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Systematics and Shell Microstructure of the Spiriferid Genera *Echinospirifer* and *Komispirifer* from the Upper Devonian of Southern Timan

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 type species of the genera *Echinospirifer* Ljaschenko, 1973 *Komispirifer* Ljaschenko, 1973 and *Mennespirifer* Ljaschenko, 1973 were revised based on material from the memorial collection of A.I. Ljaschenko. *Mennespirifer* is recognized as a junior synonym of the genus *Komispirifer*; the genera *Echinospirifer* and *Komispirifer* differ in fine ornament and the structure of the shell wall.

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Key words: Spiriferids, Upper Devonian, Frasnian, southern Timan.

INTRODUCTION

The genus *Echinospirifer*, with the type species *E. distinctus*, was established by A.I. Ljaschenko in 1973 from the Lower Frasnian of the southern Timan Mountains. In the original description, Ljaschenko (1973, p. 110) pointed out the absence of a delthyrial plate and the presence of numerous tubercles on the rib surfaces as the main distinguishing features of the genus. These features were the basis for the establishment of the family Echinospiriferidae Ljaschenko (1973, p. 109). In the same paper, the genera *Komispirifer* Ljaschenko, 1973 and *Mennespirifer* Ljaschenko, 1973 were established and assigned to the family Uchtospiriferidae (Ljaschenko, 1973, p. 87).

In the revision of some spiriferid families and genera from the Upper Devonian of Timan, Talent and Gratsianova (1988, p. 11) suggested that the genus *Echinospirifer* was a junior synonym of *Cyrtospirifer* and the family Echinospiriferidae was a synonym of Cyrtospiriferidae. They also supposed the holotypes of the type species *Uchtospirifer formosus* Ljaschenko and *Uchtospirifer menneri* Ljaschenko of the genera *Komispirifer* and *Mennespirifer* to be the juvenile and young forms (respectively) of the species *Cyrtospirifer echinosus* Ljaschenko.

In their new classification of spiriferids, Carter *et al.* (1994) recognized the validity of the family Echinospiriferidae. The genera *Uchtospirifer* Ljaschenko, 1973 and *Mennespirifer* were considered valid and placed in the subfamily Cyrtiopsinae Ivanova, 1972 from the family Cyrtospiriferidae Termier et Termier, 1949. The genus *Komispirifer* was regarded as a junior synonym of the genus *Mennespirifer* (Carter *et al.*, 1994, p. 333, 336).

The aim of this paper is to specify the taxonomic position of the genera *Echinospirifer, Komispirifer*, and *Mennespirifer*. The morphology, inner structures, and microornamentation of the type species *Echinospirifer distinctus* Ljaschenko, *Komispirifer formosus* (Ljaschenko), and *Mennespirifer menneri* (Ljaschenko), which were poorly described in the original diagnoses, were studied based on the topotypic material.

Study of *E. distinctus* has revealed that the inner structure of the type specimens does not conform to the diagnosis of the genus *Echinospirifer*. In addition to the dental plates, *E. distinctus* has a delthyrial plate, located low at the base of the dental plates near the umbo. Such an arrangement of the delthyrial plate was the probable reason for its loss during the preparation of fine sections and the subsequent erroneous conclusions about its absence. *K. formosus* certainly has a delthyrial plate.

The descriptions of the microornamentation of spiriferids are usually reduced to general information on its type. Detailed studies of the elements of the microornamentation and the structure of the shell wall are mainly episodically conducted. Opinions differ widely on the types of microornamentation, the structure and designation of shell layers. The most complete investigations along this line were performed by Vandercammen (1959, 1964), Krans (1965), MacKinnon (1974), Ivanova (1971), Dagis (1974), and others. Krans (1965, p. 92) schematically figured six different types of spiriferid microornamentation. Ivanova (1971, p. 31) assumed that the spiriferid microornamentation could be divided into two main types, i.e., capillae and spines. She supposed all microornamentation to be formed by the primary and secondary (or part of the secondary) shell layers. Dagis (1974, p. 58) considered

