Latest Famennian brachiopods from Kowala, Holy Cross Mountains, Poland

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Latest Famennian (UD-VI, "Strunian") brachiopod fauna from Kowala (Kielce Region, Holy Cross Mountains, Poland) consists of eighteen species within 6 orders, eleven of them reported in open nomenclature. Characteristic taxa include: *Schellwienella pauli*, *Aulacella interlineata*, *Sphenospira julii*, *Novaplatirostrum sauerlandense*, *Hadyrhyncha* sp., *Cleiothyridina struniensis*. New morphological details of *Schellwienella pauli*, *Sphenospira julii*, and *Aulacella interlineata* are provided. The described latest Famennian brachiopod fauna is distinctly richer than that from underlying upper Famennian deposits (11 species within 4 orders). Majority of species from Kowala seem to have been adapted to deep water settings and/or poor nutrient availability. The stratigraphic separation between *Planovatirostrum* in the UD-III to UD-V and *Novaplatirostrum* in the UD-VI observed in Sauerland and in Thuringia is valid also in the Holy Cross Mountains. This is the first comprehensive report of a relatively diversified latest Famennian brachiopod fauna from surface outcrops of Poland.

Key words: Brachiopoda, Late Devonian, Famennian, Strunian, Holy Cross Mountains, Poland.

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Introduction

Latest Famennian macrofaunas have been reported from several regions of Poland: Sudetes (Buch 1839; Tietze 1870; Schindewolf 1937; Lewowicki 1959; Gunia 1968), Holy Cross Mountains (= Góry Świętokrzyskie) (Schindewolf 1944; Czarnocki 1989; Halamski 2003; Dzik 2006), Cracow Region (Dębnik Anticline) (Baliński 1995), Carpathians (Jendryka-Fuglewicz and Fuglewicz 1987, but see comment below), Pomerania (Matyja 1976), and Eastern Poland (Kaliś 1969; see detailed review by Matyja 1976). However, these rich faunas are represented in great part by nektonic species (mainly cephalopods), while benthic ones, including brachiopods, are rare both quantitatively and qualitatively. Such a situation is similar to that described by Sartenaer (1997) for the coeval Wocklum Limestone in northern Sauerland (Germany), and, more generally, for several other Devonian deep water facies deposits. Except for two rich brachiopod faunas, one from the boreholes Babilon 1, Brda 1, and Rzeczenica 1 near Chojnice in Pomerania (several dozens of species; see Matyja 1976), the other from the boreholes Opole Lubelskie 5 and Niedrzwica 2–3 in the Lublin Basin (Kaliś 1969), other "Strunian" faunules from Poland were taxonomically quite poor; e.g., only three species have been revealed (*Sentosia* sp., rhynchonellacean gen. et sp. indet., and *Sphenospira*? sp.) from Dębnik Anticline by Baliński (1995). Several benthic species stated by Tietze (1870) to occur in the *Clymenia* (recte: *Wocklumeria*) Limestone at Dzikowiec (= Ebersdorf, Sudetes) are actually Carboniferous in age (Oberc 1957). The material described in the present paper represents therefore the third finding of a diversified brachiopod fauna of latest Famennian age in Poland. As the faunas from boreholes in Pomerania and Lublin Upland (Kaliś 1969; Matyja 1976) contain none or very few descriptions, the present paper provides the first detailed systematic description of such fauna from Poland and from surface outcrops of the Holy Cross Mountains in particular.

It may be noted that the latest Famennian (or "Strunian", an informal name denoted with quotation marks) is accepted here as the equivalent of the *Wocklumeria* ammonoid Genozone (UD-VI, do VI, Fa2d+Tn1a+partly Tn1b), corresponding therefore to the Late *Palmatolepis expansa* and *Siphonodella praesulcata* conodont zones. It is not to be confused with the earlier interval, namely the late Famennian taken here as corresponding to the *Clymenia* Genozone (UD-V), and therefore to the Early to Middle *Palmatolepis expansa* conodont zones (see Becker 1997; Ziegler 1997; Streel et al. 2006; and especially Amler and Heidelberger 2003: 1152–1153).

Institutional abbreviations.—MGL, Musée de Géologie, Lille, France; PIG, Polish Geological Institute, Warsaw, Poland; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—UD-III to UD-VI, Upper Devonian ammonoid genozones after Becker (1997); do, Upper Devonian; Fa, Famennian; Tn, Tournaisian.

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Geological setting

The described material comes from the Kowala quarry (formerly Wola) located near the village of Kowala, ca. 10 km SW from Kielce (Fig. 1). The quarry is situated in the Southern (or Kielce) Region of the Holy Cross Mountains (see locality maps in Berkowski 1991, 2002). The Famennian strata, however, are developed in the Northern (or Łysogóry) facies characterised by a thick succession of intercalated limestone and marl (about 150 m at Kowala, while elsewhere in the Southern Region this succession is strongly condensed, e.g., having only 2 m at Gałęzice; see Czarnocki 1950, 1957; Stupnicka 1992; Szulczewski et al. 1996). The age of the beds exposed in the Kowala quarry ranges from the Frasnian (Late Devonian) to the earliest Tournaisian (Early Carboniferous). Szulczewski (1995) subdivided the sequence into twelve lithological sets A–L described as "complexes" by Szulczewski (1971) and Berkowski (1990). Malec (1995), Dzik (1997), and Marynowski and Filipiak (2007) provided supplementary data on the uppermost part of the sequence.

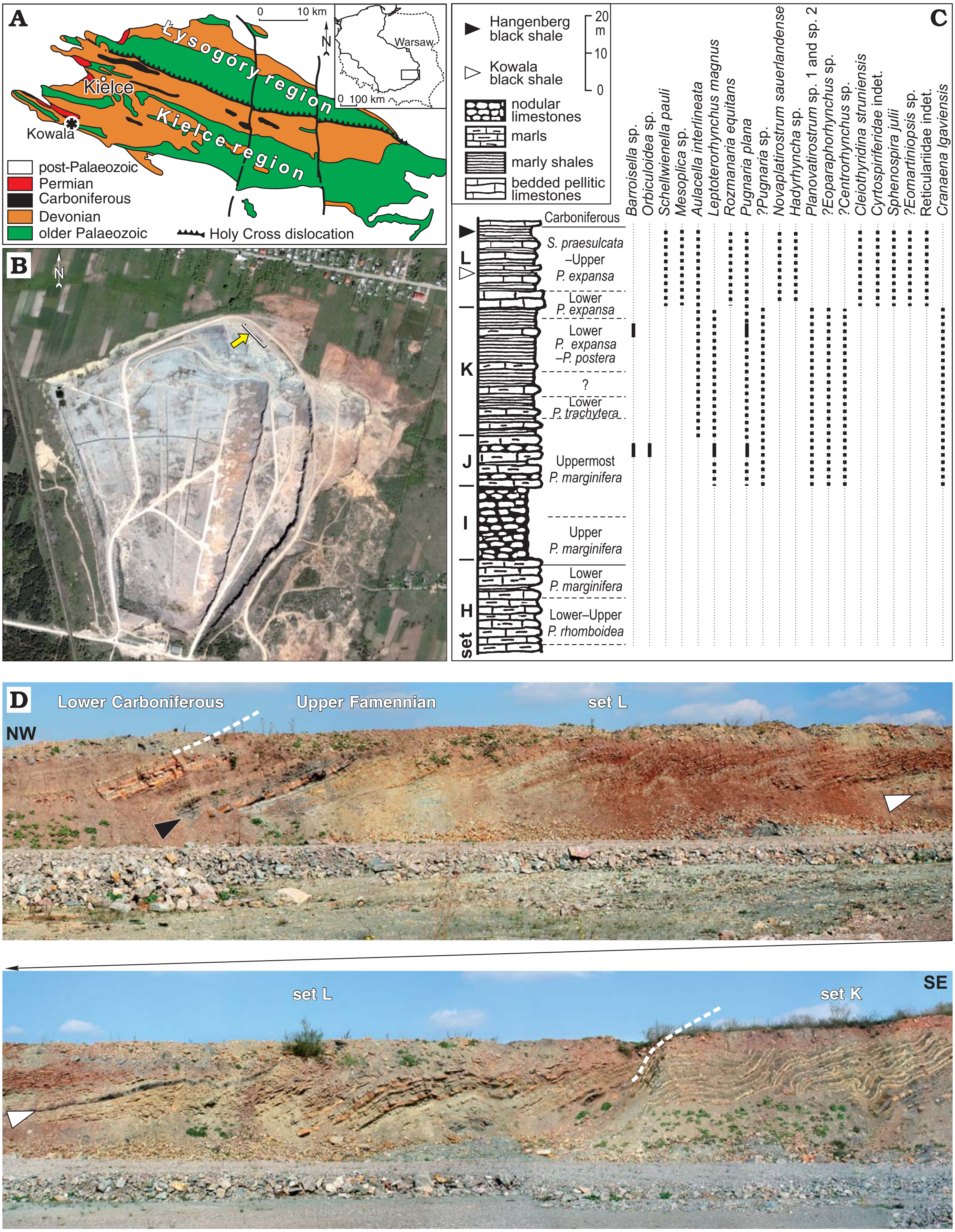
The described brachiopods were found in the "distinctly bedded pelitic limestone" (set L of Szulczewski 1995, the upper part of which corresponds to the complex A sensu Malec 1995, and Marynowski and Filipiak 2007) which is dated as the Early *Palmatolepis expansa* to *Siphonodella praesulcata* zones (Malec 1995). The great majority of the macrofauna from set L consists of cephalopods which are represented by over 30 species. Frequent and/or characteristic species include nautiloids, goniatites, e.g., *Discoclymenia cucullata*, and clymeniids, e.g., *Cymaclymenia costellata* (= *C. compressa* sensu Czarnocki 1989; the commonest species), *Glatziella glaucopis*, *Wocklumeria sphaeroides*, *Epiwocklumeria applanata*, *Kielcensia* spp. (Czarnocki 1989; Dzik 2006), therefore attesting to the latest Famennian (Wocklumian) age of the bulk part of the fauna-bearing beds within the set. Nonetheless an UD-V age of a minor part of the fauna of the set L is strongly suggested by the presence of the goniatite *Alpinites zigzag* (= *Discoclymenia zigzag*; Schindewolf 1944; Becker 2002; Dzik 2006). Benthic organisms are rare and most of them have not been studied. The latter are represented by tabulates, rugosans (*Amplexus* sp., *Oligophylloides pachythecus*, *Neaxon bulloides*; see Różkowska 1969), gastropods, crinoids, trilobites, and brachiopods. Representatives of some of these groups were previously described from the older underlying strata (sets J–K; rugosans: Berkowski 2002; trilobites: Osmólska 1958, 1963; Berkowski 1991; brachiopods: Biernat and Racki 1986a; Marynowski et al. 2007). Ostracods near the Famennian–Tournaisian boundary were investigated by Olempska (1997).

