

Late Permian Discordichthyiformes (Osteichthyes) from European Russia

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Abstract—New Late Permian fishes combining features characteristic of several classes are analyzed and redescribed. They were assigned to the family Discordichthyidae of the order Discordichthyiformes comprising three genera and four species: *Mutovinia stella* Minich, *Geryonichthys longus* A. Minich, *G. burchardi* A. Minich, and *Discordichthys spinifer* A. Minich (Minikh, 1998). A new species, *Mutovinia sennikovi* sp. nov., is described. Due to rapid evolutionary replacement, discordichthyids are rather useful stratigraphically. The photographs of the skeleton and membrane bones of these fishes are published for the first time.

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Key words: Discordichthyiform fishes, Late Permian, European Russia, scale, bones.

INTRODUCTION

In the early 1970s, I found isolated skeletal elements of fishes with unusual surface sculpturing composed of rounded, star-shaped, and elongated ganoin tubercles in the Tatarian beds (Upper Permian) of northern European Russia. The large, high scales with star-shaped tubercles from the Late Tatarian Mutovino locality on the Sukhona River in the Vologda Region were described by Minikh (1992) under the name *Mutovinia stella* and identified as the cover of high-bodied platysomids of the order Platysomiformes. In 1984, the anterior half of a fish body with a tuberculate bone sculpturing was found in Urzhumian limestones of the Kichkas locality (Orenburg Region), which was unique among the abundance of fish skeletons. This skeleton retains fin spines, scales, bony plates, scutes, and jaws with large conical teeth terminating in small transparent apices.

At the end of the 20th century, new fishes similar in morphology and bone structure were found during the survey and thematic work in the Upper Tatarian beds of northern and southeastern European Russia. The material included abdominal and dorsal fin spines, distal segments of pectoral fins, bones of the pectoral girdle, scales, bony plates, and membrane bones of the skull. More than twenty years of study of these fishes resulted in a number of reports and papers by the present author (Minikh, 1996, 1998, 2001). To date, three genera and four species of these fishes, i.e., *Mutovinia stella* Minich, *Geryonichthys longus* A. Minich, *G. burchardi* A. Minich, and *Discordichthys spinifer* A. Minich have been described and assigned to the family Discordichthyidae of the order Discordichthyiformes. Based on

the structure of membrane skull bones, jaws, and scales, this order is assigned to the class Osteichthyes.

In 2003, A.G. Sennikov made some fish bones from the Vyazniki-2 locality of the Vladimir Region available to me for identification. They included a particularly interesting large scale, which was assigned to a new species of the genus *Mutovinia*. This species is described below; in addition, refined descriptions of the previously known species and genera of Discordichthyidae are provided. Photographs of membrane skull bones, fin spines, and scales produced by M.G. Minikh are published for the first time.

On April 8, 2005, a new stratigraphic chart for the Permian System was adopted by the Bureau of the International Stratigraphic Committee. The third (Tatarian) series, including the Severodvinian and Vyatikian stages, was introduced. The former Lower Tatarian Substage is presently named the Urzhumian Stage and included in the new Biarmian Series of the Permian. In the present paper, the new divisions of the Permian are accepted.

SYSTEMATIC PALEONTOLOGY

Order Discordichthyiformes A. Minich, 1998

Type family. Discordichthyidae A. Minich, 1998.

D i a g n o s i s. Fish with blunt snout and large, conical gripping teeth. Two dorsal fin spines present; some taxa with abdominal spines. Pectoral fins possibly partially enclosed in bone shield. Scale cover of anterior upper region of body formed of high overlapping scales. One or several rows of elongated overlapping

scales with longitudinal symmetry located along midline of body; rest of surface covered with bony plates. Membrane skull bones, scales, and fin spines ornamented with high, hollow ganoin tubercles.

Composition. One family.

Comparison. The combination of characters including the presence of dorsal and abdominal fin spines, bone segments of the pectoral fins, large gripping teeth with transparent apices, and unusual body cover of scales and bony plates distinguishes the new order from all known orders of the class Osteichthyes.

Occurrence. Upper Permian of the East European Platform.

