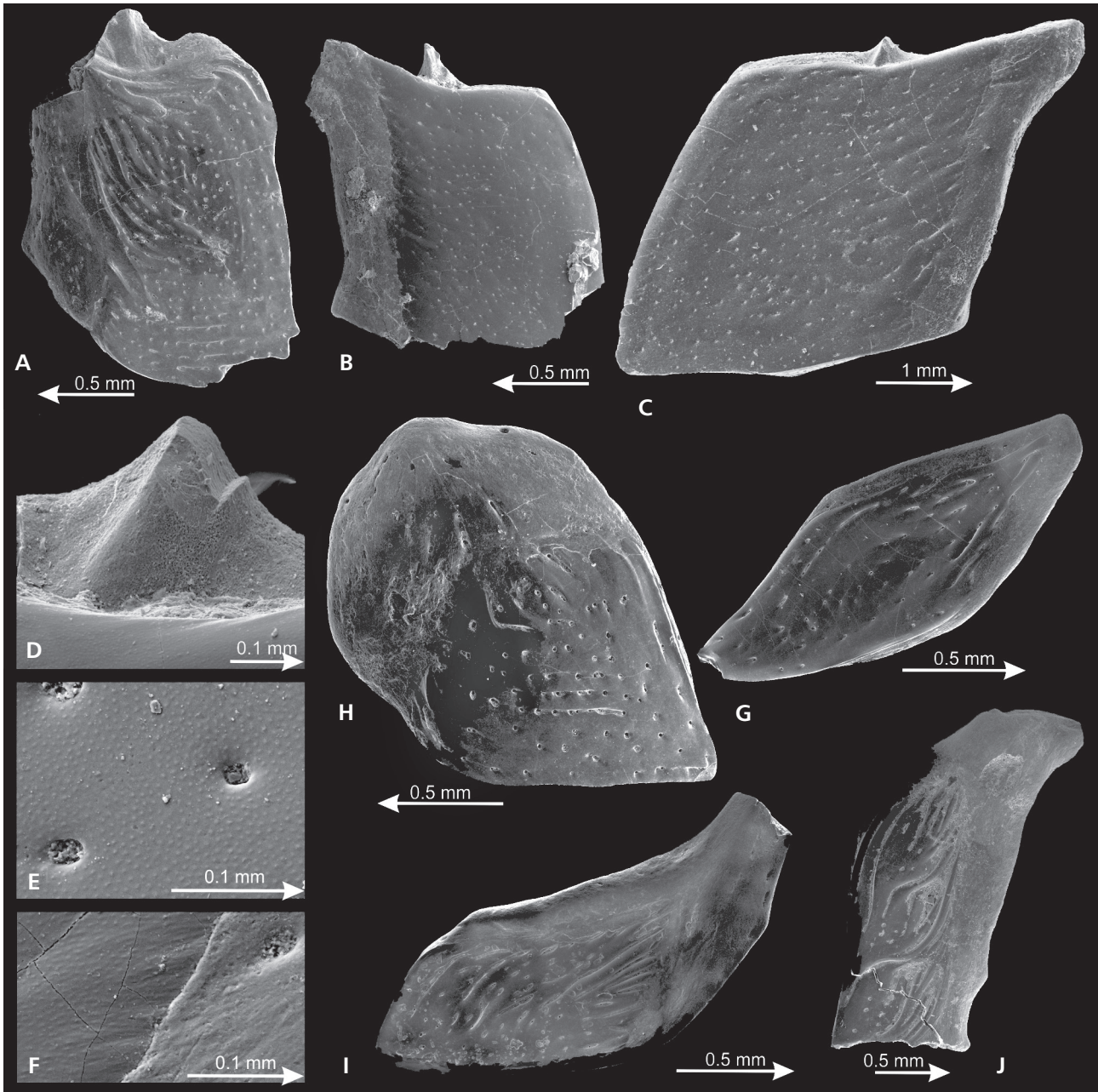
Area C (Fig. 3C–F): Rhombic scales, length exceeding height by 1.2–1.5 times. Peg and socket very small or lacking. Keel narrow, located anterior to the peg and socket. Anterior depressed field no longer than  $\frac{1}{5}$  scale length.

Area D (Fig. 3G): Scales twice longer than high. Depressed field developed as narrow bands along the anterior and the dorsal margins. Keel, peg and socket absent. Anterodorsal corner weakly developed, with a rounded tip. Anterior margin not concave. Anteroventral corner rounded and not prominent.

Area E (Fig. 3H): Scales of rounded-triangular (drop-like) shape. Anterodorsal corner rounded, large, wide, prominent, slightly bent anteriorly. Posteroventral corner pointed. Anterior margin slightly concave. Keel, peg and socket small or absent. Free field triangular, with anterior margin dissected by short furrows. Anterior ends of lobate projections of the ganoine field rounded.

Area F (Fig. 3I): Elongated scales with a well-developed depressed field. Anterodorsal corner very large, basally wide, pointing anterodorsally. Anterior margin straight or slightly concave. Dorsal and ventral margins straight. Peg and socket small or absent. Keel indistinct or absent. Scales of this area get somewhat smaller in the ventral body part, where keel, peg and socket disappear.





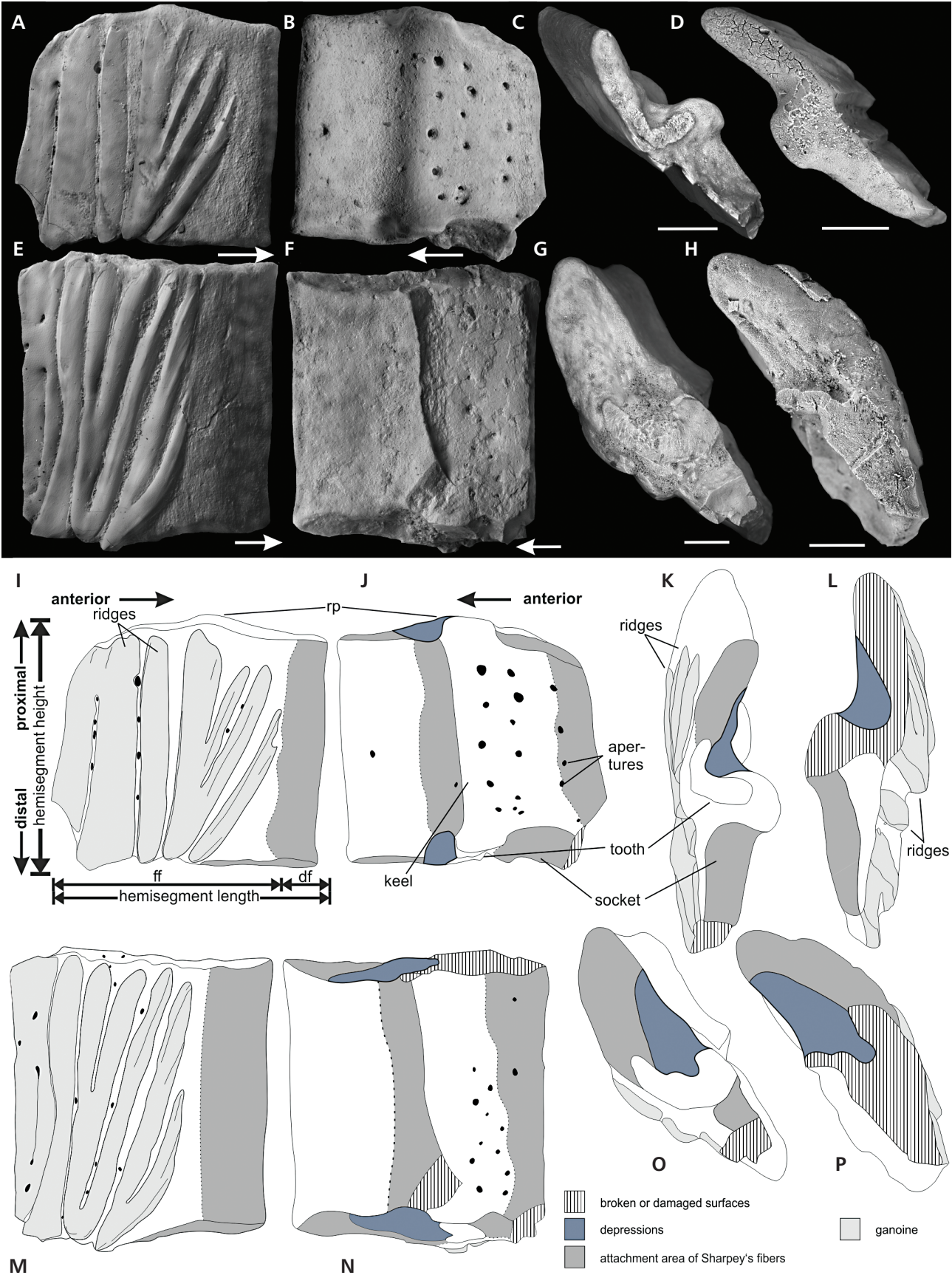
**Figure 3.** Squamation of *Toyemia tverdochlebovi* Minich, 1990, in crown view. A – area A scale, PIN 5788/55; B – area B scale, PIN 5788/56; C – area C scale, PIN 5652/226; D–F – close-ups of C; G – area D scale, PIN 5788/53; H – area E scale, PIN 5788/57; I – area F scale, PIN 5788/54; J – basal segments of a lepidotrichium, PIN 5652/227. A–B, G–I –Donguz-6 locality (Table 1: 1); C–F, J – Mikulino-3 locality (Table 1: 2).

Lepidotrichia segments (Fig. 3J, Fig. 4): Rectangular, small, thick. Height can exceed length (by up to 5 times and more), or vice versa (up to 4 times).