Besides the latest Famennian species, new brachiopod material from the underlying middle to upper Famennian strata (sets J and K, Latest *Palmatolepis marginifera* to Early *Palmatolepis expansa* zones, UD-III to UD-IV, and partly UD-V, described by Biernat and Racki (1986a), as being of "late Famennian" age) contains taxa that are previously unknown in the Kowala section. Some species from sets J–K are common within the set L, but no detailed account of the faunal content of the latter has been given. Fauna from sets H–L has only been briefly reported by Berkowski (2002: 8).

Brachiopods from set L are represented by 115 specimens belonging to 18 species (see Fig. 1C). Brachiopods, like the other benthic taxa, are quite rare, and even this scarce collection could be completed only over a period of nine years (the described strata were not cropping out before the extension of the quarry in 1999) and with assistance of several persons (see Acknowledgements).

The Kowala railroad cut and quarry represent a continuous section from the Frasnian to the lower Tournaisian. One might expect that study of brachiopods from such a geological context would contribute to our knowledge of either the mass extinction at the Frasnian–Famennian boundary or of the Hangenberg event at the end of the Devonian. Yet, in spite of the continuous character of the section, brachiopods are known only from the Frasnian (scattered material, unpublished data) and the middle to uppermost Famennian strata. Recent studies of brachiopod faunal dynamics across the Frasnian–Famennian boundary in southern Poland (ca. 100 km south of Kowala; supposedly the same palaeotectonic unit, namely the Małopolska Block) showed that brachiopods in that part of the epicontinental basin fully rebounded in the *Palmatolepis crepida* Zone, i.e., after some 1.5–2 Ma (Baliński 1996, 2002). Similar post-extinction recovery of the shelf biota during the *Palmatolepis crepida* Zone is also observed in the Holy Cross Mountains (Racki 1990, 1998; Racki and Baliński 1998). Thus, the brachiopod fauna described here, living about 8 to 15 Ma after the Frasnian–Famennian event evidently postdates the recovery process. On the other hand, absence of brachiopods from the strata overlying the black shale corresponding to the Hangenberg event (see Fig. 1D) cannot be considered as a proof of any influence of the anoxic event on the brachiopod assemblages given that benthic faunas in the section are generally scarce and, moreover, the highest part of the section is quite poorly exposed.

Fig. 1. Geological setting of the studied fauna. **A**. Solid geological map of the Palaeozoic inlier of the Holy Cross Mountains and its geographical localisation in Poland. The Holy Cross dislocation separates the Northern (Łysogóry) Region from the Southern (Kielce) Region. **B**. Aerial view of the Kowala quarry (from Google Maps: http://maps.google.com). The north-eastern wall, shown in D, is located by the arrow. **C**. Lithological column of a part of the Famennian and of the lowermost Tournasian with informal lithological sets H to L of Szulczewski (1971). After Szulczewski (1995), modified. **D**. View of the northern wall of the active Kowala quarry (state of September 2006) with informal lithological sets K and L of Szulczewski (1971). White and black arrowheads show the position of two major levels of black shales, the former corresponding to the Kowala event (Marynowski and Filipiak 2007), the latter to the Hangenberg event. →


A
0 10 km
Warsaw
0 100 km
Łysogóry region
Kielce
Kielce region
Kowala
post-Palaeozoic
Permian
Carboniferous
Devonian
older Palaeozoic
Holy Cross dislocation
B
C
Hangenberg black shale
Kowala black shale
20 m
10
0
nodular limestones
marls
marly shales
bedded pellitic limestones
Carboniferous
S. praesulcata –Upper P. expansa
Lower P. expansa
Lower P. expansa –P. postera
?
Lower P. trachytera
Uppermost P. marginifera
Upper P. marginifera
Lower P. marginifera
Lower–Upper P. rhomboidea
L
K
J
I
H
set
Barroisella sp.
Orbiculoidea sp.
Schellwienella pauli
Mesoplica sp.
Aulacella interlineata
Leptoterorhynchus magnus
Rozmanaria equitans
Pugnaria plana
?Pugnaria sp.
Novaplatirostrum sauerlandense
Hadyrhyncha sp.
Planovatirostrum sp. 1 and sp. 2
?Eoparaphorhynchus sp.
?Centrorhynchus sp.
Cleiothyridina struniensis
Cyrtospiriferidae indet.
Sphenospira julii
?Eomartiniopsis sp.
Reticulariidae indet.
Cranaena lgaviensis
D
Lower Carboniferous
Upper Famennian
set L
NW
set L
set K
SE

Systematic palaeontology

Taxa identified at least at family level are described below. Moreover, 16 indeterminate forms have been found in set L: ZPAL Bp 57/97–99 are indeterminate strophomenids, ZPAL Bp 57/7 is an indeterminate productid, ZPAL Bp 57/51, 80–84 are indeterminate rhynchonellids, and ZPAL Bp 57/52, 54–57, 60 are brachiopods indeterminate even at order level. They are neither dealt with in the systematic part nor given in the stratigraphic distribution table.

Phylum Brachiopoda Duméril, 1806

Subphylum Linguliformea Williams, Carlson, Brunton, and Popov, 1996

Class Lingulata Gorjansky and Popov, 1985

Order Lingulida Waagen, 1885

Family Lingulidae Menke, 1828

Genus *Barroisella* Hall and Clarke, 1892

Type species: *Barroisella campbelli* Cooper, 1942; Upper Devonian, Indiana, USA.

Barroisella sp.

Fig. 2A.

2007 *Barroisella* sp.; Marynowski et al. 2007: 191, fig. 4.18.

Material.—14 specimens from set K, ZPAL Bp 57/66–79.

Description.—Shell up to 20 mm in length, elongate elliptical in outline, with distinct ventral pseudointerarea, elongated median ventral muscle scar, and narrow dorsal median ridge extending for about two-third of the valve length.

Remarks.—This brachiopod is usually represented by disarticulated valves; nonetheless, the occurrence of bivalved specimens with slightly displaced valves (Fig. 2A) is noteworthy. The disposition of muscle scars in both valves suggests that the specimens are referable to the genus *Barroisella*. This form was reported from the middle Famennian set J by Marynowski et al. (2007).

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

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

Order Orthotetida Waagen, 1884

Family Pulsiidae Grant, 1974

Genus *Schellwienella* Thomas, 1910

Type species: *Spirifera crenistria* Phillips, 1836; Viséan, Lancashire, England.

Schellwienella pauli Gallwitz, 1932

Fig. 2F, H, I.

?1882 *Streptorhynchus umbraculum* Schloth.; Kayser 1882: 63–64, pl. 1: 10–11 [non *Xystostrophia umbraculum* (Schlotheim, 1820)].

?1929 *Streptorhynchus* (*Schellwienella*) cf. *umbraculum*; Dehée 1929: 36, pl. 5: 9.

1932 *Schellwienella pauli* sp. nov.; Gallwitz 1932: 104–106, pl. 6: 23–25.

1969 *Schellwienella umbraculum*; Kaliś 1969: pl. 1: 5.

1976 *Schellwienella* ?*pauli* (Gallw.); Matyja 1976: pl. 2: 1–2, 6.

Material.—15 specimens from set L, ZPAL Bp 57/3, 20, 97, 100–103.

Description.—Shell large (attaining at least 45 mm in width), transverse (length to width ratio 0.61–0.78), ventribiconvex. Outline ovate, except fot straight cardinal margin. Maximal width anteriorly to midlength. Anterior comissure rectimarginate, no sulcus or fold. Ventral interarea apsacline, triangular, relatively high (height to width ratio about 1/5), transversely striate. Pseudodeltidium well developed, convex. Dorsal interarea anacline, linear. Chilidium small, with weak median groove.

Ornamentation of costae and costellae, the latter appearing by intercalation, of different heights and thicknesses at anterior margin, 11–13 per 5 mm. Concentric microlines visible in the anterior region.

A single ventral interior (Fig. 2I) shows triangular adductor scars with their lateral borders diverged at ca. 80° and extended to about 2/5 of the valve length, anteriorly faintly flabellate, medially separated by a low ridge.

Dorsal interior unknown.

Remarks.—Ten epibiontic *Microcornus* sp. were observed on the dorsal valve of the specimen ZPAL Bp 57/101; they are grouped preferentially in the anterior region of the valve.

This species was described by Gallwitz (1932) on the basis of external casts. No revision of the this species has ever been made, and the described sample is referred to it on the basis of external characters only.

Stratigraphic and geographic distribution.—Velbert Anticline (Rhenish Slate Mountains), Holy Cross Mts., Pomerania, and Lublin Basin (Poland); Upper Devonian, Famennian, most probably "Strunian".

Order Productida Sarytcheva and Sokolskaya, 1959

Family Productidae Gray, 1840

Genus *Mesoplica* Reed, 1943

Type species: *Leptaena praelonga* Sowerby, 1840; uppermost Famennian, Devonshire, England.

Mesoplica sp.

Fig. 2K.

Material.—Single ventral valve, ZPAL Bp 57/1 from set L.

Description.—The ventral valve attains nearly 30 mm in width, is strongly convex and irregularly ornamented with both thick and fine radial ribs (only the latter in the umbonal region).

Remarks.—The single incomplete and strongly decorticated dorsal valve ZPAL Bp 57/8, which was found in the same set, is ornamented with fine continuous radial ribs (c. 7–8 per 5 mm) and most probably represents another indeterminate taxon (see Fig. 2J).

