Late Frasnian Athyridida (Brachiopoda) from Poland and the Late Devonian biotic turnover

TATJANA A. GRUNT and GRZEGORZ RACKI

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Late Frasnian representatives of the order Athyridida from the Holy Cross Mountains, Poland, support the idea that the Laurussian basins were the places of origin and radiation of the subfamilies Athyridinae and Meristinae during the middle and early late Paleozoic. At least three new species have been identified from two localities (Łgawa Hill and Kowala) in the Gałęzice Syncline. Of these, one was probaby endemic (*Merista rhenanensis* sp. n.; maybe also ?*Zonathyris* sp. A), and two (*Athyris postconcentrica* sp. n. and *Pachyplaxoides postgyralea* gen. et sp. n.) were more widely distributed in this part of the Laurussian shelf, being known also from the East European Platform and Rheinisches Schiefergebirge, respectively. This confirms an intermediate biogeographic position of the Holy Cross Mountains area, belonging to an important centre of brachiopod origin and diversification. In contrast to other articulate brachiopods, athyridids reveal a higher rate of diversification, especially at the species (and partly also generic) level, during the global Kellwasser Crisis.

Key words: Brachiopoda, Athyridida, taxonomy, biostratigraphy, biogeography, phylogeny, mass-extinction, Kellwasser Crisis, Frasnian, Famennian, Devonian, Poland.

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Introduction

Brachiopods of the order Athyridida constitute an important member of the Palaeozoic shelly benthos. Analysis of their stratigraphic distribution, both at the generic and species level, reveals cyclicity in the development of the group, that correlates well with major palaeogeographic and eustatic changes (Grunt 1989b). The late Devonian epoch represented one of the intervals when diversity of the athyridids decreased, and a closer examination of the brachiopod distribution in the context of the Frasnian-Famennian (F-F) mass extinction is one of the main goals of the present publication.

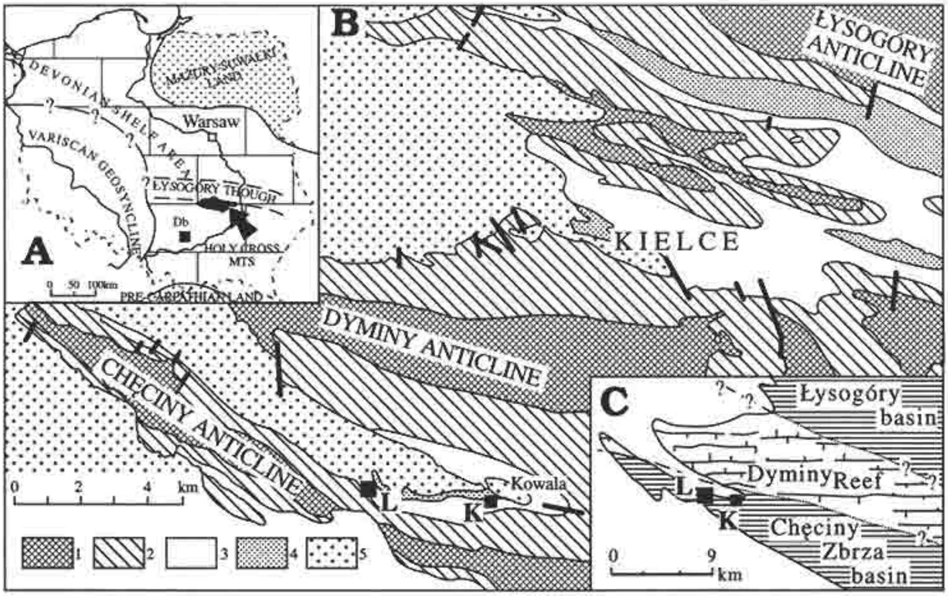

Fig. 1. **A**. Paleogeographic scheme of the Frasnian in Poland. Db – Dębnik area near Cracow; see Baliński 1979, 1995a). **B**. Geological sketch map of the western part of the Holy Cross Mountains to show location of athyridid sites. **C**. Frasnian facies pattern of the region under study. After Racki *et al.* (1993: fig. 1, modified): Abbreviations: K – Kowala quarry, L – Łgawa Hill (Jaźwica quarry); 1 – Cambrian–Silurian, 2 – Lower–Middle Devonian, 3 – Upper Devonian, 4 – Lower Carboniferous, 5 – Permian–Mesozoic cover.

Recent taxonomic revision of the Devonian athyridid faunas from different regions of Europe (Alvarez 1990; Alvarez & Brunton 1990; Racheboeuf *et al.* 1994; Gretchisnikova 1996), supplemented by the present analysis of the abundant late Frasnian material from the Holy Cross Mountains (Central Poland), have enabled a deeper insight than hitherto into the history of the group in the key crisis interval.

Four species have been identified from the late Frasnian calcareous-marly succession in two localities: Łgawa Hill ('eastern' Jaźwica quarry) near Bolechowice, and Kowala quarry (and adjacent outcrops) in the Gałęzice Syncline, SW Holy Cross Mountains (Fig. 1); the geological setting of the brachiopod-rich sites is presented in Mikłas (in Racki *et al.* 1993) and Racki & Baliński (1998). The species are richly represented in the Late *Palmatolepis rhenana* Zone, but they occur also in the Early *P. rhenana* Zone, and possibly even in the earlier part of the *Palmatolepis linguiformis* Zone.

The athyridid collection includes ca. 100 mostly silicified specimens. The material was collected by G. Racki (and collaborators), the systematic palaeontology was prepared by T.A. Grunt; the remainder of the paper was written by both of the authors.

Institutional abbrevations: GIUS – Department of Earth Sciences, Silesian University at Sosnowiec; SMF – Natur Museum und Forschungs-Institut Senckenberg in Frankfurt a.M.; PIN RAN – Paleontological Institute of Russian Academy of Sciences in Moscow.

Other abbreviations: GŁ – Łgawa Hill, KE – Kowala, L – shell length (mm), $\overline{L}$ – average value of shell length in sample, W – shell width (mm), $\overline{W}$ – average value of shell width in sample, T – shell thickness (mm), $\overline{T}$ – average value of shell thickness in sample, AA – apical angle, $\overline{AA}$ – average value of apical angle in sample, HL – hinge line (mm), $\overline{HL}$ – average value of hinge line in sample, Wdl – width of the delthyrium (mm), $\overline{Wdl}$ – average value of hinge line in sample, Ws – width of the sinus (mm), $\overline{Ws}$ – average value of width of the sinus in sample, n – number of specimens.

Systematic Palaeontology

(T.A. GRUNT)

Order Athyridida Boucot, Johnson & Staton, 1964; nom. transl. Dagys, 1974 (ex Athyridoidea Boucot, Johnson & Staton, 1964)
Suborder Athyrididina Boucot, Johnson & Staton, 1964
Superfamily Meristellacea Waagen, 1883
Family Meristidae Hall & Clarke, 1895
Subfamily Meristinae Hall & Clarke, 1895
Genus *Merista* Suess, 1851 (in Davidson 1851)
Merista rhenanensis sp. n.

Figs 2, 3.

Holotype: GIUS 4-1477/GŁ-150, complete silicified shell, illustrated in Fig. 2J–M.

Type locality: Łgawa Hill near Bolechowice, Holy Cross Mountains, Poland.

Type horizon: Late Devonian, late Frasnian, *Palmatolepis rhenana* Zone (unit R; see Racki & Baliński, 1998).

Derivation of name: From *Palmatolepis rhenana* conodont Zone.

Material. — Fourteen silicified specimens: nine complete shells, four deformed shells, and one brachial valve.