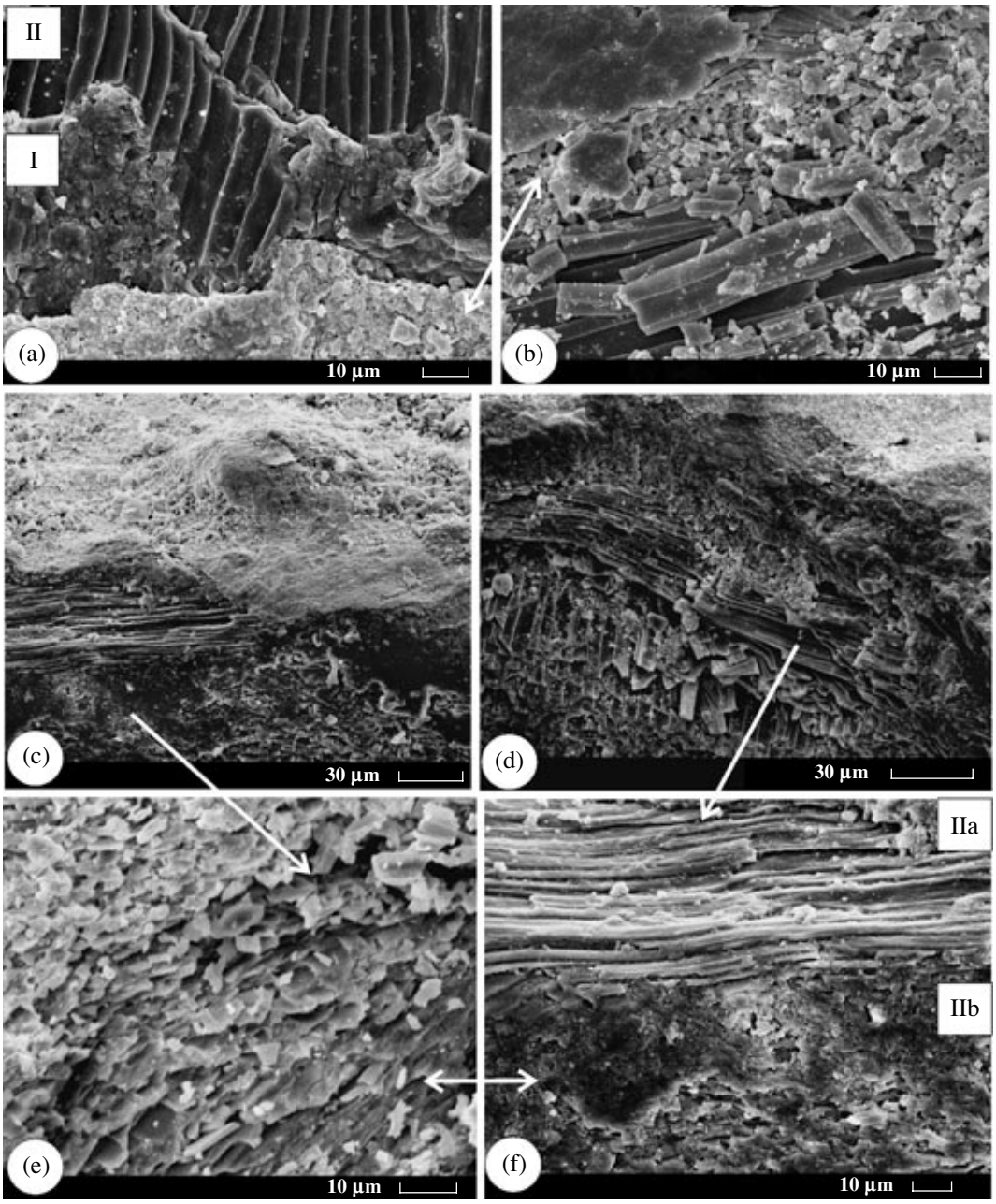


Fig. 1. Shell structure in *Echinospirifer distinctus* Ljaschenko; Frasnian Stage (Ust'-Yarega Formation), Upper Devonian; southern Timan, Yarega River (0.5 km from the mouth), specimen VNIGNI AIL, no. 2108: (a and b) juncture of the primary fine-grained (I) and the secondary fibrous (II) layers; (c) exterior of a spine and longitudinal section of the shell wall; (d) two sublayers of the fibrous layer; (e) transverse section of the second sublayer of the fibrous layer; (f) juncture of the first (IIa) and the second (IIb) sublayers of the fibrous layer.

the microornamentation (different tubercles, small spines, capillae) of the Triassic brachiopods (including spiriferids) to be formed only by the primary shell layer.

In a detailed study, new data on the microornamentation of *E. distinctus* and *K. formosus* were obtained; in both species, it is formed of spines.

The term *spine* designates external projections of the shell that are not hollow and that are formed by both the first and second layers of the shell and in length are equal to, or several times greater than, the diameter of their base.

Let us consider the structure of the shell wall and microornamentation in *E. distinctus.*

In the cross section, the shell wall consists of two layers: the primary or surface layer and the secondary (fibrous) layer; the prismatic layer is absent (Fig. 1a). The primary layer is fine-grained (Figs. 1a, 1b), 20–50 µm thick. The secondary fibrous layer is located

below it. The boundary between the layers is sharp and well pronounced (Figs. 1a, 1c).

The fibrous layer consists of two sublayers (Figs. 1c, 1f). In a tangential chip, the first sublayer is formed of long and narrow fibers. The fibers are almost parallel to the valve surface (Fig. 1d) and have an elongated, almost needlelike form (Fig. 1f). The fibers form thin stratification planes (Figs. 1d, 1f). The fibers of the underlying fibrous sublayer are inclined to the shell surface. The stratification planes of the both fibrous sublayers are almost perpendicular to each other. The boundary between the sublayers is sharp and well pronounced (Figs. 1d, 1f). The fibers of both sublayers are almost equal in size, 5–8 μm along the wide axis and 1–3 μm along the short axis. The distal surface of the prisms is rectangularly diamond-shaped (Fig. 1e). The overall thickness of the fibrous layer is about 200–300 μm.

In *E. distinctus*, the spines are positioned along the margin of the growth lamellae. Each rib has 6–8 spines (Pl. 7, fig. 2f; Fig. 2a). The height of the spines is equal to, or slightly greater than the diameter at the base. In longitudinal sections, the spines are in the shape of low ridges. The base of the spines is composed of the primary layer and the first sublayer of the fibrous layer (Fig. 2c). At the point of spine formation, fibers of the first sublayer curve or diverge in a fanlike manner, lifting the upper layer of the shell (Fig. 2c). In a disrupted spine, a circular or elongated base formed of the fibers of the second sublayer of the fibrous layer is exposed (Figs. 2e, 2f).

At low magnification, *E. distinctus* and *K. formosus* are similar in microornamentation (Pl. 7, figs. 2f, 7a). At high magnification, the microornamentation and shell structure of *Komispirifer* and *Echinospirifer* clearly differ.

In the original diagnosis of the genus *Komispirifer*, the microornamentation was characterized as follows: "when well preserved, ribs have small elongated tubercles, which are aligned in longitudinal rows" (Ljaschenko, 1973, p. 105). I revealed that the ribs of *K. formosus* bear small spines along the concentric growth lines. Each rib has 3 to 5 small elongated spines arranged in staggered rows. The space between spines corresponds to the time of development of the 4 to 6 narrowest concentric growth lines (Pl. 7, fig. 7d; Figs. 3a, 3b). In *K. formosus*, the spines are high, more or less inclined to the valve surface (Figs. 3a–3c). The length of the spine is two or three times greater than its diameter at the base. When well preserved, the elongated small spines, slightly inclined to the valve surface, look like fine capillae arranged in longitudinal rows on the rib surface.

The shell wall of *Komispirifer* also consists of two layers (Fig. 3d). The primary layer is thin and fine-grained (Fig. 3c). The underlying homogeneous fibrous layer consists of relatively wide (10–15 μm wide) fibers (Figs. 3e–3f). This layer is similar in appearance to the second fibrous sublayer of the genus *Echinospirifer*.

If the surface layer of *Komispirifer* is disrupted, the bases of the broken small spines are clearly noticeable in the shape of an elevated, rounded, columnar structures, with a basal diameter 30–35 μm (Figs. 3a–3c). The inner cavity of the small spines and the fibrous layer are composed of prismatic crystallites. Depending on the angle of inclination and section (transverse or tangential) of the small spine, the section may be rounded, oval, or elongated. Stepwise projecting prisms (Fig. 3f) or narrow lateral surfaces of the fibers (Pl. 7, figs. 7b–7d; Fig. 3e) may be exposed.

Thus, *Komispirifer* and *Echinospirifer* have both common and distinctive features in the microornamentation and shell structure:

(1) The external elements of the microornamentation are represented by spines in both genera:

(a) In *Echinospirifer*, the spines are relatively low, develop in rows at the marginal edge of each growth lamella.

