The Hirnantian (Late Ordovician) brachiopod fauna of the East Baltic: Taxonomy of the key species

LINDA HINTS and DAVID A.T. HARPER

Hints, L. and Harper, D.A.T. 2015. The Hirnantian (Late Ordovician) brachiopod fauna of the East Baltic: Taxonomy of the key species. *Acta Palaeontologica Polonica* 60 (2): 395–420.

Rhynchonelliformean brachiopods, belonging to 17 genera, are described from the East Baltic Porkuni Regional Stage, correlated with the global Hirnantian Stage. The brachiopod genera *Paromalomena*, *Proboscizambon*?, *Kinnella*, *Drabovia*, and *Coolinia,* which are described from the region for the first time demonstrate together with characteristic Hirnantian species of the genera *Hirnantia*, *Dalmanella*, *Plectothyrella*, *Eostropheodonta*, and *Hindella* a greater than previously thought commonality of the Baltic fauna with the terminal Ordovician *Hirnantia* brachiopod fauna of the Kosov Province. The samples containing brachiopods were collected from 43 drill core sections in Central East Baltic. The study area belongs to the Livonian Tongue of the Central Baltoscandian Facies Belt in the Baltic Basin. The brachiopods occur mainly in the skeletal and silty limestone of the Kuldiga Formation within the lower half of the Porkuni Stage. Few brachiopods are known from the sandy or oolitic limestone of the Saldus Formation in the upper part of the stage. Due to excellent preservation some brachiopod species (e.g., *Cliftonia psittacina* and *Dalmanella testudinaria*) yield key morphological information, relevant to their classification and phylogeny. This taxonomic study of the East Baltic brachiopods presents essential groundwork for analysis in progress on the distribution and onshore-offshore successions of the *Hirnantia* brachiopod fauna within both a Baltoscandian and global context.

Key words: Brachiopoda, taxonomy, Ordovician, Hirnantian, East Baltic.

Linda Hints [Linda.Hints@ttu.ee], Institute of Geology at Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia.
David A. T. Harper [david.harper@durham.ac.uk], Department of Earth Sciences, Durham University, Durham, DH1 3LE, UK.

Received 13 February 2013, accepted 22 October 2013, available online 22 October 2013.

Introduction

The latest Ordovician *Hirnantia* brachiopod fauna is a unique phenomenon in the evolution of Palaeozoic benthic faunas, which has received much attention in the last decades. During the latest Ordovician, restructuring of facies patterns commenced in the late Pirgu (end of the Katian) with a diachronous, upward shallowing across Baltoscandia. These changes prompted the extinction of many shallow-water shelf faunas due to habitat destruction (first phase of the mass extinction; Rong and Harper 1999; Harper et al. 2014). Due to the lowering of sea level at the beginning of the Porkuni (Hirnantian) the stromatoporoid-coral reefs developed in the shoals across northern Estonia containing specialized faunas (Ärina Formation, Fig. 1) (Nestor and Einasto 1997; Hints 2012). The previously deeper part of the basin (the Livonian Tongue), containing in places the *Foliomena* fauna (Sheehan 1973, 1979; Rong et al. 1999), also shallowed and the *Hirnantia* brachiopod fauna invaded as far as the easternmost parts of the basin. Changes in carbon isotope composition and the distribution of zonal chitinozoans (Kaljo et al. 2008; Hints et al. 2010) indicate that the development of reefs in the Estonian facies belt started at about the same time with the invasion of the *Hirnantia* brachiopod fauna into the Livonian Tongue.

In Baltoscandia, the *Hirnantia* brachiopod fauna has been studied taxonomically in Sweden (Bergström 1968) and Norway (Brenchley and Cocks 1982; Cocks 1982). Data on the distribution of Hirnantian brachiopods in Poland are presented by Temple (1965) and Podhalańska (2009). Bergström (1968) described 18 species of rhynchonelliform brachiopods from southern Sweden (Västergötland) representing the majority of the typical elements of the *Hirnantia* fauna (e.g., species of genera *Dalmanella*, *Hirnantia*, *Kinnella*, *Paromalomena*, *Eostropheodonta*, *Cliftonia*, *Plectothyrella*, and *Hindella*; Rong and Harper 1988; Jin and Bergström 2010). Additional data on the distribution of the *Hirnantia* fauna have been reported from other parts of Sweden (Bergström

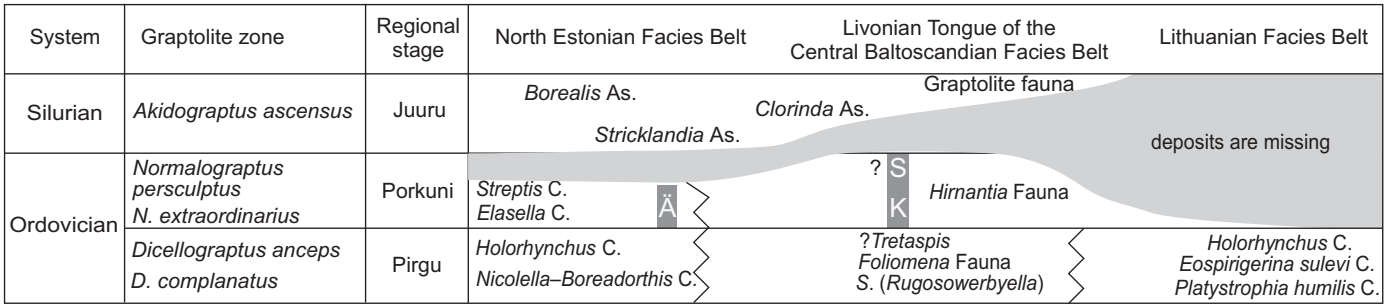


Fig. 1. Correlation and distribution of Late Ordovician–early Silurian faunal communities (C.) and associations (As.) (modified from Kaljo et al. 2008). Ä, Ärina Formation; K, Kuldiga Formation; S, Saldus Formation.

and Bergström 1996; Smelror et al. 1997; Dahlquist et al. 2010). The most diverse *Hirnantia* fauna (the *Hindella–Cliftonia* Association comprising a brachiopod fauna of up to 20 genera) has been identified in Norway (Brenchley and Cocks 1982). It includes some brachiopods (e.g., *Thebesia* and *Brevilamnulella*) indicating a similarity to the Uppermost Ordovician Midcontinent (Edgewood) fauna of North America (Amsden 1974; Rong and Harper 1988).

The distribution of some representatives of the *Hirnantia* brachiopod fauna and associated trilobites in the East Baltic has been known since the 1960s (Männil 1966, Männil et al. 1968) and refined by more recent investigations (Ulst et al. 1982; Brenchley et al. 2003; Kaljo et al. 2004; Hints et al. 2010, 2012). The most diverse *Hirnantia* brachiopod fauna occurs in westernmost Latvia, where the Porkuni Regional Stage (Hirnantian) has the thickest development in the East Baltic (over 20 m; Hints et al. 2010). However, this fauna occurs in the skeletal and silty limestone of the Kuldiga Formation, which constitutes most of the stage in the westernmost East Baltic. The oolitic and sandy limestone, and microlaminated marl of the Saldus Formation in the upper part of the Porkuni Stage comprise fragments of a few brachiopod shells possibly belonging to *Hindella*. *Hirnantia* cf. *sagittifera* (M'Coy, 1851) is the only well-preserved brachiopod of note from the Saldus Formation (Hints et al. 2012). Correlation and overviews of the lithostratigraphical units and faunas of the uppermost Ordovician in the East Baltic are presented in several publications (Ulst et al. 1982; Kaljo et al. 2001, 2004; Hints et al. 2010) and summarized in Fig. 1.

The *Hirnantia* brachiopod fauna is not known in the uppermost Ordovician Porkuni Regional Stage in northern Estonia (Ärina Formation, Fig. 1) where the corresponding strata crop out (Hints and Meidla 1997; Hints and Rõõmusoks 1997; Rõõmusoks 2004). The depositional model formulated for the Baltic Basin (Männil 1966; Jaanusson 1976) indicates that the benthic faunas of the Central East Baltic (westernmost Latvia, southern Estonia and northern Lithuania) within the Livonian Tongue of the Central Baltoscandian Facies Belt are quite different from those in the more onshore Estonian and Lithuanian belts (Hints and Harper 2003; Kaljo et al. 2011; Fig. 1). The Ordovician brachiopod fauna of the latter two belts comprises largely the common taxa, described primarily from northern Estonia and neighbouring areas (Rõõmusoks 1970, 2004; Paškevišius 1997, 2000). The species of the *Hirnantia* brachiopod fauna have not been reported from the uppermost Ordovician Porkuni Regional Stage in northern Estonia (Ärina Formation, Fig. 1).

Hirnantian brachiopods from the Central East Baltic described in this study are conspecific or closely related to brachiopods previously reported from the western parts of the Baltic Basin (in Sweden, Norway, and northern Poland) and from several other regions. But in spite of the occurrence of well-known species of brachiopods, the *Hirnantia* brachiopod fauna in the study area provides new morphological and phylogenetic data, due to excellent preservation, and new information on their distribution during the latest Ordovician. Some well-known species of the *Hirnantia* brachiopod fauna, which are abundant in the Baltic (e.g., *Cliftonia psittacina* and *Dalmanella testudinaria*), yield key morphological information, relevant to their classification and phylogeny. New palaeontological studies and taxonomic revision of Hirnantian brachiopods (Rong et al. 2008; Jin and Bergström 2010; Jin 2012; Benedetto et al. 2013) have improved our understanding of the latest Ordovician faunal provinces and documented the spatial and temporal variation of the component species. The taxonomic identification of the key species of the *Hirnantia* brachiopod fauna "may play a key role in our understanding of brachiopod faunal provisionalism during the Late Ordovician" (Jin 2012: 206). This study presents the foundation for analyses in progress on the significance of the Baltic *Hirnantia* brachiopod fauna in a more global context.

Institutional abbreviations.—GIT, Institute of Geology at Tallinn University of Technology, Tallinn, Estonia; LDM G, geological collections, Natural History Museum of Latvia (Latvijas Dabas muzejs), Riga, Latvia.

Other abreviations.—L, length; W, width.

Material and geological setting

The brachiopod samples were collected from 43 drill core sections, located in the Central East Baltic (western Latvia,

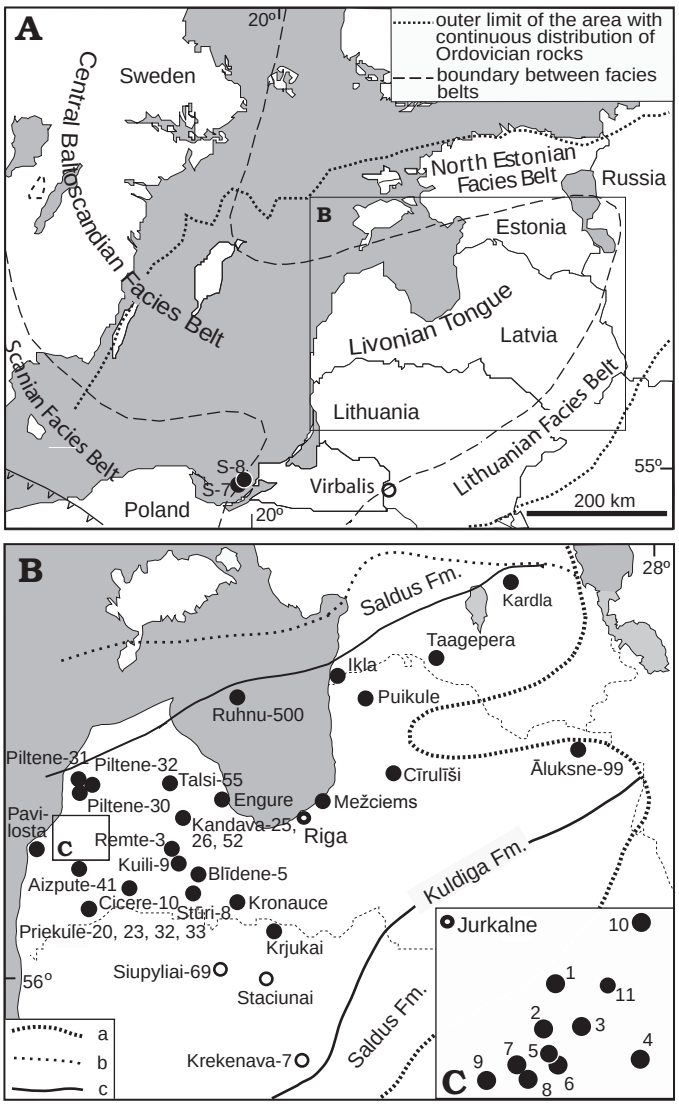


Fig. 2. **A**. The facies belts in the Baltic Basin and the study area. **B**. The location of drill core sections. **C**. Enlarged Jurkalne area. Black dots mark the locality of the drill core with brachiopods of the *Hirnantia* Fauna; empty dots indicate occurrences of the *Hirnantia* Fauna (from Paškevičius 1997, 2000). Drill cores: 1, Stirnas-18; 2, Pliekalni-14: 3, Dizrungi-17, 4, Vilcini-19; 5, Adze-6; 6, Dreimaņi-11; 7, Riekstini-15; 8, Mežmaļi-16; 9, Mežvagari-13, 10, Ēdole-60; 11, Anši. Distribution of the Hirnantian rocks: a, outer limit the the Porkuni Stage, including of the Saldus Formation on the NE areas; b, outer limit of the Saldus Formation in northern part of region; c, outer limits of the distribution area of the Kuldiga Formation.

southern Estonia, and northern Lithuania) (Fig. 2). The most fossiliferous unit, the Kuldiga Formation was sampled in some core sections (Stirna-18, Hints et al. 2010; Mežmali-16, Riekstini-15; Brenchley et al. 2003) with a view to acquiring as many fossils as possible. The other sections were sampled in less detail. However, the sandy and oolitic limestone of the Saldus Formation in the upper half of the stage were randomly sampled and thus the data available are more incomplete.

Very few brachiopod specimens from the drill cores in Lithuania have been used in this study. Their distribution is known from published data (Paškevičius 1997, 2000). Some brachiopods were collected from the drill cores in the Gulf of Gdańsk (S-7 and S-8, Ulst 1992; Fig. 1A), where the Hirnantian sequence is most similar to those in northern Poland (Podhalańska 2009).

The brachiopods are in general well preserved, although it is difficult to extract the shells from the non-weathered, carbonate rocks. Crushing the rock samples splits the brachiopods along the shell into two parts commonly obscuring the valve exterior and interior surfaces. The best-preserved specimens occur in the clay interlayers. Amongst the rare and poorly-preserved specimens are possible atrypides, which are not described in this study. Routine methods have been used (mechanical and ultrasonic techniques in some cases) for the preparation of specimens. The material studied is housed at the Institute of Geology at Tallinn University of Technology (collection 542, institutional abbreviation GIT) and the Latvian Museum of Natural History in Riga (various collections, mainly from rock samples of individual wells; institutional abbreviation LDM G). The complete data on individual specimens are accessible online in the Estonian geocollections database (http://geocollections.info) and in the Latvian national collection database (http://nmkk.lv/). The initial depths of the samples are calculated according to the drilling intervals mentioned in the core boxes, not adjusted later by geophysical data. The revised depths usually mark a somewhat higher level in the core in comparison with the initial data. For example, the lower boundary of the Porkuni Regional Stage in the Cicere drill core is identified by Ulst et al. (1982) at a depth of 900 m, which is supported by the occurrences of the Hirnantian brachiopods (*Cliftonia*, *Eostropheodonta*, and *Dalmanella*) at a depth of 899.2–899.4 m in the samples housed at the Latvian Natural History Museum. However, the geophysical studies of the borehole (Pomeranceva 1997) suggest a depth of 897 m for that boundary.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer and Popov, 1996

Class Strophomenata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Rafinesquinidae Schuchert, 1893

Subfamily Leptaeninae Hall and Clarke, 1894

Genus *Leptaena* Dalman, 1828

Type species: *Leptaena rugosa* Dalman, 1828; *Dalmanitina* Beds, Loka Formation, Hirnantian (Upper Ordovician); Borenshult, Östergötland, south Sweden.

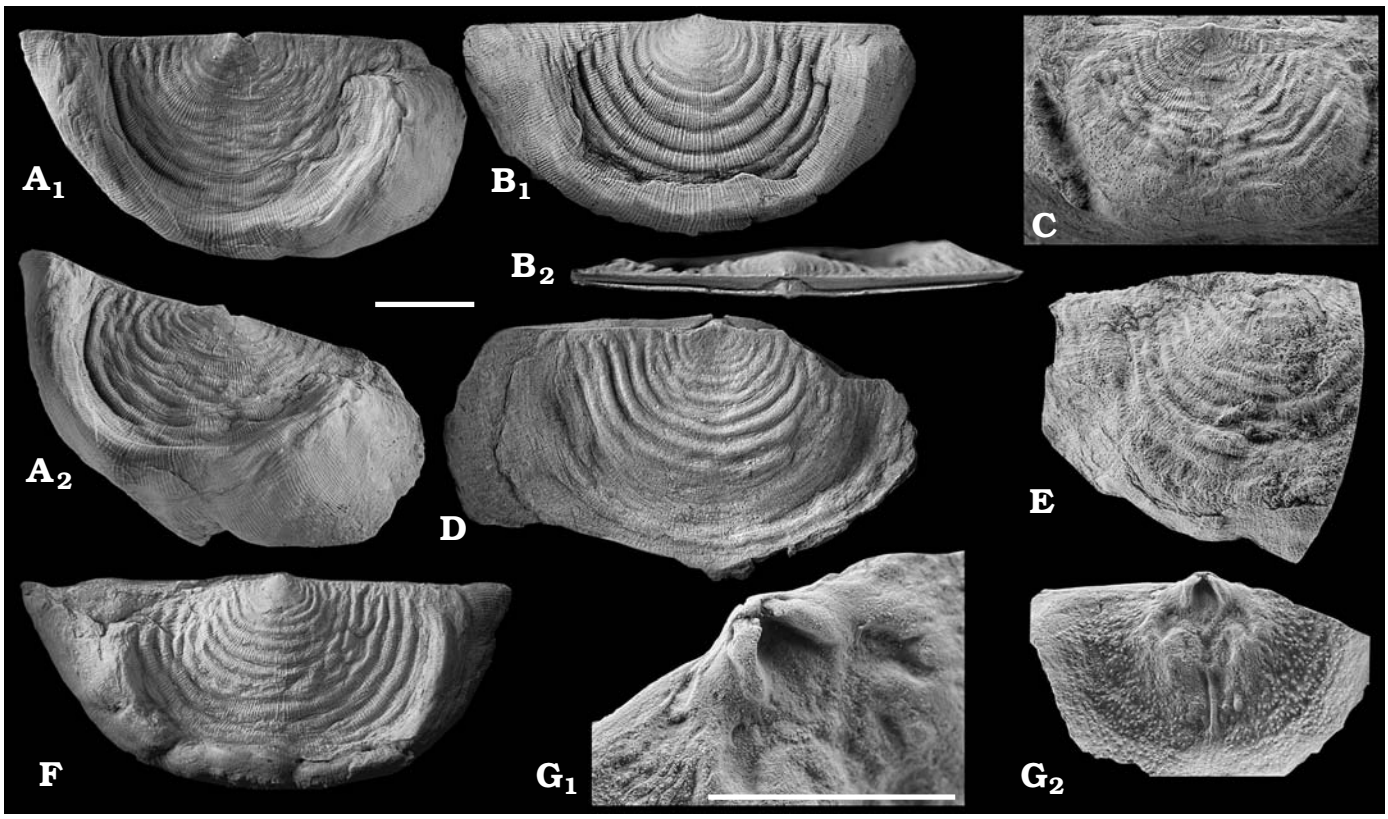


Fig. 3. Leptaenin brachiopods from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia (A–D, F–G), southwestern Estonia (E). **A**, **B**, **D**, **F**, **G**. *Leptaena* (*L.*) *rugosa* (Dalman, 1828). **A**. Shell, LDM G 273-1, Ēdole-60 drill core, depth 840.7 m, ventral (A_1) and ventro-lateral (A_2) views. **B**. Shell, GIT G 542-2, Vilcini-15, 910.35 m (figured in Kaljo et al. 2008), ventral (B_1) and posterior (B_2) views. **D**. Shell, GIT 542-17, Stirnas-18, 908.6 m, dorsal exterior view. **F**. Shell, GIT 542-18, Stirnas-18, 909.4 m, ventral view. **G**. Dorsal valve, GIT 542-197, Sturi-8, 941.8 m, view of interior (G_1) and cruralium (G_2). **C**, **E**. *Leptaena* sp. **C**. Dorsal valve, GIT 542-189, Vilcini-15, 909.3 m, exterior view. **E**. Incomplete ventral valve, GIT 542-192, Ikla, 536.5 m, exterior view. Scale bars 10 mm.