Dimensions (in mm):

Cat. No. IGUS 4–1477	L	W	T	AA	HL	Wdl	Ws	L/W	W/T	W/HL
GŁ-150 (holotype)	20.35	19.45	12.65	89	15.00	7.25	10.20	1.05	1.54	1.30
GŁ-151	17.50	17.30	10.80	100	13.15	6.45	10.50	1.01	1.60	1.31
GŁ-152	17.15	16.05	10.75	91	12.85	5.75	10.20	1.07	1.50	1.30
GŁ-153	12.90	12.65	8.35	89	7.55	3.55	7.20	1.02	1.51	1.67
GŁ-154	19.15	20.00	10.85	98	13.35	5.15	10.35	0.96	1.84	1.50
GŁ-155	21.15	20.40	11.95	100	15.80	6.35	12.35	1.04	1.71	1.29
GŁ-156	18.35	17.65	10.65	103	14.55	5.75	12.70	1.04	1.66	1.21
GŁ-157	16.25	16.70	10.00	100	12.90	4.95	9.80	0.97	1.67	1.29
GŁ-158	16.00	15.30	9.15	98	9.70	4.10	5.90	1.04	1.67	1.58

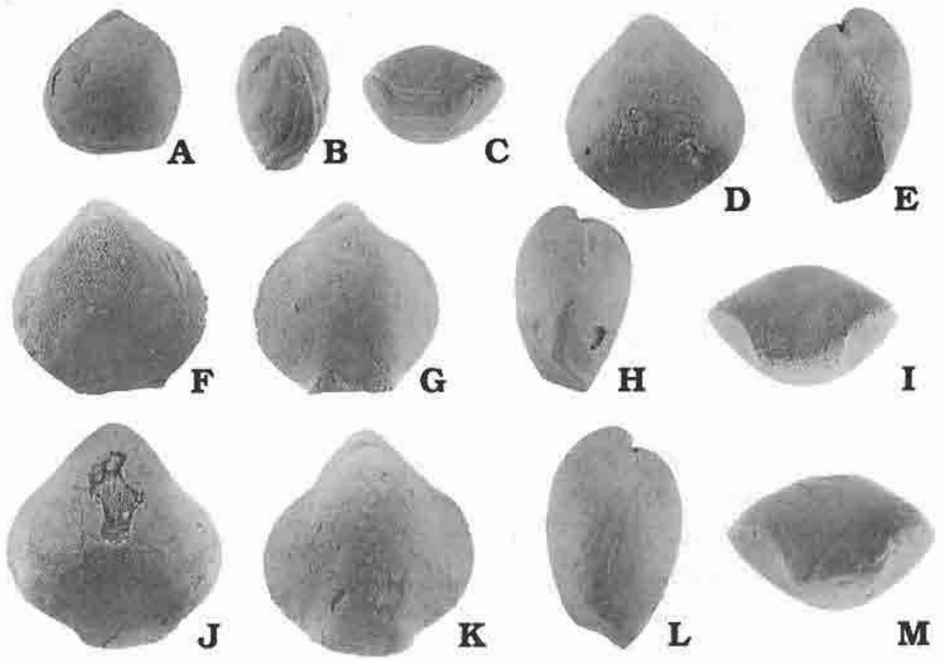

Fig. 2. *Merista rhenanensis* sp. n. from late Frasnian of Łgawa Hill near Bolechowice, Holy Cross Mts, Poland. **A–C**. Juvenile shell GIUS 4-1477/GŁ-153 in ventral, dorsal, and lateral views. **D–E**). Shell GIUS 4-1477/GŁ-152 in ventral and lateral views. **F–I**. Shell GIUS 4-1477/GŁ-151 in ventral, dorsal, lateral, and anterior views. **J–M**. Holotype GIUS 4-1477/GŁ-151 in ventral, dorsal, lateral, and anterior views. All × 1.5.

Diagnosis. — A species of *Merista* which differs from all other species of the genus in a combination of relatively large shell size (L more than 20 mm) and regular subpentagonal outline. Differs from the Eifelian species *M. turgens* Siehl, 1962 in having a more longitudinal outline (see Siehl 1962).

Description. — The shell of medium size ($\overline{L}$ = 18.18; range 12. 90–20.35; $\overline{W}$ = 18.01; range 12.65–19.45; $\overline{T}$ = 10. 52; range 8.35–12.65; n = 9), equidimensional or slightly longer than wide ($\overline{L/W}$ = 1.01; range 0.96–1.07). The maximum width and thickness at about half of the shell length. The anterior commissure strongly uniplicate to parasulcate.

The ventral valve moderately and even convex. The hinge line strongly incurved and essentially less than the maximal width of the shell ($\overline{HL}$ = 13.26; range 7.55–15.00; $\overline{W/HL}$ = 1.37; range 1.30–1.67). The beak prominent, massive, slender, incurved and perforated by a small rounded foramen ($\overline{AA}$ = 99.8; range 89–100). The small triangular delthyrium occupied by the beak of the dorsal valve ($\overline{Wdl}$ = 5.26; range: 3.55–7.25). A flattened depression initiated at about the posterior third of the valve, forming a weak tongue over the anterior margin ($\overline{Ws}$ = 10.22; range 7.20–12.70).

The dorsal valve slightly more convex than the ventral one, with the greatest convexity close to the umbo; the surface curving more gently towards the cardinal margin. The beak short, directed ventrally and exceeding the delthyrium. The median fold developed in the anterior part of the valve, distinctly developed along the anterior margin.

The surface of the shell smooth. Only rare concentric lines of growth are developed. Muscle scars not observed. The internal structures typical for the genus (Fig. 3).

Remarks. — The new species represents the stratigraphically latest occurrence of the genus in Europe.

Occurrence. — Poland, Łgawa Hill near Bolechowice, Holy Cross Mountains; Late Devonian, late Frasnian (unit R), *P. rhenana* Zone.

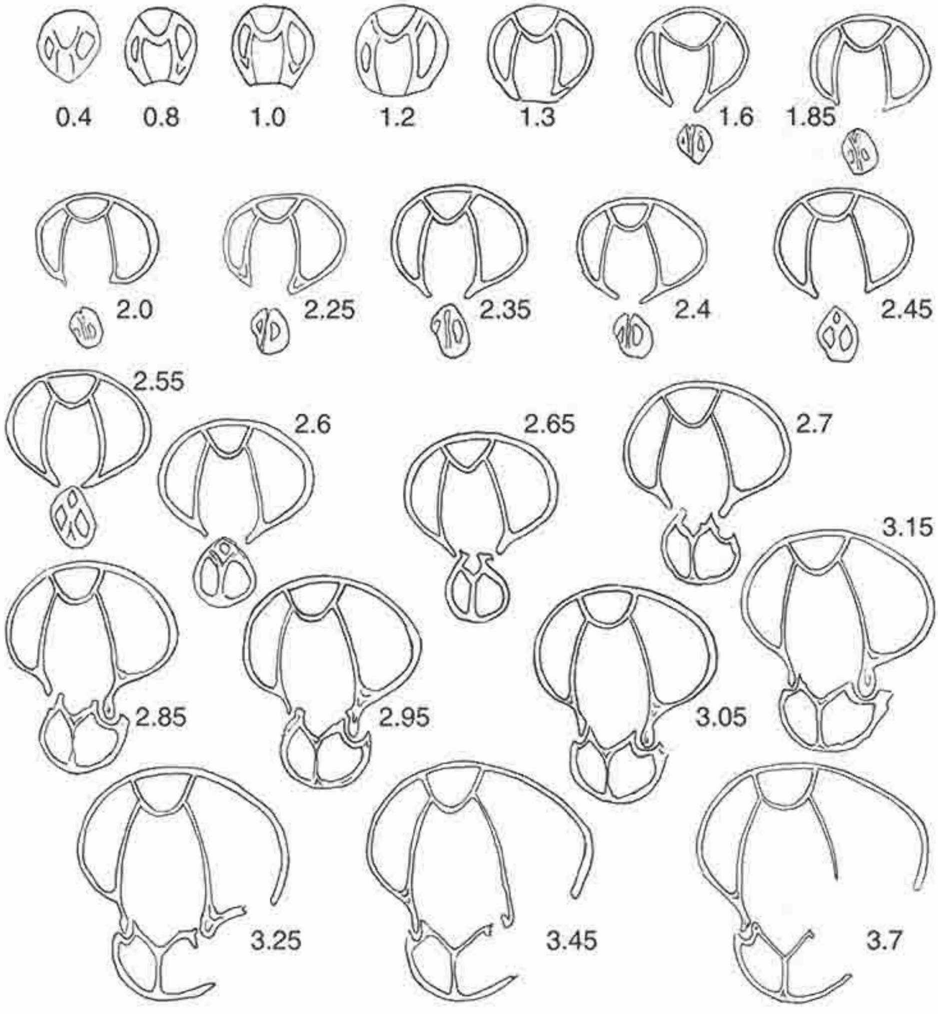

Fig. 3. *Merista rhenanensis* sp. n. Transverse serial sections of the specimen GIUS 4-1477/GŁ-70 (× 5). Distances are measured in mm from the apex of the ventral valve.