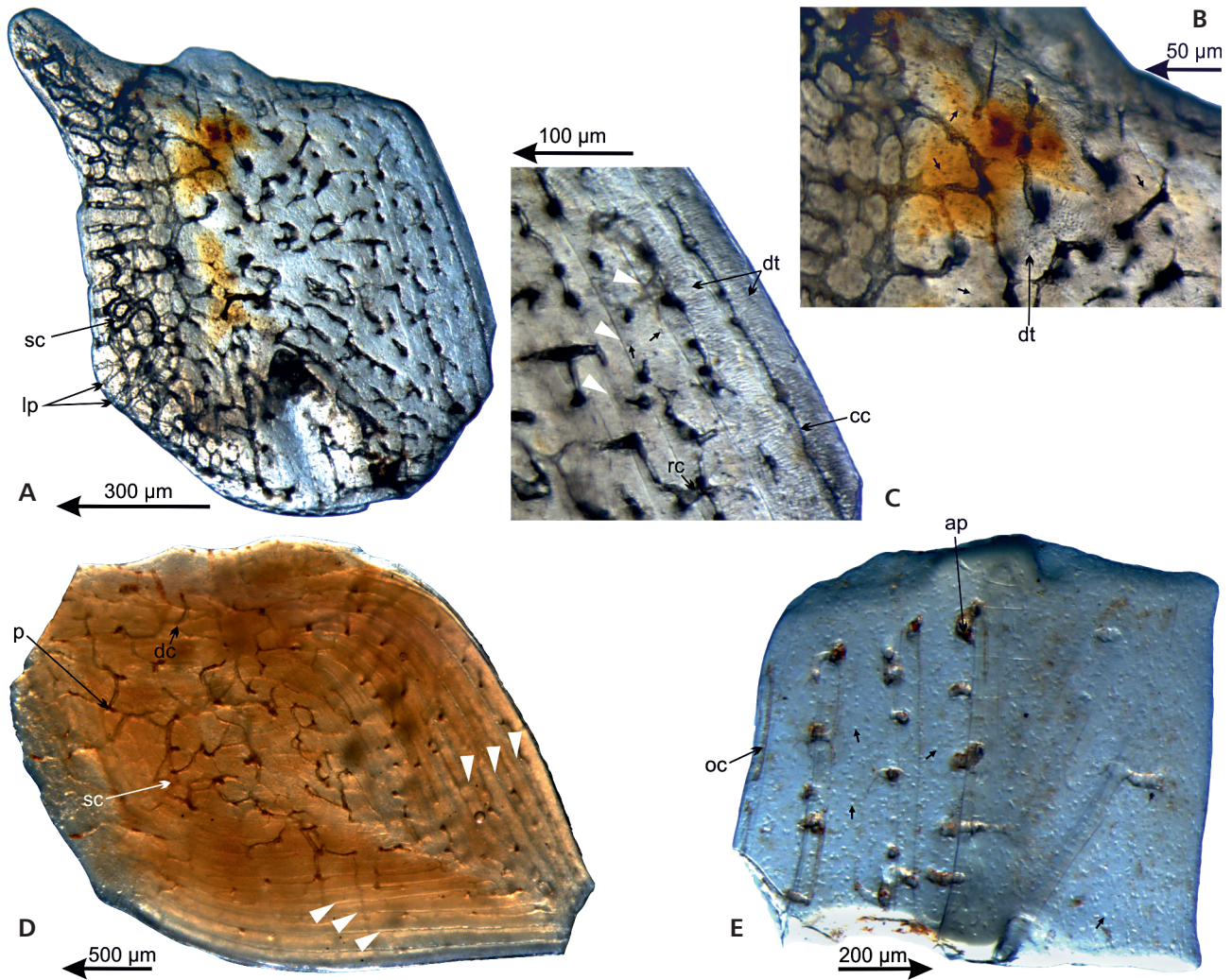
Posterodistal corner sometimes elongated. Margins straight. A keel at half length, with numerous apertures to both sides of it. Depressed field short – no more than  $\frac{1}{5}$  of the length – or lacking. Characteristic ridges directed subparallel to parallel to the axis of the fin ray, rounded or roundish-triangular in cross-section, in the anterior part

of the free field (Fig. 4A, B, E, F). Posterior part of the free field covered by a smooth ganoine surface with pores. Basal parts of the fin rays (Fig. 3J) with fused segments (with thickenings in the fusion areas) with wide depressed fields along both the anterior and the proximal margins.

The proximal and the distal margins of successive hemisegments of a ray were attached to each other by numerous Sharpey's fibers, evidenced by large attachment areas characterized by a porous surface (Fig. 4) (Gemballa







**Figure 5.** Scales and fin ray segments of *Toyemia tverdochlebovi* Minich, 1990, immersed in anise oil, Donguz-6 locality (Table 1: 1). A – juvenile area B scale, PIN 5788/58, in base view; B, C – magnified fragments of A, note the resorption lines separating odontode generations, and numerous canaliculi (dental tubules); D – area C scale, PIN 5788/59, in crown view, note the resorption lines separating odontode generations; E – lepidotrichium hemisegment, PIN 5788/60, in base view. Large white arrowheads indicate resorption lines between odontodes; small black arrows point to osteocyte lacunae. Abbreviations: ap – apertures; cc – concentric canals; dc – descending canals; dt – canaliculi (dental tubules); lp – lateral pores; oc – underlying canals; p – pores; rc – radial canals; sc – sinuously widened canals.

& Bartsch 2002). Large attachment areas of Sharpey's fibers are also located on the keel, in the posterior part of the hemisegment inside and in the anterior part of the depressed field (Fig. 4I, J, M, N). The proximal margin bears a rudiment of the peg (identified at the highest point of the margin), the distal margin exhibits a depressed area posterior to the keel that corresponds to the socket. The keel terminates in distinct, internally bending protuberances on both the distal and the proximal margin, with depressions

symmetrically placed anterior to them. The surfaces of such protuberances and depressions are free from apertures, characteristic for Sharpey's fiber attachment areas. In successive hemisegments of a fin ray, protuberances are in contact with each other and depressions lie opposite to one another. This means that protuberances and depressions do not function in the way of a 'peg and socket' of flank scales, and their immediate purpose remains unclear. Furthermore, a flat, chevron-shaped peak with a surface

**Figure 4.** Lepidotrichial hemisegments of *Toyemia tverdochlebovi* Minich, 1990, Donguz-6 locality (Table 1: 1). A–D – PIN 5788/61: A – external surface (crown view), B – internal surface (base view), C – distal margin, D – proximal margin; E–H – PIN 5788/62: E – external surface (crown view), F – internal surface (base view), G – distal margin, H – proximal margin; I–P – interpretive drawings of A–H, respectively. Scale bars equal 200 µm. Abbreviations: df – depressed field; ff – free field; rp – rudimentary peg.

free of pores, resembling the hinge teeth of bivalve mollusks, is located in the middle of the distal margin (Fig. 4C, G, K, O). We suggest that this tooth may have fitted in a groove on the proximal side of the following hemisegment (Fig. 4D, H, L, P), but the proximal margins of the hemisegments at our disposal are too damaged for verifying this suggestion. Possibly, this type of joint would have protected the lepidotrichium from both longitudinal and transversal translation and axial torsion.

Similar to body scales, there is a topological variability in fin ray hemisegments, but the scarce articulated material at our disposal does not allow for a detailed description so far.

**Ultrasculpture** (Fig. 3E, F): The free field is covered by minute tubercles (less than 10 µm in cross-section). In the central part of the free field, these micro-tubercles have a rounded shape and are regularly spaced with about 10 µm distance between tubercle tips. Along the anterior margin of the free field, in contrast, the microtubercles are elongated, with their length increasing with the curvature of the surface they are located on.

**Vascular system:** Vascular canals can be seen on scales photographed in immersive fluid (Fig. 5). They are relatively wide in the central part of the scale (and can even form small thickenings – sinuses), and do not form a flat mesh but rather separate, complex, three-dimensional junctions with loops, bends and branching points at different levels of the scale. The highest number of canals occurs around the bone/dentine boundary, and vertically and subvertically oriented descending canals pass through the lowermost layer of bone. Ascending canals of the central part of the free field open to the surface through irregularly distributed pores. Along the posterior and ventral margins, growth lines are recognizable that separate odontode generations (Fig. 5C, D) and respective layers of bone and ganoine. Concentric canals penetrating every new generation of odontodes open to the free field surface through regularly distributed pores following a concentric pattern. The concentric canals of different generations are interconnected through radial canals, which end with a row of pores on the scale margins. In this way, a flat network with regular ‘combs’ formed by the concentric and radial canals occurs on the periphery of the free field.

Vascular canals are also present in the anterior scale part, underneath the depressed field. These canals are very wide (much wider than in the central part) and mainly radially directed. Several radial canals are interconnected through short longitudinal ones. The wide radial canals open to the surface of the depressed field (mainly along the anterior margin) by pores, slightly larger than those on the free field.

The structure of the vascular canals and pores reflects the individual ontogeny. For instance, the absolute size of the pore openings does not change during growth.

Therefore, scales of young individuals will have relatively larger pores than scales from the same body area of adult fishes. Meanwhile, new odontodes form during growth of the scale, which are underpinned by vascular canals opening to the surface through new pores. Consequently, scales of same position will exhibit more pore openings in older individuals (Fig. 3C) than in younger ones (Fig. 2A, B).

**Remarks.** – *T. tverdochlebovi* differs from *T. blumentalis* in the nearly smooth free field, the lack of distinct ridges, and the smaller average size of the scales.

**Occurrence.** – Upper Severodvinian (approximately from middle part of Strena Member, Poldarsa Formation, Sukhona river basin) and lowermost Vyatkian (approximately to middle part of Erga Member, Vyatka Formation, Sukhona river basin) – numerous localities on the East European Platform.

