

Strophomenide and orthotetide Silurian brachiopods from the Baltic region, with particular reference to Lithuanian boreholes

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Epeiric seas covered the east and west parts of the old craton of Baltica in the Silurian and brachiopods formed a major part of the benthic macrofauna throughout Silurian times (Llandovery to Pridoli). The orders Strophomenida and Orthotetida are conspicuous components of the brachiopod fauna, and thus the genera and species of the superfamilies Plectambonitoidea, Strophomenoidea, and Chilidiopsoidea, which occur in the Silurian of Baltica are reviewed and reidentified in turn, and their individual distributions are assessed within the numerous boreholes of the East Baltic, particularly Lithuania, and attributed to benthic assemblages. The commonest plectambonitoids are *Eoplectodonta* (*Eoplectodonta*) (6 species), *Leangella* (2 species), and *Jonesea* (2 species); rarer forms include *Aegiria* and *Eoplectodonta* (*Ygerodiscus*), for which the new species *E. (Y.) bella* is erected from the Lithuanian Wenlock. Eight strophomenoid families occur; the rare Leptaenoidea only in Gotland (*Leptaenoidea*, *Liljevallia*). Strophomenidae are represented by *Katastrophomena* (4 species), and *Pentlandina* (2 species); *Bellimurina* (*Cyphomenoidea*) is only from Oslo and Gotland. Rafinesquinidae include widespread *Leptaena* (at least 11 species) and *Lepidoleptaena* (2 species) with *Scannomena* and *Crassitestella* known only from Gotland and Oslo. In the Amphistropiidae *Amphistropia* is widespread, and *Eoamphistropia*, *Eocymostropia*, and *Mesodouvillina* are rare. In the Leptostropiidae *Mesoleptostropia*, *Brachyprion*, and *Protomegastropia* are common, but *Eomegastropia*, *Eostropheodonta*, *Erinostropia*, and *Palaeoleptostropia* are only recorded from the west in the Baltica Silurian. In the Eopholidostrophidae, *Mesopholidostropia* is common and *Eopholidostropia* rare, and within the Shaleriidae the genus *Shaleria* is revised and found to be the only genus within the family Shaleriidae and to contain three subgenera, *S. (Shaleria)*, *S. (Shaleriella)* and *S. (Janiomya)*. In the Strophonellidae *Strophonella* was widespread and *Eostrophonella* rare. Within the Orthotetoidea, *Coolinia* and *Morinorhynchus* (with the new Ludlow and Pridoli species *M. rubeli* from the Lithuanian boreholes erected) are common, and *Fardenia*, *Saughina*, and *Valdaria* again only known from the west Baltic. Most of the genera and many of the species reviewed were very widespread and many found in the adjacent Avalonia and Laurentia: a few were even more cosmopolitan.

Key words: Brachiopoda, Silurian, Lithuania, Baltic, Strophomenoidea, Plectambonitoidea, Orthotetoidea.

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Introduction

The old terrane of Baltica was a separate entity from the time of its separation at 750 Ma until its soft oblique docking with Avalonia at about 443 Ma, Ordovician–Silurian boundary time. This was followed relatively soon afterwards by the more violent collision with Laurentia to form the Scandinavian Caledonides of Norway and Sweden, an orogeny which resulted in the much larger terrane of Laurussia.

The benthic faunas of Baltica were very endemic in the Lower Ordovician, but that endemism dwindled as Ordovician time went by, with migrants crossing the narrowing surrounding oceans from neighbouring terranes and the descendants of Baltic endemics travelling in the opposite directions. Thus by the Silurian, the brachiopod faunas were largely ho-

mogenous at the family level and to a large extent the generic level throughout Baltica, Avalonia, much of eastern Laurentia and even parts of Siberia (Cocks 2000). However, the very large consequent united terrane, Laurussia, was extensive enough for the faunas in the then-equatorial Canadian Arctic, e.g., those monographed by Zhang (1989), to be rather different to those from the Baltic area, at least at the specific level.

It is the purpose of this paper to review two of the major brachiopod orders, the Strophomenida and the Orthotetida, in the whole Baltic area during the Silurian. In general these faunas are relatively well-known from the western parts of the area, in the Oslo Region, Norway, and Gotland, Sweden, as well as from the Welsh Borderland of England in adjoining Avalonia. However, substantial undescribed collections

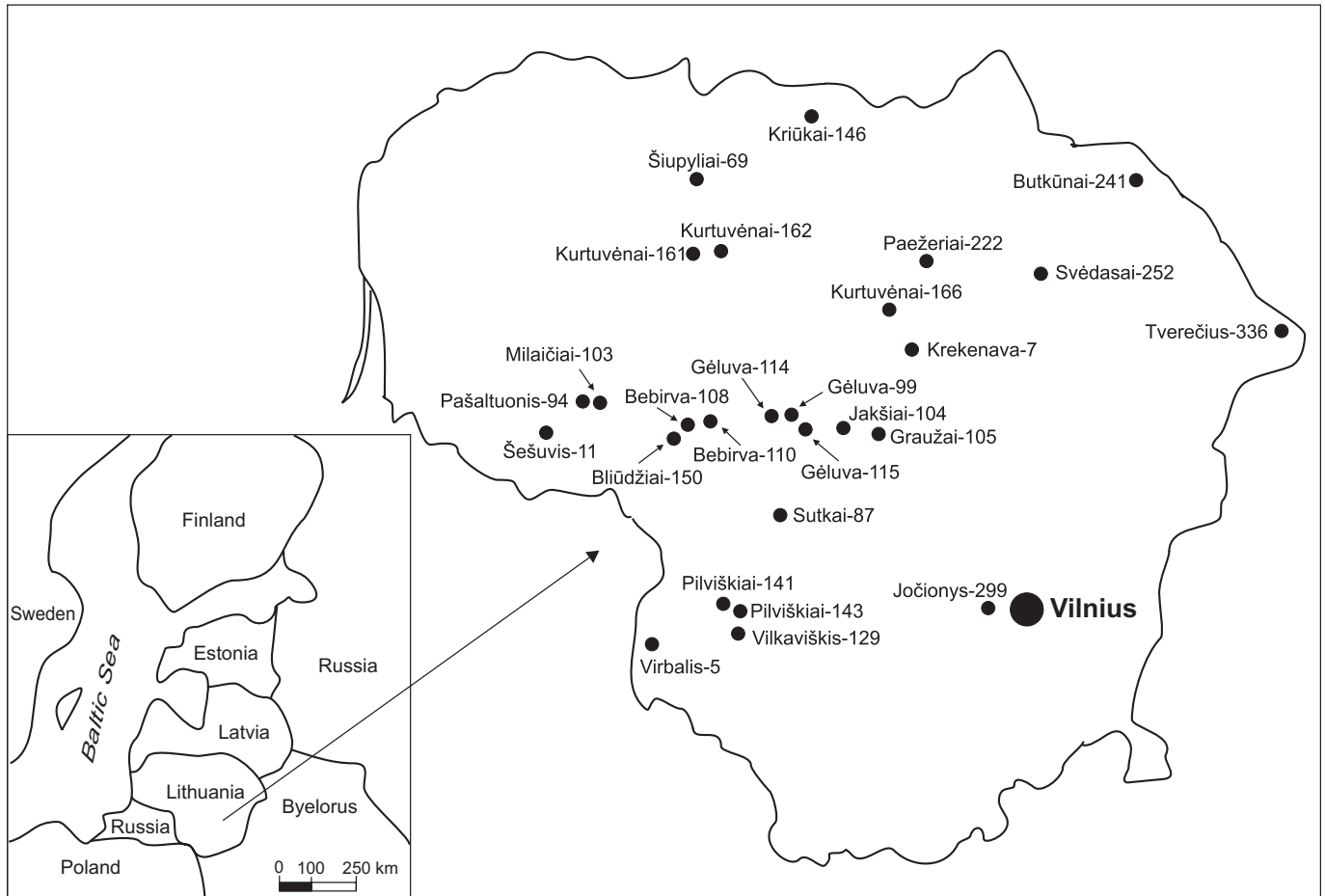


Fig. 1. Map of Lithuania showing the positions of the boreholes mentioned in the text.

are now available from the many boreholes drilled in the East Baltic Silurian, particularly Lithuania, and a further objective here is to identify and integrate these new records with those from the western Baltic and to place them within their contemporary ecological backgrounds.

Institutional abbreviations.—The material figured in this paper from Lithuania is deposited in Vilnius University Collections (VU), under Number 14, (B); there is a comparative collection in the Natural History Museum, London (NHM), in which other figured and cited materials are curated (BB and BC). We have re-illustrated some of types of Rybnikova (1966, 1967), housed in the Latvian Museum of Natural History, Riga, Latvia (LMNH, number of collection Br).

Geological background in the East Baltic area

Baarli et al. (2003) described the overall geology of Baltica in the Silurian. In the three East Baltic republics, Silurian rocks are only seen at the surface in Estonia, but in both Lat-

via (Rybnikova 1966, 1967) and Lithuania (Musteikis 1993; Musteikis and Modzalevskaya 2002) they are known subsurface from numerous boreholes (Fig. 1). Silurian strata in Lithuania formed part of the Baltic basin and represent all facies types from pelagic to lagoonal. The sequences range from 40 m to 800 m in thickness and occur at depths in the boreholes between 100 m to the east and 1200 m in the west. There are two major facies groups: pelagic, developed mainly in the Baltic syncline (western Lithuania); and shelf, on the slope of the Byelorussian-Mazurian antecline, which extends in to eastern Lithuania. The pelagic facies group consists of black argillites with graptolites, black argillites with interbeds of black, gray and greenish-gray calcareous mudstones, black argillites with thin interbeds of microcrystalline limestone, and greenish-gray calcareous mudstones and marls with interbeds of microcrystalline limestone. These facies were developed under anaerobic to dysaerobic environments below wave base and contain mainly graptolite faunas with very rare shelly faunas, including thin-shelled brachiopods. The shelf facies group consists of greenish-gray marls with benthic faunas, variegated argillaceous marls, gray and greenish-gray marls with interbeds of

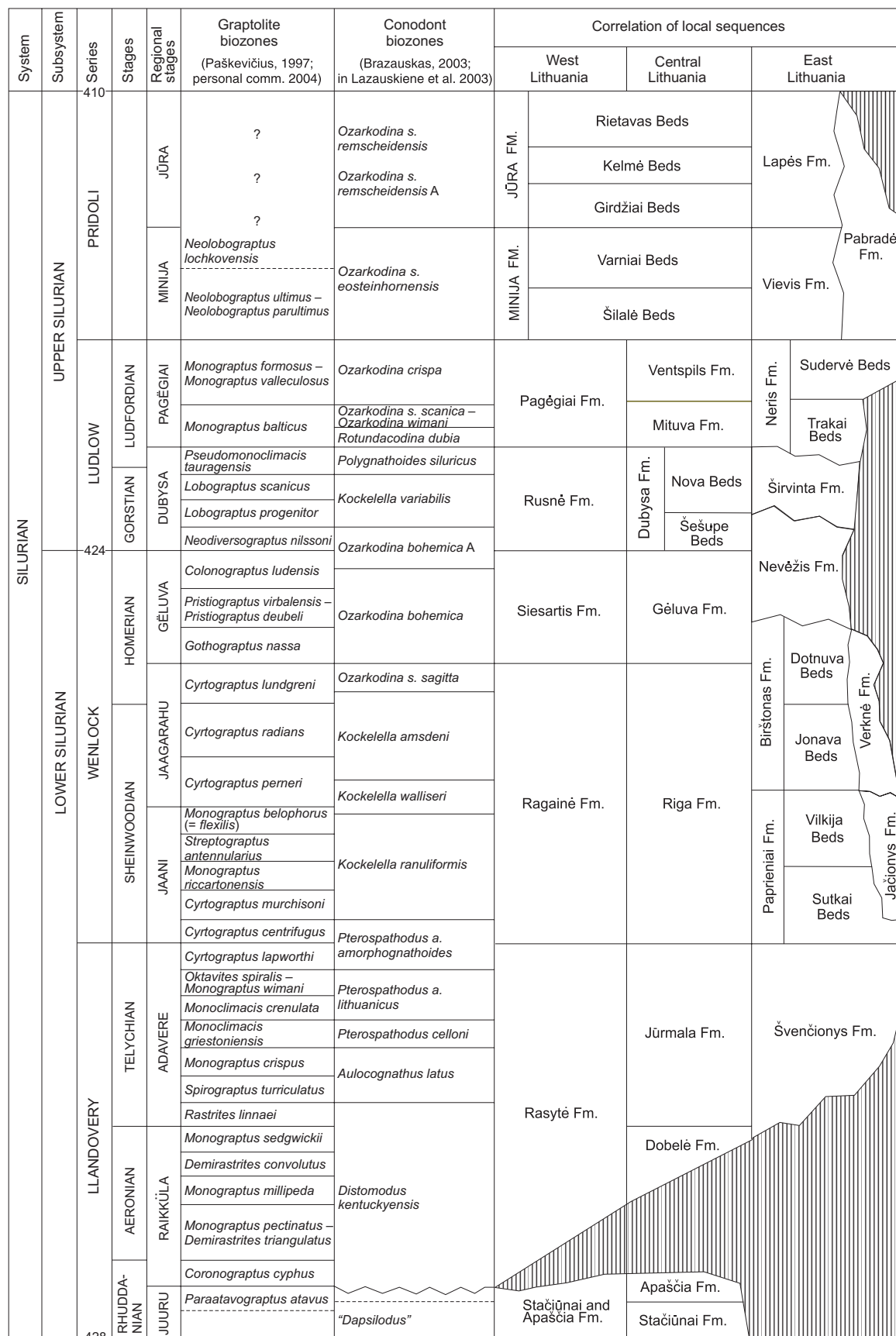


Fig. 2. Correlation of the Silurian of west, central and east Lithuania with the international Silurian stages, the East Baltic regional stages and the graptolite and conodont zones.

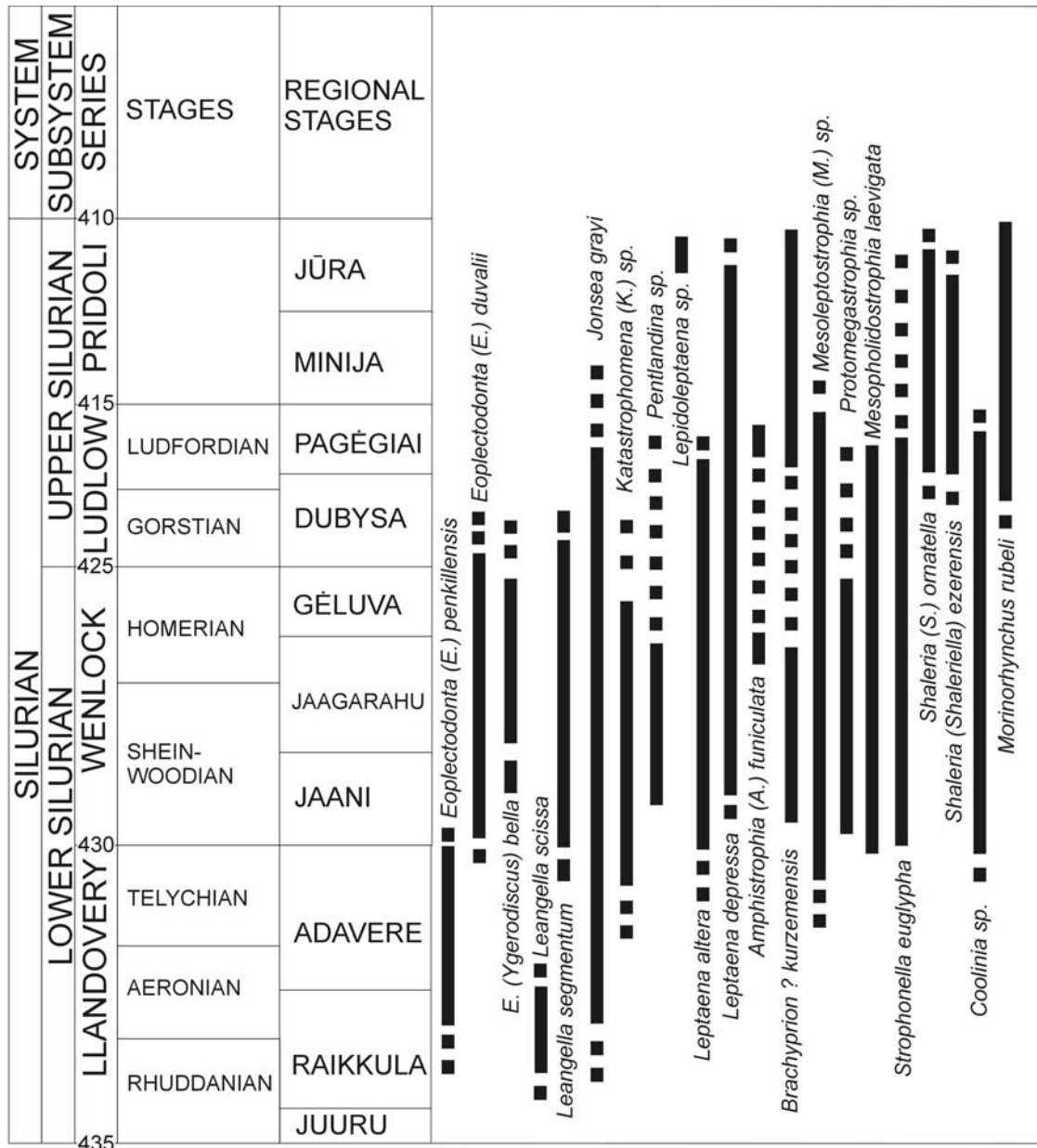


Fig. 3. Ranges of Silurian plectambonitoidean, strophomenoidean, and orthotetoidean brachiopods within the Lithuanian boreholes (see Appendix, Table 1 for details).

microcrystalline limestone, greenish-gray marls with limestone nodules, gray nodular limestone, black marl, and nodular limestone containing corals, biohermal and crinoidal limestone. The lagoonal facies consists of dolomites, dolomites with interbeds of dolomitic marl, dolomites with gypsum, and various dolomitic marls. The open shelf facies accumulated under aerobic environments of varied turbulence above wave base. The lagoonal facies formed under aerobic, shallow-water environments with increased salinity. There is a 50 to 80 km wide belt in central Lithuania in which the pelagic and shelf facies interfinger, and which contains both shelly and graptolite faunas. The correlation of the Lithuanian Silurian formations with the international standard is shown in Fig. 2.