Superfamily Athyridacea Davidson, 1881

Family Athyrididae Davidson, 1881

Subfamily Athyridinae Davidson, 1881

Genus *Athyris* McCoy, 1844

Athyris McCoy, 1844, p. 146; Grunt, 1980: p. 54 (see review of synonymy); Grunt 1986: p. 58.

Remarks. — Over 50 species are included in this genus (listed in Grunt 1989a: p. 83). Alvarez *et al.* (1996) actually recently selected a neotype for *Terebratula concentrica* Buch, 1834. In their opinion, there is not a single specimen showing even a superficial similarity to the original description of this species in the entire collection of Leopold von Buch, housed in the Museum für Naturkunde, Zentralinstitut der Humboldt-Universität, Berlin. However, detailed examination of this collection by D.Weyer and T.A. Grunt, with reference to the Quenstedt Catalogue (p. 764), confirmed that the

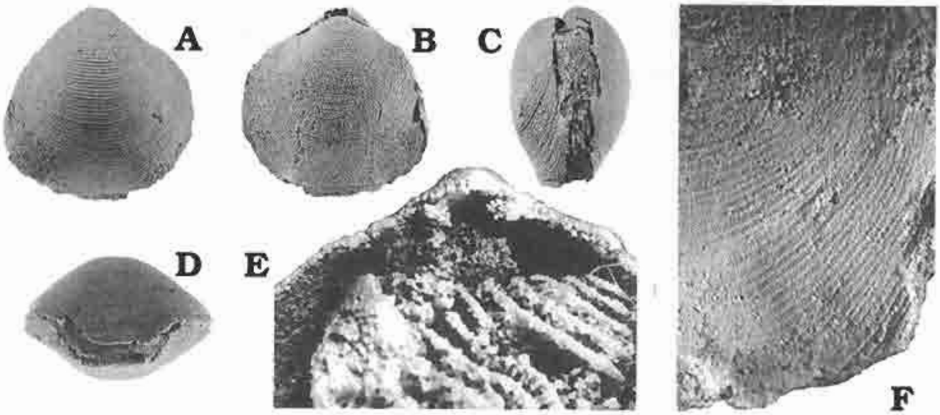

Fig. 4. *Athyris postconcentrica* sp. n. from late Frasnian of Łgawa Hill near Bolechowice, Holy Cross Mts, Poland. Shell GIUS 4-1477/GŁ-140 in ventral, dorsal, lateral and anterior views (**A–D**), sculpture (**F**); isolated brachial valve GIUS 4-1477/GŁ-161 in view on the inside (**E**). All × 1.5 except for E–F that are × 6.

original specimens (representing several species) of L. von Buch are indeed stored in this museum. Following the original description, Weyer & Grunt (in preparation) recommend that the specimen no. Mb-b. 922 from this collection be selected as lectotype of *Athyris concentrica* (Buch, 1834).

Athyris postconcentrica sp. n.

Figs 4–6.

Athyris concentrica (Buch, 1834); Lyashenko 1959: p. 213, pl. 82: 4–6.
Athyris concentrica (Buch, 1834); Grunt 1980: p. 54 (*partim*), pl. 2: 1–8, figs 14–16.
Athyris concentrica (Buch, 1834); Grunt 1989a: p. 83 (*partim*), fig. 16.
Athyris; Mikłas in Racki *et al.* 1993: p. 72, pl. 6: 1–2, 6–8, 10.

Holotype: PIN RAN 554/19; complete shell, illustrated in Grunt (1980: pl. 2:1).

Type locality: Kazaki station, Orlovski region, Russia.

Type horizon: Elets Horizon, middle Famennian (*Palmatolepis rhomboidea–Palmatolepis marginifera* Zones, Late Devonian.

Derivation of name: occurring after *Athyris concentrica* (Buch, 1834).

Material. — Thirty complete adult shells, 25 complete young and juvenile shells; all more or less silicified.

Dimensions (in mm):

Cat. No. IGUS 4-1477/	L	W	T	AA	HL	Ws	L/W	W/T	W/HL
KE-60	15.60	15.70	10.15	99	12.40	9.80	0.99	1.55	1.27
KE-61	12.65	12.75	7.80	94	9.15	8.95	0.92	1.63	1.39
GŁ-140	17.15	17.50	11.25	93	9.40	5.40	0.98	1.55	1.86
GŁ-162	17.00	18.50	10.50	96	15.40	8.50	0.92	1.76	1.20
GŁ-163	13.70	14.50	9.00	95	11.95	8.65	0.94	1.61	1.21
GŁ-164	15.75	16.50	10.50	95	11.20	8.55	0.95	1.57	1.47
GŁ-165	20.40	19.50	19.60	98	17.00	12.80	1.04	1.43	1.15
GŁ-166	16.85	18.20	12.65	96	15.30	10.05	0.92	1.44	1.19

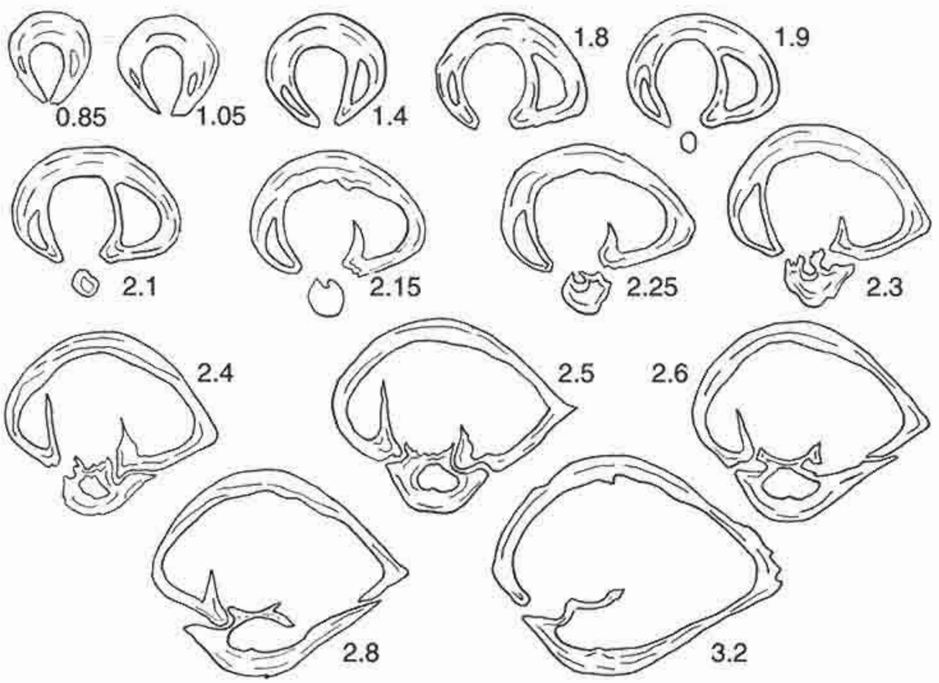

Fig. 5. *Athyris postconcentrica* sp. n. Transverse serial sections of the specimen GIUS 4-1477/GŁ-68 (× 5). Distances are measured in mm from the apex of the ventral valve.

Diagnosis. — Medium-sized species of *Athyris* distinguished from *A. concentrica concentrica* (Buch, 1834) by its smaller size and less incurved anterior margin; from *A. concentrica ventrosa* (Schnur, 1853) it differs by absence of strong vascular impressions (see Alvarez *et al.* 1996: pl. 1: 2–6, especially 4), an extremely rare feature in representatives of Athyridacea. *A. postconcentrica* sp. n. is larger, and more uniplicate at the anterior margin than *A. area* Baliński, 1995.