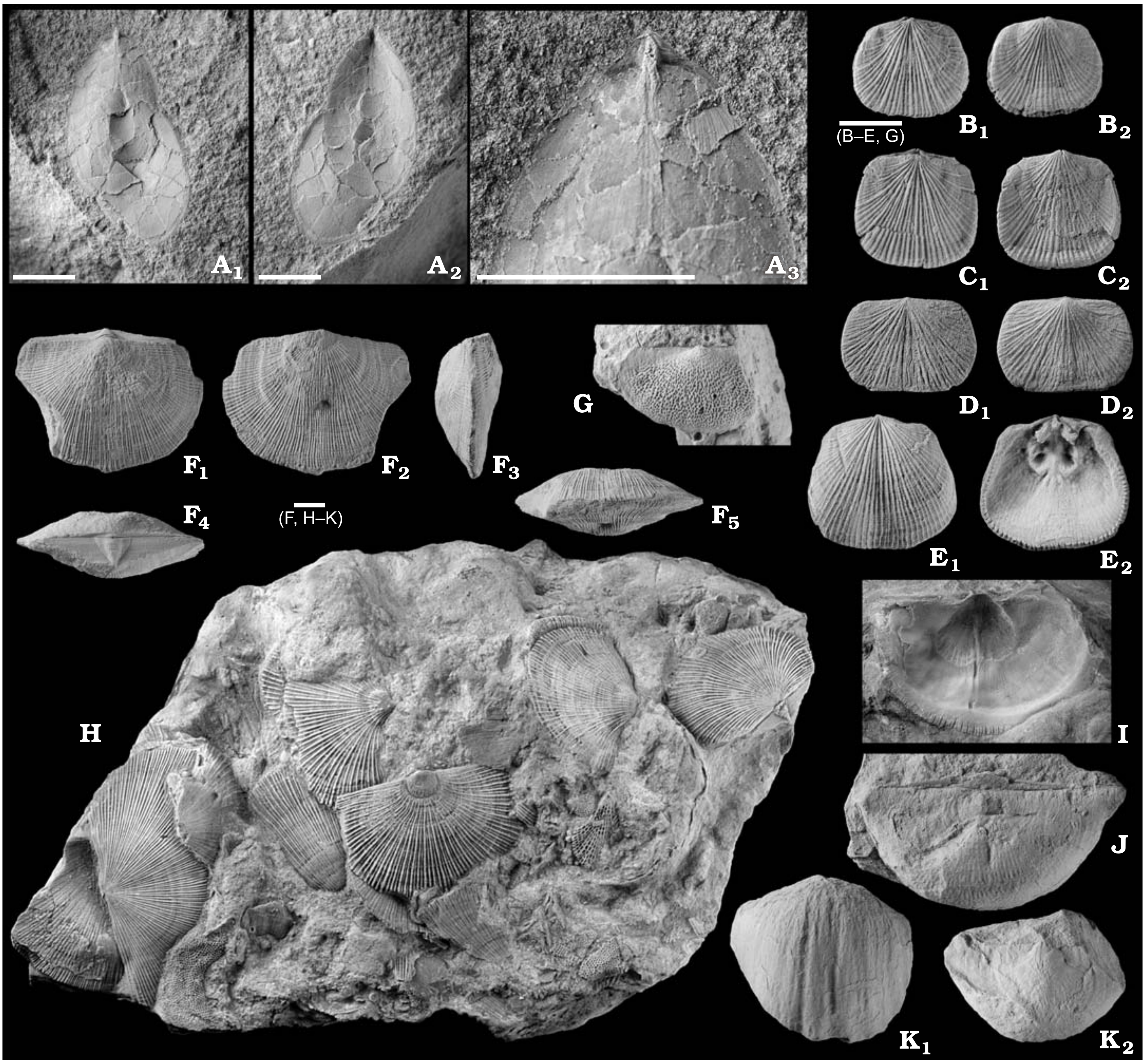


Fig. 2. Middle to Latest Famennian brachiopods from Kowala. **A**. *Barroisella* sp. The bivalved specimen ZPAL Bp 57/70a showing strongly exfoliated ventral valve (ventral internal mould) and interior of dorsal valve (lower right) (A_1) and its counterpart ZPAL Bp 57/70b (A_2); enlargement of the posterior region of the ventral valve showing pseudointerarea and elongated median muscle scar (A_3). **B**–**E**. *Aulacella interlineata* (Sowerby, 1840). **B**–**D**. Three shells ZPAL Bp 57/4a, 4b, and 86, respectively, in dorsal (B_1, C_1, D_1) and ventral (B_2, C_2, D_2) views showing variability in the shell outline. **E**. Dorsal valve ZPAL Bp 57/5 exterior (E_1) and interior (E_2). **F**, **H**, **I**. *Schellwienella pauli* (Gallwitz, 1932). **F**. Slightly destroyed shell ZPAL Bp 57/20 in dorsal (F_1), ventral (F_2), lateral (F_3), posterior (F_4), and anterior (F_5) views. **H**. Limestone block ZPAL Bp 57/103 with accumulation of shells of *S. pauli*. **I**. Interior of ventral valve ZPAL Bp 57/100. **G**. Productida indet., mould ZPAL Bp 57/7 of exfoliated dorsal valve. **J**. Productida indet. Posterior view of mostly decorticated and slightly crushed dorsal valve ZPAL Bp 57/8. **K**. *Mesoplica* sp. Ventral valve ZPAL Bp 57/1 in ventral (K_1) and posterior (K_2) views. Scale bars 5 mm.

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

Order Orthida Schuchert and Cooper, 1932

Family Rhipidomellidae Schuchert, 1913

Genus *Aulacella* Schuchert and Cooper, 1931

Type species: *Orthis prisca* Schnur, 1851 (= *Orthis eifeliensis* sensu Schuchert and Cooper 1931); Middle Devonian (Eifelian), Eifel Mountains, Germany.

Aulacella interlineata (Sowerby, 1840)

Fig. 2B–E.

1840 *Orthis interlineata*; Sowerby 1840: pl. 53: 11, pl. 54: 14.
1882 *Orthis bergica* sp. nov.; Kayser 1882: 61–63, pl. 2: 6–11.
1902 *Orthis interlineata* Phill.; Drevermann 1902: 514–515.

1926 *Orthis Bergica* Kayser; Lecointre 1926: 122.
1929 *Dalmanella interlineata* Sowerby; Dehée 1929: 31–33, pl. 5: 1–5.
1932 *Dalmanella interlineata* (Sowerby); Gallwitz 1932: 88–90, pl. 6: 6–7 [cum syn.].
1932 *Dalmanella bergica* (Kayser), nov. em.; Gallwitz 1932: 85–88, pl. 6: 3–5 [cum syn.].
non 1964 *Aulacella interlineata* (Sowerby, 1840); Sougy 1964: 437, pl. 42: 18, 19 [*A. prisca*].
1976 *Aulacella interlineata* (Sow.); Matyja 1976: pl. 1: 2, 6.

Material.—13 specimens: 12 originating from set L ZPAL Bp 57/4–6, 28–30, 35–36, 86–89; one from set K, ZPAL Bp 57/18.

Description.—Shell rather small (up to 12.1 mm in width), transverse, with maximal width near the anterior margin (4/5 to 7/8 of the shell length measured from the umbo). Some specimens are nearly rectangular in outline (Fig. 2C, D), whereas others are trapezoidal (Fig. 2E). Postero-lateral extremities frequently angular, antero-lateral ones rounded. Dorsal sulcus imperceptible (Fig. 2C) to distinct, yet shallow (Fig. 2E), U-shaped in cross-section, occupying about 1/3 of the shell width at anterior commissure. Anterior commissure rectimarginate to unisulcate.

Ornamentation of costae and costellae, the latter arising by both intercalation and bifurcation, all of comparable height and thickness at anterior margin, separated by wider furrows, 2–4 per mm at anterior margin.

The single dorsal interior ZPAL Bp 57/4 shows a stout cardinal process, strong brachiophores, a muscle area extending to 1/3 of the valve length, highly elevated peripherally and subdivided medially by a wide longitudinal elevation (Fig. 2E).

Ventral interior unknown.

Remarks.—This species differs from the type species of the genus, namely Eifelian–Givetian *Aulacella prisca* (Schnur, 1851) (= *Aulacella eifeliensis* according to several authors), as well as from Frasnian *Aulacella aggeris* Mottequin, 2008, in more subquadrate postero-lateral extremities and in the position of maximal width (at 4/5–7/8 of the shell length in the former, 3/4 in *A. prisca*, about midlength or slightly anteriorly in *A. aggeris*; Mottequin 2008). Internal structures of both taxa do not show any major difference, except for much stronger bordering of the muscle area in the described species.

Kayser (1882) and Gallwitz (1932) separated *Aulacella interlineata* (Sowerby, 1840) and *A. bergica* (Kayser, 1882) according to the size. The latter author held that both the Rhenish material he investigated and the Étrœungt material described by Dehée (1929) under *Dalmanella interlineata* consisted in fact of two species, the actual *D. interlineata* and *D. bergica* (Kayser, 1882), the former being smaller. However, the differences in form are very subtle (mean length to width ratios 0.78 and 0.77, respectively; presence or absence of a sulcus; weaker or stronger convexity of valves). A similar case occurs within the samples of *Aulacella prisca* from the Middle Devonian of the Łysogóry Region, which show high intraspecific variability (Biernat 1959 reduced to synonymy several taxa described by Gürich 1896 from the upper Eifelian of Skały); in the lower Givetian of Błonia Sierżawskie near Świętomarz some very large forms are present (Halamski 2009: pl. 11: 31, 33–36) that are, once again, best treated as representing intraspecific variability. This favours the broad interpretation of *A. interlineata* with *A. bergica* as a synonym (Drevermann 1902; Dehée 1929). This view is provisorily accepted here, but should be confirmed on the type material of both taxa.

Stratigraphic and geographic distribution.—Europe, Northern Africa; Frasnian to Famennian (Dehée 1929). Reports from Armenia (Abrahamian 1957) may require confirmation.

Order Rhynchonellida Kuhn, 1949

Family Rozmanariidae Havlíček, 1982

Genus *Leptoterorhynchus* Sartenaer, 1998

Type species: *Rozmanaria magna* Biernat and Racki, 1986; Famennian, Kowala, Poland.

Leptoterorhynchus magnus (Biernat and Racki, 1986)

Figs. 3B, C, 4.

1986 *Rozmanaria magna* sp. nov.; Biernat and Racki 1986a: 90–95, text-figs. 2–5, pls. 35: 1–5, 36: 1–5, 37: 3–5, 41: 4, 42, 43.
1986 *Rozmanaria magna* Biernat and Racki; Biernat and Racki 1986b: figs. 1A, 2C, pl. 1: 1–3.
1988 *Rozmanaria magna* Biernat and Racki; Biernat 1988: 331, pls.1: 2, 2: 6.
1998 *Leptoterorhynchus magnus* (Biernat and Racki, 1986b); Sartenaer 1998b: 121, text-fig. 1, pl. 1: 1–35.
2007 *Rozmanaria magna* (Biernat and Racki); Marynowski et al. 2007: 191, fig. 4.16a–c.

Material.—Four specimens from set K, ZPAL Bp 57/21–22, 37, 53.

Description.—Exterior: see Biernat and Racki (1986a) and Sartenaer (1998b).

Ventral interior (Fig. 4) with slightly thickened umbo and deeply ruffled inner surface of the muscle scars suggesting attachments of the ventral adjustors; teeth strong, stout, but short; dental plates absent, but low flanges may be interpreted as rudiments of these plates (see Fig. 4, distance 0.9–1.5). Dorsal interior with short, divided hinge plates which are distinctly inclined medially to the floor of the valve; crural bases distinct, thickened; crura slightly divergent, proximally crescent- to boomerang-shaped in cross section, distally calceolate and ventrally curved (Fig. 4, distance 1.6–2.4).

Remarks.—Biernat and Racki (1986a) illustrated the internal structures of the newly described species only on photographic plates which are quite illegible, wherefore their original specimens have been redrawn using a camera lucida and redescribed by the present authors.

Stratigraphic and geographic distribution.—This species is known solely from the middle Famennian of the Kowala section.