(b) In *Komispirifer*, the spines are high and grow concentrically. Subsequently, the spines appear and grow in staggered rows and positioned at a distance of 4 to 6 tiny concentric growth lines.

(2) In both *Komispirifer* and *Echinospirifer*, the spines are not hollow, and are composed of both the surface and fibrous shell layers:

(a) In *Echinospirifer*, the fibrous layer consists of two sublayers. The tubercles are formed only by the first sublayer of the fibrous layer.

(b) In *Komispirifer*, the fibrous layer covering the inner cavity of tubercles is not differentiated.

The new data on the microornamentation corroborate the earlier assumption that the genus *Komispirifer* should not be assigned to the uchtospirifers (Oleneva, 2003, 2004), where it was originally placed (Ljaschenko, 1973, p. 87). In *Uchtospirifer*, the external elements of microornamentation are represented by the capillae situated on the costae. Rarely, capillae have large false tubercles 0.1–0.5 mm in diameter, which, similar to the radial striation, are formed within the surface shell layer. In the *Uchtospirifer*, the formation of the tubercles is quite simple: as the shell grows, in some large and rare shells, the radial capillae grow with interruptions. In the place of a break or a gap of the capilla, a low thickened basement, or *nodule*, is formed. These nodules give the impression of a tuberculate ornamentation. This pattern of the formation of microornamentation substantially differs from the pattern characteristic of the genus *Komispirifer*.

Note that *Uchtospirifer* was confined to the Lower Frasnian Substage of the Upper Devonian. The first occurrence of *E. echinosus* is dated Lower Frasnian, lower beds of the Timanian Horizon. *K. formosus*

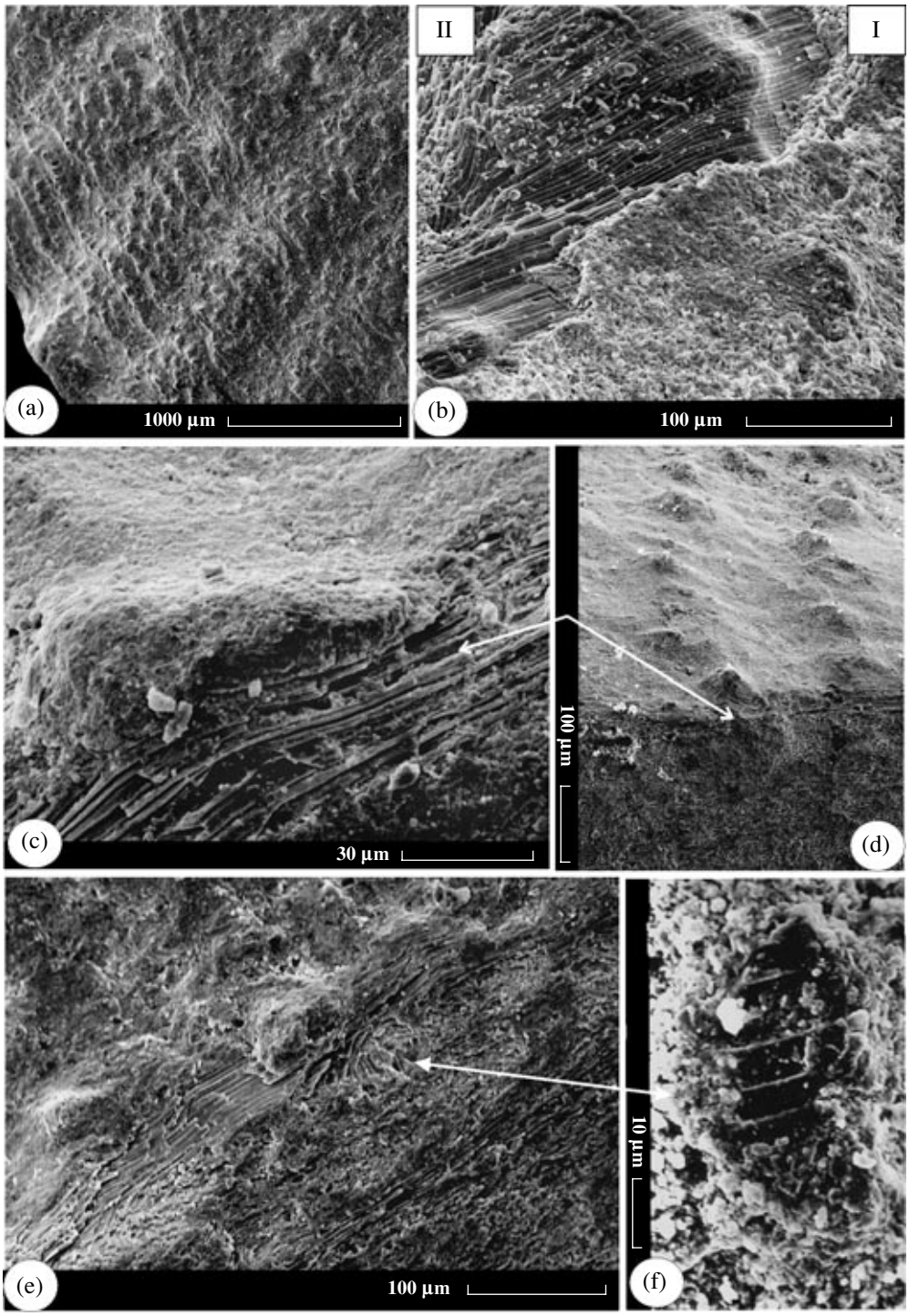


Fig. 2. Structure of the microornamentation of *Echinospirifer distinctus* Ljaschenko; Frasnian Stage (Ust'-Yarega Formation), Upper Devonian; southern Timan, Yarega River (0.5 km from the mouth), specimen VNIGNI AIL, no. 2108: (a) general appearance of microornamentation; (b) exterior of spines on the outer (I) and inner (II) shell layers; (c and d) longitudinal section of the shell and exterior of a spine composed of the first sublayer of the fibrous layer; (e) fibrous layer at the base of a spine; and (f) second sublayer of the fibrous layer at the base of a spine.

emerged later, in the upper half of the Timanian Horizon, and persisted along with *E. distinctus* in the Middle Frasnian to the upper half of the Sargaevian Horizon.