Subgenus *Leptaena* (*Leptaena*) Dalman, 1828

Leptaena (*Leptaena*) *rugosa* Dalman, 1828

Fig. 3A, B, D–F.

1828 *Leptaena rugosa* Dalman; Dalman 1828: 106, pl. 1: 1.

1968 *Leptaena rugosa* Dalman, 1828; Bergström 1968: 14–15, pl. 5: 8, 9; text-fig. 7.

2008 *Leptaena* (*Leptaena*) *rugosa* Dalman; Cocks 2008: 59 (see synonymy therein).

Material.—30 specimens (among them 15 fragmentary); mostly embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, southwestern Estonia. Drill core and depth (in meters) of sample intervals with brachiopods. Depth of fragmentary specimens is marked by "?". Collection GIT 542: Adze-6, ?844.5–845.2; Aizpute-41, 997.1–?997.8; Engure, 882.9–?884.4; Ikla, ?536.5; Mežmaļi-16, ?912.8–?913.2; Riekstini-15, ?857.3; Ruhnu-500, 610.1–?617.25; Stirnas-18, 908.6–909.4; Sturi-8, 941.8; Vilcini-15, 909.3–910.35; collections LDM G: Anši-12, 922.5; Cicere (from the sample with *Hirnantia sagittifera*; depth unknown); Ēdole-60, 840.7; Kandava-52, 932.5; Kuili-9, 948.0–?948.2; Priekule-23, 1363.0; Pliekalni-14, ?884.8; Talsi-55, ?866.5.

Remarks.—The East Baltic specimens of *Leptaena* are almost identical with *L.* (*L.*) *rugosa* from Sweden and Norway (Bergström 1968: text-fig. 7; Spjeldnæs 1957: pl. 7: 1–2, 4; Cocks and Rong 2000: fig. 150, 1d) having a transversely subquadrate shell outline, weakly convex ventral disc with up to 11 concentric rugae, multicostellate ornament with few accentuated ribs on median fascicle and 5–9 costellae per 2 mm at anterior part of the disc; the exterior of the dorsal valve is similar to the material from Norway and Sweden. The shell size, up to 45 mm wide at alate hinge line, seems to be more similar to the Norwegian specimens of the species. However, the Baltic specimens possibly have a shorter trail and less geniculated profile. The Baltic specimens have ventral interarea about twice as high as the dorsal interarea; foramen opening apical. Chilidium, up to 4 mm wide, triangular, convex with the median groove, which is characteristic for the Swedish specimens (Bergström 1968). The single dorsal interior with trapezoidal notothyrial platform and median septa on anterior half of disc (Fig. 3G_1, G_2) does not differs from the Swedish specimen (Bergström 1968: text-fig. 7). An exception is the cardinal process of the Baltic specimen where the lobes seem to be less divergent.

The species affiliation of one ventral and one dorsal valve (*Leptaena* sp.; see Fig. 3C, E) is unclear due the discontinuous nature of the rugae. Nevertheless, the latter valve has

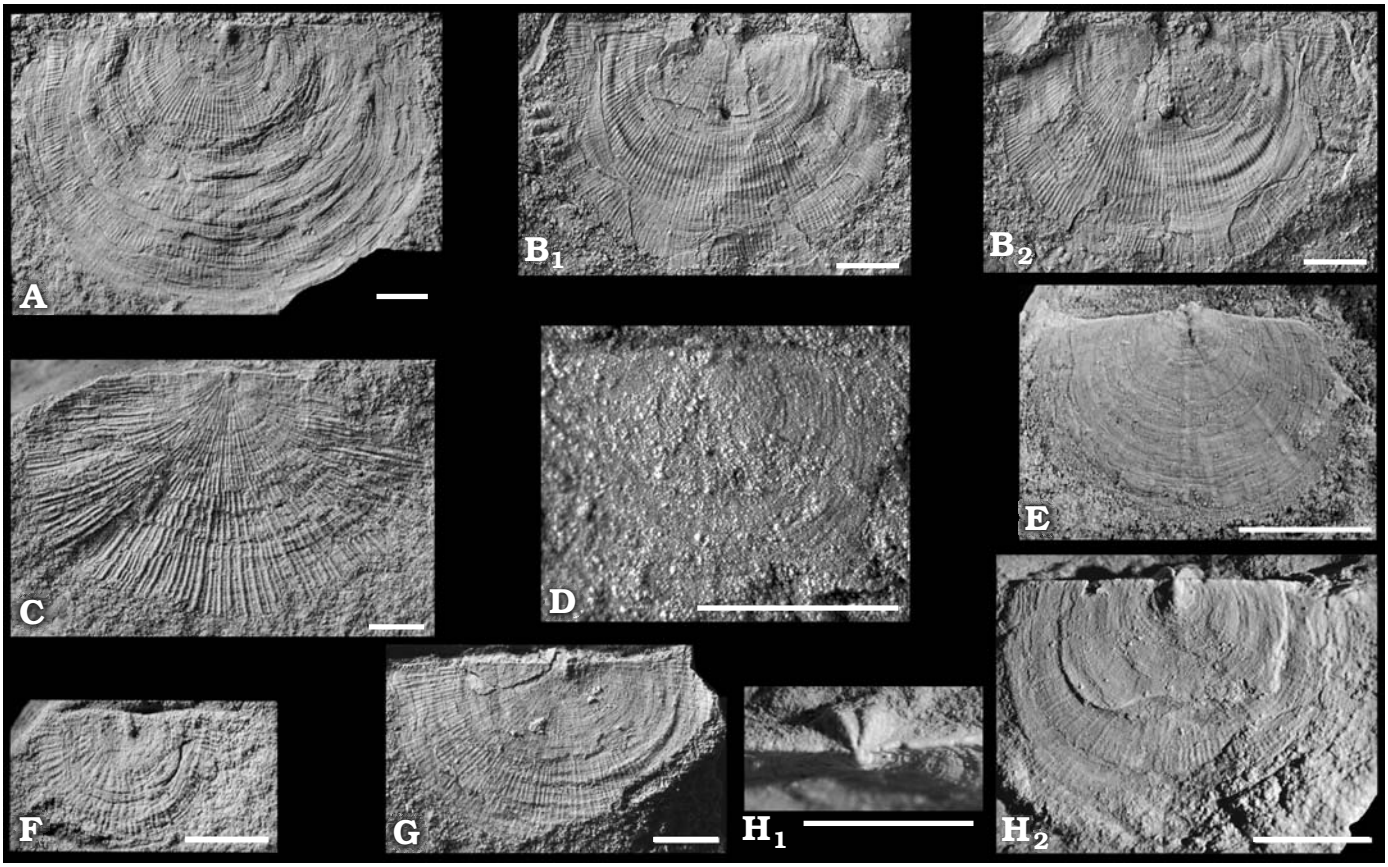


Fig. 4. Strophomenoid brachiopods from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia (A–F, H) and southwestern Estonia (G). **A**, **B**, **F**–**H**. *Paromalomena polonica* (Temple, 1965). **A**. Dorsal valve, GIT 542-299, Mežmali-16, depth 911.8 m, exterior view. **B**. Dorsal valve, GIT 542-352-1, Adze-6, 844.5 m, split into two parts: exterior view (B1) and impression (B2). **F**. Dorsal valve, GIT 542-377, Aispute-41, 884.4 m, exterior view. **G**. Dorsal valve, GIT 542-361, Ikla, 535.3 m, exterior view. **H**. Dorsal valve, GIT 542-355, Mežmali-16, 912.2 m, exterior view (H_1) and view of the chilidium (H_2). **C**. *Eostropheodonta* cf. *parvicostellata* Rong, 1984. Dorsal valve, GIT 542-365, Aispute-41, depth 988.7 m, exterior view. **D**–**E**. *Proboscisambon*? sp. **D**. Mould of dorsal valve, GIT 542-53, Stirnas-18, depth 908.2 m, exterior view. **E**. Dorsal valve, GIT 542-322-1, exterior view; Riekstini-15, 858.6 m. Scale bars 2 mm.

a peripheral ridge, similar to *L* .(*L.*) *rugosa*, but the ventral valve has smooth transition from the disc to trail, similar to the specimens of *L.* (*L.*) *rugosa* from the Killey Bridge Formation (Katian) of Ireland (Mitchell 1977).

The Baltic specimens differ from the older representatives of *L.* (*L.*) *rugosa* from Pomeroy, N. Ireland (Candela 2003) in having a more transverse disc and fewer rugae.

The early Hirnantian leptaenids *Leptaena acuteplicata* (Schmidt, 1908) and *L. friedrichi* (Rõõmusoks, 2004) (assigned to the genera *Schmidtomena* and ?*Similoleptaena* in Rõõmusoks 2004) in the reef complex (Ärina Formation) of North Estonia differ markedly from *L.* (*L.*) *rugosa*. Both Estonian species have much smaller shells; *L. acuteplicata* differs in having less prominent rugae; the *L. friedrichi* has a more robust ornament. A comparison of several Hirnantian species of *Leptaena* in Baltoscandia was presented by Cocks (2005).

Stratigraphic and geographic range.—This widespread species is mainly restricted to the Hirnantian Stage, Upper Ordovician, in Europe (Czech Republic, France, Ireland, and Wales), China (Rong and Harper 1988; Rong et al. 2002), and in North and South America. In Baltoscandia besides Norway and Sweden, it occurs in Estonia and Latvia (this paper) and also in Lithuania (Paškevičius 1997). Closely related forms occur in the highest Katian in, for example, Northern Ireland and Scotland.

Family Glyptomenidae Williams, 1965

Subgenus Glyptomeninae Williams, 1965

Genus *Paromalomena* Rong, 1984

Type species: *Platymena*? *polonica* Temple, 1965; *Dalmanitina* Beds, Hirnantian (Upper Ordovician); Stawy, Holy Cross Mountains, Poland.

Paromalomena polonica (Temple, 1965)

Fig. 4A, B, F–H.

1965 *Platymena*? *polonica* n. sp.; Temple 1965: 407–410, pl. 15: 1–4; pl. 16: 1–5.

2008 *Paromalomena polonica* (Temple); Cocks 2008: 63 (see synonyms therein).

Material.—Eight specimens embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); Latvia, Estonia. Drill core and depth (in meters) of

sample with brachiopod. Depth of fragmentary specimens is marked by "?". Collection GIT 542: Aispute-41, 1000.5; Ikla, 535.3; Mežmaļi-16, 911.8–912.5; Ruhnu-500, 616.2 (the lowermost *scabra* chitinozoan zone; Nõlvak 2003), 617.4; Vilcini-15, ?914.5; collection LDM G: Pliekalni-14, ?884.0–884.6.

Remarks.—Small semicircular shells up to 15 mm wide and 10.5 mm long with multicostellate ornament of fine and uniform costellae; the irregular growth lines, partly developed as low rugae, are most similar to those on the Polish specimens of *P. polonica* (Temple 1965: pl. 15: 2, 3). The Baltic specimens have obtuse to acute cardinal angles, hinge line 0.9 of valve width. Costellae appear at 2 to 3 mm growth stage; up to 9 costellae per 1 mm at 5 mm from apex, few costellae appear along the posterior margin. Ventral valve very weakly convex around the umbo; dorsal valve flat, anteriorly slightly concave with a low, anacline dorsal interarea with grooved chilidium (Fig. $4H_1$).

The Baltic specimens differ somewhat from the Polish specimens in shell outline, the ratios of width to length are about 1.4 and 1.6, respectively (Temple 1965).

The Baltic as well the Polish specimens differ from those from China (Rong 1984; Zhan et al. 2010) in having somewhat larger shells. The early growth stages, up to 3.5 mm generally lack radial ornament, similar to some specimens of the genus *Proboscisambon.*

Stratigraphic and geographic range.—This widespread species is mainly restricted to the Hirnantian Stage, Upper Ordovician, although similar forms occur in both the highest Katian and lowest Llandovery. It is common in deeper-water facies in Argentina, Burma, China, Thailand, and parts of Europe, for example, Austria, the Czech Republic, Poland, and England (see, e.g., Benedetto 1990; Rong and Harper 1988; Rong et al. 2002; Temple 1965). In Baltoscandia, it occurs in Sweden (Bergström 1968), Estonia, and Latvia (this paper).

Genus *Proboscisambon* Havlíček and Mergl, 1982

Type species: *Strophomena quaesita* Barrande, 1879; Královdvor Formation, Katian (Upper Ordovician); Jezerka, Bochemia, Czech Republic.

Proboscisambon? sp.

Fig. 4D, E.

Material.—Seven specimens embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); southwestern Estonia and western Latvia. Drill core and depth (in meters) of sample intervals with brachiopods. Depth interval of fragmentary specimens is marked by "?". Collection GIT 542: Aizpute-41, 997.7–1000.35; Stirnas-18, 908.2; Riekstini-15, 858.6; Ruhnu-500, 613.5; Vilcini-15, 909.5; ?Prabut Formation (Podhalańska 2009): Petrobaltic S-8, 2618.2–2618.28 (sample 47 from the interval 2614.4–2633 m).

Remarks.—Small, laterally elongated shells, up to 6.5 mm wide and 4.2 mm long with weakly developed ornament of concentric filae and few costae (nine on the largest valve) appearing at about 2.5 mm from the umbo reminiscent of the genus *Proboscisambon* first described from Bohemia (Havlíček and Mergl 1982). The Baltic specimens have obtuse cardinal angles and almost flat valves. The studied specimens are similar to those *Paramalomena* in having a fine radial ornament differing in lacking the growth lines characteristic of that genus. Depending on preservation, the small Glyptomeninae may be erroneously assigned to the genus *Foliomena*; see for example, one specimen (GIT 542-53) from the lowermost Porkuni Regional Stage in the Stirnas-18 core (Hints et al. 2010). This specimen, in fact, belongs to the genus *Proboscisambon*.

Family Leptostrophiidae Caster, 1939

Genus *Eostropheodonta* Bancroft, 1949

Type species: *Orthis hirnantensis* M'Coy, 1851; Hirnant Formation, Hirnantian (Upper Ordovician); Aber Hirnant, near Bala, Gwynedd, Wales, UK.

Eostropheodonta hirnantensis hirnantensis (M'Coy, 1851)

Figs. 5, $6A_1$.

1851 *Orthis Hirnantensis* M'Coy, 1851: 395.

2008 *Eostropheodonta hirnantensis hirnantensis* (M'Coy, 1851); Cocks 2008: 68 (see synonyms therein).

Material.—Variably preserved specimens in 129 samples with one or more specimens in each. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, southern Estonia. Drill core and depth (in meters) of sample intervals with brachiopods. Depth of fragmentary preserved material is marked by "?". Collection GIT 542: Adze-6, 840.9–844.2; Aispute-41, 987.7–1000.5; Engure, 884.3–884.4; Ikla, ?531.0–?535.7; Mežmaļi-16, 906.56–?913.4; Priekule-20, 1357.3–?1363.4; Riekstini-15, 846.15–?860.4; Ruhnu-500, ?616.3–617.4; Stirnas-18, 899.0, Taagepera, 413.7–413.9; Vilcini-19, 895.7–909.6; collections LDM G: Adze-6, ?838.1–?844.8, Dizrungi-17, ?893.8, Dreimaņi-11, ?953.6–953.75; Kandava-52, ?930.3–?931.5; Mežmali-16, ?917.8–921.35 (the revised depths are published by Gailite et al. (1989) and Hints et al. (2012) (the lower boundary of the Porkuni Stage is at a depth of 916 m); Mežvagari-13, ?871.2; Pliekalni-14, ?883.7; Priekule-20, ?1355.5–1363.4; Priekule-23, ?1392.1–1395.6; Remte-3, 958.0–958.8; Talsi-55, ?866.7–?867.1.

Description.—Plano- to concavo-convex shell, transversely subquadrate in outline, length-width ratio 0.6–0.8, maximum width commonly less than 20 mm at hinge line. Cardinal angles obtuse on smaller and acute on larger shells. Ventral valve slightly convex, maximum convexity in posterior part. Specimens less than 3 mm long have a small beak extending backward; small depression begins anterior of beak. Ventral interarea up to 0.5 mm high, delthyrium with small protegular apical deltidium. Dorsal valve commonly has small drop-shaped protegulal node covered by concentric filae, on

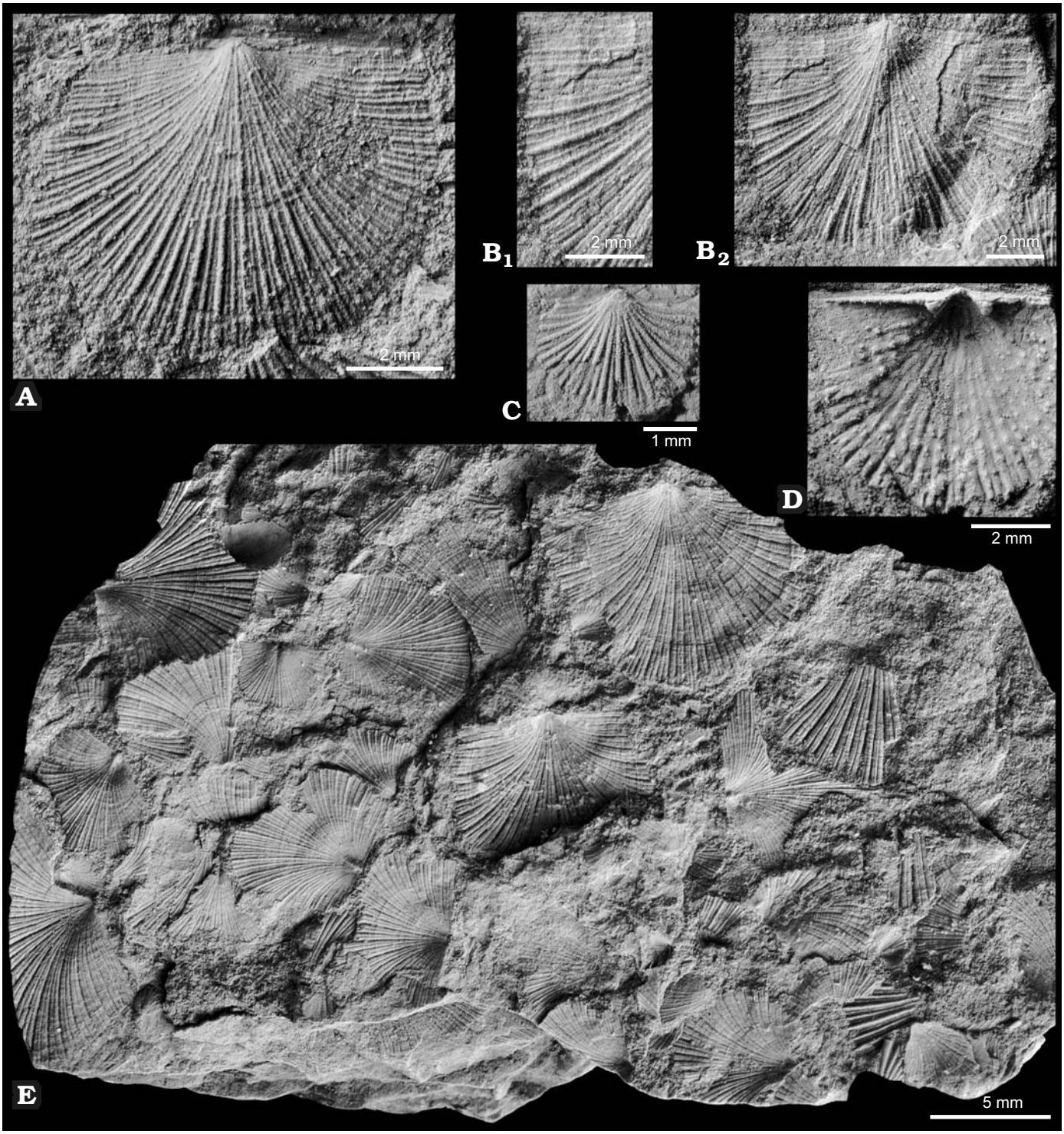


Fig. 5. Leptostrophiid brachiopod *Eostropheodonta hirnantensis* (M`Coy, 1851) from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia. **A**. Ventral valve, GIT 542-316, Riekstini-15, depth 850.3 m, ventral exterior view. **B**. Ventral valve, GIT 542-333, Riekstini-15, 854.0 m, fragment of valve with ornament (B_1) and exterior view (B_2). **C**. Juvenile specimen, GIT 542-319, Mežmali-16, 906.56 m, ventral exterior view. **D**. Ventral valve, GIT 542-385, Aispute-41, 1000.5 m, interior view. **E**. Bedding plane with numerous casts of valves, GIT 542-360, Vilcini-19, 906.5 m.

some valves it continues anteriorly as median costae. Radial ornament parvicostellate in most specimens, becoming multicostellate with faint short rugae in postero-lateral parts of shell; accentuated costae divide the ornament into 7 or more sectors, 6–12, on average 9, costellae per 2 mm at 5 mm from beak. The interspaces between ribs are densely covered by concentric filae (Fig. $5B_1$).

