

Frasnian–Famennian brachiopod extinction and recovery in southern Poland

ANDRZEJ BALIŃSKI



Baliński, A. 2002. Frasnian–Famennian brachiopod extinction and recovery in southern Poland. *Acta Palaeontologica Polonica* 47 (2): 289–305.

The new trench Z-17 situated in the Dębnik anticline (Cracow Region, southern Poland) exposed strata representing the Frasnian–Famennian boundary interval. The latest Frasnian crisis interval is characterized by the fauna of *Ryocarhynchus tumidus* interval consisting of the nominal species, *Barroisella campbelli*, *Biernatella polonica*, and representatives of *Lingulipora*, *Athyris*, *Retichonetes*, *Longispina*, *Cyrtospirifer* and *Warrenella*. The first brachiopods that appears immediately above the F–F boundary in the survival interval include the unidentified rhipidomellid, *Praewaagenoconcha* cf. *speciosa*, and *Pam-poecilorhynchus geniculatus* sp. nov. The fauna in the succeeding layer is dominated by *P. geniculatus* and *Cyrtospirifer minor*. The earliest Famennian repopulation assemblage consists of representatives of *Barroisella*, *Rhyssochonetes*, *Praewaagenoconcha*, *Nigerinoplica*, *Schizophoria*, unidentified rhipidomellid, *Pam-poecilorhynchus geniculatus* sp. nov., *Chapinella striata* sp. nov., *Crinisarina angelicoides*, and *Cyrtospirifer minor*. Low diversity and low frequency brachiopod assemblages consisting of stunted specimens characterize the succeeding brachiopod intervals spanning the remainder of the *Palmatolepis triangularis* Zone. Basinal dysoxia prevailed in the region for the duration of *Pa. triangularis* Zone. Resumption of aerobic bottom-water conditions is marked by the appearance of brachiopods of the *Dmitria gibbosa* interval (*Pa. crepida* Zone). Resumption of favorable environmental conditions during the recovery interval is marked by an increase in brachiopod diversity recording the beginning of a strong post-extinction re-diversification of the fauna.

Key words: Brachiopoda, Frasnian, Famennian, extinction, recovery, southern Poland.

Andrzej Baliński [balinski@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Devonian strata of the Dębnik anticline (Cracow Region, southern Poland) were deposited in the proximal part of the Polish epicontinental basin trending NW–SE (Fig. 1). The basin was bordered from the north and east by the Byelorussian Land (southwestern margin of the East European Craton), from the west by the Variscan Deformation Front, and from the south by the Moravian Karst and Sub-Carpathian Arch (Dadlez et al. 1994; Narkiewicz 1985, 1996; Narkiewicz and Hoffman 1989; Racki and Baliński 1998). The Devonian sequence of carbonates in the Dębnik area was deposited near the Sub-Carpathian Arch along the southern margin of the cratonic basin. Today these strata are usually poorly exposed in a small area centered around the village of Dębnik. Major advances in the understanding of the Frasnian–Famennian brachiopod and conodont faunal dynamics have been well documented in a series of studies by Baliński (1979, 1995a, 1996) and Baliński and Racki (1999). In 1998 a new supplementary trench (Z-17) was excavated by Dr. G. Racki and the present author to the south of Dębnik to investigate the Frasnian–Famennian boundary and relevant paleontological and geochemical aspects of the F–F biotic crisis. This paper documents the latest Frasnian and post-crisis brachiopod sequence and faunal dynamics in the earli-

est Famennian (Early to Middle *Palmatolepis triangularis* Zone) of the trench Z-17. For geochemical and biostratigraphical aspects of the section see Racki et al. (in press). Chondrichthyan remains from the outcrop were studied by Ginter (2002).

All specimens reported herein have been deposited at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (ZPAL) in the collection abbreviated Bp 46; for sake of brevity of the figure captions, however, I omit “ZPAL” in the abbreviation and refer to Bp 46.