The analysis is supplemented by statistical data on absolute and relative characteristics of *E. distinctus* (n = 30 specimens) and *K. formosus* (n = 76 specimens). The absolute parameters for each species show

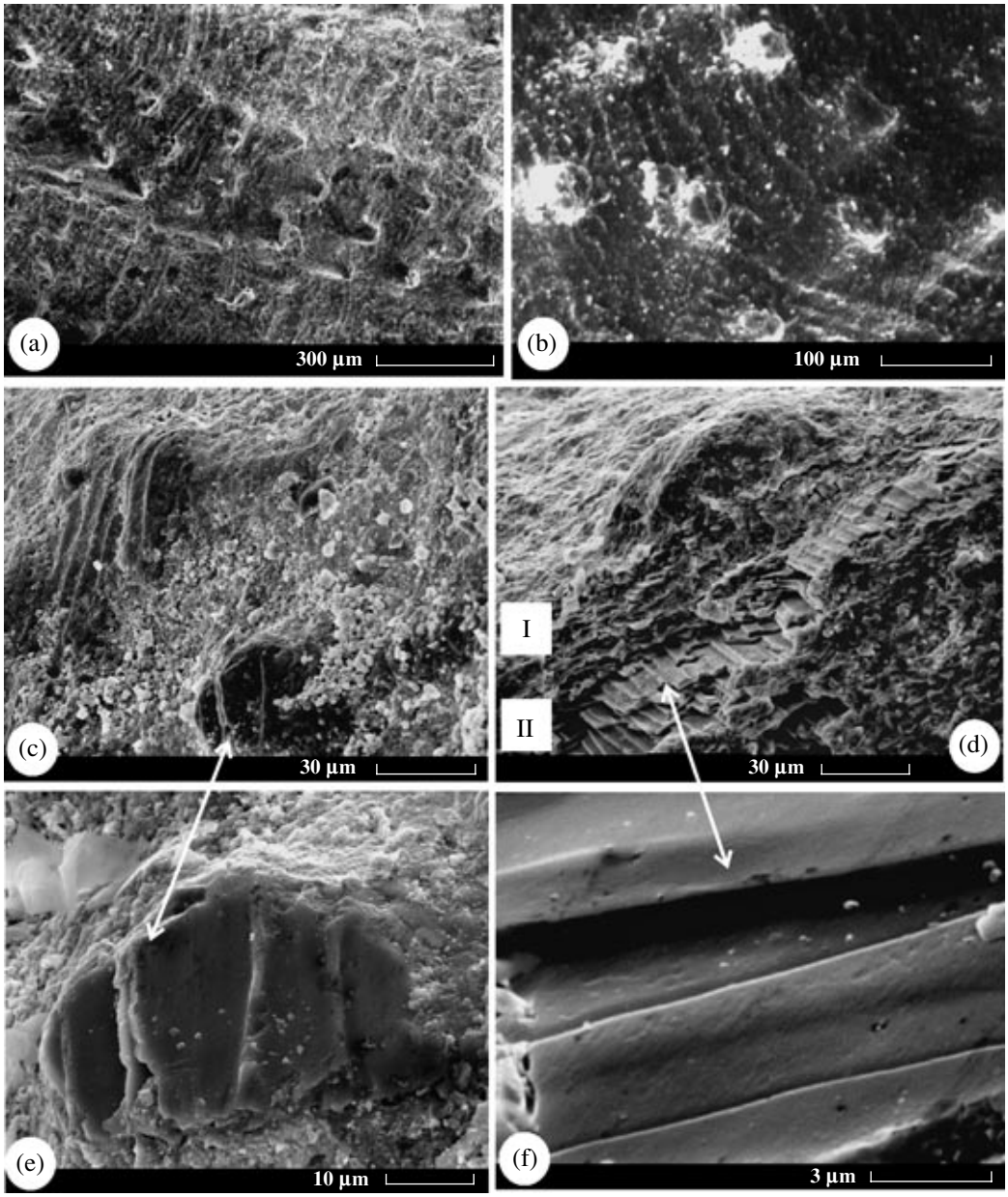


Fig. 3. Structure of microornamentation in *Komispirifer formosus* (Ljaschenko); Frasnian Stage (Upper Timanian Subhorizon), Upper Devonian; southern Timan (oil well no. 1, interval 30–45 m); specimen VNIGNI AIL, no. 2079: (a) general appearance of microornamentation; (b) spines arranged in staggered rows along concentric growth lines; (c) fragment of a small spine; (d) transverse section of the shell, fragment of the spine structure; (e) small spine composed of fibers; and (f) longitudinal view of fibers.

normal distributions with different modes. In *E. distinctus*, the modes of length (L), width (W), and height (H) are 21, 30, and 17, respectively; those of *K. formosus*, are 11, 16, and 9, respectively. The ratios also differ (Fig. 4).

The study of the type series of *Mennespirifer* revealed that this genus is invalid, because the type series of *M. menneri* (Ljaschenko, 1973, pl. 33, figs. 2–6) consists of *K. formosus* Ljaschenko (Ljaschenko, 1973, pl. 33, figs. 2–5) and juvenile *Uchtospirifer timanicus* Ljaschenko (Ljaschenko, 1973, pl. 33, fig. 6). Hence, the type series of the genus *Mennespirifer* is composed of specimens that belong to different genera.

Based on the revision of the type species of the genera *Echinospirifer, Komispirifer*, and *Mennespirifer*, the following conclusions were reached:

(1) Based on the similarity of the inner structures and microornamentation between *Echinospirifer* and *Komispirifer*, the latter is placed in the family Echinospiriferidae as a separate genus.