Palaeontological background

Although parts of the brachiopod fauna from the Silurian of the Baltic plate are well monographed, e.g., Baarli (1995), most are not. A higher proportion of the Silurian brachiopods from adjoining Avalonia, particularly from the Welsh Borderland of England, have been monographed (e.g., Davidson 1871; Bassett 1974, 1977; Temple 1987) than from Baltica, and thus the Avalonian names have been used in most of the faunal lists of Baltica. However, Silurian brachiopods have been known and described from the Baltic island of Gotland, Sweden, since the very earliest days of systematic palaeontology, e.g., Dalman (1828), and these Gotland faunas were

reviewed and partly redescribed by Bassett and Cocks (1974). In addition, the faunas from the Upper Silurian of Podolia, Ukraine, at today's eastern end of Baltica, have been well described by Kozłowski (1929), Nikiforova et al. (1985) and others. However, the important strophomenoid, plectambonitoid, and orthotetoid Silurian brachiopod faunas from today's eastern parts of Baltica have been relatively neglected, apart from those in Podolia.

Brachiopods are the most abundant benthic macrofauna and the stratigraphic ranges of key strophomenoid, plectambonitoid and orthotetoid brachiopods are shown in Fig. 3. It is the purpose of this paper to properly identify those strophomenoides and orthotetoides recovered from the Lithuanian boreholes so that the results can be incorporated into future stratigraphical and ecological analyses (although a preliminary ecological analysis has been published by Musteikis and Juškutė (1999). A general species list of East Baltic Silurian brachiopods was published by Rubel et al. (1984), but without any stratigraphical details.

This revision is timely, since all the genera of the Strophomenoidea and Orthotetoidea have been recently revised in the *Treatise on Invertebrate Paleontology* (Cocks and Rong 2000; Williams and Brunton 2000), whose familial and higher classification is followed here. The individual genera of the Plectambonitoidea, Strophomenoidea, and Orthotetoidea recorded from the whole of the Silurian of Baltica (but not Avalonia or Laurentia) will now be reviewed in turn, together with the new data on the occurrences of the various genera and species within the Lithuanian boreholes.

Systematic palaeontology

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Remarks.—It is now recognised (Rong and Cocks 1994) that only a single superfamily Strophomenoidea is needed to accommodate both denticulate and non-denticulate forms, since denticulation arose polyphyletically in several stocks and thus a separate superfamily "Stropheodontoidea" is an untenable concept. However, as a result there are now 14 families within the superfamily (Cocks and Rong 2000), of which the Strophomenidae, Rafinesquinidae, Leptaenoideidae, Amphistrophoidea, Leptostrophoidea, Eopholidostrophoidea, Shaleriidae and Strophonellidae are all known from the Silurian of Baltica. They will be considered separately here.

Family Strophomenidae Öpik, 1934

Genus *Bellimurina* (*Cyphomenoidea*) Cocks, 1968

Remarks.—The type species of this subgenus is *B. (Cyphomenoidea) wisgoriensis* (Lamont and Gilbert, 1945), whose type locality is in the Telychian of the Welsh Borderland. The species is recorded from the Telychian Lower Visby Beds of Gotland by Bassett and Cocks (1974: 15), and also from the Aeronian and Telychian Rytteråker and Vik Forma-

tions (Baarli 1995: 40) and Bruflat Formation (Cocks and Baarli 1982) of the Oslo region. The genus is not known from the East Baltic.

Genus *Katastrophomena* (*Katastrophomena*)

Cocks, 1968

Remarks.—The type species, *Katastrophomena (K.) woodlandensis* (Reed, 1917), whose type locality is from the Rhuddanian of Girvan, Scotland (then part of Laurentia), was recorded from Baltica by Baarli (1995: 31) from the Rhuddanian Solvik Formation of the Oslo region. Two species, *Katastrophomena (K.) penkillensis* (Reed, 1917), from the upper part of the Rhuddanian Solvik Formation of the Oslo region (Baarli 1995: 32), and *Katastrophomena (K.) scabrosa* (Davidson, 1847) from the Upper Wenlock Slite and Klinteberg formations of Gotland (Bassett and Cocks 1974: 13), are also recorded from Baltica. Subsequently Bassett (1974: 107) included *K. (K.) scabrosa* as merely a subspecies of *K. antiquata* (J. de C. Sowerby, 1839) (but which he incorrectly listed as the type species of the genus), and we follow him here in regarding *K. antiquata* as the widespread but rather rare species in the Wenlock and early Ludlow of the Baltic, including Lithuania. Nikiforova (1954: 80) identified *K. antiquata* from the Wenlock and Ludlow of Podolia, and Rubel et al. (1984: 13) recorded *Katastrophomena (K.)* sp. from the East Baltic area. When individuals are small, they are very difficult to separate from *Pentlandina*, but we have identified small specimens from the Wenlock of the Graužai-105 borehole (see Appendix) of Lithuania as *Katastrophomena (K.)* sp. (Fig. 4G). They occur in the Vilkijsa Beds of the Paprieniai Formation (Sheinwoodian) in east Lithuania; at the top of the Jūrmala (Telychian) and Gėluva formations (Homerian) in central Lithuania, and the Dubysa Formation (Gorstian) in west Lithuania.

Genus *Pentlandina* Bancroft, 1949

Remarks.—The type species of the genus is *P. tartana* Bancroft, 1949, from the Telychian of Scotland. From Baltica *Pentlandina loveni* (Verneuil, 1848) was described from the Wenlock of Gotland and revised by Bassett and Cocks (1974: 14), who also listed *Pentlandina* sp. from the Telychian and Wenlock of Gotland. It has not so far been recorded from elsewhere in Baltica, apart from as *Pentlandina* sp. from an unspecified locality and horizon by Rubel et al. (1984: 14). Similar poorly preserved shells which may belong to the genus are known from the Vilkijsa Beds of the Paprieniai (Sheinwoodian) and Jonava Beds of the Birđtonas formations (Sheinwoodian) in east Lithuania from Graužai-105 (776.0–742.7 m) and the Pagėgiai Formation (Ludfordian) in west Lithuania in Šiupyliai-69 (823.2 m).

Family Rafinesquinidae Schuchert, 1893

The Silurian rafinesquinid genera recorded from Baltica are *Crassitestella*, *Lepidoleptaena*, *Leptaena*, and *Scammomena*.

Genus *Crassitestella* Baarli, 1995

Remarks.—Only the type species, *Crassitestella reedi*, originally described from the Rhuddanian of Girvan, Scotland, by Cocks (1968: 310) is known from Baltica, and this was redescribed and revised by Baarli (1995: 39) from the Rhuddanian Solvik Formation of the Oslo Region. The genus is not known from elsewhere in Baltica.

Genus *Lepidoleptaena* Havlíček, 1963

Remarks.—The type species of the genus is *Lepidoleptaena lepidula* (Barrande, 1879), from the Lower Devonian Koněprusy Limestone of Bohemia, which was revised by Havlíček (1967: 107). Silurian species of the genus are known and Modzalevskaya and Pushkin (1989: 96) have recorded *Lepidoleptaena* cf. *poulsenii* Kelly, 1967 from the Ludlow–Pridoli of Belarus; and Basset and Cocks (1974:) recorded *Lepidoleptaena* sp. from the Upper Ludlow of Gotland. There are no other previous records of the genus from the East Baltic, apart from *Lepidoleptaena* sp. recorded by Rubel et al. (1984: 13) from an unspecified locality and horizon. The genus is poorly represented in the Lithuanian boreholes, but wider specimens of which we have no interiors may represent the genus there, and there is a single incomplete ventral interior, VU B20495, from the central Lithuanian Pridoli Jūra Formation in the Vilkaviškis-129 borehole (596.3 m), which shows the rim to the ventral disc which is characteristic of the genus and is therefore identified as *Lepidoleptaena* sp.

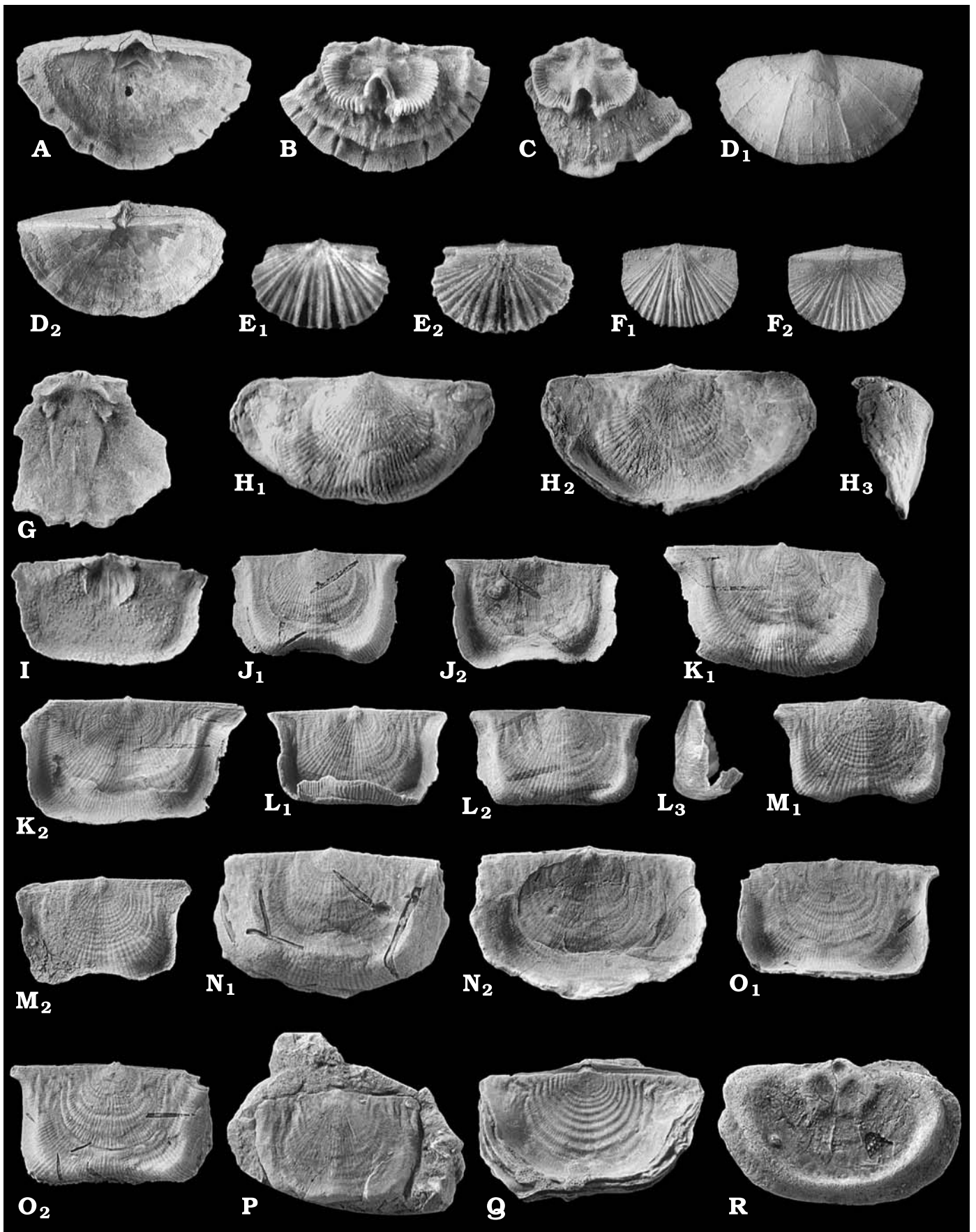
Genus *Leptaena* Dalman, 1828

Remarks.—The type species of the genus is *Leptaena rugosa* Dalman, 1828, from the Ashgill of Sweden. There is a great number of species of *Leptaena* from the Baltic area and worldwide—the variability of both the genus and the individual species within it are very substantial and a comprehensive review of this genus would be desirable, although Rong and Cocks (1994: 678) discussed the many generic names within its synonymy. Those species recorded from the Baltic Silurian are: *Leptaena altera* Rybnikova, 1966, *Lepta-*

ena depressa (J. de C. Sowerby, 1825), *Leptaena haverfordensis* Bancroft, 1949, *Leptaena purpurea* Cocks, 1968, *Leptaena rhomboidalis* (Wahlenberg, 1818), *Leptaena valentia* Cocks, 1968, *Leptaena valida* Bancroft, 1949, and *Leptaena venezavensis* (Rybnikova, 1966). Five species are known from the Llandovery of the Oslo Region (Baarli 1995; Cocks and Baarli 1982), but are not yet recorded from elsewhere in Baltica. One of these species, *Leptaena dejecta*, Baarli (1995: 34, was assigned originally to the Ordovician genus *Dactylogonia*), but the side septa and other structures characteristic of that genus are not seen, and we reassign the species here to *Leptaena*. *L. haverfordensis*, *L. purpurea*, and *L. valida*, also recorded by Baarli (1995), all have their type localities in the Llandovery of Wales and the Welsh Borderland, whilst the type locality of *L. valentia* is in the Rhuddanian of Scotland (Cocks 1968).

