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Revision of Spiriferid Brachiopods of the Family Uchtospiriferidae from the Devonian of Southern Timan

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Abstract—Spiriferid brachiopods of the family Uchtospiriferidae are revised based on the restudy of the original material from the memorial collection of A**.I.** Ljaschenko. The fact that the changes in the shell micro-ornamentation of *Uchtospirifer* are controlled both by the ontogenetic development and the degree of preservation is reported for the first time. The variability of the external morphology of spiriferid shells is studied on the basis of biometric analysis. The taxonomic revision results in the recognition of *Timanospirifer, Nordispirifer, Clivospirifer,* and *Acutella* as junior synonyms of the genus *Uchtospirifer.* The description of the type species of the genus, *Uchtospirifer nalivkini,* is supplemented by new observations.

Key words: brachiopods, Spiriferida, micro-ornamentation, Devonian, Frasnian, Timan, Russia.

INTRODUCTION

The genus *Uchtospirifer* was established by A.I. Ljaschenko in 1957 with the type species *U. nalivkini* Ljaschenko, 1957. Later, in the description of *U. nalivkini* and new species, *U. timanicus* and *U. angulosus,* Ljaschenko (1958) pointed out that the shape of the shell, sinus, and fold and micro-ornamentation vary widely. He also introduced features of micro-ornamentation into the definition of species (Ljaschenko, 1959, 1969). In a more recent paper (Ljaschenko, 1973), he used such characters as the form of the shell, sinus, and fold and the pattern of micro-ornamentation as a basis for the definition of the genera *Timanospirifer, Mennespirifer, Clivospirifer, Komispirifer,* and *Acutella.* The species that were earlier described within the genus *Uchtospirifer* became type species of the new genera (Table 1). Ljaschenko placed the genus *Acutella* into the family Spinocyrtidae and all the other genera together with a new genus, *Nordispirifer* Ljaschenko, 1973, into the family Uchtospiriferidae.

Talent and Gratsianova (1988) pointed to the morphological similarity of the new genera. These authors suggested that the only valid taxon assignable to the family Cyrtospiriferidae Termier et Termier, 1949 is the genus *Uchtospirifer,* all the others being junior synonyms of the earlier described genera. Thus, they listed *Mennespirifer* and *Komispirifer* as synonyms of *Cyrtospirifer. Timanospirifer, Nordispirifer,* and *Clivospirifer* were synonymized with *Uchtospirifer.* The genus *Acutella* was synonymized with *Spinocyrtia* (Talent and Gratsianova, 1988).

In their new classification of spiriferids, Carter *etal.* (1994) recognized *Uchtospirifer, Mennespirifer,* and *Acutella* as valid members of the family Cyrtiopsinidae Ivanova, 1972. The other genera were placed into the synonymy of the first two genera: *Uchtospirifer (= Timanospirifer, Nordispirifer,* and *Clivospirifer)* and *Mennespirifer (= Komispirifer).*

Thus, *Uchtospirifer* is recognized as valid by the cited researchers, whereas the genera *Timanospirifer, Mennespirifer, Nordispirifer, Komispirifer, Clivospirifer,* and *Acutella* are variably regarded as junior synonyms of other genera, including the genus *Uchtospirifer.* These contradictory opinions account for analyses of incomplete data contained in the published sources.

I had a possibility to revise the above-listed spiriferid forms (Oleneva, 2003). They are represented by the type materials of the memorial collection of Ljaschenko stored at the Collection Department of the All-Russia Research Institute of Petroleum Geology (VNIGNI). Similarities and dissimilarities of the genera were investigated on the basis of a detailed study of their micro-ornamentation. Below the micro-ornamentation is described according to the original diagnoses made by Ljaschenko (1973); this description is followed by new data acquired in the course of the present revision.

Uchtospirifer. "In case of good preservation, the surface of plications and interspaces bears micro-ornamentation of longitudinal and transverse, frequently reticulate, striae. Sometimes the longitudinal striae bear small spines or elongated tubercles" (Ljaschenko, 1973, p. 89). The description of the type species *U. nalivkini* (Ljaschenko, 1973, p. 80) adds ".. .longitudinal striae converge toward the tops of the ribs at small angles."

Table 1. Changes in the taxonomic position of species of the genus *Uchtospirifer*

Ljaschenko, 1957-1969		Ljaschenko, 1973		Oleneva, 2003	
Uchtospirifer	*nalivkini* Ljaschenko, 1957	—•	*Uchtospirifer,* 1957	*Uchtospirifer*	*nalivkini*
	timanicus Ljaschenko, 1958	—»•	*Timanospirifer,* 1973		*timanicus*
	angulosas Ljaschenko, 1958	—-	*Acutella,* 1973		*angulosus*
	clivosus Ljaschenko, 1969	—*	*Clivospirifer,* 1973		*clivosus*
	menneri Ljaschenko, 1959	—-	*Mennespirifer,* 1973		-
	formosus Ljaschenko, 1960	—•	*Komispirifer,* 1973		-

Table 2. Micro-ornamentation features after A. I. Ljaschenko

Diagnostic characters of the genera	*Uchto-spirifer*	*Timano-spirifer*	*Menne-spirifer*	*Nordi-spirifer*	*Komi-spirifer*	*Clivo-spirifer*	*Acutella*
Longitudinal striae	+	+	+	-	+	-	+
Concentric growth lines	+	+	+	+	+	-	+
Longitudinal striae converge	+	+	-	-	-	-	+
Tubercles	+	+	+	+	+	+	+
Tubercles converge	-	-	-	-	-	+	-

\+ character is present in the diagnosis of the genus.
\- character is absence in the diagnosis of the genus.

Timanospirifer. "The surface is covered with a micro-ornamentation of longitudinal striae, converging at small angles, and thinner wavy concentric striae" (Ljaschenko, 1973, p. 92). In the description of *T. exelsus* Ljaschenko noted that "in case of perfect preservation the longitudinal striae preserve small tubercles" (Ljaschenko, 1973, p. 95).

Mennespirifer. "In case of perfect preservation the shell bears weakly radial striae and, occasionally, small tubercles." The type species *M. menneri* is noted to have its surface covered with very thin, intermittent, longitudinal, nearly parallel striae. When perfectly preserved, the striae show small elongated tubercles, which are aligned in a row (Ljaschenko, 1973, p. 102).

