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Revision of the Ordovician plectambonitoid brachiopod Ujukella Andreev and related genera

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Revision of the Ordovician plectambonitoid brachiopod *Ujukella* Andreev and related genera

EVA EGERQUIST

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Abstract: New material of the poorly known plectambonitoid brachiopod *Ujukella fastigata* (Rubel) is described from the Lower Ordovician (upper Volkhov) of Ingria, Russia. The closely related plectambonitoid brachiopods, *U*.? *geometrica* (Kutorga), from the Lower Ordovician of Ingria, Russia, *U*. sp. from the Lower Ordovician of Öland, Sweden, and *U. alexandrae* Andreev (= *U. minima* Andreev) from the Middle Ordovician of southern Siberia, Russia are redescribed in order to draw comparison with *U. fastigata*. These taxa are referred to the Family Leptesti-idae, based on a new cladistic analysis.

Keywords: Brachiopoda, Rhynchonelliformea, Plectambonitoidea, Leptestiidae, *Ujukella*, Lava River, Ingria, Russia, Tuva, Öland, Sweden, early Ordovician, late Oeland, cladistics.

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Only a few plectambonitoid brachiopods are known from the lower to middle Ordovician (Oeland Regional Series) of Baltoscandia. These include *Plectella* Lamansky, 1905 (Billingen Regional Stage) and *Ingria* Öpik, 1930 (Volkhov Regional Stage). From the Kunda Regional Stage *Ahtiella* Öpik, 1932, *Inversella* Öpik, 1933, and *Ukoa* Öpik, 1932 have been described. A member of another group of Baltoscandian plectambonitoids was described by Kutorga (1846) as *Leptaena geometrica*, coming from the middle Ordovician (presumably Kunda Stage). The taxonomic position of these specimens, however, has remained unclear because of a lack of specimens showing interiors. None of these brachiopods has been revised since the 1930's.

Rubel (1961) described two specimens, quite similar to *L. geometrica*, under the name *Eostrophomena*? *fastigata*. These specimens, from the middle Volkhov beds of the St. Petersburg district, also show exteriors only. In 1993, three new taxa from this group were described by Andreev: *Onegia vitrea*, *Ujukella alexandrae*, and *Ujukella minima*.

The object of this paper is to compare some of these taxa with new material from Ingria and to discuss possible revision of some previously described taxa.

Geological setting and localities

Figures 1 and 6 show the localities from where the brachiopod material described herein was obtained. The described material of *Ujukella fastigata* comes from the Volkhov Formation at the Lava River, St. Petersburg district (sampled in 1991 by L. Holmer and L. Popov). The sample consists of a soft, calcareous, glauconitic clay intercalation between beds of glauconitic limestone within the uppermost part of the Volkhov Formation (BIIγ; *Microzarkodina parva* Conodont Biozone; Fig. 1). After washing and sieving, fragments and well preserved complete shells from at least 37 specimens were found. The sampled outcrop is situated on the eastern side of the Lava River which flows out into Lake Ladoga not far to the north of the sampling locality. Additional sampling in 1997 at the Lava River and at the closely situated Putilovo Quarry yielded more than 100 specimens of this species, from the *Paroistodus originalis* and *M. parva* Bio-zones (BIIβ & BIIγ; Fig. 1). The specimens described by Rubel (1961) as *Eostrophomena*? *fastigata* also come from middle Volkhov strata (BIIβ and BIIγ) at the Lava and Syas Rivers. The general lithology of the Volkhovian and Kundan rocks in the area is characterised by limestone beds, interrupted by numerous clay-horizons and discontinuity surfaces.

Ujukella? *geometrica* (Kutorga) comes from the middle Ordovician at Pulkova near St. Petersburg. This locality is now unfortunately unavailable and the exact stratigraphic position of the specimens is not clear. The preservation of the fossils, however, suggests that they were collected in the oolitic Kunda beds (BIIIβ; *Amorphognathus*? *variabilis* Conodont Biozone).

All these localities are part of a series of quarries and outcrops along the so-called Baltic–Ladoga Clint (=cliff), a more than 250 km long exposure of shallow Ordovician shelf deposits, extending from the north-western coast of Estonia to the southern shore of Lake Ladoga (Popov et. al. 1989; Dronov et. al. 1996). The Baltic–Ladoga Clint forms the northern edge of the Ordovician outcrop area in the East Baltic region (Fig. 1). In contemporaneous deposits, on the island of Öland, another similar, yet undescribed brachiopod, *Ujukella* sp. has been found in the middle Kundan ("*Raniceps* limestone").

Only one of the discussed species, *Ujukella alexandrae* Andreev (= *Ujukella minima* Andreev), comes from Llanvirn beds (middle part of the Malinovskaya Fm.) in Tuva, Siberia, close to the Kazakhstan border (Andreev 1993).

Systematic palaeontology

The discussed material is deposited in the Palaeontological Museum, Uppsala University (PMU), the Geological Institute in Tallinn (GT), the Swedish Museum of Natural History (RM) in Stockholm, the Museum of the Palaeontological Institute (PIN) Russian Academy of Sciences in Moscow, and the Central Research Geological Exploration Museum (CNIGR) in St. Petersburg.

The terminology used here follows Cocks & Rong (1989).

Superfamily Plectambonitoidea Jones, 1928

Systematic position. – Order Strophomenida Öpik, 1934; Suborder Strophomenidina Öpik, 1934.

