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Pyramidal Spiriferids (Brachiopods) from the Middle and Upper Devonian of the Russian Plate: Morphology, Systematics, and Shell Wall Structure

N. V. Oleneva

All-Russia Research Institute of Geology and Petroleum (VNIGNI), sh. Entuziastov 36, Moscow, 105819 Russia
e-mail: nat_oleneva@mail.ru

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Abstract—The pyramidal spiriferids *Thomasaria* Stainbrook, 1945 and *Pyramina* Ljaschenko, 1969 from the collection of brachiopods of Ljaschenko are examined. New data on the shell microornamentation and inner structure support the validity of the genus *Piramina* and its type species *P. oskolensis* Ljaschenko. A new species of the genus *Thomasaria*, *T. rotunda* is described.

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Key words: Brachiopods, pyramidal spiriferids, Devonian, Frasnian, Russian Plate.

INTRODUCTION

The genus *Pyramidalia* Nalivkin, with the type species *Spirifer simplex* Phillips, 1841 was established by Nalivkin in 1947. The diagnosis of *Pyramidalia* included the following characters, "Relatively small-sized, sharply inequivalve, smooth or coarse-plicate. Ventral valve pyramidal, with very high, triangular, straight or slightly curved area, sulcus more or less developed." The internal side of the ventral valve has dental plates and an umbonal thickening (callus deposition) (Nalivkin, 1947, p. 124). Microornamentation was not marked in the original description.

This genus was probably established based on the distinctive pyramidal shape of the ventral valve. Such a shape is characteristic of many spiriferid genera and is usually regarded as a character of uncertain taxonomic rank. Therefore, the genus *Pyramidalia* is frequently considered to be invalid.

In his revision of reticulariids from the Devonian of Belgium, Vandercammen (1957, p. 12) assigned *Spirifer simplex* to the genus *Plectospirifer* Grabau, 1931. The list of synonyms from this work shows that, from 1841 to 1950, this species was referred to the genera *Spirifer* Sowerby, 1818, *Reticularia* McCoy, 1844, *Eoreticularia* Nalivkin in Frederiks, 1924, and *Cyrtia* Dalman, 1828. Later, considering some genera of the family Cyrtinidae Frederiks, 1911, Ivanova 1916 (1962, p. 119) proposed that until a detailed reexamination of microornamentation and spondylium, *Pyramidalia* should be placed in the genus *Squamulariina* Frederiks, 1916. At the same time, Ch. Pitra tentatively treated *Pyramidalia* as a junior synonym of *Cyrtinaella* Frederiks, 1916 (*Treatise*…, 1965, p. 678).

Two years earlier than Nalivkin, Stainbrook (1945) described brachiopods with a pyramidal ventral valve and assigned them to the genus *Thomasaria* Stainbrook, 1945. In the diagnosis of the type species *T. altumbona*, Stainbrook (1945, p. 58, pl. 4, figs. 22–30) indicated the presence of well-developed dental plates, which extend along the valve bottom and gradually decrease in height to the base of the hinge teeth. Regarding the microornamentation, he indicated that the outer surface of both valves has many narrow growth lines with spines, which are usually separated from each other by regular spaces. The characters listed, i.e., the pyramidal shape, long dental plates diverging anteroventrally, are clearly seen in the figures of the type species *T. altumbona* presented by Cooper and Dutro (1982, p. 102, pl. 35, figs. 1–3). Based on these characters, Cooper and Dutro regarded *Thomasaria* as the type genus of the family Thomasariidae Cooper et Dutro, 1982.

When discussing the taxonomic position of *Thomasaria* and *Pyramidalia*, Baliński (1979, p. 70) regarded *Pyramidalia* as a junior synonym of the genus *Thomasaria*. Brice (1985, p. 145) also proposed that these genera could have been synonyms and indicated that morphological structures of the type specimens of *P. simplex* and *T. altumbona* should be compared.

In the spiriferid classification of Carter et al. (1994), the family Thomasariidae and its type genus *Thomasaria* are accepted; following Ivanova, the genus *Pyramidalia* is included in the family Cyrtinidae as a junior synonym of the genus *Squamulariina*; and the *Pyramina* Ljaschenko, 1969 is regarded as a junior synonym of the genus *Echinocoelia* Cooper et Williams, 1935 of the family Ambocoeliidae George, 1931.

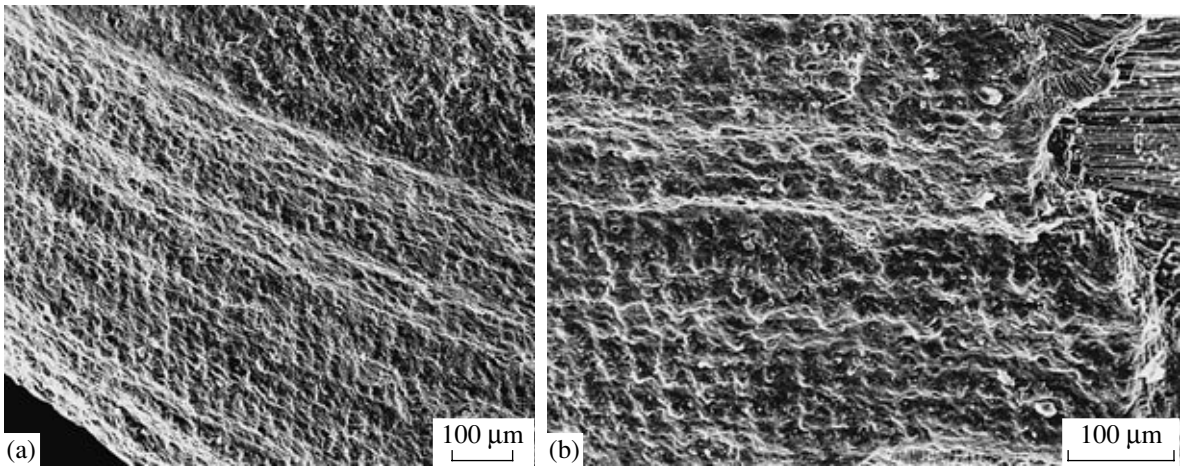


Fig. 1. *Pyramina oskolensis* Ljaschenko from the Staryi Oskol Horizon of the Givetian Stage, Middle Devonian; Voronezh Region (southern Voronezh GSP, borehole 512, depth of 161.1 m); specimen VNIGNI, no. 1671, microornamentation fragment: (a) concentric lines and (b) false radial striation composed of densely spaced, undulating concentric growth lines.