Ventral interior (Fig. 5D) has small teeth with minute crenulations on upper side; crural fossettes strong, dental plates short, divergent.

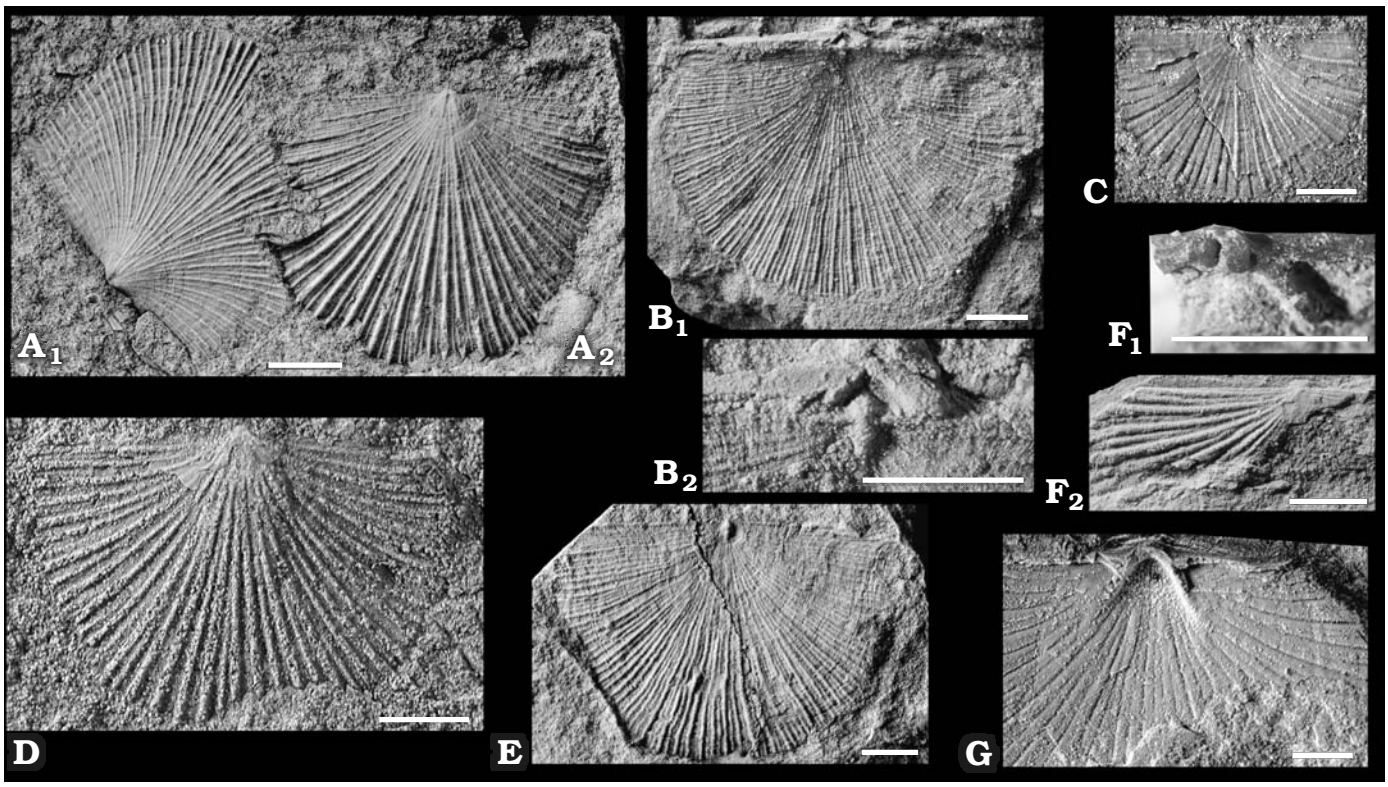


Fig. 6. Leptostrophiid brachiopods from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia (A–E, G) and southwestern Estonia (F). **A**. *Eostropheodonta hirnantensis* (M`Coy, 1851), Taagepera, depth 413.9 m, moulds of ventral valves, GIT 542-337/1 (A_1) and GIT 542-337/2 (A_2), exterior views. **B**, **E**. *Eostropheodonta* cf. *parvicostellata* Rong, 1984. **B**. Shell, GIT 542-381, Vilcini-19, 906.4 m, exterior view of dorsal valve (B_1) and view on interarea (B_2). **E**. Mould of dorsal valve, LDM G328-12, Priekule-33, 1395.6 m, exterior view. **C**, **D**, **F**, **G**. *Coolinia* sp. **C**. Mould of ventral valve, LDM G328-26, Dižrungi-17, 984.5 m, exterior view. **D**. Ventral valve, LDM G328-26, Dizrungi-17, 984.5 m, exterior view. **F**. Fragment of dorsal valve, GIT 542-364, Ruhnu-500, depth 612.9 m, view of cardinalia (F_1) and exterior view (F_2). **G**. Incomplete ventral valve, GIT 542 48-2, Stirnas-18, 899.0 m, interior view. Scale bars 2 mm.

Remarks.—The material is insufficient for precise differentiation between the subspecies *E. hirnantensis hirnantensis* (M'Coy, 1851) and *E. hirnantensis siluriana* (Davidson, 1871), which are defined mainly by the ribbing. The latter subspecies (Hiller 1980) has coarser, more fascicostellate ribbing than *E. h. hirnantensis*. Ornament of a few specimens reminiscent of *E. h. siluriana* (Fig. $6A_2$) co-occurring in some samples with specimens more similar to *H. h. hirnantensis* (Fig. $6A_1$).

The Baltic specimens are similar to *E. h. hirnantensis* from Poland and England (Temple 1965) in shape and size and in the radial ornament, showing a strong median costa on the ventral valve and in the arrangement of ribs into the sectors between the stronger ribs. In many samples, indeterminate strophomenoid brachiopods are represented by incomplete valves and fragments having an ornament similar to *Eostropheodonta* and, more specifically, to *E. h. hirnantensis*.

Stratigraphic and geographic range.—This key taxon occurs mainly in the Hirnantian Stage, Upper Ordovician. The species is a characteristic component of the globally distributed *Hirnantia* brachiopod fauna in Africa, Canada, China, the Czech Republic, England, and Ireland (Rong and Harper 1988). In Baltoscandia it occurs in Norway (Cocks 1982), Sweden (Bergström 1968), Estonia, Latvia (this paper), and Lithuania (Paškevičius 1997).

Eostropheodonta cf. *parvicostellata* Rong, 1984

Figs. 6B, E.

Material.—Six specimens embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia. Drill core and depth (in meters) or sample intervals with brachiopods. Collection GIT 542: Adze, 844.2; Aispute-41, 995.9; Riekstini-15, 850.0; Vilcini-19, 894.7–906.4; collection LDM G: Priekule-23, 1395.6.

Remarks.—Some specimens, amongst those assigned to the genus *Eostropheodonta*, are particularly distinctive, having a parvicostellate ornament of fine costae and costellae of nearly equal strengths, 9–11 costellae per 2 mm at 5 mm from umbo. The shells are small up to 13 mm wide at the hinge line and about 9 mm long. Cardinal extremities are acute. Ventral interarea is 0.3 mm high, delthyrium is open (Fig. $6B_1$). Dorsal valve is flat, interarea low, notothyrium covered by small, convex chilidium. The radial ornament of these Baltic specimens is most similar to *E. parvicostellata* from the Hirnantian of China (Rong 1984). However, our specimens are relatively small. The lack of interiors negates precise species level identification. *E. parvicostellata* differs

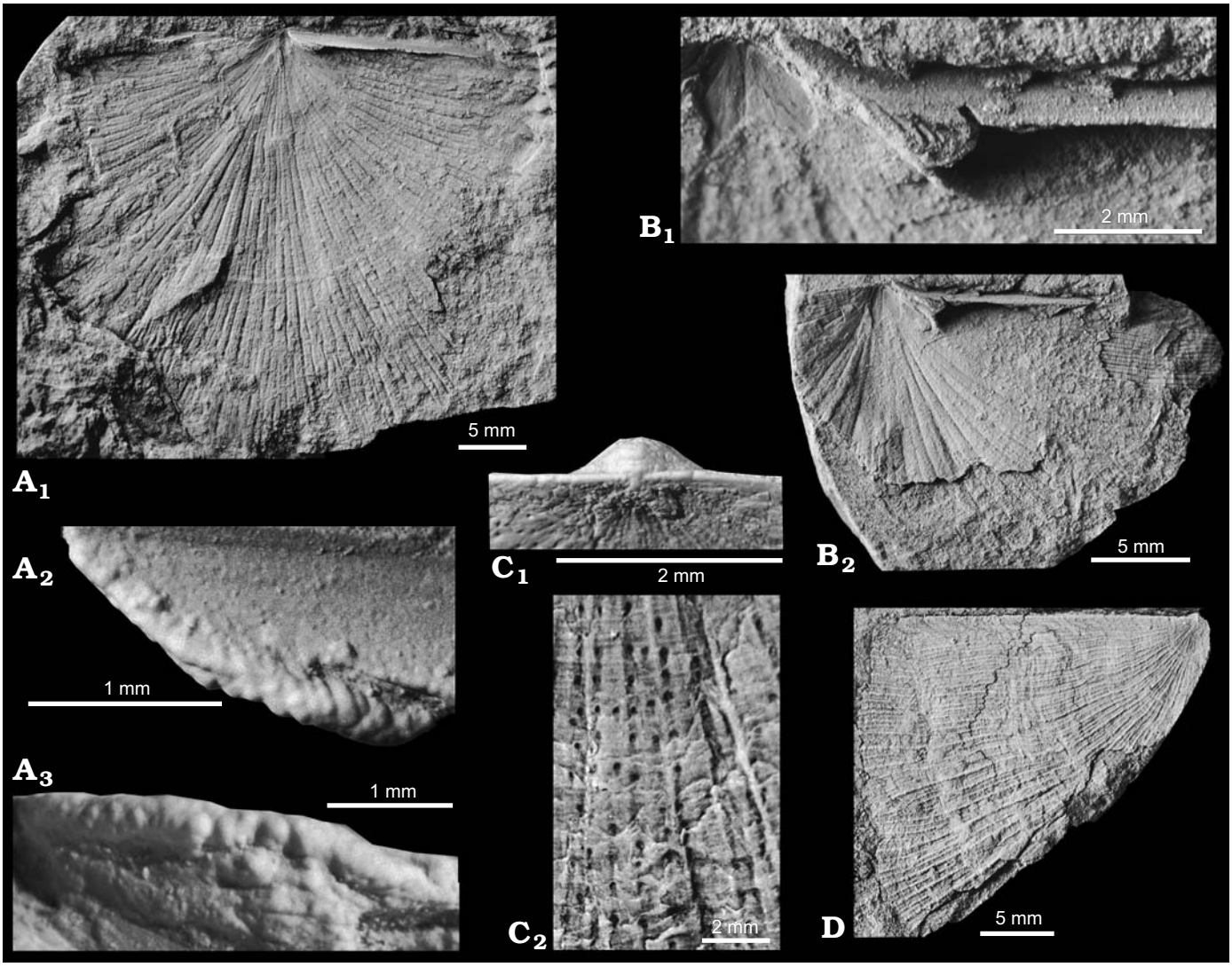


Fig. 7. Leptostrophiid brachiopod *Eostropheodonta* cf. *schmalenseei* (Bergström, 1968) from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, southwestern Estonia (A) and western Latvia (B–D). **A**. Ventral valve, GIT 542-218, Ruhnu-500, depth 616.9 m, interior (A_1), posterior (A_2), and lateral (A_3) views of the teeth. **B**. Incomplete ventral valve, LDM G328-10, Talsi-55, 866.7 m, interior view (B_2) and view of interarea (B_1). **C**. Dorsal valve, GIT 542-220, Mežmali-16, 913.0 m, view of posterior part with convex chilidium (C_1) and view of surface with endopunctae on the middle part of the valve (C_2). **D**. Incomplete ventral valve, LDM G 328-9, Talsi-55, 866.7 m, exterior view.

from *E. h. hirnantensis* in having a median process between the cardinal process lobes (Rong 1984: fig. 15). However, the very high variability of radial ornament of the latter species (Rong and Cocks 1994) does not exclude possible assignment to *E. h. hirnantensis*.

Eostropheodonta cf. *schmalenseei* (Bergström, 1968)

Fig. 7.

Material.—11 variably preserved specimens, embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, southwestern Estonia. Drill core and depth (in meters) of sample intervals with brachiopods: collection GIT 542: Engure, 882.9; Mežmaļi-16, 913.0, 913.4; Piltene-1, 1017.1; Ruhnu-500, 616.9; collections LDM G: Cicere (depth is unknown); Kronauce, 1055.1; Talsi-55, 866.7–867.1; Pāvilosta,1097.0–?1097.5; Remte-3, 965–966.

Description.—Large oval, thin-shelled specimens. Ventral valve is very weakly convex in posterior part, dorsal valve is almost flat with weak concavity in the middle. The largest specimen is 52.3 mm wide and over 37 mm long. Ornamentation parvicostellate, with about 50 ribs at the 10 mm growth stage along the valve margins, 28 of which are accentuated; 5 ribs occur per 2 mm at 20 mm from umbo; 2–3 stronger ribs with 1–2 finer costellae between them occur per 2 mm on the anterior margin. Concentric growth lines very fine with 8–10 lines per 1 mm.

Ventral interarea is flat, 0.5 mm high. The denticulate teeth diverge at 110°. Dental plate with about 12 denticles capping the teeth and with crenulations on the antero-median faces. The denticles and crenulations continue along the

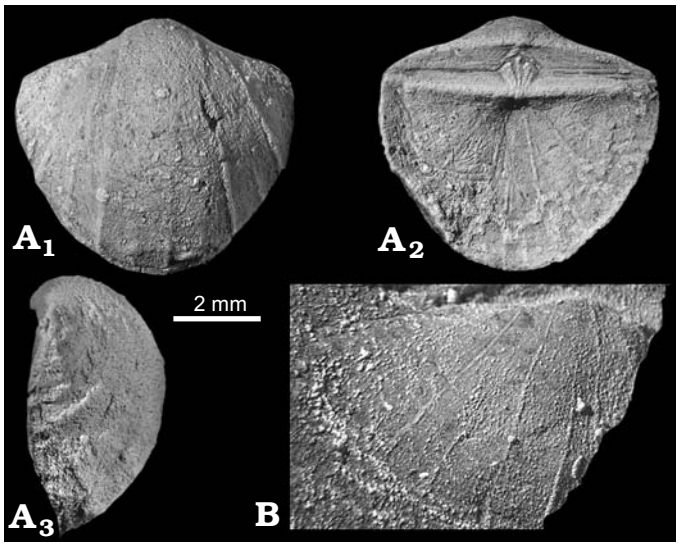


Fig. 8. Plectambonitoid brachiopods from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia. **A**. *Leangella* sp., shell, GIT 542-222, Riekstini-15, depth 859.3 m, ventral (A_1), dorsal (A_2), and lateral (A_3) views. **B**. *Eoplectodonta* sp., incomplete ventral valve, GIT 542-21, Stirnas-18, 911.9 m, ventral view.

edge of the delthyrium as small protuberances (Fig. 7A_2, A_3, B_1). Dental plates very short. Muscle scars not visible. The external ornament is impressed on the interior valve surface; tubercles (pseudopunctae) are sporadically developed.

Two dorsal valves have low interareas with notothyrium covered by convex, non-grooved chilidium (Fig. 7D_1); interior is unknown.

Remarks.—*Eostropheodonta* cf. *schmalenseei* differs from *E. h. hirnantensis* by its larger size and less well-differentiated ornament. The ventral valves of *E*. cf. *schmalenseei* differ from *E. h. hirnantensis* in having teeth, developed as oblique plates with about 12 denticles on the anterior margin of the interarea. The latter species has antero-laterally directed teeth with 4–6 denticles (Temple 1965: pl. 17: 4, 5; Bergström 1968, pl. 6: 7; Rong and Cocks 1994). The lack of a median groove on the chilidium (Fig. 7D_1) in the East Baltic species confirms the close relationship with *E. schmalenseei* from Sweden.

Eostropheodonta cf. *schmalenseei* is similar to *Eostropheodonta luna* from the Boda Limestone (Cocks 2005: pl. 9: 11–15) and to the Estonian species *Pirgumena* (= *Eostropheodonta* by Cocks 2005: 269) *martnai* (Rõõmusoks 2004: pl. 15: 8–10; pl. 16: 1–5) by the shell size. However, *E.* cf. *schmalenseei* has a more uniform ornament with wider interspaces between costellae, especially on the postero-lateral parts of valves. *E. luna* and the Estonian species have ornaments bearing accentuated ribs. There are insufficient data on the interiors of related species to permit their clear comparison.

Superfamily Plectambonitoidea Jones, 1928
Family Leptestiidae Öpik, 1933

Genus *Leangella* Öpik, 1933

Type species: *Plectambonites scissa* var. *triangularis* Holtedahl, 1916; Solvik Formation, Lower Llandovery (Silurian); Asker, Norway.

Leangella (*Leangella*) cf. *scissa* (Davidson, 1871)

Fig. 8A.

Material.—Two specimens. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia. Drill core and depth (in meters) of brachiopod samples: collection GIT 542: Riekstini-15, 859.3, 861.8–861.85.

Remarks.—Small, strongly concavo-convex shells, sub-triangular in outline with 5 primary ribs, similar to *L.* (*L.*) cf. *scissa* from the *Dalmanitina* Beds in Sweden (Bergström 1968) and also to *L.* (*L.*) *scissa* from the lowermost Silurian in the East Baltic (Rubel 2011). The larger of two specimens is 6.4 mm wide, 5.8 mm long and 2.9 mm deep, the smaller is only 1.5 mm wide. Cardinal angles rounded; anterior commissure slightly sulcate. Ventral interarea almost orthocline, slightly concave at the apex, 0.6 mm high. Delthyrium with small deltidial plates in apical part. Dorsal interarea flat, hypercline, 0.4 mm high. Notothyrium filled with trilobate cardinal process. Radial ornament of five primary and 4 additional ribs on ventral valve with very fine intercalated costellae. The Swedish species apparently differs from the Baltic material in lacking fine costellae between the primary costae; the Silurian *L.* (*L.*) *scissa* has a wider shell and more convex ventral valve.

Although rare in the *Hirnantia* brachiopod fauna, *Leangella* is common in the Boda Limestone (Sheehan 1979; assigned to *Diambonia,* Jaanusson 1982). The species *L.* (*L.*) *longae* Cocks, 2005 from the lowermost Boda flank facies at Osmundsberget differs from the Hirnantian specimens in having more numerous (up to 14) primary costae.

The Hirnantian material of *Leangella* from the central Oslo Region in Norway, identified as *L.* aff. *cylindrica* (Reed, 1917) by Cocks (1982), is insufficiently known for adequate comparison.

Family Sowerbyellidae Öpik, 1930
Subfamily Sowebyellinae Öpik, 1930
Genus *Eoplectodonta* Kozłowski, 1929

Type species: *Sowerbyella precursor* Jones, 1928; Upper Haverford Mudstone Formation, Lower Llandovery (Silurian); Haverfordwest, Dyfed, Wales, UK.

Eoplectodonta sp.

Fig. 8B.

