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Maximizing diductor adhension: An unusual cardinal process in Late Ordovician brachiopods from Estonia

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Cardinal process is a structure on dorsal valve of brachiopods serving for separation or attachment of diductor muscles. A cardinal process with a peculiar folded myophore is described from Late Ordovician *"Orthis" kukersiana*-group brachiopods assigned to the genus *Cyrtonotella* (order Orthida). This structure differs from those of other rhynchonelliformean brachiopods and can be considered as a separate type among about twenty varieties of processes described up to now.

Large Late Ordovician orthoidean brachiopods of the "*Orthis*" *kukersiana* group of Öpik (1930) were later (Öpik 1934) assigned to the genus *Cyrtonotella* Schuchert and Cooper, 1932. These brachiopods are distributed in the East Baltic through the Kukruse to Keila stages (lowermost Upper Ordovician) (Öpik 1930, 1934; Alikhova 1969; Paškevičius 1997; Rõõmusoks 1970; Ropot and Pushgin 1987) (Fig. 1). The aim of this paper is to provide an improved description of the cardinal process of the "*Orthis*" *kukersiana*-group brachiopods (*Cyrtonotella kukersiana*, *C. frechi* and other related Upper Ordovician taxa) first described by Öpik (1930: 73, 75, 80, text-fig. 8). Öpik characterised the cardinal process of "*Orthis*" *kukersiana* as a thick, flat and stocky structure, which reaches slightly above the notothyrium, and consists of folds lying one on top of another, in posterior view. Lesnikova (1949) followed Öpik's description of the process in a short description of *C. kukersiana*, and Alikhova (1960) noted the folded myophore of the process as a characteristic of the genus *Cyrtonotella*. In spite of these observations the folded myophore has received little attention.

Institutional abbreviations.—The material described in the paper is from the collection of the Institute of Geology at Tallinn University of Technology, Estonia (GIT) and from the Estonian Museum of Natural History, Tallinn (RLM).

Description of the cardinal process.—The cardinal process of the *C. kukersiana*-group brachiopods is situated on an elevated notothyrial platform. Together with widely divergent brachiophores and a wide median septum it forms a cross-like structure in the posterior part of the valve (Figs. $2A_1$, $3A_1$). The cardinal process appears as a thick structure, in some cases with a sharp middle part, extending above the dorsal interarea (Figs. 2A, 3A, B). In the dorsal valves (Figs. $2A_1$, B_3) of the Baltic taxa the cardinal process differentiates into a shaft and myophore; the latter consists of a thin ridge crenulated by up to 8 closely spaced folds (Figs. $2A_2$, C, D, $3A_3$, B, C, D_1, E, G). The folds occupy about one-third to a quarter of the width of the notothyrial cavity (Figs. $3A_3$, B_2, D_1, E_1,). The upper surfaces of the folds are almost on the same level (Figs. $2C_2$, C_3, $3E_2$) but rise anteriorly in relation to the interarea (Figs. $3A_2$, C_2, E_2). On some specimens the folded myophore is rimmed anteriorly by a separate ridge, rampant, surrounding laterally some of the folds (Fig. $3C_1$). The length of the myophore is somewhat shorter or about equal to

B

Global series	Graptolite biozones	Regional Stage	Stratigraphic range of studied brachiopods
Upper Ordovician	*Dicranograptus foliaceous*	KEILA	*Cyrtonotella k. frechi*
		HALJALA	
	Normalograptus gracilis	KUKRUSE	*Cyrtonotella k. kukersiana*

Fig. 1. Locality map (**A**) with the outcrop belt (grey) of the Kukruse to Keila Stage and stratigraphic range of studied brachiopods (**B**). Correlation of the regional stages with the graptolite biozones by Webby et al. (2004).