Description. — The shell of medium size ($\overline{L}$ = 14.96; range 12.10–20.40; $\overline{W}$ = 15.51; range 12.75–19.50; $\overline{T}$ = 10.01; range 7.80–12.45; n = 30); equidimensional to slightly wider than long or sometimes slightly longer than wide ($\overline{L/W}$ = 0.95; range 0.92–1.03) rounded-subpentagonal in outline with gently arched lateral margins, moderately equally biconvex to dorsibiconvex. The maximum width at about half the shell length. The maximum thickness within the posterior third of the shell. The anterior commissure rectimarginate to strongly uniplicate.

The ventral valve moderately and evenly convex with the surface curving more strongly from the umbo towards the cardinal margins and less towards the anterior margin. The hinge line moderately incurved and slightly less than maximum width of the shell ($\overline{HL}$ = 11.6; range 8.65–15.40). The beak prominent, recurved over the cardinal margin and perforated by a small rounded permesothyrid foramen ($\overline{AA}$ = 99; range 92–105). The small triangular delthyrium occupied by the beak of the dorsal valve. There is an indistinct median sulcus. A flattened depression originates at about mid-length or in anterior third of the valve, forming a weak tongue over the anterior margin ($\overline{Ws}$ = 9.06; range 5.40–10.90).

The dorsal valve more convex than the ventral, with the greatest convexity in the posterior third close to the umbo, with the surface curving strongly from the umbo towards the cardinal margin. The beak directed ventrally and over the delthyrium. The median fold indistinct, developed in the anterior part of the valve.

Both valves ornamented by concentric, closely spaced and imbricated growth lamellae (Fig. 4F).

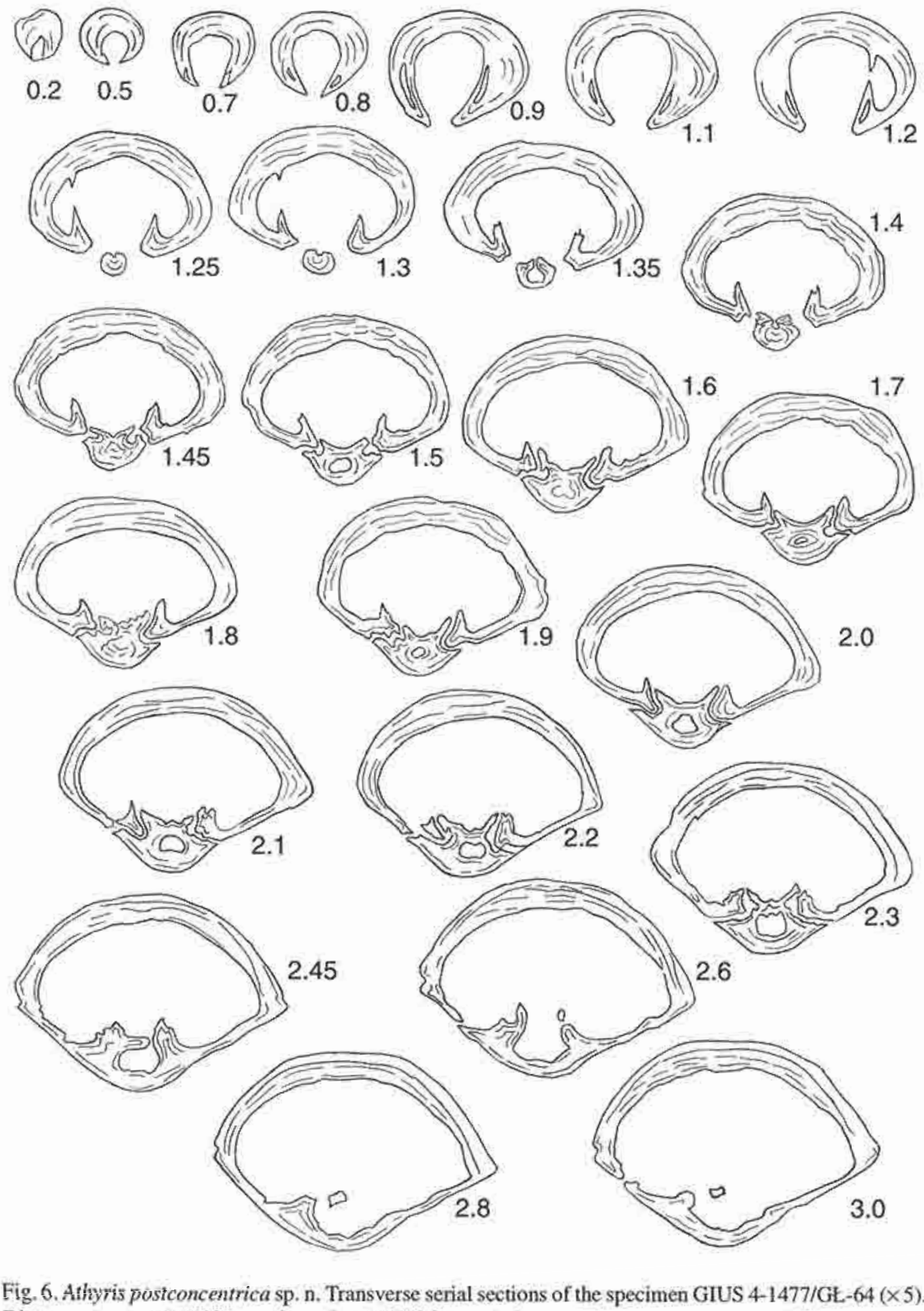

Fig. 6. *Athyris postconcentrica* sp. n. Transverse serial sections of the specimen GIUS 4-1477/GŁ-64 (×5). Distances are measured in mm from the apex of the ventral valve.

The dental plates begin at 0.9 mm from the apex of the ventral valve and extend anteriorly for about 4 mm. They are thin and slightly concave in the apex-region, becoming parallel anteriorly. They are differentiated from the lateral walls of the valve at about 1 mm from the apex. In the plane

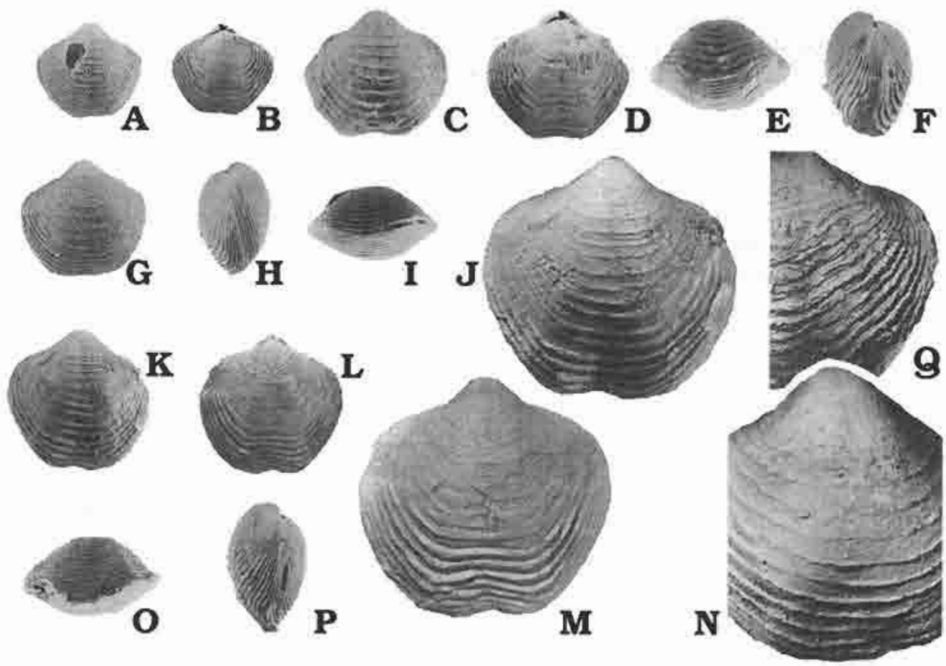

Fig. 7. *Pachyplaxoides postgyralea* sp. n. from late Frasnian of Łgawa Hill near Bolechowice, Holy Cross Mts, Poland (**A–B**, **G–O**) and Quarry Reichle, Prümer Mulde, Eifel Hills, Germany (**C–F**, **Q**). **A–C**. Juvenile shell GIUS 4-1477/GŁ-153 in ventral and dorsal views. **C–F**. **Q**. Holotype SFM 59509 in ventral, dorsal, lateral, and anterior views (**C–F**), sculpture (**Q**). **G–I**, **N**. Shell GIUS 4-1477/GŁ-102 in ventral, dorsal, lateral, and anterior views (**G–I**), sculpture (**N**). **J–M**, **O**, **P**. Shell GIUS 4-1477/GŁ-101 in ventral (**J–K**), dorsal (**L–M**), anterior (**O**), and lateral (**P**) views. All × 1.5 except for **J** and **M–N** that are × 6, **N** × 10, and **Q** × 3.