The collection of A.I. Ljaschenko, which is housed in All-Russia Research Institute of Geology and Petroleum (VNIGNI), includes brachiopods with a pyramidal ventral valve and a flattened dorsal valve from the Middle and Upper Devonian of the Russian Plate. Of these, more than 30 complete shells come from the Frasnian beds of the Upper Devonian of southern and central Timan, and three complete shells and about 40 isolated valves are from the Givetian beds of the Middle Devonian of the Volga–Ural Region. Ljaschenko assigned Upper Devonian spiriferids to *Pyramidalia simplex* (Phillips), while similar spiriferids from the Middle Devonian were determined as *Pyramina oskolensis* Ljaschenko, 1969.

Similar appearance and indistinct diagnostic characters in some cases could have resulted in incorrect assignment of species to particular genera. Thus, Sapel'nikov and Mizents (2000) indicated that the inner structure of *S. simplex* should be reexamined and, at the same time, figured specimens from the Middle Devonian of the Middle Ural Mountains (which are similar in my opinion to the genus *Pyramina*) under the name *Cyrtinaella simplex* (Sapel'nikov and Mizents, 2000, p. 125, pl. 36, fig. 8; pl. 41, fig. 5).

I examined Middle and Upper Devonian pyramidal spiriferids from the collection of Ljaschenko and obtained new data on the microornamentation, shell wall structure, and other morphological features. This resulted in the following conclusions.

(1) Spiriferids from the Upper Devonian of Timan and the Volga–Ural Region which were previously assigned to the genus Pyramidalia should be referred to *Thomasaria* (described as *T. rotunda* sp. nov.).

(2) *Pyramina* from the Middle Devonian of the Volga–Ural Region should be regarded as a distinct genus of the subfamily Ambocoeliinae George, 1931 rather than as a junior synonym of the genus *Echinocoelia*, as was previously proposed.

The microornamentation and structure of the shell wall were examined in the Paleontological Institute of the Russian Academy of Sciences using a scanning microscope MicroScan. The material is housed in VNIGNI, Moscow, collection nos. 16 and 31.

RESULTS AND DISCUSSION

The study of the external surface of *Thomasaria rotunda* sp. nov. showed that its microornamentation is composed of concentric growth lines and elongated spines arranged in concentric rows. Depending on the preservation of the external surface, the microornamentation of *T. rotunda* ranges from rounded tubercles with narrow concentric growth lines (Pl. 9, fig. 1e) to rounded drop-shaped structures (Pl. 9, fig. 1) or elongated spines arranged in concentric rows (Pl. 8, fig. 9g, Pl. 9, fig. 1b). In some cases, a fine calciferous layer coating spines gives the impression that the shell interior is covered with spines.

In *T. rotunda*, the spines are positioned tangential to the shell surface, the spine bases are 30–60 μm in diameter, the spine length ranges from 30 to 100 μm. It has been shown that the spines are formed and grow on the extension of the pore canals (Pl. 9, figs. 1e, 2a). In distal sections or broken spines, the central area of each spine has a rounded hole, that is, the pore canal (Pl. 9, fig. 1c). In longitudinal sections of spines, the pore canal is in the shape of a narrow trough extending throughout the spine length (Pl. 9, figs. 1d, 1e). The pore canal is approximately 10 μm in diameter and is as long as a spine, i.e., 70–100 μm. It has been established that the pore canals are conical in shape, and the diameter of the opening of the pore canals increases from 1–1.5 μm in the fibrous layer (Pl. 9, fig. 2a) to 10–12 μm on the shell surface (Pl. 9, figs. 1c, 1e).