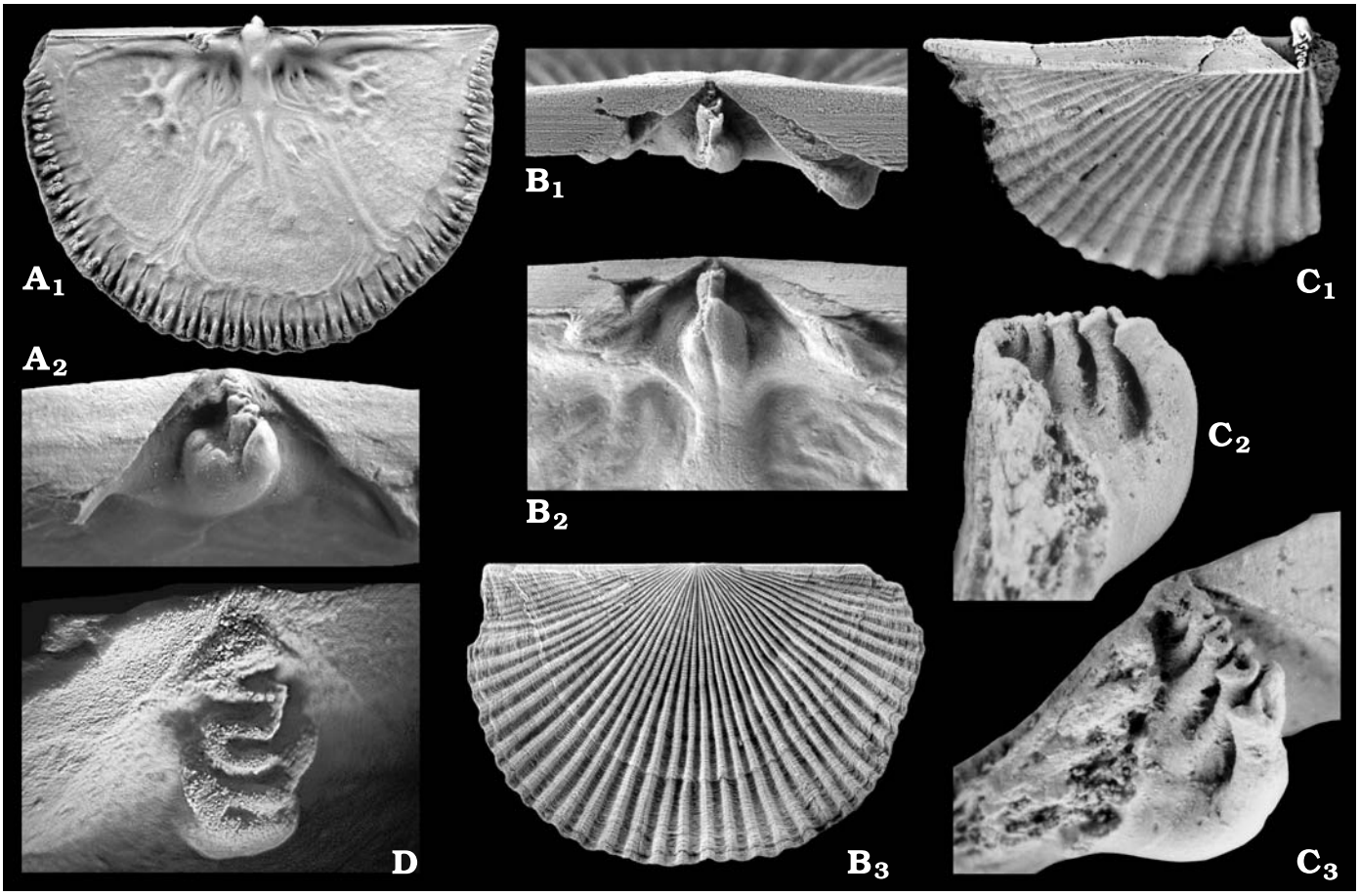

Fig. 2. **A**–**C**. *Cyrtonotella kukersiana kukersiana* (Wysogorski), lowermost Upper Ordovician, Kukruse Stage. **A**. Dorsal valve GIT 400-1, interior (A_1, × 1.7) and dorso-lateral (A_2, × 6), view of the cardinal process; NE Estonia, Küttejtu quarry. **B**. Dorsal valve RLM 1201g/5811, posterior (B_1, × 5.5) and dorso-lateral (B_2, × 5.5) views of the cardinalia, exterior of the valve (B_3, × 1.9); NE Estonia, Kivitli. **C**. Dorsal valve GIT 400-3, posterior view of the interarea (C_1, × 3), lateral (C_2, × 10), and dorso-lateral (C_3, × 10), views of the cardinal process; NE Estonia, Küttejtu quarry. **D**. *Cyrtonotella* sp. Incomplete dorsal valve, GIT 400-54, view of the notothyrium with small antygidium and folded cardinal process, drill core No 1046 (7 km south of Vasalemma in NW Estonia), Upper Ordovician, Keila Stage, × 15.