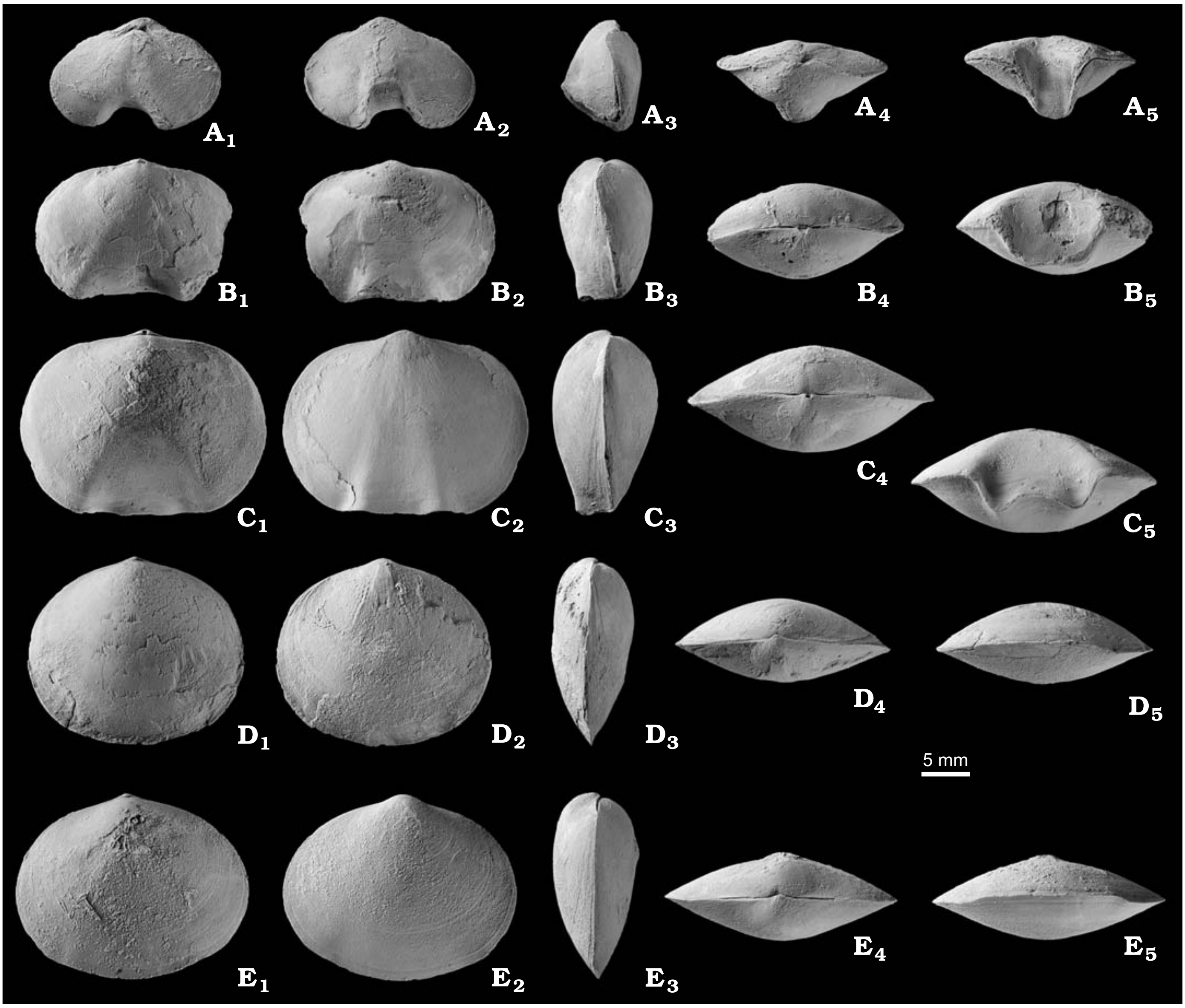


Fig. 3. Middle to Latest Famennian brachiopods from Kowala. **A**. *Rozmanaria equitans* (Schmidt, 1924); shell ZPAL Bp 57/104 in dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), and anterior (A_5) views. **B**, **C**. *Leptoterorhynchus magnus* (Biernat and Racki, 1986); two shells ZPAL Bp 57/53 and 37, respectively, in dorsal (B_1, C_1), ventral (B_2, C_2), lateral (B_3, C_3), posterior (B_4, C_4), and anterior (B_5, C_5) views. **D**, **E**. *Pugnaria plana* Biernat and Racki, 1986; two shells ZPAL Bp 57/58 and 59, respectively, in dorsal (D_1, E_1), ventral (D_2, E_2), lateral (D_3, E_3), posterior (D_4, E_4), and anterior (D_5, E_5) views.

Genus *Rozmanaria* Weyer, 1972

Type species: *Liorhynchus*? *equitans* Schmidt, 1924; Famennian, Sauerland, Germany.

Rozmanaria equitans (Schmidt, 1924)

Fig. 3A.

1924 *Liorhynchus*? *equitans* sp. nov.; Schmidt 1924: 145, pl. 7: 16, 17.
1962 *Plectorhynchella equitans eguitans* (Schmidt), 1923; Rozman 1962: 176–177, pl. 30: 12 [spelling error for *equitans equitans*].
1972 *Rozmanaria equitans* (H. Schmidt, 1924); Weyer 1972: 87–91, pls. 1–4 [cum syn.].
1983 *Rozmanaria equitans* (H. Schmidt, 1924); Biernat 1983: 139–140, pl. 5: 4.
1986 *Rozmanaria equitans* (Schmidt); Biernat and Racki 1986b: fig. 2a.
1988 *Rozmanaria equitans* (H. Schmidt); Biernat 1988: 329, pl. 2: 5.

Material.—A single specimen from set L, ZPAL Bp 57/104.

Stratigraphic and geographic distribution.—Latest Famennian (UD-VI) of the Rhenish and Thuringian Slate Mts., as well as (most probably) of the Holy Cross Mts.; late Famennian (UD-V) of the Rhenish Slate Mts. and Ural (Rozman 1962; Weyer 1972; present study). The report of this species by Biernat (1983: 140) from the lower Famennian of the Holy Cross Mts. is doubtful.

Genus *Pugnaria* Biernat and Racki, 1986

Type species: *Pugnaria plana* Biernat and Racki, 1986; Famennian, Kowala, Poland.

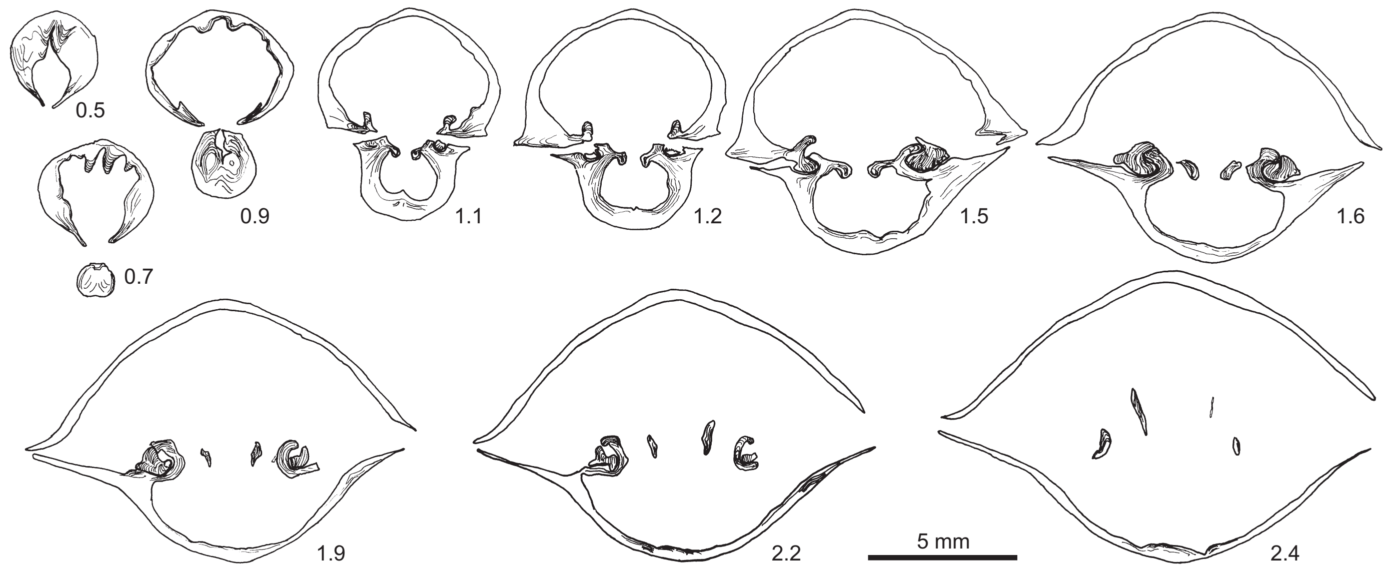


Fig. 4. Transverse serial sections of *Leptoterorhynchus magnus* (Biernat and Racki, 1986) through shell ZPAL Bp 31/145 from Kowala, sets J–K. Numbers indicate distances in mm from ventral umbo.

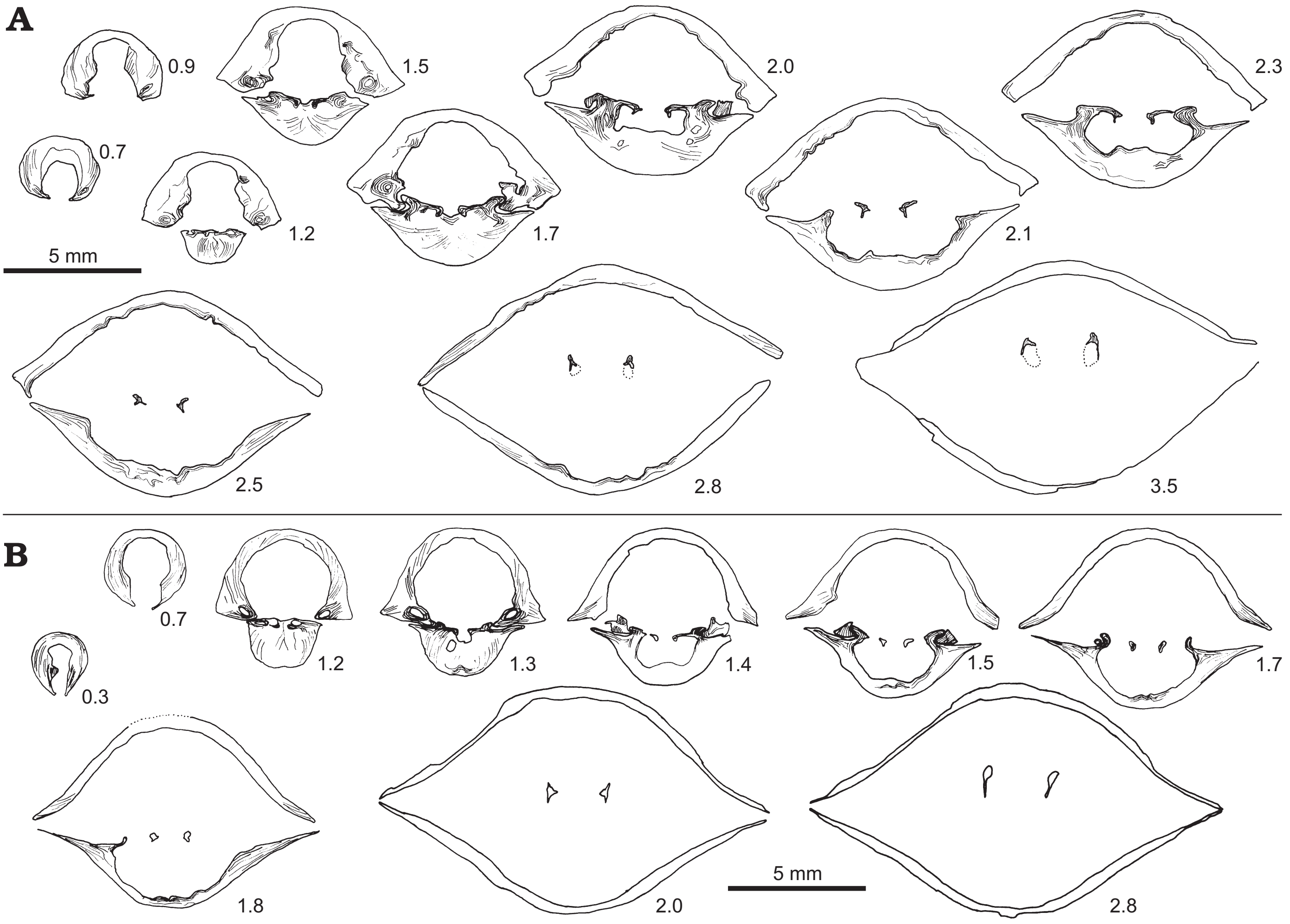


Fig. 5. Transverse serial sections of *Pugnaria plana* Biernat and Racki, 1986 through shells ZPAL Bp 31/107 (**A**) and ZPAL Bp 31/154 (**B**) from Kowala, sets J–K. Numbers indicate distances in mm from ventral umbo.