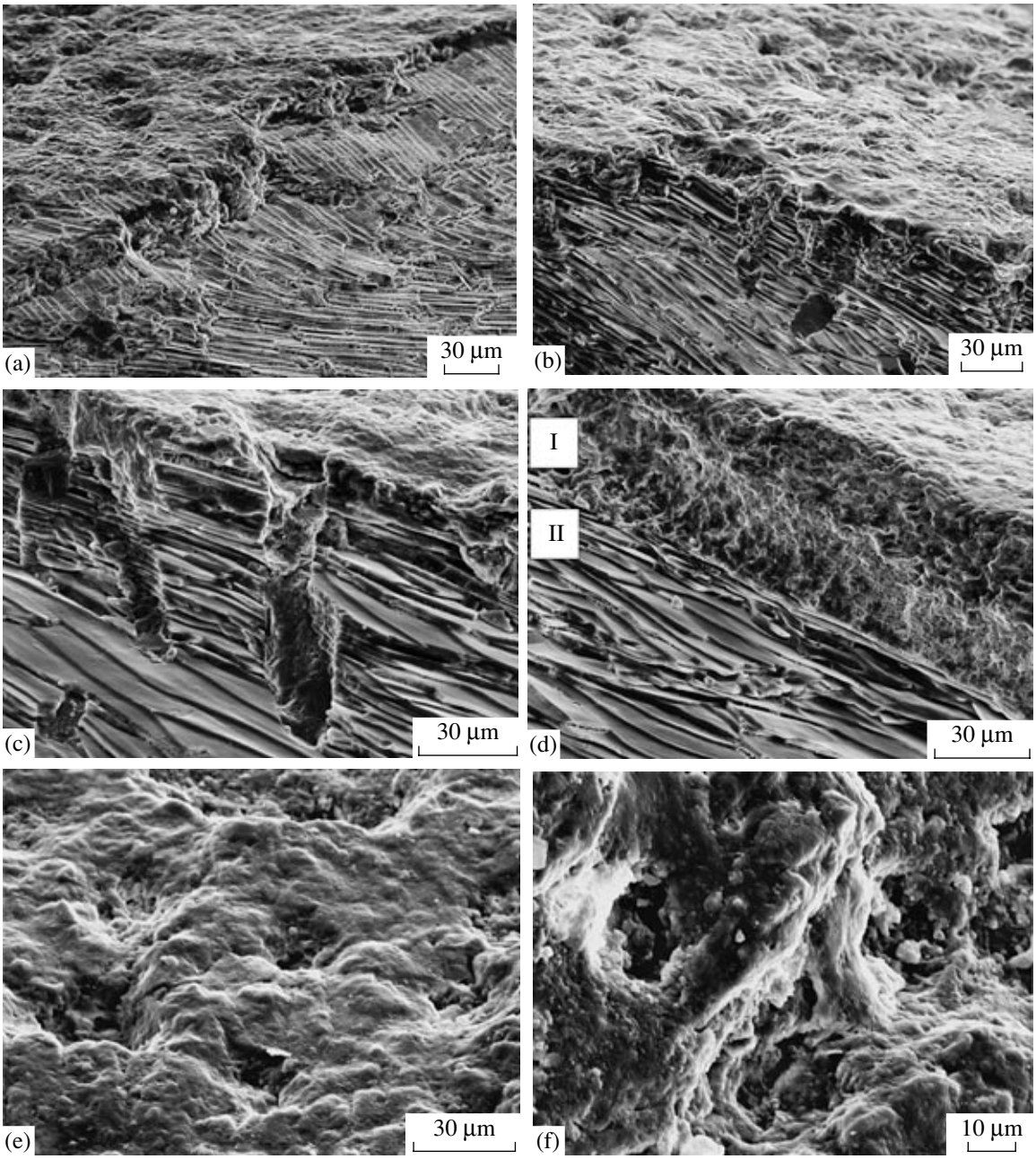
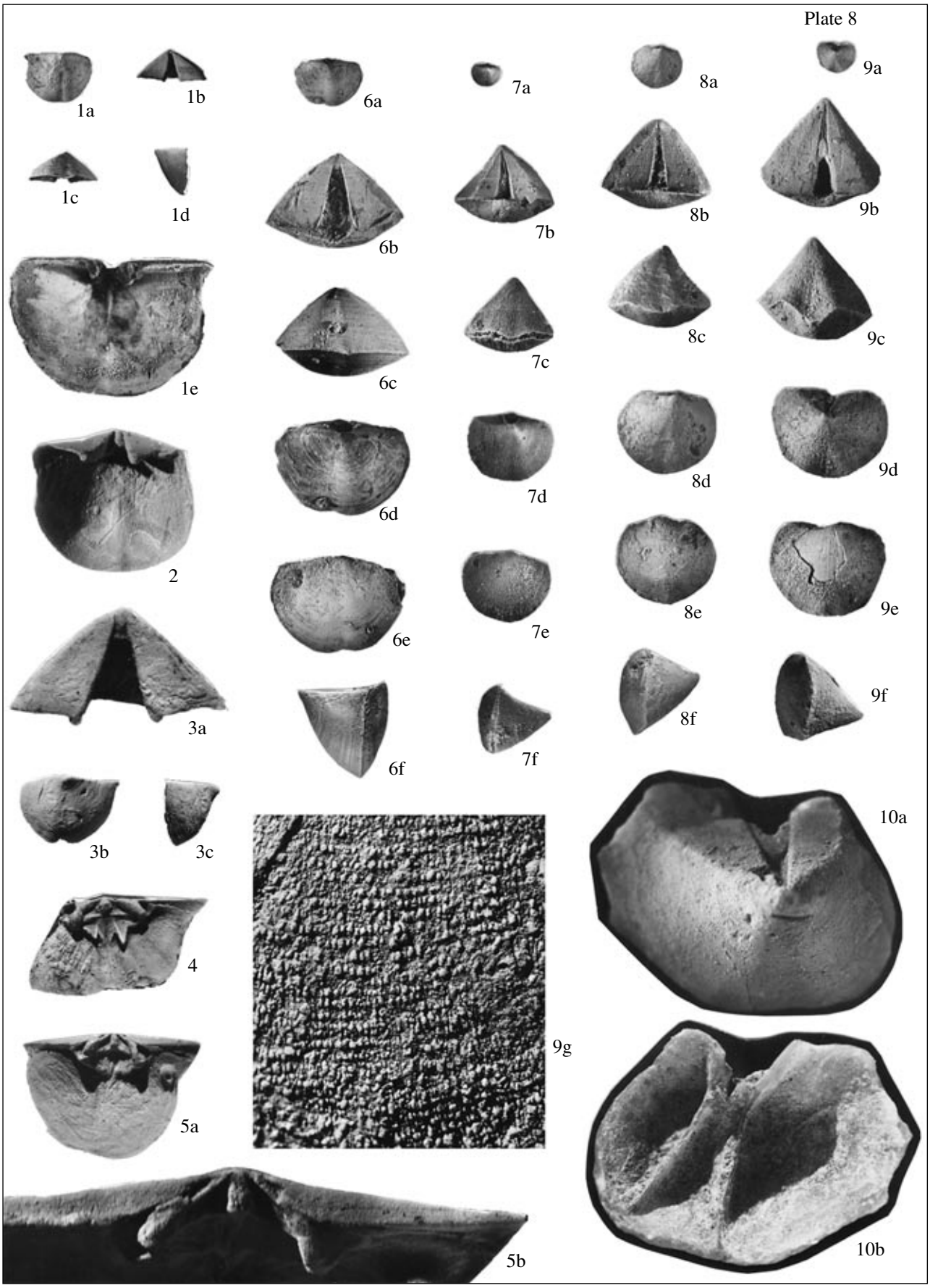


Fig. 2. *Pyramina oskolensis* Ljaschenko from the Staryi Oskol Horizon of the Givetian Stage, Middle Devonian; Voronezh Region (southern Voronezh GSP, borehole 512, depth of 161.1 m); specimen VNIGNI, no. 2607/2: (a, b) surface shell layer with traces of pore canals, (c) tangential split of the shell, the external and prismatic layers are visible; (d) boundary between the primary (I) and fibrous (II) shell layers; and (e, f) longitudinal section of the shell through the pore canals.