the length of the notothyrial platform, but along the upper surface of the folds it is about two times longer. In most of the specimens the notothyrium and delthyrium are open and the folded myophore is visible as a structure occupying part of these openings (Figs. $2C_1$, 3F). An exception was observed in two valves, which have an antygidium at the apex of the notothyrium (Fig. 2D).

Radial ridges occurring laterally on both sides of the cardinal process on the notothyrial platform are variably developed. These ridges of secondary shell material (Fig. $3E_2$) are developed extravagantly on gerontic specimens (Figs. $2A_2$, $3A_3$) and the whole structure becomes similar to a trilobed or stout cardinal process in dorsal view (Figs. $2A_1$, $3A_1$, A_2, $3C_2$, $3D_2$). The cardinal process figured by Öpik (1930: text-fig. 8) represents a similarly thickened structure, which in a two-dimensional view is poorly visible without well-oriented photographs or the specimens themselves for comparison. Sometimes two wedge-like plates are developed on the surface of the interarea on both sides of the notothyrium (Figs. $2B_2$, $3E_1$).

Comparison and significance of the folded myophore.—The adult specimens of the *C. kukersiana*-group brachiopods with relatively large plano- to concavo-convex shells presumably had rather strong muscles for opening and closing the valve. In the opinion of Alwyn Williams (personal communication 2004), the folded myophore can serve as a structure, to which each fold binds the tendonous base of inserted diductors. In ventral view the tendonous bases of the right diductor are located alternately with these of the left diductor. The cardinal process of the Estonian specimens described here differs from cardinal processes known among the rhynchonelliformean brachiopods (Williams and Rowell 1965: H117–H119; Williams et al. 1997: 396–399). It is a peculiar modification of ridge-like cardinal process, which commonly separates the diductor scares of several orthids, for example, of *Glossorthis* and *Glyptorthis* (Williams et al. 1997: fig. 360: 1, 4). Some Baltic specimens have subsidiary ridges laterally to the cardinal process similarly to that of the first genus.

The folded form and supposedly alternate location of the left and right diductors differentiate the studied brachiopods from

