

The Ordovician brachiopod genus *Cyrtonotella*: taxonomy and distribution in the Baltic Basin

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Abstract. The taxonomy of the Baltic Ordovician orthoidean brachiopods of the genus *Cyrtonotella* Schuchert & Cooper, 1931 is discussed, two neotypes are suggested and emended descriptions of species and subspecies are presented. This taxonomic revision of *Cyrtonotella*-like brachiopods highlights their differences from the family Nanorthidae Havlíček, 1977 in which they have been included up to now. The well-preserved Baltic representatives of the genus *Cyrtonotella* display several morphological features, which are unique to this group of brachiopods and may have a family-level importance. The studied brachiopods belong to the shallow-water faunal associations of the Baltic Basin, including its easternmost parts (the Moscow Basin). These brachiopods disappear during the faunal crisis at the Sandbian–Katian transition. The global distribution of *Cyrtonotella* is poorly known due to taxonomic problems. New data on the Baltic species, which specify their stratigraphic and spatial distribution in the Baltic Basin, is a step towards reducing the taxonomic confusion among *Cyrtonotella* species.

Key words: rhynchonelliformean brachiopods, taxonomic revision, distribution, Ordovician, Baltica.

INTRODUCTION

The Ordovician brachiopods of the genus *Cyrtonotella* occur in the shallow-water environments of the Baltic Basin, especially in areas of the distribution of kukersite kerogen. They are also found in more or less argillaceous deposits of its easternmost parts, known as the Moscow Basin (Alikhova 1969). The specimens included in *Cyrtonotella* are well recognizable by their unique cardinal process (Hints 2004). Presently, the systematics of *Cyrtonotella* requires revision in order to assess the biogeographic and stratigraphic distribution of this genus. This paper presents the first modern systematic revision of *Cyrtonotella* species from Baltica, which enables better understanding of their taxonomy on the genus and family level in future studies.

The taxonomic study of the Ordovician orthoidean brachiopods presently assigned to the genus *Cyrtonotella* Schuchert & Cooper, 1931 dates back to the classical papers of Eichwald (1829, 1861). Eichwald (1829) described the species *Terebratula semicircularis*, which was selected by Schuchert & Cooper (1932) as a type species of their new genus *Cyrtonotella* Schuchert & Cooper 1931. Eichwald (1861) illustrated a specimen of *Cyrtonotella kuckersiana* under the name of *Orthis rustica* [= *Dolerorthis rustica* (Sowerby)]. When describing the *Orthis calligramma* group of brachiopods, Wysogórski

(1900) mentioned two new species: *Orthis kuckersiana* and *Orthis frechi*. The third name, *O. concava*, mentioned by him comes from the manuscript by Schmidt (see Alikhova 1951, p. 26) and should be considered as *nomen nudum*. Some small Middle Ordovician orthides described by Rubel (1961) were excluded from the genus *Cyrtonotella* by Hints (2014). The descriptions of species of the genus *Cyrtonotella* in the Baltic region have been provided by Öpik (1930a, 1930b, 1934) and Alikhova (1951, 1953, 1969). Öpik (1930a, 1934) mentioned six taxa related to *O. kuckersiana* Wysogórski and *O. frechi* Wysogórski, which occur mainly in the lowermost Upper Ordovician Kukruse Regional Stage (RS) and Haljala RS. The species *Orthis bekkeri* (Öpik 1930a, pl. III, fig. 25) was excluded from the present study because it is more similar to members of the genus *Sivorthis* Jaanusson & Bassett, 1993 than other *Cyrtonotella* species.

The present study is the first step towards the taxonomic stability of the Baltic species of *Cyrtonotella*. For that, two neotypes are selected and detailed descriptions of two subspecies and two species are presented. The description of the type species *Cyrtonotella semicircularis* (Eichwald) will be presented in another paper which deals with the genus- and family-level taxonomy of cyrtoneid brachiopods.

The specimens used in this study (in total about 400 specimens) are housed in Estonia at the Department of Geology, Tallinn University of Technology (institutional abbreviation GIT), Natural History Museum, University of Tartu (TUG, including the type material of A. Öpik) and the Estonian Museum of Natural History in Tallinn (ELM, including the specimens collected in the 19th century by F. Schmidt and A. Mickwitz). Some specimens are kept in the Peabody Museum (YPM, collections of C. Schuchert and G. A. Cooper), Swedish Museum of Natural History (RM, about 30 specimens collected from Estonia) and F. N. Chernyshev Central Geological Scientific Research and Exploration Museum (CNIGR) in St Petersburg (material described by T. N. Alikhova).

SYSTEMATIC PALAEOLOGY

Order ORTHIDA Schuchert & Cooper, 1932
 Suborder ORTHIDINA Schuchert & Cooper, 1932
 Superfamily ORTHOIDEA Woodward, 1852
 Genus *Cyrtonotella* Schuchert & Cooper, 1931

Type species. Terebratula semicircularis Eichwald, 1861, Middle Ordovician, Aseri RS (upper Darriwilian), northwestern Russia (St Petersburg region).

Discussion. The orthoidean genus *Cyrtonotella* is included in the family Nanorthidae Havlíček, 1977 (Williams & Harper 2000). However, the brachiopods described below, which are assigned to that genus, differ essentially from Nanorthidae in the much larger shell size and interior of the dorsal valve, especially in the unique cardinal process (Hints 2004), and supposedly belong to a distinct new family-level group. The identification of a new family and revision of the type species of the genus *Cyrtonotella semicircularis* (Eichwald) are addressed in another paper in progress and thus the family-level status is not defined here.

Distribution. The brachiopods assigned to the genus *Cyrtonotella* are not very common outside the Baltic Basin. Just over ten species have been mentioned from North America (Butts 1942; Cooper 1956; Kraft 1962; Ross & Ingham 1970; Ross & Ethington 1992; Potter & Boucot 1992), Great Britain (Cocks 2008), Ireland (Mitchell 1977; Candela 2003), Peru (Villas et al. 2015) and Thailand (Hamada 1964). The total stratigraphic range of cyrtoneid brachiopods in the Baltic and Moscow basins covers the Darriwilian (Aseri, Lasnamägi? and Uhaku RSs), Sandbian (Kukruse and Haljala RSs) and lowermost Katian stages (Keila RS). The total global stratigraphical range of the cyrtoneid brachiopods varies according to the above-mentioned publications in the same interval as in the East Baltic, however, with differences between different regions.

Cyrtonotella kuckersiana (Wysogórski, 1900)

Diagnosis. Medium-sized to large, plano-convex to weakly concavo-convex orthoideans. Ornament costate with well-developed filae; 30 to about 50 ribs occur along the commissure. Brachiophores plate-like, disposed at about 90–100° in ventral view, 110–150° in basal parts. Cardinal process, which extends beyond hinge line, in posterior plan ridge- or wedge-like with myophore folded up to ten times.

Discussion and comparison. In literature, two different spellings of the species name have been used. Wysogórski (1900) derived the name *kuckersiana* from *Kuckers*, an old German name for a locality in northeastern Estonia. Based on the Estonian spelling of the locality, Öpik (1930a), used *kukersiana* instead of the original name, which still has priority (Article 32.1 in ICZN 1999).

Cyrtonotella kuckersiana and related Ordovician taxa described below differ from the type species of the genus *C. semicircularis* in the costate ornament, consisting of ribs bifurcating very close to the umbo, and in a smaller number of costae along the shell margin (see Hints 2014, fig. 1). The cardinal process on the type species is a delicate folded ridge instead of the wedge-like strong process in Upper Ordovician species.

