Early Silurian brachiopods (Rhynchonellata) from the Sælabonn Formation of the Ringerike district, Norway

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Thomsen, E., Jin, J. & Harper, D.A.T. 2006–12–11: Early Silurian brachiopods (Rhynchonellata) from the Sælabonn Formation of the Ringerike district, Norway. *Bulletin of the Geological Society of Denmark*, Vol. 53, pp. 111–126. © 2006 by Geological Society of Denmark. ISSN 0011–6297. (www.2dgf.dk/publikationer/bulletin).

A revision of Kiær's index fossils of "Etage" 6 in the Ringerike district of Norway reveals the presence of four species: *Rostricellula wadti* sp. nov., *Platytrochalos ringerikensis* sp. nov., *Platytrochalos rabbei* sp. nov., and *Zygospiraella duboisi*. *Rostricellula* is a common Ordovician rhynchonellide brachiopod and is known to occur in the Lower Silurian as a holdover taxon in only a few localities worldwide. Previously, *Platytrochalos* was known only from the Lower Silurian (Llandoverian) rocks of Anticosti Island, eastern Canada. The occurrence of this rare genus in the Ringerike district provides additional information for the early evolution and palaeogeography of the taxonomically enigmatic family Leptocoeliidae. *Zygospiraella* is regarded as an index genus for the Rhuddanian, and the presence of *Z. duboisi* provides a useful biostratigraphic control on the age of the Sælabonn Formation.

Key words: Rhynchonellate brachiopods, Early Silurian, biostratigraphy, taxonomy, Norway.

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Despite their potential importance for the study of biotic recovery immediately after the Late Ordovician mass extinction event, Rhuddanian (earliest Silurian) brachiopod faunas are generally poorly known compared to the large amount of data on the pre-extinction Ashgill, or post-extinction Aeronian and Telychian brachiopods worldwide. Early Llandovery brachiopods from Wales (Temple 1970, 1987) are preserved mostly as moulds, making them difficult to compare with the better preserved shelly material of North America, Siberia, Kazakhstan, and northern Urals (for a summary see Kovalevskii *et al.* 1991; Beznosova 1994). In North America, most Rhuddanian brachiopods remain to be studied systematically, except for those of the American mid-continent (e.g. Amsden 1974) and the well-known *Virgiana* fauna (Jin *et al*. 1993, 1996). Some of the well-preserved Rhuddanian brachiopod faunas from Anticosti Island (eastern Canada), Manitoulin Island (Ontario, Canada), and the Illinois Basin (USA) are dominated by dalmanellid orthides, plectambonitoid strophomenides, and smooth athyridides, which are notoriously time-consuming for taxonomic examination.

Rhuddanian brachiopod faunas usually contain a mixture of holdover taxa from the Late Ordovician and newly evolved forms typical of the Early Silurian. Genera such as *Mendacella*, *Eoplectodonta*, *Leptaena*, *Eospirigerina*, and *Cryptothyrella* are probably the most common brachiopods that survived the Late Ordovician mass extinction event to become the common brachiopods during the earliest Silurian. Some newly evolved forms (e.g. *Viridita* and *Virgiana*) may be widespread across several tectonic plates during the Rhuddanian, whereas others are highly endemic taxa, among which is *Platytrochalos* dealt with in this study, a genus known previously only from Anticosti Island.

During a Cand. scient. study (University of Copenhagen), Thomsen (1981) described 31 brachiopod species from Rhuddanian and Aeronian strata of the Ringerike district, including the index species of Kiær (1908), i.e. *Rostricellula* n. sp. *a*, *Rostricellula* n. sp. *b*, Rhynchonellida n. gen. *a* n. sp. *a,* and *Zygospiraella duboisi* (Thomsen 1982). These species have been regarded to have important regional biostratigraphic utility because of their distinct morphological characteristics and stratigraphic ranges. Their taxonomic identities, however, have not been examined in detail, which has hampered the study of their biostratigraphical and palaeobiogeographical significance. A comparison of these Norwegian brachiopods with the Rhuddanian and Aeronian brachiopods of North America indicates the presence of *Platytrochalos* in the Ringerike district. The Rhuddanian index fossil, *Zygospiraella*, was widespread across several tectonic plates and terranes (Copper 2002). The present study, therefore, aims to clarify the taxonomic positions of some key brachiopod taxa from the Ringerike district and compare them with Rhuddanian-Aeronian brachiopods of other regions, particularly those well-preserved forms from Anticosti Island.

Materials and methods

The brachiopod specimens from the Ringerike district of Norway were collected either directly from outcrops or subsequently isolated from relatively large bulk samples by the first author. Most of the shells, however, come from the bulky limestone samples, which were treated by heating-and-quenching to obtain free specimens. Type specimens from the Norwegian material were deposited at the Natural History Museum of Oslo, Department of Geology (PMO).

Specimens of *Platytrochalos* from Anticosti Island, eastern Canada, were collected by Paul Copper of Laurentian University, Canada (sample numbers prefixed with the letter C or A), with subsequent additions collected by Jisuo Jin. The type specimens of various species of *Platytrochalos* described by Jin (1989) were deposited in the Type Collections of Invertebrate and Plant Fossils, Geological Survey of Canada (GSC), Ottawa. Specimens illustrated in this paper and numerous topotype specimens are currently stored at the Department of Earth Sciences, University of Western Ontario (W). Detailed locality data for the Anticosti Island collections are available from Jin.

Serial sections of brachiopod specimens were prepared separately and independently in Canada and Norway by the co-authors. A parallel grinder was used to grind the shells and acetate peels were taken at 0.05–0.1 mm intervals. For the Anticosti Island material, the peel sections were photographed digitally on a stereomicroscope with a transmitted light base. The digital images then are traced digitally using Corel Photopaint to produce the line drawings of serial sections. The serial acetate peel sections made it possible to depict detailed shell structures. For the Norwegian material, the technique for making serial sections and wax models essentially follows that of St. Joseph (1938). The peels were traced directly using a camera lucida to produce the solid outline drawings of shell structures. The serial drawings were used further to construct wax models for two of the serially sectioned shells, with an emphasis on their internal structures. Finally, durable silicon casts were made from the wax models and plaster of Paris models from these (illustrated in this paper).

Geological and stratigraphical settings

The Ringerike district

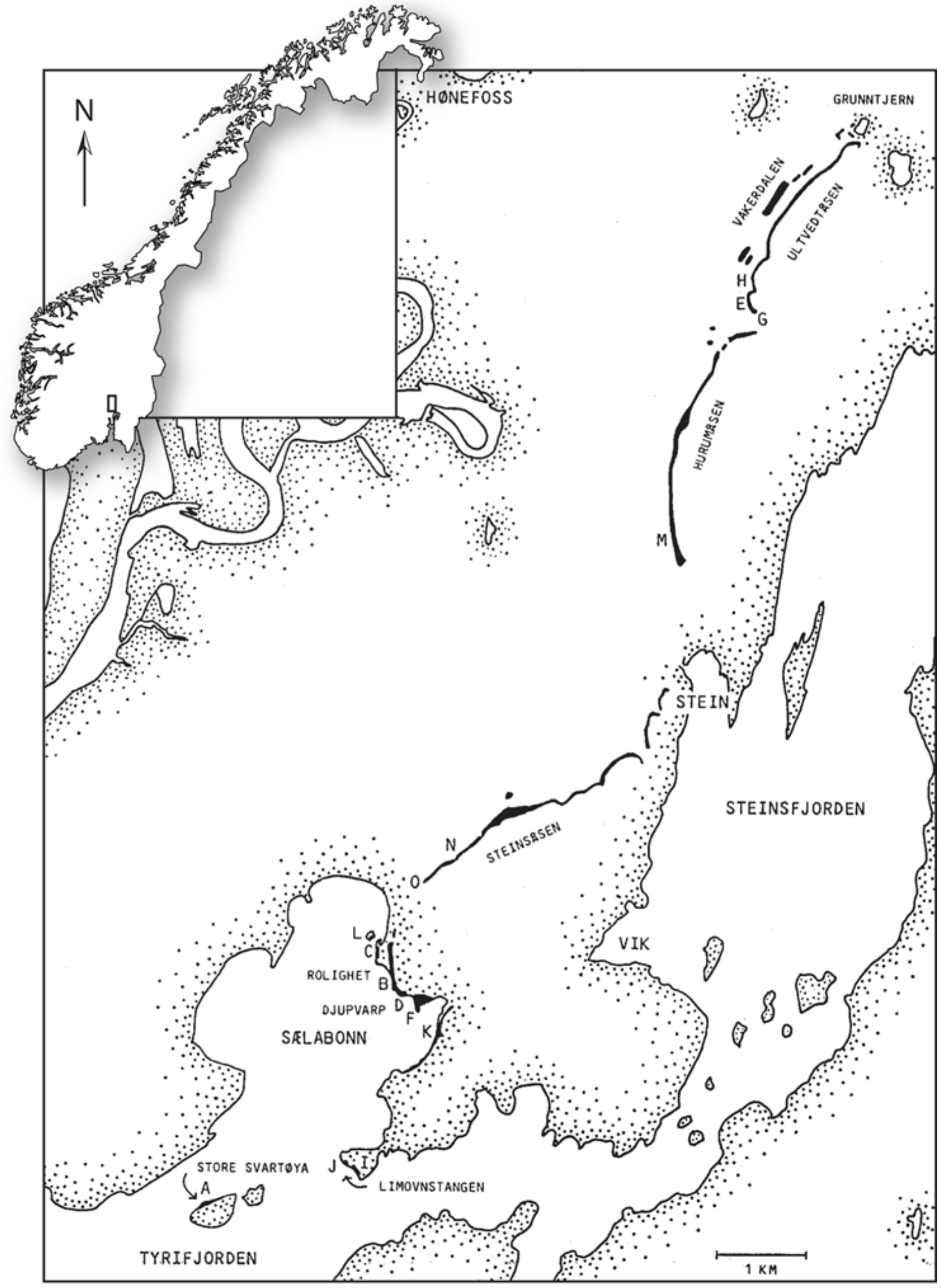
In the Ringerike district about 40 km northwest of Oslo, the lowermost Silurian (largely Rhuddanian) strata of the Sælabonn Formation are exposed in the northeast-southwest belt, from Lake Grunntjern to the island Store Svartøya (Fig. 1). Kiær (1908) was the first to describe the Silurian fauna of the Ringerike district, although the general geology had been investigated by such pioneer geologists as Murchison (1845, 1846, 1847), Kjerulf (1855, 1862, 1879), and Kjerulf and Dahll (1857). Kiær (1908) initially divided the Oslo region into smaller districts based on their differences in facies, with Ringerike being the type district for his "western facies." The well-known "Etage" divisions, introduced by Kjerulf (in Kjerulf & Dahll 1857), were revised and developed by Kiær to form the local Silurian stratigraphical framework, which was used until the early 1980s.