***Toyemia blumentalis* A. Minich, 2009 in Minikh & Minikh (2009)**

Figures 2C, 6, 7, 8

1995 *Toyemia blumentalis* A. Minich. – Minikh, p. 3, fig. 2. [nomen nudum]

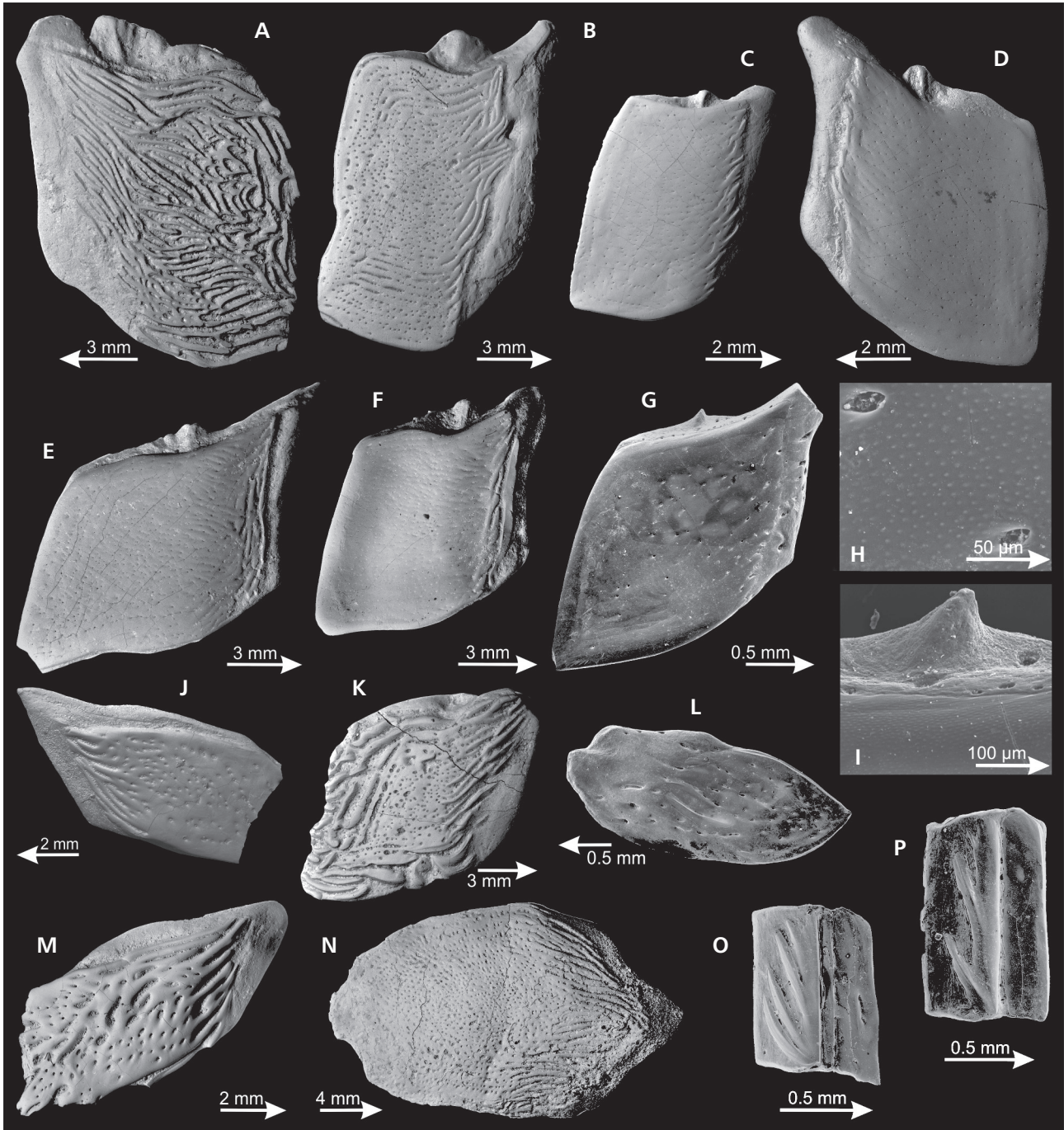
2009 *Toyemia blumentalis* A. Minich; Minikh & Minikh, p. 80, text-figs 10, 11, pl. 24.

**Material.** – Isolated scales, PIN collection nos. 5674, 5676, 5787.

**Description.** – Area A (Fig. 6A, B): Rectangular scales, twice higher than long. Anterior margin slightly concave. Anterodorsal corner well-developed, with a rounded tip, strongly bent anteriorly. Anteroventral corner slightly pointed and often directed anteriorly. Dorsal margin slightly concave at the level of the peg. Ventral margin slightly convex at the level of the socket. Posterior margin smooth, usually undenticulated. Posterodorsal corner rounded, posteroventral corner pointed. Anterior depressed field accounting for about 1/4 of the scale length. Peg and socket triangular. Peg directed dorsally, with a pointed tip and a prominent vertical crest. Socket deep. Keel narrow, located somewhat anterior to peg and socket. Free field sculptured with prominent, thick ridges, rounded-triangular in cross-section, especially well-developed close to the anterior margin. Posterior part usually with concentric rolls with numerous pores in cannelures between them. In some scales, the whole free field covered with thick ridges.

Area B (Fig. 6C, D): Rhombic scales, with length equal to or slightly exceeding the height. Sculpture of the free field consisting of quite sharply descending furrows,





**Figure 6.** Squamation of *Toyemia blumentalis* A. Minich, 2009, in crown view. A – area A scale, PIN 5674/13; B – area A–B scale, PIN 5674/11; C – area B scale, PIN 5674/12; D – area B scale, PIN 5674/14; E – area B–C scale, PIN 5674/16; F – area B–C scale, PIN 5674/17; G – area B–C scale, PIN 5787/10; H–I – close-ups of G; J – area D scale, PIN 5674/30; K – area A–E scale, PIN 5674/18; L – area E scale, PIN 5787/9; M – area F scale, PIN 5674/15; N – ridge scale, PIN 5674/19; O – lepidotrichium hemisegment, PIN 5787/12; P – lepidotrichium hemisegment, PIN 5787/11. A–F, J–K, M–N – Gorokhovets locality (Table 1: 5); G–I, L, O, P – Galibikha locality (Table 1: 4).

separating ridges with a rounded cross-section. Lobate projections of ganoine rounded or roundish-pointed. These ornamentation elements occupy no more than  $\frac{1}{8}$  of the free field length. Rest of the free field is ornamented with flat concentric rolls, separated from each other by shallow

cannelures with numerous pores. Further characters as in area A.

Area C (Fig. 6E–I): Rhombic scales, 1.2–1.5 times longer than high. Peg and socket very small, but a prominent crest present on the peg and the socket of con-

siderable depth. Keel narrow, located anterior to peg and socket. The depressed field accounts for no more than  $\frac{1}{5}$  of the scale length.

Area D (Fig. 6J): Scale length exceeding their height twice. Depressed field developed as narrow stripes along the anterior and the dorsal margins of the scale. Anterodorsal corner weakly developed, with a rounded tip. Anterior margin not concave, anteroventral corner rounded and not prominent.

Area E (Fig. 6K, L): Rounded-triangular, drop-shaped scales. Anterodorsal corner rounded, short, with a wide base. Posterior margin straight or slightly convex, usually smooth, sometimes wavy due to slightly prominent sculptural ridges. Anterior margin convex or straight. Keel, peg and socket weakly developed or absent. Anterior part of the free field ornamented with prominent ridges triangular or rounded-triangular in cross-section, its anterior margin is dissected by deep furrows. The posterior part of the free field is made of concentric rolls separated by shallow canelures, or of ridges separated by furrows. The length of the depressed field can make up to half of the scale length.

Area F (Fig. 6M): Elongated scales with a well-developed depressed field. Anterodorsal corner basally wide, pointing anterodorsally. Anterior margin straight or slightly concave. Peg and socket small. Keel indistinct or absent. The size of area F scales somewhat decreases towards the ventral body part, and the keel, peg and socket disappear. Free field ornamented with ridges separated by furrows along the anterior and the dorsal margins.

Ridge scales (Fig. 6N): Large ovoid scales, pointed on their anterior and posterior ends. Extension of the

depressed field highly variable. Anterior part of the free field ornamented with ridges rounded-triangular in outline and dissected by furrows. Posterior part of the free field sculptured with concentric rolls separated by shallow canelures.

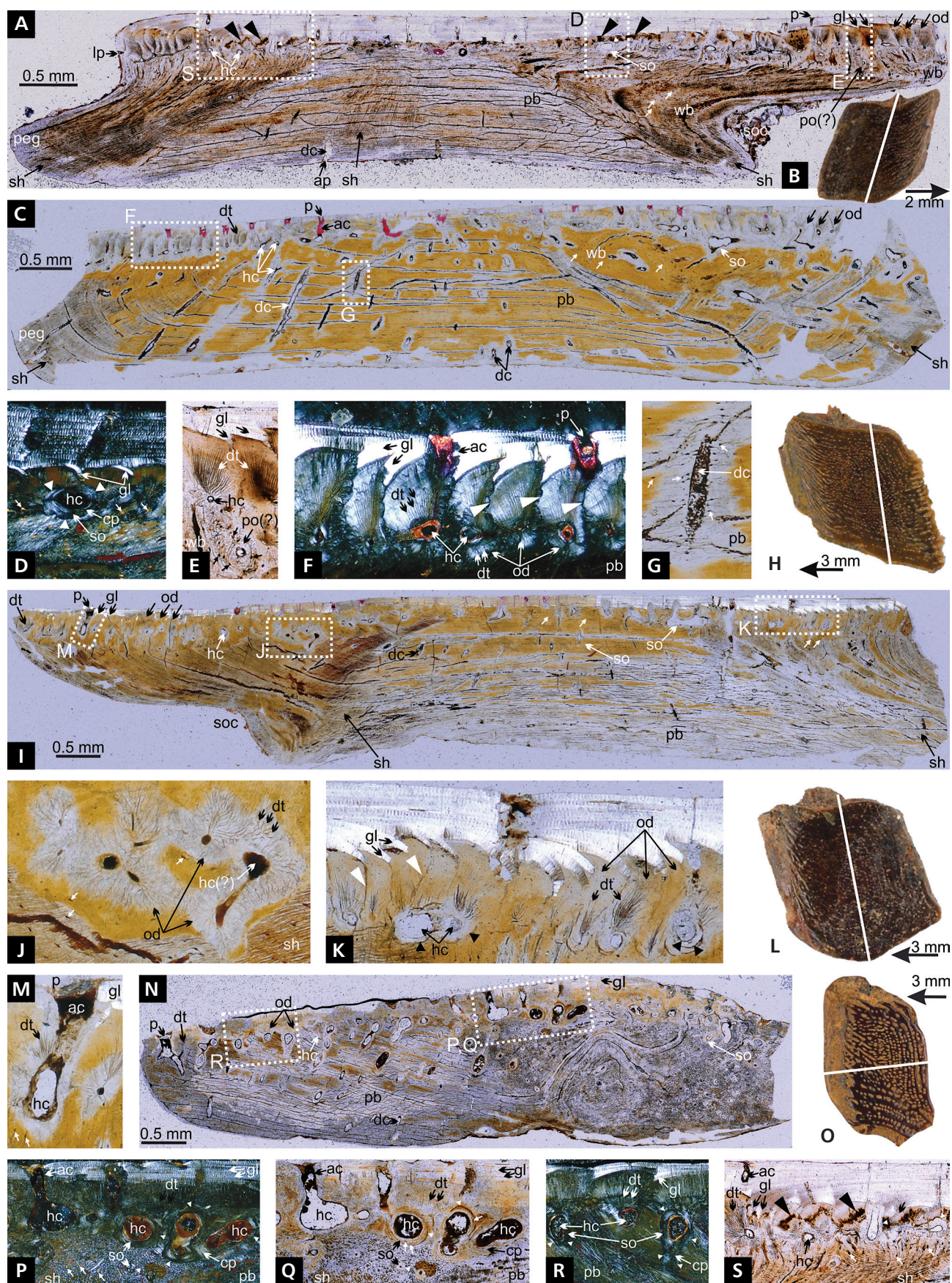
Lepidotrichia segments (Fig. 6O, P): Similar to those in *T. tverdochlebovi*.