Pugnaria plana Biernat and Racki, 1986

Figs. 3D–E, 5.

1986 *Pugnaria plana* gen. et sp. nov.; Biernat and Racki 1986a: 95–97; text-figs. 2, 5–7, pls. 38, 39, 44: 2a–g, 45.

1986 *Pugnaria plana* Biernat and Racki; Biernat and Racki 1986b: fig. 1C, pl. 1: 5, 6.

1988 *Pugnaria plana* Biernat and Racki; Biernat 1988: 329, pl. 1: 3.

2007 *Pugnaria plana* (Biernat and Racki); Marynowski et al. 2007: 191, fig. 4.17a, b.

Material.—Seven specimens: 5 from set L, ZPAL Bp 57/24–27, 31; 2 from set K, ZPAL Bp 57/58–59.

Description.—Exterior, see Biernat and Racki (1986a).

Ventral interior without dental plates although very small dental nuclei are observed in both sectioned specimens (Fig. 5A, distance 0.9–1.7; Fig. 5B, distance 1.2–1.3). Teeth stout and short. Dorsal interior without median septum; hinge plates short, nearly horizontal, divided; crural bases well marked, crura crescent-shape in cross-section proximally, more triangular and dorsally concave at distal ends, slightly divergent and curved ventrally (Fig. 5A, B).

Remarks.—Although the shell serial sections were illustrated by Biernat and Racki (1986a: pls. 44: 2, 45), they are quite difficult to analyse as they are shown in photographs only. Here, we illustrate the sections of two shells by camera lucida drawings (Fig. 5A, B).

Stratigraphic and geographic distribution.—This species, known solely from the Kowala section, was described by Biernat and Racki (1986a) from set K, subsequently reported by Marynowski et al. (2007) from set J, and now has been found in set L.

Genus *Novaplatirostrum* Sartenaer, 1997

Type species: *Novaplatirostrum sauerlandense* Sartenaer, 1997; uppermost Famennian, Sauerland, Germany.

Novaplatirostrum sauerlandense Sartenaer, 1997

Figs. 6, 7A–D, 8.

1997 *Novaplatirostrum sauerlandense* gen. et sp. nov.; Sartenaer 1997: 31–35, pl. 1: 1–40, fig. 1 [cum syn.].

Material.—26 specimens from set L, ZPAL Bp 57/38–39, 40–50, 105–112; PIG 163.II.66.2–6, some of them poorly preserved.

Description.—Shells slightly asymmetrical, ovate, transverse, up to 28.1 mm in width, moderately ventribiconvex. Maximal width at 2/3 of the length, maximal thickness in the posterior region. Anterior commissure uniplicate, deflection broad (0.45–0.65 of the shell width) and very low. Costae apparent only in the anterior third (often less), 2–7 on the fold and 1–3 on lateral slopes.

Ventral interior with dental plates not discernible in the thickened umbonal cavity (Fig. 6); teeth stout, strong; muscle scars deeply impressed on the valve floor. Dorsal interior without median septum; hinge plates divided, posteriorly concave, more anteriorly nearly horizontal; crural bases well marked, with sharp longitudinal, dorsally directed ridge, which continues till the distal ends of crura (Fig. 6).

Remarks.—The described material from Kowala is similar both externally and internally to the type collection from the Wocklumian of Sauerland (Germany) figured by Sartenaer (1997: pl. 1). The difference between values of the length to width ratio (0.73 to 0.98, mean 0.86 at Kowala; 0.72 to 0.88, mean 0.82 in Sauerland) is not significant. The pattern of variation of number of ventral costae is also broadly similar in both samples, even if Kowala material is clearly more variable than that from Sauerland (a smaller sample is more varied, Fig. 8): the extreme representatives, with 3 and 7 ventral costae respectively are shown in Fig. 7A and D.

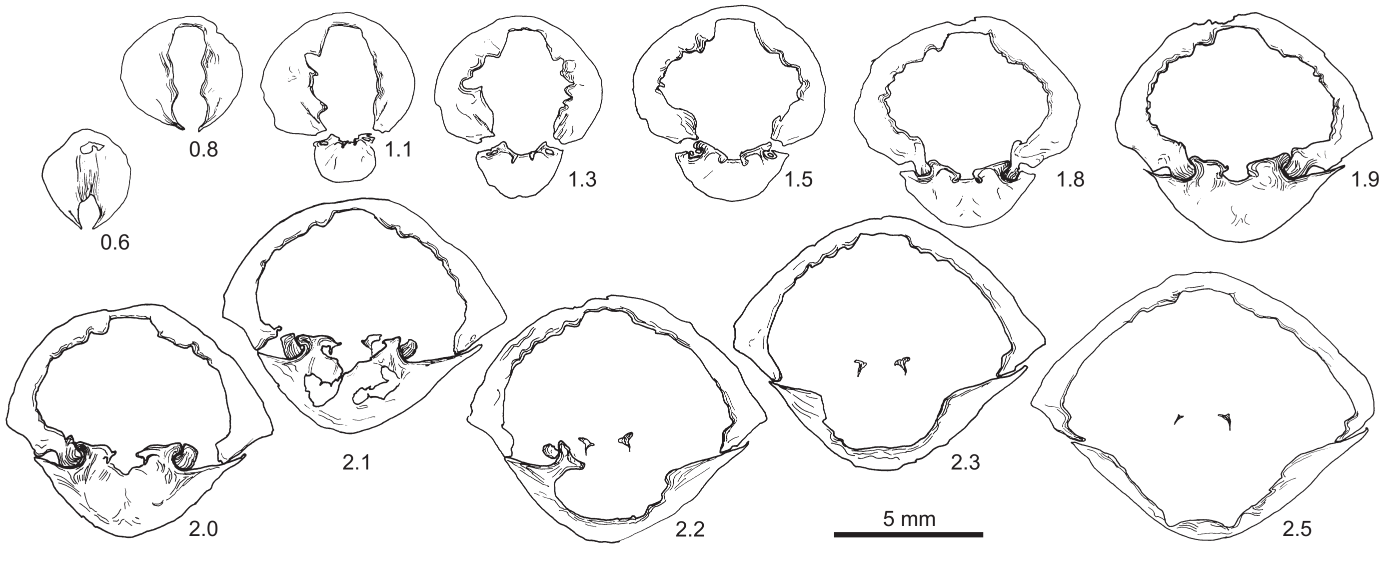


Fig. 6. Transverse serial sections of *Novaplatirostrum sauerlandense* Sartenaer, 1997 through shell ZPAL Bp 57/40 from Kowala, set L. Numbers indicate distances in mm from ventral umbo.

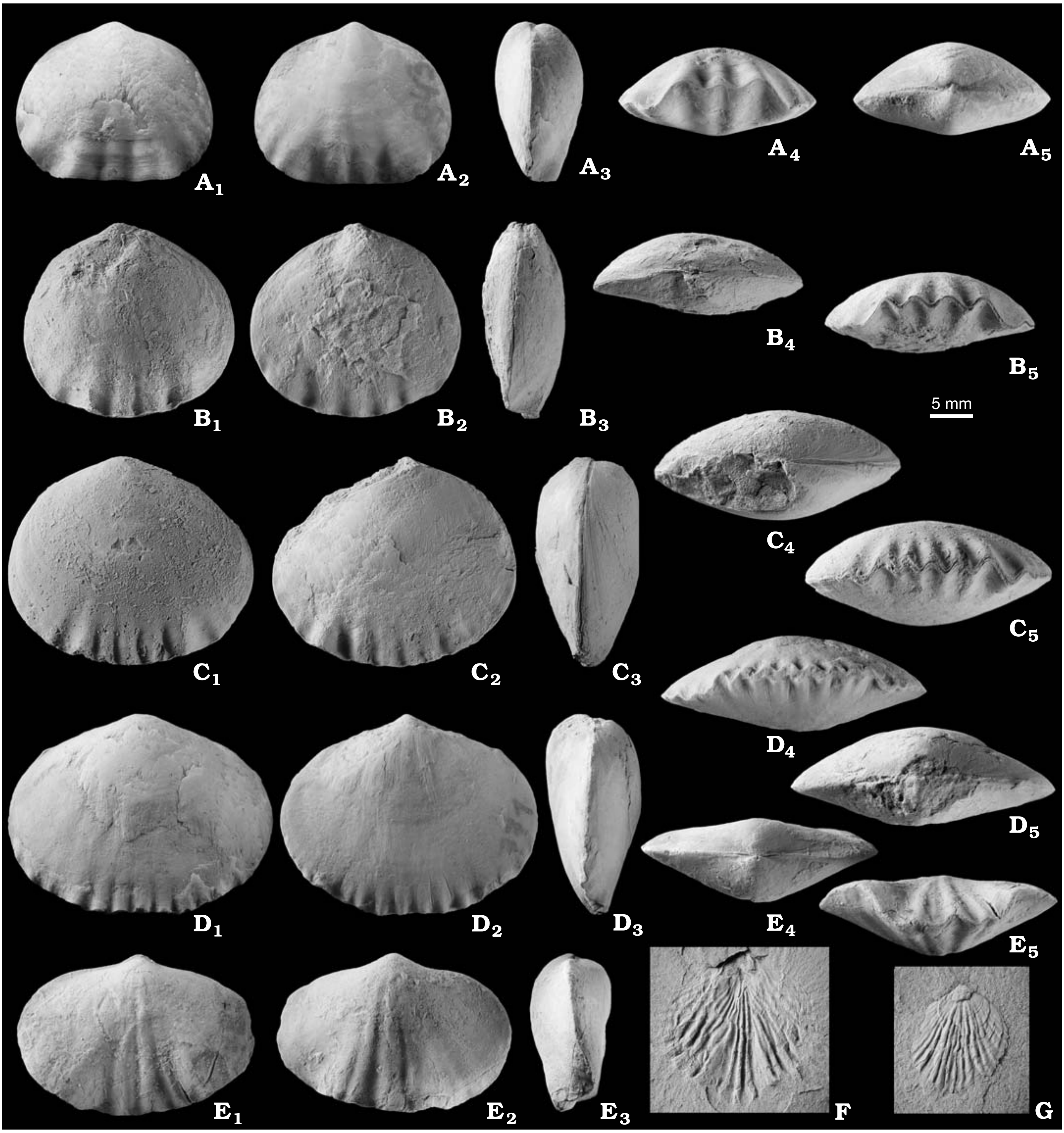
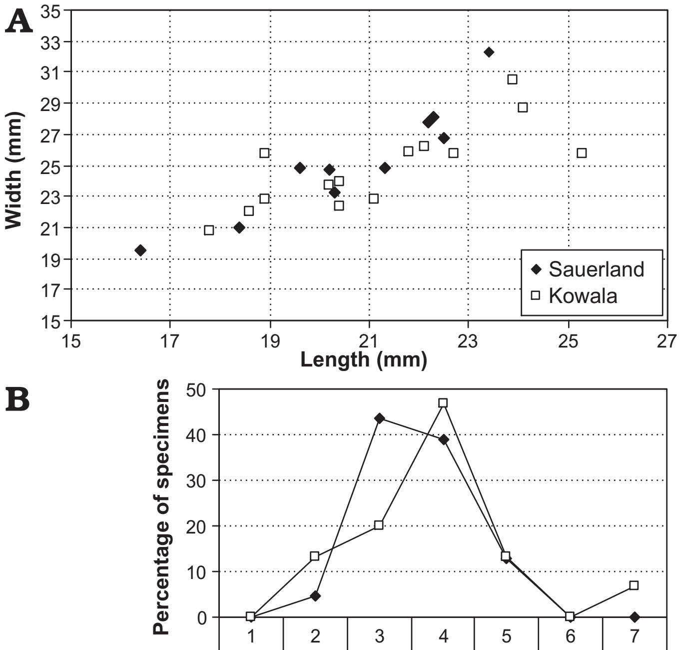