Nordispirifer. The micro-ornamentation is characterized by ".. .the presence of distinct tubercles and the absence of longitudinal and concentric striae." This diagnosis does not match the description of the micro-ornamentation of the type species, *N. celeber,* which has "plications and interspaces covered with small elongated tubercles and numerous thin tightly spaced growth lines" (Ljaschenko, 1973, p. 105).

Komispirifer. "When well preserved, plications bear small elongated tubercles, which are aligned in longitudinal rows" (Ljaschenko, 1973, p. 105). The type species, *K. formosus,* is described as "occasionally having thin, weakly developed longitudinal striae" (Ljaschenko, 1973, p. 106).

Clivospirifer. The type species, *C. clivosus,* has the following micro-ornamentation: "The flank plications and interspaces, as well as the fold and sinus, bear numerous small elongated tubercles, which are aligned in longitudinal, somewhat converging rows. On the plications they converge anteriorly; in the grooves, toward the apex" (Ljaschenko, 1973, p. 109).

Acutella. "The plications and interspaces, as well as the sinus and fold, are covered with thin longitudinal, typically converging striae (micro-plications) and still thinner concentric striae" (Ljaschenko, 1973, p. 119). The micro-ornamentation of *A. acuminata* (Ljaschenko, 1973, p. 120) and *A. mucronata* (Ljaschenko, 1973, p. 124) shows itself in the presence of short spines and thin elongated tubercles on radial striae.

To facilitate the discussion, all above-listed features of micro-ornamentation are summarized in Table 2. The table shows that, according to Ljaschenko's data, the micro-ornamentation coincides in the genera (1) *Uchtospirifer, Timanospirifer,* and *Acutella* and (2) *Mennespirifer* and *Komispirifer.*

The revision has showed that micro-ornamentation patterns change in the course of ontogeny and depend on the degree of preservation of the shell layer.

DISCUSSION

Ontogenetic Changes of Micro-ornamentation

The basic elements of micro-ornamentation in *Uchtospirifer* are narrow (0.06-0.1 mm wide) weakly convex riblets (striae) and still thinner concentric growth lines (14 or 15 per mm) (PI. 7, figs. 3, 4, 10). Young specimens of *Uchtospirifer* (shell lengths no more than 15-20 mm) have tightly spaced plications.

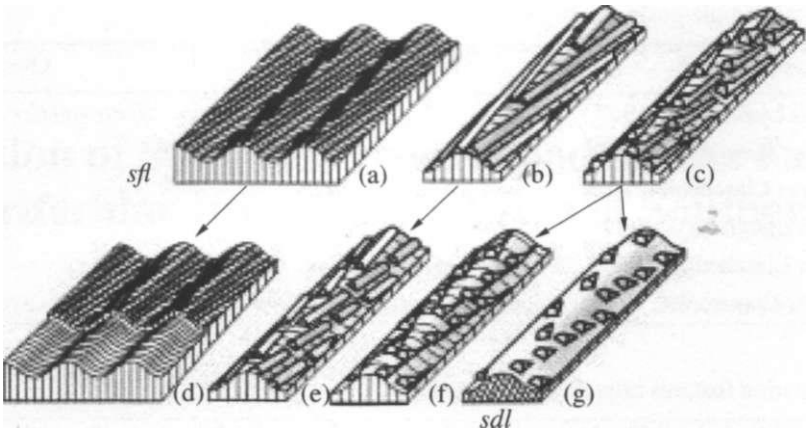


Fig. 1. Changes in the micro-ornamentation of *Uchtospirifer*. (a)-(c) in ontogeny; (d)-(g) due to the destruction of the surface layer. Designations: *(sfl)* surface layer; *(sdl)* secondary layer.

At the anterior edge of the shell, each plication bears four to six striae. Along the entire length of the shell, the number of striae and the width of intervals between them remain constant.

During the next growth stage (shell length more than 20 mm), the plications and interspaces gradually widen. At a distance of 15 mm from the apex, each 5 mm of the shell surface bear about seven plications; closer to the anterior edge, up to four plications. The widening and enlargement of plications change the direction of striae alignment. They meet on plications at acute angles (6°-10°). The number of striae in interspaces increases by the intercalation. Close to the anterior edge of large shells, a plication can have 10 to 14 striae, i.e., up to 15 striae per 1 mm.

The subsequent complication of the micro-ornamentation proceeds through the appearance of elongated or nodular tubercles. Tubercles are more common on striae occurring on plications and less frequent in interspaces. There is no observable relationship between tubercles and concentric growth lines.

Tubercles are formed by elongation and fracturing of a stria perpendicularly to the shell's surface. In the fracture point the stria expands forward and upward and forms a low stepped ledge, or a tubercle (PI. 7, figs. 4a-4c; Fig. lc). The base of the tubercle is equal to or slightly wider than the parental stria. Tubercles vary in length from 0.1 to 0.5 mm. Differences in the height and width of their basal parts result in different shapes of tubercles: droplike (PI. 7, fig. 5); elongated (PI. 8, fig. la); or elevated, shaped like a rounded nodule (PI. 7, fig. 4a). Axial parts of tubercles sometimes bear indistinct relics of the central channel (PI. 8, fig. 2). At the point of interruption, some distance away from the tubercle's ledge or sometimes its base (PI. 7, figs. 4b, 4c), the stria reappears uniform and continuous, thus giving an impression of its continuity.

It is noteworthy that tubercles are rather rare in *Uchtospirifer* and occur only in specimens with a well-preserved external surface. The tubercles' arrangement lacks regularity. Most frequently they concentrate close to the anterior edge of adult, large shells (PI. 7, figs. 2,4a).