Ultrasculpture (Fig. 6H, I): Indistinguishable from that of *T. tverdochlebovi*, consisting of microtubercles, circular in the central part and elongated towards scale margins and on the sculptural ridges.

Histology (Figs 7, 8): Layers of ganoine, dentine and bone are well-developed in the scales. The ganoine has a multilayered structure (onion-like pattern). Rod-like structures are well-visible in polarized light (Figs 7D, F, P, R; 8E). Usually, ganoine layers correspond 1:1 to odontodes (Fig. 7F, K). Ganoine layers are wedged between odontodes sequentially joining one another (= odontocomplexes) (Fig. 7D–F, K, P–R). During formation of a new odontode, partial resorption of an old one occurs (lines of resorption, which mark the boundary between odontode generations, are visible) (Figs 7F, K; 8T). A horizontal network of relatively thin canals with circular cross-section, completely embedded in dentine, is located at the base of the odontodes (Fig. 7F). In the central scale part, the canals (as well as the odontodes) seem not to follow any regular pattern, while in the ventral and posterior regions they form a regular network of concentric and perpendicular canals. The dentine layer is thinner (because of smaller-sized odontodes) in the central part of the scales, but much more pronounced in the ventral and posterior

**Figure 7.** Histological sections of scales of *Toyemia blumentalis* A. Minich, 2009, Gorokhovets locality (Table 1: 5). A – vertical section of area B–C scale PIN 5674/20 in linearly polarized light; B – crown view of scale before sectioning, with indication of the cutting plane; C – vertical section of area C scale PIN 5674/21 in linearly polarized light; D – magnified fragment of A in cross-polarized light showing a secondary osteon on the boundary of the dentine and bone layers, note that the lumen of the horizontal canal is enclosed in lamellar centripetal bone and the secondary osteon is separated from surrounding primary bone by a resorption line; E – magnified fragment of A showing a probable primary osteon, note that the lumen of the horizontal canal is surrounded concentrically by elongated osteocyte lacunae (but a resorption line is absent), and the chaotically distributed osteocyte lacunae in the surrounding woven-fibered bone; F – magnified fragment of C in cross-polarized light showing details of the ganoine and dentine layers, note that odontodes are separate by resorption lines, generations of ganoine are wedged between odontodes, and horizontal canals are completely enclosed in dentine; G – magnified fragment of C showing a descending canal, note numerous satellite cells surrounding the canal; H – crown view of scale before sectioning, with indication of the cutting plane; I – vertical section of area B scale PIN 5674/22 in linearly polarized light; J – magnified fragment of I showing odontodes embedded deeply into the bone, note the numerous canaliculi radiating from canal lumina, as well as the irregular shape of the odontodes and the depth of their embedding into the parallel-fibered bone; K – magnified fragment of I showing odontodes, note that the tissue around the horizontal canal lumina is separated from surrounding dentine by one or several resorption lines; L – crown view of scale before sectioning, with indication of the cutting plane; M – magnified fragment of I showing horizontal and ascending canals, note the secondary widening of primary canals by resorption of dentine (indicated by remnants of canaliculi) and ganoine; N – horizontal section of area B scale PIN 5674/30 in linearly polarized light; O – crown view of scale before sectioning, with indication of the cutting plane; P, Q – magnified fragment of N in linear (P) and cross-polarized light (Q), note the presence of secondary osteons with concentrically arranged osteocyte lacunae in the centripetal bone surrounding the canal lumina and the crossing pattern of Sharpey's fibers; R – magnified fragment of N in cross-polarized light showing secondary osteons formed around horizontal canals, note the resorption lines separating the osteons from both dentine and bone and the fact the canal lining made of the same tissue in both the dentine and the bone layers; S – magnified fragment of A showing the presumed recrystallization of odontodes. Small arrows point to osteocyte lacunae; small arrowheads indicate resorption lines; large white arrowheads indicate resorption lines between odontodes; large black arrowheads indicate probable recrystallized dentine. Abbreviations: ac – ascending canals; ap – apertures; cp – centripetal bone; dc – descending canals; dt – canaliculi (dental tubules); gl – ganoine layers; hc – horizontal canals; lp – lateral pores; od – odontodes; p – pores; pb – parallel-fibered bone; po – primary osteon; sh – Sharpey's fibers; so – secondary osteon; soc – socket; wb – woven-fibered bone.







parts (Fig. 7A, C, I). Conversely, the ganoine layer is much thicker in the middle scale part due to the higher number of superimposed layers (Fig. 7A). Numerous, sometimes dichotomising canaliculi pierce the dentine from the horizontal canal lumina (Figs 7D–F, G, K, P–S). Most of the longer canaliculi are directed upwards, while the shorter canaliculi can also point downwards or laterally (Fig. 7E, F, M, S), which is especially pronounced in odontodes embedded into the bone (Fig. 7J). In larger scales, in some older odontodes located closer to the anterodorsal part of the free field, the distal parts of the canaliculi appear much darker and converge into a fan-shaped dark area (Fig. 7A, S). In both linear and cross-polarized light (Fig. 7D), the dentine in older odontodes is much darker than the dentine in younger ones, located closer to the scale margins (Fig. 7F). This can be a preservational artifact, but might also point to recrystallisation of dentine.

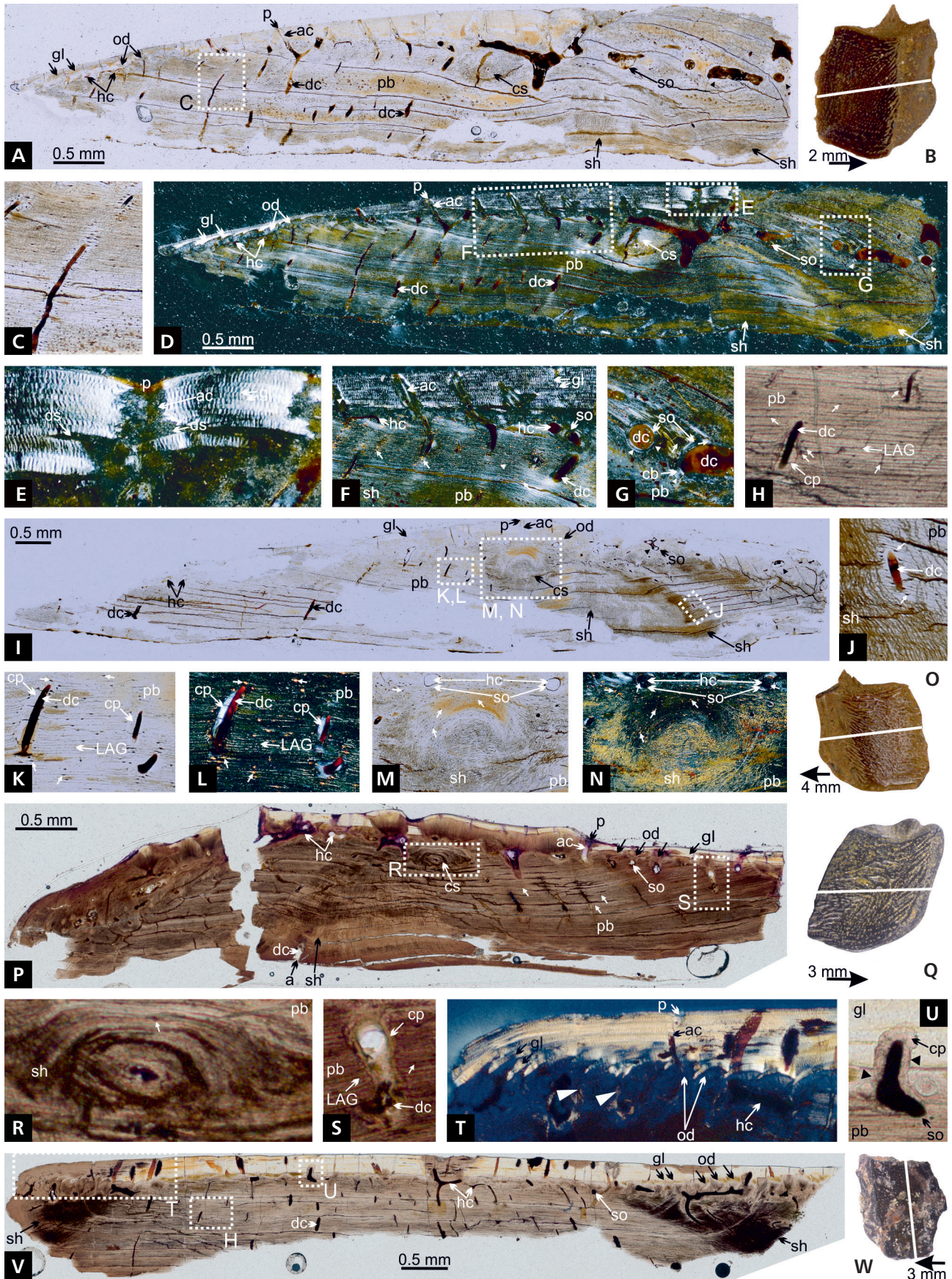
Short ascending canals trend crownward from the main horizontal canal system through the ganoine and dentine layer and open in pores on the ganoine surface. The canal inside has a lining of dentine (Fig. 8E, F). The dentine forms a homogeneous layer in most cases, but sometimes it is composed of smaller inlays ('Kosminleisten' *sensu* Aldinger, 1937), between which the ganoine layers are wedged (Fig. 8E). Sometimes, odontodes of the dentine layer are deeply embedded into the bone layer (which may be interpreted as evidence for remodeling of the dentine and bone layers); in these cases, canaliculi diverge radially from the canals (Fig. 7J). A layer of woven-fibered bone that can be seen in larger scales under the younger odontodes as well as in the region of the socket contains chaotically scattered osteocytes (seen in various views) with long, branching canaliculi (Fig. 7A, E).