We only recognise two species of *Leptaena* from the Wenlock and Ludlow of the East Baltic, *Leptaena depressa* and *L. altera*. *Leptaena venezavensis* was originally erected under *Rugoleptaena* by Rybnikova (1966: 76) from the Pagėgiai Horizon of Latvia, which she declared as Lower Ludlow, but which is now known to be Upper Ludlow. We here synonymise that species with *Leptaena depressa*. *L. depressa* is up to four times the size of *L. altera* and occurs in the shallow-water assemblages of the East Baltic (Figs. 4P–R, 5A–D). *L. depressa*, whose type locality is in the Upper Wenlock of England, is accompanied in Gotland by the much-quoted *L. rhomboidalis* (Wahlenberg, 1818): the differences between the two species were discussed and illustrated by Basset and Cocks (1974: 14), and chiefly consist of the enhanced genicular rim and stronger rugae in *L. rhomboidalis*; but the latter is not known from Baltica east of Gotland. *Leptaena* is present in the Pridoli of Lithuania; but, as discussed above, most of the specimens known only show the valve exteriors, and thus may be either *Leptaena* or *Lepidoleptaena*. *Leptaena depressa* is known from the Švenčionys (Telychian), Paprieniai, Jačionys, Birštonas, Verknė and Nevėžis formations (Sheinwoodian and Homerian) in east Lithuania; the upper part of the Riga (Homerian), Gėluva (Homerian), Dubysa (Gorstian) and Miniija

Fig. 4. **A–D.** *Leangella* (*L.*) *segmentum* (Lindström, 1861). **A.** VU B10064, ventral interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* Zone), Butkūnai-241, 493.2 m, × 4. **B.** VU B10066, dorsal interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* Zone), Butkūnai-241, 491.4 m, × 4. **C.** VU B10067, dorsal interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* Zone), Butkūnai-241, 483.1 m, × 5. **D.** VU B10055, ventral (D_1), and dorsal (D_2) views of a conjoined shell, Riga Formation (Sheinwoodian, *M. riccartonensis* Zone), Sutkai-87, 893.6 m, × 5. **E, F.** *Jonesea grayi* (Davidson, 1849) (= *Plectodonta aknistensis* Rybnikova, 1967). **E.** LMNH Br. 30/5, holotype of *aknistensis*, ventral (E_1), and dorsal (E_2) views of a conjoined shell, Upper Wenlock, Akniste borehole, Latvia, 545.7–549.9 m, × 7. **F.** VU B10079, ventral (F_1), and dorsal (F_2) views of a conjoined shell, Siesartis Formation (Homerian, *M. ludensis* Zone), Kriūkai-141, 759.3 m, × 5. **G.** *Katastrophenomena* (*K.*) sp., VU B21150, dorsal interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian), Graužai-105, 776.0 m, × 4. **H–O.** *Leptaena altera* Rybnikova, 1966. **H.** LMNH Br. 30/58, holotype, ventral (H_1), dorsal (H_2), and lateral (H_3) views of a conjoined shell, Pagėgiai Formation (Ludfordian), Ezere borehole, Latvia, 1081.3 m, × 3. **I.** LMNH Br. 30/59, ventral interior, Wenlock, Akniste borehole, Latvia, 556.0 m, × 3. **J.** VU B10037, ventral (J_1), and dorsal (J_2) views of a conjoined shell, Riga Formation, (Homerian, *C. radians–M. testis* Zone), Gėluva-99, 912.2 m, × 3. **K.** VU B10036, ventral (K_1), and dorsal (K_2) views of a conjoined shell, Riga Formation, (Homerian, *C. radians–M. testis* Zone), Gėluva-99, 911.6 m, × 3. **L.** VU B10051, ventral (L_1), dorsal (L_2), and lateral (L_3) views of a conjoined shell, Riga Formation, (Sheinwoodian, *C. radians–M. flexilis* Zone), Sutkai-87, 846.4 m, × 3. **M.** VU B20496, ventral (M_1), and dorsal (M_2) views of a conjoined shell, Riga Formation, (Sheinwoodian, *C. radians–M. flexilis* Zone), Sutkai-87, 846.4 m, × 3. **N.** VU B10042, ventral (N_1), and dorsal (N_2) views of a conjoined shell, Vilkija Beds of Paprieniai Formation, (Sheinwoodian), Krekenava-7, 774.85 m, × 3. **O.** VU B10044, dorsal (O_1), and ventral (O_2) views of a conjoined shell, Jonava Beds of Birštonas Formation, (Sheinwoodian), Krekenava-7, 717.5 m, × 3. **P–R.** *Leptaena depressa* (J. de C. Sowerby, 1825). **P.** VU B10047, ventral exterior, Dubysa Formation (Gorstian, *O. s. bohémica* Zone), Sutkai-87, 765.3 m, × 1.5. **Q.** VU B10073, dorsal exterior, Jonava Beds of Birštonas Formation (Sheinwoodian–Homerian, *K. amsdeni* Zone), Svėdasai-252, 461.0 m, × 1.5. **R.** VU B10075, dorsal interior, Dotnuva Beds of Birštonas Formation (Homerian, *K. amsdeni* Zone), Svėdasai-252, 448.7 m, × 2.



(Lower Pridoli) formations in central Lithuania, and the Rusnė, Dubysa, Pagėgiai, Mituva, Ventspils (Gorstian and Ludfordian), Miniija and Jūra (Pridoli) formations in west Lithuania (Appendix).

Rybnikova (1966: 78; 1967: 193) described *Leptaena altera* as from the Wenlock–Lower Ludlow of Latvia, and we reillustrate her types here (Fig. 4H, I). The species may be the same as *L. holcrofti* which Bassett described (1974: 121) from the Upper Wenlock of Wales. *L. altera* differs in size from slightly larger specimens in shallower-water to smaller specimens from deeper-water facies (Fig. 4H–O). Its distribution in Lithuania is in the Švenčionys (Telychian), Paprieniai (Sheinwoodian) formations and the Jonava Beds of the Birštonas Formation (Sheinwoodian) in east Lithuania; the Jūrmala (Telychian), Riga and Gėluva (Sheinwoodian and Homeric), and the Šešupė Beds of the Dubysa formations (Gorstian) in central Lithuania; and the Siesartis (Homeric), Rusnė, Dubysa (Gorstian) and Pagėgiai (Ludfordian) formations in west Lithuania (Appendix).

Genus *Scannomena* Bassett, 1977

Remarks.—The type species, *Scannomena rugata* (Lindström, 1861) has its type locality in the early Wenlock Upper Visby Beds of Gotland (Bassett and Cocks 1974: 14; Bassett 1977: 135). It has not been recorded from elsewhere in Baltica.

Family Leptaenoideidae Williams, 1953

Genus *Leptaenoidea* Hedström, 1917

Remarks.—The type locality of the type and only known species, *Leptaenoidea silurica* Hedström, 1917, is in the Upper Wenlock Halla Beds of Gotland (Bassett and Cocks 1974: 15). It has not been recorded from elsewhere, and is thus one of the few Silurian brachiopod genera endemic to Baltica.

Genus *Liljevallia* Hedström, 1917

Remarks.—The type and only known locality of the genus and species, *Liljevallia gotlandica* Hedström, 1917, and thus another Baltic endemic species, is from the Upper Visby

Beds of Telychian age of Gotland. It was revised and illustrated by Bassett and Cocks (1974: 18) and a ventral valve was illustrated for the first time by Cocks and Rong (2000: fig 161).

Family Amphistropiidae Harper, 1973

Genus *Amphistrophia* (*Amphistrophia*) Hall and Clarke, 1892

Remarks.—The type species, *Amphistrophia* (*A.*) *striata* (Hall), is from the Wenlock of New York State, U.S.A. A common species in Baltica is *A.* (*A.*) *funiculata* (M'Coy, 1846), whose type locality is in the Upper Wenlock of England, it is known from the Wenlock Slite and Mulde Beds of Gotland (Bassett and Cocks 1974: 16) and elsewhere. The genus is rare in Lithuania, but one poorly preserved specimen from the Svėdasai-252 borehole of eastern Lithuania shows unequally parvicostellate ribbing different from the more equal parvicostellae of *A.* (*A.*) *funiculata*. We have identified *A.* (*A.*) *funiculata* itself, and the species is figured here (Fig. 5E), from the Birštonas Formation (Homeric) in east Lithuania and the Mituva Formation (Ludfordian) in west Lithuania. Nikiforova et al. (1985) reassigned *Strophomena podolica* Siemiradzki, 1906, from the Lower Devonian of Podolia, to *Amphistrophia*: it was also revised by Kozłowski (1929: 101). Rybnikova (1966: 87; 1967: 194) recorded that species from the Ludlow of the Latvian boreholes, but her illustrations appear unidentifiable and we cannot confirm the species as present in the Silurian of Latvia.

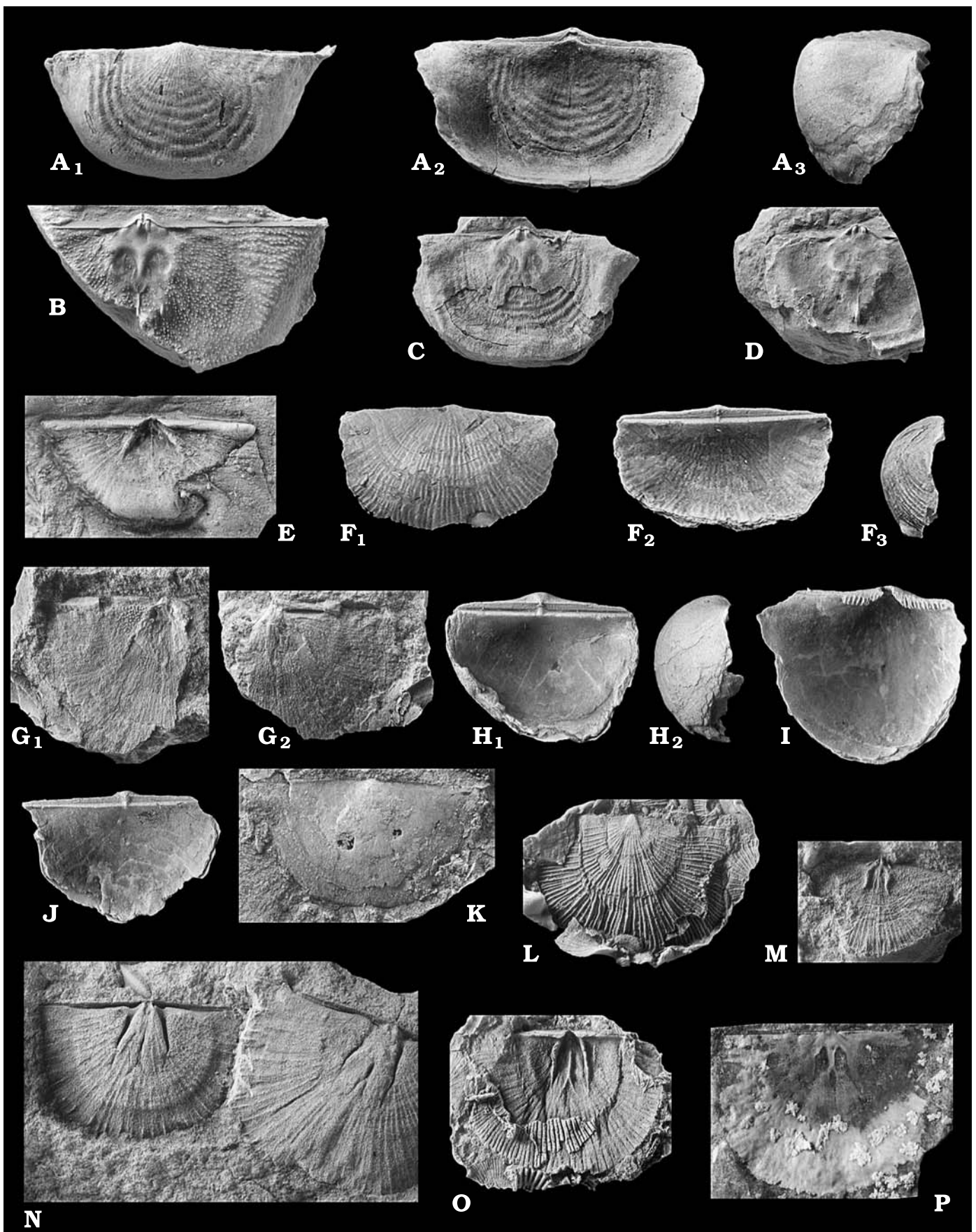
Genus *Eoamphistrophia* Harper and Boucot, 1978

Remarks.—The type species, *Eoamphistrophia whittardi* (Cocks, 1967), is recorded from the Telychian Lower Visby Beds of Gotland (Bassett and Cocks 1974: 16), but is not known from elsewhere on Baltica.

Genus *Eocymostrophia* Baarli, 1995

Remarks.—*Eocymostrophia balderi* Baarli, 1995, the type and only known species of the genus, is described from the Telychian Vik Formation of the Oslo Region (Baarli 1995: 48). It is not yet known from elsewhere.

Fig. 5. **A–D.** *Leptaena depressa* (J. de C. Sowerby, 1825). **A.** VU B10074, ventral (A₁), dorsal (A₂), and lateral (A₃) views of a conjoined shell, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* Zone), Svėdasai-252, 482.7 m, × 2.5. **B.** VU B10049, dorsal interior, Riga Formation (Sheinwoodian, *C. radians–M. flexilis* Zone), Sutkai-87, 765.3 m, × 2. **C.** VU B10048, dorsal interior, Riga Formation (Sheinwoodian, *C. radians–M. flexilis* Zone), Sutkai-87, 765.8 m, × 1.5. **D.** VU B10050, dorsal interior, Riga Formation (Sheinwoodian, *C. radians–M. flexilis* Zone), Sutkai-87, 765.8 m, × 1.5. **E.** *Amphistrophia* (*A.*) *funiculata* (M'Coy, 1846), VU B21101, ventral interior, Birštonas Formation (Sheinwoodian–Homeric), Paežeriai-222, 694.7 m, × 2.5. **F.** *Brachyprion? kurzemensis* Rybnikova, 1966, VU B21000, ventral (F₁), dorsal (F₂), and lateral (F₃) views of a conjoined shell, Pagėgiai Formation (Ludfordian), Milaičiai-103, 1206.25 m, × 2.5. **G.** *Mesoleptostrophia* (*M.*) sp., VU B20491, dorsal interior (G₁), and its counterpart (G₂), Dubysa Formation (Gorstian), Vilkaviškis-129, 709.4 m, × 2. **H–K.** *Mesopholidostrophia laevigata* (J. de C. Sowerby, 1825). **H.** VU B10060, dorsal (H₁) and lateral (H₂) views of a conjoined shell, Jonava Beds of Birštonas Formation (Sheinwoodian, *K. amsdeni* Zone), Butkūnai-241, 476.2 m, × 4. **I.** VU B10060, ventral interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* Zone), Butkūnai-241, 484.3 m, × 5. **J.** VU B10061, dorsal view of a conjoined shell, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* Zone), Butkūnai-241, 482.2 m, × 5. **K.** VU B20490, ventral exterior, Gėluva Formation (Homeric), Jakšiai-104, 788.7 m, × 3. **L–O.** *Shaleria* (*S.*) *ornatella* (Davidson, 1871). **L.** NHM BC13115a, ventral exterior, Leintwardine Formation (Ludlow), Court Perrott Quarry, Usk, Gwent, Wales, × 2. **M.** NHM BC13112, Usk, × 2. **N.** NHM B842, Whitcliffe Formation (Ludlow), Whitcliffe Quarry, Ludlow, Shropshire, England, × 2.5. **O.** NHM BC13115b, Leintwardine Formation (Ludlow), Court Perrott Quarry, Usk, Gwent, Wales, × 2. **P.** *Shaleria* (*Shaleriella*) *ezerensis* (Rybnikova, 1966) (= *delicata* Harper and Boucot, 1978), NHM BB32970, Hemse Beds (Ludlow), Millklint, Gotland, Sweden, × 2.



Genus *Mesodouvillina* Williams, 1950

Remarks.—The type species of the genus is *M. subinterstitialis* (Kozłowski, 1929) from the Lower Devonian Borshchov horizon of Podolia. Nikiforova et al. (1985: 22) reassigned Kozłowski's (1929) *Stropheodonta (Brachyprion) dzwinogradensis* from the Pridoli Skala horizon of Podolia to *Mesodouvillina*? Unfortunately neither Kozłowski nor Nikiforova et al. illustrated or described the interior of any specimens of either valve of that species and we therefore regard the species as a *nomen dubium*. Thus it is not clear whether or not the genus is truly present anywhere in the Silurian. Rybnikova (1966: 83, 1967: 194) identified "*B. dzwinogradensis* Kozłowski" from the Pridoli Piltene and Ezere boreholes of Latvia, but the specimens are reassigned here to *Shaleria* (see below).

Strophodonta colongensis (Sapelnikov 1968: 87, pl. 33: 1, 2; Sapelnikov and Mizens, 1991: 90, pl. 38: 5, 6), from the Lower Pridoli of the eastern slope of the northern Urals, is unlikely to belong to that Devonian genus, but the species has not been reallocated to another genus here.

Family Leptostrophiidae Caster, 1939

Genus *Brachyprion* Shaler, 1865

The type species of *Brachyprion* is *B. leda* from the mid-Aeronian to Telychian Jupiter Formation of Anticosti Island, Canada, revised by Rong and Cocks (1994: 682). This is much less convex than the *Brachyprion arenacea* (Davidson, 1871), which was placed within *Brachyprion* by Cocks (1967) and which was recorded from the Aeronian Rytteråker Formation of the Oslo region by Cocks and Baarli (1982: 88). Similarly convex shells were recorded as *Brachyprion* sp. from the Wenlock and Ludlow of Gotland by Bassett and Cocks (1974: 15). Following the revision of *B. leda* by Dewing (1999), the generic identity of all these forms requires revision. Modzalevskaya (1985: 60, pl. 1: 1, 2) recorded *Brachyprion* cf. *robustum* Twenhofel from the Llandovery of Novaya Zemlya. *B. robustum* itself, which was originally described from Anticosti Island, Canada, has now been placed within the synonymy of *B. leda* by Dewing (1999), but we have seen no material from Baltica that could be included within that species. Rybnikova (1966: 85; 1967: 194) described and illustrated what she determined as *Brachyprion costatula* (Barrande) from the Lower Ludlow of Latvia, Lithuania, Podolia, the Urals and central Asia. Her illustrated shells may be reassigned to *Shaleria* (Rubel et al. 1984, and see below).

Rybnikova (1966: 80; 1967: 194) also described a new species, *Brachyprion kurzemensis* from the Ludlow of Latvia, but without illustrating the ventral interior. The cardinalia of the dorsal valve are not identical to the type species of *Brachyprion*, and the species remains unassigned to a definite genus until better material becomes available. We have also found similar material from the Upper Ludlow of the Milaičiai-103 borehole (1206.5–1202.75 m) (Fig. 5F), which we have identified here as *Brachyprion? kurzemensis*, but there are no interiors available from Lithuania. It occurs in the Paprieniai and Birštonas formations (Sheinwoodian and

Homerian) in east Lithuania; Rusnė (Gorstian), Pagėgiai (Ludfordian), Miniija and Jūra (Pridoli) formations in west Lithuania (Appendix).