Changes in Micro-ornamentation Associated with the Degree of Preservation

As noted above, the micro-ornamentation of *Uchtospirifer* is formed by a combination of radial and concentric elements that produce a fine, reticulate pattern (PI. 7, figs. 3,4; Fig. la). Partial damage to the surface layer gives an impression of a lack of radial elements and the presence of only concentric ornamentation (PI. 7, fig. 10; Fig. Id). Moreover, the processes of dissolution or abrasion variably destroy the finest striae and can form intermittent, dotted lines that appear as elongated or "false" tubercles (PI. 7, fig. 7; Fig. le). In the case of the worse preservation of the shell layer, when both radial and concentric elements are obliterated, tubercles appear as pointlike rounded structures aligned in dotted rows. Being higher, the tubercles form lines converging on the tops of plications (PI. 7, fig. 6; Figs. If, lg). Thus, they mimic the typical micro-ornamentation of uchtospiriferids.

To improve understanding of the micro-ornamentation of *Uchtospirifer*, the shell structure was studied. The study was based on ventral valves of *U. nalivkini* (PI. 8, fig. 1) and *U. rotundas* (PI. 7, fig. 4) with a well-preserved shell layer.

The shell of *Uchtospirifer* consists of the surface, fibrous, and prismatic layers. Obliteration of the surface layer strongly levels the striae, up to their complete disappearance, and exposes the inner layers.

The fibrous layer has a coarsely crystalline texture. Fibers are oriented at a small angle to the valve surface and have an elongated oval, almost needlelike or irregular form (PI. 8, figs. 3a-3d). The width of fibers measured along the long axis is up to 10 um, their thickness measured along the short axis amounts to 3-4 ***im.** The

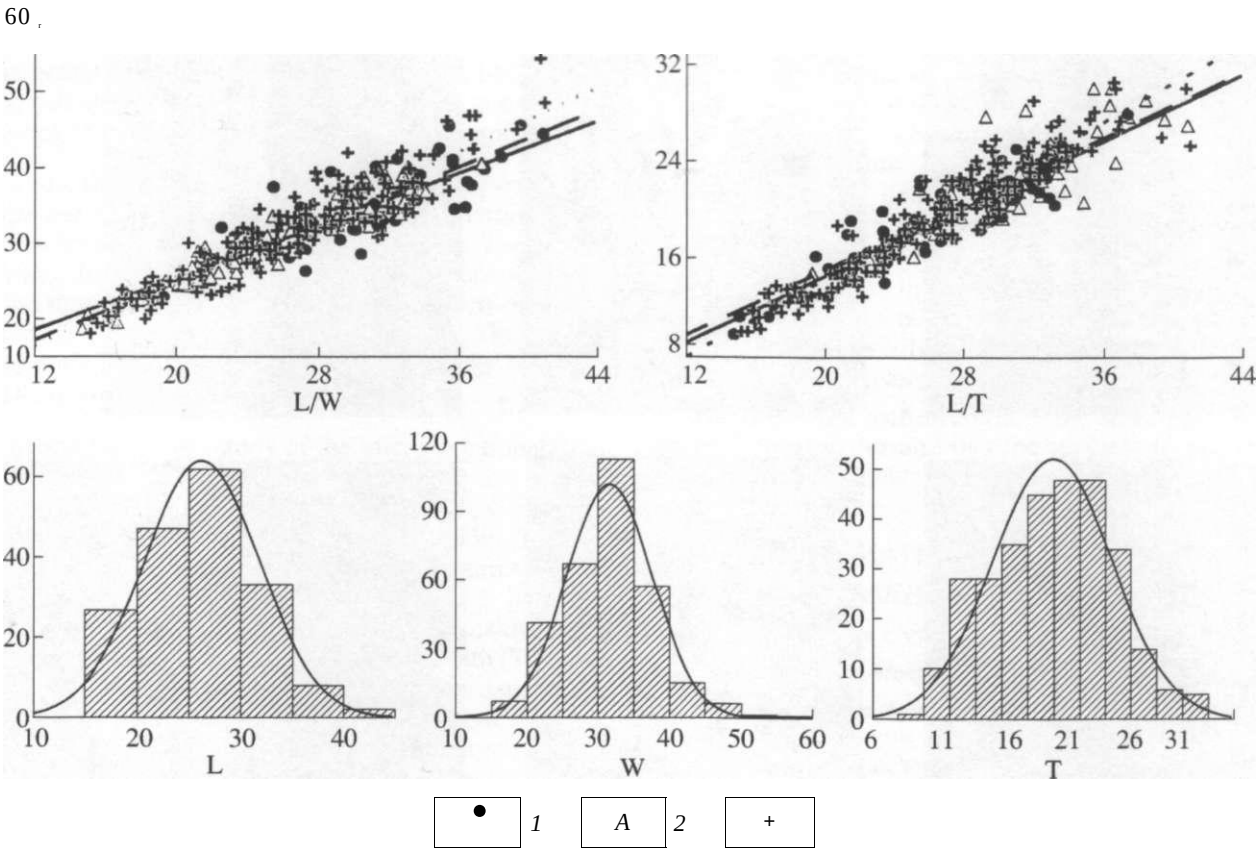


Fig. 2. Scatter diagram (LAV, L/T) and histograms of the main measurements (L, W, T) in the complete sample (n = 330) of the type species *(1) Uchtospirifer,* (2) *Timanospirifer,* and *(3) Acutella.*

width of the fibrous layer varies from 400 um to considerably lower values of 250-300 um in interspaces.

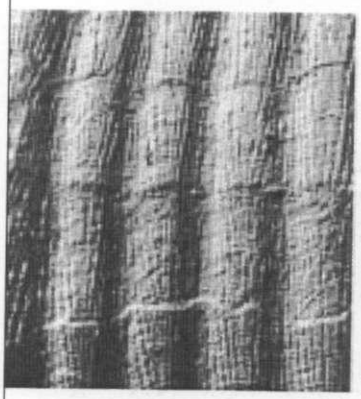
The Prisms of the prismatic layer appear differently depending on the orientation of the section, i.e., frontal (PI. 8, fig. 3e) or longitudinal (PI. 8, fig. 3g). Tangential sections show crystallites oriented at a small angle to the valve surface and arranged in parallel rows. Relatively larger crystallites have an elongated rectangular, or narrow, nearly needlelike shape. Less frequently they are interconnected by short transverse prisms (PI. 8, fig. 3e). In longitudinal shears prisms look like flattened, low trapezoids with the outer surface shaped as longitudinal carinated elevations (PI. 8, fig. 3d, top). The relative dimensions of prisms typically vary: in length from 10 to 35 Jim and in width from 4 to 6 um. The overall thickness of the prismatic layer reaches 200 u.m.