Material.—Eight specimens embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); southwestern Estonia and western Latvia. Drill core and depths (in meters) of sample with brachiopod. Collection GIT 542: Ikla, 534.7, 539.6; Stirnas-18, 911.9, 912.2, Riekstini-15, 861.85; Aispute-41, 983.25.

Remarks.—Poorly-preserved sowerbyellid brachiopods are tentatively assigned to the genus *Eoplectodonta.* The shells

are relatively small, transversally semioval, up to about 13 mm wide at the hinge line and 6–7 mm long; cardinal angles acute. Ventral valve weakly convex, dorsal one concave. Radial ornament consists of a few strong ribs with about 7 fine costellae between them on the anterior margin of the valve. Interiors, including the occurrence of hinge denticles, unknown. The Baltic specimens are similar to *Eoplectodonta* (*Eoplectodonta*) sp. nov. 1 (Cocks 2005) from the Boda Limestone in Sweden in their small size, however, they differ in having more accentuated costae.

Order Orthotetida Waagen, 1884
Suborder Othotetidina Waagen, 1884
Superfamily Chilidiopsoidae Boucot, 1959
Subfamily Chilidiopsinae Boucot, 1959
Family Chilidopsidae Boucot, 1959
Genus *Coolinia* Bancroft, 1949

Type species: *Orthis applanata* Salter, 1846; Telychian, Upper Llandovery (Silurian); Coolin, Cong, Galway, Ireland.

Coolinia sp.

Fig. 6C, D, F, G.

Material.—Seven specimens embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, southwestern Estonia. Drill core and depth (in meters) with brachiopod samples. Collection GIT 542: Mežmaļi-16, 912.6; Krjukai, 968.6; Ruhnu-500, 612.9, Stirnas-18, 899.0, 908.3 m; Vilcini-15, 906.4; collection LDM G: Dizrungi-17, 894.5.

Remarks.—Only few specimens of the genus *Coolinia* are known from the East Baltic sections. *Coolinia dalmani* Bergström, 1968 from the *Dalmanitina* Beds in Västergötland, Sweden, and some comparative species from the topmost Ordovician and lowermost Silurian in USA (Amsden 1974) have posterior costae and costellae curving towards the posterior margin of the valve. This type of ribbing is developed most clearly on specimens of another chilidopsid genus, *Valdaria* (Bassett and Cocks 1974) first described from the Silurian rocks of Gotland. However, the position of the posterior costae, which may have some taxonomic value, is not clear on the Baltic specimens; they are subparallel rather than curving toward the margin.

Description.—The Baltic specimens have transversely suboval, weakly biconvex shells, up to about 12 mm wide and 7 mm long; the maximum width corresponds to width of the hinge line or is a little shorter. Radial ornament of up to 40 costae and costellae, among them 18 primary costae.

One dorsal fragment (Fig. 6F) displays prominent cardinal lobes partly covered by a short chilidium, and socket ridges divergent postero-laterally like those of the genus *Coolinia*. Interior of one incomplete ventral valve (Fig. 6G) has a small delthyrial chamber and dental plates diverging at about 70 degrees; the muscle field is not differentiated on the valve floor which is covered by impressions of the external ornament.

Suborder Triplesiidina Moore, 1952
Superfamily Triplesioidea Schuchert, 1913
Family Triplesiidae Schuchert, 1913
Genus *Cliftonia* Foerste, 1909

Type species: *Cliftonia striata* Foerste, 1909; Clinton Formation, Llandovery (Silurian); Tennessee, USA.

Cliftonia psittacina (Wahlenberg, 1821)

Fig. 9A–F, H–K; Table 1.

1821 *Anomites psittacinus* Wahlenberg; Wahlenberg 1821: 65.
1965 *Cliftonia psittacina* (Wahlenberg, 1821); Bergström 1968: 11–12 (see synonyms therein), pl. 4: 7, 8; pl. 5: 1, 2.

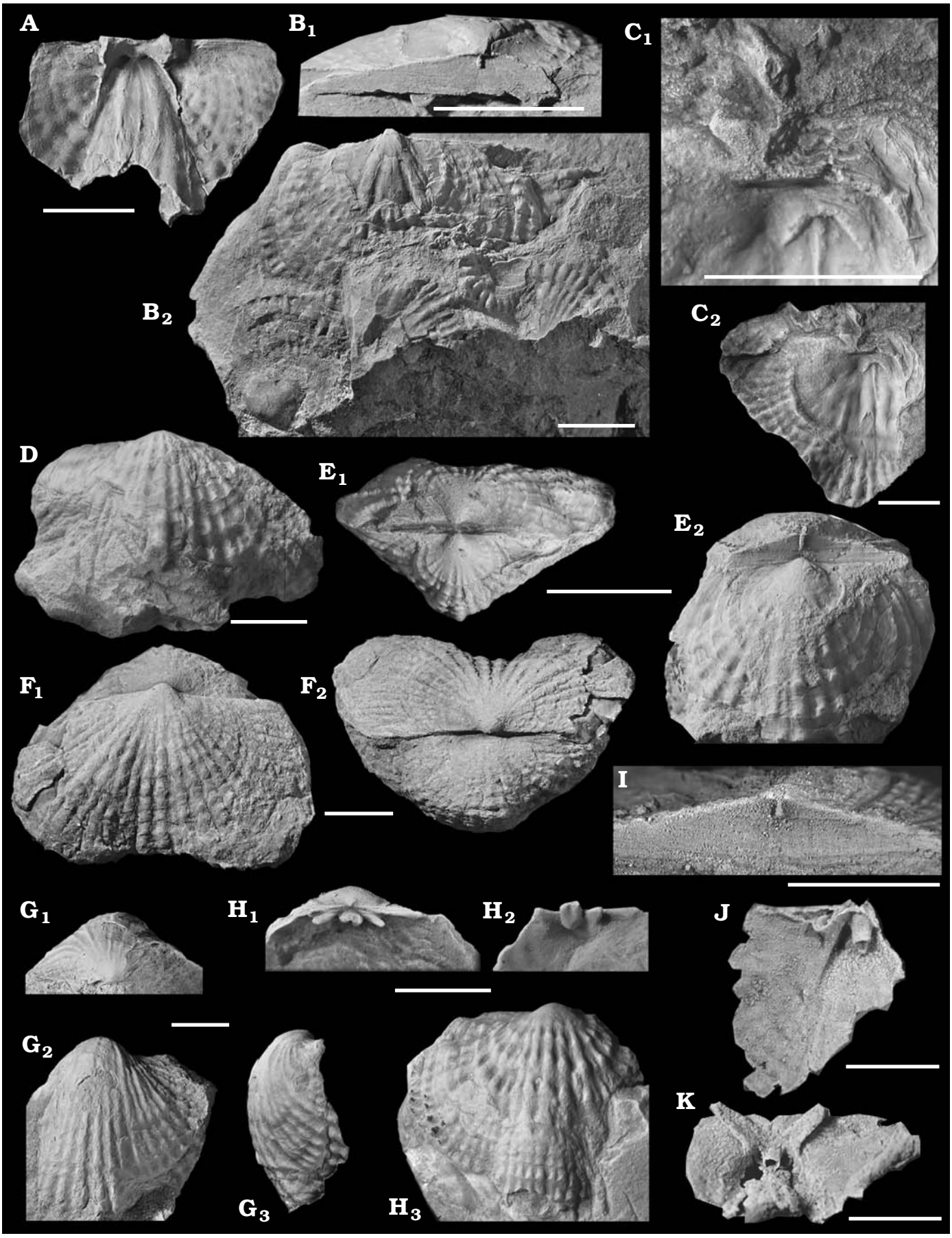
Material.—122 differently preserved specimens. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, southern Estonia. Drill core and depth (in meters) of sample intervals with brachiopods. Depth of fragmentary preserved specimens is marked by "?". Collection GIT 542: Adze-6, 844.2–?844.9; Aizpute-41, 994.65–?1001.3; Blīdene-5, 815.75; Engure, 882.15–884.4; Ikla, ?538.5; Kandava-26, ?962.7–962.8; Kardla-570, 175.0; Mežmaļi-16, 911.8–?915.0; Priekule-20, 1369.6–1369.7; Riekstini-15, 857.5–?861.3; Ruhnu-500, ?615.3–?617.2; Stirnas-18, ?901.7–?911.8; Sturi-8, ?940.5; Vilcini-19, 904.9–914.8; collections LDM G: Adze, 844.1; Anši, ?919.45–?921.5; Blīdene-5, 815.75–820.7.0; Dižrungi-17, ?894.4–?896.2; Cicere, ?899.4; Ēdole-60, 837.5–838.78; Kuili, ?948.0; Mežvagari-13, ?875.0–?877.6; Pāvilosta, ?1082.6–?1099.0; Piltene-32, 939.0; Pliekalni-14, 884.0–?888.0; Priekule-23, ?1368.6; Remte-3, ?965-966; Talsi-55, ?866.7

Description.—Dorsi-biconvex shell with subcircular to oval outline, maximum width up to 30 mm at about mid valve length, ratio of shell length/width is 0.8 (variation 0.6 to 0.9), cardinal angles obtuse (Table 1). Ventral sulcus shallow with six to ten costae; dorsal fold with four to nine, or occasionally more.

The valve surface around the umbo is covered by fine filae prior to the first concentric lamellae with about 13 costae. Up to 7 costae and costellae occur per 5 mm at 5 mm in front of umbo, and up to 30 along the commissure. Anteriorly, the distance between growth lines decreases. Ventral interarea up to 2 mm high, weakly apsacline, concave under the beak. Interarea smooth with numerous parallel growth lines. Pseudodeltidium with short monticulus with length of one third to

Table 1. Measurements (in mm) of *Cliftonia psittacina* (Wahlenberg, 1821).

Specimen	Ventral/ dorsal length	Width	Height of interarea	Number of ribs on fold/sulcus/ laterally
Shell GIT 542-24	11.0 /–	11.0	7.5	5 / – / 8
Ventral valve GIT 542-26	17+ /	24+	?	–/ 10 / 11+
Ventral valve GIT 542-162	16.5 /	c. 18	10.4	–/ 8 / 13
Ventral valve GIT 542-169	c. 11 /	c. 12	?	–/ 6 /–
Shell LDM G 328-175	? / ?	22.5	17.0	? / 6 / 8


A
B1
B2
C1
C2
D
E1
E2
F1
F2
I
G1
G2
G3
H1
H2
H3
J
K

a half of the height of the interarea. Foramen small, circular, apical. Dorsal interarea low, slightly concave.

Interior of the ventral valve is represented by only a few specimens. Teeth supported by thin subvertical dental plates which join with slightly divergent thin septa, bounding the muscle field laterally. The cavity under the pseudodeltidium is filled by secondary shell material, centrally penetrated by the foramen opening or tube, which is exposed on two fragments of small, silicified ventral valves with platelike teeth rising from the valve floor and extending at right angles; dental plates not clearly developed (Fig. 9J, K).

Dorsal valve has slightly keeled cardinal process lacking a cowel. Brachiophores triangular, divergent postero-laterally. Short wedge-shaped septa is separated from cardinalia by callosity on shell floor (Fig. 9C). Muscle fields obscure in both valves. The lamellae on the costae are displayed as small depressions on the interior surface.

Remarks.—The development of a monticulus has proved to be a controversial character at genus-level taxonomy in the triplesiids. All ventral valves from the East Baltic sections have a pseudodeltidium with a short fold or monticulus developed only during early growth stages. The development and taxonomic value of the monticulus has been discussed by Amsden (1973, 1974), Wright (1993, 1971) and Wright and Jaanusson (1993). The presence of a short monticulus, only early in ontogeny, separates the Baltic specimens from typical representatives of the genus *Cliftonia*, which had a monticulate pseudodeltidium throughout life (Wright 2000). Nevertheless the East Baltic specimens are similar to the North American *Cliftonia tubulistriata* (Savage, 1913) from the Edgewood Group (Amsden 1974), that also has a short monticulus on the pseudodeltidium. The American species differs from both Hirnantian species, *C. psittacina* and *C. oxoplecioides*, in having a circular rather than transverse outline. The Scandinavian (Bergström 1968; Cocks 1982) and Baltic specimens of *Cliftonia* clearly differ from the types of *C. oxoplecioides* from the Kildare Limestone in Ireland (Wright 1963) in having a stronger external ornament, stronger concentric growth lamellae and a less obvious fold and sulcus. *C. oxoplecioides plicata* Benedetto, 1990, from the Don Braulio Formation (Hirnantian) in the Argentian Precordillera, is similar to the nominate subspecies but in contrast possesses an unusually high fold and deep sulcus together with a striking reticulate ornament. The reduction of monticulus on *C. psittacina* is one of the features which potentially differentiates it from the type species.

The monticulus described here has some similarity with those of the related genus *Oxoplecia*, which has variably developed monticulus, that may be lost towards the hingeline. *Oxoplecia*, however differs from the *Cliftonia* by lacking a ventral tube (Wright 1963), which is present in the East Baltic specimens.

Stratigraphic and geographic range.—This widespread species occurs in the Hirnantian Stage, Upper Ordovician. It is a key element of the *Hirnantia* brachiopod fauna in Argentina, Canada, China, the Czech Republic, England, Ireland, Norway, Sweden, Thailand, and Wales (see Rong and Harper 1988; Rong et al. 2002; Benedetto et al. 1990). It also occurs in Estonia and Latvia (this paper).

Cliftonia sp. A

Fig. 9G.

Material.—Seven specimens embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia. Drill core and depth (in meters) of sample intervals with brachiopods. Collection GIT 542: Aizpute-41, 1000.3; Mežmaļi-16, 915.6; 916.1; Sturi-8, 943.0, Priekule-20, 1363.0; Riekstini-15, 860.8–860.9, Vilcini-19, 913.5.

Remarks.—These specimens may represent a subspecies of *Cliftonia* cf. *psittacina.* They are distinctive, being small, less than 15 mm in length, with a strongly convex dorsal valve, weakly impressed sulcus with five costae, cardinal process is grooved. These specimens occur in the lowermost part of the Porkuni Stage, commonly below the first appearance of *C. psittacina* (in the Stirnas-18 core in the chitinozoan *Spinachitina taugourdeaui* Zone; Hints et al. 2010).

Class Rhynchonellata Williams, Carlson, Brunton, Holmer, and Popov, 1996

Order Orthida Schuchert and Cooper, 1932

Suborder Dalmanellidina Moore, 1952

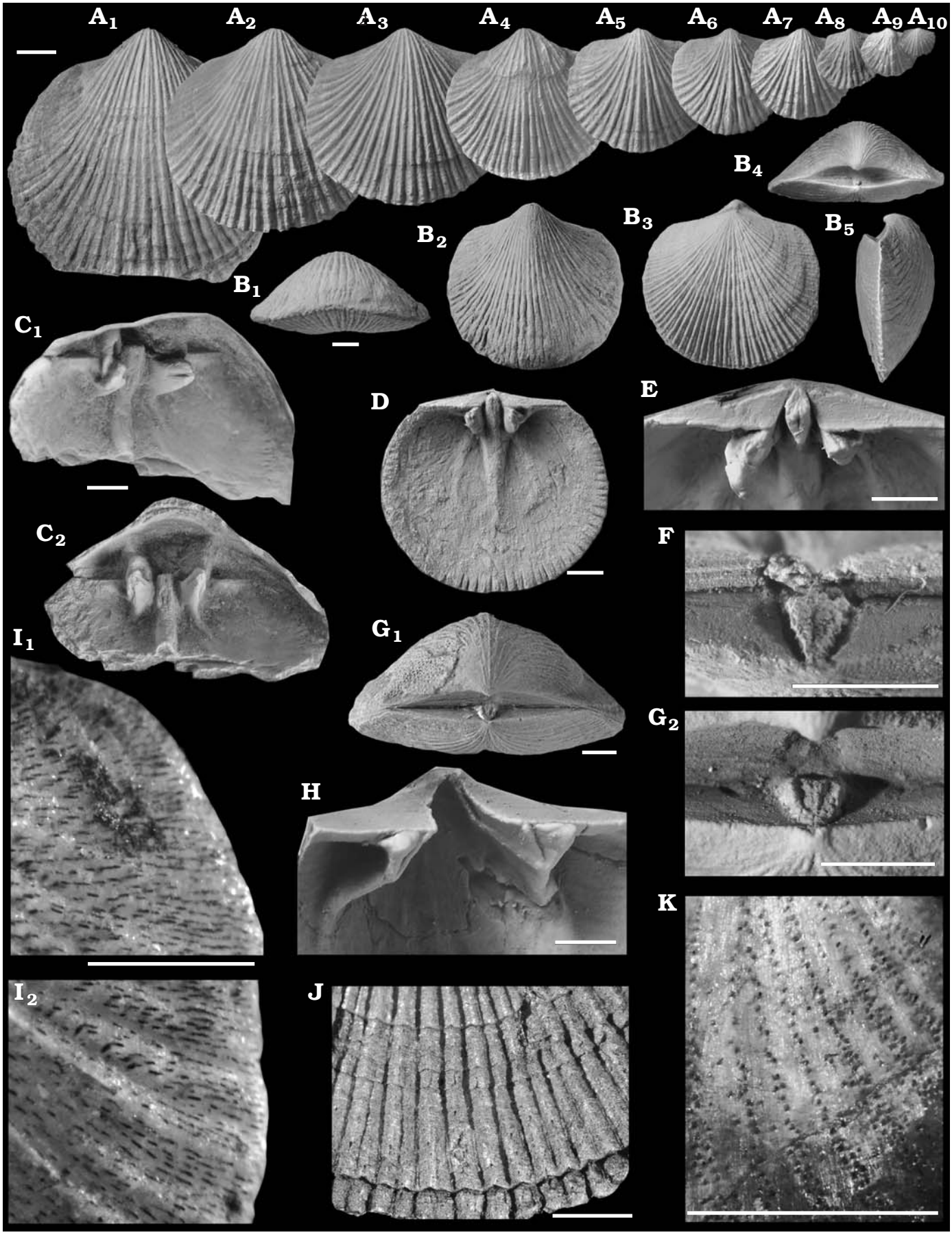
Superfamily Dalmanelloidea Schuchert, 1913

Family Dalmanellidae Schuchert, 1913

Genus *Dalmanella* Hall and Clarke, 1892

Type species: *Orthis testudinaria* Dalman, 1828; *Dalmanitina* Beds, Loka Formation, Hirnantian (Upper Ordovician), Borenshult, Östergötland, Sweden.

← Fig. 9. Triplesiid brachiopods of the genus *Cliftonia* from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia (A–I) and southern Estonia (J, K). **A**–**F**, **H**–**K**. *Cliftonia psittacina* (Wahlenberg, 1821). **A**. Ventral valve, GIT 542-166-1, Aispute-41, depth 997.25 m, interior view. **B**. Ventral valve, GIT 542-166-2, Aispute-41, 997.25 m, view of ventral interarea with short monticules (B_1) and exterior on the bedding plane with fragments of *Cliftonia* (B_2). **C**. Dorsal valve, GIT 542-22, Stirnas-18 core, 909.0 m, view of cardinalia with broken lobes of cardinal process (C_1) and interior view (C_2). **D**. Ventral valve, GIT 542-163, Stirnas-18, 908.0 m, exterior view. **E**. Shell, GIT 542-24, Stirnas-18, 908.9 m, posterior (E_1) and inclined view of ventral area with monticulus (E_2). **F**. Shell, LDM G 328-59, Adze, 844.1 m, ventral (F_1) and posterior (F_2) views. **H**. Dorsal valve, GIT 542-171, Aizpute, 997.25 m, views of cardinalia (H_1, H_2) and exterior view (H_3). **I**. Ventral interarea with short monticulus on valve, GIT 542-25, Stirnas-18 core, 909.5 m, view on ventral interarea with monticulus. **J**, **K**. Fragments of ventral valves, Kardla, 175.0 m, GIT 542-153 (**J**) and GIT 542-154 (**K**), views on ventral interior. **G**. *Cliftonia* sp., ventral valve, GIT 542-161-1, Mežmali-16, 916.1 m, posterior (G_1), exterior (G_2), and lateral (G_3) views. Scale bars 5 mm.


A1
A2
A3
A4
A5
A6
A7
A8
A9
A10
B1
B2
B3
B4
B5
C1
C2
D
E
F
G1
G2
H
I1
I2
J
K

Dalmanella testudinaria (Dalman, 1828)

Fig. 10.