Fig. 7. Middle to Latest Famennian brachiopods from Kowala. **A**–**D**. *Novaplatirostrum sauerlandense* Sartenaer, 1997; four shells ZPAL Bp 57/106, 39, 38, and 105, respectively, in dorsal (A_1, B_1, C_1, D_1), ventral (A_2, B_2, C_2, D_2), lateral (A_3, B_3, C_3, D_3), posterior (A_4, B_4, C_4, D_4), and anterior (A_5, B_5, C_5, D_5) views. **E**. *Hadyrhyncha* sp.; shell ZPAL Bp 57/115 in dorsal (E_1), ventral (E_2), lateral (E_3), posterior (E_4), and anterior (E_5) views. **F**, **G**. *Centrorhynchus* sp.; external imprints ZPAL Bp 57/61 and 62, respectively, of two strongly flattened ventral valves on a shale surface.

Poorly preserved middle to late Famennian *Planovatirostrum planoovale* sensu Biernat and Racki (1986a) (= *Planovatirostrum* sp. 1 here) and *Planovatirostrum* cf. *undulatum* sensu Biernat and Racki (1986a) (= *Planovatirostrum* sp. 2 here; both from Kowala) differ in being more transverse (length to width ratio 0.72 to 0.82 in the former, 0.70 in the later). Even if their specific identification can hardly be attempted, they may be attributed to the genus *Planovatirostrum* Sartenaer, 1970 (Sartenaer and Xu 1989). The stratigraphic separation between two members of the same evolu-



Number of ventral costae	1	2	3	4	5	6	7
Sauerland (N = 46)	0	4.5	43.5	39	13	0	0
Kowala (N = 15)	0	13.3	20	46.7	13.3	0	6.7

Fig. 8. Biometrical characteristics of *Novaplatirostrum sauerlandense* Sartenaer, 1997 from the type section (after Sartenaer 1997) and from Kowala. **A**. Comparison of the shell outline of representatives of the two collections on a width to length scatter diagram. **B**. Comparison of costation of the two collections.

tionary lineage, namely *Planovatirostrum* in the middle and late Famennian (UD-III to UD-V) and *Novaplatirostrum* in the latest Famennian (UD-VI) observed by Sartenaer (1997) in Sauerland and in Thuringia is therefore valid also at Kowala, even if the age of the latter taxon cannot be given in such detail as in Germany.

Stratigraphic and geographic distribution.—Holy Cross Mountains, Sauerland; Famennian, most probably UD-VI (Sartenaer 1997).

Genus *Hadyrhyncha* Havlíček, 1979

Type species: *Hadyrhyncha hadyensis* Havlíček, 1979; Famennian, Moravia, Czech Republic.

Hadyrhyncha sp.

Fig. 6E.

Material.—A single articulated shell, most probably from set L, ZPAL Bp 57/115.

Description.—Shell ovate, 27.3 mm wide, 18.5 mm long, and 9.5 mm thick, distinctly transverse (length to width ratio 0.68), moderately ventribiconvex. Maximal width slightly anteriorly to midlength, maximal thickness in the posterior region. Umbo fine, incurved at ca. 45° in relation to the commissural plane. Dorsal valve with a broad (16.8 mm at anterior commissure or 0.62 of the total width), flat-bottomed sulcus appearing at 1/3 of the valve length. Ventral fold very low, flat, apparent only in the anterior region. Anterior commissure unisulcate, deflection broad and low. Ornamentation of low, rounded costae, three dorsal ones appearing at ca. 1/3 of the valve length and four ventral ones appearing at ca. 1/5 of the valve length.

Remarks.—This form is included into *Hadyrhyncha* on account of its transverse outline, inverse sulcation, and weak, rounded costae. It differs from the two species described within this genus, namely *H. hadyensis* Havlíček, 1979 from the Famennian (UD-V to UD-VI) of Moravia and *H. meridionalis* Sartenaer, 1998 from the Famennian (UD-V) of Morocco in possessing broader costae, and from the former moreover in having a higher deflection of the anterior commissure (Sartenaer 1998a). Consequently, it represents a new species within the genus *Hadyrhyncha*, which is not named because of lack of sufficient material.

Family Trigonirhynchiidae Schmidt, 1965

Genus *Centrorhynchus* Sartenaer, 1970

Type species: *Camarotoechia baitalensis* Reed, 1922; Famennian, Pamir.

Centrorhynchus sp.

Fig. 6F, G.

Material.—Five specimens from set K, ZPAL Bp 57/61–65.

Description.—Shell suboval in outline, attaining up to 18 mm in length. Ventral sulcus and dorsal fold present. Shell strongly costate with 3–5 costae in sulcus and up to 6 costae on each flank. Concentric growth lines distinct. Other details not preserved.

Remarks.—All specimens came from shales and are invariably strongly flattened and slightly distorted. General aspect of the shell and character of its costation suggest that they probably represent a species of *Centrorhynchus*.

Order Athyridida Boucot, Johnson, and Staton, 1964

Family Athyrididae Davidson, 1881

Subfamily Cleiothyridininae Alvarez, Rong, and Boucot, 1998

Genus *Cleiothyridina* Buckman, 1906

Type species: *Atrypa pectinifera* Sowerby, 1840; Upper Permian (Kazanian), Durham, United Kingdom.

Cleiothyridina struniensis (Dehée, 1929)

Fig. 9C–F.

1929 *Seminula*? *struniensis* sp. nov.; Dehée 1929: 27–28, pl. 4: 1–3.
1976 *Composita struniana* (Dehée); Matyja 1976: pl. 10: 1, 3, 5 [spelling error for *struniensis*].
?1983 *Cleiothyridina* sp.; Biernat 1983: 140–141, pl. 6: 3.

Material.—Two shells (ZPAL Bp 57/85, 2, 113) and a single ventral valve (ZPAL Bp 57/34).

Description.—Shell up to 25.4 mm in length, moderately to strongly elongate, ventribiconvex. Maximal width at 3/5–3/4 of the length. Interareas not apparent. Umbo thick, incurved, with large pedicle foramen attaining up to 2.4 mm in diametre.

Anterior commissure uniplicate, deflection subtriangular to trapezoidal, occupying 3/5–4/5 of the shell width. Ornamentation of spine bases arranged along concentric lines (Fig. 9C_6).

The single ventral interior ZPAL Bp 57/34 shows short dental plates and small, deeply impressed rhomboidal posterior adductor scars, and faintly impressed, large anterior adductor scars (Fig. 9E).

Remarks.—The material is described here as belonging to one species; however, differences in shape between the specimens illustrated in Fig. 9C and D are quite notable; the former is nearly identical to the specimens from the type collection (Dehée 1929); the latter, wider and more pentagonal, is more alike to *Cleiothyridina royssii* (L'Éveillé, 1835) as illustrated by Matyja (1976: pl. 15: 1–3). However, this species is more rounded in outline. The shell shown in Fig. 9F reveals a prominent ventral sulcus. The interior figured in Fig. 9E is fragmentary, and it cannot be precised to which morphotype it is more similar.

The micro-ornamentation of the described shells is characteristic of the subfamily Cleiothyridininae. They are very similar externally to specimens from the "calcaires d'Étrœungt" described and illustrated by Dehée (1929) as *Seminula* (?) *struniensis* Dehée, 1929. Brice (in Hubert et al. 2007) referred the Étrœungt material to the genus *Composita* considered by Alvarez and Rong (2002) to include *Seminula*. The Holy Cross Mountains species (and, consequently, the putatively conspecific Ardennes specimens) is referred here rather tentatively to the genus *Cleiothyridina* on account of longitudinally ovate outline (pentagonal in *Crinisarina*) and fine growth lamellae (large in *Carteridina*); however, diagnostic internal characters of both type specimens and shells from Kowala are unknown.

The muscle scars figured in Fig. 9E show notable similarity to those of *Cleiothyridina dilimensis* Grunt, 1997 from the lower–middle Carboniferous of Kolyma-Omolon Massif (Grunt 1989: fig. 31).

The specimen from the early Famennian (Late *Palmatolepis crepida* or Early *Palmatolepis rhomboidea* Zone) of Jabłonna described as *Cleiothyridina* sp. by Biernat (1983: pl. 6: 3), with length approximately equal to the width and poorly developed sulcus and fold, might also belong to the described species.

Stratigraphic and geographic distribution.—Avesnois (France), latest Famennian (Dehée 1929); Holy Cross Mountains (Poland), most probably latest Famennian.

Order Spiriferida Waagen, 1883

Family Cyrtospiriferidae Termier and Termier, 1949

Cyrtospiriferidae gen. et sp. indet.

Fig. 9G.

Material.—One shell ZPAL Bp 57/10, lacking postero-lateral parts, otherwise well preserved.