Diversity dynamics of the brachiopod fauna near the F–F boundary

The Frasnian–Famennian brachiopod sequence from the Dębnik anticline was described in detail by Baliński (1995a, 1996) and Baliński and Racki (1999). Recent investigation of the new outcrop (Z-17) revealed the occurrence of a new brachiopod assemblage unknown to those earlier investigators. The newly discovered assemblage was recovered just above the F–F boundary, and is dominated by the rhychnelloid brachiopod *Pam-poecilorhynchus geniculatus* sp. nov. and the cyrtospiriferid *Cyrtospirifer minor*. This new assem-

Latest Frasnian “crisis” assemblage

In the Dębnik area the highest Frasnian assemblage in the brachiopod sequence is the *Ryocarrhynchus tumidus* interval (Fig. 2) represented in trench Z-6 and lowermost part of Z-17. Generally, the sparse brachiopod fauna of the interval occurs 0.5 m below the F–F boundary in a shell bed yielding abundant *R. tumidus*, associated with linguloids, the helenathyrin *Biernatella polonica*, and rare ?*Rysochonetes* sp., *Longispina* sp., *Athyris* cf. *concentrica*, *Warrenella* (*Warrenella*) sp., *Cyrtospirifer minor*, and ?*Tenticospirifer* sp. *Ryocarrhynchus tumidus* is also known from the highest Frasnian of the eastern Holy Cross Mountains (Racki and Baliński 1998: 296) and Senzeille, Belgium (Bouckaert et al. 1972). In Poland the highest part of the *R. tumidus* interval is defined by the last occurrence of *Biernatella polonica*. The latter species is the youngest member of the diplospiridium-bearing helenathyrin that first appear in the early Devonian (see Alekseeva 1969; Alvarez et al. 1998; Baliński 1977, 1995b). The last atrypoids disappear from the record slightly earlier within *R. tumidus* interval.

The uppermost beds of the *Ryocarrhynchus tumidus* interval exposed in trench Z-6 and at the base of the section in trench Z-17 probably represent the “crisis” or “extinction” zone that yield a low diversity assemblage dominated by *R. tumidus* (Fig. 2.3; see also Baliński 1995a). This rhynchonellid was probably adapted to dysoxic conditions (see Bowen et al. 1974). Hałas et al. (1992) noted a shift to more positive values in the carbon isotopic curve at the F–F boundary at Dębnik, that is probably related to development of an upwelling system that brought anoxic waters up onto the shelf. The recent studies of heavy metals composition (V, Ni, Cr) of the section in trench Z-17 suggest fluctuating oxic to dysoxic bottom-water conditions in the highest Frasnian and its deterioration towards hypoxic levels in the Early Famennian (Racki et al. in press).

The only articulated brachiopods that carryover from the late Frasnian faunas recovered immediately above the F–F boundary are *Cyrtospirifer minor* and ?*Rysochonetes* sp. Both of these possibly represent ecological opportunists in the sense of Harries and Kauffman (1992) or short-term Lazarus taxa (Kauffman and Hart 1996).

Earliest Famennian survivors

A number of brachiopod taxa have their first (lowest) occurrences immediately above the F–F boundary in the survival interval (= *Pamwoecilorhynchus geniculatus* interval of Fig. 2) with *Cyrtospirifer minor* and ?*Rysochonetes* sp. These include: the productid *Praewaagenoconcha* cf. *speciosa*, undetermined rhipidomellid, and the rhynchonelloid *Pamwoecilorhynchus geniculatus* sp. nov. Slightly higher, *P. geniculatus* (nominal species for the post-extinction survivor assemblage) becomes abundant in bed 12 (upper part of the set II) at 0.8 m above the F–F boundary. Species of *Pamwoecilorhynchus* occur elsewhere in early Famennian deposits of

Asia and Europe (Brice et al. 2000). The oldest Famennian occurrence of *Cyrtospirifer minor* is in this bed after a temporary absence in the area during the most severe environmental disturbance. This opportunist or short-term Lazarus species increases in abundance, although represented by smaller morphotypes, in younger beds.