Discussion. – The classification of the early plectambonitoids is presently rather confusing. Cocks & Rong (1989) made an effort to simplify it by introducing specific key characters for family belonging. This classification, however, has been criticised by

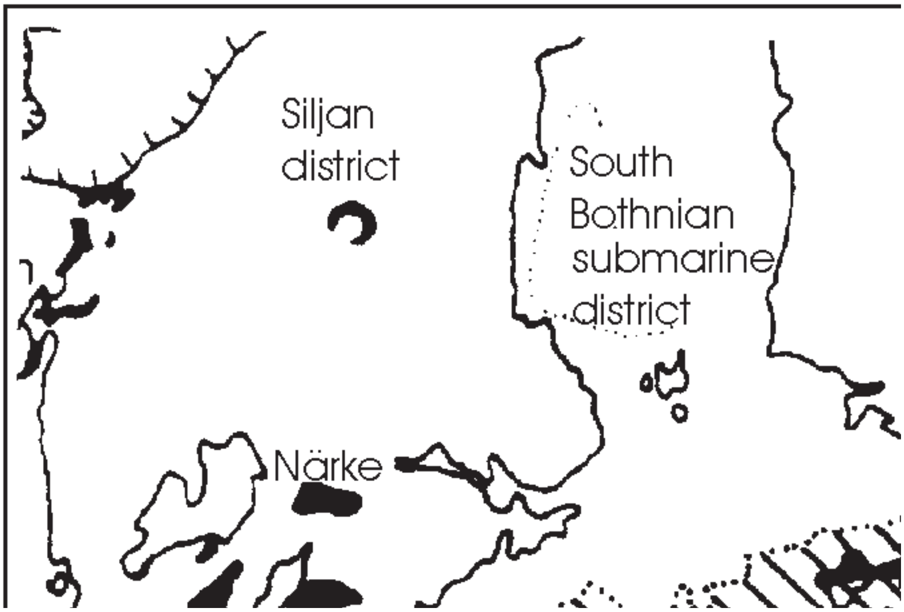


Fig. 1. Maps showing localities. A: Tuva, Siberia. B: Location of the larger map showing Baltoscandia with sampling localities and distribution of Ordovician deposits: outcrop areas black, subsurface and submarine Ordovician shaded (modified after Jaanusson 1982 and Nielsen 1995). 1: Lava River and Putilovo Quarry, 2: Syas River, 3: Ölands norra udde. Section from the Lava River with finds of *Ujukella fastigata*.

Table 1. Dimensions in mm of discussed taxa. V v = ventral valve, d v = dorsal valve, ia =interarea.

Species	Specimen	Max. width	Length v v	Length d v	Length ia	Width ia	Comments
Ujukella alexandrae	4461/2	10	5	-	-	-	Holotype v v
(after Andreev 1993)	4461/3	9	-	4.5	-	-	dorsal valve
	4461/4	8	5	-	-	-	ventral valve
	4461/7	8	-	4	-	-	dorsal valve
	4461/9	11	4	-	-	-	ventral valve
	4461/10	9	5	-	-	-	ventral valve
	4461/11	10	5	-	-	-	ventral valve
(*Ujukella minima*)	4461/20	5	-	3.5	-	-	Holotype d v
	4461/24	5.1	-	3.0	-	-	dorsal valve
Ujukella fastigata	1	4.7	2.0	1.8	4.6	0.4	conjoined
	2	4.7	2.6	2.1	4.7	0.5	conjoined
	3	4.8	2.4	1.7	4.8	0.4	conjoined
	4	4.8	2.6	2.1	4.8	0.4	conjoined
	5	5.6	3.25	-	5.6	0.2	ventral valve
	6	5.4	2.9	2.3	5.4	0.5	conjoined
	7	4.3	2.2	1.8	4.15	0.25	conjoined
	8	5.6	3.25	-	5.6	0.5	ventral valve
	9	4.75	2.7	-	4.7	0.4	ventral valve
(*Eostrophomena fastigata*)	Br 2592	6.3	3.4				ventral ext
(after Rubel 1961)	Br 2577	5.4	2.5				ventral ext
Ujukella sp.	Br 21269	7.0	2.5	-	-	-	ventral ext
	Br 21270	7.0	-	3.0	-	-	dorsal ext
	Br 21271	6	3.5	-	-	-	ventral ext
	Br 21272	8.0	3.5	-	-	-	ventral ext
	Br 21273	7.0	3.6	-	-	-	ventral ext
	Br 21274	7.0	-	3.0	-	-	dorsal ext
Ujukella? *geometrica*	1	6.0	3.3	3.2	5.7	0.7	conjoined
	2	7.4	3.8	3.7	6.8	0.8	conjoined

other authors (Potter 1991; Laurie 1991). As an attempt to remedy this situation, a cladistic analysis was carried out as a part of this investigation. Twenty characters were compared between the new material of *Ujukella fastigata*, *U. alexandrae* and eight other early plectambonitoid taxa. The analysis indicates that *Grorudia*, *Tetraodontella*, *Taphrodonta*, *Anechophragma*, and *Ujukella* are related. The first three of these genera were originally assigned to the Family Leptestiidae and it is here suggested that *Ujukella* and *Anechophragma* also belong to this family, although *Anechophragma* was described as a leptellinid by Neuman (1976).

For further discussion of the cladistic analysis see below. For characters and character states see the Appendix.

Family Leptestiidae Öpik, 1933

Emended diagnosis. – Teeth simple, in some taxa supplemented by a pair of accessory teeth. Dorsal adductor field with variable number of septa, in some taxa with an anteriorly raised bema. Pseudodeltidium commonly narrow, arched, covering main part of the delthyrium. Socket plates short, divergent and commonly pointed distally, in some taxa fused to the cardinal process.

Discussion. – Andreev (1993) placed *Ujukella* in the Family Sowerbyellidae because of the cardinal process that he characterised as trifid and undercut. However, as discussed below, the cardinal process is better described as simple and undercut. Thus, it cannot be referred to the Sowerbyellidae, as defined by Cocks & Rong (1989). The cladistic analysis confirms this conclusion by placing Sowerbyella quite far from the *Anecho-phragma* - *Ujukella* group.

The results of the cladistic analysis (see further below) do not give strong support for a drastic revision of the early plectambonitoids, which remain a problematic group. Because of this no attempt has been made to assign the different genera to subfamilies although it seems that the *Anechophragma* - *Ujukella* group should form one subfamily. Further analysis, involving additional taxa and characters, should be carried out prior to recognition of subfamilies.