The layer of parallel-fibered bone is much thicker than the ganoine and dentine layers. Numerous Sharpey's fibers, directed towards the center of the scale, enter the bone layer along the ventral and dorsal scale margin (Figs 7A, C, I; 8V) and through the keel (Fig. 8A, D, I, P). Lines of arrested growth (LAG), at which most of the osteocyte

lacunae are concentrated (Fig. 8H, K, L), are well-visible in the bone. The lacunae appear elongate in vertical section (Fig. 7A, C, G) and rounded in horizontal section (Fig. 8H, K–N), without visible canaliculi. The canaliculi are not observable because they lie in the same plane as the LAG. Thus, the osteocytes had a fusiform-flattened shape. In horizontal sections, a circular structure can be observed in the middle of scales, formed by pseudo-lamellar bone with traces of centripetal deposition (Fig. 8A, D, I, M, N, R). This structure is located slightly posterior to the Sharpey's fibers, which enter the bone through the keel, but is pervaded by numerous collagen fibers. Part of the fibers is parallel to the vertical axis of the scale (orthogonal to the sectioning plane). Another part comes from the scale inside, converges to the centre of the circular structure, and strikes the sectioning plane obliquely. As a result, the fibers cross (Fig. 7P). Descending canals starting from the junctions and canal networks pierce the bone layer (Figs 7A, C, I; 8A, D, F, P, V). These vascular canals form three-dimensional junctions in the basal bone. The canals are surrounded by a number of osteocyte lacunae ('satellite cells') (Figs 7G; 8C, J), which are separated from the canal lumen by centripetally deposited bone (Fig. 8H, K, L, S), much brighter in polarized light than the surrounding bone and thus reminiscent of primary osteons in cross-section. However, the centripetal bone layer of vascular canals is relatively thin and does not enclose cells (as it would be the case in osteons), the canals are orthogonal to the LAGs of the parallel-fibered basal bone (while primary osteons are usually parallel to LAGs), the osteocytes are rounded, and the canaliculi point radially from the canal lumen (while osteocyte canaliculi in osteons are concentrically arranged, as are the bone fibers). Some canals (Fig. 7E) are possibly enclosed in primary osteons, which is indicated by the flattened, concentrically arranged (including canaliculi) osteocyte lacunae. Nonetheless, the bony matrix of the supposed primary osteons exhibits no lamellar structure in polarized light, which constitutes a difference to typical primary osteons.

**Figure 8.** Histological sections of scales of *Toyemina blumentalis* A. Minich, 2009. A – horizontal section of area B scale PIN 5674/23 in linearly polarized light; B – crown view of the scale before sectioning, with indication of the cutting plane; C – magnified fragment of A; D – same section in cross-polarized light; E – magnified fragment of D showing the opening of an ascending canal, note the presence of dentine strips interposed between ganoine layers; F – magnified fragment of D, note the resorption of ganoine in ascending canals and rounded osteocyte lacunae; G – magnified fragment of D showing secondary odontodes, note the lamellar (alternately dark and light) centripetal bone; H – magnified fragment of V showing descending canals, note the presence of centripetal bone separating separate satellite cells from the canal; I – horizontal section of area B scale PIN 5674/31 in linearly polarized light; J, K – magnified fragments of I showing descending canals; L – same fragment as K in cross-polarized light, note the lighter centripetal bone; M – magnified fragment of I showing the 'circular structure', note numerous Sharpey's fibres; N – same in cross-polarized light; O – crown view of the scale before sectioning, with indication of the cutting plane; P – horizontal section of area B scale PIN 5676/25 in linearly polarized light; Q – crown view of the scale before sectioning, with indication of the cutting plane; R – magnified fragment of P showing the 'circular structure'; S – magnified fragment of P showing a descending canal; T – magnified fragment of V in cross-polarized light; U – magnified fragment of V showing an ascending canal, note the resorption of ganoine; V – vertical section of area C scale PIN 5676/26; W – crown view of scale before sectioning, with indication of the cutting plane. A–G, I–O – Gorokhovets locality (Table 1: 5), P–W – Klimovo-I locality (Table 1: 3). Small arrows point to osteocyte lacunae; small arrowheads indicate resorption lines; large white arrowheads indicate resorption lines between odontodes. Abbreviations as in Figure 7, with addition of: cs – circular structure; ds – dentine strips; LAG – line of arrested growth.







Wide canals of various (not only cylindrical) shape, distributed without apparent regularity, occur in both the dentine and the bone layer (Figs 7D, P–R; 8F, G). They can be parallel or oblique to the scale surface. These canals are always enclosed in centripetal bone of varying thickness, which includes concentrically oriented osteocyte lacunae (Fig. 7Q). The centripetal bone is composed of a succession of thin layers (lamellae), appearing alternately light and dark in cross-polarized light, and is clearly separated from the surrounding primary bone by one (Fig. 7A, D, P, R, F, G) or several (Fig. 7K) resorption lines. These structures remind of secondary osteons in bones of tetrapods and some sarcopterygians, and are indicative of remodeling of the bone.

**Remarks.** – Scales of *T. blumentalis* differ from *T. tverdochlebovi* in the more pronounced sculptural ridges (especially in the anterior part of the free field) and the larger average size of the scales.

**Occurrence.** – Uppermost Severodvinian (approximately from uppermost part of Kichuga Mb. on Sukhona River) and entire Vyatkian (to Permian–Triassic boundary) – numerous localities on the East European Platform.

### Genus *Evenkia* Berg, 1941

**Type and only species.** – *Evenkia eunoptera* Berg, 1941.

### *Evenkia eunoptera* Berg, 1941

Figures 9A–E; 10A–G, L, M

1941 *Evenkia eunoptera* Berg; Berg, p. 458, figs 1–6.

1985 *Evenkia eunoptera* Berg. – Selezneva, p. 73, fig. 2.

1999 *Evenkia eunoptera* Berg. – Sytchevskaya, p. 447, figs 2, 3.

**Material.** – Isolated scales, PIN collection no. 1876.

**Description.** – Area B (Fig. 9A, B): Rhombic scales of length equal to or slightly below their height. Anterodorsal corner well-developed, bent anteriorly. Anteroventral corner pronounced, pointed, directed anteriorly. Dorsal scale margin slightly concave at the level of the peg. Ventral margin slightly convex at the level of the socket. Posterodorsal corner rounded, posteroventral corner pointed. Anterior depressed field accounting for about  $\frac{1}{6}$  of scale length, with pore openings concentrated along its anterior, ventral and, less abundantly, dorsal margins. Peg triangular, with an indistinct vertical crest along its midline. Socket corresponding to the size of the peg. Keel flattened, located slightly anterior to peg and socket.

Anterior margin of the free field straight, not dissected. Free field smooth anteriorly. Posterior part of the ganoine

field sculptured with concentric, flattened rolls (especially distinctive in the ventral part) separated by shallow cannelures. The cannelures bear numerous small pores, arranged concentrically following growth lines of the scale. Posterior to the keel, numerous chaotically distributed apertures occur.

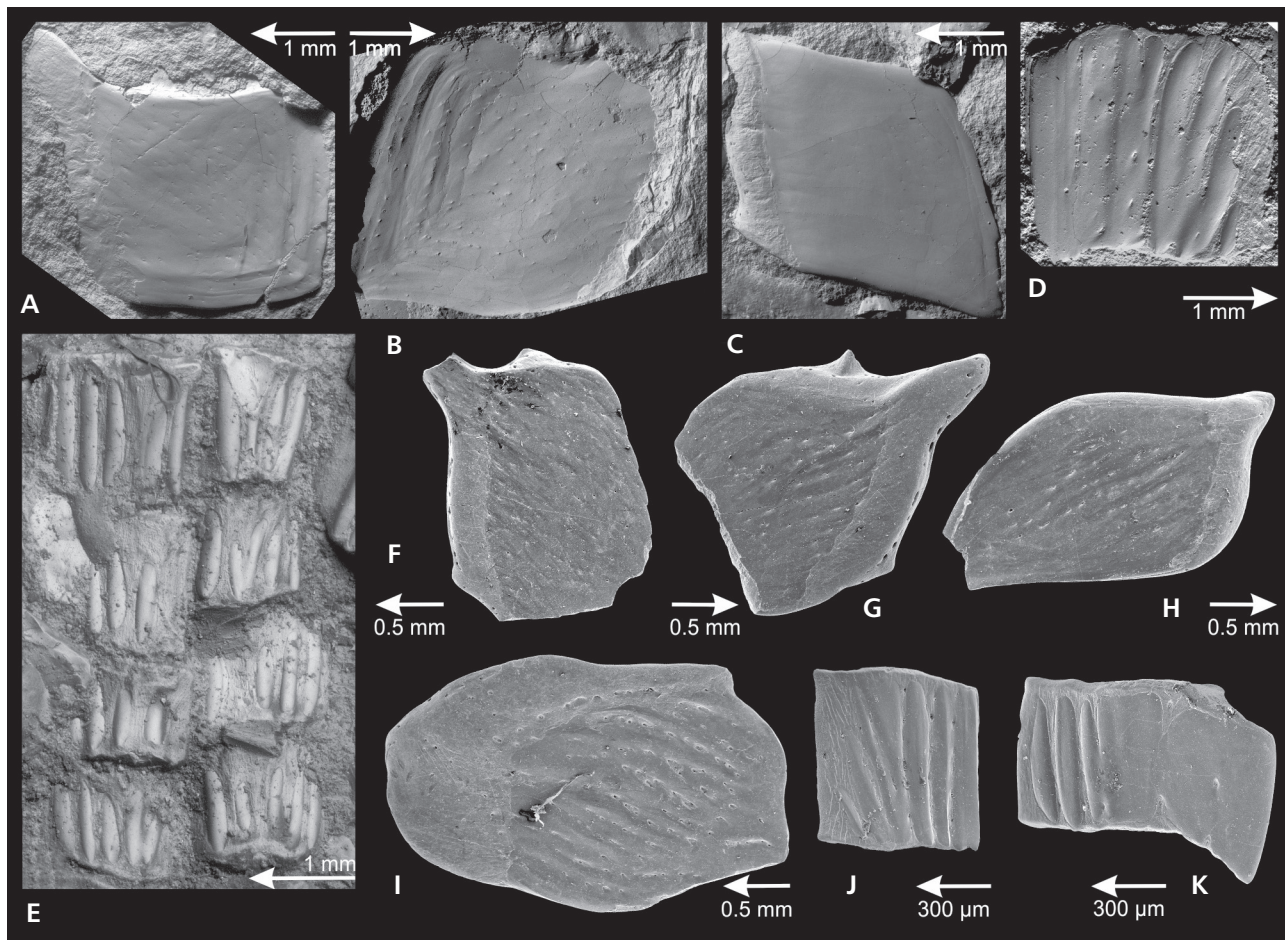
**Area C** (Fig. 9C): Scales of rhombic to nearly rectangular shape. Length 1.5–2 times exceeding height. Peg and socket very small or absent. Keel narrow, located anterior to peg and socket. Depressed field accounting for no more than  $\frac{1}{5}$  of scale length.