1828 *Orthis testudinaria* Dalman; Dalman 1828: 115–116; pl. 2: 4a–e.
1968 *Dalmanella testudinaria* (Dalman, 1828); Bergström 1968: 8; pl. 2: 5.
2010 *Dalmanella testudinaria* (Dalman, 1828); Jin and Bergström 2010: 20–23 (see synonyms therein); figs. 3–6.

Material.—355 specimens (including 207 measured specimens), partly embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, southern Estonia. Drill core and depth (in meters) of sample intervals with brachiopods. Depth of fragmentary preserved specimens is marked by "?". Collection GIT 542: Adze-6, 837.8–?846.5; Aispute-41, 991.6–?1000.75; Engure, 882.15–882.3 m; Ikla, ?532.8–533.6; Mežmaļi-16, 902.6–910.95; Piltene-30, 1017.1; Riekstini-15, 846.15–?860.2; Ruhnu-500, 610.7–?616.1; Stirnas-18, 898.8–906.8; Vilcini-19, ?899–907.0; collections LDM G: Anši-12, 913.7–918.7; Blīdene-5, 815.75–819.3; Dizrungi-17, 881.6–?893.8; Dreimaņi-11, 952.8–955.45; Ēdole-60, 832.5–836.8; Kronauce-20, 1049.1–1050.9; Mežvagari-13, 869.5–?879.1; Pāvilosta, 1082.6; Pliekalni-14, 877.0–883.1; Priekule-23, ?1386.5; Remte-3, 958.0–958.8.

Discussion.—The Swedish type material of *Dalmanella testudinaria* was recently revised by Jin and Bergström (2010). The interpretation of *D. testudinaria* in the East Baltic (Hints 1975) is not substantially different from the revised concept of the species. The East Baltic specimens have a consistent shell shape, illustrated by the ratios of different measurements (shell length, width, thickness, width of interarea, distance of the maximum width from the umbo; Hints 1975). The average shell length/width ratio (L/W) is 0.91. The extreme values of that ratio 0.69 and 1.10 occur accordingly in 2 and 5 cases of 203 measured specimens. The L/W ratio slightly less than 1, is characteristic of the topotype specimens from Östergötland (Jin and Bergström 2010: fig. 6). The hinge line is on average 0.64 of the shell width (variation from 0.52 to 0.78), close to that for the type material of *D. testudinaria* (Jin and Bergström 2010). The maximum width of shell occurs slightly behind the shell mid-length (ratio of the distance of maximum width from the umbo and shell length is 0.43 based on 42 measurements). The shell thickness is on average 0.43 of the shell length. The larger shells can be variably compacted, which increase the variation of measurements of shell thickness. The largest specimens from Latvia slightly exceed the size of the largest specimens from Borenshult in Sweden.

The number of costae and costellae is the most variable feature. The shells with an average length of 10.4 mm have a combined total of 48 costae and costellae. Shells that are 3.3 to 17.2 mm long have 30 to 75 ribs. The variation in rib number is larger than that of the measured linear characters. There are some regional differences in *D. testudinaria* particularly in the number of ribs per 2 mm at 2 mm from the umbo: 6–9 on Latvian, 7–10 on Swedish and 8–12 on Polish specimens. Capillae occur between the costae and costellae, similar to those on the Swedish specimens. All the specimens have a median interspace on the dorsal valve and well-developed, large punctae which have often pyrite infillings (Fig. 10I, J).

However, there are two characteristics which were noted by Jisuo Jin (personal communication 2010), who studied some specimens from the Riekstini core (depth 851.0 m). These are the occurrences of aditicules and a prominent cardinal process. The Swedish specimens have a relatively small cardinal process with a shaft and bilobate myophore, which occupies half or one-third the width of the notothyrial cavity. The specimen from the Riekstini core prepared by Jisuo Jin has incipient trilobate cardinal process, which is similar to the shell on Fig. 10G. In their cardinal process and aditicules, therefore, the East Baltic specimens resemble the North American *Cincinnetina* Jin, 2012 (formerly known as "*Dalmanella*" of the Cincinnati type area), but they lack the dorsal medial costa that is diagnostic of *Cincinnetina*. Three other specimens from the same sample have a prominent cardinal process bilobate with weakly developed crenulations, but not trilobate. Most of the Baltic specimens have cardinal process with bilobate, more or less strongly crenulated myophore (Fig. 10C–F), which is more robust and extends more posteriorly over the interarea compared with that of Swedish specimens. Such a cardinal process is more typical of other species, for example, the cardinal process of *Cincinnetina multisecta* (Meek, 1873) from Laurentia (Jin and Bergström 2010; Jin 2012). However, the faint capillae interrupted by strong growth lines ("pitted" ornament between the ribs), which are characteristic of the latter and several other species of *Onniella* and *Cincinnetina* in North America (Jin and Zhan 2008; Jin and Bergström 2010; Jin 2012) are not apparent on Baltic specimens of *D. testudinaria*. However, such ornament (reticulated growth lines of Jin 2012) is described on the Baltic species *Onniella trigona* from the Porkuni Stage and lowermost Silurian (Hints 1975; Rubel 2011).

← Fig. 10. Dalmanellid brachiopod *Dalmanella testudinaria* (Dalman, 1828) from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia (A, B, D–K) and southwestern Estonia (C). **A**. Ventral valves, GIT 542-63/1–10, Adze, depth 842.6 m (A_1–A_{10}), exterior views. **B**. Shell, GIT 542-41/1, Stirnas-18, 899.55 m, anterior (B_1), ventral (B_2), dorsal (B_3), posterior (B_4), and lateral (B_5) views. **C**. Shell interior, GIT 542-76, Ikla, 533.6 m, antero-lateral (C_1) and anterior (C_2) views. **D**. Dorsal valve, LDM G328-121, Ēdole, 835.6 m, interior view. **E**. Dorsal valve, GIT 207-17, Engure, 882.15 m, views of cardinalia and interarea. **F**. Shell, GIT 542-111, Stirnas-18, 899.2 m, view of cardinal process. **G**. Shell, LDM G328-74, Mežvagari-17, 869.5 m, posterior view (G_1) and view of cardinal process (G_2). **H**. Ventral valve, GIT 542-69, Mežmali-16, 918.6 m, view of interarea and teeth. **I**. Pyritized pores on posterior and lateral parts of ventral valves, Stirnas-18, 903.8 m, GIT 542-114/1 (I_1) and 542-114/2 (I_2), exterior views. **J**. Ornament of the shell with few aditicules, LDM G328-97; Dizrungi-17, 888.3 m. **K**. Punctae on the broken shell surface, LDM G328-68; Kronauce, 1049.1 m. Scale bars 2 mm, except I_1 1 mm.

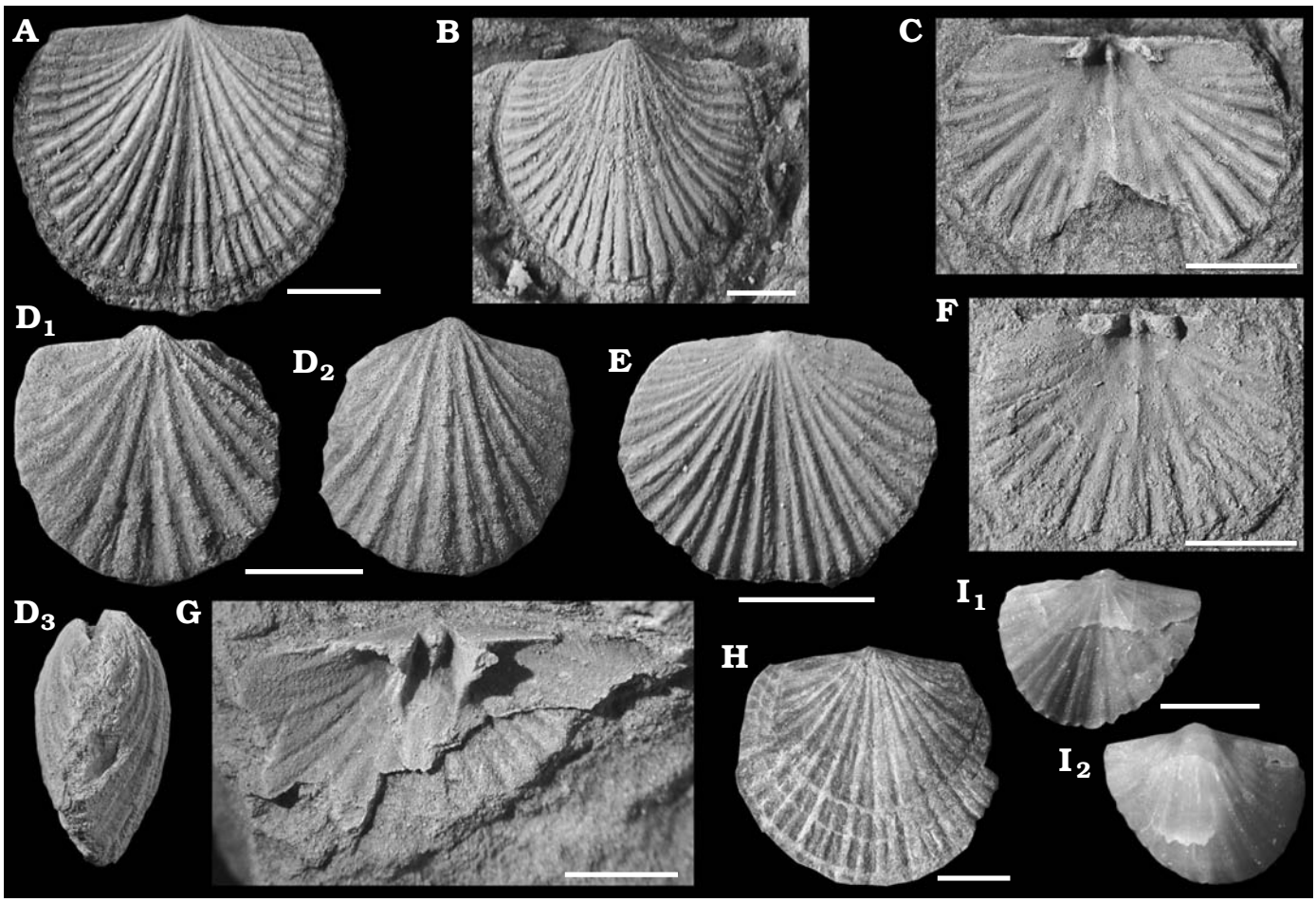


Fig. 11. Dalmanellid brachiopods from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia (A–D, F–I) and southwestern Estonia (E). **A**, **B**, **D**, **H**, **I**. *Onniella* sp. **A**. Dorsal valve, GIT 542-66, Aispute-41, depth 1001.15 m, exterior view. **B**. Ventral valve, LDM 382-50, Dižrungi-17, 896.0 m, ventral view. **D**. Shell, GIT 542-471, Riekstini-15, 860.85, dorsal (D_1), ventral (D_2), and lateral (D_3) views. **H**. Dorsal valve, GIT 542-480, Krjukai, 968.6 m, dorsal exterior view. **I**. Shell, GIT 542-472, Kandava-26, 964.5 m, ventral (I_1) and dorsal (I_2) views. **C**, **E**, **F**. *Draborthis* cf. *caelebs* Marek and Havlíček, 1967. **C**. Dorsal valve, GIT 542-392, Riekstini-15, 857.5, interior view. **E**. Dorsal valve, GIT 542-67, Ruhnu-500, 914.0 m, exterior view. **F**. Dorsal valve, GIT 542-4393, Mežmali-16, 913.2 m, interior view. **G**. *Drabovia* sp., dorsal valve, GIT 542-473, Mežmali-16, 910.1 m, interior view. Scale bars 2 mm.

The presence of aditicules separates at least some of the East Baltic specimens from the Swedish type material and thus should be rejected from *D. testudinaria* following Jin and Bergström (2010). The type of cardinal process and occurrence of additicules is currently difficult to establish in differently preserved specimens from different localities in the Central East Baltic. More detailed studies of the punctae and shell microstructures of *D. testudinaria* are needed to confirm the diagnostic value of the aditicules. Currently the differences noted between the East Baltic specimens and those from the type locality in Sweden is considered as intraspecific variation.

Stratigraphic and geographic range.—This near-cosmopolitan species is mainly restricted to the Hirnantian Stage, Upper Ordovician, although related forms occur in the underlying Katian Stage. The species is a common component of the *Hirnantia* brachiopod fauna (Rong and Harper 1988), particularly in Europe, including England, Ireland and Wales, Austria, Czech Republic, France, Norway, Sweden, Estonia, Latvia (this paper), and Lithuania (Paškevičius 1997). The species also occurs in China, Burma, North America (Canada), South America (Argentina), and Asia (Kazakhstan).

Genus *Onniella* Bancroft, 1928

Type species: *Onniella broeggeri* Bancroft, 1928; Onny Shale Formation, lower Katian (Ordovician); Salop, UK.

Onniella sp.

Fig. 11A–B, D, H–I.

Material.—Eight specimens. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia. Drill core and depth (in meters) of sample intervals with brachiopods. Collection GIT 542: Adze-6, 822.5; Aispute-41, 1001.15; Kandava-26, 964.5; Krjukai, 968.6; Mežmaļi, 916.3; Riekstini-15, 860.85–861.8; Vilcini-19, 914.5. Collection LDM G: Dižrungi-17, 896.0.

Remarks.—Shell small, biconvex, ventral valve slightly car-

inate, dorsal valve sulcate. The shell outline and fascicostellate ornament is similar to that of *Onniella trigona* from the East Baltic (Rubel 1962, 2011; Hints 1975) and *Onniella tricapitata* Jin and Zhan, 2008 from the Ellis Bay Formation on Anticosti Island (Jin and Zhan 2008). However, the Latvian specimens differ from both species in lacking reticulated growth lines (Jin 2012). Comparisons are difficult with *Onniella kalvoy*a Cocks, 1982 from the central Oslo Region, Norway (Cocks 1982) due to insufficient data on the East Baltic specimens. Two smaller specimens (Fig. 11D, I) with stronger costae and costellae, however, could belong to another species or merely represent early growth stages.

Family Heterorthidae Schuchert and Cooper, 1931

Genus *Heterorthina* Bancroft, 1928

Type species: *Heterorthina praeculta* Bancroft, 1928; Crosspipes Member of the Cheney Longville Formation, Cheneyan, lower Katian (Ordovician); Wales, UK.

Heterorthina? sp.

Fig. 12.

Material.—One specimen, the single shell DML G 328-75 from the Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia. The Blīdene-5 drill core (depth 819.3 m).

Remarks.—Specimen has, on the basis of outline, convexity of valves, its rectimarginate commissure and occurrence of aditicules similarities to the rhipidomellinae genera *Mendacella* and *Dalejina.* The external ornament with a median interspace on the dorsal valve, however, is similar to the ribbing pattern on *Heterorthina*. It differs from the first two genera (Jin and Zhan 2008; Hints 1975, 2012; Rubel 2011) in having the interspace between the ribs on dorsal valve, a characteristic of *Heterorthina*. The relatively short hingeline and lack of a fold and sulcus, however, introduces some uncertainty with that assignment *Heterorthina*.

This species is medium-sized, transversely oval, moderately biconvex, 13.2 mm wide at mid valve length, 11.7 mm long, and 5.3 mm thick. Hinge line forms about 60% of the shell width.

Ventral valve convex, maximum convexity in posterior half. Interarea, low apsacline. Dorsal valve weakly sulcate in posterior part, anteriorly evenly convex, anterior commissure essentially rectimarginate. Dorsal interarea low (0.7 mm) anacline, notothyrium open, partly filled by bi(?)-lobate myophore.

Radial ornament fascicostellate with median costa on ventral valve and corresponding interspace on dorsal valve; posterior costellae curve towards interarea; ribs are triangular in cross-section. Along the commissure 65 costae and costellae; of which 16 primary, at 5 mm from umbo, 6 ribs per 2 mm. Growth lines strong on the anterior half. Aditicules on the rib crests are developed close to the growth lines. The shell external surface is covered by a dense, minute concentric ornament best visible in interspaces. The endopunctae are not visible.

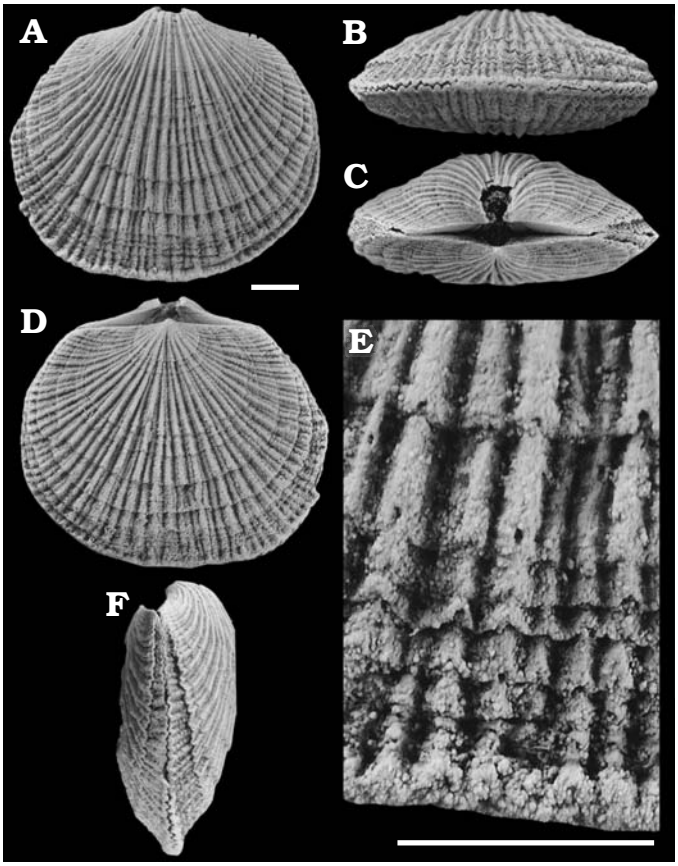


Fig. 12. Heterorthid brachiopod *Heterorthina*? sp. from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia. Shell, LDM 328-75, Blīdene-5, depth 819.3 m, ventral (**A**), anterior (**B**), posterior (**C**), dorsal (**D**), and lateral (**F**) views, and detail of external ornament (**E**) of the ventral valve showing the growth lines and aditicules. Scale bars 2 mm.

Superfamily Enteletoidea Waagen, 1884

Family Draboviidae Havlíček, 1950

Subfamily Draboviinae Havlíček, 1950

Genus *Hirnantia* Lamont, 1935

Type species: *Orthis sagittifera* M'Coy, 1851; Foel-y-Ddinas Mudstone Formation, Hirnantian, (Upper Ordovician); Wales, UK.