of articulation, the dental plates occupy the total height of the ventral cavity. The teeth subrectangular and slightly curved. The corresponding dental sockets bordered laterally by low inner socket ridges. The cardinal plate extends anteriorly for a length of 3.05 mm from the umbo. It is subtriangular, concave and apically perforated (Figs 4E, 5, 6). The inner cardinal plate relatively wide, gently concave, and subtriangular. The outer cardinal plates small and subtriangular. The brachidium consists of at least 10 whorls (Fig. 4E). The muscle scars poorly differentiated.

Remarks. — This species was previously identified as *Athyris concentrica* Buch (e.g., Grunt 1980). However, the investigation of the original collection of L. von Buch (1834), housed in the Museum of Natural History in Berlin, has allowed the separation of these two species.

Occurrence. — Russia: Orlovski region, Kazaki station; Late Devonian, middle Famennian (*P. rhomboidea–P. marginifera* Zones), Elets Horizon. Poland: Holy Cross Mountains, Łgawa Hill near Bolechowice, unit R, and Kowala Quarry (eastern wall), unit H-2; Late Devonian, late Frasnian, *P. rhenana* Zone, mostly the late part (?also *P. linguiformis* Zone).

Genus *Pachyplaxoides* gen. n.

Derivation of name: Showing a close external similarity to *Pachyplax* Alvarez & Brunton, 1990.

Diagnosis. — *Pachyplaxoides* differs from the majority of athyridoid genera in the absence of dental plates within the ventral valve. It resembles *Planalvus* Carter, 1971 in the absence of dental plates, and in having a small shell size and a subcircular outline; it differs in the thin-shelled ventral valve and in the presence of a perforation within the cardinal plate.

Remarks. — Like *Pachyplaxoides* gen. n., *Lamellosathyris* Jin & Fang, 1983 (type species *Spirifer lamellosa* Leiveille, 1835) is also characterized by the absence of dental plates within the ventral valve, as was shown by Jin & Fang (1983: p. 148, fig. 1) in the material from the Tournaisian of Western Yunnan, China. Brunton (1980: figs 16, 17) selected a neotype of *Spirifer lamellosa* and illustrated two specimens from the Tournaisian of Belgium; the specimen in his fig. 17 shows the interior of the umbonal regions of a silicified specimen revealing the articulation, dental plates, perforated cardinal plate and pedicle cavity. The specimens from China, as well as those from Belgium, are externally marked by strong lamellose ornamentation, but fine radially arranged grooves or spines remain undeveloped. In contrast to the European forms, however, the Chinese specimens are typified by the absence of dental plates. Thus, revision of the Carboniferous group is necessary, also in the context of the new genus proposed herein.
Species included. — *Pachyplaxoides postgyralea* sp. n.

Pachyplaxoides postgyralea sp. n.

Figs 7, 8.
Holotype: SFM 59509, complete shell, illustrated in Fig. 7C–F.
Type locality: Reichle Quarry, Prüme Syncline, Eifel Hills, Germany.
Type horizon: Late Devonian, late Frasnian; Early *Palmatolepis rhenana* Zone.
Derivation of name: Occurring after *Pachyplax gyralea* Alvarez & Brunton, 1990.
Material. — Twenty complete silicified shells in good preservation.
Dimensions (in mm):

Cat. No. IGUS 4-1477/	L	W	T	AA	HL	Ws	L/W	W/T	W/HL
GŁ-101	12.10	12.60	7.10	102	10.90	6.45	0.96	1.77	1.22
GŁ-102	10.35	11.50	6.45	107	10.45	6.05	0.90	1.78	1.10
GŁ-103	8.05	9.25	4.85	102	8.30	5.10	0.91	1.90	1.11
GŁ-104	12.00	12.45	7.75	103	10.95	6.45	0.96	1.67	1.14
GŁ-105	11.50	12.75	8.05	96	11.55	7.75	0.90	1.58	1.10
GŁ-106	11.55	13.20	7.70	101	11.75	6.45	0.87	1.71	1.12
GŁ-107	12.20	12.55	7.35	102	11.30	6.80	0.97	1.70	1.11
GŁ-108	10.50	11.15	7.10	106	10.55	6.45	0.94	1.57	1.06

Diagnosis. — *Pachyplaxoides postgyralea* sp. n. in its outline, dimensions and ornamentation, demonstrates close similarity to representatives of *Pachyplax* Alvarez & Brunton, 1990, but essentially differs in the absence of dental plates within the ventral valve.
Description. — The shell small to medium size ($\overline{L}$ = 10.51; range 8.05–13.00; $\overline{W}$ = 11.31; range 9.25–12.60; n = 20) from slightly to moderately biconvex ($\overline{T}$ = 6.73; range 4.85–8.05) equidimensional to slightly wider than long ($\overline{L/W}$ = 0.89; range 0.85–1.01), rounded subpentagonal to subcircular in outline. The almost straight hinge line slightly shorter than the maximum width, which is about half of the shell length ($\overline{HL}$ = 11.15; range 8.30–11.75). The maximum thickness within the posterior third of the shell. The anterior commissure gently uniplicate.

The ventral valve has an even median convexity. The triangular delthyrium largely occupied by the dorsal beak. The median sulcus poorly developed, originating at about one third of the the valve length, becoming more conspicuous anteriorly (Ws 6.27; range 3.10–7.75). The beak prominent, short, slightly recurved over the cardinal margin and perforated by a small rounded permesothyrid foramen; $\overline{AA}$ = 102.55; range 95–108.

The dorsal valve most strongly curved over the umbonal region. The beak directed ventrally and over the delthyrium. The median fold poorly defined, gently rounded, originating at about one third of the the valve length, becoming more prominent anteriorly.