Comparison between the micro-ornamentations of the above-discussed genera has showed that *Timanospirifer, Nordispirifer, Clivospirifer,* and *Acutella* have a pattern similar to that of *Uchtospirifer* (PI. 7, figs. 7,10). The genera *Clivospirifer* and *Nordispirifer* exemplify the overestimated importance of micro-ornamentation details. The type species of the genera *Clivospirifer, C. clivosus* (Ljaschenko, 1969), and *Nordispirifer, N. celeber* (Ljaschenko, 1973), are based on specimens with varying degrees of the micro-ornamental preservation. Among them, *C. clivosus* has the worst preservation (PI. 7, fig. 6). In the absence of radial and concentric micro-ornamentations, the elevated tubercles form dotted rows converging on the tops of plications. As already mentioned, the diagnosis of the genus *Nordispirifer* refers to the absence of concentric striae, whereas the type species *N. celeber* has both elongated droplike tubercles and concentric growth lines, which are well preserved in the interspaces (PI. 7, fig. 5).

The genus *Acutella* is not a synonym of *Spinocyrtia* as suggested by Gratsianova and Talent. Likewise, it cannot be assigned to Spinocyrtidae because the genus has characters that do not match the diagnosis of the type genus of the family. Contrary to *Spinocyrtia, Acutella* has a delthyrium with well-developed deltidial plates and smoothed plications in the sinus and on the fold. Its micro-ornamentation is similar to that of *Uchtospirifer* (PI. 7, figs. 2, 3).

The shell shape and micro-ornamentation of the type specimens of the genera *Mennespirifer* and *Komispirifer* do not fit the diagnosis of the family Uchtospiriferidae, to which these genera were assigned. Representatives of these genera differ from the type genus, *Uchtospirifer,* in having transversely expanded shells of small and medium size, with angular rather than rounded cardinal angles, low ventral inter-

Plate 7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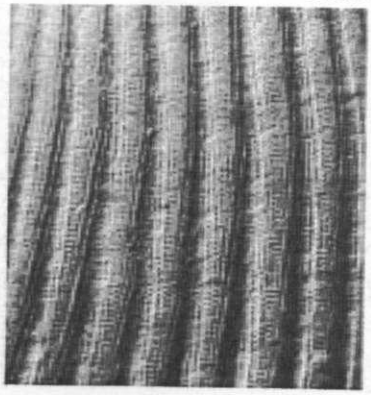
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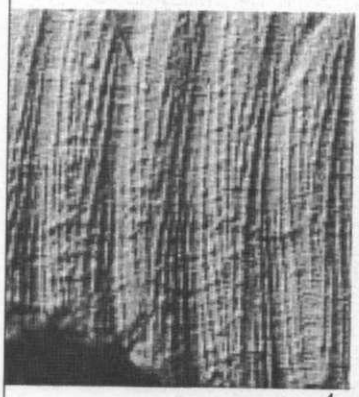
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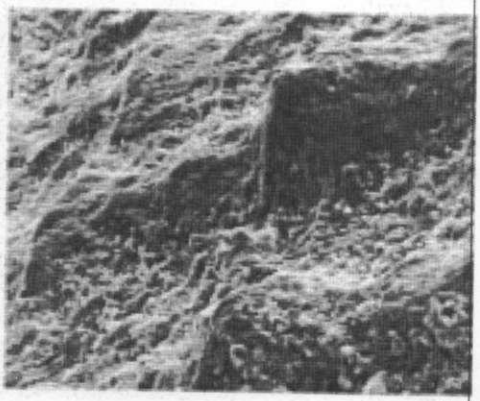
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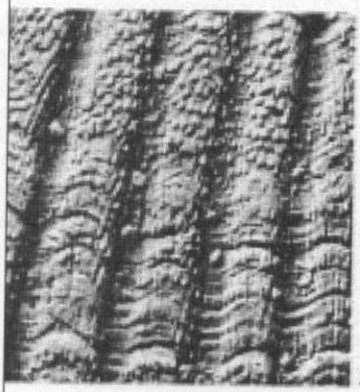
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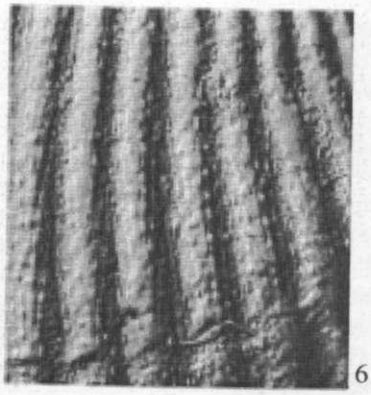
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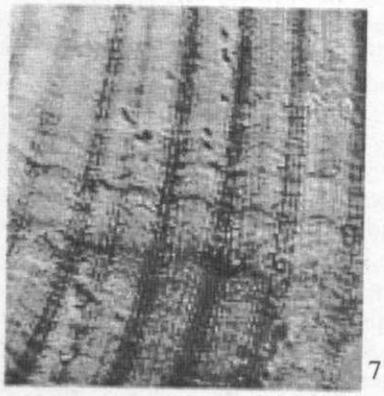
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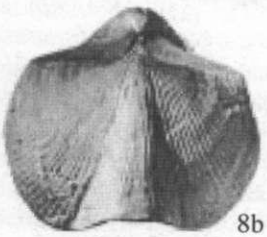
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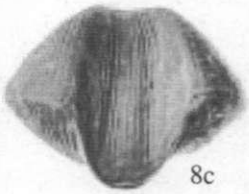
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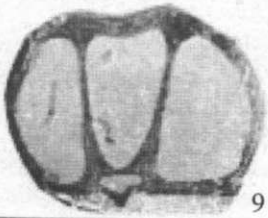
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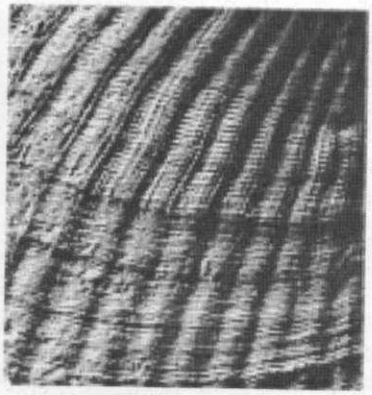
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area, and a delthyrial opening that always remains unclosed being devoid of deltidial plates. The micro-ornamentation is represented by concentric lines, tubercles, and striae that are parallel and do not converge on the tops of plications as in the genus *Uchtospirifer.*

Thus, the genera *Timanospirifer, Nordispirifer, Clivospirifer,* and *Acutella* have micro-ornamentations similar to that of the genus *Uchtospirifer.* The genera *Mennespirifer* and *Komispirifer* differ from members of the family Uchtospiriferidae in the micro-ornamentation, shape, and morphology of shells. These close genera are similar to the genus *Cyrtospirifer* Nalivkin, 1918 and are not addressed thereafter.