Hirnantia sagittifera (M'Coy, 1851)

Material.—57 variably preserved specimens. Porkuni Regional Stage, Hirnantian (Upper Ordovician); Latvia and southwestern Estonia. Drill core and depth (in meters) of sample intervals with brachiopods. Depth of fragmentary preserved specimens is marked by "?". Kuldiga Formation: collection GIT 542: Adze, ?846.70; Aizpute-41, ?1000.3; Engure, ?882.45–882.80; Mežmaļi-16, ?903.50–?914.8; Ruhnu-500, ?616.5–616.90; Stirnas-18, ?910 (lowermost *Conochitina scabra* Biozone, Hints et al. 2010); Riekstini-15, ?855.7–?857.5; (*C. scabra* Biozone, Brenchley et al. 2003); Vilcini-15, 910.8. ?Prabut Formation: Petrobaltic S-8, 2618.2–2618.8 m; collections LDM G: Blīdene-5, ?815.75–?819.3; Cicere, ?897.8–898.2; Dižrungi-17, 895.7–?895.9;

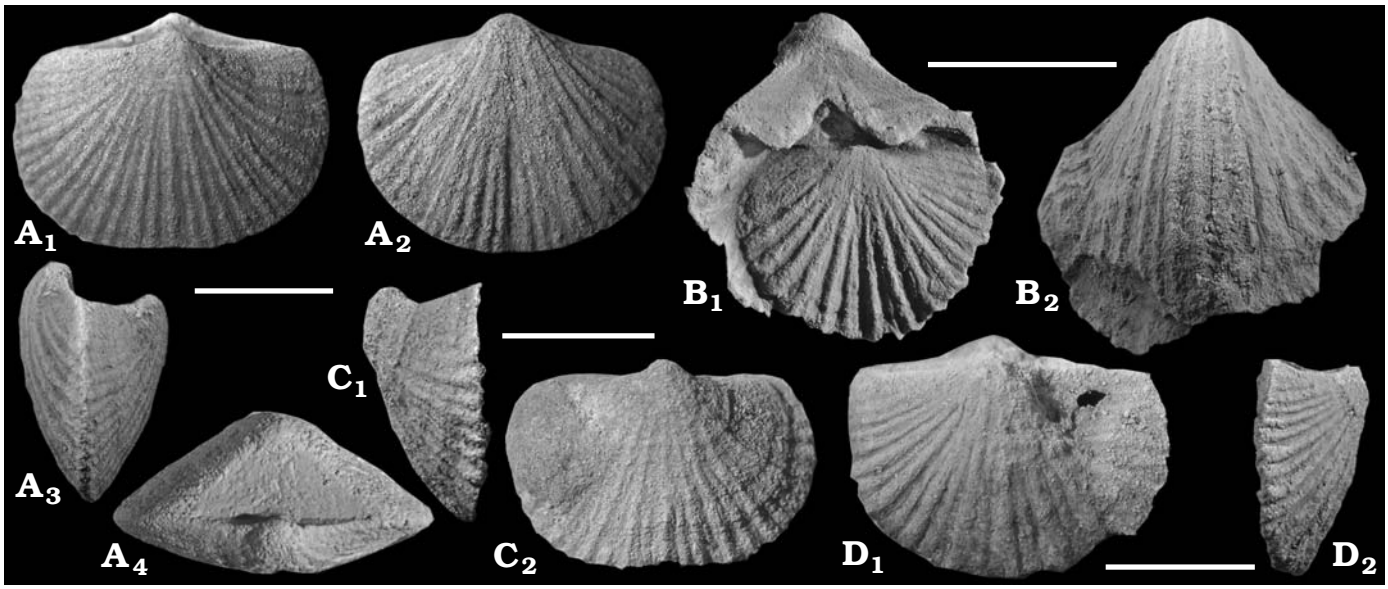


Fig. 13. Draboviid brachiopods of the genus *Kinnella* from the East Baltic, Upper Ordovician. **A**, **C**. *Kinnella* cf. *kielanae* (Temple, 1965) from Kuldiga Formation, Porkuni Regional Stage, western Latvia. **A**. Shell, GIT 542-229, Riekstini-15, depth 859.9 m, ventral (A_1), dorsal (A_2), lateral (A_3), and posterior (A_4) views. **C**. Ventral valve, GIT 542-226, Aispute-41, 1001.15 m, lateral (C_1) and ventral (C_2) views. **B**, **D**. *Kinnella* sp. **B**. Shell with shifted valves, LDM 328-43, Kuili Formation, Pirgu Regional Stage, western Latvia, Blīdene-5, 822.6 m, view of dorsal exterior and ventral interarea (B_1) and ventral exterior (B_2). **D**. Shell, GIT 509-71, Tudulinna? Formation, Vormsi Regional Stage (Katian), central Estonia, Lelle (102), 147.96–148.0 m, ventral (D_1) and lateral (D_2) views. Scale bars 2 mm.

Kandava-25, ?930.3–?930.5; Kronauce, ?1053.7; Kuili, ?948.0–948.5; Mežciems, ?379.5; Mežvagari-13, 872.1–879.10; Piltene-30, 938.0–945.0; Piltene-31, 971.2–?977.8; Piltene-32, 923.5; Pliekalni-14, 884.8; Remte-3, ?965–?966. Saldus Formation: Alūksne, ?872.45–872.52.

Remarks.—The species *Hirnantia sagittifera* from the East Baltic has been recently described in a separate paper (Hints et al. 2012) and need not be repeated here.

Stratigraphic and geographic range.—The Hirnantian Stage, Upper Ordovician. This cosmopolitan species is the eponymous taxon for the *Hirnantia* brachiopod fauna. The species is common in both the typical and atypical *Hirnantia* faunas and has a near global distribution (Rong and Harper 1988). In Baltoscandia it occurs in Norway (Cocks 1982), Sweden (Bergström 1968), Estonia, Latvia (this paper), and Lithuania (Paškevičius 1997).

Genus *Kinnella* Bergström, 1968

Type species: *Hirnantia*? *kielanae* Temple, 1965; *Dalmanitina* Beds, Hirnantian (Upper Ordovician); Stawy, Holy Cross Mountains, Poland.

Kinnella cf. *kielanae* (Temple, 1965)

Fig. 13A, C.

Material.—Two specimens. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia. Drill core and depth (in meters) of brachiopod samples. Collection GIT 542: Aispute-41, 1001.15; Riekstini-15, ?858.6–?860.85.

Description.—Small biconvex shells up to 4.7 mm wide, ventral interarea high, catacline to slightly procline, weakly concave below the beak. Shell transversely oval with rounded cardinal angles. Anterior commissure sulcate, may have a slight indention in the anterior part. Delthyrium is open, twice as high as wide. Dorsal valve is weakly convex in posterior part, anteriorly flattened; sulcus developed between the median primary costae; interarea is low, anacline with open notothyrium. Radial ornament is fascicostellate with medial costa on the ventral valve. Sixteen costae appear at umbo of the ventral valve, which increase in number by bifurcation up to 35 along the shell commissure; at 5 mm from umbo, 6 costae per 2 mm.

Remarks.—The position of the ventral interarea suggests that the Baltic specimens are most similar to those described from South China (Rong 1979: pl. 1: 7, 1984: fig. 3). However, that feature is very variable (Lespérance and Sheehan 1976; Stott and Jin 2007) and cannot be used as diagnostic. The Baltic specimens differ from the type species *K. kielanae* (Temple 1965: 403) by less convex dorsal valve, more transverse outline and more robust ornament. The pre-Hirnantian *Kinnella laurentiana* Stott and Jin, 2007 from Canada (Manitoulin Island) differs from the Baltic specimens in having more convex valves, apsacline ventral area and arrangement of ribs with median costa on the dorsal valve instead of "a strong axial interspace in brachial valve…" on *K. kielanae* (Temple 1965: 403) and the Baltic specimens.

In the East Baltic, *Kinnella* was probably present already in the upper Katian, in the Vormsi Stage (Hints et al. 2007). *Kinnella* sp. (Fig. 13D) from that stage differs in the more variable size of costae and costellae and by an almost catacline ventral area. Another specimen (Fig. 13B) from the Pirgu Regional Stage in the Blidne-5 core probably belonging to

Kinnella, differs from the others in the less transverse outline of the shell and by more robust ornament.

Genus *Drabovia* Havlíček, 1950

Type species: *Orthis redu*x Barrande, 1848; Letná Formation, Upper Sandbian (Ordovician); Drabov Hill near Beroun, Czech Republic.

Drabovia sp.

Fig. 11G.

Material.—Two specimens from the Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, Vilcini-19 core (on depths 901.1 m and 901.2 m; collection GIT 542)

Remarks.—Two small, dorsal valves with a suboval outline, a nodule-like myophore and short anteriorly-narrowing cardinal process shaft and erect subparallel brachiophore plates are similar to those of *Drabovia westrogothica* Bergström from Västergötland, Sweden (Bergström 1968) and *Drabovia*? *minuta* Hints, 2012). However, the Latvian specimens are insufficient for detailed comparison with the other species of *Drabovia*.

Genus *Draborthis* Marek and Havlíček, 1967

Type species: *Draborthis caelebs* Marek and Havlíček, 1967; Kosov Formation, Hirnantian (Upper Ordovician); Bohemia, Czech Republic.

Draborthis cf. *caelebs* Marek and Havlíček, 1967

Fig. 11C, E, F.

Material.—Six specimens embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia. Drill core and depth (in meters) of brachiopod samples. Collection GIT 542: Engure, 884.3; Mežmaļi-16, 913.2; Riekstinis-15, 857.5–858.6.

Remarks.—Small, weakly sulcate suboval to subquadrate dorsal valves with the valve width 7.1 mm and length 4.8 mm. Brachiophores widely divergent (Fig. 11C, F), cardinal process with small nodule-like myophore on the floor of notothyrial cavity, narrow septum reaches the anterior half of the valve. Although the Baltic valves are small, in comparison with *D. caelebs* from Sweden (Bergström 1968) and Bohemia (Marek and Havlíček 1967), they are based on dorsal internal characters clearly related to that species and distinguish it from other small dalmanellidine brachiopods in the Baltic area.

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Trigonorhynchiidae Schmidt, 1965

Subfamily Rostricellulinae Rozman, 1969

Genus *Plectothyrella* Temple, 1965

Type species: *Plectothyrella platystrophoides* Temple, 1965; Ashgill Shales, Hirnantian (Upper Ordovician); Hol Beck, near Ambleside, Westmorland, UK.

Plectothyrella crassicostis (Dalman, 1828)

Fig. 14; Table 2.

1828 *Atrypa*? *crassicostis* Dalman; Dalman 1828: 47–48.
1968 *Plectothyrella platystrophoides* Temple, 1965; Wright 1968: 357, fig. 4.
2002 *Plectothyrella crassicosta* (Dalman, 1828); Bergström 1968: 19, pl. 7: 5–8.
2008 *Plectothyrella crassicostis* (Dalman, 1828); Cocks 2008: 187 (see synonyms therein).

Material.—98 specimens, partly fragmentary embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia, southwestern Estonia, and Kaliningrad Region (Russia). Drill core and depth (in meters) of sample intervals with brachiopods. Depth of fragmentary preserved specimens is marked by "?". Collection GIT 542: Adze-6, 838.5–?844.4; Aispute-41, ?993.55–996.35; Blīdene-5, 815.75; Engure 882.1–?884.4; Ikla, ?584; Malinovskaya (Russia, Kaliningrad Region; depth is unknown); Mežmaļi-16, ?905.9–914.55; Riekstini-15, 846.0–855.7; Ruhnu-500, 609.8–?611.8; Stirnas-18, ?899.0–?910.0; Sturi-8, ?942.6; Vilcini-19, 901.0–907.9. Collections LDM G: Anši-12, 914.6–914.8; Blīdene-5, 816.6–819.3; Cicere-10, ?897.8–898.0; Dizrungi-17, ?881.6; Dreimaņi-11, 954.65–?955.5; Ēdole-60, ?836.8–848.0; Kronauce-20, 1050.9; Mežvagari-13, 869.5–878.3; Pāvilosta, ?1098.6; Piltene-31, 970.7; Pliekalni-14, ?882.0–?884.8; Puikule, 1398.3.

Description.—Ventribiconvex rostrate, costate shell with subcircular to anteriorly elongate outline, anterior commissure sulcate, lateral undulating. Ratio of ventral valve length/width varies from 0.77 to 0.90; thickness up to 90% of shell width. Maximum convexity at about mid length in dorsal valve, and in the posterior half of ventral valve. Ventral beak incurved or overhanging the umbonal part of dorsal valve. Palintrope variably developed. Dorsal fold and ventral sulcus originating 2–3 mm from beaks (Table 2).

Ornament consists of high, angular costae, 17 to 23 around the beak. Dorsal fold consists of two anteriorly-broadening costae bifurcating at 3–6 mm from umbo and separated from each by a deep median interspace. The fold is flanked laterally on both sides by one thin and 10 to 13–14 stronger costae, which become thinner towards the posterior edge. Ventral sulcus with strong median and two or more thinner costae; sulcus is limited on both sides by

Table 2. Measurements (in mm) of *Plectathyrells crassicistis* (Dalman, 1828).

Specimen	Ventral/dorsal length	Shell width	Thickness	No of ribs in sinus/fold	Ribs no in flanks
GIT 542-37, dorsal valve	–/27	–	–	–/2–4–7	9
GIT 542-38, shell	16/–	20.0	7.1	1–3/2–4	–
GIT 542-202, shell	27.4/–	–	–	1–3/2–4	11
GIT 542-230, shell	20.8/18.5	21.8	11.8	1–3/2–4	11
LDM G 328-135, shell	29.8/27.1	27.3+	1–0.9	–/4	–
LDM G 328-133, shell	18.2/16.7	16?	–	–/2–4–5	–

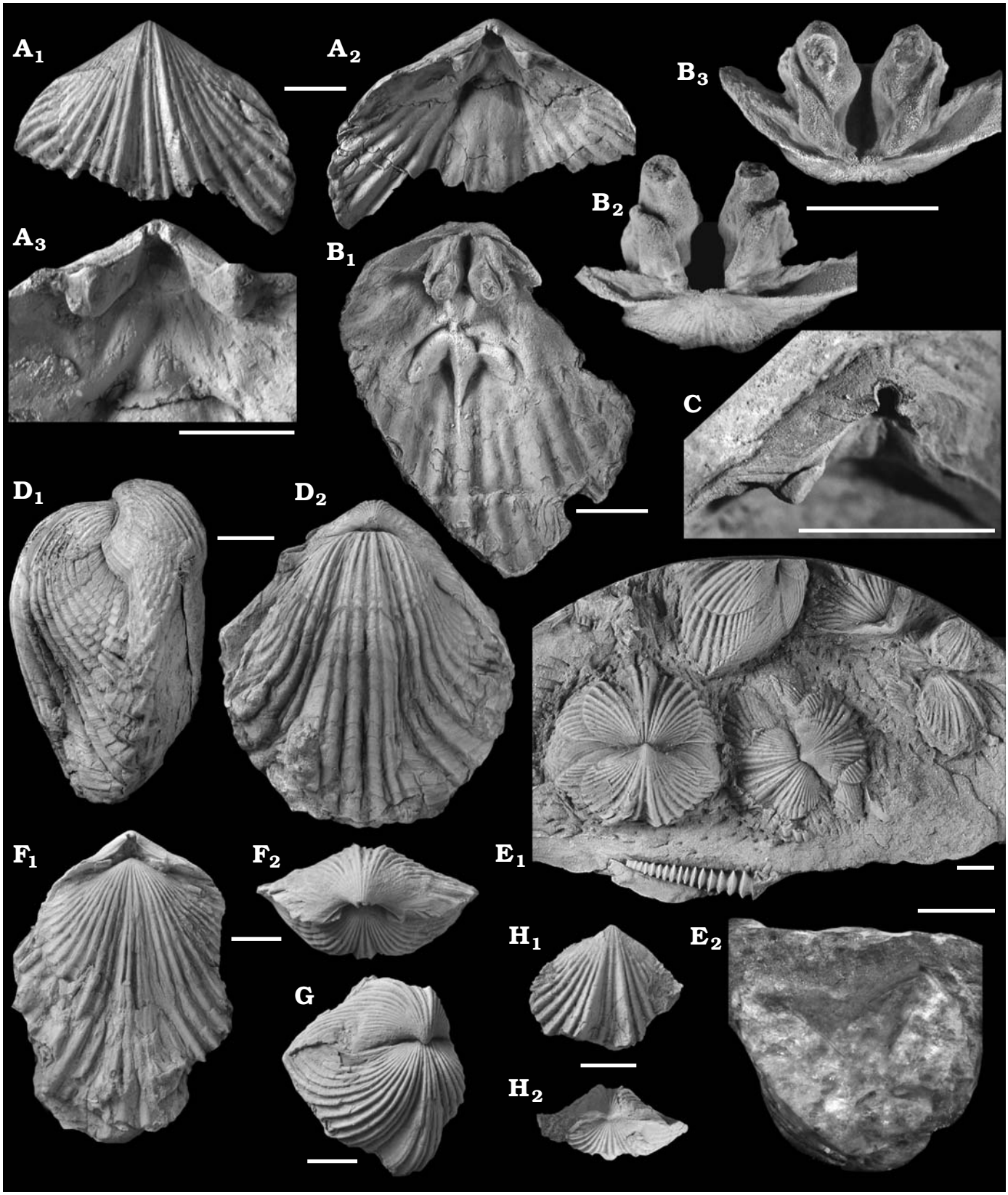


Fig. 14. Trigonorhynchiid brachiopod *Plectothyrella crassicostis* (Dalman, 1828) from the Kuldiga Formation of the Porkuni Regional Stage, Hirnantian (Upper Ordovician), East Baltic, western Latvia. **A**. Ventral valve, LDM G 328-15, Blīdene-5, depth 816.6 m, exterior view (A_1), interior view (A_2) and the detail of the posterior part of the same (A_3). **B**. Incomplete dorsal valve, GIT 542-16, Riekstini-15, 854.8 m, dorsal interior (B_1), posterior (B_2), and posteriorly tilted (B_3) views of cruralium. **C**. Ventral valve, LDM G 328-149, Mežmali-16, depth 914.9 m, view of pedicle opening. **D**. Shell, LDM G 328-135, Ēdole-61, 848.1 m, lateral (D_1) and dorsal (D_2) views. **E**. Shells, GIT 542-3/1–3, Adze-6, 838.5 m, posterior views of shells in live position and →

one or two strong costae. In some cases additional costellae appear on fold and sulcus. The growth lines are variably developed, very strong on some specimens. The palintrope and shell surface are filated.

Ventral valve (Fig. 14A, F) has wide open delthyrium, about twice as wide as high with somewhat elevated (thickened?) edges (Fig. 14A_2, A_3); the permesothyrid pedicle opening, circular in diameter, about 0.7 mm; stout cyrtomatodont teeth have postero-laterally, divergent thickenings. Delthyrial chamber short thickened in umbonal part.

Dorsal interior is represented by one valve. Sockets form oblique grooves below the posterior edge of the valve, inner socket ridges are connected to the thick outer hinge plates. Crura strong, curved antero-ventrally, rod-like, rising from thickened shell floor (Fig. 14B). Trilobated thickening of shell floor occurs in front of the cardinalia. Muscle field not impressed. Ribs impressed on interior surface of valve.

Remarks.—The Baltic specimens are similar to *P. crassicostis* from Sweden (Bergström 1968) and also to specimens previously described as *P. platystrophoides* (a junior synonym of *P. crassicostis*) in Ireland (Wright 1968), England and North Wales (Temple 1965). The preservation of specimens (mostly moulds) from the latter and several other areas (e.g., China, Chen et al. 2006; Sardinia, Leone et al. 2009) hinders accurate comparisons with the Baltoscandian specimens. The Baltic specimens are of medium size (width about 20 mm), and very similar to those from Québec in posterior view (ventral beak covers the dorsal umbo) and by the arrangement of costae (Lespérance and Sheehan 1976: pl. 110: 7–9, 12). The thick inner socket ridges mentioned by Lespérance and Sheehan (1976: pl. 110: 16) are also similar to the Baltic specimen (Fig. 14B).

The lateral branches of the median septum are similar to those in *P. crassicostis* from Kildare (Wright 1968: fig. 4B) and Québec (Lespérance and Sheehan 1976).

The dorsal interiors of the Chinese specimens figured by Sheng (1982: pl. 3: 5, 6) seems to differ from the Baltic and other specimens of *P. crassicostis* by a much greater number of costae, revealed by the ribbing impressions on the interior surface of the valve.

Stratigraphic and geographic range.—The Hirnantian Stage, Upper Ordovician. A similar form is reported from the lowest Llandovery in England. This characteristic taxon of the *Hirnantia* fauna occurs on a range of different continents (Africa, Asia, Europe, North and South America), across the Bani and Kosov provinces (see Rong and Harper 1988; Rong et al. 2002; Benedetto et al. 1990). In Baltoscandia it occurs in Sweden (Bergström 1968), Estonia, and Latvia (this paper).

Tentaculites sp. in the lower part of sample (figured in Kaljo et al. 2008) (E_1). Polished cross section of the shell (GIT 542-3/3) cut by drilling of the upper edge on E_1 showing due compression broken anterior part and long crura (E_2). **F**. Shell, GIT 542-202, Engure, 882.1 m, dorsal (F_1) and posterior (F_2) views. **G**. Shell, LDM G 272-1, Piltene-31, 970.7 m, postero-lateral view. **H**. Shell, LDM G 328-126, Blīdene-5, 818.3 m, ventral (H_1) and posterior (H_2) views. Scale bars 5 mm.

Order Athyridida Boucot, Johnson, and Staton, 1964

Suborder Athyrididina Boucot, Johnson, and Staton, 1964

Superfamily Meristelloidea Waagen, 1883

Family Meristellidae Waagen, 1883

Subfamily Meristellinae Waagen, 1883

Genus *Hindella* Davidson, 1882

Type species: *Athyris umbonata* Billings, 1862; Ellis Bay Formation, Ashgill (Ordovician); Anticosti Island, Quebec, Canada.

Hindella cf. *crassa incipens* (Williams, 1951)

Fig. 15A, E, F.