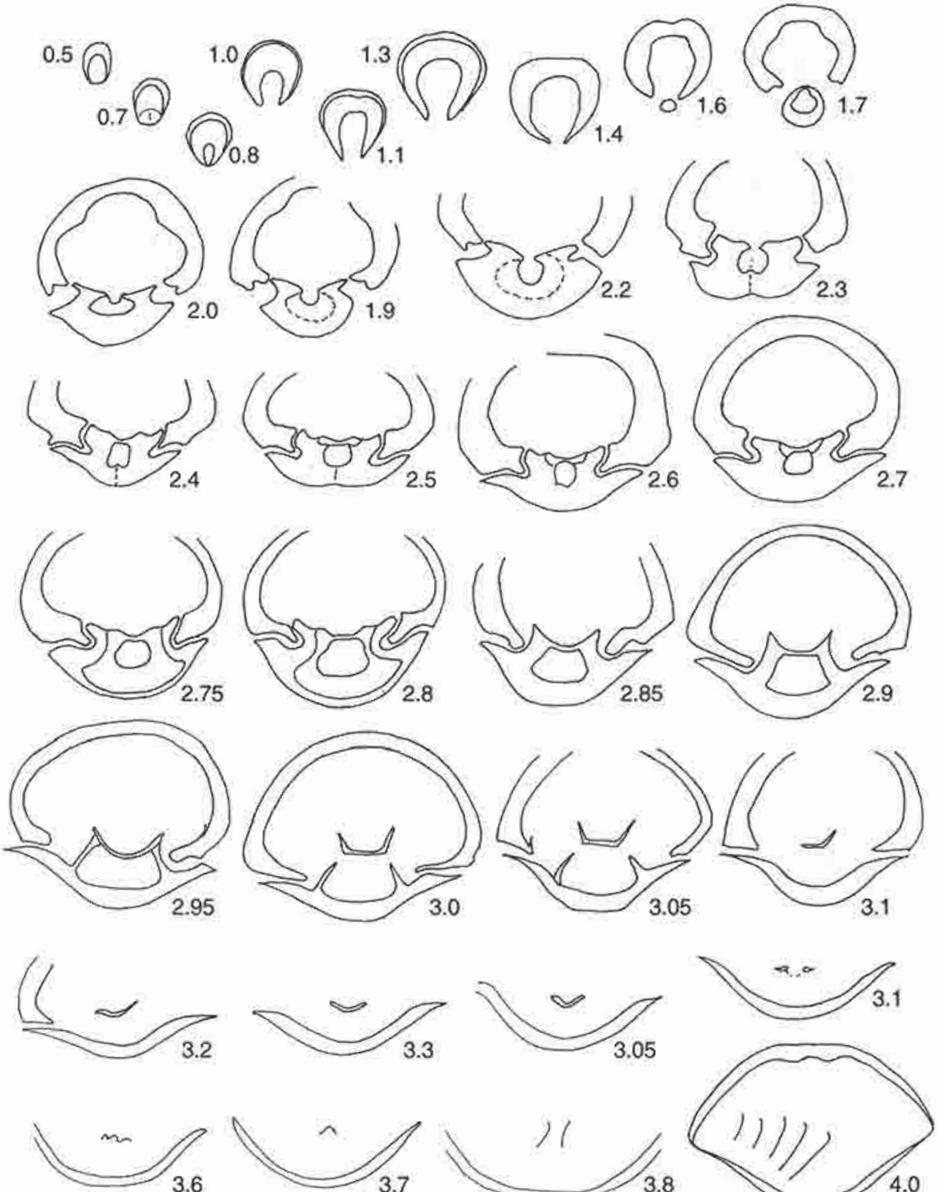

Fig. 8. *Pachyplaxoides postgyralea* sp. n. Transverse serial sections of the specimen GIUS 4-1477/GŁ-140 from late Frasnian of Łgawa Hill near Bolechowice, Holy Cross Mts, Poland (× 3.5). Distances are measured in mm from the apex of the ventral valve.

The surface of the shell covered by concentric, imbricated and widely spaced growth lamellae (up to 20 lamellae on each valve; Fig. 7N–Q)

Dental plates and apical lateral cavities lacking. The central pedicle cavity wide and subcircular. The hinge plate subtrapezoidal, thin, and apically perforated. A clearly differentiated elongate visceral

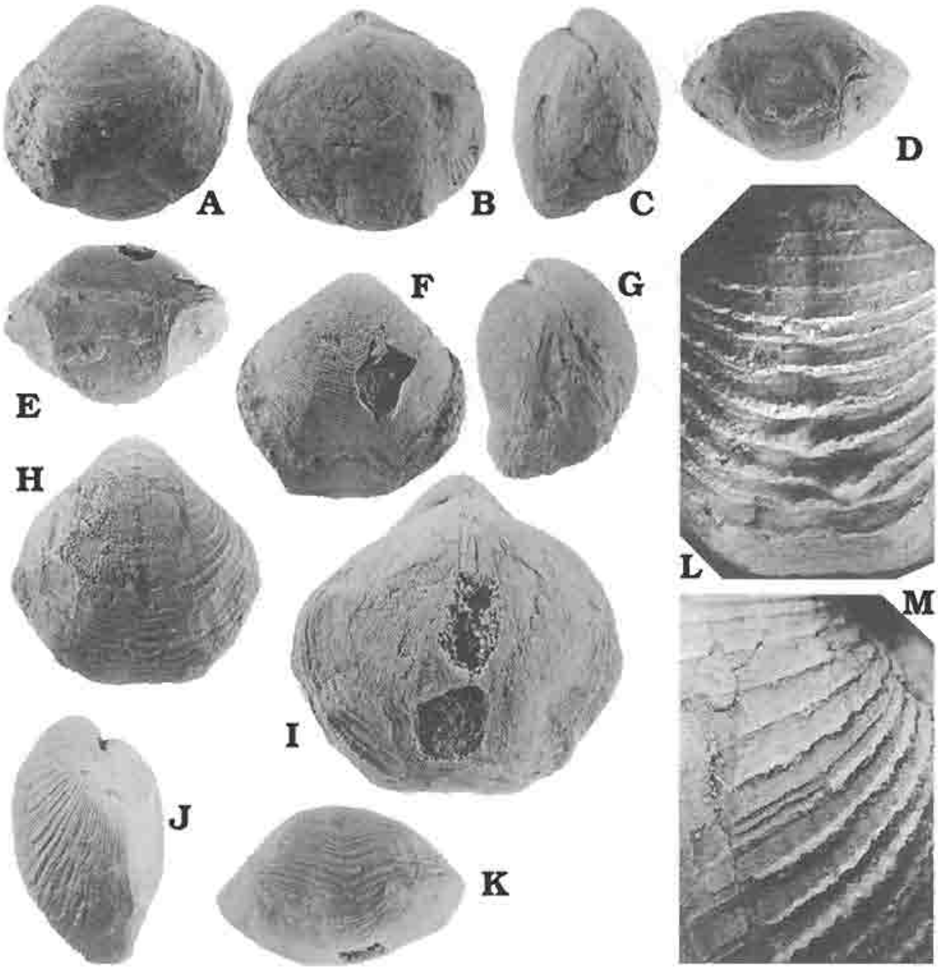

Fig. 9. ?*Zonathyris* sp. A from late Frasnian of Łgawa Hill near Bolechowice, Holy Cross Mts, Poland. **A–G**. Shells GIUS 4-1477/GŁ-143 (**A–D**) and 4-1477/GŁ-142 (**E–G**) in anterior, ventral, and lateral views. **H–M**. GIUS 4-1477/GŁ-141 in ventral, dorsal, lateral, and anterior views (**H–K**); sculpture on ventral valve (**L–M**). All × 1.5 except for **I** that is × 2 and **L–M** × 6.

foramen connects the dorsal cavity and central pedicle cavity of the ventral valve. The outer hinge plates poorly defined, difficult to distinguish from the inner socket ridges, as well as from crural bases.

Occurrence. — Germany: Ardennes-Rheinisches Schiefergebirge, Reichle Quarry, Prüme Syncline, Eifel Hills; Late Devonian, late Frasnian; Early *P. rhenana* Zone. Poland: Holy Cross Mountains, Łgawa Hill near Bolechowice; Late Devonian, late Frasnian (unit R), *P. rhenana* Zone.

Subfamily Flexathyridinae Grunt, 1980

Genus *Zonathyris* Struve, 1992

Remarks. — *Zonathyris* was inadequately documented by Struve (1992), due to lack of dàta on the internal morphology. The main diagnostic feature remains the characteristic coarse concentric,