Genus *Ujukella* Andreev, 1993

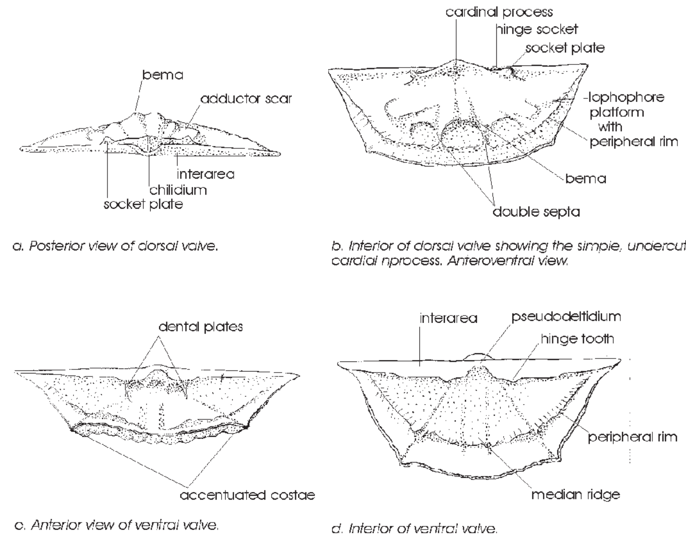
Type species. – *Ujukella alexandrae* Andreev, 1993; Llanvirn, Malinovskaya Fm., Tuva, Siberia.

Diagnosis. – Shell concavo-convex, wider than long, with maximum width along the cardinal margin. Cardinal angles drawn out into pointed alae. Radial ornamentation equally parvicostellate with two diverging, accentuated costae. Ventral interior with median ridge anterior to the muscle field and a medianly divided peripheral rim. Dorsal interior with low lophophore platform surrounded by a rim. Bema with the anterior part elevated on two submedian septa. Socket plates fused to a simple, undercut cardinal process.

Species assigned. – *Ujukella alexandrae* Andreev, 1993 (= *Ujukella minima* Andreev, 1993); *Ujukella fastigata* (Rubel, 1961); *Ujukella* sp.; *Ujukella*? *geometrica* (Kutorga, 1864).

Geographic and stratigraphic distribution. – *Ujukella alexandrae*, Llanvirn, middle part of Malinovskaya Fm., Tuva, Siberia; (*U. minima*, Llanvirn, middle part of Malinovskaya Fm., Tuva, Siberia); *U. fastigata*, upper Oeland, Volkhov Stage, St. Petersburg district, Russia; *U.*? *geometrica*, upper Oeland, Kunda Stage, St. Petersburg district, Russia; *U.* sp., upper Oeland, Kunda stage, Öland, Sweden.

Remarks. – Another early plectambonitoid, *Onegia vitrea*, was described by Andreev (1993) based on specimens from the Volkhov River, St. Petersburg district. These specimens come from the same horizon (upper Volkhov) as *Ujukella fastigata* and it would have been important to include these in the cladistic analysis. Unfortunately the specimens are lost. Moreover, judging from the illustrations of the specimens described by Andreev (1993), it seems likely that at least two genera are mixed. Thus, for example, figures 15 and 16 on plate 7 can probably be assigned to *Ujukella*. Because of these uncertainties, it is suggested that *O. vitrea* is considered as a nomen dubium.



a. Posterior view of dorsal valve.
b. Interior of dorsal valve showing the simple, undercut cardial nprocess. Anteroventral view.
c. Anterior view of ventral valve.
d. Interior of ventral valve.

Fig. 2. Ujukella fastigata in different views with terms used in this paper.

Ujukella alexandrae Andreev, 1993

Fig. 3 L–Y.

Ujukella alexandrae sp. nov. – Andreev (1993, pp. 50–55, pl. 7).
?*Ujukella minima* sp. nov. – Andreev (1993, pp. 50–55, pl. 7).

Material. – Holotype, PIN 4461/2a. Figured: 4461/2a holotype, exterior of ventral valve, 4461/2b exterior of ventral valve, 4461/3 external cast of dorsal valve, 4461/6 internal cast of dorsal valve, 4461/8 internal cast of ventral valve, 4461/9 interior of dorsal valve, 4461/20 external cast of dorsal valve, 4461/24 internal cast of dorsal valve (the last two specimens *U. minima*). For dimensions see Table 1.

Thirty-eight specimens and ten natural casts were examined by Andreev. Thirteen of those have been made available to me and the following description is mostly based on them.

Locality and horizon. – Tuva, Siberia; Llanvirn, middle part of the Malinovskaya Formation.

Diagnosis. – Shell concavo-convex, with maximum width along the cardinal margin, cardinal angles drawn out into pointed alae. Radial ornamentation equally parvicostellate with two diverging accentuated costae. A convex pseudodeltidium covers main part of the delthyrial aperture. Ventral interior with median ridge anterior to the muscle field and a medianly divided peripheral rim. Dorsal interior with low lophophore platform surrounded by a rim; the bema is anteriorly elevated on two submedian septa. Socket plates fused with simple, undercut cardinal process.