Following Alikhova (1953), Rõdmusoks (1970) accepted two subspecies, *Cyrtonotella kuckersiana kuckersiana* and *C. kuckersiana frechi*, which are distributed in the Kukruse and Haljala RSs and in the lowermost Keila RS. The oldest and youngest specimens of *C. kuckersiana* from the Kukruse RS and Jõhvi Substage of the Haljala RS, respectively, differ clearly from each other (Fig. 1A1–A5, B1–B5). They could be treated as separate species by analogy with two other species, *C. laine* and *C. barbara*. However, it is complicated in practise. Supposing the evolutionary trend in changes of shell morphology from large, planoconvex shells to smaller, weakly concavo-convex shells, there occur specimens with transitional characteristics. For this reason many species have been identified not on the subspecies, but on the species level. In the present study, the descriptions of the subspecies characterize the two groups of related brachiopods belonging to *C. kuckersiana*.

Distribution. The *C. kuckersiana kuckersiana*-type shells occur mainly in the Kukruse RS. The distribution of that species in different localities of the Kukruse RS is shown already by Bekker (1921). The *C. kuckersiana frechi*-type shells are most common in the Haljala RS. In the Baltic region, the type of the genus *C. semicircularis* is the oldest, occurring in the Aseri RS of northwestern Russia (St Petersburg region). In the studied collections one *C. kuckersiana kuckersiana*-type brachiopod shell

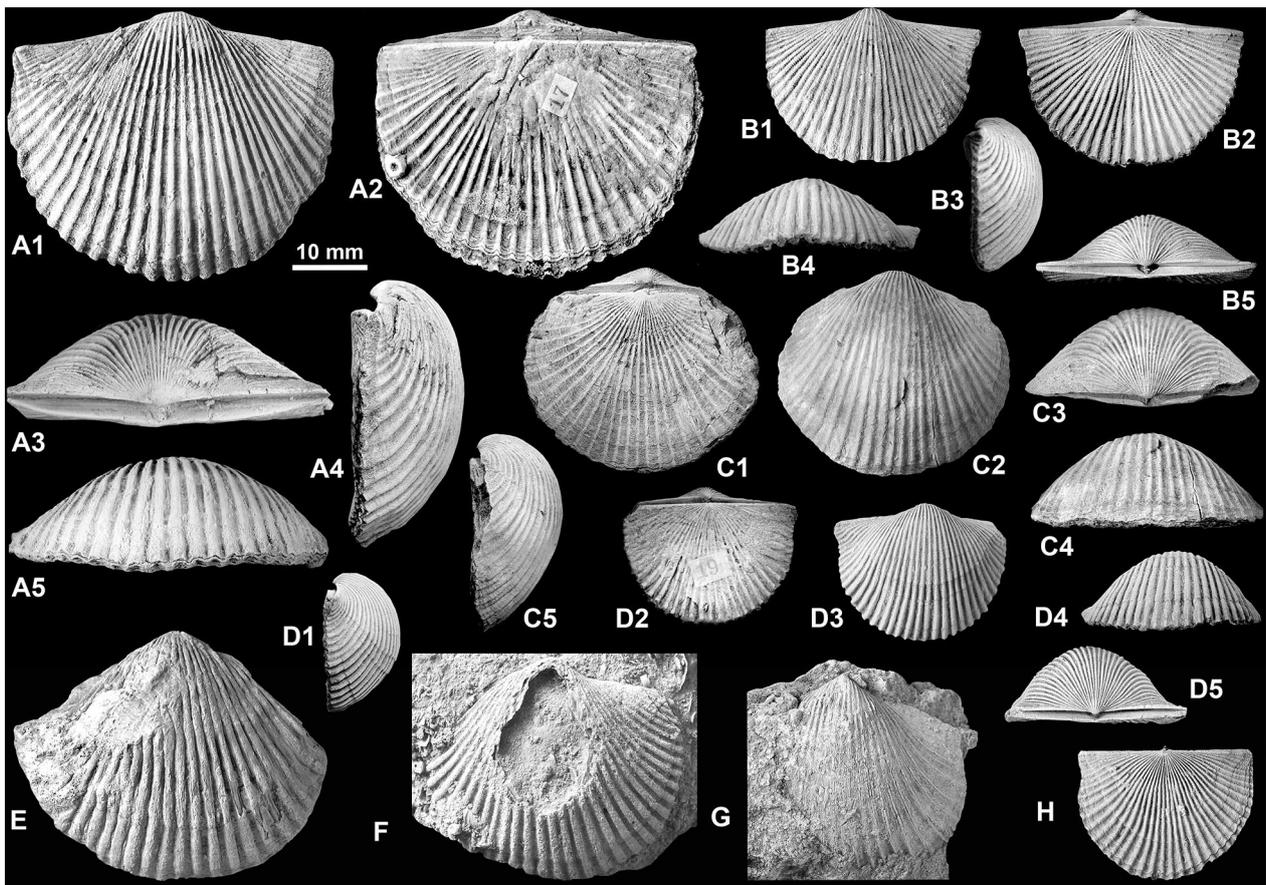


Fig. 1. A1–A5, *Cyrtototella kuckersiana kuckersiana* (Wysogórski, 1900), neotype, shell TUG 1054-17 (Br 077), ventral, dorsal, posterior, lateral and anterior views, Ubja, northeastern Estonia, Kukruse Regional Stage (RS). B1–B5, *Cyrtototella kuckersiana frechi* (Wysogórski, 1900), neotype, shell GIT 400-70, ventral, dorsal, lateral, anterior and posterior views, Pääsküla (western part of Tallinn), Jõhvi Substage of the Haljala RS. C1–C5, *Cyrtototella barbara* (Öpik, 1930a), holotype, shell TUG 1054-24 (Br 084), dorsal, ventral, posterior, anterior and lateral views, Sõjamägi (Tallinn), Haljala RS. D1–D5, *Cyrtototella laine* (Öpik 1930a), holotype, shell TUG 1054-19 (Br 084), lateral, dorsal, ventral, anterior and posterior views, Kohtla, northeastern Estonia, Kukruse RS. E, *Cyrtototella kuckersiana kuckersiana* (Wysogórski, 1900), ventral valve ELM G1:7957, Jõhvi, northeastern Estonia, Jõhvi Substage of the Haljala RS. F, *Cyrtototella kuckersiana kuckersiana* (Wysogórski, 1900), ventral valve ELM G1:7724, Kavastu, northeastern Estonia, Jõhvi Substage of the Haljala RS. G, *Cyrtototella kuckersiana* cf. *kuckersiana* (Wysogórski, 1900), ventral valve ELM G1:4948, Tallinn, Uppermost Darriwilian (Uhaku RS). H, *Cyrtototella kuckersiana kuckersiana* (Wysogórski, 1900), exterior of dorsal valve GIT 400-124, Kukruse, northeastern Estonia, Kukruse RS. The scale is the same for all figures.

(ELM G1:4948) is labelled as a specimen from the stage C₁ in Tallinn (Fig. 1G). This is the oldest occurrence of *Cyrtototella* in Estonia. The occurrence of *C. kuckersiana* in the Middle Ordovician Uhaku RS (C_{1c}) is shown also by Öpik (1930a, p. 237, in C₂α; = C_{1c} by Rõõmusoks 1970). The total stratigraphic range of brachiopods of the genus *Cyrtototella* in Baltica comprises the interval from the Aseri RS to Keila RS, which corresponds to about 11 Ma (Kaljo et al. 1996). An exception is the Lasnamägi RS, where the occurrence of *Cyrtototella* is not identified up to now.

Material. More than 300 specimens belong to the *C. kuckersiana* group, however, about 100 additional

specimens in the collections of GIT and ELM have not been identified on the subspecies level due to insufficiently clear subspecies characteristics or poor preservation.