In addition to the study of the micro-ornamentation, the inferred close affinities between the genera *Uchtospirifer, Timanospirifer, Nordispirifer, Clivospirifer,* and *Acutella* were checked biometrically. The statistical sample complies with the main requirements of biometry. In each specimen the following measurements were taken: length (L), width (W), thickness (T), length of the cardinal margin (H), sinal width (Ws), and length of the linguae extention (LL). All measurements are accurate to 0.1 mm. The complete sample from the type localities included specimens of the type species of *Uchtospirifer* (n = 52), *Timanospirifer* (n = 170), *Acutella* (n = 83), *Nordispirifer* (n = 2), and *Clivospirifer* (n = 6). The values of L, W, and T and their ratios (LAV, L/T) were represented diagrammatically with the use of the STATISTICA software package, which was developed by StatSoft Inc.

Histograms (Fig. 2) indicate that the values of L, W, and T of the complete sample have normal distributions and show nearly symmetrical unimodal curves'. Bivariate diagrams of LAV and L/T show a high positive correlation of the parameters (R equals 0.92 and 0.93, respectively) and low values of standard deviation (Sd= 0.07, for LAV; Sd = 0.12, for L/T). The data points are clustered closely about the estimated regression lines.

These statistical parameters suggest that the complete sample consists of closely related brachiopods. The type specimens of *Timanospirifer, Nordispirifer, Clivospirifer,* and *Acutella* are similar to the type species of the genus *Uchtospirifer* in the body plan and micro-ornamentation. Therefore, these taxa are junior synonyms of the genus *Uchtospirifer.* Members of Spinocyrtidae have not been found in the Timanian deposits.

It is worth noting that the material under study originates from localities restricted to a small area along the Uchta River and its tributaries, the Neft'yole, Polovinny Yole, and Yarega Rivers in Southern Timan (Fig. 3).

The following section contains the description of the genus *Uchtospirifer* and its type species, *U. nalivkini,* supplemented by new observations.

SYSTEMATIC PALEONTOLOGY

Family Cyrtospiriferidae Termier and Termier, 1949

Subfamily Cyrtiopsinae Ivanova, 1972

Genus *Uchtospirifer* Ljaschenko, 1957

Uchtospirifer: Ljaschenko, 1957, p. 885; 1958, p. 148; 1959, p. 247; 1973, p. 88; Ivanova, 1960, p. 266; Vandercammen, 1967, p. 3;

Timanospirifer: Ljaschenko, 1973, p. 92;

Nordispirifer: Ljaschenko, 1973, p. 104;

Clivospirifer. Ljaschenko, 1973, 108;

Acutella: Ljaschenko, 1973, p. 119.

Type species. *Uchtospirifer nalivkini* Ljaschenko, 1957, Southern Timan; Lower Frasnian, Timanian Horizon.

Diagnosis. Shells from medium to large size, elongated oval, both valves moderately or strongly inflated. Cardinal margin straight, shorter than maximal shell width. Cardinal angles blunt, less frequently right, lateral sides rounded. Apex of ventral valve high, variably curved. Ventral interarea moderately high, flat or variably concave. Delthyrial opening uncovered or partly covered by deltidium plates. Fold and sinus broad, from gently rounded to angular triangular. Sur-

Explanation of Plate 7

Figs. 1,8, and 9. *Uchtospirifer nalivkini* Ljaschenko: (1) specimen VNIGNI AIL, no. 1937, fragment of micro-ornamentation, xlO; Southern Timan, village of Yarega, oil mine no. 1, depth 80-85 m; Lower Frasnian, Lower Timanian Subhorizon; (8) holotype VNIGNI AIL, no. 1916 [60/365], complete shell, xl (Ljaschenko, 1973, pi. 27, fig. 2); (8a) ventral valve; (8b) dorsal valve; (8c) frontal view; (8d) lateral view; same age; (9) specimen VNIGNI AIL, no. 1918, ventral interior, x5; same age.

Figs. 2 and 3. *Uchtospirifer angulosus* Ljaschenko: (2) specimen VNIGNI AIL, no. 2539 [60/391], fragment of micro-ornamentation, xlO (= holotype of *Acutella acuminata* Ljaschenko, 1973, pi. 40, fig. 5); Southern Timan, village of Yarega, oil mine no. 1, depth 55-56 m; Lower Frasnian, Upper Timanian Subhorizon; (3) specimen VNIGNI AIL, no. 2522, fragment of micro-ornamentation, xlO *{Acutella angulosa* Ljaschenko, 1973, pi. 42, fig. 1; Southern Timan, village of Domanik, oil mine no. 2, depth 50-75 m; same age.

Figs. 4 and 6. *Uchtospirifer rotundus* Ljaschenko: (4) specimen VNIGNI AIL, no. 2020, fragment of micro-ornamentation: (4a) tubercles near the frontal margin, xlO; (4b) striae and tubercles, x500; (4c) lateral view of a tubercle, x600; oil mine no. 1, depth 35^-5 m, same age; (6) specimen VNIGNI AIL, no. 2055 [32/237], fragment of micro-ornamentation, xlO (= *Clivospirifer clivosus* Ljaschenko, 1973, pi. 34, fig. 3, same location and age).