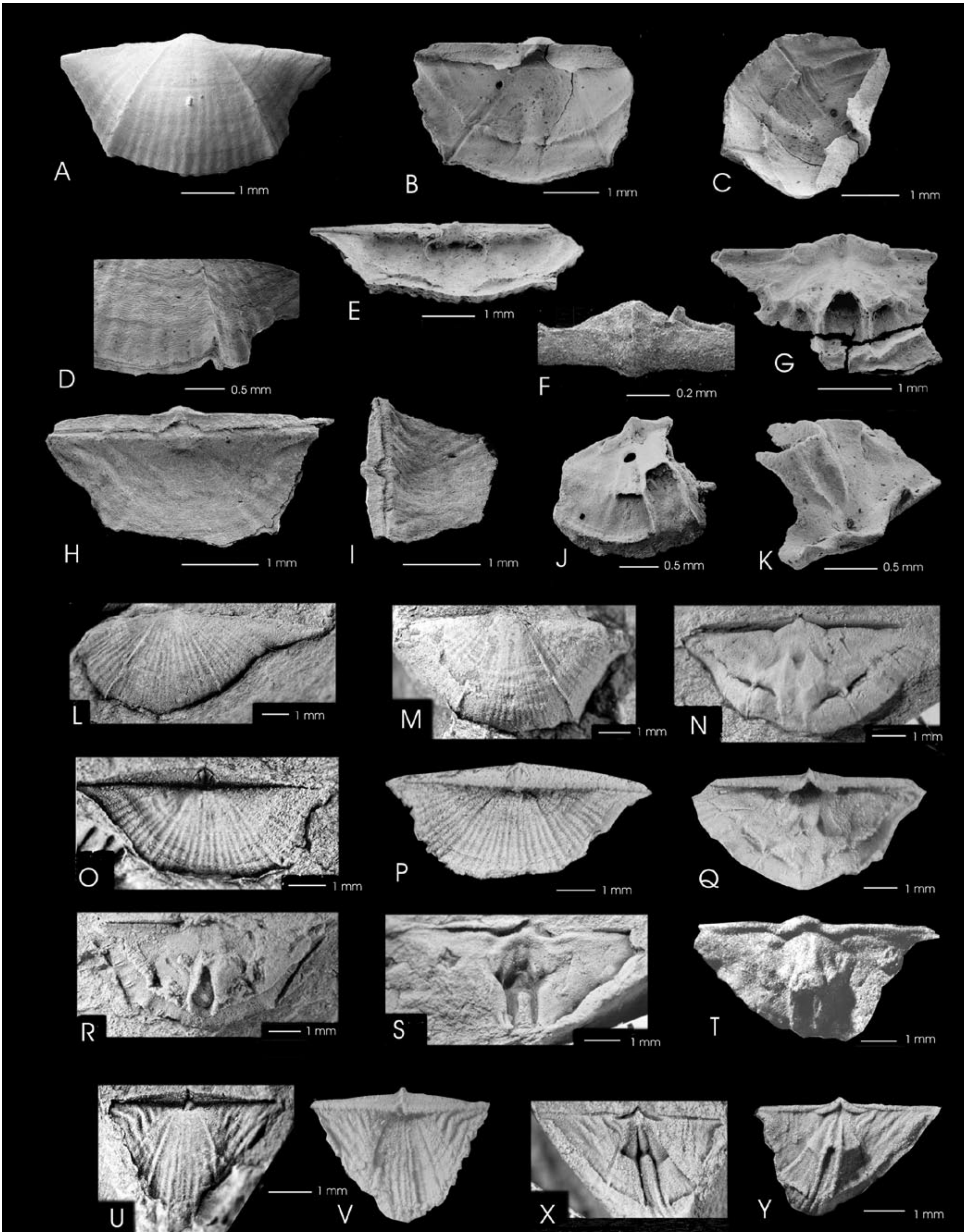
Description. – Outline: Shell up to 10 mm wide and 5 mm long. Ventral and dorsal valve on average 50% as long as wide. The shell is strongly concavo-convex with its maximum width along the cardinal margin. The cardinal angles are drawn out into pointed alae.

Ventral valve: The radial ornamentation is equally parvicostellate with two diverging accentuated costae, which are visible also inside the shell and have corresponding grooves in the dorsal valve. A fine concentric striation is visible on both valves. On some specimens indistinct rugae are visible on the alae. A convex pseudodeltidium covers the main part of the delthyrial aperture and a linear, quite narrow interarea extends along the whole hinge line. The hinge teeth are simple; dental plates are present but small, so that they are covered by the interarea in strict dorsal view. The interior of the ventral valve shows a well-defined medium septum anterior to the muscle field and an undulating rim that corresponds to the platform in the dorsal valve. The muscle field is tripartite with diductor scars larger than the adductor scars.

Dorsal valve: A narrow, hypercline interarea extends along the whole cardinal margin. The chilidial plates seem to be separated and the cardinal process is simple, undercut and connected with the socket plates by a ridge. The structure is rather high and covers the whole delthyrium when the shell is closed. The posterior part of the cardinal process has a distinct ridge that extends from the base of the chilidial plates to the top of the process. Inside the valve is a platform, which is quite low, but prominent due to an undulating rim that extends along the periphery. A high bema is elevated on two submedian ridges (double septa), which do not reach the edge of the shell.

Remarks. – In their criteria for classification Cocks & Rong (1989) recognised three kinds of cardinal processes: simple, trifid not undercut, and trifid undercut, thus excluding the simple undercut alternative. Andreev (1993) refers to the cardinal process as trifid, but on the specimens available the cardinal process is not lobed and since no notothyrial platform is present, simple and undercut appears to be the most proper way to classify the structure. Potter (1991) refers to this type of cardinal process as transverse-ridge type.

Discussion. – Compared to *U. alexandrae*, the specimens referred to as *U. minima* by Andreev (1993) are smaller and more triangular in outline. The shell is up to 5.1 mm wide and 3.5 mm long, and the dorsal valve is about 64% as long as wide. The triangular outline, however, might be due to the tectonic strain which obviously affects the specimens. Other differences from *U. alexandrae* are that the submedian ridges seem to reach the edge of the shell and that four distinct rugae are visible on the alae. It is however possible to trace rugae also on *U. alexandrae*, although they are much less prominent on these specimens. Unfortunately only four valves of *U. minima*, all dorsal, have been found, which makes detailed comparisons difficult. In spite of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this, the similarity between *U. alexandrae* and *U. minima* seems to be close enough to regard them as the same species. The fact that they come from the same stratigraphic level from the same region strengthens this suggestion. In my opinion it is most likely that the specimens referred to as *U. minima* by Andreev (1993) are juveniles of *U. alexandrae*, a suggestion that also may explain the difference in outline. Another important source of confusion may be that Andreev (1993) mistakenly classified the holotype of *U. minima* (PIN 4461/20) as a ventral valve. However a silicon cast of the specimen clearly shows that it is a natural cast of a dorsal valve (Fig. 3V).

Ujukella fastigata (Rubel, 1961)

Figs. 2, 3A–K.

Eostrophomena? *fastigata* sp. nov. – Rubel (1961, pp. 186, 187, pl. XV Fig. 10, 11).

Material. – Holotype, GT Br 2592, exterior of ventral valve. Figured: PMU In 1-2 interior of ventral valve, In 3-5 interior of dorsal valve, In 6 cardinalia, In 7 exterior of dorsal valve, In 10 exterior of ventral valve. Total of 42 complete and fragmented shells in PMU, two ventral valves in GT. For dimensions see Table 1.

Localities and horizon. – Putilovo Quarry, Lava and Syas Rivers, St. Petersburg district, Russia; upper Oeland, Volkhov (BIIβ & BIIγ; *Paroistodus originalis – Microzarkodina parva* Cono-dont Biozones).

Emended diagnosis. – Shell concavo-convex, with maximum width along the cardinal margin, cardinal angles drawn out into pointed alae. Radial ornamentation equally parvicostellate with two diverging accentuated costae. A convex pseudodeltidium covers the main part of the delthyrial aperture. Ventral interior with median ridge anterior to the muscle field and a medianly divided peripheral rim. Dorsal interior with a low lophophore platform surrounded by a rim; bema anteriorly elevated on two submedian septa. Socket plates fused with simple, undercut cardinal process.