Kiær (1908) designated "Zones" within each "Etage" based on index fossils (mostly brachiopods) and/or lithology. The Sælabonn Formation corresponds more or less to Kiær's "Etage" 6, which is divided into three Zones, a, b and c:

6c: The Zone with *Rhynchonella 10-plicata*, Sow.
6b: The Zone with *Rhynchonella Weaveri*, Salt.
6a: The Zone with *Leptocoelia hemisphaerica*, Sow.

For each stratigraphic zone, Kiær provided a faunal list, without any systematic descriptions of the brachiopods. From his collection stored at the Natural History Museum of Oslo, Department of Geology, however, it has been possible to identify most of

Fig. 1. Locality map of the Ringerike district, Norway; the investigated exposures are marked in black. The capital letters indicate the location of the different sections, see Fig. 2.



Kiær's taxa (Thomsen 1981, 1982; Thomsen & Baarli 1982).

More recent studies of the geology and biostratigraphy of the Sælabonn Formation have been published by Thomsen (1981, 1982) and Thomsen & Baarli (1982). In the study area, the formation is about 110 m thick, underlain by the Upper Ordovician Langøyene Formation and overlain by the Rytteråker Formation (upper Aeronian–lower Telychian). The Sælabonn Formation consists of interbedded marine calcareous sandstone, calcareous siltstone, shale, and microsparite to biosparite limestones (Fig. 2). On the basis of sedimentological and faunal data, these strata were interpreted to have been deposited in a shallow-water, storm-influenced shelf environment (Thomsen 1981, 1982). The formation is divided, from base to top, into the Store Svartøya, the Djupvarp and the Steinsåsen members, ranging from the Rhuddanian to mid-Aeronian in age (Thomsen 1981, 1982).

From the Sælabonn Formation in Ringerike, Thomsen (1981) described 31 species of brachiopods and recognized two brachiopod assemblages. Brachiopod biostratigraphy, the occurrence of other faunas and the depositional environments of the Sælabonn For-

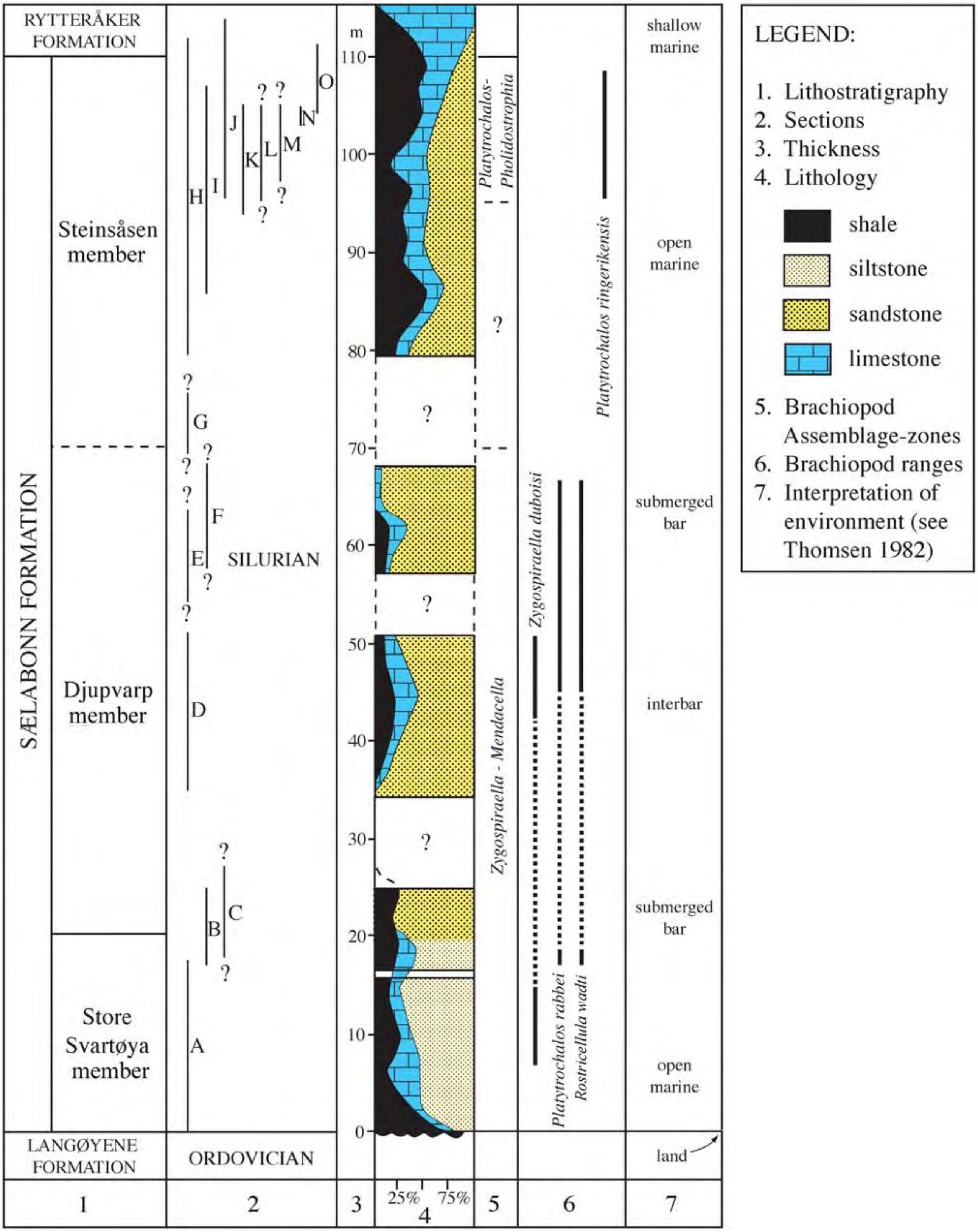
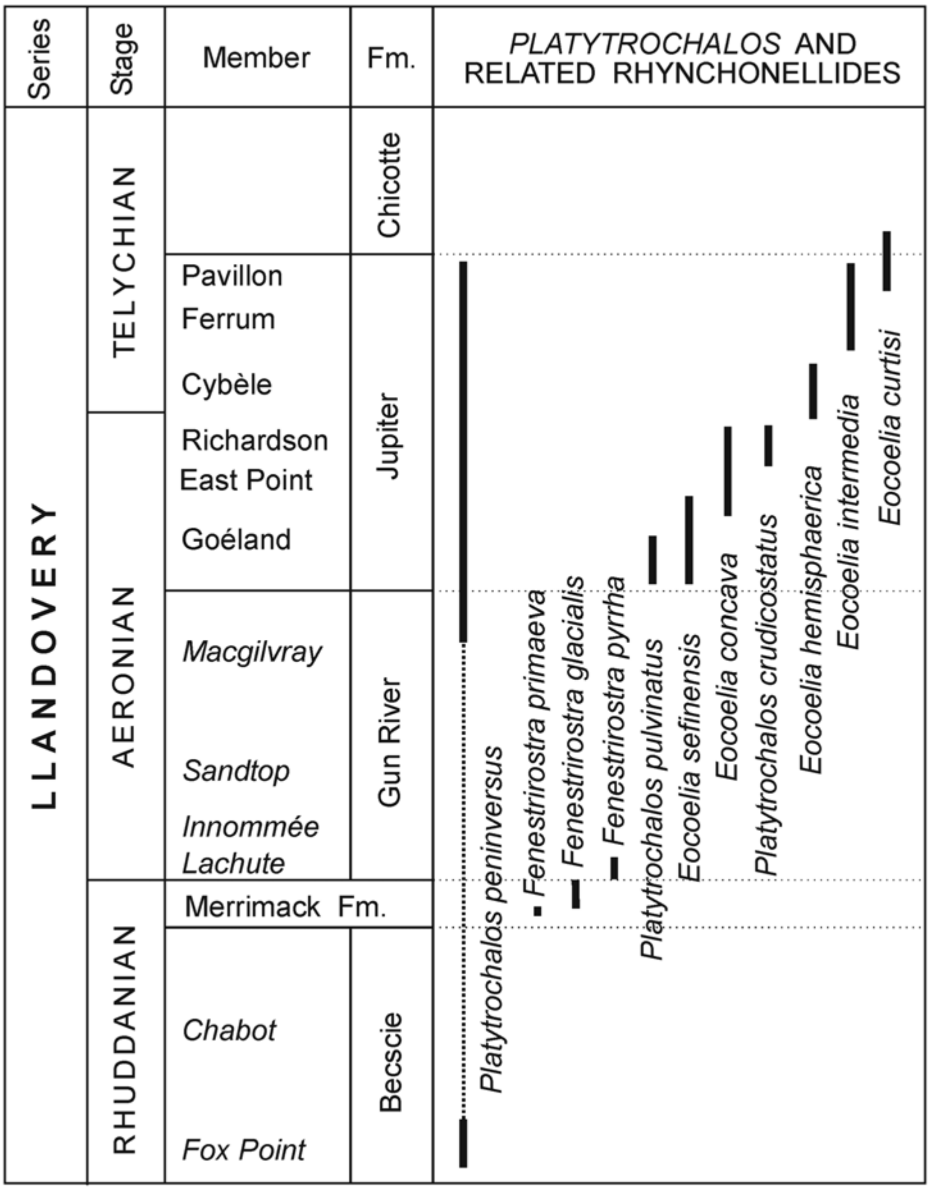