Description.—Shell 14.3 mm long, transverse, strongly ventribiconvex. Cardinal margin straight. Dorsal fold distinct but low and flattened. Ventral sulcus distinct but shallow. Ventral interarea apsacline, incurved, transversely striate; delthyrium 4.2 mm wide; remnant of a convex pseudodeltidium is visible. Dorsal interarea linear, catacline. Anterior commissure uniplicate, tongue rounded, 9.1 mm wide. Ornamentation of radial costae and costellae separated by narrower furrows, 10 on dorsal lateral flanks, 14 on ventral lateral flanks, 10 in fold and sulcus. Sinal pattern with numerous main plications, one group of densely crowded central plications and rare lateral plications (Fig. 9G_6). Fold pattern poorly preserved, with more dense central plications (Fig. 9G_1). Micro-ornamentation of fine radial capillae both on costae and between them (Fig. 9G_7), preserved in the ventral sulcus only.

Interior unknown.

Remarks.—The general form and sinal pattern of the discussed specimen remind of *Sinospirifer* Grabau, 1931; on the contrary, the micro-ornamentation is strongly similar to the *davidsoni*-pattern sensu Ma and Day (2007), characteristic of *Cyrtiopsis*. The form cannot be determined taxonomically with confidence due to inadequate preservation of the studied material (in particular, absence of internal characters).

Genus *Sphenospira* Cooper, 1954

Type species: *Spirifera alta* Hall, 1867; Famennian, Ohio, USA.

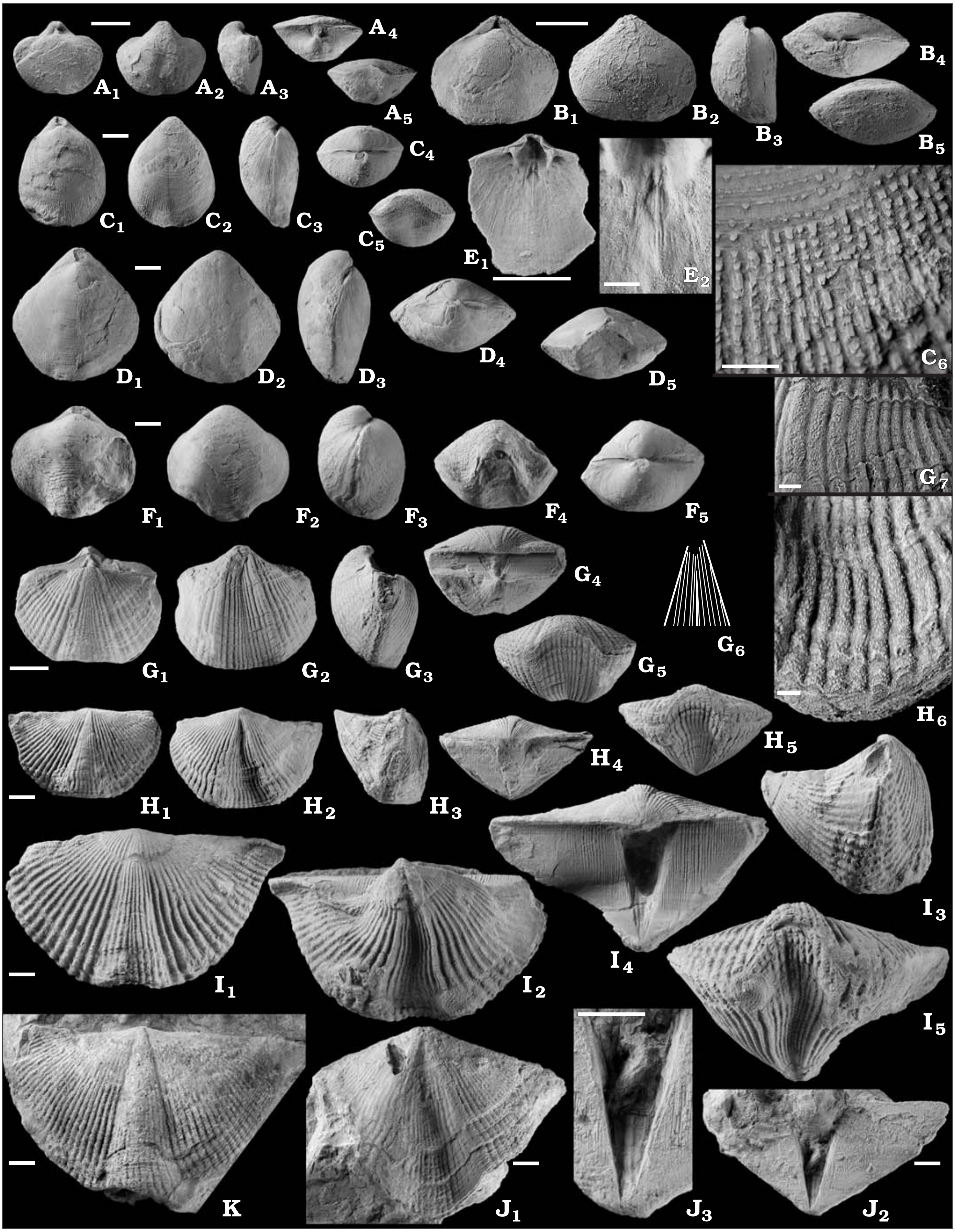
Sphenospira julii (Dehée, 1929)

Figs. 8, 9H–K.

1929 *Spirifer Julii* nom. nov.; Dehée 1929: 19–21, pl. 2: 1–8.
1969 *Sphenospira julii* (Dehée); Kaliś 1969: 812, pl. 2: 3.
1976 *Sphenospira julii* (Dehée); Matyja 1976: 504, 509, pl. 14: 1, 2, 4, 5.
non 1987 *Sphenospira julii* (Dehée, 1929); Jendryka-Fuglewicz and Fuglewicz 1987: 87–88, pls 1, 2.
?1995 *Sphenospira*? sp.; Baliński 1995: 75–77, pl. 15: 3–5, fig. 22.

Material.—15 shells, most often preserved only fragmentarily, ZPAL Bp 57/9, 11–16, 19, 23, 91–96, 114.

Fig. 9. Latest Famennian brachiopods from Kowala. **A**. ?*Eomartiniopsis* sp.; complete shell ZPAL Bp 57/68 in dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), and anterior (A_5) views. **B**. Reticulariidae gen. et sp. indet.; shell ZPAL Bp 57/32 in dorsal (B_1), ventral (B_2), lateral (B_3), posterior (B_4), and anterior (B_5) views. **C–F**. *Cleiothyridina struniensis* (Dehée, 1929). **C**. Elongate shell ZPAL Bp 57/85 in dorsal (C_1), ventral (C_2), lateral (C_3), posterior (C_4), and anterior (C_5) views and enlargement of the dorsal valve (C_6) showing micro-ornamentation. **D**. More transverse shell ZPAL Bp 57/2 in dorsal (D_1), ventral (D_2), lateral (D_3), posterior (D_4), and anterior (D_5) views. **E**. Ventral interior ZPAL Bp 57/34, general aspect (E_2) and detailed view of muscle scars (E_2). **F**. Shell ZPAL Bp 57/113 in dorsal (F_1), ventral (F_2), lateral (F_3), posterior (F_4), and anterior (F_5) views. **G**. Cyrtospiriferidae gen. et sp. indet.; slightly incomplete shell ZPAL Bp 57/20 in dorsal (G_1), ventral (G_2), lateral (G_3), posterior (G_4), and anterior (G_5) views; schematic diagram of sinal pattern (G_6); enlargement of the ventral valve (G_7) showing micro-ornamentation. **H–K**. *Sphenospira julii* (Dehée, 1929). **H**. Complete shell ZPAL Bp 57/96 in dorsal (H_1), ventral (H_2), lateral (H_3), posterior (H_4), and anterior (H_5) views and an enlargement of the ventral valve (H_6) showing micro-ornamentation. **I**. Complete shell ZPAL Bp 57/114 in dorsal (I_1), ventral (I_2), lateral (I_3), posterior (I_4), and anterior (I_5) views. **J**. Ventral valve ZPAL Bp 57/93 in ventral (J_1) and posterior (J_2) views with an enlargement of the delthyrium (J_3). **K**. Exterior of the dorsal valve ZPAL Bp 57/91. Scale bars 5 mm except C_6, E_2, G_7, and H_6 1 mm. →


A1
A2
A3
A4
A5
B1
B2
B3
B4
B5
C1
C2
C3
C4
C5
C6
D1
D2
D3
D4
D5
E1
E2
F1
F2
F3
F4
F5
G1
G2
G3
G4
G5
G6
G7
H1
H2
H3
H4
H5
H6
I1
I2
I3
I4
I5
J1
J2
J3
K

Description.—Shell large (up to 56 mm wide), transverse, strongly ventribiconvex. Ventral valve subconical. Maximal width at cardinal margin. Dorsal fold distinct, semi-ovate in transverse section, relatively narrow (up to one fourth of the shell width). Ventral sulcus distinct, U-shaped in transverse section, moderately deep. Anterior commissure uniplicate to paraplicate. Ventral interarea apsacline to procline (in older shells), very high (height to width ratio 0.43–0.52), sometimes concave, longitudinally striate. Deltidium occupying one fifth to one fourth of the interarea; delthyrial plate, with median longitudinal, rounded ridge, visible in one specimen (Fig. 8J_3). Dorsal interarea catacline, linear.

Ornamentation of strong radial costae, separated by narrower furrows, in the largest two specimens 13 in the fold, 15 in the sulcus, and 19?–24 on lateral flanks.

Interior unknown.

Remarks.—The material reported under this name by the present authors consists mostly of smaller specimens than the major part of the type collection of the species from Étrœungt (Dehée 1929): the largest specimen from Kowala (ZPAL Bp 57/91, Fig. 9K) is 56 mm wide, whereas in the French ones a width of ca. 60–80 mm is rather a rule than an exception. Moreover, the discussed material is quite diversified in the density of costation: in the median region of the dorsal valve (near the fold) from 3 costae per 5 mm (ZPAL Bp 57/14) to 4 per 5 mm (ZPAL Bp 57/96); in the median region of the ventral valve (near the sinus) from 3.5 per 5 mm (ZPAL Bp 57/96) to 4.5 per 5 mm (ZPAL Bp 57/9; 11 per 5 mm in the lateral region). A similar phenomenon occurs in the type collection from Étrœungt: for example, the holotype MGL 1582 has about 3 costae per 5 mm in the median region of the dorsal valve, and 5 costae per 5 mm in the lateral regions thereof, whereas the corresponding values for the ventral valve are, respectively, 4 and 9, whereas the dorsal valves MGL 1581 and MGL 1579 (Dehée 1929: pl. 8: 4 and 2, respectively) show the following pairs of values: 1.5 and 4, 3.5 and 10 (Dehée 1929; Nicollin 2004). In both collections therefore, the variation is strong, but ventral valves are usually more finely costate than dorsal ones. Poor stratigraphic resolution of the type collection and lack of better material in the type locality (Nicollin 2008) hampers recognition of the abovementioned morphotypes from the type area as representing intraspecific variability or being consecutive stages of a chronophyletic evolution. The first possibility was preferred and a wide understanding of the discussed taxon is admitted.

In Poland, this species was reported from Pomerania by Matyja (1976) and from the Lublin Basin by Kaliś (1969). A similar form (poorly preserved, described as *Sphenospira* sp.) was found by Baliński (1995) in approximately coeval strata of the Dębnik Anticline.