Cyrtototella kuckersiana kuckersiana (Wysogórski, 1900)
Figures 1A1–A5, E, F, H; 2A; 3; 4A1, A2, H; 5A1, A2

- 1861 *Orthis rustica* Eichwald, p. 238, pl. 12, fig. 23.
1900 *Orthis kuckersiana* n. sp.; Wysogórski, p. 12, pl. 8.
1930a *Orthis kuckersiana* Wysogórski; Öpik, pp. 70–76, pl. 2, figs 14–18, text-figs 7, 8; Öpik 1930b, p. 14, pl. I, fig. 6; Öpik 1934, pp. 58–61, pl. 45,

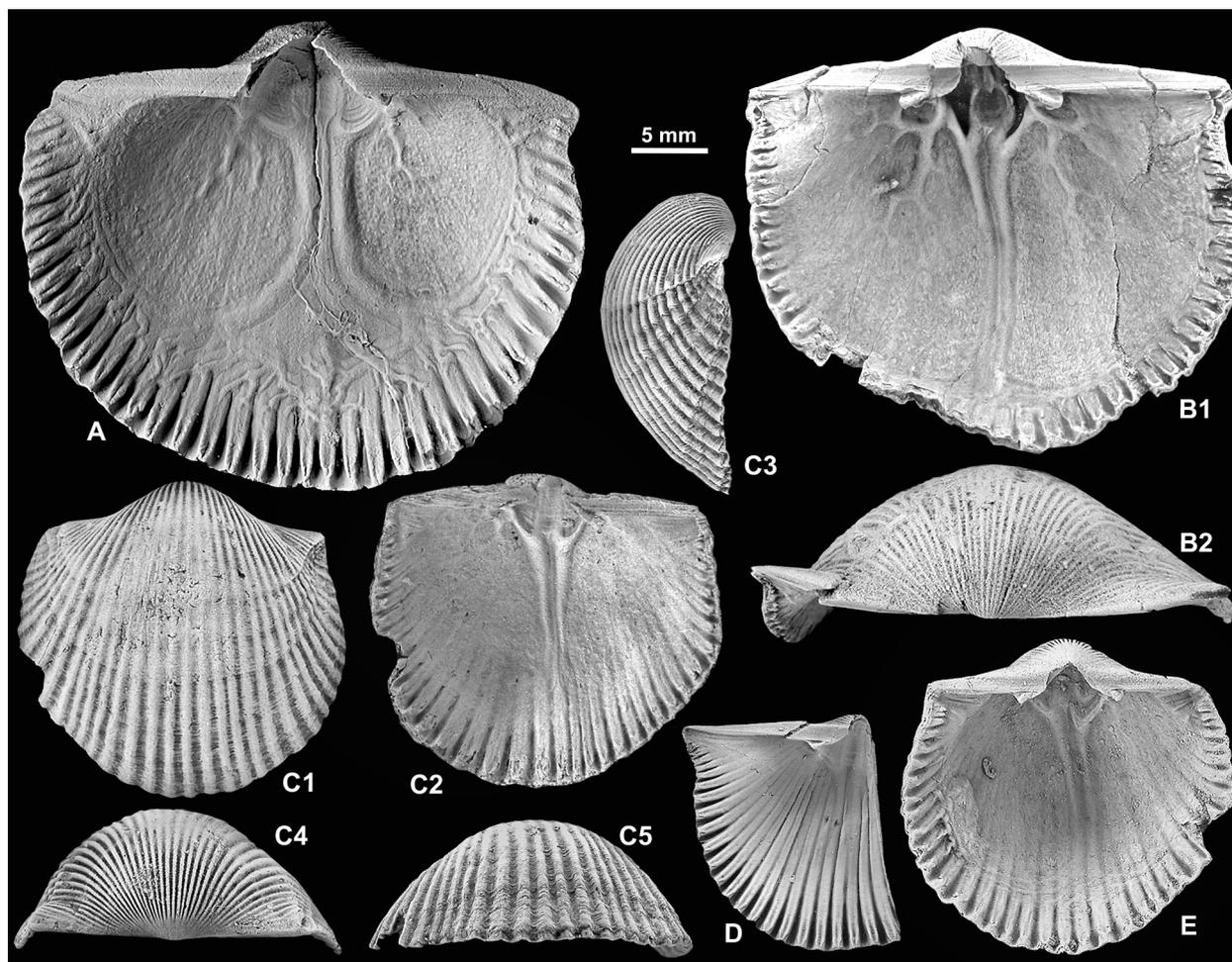


Fig. 2. A, *Cyrtanotella kuckersiana kuckersiana* (Wysogórski, 1900), ventral interior, TUG 1954-16 (Br 074), Kohtla, northeastern Estonia, Kukruse Regional Stage (RS). B1, B2, *Cyrtanotella laine* (Öpik 1930a), ventral valve GIT 400-19, interior and posterior views. Kohtla-Nõmme, northeastern Estonia, Kukruse RS. C1–C5, *Cyrtanotella laine* (Öpik 1930a), ventral valve GIT 400-50, exterior, interior, lateral, posterior and anterior views, GIT 400-50, Kohtla, northeastern Estonia, Kukruse RS. D, *Cyrtanotella kuckersiana* cf. *kuckersiana* (Wysogórski, 1900), interior of ventral valve GIT 400-7, Küttejõu quarry, northeastern Estonia, Kukruse RS. E, *Cyrtanotella laine* (Öpik 1930a), ventral valve GIT 400-11, ventral interior, Kohtla, northeastern Estonia, Kukruse RS. The scale is the same for all figures.

- figs 1, 2; pl. 46, fig. 1; pls 47, 48; Lesnikova 1949, p. 203, pl. 32, figs 1–3b. Alikhova 1951, pp. 24–25, pl. 2, figs 21, 22.
- 1951 *Cyrtanotella concava* (Schmidt); Alikhova, pp. 25–26, pl. 2, figs 22, 23.
- 1953 *Cyrtanotella kuckersiana kuckersiana* (Wysogórski); Alikhova, pp. 32–36, pl. 2, figs 11–13; Alikhova 1969, pp. 22–23, pl. 1, figs 10, 11; Hints 2004, pp. 636–637, pl. 2A–C, pl. 3B–G.

Neotype (designated here). Shell TUG 1054-17 (old number Br 077) (Fig. 1A1–A5) with ventral length 35.4 mm, dorsal length 31.3 mm, width 42.9 mm and thickness 14.8 mm; 42 ribs occur along the sell margin,

27 of which appear around the umbo and along the posterior edge. The type specimen is described and figured by Öpik (1930a, pl. 2, fig. 17); Ubja, northeastern Estonia; Kukruse RS, lowermost Upper Ordovician (Sandbian).

Öpik considered this specimen one of the ‘typoids’, whose exterior features (size, outline) coincide with those of the specimen figured by Wysogórski (1900, pl. 8). Alikhova (1951) proposed for the lectotype Wysogórski’s specimen on plate 8. Unfortunately, Wysogórski’s specimens are lost and Öpik’s specimen is suitable for the neotype to ensure the stability of the taxonomic status of the species (Article 75.1, ICZN 1999).

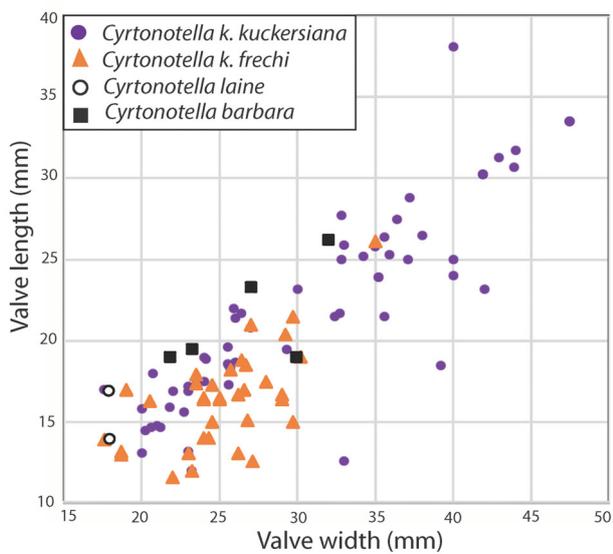


Fig. 3. Measurements of 105 dorsal valves of the species of *Cyrtototella*.