Family *Discordichthyidae* A. Minich, 1998

Diagnosis. Dorsal fin spines extending rather deep into body and covered laterally and posteriorly with high thick tubercles. Posterior edge lacking serration. Abdominal fin spines (if present) containing long and deep longitudinal grooves for fins. Distal bony segments (spines) of pectoral fins asymmetrical, thornlike, with ventrally open longitudinal cavity. Jaw dentition composed of series of large, closely positioned, transversely compressed conical teeth with transparent apices and series of smaller labial teeth. Body covered with ganoin scales, scutes, and bony plates.

Generic composition. Three genera: *Mutovinia* Minich, 1992; *Discordichthys* A. Minich, 1998; and *Geryonichthys* A. Minich, 1998.

Occurrence. Upper part of the Biarmian Series and the Tatarian Series of the East European Platform.

Genus *Discordichthys* A. Minich, 1998

Discordichthys: A. Minich, 1998, p. 53.

Type species. *D. spinifer* A. Minich, 1998.

Diagnosis. Small fishes with blunt snout and two dorsal fin spines. Operculum triangular. Orbit bordered posteriorly by three longitudinally extended postorbitalia. Jaws with series of large, conical, closely positioned lingually curved teeth with transparent apices and series of small teeth on external margin. Ichthyodorulites ornamented with several almost regular longitudinal rows of long, high, dorsally rounded tubercles; interridge spaces relatively wide. In anterior dorsal part of body, scales high, widely overlapping, longitudinally extended at midline of body, symmetrical; rest of body covered with scales and bony plates varying in size. Surface sculpturing of bones and scales composed of high tubercles varying in size and shape.

Species composition. Type species.

Comparison. *Discordichthys* differs from *Mutovinia* Minich and *Gerionichthys* A. Minich in the minor structural features and ornamentation of fin spines and surface sculpturing of membrane bones. In addition, it differs from *Gerionichthys* in the shape of the operculum and postorbitale.

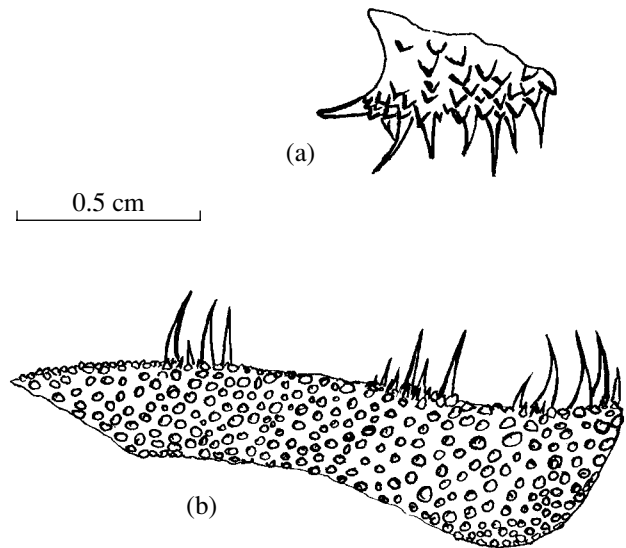


Fig. 1. Fragments of jaw bones of *Discordichthys spinifer* A. Minich, holotype SGU, no. 104-B/B-1: (a) rostro-praemaxillare and (b) anterior region of the lower jaw with teeth.

Discordichthys spinifer A. Minich, 1998

Plate 16, figs. 1–6

Discordichthys spinifer: A. Minich, 1998, p. 54, pl. 1, fig. 1.

Holotype. SGU, no. 104-B/V-1, incomplete skeleton; Orenburg Region, Perevolotskii District, Kichkas locality; Upper Permian, Biarmian Series, Urzhumian Stage, upper part of the Amanak Formation.

Description (Fig. 1). The specimen is 110 mm long, the greatest body depth is in line with the anterior dorsal spine (45 mm). Cranial bones are represented by the hyomandibulare, rostro-praemaxillare, operculum, mandibulare, postorbitalia, and fragments of unidentified bones.