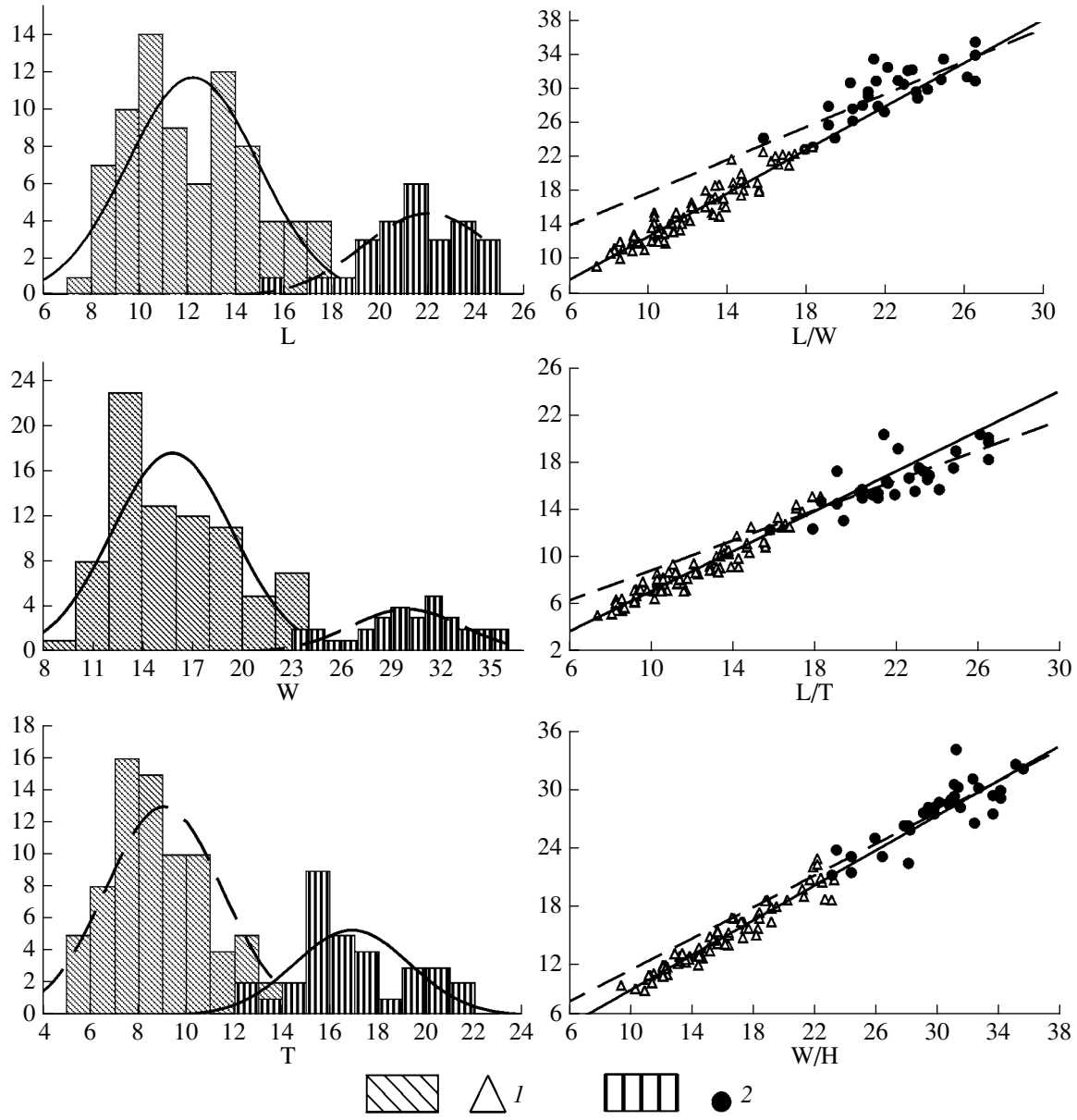


Fig. 4. Correlation diagrams of the absolute measurements (L, W, T) and ratios (L/W, L/T, W/H) of (*1*) *Komispirifer formosus* and (*2*) *Echinospirifer sublimes.* Designations (L) length of the ventral valve, (W) width, (T) thickness, and (H) length of the hinge line.

(2) The morphological similarity, successive appearance, and simultaneous existence of the two genera suggest their close phylogenetic relationships.

(3) The diagnosis of the genus *Mennespirifer* does not contain special features of an isolated spiriferid group. The majority of specimens of the type series belong to the genus *Komispirifer.* Therefore, *Mennespirifer* is considered to be a synonym of *Komispirifer.*

The new data received on the structure and microornamentation of *Echinospirifer* possibly require revision of the family Echinospiriferidae, in particular, the position of the genera *Adolfispirifer* Krylova, 1962; *Arctospirifer* Stainbrook, 1950; *Enchondrospirifer* Brice, 1973; *Hispidaria* Cooper et Dutro, 1982; *Howittia* Talent, 1956; *Indospirifer* Grabau, 1931; *Regauxia* Brice, 1988; and *Sergunkovia* Nalivkin, 1979, which were placed in this family by Carter *et al.* (1994). Among them, there are genera with, without, or with questionable delthyrial plate in the diagnosis. The microornamentation also varies.

MATERIAL

The structure of the shell layers and microornamentation were studied using a scanning electron microscope CamScan in the Paleontological Institute of the Russian Academy of Sciences.

The material is housed at the Collection Fund of the All-Russia Research Institute of Geology and Petroleum, Moscow (VNIGNI), coll. no. 30.

SYSTEMATIC PALEONTOLOGY

Superfamily Spinelloidea Johnson, 1970

Family Echinospiriferidae Ljaschenko, 1973

Genus *Echinospirifer* Ljaschenko, 1973

Echinospirifer: Ljaschenko, 1973, p. 109.

Type species. *Echinospirifer distinctus* Ljaschenko, 1973; southern Timan, Lower Frasnian, Ust'-Yarega Formation.

Diagnosis. Shell small or medium-sized, transversely elongated. Hinge line long. Lateral sides forming acute angles. Area low. Sulcus and fold well developed and costate. Ribs numerous. Microornamentation composed of small spines located on ribs along growth lamellae. Ventral valve containing long and wide dental plates. Delthyrial plate low, present only at early developmental stages. Dorsal valve with cardinal process, crural plates not reaching shell bottom, dental sockets elongated.

Species composition. Type species and *E. echinosus* (Ljaschenko); southern Timan; Upper Devonian, Frasnian.

Comparison. *Echinospirifer* is similar to *Regauxia* Brice, 1988 in microornamentation, which is formed of small spines on the shell surface, and differs in the larger, transversely elongated, acute-angled shell, a twice greater number of ribs, and in the low delthyrial plate. The genus considered differs from *Adolfispirifer* Krylova, 1962 and *Arctospirifer* Stainbrook, 1950 in the long and sharply cornered hinge line. It also differs from *Adolfispirifer* in the microornamentation and the presence of a delthyrial plate. *Echinospirifer* differs from *Arctospirifer* in the numerous lateral ribs and the absence of earlike outgrowths.

***Echinospirifer distinctus* Ljaschenko, 1973**

Plate 7, figs. 1–3

Cyrtospirifer sublimis: Ljaschenko, 1973, p. 86, pl. 26, figs. 3 and 4.

Echinospirifer distinctus: Ljaschenko, 1973, p. 109, pl. 26, figs. 1 and 2.

Mennespirifer tichonovischi: Ljaschenko, 1973, p. 103, pl. 33, fig. 1.

Holotype. VNIGNI AIL, no. 2401 [60/561], complete shell; southern Timan, 0.5 km of the mouth of the Yarega River; Upper Devonian, Middle Frasnian, Ust'-Yarega Formation.