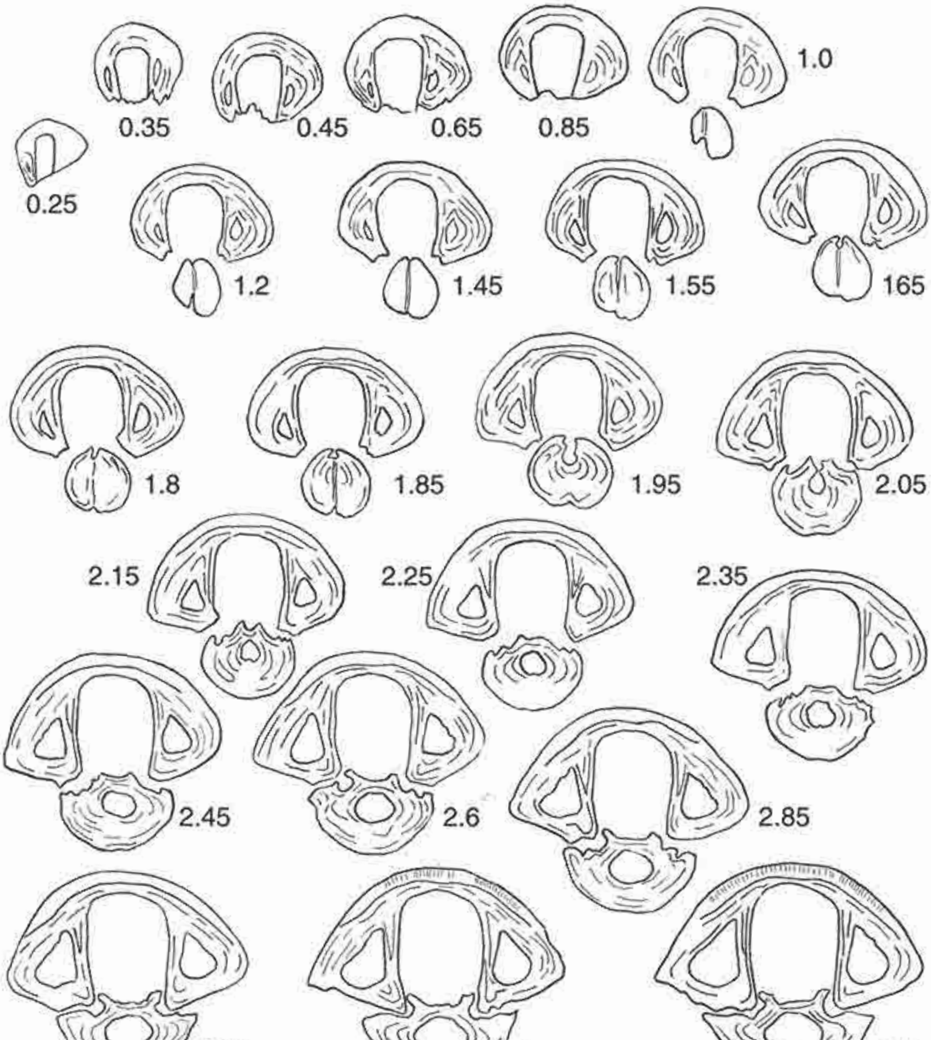

Fig. 10. ?*Zonathyris* sp. A. Transverse serial sections of the specimen GIUS 4-1477/GŁ-67 (× 5). Distances are measured in mm from the apex of the ventral valve.

weakly imbricated sculpture (Alvarez *et al.* 1996: pl. 4: 19), closely resembling growth lamellae of the Early Carboniferous genus *Lamellosathyris* (see Carter 1971, 1972; Grunt 1980, 1986). The latter is characterized by lacking dental plates within the ventral valve. Based on this sculptural character, and in view of the very limited material available, an athyridid taxon described below is tentatively referred to the genus *Zonathyris*.

?*Zonathyris* sp. A

Figs 9–10.

Material. — Four complete shells.

Description. — The shell of medium size ($\overline{L}$ = 21.22; range 20.45–22.95; $\overline{W}$ = 22.01; range 21.50–23.35; n = 4), equidimensional or slightly wider than long ($\overline{L/W}$ = 0.96; range 0.95–0.98); rounded-subpentagonal in outline, moderately equally biconvex ($\overline{T}$ = 13.85; range 13.25–14.45). The maximum width at about half of the shell length. The maximum thickness within the posterior third of the shell. The anterior commissure strongly uniplicate. The lateral margins moderately arched. The hinge line slightly shorter than the maximal width of the shell ($\overline{HL}$ = 18.09; range 17.05–19.95; $\overline{W/HL}$ = 1.22; range 1.17–1.26).

The ventral valve moderately and evenly convex, with the surface curving more strongly from the umbo towards the cardinal margins and less towards the anterior margin. The beak prominent, thick, not strongly recurved over the cardinal margin and perforated by a small rounded permesothyrid foramen ($\overline{AA}$ = 13.85; range 13.25–14.45). The small and low triangular delthyrium occupied by the beak of the dorsal valve. The median sulcus developed in the frontal part of the valve only ($\overline{Ws}$ = 11.8; range 10.45–12.55). The sharp subrectangular tongue developed over the anterior margin of the valve.

The dorsal valve usually as convex as the ventral one, with the greatest convexity in the posterior part, close to the umbo; in lateral profile strongly arched in umbonal region and gently sloping towards the anterior margin. The beak weakly developed, directed ventrally and exceeding the delthyrium. The distinct median fold developed in the anterior part of the valve.

The surfaces of both valves covered by 15–20 coarse concentric, weakly imbricated growth lamellae (Fig. 9L, M).

The dental plates thick, straight, and subparallel. They become differentiated early at 0.25 mm from the apex of the ventral valve and separate a wide subrectangular pedicle chamber. The lateral apical cavities small and subtriangular. In the articulation plane (at 1.2–1.4 mm from the apex of pedicle valve) the dental plates occupy the total height of the ventral cavity. The teeth large and subtriangular. The dental sockets shallow and poorly developed. The outer socket ridges not developed. The visceral foramen within the brachial valve large and oval. The inner cardinal plate rather wide and flattened. The outer cardinal plates reduced (Fig. 10).

Remarks. — Rare specimens from Bolechowice differ from *Z. occulta* (Quenstedt, 1871) in larger dimensions, shorter hinge line and in rounded cardinal extremities (see Struve 1992). From *Z. conchoides* Alvarez *et al.*, 1996 it differs by isometric subpentagonal outline, strongly uniplicate anterior margin and subrectangular tongue. Poor material excludes possibility of erection of a new species.

Occurrence. — Poland, Łgawa Hill near Bolechowice, Holy Cross Mountains; Late Devonian, late Frasnian (unit R), *P. rhenana* zone.

Stratigraphic and biogeographic aspects of the Holy Cross Mountains fauna

(T.A. GRUNT & G. RACKI)

As shown by Racki *et al.* (1993), the athyridid association from the late Frasnian marly-calcareous deposits of the Holy Cross Mountains forms an important element of the diverse and rich brachiopod- and sponge-dominated assemblage, thriving in different habitats over the southern foreslope of the Dyminy Reef (see Fig. 1C). The diverse athyridids described herein constitute almost 8% of the collected material at the Łgawa Hill locality (see Table 1 in Racki *et al.* 1993). The athyridids are unknown from autochthonous shell nests, and post-mortem transport precluded the possibility of a more detailed ecological analysis of the mostly coquinite taphofacies (see Mikłas in Racki *et al.* 1993: pls 2–4). The good overall preservation suggests, however, that some athyridid populations colonized muddy, stagnant habitats, maybe even in association with the deeper-water rhynchonellids, such as *Pammegetherhynchus* (see Sartenaer *et al.* 1998).

One of the most unusual features is the occurrence of the meristellaceans. This stratigraphically old superfamily, known from the Early Silurian, has not yet been reported later than the early Frasnian in European successions. Thus, *Merista rhenanensis* sp. n. obviously represents an infrequently occurring relic species in this part of the Laurussian shelves, even if the genus persisted until the Tournaisian in North American basins (*M. macullochensis* Carter, 1967).

Athyridacean brachiopods are far more common, and include three species belonging to different genera. Of these, *Athyris postconcentrica* sp. n. is the most abundant in the athyridid association under study. This species is also typical of the middle Famennian of the East European Platform (Grunt 1980), but its exact range remains unknown. The widely distributed Late Devonian representatives of *Athyris* were usually identified hitherto as *A. concentrica* (Buch, 1834), but the observations of one of the authors (T.A.G), together with D. Weyer, on the original collection of L. von Buch, clearly indicated that the type species of *Athyris* was restricted to the Middle Devonian, and probably to a short stratigraphic interval only (see also Alvarez *et al.* 1996). Revision of this species group is still urgently needed because of the absence of serial sections for the recently proposed new subgenera *Bruntonites* Struve, 1992; *Zonathyris* Struve, 1992; *Alvarezites* Struve, 1992; and *Eifuris* Struve, 1992, which are based on external morphology only. That is why the assignement of several Devonian, as well as Early Carboniferous species, to these genera (or subgenera) is still under discussion.