The hyomandibulare (Pl. 16, fig. 4) curves slightly and narrows somewhat at the middle. Its dorsal margin is overlapped by the operculum, which is in the shape of a low isosceles triangle. The operculum (Pl. 16, fig. 4) is ornamented with very high tubercles. In the central part of the bone, they are large and rounded; towards the bone edges, they become smaller, thinner, and pointed and change in shape from triradiate to pointed odontoid. The upper and anteromedial margins of the bone lack ornamentation. The anterior margin contains small rounded foramina, which probably open a sensory canal. Three postorbitalia form two-thirds of the posterior upper border of the orbit. These bones are small, longitudinally extended and have the same ornamentation as the operculum.

In the lower jaw (Fig. 1b; pl. 16, fig. 2), the upper margin is straight, while the proximal and distal regions are ventrally widened. The dentition consists of large, closely positioned, transversely compressed, strongly pointed, and lingually curved teeth with tiny enamel apices. A series of small teeth extends along the labial

margin. The mandibulare is covered with high, rounded, needle-shaped or hooked ganoin tubercles varying in size. The rostro-praemaxillare has similar teeth and ornamentation of ventrally pointed tubercles (Fig. 1a; Pl. 16, fig. 2).

The dorsal fin spines are bilaterally symmetrical (Pl. 16, fig. 3), relatively wide at the base. Their lateral surfaces are almost completely (except for the immersed area at the anterior lower end) ornamented with several (5 or 6) longitudinal rows of high, elongated-oval tubercles. The posterior edges of the tubercles are much higher than the anterior edges. A longitudinal groove extends up to two-thirds of the spine extent; the rest of the caudal surface of the spine is covered with the same ornamentation as the lateral sides.

Because of incomplete preservation of the skeleton, it is difficult to reconstruct the position of scales on the body. It is evident that, below the anterior ichthyodorulite, there were several rows of high and large scales (11 vertical and four horizontal rows are preserved; Pl. 16, fig. 4), which were similar in shape to the scales of high-bodied platysomiform fish. These scales have a large anterior articular facet, a nonserrated posterior edge, and a stout articular spine, the base of which is equal to the length of the scale. The spine base of many scales is pierced by one or two small foramina. The ornamentation of the free area is composed of very high, usually posteriorly pointed tubercles varying in size and shape. Long and relatively low symmetrical scales, with a considerably anteriorly extended articular spine and broad lateral articular facets (Pl. 16, fig. 6), are located at the midline of the body. Other scales and bony plates, the position of which on the body is not entirely known, vary in shape from rounded to polygonal. They also widely vary in size and area of overlapped surface. Many scales are convex. The ornamentation is always composed of high, pointed tubercles varying in size (Pl. 16, fig. 5) and sometimes overhanging the posterior margin of the scale.

M a t e r i a l. Holotype.

Genus *Mutovinia* Minich, 1992

Mutovinia: Minikh, 1992, p. 144; A. Minikh, 1998, p. 49.

T y p e s p e c i e s. *Mutovinia stella* Minich, 1992.

D i a g n o s i s. Fish up to 70 cm long. Dorsal fin spines straight, with broad base and roundly narrowed distal end, immersed rather deeply. Scales large, high, overlapping. Bony segment of pectoral fin pointed distally and containing deep longitudinal cavity. Supraorbital-postorbital with slightly concave orbital margin. Scales, ichthyodorulites, and membrane bones of skull

and pectoral girdle ornamented with high ribbed tubercles.

S p e c i e s c o m p o s i t i o n. *M. stella* Minich and *M. sennikovi* sp. nov. from the Tatarian Series of European Russia.

C o m p a r i s o n. *Mutovinia* differs from all other genera of the family in the shape of the distal segment of the pectoral fin and supraorbital-postorbital and in the ornamentation of membrane bones.

R e m a r k s. The genus *Mutovinia* was originally described based on isolated scales from the Tatarian beds of the Upper Permian of European Russia (Minikh, 1992) and referred to high-bodied actinopterygians of the family Platysomidae Young. This was supported by the similarity in scale morphology. Additional material enables a new hypothesis for the taxonomic position of this fish to be developed.

Mutovinia stella Minich, 1992

Plate 17, figs. 1–4

Mutovinia stella: Minikh, 1992, p. 145, pl. 2, fig. 3; A. Minikh, 1998, p. 50, pl. 1, figs. 2a and 2b.