Genus *Eomegastrophia* Cocks, 1967

Remarks.—Baarli (1995: 45) recorded and illustrated *Eomegastrophia* spp.?, from the Rhuddanian Lower Solvik Formation of the Oslo region, but the genus is not known from elsewhere on Baltica: the type species is from the Aeronian of England.

Genus *Eostropheodonta* Bancroft, 1949

Remarks.—*Eostropheodonta* is a widespread and almost cosmopolitan genus in the Ashgill, Llandovery (Cocks 1967), and Wenlock (Bassett 1977), and its type species is from the Hirnantian of Avalonia. Baarli (1995: 43) erected and described a new species *E. delicata* from the Lower Llandovery Solvik Formation of the Oslo Region, and also *E. multiradiata*? Bancroft, 1949 from the same formation. However, the genus is not yet known from eastern Baltica in rocks younger than Ashgill.

Erinostrophia Cocks and Worsley, 1993

Remarks.—The type and only known species of the genus is *Erinostrophia undata* (M'Coy, 1846) from the Telychian Uggool Beds of Ireland, then in Avalonia, which was revised and figured from its type locality by Cocks and Worsley (1993). The same species has long been known by the name of its junior synonym, *Strophomena walmstedti* Lindström, 1861, whose type locality is from the Telychian Lower Visby Beds of Gotland, and which was revised and illustrated by Bassett and Cocks (1974: 16). It was also redescribed and figured from the Telychian Bruflat Beds of the Oslo region by Cocks and Worsley (1993), but is not known from further east in Baltica.

Mesoleptostrophia (Mesoleptostrophia) Harper and Boucot, 1978

Remarks.—The type species of this long-lived genus, which lasted from the Aeronian to the Middle Devonian, is *M. (M.) kartalensis* from the Emsian of Turkey. Species attributed to the genus from Baltica include *Mesoleptostrophia (M.) filosa* (J. de C. Sowerby, 1839), originally described from the Wenlock of England, but identified by Bassett and Cocks (1974: 15) from the Wenlock and Lower Ludlow of Gotland, and "*Leptostrophia? filosa?*" *lata* Holtedahl, 1916, from the Wenlock of the Oslo Region, Norway (Harper and Boucot 1978: 68). Rubel et al. (1984) listed *Leptostrophia compressa* from the East Baltic without giving details of any localities—the species is known only from the Aeronian and Telychian of Wales and the Welsh Borderland (Cocks 1967). Sokolskaya (1954: 40) also described and illustrated forms which she determined as *Rafinesquina compressa* (Davidson, 1871) from the Aeronian Raikküla Beds of Estonia, but without figuring interiors—these forms may possibly be true

Mesoleptostrophia, but their identification as *R. compressa* cannot be confirmed. Gagel (1890: 43) erected *Strophomena lindströmi* from the glacial erratic boulders of the north German plain, but without illustrating interiors: its age and generic affinity are unknown, and therefore we treat the species as a *nomen dubium*. However, Sokolskaya (1954) identified and illustrated what she determined as *S. lindströmi* from the Aeronian Raikküla Beds of Estonia, but again she did not illustrate interiors—from the pictures of the exteriors her specimens appear more likely to be attributable to the orthotetoid *Coolinia*. In the Lithuanian boreholes we have identified *Mesoleptostrophia* (*M.*) sp. (Fig. 5G) from the Birštonas Formation (Sheinwoodian and Homerian) in east Lithuania, the top of the Jūrmala (Telychian), Riga and Gėluva formations (Sheinwoodian and Homerian) in central Lithuania, and the Dubysa, Rusnė, Mituva, Pagėgiai (Gorstian and Ludfordian) formations and the Šilalė Beds of the Minija Formation (Lower Pridoli) in west Lithuania (Appendix).

Palaeoleptostrophia Rong and Cocks, 1994

Remarks.—The type species of the genus is *P. jamesoni* (Reed, 1917) from the Rhuddanian of Girvan, Scotland, revised by Rong and Cocks (1994). Baarli (1995: 44) has described and illustrated what she termed *Palaeoleptostrophia ostrina?* (Cocks, 1967) from the Rhuddanian Solvik Formation of the Oslo Region, but that species is known only from the Telychian of the Welsh Borderland. The genus is not known from the East Baltic.

Protomegastrophia Caster, 1939

Remarks.—The type species, *P. profunda* (Hall) comes from the Wenlock of Wisconsin, U.S.A. Bassett and Cocks (1974: 17) have recognised *Protomegastrophia semiglobosa* (Davidson, 1871), whose type locality is the Upper Wenlock of Walsall, England, from the Lower Wenlock Upper Visby and Högkint Beds of Gotland. We have identified *Protomegastrophia* sp. from the Riga and Gėluva formations (Sheinwoodian and Homerian) in central Lithuania, and from the Mituva Formation (Ludfordian) in west Lithuania (Appendix).

Eopholidostrophiiidae Rong and Cocks, 1994

Eopholidostrophia Harper, Johnson, and Boucot, 1967

Remarks.—The type species is *E. sefinensis* Williams, 1951, from the Aeronian of the type Llandovery district, Wales. *Eopholidostrophia* spp., have been recorded from the Lower Llandovery of the Oslo region by Baarli (1995: 47). As discussed above under *Jonesea*, the species *Plectambonites aequalis* Teichert, 1928, from the Lower Llandovery Tamalu Formation of Estonia, may be attributable to *Eopholidostrophia*, but the genus is not otherwise known from the East Baltic. Teichert's type specimens have not been traced, because they were lost in World War II.

Mesopholidostrophia Williams, 1950

Remarks.—The type species of *Mesopholidostrophia* is *M. nitens* (Williams, 1950) from the Wenlock Mulde Marl of Gotland, a junior subjective synonym of *M. laevigata* (J. de C. Sowerby, 1839), whose type locality is from the Upper Wenlock of the type Wenlock area, England. The species was revised by Bassett and Cocks (1974: 18) from Gotland and by Bassett (1977) from Britain. From Baltica are recorded *Mesopholidostrophia* aff. *fletcheri* (Davidson, 1847), whose type locality is also from the Upper Wenlock of the type Wenlock area, from the Upper Wenlock Mulde Beds of Gotland (Bassett and Cocks 1974: 18), and *Mesopholidostrophia sifae* Baarli, 1995 from the Aeronian Rytteråker Beds of the Oslo region (Baarli 1995: 46).

The Lithuanian distribution of *M. laevigata* (Fig. 5H–K) is in the Švenčionys (Telychian), Paprieniai, Jačionys formations and the Jonava Beds of the Birštonas Formation (Sheinwoodian) in east Lithuania, the upper part of the Jūrmala Formation (Telychian), Riga and Gėluva formations (Sheinwoodian and Homerian), the Šešupė Beds of the Dubysa Formation (Gorstian) in central Lithuania, and the Dubysa, Rusnė, Mituva and Pagėgiai formations (Gorstian and Ludfordian) in west Lithuania (Appendix).

Family Shaleriidae Williams, 1965

Genus *Shaleria* Caster, 1939

Remarks.—The type species of *Shaleria*, by the original designation of Caster (1939: 33), is *Strophomena gilpeni* Dawson, 1881, whose type locality is the Lower Devonian Stonehouse Formation of Arisaig, Nova Scotia, Canada. This type species was revised from new collections by Harper (1973). The genus was revised by Harper and Boucot (1978: 161), who also revised the family, in which they included only two genera, *Shaleria*, with three subgenera *S.* (*Shaleria*), *S.* (*Janio-myia*) Havlíček, 1967, and *S.* (*Protoshaleria*) subgen. nov., and *Shaleriella* gen. nov. Subsequent revision by Cocks and Rong (2000), put *S.* (*Protoshaleria*) within the synonymy of *S.* (*Shaleria*), and included *Shaleria* and *Shaleriella* as the only two separate genera within the family. The type species of *Shaleriella* is *S. delicata* Harper and Boucot, 1978, from the Silurian of Gotland, Sweden (see below under *S.* (*S.*) *ezerensis*). Harper and Boucot (1978: 123, 160–161) distinguished *Shaleria* from their new genus *Shaleriella* on (i) the geniculate profile of the latter, as opposed to the gently convex profile of the former, (ii) the lack of dorsal “brace plates” (termed here dorsal side septa) in the latter, and (iii) the “uniformly costellate” ornament of *Shaleria*. The latter is puzzling, since Harper (1973: 39), in his revision of the type species of *Shaleria*, described its ornament as “some specimens unequally parvicostellate; others parvicostellate with inserted costellae separated by interspaces of about the same width, which may bear a single fine costella,” and these observations are borne out by his illustrations, and thus the ornamental distinction between the two genera is negated. The dorsal side septa, which are often curved in a bow shape in their posterior

parts, are more difficult in assessing generic importance and differentiation. Harper and Boucot (1978: 34) illustrate only two dorsal interiors of *S. delicata*, one of which (fig. 21 in their paper) lacks side septa and the other of which (fig. 22) possesses them, although they are weakly developed in that specimen. The geniculate profile is a genuine difference, and that is consistently linked with a valve outline which is squarer anteriorly (a feature not mentioned by Harper and Boucot). However, we do not consider those two features alone as a firm basis for good generic differentiation, but they appear to be consistent between populations and thus we assess *Shaleriella* here not as a separate genus but as a subgenus of *Shaleria*. Havlíček (1967: 174) erected *Janiomya* as a new independent genus which differed from *Shaleria* only in the lack of “strong subparallel plates” in the dorsal valve. Since Havlíček only illustrated a single dorsal interior of *Janiomya parallelomya*, the type species of his new genus, from the Pridoli of Bohemia, it is difficult to be certain of its status because of the wide range of variation that we have seen in the strength of these plates in large populations of, for example, *Shaleria ornatella* from the Welsh Borderland, and we follow Cocks and Rong (2000) in provisionally placing *Janiomya* as a subgenus of *Shaleria* until larger collections of material become available from Bohemia. Thus, to summarise, *Shaleria* is now considered to be the only genus within the family Shaleriidae, and includes the three subgenera *S. (Shaleria)*, *S. (Janiomya)* and *S. (Shaleriella)*.

Shaleria (Shaleria) ornatella (Davidson, 1871)

Figs. 5L–O, 6B–H.

Strophomena ornatella Davidson 1871: 309, pl. 43: 16–20.

Strophomena impressa Munthe 1902: 233, figs. 3, 4 *nomen nudum*.

Shaleria ornatella (Davidson) Caster 1939: 34.

Shaleria aff. *ornatella* (Davidson); Bassett and Cocks 1974: 17.

Shaleria (Protoshaleria) ornatella (Davidson) Harper and Boucot 1978: 162, pl. 35: 1–10.

Shaleriella tenuis Nikiforova, Modzalevskaya, and Bassett 1985: 23, pl. 5: 1–6.

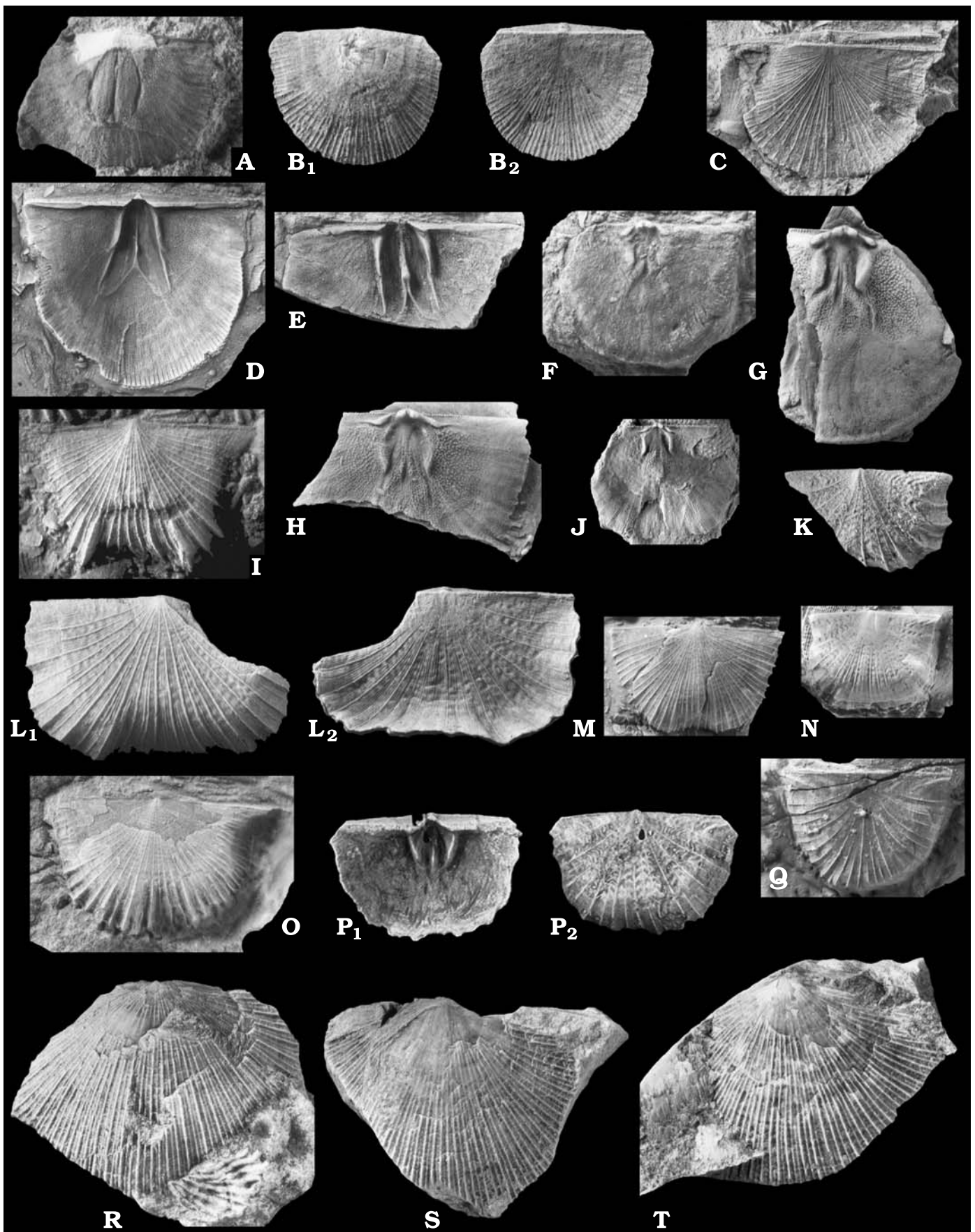
Shaleria (Janiomya) ornatella (Davidson); Rong and Cocks 1994: 661, fig. 11.

Remarks.—The type locality, from which the lectotype was selected by Cocks (1978: 129), is from the Upper Ludlow of

Shropshire, England. *Shaleriella tenuis* of Nikiforova et al. (1985), from the Pridoli Skala Horizon of Podolia, has dorsal side septa, whose presence is characteristic of *Shaleria* rather than their absence from *Shaleriella*, and should thus be reassigned to the former genus, and is also placed here within the synonymy of *S. (S.) ornatella*. *S. (S.) tenuis* is also listed from the Ludlow–Pridoli of Belarus by Modzalevskaya and Pushkin (1989: 96), but cannot be confirmed without illustration. There is considerable variation in the ornamentation of the species: some specimens have zig-zag rugellae between some, or in some cases nearly all, of the parvicostellae, whilst in some populations these rugellae are rare or even apparently absent. The convexity also varies from flat to medium, but the profile does not show the geniculation or rather square anterior outline present in *S. (S.) ezerensis* (see below). Harper and Boucot (1978:162) erected the separate subgenus *Protoshaleria* within *Shaleria*, with *S. ornatella* as its type species, on the basis that *Protoshaleria* had a single pair of “brace plates” in contrast to the “second pair of brachial ridges which flank the brace plates and are almost identical to them, and commonly two pairs of parallel-sided diductor tracks in the pedicle valve”. However, as can be seen from the excellent illustrations of the type species of *Shaleria* in Harper (1973: 13), these features are variably developed in the topotype population and thus a separate subgenus is not warranted. As discussed in Bassett and Cocks (1974: 17), Munthe (1902) figured specimens from Gotland as “*Strophomena impressa* Lindström”; however, that name was never published by Gustav Lindström and the species name is a *nomen nudum*.