Diagnosis. Large, up to 33 mm long and 46 mm wide suboval plano- to weakly concavo-convex shell; cardinal angles rounded; anterior commissure rectimarginate; hinge line corresponds to 0.9 shell width or is equal to it. Ornament consists of up to 47 filated ribs of almost equal size along the lateral and anterior margins; 12–14 primary costae appearing at the umbo bifurcate at a distance of about 2 mm; fine filae, up to 11 in 2 mm, occur on ribs and interspaces, capillae are rare. Ventral valve has *vascula media* which smoothly curve laterally; dorsal valves have plate-like brachiophores whose tops diverge at about 90°, basal parts at about 120° or more from each other.

Description. Large, up to about 50 mm wide and over 30 mm long suboval shell (Fig. 3) with a moderately convex ventral valve, whose length corresponds to 0.73–0.81 width and to 0.3–0.4 thickness; the highest convexity is in the midline or posterior half; dorsal valve flat or very weakly concave at the umbo. Cardinal angles sharp to obtusely rounded on mature shells; hinge line corresponds to 0.9 shell width or is equal to it. Anterior commissure rectimarginate or very weakly sulcate. Ventral umbo rounded, interarea concave, apsacline, 1.7–2.5 mm high; delthyrium open, delthyrial angle about 90°. Dorsal umbo flattened; interarea catacline, up to 2 mm high; notothyrium open, partly occupied by the cardinal process.

Ornament costate, on dorsal valve 12–14 costae appear at the umbo. The number of costae increases by bifurcation at a distance of 2–3 mm from the umbo, additional new costae appear along the posterior margin during the growth of the shell. On average 38 costae

(variation 33–47) are counted along the lateral and anterior margins. Capillae are visible on the lateral parts of some mature shells, mainly on the interspaces. Fine filae (lamellae), 7–11 in 2 mm, occur on costae and interspaces (Fig. 5A1, A2); anterior one third of the valve length may be formed during hemiperipheral growth (Fig. 5A1); stronger growth lines mark changes in shell outline from suboval with acute cardinal angles to subrectangular with obtuse angles.

Ventral interior (Fig. 2A) with small triangular teeth; crural fossettes form straight notches on inner sides of teeth; dental plates slightly arched laterally, convergent on the valve floor and merging with low ridges surrounding antero-laterally the muscle field which occupies about 0.2 valve length; diductor scars elongately oval, occupying partly interior sides of the dental plates; adductor scar suboval, slightly shorter than diductor scars. A pair of parallel vessel-like septa marking the *vascula media* arise in front of diductors and curves smoothly laterally at a distance of 2/3 valve length from the umbo. A thin septum occurs between the *vascula media*.

Mature dorsal valves have expressive cardinalia with an elevated notothyrial platform parallel to the interarea. Cardinal process is wedge-shaped in posterior view, with up to 10 closely spaced folds extending above the interarea and fills about one third to a quarter of the width of the notothyrial cavity. Details of the cardinal process have been described earlier (Hints 2004). In ventral view brachiophores are arranged at about 90° from each other, on basal parts at about 120°; sockets occur as small triangular depressions between the brachiophores and posterior edge of the valve. Small triangular tooth-like structures above the sockets on the anterior edge of interarea provide a secure lock of the shell. The notothyrial platform continues anteriorly as a short and wide myophragm; lateral septa separate the anterior and posterior adductors. The adductor muscle field extends about to the middle of the valve; its width corresponds to 0.3 valve width and it is postero-laterally bordered by arched ridges. The crenulation on the inner peripheral margin occupies about 0.2 valve length or is practically missing on postero-lateral corners close to *vascula cardinalia*.

Discussion and comparison. Some specimens from the Jõhvi Substage of the Haljala RS (Fig. 1E, F) are included here within *C. kuckersiana kuckersiana* mainly because of large size (shell width up to 35 mm) and costate ornamentation. Weak concavity of the dorsal valve and somewhat more strongly developed filae supposedly indicate intraspecific variability, although marking some similarity with *C. kuckersiana frechi*. The comparison with *C. kuckersiana frechi* and other species is presented below.