Fig. 2. Stratigraphy of the Sælabonn Formation, Ringerike district, Norway, showing litho- and biostratigraphy, ranges of brachiopods and interpretation of environments.

Fig. 3. Stratigraphic ranges of *Platytrochlos* and related brachiopods in the Lower Silurian succession of Anticosti Island, eastern Canada. Informal members are italicized.



mation and its members were discussed in detail by Thomsen (1982). Thomsen and Baarli (1982) compared the brachiopod biostratigraphy of the Sælabonn Formation of Ringerike and the correlative Solvik Formation in the Asker and Oslo districts. The focus of the present study is a systematic revision of the brachiopod index species of the Sælabonn Formation of Ringerike.

Anticosti Island

The leptocoeliid brachiopod, *Platytrochalos* Jin, 1989, was first described from the Rhuddanian–middle Telychian strata of Anticosti Island, eastern Canada (Fig. 3). Before the present study, the genus had not been recognized in other regions and thus has been regarded as an endemic taxon to the Anticosti Basin. On Anticosti Island, the Upper Ordovician to Lower Silurian succession was largely continuous, dominated by carbonate strata, with several stages of reef buildups (Copper 2001).

The Rhuddanian strata of the Becscie Formation are divided informally into a lower Fox Point, and upper Chabot members (Long & Copper 1994). The oldest representative of *Platytrochalos*, *P. peinversus*, occurs as a rare taxon in the Fox Point member, in micritic mudstone partings in the predominantly wackestone/packstone/grainstone facies accumulated on a relatively shallow-water carbonate shelf. Holdover taxa from the Late Ordovician, such as

Eospirigerina, *Leptaena*, *Mendacella*, *Cryptothyrella*–like smooth athyridids, and *Viridita lenticularis* (related to *Brevilamnulella*) form sporadic, virtually monospecific shell beds. *Platytrochalos* is absent in the overlying Chabot member, which consists of biogenic grainstones and intraformational conglomerates, with common coral-stromatoporoid biostromes and *Virgiana* shelly packstones.

The succeeding Merrimack Formation is characterized by recessive-weathering, micritic mudstones and interbeds of shelly packstones of outer shelf origin (Copper & Long 1989). *Platytrochalos* and *Rostricellula* are absent, but the brachiopod fauna is dominated by unusually large rhynchonellids (*Fenestrirostra glacialis* and *Rhynchotrema fringilla*), with locally common *Mendacella*, *Leptaena*, *Coolinia*, *Virgiana*, and *Stricklandia*.

The Gun River Formation was divided by Long and Copper (1994) into four informal members (Fig. 3). The formation consists largely of micritic mudstone of relatively deep shelf origin. It reverses to a shallowing-upward sequence near the top, within the Macgilvray member. After a hiatus in the upper Becscie, Merrimack, and much of Gun River formations, *Platytrochalos* re-appears in the top part of the Gun River Formation, coeval with the invasion of a diverse brachiopod fauna (e.g. *Katastrophomena*, *Pentamerus*, *Stricklandia*, and *Kulumbella*).

The Jupiter Formation was divided into six members by Copper & Long (1990) and consists of two large-scale shallowing-upward cycles from micritic mudstone to crinoid-shelly packstone/grainstones or coral-stromatoporoid reefs. Pentamerids and atrypids are particularly abundant, forming numerous shell beds in micritic mudstone-dominated facies. Relatively small-shells of rhynchonellids and leptocoelids (e.g. *Stegerhynchus*, *Platytrochalos*, *Ancillotoechia*, and *Eocoelia*) may also be abundant in soft-weathering, calcareous mudstones in the Goéland, Richardson, and Cybèle members.

Comparison between the brachiopod faunas of Ringerike and Anticosti Island

In comparison to the Early Silurian brachiopods of Norway, the generally cosmopolitan *Rostricellula* and *Zygospiraella* are absent from the Lower Silurian strata of Anticosti Island, although *Rostricellula* is locally common in the Upper Ordovician (Rawtheyan–Hirnantian) of Anticosti Island (Jin 1989) and *Zygospiraella* is known from Rhuddanian rocks of the Michigan Basin of North America (Copper 1982). This makes it difficult to explain why the largely endemic taxon, *Platytrochalos*, occurs on Anticosti Island of Laurentia and in the Ringerike district of Baltica.