Description (Figs. 1, 2, 5). The shell is medium-sized (L = 20–26 mm), transversely elongated, inflated, and equivalve. The hinge line is straight and long, equal to, or slightly shorter than the maximum shell width. The hinge line and the lateral side form an acute angle. The lateral commissures are rounded. The anterior margin is paraplicate.

The ventral valve is convex. The maximum convexity is situated posteriorly from the shell midline, closer to the umbonal region. The lateral slopes are slightly convex. The sulcus is deep and narrow, angularly rounded, sharply bordered laterally. It starts from the umbo and terminates at the anterior margin in the moderately high linguiform extension with angular and concave bottom and narrow and rounded apex. The umbo is low, wide, sharp, curved, and overhanging the dorsal valve. The area is triangular, long, moderately high, flattened in the lower region, and perpendicular to the commissural plane. In the upper region, the area is strongly concave with vertical hatching and horizontal growth lines. The apical angle is 110°–120°. The delthyrium is narrow and open, with narrow grooves along its edges. Its basal width is two-thirds of its height.

The dorsal valve is convex, with the maximum height near the anterior margin. The lateral slopes are moderately convex in the upper and middle regions and almost flat near the ears. The fold is relatively narrow, high, narrowly rounded, and sharply bordered by two grooves; it extends from the umbo and, reaching the anterior margin, terminates in a rounded angular linguiform extension. The umbo is small and curved.

The external ornamentation is formed by simple, rounded, and high radial ribs separated by equally wide or slightly narrower interspaces with a narrowly rounded bottom. The middle ribs are somewhat smoothed and dichotomizing. The number of lateral ribs is about 25 on the each side. The number of middle ribs is 8–10. Except the area, the shell is covered with closely spaced wavy concentric growth lines and small, elongated spines positioned along the growth lamellae.

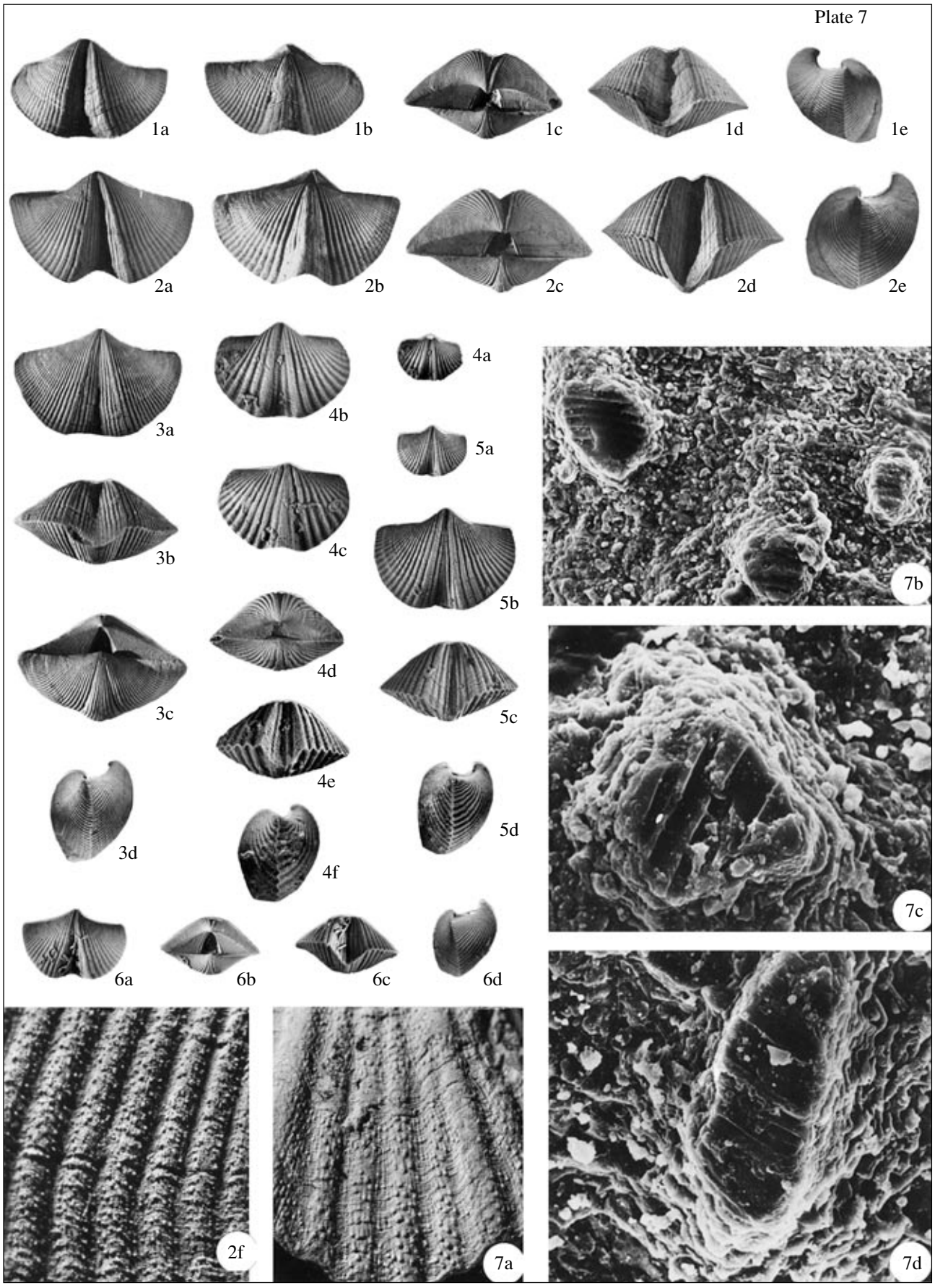
Inside the ventral valve, there are wide dental plates, which converge at a small angle and reach the midlength of the valve. The delthyrial plate is low and connects dental plates. It presents only at early developmental stages. The dorsal valve contains a lamellar bilobate cardinal process and crural plates, which terminate short of the shell bottom. The dental sockets are narrow and elongated (Fig. 5).