The genus *Zonathyris* is newly erected and its distribution is rather incompletly known. This genus was poorly documented by Struve (1992), but the peculiar sculpture, very reminiscent of the ornamentation of the Early Carboniferous genus *Lamellosathyris*, allows us to conclude that the genus encompasses Middle to Late Devonian ancestors of the common Carboniferous athyridids (Carter 1971; Grunt 1986, 1989a). Hence, ?*Zonathyris* sp. A can be an endemic species and transitional link between these distinctive Eifelian and Carboniferous athyridids.

In summary, the Holy Cross part of the Laurussian shelf represents a unique region of athyridid development, as demonstrated especially by the high generic diversity of the association, coupled with a prolonged persistence of the meristellaceans. In addition, the transitional nature of the Polish basin is obvious from a biogeographic viewpoint. Affinity with Russian faunas is strongly suggested by the wide distribution of *Athyris*, which is also evident in the Famennian of the Cracow area (Fig. 1A; see Baliński 1995a); however, the sporadically occurring Frasnian species at Dębnik (with a distinct median sulcus in the ventral valve; Baliński 1979) seems to represent separate species from *A. postconcentrica*, which is known from the Holy Cross Mountains and East European Platform (close e.g., to North American-Asiatic *Athyris angelica* Hall, 1867; see Grunt 1996). Links with the Variscan biotas suggest the presence of ?*Zonathyris*. Furthermore, the European Palaeozoic domains are confirmed as the major centre of the origin and diversification for the subfamilies Athyridinae and Meristinae (Grunt 1989a). All the revealed biogeographic characters agree with the conclusions derived from the more comprehensive analysis of the Holy Cross biotas from the Middle–Late Devonian transition (Racki 1988).

Athyridids and the Frasnian-Famennian mass extinction

(T.A. GRUNT & G. RACKI)

Athyridid brachiopods played a significant role in the composition of benthic communities from the late Ordovician utill the end of the Triassic (e.g., Grunt 1989a; Copper & Gourvennec 1996). The stratigraphic distribution of athyridid genera and species reveals a distinctive cyclic pattern, recording the major eustatic changes and consequent palaeogeographic turnovers (Grunt *et al.* 1995). In fact, some extinction events were coupled with the end-Silurian, end-Devonian and end-Carboniferous episodes, representing more or less distinctive global crises in overall regressive settings (see summary in Walliser 1996). Nevertheless, the major crisis in the athyridid history is linked with the end-Paleozoic mass extinction.

During the Middle and Late Devonian, athyridid history was marked by the progressive elimination of the Early Devonian survivors (Grunt 1980, 1989a). After the Eifelian acme of Meristellacea, only infrequent single species occurring in the Late Devonian, exemplified by *Merista rhenanensis* and *Dicamara lacryma* (Sowerby, 1840), flourished on the European shelves. However, the athyridids survived in the western Laurussian domains to the Early Carboniferous, as shown by *Merista*, *Camarophorella* and *Camarospira*. Within the Athyridacea, the two genera *Athyris* and *Atrythyris* appeared in the late Emsian successions of Variscan Europe (Rhine-Czech area). Gradual expansion of the former genus is well recorded during the Middle and Late Devonian, and e.g., the first species of *Athyris* colonized the north-eastern Siberian Basin during late Frasnian (Grunt 1996). The Frasnian rise of species diversity is well known from Central and Western Europe. Although single species were reported from the Tournaisian, the main demise of the species group is referred to the end-Famennian global bio-crisis (D/C or Hankenberg Event; Walliser 1996); survivors locally formed locally new lineages in this key interval (e.g., in the Transcaucas; Gretchishnikova 1996). Otherwise, *Atrythyris* developed during the Eifelian and early Givetian only, but its survival even into the late Famennian is possible. The characteristic reticulate ornamentation has occasionally been found in well preserved shells of several Late Devonian species, including *A. postconcentrica* (see Grunt 1980: pl. 2: 7), and the diagnostic significance of the character needs further explanation. The genus *Planalvus*, also originated in the Early Devonian European basins (Spain, France), but existed during the late Frasnian of the Central European seas (Grunt *et al.* 1995), and the latter continued to the Carboniferous (Carter 1971). The Flexathyridinae also possibly passed across the fatal Devonian–Carboniferous boundary, although the genus *Zonathyris* is possibly limited in the Frasnian to the endemic species in the Holy Cross Mountains area.

A similar overall distributional pattern is typical for the subfamily Plicathyridinae, and the Frasnian expansive development of *Plicathyris* and *Anathyris* in the eastern Laurussian and Siberian (Kuznetsk) domains is especially noteworthy; in addition, the endemic genus *Anathyrella* comprises four later Frasnian species in the Kuznetsk Basin (Rzhonsnitskaya & Modzalevskaya 1996). Other athyridid groups (Spirigerellidae, Nucleospiracea) and retziids persisted to the Late Paleozoic but, with the exception of *Retzia tulensis* Pander, 1856, outside of European domains (for details see Grunt 1989a).

In addition, the family Biernatellidae Baliński, 1977 constitutes an unusual athyridid lineage, marked by double spiralia. This group was one of the possible victims of the F-F ecosystem collapse, at least on the South Polish shelf (see Baliński 1995b; Racki & Baliński 1998).

To summarize the Devonian athyridid development (see species lists in Grunt 1989a: pp. 80–94), Eifelian faunas include 64 species belonging to 20 genera, but also from the Frasnian ca. 60 species from 10 genera have been still reported. During the Givetian and Frasnian only one new genus originated, although intensive speciation was a marked feature of *Athyris* and *Anathyris*, forming for the first time such a strongly predominating and widespread component of the athyridid faunas. The F-F boundary is hardly recognizable as a turning point in the athyridid history, although the demise of Plicathyridinae (Rzhonsnitskaya & Modzalevskaya 1996), and a few other genera, was linked with the global ecosystem collapse. In contrast to other articulate brachiopods (see Racki 1998), the athyridids successfully survived the eustatic and thermal fluctuations, and hypoxic events in the Kellwasser (KW) Crisis, as well as the common regressive and progressively cooler water conditions during the Famennian (see e.g., Walliser 1996), and recovered as a result of transgressive pulses. Thus, the Famennian assemblages are especially distinctive in taxonomic composition, despite the continued trend towards overall reduction of diversity: ca. 30 species representing seven genera are known at present. Only two genera, *Athyris* (15 species) and *Retzia* (7 species) belong to the typical Early–Middle Devonian survivors, and the widespread flourishing of diverse species of *Athyris* was a particular feature of Famennian benthic biotas (see examples in Baliński 1995a and Grunt 1996; also Racki & Baliński 1998). The first appearance of four genera, mostly ancestors of the Late Paleozoic taxa, as well as the Lazarus aspect of several genera (e.g., *Merista, Plectospira, Nucleospira*), revealed the still erratically known pattern of the brachiopod recovery and radiation in the post-extinction age. In particular, details of phylogenetic relationships at the species level are lacking.

In conclusion, the KW Crisis exhibits, in fact, a rather higher rate of diversification among athyridids, especially at species (and partly also generic) level. According to Copper in Copper & Gourvennec (1996), the spire-bearing articulates survived the F-F and end-Permian mass extinctions possibly because they had a wide geographic range which included cold climate, high latitude siliciclastic shelf settings (generalist strategy *sensu* Harries *et al.* 1996). Racki *et al.* (1993) noted the possibility that the less devastated level-bottom (non-reef) and nearshore communities were a source of eurytopic recolonizers, with athyridids in a main role, which invaded the ecospace vacated by the F-F extinction. Athyridids reveal, in fact, several progressive adaptative features (Grunt 1989a: pp. 122–126). In particular the neostrophic mode of shell growth resulted in a pedunculate life habit and compound cardinal structures, enabling a tight closure of valves. The absence of a prismatic layer in the shell wall and cardinal structures also appears suitable for an evolutionary plasticity of this group, whilst the development of a prismatic layer (e.g., in atrypids) was a distinctively 'gerontic' evolutionary character. In addition, some athyridids had a punctate shell, which probably enhanced the function of metabolic exchange. All these advantages are evidenced in successful lineages of modern brachiopods (rhynchonellids and especially terebratulids).

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