Description. – Outline: Shell up to 6.3 mm wide and 3.4 mm long. Ventral and dorsal valves on average 53% and 41% as long as wide, respectively. The shell is strongly concavo-convex with maximum width along the cardinal margin. The cardinal angles are drawn out into alae, which vary in length from specimen to specimen.

Ventral valve: The radial ornamentation is equally parvicostellate with two diverging accentuated costae, which are visible also on the interiors and have corresponding grooves in the dorsal valve. Both valves with fine concentric external striation. A convex pseudodeltidium covers half of the delthyrial aperture and a straight, quite narrow interarea extends along the entire hinge line. Hinge teeth are simple and dental plates are present but small, so that they are covered by the interarea in full dorsal view. Ventral interior with well-defined medium septum anterior to the muscle field and an undulating ridge that corresponds to the platform in the dorsal valve. Muscle field is indistinctly visible, but appears to be tripartite with the diductor scars larger than the adductor scars.

Dorsal valve: A narrow, hypercline interarea extends along the whole cardinal margin. The cardinal process is simple, undercut and fused with the socket plates (see discussion above under *U. alexandrae*). The structure is rather high and covers the whole delthyrium when the shell is closed. The posterior part of the cardinal process has a distinct ridge that extends from the apically fused chilidial plates to the top of the process. Valve interior with platform, which is quite low, but prominent due to an undulating rim that extends along the periphery. A high bema is elevated on two submedian ridges (double septa), which do not reach the edge of the shell.

Discussion. – The new material of this brachiopod, including the well-preserved interiors, makes it possible to revise the taxon in detail. The resemblance between this species and *U. alexandrae* is, in my opinion, close enough to regard the two taxa as the same genus, but belonging to different species. *Eostrophomena*? *fastigata* Rubel (1961) was based on two specimens from the middle Volkhov (BIIβ & BIIγ; *P. originalis – M. parva* Biozones) at the Lava and Syas Rivers, St. Petersburg district. These two specimens show exteriors only. However, since they are very similar to the new specimens, from the same formation and the same locality (Lava River), it is most likely that they are conspecific. Thus *Eostrophomena*? *fastigata* is here referred to *Ujukella*.

The small differences between *U. alexandrae* and *U. fastigata* indicated by the cladistic analysis (see below), might be regarded as variations within the same species. Taking into consideration that *U. fastigata* occurs in Volkhov strata in western Russia whereas *U. alexandrae* comes from Llanvirn strata in southern Siberia close to the Kazakhstan border, a division into two species currently seems to be the most proper solution.

Ujukella sp.

Fig. 4A, B.

Material. – Exteriors of two dorsal and four ventral valves are examined: RM Br 21269-21274. Figured: Br 21270 exterior of dorsal valve, Br 21272 exterior of ventral valve. For dimensions see Table 1.

Locality and horizon. – Ölands norra udde (northern point of Öland), Sweden; upper Oeland, Kunda Stage (*A. variabilis* Conodont Biozone; "*Raniceps* limestone").

Description. – Shell up to 8 mm wide and 3.6 mm long. Ventral and dorsal valves on average 47% and 43% as long as wide, respectively. The shell is strongly concavo-convex, with maximum width along the cardinal margin. The cardinal angles are drawn out into pointed alae. Radial ornamentation is equally parvicostellate, the ventral valve has two diverging accentuated costae with corresponding grooves on the dorsal valve. Due to the poor preservation, it is not possible to recognise any finer striation on

Fig. 3. **A**–**K**. *Ujukella fastigata* (Rubel). A, D: PMU In 10, ventral valve exterior, ×10 (A); magnification of striation, ×15 (D). B, C: PMU In 2, ventral valve interior, ×11. E: PMU In 1, ventral valve interior, anterior view showing the vestigial dental plates, ×10. F: PMU In 6, magnification of cardinalia, posterior view showing the apically fused chilidial plates and the ridge on the posterior part of the cardinal process, ×40. G: PMU In 3, dorsal valve interior, ×14. H, I: PMU In 7, dorsal valve exterior, ×14. J: PMU In 4, dorsal valve interior, oblique anterior view, ×15. K: PMU In 5, dorsal valve interior, oblique posterior view, ×20. **L**–**Y**. *Ujukella alexandrae* Andreev. L: PIN 4461/2a, holotype, ventral valve exterior, ×5. M: PIN 4461/2b (from the same stuff as the holotype), ventral valve exterior, ×6. N, Q: PIN 4461/8, ventral valve interior; natural cast (N), silicon cast of N (Q), ×6. O, P: PIN 4461/3, dorsal valve exterior; natural cast (O), silicon cast of O (P) ×7. R: PIN 4461/9, dorsal valve interior, ×6. S, T: PIN 4461/6, dorsal valve interior; natural cast (S), silicon cast of S (T), ×7. (U–Y. *Ujukella minima* Andreev) U, V: PIN 4461/20, (holotype), dorsal valve exterior; natural cast (U), silicon cast of U (V), ×8. X, Y: PIN 4461/24, dorsal interior; natural cast (X), silicon cast of X (Y) ×8.