When describing the internal structures (delthyrium and spiral of the brachial support) of species of the genus *Thomasaria*, *T. gibbosa* (Vandercammen, 1956, p. 20, fig. 12) and *T. parallela* (Vandercammen, p. 28, fig. 23), Vandercammen recognized three shell layers. Of these, he referred the fibrotest and prismotest to structural elements of the shell wall, while the layer covering the internal structures of the skeleton he named the callotest (not considered in the present study).

The study of *T. rotunda* has shown that its shell consists of two layers, including the outer (primary) and secondary or fibrous layers. The primary layer is thin, cryptocrystalline in structure, and has a sharp boundary with the underlying fibrous layer. The fibrous shell layer consists of two sublayers. The first sublayer is very thin (20–30 μm), composed of narrow fibers, which form a rectangular prism in section, the sides of which are 2–3 μm long (Pl. 9, fig. 1g). It is underlain by

Plate 8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the second sublayer of the fibrous layer (Pl. 9, figs. 2a, 2b), which is up to 100 μm high and has wider prisms (up to 10 μm). The planes of the fibrous sublayers are positioned at a sharp angle to one another (Pl. 9, fig. 2b). The plains of fibers of the layer show distinct small bases of pore openings arranged in radial rows (Pl. 9, fig. 2a).

Thus, it is shown that, in *T. rotunda*, the spines are restricted to the primary shell layer. The spines are arranged in concentric rows on the shell surface and have a hollow central canal. The central canal of the spines continues from small pores inside the shell, which pierce the primary layer and reach the fibrous layer.

Let us consider the structure of microornamentation and shell wall in the genus *Pyramina*. The diagnosis of the type species *P. oskolensis* reads that microornamentation is absent, but narrow concentric growth lines and weak longitudinal striation are sometimes observed (Ljaschenko, 1969, p. 24).

The study of available specimens has shown that the sculptural elements of *P. oskolensis* should not be taken for longitudinal striation; the impression of radial striation is formed by concentric growth lines. At the anterior margin, the concentric lines become wavy, and each subsequent curvature follows exactly the preceding one. Fine, closely spaced sinusoidal curves look like narrow radial striae (Fig. 1).

In *P. oskolensis*, intact external surface of the shell is almost smooth. As the surface layer is damaged, the pore canals open. On the surface of the ventral valve near the umbo, the pores are arranged in regular rows. The pores are very small, circular, 15–20 μm wide (Figs. 2a, 2b). In the transverse plane of the shell, the pores are shaped as hollow, tubular, conical canals. Inside the shell, the pore canals are positioned perpendicular to the internal shell surface; in tangential sections of lateral slopes, the canals seem inclined (Fig. 2e). The boundary between the pore canals and the fibrous layer is sharp, distinct, without a trace of fiber curvature. The pore canals pierce both the primary and secondary shell layers (Figs. 2e, 2f).

It has been established that, in the genus *Pyramina*, the shell consists of two layers, the primary (I) and secondary (II) shell layers (Figs. 2c, 2d). The primary layer is cryptofilamentary in structure, 30–40 μm thick. The secondary layer is formed by narrow, long fibers positioned in parallel to the shell surface. The fibers are regular, distinct, and vary in length. On the tangential slopes of the shell, the fibers are in the shape of narrow lateral steps projecting one above the other (Fig. 2d).

Thus, the genus *Pyramina* is characterized by a porous shell. Small, closely spaced pores in the shape of narrow tubular canals pierce the primary layer and are well-developed in the fibrous layer. According to the classification proposed by Ivanova (1971, p. 23), this pore pattern belongs to the first type of internal porosity.

Below, the genera *Thomasaria* and *Pyramina* are described, new data on the inner structure and surface ornamentation of *T. rotunda* sp. nov. and *P. oskolensis* are provided.

SYSTEMATIC PALEONTOLOGY

Order Spiriferida

Suborder Delthyridina

Superfamily Reticularioidea Waagen, 1883

Family Thomasariidae Cooper et Dutro, 1982

Genus *Thomasaria* Stainbrook, 1945

Thomasaria: Stainbrook, 1945, p. 57; Vandercammen, 1956, p. 19; *Treatise…*, 1965, p. 711; Brice, 1970, p. 94; Cooper and Dutro, 1982, p. 102; Carter et al., 1994, p. 358.

Pyramidalia: Nalivkin, 1947, p. 124.

Type species. *Thomasaria altumbona* Stainbrook, 1945; North America; Upper Devonian, Frasnian.