Dimensions in mm and ratios:

Specimen no.	L	W	T	L/W	L/T	AA
2903	20.3	27.8	15.1	0.73	1.84	120
2107	20.8	28.2	15.4	0.73	1.83	119
2903/2	21.1	29.8	15.5	0.70	1.92	126
Holotype 2401	22.6	31.2	16.8	0.72	1.85	127
2104	23.1	32.3	17.7	0.71	1.82	117
2903/1	24.8	31.3	17.7	0.79	1.75	112
3051	26.5	35.6	20.2	0.74	1.76	121

Variability. In the collection under study, shells are represented only by elongated morphotypes. The

Plate 7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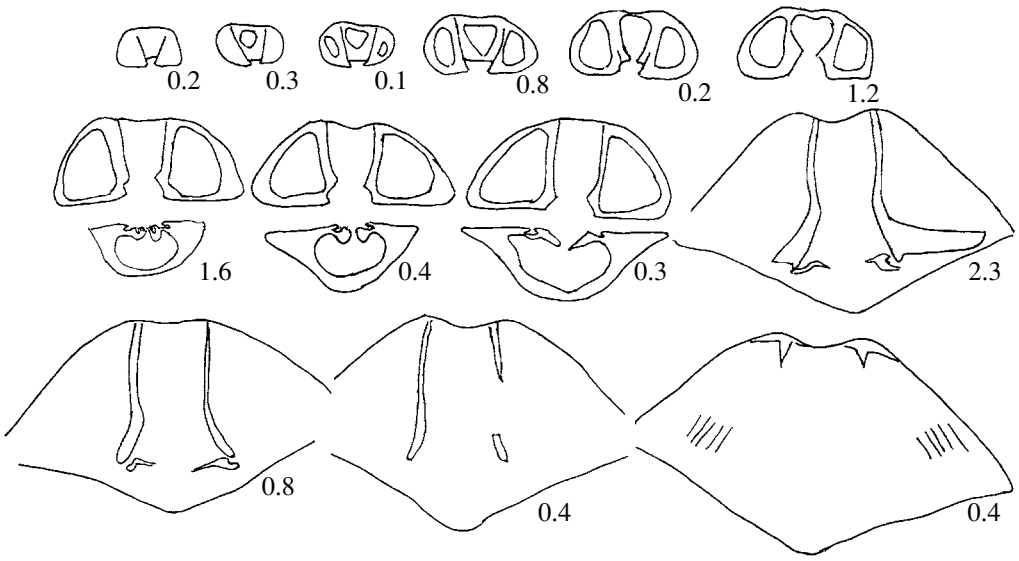

Fig. 5. Shell interior of *Echinospirifer sublimis* Ljaschenko; specimen VNIGNI AIL, no. 2107; southern Timan, 0.5 km of the mouth of the Yarega River, right bank; Upper Devonian, Frasnian Stage, Lower Ust'-Yarega Formation.

isometry ratio ranges from 0.71 to 0.79. The convexity varies from 1.75 to 1.92.

Comparison. The type species differs from *E. echinosus* (Ljaschenko) in the acute (rather than relatively short) ears and the curved umbo overhanging the dorsal valve.

Remarks. The specimens described as *M. tichonovischi* and *C. sublimis* (see synonymy) do not show significant differences from *E. distinctus* in their exterior, inner structure, and microornamentation. In addition to the morphological similarity, these species were described from the same layers (Lower Ust'-Yarega Formation) of the southern Timan. On this basis, they were regarded as synonyms of *E. distinctus.*

Material. Ten well-preserved specimens: 6 specimens come from the southern Timan, 0.5 km of the mouth of the Yarega River, right bank; 2 specimens are from the left bank of the Ukhta River, above the Neft'iol' River; and 2 specimens are from the Gerdiol' Creek, 0.5 km of its mouth; Middle Frasnian, Lower Ust'-Yarega Formation.

Genus *Komispirifer* Ljaschenko, 1973

Komispirifer: Ljaschenko, 1973, p. 105.

Mennespirifer: Ljaschenko, 1973, p. 101.

Type species. *Uchtospirifer formosus* Ljaschenko, 1960, southern Timan, Lower Frasnian; Upper Timanian Subhorizon.

Diagnosis. Shells small and medium-sized, semioval, transversely elongated, and ribbed. Hinge line slightly shorter than, or equal to maximum shell width. Sulcus and fold well developed, ribbed and angular. Area high. Ribs numerous. Microornamentation formed of small spines arranged along growth lines

Explanation of Plate 7

Figs. 1–3. *Echinospirifer distinctus* Ljaschenko; (1) specimen VNIGNI AIL, no. 2105 [60/536], compete shell (= *E. distinctus*; Ljaschenko, 1973, pl. 26, fig. 2), ×1: (1a) ventral valve; (1b) dorsal valve; (1c) posterior view; (1d) anterior view; and (1e) lateral view; southern Timan, 0.5 km of the mouth of the Yarega River; Upper Devonian, Frasnian, Ust'-Yarega Formation; (2) holotype VNIGNI AIL, no. 2401 [60/535], compete shell (= *E. distinctus*; Ljaschenko, 1973, pl. 26, fig. 1), ×1: (2a) ventral valve, ×1; (2b) dorsal valve, ×1; (2c) posterior view, ×1; (2d) anterior view, ×1; (2e) lateral view, ×1; (2f) fragment of microornamentation, ×10; (3) specimen VNIGNI AIL, no. 2104 [60/561], compete shell (= *C. sublimis*; Ljaschenko, 1973, pl. 26, fig. 4), ×1: (3a) ventral valve; (3b) anterior view; (3c) posterior view; (3d) lateral view; southern Timan, Ukhta River, 1 km above the mouth of the Neft'iol' River; the same age as above.

Figs. 4–7. *Komispirifer formosus* (Ljaschenko); (4) specimen VNIGNI AIL, no. 2057 [60/506], compete shell (= *K. acceptus*; Ljaschenko, 1973, pl. 35, fig. 7): (4a) ventral valve, ×1; (4b) ventral valve, ×2; (4c) dorsal valve, ×2; (4d) posterior view, ×2; (4e) anterior view, ×2; (4f) lateral view, ×2; southern Timan, oil well no. 1, interval 30–45 m; Upper Devonian, Frasnian, Upper Timanian Subhorizon; (5) specimen VNIGNI AIL, no. 2074, compete shell: (5a) ventral valve, ×1; (5b) ventral valve, ×2; (5c) anterior view, ×2; (5d) lateral view, ×2; the same locality and age; (6) holotype VNIGNI AIL, no. 2074 [60/381], compete shell (= *K. formosus*; Ljaschenko, 1973, pl. 35, fig. 1), ×1: (6a) ventral valve; (6b) anterior view; (6c) posterior view; (6d) lateral view; (7) specimen VNIGNI AIL, no. 2079, compete shell: (7a) fragment of microornamentation, ×10; (7b, 7c) cavity of small spines filled with fibers, transverse section, ×200 and ×600, respectively; (7d) longitudinal section of a spine and concentric growth lines at its base, ×600; the same locality and age.