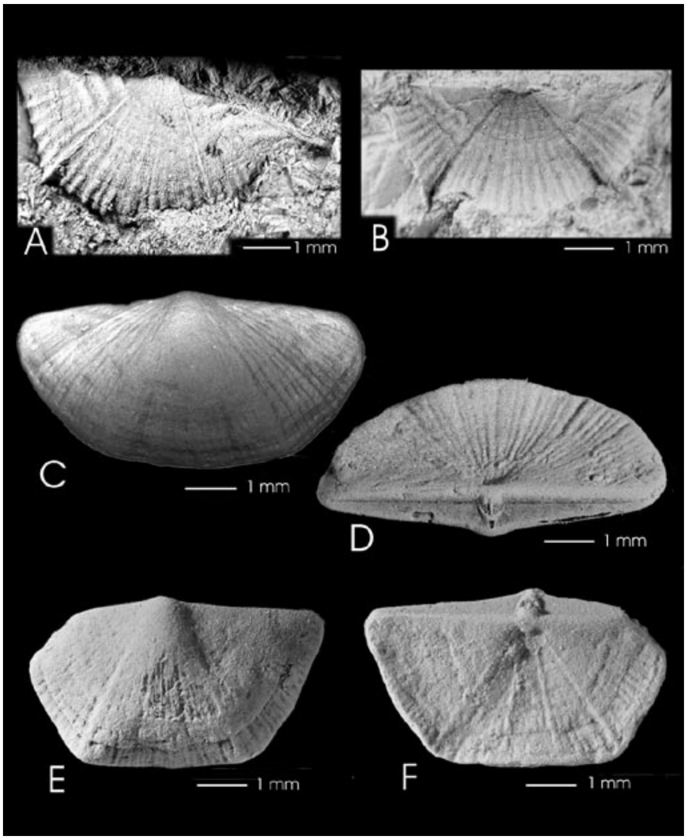

Fig. 4. **A**–**B**. *Ujukella* sp. A: RM Br 21272, ventral valve exterior, ×6. B: RM Br 21270, dorsal valve exterior, ×6. **C**–**F**. *Ujukella*? *geometrica*. (Kutorga), two conjoined specimens from CNIGR collection 3785. C, D: lectotype; ventral valve exterior (C), dorsal valve exterior, posterior view showing cardinalia with fused chilidial plates and ridge on cardinal process (D), ×7. E, F ventral valve exterior (E), dorsal valve exterior (F) of conjoined specimen, ×7.

the shells, but some specimens have indistinct rugae on the cardinal angles. Narrow interareas extend along the whole hinge line, of which the dorsal one is hypercline. A convex pseudodeltidium covers part of the delthyrial aperture, the rest of which is covered by the cardinal process that has a ridge on its posterior surface. Chilidial plates are completely fused.

Discussion. – The Öland specimens possess the same outline, convexity and ornamentation as *U. fastigata*, except for some indistinct rugae on some of the specimens (Fig. 4A). On the other hand, rugae of this type are clearly visible on *U. alexandrae*. Since all specimens show exteriors only, it is difficult to define the species. However the resemblance to the previously described *Ujukella* species is close enough to consider this taxon as belonging to the same genus.

Ujukella? *geometrica* (Kutorga, 1846)

Fig. 4C–F.

Leptaena geometrica – Kutorga (1846, pp.104–105, pl. 4, Fig. 3).

Material. – Two complete shells from CNIGR collection 3785, St. Petersburg, have been available to me, both figured. Lectotype (here selected) Fig. 4C, D. For dimensions see Table 1.

Locality and horizon. – Pulkova, St. Petersburg district, Russia; stratigraphic position uncertain but presumably upper Oeland, Kunda Stage (BIIIβ; *A*.? *variabilis* Biozone).

Description. – Shell up to 7.4 mm wide and 3.8 mm long. Ventral and dorsal valves on average 53% and 51% as long as wide, respectively. The outline of the shell is semioval to trapezoid, with maximum width along the cardinal margin. It lacks pointed alae (probably due to abrasion), but the angle between the cardinal margin and the edge of the shell is acute. The shell is moderately concavo-convex. Radial ornamentation is equally parvicostellate with two diverging accentuated costae on the ventral valve and faint corresponding grooves on the dorsal valve. Some indistinct rugae are visible on the posterior portion of the ventral valve. The ornamentation of the dorsal valve is somewhat different to that on the ventral valve with four to six accentuated costellae. A fine concentric striation is visible on both valves. A convex pseudodeltidium covers half part of the delthyrial aperture and a straight, quite narrow interarea extends along the whole hinge line. The inclination of the dorsal interarea is hypercline to anacline. The cardinal process covers the rest of the delthyrial aperture when the shell is closed. It also has a distinct ridge on the posterior part, which is visible from the apically fused chilidial plates to the deltidium.

Discussion. – *Leptaena geometrica* was questionably assigned to the genus *Sowerbyella* by Cocks & Rong (1989). This species, however, seems to be more close to the *Anechophragma* - *Ujukella* group and might well be congeneric with *Ujukella*. The ornamentation on the ventral valve is quite similar to that of *Ujukella* although that on the dorsal valve differs in having the above-mentioned accentuated costellae. In posterior view there is also a similarity in, for example, the distinct ridge on the cardinal process. The specimens differ from the other species of *Ujukella* in being flatter and not having pointed alae. The latter feature, however, is probably due to the abraded nature of the available specimens. The specimens illustrated by Kutorga (1846) have pointed alae and are very similar to *Ujukella* in outline. Like the specimens of *U*. sp. from Öland, these have no visible interiors, making precise taxonomic discrimination difficult and the species is tentatively referred to *Ujukella*.

Cladistic analysis

A cladistic analysis based on twenty characters from ten taxa was carried out using the PAUP program (Phylogenetic Analysis Using Parsimony 3.1.1; Swofford 1993). For characters and character states see the Appendix; distribution of discussed taxa is shown in Fig. 6.

The analysed ten taxa are:

1. *Plectella uncinata* (Pander, 1830), Billingen Stage (*P. elegans* – lower *O. evae* Conodont Biozones), East Baltoscandia.
2. *Plectambonites planissimus* (Pander, 1830), Aseri Stage (*D. murchisoni* Graptolite Biozone), St. Petersburg district.
3. *Anechophragma rarum* (Neuman, 1976), upper Arenig – lower Llanvirn (*D. hirundo* – *D. artus* Graptolite Biozone), New World Island, Newfoundland.
4. *Calyptolepta diaphragma* (Neuman, 1976), upper Arenig – lower Llanvirn (*D. hirundo* – *D. artus* Graptolite Biozone), New World Island, Newfoundland.
5. *Grorudia* spp. (Spjeldnæs, 1957), Vollen and Arnestad Formations, (*N. gracilis* – *D. multidens* Graptolite Biozones), Oslo region, Norway.
6. *Tetraodontella biseptata* (Jaanusson, 1962), Dalby Limestone (*N. gracilis* Graptolite Biozone), Sweden.