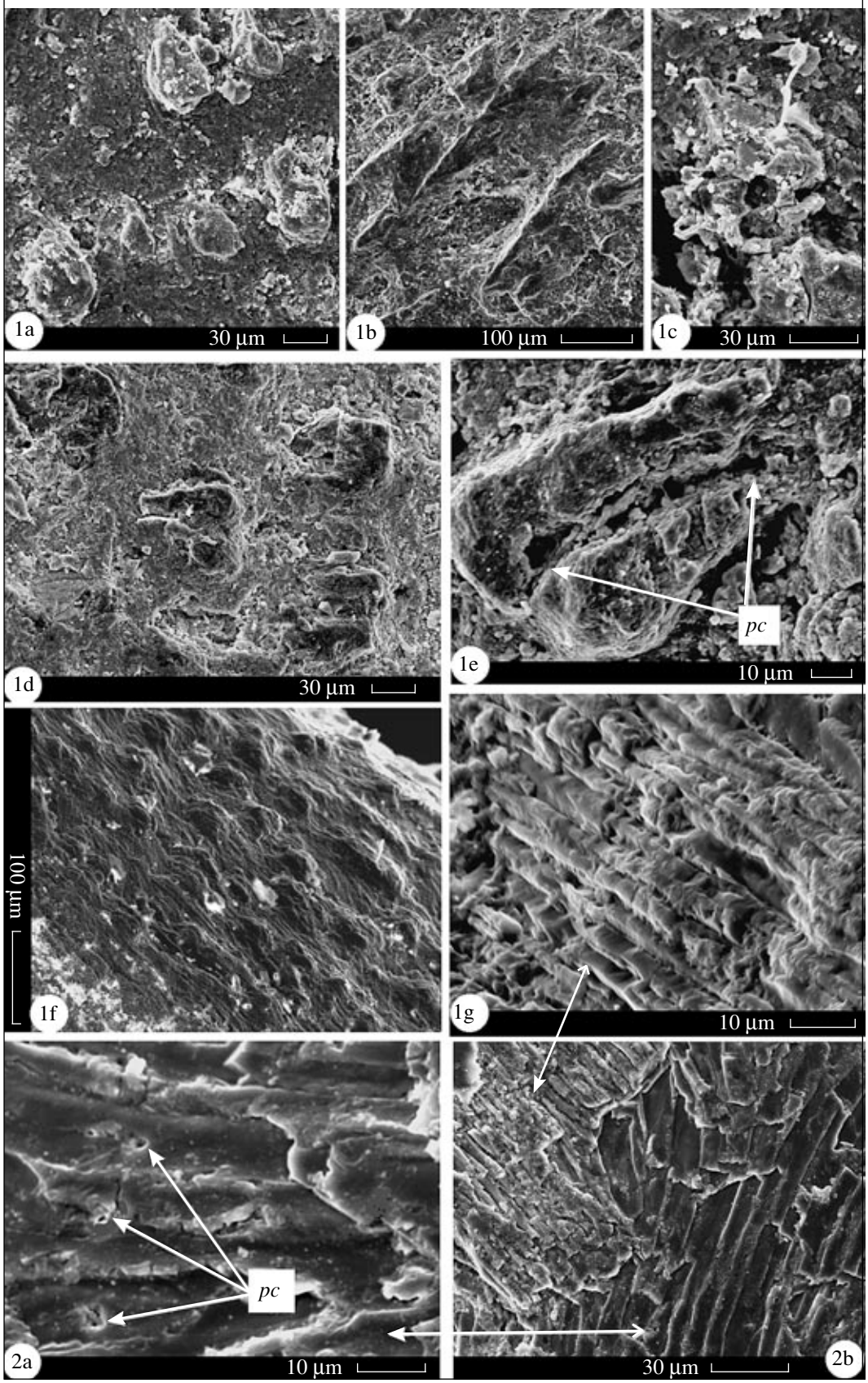
Diagnosis. Relatively small, smooth shells expanded slightly transversely. Ventral valve semipyra-

Explanation of Plate 8

Figs. 1–6. *Pyramina oskolensis* Ljaschenko: (1) specimen VNIGNI, no. 2606, ventral valve: (1a) umbonal view, ×1; (1b) areal view, ×1; (1c) view of anterior margin, ×1; (1d) lateral view, ×1; and (1e) inner structure of the ventral valve, ×3; Voronezh Region, village of Nizhnii Kurlak, borehole 24, depth of 126.1 m; Middle Devonian, Givetian Stage, Staryi Oskol Horizon; (2) specimen VNIGNI, no. 1671, inner structure of the dorsal valve, ×3; Voronezh GSP, borehole 512, depth of 161.5 m; the same age; (3) specimen VNIGNI, no. 2607, ventral valve: (3a) areal view, ×3; (3b) umbonal view, ×1; and (3c) lateral view, ×1; the same locality and age; (4) specimen VNIGNI, no. 2607/1, inner structure of the dorsal valve, ×3; the same locality and age; (5) specimen VNIGNI, no. 2822, dorsal valve: (5a) inner structure of the dorsal valve, ×3; (5b) areal view, ×10; (6) holotype VNIGNI, no. 3032 [32/168], complete shell: (6a) ventral valve, ×1; (6b) areal view, ×2; (6c) view of the anterior margin, ×2; (6d) umbonal view, ×2; (6e) dorsal valve, ×2; and (6f) lateral view, ×2; Voronezh Region, town of Borisoglebsk, borehole 118, depth of 446.5 m; Middle Devonian, Givetian Stage, Staryi Oskol Horizon.

Figs. 7–10. *Thomasaria rotunda* sp. nov.; (7) specimen VNIGNI, no. 2616, complete shell: (7a) ventral valve, ×1; (7b) areal view, ×3; (7c) view of the anterior margin, ×3; (7d) umbonal view of top, ×3; (7e) dorsal valve, ×3; and (7f) lateral view, ×3; southern Timan, Lyaiol River, 11 km from the mouth, outcrop 698; Upper Devonian, Frasnian Stage, Lyaiol Formation; (8) specimen VNIGNI, no. 2610, complete shell: (8a) ventral valve, ×1; (8b) areal view, ×2; (8c) view of the anterior margin, ×2; (8d) umbonal view, ×2; (8e) dorsal valve, ×2; and (8f) lateral view, ×2; the same locality and age; (9) holotype VNIGNI, no. 2609, complete shell: (9a) ventral valve, ×1; (9b) areal view, ×3; (9c) view of the anterior margin, ×3; (9d) umbonal view, ×3; (9e) dorsal valve, ×3; (9f) lateral view, ×3; and (9g) fragment of microornamentation, ×10; the same locality and age; (10) specimen VNIGNI, no. 2608, inner structure of the ventral valve: (10a) umbonal view, ×20; (10b) inner structure of the ventral valve, ×20; southern Timan, right bank of the Vezha-Vozh River, outcrop 65; the same age.

Plate 9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midal, with high, straight area. Dorsal valve moderately convex; delthyrium high and narrow, covered by two connected deltidial plates. Ventral valve with long dental plates diverging anteriorly and ventrally and separated by low euseptum. Dorsal valve with short crural plates and undulate cardinal process. External surface smooth, microornamentation consisting of narrow hollow spines arranged in concentric rows.