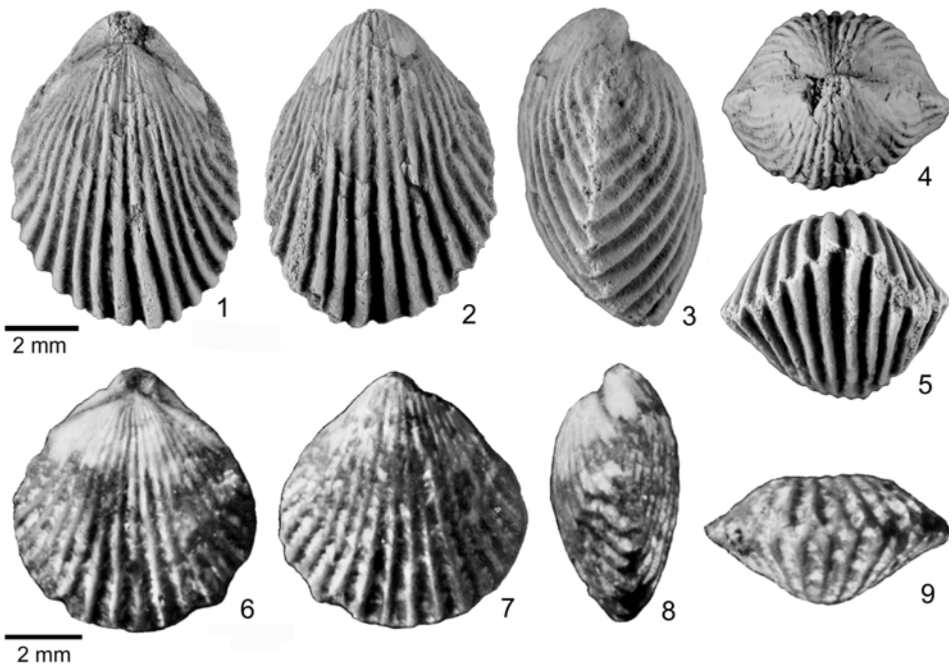
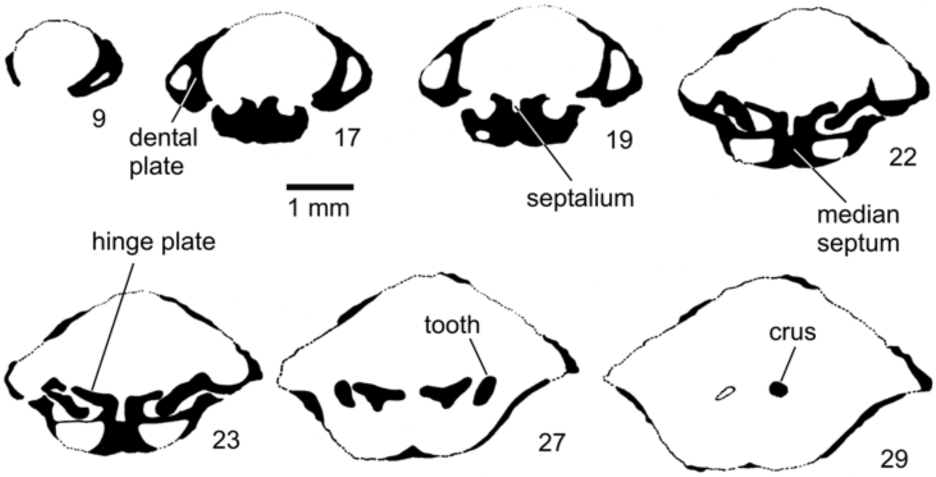
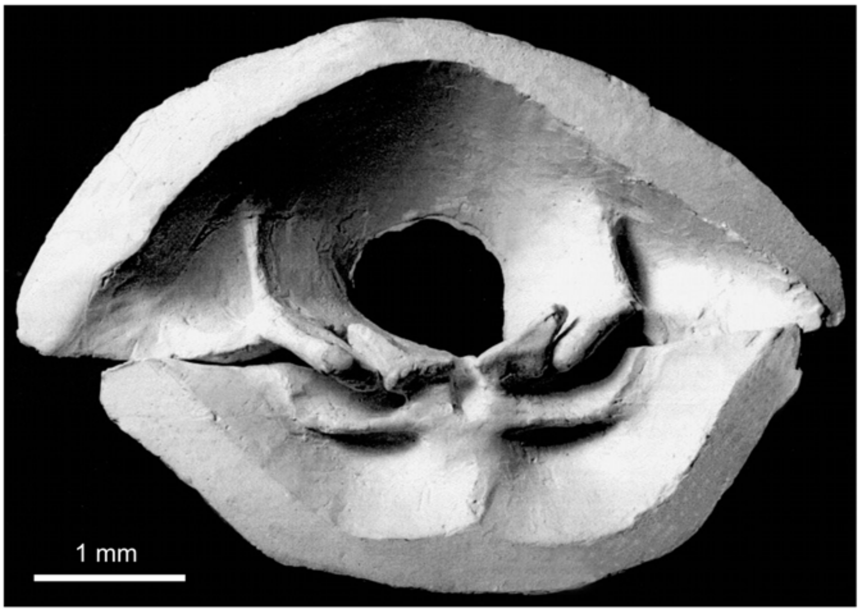


Fig. 4. *Rostricellula wadti* sp. nov. from the Djupvarp member, Sælabonn Formation (Ringerike district, Norway, locality Djupvarp-Borgen Isthmus, section F, upper Rhuddanian). 1–5, PMO 208.787, holotype, dorsal, ventral, lateral, posterior, and anterior views of elongate form. 6–9, PMO 106.619, paratype, dorsal, ventral, lateral, and anterior views of serially-sectioned shell.

Fig. 5. Selected serial sections and plaster of Paris model of *Rostricellula wadti* sp. nov. reconstructed from the serial sections, PMO 106.619, Djupvarp member, Sælabonn Formation (Ringerike district, Norway, locality Djupvarp-Borgen Isthmus, section F, upper Rhuddanian). Numbers refer to sections.





Systematic Palaeontology

Order *Rhynchonellida* Kuhn, 1949

Superfamily *Rhynchotrematoidea* Schuchert, 1913

Family *Trigonirhynchiidae* McLaren, 1965

Genus *Rostricellula* Ulrich & Cooper, 1942

Rostricellula wadti sp. nov.
Figures 4, 5

1908 *Rhynchonella Weaveri* Salter; Kiær, pp. 40–46, 590 (*pars*)
1960 *Camarotoechia weaveri*; Henningsmoen, pl. 7
1982 N. gen. *a* n. sp. *a*; Thomsen, p. 7, fig. 3
1982 Rhynchonellida sp. *a*; Thomsen & Baarli, p. 66.

Derivation of name. After the late Dr. J. Wadt, Copenhagen.

Types. Holotype, PMO 208.787 (Fig. 4.1–4.5), Paratype, PMO 106.619, partly exfoliated, with shell material preserved posteriorly (Fig. 4.6–4.9), serially sectioned after it was photographed (Fig. 5). *Zygospiraella duboisi-Mendacella mullockiensis* Assemblage Zone, upper Rhuddanian, Djupvarp member, Sælabonn Formation, Djupvarp-Borgen Isthmus, Ringerike, Norway.

Other material. Several internal moulds (some with shell material preserved posteriorly) and numerous external moulds of separated ventral and dorsal valves. Same locality and horizon as for the types.

Diagnosis. Small, suboval, biconvex shells of *Rostri-*

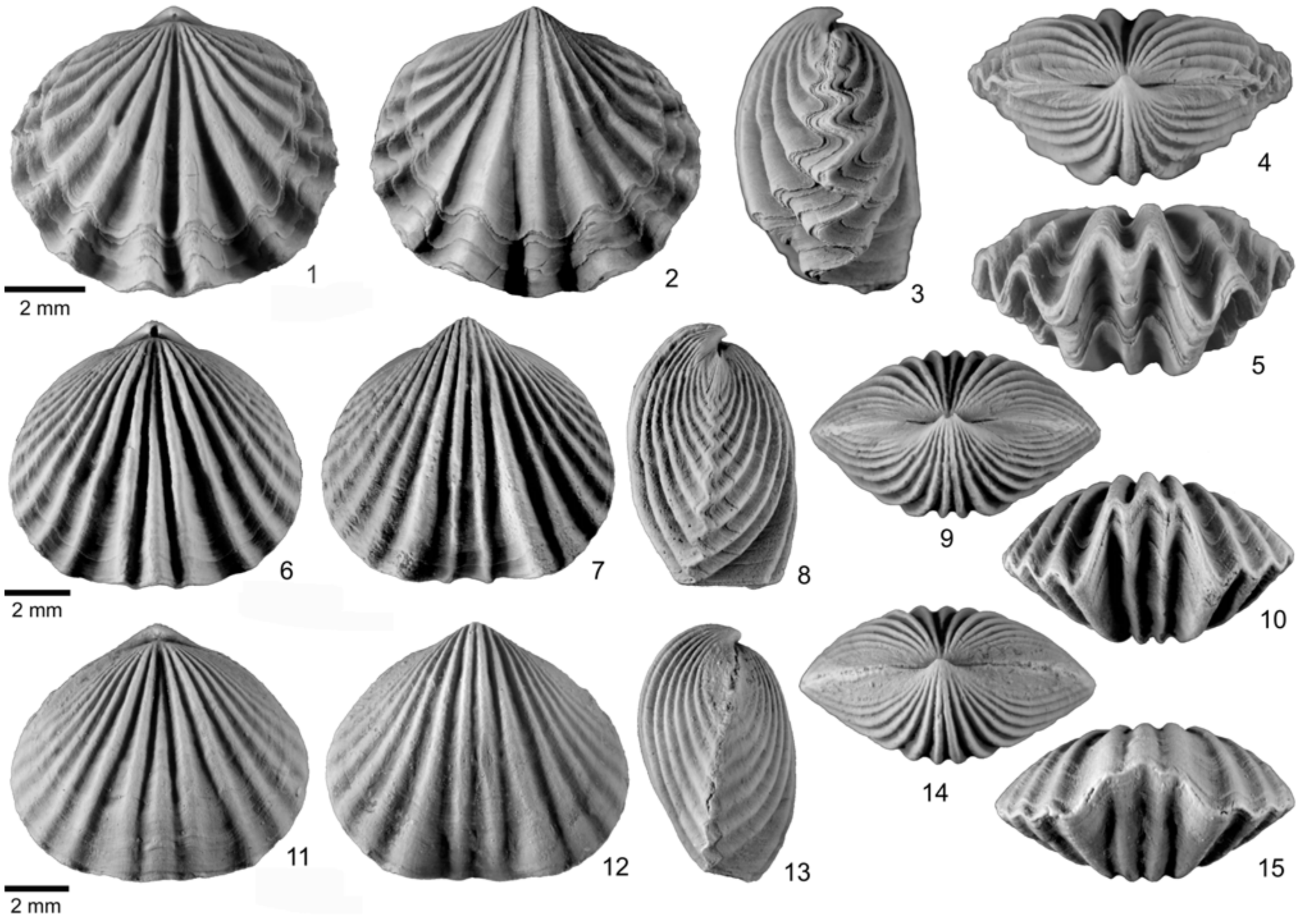


Fig. 6. *Platytrochalos* from the Lower Silurian of Anticosti Island, eastern Canada. 1–5, *Platytrochalos crudicostatus* Jin, 1989, W2824, dorsal, ventral, lateral, posterior, and anterior views, lower Cybèle Member, Jupiter Formation (locality A59, lower Telychian). 6–15, *Platytrochalos peninversus* Jin, 1989, W2825 and W2826, dorsal, ventral, lateral, posterior, and anterior views of two shells, from the top Gun River Formation (locality C633, middle Aeronian) and the lower Becscie Formation (locality A86, lower Rhuddanian), respectively.

cellula with thickened notothyrial platform, swollen dorsal median septum and deep, narrow septalium.