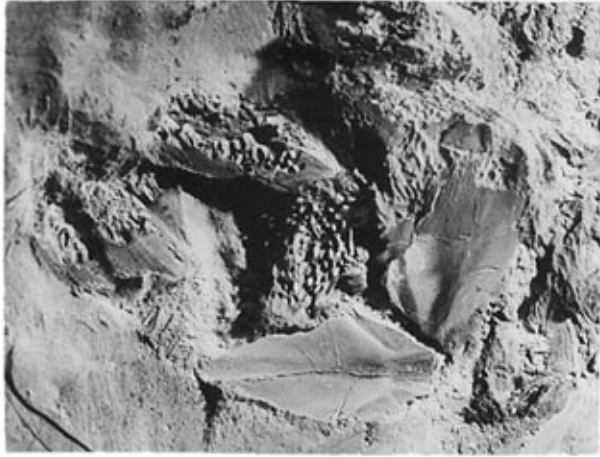
H o l o t y p e. SGU, no. 104-B/1102-1, scale; Vologda Region, Velikoustyugskii District, Mutovino locality; Upper Permian, Tatarian Series, Severodvinian Stage, Poldarsa Formation.

D e s c r i p t i o n. Medium-sized fish. The posterior margin of scales is smooth; the free area, which is not overlapped by neighboring scales, is three times as large as the anterior area covered by scales. The base of the articular spine is equal to the scale length. The ornamentation of the free surface is composed of numerous large, widely spaced tubercles, which are supplemented at the periphery by ridges in the shape of sharpened rays. The supraorbital-postorbital (specimen SGU, no. 104-B/1325-8; Pl. 17, fig. 4) is flattened, with a slightly concave anterior margin and a convex posterior margin. Its internal surface has a relatively deep, short depression in the lower part of the orbital margin. This depression was probably articulated with the underlying infraorbital, which has not yet been recorded. The ornamentation on the anterior and lower parts of the supraorbital-postorbital consists of high serrated bracket-shaped tubercles, which are replaced on the rest of the surface by star-shaped tubercles.

The pectoral fin was probably enclosed in a bony shield (specimen SGU, no. 104-B/1325-5; Pl. 17, figs. 2a–2c). This is evident from the presence of bony elements in the shape of strongly convex spines resembling in appearance the spinalia of placoderms. These bony elements are assymmetrical, expanded proxi-

Explanation of Plate 16

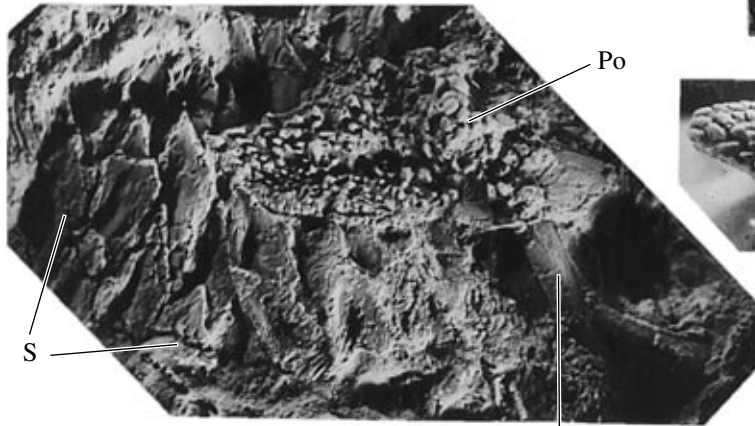
Figs. 1–6. *Discordichthys spinifer* A. Minich, holotype SGU, no. 104-B/V-1: (1) skeleton, $\times 1.3$; (2) lower jaw and premaxilla, $\times 2.3$; (3) anterior dorsal fin spine, lateral view, $\times 4.3$; (4) fragment of scale cover in the anterior part of the body (*s*), operculum (*Po*), and hyomandibulare (*Hm*), $\times 4.2$; (5) scales and bony plates, $\times 5$; and (6) scales of the lateral row, $\times 4$; Orenburg Region, Perevolotskii District, Kichkas locality; Biarmian Series, Urzhumian Stage, Amanak Formation.