Species composition. In addition to the type, nine species: *T. simplex* (Phillips, 1841), *T. pyramidalis* (Schnur, 1853), *T. gibbosa* Vandercammen, 1956, *T. parallela* Vandercammen, 1956 and *T. serrensis* Brice, 1985 from the Middle Devonian–Frasnian of the Upper Devonian of Western and Central Europe (England, Belgium, Germany, Poland, France), and from Morocco, the Ural Mountains, Kuznetsk Basin, Central Asia; *T. rockymontana* (Warren, 1928), *T. altumbona* Stainbrook, 1945, *T. demissa* Cooper et Dutro, 1982 and *T. warreni* Cooper et Dutro, 1982 from the Frasnian Stage of the Upper Devonian of North America and Canada; and *T. rotunda* sp. nov.

Comparison. *Thomasaria* is closely similar in shell shape to *Squamulariina* and *Cyrtinaella* and sharply differs from these genera in the inner structure of the ventral valve. In the type species of the genus *Squamulariina*, *Cyrtina parva* Gurich, 1896, figured by Biernat (1966, p. 136, pl. 32, figs. 1–13), the high septal part of the spondylium is almost as long as the diverging dental plates, which is atypical for *Thomasaria*. The type species of the genus *Cyrtinaella*, *Cyrtina biplicata* Hall, 1857, is similar in internal structure to *Cyrtina*, as follows from the diagnosis provided by Pitra (*Treatise...*, 1965, p. 678, fig. 549.2). *Thomasaria* differs from both genera in its microornamentation composed of hollow spines (which has not been recorded in *Cyrtinaella* and *Squamulariina*).

Thomasaria rotunda Oleneva, sp. nov.

Plate 8, figs. 7–10; Plate 9, figs. 1 and 2

Pyramidalia simplex: Nalivkin, 1947, p. 124, pl. 31, fig. 4; Mikryukov, 1955, p. 247, pl. 6, fig. 9; Petreneva, 1955, p. 286, pl. 3, fig. 6; Adrianova, 1955, p. 378, Pl. 9, fig. 4.

Etymology. From the Latin *rotundus* (circular).

Holotype. VNIGNI, no. 2609, complete shell; southern Timan, Lyaiol River, outcrop 698; Upper Devonian, Upper Frasnian, terminal Lyaiol Horizon.

Description. The shell is small (Lp = 5.8 mm), semipyramidal, rounded. The hinge line is shorter than the greatest width of the shell. The lateral sides and cardinal angles are rounded. The sulcus is small, visible near the anterior margin only in large shells, the linguiform extension is small, trapezoidal.

The ventral valve is high, semipyramidal, with a sharp straight umbo. The area is high and straight, or, less frequently, gently concave, with a narrow, high triangular delthyrium, which is sometimes partially or completely covered by the deltidial plates. In the case of incomplete fusion, a small part near the hinge line of the valve remains open. The area is high and straight, the umbo is sharp. The apical angle is 84°–94°.

The dorsal valve is slightly, gently convex, the greatest convexity is near the hinge line of the shell. The fold is low, only seen near the anterior margin of the shell.

The external shell surface is smooth, the microornamentation is formed of narrow, concentric growth lines and very narrow spines or circular tubercles at their bases.

Inside the ventral valve, there are long, narrow dental plates, which diverge anteriorly and ventrally and reach the valve bottom. The euseptum is low, short, and not lower than the dental plates.

In the dorsal valve, the crural plates are short and the undulate cardinal process is low; the dental sockets are small, rounded. A low euseptum extends from the base of the cardinal process for one-third of the valve length (Fig. 3).

Measurements, mm and ratios:

Specimen VNIGNI, no.	Lp	Lb	W	T	Lp/W	Lp/T	AA
2615	4.5	4.4	6.8	4.7	0.66	0.96	94
Holotype 2609	5.8	5.5	6.9	5.9	0.84	0.98	79
2614	7.9	6.3	9.5	7.4	0.83	1.07	84
2613	9.8	9.8	13.4	10.4	0.73	0.94	89
2608	10.9	8.5	11.2	8.1	0.97	1.35	85
2615/1	11.4	10.4	14.7	10.5	0.78	1.09	90

Variability. The age variation is insignificant. In small specimens, sulcus and fold are absent, the shell width is always greater than the height; in large specimens, the fold and sulcus are present, the shell height is equal to, or greater than, the width.

Comparison. *T. rotunda* sp. nov. is most similar in shell outlines to *T. altumbona* (Stainbrook, 1945, p. 58, pl. 4, figs. 22–30) and *T. demissa* (Cooper and Dutro, 1982, p. 103, pl. 33, figs. 55, 56; pl. 35, figs. 4–24; pl. 39, figs. 35–37; pl. 41, figs. 27–33) and differs from both species in the hemispherical shell shape, the short hinge line, and the rounded cardinal angles. In *T. altum-*

Explanation of Plate 9

Figs. 1 and 2. *Thomasaria rotunda* sp. nov.; holotype VNIGNI, no. 2609: (1a) microornamentation composed of rounded tubercles; (1b) microornamentation composed of elongated procumbent spines; (1c) distal section of the spine, with a pore canal in the center; (1d, 1e) longitudinal sections of spines, (1f) surface microornamentation composed of rounded tubercles; and (1g) fibrous layer; southern Timan, Lyaiol River, 11 km from the mouth, outcrop 698; Upper Devonian, Frasnian Stage, Lyaiol Formation; (2) specimen VNIGNI, no. 2618: (2a) fibrous layer with traces of pore canals (*pc*), (2b) two sublayers of the fibrous layer; southern Timan, left bank of the Vezha-Vozh River, 4 km from the mouth, outcrop 57; the same age.