From Baltica *Shaleria* aff. *ornatella* (Davidson, 1871) was identified from the Ludlow Hemse, Eke and Burgsvik Beds of Gotland by Bassett and Cocks (1974: 17), but this is now here revised to *S. (S.) ornatella*. The same species name also includes the specimens termed *Shaleriella tenuis* Nikiforova et al. (1985: 23), from the Pridoli of Podolia. *Shaleria* is widespread in the East Baltic Upper Ludlow and Pridoli. It was illustrated under the name of *Brachyprion dzwinogradensis* by Rybnikova (1967), but, as discussed above under *Brachyprion*, that species name is a *nomen dubium*. We have identified *Shaleria* from the boreholes,

Fig. 6. **A.** *Shaleria (Shaleriella) ezerensis* (Rybnikova, 1966) (= *S. (S.) delicata* Harper and Boucot, 1978), NHM BB22923, Hemse Beds (Ludlow), Millklint, Gotland, Sweden, × 2. **B–H.** *Shaleria (S.) ornatella* (Davidson, 1871). **B.** VU B10045, ventral (B_1), and dorsal (B_2) views of a conjoined shell, Lapès Formation (Pridoli), Krekenava-7, 574.8 m, × 2. **C.** VU B20493, dorsal exterior, Jūra Formation (Pridoli), Sutkai-87, 623.8 m, × 2. **D.** VU B10081, ventral interior, Kelmė-Rietavas Beds of Jūra Formation (Pridoli), Šešuvis-11, 1117.5 m, × 2. **E.** VU B20492, ventral interior, Jūra Formation (Pridoli), Sutkai-87, 623.6 m, × 2. **F.** VU B10046, dorsal interior, Lapès Formation (Pridoli), Krekenava-7, 574.8 m, × 2. **G.** VU B10053, dorsal interior, Jūra Formation (Pridoli), Sutkai-87, 624.7 m, × 3. **H.** VU B10052, dorsal exterior, Jūra Formation (Pridoli), Sutkai-87, 624.7 m, × 3. **I–P.** *Shaleria (Shaleriella) ezerensis* (Rybnikova, 1966). **I.** LMNH Br. 30/12, holotype, ventral exterior, Jūra Formation (Pridoli), Ezere borehole, Latvia, 926.8 m, × 3. **J.** LMNH Br. 30/14, dorsal interior, Jūra Formation (Pridoli), Ezere borehole, Latvia, 926.8 m, × 3. **K.** VU B20494, ventral exterior, Mituva Formation (Ludfordian), Šešuvis-11, 1323.0 m, × 3. **L.** VU B10084, ventral (L_1) and dorsal (L_2) views of a conjoined shell, Mituva Formation (Ludfordian), Virbalis-5, 881.0 m, × 4. **M.** VU B10085, ventral exterior, Mituva Formation (Ludfordian), Virbalis-5, 878.3 m, × 2. **N.** VU B10086, ventral exterior, Mituva Formation (Ludfordian), Virbalis-5, 871.0 m, × 2. **O.** VU B10082, ventral exterior, Varniai Beds of Minija Formation (Pridoli), Šešuvis-11, 1150.0 m, × 2. **P.** VU B21131, ventral interior (P_1), and exterior (P_2), Pagėgiai Formation (Ludfordian), Milaičiai-103, 1213.95 m, × 4. **Q.** *Strophonella euglypha* (Dalman, 1828), VU B21102, ventral exterior, Šešupė Beds of Dubysa Formation (Gorstian, *L. scanicus*–*L. progenitor* Zone), Virbalis-5, 969.8 m, × 1.5. **R–T.** *Morinorhynchus rubeli* sp. nov. **R.** VU B20503, ventral exterior, Šilalė Beds of Minija Formation (Pridoli), Bebirva-108, 969.0 m, × 3. **S.** VU B20504, dorsal exterior, Šilalė Beds of Minija Formation (Pridoli), Bebirva-108, 972.5 m, × 3. **T.** VU B20502, ventral exterior, Šilalė Beds of Minija Formation (Pridoli), Bebirva-110, 924.4 m, × 3. →



such as Gėluva-114 and others, from central Lithuania and Šešuvis-11 and others from western Lithuania, as *S. (S.) ornatella*.

Distribution.—The distribution of *S. (S.) ornatella* in Lithuania is from the Vievis and Lapės formations (Pridoli) in east Lithuania; Neris, Mituva, Ventspils (Ludfordian), Miniija and Jūra (Pridoli) formations in central Lithuania; upper part of the Rusnė Formation, Mituva, Ventspils, Pagėgiai (Ludfordian), Miniija and Jūra (Pridoli) formations in west Lithuania (Appendix).

Shaleria (Shaleriella) ezerensis (Rybnikova, 1966)

Figs. 5P, 6A, I–P.

Brachypriion ezerensis Rybnikova 1966: 80, pl. 1: 9, 10.

Brachypriion ezerensis Rybnikova; Rybnikova 1967: 193, pl. 21: 1, 2.

Shaleriella delicata Harper and Boucot 1978: 161, pl. 34: 11–25, 29.

Shaleriella delicata Harper and Boucot; Cocks and Rong 2000: 302, fig. 192: 2a–c.

Remarks.—The type locality of *S. (S.) ezerensis* is from the Ezere borehole of Latvia from 926.8 m from the Pridoli Jūra Formation (Rybnikova 1966, 1967). From her figured dorsal interior (Rybnikova 1967, pl. 21: 2A) it should also be referred to *Shaleria*, but the species shows the characteristics of the subgenus *Shaleriella* discussed above. We consider it the same as the species described as the type species of *Shaleriella* by Harper and Boucot (1978). There is some confusion as to the type locality of *S. delicata*; the caption to the figure of the holotype states “Eke Marl, Gotland, USNM loc. 10039.” That locality (Harper and Boucot 1978: 63) is stated to be “Hemse Marl, Gogs Lau parish, north-road-ditch, Ronehamn quadrangle, Gotland.” All Harper and Boucot’s (1978: pl. 34) figured specimens come from either USNM loc 10038 or USNM loc 12834; the latter is within the Eke Beds. Material from both the Hemse Marl and the immediately overlying Eke Marl in the Natural History Museum both contain shaleriids similar to the holotype of *S. delicata*, and we assume here that the Hemse Marl at USNM loc. 10039 is correct, with the plate caption an error. *S. delicata* was listed from the Ludlow of Belarus by Modzalevskaya and Pushkin (1989: 95), but is considered here as a synonym of *S. (S.) ezerensis*.

Distribution.—In Lithuania the species is here recorded from the Lapės Formation (Pridoli) in east Lithuania; Dubysa, Neris, Mituva, Ventspils (Gorstian and Ludfordian), Miniija and Jūra (Pridoli) formations in central Lithuania; Rusnė (Gorstian), Mituva, Ventspils, Pagėgiai (Ludfordian), Miniija and Jūra formations in west Lithuania (Appendix Table 1).

Family Strophonellidae Caster, 1939

Genus *Eostrophonella* Williams, 1950

Remarks.—The type species is *Eostrophonella davidsoni* (Holtedahl, 1916), from the Lower Llandovery of the Oslo Region. The species was revised by Baarli (1995: 49) and is only known from the Rhuddanian Solvik Formation at Oslo.

Genus *Strophonella* Hall, 1879

Remarks.—The type species is *S. semifasciata* (Hall, 1879) from the Wenlock of Indiana, U.S.A. A long-known Baltic species is *Strophonella euglypha* (Dalman, 1828) from the Wenlock and Ludlow of Gotland and elsewhere, which was revised by Bassett and Cocks (1974: 17) and Bassett (1977: 143). Harper and Boucot (1978: 96) listed *Amphistrophia euglyphoides* Holtedahl, 1916, from the Wenlock of the Oslo region, as a species of *Strophonella*, but, even assuming that the generic assignment is correct, that species requires revision to see whether or not it is truly separate from *S. euglypha*. Modzalevskaya and Pushkin (1989: 94) and Pushkin et al. (1991: 18) identified *S. euglypha* from the Upper Wenlock and Lower Ludlow of Belarus. Rybnikova (1966:87; 1967: 194) identified *Strophonella* “cf. *podolica* (Siemiradzki, 1906)” from the Ludlow of Latvia, but a revision of that species by Kozłowski (1929: 101) established that it was confined to the Lower Devonian Borshchov horizon of Podolia.

We identify all of the Wenlock and Ludlow strophonellids in the Lithuanian boreholes as *Strophonella euglypha* (Fig. 6Q). Its distribution is from the Švenčionys (Telychian), Paprieniai, Jačionys and the Birštonas formations (Sheinwoodian) in east Lithuania; the Riga, Gėluva (Sheinwoodian and Homeric) and Dubysa (Gorstian) formations in central Lithuania; the Dubysa, Rusnė, Pagėgiai (Gorstian and Ludfordian) formations and possibly the Girdžiai Beds of the Jūra Formation (Pridoli) in west Lithuania (Appendix).

Superfamily Plectambonitoidea Jones, 1928

Family Leptestiidae Öpik, 1933

Leangella (Leangella) Öpik, 1933

Remarks.—The species recorded from the Silurian of Baltica are *Leangella scissa* (Davidson, 1871), *Leangella triangularis* (Holtedahl, 1916), and *Leangella segmentum* (Lindström, 1861). *Leangella* was erected by Öpik (1933: 42), with *Plectambonites scissa* var. *triangularis* Holtedahl, 1916, from the Lower Llandovery of the Oslo region as its type. However, Cocks (1970) and Cocks and Rong (1989) did not recognize *L. triangularis* as a separate taxon, putting it within the synonymy of *Leangella scissa*. Later Baarli (1995: 24) distinguished *L. triangularis* as a valid and separate subspecies of *L. scissa* and the only *Leangella* in the Solvik Formation of the Oslo area; however, we do not follow Baarli’s differentiation and identify of all Baltic early Llandovery specimens, including those from the Lithuanian boreholes, as *L. scissa*. It occurs in the Dobelė Formation (Aeronian) in west Lithuania (Figs. 2, 3) in the Kurtuvėnai-161 (1478.9 m) and Šešuvis-11 (1620.1 m) boreholes. Rybnikova (1967: 186) recorded and illustrated *L. scissa* from the Lower and Middle Llandovery of Latvia.

Leangella segmentum is the only known species of the genus from the Wenlock or later rocks of Baltica, its type locality of Djupvik is within the Upper Wenlock Mulde Marl of Gotland, and the lectotype was selected by Cocks (1970:



Fig. 7. *Eoplectodonta* (*E.*) *penkillensis* (Reed, 1917), B20497, Riga Formation (Sheinwoodian, *M. riccartonensis* Zone), eroded bedding plane with the *Clorinda* sp., Vilkaviškis-129, 837.1 m, $\times 3.4$.

163) and the species further revised by Bassett and Cocks (1974: 13). We illustrate here (Figs. 4A–D, 8R–T) specimens which were identified as *L. segmentum* from the Wenlock and Lower Ludlow of the Lithuanian boreholes. The species occurs in the Švenčionys (Telychian), Paprieniai, and Jonava Beds of the Birštonas formations (Sheinwoodian) in east Lithuania; in the Jūrmala (Telychian), Riga and Gēluva formations (Sheinwoodian and Homerian), Šešupė Beds of Dubysa Formation (Gorstian) in central Lithuania; the upper part of the Ragainė, the Siesartis (Homerian), and the lower part of Dubysa and the Rusnė formations (Gorstian) in west Lithuania. For localities see Appendix.

Family Xenambonitidae Cooper, 1956

Genera *Jonesea* Cocks and Rong, 1989 and *Aegiria* Öpik, 1933

Remarks.—The species recorded from the Silurian of Baltica are *Jonesea grayi* (Davidson, 1849) from the Lower Ludlow of Gotland (Bassett and Cocks 1974: 13), *Jonesea aknistensis* (Rybnikova, 1967), and *Aegiria norvegica* Öpik, 1933.

These small plectambonitoids, which can be very abundant at certain horizons from the Late Ordovician to the Ludlow, have often been assigned to *Chonetoidea*, but that genus is now known to be restricted to the Ordovician (Cocks and Rong 2000).

Öpik (1933) erected the genus *Aegiria*, with the type species *A. norvegica* from the Lower Llandovery Solvik Formation of Leangen, Oslo, and which was revised by Baarli (1995: 26). However, *Aegiria* is not known from beds younger than the Lower Llandovery, and is not yet recorded from the East Baltic. Rybnikova (1967: 188) erected the new species *Plectodonta aknistensis*, with the holotype from the Upper Wenlock of the Akniste borehole in Latvia. Unfortunately only exteriors were figured by Rybnikova (1967), and we reillustrate her type specimen here (Fig. 4E), but nevertheless the distinctive outline, profile and angular ribbing of this small species places it without doubt within the genus *Jonesea*. *Plectodonta* itself is known only from the Lower Devonian of Podolia, Ukraine, and its type species was also reillustrated by Cocks and Rong (1989). Although Cocks and Rong (1989: 127) doubtfully referred *Plectambonites aequalis* Teichert (1928), from the Lower Llandovery Tamsalu Formation of Estonia, to *Jonesea*, we now think that that species is more likely to belong to the strophomenoid *Eopholidostrophia* (see above). Thus the only recorded species of *Jonesea* from Baltica, apart from *J. aknistensis*, is the type species, *J. grayi* (Davidson, 1849), whose type locality is in the Wenlock of England. Baltic *J. grayi* has not previously been illustrated, merely listed (e.g., by Modzalevskaya and Pushkin 1989: 96, from the Ludlow of Belarus, and Rubel et al., 1984: 12) from the East Baltic. *Jonesea* occurs in the Lithuanian boreholes

sporadically in the Upper Llandovery, Wenlock and Ludlow: a few specimens are also recorded from the Lower Pridoli (Minija Formation in the Bebirva-110 borehole): we identify it as *J. grayi* by comparison with English material. More revision of the East Baltic material is necessary, but there are few interiors recorded from the East Baltic, and we can only illustrate an exterior here (Fig. 4F). Since the interiors of *J. aknistensis* are not known, we provisionally place the species within the synonymy of the very variable *J. grayi* until more data and specimens become available.

Lithuanian distribution of *Jonesea grayi* is in the Šenčionys (Telychian), Paprieniai (Sheinwoodian) and Jonava Beds of Birštonas formations (Sheinwoodian) in east Lithuania; the Jūrmala (Telychian), Riga and Gėluva (Sheinwoodian and Homerian) formations in central Lithuania; the Dobelė (Aeronian), Jūrmala (Telychian), Riga, Ragainė and Siesartis (Sheinwoodian and Homerian), Rusnė, Dubysa, Mituva and Pagėgiai (Gorstian and Ludfordian) and Minija (Lower Pridoli) formations in west Lithuania (Appendix)

Family Sowerbyellidae Öpik, 1930

Remarks.—Sowerbyellidae in the Silurian of Baltica include only one genus *Eoplectodonta* Kozłowski, 1929, with two subgenera, the nominal subgenus *Eoplectodonta* (*Eoplectodonta*) and *Eoplectodonta* (*Ygerodiscus*) Havliček, 1967.