Material.—102 specimens, mostly fragmentary, embedded in rock. Porkuni Regional Stage, Kuldiga Formation, Hirnantian (Upper Ordovician); western Latvia and southwestern Estonia. Drill core and depth (in meters) of sample intervals with brachiopods. Depths of fragmentary preserved specimens are marked with "?" *Hindella* cf. *crassa incipiens* (Williams, 1951) in collection GIT 542: Adze-6, ?844.0–?844.5; Aispute-41, 990.95–998.55; Engure, ?882.8–?884.3; Ikla, ?527.0; Krjukai, ?968.0; Mežmaļi-16, ?912.0–?913.8; Piltene-1, ?1016.2; Piltene-30, ?938.0; Priekule-20, ?1357.3; Riekstini-15, ?858.7; Ruhnu-500, 616.9; Stirnas-18, ?899.5–?908.9; Vilcini-19, ?906.3–?912.9; collections LDM G: Cicere, ?897.8–?898.2; Dižrungi-17, ?893.7–?894.5; Plikalne-14, ?884.0–888.0; Adze-6, ?837.0–?845.4; Mežvagari-13, ?870.2–?875.0; Kandava-52, ?930.3–?932.5; Remte-3, ?958.0–?958.8; Kuili-9, ?948.7; Ēdole-60, ?837.5–?841.4; Dreimaņi, ?952.2; Blīdene-5, ?815.75–?818.0; Piltene-30, ?937.6–?942.1; Talsi-55, ?866.4–?866.7.

Remarks.—Brachiopods characterized by a biconvex shell with weakly developed concentric growth lines occur in many of the studied samples, mostly as fragments and incomplete valves. A few more or less complete shells and valves reminiscent of *H. crassa incipiens* (Sheehan 1977; pl. 2: 7, 9, 11) the common Hirnantian brachiopod in many parts of northern Europe and China (Harper 1981, 1988; Rong and Li 1999; Chen et al. 2000, 2006; Brenchley et al. 2006, Rong et al. 2002). It is highly probable that the fragments of brachiopod valves with weak concentric ornaments belong to the same taxon group. These moderately biconvex specimens have a sub-circular outline with a length up to 17 mm and width up to about 20 mm. One dorsal valve has an anteriorly-thinning, long, dorsal septum (Fig. 15E) and one ventral valve has a pedicle chamber that widens slightly anteriorly (Fig. 15F). The East Baltic specimens differ from the other Upper Ordovician species, *H. cassidea* (Sheehan 1977), in having less convex valves, a less incurved ventral umbo which does not overhang the dorsal umbo, and by a more circular outline. *H. cassidea* is most similar to *Hindella*

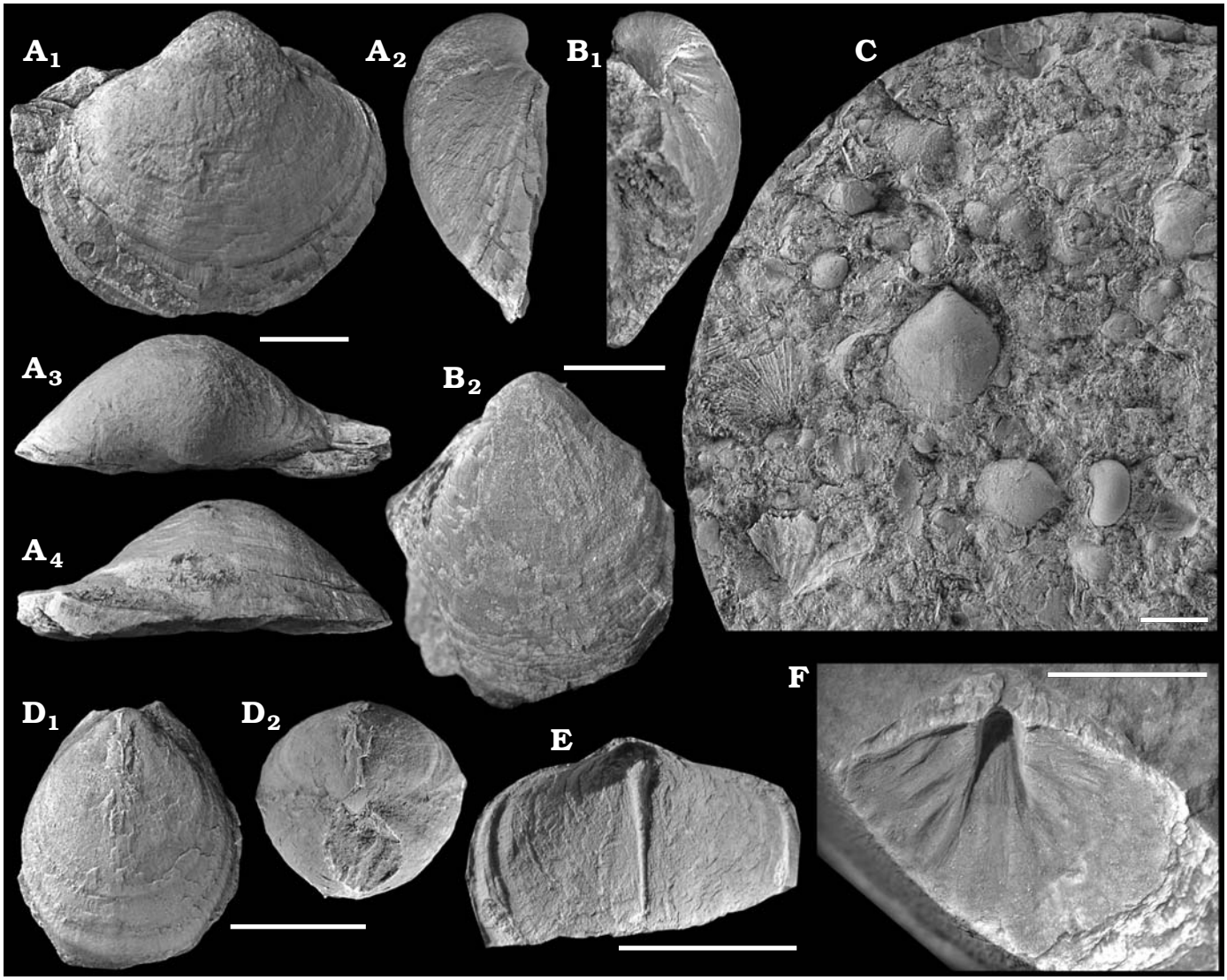


Fig. 15. Meristellid brachiopods of the genus *Hindella* from Porkuni Regional Stage, East Baltic, Kuldiga Formation, western Latvia (A–C, E, F) and Ärina Formation, northern Estonia (D). **A**, **E**, **F**. *Hindella* cf. *crassa incipiens* (Williams, 1951). **A**. Ventral valve, GIT 542-273, Aispute-41, depth 991.0 m, exterior (A_1), lateral (A_2), posterior (A_3), and anterior (A_4) views. **E**. Incomplete dorsal valve, GIT 542-278, Aispute-41, 991.0 m, interior view. **F**. Incomplete ventral valve, GIT 542-35, Stirnas-18, 907.5 m, interior view. **B**, **C**. *Hindella* sp. **B**. Ventral valve, GIT 542-34, Stirnas-18, 908.2 m, lateral (B_1) and exterior (B_2) views. **C**. The bedding plane with brachiopods, including *Hindella* sp., GIT 542-4 (figured in Kaljo et al. 2008), Aispute-41, 998.25 m. **D**. *Hindella* cf. *cassidea* (Dalman, 1828), shell, GIT 542-267, erratics from the Kõnnu village, dorsal (D_1) and posterior (D_2) views. Scale bars 5 mm.

from northern Estonia (*H*. cf. *cassidea* in Modzalevskaya 1985) (Fig. 15D).

Concluding remarks

The *Hirnantia* brachiopod fauna of the East Baltic, occurring in the Livonian Tongue of the Baltoscandian Facies Belt, is represented by at least 17 brachiopod genera. Thus the diversity of brachiopods is relatively high in view of the restricted number of finds from drill core sections. Based on the dominance of the genera *Leptaena*, *Paramalomena*, *Eostropheodonta*, *Plectothyella*, *Hindella*, *Dalmanella*, and *Hirnantia*, and several others established for the first time in the region (*Proboscisambon*, *Leangella*, *Eopletodonta*, *Onniella*, *Drabovia*, *Draborthis*), the East Baltic assemblage can be reliably assigned to the Kosov Province (Rong and Harper 1988; Dahlquist et al. 2010). The exceptional occurrence of some brachiopods (e.g., *Thebesia*, *Brevilamnulella*) common in Norway (Brenchley and Cocks 1982; Dahlquist et al. 2010) and North America (Edgewood Province; Rong and Harper 1988) deserves some discussion. The restricted distribution of these species in Baltoscandia may be partly due to the varied stratigraphical completeness of the Hirnantian Stage in different parts of Baltoscandia. Future detailed biostratigraphical and chemostratigraphical studies may clarify more fully the spatial and temporal relationships of faunas in different provinces.

A number of species deserve some concluding discussion.

The specimens described in this paper under the name *Cliftonia psittacina* hint at the possible presence of two species or subspecies in Sweden. The type material within the Boda Limestone from Osmundsberget (Bergström 1968) is mainly pre-Hirnantian in age (Ebbestad and Högström 2007). The Boda Limestone is described as high relief carbonate mud mound deposits (Riding 2002) where the fauna in general exhibits strong endemism (Ebbestad and Högström 2007). *C. psittacina* (Bergström 1968) in the silty carbonate facies of the *Dalmanitina* Beds differ from the specimens of the Boda Limestone in shape and size, which are considered by Bergström (1968) within the range of intraspecific variation. If the future studies of the Swedish specimens confirm the occurrence of two different species or subspecies, the specimens from the *Dalmanitina* Beds and from the Kuldiga Formation in the East Baltic should be defined under a new species name. Outside Baltoscandia (e.g., Ireland and Wales, Wright 1963, 1968; Cocks and Price 1975; China and Gorny Altai, Rong et al. 2002; Zhan and Jin 2007) *Cliftonia oxoplecioides* Wright (1963) is a common species in the Hirnantian, including the stratotype, the Wangjiawan North Section in China (Chen et al. 2006). This species is most similar, externally, to the North American species *C. tubulistriata* (Savage, 1913) from the Noix, Leemon and Keel formations of the lowermost Edgewood Group in the American midcontinent (Amsden 1974). The type species *C. psittacina* is at least partly older than *C. oxoplecioides* and *C. tubulistriata.*

The Baltic thin-shelled leptostrophide brachiopods form the taxonomically most complicated group. Besides preservational problems (the valves split into two parts during crushing the samples), the taxonomy of related taxa is sometimes confusing. *Aphanomena schmalenseei,* described by Bergström (1968) from the *Dalmanitina* Beds from Västergötland in Sweden, is according to Cocks (2005) conspecific with *Eostropheodonta hirnantensis*. The East Baltic specimens nevertheless indicate that the large shells may represent a separate species, related to *Aphanomena luna* (Lindström in Angelin and Lindström, 1880) from the Boda Limestone (Cocks 2005) and *Pirgumena martnai* Rõõmusoks, 1993 from the reef complex of the Ärina Formation in northern Estonia (Rõõmusoks 2004), a hypothesis that requires the support of further data.

The restricted amount of rock material available from drill cores limits the statistical analysis of the brachiopod fauna, although densely sampled sections have revealed the dominance of *Cliftonia* and *Hindella* in the lower and of *Dalmanella testudinaria* in the middle part of the Porkuni Regional Stage (Hints et al. 2010). The same results were reached by preliminary multivariate investigations (Harper and Hints 2013) of the *Hirnantia* brachiopod fauna in the East Baltic.

In conclusion, the above taxonomic study of the *Hirnantia* brachiopod fauna shows for the first time that not just random representatives are found in the East Baltic, but rather there are the main components of the Kosovo Province with a significant diversity. Some perfectly preserved brachiopods reveal details of brachiopod interiors and comparison of related species indicates differences in stratigraphical ranges, which is important for mapping Late Ordovician faunal provinces and their mutual relationships.

Acknowledgements

The authors are indebted to Anita Saulite and Ligita Lukševiča (LDM) for help during studies at the museum in Riga. We are grateful to Raisa Pomeranceva (Geological Survey of Latvia [now Latvian Environment, Geology and Meteorology Agency], Riga, Latvia) for help in the interpretation of stratigraphy of studied core sections. Thanks are also to Jin Jisuo (Western University, London, Ontario, Canada) for comments on the Baltic brachiopods. Gennadi Baranov (GIT) is acknowledged for taking photos of the brachiopods. The reviewers Jisuo Jin, Juan Luis Benedetto (National University of Córdoba, Córdoba, Argentina), and Rémy Gourvennec (Université de Bretagne Occidentale, Brest, France) are acknowledged for useful comments and suggestions. LH was supported by the Estonian Research Council and by the Council for International Exchanges of the Estonian Academy of Sciences, who financed the research in Riga. DATH acknowledges support from the Carlsberg Foundation and Danish Council for Independent Research.

References

Amsden, T.W. 1973. The pseudodeltidium in *Triplesia* and *Placotriplesia*. *Lethaia* 6: 253–274.

Amsden, T.W. 1974. Late Ordovician and early Silurian articulate brachiopods from Oklahoma, southwestern Illinois, and eastern Missouri. *Bulletin of the Oklahoma Geological Survey* 119: 1–154.

Angelin, N.P. and Lindström, G. 1880. *Fragmenta Silurica e dono Caroli Henrici Wegelin*. 60 pp. Holmiae, Stockholm.

Bancroft, B.B. 1928. On the notational representation of the rib-system in Orthacea. *Manchester Literary and Philosophical Society, Memoirs and Proceedings* 72: 53–90.

Bancroft, B.B. 1949. *Welsh Valentian brachiopods and the* Strophomena antiqua *group of fossil brachiopods* (Lamont, A. ed.). 16 pp. Privately printed, Mexborough.

Barrande, J. 1848. Überdie Brachiopoden der silurischen Schichten von Böhmen. *Naturwissenschaftliche Abhandlungen* 2: 155–256.

Barrande, J. 1879. *Système Silurien du Centre de la Bohême. Ière Partie. Rechercher Paléontologiques, Vol. 5, Classe de Mollusques: Ordre des Brachiopodes*. 226 pp. Published by the author, Prague.

Bassett, M.G. and Cocks, L.R.M. 1974. A review of Silurian brachiopods from Gotland. *Fossils and Strata* 3: 1–56.

Benedetto, J.L. 1990. Los generos *Cliftonia* y *Paromalomena* (Brachiopoda) en el Ashgilliano de la Sierra de Villicum, Precordillera de San Juan, Argentina. *Ameghiniana* 27: 151–159.

Benedetto, J.L., Halpern, K., and Inchausti, J.C.G. 2013. High-latitude Hirnantian (Latest Ordovician) brachiopods from the Eusebio Ayala Formation of Paraguay, Paraná Basin. *Palaeontology* 56: 61–78.

Bergström, J. 1968. Upper Ordovician brachiopods from Västergötland, Sweden. *Geologica et Palaeontologica* 2: 1–35.

Bergström, S.M. and Bergström, J. 1996. The Ordovician–Silurian boundary succession in Östergötland and Västergötland. *GFF* 118: 25–42.

Billings, E. 1862. New species of fossils from different parts of the lower, middle, and upper Silurian rocks of Canada. *Palaeozoic Fossils* 1 (4): 96–185.

Boucot, A.J. 1959. A new family and genus of Silurian orthotetacid brachiopods. *Journal of Paleontology* 33: 25–28.

Boucot, A.J., Johnson, J.G., and Staton, R.D. 1964. On some atrypoid,

retzioid, and athyridoid Brachiopoda. *Journal of Paleontology* 38: 805–822.

Brenchley, P.J. and Cocks, L.R.M. 1982. Ecological associations in a regressive sequence: The latest Ordovician of the Oslo-Asker district, Norway. *Palaeontology* 25: 783–815.

Brenchley, P.J., Carden, G.A., Hints, L., Kaljo, D., Marshall, J.D., Martma, T., Meidla, T., and Nõlvak, J. 2003. High-resolution stable isotope stratigraphy of the Upper Ordovician sequence: Constraints on the timing of bioevents and environmental changes associated with mass extinction and glaciation. *Geological Society of America Bulletin* 115: 89–104.

Brenchley, P.J., Marshall, J.D., Harper, D.A.T., Buttler, C.J., and Underwood, C.J. 2006. A late Ordovician (Hirnantian) karstic surface in the submarine channel, recording glacio-eustatic sea-level changes: Meifod, central Wales. *Geological Journal* 41: 1–22.

Candela, Y. 2003. Late Ordovician brachiopods from the Bardahessiagh Formation of Pomeroy, Ireland. *Monograph of the Palaeontological Society* 156 (618): 1–95.

Caster, K.E. 1939. A Devonian fauna from Colombia. *Bulletin of American Paleontology* 24: 1–218.

Chen, X., Rong, J., Fan, J., Zhan, R., Mitchell, C.E., Harper, D.A.T., Melchin, M.J., Peng, P., Finney, S.C., and Wang, X. 2006. The Global Boundary Stratotype Section and Point (GSSP) for the base of the Hirnantian Stage (the uppermost of the Ordovician System). *Episodes* 29: 183–196.

Chen, X., Rong, J., Mitchell, C.E., Harper, D.A.T., Fan, J., Zhan, R., Zhang, Y., Li, R., and Wang, Y. 2000. Late Ordovician to earliest Silurian graptolite and brachiopod biozonation from the Yangtze region, South China, with a global correlation. *Geological Magazine* 137: 623–650.

Cocks, L.R.M. 1982. The commoner brachiopods of the latest Ordovician of the Oslo-Asker district, Norway. *Palaeontology* 25: 755–781.

Cocks, L.R.M. 2005. Strophomenate Brachiopods from the Late Ordovician Boda Limestone of Sweden: their systematics and implications for palaeogeography. *Journal of Systematic Palaeontology* 3: 243–282.

Cocks, L.R.M. 2008. A revised review of British Lower Palaeozoic brachiopods. *Monograph of the Palaeontographical Society London* 161 (629): 1–276.

Cocks, L.R.M. and Price, D. 1975. The biostratigraphy of the upper Ordovician and lower Silurian of south-west Dyfed, with comments on the *Hirnantia* fauna. *Palaeontology* 18: 703–724.

Cocks, L.R.M. and Rong, J. 2000. Order Strophomenida. *In*: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology Part H Brachiopoda Revised Volume 2: Linhuliformea, Craniiformea, and Rhynchonelliformea (part)*, 216–348. Geological Society of America and University of Kansas Press, Boulder.

Dahlquist, P., Harper, D.A.T., and Wickström, L. 2010. Late Ordovician shelly faunas from Jämtland: palaeocommunity development along the margin of the Swedish Caledonids. *Bulletin of Geosciences* 85: 505–512.

Dalman, J.W. 1828. Uppställning och Beskrifning af de i Sverige funne Terebratuliter. *Kongliga Svenska Vetenskapsakademien Handlingar for År* 1827: 85–155.

Davidson, T. 1871. A Monograph of the British Brachiopoda. Part 7. The Silurian Brachiopoda. *Monograph of the Palaeontographical Society* 4: 249–397.

Davidson, T. 1882. A Monograph of the British Fossil Brachiopoda. Part 1. Devonian and Silurian Supplements. *Monograph of the Palaeontographical Society London* 5: 1–134.

Duméril, A.M.C. 1806. *Zoologie analytique ou méthode naturelle de classification des animaux*. xxiv + 344 pp. Allais, Paris.

Ebbestad, J.O. and Högström, A.E.S. 2007. Ordovician of the Siljan District, Sweden. *In*: J.O. Ebbestad, L.M. Wickström, and A.E.S. Högström (eds.), WOGOGOB 2007, 9th meeting of the Working Group on Ordovician Geology of Baltoscandia. IGCO503 Ordovician Palaeogeography and Palaeoclimate Regional Meeting 2007. Field guide and Abstracts. *Rapporter och meddelanden* 128: 7–26.

Foerste, A.F. 1909. Fossils from the Silurian formations of Tennessee, Indiana and Kentucky. *Bulletin of the Denison University Science Laboratories* 14: 61–116.