Figs. 5, 7, and 10. *Uchtospirifer timanicus* Ljaschenko: (5) specimen VNIGNI AIL, no. 2054 [60/466]. fragment of micro-ornamentation, x20 (= holotype of *Nordispirifer celeber* Ljaschenko, 1973, pi. 34, fig. 1); oil mine no. 2. depth 50-70 m. same age; (7) VNIGNI AIL, no. 1845, xlO; oil mine no. 1, depth 30-40 m, same age; (10) VNIGNI AIL, no. 1839, fragment of micro-ornamentation, xlO, same age.

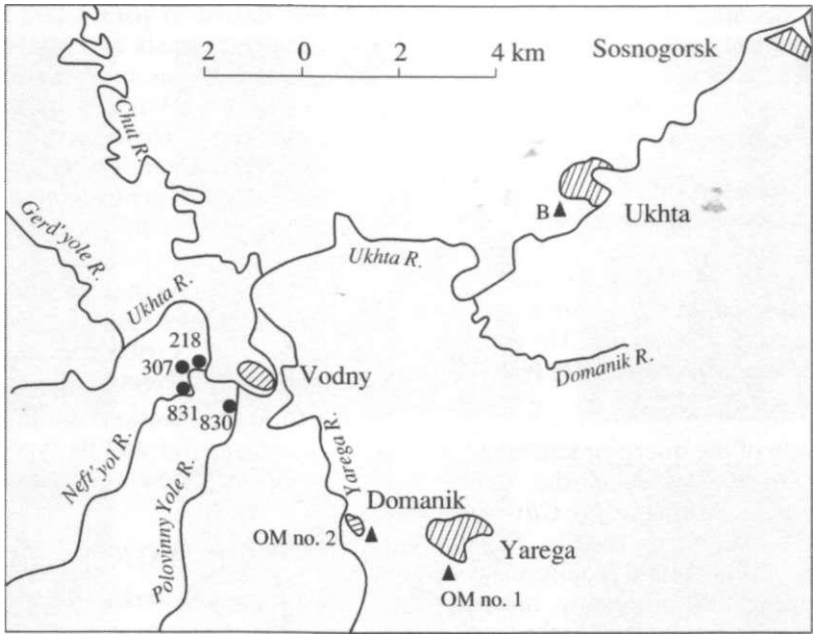


Fig. 3. Schematic map of the localities with *Uchtospirifer* in Southern Timan: **(7)** nos. of exposures; (2) oil mine; *(3)* balneology borehole.

face ornamentation consists of numerous plications, strongly smoothed on fold and sinus up to complete disappearance. Micro-ornamentation consists of striae converging on tops of plications at acute angles and concentric striae. Radial micro-ornamentation occasionally complicated by tubercles. Interior of ventral valve contains dental plates connected by delthyrial plate. Apical thickening not developed. Crural plates of dorsal valve fuse at base of cardinal process. Cardinal process lamellar, bifurcate.

Composition. The genus *Uchtospirifer* comprises about ten species. Among them, in addition to the type species *U. nalivkini (= U. solnzevi* Ljaschenko, *U. concentricus* Ljaschenko), the Frasnian deposits are characterized by *U. timanicus (= Timanospirifer kruglovi* Ljaschenko, *Spinocyrtia recta* Ljaschenko, *S.* ex gr. *eurutenes* Owen, *S. spatiosa* Ljaschenko, *Nordispirifer celeber* Ljaschenko); *U. clivosus (= Timanospirifer optatus* Ljaschenko, *T. exelsus* Ljaschenko, *Spinocyrtia uchtensis* Ljaschenko, 5. *uchtensis* var. *aperta* Ljaschenko); *U. angulosus (= Acutella neftiolica* Ljaschenko, *A. mucronata* Ljaschenko, *A. acuminata* Ljaschenko, *A. lepida* Ljaschenko); *U. rotundus (= Spinocyrtia globosa* Ljaschenko). Also known are *U. baituganicus* from the Frasnian of the Volga-Urals region, and *U. murchisoniana* (Verneuil) and *U. bironensis* Vandercammen from the Frasnian of Belgium and France.

Comparison. This genus differs from the genus *Cyrtospirifer* Nalivkin (Nalivkin, 1918, p. 123) in the short cardinal margin, absence of elongated cardinal angles, rounded flanks, presence of deltidial plates, and the character of micro-ornamentation. It differs from *Cyrtiopsis* Grabau (Grabau, 1923-1924, p. 195) in the missing foramen in the top of the pseudodeltidium and in the micro-ornamentation composed of striae converging on tops of plications instead of longitudinal striae as in *Cyrtospirifer* and *Cyrtiopsis.*