Genus *Eoplectodonta* Kozłowski, 1929

Subgenus *Eoplectodonta* (*Eoplectodonta*)

Kozłowski, 1929

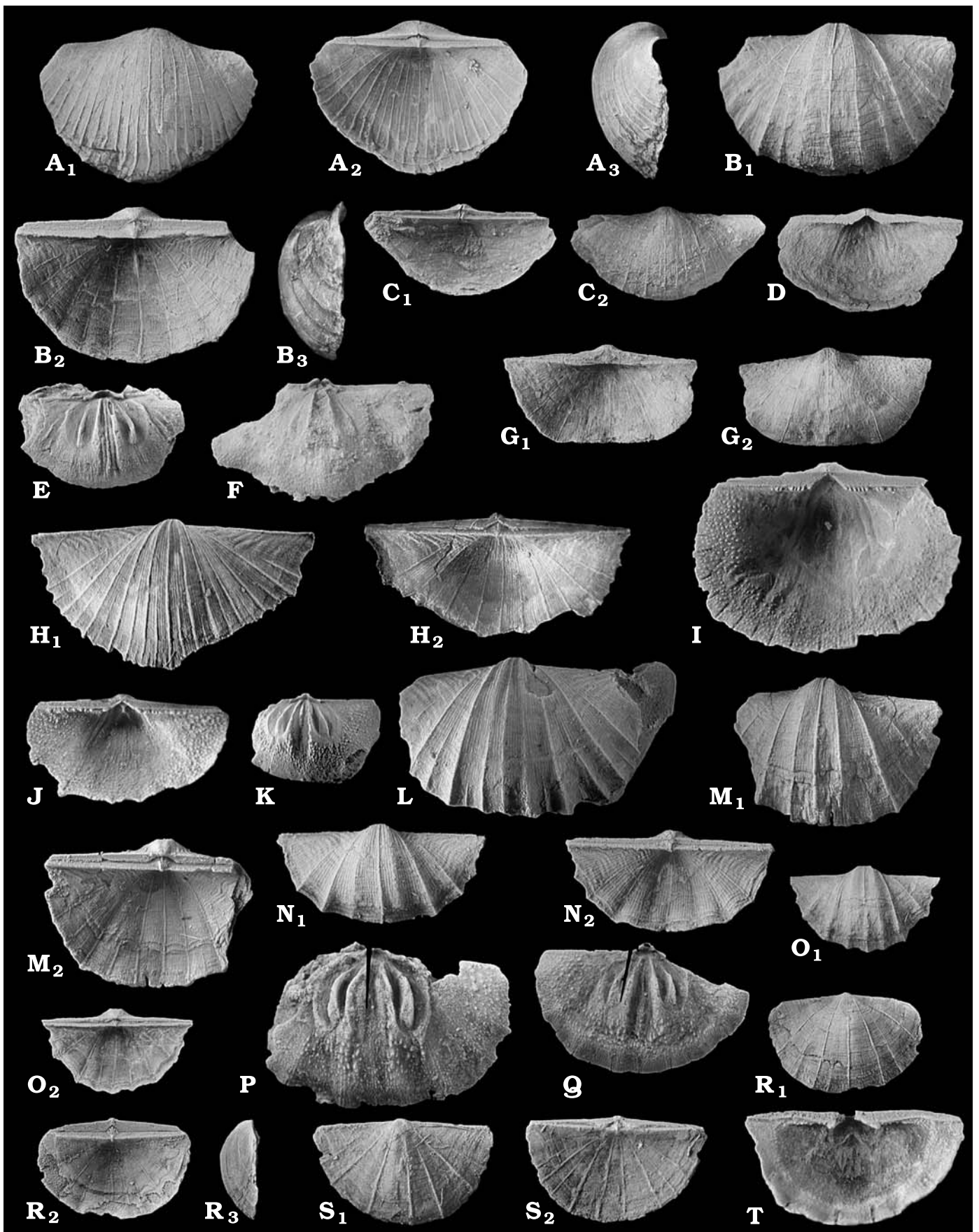
Remarks.—Kozłowski (1929) erected *Eoplectodonta* with the type species *Sowerbyella praecursor* Jones, which was later placed into the synonymy of *Orthis duplicata* J. de C. Sowerby (1839) by Cocks (1970); both species are from the early Llandovery of the Llandovery type area, Wales. From Baltica, the following species have been recorded: *E. (E.) duplicata* (J. de C. Sowerby, 1839), *E. (E.) duvalii* (David-

son, 1847), *E. (E.) exceptionis* (Rybnikova, 1967), *E. (E.) penkillensis* (Reed, 1917), *E. (E.) transversalis* (Wahlenberg, 1818), and *E. (E.) jongensis* Baarli, 1995, which will now be considered in turn.

We have recognised *Eoplectodonta* (*Eoplectodonta*) *penkillensis* (Reed, 1917) as common in the East Baltic (Fig. 7); this species was originally described from the Penkill Formation of Girvan, Scotland and revised by Cocks (1970). Most of the Lithuanian specimens are small, with an average width of less than 6 mm. They occur in the strata near the middle of the Llandovery and the bottom of the Wenlock: Dobele, Jūrmala and Riga formations in the central Lithuania and Rasytė Formation in the west Lithuania (Figs. 7, 8G; occurrences see in Appendix). Cocks and Baarli (1982) have also determined the species from the Telychian Vik and Bruflat formations of the Oslo region, Norway.

E. (E.) transversalis is known only from Telychian rocks in Gotland—the differences between it and *E. (E.) penkillensis* were discussed by Cocks (1970). Despite a record of *E. (E.) transversalis* by Modzalevskaya and Pushkin (1989) from the Llandovery of the Brest Depression of Belarus, this was subsequently revised (Pushkin et al. 1991) to *E. (E.) penkillensis*, and thus *E. (E.) transversalis* is not known from the East Baltic. Baarli (1995) erected the subspecies *E. transversalis jongensis* from the Aeronian Rytteråker Formation of the Oslo region, Norway: however, her statistics only compared that taxon with *E. duplicata*. The length/width ratios of *E. jongensis*, as seen in her figured specimens, are too wide to be included within *E. (E.) transversalis*, and *E. jongensis* therefore needs further detailed consideration in relation to the other Aeronian species of *Eoplectodonta*, such as those listed by Cocks (1970). Not many Aeronian specimens of *E. (Eoplectodonta)* have been recorded from Lithuania, and those that we have appear similar to *E. (E.) penkillensis*. *E. (E.) exceptionis* is known only from late Rhuddanian *Coronograptus cyphus* and early Aeronian *C. gregarius*

Fig. 8. A–F. *Eoplectodonta* (*E. duvalii*) (Davidson, 1847). A. VU B10069, ventral (A₁), dorsal (A₂), and lateral (A₃) views of a conjoined shell, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* biozone), Butkūnai-241, 493.2 m, × 2.5. B. VU B10039, ventral (B₁), dorsal (B₂), and lateral (B₃) views of a conjoined shell, Riga Formation (Homerian, *M. testis* biozone), Gėluva-99, 882.4 m, × 5. C. VU B19562, ventral (C₁), and dorsal (C₂) views of a conjoined shell, Jonava Beds of Birštonas Formation (Sheinwoodian, *K. ranuliformis* biozone), Svėdasai-252, 472.8 m, × 2.5. D. VU B20158, ventral interior, Sutkai Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* biozone), Butkūnai-241, 516.2 m, × 3. E. VU B10070, dorsal interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* biozone), Butkūnai-241, 493.2 m, × 3. F. VU B19810, dorsal interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* biozone), Graužai-105, 776.0 m, × 5. G. *Eoplectodonta* (*E. penkillensis*) (Reed, 1917), VU B10038, dorsal (G₁), and ventral (G₂) views of a conjoined shell, Jūrmala Formation (Telychian, *M. griestonensis*–*O. spiralis* biozone), Gėluva-99, 1003.4 m, × 5. H, I. *Eoplectodonta* (*E. exceptionis*) (Rybnikova, 1967). H. LMNH Br. 30/112, holotype, ventral (H₁), and dorsal (H₂) views of a conjoined shell, Aeronian (*C. gregarius*–*D. triangulatus* biozone), Choldre borehole (Latvia), 336.2 m, × 4. I. LMNH Br. 30/116, ventral interior, Rhuddanian (*C. cyphus* biozone), Choldre borehole (Latvia), 352.4 m, × 4. J–L. *Eoplectodonta* (*Ygerodiscus undulata*) (Salter, 1848) (= *E. propinqua* Rybnikova, 1967). J. LMNH Br. 30/121, ventral interior, Rhuddanian (*C. cyphus* biozone), Choldre borehole, Latvia, 367.2–367.6 m, × 4. K. LMNH Br. 30/119, dorsal interior, Rhuddanian (*C. cyphus* biozone), Choldre borehole, Latvia, 363.7 m, × 3. L. LMNH Br. 30/124, holotype, ventral exterior, Rhuddanian (*C. cyphus* biozone), Choldre borehole, Latvia, 352.4 m, × 4. M–Q. *Eoplectodonta* (*Ygerodiscus bella*) sp. nov. M. VU B10040, holotype, ventral (M₁), and dorsal (M₂) views of a conjoined valves, Riga Formation (Homerian, *M. testis* biozone), Gėluva-99, 890.6 m, × 5. N. VU B10054, ventral (N₁), and dorsal (N₂) views of a conjoined valves, Riga Formation (Sheinwoodian, *C. radians*–*M. flexilis* biozone), Sutkai-87, 843.9 m, × 5. O. VU B10078, ventral (O₁), and dorsal (O₂) views of a conjoined valves, Riga Formation (Homerian, *M. testis* biozone), Gėluva-114, 998.0 m, × 3. P. VU B21052, dorsal interior, Gėluva Formation (Homerian), Pilviškiai-143 borehole, 799.4 m, × 5. Q. VU B21051, dorsal interior, Gėluva Formation (Homerian), Pilviškiai-143, 799.4 m, × 5. S–U. *Leangella* (*L. segmentum*) (Lindström, 1861). R. 10063, ventral (R₁), dorsal (R₂), and lateral (R₃) views of a conjoined shell, Sutkai Beds of Paprieniai Formation (Sheinwoodian, *K. ranuliformis* biozone), Butkūnai-241, 517.2 m, × 3. S. VU B10041, ventral (S₁), and dorsal (S₂) views of a conjoined shell, Riga Formation (Homerian, *G. nassa* biozone), Gėluva-99, 873.7 m, × 5. T. VU B20022, ventral interior, Vilkija Beds of Paprieniai Formation (Sheinwoodian), Graužai-105, 768.0 m, × 5.



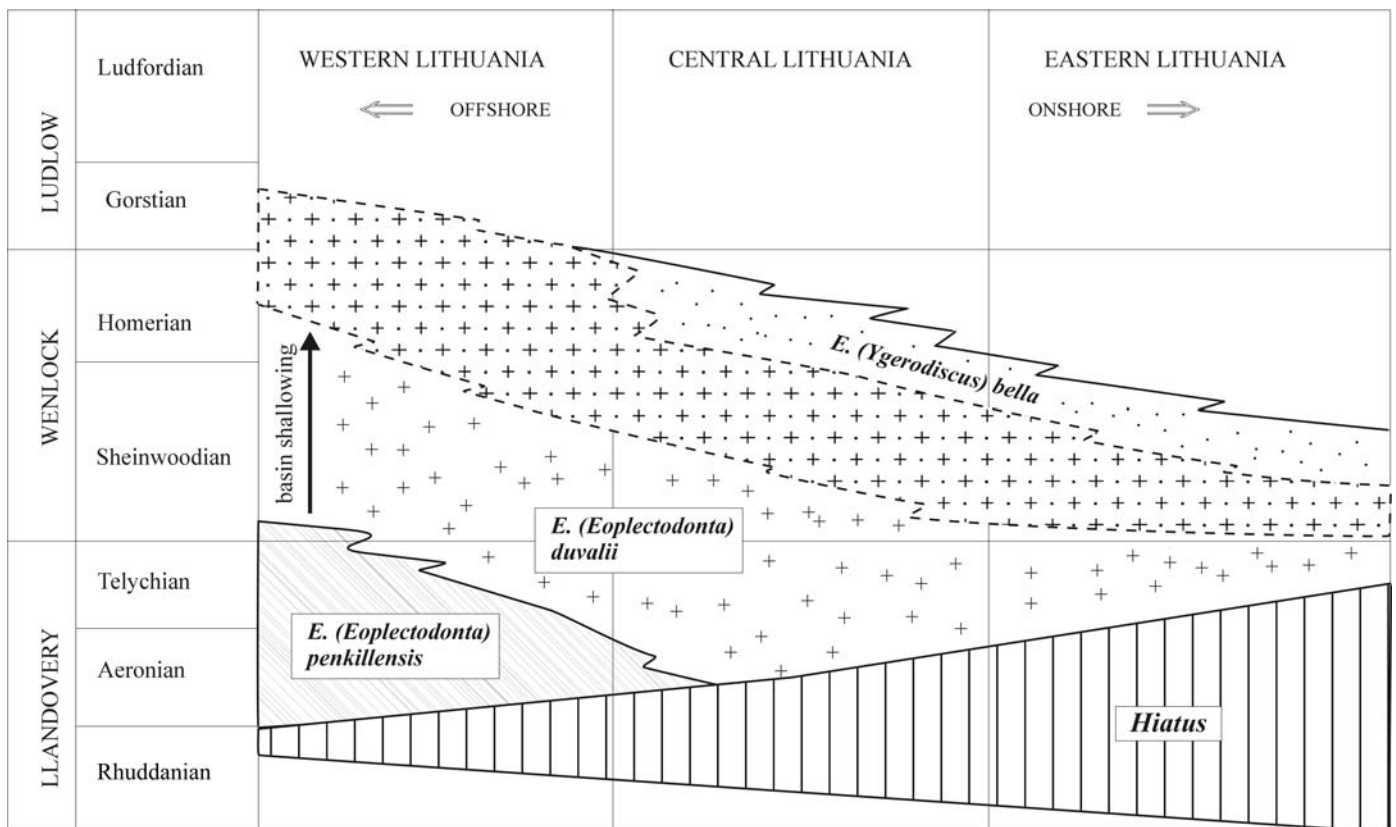


Fig. 9. Diagram showing the relative dispositions of *E. (Eoplectodonta)* and *E. (Ygerodiscus)* from west to east in the East Baltic platform.

zones calcareous nodular limestones in the Choldre borehole of Latvia (Rybnikova 1967: 189), and Rybnikova's types are reillustrated here (Fig. 8H, I). This interval is represented only by graptolitic shales in Lithuania, and thus *E. (E.) exceptionis* is not recorded there.

At higher levels in various boreholes, small specimens of *Eoplectodonta* are found abundantly in the Wenlock; however the preservation is not good enough to identify most of them more narrowly than as *Eoplectodonta (E.)* sp., although a few larger specimens (Fig. 8A–F), e.g., from 926–930 m in the Pilviškiai-141 borehole, we identify as *E. (E.) duvalii*. In slightly younger beds in the same sequence, some specimens show incipient undulations, although these are not strong enough to warrant attribution to *Ygerodiscus*. In general, the size of the specimens increases towards the shoreline and in time. The diachronous sequences of *E. (E.) penkillensis*, *E. (E.) duvalii* and *E. (Ygerodiscus) bella* sp. nov. (see below) suggest their distribution to be rather environmentally than evolutionarily controlled and show the overall basin shallowing in time, especially in the eastern and central Lithuania (Fig. 9).

Nikiforova (1954: 76) identified "*Sowerbyella transversalis* var. *lata* Jones" from the Wenlock and Ludlow of Podolia; however, we include her material within *E. (E.) duvalii*. Alichova et al. (1954: 36, pl. 22: 6, 7) described "*Sowerbyella transversalis* (Wahlenberg) var. *lata* Jones,

1928" from the Wenlock of southern Lithuania; judging from the figures this species should also be attributed to *E. duvalii*. From Lithuania we have identified *Eoplectodonta (E.) duvalii* from the Švenčionys (Telychian), Paprieniai and Birštonas (Sheinwoodian) formations in the east Lithuania; Jūrmala (Telychian), Riga and Gēluva (Sheinwoodian–Homerian) formations and in the Šešupė Beds of Dubysa Formation in the central Lithuania; Ragainė, Siesartis (Sheinwoodian–Homerian) and Dubysa (Gorstian) formations in the west Lithuania (Appendix).

Subgenus *Eoplectodonta (Ygerodiscus)* Havlíček, 1967

Remarks.—The type species of the subgenus is *E. (Y.) undulata* (Salter in Phillips and Salter, 1848), from the Middle Llandovery of Wales, revised by Cocks (1970). There is disagreement whether *Ygerodiscus* should be recognised as a separate taxon. Temple (1987) put *E. (Y.) undulata* within the synonymy of *E. (E.) duplicata*, the type species of *Eoplectodonta (Eoplectodonta)*; however, whole populations of plectambonitoids appear to have the undulose shell so typical of *Ygerodiscus*, and so we retain the name as a subgenus here within *Eoplectodonta* so as to be able to distinguish such specimens. From Baltica *E. (Y.) undulata* has been recorded (as *Sowerbyella undulata*) from the Middle Llandovery of the Choldre borehole, Latvia, by Rybnikova (1967: 187), but it is

doubtful from her illustrations that the specimens are actually *E. (Ygerodiscus)* and are more probably *E. (Eoplectodonta)* and possibly *E. (E.) penkillensis*. Rybnikova (1967: 191) also described the species *Plectodonta propinqua* (from the Lower Llandovery of the same borehole), which from her illustrations should be attributed to *E. (Ygerodiscus)*, but we consider that *E. (Y.) propinqua* is probably a junior synonym of *E. (Y.) undulata* (Fig. 8J–L). From Lithuania we have recognised undulate *Eoplectodonta* from the lower Wenlock upwards, with the quantity becoming greater in the middle and upper Wenlock, this species is described below as *Eoplectodonta (Ygerodiscus) bella* sp. nov. Rare shells in the Riga Formation (lower Homeric) can be identified as *E. (Y.) cornuta* (Davidson, 1883), whose distribution is also listed in the Appendix.

Eoplectodonta (Ygerodiscus) bella sp. nov.

Fig. 8M–Q

Holotype: VU B10040, a dorsal valve interior (Fig. 8M), from the Wenlock Riga Formation at 890.6m in the Gėluva-99 borehole, Lithuania.

Derivation of the name: From Latin *bellus*, beautiful.

Distribution.—Vilkija Beds of Paprieniai Formation (Sheinwoodian) and Jonava Beds of Birštonas Formation (Sheinwoodian) in east Lithuania; Riga and Gėluva formations (Sheinwoodian and Homeric) in central Lithuania; Siesartis (Homeric), Dubysa and Rusnė (Gorstian) formations in west Lithuania (Figs. 2, 3, 9). For localities see Appendix.

Diagnosis.—*Ygerodiscus* of small size with relatively high length/width ratio, sharp ridge crests, some of which are variably enhanced: erect and open delthyrium.