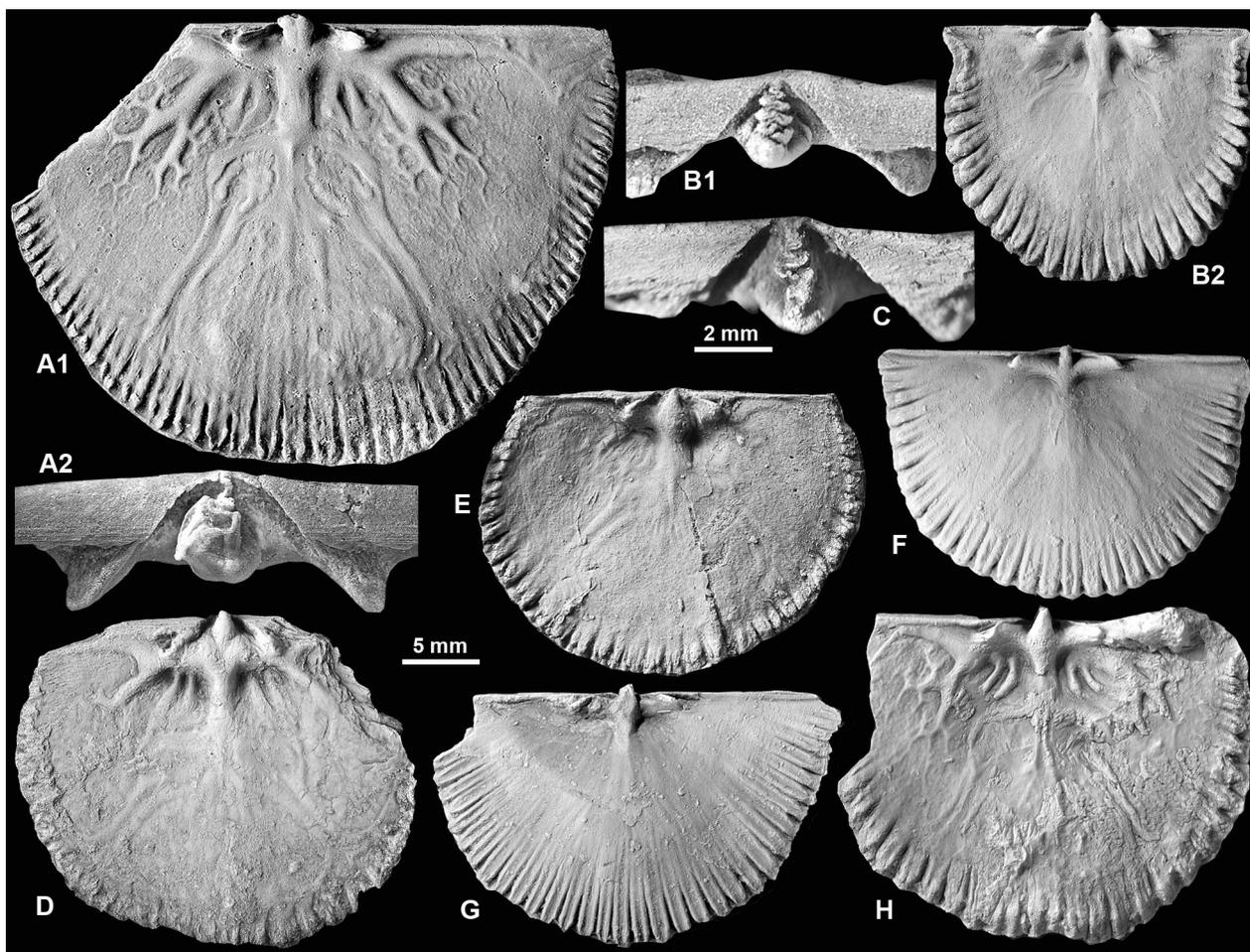


Fig. 4. **A1, A2**, *Cyrtototella kuckersiana kuckersiana* (Wysogórski, 1900), interior and cardinal process of dorsal valve TUG 1054-15, Kohtla, northeastern Estonia, Kukruse Regional Stage (RS). **B1, B2**, *Cyrtototella laine* (Öpik 1930a), posterior view of the cardinal process and interior of dorsal valve GIT 400-118, Pääsküla (western part of Tallinn), Jõhvi Substage of the Haljala RS. **C, D**, *Cyrtototella barbara* (Öpik, 1930a), posterior view of the cardinal process and interior of dorsal valve GIT 400-78. Tallinn (Pirita–Ülemiste channel), Kukruse RS. **E**, *Cyrtototella barbara* (Öpik, 1930a), interior of dorsal valve GIT 400-86, Tallinn? (locality HN 32), Kukruse RS. **F**, *Cyrtototella kuckersiana frechi* (Wysogórski, 1900), interior of dorsal valve TUG 72-278, Alliku (western Estonia), Jõhvi Substage of the Haljala RS. **G**, *Cyrtototella kuckersiana frechi* (Wysogórski, 1900), interior of dorsal valve TUG 243-151, Aluvere, northeastern Estonia, Haljala RS. **H**, *Cyrtototella kuckersiana kuckersiana* (Wysogórski, 1900), interior of dorsal valve GIT 400-138, Alliku (western Estonia), Jõhvi Substage of the Haljala RS. Scale 5 mm for dorsal valve, 2 mm for cardinal process.

Occurrence and material. Uhaku, Kukruse and Haljala RSs in northern Estonia, southern Lithuania (Paškevičius 1997) and the northwestern part of Russia (Alikhova 1951, 1953). The Estonian collections GIT, TUG and ELM comprise 64 specimens.

Cyrtototella kuckersiana frechi (Wysogórski, 1900)
 Figures 1B1–B5; 3; 4F, G; 5B, C

1900 *Orthis frechi* n. sp.; Wysogórski, p. 12, pl. 8.

1930a *Orthis* aff. *frechi* Wysogórski; Öpik, p. 79, pl. 3, figs 20, 23.

1930b *Orthis* cf. *frechi* Wysogórski; Öpik, pp. 14–15, pl. 1, fig. 5.

1953 *Cyrtototella kuckersiana frechi* (Wysogórski); Alikhova, p. 36, pl. 2, figs 7, 10; Hints 2004, pp. 636–637, pl. 2A–C, pl. 3B–G.

1953 *Cyrtototella concava* (Schmidt in manuscript 1900); Alikhova, p. 23, pl. 12, figs 5–7.

1969 *Cyrtototella* cf. *kuckersiana frechi* (Wysogórski), Alikhova, pp. 23–24, pl. 1, figs 12, 13.

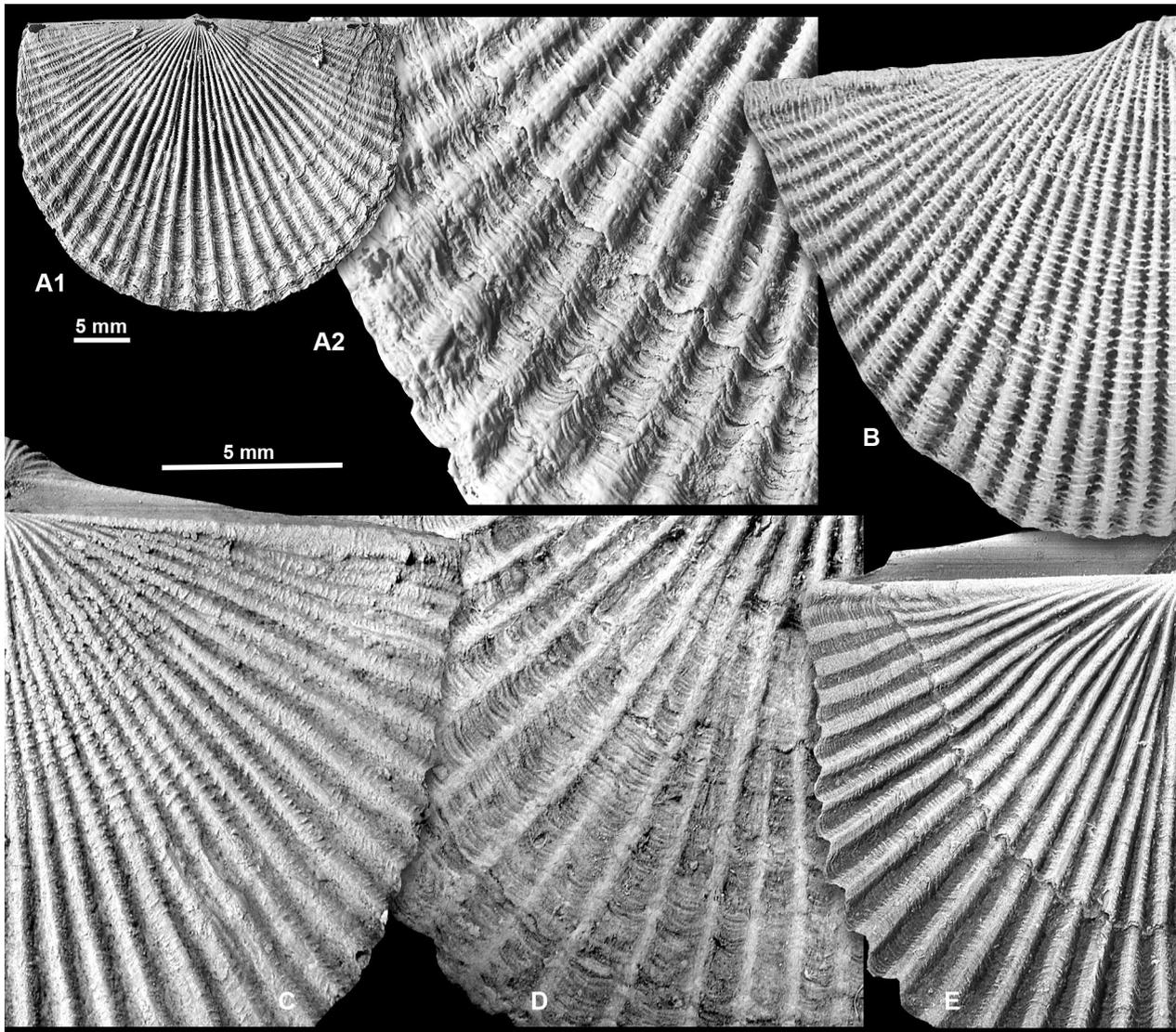


Fig. 5. Exterior sculpture. **A1, A2**, *Cyrtonotella kuckersiana kuckersiana* (Wysogórski, 1900), dorsal valve TUG 1054-18 (Br 075). **B**, *Cyrtonotella kuckersiana frechi* (Wysogórski, 1900), shell GIT 400-40, filate ribbing on ventral valve. **C**, *Cyrtonotella kuckersiana frechi* (Wysogórski, 1900), holotype, shell GIT 400-70, filate ribbing on dorsal valve. **D**, *Cyrtonotella barbara* (Öpik, 1930a), holotype, shell TUG 1054-24 (Br 084), exterior sculpture on dorsal valve. **E**, *Cyrtonotella laine* (Öpik, 1930a), shell GIT 400-47, exterior sculpture on dorsal valve. Scale 5 mm for A1, 5 mm for A2–F.