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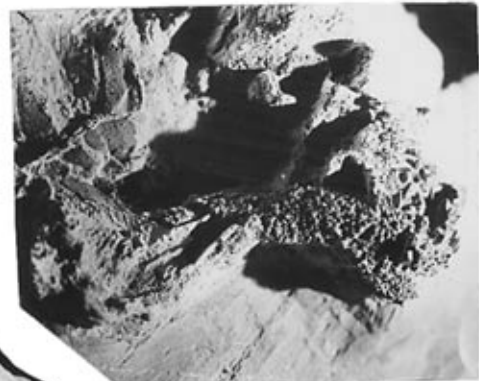
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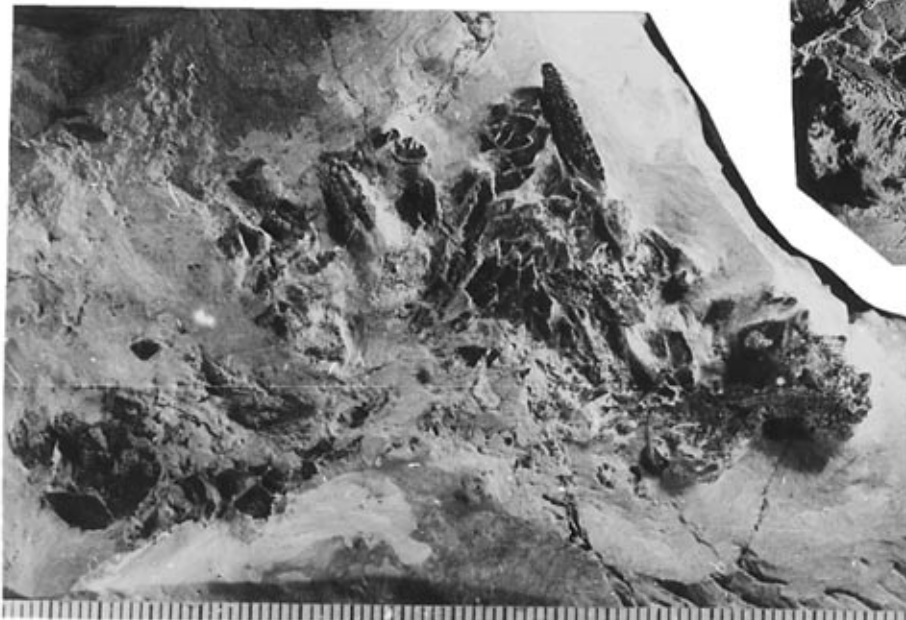
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1

mally, and claw-shaped, with a convex dorsal surface, in lateral view. There is a deep, caudally open cavity.

The dorsal fin spines (specimen SGU, no. 104-B/938; Pl. 17, fig. 3) resemble in shape the ichthyodorulites of hybodont sharks. They are rather massive, slightly convex anterodorsally, and have widely spaced lateral sides. The ornamentation consists of tubercles of two types; the dorsal surface is covered with large smooth tubercles irregular in shape, while the lateral surface has star-shaped tubercles. Distally, the spines taper gradually to a blunt rounded tip. The pulp groove extends for two-thirds of the spine extent, the distal third of its caudal surface is covered with star-shaped tubercles.

Measurements, mm. Spines: specimen SGU, no. 104-B/938: length, 28; greatest width, 6; greatest thickness, 5; specimen SGU, no. 104-B/939: length, 45; width, 9; both specimens come from the type locality.

Occurrence. Upper Permian, Tatarian Series, upper part of the Severodvinian Stage and the Vyatkian Stage of European Russia.

Material. In addition to the holotype, numerous membrane bones and scales from several localities of the Vologda Region: type locality and Ust'e Strel'ny (specimens SGU, nos. 104-B/2611, 2613); Salarevo (SGU, nos. 104-B/1332-6, 1336-1, 1339); Monastyr-ikha (SGU, no. 104-B/1335); Mikulino-2 (SGU, no. 104-B/1323-2); and Navoloki (SGU, no. 104-B/1341); in the Orenburg Region: Preobrazhenka locality (SGU, no. 104-B/1399) and Boevaya Gora locality (SGU, no. 104-B/2649).

Mutovinia sennikovi A. Minich, sp. nov.

Plate 17, fig. 14

Etymology. The species is named in honor of the paleontologist Andrei G. Sennikov, who collected the type material.