Description.—Exterior with evenly convex ventral valve with enhanced umbo, and strongly concave dorsal valve: semicircular outline with small alae slightly extending laterally: small pair of chilidial plates, but with delthyrium otherwise open to reveal cardinal process. Unequally parvicostellate ornament, with enhanced central costella and between three and six equally enhanced costella to each side of it; the enhanced costellae are at the crest of undulations which originate near the umbo and continue to the anterior: in larger specimens smaller subsidiary undulations and slightly enhanced costellae are only present anteriorly. Ventral interior with denticulate hinge line, weak divergent dental plates: well-impressed diductor muscle field enclosing less well-impressed lanceolate adductor scars separated by a variably developed very thin myophragm. Dorsal interior with fossettes on hinge line; prominent trifid undercut cardinal process between well-developed flaring socket plates which antero-laterally extend into the lateral edges of the variably-developed bema which bears two pair of side septa, with the central pair longer than the lateral pair and extending to two-thirds valve length: the exterior undulations can be seen internally: mantle canal system not known.

Discussion.—The Wenlock Lithuanian material is of smaller size than *E. (Y.) undulata* and also the contemporary *E. (Y.) novemplicata* (Havliček, 1967) from Perunica, which also has a rather different ribbing style, and we differentiate the

East Baltic material here as *E. (Y.) bella* sp. nov. The average width is 9.1 mm and the maximum (estimated) width is 11 mm, in contrast to the 16 mm (Cocks 1970) achieved by *Y. undulata* and 15 mm by *E. (Y.) novemcostata*. *E. (Y.) undulata* also has much more prominently developed lateral alae than *E. (Y.) bella*, leading to a smaller length/width ratio. The only formally erected species of *E. (Ygerodiscus)* from rocks younger than the Llandovery is *E. (Y.) cornuta* (Davidson, 1883) from the Wenlock of England, which was revised by Bassett (1974: 90); however, that species has a very distinctive pair of shell projections anteriorly, and thus that name cannot be used for the bulk of the Lithuanian borehole specimens, although we record true *E. (Y.) cornuta* rarely from the Riga Formation (Lower Homeric) in boreholes Gėluva-99 (890.6 m) and Pilviškiai-141 (908.0 and 866.5 m).

Order Orthotetida Waagen, 1884

Superfamily Orthotetoidea Waagen, 1884

Family Chilidiopsidae Boucot, 1959

Genus *Coolinia* Bancroft, 1949

Remarks.—The type species of the genus is *Coolinia applanata* (Salter in M'Coy 1846), originally described from the Telychian of Ireland, and which has also been recorded and illustrated from the Upper Llandovery Bruflat Formation of the Oslo region by Cocks and Baarli (1982: 85) and as *C. aff. applanata* from the Upper Llandovery of Belarus by Modzalevskaya and Pushkin (1989: 93). The most common species recorded from the Wenlock and Ludlow of Gotland is *Coolinia pecten* (Linnaeus, 1758), whose Lower Wenlock type locality is either from the Upper Visby or the Högklint Beds of Gotland (Bassett and Cocks 1974: 18). A form identified as *C. pecten* was illustrated from the Lower Llandovery Juuru Formation of Estonia by Sokolskaya (1954:90) which is certainly *Coolinia* but the species (rather than the genus) is not known from beneath the Wenlock elsewhere and we identify the material from the illustrations as *Coolinia* sp., following Rubel et al. (1984: 15). *Coolinia deflexa* was described within *Fardenia* from the Wenlock of Podolia by Tsegelnyk (1976: 75), but it has the large chilidium characteristic of *Coolinia* and it is uncertain from the published illustrations whether or not it is a synonym of *C. pecten*. The *Schellwienella* sp. of Rybnikova (1967: 195), from the Ludlow of Latvia, was reassigned to *Morinorhynchus orbignyi* (Davidson, 1848) by Rubel et al. (1984: 16), but re-examination of Rybnikova's 1967: pl. 21: 7 shows her material to lack the strong pseudodeltidium of *Morinorhynchus* and the material is reassigned here to *Coolinia*.

Distribution.—The genus occurs rarely in the Lithuanian boreholes, but it is not abundant and often fragmentary, and is identified here as *Coolinia* sp. Its distribution is the Paprieniai, Jačionys and Jonava Beds of the Birštonas formations (Sheinwoodian) in east Lithuania; Riga (Sheinwoodian and lower Homeric) Formation in central Lithuania; upper part of the Ragainė Formation, Siesartis (Homeric), Dubysa,

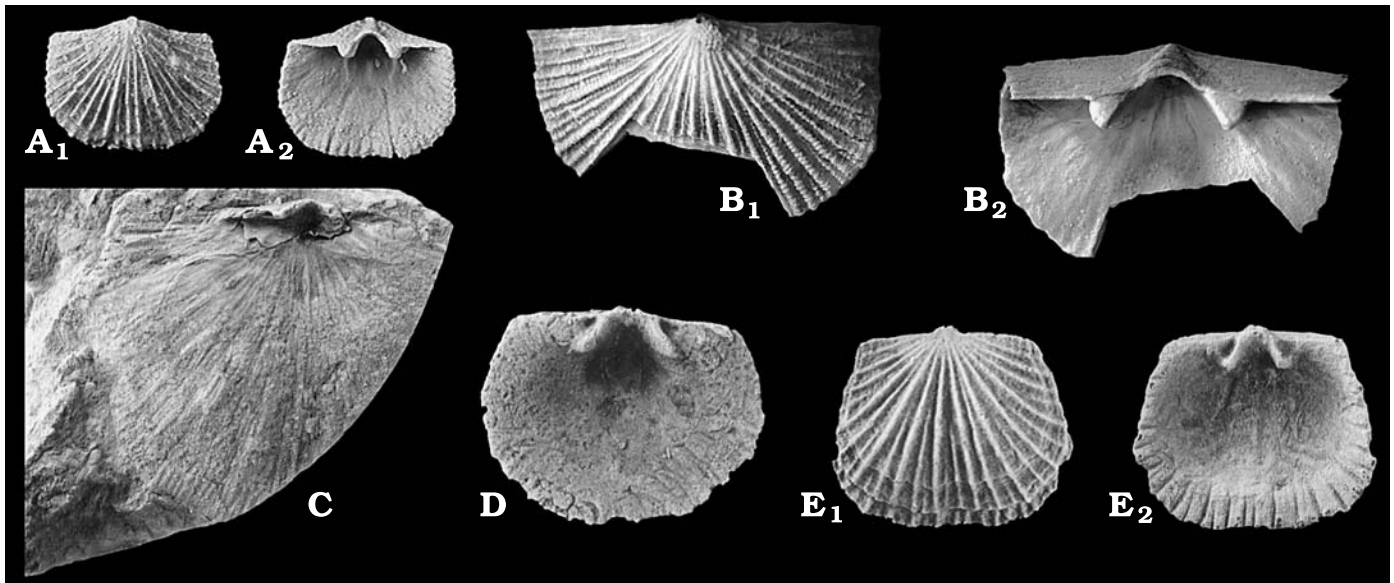


Fig. 10. *Morinorhynchus rubeli* sp. nov. A. VU B20499, ventral exterior (A₁), and interior (A₂), Nova Beds of Dubysa Formation (Gorstian–Ludfordian), Šiupyliai-69, 879.4 m, × 6. B. VU B20498, holotype, ventral exterior (B₁), and interior (B₂), Mituva Formation (Ludfordian), Virbalis-5, 881.5 m, × 4. C. VU B20501, dorsal interior, Ventspils Formation (Ludfordian), Kurtuvėnai-162, 1097.2 m, × 2. D. VU B20500, dorsal interior, Vievis Formation (Pridoli), Graužai-105, 580.9 m, × 5. E. VU B10146, dorsal exterior (E₁), and interior (E₂), Mituva Formation (Ludfordian), Virbalis-5, 887.45 m, × 5.

Rusnė, Mituva and Pagėgiai (Gorstian and Ludfordian) formations in west Lithuania (Appendix).

Fardenia Lamont, 1935

Remarks.—The type species is from the Ashgill of Girvan, Scotland. The chief difference between *Coolinia* and *Fardenia* lies in the large chilidium present in the former and lacking in the latter. *Fardenia oblectator* Baarli, 1995, from the Lower Llandovery Solvik Formation of the Oslo region (Baarli 1995: 51), can be attributed to the genus. “*Fardenia flabellata*” was described by Beznosova (1985) from the Wenlock of north-east Timan, but the illustrations of the species in Beznosova (1994: pl. 1: 3, 4) do not show the distinguishing features, and we treat the species here as a *nomen dubium*.

Genus *Morinorhynchus* Havliček, 1965

Remarks.—The type species of the genus is *M. dalmanelliformis* Havliček, 1965, from the Ludlow of Bohemia. The genus differs from *Coolinia* in having a large pseudodeltidium and a small or even absent pair of chilidial plates, in contrast to the latter whose delthyrium is filled by only a vestigial pseudodeltidium (or deltidial plates) and a large chilidium. From Baltica are recorded the species *Morinorhynchus adnatus* (Hedström, 1917), whose type locality is in the Wenlock Halla Beds of Gotland, revised by Bassett and Cocks (1974: 21), *Morinorhynchus crispus* (Lindström, 1861), whose type locality is in the Ludlow Hemse Beds of Gotland, revised by Bassett and Cocks (1974: 20), and which is also recorded from the Ludlow of Podolia by Nikiforova et al. (1985: 26), and *Morinorhynchus wieniukowi* (Kozłowski,

1929), whose type locality is in the Pridoli Rashkov Beds of the Skala Horizon of Podolia, and which was revised by Nikiforova et al. (1985: 26). From the Upper Wenlock of the Welsh Borderland, England, *Morinorhynchus orbignyi* (Davidson, 1848) is known: this species was revised by Bassett (1974: 98), but is not known from Baltica. *M. crispus* and *M. wieniukowi* (Kozłowski), both revised by Nikiforova et al. (1985), occur in the Ludlow and Pridoli of Podolia. *Morinorhynchus cf. dalmanelliformis* Havliček, 1965 was recorded by Sapelnikov et al. (1975: 9, pl. 1: 1–4) and Sapelnikov and Mizens (1991: 94, pl. 38: 1–4) from the Lower Pridoli of the eastern slope of the northern Urals, but we have not revised those records here.

Morinorhynchus rubeli sp. nov.

Figs. 6R–T, 10.

Fardenia cf. *attenuata* Amsden; Nikiforova 1970: 99, pl. 1: 5–12 (non Amsden 1951).

Holotype: VU B20498 (Fig. 10B) from the Upper Ludlow Mituva Formation, at 881.5 m depth in the Virbalis-5 borehole, Lithuania.

Derivation of name: After Madis Rubel, in honour of his work on Baltic brachiopods.

Distribution.—Neris (Ludfordian), Vievis and Lapės (Pridoli) formations in east Lithuania; Ventspils (Ludfordian), Miniija and Jūra (Pridoli) formations in central Lithuania; Nova Beds of Dubysa Formation and upper part of Rusnė Formation (Gorstian–Lower Ludfordian), Mituva, Ventspils, Pagėgiai (Ludfordian), Miniija and Jūra (Pridoli) formations in west Lithuania (Appendix).

Diagnosis.—*Morinorhynchus* with plastic shell shape and outline; originally biconvex but adult parts of ventral valve

varying from convex to concave; relatively strong socked plates with relatively small angle of separation; variable ornament.

Description.—Exterior: profile biconvex in juveniles but ranging in adults from biconvex to a largely convex dorsal valve with a convex, irregularly planar or in part even concave ventral valve: outline subcircular with weakly developed alae, maximum width on average at half to two-thirds valve length. Characteristic pseudodeltidium strongly developed, very small low chilidial plates are present, but are scarcely visible in many specimens. Ornament of subequal parvicostellae with new costellae arising by intercalation: variably-developed growth-lines sometimes accentuated to form fine concentric filae. Ventral interior with flaring teeth: muscle field very weakly impressed and merging anteriorly with valve floor: mantle canals not known. Dorsal interior with substantial upstanding cardinal process partly projecting over the valve posterior margin and conjoined laterally to substantial recurved socket plates; muscle field poorly impressed, but with suboval adductor scars present in some specimens: mantle canals not known.

Discussion.—A key feature, which distinguishes the new species from all others in the genus is the plastic shape of the shell. Whilst originally biconvex in smaller specimens, like the type species *M. dalmanelliformis*, and also *M. adnatus*, *M. crispus*, *M. orbignyi*, and *M. wieniukowi*, in adult specimens of *M. rubeli* the pedicle valve can vary from convex to concave, but through all combinations of the two in different parts of the same individual shell. We presume from these inconstant shapes that the adult shell lay subparallel to, and was influenced in form by, the ocean floor; rather than, as in the other species, being more erect and therefore more independent of the ocean floor topography. In addition, the socket plates in *M. rubeli* are more strongly developed, and at a less acute angle of separation, in contrast to the more antero-laterally flaring socket plates of *M. adnatus*, *M. crispus*, *M. dalmanelliformis*, and *M. orbignyi*: the dorsal interior of *M. wieniukowi* is not known. Various authors have used the “distinctive” concentric radial ornamentation to differentiate between different species of *Morinorhynchus*; however, we have found (following examination of many specimens of the genus from the Welsh Borderland and Gotland, as well as the Lithuanian boreholes) that there is considerable variation of this attribute within populations and cannot use it to characterise the various species. *Morinorhynchus miniparvicostellus* from the Wenlock of Arctic Canada (Zhang 1989; Jin and Chatterton 1997) is relatively wider than the new species and has a higher degree of parvicostellation in the ornament. *M. subcarinatus* from the Ludlow of Nevada is also more parvicostellate than *M. rubeli* and has finer ornament: also the socket plates diverge at a wider angle (Johnson, Boucot, and Murphy 1976). *M. variatus* from the Pridoli of Urals (Brevel and Breivel 1988) differs from the new species in convex brachial valve and wider angle of separation of socket plates.

Many *Morinorhynchus* from northern and eastern parts of Baltica have been attributed as being related to “*M. attenuata* Amsden”. These records include the *M. cf. attenuata* of Sapelnikov and Mizens (1991: 93, pl. 9: 13, 14), Modzalevskaya, (1980: 82, pl. 1: 1, 2; 1997: 40, pl. 7: 3, 4), from the Wenlock to Pridoli beds of Vaigach Island, the Polar Urals west slope, Chernov Range (Pechora), and Dolgij island. Nikiforova (1970: 99, pl. 1: 5–12) identified *Fardenia cf. attenuata* from the Ludlow and Pridoli of Vaigach Island. However, Amsden’s species *M. attenuata*, whose type is from the Wenlock Henryhouse Formation of Oklahoma, U.S.A. (Amsden 1951) is not an orthotetoid and is actually attributable to the strophomenoid *Mesopholidostrophia*. The Vaigach form identified by Nikiforova and Modzalevskaya is undoubtedly *Morinorhynchus*, as can be seen from the published illustrations of the interareas: we reassign the Vaigach material here to *M. rubeli* sp. nov., and suspect that the other quoted records from north-east Baltica are also that species.

Saughina Bancroft, 1949

Remarks.—The type species is *Saughina pertinax* (Reed, 1917), from the Rhuddanian of Scotland. Williams and Brunton (2000) put the genus into the synonymy of *Fardenia*, but we consider both genera valid and separate here. Baarli (1995: 50) identified and illustrated the subspecies *Saughina pertinax gentilis*, originally described from the Rhuddanian of Wales by Bancroft (1949), from the Lower Llandovery Solvik Formation of the Oslo region. The genus is not definitely known from elsewhere in Baltica. However, “*Fardenia pertinax*” was recorded from the Lower Llandovery of Juzhnyj island, Novaya Zemlya and the Chatanzeyan Peninsula (Modzalevskaya 1985: 60, pl. 1: 3, 4; Sapelnikov and Mizens 1991: 92, pl. 2: 5a, 5b), but we have not seen the relevant material and do not know whether or not it is truly *Saughina*.

Valdaria Bassett and Cocks, 1974

Remarks.—The type and only known species of this distinctive genus is *Valdaria testudo*, described by Bassett and Cocks (1974: 19) from the Lower Wenlock Upper Visby Beds of Gotland. It has not been recorded from elsewhere.

Concluding remarks

Following this review, it is now possible to place the Silurian East Baltic strophomenides and orthotetides in perspective by comparison with those hitherto better-known faunas from the western Baltic areas of Oslo and Gotland and adjacent Avalonia (Wales and the Welsh Borderland of England). It may be declared with confidence that Baltica-Avalonia was a single faunal province during the whole of Silurian time, and that broadly similar brachiopod faunas colonised everywhere between Newfoundland and the Urals, although some

rarer genera and species had a much more restricted geographical range. There were also the same faunal associations, which reflect the contemporary benthic animal communities, throughout the area and the commonest strophomenide and orthotetidean genera within those assemblages are the same, often to the species level, and are attributed to assemblages here.