***Uchtospirifer nalivkini* Ljaschenko, 1957**

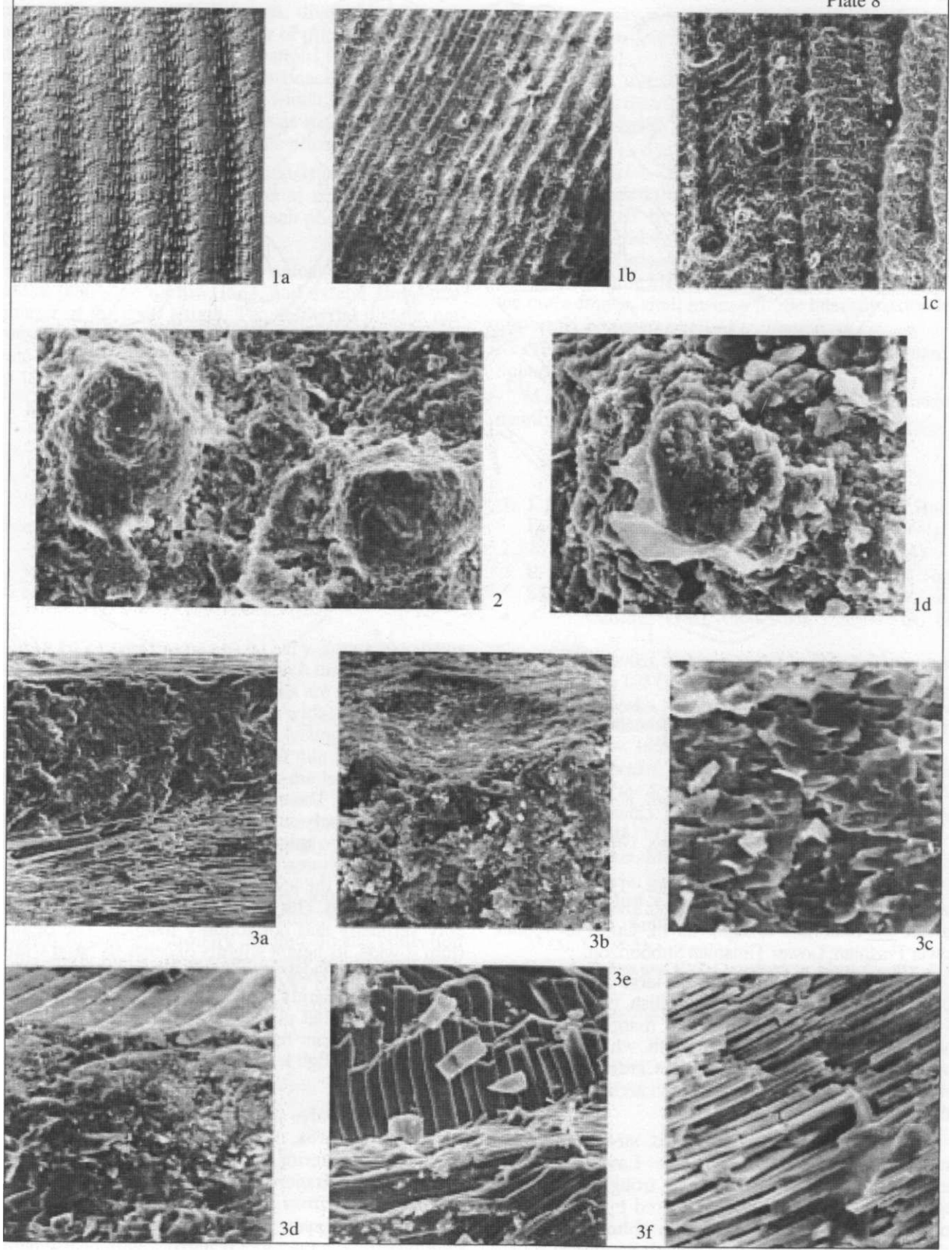
Plate 7, figs. 1, 8, and 9; Plate 8, figs. 1 and 3

Uchtospirifer nalivkini: Ljaschenko, 1957, p. 885, pi. 1, fig. 1; 1958, p. 148, pi. 11, figs. 1-3; 1959, p. 122, pi. 14, fig. 1-9; 1973, p. 88, pi. 27, figs. 1-7; pi. 51, fig. 2;

Explanation of Plate 8

Figs. 1 and 3. *Uchtospirifer nalivkini* Ljaschenko: (1) specimen VNIGNI AIL, no. 1917 [60/371] (= *Uchtospirifer nalivkini,* Ljaschenko, 1973, pi. 27, fig. 7): (la-Id) fragments of micro-ornamentation, xlO, x300, x500, and x900; (3) structure of the shell layer: (3a) juncture of fibrous and prismatic layers, x250; (3b) fragment of external surface and fibrous layer, x650; (3c) fibrous layer, x800; (3d) fibrous layer (below) and transverse section of prismatic layer (above), x540; (3e, 3f) prismatic layer, x450 and x900; Southern Timan, village of Yarega, oil mine no. 1, depth 80-85 m, Lower Frasnian, Lower Timanian Subhorizon.
Fig. 2. *Uchtospirifer rotundus* Ljaschenko: specimen VNIGNI AIL, no. 2020, fragment of micro-ornamentation, x900; Designations: (CO central channel, see Plate 7, fig. 4.