Holotype. SGU, no. 104-B/2984, scale; Vladimir Region, Vyaznikovskii District, Vyazniki-2 locality; Upper Permian, Tatarian Series, upper part of the Vyatkian Stage.

Description. A relatively large fish. The scales are high and flat, with a smooth posterior margin. A small articular spine with a wide base is pierced by three small foramina, which open the sensory canal. The anterior articular surface of the scale is very small. The membrane bones and free field on the scales are densely covered with flattened wedge-shaped tubercles, which are pointed posteriorly and ventrally. The wide anterior margin of these tubercles has several fine, thin ridges. A large articular fossa on the internal surface of the scale extends for one-third of its height. The ichthyodorulites are large, with the walls widely spaced proximally. They are ornamented with large, rounded or wedge-shaped tubercles; the wedge-shaped tubercles have ridges.

Measurements, mm. Scale height, 25; scale length, 8.

Comparison. The new species differs from *M. stella* Minich in the larger size, the shape of scales, and in the ornamentation of the bone surface.

Occurrence. Upper Permian, Tatarian Series, upper part of the Vyatkian Stage of the Vladimir Region.

Material. In addition to the holotype, fragments of membrane bones and ichthyodorulites from the type locality, specimens SGU, nos. 104-B/2971-1 and 104-B/2971-2; specimens SGU, nos. 104-B/2931-2a and 104-B/2931-2b from the Gorokhovets locality, Vladimir Region; and specimen SGU, no. 104-B/3001 from the Zhukov Ovrag locality, Vladimir Region.

Genus *Geryonichthys* A. Minich, 1998

Geryonichthys: A. Minich, 1998, p. 51.

Type species. *Geryonichthys longus* A. Minich.

Diagnosis. Medium-sized fish. Operculum irregularly quadrangular, with height slightly greater than length. Posterior infraorbitale high and narrow. Supraorbito-postorbitale convex medially, with abruptly concaved orbital margin and rounded convex upper margin. Cleithrum composed of rounded convex dorsal plate and large triangular process. Ichthyodoru-

Explanation of Plate 17

Figs. 1–4. *Mutovinia stella* Minich: (1) holotype SGU, no. 104-B/1102-1, scale, $\times 3$; (2) specimen SGU, no. 104-B/1325-5, distal element of the pectoral fin, $\times 3$: (2a) lateral, (2b) ventral, and (2c) dorsal views; (3) SGU, no. 104-B/938, dorsal fin spine, lateral view, $\times 3$; and (4) SGU, no. 104-B/1325-8, supraorbito-postorbitale, $\times 3$; Vologda Region, Velikoustyugskii District, Mutovino locality; Tatarian Series, Severodvinian Stage, Poldarsa Formation.

Figs. 5–10. *Gerionichthys longus* A. Minich; Vologda Region; Tatarian Series, Severodvinian Stage, Poldarsa Formation: (5) specimen SGU no. 104-B/940, dorsal fin spine, lateral view, $\times 3$; (6) holotype SGU, no. 104-B/898, abdominal fin spine, lateral view, $\times 3$; (7) specimen SGU, no. 104-B/1325-4, infraorbitale, $\times 3$; (8) SGU, no. 104-B/1325-1, operculum, $\times 3$; (9) SGU, no. 104-B/1325-6, bone element of the pectoral fin, dorsal view, $\times 3$; Mutovino locality; and (10) SGU, no. 104-B/1323-5, cleithrum, $\times 1.5$; Mikulino locality.

Figs. 11–13. *Gerionichthys burchardi* A. Minich: (11) specimen SGU, no. 104-B/1320-1, supraorbito-postorbitale, $\times 3$; (12) SGU, no. 104-B/1320-6, distal element of the pectoral fin, $\times 3$; and (13) holotype SGU, no. 104-B/1320-4, dorsal fin spine, $\times 3$; Orenburg Region, Grachevskii District, Babintsevo locality; Tatarian Series, upper part of the Severodvinian Stage.

Fig. 14. *Mutovinia sennikovi* sp. nov., holotype SGU, no. 104-B/2984, scale, $\times 3$; Vladimir Region, Vyaznikovskii District, Vyazniki-2 locality; Tatarian Series, upper part of the Vyatkian Stage.



lites and long fin spines on abdomen and relatively short prominent spines of pectoral fin present. Ornamentation of bones composed of high oval tubercles.