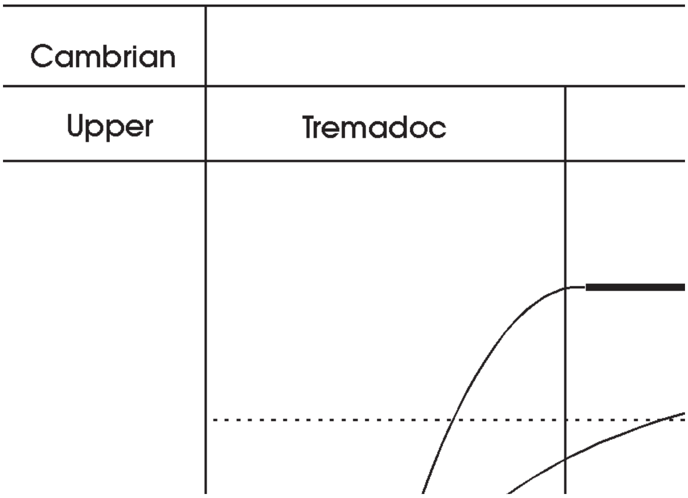

Fig. 5. Cladogram derived in this study from PAUP analysis of ten early plectambonitoid taxa. Dotted lines separate the groups discussed in the text.

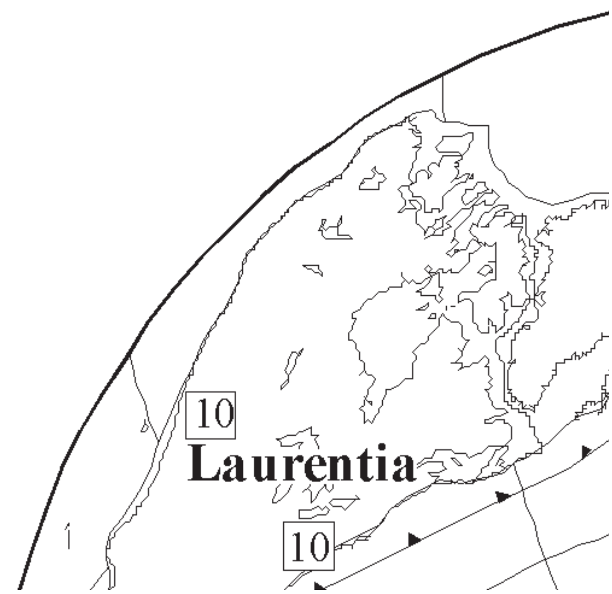

Fig. 6. Early Llanvirn plate tectonic reconstruction with occurrences of taxa used in the cladistic analysis (modified after Torsvik & Smethurst 1997).

7. *Sowerbyella antiqua* (Jones, 1928), upper Llanvirn, Llandeilian Stage; (*G. teretiusculus* Graptolite Biozone), England – Wales.
8. *Ujukella alexandrae* (Andreev, 1993), Llanvirn (Malinkovskaya Formation), Tuva, Altai, SW Siberia.
9. *Ujukella fastigata* (Rubel, 1961), Volkhov Stage (BIIβ & BIIγ; upper *P. originalis – M. parva* Conodont Biozones), St. Petersburg district, Russia.
10. *Taphrodonta parallela* (Cooper, 1956), lower Llanvirn, upper Pogonip Group (*D. artus* Graptolite Biozone), Nevada, USA. (Other species of *Taphrodonta* have been found in Kazakhstan [Nikitina & Timofeeva 1992] and Tibet [Liu 1976; syn. *Nanambonites* Cocks & Rong 1989].)

Table 2. Character state matrix used in PAUP analysis of characters 1–20 as listed in the Appendix.

	Character number no Taxon	1 out	2 prt	3 ror	4 gra	5 dia	6 dpm	7 pdl	8 chp	9 tee	10 dpl	11 mdr	12 mfd	13 vpr	14 cpr	15 spl	16 lpl	17 bem	18 mrd	19 smr	20 sds
	1 *Plectella*		0	0	1	1	1	1	1	1	0	2	0	0	0	0	1	1	0	1	0
2	2 *Plectambonites*		2	0	1	2	1	1	1	2	0	2	0	0	0	0	1	1	0	1	0
2	3 *Anechophragma*		0	0	0	0	1	0	1	0	2	0	1	0	2	1	2	1	1	0	1
0	4 *Calyptolepta*		0	0	2	0	1	0	1	2	1	1	1	0	2	0	0	1	0	0	1
0	5 *Grorudia*		1	1	2	0	0	0	1	?	3	1	1	1	0	2	1	0	1	1	1
1	6 *Tetraodontella*		1	0	0	0	0	0	1	?	3	0	1	0	0	2	0	1	1	1	1
1	7 *Sowerbyella*		0	0	2	0	0	0	0	0	1	1	0	2	0	3	2	0	2	2	1
2	8 *U. alexandrae*		1	0	3	0	1	0	1	0	2	1	1	1	2	1	2	1	1	1	1
0	9 *U. fastigata*		1	0	3	0	1	0	1	1	2	1	1	1	2	1	2	1	1	1	1
0	10 *Taphrodonta*		0	1	0	0	0	0	1	0	3	2	0	1	2	0	0	1	0	0	1
0																					

The analysed taxa were chosen because they represent the earliest known plectambonitoid brachiopods. Moreover, all except *Plectella* and *Plectambonites* (which serve as an outgroup) have double septa. The analysis does not include *Ujukella*? *geometrica*, the two specimens named *Eostrophomena*? *fastigata* by Rubel (1961) or *Ujukella* sp. from Öland because no interiors are visible on these specimens. Neither are the specimens referred to as *Ujukella minima* by Andreev (1993) included because there is no ventral valve available. The characters are not ranked in the way proposed by Cocks & Rong (1989) because there are some uncertainties concerning the reliability in this ranking, as discussed below.

Five trees of equal length were produced, all with a consistency index of 0.67 (excluding uninformative characters).

A 50-percent majority-rule consensus of the five trees (Fig. 5) divides the ten taxa into three distinct groups, leaving *Calyptolepta* and *Sowerbyella* aside as sister groups. The first group consists of *Plectella uncinata* and *Plectambonites planissimus* which were chosen to serve as a comparable outgroup belonging to the family Plectambonitidae. The second group consists of *Anechophragma*, *Ujukella alexandrae*, and *U. fastigata*. The two *Ujukella* species are grouped together in all five trees, separated by different arrangement of the chilidial plates only (separated or apically fused). This confirms the suggestion that they are congeneric. *Anechophragma* is grouped together with *Ujukella* in four of the five trees and differs from *Ujukella* in four characters. 1: outline (not alate instead of alate), 3: radial ornamentation (multicostellate instead of parvicostellate with two accentuated costae), 10: dental plates (absent instead of vestigial), and 12: muscle field (with smaller diductor scars than *Ujukella*). This resemblance indicates that they belong to the same family and probably also to the same subfamily. The difference in outline is not necessarily a significant character considering that the pointed alae vary quite a lot in length within the *Ujukella* genera. Since only few specimens of *Anechophragma* are found there is a possibility that this genus also has variable shape of the cardinal angles.