The spiriferid described as *Sphenospira julii* (Dehée, 1929) by Jendryka-Fuglewicz and Fuglewicz (1987) from exotic material of Kruhel Wielki (Carpathians, southern Poland) differs from *S. julii* in having curved hinge margin (straight in the latter), very faint costation (strong in *S. julii*), and less distinct sinus and fold. In consequence, the form from Kruhel Wielki represents most probably another species. The age determination of the brachiopod-bearing level by Jendryka-Fuglewicz and Fuglewicz (1987), based primarily on stratigraphic occurrence of *S. julii* may therefore be considered as unwarranted.

Stratigraphic and geographic distribution.—Dinant Synclinorium (Belgium), Avesnois (France), Velbert Anticline (Germany), Holy Cross Mts., Pomerania, Lublin Basin (Poland), Dniepr-Donets Trough, Kuznetsk Basin, Ural (Russia), Transcaucasia, Mongolia (Nicollin and Brice 2004: 440; present study). Famennian, in all cases where satisfactory stratigraphic precision is available the age of beds with *S. julii* is latest Famennian (Strunian).

Family Martiniidae Waagen, 1883

Genus *Eomartiniopsis* Sokolskaya, 1941

Type species: *Eomartiniopsis elongata* Sokolskaya, 1941; Famennian–Tournaisian, Moscow Basin, Russia.

?*Eomartiniopsis* sp.

Fig. 9A.

Material.—A single specimen, ZPAL Bp 57/68.

Description.—Shell small, transverse, strongly ventribiconvex. Maximal width posteriorly to midlength. Hinge line long, ventral interarea apsacline, poorly delineated. Umbo incurved. Ventral sulcus visible in the anterior half. Anterior commissure uniplicate, tongue low, rounded. Micro-ornamentation not preserved. Long, subparallel dental plates.

Remarks.—The general form suggests the appurtenance to the genus *Eomartiniopsis* Sokolskaya, 1941.

Family Reticulariidae Waagen, 1883

Reticulariidae gen. et sp. indet.

Fig. 9B.

Material.—Five rather poorly preserved shells, ZPAL BP 57/17, 32, 33, 90; PIG 163.II.66.1.

Description.—Shells small (8.1–10.5 mm in length), ovate, moderately transverse, slightly ventribiconvex. Maximal width slightly anteriorly to midlength. Anterior commissure rectimarginate to slightly uniplicate. Micro-ornamentation usually not preserved but one of the shells shows concentric growth lamellae and very fine spines.

Stratigraphic and palaeogeographic distribution

A comparison of the brachiopod content of the upper to uppermost Famennian set L with that of the middle to upper Famennian sets J and K is shown in Table 1.

Among twenty three analysed taxa, only four are in common between the two analysed faunas. Even if such a low ratio may be partly explained by insufficient data (several spe-

Table 1. Comparison of brachiopod faunas from upper Famennian sets J–K (data after Biernat and Racki 1986a; supplemented by Marynowski et al. 2007 and by the present authors) and uppermost Famennian set L (this work). +, species present; 1, a single specimen of the species present; –, species absent.

Taxon		Stratigraphic set	
Order	Species	J–K	L
Lingulida	*Barroisella* sp.	+	–
	Orbiculoidea sp.	+	–
Strophomenida	*Schellwienella pauli*	–	+
	Strophomenida indet.	–	+
Productida	*Mesoplica* sp.	–	+
	Productida indet.	–	+
Orthida	*Aulacella interlineata*	+	+
Rhynchonellida	*Leptoterorhynchus magnus*	+	+
	Rozmanaria equitans	–	1
	Pugnaria plana	+	1
	?*Pugnaria* sp.	+	–
	Novaplatirostrum sauerlandense	–	+
	Hadyrhynchia sp. nov.	–	1
	Planovatirostrum sp. 1 (= *P. planoovale* sensu Biernat and Racki 1986a)	+	–
	Planovatirostrum sp. 2 (= ?*P.* cf. *undulatum* sensu Biernat and Racki 1986a)	1	–
	?*Eoparaphorhynchus* sp.	1	–
	Rhynchonellida indet. 1	–	+
	Rhynchonellida indet. 2	+	–
	?*Centrorhynchus* sp.	+	–
Athyridida	*Cleiothyridina struniensis*	–	+
Spiriferida	Cyrtospiriferidae indet.	–	1
	Sphenospira julii	–	+
	?*Eomartiniopsis* sp.	–	1
	Reticulariidae indet.	–	+
Terebratulida	*Cranaena lgaviensis*	+	–
Indeterminate		–	+
TOTAL: species present		11	18
TOTAL: orders present		4	6

cies represented only by single specimens), it attests nevertheless to a major faunal turnover in the Kowala section before the latest Famennian (even if a precise dating cannot be given). This phenomenon may be explained by a facies change caused by the global Strunian transgression (T-R cycle IIf of Johnson et al. 1985; Dreesen et al. 1988; Matyja 1993). An analogous "Strunian" immigration event among Rugosa was noted by Berkowski (2002, and references therein). Moreover, it should be emphasised that the species in common between the faunas of sets J–K and L belong to the orders Rhynchonellida and Orthida; on the contrary, representatives of the Strophomenida, Productida, Athyridida, and Spiriferida are known solely from set L, whereas representatives of the Lingulida and Terebratulida only from the sets J–K. This might suggest a greater ecologic plasticity of representatives of the rhynchonellids and orthids.

Table 2. Geographic distribution of latest Famennian brachiopods from Kowala. Only taxa identified at species level have been taken into account. Sources of data: Pomerania after Matyja (1976); Lublin Basin after Kaliś (1969), corrected; Étrœungt after Dehée (1929) and Gallwitz (1932); SW England after sources reported in Amler and Heidelberger (2003), Rhenish Slate Mountains after Gallwitz (1932) and Weyer (1972), Mugodzhary and the Russian Platform after various sources reported in Nicollin and Brice (2004). Species in common with the Kowala section are counted twice, the first time with dubious presences counted as absences, the second one (in brackets) with dubious presences counted as presences.

Taxon / Region	Kowala	Pomerania	Lublin Basin	Étrœungt	Rhenish Slate Mts.	SW England	Mugodzhary and S Urals	Russian Platform
Schellwienella pauli	+	+	+	?	+			
Aulacella interlineata	+	+	+	+	+	+		
Leptoterorhynchus magnus	+							
Rozmanaria equitans	+				+		+	
Pugnaria plana	+				?			
Novaplatirostrum sauerlandense	+				+			
Cleiothyridina struniensis	+			+				
Sphenospira julii	+	+	+	+		+	?	+
Species in common with Kowala	7	3	3	3(4)	3(5)	2	1(2)	1

The geographical distribution of "Strunian" brachiopods from Kowala is presented in Table 2.

As far as it can be judged from the limited sample (eight species; the other taxa, described in open nomenclature, were unfit for this analysis), the "Strunian" fauna of Kowala is composed in major part of species widely distributed geographically. Such a situation is quite common among coeval brachiopod faunas (Nicollin and Brice 2004).

Palaeoecology

The described latest Famennian brachiopod fauna from Kowala inhabited deep-water soft-bottom settings located presumably below the photic zone (Szulczewski 1971; Biernat and Racki 1986a). Characteristic is the co-occurrence of sulcate (*Rozmanaria*, *Leptoterorhynchus*) and uniplicate (*Pugnaria*, *Novaplatirostrum*) rhynchonellids.

All Recent rhynchonellids have spirally coiled lophophore known as spirolophous. It is highly probable that the same type of the lophophore was characteristic for all fossil representatives of the order since its origin in the Early Ordovician (Rudwick 1970), including those from the latest Famennian of Kowala. This type of lophophore is regarded as an efficient filtering system (e.g., Fürsich and Hurst 1974; Vogel 1975). It is also probable that the rhynchonellids studied here, which possess very limited proximal skeletal support of the lophophore in the form of crura and lack of rigid calcareous spiralia, could uncoil and extend their lophophore beyond the shell for feeding purposes similarly as it was observed among Recent representatives of the group (see Ager 1987). As Ager remarked (1987: 853) such a capability is an advantage for a suspension feeder since it greatly extends the area for trapping food particles in the water. Recently Lee (2008) remarked, however, that the ability of rhynchonellids and terebratulids to extend their lophophore outside the shell seems unlikely.

The adult shells of the rhynchonellids from Kowala have thin and largely smooth shells, very small pedicle foramen combined with a median deflection of the anterior commissure, either ventrally (sulcate) or dorsally (uniplicate) directed. According to Fürsich and Hurst (1974) and Vörös (2005) these features suggest adaptation to deep and quiet water environment. The deflection of the anterior commissure of the rhynchonellids guides the exhalant water current more ventrally (in sulcate) or dorsally (in uniplicate forms) and consequently separates the exhalant apertures from inhalant ones (Copper 1986; Emig 1992), thereby increasing efficiency of filtering process. Similar enhancing of feeding efficiency was also presumed for sulcate adult terebratulids (Lee 2008). Although the deflection of the commissure may be found in rhynchonellids inhabiting various water depths, this feature might have been particularly advantageous for forms dwelling in deep quiet water environment.

Besides rhynchonellids several other brachiopods from Kowala are also characterised by possessing spirolophe type of lophophore (as it can be concluded from their brachidia) and deflection (uniplication) of the anterior commissure, i.e., *Cleiothyridina struniensis*, Cyrtospiriferidae gen. et sp. indet., *Sphenospira julii*, ?*Eomartiniopsis* sp., and Reticulariidae gen. et sp. indet. According to Fürsich and Hurst (1974) the lophophore of Spiriferida (in broad sense, including athyrididids) is regarded as most advanced, powerful, and efficient filtering system of any brachiopod group. It seems that these adaptations of brachiopod fauna from Kowala (spirolophous lophophore and deflection of the commissure) may be regarded as advantageous for this particular environment characterised by a deep water setting and lower concentrations of nourishment.

Conclusions

- The thick sequence of intercalated limestone and marl (set L of the Kowala quarry, Kielce Region of the Holy Cross Mountains) contains a moderately diversified brachiopod fauna (eighteen species). The bulk of this fauna is dated to the latest Famennian ("Strunian"); its minor part may belong to the late Famennian. It is the richest brachiopod fauna of this age reported up to now from the Holy Cross Mountains.
- Faunal content of the middle to upper Famennian grey limestone and slate (sets J–K) and uppermost Famennian cephalopod limestone and marl (set L) are quite different: only five species (out of twenty two) are common for both faunas. They belong to the Rhynchonellida and Orthida, whereas representatives of other orders are limited to one of the two faunas.
- The stratigraphic separation between two members of the same evolutionary lineage, namely *Planovatirostrum* in the middle and late Famennian (UD-III to UD-V) and *Novaplatirostrum* in the latest Famennian (UD-VI) observed in Sauerland and in Thuringia is valid also in the Holy Cross Mountains.
- Majority of species from Kowala possessed spirolophe type of lophophore and deflection (sulcation or uniplication) of the anterior commissure. These seem to have been adaptations to deep water settings and/or poor nutrient availability.
- The described latest Famennian brachiopod fauna from the set L consists mainly of species widely distributed geographically.

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