Species composition. Type species and *G. burchardi* A. Minich, 1998 from the Severodvinian and Vyatkian stages of the Upper Permian of Eastern Europe.

Comparison. *Geryonichthys* differs from *Mutovinina* Minich and *Discordichthys* A. Minich in the presence of abdominal fin spines and ornamentation of membrane bones. In addition, it differs from *Discordichthys* in the triangular shape of the operculum and from *Mutovinina* in the structural features of the supraorbito-postorbitale.

Geryonichthys longus A. Minich, 1998

Plate 17, figs. 5–10

Geryonichthys longus: A. Minikh, 1998, p. 51, pl. 1, figs. 3a and 3b.

Holotype. SGU, no. 104-B/898, abdominal fin spine without distal end; Vologda Region, Velikoustyugskii District, Mutovino locality; Upper Permian, Tatarian Series, Severodvinian Stage, Poldarsa Formation.

Description. The abdominal fin spines are long, wide, slightly curved, and asymmetric (holotype; Pl. 17, fig. 6). The proximal end of the spine is hyperbolic in cross section. The spine is hollow; a deep longitudinal groove for the fin reached its distal end. The lateral surfaces are ornamented with numerous, rather high, narrow, elongated, and externally flattened tubercles of irregular shape and irregular arrangement. The tubercles are larger on the anterior margin and smaller at the periphery. The tubercles are hollow and pointed caudally. Judging from the width (2 to 8 mm) and extent of the nonornamented area, which is at most one-fourth of the bone length, the spines were only slightly immersed.

The dorsal fin spines are triangular in lateral view (SGU, no. 104-B/940; Pl. 17, fig. 5). Their lateral surfaces are ornamented with seven or eight irregular rows of high elongated tubercles varying in size. The distal area of the caudal surface has similar tubercles.

The operculum is convex, trapezoid (SGU, no. 104-B/1325-1; Pl. 17, fig. 8). Its height is slightly greater than the length; the anterior edge is almost straight, while the corners are slightly attenuate and rounded. The ornamentation is formed of numerous high oval ganoin tubercles, which are relatively widely spaced. The infraorbitale is high, medially convex, with a large articular facet (SGU, no. 104-B/1325-4; Pl. 17, fig. 7). The ornamentation is formed of dorsally flattened tubercles, which are relatively large and rounded in the central zone of the bone and become narrower at the periphery.

In the pectoral girdle, only one bone, presumed cleithrum, in preserved (specimen SGU, no. 104-B/1323-5).

This bone is complex in shape and consists of a rounded, slightly convex plate ornamented with elongated tubercles and a large long process attached to the internal side on the plate at an almost right angle. The process is thin, triangular in lateral view; its base occupies almost the entire extent of the long diagonal of the cleithrum plate. The internal surface of the process has a longitudinal median crest. At the base, in the area of contact with the margin of the plate, the process is ornamented with elongated tubercles.

The bone segment of the pectoral fin (specimen SGU, no. 104-B/1325-6; Pl. 17, fig. 9) is rather strongly convex and has a deep longitudinal cavity. Near the cavity, its lateral walls curve laterally. The surface is ornamented with high, elongated, flattened, irregularly arranged tubercles.

Occurrence. Upper Permian, Tatarian Series, Severodvinian and Vyatkian stages of European Russia.

Material. In addition to the holotype, scales and bones from the type and some other localities in the Vologda Region: specimens SGU, nos. 104-B/2936-3 and 104-B/2872-2 from the Mutovino locality; SGU, nos. 104-B/1323-5 and 104-B/1392-1 (Mikulino-2 locality); SGU, nos. 104-B/1387–1389 (Poteryakha locality); SGU, nos. 104-B/R-157 and 104-B/1322-12 (Strel'na locality); and SGU, no. 104-B/2918 (Salarevo locality); from the Vladimir Region: SGU, no. 104-B/2931-1a (Gorokhovets locality); and from the Orenburg Region: SGU, nos. 104-B/1383 and 104-B/2743 (Preobrazhenka locality); SGU, no. 104-B/1623 (Baleika locality); SGU, nos. 104-B/2911 and 104-B/2919 (Yashino-1 locality); and SGU, nos. 104-B/1324-13 and 104-B/1799 (Kul'chumovo locality).