Neotype (designated here). GIT 400-70, shell (Figs 1B1–B5, 5C) with length of the ventral valve 20.1 mm and of the dorsal valve 17.7 mm, shell width 28.4 mm and thickness 8.4 mm. Forty costae appear around the shell margins and 14 around the umbo. Pääsküla (western part of Tallinn), Jõhvi Substage of the Haljala RS.

Öpik (1930a) recommended for the type of *O. frechi* one of the two specimens shown by him in table 3, figs 21 and 22. However, neither of them can be referred to *O. frechi*. The first specimen exhibits subparallel *vascula media* very similar to those of the species

C. laine described below, and the second specimen represents a relatively younger *C. kuckersiana kuckersiana*.

Alikhova (1953, p. 36) has selected for the holotype of the subspecies *C. kuckersiana frechi* a specimen figured by Wysogórski (1900, pl. 8). However, that specimen is lost and its locality is unknown. Thus, it is necessary to designate a new type specimen. Shell GIT 400-70 from the Jõhvi Substage of the Haljala RS designated as the neotype shows great similarity with the drawing of *O. frechi* by Wysogórski (1900, pl. 8) by the shell outline and also by the stratigraphic position.

Diagnosis. Medium-sized, suboval to subtriangular shell, with ventral valve length up to 31 mm (Fig. 3) and width up to 27 mm; cardinal angles acute; anterior commissure slightly sulcate; hinge line corresponds to shell width. Ornament consists of up to about 40 filated costae, 14–16 costae around the umbo bifurcate within the distance 2–5 mm. Brachiophore plates widely divergent, their tops diverge at about 110°, basal parts at about 140° or more from each other.

Description. Medium-sized for the genus plano- or slightly concavo-convex shell; ventral valve length corresponds to about 0.6–0.8 and thickness to 0.4–0.5 valve width. Cardinal angles acute to obtuse, length of hinge line corresponds to shell width. Ventral valve moderately convex; dorsal valve weakly concave in the middle; anterior commissure sulcate. Ornament costate, with second-order costae appearing within 2–5 mm from the umbo and along the posterior margin; on average 38 ribs are counted along the shell margin. Filae fine, about 7–12 filae in 2 mm (Fig. 5B, C). Ventral umbo is curved up to the hinge line; interarea apsacline to orthocline, concave, 1.5–2 mm high; dorsal interarea anacline, 1–1.3 mm high; delthyrium and notothyrium wide. Ventral interior is unknown. Brachiophores are short, tilted postero-laterally, disposed in ventral view at about 110°, basally on the valve floor at about 140° from each other. Sockets triangular between the brachiopore and posterior edge of the valve. Cardinal process with a folded myophore directed backwards and fills about 1/3 of the notothyrium. Muscle scars weakly developed with anteriorly developed *vascula antemyaria*. The peripheral ribbing occupies up to 0.3 valve length, becoming shorter laterally. Dorsal muscle field weakly expressed.

Comparison and discussion. *Cyrtototella kuckersiana kuckersiana* and *C. kuckersiana frechi* differ in shell size (Fig. 3), outline and details of ornament. The oval shell of *C. kuckersiana kuckersiana* is up to 50 mm wide, which corresponds to 0.7–0.8 shell length and 0.3–0.4 shell thickness. The medium-sized, suboval to subtriangular shell of *C. kuckersiana frechi* has shells whose length corresponds to 0.6–0.7 width and about 0.4 thickness.

The hemiperipheral growth of the shells of *C. kuckersiana kuckersiana* shows that younger specimens have shell outline similar to that of *C. kuckersiana frechi*, which does not reach the size of the first subspecies. This could be related to changes in environments – the larger specimen (*C. kuckersiana kuckersiana*) originates from the kukerite kerogen-rich facies and the smaller one (*C. kuckersiana frechi*) from the siliciclastic carbonate facies with a low content of kerogen. The subspecies presumably represent facies-dependent groups of the species *C. kuckersiana*.

Cyrtototella kuckersiana kuckersiana has an almost flat dorsal valve while the shell of *C. kuckersiana frechi* has an anteriorly widening low sulcus and weakly sulcate anterior commissure. The differences in shell outline and cardinal angles are age-dependent, especially in *C. kuckersiana kuckersiana*, whose younger specimens have a suboval outline with acute cardinal angles resembling the specimens of *C. kuckersiana frechi*. Both subspecies exhibit costate ornament with 13–14 costae appearing around the umbo, and some ribs appear during the growth of the shell on the posterior edge. The branching of ribs occurs close to the umbo, within 2–4 mm (*C. kuckersiana kuckersiana*) or up to 5 mm from the umbo (*C. kuckersiana frechi*). The total number of costae varies from 35 to 43, reaching about 50 on the largest specimens.

The shell surface is covered by fine filae, whose number in 2 mm varies from 7 to 10, being somewhat denser on *C. kuckersiana kuckersiana* than on *C. kuckersiana frechi*. Capillae occur on some mature shells of *C. kuckersiana kuckersiana* but not on other taxa.

Öpik (1930a) attributed taxonomic value to the vascular pattern. *Cyrtototella kuckersiana kuckersiana* has *vascula media* curving smoothly laterally close to the midline. One specimen, identified by Öpik as *O. cf. frechi*, is included here in the species *C. laine* by the similarity in long subparallel *vascula media* observed on several specimens of the latter species. Most specimens of *C. laine* differ clearly from *C. kuckersiana* in a smaller size, strongly convex ventral valve and finer filae on the shell surface (Figs 1D1–D5, 5E). Both subspecies of *C. kuckersiana* have plate-like tilted and laterally divergent brachiophores, whereas brachiophores in *C. kuckersiana frechi* are more widely tilted than in *C. kuckersiana kuckersiana*.

Occurrence and material. Haljala and Keila RSs. *Cyrtototella kuckersiana frechi* (Wysogórski) is represented in the collections of GIT, TUG and ELM by 163 specimens.

Cyrtototella laine (Öpik, 1930a)

Figures 1D1–D5; 2B1, B2, C1–C5, E; 4B1, B2; 5E

- 1930a *Orthis laine* n. sp.; Öpik, p. 79, pl. 3, fig. 19.
 1930a *Orthis cf. frechi* Wysogórski; Öpik, p. 76, pl. 3, fig. 21.
 ?1951 *Cyrtototella kuckersiana* (Wysogórski), Alikhova, pl. 1, fig 21.

Holotype. TUG 1054-19 (Br 082 in Nestor 1974), shell about 23 mm wide, ventral valve 18.4 and dorsal valve 16.2 mm long, thickness about 23 mm. The specimen is figured by Öpik (1930a, pl. 3, fig. 19); in this paper

Fig. 1D1–D5; Kohtla, northeastern Estonia, Kukruse RS (Sandbian).

Diagnosis. Small to medium-sized suboval shell with strongly convex ventral valve. Ventral interarea orthocline, dorsal interarea catacline. Ribs appear at 2 mm distance around umbo and along posterior edge, 35–39 ribs occur on valve margins. Ventral muscle field with elongated oval diductor scars impressed on valve floor. *Vascula media* expressed as two parallel septa originating before muscle scars and reaching up to the first half of valve. A thin thread-like septa separates the branches of *vascula media*.