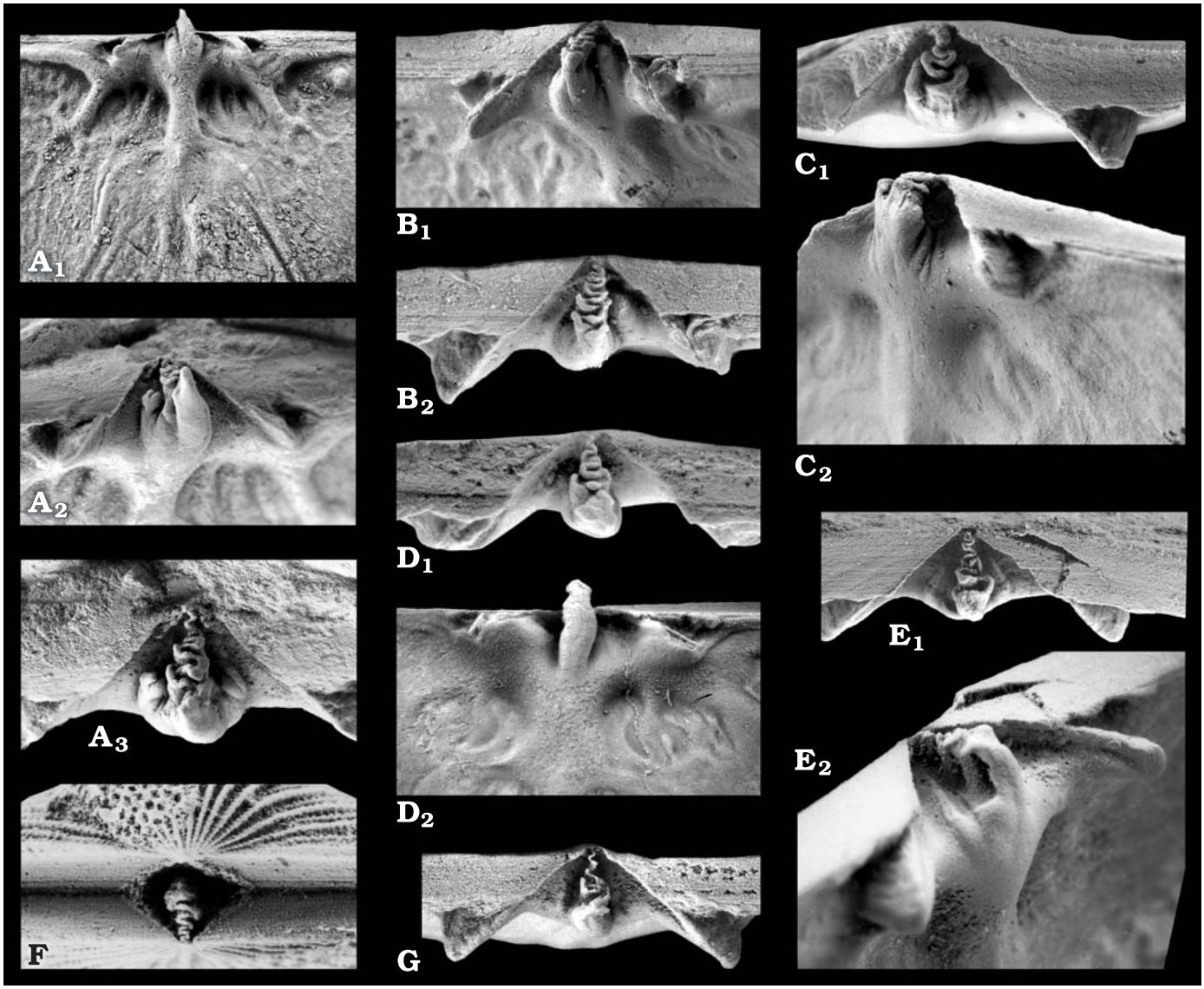

Fig. 3. **A**. *Cyrtonotella kukersiana frechi* (Wysogorski), dorsal valve GIT 400-8, detail of posterior part (A_1, × 1.4), dorso-lateral (A_2), and posterior (A_3) views of the cardinal process, × 6.4; northern Estonia, Alliku, Upper Ordovician, Haljala Stage. **B**–**G**. *Cyrtonotella kukersiana kukersiana* (Wysogorski), lowermost Upper Ordovician, Kukruse Stage. **B**. Dorsal valve RLM 1201g-5813, dorso-lateral (B_1) and posterior (B_2) view of the cardinalia; NE Estonia, Kivitli, × 4,5. **C**. Dorsal valve GIT 400-4, posterior (C_1) and dorso-lateral (C_2) views of the cardinalia; NE Estonia, Küttejtu quarry, × 10. **D**. Dorsal valve RLM 1209/g9.3a, posterior (D_1, × 7) and dorsal (D_2, × 5) views of the cardinalia; NE Estonia, Kohtla. **E**. Dorsal valve GIT 400-2, posterior (E_1, × 6) and dorso-lateral (E_2, × 7) views of the cardinalia; NE Estonia, Küttejtu. **F**. Posterior view of the complete shell GIT 400-40, NE Estonia, Kohtla-Järve, × 7. **G**. Dorsal valve RLM 1201g/5810, view of the cardinalia, NE Estonia, Kivitli, × 5.6.

those which have left and right diductor attachments symmetrically on the left and right side of crenulated myophore, for example from *Herbertella* and *Dinorthis* (see Williams et al. 1997: fig. 360: 2, 3).

The described above cardinal process is characteristic for at least two subspecies *Cyrtonotella kukersiana kukersiana* (Wysogorski) and *C. kukersiana frechi* (Wysogorski).

Its use in higher level taxonomy may contribute for better understanding of the genus *Cyrtonetella* with type species of the genus *C. semicircularis* (Eichwald, 1829) from the uppermost Middle Ordovician in north-western Russia (*Echinosphaerites*-limestone; Schuchert and Cooper 1932).

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