Description. Shell small, rarely exceeding 10 mm in length, suboval in outline, slightly longer than wide, biconvex. Hinge line short, curved, with rounded, sloping cardinal extremities. Ventral umbo moderately convex, relatively low, with apical angle about 108° (in specimen PMO 106.619). Delthyrium open. Dorsal umbo weakly convex, with small, suberect beak. Small, shallow medial groove present in umbonal area of dorsal valve, inverting to fold in anterior half of valve. Ventral sulcus well developed anteriorly in relatively large forms, occupying approximately 36% of shell width at anterior margin (Fig. 4.5). Costae simple, weakly developed posteriorly, subangular anteriorly, averaging 20 per valve, with three in sulcus and four on fold. Growth lines best developed near anterior margin.

Teeth small, delicate, cyrtomatodont; dental plates short, relatively thick, separating umbonal interior into large delthyrial cavity and small lateral cavities (Fig. 5). Ventral muscle field poorly preserved. Sockets narrow, diverging antero-laterally. Notothyrial platform thickened, anteriorly forming floor of septalium and supported by very thick median septum. Cardinal process absent. Crural plates subparallel to each other, forming narrow septalium. Hinge plates strongly diverging in lateral direction, nearly parallel to hinge line. Crura short, rod-like.

Remarks. For a rhynchonellide shell with a rather simple external morphology and internal structures, *Rostricellula* contains an unusually large number of species. Among the 40 species described by Cooper (1956) and eleven by Cocks (1978), nearly all are Ordovician in age. In recent years, about six more species have been added (see list of species in Jin et al.

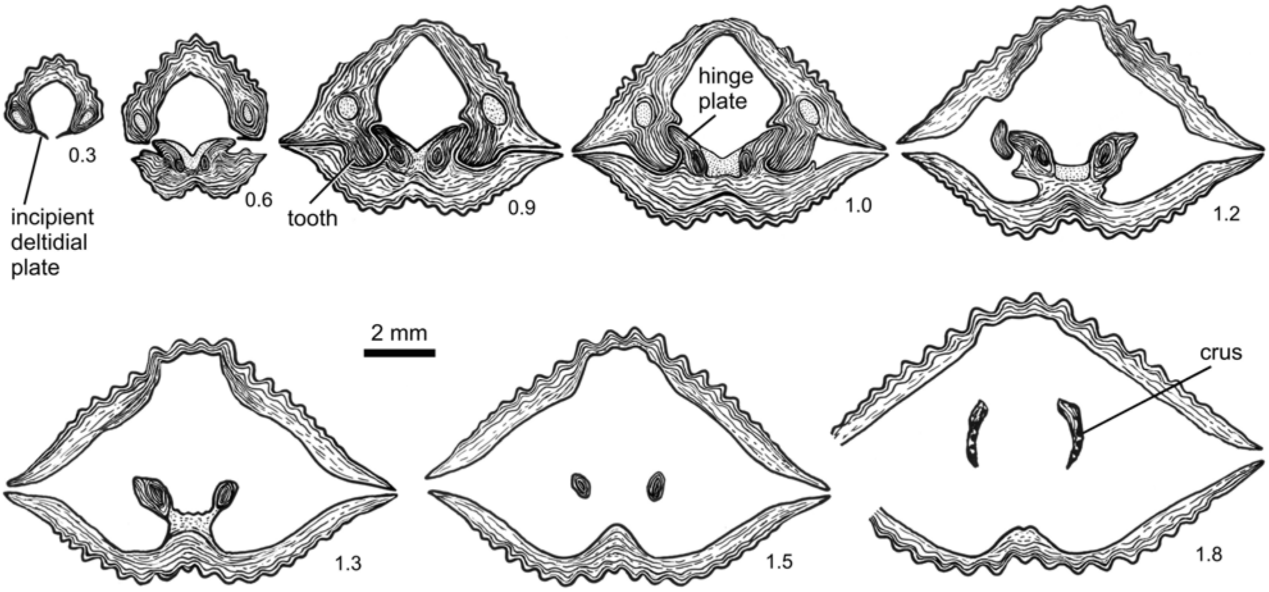


Fig. 7. Serial sections of *Platytrochalos peninversus* Jin, 1989. Paratype GSC 102.522, Goéland Member, Jupiter Formation, (Anticosti Island, eastern Canada, locality C635, middle Aeronian). Note sessile hinge plates and sockets.

1993). In addition to the new species described in this paper, only one other species, *Rostricellula subtilicostata* Jin, Caldwell, & Norford, 1993, has been identified positively as a Silurian representative of the genus.

The Ringerike specimens assigned to *Rhynchonella weaveri* Salter by Kiær (1908) are, in fact, a mixture of two species, recognized in this study as *Rostricellula wadti* sp. nov. and *Platytrochalos rabbei* sp. nov. Despite a certain degree of similarity in external morphology, *R. wadti* has a well-developed dorsal median septum and a typical rhynchonellide septalium (= cruralium), whereas *P. rabbei* has sessile hinge plates and lacks a dorsal median septum. A swollen dorsal median septum and a small septalium that is subrectangular in cross section are typical features of the latest Ordovician and Early Silurian forms of *Rostricellula*, such as *R. transversa* Cooper, 1956 from the Ellis Bay Formation (Hirnantian) of Anticosti Island (Jin 1989, 2003) and *R. subtilicostata* Jin, Caldwell & Norford, 1993 from the Ekwan River Formation (Telychian) of the Hudson Bay Lowlands, Canada (Jin *et al.* 1993).

Incertae sedis

Family *Leptocoeliidae* Boucot & Gill, 1956

Genus *Platytrochalos* Jin, 1989

Type species. *Platytrochalos crudicostatus* Jin, 1989, Richardson Member, Jupiter Formation, lower Telychian, Anticosti Island, eastern Canada.

Remarks. In the revised Treatise on Invertebrate Paleontology, Savage (2002) assigned the Leptocoeliidae to the rhynchonellide superfamily Rhynchotrematoidea. As discussed recently by Jin (2003), the systematic position of the leptocoeliids remains uncertain because of its sessile hinge plates. The two common Early Silurian genera of the family, *Platytrochalos* and *Eocoelia*, are probably closely related to each other because of their largely identical internal structures, especially in their hinge sockets and hinge plates that sit directly on the dorsal valve floor (Figs. 6, 7). *Platytrochalos* can be distinguished from *Eocoelia* by having a biconvex shell with a ventral sulcus and a dorsal fold, whereas *Eocoelia* typically has a planoconvex shell. *Anabaia* Clarke, 1893 (=*Harringtonina* Boucot, 1972), which ranges from the lower Llandovery to Prídolí and is confined to South America (Melo & Boucot 1990), is similar to *Platytrochalos* externally in having a biconvex shell, strong and simple costae, and a ventral sulcus and dorsal fold, but differs in bearing a strong, blade-like cardinal process and notably shorter crura (see Benedetto 1988). The internal structures of these early leptocoeliids are unlike any other groups of rhynchonellides but are similar to some spire-bearing atrypides and athyridides, even though no spiralia have been found in any leptocoeliids. This was the main reason for this group to be assigned to the Spiriferida by Boucot *et al.* (1965). In any case, the sessile sockets and hinge