The entire repopulation assemblage from bed 12 of the set II (spans the early part of the Early *Pa. triangularis* Zone) consists of one linguloid and nine articulated species (Fig. 2). These include: *Barroisella campbelli*, *Nigerinoplica* sp., *Praewaagenoconcha* cf. *speciosa*, ?*Rysochonetes* sp., rhipidomellid gen. et sp. indet., *Schizophoria* (*Schizophoria*) sp., *Pamwoecilorhynchus geniculatus* sp. nov., *Chapinella striata* sp. nov., *Crinisarina angelicoides*, and *Cyrtospirifer minor*.

The younger layers of the trench Z-17 (base of set III; Fig. 1; the earliest Middle *Pa. triangularis* Zone) reveal an important change in the brachiopod sequence. *Pamwoecilorhynchus geniculatus* gradually disappears and is replaced by another rhynchonelloid *Orbiculatisinurostrum leave*. The first occurrence of the latter defines the base of the succeeding *O. laeve* interval (Fig. 2). Strata of the *O. laeve* interval consist of platy, micritic, dark-grey to almost black limestones that crop out in the area of trench Z-17, and are seen in several nearby trench sections (Baliński 1979, 1995a). The *O. laeve* interval spans part of the *Pa. triangularis* Zone, and is characterized by a low diversity and low abundance assemblage consisting of small phenotypes of *O. laeve*, *Cyrtospirifer minor*, and *Pygmis jablonensis*.

Low diversity and sparse assemblages characterize the succeeding *Iloerhynchus mesoplicatus*, *Cyrtospirifer brodi*, and *Cyrtospirifer wesgensis* intervals (Baliński 1995a). These three intervals above the *O. leave* interval span part of the Late *Pa. triangularis* Zone. The *I. mesoplicatus*, *C. brodi*, and *C. wesgensis* intervals characterize the post-extinction survival interval. Each assemblage consists of two to four brachiopod taxa (Fig. 2). The low species and generic diversity (oligophyly *sensu* Urbanek 1997, 1998) show the characteristics of post-extinction survivor assemblages (e.g., Urbanek 1998; Walliser 1996) following major diversity reduction bio-events (Kauffman and Hart 1996).

Early Famennian recovery faunas

The succeeding *Dmitria gibbosa* interval (*Palmatolepis crepida* Zone; Fig. 2) records termination of basinal episodic hypoxia that persisted throughout the region during the entire *Pa. triangularis* Zone. A change to more favorable environmental conditions are reflected in a distinct increase of brachiopod species diversity from 2 to 4 to 13 species. This recovery interval (diversification bio-event of Kauffman and Hart 1996; radiation events of Walliser 1996) records the beginning of a strong re-diversification of brachiopod fauna in the Dębnik area. Diversity peaks at 14 species in the succeeding *Cavatisinurostrum longililnguis* interval (see Baliński 1995a; Baliński and Racki 1999). Species characterizing assemblages of the *D. gibbosa* and *C. longililnguis* intervals are