Geryonichthys burchardi A. Minich, 1998

Plate 17, figs. 11–13

Geryonichthys burchardi: A. Minikh, 1998, p. 53, pl. 1, fig. 4.

Holotype. SGU, no. 104-B/1320-4, large fragment of the dorsal fin spine; Orenburg Region, Grachevskii District, Babintsevo locality; Upper Permian, Tatarian Series, upper part of the Severodvinian Stage.

Description. The dorsal fin spine has a slightly convex anterodorsal margin and a long and deep longitudinal groove. The lateral surfaces and a large area on the caudal surface of the distal end of the spine are ornamented with 10 to 12 closely and almost regularly positioned longitudinal rows of narrow elongated tubercles.

The supraorbito-postorbitale is prominent medially (specimen SGU, no. 104-B/1320-1; Pl. 17, fig. 11). The orbital margin is distinctly concave. The ornamentation is composed of numerous closely positioned high elongated tubercles, which are relatively large in the central part of the bone.

The distal bony segment of the pectoral fin is slightly convex, flattened, with a short longitudinal

groove (specimen SGU, no. 104-B/1320-6; Pl. 17, fig. 12). The dorsal surface is covered with densely spaced rows of longitudinally extended tubercles flattened from above. The caudal surface is flat and ornamented with pointed tubercles at the margins.

Comparison. *G. burchardi* differs from *G. longus* in the structure of the dorsal fin spine and the distal segment of the pectoral fin and in the more regularly arranged and more densely spaced rows of tubercles composing surface ornamentation of bones.

Occurrence. Upper Permian, Tatarian Series, upper part of the Severodvinian Stage and the Vyatkian Stage of the Orenburg Region.

Material. In addition to the holotype, membrane bones of the skull and other fragments of the skeleton from the type and other localities of the Orenburg Region: specimen SGU, no. 104-B/2765-1 from the Babintsevo locality; SGU, no. 104-B/2737 (Novogorodskoe locality); and SGU, no. 104-B/998 (Zubochistenka locality).

CONCLUSIONS

The analysis of the distribution of discordichthyids, which are widespread in the Tatarian Series of the Upper Permian of European Russia, has shown the following features of their historical development:

(1) This large group first appeared in the basins of European Russia in the terminal Urzhumian of the Biarmian Series of the Permian and persisted to the terminal Vyatkian of the Tatarian Series.

(2) The upper part of the Urzhumian Stage is characterized by *Discordichthys spinifer*.

(3) The Severodvinian and Vyatkian stages are characterized by *Mutovinia stella*, *Geryonichthys longus*, and *G. burchardi*.

(4) The genus *Geryonichthys* first appeared in the basal Severodvinian Stage, while the genus *Mutovinia* emerged in the upper half of the Severodvinian (M. Minikh and A. Minikh, 1997; A. Minikh and M. Minikh, 2001).

(5) *Mutovinia sennikovi* appeared at the end of the Vyatkian (at the Permian–Triassic transition); it occurs in the Vyazniki-2 locality along with an ichthyofauna typical of both the Tatarian Series (*Mutovinia stella*, *Toyemia blumentalis*, *Geryonichthys* sp., and *Xenosynchodus* sp.) and the Triassic (*Saurichthys* sp.) (determined by the author). To date, *Saurichthys* has only been recorded in the Triassic beds of the world.

Thus, the boundary beds of the Biarmian and Tatarian series are marked by the emergence of the order Discordichthyiformes. Apparently, the appearance of the new fish order at this boundary of European Russia coincided with a crucial point in the global history of early tetrapods, i.e., the replacement of the dinoccephalian fauna by the pareiasaurian–theriodont fauna (Ivakhnenko et al., 1997; Ochev, 1999).

The unique fish assemblage from the Vyazniki beds, which includes elements of Late Permian and Triassic ichthyofaunas, allows us to supplement the Upper Permian biozonation based on fishes (Minikh and Minikh, 1999) and recognize a new ichthyofaunal zone in its terminal part.

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