**Lepidotrichia segments** (Fig. 9D, E): Rectangular, small, thick hemisegments, whose height can distinctly exceed the length or vice versa. Posterodistal corner straight or extending distally. Margins straight. Keel flattened, located at mid-length of the hemisegment. Depressed field narrow, no more than  $\frac{1}{5}$  of segment length, or absent. Characteristic vertical ridges, rounded or rounded-triangular in cross-section, located in the anterior part of the free field. In the posterior part, they are replaced by a continuous, smooth ganoine field bearing pores. Segments at the base of the fin rays fused (with thickenings in places of fusion), with a wide depressed field along the anterior and the proximal margin.

**Vascular system:** Thin sections (Fig. 10A–G, L, M) show that vascular system canals lie at different levels, as in *Toyemia*. Probably, they also formed complex, three-dimensional junctions at different levels, giving rise to loops, bends, and branching points. Judging from their density, the canals were more flexuous, numerous and closely packed, than in *Toyemia*.

Parallel to the posterior and the ventral margin, growth lines separating odontode generations and the respective layers of bone and ganoine from one another are visible. In this part of the scale, the vascular canals mainly lie between the dentine and bone layers (although the canal lumen is usually fully enclosed in dentine). Concentric canals are present in every new generation of odontodes. Numerous large pores along the margin of the depressed field suggest that wide vascular canals were located underneath it as well. Generally, the histological structure of *Evenkia* scales is not much different from that in *Toyemia*.

**Remarks.** – Scales of *E. eunoptera* differ from both *Toyemia* and *Oshia* in the more pronounced anterodorsal and anteroventral corners. Furthermore, they differ from *Toyemia* in the less dissected, nearly smooth free field, especially in its anterior and dorsal part. From *Oshia*, they differ in the better development of the pointed anteroventral corner; a higher complexity and density of the vascular canals within the bone layer: the lack of diagonal and the presence of concentric ornamenting rolls; the regular distribution of pores in the posterior part of the free field and their chaotic scattering in the anterior part; the concave dorsal scale margin; and a more pronounced peg.



**Figure 9.** Squamation of Evenkiidae Selezneva, 1985, in crown view. • A–E – *Evenkia eunotoptera* Berg, 1941, Anakit locality (Table 1: 7); A – area B scale, PIN 1876/119; B – area B–C scale, PIN 1876/119; C – area C scale, PIN 1876/121; D – lepidotrichium hemisegment, PIN 1876/119; E – caudal fin lepidotrichia in articulation, PIN 1876/37. • F–K – *Oshia ferganica* Sytchevskaya, 1999, Madygen locality (Table 1: 8); F – area A scale, FG 596/III/220; G – area B–C scale, FG 596/III/221; H – area C scale, FG 596/III/222; I – area E scale, FG 596/III/223; J – lepidotrichium hemisegment, FG 596/III/224; K – lepidotrichium hemisegment, FG 596/III/225.

**Occurrence.** – Dvuroginsky Regional Stage, Bugarikta Fm., Early Triassic; Tunguska River basin, Central Siberia.

### Genus *Oshia* Sytchevskaya, 1999

**Type and only species.** – *Oshia ferganica* Sytchevskaya, 1999.

### *Oshia ferganica* Sytchevskaya, 1999

Figures 9F–K; 10H–K, N–P

1999 *Oshia ferganica* Sytchevskaya; Sytchevskaya, p. 458, fig. 8.

**Material.** – Isolated scales, PIN collection no. 3267, FG collection no. 596/III.

**Description.** – Area A (Fig. 9F): Rectangular scales, height 1.5–2 times exceeding length. Anterior margin

slightly concave at the anterodorsal and anteroventral corners, but convex in the central part. Anterodorsal corner well-developed, extended anteriorly and dorsally. Anteroventral corner less pronounced, slightly pointed and directed anteriorly. Dorsal scale margin convex, dorsal margin of the free field slightly concave at the level of the peg. Ventral margin slightly convex at the level of the socket. Posterior margin somewhat wavy, with wave crests pointing posteroventrally. Posterodorsal corner rounded, posteroventral corner acute. Anterior depressed field accounting for about  $\frac{1}{6}$  of the scale length, bearing numerous large pore openings concentrated along its anterior, ventral and, to a lesser extent, dorsal margin. Peg and socket triangular, of small size. Peg rather short, bearing a weakly developed vertical crest along the midline. Socket corresponding to the size of the peg. Keel flattened, located slightly anterior to peg and socket.

Anterior margin of the free field somewhat wavy, not dissected. Free field sculptured with low diagonal rolls,

starting at its dorsal and anterior margins and separated by shallow cannelures. Rolls most distinct close to the anterodorsal corner of the free field, flattening to form a continuous surface in the posterior part. Small pores located in the cannelures between the ridges, and distributed chaotically in the posterior part of the free field.

Area B, C (Fig. 9G): Rhombic scales, of length equal or slightly inferior to their height. Unlike in area A scales, a depressed field is developed not only anterior, but also dorsal to the free field. Anterodorsal corner pointing anteriorly, with a flat longitudinal crest and a rounded tip. Peg with an acute tip and an essentially vertical crest along the midline. Otherwise similar to area A scales.

Area C (Fig. 9H): Scales rhombic to rectangular, 1.5–2 times longer than high. Peg and socket small or lacking. Keel narrow, located anterior to peg and socket. Anterior depressed field accounting for no more than  $\frac{1}{5}$  of scale length.

Area E (Fig. 9I): Rounded-rectangular scales. Anterodorsal corner large, blunt and broad. Posterodorsal and posteroventral corners pronounced, slightly pointed. All margins convex. Peg and socket broad and short or lacking. Depressed field developed along the anterior and the dorsal margin, making up to  $\frac{1}{3}$  of the scale length. Free field rectangular, with a more distinct ornamentation than in other areas, consisting of diagonal rolls with numerous pores in between, opening towards posteriorly. The anterior and proximal margins of the free field have a more wavy outline than in other body areas.

Lepidotrichia segments (Fig. 9J, K): Straight, small, thick hemisegments, whose height can distinctly exceed the length or be much inferior to it. Posterodistal corner extended distally or straight. Margins straight. Small articulating elements, complex joint surfaces. Keel flattened, located at the middle of the length, with numerous apertures to both sides (especially posteriorly). Depressed field narrow – no more than  $\frac{1}{5}$  of the length – or lacking. Characteristic vertical and subvertical ridges, rounded or rounded-triangular in cross-section, in the anterior part of the free field. In the posterior part, the ridges are replaced by a continuous, smooth, pore-bearing ganoine field. At the base of the fin rays, segments are fused (fusion lines are developed as thickenings) and exhibit depressed fields along both the anterior and the proximal margins.

Ultrasculpture: Free field of the scales covered by small ( $>10\ \mu\text{m}$  in cross-section) tubercles. On the smooth central part of the free field, the tubercles have a rounded shape and a spacing of *ca.*  $10\ \mu\text{m}$  between their tips. On

the anterior margin of the ornamental ridges of the free field, in contrast, the tubercles are elongated, and stretched the stronger, the less even the surface is on which they are placed.

Vascular system (Fig. 10H–K, N–P): As in *Toyemia*, canals of the vascular system do not constitute a simple horizontal network, but lie on several levels. Most probably, they formed complex three-dimensional junctions on several levels, giving rise to loops, bends and branching points. The highest vascular canal concentration is seen along the contact of bone and dentine, while vertical and subvertical canals pass through the lower layer of the bone. Distributed underneath the whole free field, the canals open to the surface through chaotically scattered pore openings.