Plate 8



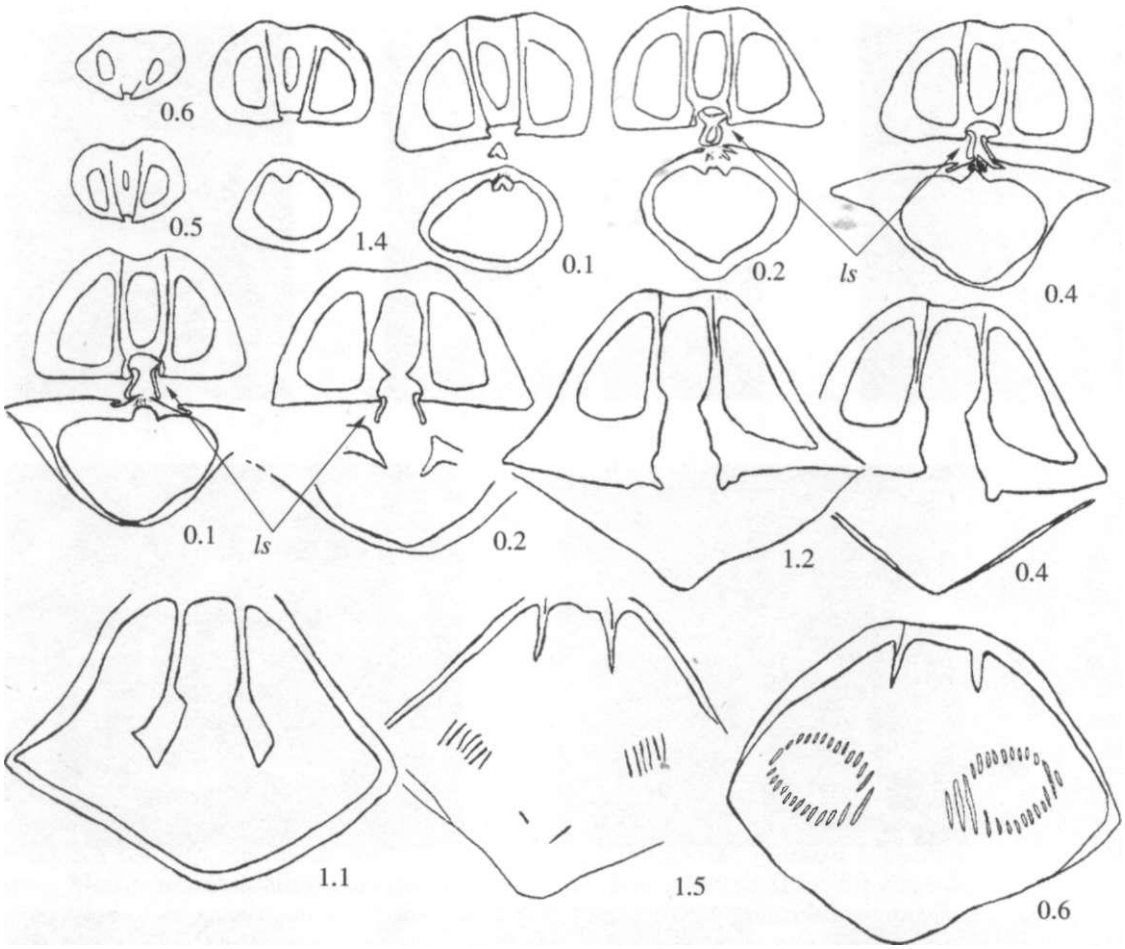


Fig. **4.** Internal structure of *Uchtospirifer nalivkini* Ljaschenko; VNIGNI AIL, no. 1918; L = 26.3 mm; *(Is)* longitudinal section of the high deltidial plate.

Uchtospirifer solnzevi: Ljaschenko, 1969, p. 50, pi. 10, fig. 2; 1973, p. 90, pi. 28, figs. 2 and 3;

Uchtospirifer concentricus: Ljaschenko, 1969, p. 51, pi. 10, fig. 1; 1973, p. 91, pi. 28, fig. 1.

Holotype. VNIGNI AIL, no. 1916 [60/365], complete shell; Southern Timan, Ukhta District, village of Yarega, oil mine no. 1, depth 85 m, Upper Devonian, Lower Frasnian, Lower Timanian Subhorizon.

Description. Shells are of large size (L = 19-40 mm), valves are elongated roundish, from moderate to strongly inflated. The cardinal margin is straight, shorter than the shell maximal width, which is situated anteriorly from the shell mid-line. Cardinal angles are rounded, grading imperceptibly into arch-shaped commissures.

The ventral valve is pear-shaped, strongly inflated, more concave than the dorsal valve. Lateral edges are gently rounded. The sinus is wide, troughlike, extending from the apex, laterally bordered by wider plications. The frontal margin bears an obliquely rounded sinal lobe, extending anteriorly, with a rounded square top. The width of the sinal lobe amounts to one-third of the shell width. The apex is massive, elevated, broadly triangular, strongly curved; the apical tip hangs over the dorsal valve. The apical angle varies from 100° to 120°. The ventral interarea is triangular, distinct, moderately elevated, flat in the lower region and weakly concave in the upper region. The surface of the interarea is observably vertically and horizontally hatched. The delthyrium is wide, its height slightly exceeds its basal width. The delthyrium shows narrow, distinct grooves running parallel to its margin. Occasionally, the delthyrium is closed by deltidial plates. The growth of the deltidial plates commences from the apex and leads to their occlusion, although leaving a crescent orifice above the commissure.

The dorsal valve is rounded rectangular in outline, moderately convex, with the maximal bulge located closer to the anterior margin of the shell. The fold is high, rounded trapezoidal, sharply bordered by two grooves, starts from the apex, and gradually widens anteriorly. The apex is low, slightly overlapping the commissure; the interarea is narrow, with nearly parallel margins.

The external ornamentation is formed by simple, narrow, flatly rounded plications, divided by twice as narrow interspaces. The number of plications increases through dichotomy and intercalation. The lateral flanks of the fold bear 30-40 plications each. The sinus and fold are covered by plications, which are less distinct, more flattened, and about twice as narrow as those on the flanks. The number of middle plications is 20-30.

The micro-ornamentation consists of thin, radial striae, converging on plications at acute angles, and intersecting concentric striae. Each plication bears 10-14 superfine radial striae.

The ventral interior has no apical thickening. The dental plates are narrow, long, and extend along one-quarter of the shell length. The delthyrial plate is narrow and distinct. The dorsal interior contains a bifurcate lamellar cardinal process. The lophophore has up to 13 spiralia (Fig. 4).

Measurements in mm and ratios:

	w		H	L/W	L/T	W/H	AA
2012	19.8	22.6	14.7	18.5	0.87	1.54	1.22	96
2154	27.7	34.8	19.5	29.6	0.79	1.42	1.17	120
holotypel916	32.3	32.7	21.4	27.9	0.98	1.50	1.17	97
1955	35.6	40.3	26.7	33.9	0.88	1.51	1.19	103
1954	38.4	41.1	29.3	34.2	0.93	1.40	1.20	97
1962	40.8	44.2	27.2	34.5	0.92	1.62	1.28	105

Ontogenetic variability. Young specimens have weakly convex valves, in which the apices of both valves are low. Gerontic individuals are strongly biconvex and rounded square in shape, with the ventral apex closely adjoining the dorsal valve. Young shells demonstrate the apical thickening and the thin fusion of crural plates below the cardinal process, the latter feature has not been observed in large specimens. Small shells do not show deltidial plates. During late growth stages, the deltidial plates can be high and strongly convex (Fig. 4).

Variability. The species is highly variable. Shell outlines vary from elongated roundish to transversely oval, almost round. Shells are from moderately inflated to convex, strongly inflated. In the collection under study shells are predominantly nearly isometric, with the LAV ratio ranging from 0.87 to 0.93. The shell convexity (L/T) varies from 1.40 to 0.62; the circularity (W/H) varies from 1.17 to 1.28.

The height of the interarea and the expression of deltidial plates may also be regarded as variable features. The delthyrial opening of some shells is completely closed by deltidial plates except for only the crescent incision near the delthyrial base. More often these plates are not developed or cover only the periapical region of the shell.

Comparison. This species differs from *U. murchisoniana* (Sartenaer, 1965, p. 3) in the more laterally extended shell; in the sinus and fold being distinctly bordered by lateral, larger plications; in the broadly trapezoidal sinus instead of the narrow rounded sinus. From *U. timanicus* it differs in the rounded elongated shell, in the high and strongly curved apex, and in the more convex shell instead of the laterally extended, uniformly biconvex shell of *U. timanicus.*

Occurrence. Lower Frasnian, Lower Timanian Subhorizon; Southern Timan.

Material. Fifty-two complete and 144 damaged, mainly ventral valves.

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