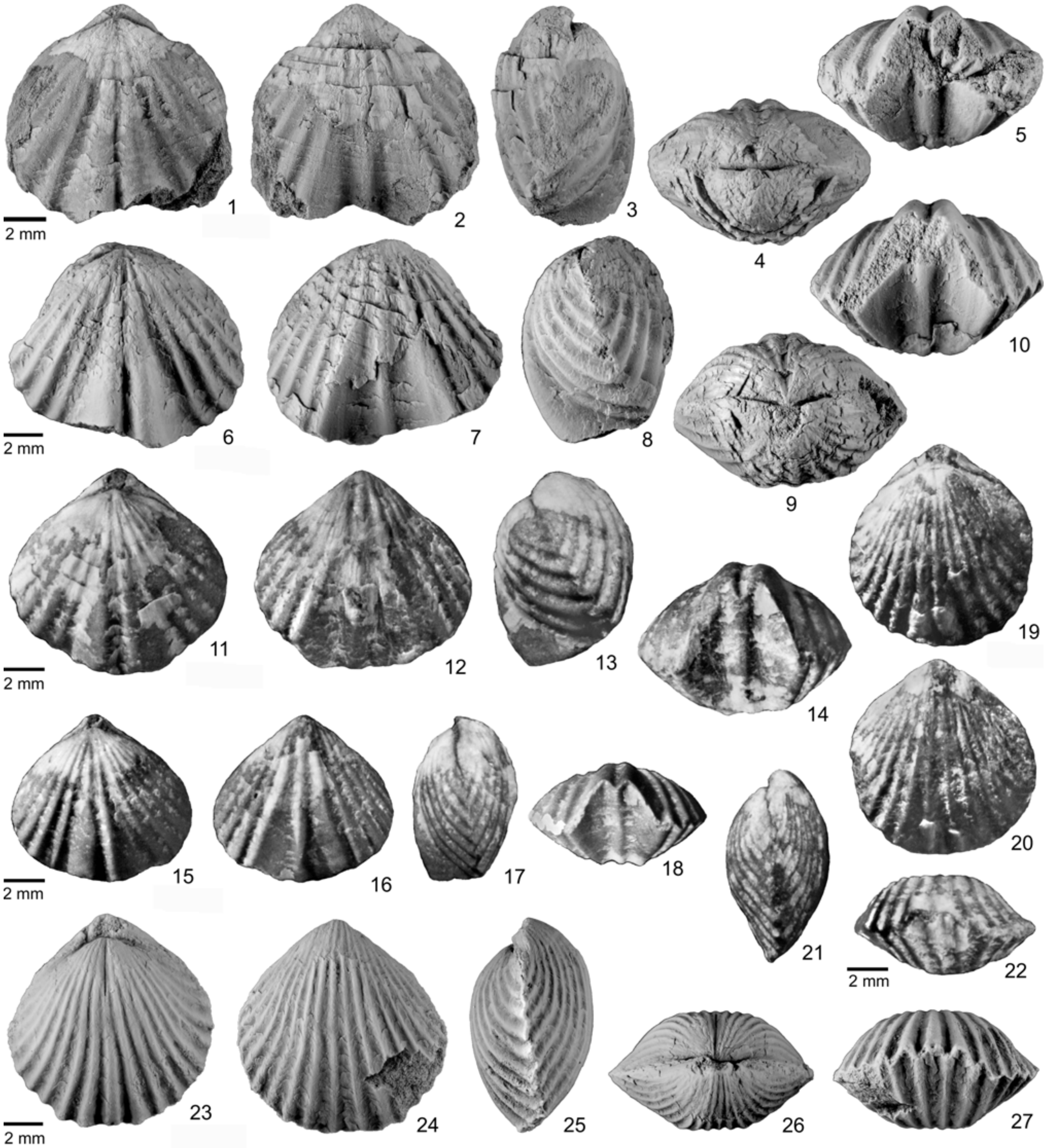


Fig. 8. *Platytrochalos* from the Lower Silurian of the Ringerike district, Norway. 1–18, *Platytrochalos ringerikensis* sp. nov. from the Steinsåsen member, Sælabonn Formation; 1–5, PMO 208.788, holotype, dorsal, ventral, lateral, posterior, and anterior views, (locality Steinsåsen, section N, lower Aeronian) 6–10, PMO 208.789, paratype, dorsal, ventral, lateral, posterior, and anterior views, (locality Steinsåsen, section N, lower Aeronian) 11–14, PMO 106.649, paratype, dorsal, ventral, lateral, and anterior views, (locality Steinsåsen, section N, lower Aeronian) 15–18, PMO 106.647, paratype, dorsal, ventral, lateral, and anterior views, (locality Steinsåsen, section N, lower Aeronian) 19–27, *Platytrochalos rabbei* sp. nov. from the Djupvarp member, Sælabonn Formation 19–22, PMO 106.618, paratype, dorsal, ventral, lateral, and anterior views of shell (subsequently serial-sectioned), (locality Djupvarp-Borgen Isthmus, section F, upper Rhuddanian); 23–27, PMO 208.790, holotype, dorsal, ventral, lateral, posterior, and anterior views of largely exfoliated shell, (locality Djupvarp-Borgen Isthmus, section F, upper Rhuddanian).

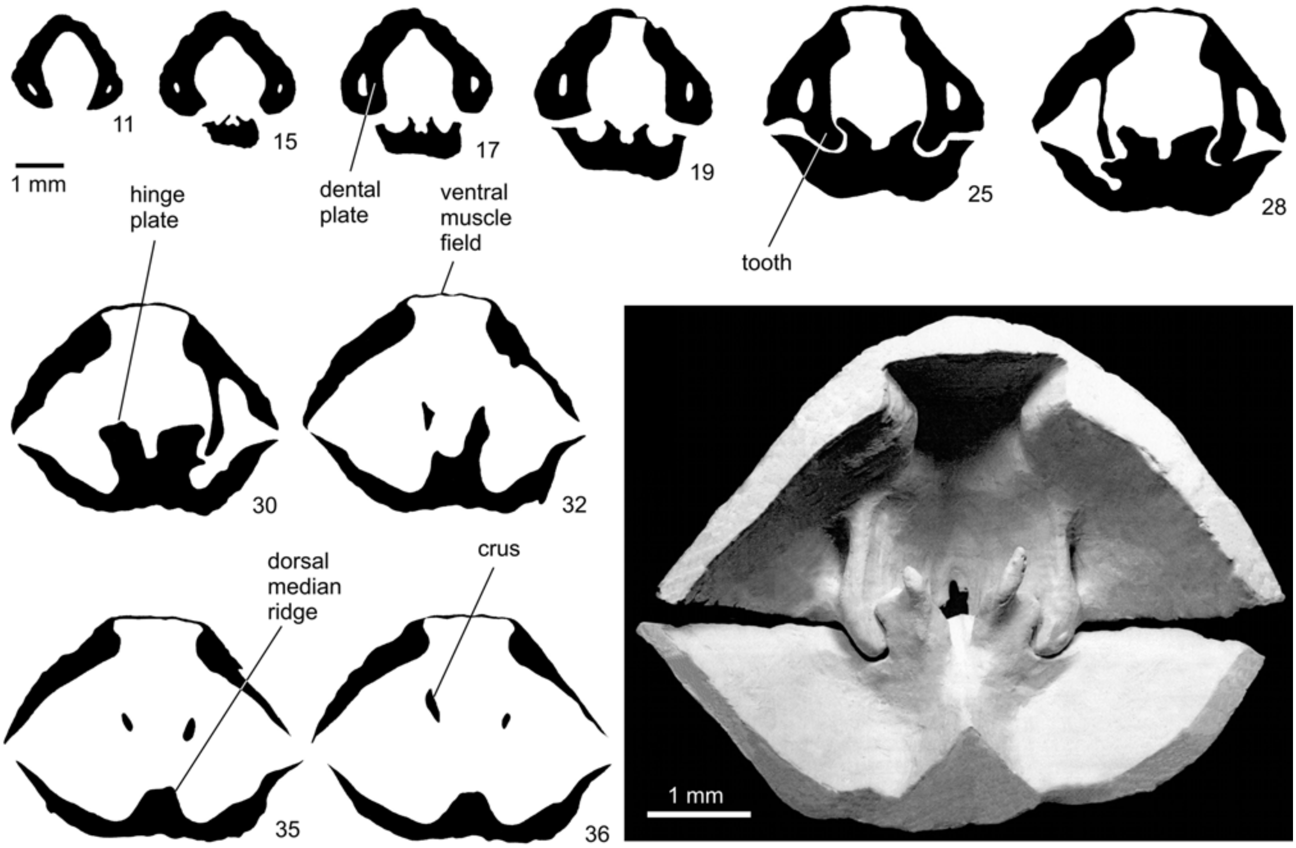


Fig. 9. Selected serial sections and plaster of Paris model of *Platytrochalos ringerikensis* sp. nov. Paratype, PMO 106.648, Steinsåsen member, Sælabonn Formation (Ringerike district, Norway, locality Steinsåsen, section N, lower Aeronian). Numbers refer to sections.

plates and the lack of a median septum-supported septalium (= cruralium) make the leptocoeliids an aberrant group of brachiopods, which are not likely to have a close affinity to the Rhynchotrematoidea.

Species assigned:

Platytrochalos crudicostatus Jin, 1989 (type species).

Platytrochalos peninversus Jin, 1989, Becscie, Gun River, and lower Jupiter formations, Rhuddanian-upper Aeronian, Anticosti Island, eastern Canada.

Platytrochalos pulvinatus Jin, 1989, Goéland Member, Jupiter Formation, upper Aeronian, Anticosti Island.

Platytrochalos ringerikensis sp. nov. (herein)

Platytrochalos rabbei sp. nov. (herein)

Platytrochalos ringerikensis sp. nov.
Figures 8.1–8.18, 9, 10

1908 *Rhynchonella 10-plicata* Sowerby; Kiær, pp. 49–52, 590, pl. 2, fig. 12.
1960 *Rhynchotreta decemplicata*; Henningsmoen, pl. 7
1982 *Rostricellula* n. sp. *b*; Thomsen, p. 9, fig. 3.
1982 *Stegerhynchus decemplicatus*; Cocks & Baarli, p. 80, fig. 1.
1982 *Rostricellula* sp. *b*; Thomsen & Baarli, p. 66, fig. 1; pl. 3, figs. 3, 4.

Derivation of name. After Ringerike, the district where the species occurs.