The third group consists of *Grorudia*, *Tetraodontella* and, in three trees out of five, of *Taphrodonta*. In this group more characters differ than in the previous group (Fig. 5, Tables 2–3), a matter that makes this relationship somewhat more uncertain. Cocks & Rong (1989) placed *Grorudia* and *Tetraodontella* in the Grorudiidae and *Taphrodonta* in the Plectambonitidae. This placement, however, is not supported by the cladistic analysis. On the other hand, Laurie (1991) proposed that both *Tetra-odontella* and *Taphrodonta* belong to the same family, and since they were originally placed within the Leptestiidae, this systematic position is preferred here.

Table 3. Synapomorphy scheme for internal nodes shown in the cladogram. Numbers in brackets show the amount of homoplasy (1.0 = no homoplasy).

Node	Character state changes
1→*Plectella*	4:0→1(1.0), 8:0→1(0.5)
1→*Plectambonites*	1:0→2(0.667), 4:0→2(1.0), 8:0→2(0.5)
1→2	3:1→2(0.75), 6:1→0(1.0), 9:0→1(1.0), 10:2→1(0.5), 15:1→0(0.5), 18:1→0(1.0), 19:0→1(1.0)
2→*Sowerbyella*	5:1→0(0.5), 7:1→0(1.0), 12:0→2(0.5), 14:0→3(1.0), 15:0→2(0.5), 16:1→0(0.5), 17:0→2(0.667), 18:0→2(1.0)
2→3	11:0→1(0.5), 13:0→2(0.5), 20:2→0(1.0)
3→*Calyptolepta*	8:0→2(0.5)
3→4	3:2→0(0.75), 9:1→2(1.0), 12:0→1(0.5), 17:0→1(0.667)
4→5	2:0→1(0.5), 5:1→0(0.5), 9:2→3(1.0)
5→*Taphrodonta*	10:1→2(0.5), 11:1→0(0.5), 17:1→0(0.667)
5→6	1:0→1(0.667), 13:2→0(0.5), 14:0→2(1.0), 20:0→1(1.0)
6→*Tetraodontella*	2:1→0(0.5), 10:1→0(0.5), 12:1→0(0.5)
6→*Grorudia*	3:0→2(0.75), 15:0→1(0.5), 16:1→0(0.5), 18:0→3(1.0)
4→7	14:0→1(1.0), 15:0→2(0.5)
7→*Anechophragma*	10:1→0(0.5), 12:1→0(0.5)
7→8	1:0→1(0.67), 3:0→3(0.75),
8→*U. alexandrae*	——
8→*U. fastigata*	8:0→1(0.5)

It is relevant to consider if these two groups belong to different families or to the same family but different subfamilies. The brachiopods in the *Anechophragma – Ujukella* group have undercut cardinal process which *Grorudia*, *Tetraodontella*, and *Taphrodonta* lack. This character was considered as important on the family level by Cocks & Rong (1989). Potter (1991), however, considered the same character to be of only subgeneric significance in his study of *Bimuria*. This feature may thus not be as essential for classification as Cocks & Rong (1989) claimed. Considering that only five characters separate the two groups, they probably belong to the same family, which in this case should be the Leptestiidae.

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Appendix: Characters and character states used in the cladistic analysis

EXTERIOR

1. Outline (out) 0: semicircular to semioval, not alate to slightly alate. 1: strongly alate. 2: subrectangular.
2. Profile, transverse (prt) 0: concavo-convex. 1: flat to weakly concavo-convex.
3. Radial ornamentation (ror) 0: multicostellate. 1: equally parvicostellate with wide interspaces between costellae. 2: Unequally parvicostellate with two or three generations of accentuated costellae. 3: equally parvicostellate with two accentuated costae.
4. Granulation (gra) 0: absent. 1: present, randomly arranged. 2: radial rows of tubercles, built up by costellae and the concentric striation.
5. Dorsal interarea, inclination (dia) 0: anacline. 1: hypercline
6. Denticulate posterior margin (dpm) 0: absent. 1: present.
7. Pseudodeltidium (pdl) 0: apical. 1: covers main part of the delthyrium.
8. Chilidial plates (chp) 0: separated. 1: apically fused. 2: completely fused.

VENTRAL VALVE INTERIOR

9. Teeth (tee) 0: simple, small, pointed, 1: simple, obliquely arranged, 2: simple wide transversely arranged, 3: double.
10. Dental plates (dpl) 0: absent, 1: vestigial, 2: well developed.
11. Median ridge anterior to the muscle field (mdr) 0: absent, 1: present.
12. Muscle field (mfd) 0: with adductor scars not enclosed by the diductor scars, of about equal length, 1: with adductor scars not enclosed by the larger diductor scars, 2: with adductor scars enclosed by the diductor scars.
13. Peripheral or subperipheral rim (vpr) 0: absent, 1: present, complete, 2: present, divided medianly.

DORSAL VALVE INTERIOR

14. Cardinal process (cpr) 0: simple, not undercut, 1: simple, undercut, 2: trifid, not undercut, 3: trifid, undercut.
15. Socket plates (spl) 0: widely diverging, 1: wide, curved, subparallel to the posterior margin, 2: fused to the cardinal process.
16. Lophophore platform (lpl) 0: absent, 1: present, bordered by rim.
17. Bema (bem) 0: absent, 1: present, anteriorly raised, 2: present, not raised anteriorly.
18. Median ridge (mrd) 0: absent, 1: present, originating from the notothyrial platform, 2: present, originating from the callosity anterior to the pit which is formed by the undercut cardinal process, 3: present, originating quite far from the notothyrial platform (anterior to the posterior margin of the submedian ridges).
19. Submedian ridges (double septa) (smr) 0: absent, 1: one pair.
20. Side septa (sds) 0: absent, 1: one pair, 2: more than one pair.