Description. Suboval shell, small to medium in size, commonly less than 25 mm wide; ventral length corresponds to 0.8 shell width or is equal to it. Ventral valve strongly convex; valve thickness corresponds to 0.5–0.6 shell length; cardinal angles rounded to sharp. Dorsal valve weakly concave; anterior commissure weakly sulcate. Radial ornamentation consists of 35–39 ribs, 13 or more appear at 2 mm distance around the umbo and 5–7 along the posterior edge on both sides of the umbo. Filae fine, about 15 in 2 mm. Growth lines mark the change in shell outline from laterally elongated with sharp cardinal angles to suboval in mature shells (Fig. 5E).

Ventral interarea orthocline, concave, 1.5–2 mm high; dorsal area catacline, flat, 1.5–1.7 mm high. Interarea as wide as shell width or forms 0.9 of it; cardinal process reaches over the hinge line and fills partly the notothyrium and delthyrium.

Ventral umbo is curved over the hinge line; delthyrium right-angled; teeth small; dental plates subparallel, joining on valve floor with low ridges bounding the oval diductor scars; crural fossettes developed as small depressions in the middle of dental plates. Two parallel, low ridges before diductor scars reaching anterior half of the valve mark the *vascula media*; on six of seven specimens these ridges have asymmetrical position. Peripheral ribbing on the inner surface of valves occupies about 0.3 valve length in the middle of the valve.

Cardinal process on the raised notothyrial platform is wedge-shaped, with lobated myophore which reaches over the hinge line and fills partly the notothyrium and delthyrium. Brachiophores are short, divergent, connected with the raised notothyrial platform. Muscle field extends to the middle of the valve; posterior scars are shorter than anterior scars. Vascular system weakly developed.

Discussion and comparison. The described species differs from the *C. kuckersiana*-type brachiopods in having a relatively small size, high and strongly convex ventral valve and parallel branches of *vascula media*, which tend to have an asymmetrical position in relation to valve midline. One ventral valve (GIT 400-19;

Fig. 2B1, B2) differs from other specimens of *C. laine* in the large size. This specimen, like a specimen identified by Öpik (1930a, pl. 3, fig. 21) as *C. cf. kuckersiana*, is included in *C. laine* having parallel and asymmetrical *vascula media*.

Cyrtonotella laine has some similarity with Wysogórski's (1900) figure of *Orthis concava* Schmidt *mscr.* The description of Lithuanian specimens with the name *O. concava* by Alikhova (1953) should be treated as *nomen nudum* as the species has not been described and the original material is lost. Alikhova (1951) considered the specimen figured by Wysogórski as the lectotype of the species *Cyrtonotella concava* (Schmidt). She described it on the basis of Wysogórski's figure and few specimens from Leningrad District. However, the Leningrad specimens differ from the figured one in smaller convexity and ribbing of the ventral valve, and presumably belong to the *C. kuckersiana kuckersiana*-group species.

Occurrence and material. This specimen is relatively rare in the Kukruse and Haljala RSs (Sandbian) in northern Estonia; 28 specimens are represented in the GIT, TUG and ELM collections.

Cyrtonotella barbara (Öpik, 1930a)
Figures 1C1–C5; 3; 4C–E; 5D

1930a *Orthis barbara* n. sp.; Öpik, pp. 80–81; pl. 3, fig. 24; in this paper Fig. 1C1–C5.

Holotype. TUG 1054-24 (Br 084, old number in Nestor 1974), shell 26.4 mm long and 30.0 mm wide and ca 11.9 mm thick. The specimen is figured in Öpik (1930a, pl. 3, fig. 24; in this paper Fig. 1C1–C5); Sõjamägi (Tallinn), Haljala RS.

Diagnosis. Medium-sized subcircular shell up to about 30 mm wide (Fig. 3). Flat to weakly concave dorsal and moderately convex ventral valve. Ornament costate with up to 40 rounded-triangular ribs on shell margins, few second-order costellae appear in anterior half of valves; filae thin, weak; ventral umbo curved over hinge line; cardinal process on notothyrial platform has thickened basal part with ridge-like folded myophore reaching backwards over interarea.

Description and discussion. Medium-sized subcircular shell; hinge line corresponds to 0.7–0.8 shell width; ventral valve convex, its length corresponds to 0.8 and thickness to 0.4 shell width; dorsal valve weakly concave in the middle; anterior commissure rectimarginate. Radial ornamentation consists of 40 low rounded costae, few second-order ribs appear on the anterior half of valves; interspaces between costae are wider than ribs. About 30 ribs appear around the umbo at a distance of 2 mm;

3–4 ribs and 3 ribs occur in 5 mm on the anterior and lateral margins, respectively. Filae, 6–8 in 2 mm, are thin and weakly developed (Fig. 5D). Ventral umbo extends over the hinge line; interarea strongly apsacline, up to 2 mm high, dorsal interarea flat, anacline; delthyrium wide, open, notothyrium partly filled with a narrow, weakly folded cardinal process; myophragm short, separates posterior adductor scars (Fig. 4D–E). Ventral interior is unknown.

The specimen of *C. barbara* differs from the *C. kukersiana*-type specimens and from *C. laine* in having subcircular outline, a shorter hinge line and low and rounded ribs with few second-order ribs. The taxonomically unclear specimen figured by Wysogórski (1900) as *Orthis concava* Schmidt *mscr.* differs from *C. barbara* in the more oval outline and seemingly in a higher number of ribs.

Distribution and material. Kukruse and Haljala RSs; 13 specimens in GIT, TUG and ELM collections.

DISTRIBUTION OF CYRTONOTELLA IN BALTICA

The earliest occurrence of *Cyrtototella* in Baltica is *C. semicircularis* in the Aseri RS (Alikhova 1953).

However, most Baltic *Cyrtototella* records come from the interval from the Uhaku RS to the Keila RS (Darrivilian to Sandbian stages; Fig. 6). The occurrence of cyrtoneilids (*Cyrtototella* sp. nov. 1 and *Cyrtototella* sp. A, in Ropot & Pushkin 1987) in the Oandu and Vormsi stages of Belarus is not clear because neither descriptions nor figures are available. The Baltic brachiopods of the genus *Cyrtototella* became extinct during the mid-Caradoc (Keila–Oandu) faunal turnover in the Baltic Basin (Meidla et al. 1999; Ainsaar et al. 2004).

The Ordovician brachiopods of the genus *Cyrtototella* inhabited the temperate-water carbonate ramp environments of the Baltic Basin (Dronov & Rozhnov 2007), especially areas of the occurrence of the kukersite kerogen in northern Estonia and in the eastern neighbouring regions of Russia (Fig. 6II). The kukersite organic matter was transported from tidal flats to subtidal shallow-water environments (Bauert & Puura 1990) with diverse shelly fauna. On the southern shallow shelf, in Lithuania, *Cyrtototella* occurs in detrital limestones and dark marls with different pyritic traces indicating the burial of abundant organic matter (Paškevičius 2000). The brachiopod community of the Kukruse RS with *C. kukersiana kukersiana* is considered (Paškevičius 2000) to belong to the Benthic Assemblage BA2. The taxonomic composition of that community is similar to