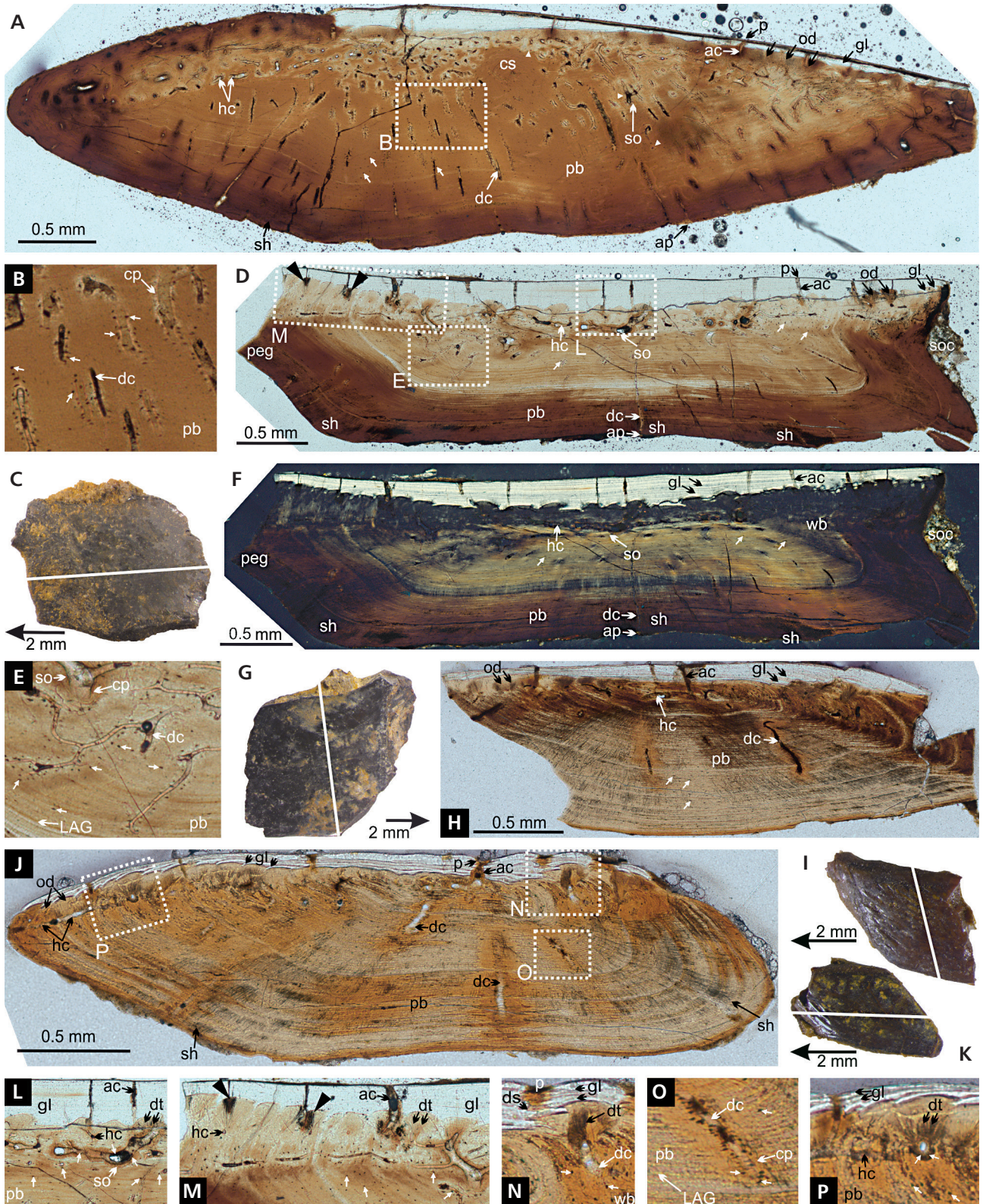
Parallel to the posterior and the ventral margins, growth lines are discernible in the peripheral part of the free field, separating from each other the successive generations of odontodes and the respective layers of bone and ganoine. In this part of the scale, the vascular canals mainly occur between dentine and bone (but the canal lumen is usually enclosed in dentine). As in *Toyemia*, ascending canals have a lining of dentine, more frequently than in *Toyemia* subdivided into small inlays ('Kosminleisten' *sensu* Aldinger, 1937) with ganoine layers wedged between them (Fig. 10L). Concentric canals are seen within each new generation of odontodes. Judging from the numerous large pores along the margin of the depressed field, wide vascular canals are probably located underneath the depressed field. In general, the histological structure of *Oshia* scales is similar to that of *Toyemia*.

**Remarks.** – Scales of *O. ferganica* differ from both *Toyemia* and *Evenkia* in the presence of distinct diagonal rolls, beginning from the anterior and the dorsal scale margins; the regular distribution of pores in the anterior part of the scale and their chaotic scattering in the posterior part; the convex dorsal scale margin; the less pronounced peg. Furthermore, they differ from *Toyemia* in the more rectangular shape of area A scales. From *Evenkia*, they differ in the less developed, anteriorly pointing anteroventral corner, and the lower density and complexity of the vascular canal branchings within the bone layer. In general, scales of *Oshia* appear to be most diagnostic and easily distinguishable from other evenkiids.

**Occurrence.** – Madygen Fm., Middle–Late Triassic boundary (Ladinian–Carnian boundary); Madygen locality, Fergana Valley, Batken Region, Kyrgyzstan.

**Figure 10.** Histological sections of scales of Evenkiidae Selezneva, 1985. • A–G, L, M – *Evenkia eunoptera* Berg, 1941, Anakit locality (Table 1: 7); A – horizontal section of area C scale PIN 1876/122 in linearly polarized light; B – magnified fragment of A showing descending canals, note numerous satellite cells surrounding the canals; C – scale in crown view before sectioning, with indication of the cutting plane; D – vertical section of area B scale PIN 1876/123 in linearly polarized light; E – magnified fragment of D, note numerous satellite cells surrounding the canals; F – vertical section of area B





scale PIN 1876/123 in cross-polarized light; G – crown view of scale before sectioning, with indication of the cutting plane; • H–N – *Oshia ferganica* Sytchevskaya, 1999, Madygen locality (Table 1: 8); H – vertical section of area C–F scale PIN 3267/300; I – scale in crown view before sectioning, with indication of the cutting plane; J – horizontal section of area C–F scale PIN 3267/301 in linearly polarized light; K – scale in crown view before sectioning, with indication of the cutting plane; L, M – magnified fragments of D, note the secondary osteons; N–P, magnified fragments of J. Small arrows point to osteocyte lacunae; large black arrowheads indicate probable recrystallized dentine. Abbreviations as in Figures 7 and 8.



## Discussion

Most Palaeozoic actinopterygians had a squamation formed by rhombic scales of the palaeoniscoid type (Aldinger 1937; Schultze 2016, 2018). Palaeoniscoid scales are composed of three types of tissue (from outside to inside): ganoine, orthodentine and bony base (Sire *et al.* 2009, Schultze 2016). The ganoine unit is usually thick and consists of several well-distinguishable layers showing birefringence (rodlet structure) in polarized light (Richter & Smith 1995). The dentine layer is formed by odontodes, which usually fuse into odontocomplexes – agglomerations or clusters of odontodes, deposited besides or above each other during successive growth phases. Numerous tubules (canaliculi) pass through the dentine layer (Sire *et al.* 2009). The bony scale base is quite thick and made of pseudolamellar (parallel-fibered) bone with abundant osteocyte lacunae. The vascular system of palaeoniscoid-type scales is represented by vertical (ascending and descending) canals opening through pores to the outer and apertures to the inner surfaces of the scale and passing through the ganoine and the bone layers, and a rich network of horizontal canals located between the dentine and bone layers (Goodrich 1907; Schultze 2016, 2018). Horizontal vascular system canals lie in the base of the odontodes, enclosed in dentine (Aldinger 1937). Palaeoniscoid-type scales articulate to each other by means of the ‘peg and socket’ articulation.

Knowledge on the dermal skeleton of fishes and fish-like vertebrates has greatly increased over the last decade. Thus, light has been shed on the origin and phylogenetic development of cosmine; the term cosmine, previously used only for the eucosmine of relatively advanced sarcopterygians, has been broadened; the possession of cosmine (but not eucosmine) has been demonstrated to be the primitive condition for osteichthyans, including actinopterygians; the three-dimensional structure and the formation mechanism of cosmine during ontogenesis has been reconstructed (Qu *et al.* 2013a, b, 2017; Jerve *et al.* 2016; Mondéjar-Fernández 2018; Mondéjar-Fernández & Meunier 2021). In contrast, ganoid scales (including the palaeoniscoid type) have received less attention than cosmoid scales. For this reason, the terminology for describing cosmoid scales is better elaborated than ganoid scale terminology. Furthermore, the homologies of the two scale types are not conclusively clarified, and the phylogenetic origin of ganoine remains obscure.

Qu *et al.* (2017) proposed that the horizontal canal network of palaeoniscoid-type scales is homologous to the cross canal system of sarcopterygians, while ascending canals and their pores might be homologous to cross canal openings to the scale neck. This hypothesis was supported by the topological similarity between the sarcopterygian cross canal system and the actinopterygian horizontal canal network. In sarcopterygians (Gross

1956, Qu *et al.* 2017, Mondéjar-Fernández 2018) and the basal osteichthyan *Andreolepis* (Gross 1968), the cross canal network is fully enclosed in bony tissue. In contrast, in most previously studied basal actinopterygians (Aldinger 1937), including the earliest unequivocal representative *Cheirolepis* (Zylberberg *et al.* 2016), as well as the Evenkiidae discussed herein, the horizontal canals are enclosed in dentine. Moreover, canaliculi radiate directly from the horizontal canals, which gives them more similarity with the pulp canals of *Andreolepis* than with its cross canals. It should be pointed out that the pore cavities in *Andreolepis* are ascending from the pulpal canal system. In early sarcopterygians, including *Psarolepis*, pore cavities are incorporated into a single enamel layer (Qu *et al.* 2016). Meanwhile, the same and further authors (Zhu *et al.* 2006, 2010; Giles *et al.* 2015; Lu *et al.* 2016; Mondéjar-Fernández 2018) noted that pore cavities in the basalmost actinopterygians *Meemannia* and *Cheirolepis* as well as in the basalmost actinistian *Styloichthys* pierce several enamel layers, which does not contradict considering this combination of tissues and pore-canal-system as cosmine. Unfortunately, the histology of *Meemannia* scales remains unknown and the structure of dermal bones is little informative for reconstructing the morphogenesis of ganoine, given that even in relatively derived basal actinopterygians such as *Birgeria*, *Scanilepis* or *Polypterus* (Ørvig 1978) the ‘ganoine’ layers on dermal bones are separated from one another by dentine and form no onion-like pattern, resembling more the cosmine of the dermal bones of *Meemannia* and *Cheirolepis* (apart from the pore-canal system) than the ganoine on scales of the same taxa. In our opinion, the ascending canals of the actinopterygian scales may well be homologues of the sarcopterygian pore cavities, and their horizontal canals may be homologous with the pulpal canals of *Andreolepis* or the mesh canals of derived sarcopterygians. Therefore, we use a functional terminology for describing the pore-canal network of actinopterygians.