Gailite, L.K., Stringis, T.K., Ulst, R.Ž., and Jakovleva, V.I. 1989. Stratotype sections of the regional stratigraphic units [in Russian]. *In*: A.P. Brangulis (ed.), *Stratotipičeskie i opornye razrezy venda, kembriâ i ordovika Latvii*, 79–151. Zinatne, Riga.

Hall, J. and Clarke, J.M. 1892. An introduction to the study of the genera of Palaeozoic Brachiopoda. *New York State Geological Survey, Palaeontology of New York* 8 (1): 1–367.

Hall, J. and Clarke, J.M. 1894. An introduction to the study of the genera of Palaeozoic Brachiopods. *New York State Geological Survey, Palaeontology of New York* 8 (2): 1–394.

Harper, D.A.T. 1981. The Stratigraphy and faunas of the Upper Ordovician High Mains Formation of the Girvan District. *Scottish Journal of Geology* 17 (4): 247–255.

Harper, D.A.T. 1988. Ordovician–Silurian junctions in the Girvan district S.W. Scotland. *Bulletin of British Museum (Natural History), Geology* 43: 45–52.

Harper, D.A.T. and Hints, L. 2013. The *Hirnantia* brachiopod fauna in the East Baltic: Offshore-onshore gradients in Estonia and Latvia. *In*: A. Lindskog and K. Mehlqvist (eds.), *Proceedings of the 3rd IGCP 591 Annual Meeting–Lund, Sweden, 9–19 June 2013*, 119–120. Lund University, Lund.

Harper, D.A.T., Hammarlund, E.U., and Rasmussen, C.M.Ø. 2014. End Ordovician extinctions: A coincidence of causes. *Gondwana Research* 25 (4): 1294–1307.

Havlíček, V. 1950. The Ordovician Brachiopoda from Bohemia. *Rozpravy Ústředního ŭstavu geologického* 13: 1–135.

Havlíček, V. and Mergl, M. 1982. Deep water shelly fauna in the latest Kralodvorian (upper Ordovician, Bohemia). *Véstnik Ústředního ústavu geologického* 57: 37–46.

Hiller, N. 1980. Ashgill Brachiopoda from the Glyn Ceiriog District, north Wales. *Bulletin of the British Museum (Natural History)*, *Geology* 34 (3): 109–216.

Hints, L. 1975. *Brahiopody Enteletacea ordovika Pribaltiki*. 119 pp. Punane Täht, Tallinn.

Hints, L. 2012. New Hirnantian orthide brachiopods from the type section of the Porkuni Stage (Porkuni quarry, north-eastern Estonia). *Estonian Journal of Earth Sciences* 61 (4): 227–241.

Hints, L. and Harper, D.A.T. 2003**.** Review of the Ordovician rhynchonelliformean Brachiopoda of the East Baltic: Their distribution and biofacies. *Bulletin of Geological Society of Denmark* 50: 29–43.

Hints, L. and Meidla, T. 1997. Porkuni Stage. *In*: A. Raukas and A. Teedumäe (eds.), *Geology and Mineral Resources of Estonia*: 85–88. Estonian Academy Publishers, Tallinn.

Hints, L. and Rõõmusoks, A. 1997. Ordovician articulate brachiopods. *In*: A. Raukas and A. Teedumäe (eds.), *Geology and Mineral Resources of Estonia*: 226–228. Estonian Academy Publishers, Tallinn.

Hints, L., Hints, O., Kaljo, D., Kiipli, T., Männik, P., Nõlvak, J., and Pärnaste, H. 2010. Hirnantian (latest Ordovician) bio- and chemostratigraphy of the Stirnas-18 core, western Latvia. *Estonian Journal of Earth Sciences* 59 (1): 1–24.

Hints, L. Hints, O., Nemliher, R., and Nõlvak, J. 2007. Hulterstad brachiopods and associated faunas in the Vormsi Stage (Upper Ordovician, Katian) of the Lelle core, Central Estonia. *Estonian Journal of Earth Sciences* 56 (3): 131–142.

Hints, L., Pärnaste, H., and Gailite, L.-I. 2012. *Hirnantia sagittifera* (Brachiopoda) and *Mucronaspis mucronata s.l.* (Trilobita) in the Upper Ordovician of the East Baltic: taxonomy and distribution. *Estonian Journal of Earth Sciences* 61 (2): 65–81.

Holtedahl, O. 1916. The Strophomenidae of the Kristiania region. *Skrifter utgit av videnskapsselskapet i Kristiania, I. Matematisk-Naturvidenskabelig Klasse* 12: 1–118.

Jaanusson, V. 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Balto-Scandia. *In*: M.G. Bassett (ed.), *The Ordovician System: Proceedings of a Palaeontological Association Symposium, Birmingham, September 1974*, 301–326. University of Wales Press and National Museum of Wales, Cardiff.

Jaanusson, V. 1982. The Siljan District. *In*: D.L. Bruton and S.H. Williams

(eds.), Field Excursion Guide. IV International Symposium on the Ordovician System. *Paleontological Contributions from the University of Oslo* 279: 15–42.

Jin, J. 2012. *Cincinnetina*, a new Late Ordovician dalmanellid brachiopod from the Cincinnati type area, USA: Implications for the evolution and palaeogeography of the epicontinental fauna of Laurentia. *Palaeontology* 55: 205–228.

Jin, J. and Bergström, J. 2010. True *Dalmanella* and taxonomic implications for some Late Ordovician dalmanellid brachiopods from North America. *GFF* 132: 13–24.

Jin, J. and Zhan, R. 2008. *Late Ordovician Orthide and Billingsellide Brachiopods from Anticosti Island, Eastern Canada: Diversity Change through Mass Extinction*. 152 pp. NRC Research Press, Ottawa.

Jones, O.T. 1928. *Plectambonites* and some allied genera. *Memoirs of the Geological Survey of Great Britain, Palaeontology, London* 1: 367–527.

Kaljo, D., Hints, L., Hints, O., Männik, P., Martma, T., and Nõlvak, J. 2011. Katian prelude to the Hirnantian (Late Ordovician) mass extinction: a Baltic perspective. *Geological Journal* 46: 464–477.

Kaljo, D., Hints, L., Männik, P., and Nõlvak, J. 2008. The succession of Hirnantian events based on data from Baltica: brachiopods, chitinozoans, conodonts, and carbon isotopes. *Estonian Journal of Earth Sciences* 57 (4): 197–218.

Kaljo, D., Hints, L., Martma, T., and Nõlvak, J. 2001. Carbon isotope stratigraphy in the latest Ordovician of Estonia. *Chemical Geology* 175: 49–59.

Kaljo, D., Hints, L., Martma, T., Nõlvak, J., and Oraspõld, A. 2004. Late Ordovician carbon isotope trend in Estonia, its significance in stratigraphy and environmental analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 210: 165–185.

King, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals and Magazine of Natural History* (series 1) 18: 28–42, 83–94.

Kozłowski, R. 1929. Les Brachiopodes gotlandiens de la Podolie Polonaise. *Palaeontologia Polonica* 1: 1–254.

Kuhn, O. 1949. *Lehrbuch der Paläozoologie*. 326 pp. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Lamont, A. 1935. The Drummuck Group, Girvan, a stratigraphical revision with descriptions of new fossils from the lower part of the group. *Geological Society of Glasgow Transactions* 19: 288–334.

Leone, F., Loi, A., Pillola, G.L., and Štorch, P. 2009. The Late Ordovician (Hirnantian) deposits in the Domusnovas area (SW Sardinia). *Rendiconti della Societa Paleontologica Italiana* 3 (2): 227–237.

Lespérance, P.J. and Sheehan, P.M. 1976. Brachiopods from the Hirnantian stage (Ordovician–Silurian) at Percé, Québec. *Palaeontology* 19: 719–731.

M'Coy, F. 1851. On some new Cambro-Silurian fossils. *Annals and Magazine of Natural History* (series 2) 8: 387–409.

Männil, R.M. 1966. *Istoriâ razvitiâ Baltijskogo bassejna v ordovike*. 200 pp. Valgus, Tallinn.

Männil, R., Põlma, L., and Hints, L. 1968. Stratigraphy of the Viru and Harju Series (Ordovician) of the central East Baltic area [in Russian with English summary]. *In*: A.A. Grigelis (ed.), *Stratigraphiâ nižnego paleozoâ Pribaltiki i korrelâciâ s drugimi regionami*, 81–110. Mintis, Vilnius.

Marek, L. and Havlíček, V. 1967. The articulate brachiopods of the Kosov Formation (Upper Ashgillian). *Věstník Ústředního ústavu geologického* 42: 275–284.

Meek, F.B. 1873. Section I. Descriptions of invertebrate fossils of the Silurian and Devonian systems. *Ohio Geological Survey, Palaeontology* 1: 1–243.

Mitchell, W.I. 1977. The Ordovician Brachiopoda from Pomeroy, Co. Tyrone. *Monograph of the Palaeontographical Society, London* 545 (130): 1–138.

Modzalevskaya, T.L. [Modalevskaâ, T.L.] 1985. *Brachiopody silura i rannego devona evropejskoj casti SSSR. Otrâd Athyridida*. 128 pp. Nauka, Moskva.

Moore, R.C. 1952. Brachiopoda. *In*: R.C. Moore, C.G. Lalicker, and A.G. Fischer (eds.), *Invertebrate Fossils*, 197–267. McGraw-Hill, New York.

Nestor, H. and Einasto, R. 1997. Ordovician and Silurian carbonate sedimentation basin. *In*: A. Raukas and A. Teedumäe (eds.), *Geology and Mineral Resources of Estonia*, 192–204. Estonian Academy Publishers, Tallinn.

Nõlvak, J. 2003. Distribution of Ordovician chitinozoans. *In:* A. Põldvere (eds.), Ruhnu (500) Drill Core. *Estonian Geological Sections* 5: 23–25.

Öpik, A. 1930. Brachiopoda Protremata der Estländischen Ordovizishen Kukruse-Stufe. *Universitatis Tartuensis (Dorpatensis) Acta et Commentationes (series A)* 17: 1–262.

Öpik, A. 1933. Über Plectamboniten. *Universitatis Tartuensis (Dorpatensis) Acta et Commentationes (series A)* 24 (7): 1–79.

Öpik, A. 1934. Über Klitamboniten. *Universitatis Tartuensis (Dorpatensis) Acta et Commentationes (series A)* 26 (5): 1–239.

Paškevičius, J. 1997. *The Geology of the Baltic Republics*. 387 pp. Vilnius University, Geological Survey of Lithuania, Vilnius.

Paškevičius, J. 2000. Brachiopod communities of the Lithuanian facies zone in the Baltic Ordovician Basin. *Geologija* 32: 14–35.

Podhalańska, T. 2009. The Late Ordovician Gondwana glaciation—a record of environmental changes in the depositional succession of the Baltic Depression (Northern Poland). *Prace Państwowego Institutu Geologicznego* 193: 1–96.

Pomeranceva, R. 1997. *Pārskats "Pamaturbumi", I sējums. Report "Reference cores, I. Manuscript ID 2828.* 74 pp., 37 figs. Valsts ģeoloģijas dienests (State Geological Agency), Riga.

Reed, F.R.C. 1917. The Ordovician and Silurian Brachiopoda of the Girvan District. *Transactions of the Royal Society of Edinburgh* 51: 795–998.

Riding, R. 2002. Structure and composition of organic reefs and carbonate mud mounds: concepts and categories. *Earth-Science Reviews* 58: 63–231.

Rong, J.-Y. 1979. The Hirnantian fauna of China with comments on the Ordovician–Silurian boundary [in Chinese]. *Acta Stratigraphica Sinica* 3 (1): 1–28.

Rong, J.-Y. 1984. Brachiopods of latest Ordovician in the Yichang district, Western Hubei, Central China. *In*: Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.), *Stratigraphy and Palaeontology of Systemic Boundaries in China. Ordovician–Silurian Boundary 1*, 111–176. ANHUI Science and Technology Publishing House, Hefei.

Rong, J.-Y. and Cocks, L.R.M., 1994. True *Strophomena* and a revision of the classification and evolution of strophomenoid and strophodontoid brachiopods. *Palaeontology* 37: 651–694.

Rong, J.-Y. and Harper, D.A.T. 1988. A global synthesis of latest Ordovician Hirnantian brachiopod faunas. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 79: 383–402.

Rong, J.-Y. and Harper, D.A.T. 1999. Brachiopod survival and recovery from the latest Ordovician mass extinctions in South China. *Geological Journal* 34: 321–348.

Rong, J.-Y. and Li, R.-Y. 1999. A silicified *Hirnantia* fauna (Latest Ordovician brachiopods) from Guizhou, southwest China. *Journal of Paleontology* 73: 831–849.

Rong, J.-Y., Chen, X., and Harper, D.A.T. 2002. The latest Ordovician *Hirnantia* fauna (Brachiopoda) in time and space. *Lethaia* 35: 231–249.

Rong, J.-Y., Zhan, R., and Harper, D.A.T. 1999. Late Ordovician (Caradoc–Ashgill) Brachiopod Faunas with *Foliomena* Based on Data from China. *Palaios* 14: 412–431.

Rong, J.-Y., Jin, J., Zhan, R., and Bergström, J. 2008: The earliest known *Stegerhynchus* (Rhynchonellida, Brachiopoda) from the Hirnantian strata (uppermost Ordovician) at Borenshult, Östergötland, Sweden. *GFF* 130: 21–30.

Rõõmusoks, A. 1993. Some brachiopod genera of the superfamily Strophomeninae from the Ordovician of Estonia. *Proceedings of the Academy of Sciences of the Estonian SSR. Geology* 42 (2): 48–57.

Rõõmusoks, A. 1970. *Stratigrafiâ Viruskoj i Har'ûskoj serij (Ordovik) cevernoj Estonii 1*. 346 pp. Valgus, Tartu.

Rõõmusoks, A. 2004. Ordovician strophomenoid brachiopods of northern Estonia. *Fossilia Baltica* 3: 1–72.

Rozman, H.S. 1969. Late Ordovician brachiopods of the Siberian Platform [in Russian]. *Paleontologičeskij žurnal* 3: 86–108.

Rubel, M. 1962. New species of brachiopods (Dalmanellidae) from the Llandoverian of Estonia [in Russian]. *Eesti NSV Teaduste Akadeemia Uurimused* 13: 109–160.

Rubel, M. 2011. Silurian brachiopods Dictyonellida, Strophomenida, Productida, Orthotetida, Protorthida and Orthida from Estonia. *Fossilia Baltica* 4: 1–133.

Salter, J.W. 1846. Addendum containing descriptions of new species. *In*: F. McCoy (ed.), *A Synopsis of the Silurian Fossils of Ireland, Collected from the Several Districts by Richard Griffith, F.G.S.,* 69–72. Dublin University Press, Dublin.

Savage, T.E. 1913. Alexandrian Series in Missouri and Illinois. *Geological Society of American Bulleti*n 24: 351–376.

Schmidt, F. 1908. Beitrag zur Kenntnis der ostbaltischen, vorzüglich untersilurischen, Brachiopoden der Gattungen *Plectambonites* Pand., *Leptaena* Dalm. und *Strophomena* Blainv. *Bulletin de l´Académie Impériale des Sciences de St.-Pétersbourg, sér. 6* 2 (9): 717–726.

Schmidt, H. 1965. Neue Befunde an Paläozischen Rhynchonellacea (Brachiopoda). *Senckenbergiana Lethae* 46 (1): 1–25.

Schuchert, C. 1893. Classification of the Brachiopoda. *American Geologist* 11: 141–167.

Schuchert, C. 1913. Class 2. Brachiopoda. *In*: K.L. von Zittel (translated and edited by C.R. Eastman). *Text-book of Palaeontology, Vol. 1, Part 1, 2nd*: 355–420. MacMillian and Co. Ltd., London.

Schuchert, C. and Cooper, G.A. 1931. Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea with notes on the Telotremata. *American Journal of Science* 22: 241–251.

Schuchert, C. and Cooper, G.A. 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Memoirs of the Peabody Museum of Natural History* 4 (1): 1–270.

Sheehan, P.M. 1973. Brachiopods from the Jerrestad Mudstone (Early Ashgillian, Ordovician) from a Boring in Southern Sweden. *Geologica et Palaeontologica* 7: 59–76.

Sheehan, P.M. 1977. Late Ordovician and earliest Silurian meristellid brachiopods in Scandinavia. *Journal of Paleontology* 51: 23–43.

Sheehan, P.M. 1979. Swedish Late Ordovician Marine Benthic Assemblages and their Bearing on Brachiopod Zoogeography. *In*: J. Gray and A.J. Boucot (eds.), *Historical Biogeography, Plate Tectonics, and the Changing Environment*, 61–72. Oregon State University Press, Corvallis.

Sheng, X. 1982. On the distribution and age of the *Hirnantia* fauna and *Dalmanitina* Beds in China. *Bulletin of the Institute of Geology Chinese Academy of Geological Sciences* 6: 33–56.

Smelror, M., Cocks, L.R.M., Mork, A., Neuman, B.E.E., and Nakrem, H.A. 1997. Upper Ordovician–Lower Silurian strata and biota from offshore South Norway. *Norsk Geologisk Tidsskrift* 77: 251–268.

Spjeldnæs, N. 1957. The Middle Ordovician of the Oslo region, Norway. *Norsk Geologisk Tidsskrift* 37: 1–214.

Stott, C.A. and Jin, J. 2007. The earliest known *Kinnella*, an orthide brachiopod from the Upper Ordovician of Manitoulin Island, Ontario, Canada. *Acta Palaeontologica Polonica* 52: 535–546.

Temple, J.T. 1965. Upper Ordovician brachiopods from Poland and Britain. *Acta Palaeontologica Polonica* 10: 379–450.

Ulst, R.Z. 1992. Ordovician and Silurian in deep borings on the shelf of the Baltic sea [in Russian]. *In*: V.S. Sorokin (ed.), *Paleonontologiâ i stratigrafiâ fanerozâ Latvii i Baltijskogo morâ*, 139–144. Zinatne, Riga.

Ulst, R.Z., Gailite, L.K., and Jakovleva, V.I. 1982. *Ordovik Latvii*. 294 pp. Zinatne, Riga.

Waagen, W. 1883. Salt-Range fossils, vol. I, Part 4, *Productus* Limestone fossils, Brachiopoda. *Memoirs of the geological Survey of India, Palaeontologia Indica*, *series 13* 2: 391–546.

Waagen, W. 1884. Salt Range fossils. Vol. I, Part 4. *Productus* Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica, series 139* 3–4: 547–728.

Wahlenberg, G. 1821. Petrifacta Telluris svecanae examinata. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 8: 1–116, 293–297.

Williams, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery District. *Quarterly Journal of Geological Society, London* 107: 85–136.

Williams, A. 1965. Suborder Strophomenidina. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda*, 362–412. The Geological Society of America and the University of Kansas Press, New York.

Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E., and Popov, L.E. 1996. A supra-ordinal classification of the Brachiopods. *Philosophical Transactions of the Royal Society of London B* 351: 1171–1193.

Wright, A.D. 1963. The fauna of the Portrane Limestone, I. *Bulletin of the British Museum (Natural History), Geology* 8 (5): 223–254.

Wright, A.D. 1968. A westward extension of the upper Ashgillian *Hirnantia* fauna. *Lethaia* 1: 352–367.

Wright, A.D. 1971. Taxonomic significance of the pseudodeltidium in triplesiacean brachiopods. *Palaeontology* 14: 342–356.

Wright, A.D. 1993. Subdivision of the Lower Palaeozoic articulate brachiopod family Triplesiidae. *Palaeontology* 36: 481–493.

Wright, A.D. 2000. Triplesiidina. *In*: R.L. Kaesler (ed.) *Treatise on Invertebrate Paleontology Part H Brachiopoda Revised. Volume 3: Linguliformea, Craniformea, and Rhynchonelliformea (Part)*, 681–689. The Geological Society of America and the University of Kansas, Boulder.

Wright, A.D. and Jaanusson, V. 1993. New genera of Upper Ordovician triplesiid brachiopods from Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 115 (2): 93–108.

Zhan, R. and Jin, J. 2007. *Ordovician–Early Silurian (Llandovery) Stratigraphy and Palaeontology of the Upper Yangtze Platform, South China*. 169 pp. Science Press, Beijing.

Zhan, R., Liu, J.-B., Percival, I.G, Jin, J., and Li, G.-P. 2010. Biodiversification of Late Ordovician *Hirnantia* fauna on the Upper Yangtze Platform, South China. *Science China Earth Sciences* 53 (12): 1800–1810.