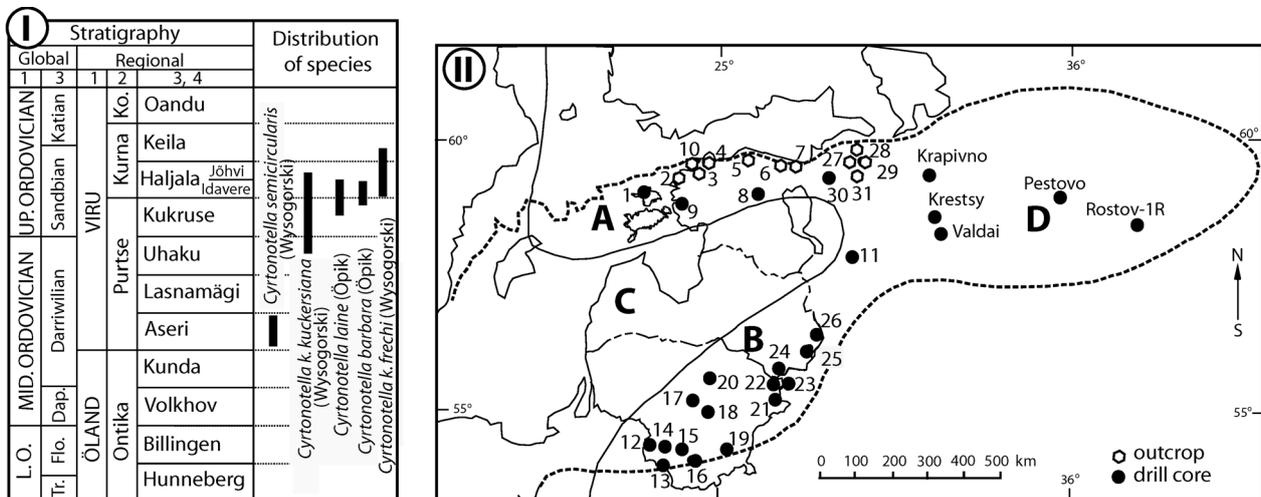


Fig. 6. Stratigraphical (I) and spatial (II) distribution of brachiopods of the genus *Cyrtototella* (Schuchert & Cooper, 1931) in the Baltic Basin with the Estonian (A) and Lithuanian (B) shelves, Livonian Basin (C) and Moscow Basin (D). *Explanations of the stratigraphic scheme:* 1, global or regional series; 2, regional subseries; 3, global or regional stage; 4, regional substage. *Abbreviations:* L.O., Lower Ordovician; Mid., Middle; Up., Upper; Tr., Tremadocian; Flo., Floian; Vi., Vinni. *Localities:* 1, Kõrgessaare; 2, Põðsaspea; 3, Alliku; 4, localities in the limits of Tallinn; 5, Aluvere; 6, Kohtla; 7, Jõhvi; 8, Ellavere; 9, Haapsalu; 10, Ristna; 11, Porkhov; 12, Virbalis; 13, Kalvarija; 14, Sasnava-6; 15, Prienai-3; 16, Ilgai-54; 17, Krekenava-7; 18, Ukmerge-10; 19, Tauçionys-49; 20, Svedasai-252; 21, Vidzy; 22, Kazimirovo; 23, Vangishki-205; 24, Vishki-25; 25, Škaune-103; 26, Berzini; 27, Veimarn; 28, Džatlitsy; 29, Volgovo; 30, core No. 139; 31, Khrevitsa. Data from Alikhova (1951, 1953, 1969), Rõðmusoks (1970), Dmitrovskaya (1991), Laškovas et al. (1993), Paškevičius (2000), Estonian geoscience collections database and unpublished reports.

the contemporaneous faunas in the northern part of the basin in Estonia (Hints et al. 2018). Differently from Lithuania, the North American relatives occur along the facies transect from the benthic association BA3 to BA4 and BA5 (Potter & Boucot 1992).

The brachiopods of the genus *Cyrtonotella* have been identified in the Moscow Basin in the Kukruse RS (Alikhova 1969) and Haljala RS (Dmitrovskaya 1977) in relatively shallow-water environments as in the East Baltic. The marls and limestones enriched in kukersite kerogen occur in the Kukruse RS up to the middle part of the Moscow Basin (Krestsy, Valdai and Porkhov drill cores, Alikhova 1969; Fig. 6II). The easternmost finds of *Cyrtonotella* in the southeast of the basin (Rostov R-1 drill core; specimens GIT 154-314-1, 154-478) come from the Kukruse and Haljala RSs. The transition from the Kukruse RS to the Haljala RS (lower half of the Sandbian) in this core coincides with a change in brachiopod composition. There appear several new brachiopods (*Eorhipidomella ovalis*, Hints 1971, *Multicostella rostovensis* nom. nud. in the collection GIT 154) unknown in the East Baltic. The latter species, however, could be related to the Baltic plaesiomyd genus *Madiorthis* (Zuykov et al. 2008) from the Haljala RS of the same interval.

The cluster analysis of the dynamics of the rhychnelliformean brachiopods in the Baltic Basin (Hints et al. 2018) reveals the same trend of faunal diversity changes during the transition of the Kukruse and Haljala times. In the Moscow Basin, the brachiopods common with the Baltic Basin (such as *Leptelloidea*, *Estlandia*, *Clitambonites*; Alikhova 1969) dominated up to that time. Subsequent development of faunas in the Moscow Basin is poorly known due to the development of facies (dolomites, sandstones) unsuitable for many groups of benthic organisms (Alikhova 1969; Kheraskova et al. 2005). Besides, on different stratigraphic levels there occur erosional gaps and the Devonian deposits overlie the Ordovician deposits of different age (Alikhova 1969).

The distribution of *Cyrtonotella* and associated brachiopods (Hints et al. 2018) in the Baltic and Moscow basins highlights their close palaeobiogeographical relationships through the early Sandbian Stage.

CONCLUSIONS

The cyrtonellid brachiopods are represented by four species (one of these with two subspecies) in the shallow sea environments of the Middle and Upper Ordovician of the Baltic Basin.

The type specimens have been selected for two subspecies, and the emended descriptions of all species

and subspecies are presented. The cyrtonellid brachiopods are easily identifiable by their cardinal process, whose folded myophore reaches backwards from the notothyrium.

The stratigraphic range of the Baltic Ordovician cyrtonellids, together with the type species *C. semicircularis* from the Middle Darriwilian, covers about 11 Ma, which corresponds to the interval from the Aseri RS to Keila RS (mid-Darriwilian–Katian). The cyrtonellid brachiopods became extinct in the Baltic Basin during the Sandbian faunal turnover at the transition from the Keila RS to the Oandu RS.

In the easternmost parts of the Moscow Basin *Cyrtonotella* disappeared already during the Kukruse Age. Up to that time, the faunas of the Baltic and Moscow basins had a close relationship. The global distribution of the representatives of the genus *Cyrtonotella* is still insufficiently known due to the taxonomic problems on the species and genus levels.

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Ordoviitsiumi brahhiopood perekonnast *Cyrtonotella*: taksonoomia ja levik Balti basseinis

Linda Hints

On esitatud Ordoviitsiumi brahhiopoodide perekonna *Cyrtonotella* kolme liigi ja kahe alamliigi täiustatud kirjeldused. Kahele liigile on valitud tüüpeksemplarid (lektotüübid). Perekond on arvatud kuuluvaks sugukonda Nanorthidae, kuid tõenäoliselt esindab see eraldi gruppi (sugukonda) brahhiopoodide, mida iseloomustab suhteliselt suur koda ja omapärane kardinaaljätik.

Perekonna *Cyrtonotella* brahhiopoodide stratigraafiline levik Balti basseinis haarab koos perekonna tüüpliigi *C. semicircularis*'ega ligi 11 miljoni pikkuse ajalõigu Kesk-Ordoviitsiumi Aseri east kuni Hilis-Ordoviitsiumi Keila eani. Nende geograafiline levik ulatub Baltikumist kuni nn Moskva Basseini idapoolsemate piirkondadeni.

Perekond *Cyrtonotella* brahhiopoodide on kirjeldatud eri regioonidest Euroopas, Ameerikas ja Aasias, aga nende seosed Balti basseinis esinevate liikidega ei ole selged, nagu ka nende võimalik sugukondlik ning perekondlik staatus.