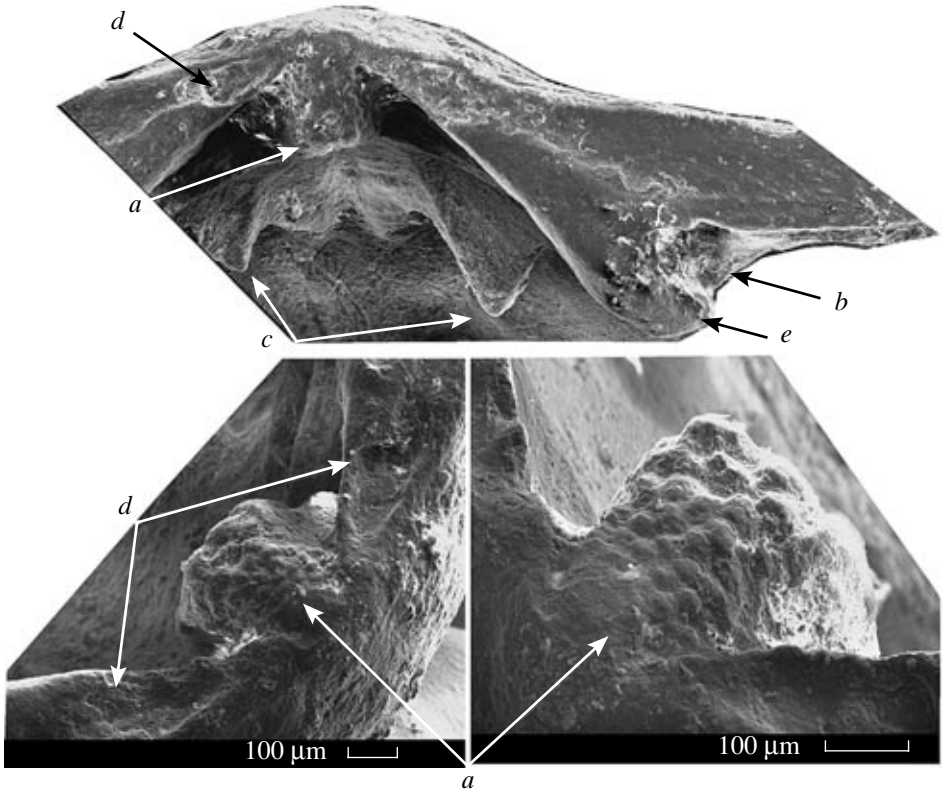

Fig. 3. *Thomasaria rotunda* sp. nov. from the Lyaiol Formation of a Frasnian Stage, Upper Devonian; southern Timan (right bank of the Vezha-Vozh River, 7 km from the mouth, outcrop 65); specimen VNIGNI, no. 2608, inner structure of the dorsal valve. Designations: (*a*) cardinal process, (*b*) dental sockets, (*c*) crural plates, (*d*) socket ridges, and (*e*) euseptum.

bona, the shell is larger, rectangular, with almost right cardinal angles; in *T. demissa*, the shell is trapezoidal, transversely expanded; the hinge line is long, straight, positioned at a sharp angle to the lateral sides. The new species differs from *T. simplex* (figured by Vandercammen, 1957, pl. 2, figs. 11–14, 17) in the rounded shape of its shell, the high straight area, and the poorly pronounced sulcus (in *T. simplex*, the shell is rounded square with a lower, dorsally inclined area and a distinct deep sulcus).

Occurrence. Upper Devonian, Upper Frasnian, Lyaiol Horizon; southern Timan, Mendymskii Horizon, Volga–Ural Region.

Material. About 30 complete, well-preserved shells: 17 from southern Timan, Lyaiol River, outcrop 698; eight from the Vezha-Vozh River, outcrop 57; one from central Timan, Srednyaya River, outcrop 665; two from the Orenburg Region, Salmysh, borehole 619, depth of 3277.7–3280.5 m; and one from Tatarstan, borehole Yanchikovskaya no. 12, depth of 1529.35–1534.65 m.

Family Ambocoeliidae George, 1931
Subfamily Ambocoeliinae George, 1931
Genus *Pyramina* Ljaschenko, 1969

Pyramina. Ljaschenko, 1969, p. 23.

Type species. *Pyramina oskolensis* Ljaschenko, 1969; Russian Plate; Middle Devonian, Givetian Stage.

Diagnosis. Relatively small, rounded trapezoidal, semipyramidal smooth shells, with small longitudinal depressions on both valves. Areas of ventral and dorsal valves high. Umbonal region of ventral valve inclined ventrally. Inside ventral valve, margins of delthyrium with thick delthyrial ridges, relatively small deltidial plate covering apex of delthyrium always present at base; umbonal region of valve with short median septum. In dorsal valve, notothyrium open, cardinal process tuberculate; hinge plate and socket ridges well developed; crural plates converging, reaching valve bottom, euseptum short; elongated pits located on lateral sides of notothyrium. External shell surface porous.

Species composition. Type species.

Comparison. *Pyramina* is similar to the genera *Crurithyris* George, 1931, *Cyrtinoides* Iudina et Rzonsnitskaia, 1985, and *Echinocoelia* Cooper et Williams, 1935 of the subfamily Amdocoeliinae. It is similar to the type species of the genus *Crurithyris*, *Spirifer urei* Fleming, 1828, in the shape of the cardinal process, which is elongated, triangular, tuberculate rather than thick and bilobate (as in *Echinocoelia*). It is distinguished from *Crurithyris* and *Echinocoelia* by the