Types. Holotype, PMO 208.788 (Fig. 8.1–8.5); paratypes, PMO 208.789 (Fig. 8.6–8.10), PMO 106.647 (Fig. 8.15–8.18 serially sectioned after it was photographed), PMO 106.648 (serially sectioned after it was photographed; Fig. 9), 106.649 (Fig. 8.11–8.14 serially sectioned after it was photographed). *Platytrochalos-Pholidostrophia* Assemblage Zone, lower Aeronian, Steinsåsen member, Sælabonn Formation, Steinsåsen, Ringerike, Norway.

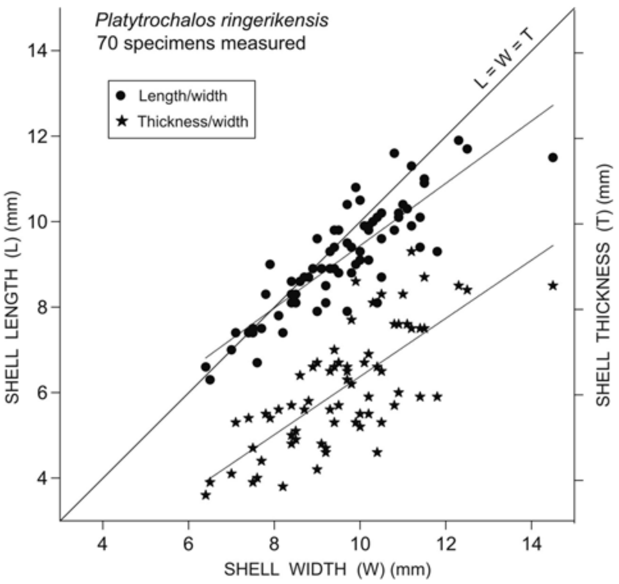


Fig. 10. Shell measurements of a population of *Platytrochalos ringerikensis* sp. nov. from the Steinsåsen member, Sælabonn Formation (Ringerike district, Norway, locality Steinsåsen, section N, lower Aeronian). Note that the shells become more transversely extended with ontogeny.

Other material. More than 100 specimens, mostly internal moulds with shell material preserved posteriorly, two slightly deformed internal moulds, numerous external moulds of separated ventral and dorsal valves, and some fragmentary material from the Steinsåsen member, Sælabonn Formation at Limovnstangen, Borgen, Evangelieholmen, Steinsåsen, Ultvedtåsen, and Grunntjern (Fig. 1).

Diagnosis. Small, suboval, biconvex shells of *Platytrochalos*, with anteriorly prominent ventral sulcus and dorsal fold. Each valve bearing 15–18 simple, subangular costae, including one in sulcus and two on fold. Dental plates well developed. Hinge plates sessile posteriorly, raised anteriorly by secondary shell thickening. Crura rod-like, directed antero-ventrally.

Description. Shell small, suboval to subpentagonal in outline, with width equal to, or slightly greater than, length (Fig. 10); average length 9.1 mm (std = 1.3 mm, max = 11.9 mm), width 9.6 mm (std = 1.5 mm, max = 14.5 mm), and thickness 6.1 mm (std = 1.4 mm, max = 9.3 mm); nearly equibiconvex or with dorsal valve slightly deeper. Hinge line short, curved, with rounded, sloping cardinal extremities. Ventral umbo moderately high, strongly convex, with small, dorsally curved beak; apical angles ranging between 101–110 degrees; delthyrium open. Dorsal umbo weakly to moderately convex, with apex and small beak buried under ventral beak. Sulcus beginning 4–5 mm from ventral apex, becoming deeper and wider anteriorly to form subtriangular tongue and occupy about one-half of shell width at anterior margin, bearing one simple, subrounded costa. Dorsal umbonal area marked by shallow and narrow medial groove, which inverts to bicostate fold at about one-fourth of shell length from dorsal apex. Costae simple, subrounded, usually 15 or 17 in ventral valve, 16 or 18 in dorsal valve; costae associated with fold and sulcus usually stronger than those on shell flanks. Concentric growth lines present, best developed near anterior margin.

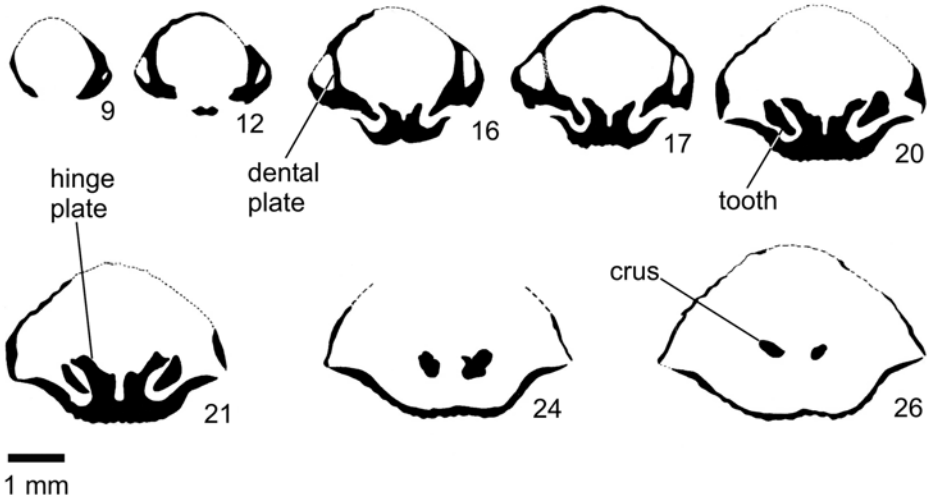
Teeth relatively large, cyrtomatodont. Dental plates well developed, subparallel to each other, relatively long and high for genus, forming small lateral cavities (Fig. 9). Ventral muscle field deeply impressed, flabellate in outline, lacking anterior bounding ridge. Notothyrial platform moderately thickened; sockets largely sessile on valve floor, bounded medially by hinge plates and anteriorly by low bounding ridge; hinge plates robust, swollen, diverging from each other more strongly in their posterior than anterior portions; septalium sessile posteriorly, raised anteriorly by secondary shell thickening; dorsal median ridge low, thick, highest in mid-length of valve; crura rod-like, antero-ventrally directed.

Remarks. *Platytrochalos ringerikensis* is similar to *P. crudicostatus* (Fig. 6) and *P. pulvinatus* from Anticosti Island in its anteriorly developed ventral sulcus with one costa and dorsal fold with two costae. The Norwegian species, however, has a larger, more strongly biconvex shell with considerably higher and longer dental plates developed. The type species of *P. crudicostatus* has very coarse costae of high amplitude on the shell flanks (Fig. 6.1–6.5; see also Jin, 1989, pl. 22, figs. 6–20), whereas *P. ringerikensis* has relatively low and rounded costae on the flanks. *Platytrochalos pulvinatus* has a prominent notothyrial pad that posteriorly resembles a cardinal process; this structure is absent in the Norwegian forms of *Platytrochalos*. In some specimens of the new species, the costa in the sulcus may be very weak in some specimens to give the sulcus a quasi-smooth appearance.

Platytrochalos rabbei sp. nov.
Figures 8.19–8.27, 11

1908 *Rhynchonella weaveri* Salter; Kiær, pp. 40–46 (*pars*), 590 (*pars*)
1960 *Camarotoechia weaveri*; Henningsmoen, pl. 7
1982 *Rostricellula* sp. *a*; Thomsen, p. 7, fig. 3.

Fig. 11. Selected serial sections of *Platytrochalos rabbei* sp. nov. Paratype, PMO 106.618, Djupvarp member, Sælabonn Formation (Ringerike district, Norway, locality Djupvarp-Borgen Isthmus, section F, upper Rhuddanian). Numbers refer to sections.



1982 *Rostricellula* sp. *a*; Thomsen & Baarli, p. 65–66, fig. 1, pl. 2, figs. 11, 12.

Derivation of name. After the late Dr. Aase Rabbe, Copenhagen.

Types. Holotype, PMO 208.790 (Fig. 8.23–8.27); paratype, PMO 106.618 (Fig. 8.19-8.22 serially sectioned after it was photographed; Fig. 11). *Zygospiraella duboisi*-*Mendacella mullockiensis* Assemblage Zone, upper Rhuddanian, Djupvarp member, Sælabonn Formation, Djupvarp-Borgen Isthmus, Ringerike, Norway.

Other material. Mostly internal moulds with shell material preserved posteriorly, and numerous external moulds of ventral and dorsal valves; *Zygospiraella duboisi*-*Mendacella mullockiensis* Assemblage Zone, Djupvarp member, Sælabonn Formation at Store Svartøya, Rolighet south, Djupvarp, Djupvarp-Borgen Isthmus, and Ultvedtåsen south.

Diagnosis. Small, biconvex shells of *Platytrochalos* with weakly developed ventral sulcus and dorsal fold. Dental plates well developed. Hinge plates completely sessile; dorsal median ridge absent or poorly defined.