Eoplectodonta, *Leangella*, and *Jonesea* are the most abundant plectambonitoids, all of which had their local acmes in the deeper-water BA4 and BA5 benthic communities. However, the strophomenoids were far more diverse (although no more abundant) than the plectambonitoids. We recognise 25 named strophomenide genera, with 40 named and at least 12 unnamed species; a substantial diversity. Most occupied ecological niches in mid-shelf BA2 to BA 4 benthic assemblages. More genera are recorded from Norway and Sweden (as well as England in adjoining Avalonia) than from the East Baltic, but that may be a distorted result reflecting both larger and more accessible outcrops in the west than the east as well as more past palaeontological work. We have included a more general and global review of the strophomenoid genus *Shalerialia*, in which we have recognised three subgenera *Shalerialia* (*Shalerialia*), *Shalerialiella*, and *Janiomya* and identified it as the only genus within the family Shalerialiidae. The Orthotetioidea, all of which are within the family Chilidiopsidae, comprise five genera in the Silurian Baltic, of which only *Coolinia* and *Morinorhynchus* are common.

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Appendix

Occurrence of strophomenid and orthotetid brachiopods in Lithuanian boreholes.

	Bebirva-108	Bebirva-110	Butkūnai-150
<i>Eoplectodonta (E.) penkillensis</i> (Reed, 1917)		1128.9–1128.0	1314.1–1292.4
<i>Eoplectodonta (E.) duvalii</i> (Davidson, 1847)		1111.7–1082.5	
<i>E. (Ygerodiscus) bella</i> sp. nov.		1115.4–1082.1	
<i>Leangella scissa</i> (Davidson, 1871)			
<i>Leangella segmentum</i> (Lindstrom, 1861)		1097.0–1077.8	
<i>Jonesea grayi</i> (Davidson, 1849)	1310.2–1078.7	1244.8–1004.3	1320.8–1040.7
<i>Katastrophomena (K.)</i> sp.			
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966		1091.9–1026.2	
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)	1016.8–838.9	1012.5–862.0	917.8–915.8
<i>Amphistrophia (A.) funiculata</i> (M' Coy, 1846)		968.8	
<i>Brachyprion? kurzemensis</i> Rybnikova, 1967		899.6	
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)		966.5–962.4	
<i>Mesoleptostrophia (M.)</i> sp.	1029.2	981.8–916.1	
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)	1133.5	1077.8–943.1	
<i>Shaleria (S.) ornatella</i> (Davidson, 1871)	1032.5–879.8	968.8–859.5	1031.6–849.9
<i>S. (Shaleriella) ezerensis</i> (Rybnikova, 1966)		920.3–914.4	1036.1
<i>Strphonella euglypha</i> (Dalman, 1828)	1099.0	1066.8–832.4	
<i>Coolinia</i> sp.		962.4	
<i>Morinorhynchus rubeli</i> sp. nov.	972.5–843.0	981.8–811.6	1001.6–960.7
	Butkūnai-241	Gėluva-99	Gėluva-114
<i>Eoplectodonta (E.) penkillensis</i> (Reed, 1917)		1007.7–916.1	
<i>Eoplectodonta (E.) duvalii</i> (Davidson, 1847)	545.4–474.2	993.7–889.9	1091.4–960.2
<i>E. (Ygerodiscus) bella</i> sp. nov.	476.2–464.4	894.0–855.3	997.3–960.2
<i>Leangella scissa</i> (Davidson, 1871)			
<i>Leangella segmentum</i> (Lindstrom, 1861)	517.2–481.2	1007.4–854.5	977.3–957.9
<i>Jonesea grayi</i> (Davidson, 1849)	545.1–503.0	1007.7–862.0	991.0
<i>Katastrophomena (K.)</i> sp.			
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966		937.6–870.7	
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)		873.7–695.8	974.1–871.3
<i>Amphistrophia (A.) funiculata</i> (M' Coy, 1846)			
<i>Brachyprion? kurzemensis</i> Rybnikova, 1967			
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)			
<i>Mesoleptostrophia (M.)</i> sp.			
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)	503.0–475.3	975.4–851.0	
<i>Shaleria (S.) ornatella</i> (Davidson, 1871)		801.1–690.6	829.3
<i>S. (Shaleriella) ezerensis</i> (Rybnikova, 1966)			832.6
<i>Strphonella euglypha</i> (Dalman, 1828)		907.8–823.4	
<i>Coolinia</i> sp.	505.9–473.3	1005.2–972.8	1080.5–1073.8
<i>Morinorhynchus rubeli</i> sp. nov.		668.0–644.7	
	Gėluva-115	Grauzai-105	Jakšiai-104
<i>Eoplectodonta (E.) penkillensis</i> (Reed, 1917)			
<i>Eoplectodonta (E.) duvalii</i> (Davidson, 1847)	962.8–923.3	823.3–685.8	
<i>E. (Ygerodiscus) bella</i> sp. nov.	938.1–903.5	744.8–703.0	

<i>Leangella scissa</i> (Davidson, 1871)			
<i>Leangella segmentum</i> (Lindstrom, 1861)	963.7–886.7	823.2–725.7	
<i>Jonesea grayi</i> (Davidson, 1849)	1034.4–927.0	823.2–763.2	
<i>Katastrophomena</i> (K.) sp.		776.0	
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966		750.6–742.7	
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)	960.5–888.8	806.2–672.5	
<i>Amphistrophia</i> (A.) <i>funiculata</i> (M'Coy, 1846)			
<i>Brachyprion?</i> <i>kurzemensis</i> Rybnikova, 1967			
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)			
<i>Mesoleptostrophia</i> (M.) sp.			
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)			788.7
<i>Shaleria</i> (S.) <i>ornatella</i> (Davidson, 1871)	770.8	551.5–530.2	
<i>S.</i> (<i>Shaleriella</i>) <i>ezerensis</i> (Rybnikova, 1966)			
<i>Strphonella euglypha</i> (Dalman, 1828)		821.2–696.5	
<i>Coolinia</i> sp.	1007.0	803.0–768.0	
<i>Morinorhynchus rubeli</i> sp. nov.		580.9–555.5	
	Jočionys-299	Krekenava-7	Kriūkai-146
<i>Eoplectodonta</i> (E.) <i>penkillensis</i> (Reed, 1917)			939.7
<i>Eoplectodonta</i> (E.) <i>duvalii</i> (Davidson, 1847)		848.9–764.45	
<i>E.</i> (<i>Ygerodiscus</i>) <i>bella</i> sp. nov.		765.3–725.7	
<i>Leangella scissa</i> (Davidson, 1871)			
<i>Leangella segmentum</i> (Lindstrom, 1861)		783.3–725.9	747.2–740.0
<i>Jonesea grayi</i> (Davidson, 1849)		860.0–783.0	936.5–713.4
<i>Katastrophomena</i> (K.) sp.			
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966		830.2–719.1	734.8
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)		779.6–790.8	
<i>Amphistrophia</i> (A.) <i>funiculata</i> (M'Coy, 1846)			
<i>Brachyprion?</i> <i>kurzemensis</i> Rybnikova, 1967		820.0	
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)			
<i>Mesoleptostrophia</i> (M.) sp.			
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)			
<i>Shaleria</i> (S.) <i>ornatella</i> (Davidson, 1871)		578.4–543.1	
<i>S.</i> (<i>Shaleriella</i>) <i>ezerensis</i> (Rybnikova, 1966)		543.1	
<i>Strphonella euglypha</i> (Dalman, 1828)	181.0–179.1	747.3	
<i>Coolinia</i> sp.	190.7	828.3–828.1	
<i>Morinorhynchus rubeli</i> sp. nov.			
	Kurtuvėnai-161	Kurtuvėnai-162	Kurtuvėnai-166
<i>Eoplectodonta</i> (E.) <i>penkillensis</i> (Reed, 1917)	1480.5–1431.0		1022.5–980.0
<i>Eoplectodonta</i> (E.) <i>duvalii</i> (Davidson, 1847)	1307.0	1275.0	882.0–809.5
<i>E.</i> (<i>Ygerodiscus</i>) <i>bella</i> sp. nov.			
<i>Leangella scissa</i> (Davidson, 1871)	1478.9		
<i>Leangella segmentum</i> (Lindstrom, 1861)	1392.0–1301.0	1260.5	811.0
<i>Jonesea grayi</i> (Davidson, 1849)	1393.9–1180.3	1275.0–1160.6	893.0–868.8
<i>Katastrophomena</i> (K.) sp.	1474.5		
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966	1319.0–1287.4	1275.0–1260.5	874.5–856.0
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)	1227.4–1103.0	1237.0–1156.5	811.0–664.0
<i>Amphistrophia</i> (A.) <i>funiculata</i> (M'Coy, 1846)			

<i>Brachyprion? kurzemensis</i> Rybnikova, 1967	1120.0–1049.0		
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)			
<i>Mesoleptostrophia</i> (M.) sp.			842.8
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)		1202.3–1197.8	843.8–801.8
<i>Shaleria</i> (S.) <i>ornatella</i> (Davidson, 1871)	1182.3–1049.3		796.2–667.0
<i>S.</i> (<i>Shaleriella</i>) <i>ezerensis</i> (Rybnikova, 1966)	1180.3–1109.0	1141.8–1056.0	803.0–797.0
<i>Strphonella euglypha</i> (Dalman, 1828)	1269.0–1265.2	1237.0–1196.2	845.5–839.0
<i>Coolinia</i> sp.	1420.0–1321.0	1266.5–1260.5	1017.6–804.0
<i>Morinorhynchus rubeli</i> sp. nov.	1179.3–1116.0	1112.5–1029.0	676.8–667.9
	Milaičiai-103	Paežeriai-222	Pašaltuonis-94
<i>Eoplectodonta</i> (E.) <i>penkillensis</i> (Reed, 1917)			
<i>Eoplectodonta</i> (E.) <i>duvalii</i> (Davidson, 1847)		738.0–626.1	
<i>E.</i> (<i>Ygerodiscus</i>) <i>bella</i> sp. nov.		612.4–658.0	
<i>Leangella scissa</i> (Davidson, 1871)			
<i>Leangella segmentum</i> (Lindstrom, 1861)	1286.0	671.1	
<i>Jonesea grayi</i> (Davidson, 1849)	1517.7–1202.75	738.0–704.0	
<i>Katastrophomena</i> (K.) sp.			
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966		730.0–693.0	1218.0–1222.0
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)	1228.0–1055.0	699.1–667.6	1118.0
<i>Amphistrophia</i> (A.) <i>funiculata</i> (M' Coy, 1846)		694.7	
<i>Brachyprion? kurzemensis</i> Rybnikova, 1967	1206.5–1202.75		1147.6
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)		678.1–645.9	
<i>Mesoleptostrophia</i> (M.) sp.			1193.5
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)	1245.6–1216.35		
<i>Shaleria</i> (S.) <i>ornatella</i> (Davidson, 1871)	1196.95–944.1		
<i>S.</i> (<i>Shaleriella</i>) <i>ezerensis</i> (Rybnikova, 1966)	1216.42–1133.65		1204.9–1121.0
<i>Strphonella euglypha</i> (Dalman, 1828)	1208.7–1210.9	694.7	1216.0–1196.5
<i>Coolinia</i> sp.	1216.42–1208.0		
<i>Morinorhynchus rubeli</i> sp. nov.	1206.3–1057.6		
	Pilviškiai-141	Pilviškiai-143	Sutkai-87
<i>Eoplectodonta</i> (E.) <i>penkillensis</i> (Reed, 1917)	958.1–940.0		917.8–903.2
<i>Eoplectodonta</i> (E.) <i>duvalii</i> (Davidson, 1847)	938.4–851.2	791.7–752.1	917.8–823.3
<i>E.</i> (<i>Ygerodiscus</i>) <i>bella</i> sp. nov.	903.6–864.5		875.8–797.3
<i>Leangella scissa</i> (Davidson, 1871)			
<i>Leangella segmentum</i> (Lindstrom, 1861)	958.6–810.8	812.2–600.4	915.2–797.3
<i>Jonesea grayi</i> (Davidson, 1849)	958.6–848.2	771.8	916.9–810.6
<i>Katastrophomena</i> (K.) sp.	834.3		
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966	956.0–808.7	875.9–752.1	875.0–797.3
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)	634.8–626.9		775.2–760.0
<i>Amphistrophia</i> (A.) <i>funiculata</i> (M' Coy, 1846)			
<i>Brachyprion? kurzemensis</i> Rybnikova, 1967			
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)			880.7
<i>Mesoleptostrophia</i> (M.) sp.	958.1–872.4		780.8
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)	958.1–789.2	837.8–752.1	801.0–769.1
<i>Shaleria</i> (S.) <i>ornatella</i> (Davidson, 1871)	674.4–594.3	720.7–583.6	669.9–578.5
<i>S.</i> (<i>Shaleriella</i>) <i>ezerensis</i> (Rybnikova, 1966)	678.4–620.9		
<i>Strphonella euglypha</i> (Dalman, 1828)		861.0	

<i>Coolinia</i> sp.	958.1–887.2		896.4–885.7
<i>Morinorhynchus rubeli</i> sp. nov.	634.8	766.4	624.3
	Svėdasai-252	Šešuvis-11	Šiupyliai-69
<i>Eoplectodonta</i> (<i>E.</i>) <i>penkillensis</i> (Reed, 1917)			
<i>Eoplectodonta</i> (<i>E.</i>) <i>duvalii</i> (Davidson, 1847)	535.5–449.5		
<i>E.</i> (<i>Ygerodiscus</i>) <i>bella</i> sp. nov.	449.5–448.1		
<i>Leangella scissa</i> (Davidson, 1871)		1620.1	
<i>Leangella segmentum</i> (Lindstrom, 1861)	511.8–471.0		
<i>Jonesea grayi</i> (Davidson, 1849)	535.5–448.7	1620.1–1339.5	968.6–829.1
<i>Katastrophomena</i> (<i>K.</i>) sp.	495.0		
<i>Lepidoleptaena</i> sp.			
<i>Leptaena altera</i> Rybnikova, 1966			
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)	514.5–427.9	1323.0–1136.2	881.4–846.0
<i>Amphistrophia</i> (<i>A.</i>) <i>funiculata</i> (M'Coy, 1846)			
<i>Brachyprion?</i> <i>kurzemensis</i> Rybnikova, 1967	480.8–442.5		
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)			
<i>Mesoleptostrophia</i> (<i>M.</i>) sp.	441.9		918.0
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)	507.0–472.8		
<i>Shaleria</i> (<i>S.</i>) <i>ornatella</i> (Davidson, 1871)		1323.0–1010.6	828.0–790.0
<i>S.</i> (<i>Shaleriella</i>) <i>ezerensis</i> (Rybnikova, 1966)		1216.6–1150.0	
<i>Strphonella euglypha</i> (Dalman, 1828)	480.0–447.6		
<i>Coolinia</i> sp.	514.5–443.7	1379.0	
<i>Morinorhynchus rubeli</i> sp. nov.			881.4–794.5
	Tverečius-336	Vilkaviškis-129	Virbalis-5
<i>Eoplectodonta</i> (<i>E.</i>) <i>penkillensis</i> (Reed, 1917)		894.0–860.2	1150.4–1120.7
<i>Eoplectodonta</i> (<i>E.</i>) <i>duvalii</i> (Davidson, 1847)	228.7–191.8	854.3–795.1	1115.0
<i>E.</i> (<i>Ygerodiscus</i>) <i>bella</i> sp. nov.		851.3–795.1	
<i>Leangella scissa</i> (Davidson, 1871)			
<i>Leangella segmentum</i> (Lindstrom, 1861)		894.0–771.0	1051.0
<i>Jonesea grayi</i> (Davidson, 1849)		894.0–761.5	1150.27–983.0
<i>Katastrophomena</i> (<i>K.</i>) sp.		879.9	
<i>Lepidoleptaena</i> sp.		596.3	
<i>Leptaena altera</i> Rybnikova, 1966		875.0–741.3	1035.4
<i>Leptaena depressa</i> (J. de C. Sowerby, 1825)	210.2–162.6	737.9–593.5	893.0–760.2
<i>Amphistrophia</i> (<i>A.</i>) <i>funiculata</i> (M'Coy, 1846)			
<i>Brachyprion?</i> <i>kurzemensis</i> Rybnikova, 1967			
<i>Protomegastrophia semiglobosa</i> (Davidson, 1871)			
<i>Mesoleptostrophia</i> (<i>M.</i>) sp.		781.1	
<i>Mesopholidostrophia laevigata</i> J. de C. Sowerby, 1839)	203.0–175.3	815.0–741.3	
<i>Shaleria</i> (<i>S.</i>) <i>ornatella</i> (Davidson, 1871)		593.5–586.6	847.0–738.4
<i>S.</i> (<i>Shaleriella</i>) <i>ezerensis</i> (Rybnikova, 1966)		709.4	875.0–802.15
<i>Strphonella euglypha</i> (Dalman, 1828)			981.5–969.8
<i>Coolinia</i> sp.		894.0	
<i>Morinorhynchus rubeli</i> sp. nov.		626.5–589.3	881.5–757.2