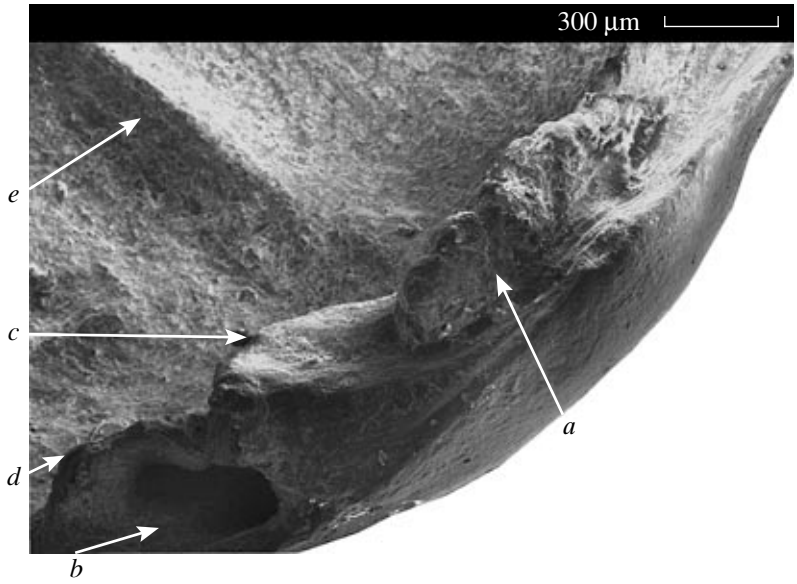

Fig. 4. *Pyramina oskolensis* Ljaschenko from the Staryi Oskol Horizon of the Givetian Stage, Middle Devonian; Voronezh Region (southern Voronezh GSP, borehole 512, depth of 161.1 m); specimen VNIGNI, no. 3042, inner structure of the dorsal valve. Designations: (*a*) cardinal process, (*b*) dental sockets, (*c*) crural plates, (*d*) euseptum, and (*e*) pits.

shape of its ventral valve with the straight, high area adjoining the dorsal valve at an almost right angle and by the umbo, which is inclined ventrally. In addition, it differs from both genera in the structure of the dorsal valve, the crural plates of which are short, converging, and reaching the valve bottom and the euseptum is short. In *Echinocoelia*, the crural plates are positioned parallel to one another, and the euseptum is long and high, as in *E. denayensis* Johnson (Johnson, 1966, pl. 26, figs. 23–30; Johnson, 1971, pl. 42, figs. 14–25) and *E. careocamera* Johnson (Johnson, 1978, pl. 7, figs. 1–8). In *Crurithyris*, on the contrary, the crural plates diverge at an angle and do not reach the valve bottom, as in *C. calendae* Johnson (Johnson, 1971, pl. 42, figs. 1–13). The dorsal valve of *Crurithyris* and *Echinocoelia* has a long, high septum, which reaches the anterior margin of the shell (*Pyramina* lacks this character). In addition, *Pyramina* differs from the two genera in the smooth shell with numerous internal pores and the microornamentation composed of only concentric growth lines (instead of short spines, which are characteristic of *Crurithyris* and *Echinocoelia*). *Pyramina* is similar to *Cyrtinoides* in the shape of the ventral valve, but differs in its structure, i.e., dental plates and tichorhinum are absent and the shell surface is porous (which is atypical for *Cyrtinoides*).

***Pyramina oskolensis* Ljaschenko, 1969**

Plate 8, figs. 1–6

Pyramina oskolensis: Ljaschenko, 1969, p. 24, pl. 5, figs. 1 and 2.

Cyrtinaella simplex: Sapel'nikov and Mizents, 2000, p. 125, pl. 36, fig. 8; pl. 41, fig. 5.

Holotype. VNIGNI, no. 3032 [32/168], complete shell; Voronezh Region, town of Borisoglebsk, borehole 1, depth of 446 m; Middle Devonian, Givetian Stage, Staryi Oskol Horizon.

Description. The shell is small (Lp = 8–10 mm), rounded trapezoidal, semipyramidal. The hinge line is equal to, or slightly shorter than, the greatest width of the shell. The cardinal angles and lateral sides are rounded, the anterior margin is narrow, almost straight or gently convex.

The ventral valve is high, semipyramidal, with gently convex, almost flat lateral slopes. A relatively narrow longitudinal depression is located in the central part of the valve, extending from the umbonal region to the anterior margin. The area is triangular, high, flat, positioned perpendicular to the commissural plane, distinctly separated from the lateral slopes of the valve. The delthyrium is high, broad, with the width at the base half as great as its height. In upper part of the delthyrium is always covered by a short delthyrial plate. The umbo is small, narrow, pointed, with its tip inclined sharply ventrally.

The dorsal valve is slightly convex, the greatest height is at the middle of the valve length. The lateral slopes are slightly convex, almost flat; a relatively narrow, gentle longitudinal depression extends in the middle of the valve. The area of the dorsal valve is relatively wide, linear, with parallel margins and a wide, open chilidium in the central part. The dorsal valve is articulated with the plain of the area of the ventral valve at a blunt angle. The umbo is small, wide, only slightly differentiated, not curved. Small, elongated triangular pits are located on the surface of the area lateral to the umbo.

The external shell surface is smooth, the microornamentation is only composed of concentric growth lines. The shell is pierced by many small, internal pores.

Narrow, high delthyrial ridges are seen inside the ventral valve, the teeth are large, elongated oval, the median septum is relatively low, short, terminates short of reaching the midlength of the valve.

In the dorsal valve, the surface of the narrow area has pits located lateral to the notothyrium. A high, triangular cardinal process with a tuberculate surface is located at the base of the notothyrium (Fig. 4). A high hinge plate and short crural plates deviate from the base of the cardinal process. The crural plates reach the valve bottom and come in contact; a low, narrow euseptum extends from this contact.

Measurements, mm and ratios:

Specimen VNIGNI, no.	Lp	Lb	W	T	Lp/W	Lp/T
2606	8.9	–	11.7	–	0.76	–
Holotype 3032	9.6	8.8	11.8	7.9	0.81	1.22
2605	9.9	9.4	11.9	7.5	0.83	1.32

Variability. The angle of inclination of the umbo ranges from slightly to sharply curled ventrally, the longitudinal depression on either valve ranges from sharp, distinct to hardly visible.

Occurrence. Middle Devonian, Givetian Stage, Staryi Oskol Horizon; central region of the Russian Plate.

Material. Three complete shells and more than 40 isolated (mostly ventral) valves from the Voronezh Region, GSP, borehole 512, depth of 161.1 m; town of Borisoglebsk, borehole 1, depth of 446 m; Annenskii District, village of Nizhnii Kurlak, borehole 24, depth of 125–126 m; Tambov Region, village of Rzhaksa, borehole 1, depth of 700.3–706 m.

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