Description. Shell small, suboval to subpentagonal in outline, slightly elongate to equidimensional, subequally biconvex, with dorsal valve slightly deeper; maximum width and thickness attained near midlength of shell. Hinge line relatively short, curved, with round cardinal extremities. Anterior commissure gently uniplicate to nearly rectimarginate. Ventral umbo moderately convex, with apical angles around 92 degrees (in specimen PMO 106.618). Delthyrium open. Ventral sulcus absent or very shallow when present anteriorly to occupy about one-third of shell width. Dorsal umbonal area marked by shallow and narrow medial groove, which may invert into faintly delimited fold anteriorly in some specimens. Each valve bearing up to 20 simple, subangular costae, with postero-lateral ones being generally weak. Growth lines poorly preserved.

Shell measurements (mm):

	Length	Width	Thickness
PMO 208.790 (holotype)	9.0	8.8	5.1
PMO 208.791	8.6	7.9	5.6
PMO 208.792	6.9	6.4	3.1
PMO 208.793	5.5	4.6	2.4

Teeth large and strong for shell size, medially directed cyrtomatodont. Dental plates well developed, subparallel to each other, laterally position to form small lateral cavities and large delthyrial cavity (Fig. 11). Ventral muscle field clearly delimited only posteriorly. Sockets sessile on valve floor, diverging from each other antero-laterally, bounded medially by hinge plates. Crural plates low, thick, discrete, sitting directly on valve floor. Hinge plates relatively broad, diverging from each other ventro-laterally at 85–95 degrees. Median ridge absent or poorly developed. Crura robust, rod-like, not strongly curved in ventral direction. Dorsal muscle field poorly impressed.

Remarks. Despite their small size, the shell of *Platytrochalos rabbei* are biconvex with the dorsal valve slightly deeper than the ventral valve. This implies that these are not immature shells, which would have

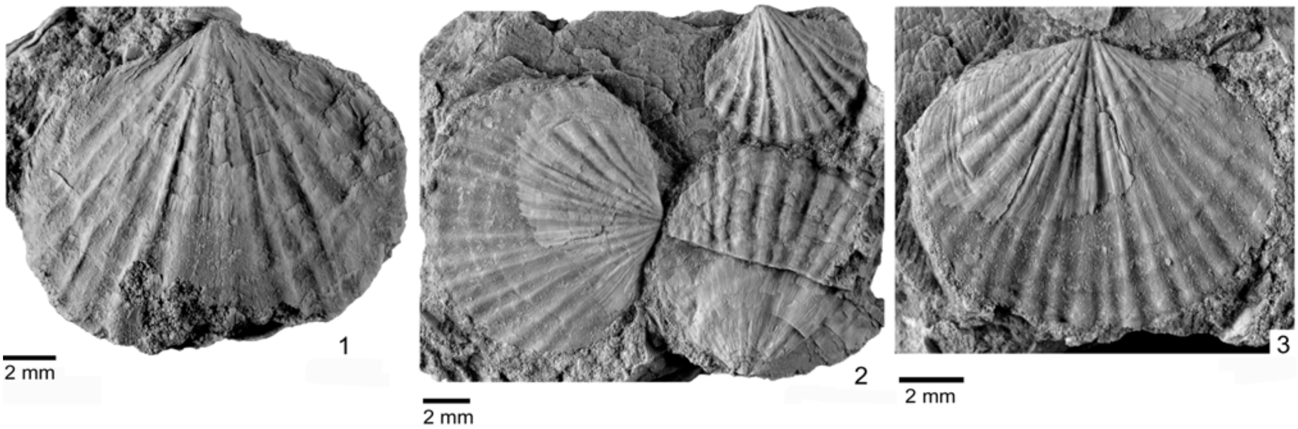


Fig. 12. *Zygospiraella duboisi* (Verneuil, 1845), Djupvarp member, Sælabonn Formation, (Ringerike district, Norway, locality Djupvarp, section D, upper Rhuddanian). 1, PMO 208.794, exterior of ventral valve partly embedded in rock matrix; 2, PMO 208.795-208.798, exterior views of one immature ventral valve and two dorsal valves embedded in rock matrix. 3, one dorsal valve from 2, reoriented and further enlarged, showing planoconvex profiles with broad sulcus.

been nearly planoconvex for *Platytrochalos*. Thus, *P. rabbei* can be distinguished from *P. ringerikensis* by its smaller shell size, weaker fold and sulcus associated with more numerous costae, better developed crural plates, and absence or poor development of a dorsal median ridge. In *Platytrochalos rabbei*, there are usually three or four costae on the fold and two or three in the sulcus, but the number may become difficult to assess because, in some specimens, the fold and sulcus are poorly delimited to produce a largely rectimarginate anterior commissure. The new species resembles *P. peninversus* (Fig. 6.6–6.15) in its moderately biconvex shell with two or three costae in the sulcus and completely sessile hinge plates, but differs in having a shell with greater length/width ratio and much better developed dental plates in spite of its small shell size. The notothyrial cavity in *P. peinversus* may or may not be filled by a thickened muscle pad to form a raised notothyrial platform (see Jin, 1989).

Order *Atrypida* Rzhonsnitskaya, 1960

Superfamily *Atrypoidea* Gill, 1871

Family *Atrypidae* Gill, 1871

Genus *Zygospiraella* Nikiforova (in Nikiforova & Andreeva), 1961

Zygospiraella duboisi (Verneuil, 1845)
Figure 12

1845 *Zygospiraella duboisi* Verneuil, p. 97, pl. 10, fig. 16
1908 *Leptocoelia hemisphaerica* Sowerby; Kiær, pp. 37–46, 589
1961 *Zygospira* (*Zygospiraella*) *duboisi* (Verneuil); Nikiforova & Andreeva, p. 237, pl. 51, figs 1–21
1970 *Zygospiraella duboisi* (Verneuil); Rubel, p. 28, pl. 13, figs 1–15
1982 *Zygospiraella duboisi* (Verneuil); Thomsen, p. 7, fig. 3
1982 *Zygospiraella duboisi* (Verneuil); Thomsen & Baarli, pp. 64–65, fig. 1, pl. 3, fig. 14.

Types. Type material not currently available; *Terebratula duboisi* Verneuil, p. 97, pl. 10, fig. 16; the Juuru Formation, Rhuddanian, Estonia.

Other material. Numerous separated ventral and dorsal valves embedded in shelly packstone blocks PMO 208.794-208.798. *Zygospiraella duboisi-Mendacella mullockiensis* Assemblage Zone, Djupvarp member, Sælabonn Formation at Store Svartøya, Sørumshaugen, and Djupvarp.

Description. Shell small, subcircular to transversely suboval in outline, planoconvex to ventribiconvex. Hinge line relatively long, straight, with round cardinal extremities. Ventral umbo moderately convex, carinated, with erect to suberect beak. Gentle, fold-like medial ridge present in ventral valve, and shallow sulcus in dorsal valve. Costae subrounded to subangular, increasing anteriorly mainly by bifurcation to reach 20 at anterior margin in adult shells. Growth lamellae prominent, widely spaced.

Dental plates short, low. Ventral muscle field well impressed posteriorly. Sockets narrow, diverging from each other antero-laterally at about 90 degrees. Hinge plates discrete, sessile on valve floor. Dorsal muscle field divided by thick median ridge.

Remarks. These small specimens of *Zygospiraella* were assigned to *Z. duboisi* by both Thomsen (1982) and Thomsen & Baarli (1982) and form a key element of the *Zygospiraella duboisi-Mendacella mullockiensis* Assemblage Zone. Copper (1982) has discussed the possible synonymies between *Z. planoconvexa* (Hall) from the Manitoulin Formation (Rhuddanian), Ontario and *Z. duboisi* (Verneuil), the genotypic species, noting that the latter species has a less protruding beak with a commonly developed apical perforation at the umbo and with anteriorly fading ribs. *Z. scotica* (Salter, 1851) from the Mulloch Hill Sandstone (middle Rhuddanian) of the Girvan district, SW Scotland (Floyd & Williams 2003) is similar in shape and ribbing pattern. All three species, however, have different modes of preservation; the Girvan material is mouldic preserved in sandstone whereas the Ringerike material preserves shell and the Canadian material is silicified or dolomitized. The three species are clearly similar but a statistical analysis of all three is required to establish their precise mutual relationships. The Ringerike material is thus retained within *Z. duboisi*.

Acknowledgements

Material from Norway was collected by Elsebeth Thomsen with kind permission and help from the Natural History Museum in Oslo, Department of Geology and the Institute of Geology, University of Oslo, together with the people of Ringerike. Specimens from Anticosti Island were collected by Paul Copper of Laurentian University, Canada. The wax and plaster models were made by the late Erna Nordmann and some of the photographs by Jan Aagaard, both University of Copenhagen. Anne Gundersen of Tromsø University Museum drafted some of the text-figures. Funding of this collaborative research project was provided by the University of Copenhagen, the University of Tromsø, as well as private means (Thomsen), the Natural Sciences and Engineering Research Council of Canada (Jin) and the Carlsberg Foundation (Harper). We thank Art Boucot (Oregon State University, Corvallis) and Robin Cocks (Natural History Museum, London) for their helpful review comments.

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