When describing and depicting the first scales referable to *Toyemia*, Krotow (1904, pp. 7, 8, figs 3, 4) emphasized morphological similarity between these (purported crossopterygian) scales and those of the recent *Polypterus senegalus* Cuvier, 1829. Similarities in the histology of *Toyemia* and polypterid scales have been pointed out by Esin (1989, 1995). Based on scale morphology, A.V. Minikh (personal communication) considers *Toyemia* as ancestral to the scanilepiforms *Evenika* and *Oshia*. Currently, Scanilepiformes Sytchevskaya, 1999, comprise seven genera from Triassic deposits of the Northern hemisphere (in stratigraphic order): *Evenika* Berg, 1941, *Beishanichthys* Xu & Gao, 2011, *Fukangichthys* Su, 1978, *Oshia* Sytchevskaya, 1999, *Mizhilepis* Liu & Shen, 2006, *Tanaocrossus* Schaeffer, 1967, and *Scanilepis* Aldinger, 1937. All these taxa are characterized by a long-based

dorsal fin, undenticulated and little-ornamented scales with numerous large pores, and fin rays with short segments that carry pronounced longitudinal ridges. Data on scale histology have only been published for *Scanilepis* (Aldinger 1937, Schultze 1968, Ørvig 1978), which is also characterized by wide vascular canals, partly opening to the surface and surrounded by concentric lamellae and cellular bone.

Morphological characters shared by *Toyemia*, *Evenkia*, *Oshia* and the polypteriforms comprise the scale shape and ornamentation, the size and distribution of pores on the scales, the peg bearing a median crest (without trace of Sharpey's fiber attachment) that fits into a corresponding depression in the socket (Gemballa & Bartsch 2002, fig. 9), and the typical shape, ornamentation and histology of lepidotrichia segments. Scale histology and the features of the vascular system are discussed in the following.

Generally, the scales of *Toyemia*, *Evenkia* and *Oshia* described herein conform to the palaeoniscoid type, but exhibit some notable differences. In the investigated scales of scanilepiforms, dentine inlays in the ascending canals ('Kosminleisten', Figs 7E, 8L) occur less frequently than in most palaeoniscoid scales (Aldinger 1937). Probably, the ascending canals, just as the horizontal and descending ones, were subject to remodeling. In most cases, the dentine inlays, as well as the margins of ganoine wedged between them (Fig. 7M), have been resorbed and replaced by centripetally deposited bone (Figs 7F, P–S; 8G, U), and are only preserved in unaltered canals. This may be caused by the necessity of lumen widening in the growing scale. Presumed dentine recrystallization, observed in some *Toyemia* scales (Fig. 7A, D, S), has not been described earlier in ganoid scales. Nonetheless, even more distinct recrystallization occurs in other osteichthyans, e.g. in *Psarolepis* (Qu *et al.* 2013b).

The architecture of vascular canals of *Toyemia* is more complex than in palaeoniscoid scales: a part of the canals (the thinner, horizontal canals) lie within the dentine layer, the other part (the wider, three-dimensionally sinuous canals) – usually within the bone layer, where vascular canals form three-dimensional junctions. Wide canals represent secondary osteons (Figs 7D, F–R; 8F, G), enclosed in concentric bone layers, that formed by remodeling of bone and dentine (evidenced by the resorption lines). Secondary osteons frequently occur in the scales of various sarcopterygians and tetrapods (Zylberberg *et al.* 2010, Witzmann 2011, Mondéjar-Fernández & Clément 2012). In palaeoniscoid scales of basal actinopterygians, in contrast, secondary osteons are very rare (although they do occur in dermal bones) and have been only positively reported in *Plegmolepis groenlandica* (Aldinger 1937). We suggest that in palaeoniscoid (and polypteroid) scales, secondary osteons only occurred in relatively old individuals, which were rather rare in populations. This assumption is confirmed by the fact that most secondary osteons in the

material studied by us were observed in the largest scales with the highest number of odontode generations (Figs 7D, F–R; 8F, G). If true, this might explain why secondary osteons have only been described in a small number of basal actinopterygians.

Secondary osteons may be present in Polypteridae. In the dentine layer of *Dajetella sudamericana* Gayet & Meunier, 1992, primary and secondary denteons have been observed (Gayet & Meunier 1992), which are reminiscent of the secondary canals in the dentine layer of Evenkiidae. While in *Dajetella* these structures only occur in the dentine layer, there is no difference between the wide canals of Evenkiidae in the dentine and in the bone layer (including the tissue forming them, which, in our opinion, is of osteogenic origin). We propose that the 'secondary denteons' of *Dajetella* may also be secondary osteons.

Furthermore, while in most basal actinopterygians, the vascular canals only lie underneath the sculptural ridges of the free field (Aldinger 1937), in *Toyemia*, *Evenkia* and *Oshia*, as in *Polypterus*, large and wide canals occur as well underneath the depressed field, opening to its surface through large pores. Compared to palaeoniscoid scales, a more complex pore-canal system has been documented in several scanilepiforms (Aldinger 1937, Giles *et al.* 2017).

Osteocyte lacunae ('satellite cells') are concentrated around the primary vascular canals. This structure of vascular canals has first been described in *Scanilepis* (Aldinger 1937, Schultze 1968, Ørvig 1978), where the 'satellite cells' are separated from the lumen by a layer of centripetally deposited bone (Schultze 1968) – just as in the here discussed Evenkiidae. It is worth noting that the number and the density of 'satellite cells' in *Scanilepis* scales is much higher than in *Toyemia*, while *Evenkia* and *Oshia* occupy an intermediate position for this character. Osteocyte concentration around vascular canals has also been observed in scales of the recent *Polypterus* (Schultze, 1966, 1968), but is unusual for palaeoniscoid-type scales.

A bony base consisting of pseudolamellar (parallel-fibered) cellular bone is typical for rhombic scales (Aldinger 1937, Kerr 1952, Schultze 1968, Ørvig 1978, Bakaev & Kogan 2020, Ivanov *et al.* 2021), although this type of tissue has not been distinguished in the early works. There is some controversy related to this part of the scale. Some authors refer to this layer as 'isopedine' (Schultze 2016, 2018), while others reserve this term for true lamellar bone (Zylberberg *et al.* 2010, Mondéjar-Fernández 2018). We refrain from using the term 'isopedine', since it has been originally proposed by Pander (1856) for describing lamellar bone (Mondéjar-Fernández & Meunier 2021). The osteogenesis of parallel-fibered bone advances slower than that of woven-fibered bone, but leads to more regular, anisotropic distribution of collagen fibers (Francillon-Vieillot *et al.* 1990). Woven-fibered bone usually forms at early ontogenetic stages (Francillon-Vieillot *et al.* 1990), so it is expected to occur

in the oldest, central part of a scale. This pattern has been reported for some basal actinopterygians, such as *Plegmolepis groenlandica*, depicted by Aldinger (1937, text-fig. 20, pl. 18), where in the middle part of the scale (on the left side of the figure) LAGs are lacking, osteocyte lacunae are chaotically scattered, not flattened, and some are shown in a stellar shape. In contrast, in evenkiid scales the woven-fibered bone is located underneath the youngest, most distal odontodes, which points to either a slower scale growth during early ontogeny or resorption and remodeling of bone under the older odontodes, and a fast growth in the adult fish.

Despite the similarity to polypteroid scales, scales of Evenkiidae do not exhibit the highly characteristic layer of plywood-like tissue, usually termed ‘elasmodine’ (Sire *et al.* 2009). However, an enigmatic circular structure is present in evenkiid scales in nearly the same position as the elasmodine layer in the scales of *Polypterus*, well-visible in scales of *Evenkia* (Fig. 10A) and especially *Toyemia* (Figs 7; 8A, D, M, N, P, R), but not observed in *Oshia* (Fig. 10J). This might either be explained by the fact that the sectioned *Oshia* scale comes from a posterior body region, or by the location of the section that did not cut the circular structure. We hypothesize that the elasmodine layer of polypteroid scales might be derived from the interwoven collagen fibers of this circular structure in scales of evenkiids. To test this hypothesis, and to trace the evolution of polypteroid scales, more studies on intermediate forms are needed. A stratigraphic gap of *ca.* 100 million years is still to close, as the latest currently known scanilepiforms date from the Late Triassic (Rhaetian) of Sweden (Aldinger 1937, Lehman 1979) and the USA (Schaeffer 1967, Schaeffer & McDonald 1978), while the earliest known polypteriforms come from the Late Cretaceous (Cenomanian) of Africa (Gayet *et al.* 2002, Grandstaff *et al.* 2012).

## Conclusion

The little-known actinopterygian taxon *Toyemia* Minich, 1990, from the continental late Permian of European Russia possessed characteristic scales and fin rays, used as index fossils for biostratigraphy. Morphological and histological similarities of these structures to representatives of Scanilepiformes, an essentially freshwater group of Triassic actinopterygians with well-established polypteriform affinity (Giles *et al.* 2017), as well as to the extant *Polypterus*, support our earlier interpretation of *Toyemia* as the oldest known scanilepiform (Bakaev *et al.* 2017, 2020; Kogan & Bakaev 2019). The appearance of *Toyemia* in the fossil record coincides with a shift in aquatic ecosystems – the so-called Severodvinian biotic crisis – which has been explained by a tectonically induced fractioning and restriction of aquatic habitats on a regional

scale. If scanilepiforms and their allied taxa possessed the polypterid-specific ability to breathe atmospheric oxygen, this may have contributed to their success under the restricted environmental conditions during the Permian.

We suppose that the higher complexity of the vascular system in the scales of *Toyemia* and the Triassic scanilepiforms, when compared to the palaeoniscoid-type scales, is a secondary acquisition illustrating the evolutionary pathway towards the polypteroid scale. The ‘circular structure’ with its crossing pattern of collagen fibers, observed in scales of *Toyemia* and *Evenkia*, may be a predecessor of the elasmodine layer, which occupies the same topological position in polypteroid scales.

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