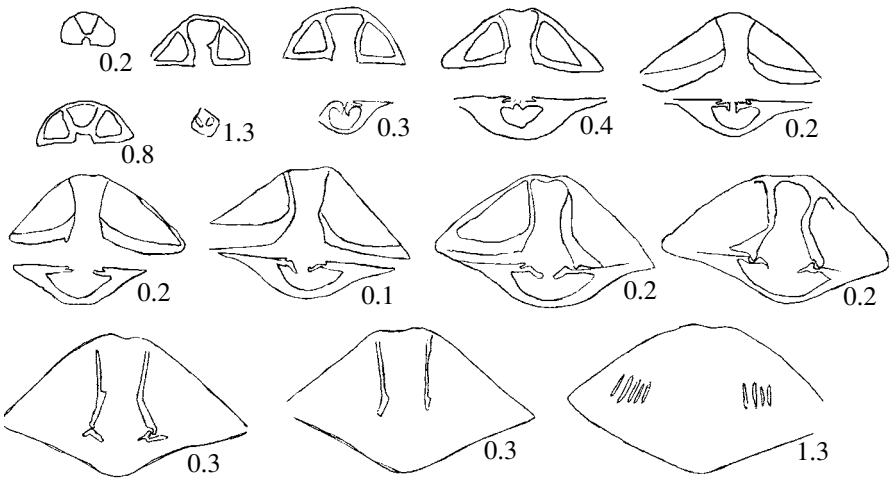

Fig. 6. Shell interior of *Komispirifer formosus* (Ljaschenko); specimen VNIGNI AIL, no. 7033; southern Timan, oil well no. 1, interval 30–45 m; Upper Devonian, Frasnian Stage, Upper Timanian Subhorizon.

on ribs in staggered rows. Inside ventral valve, delthyrial plate well developed.

Species composition. Type species.

Comparison. This genus differs from *Echinospirifer* in the smaller shell, well developed delthyrial plate, and microornamentation composed of small spines located on the robs in staggered rows rather than on along the marginal edge of the growth lamellae (as in *Echinospirifer*).

***Komispirifer formosus* (Ljaschenko, 1960)**

Plate 7, figs. 4–7

Uchtospirifer formosus: Ljaschenko, 1960, p. 25, pl. 7, figs. 1–5.

Mennespirifer menneri: Ljaschenko, 1973, p. 101, pl. 33, figs. 2–5.

Komispirifer formosus: Ljaschenko, 1973, p.105, pl. 35, figs. 1–5.

Komispirifer acceptus: Ljaschenko, 1973, p. 107, pl. 35, figs. 6 and 7.

Holotype. VNIGNI AIL, no. 2074 [60/381], complete shell; southern Timan, oil well no. 1, interval 35–40 m; Upper Devonian, Lower Frasnian, Upper Timanian Subhorizon.

Description (Figs. 3, 6). Shells are small or medium-sized (L = 10–16 mm), slightly convex, equivalve. The hinge line is straight, slightly shorter the maximum shell width. The ears are rounded, gradually passing into arched lateral commissures.

The ventral valve is strongly convex, rectangular, with the maximum height in the umbonal region. The lateral sides are slightly convex. The umbo is low and pointed. The area is triangular, moderately high, almost vertical, flattened in the lower region and slightly concave in the upper region. The apical angle is 106°–116°. The delthyrium is wide, open, with its height slightly exceeding the basal width and with narrow grooves along its edges. The area has vertical hatching and horizontal growth lines.

The sulcus is relatively narrow, moderately deep, well-pronounced, with an angularly rounded bottom, and bordered laterally by wider ribs. The sulcus starts from the umbo and terminates at the anterior margin with the angularly rounded linguiform extension.

The dorsal valve is elongated rectangular, slightly convex, with the maximum convexity situated close to the anterior margin. The umbo is low. The area is narrow and linear. The fold is moderately high, wide, gently sloping, and clearly bordered laterally by deep grooves. The fold starts from the umbo and gradually widens anteriorly.

The ornamentation is formed of simple, high, flatly rounded radial ribs, separated by interspaces of half their width. Each lateral side bears 15–18 ribs. The sulcus and the fold bear 6–8 thinner rounded ribs.

The microornamentation is represented by thin concentric growth lines and small spines arranged in staggered rows on the ribs along the growth lines. Each rib bears 4 to 6 small spines.

Inside the ventral valve, the dental plates are wide, converge at a small angle, and reach the midlength of the valve. The delthyrial plate connects the dental plates and covers the delthyrium, reaching the middle of its length. The dorsal interior contains the lamellar bilobate cardinal process, long crural plates, and narrow and elongated dental sockets (Fig. 6).

Dimensions in mm and ratios:

Specimen no.	L	W	T	L/W	L/T	AA
2071/9	6.6	10.2	5.1	0.64	1.54	113
2057	8.3	11.4	6.4	0.72	1.78	106
2976	10.3	15.7	8.6	0.65	1.82	116
Holotype 2074	12.2	16.8	9.1	0.72	1.84	109
1982	14.7	19.5	9.9	0.75	1.96	106
2061/3	16.4	22.2	12.6	0.73	1.76	116
2062	18.3	23.3	15.2	0.78	1.53	117

Ontogenetic changes. Small shells are semicircular, flattened, with a low area, while large shells become transversely expanded. As the shell grows, the area increases in height, the umbo changes from straight to slightly curved. The sulcus and the fold are well-pronounced only in large shells.

Variability. Two morphotypes are present in the collection: more inflated with gently rounded lateral sides and more transversely expanded with angularly rounded lateral sides. The transversely expanded morphotype prevails in the collection, with the isometry ratio ranging from 0.64 to 0.78. The convexity ratio ranges from 1.54 to 1.84, while the extent of circularity varies insignificantly from 1.11 to 1.26.

Remarks. *Komispirifer acceptus* is considered to be invalid, because it is a morphological variety of the species *K. formosus.* These varieties differ only in the convexity and circularity of the shell and are usually found in the same localities and layers in equal number. Thus, *K. acceptus* is a junior synonym of the species *K. formosus.*

Occurrence. Upper Devonian, Lower Frasnian, Upper Timanian Subhorizon; southern Timan.

Material. Over 200 well-preserved complete shells: oil well no. 1, interval 35–40 m; oil well no. 2, interval 50–70 m; Ukhta River, 200 m below the mouth of the Neft'iol' River.

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