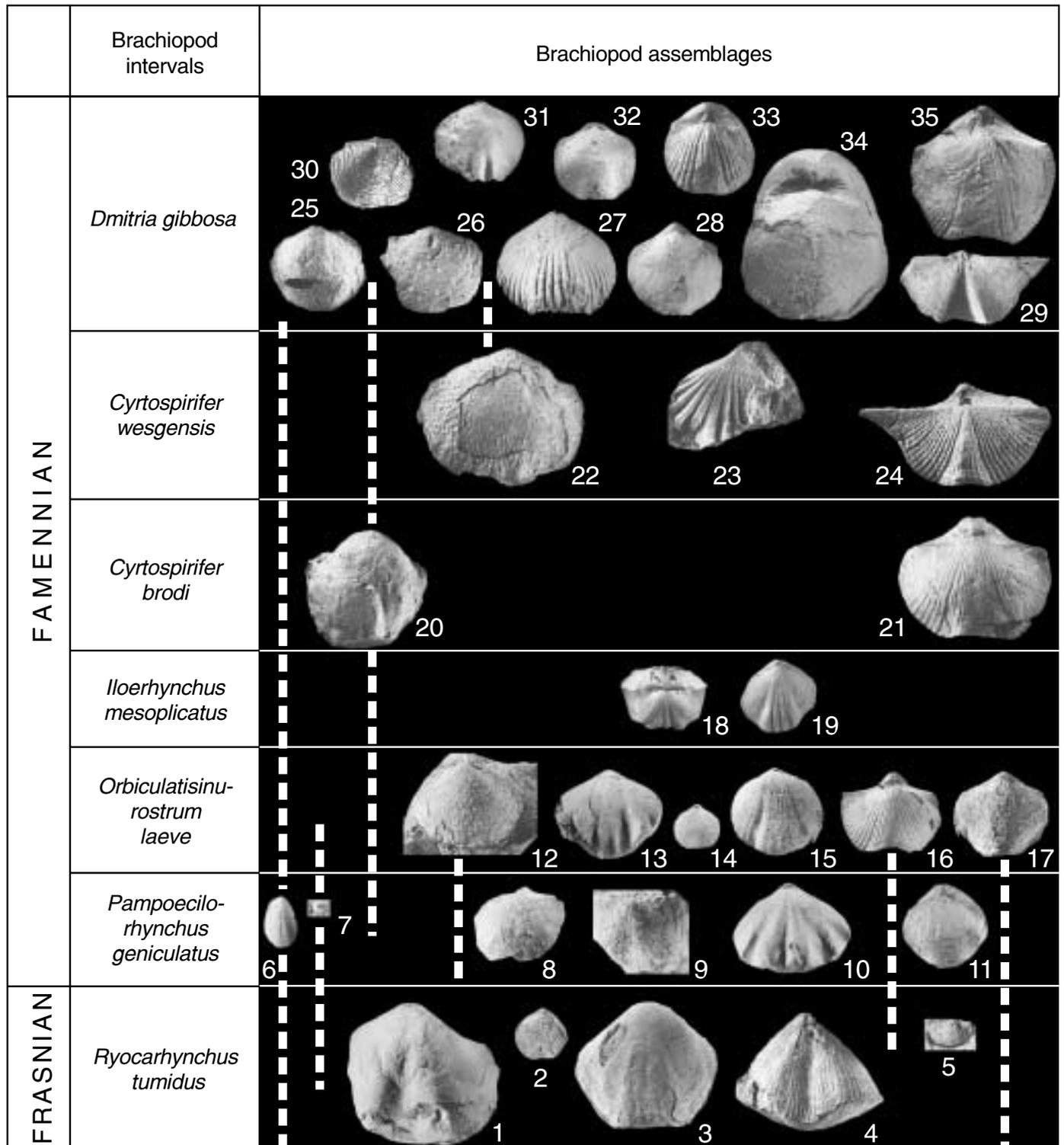


Fig. 2. The sequence of the Late Frasnian–Early Famennian brachiopod assemblages in Dębniak anticline, Cracow Region, southern Poland. Explanations: 1, *Warrenella* sp.; 2, *Biernatella polonica* Baliński, 1977; 3, *Ryocarhynchus tumidus* (Kayser, 1872); 4, *?Tenticospirifer* sp.; 5, *Longispina* sp.; 6, *Barroisella campbelli* Cooper, 1942; 7, *?Ryssochonetes* sp.; 8, *Schizophoria* (*Schizophoria*) sp.; 9, rhipidomellid gen. et sp. indet.; 10, *Pampoecilorhynchus geniculatus* sp. nov.; 11, *Crinisarina angelicoides* (Merriam, 1940); 12, *Praewaagenoconcha* cf. *speciosa* (Hall, 1867); 13, *Chapinella striata* sp. nov.; 14, *Pygmis jablonensis* (Biernat, 1983); 15, *Orbiculatisinu-rostrum laeve* (Gürich, 1903); 16, *Cyrtospirifer minor* (Gürich, 1903); 17, *Athyris* cf. *concentrica* (v. Buch, 1834); 18, *Miniostrella rara* Baliński, 1995; 19, *Iloerhynchus mesoplicatus* Baliński, 1995; 20, *Nigerinoplica* sp.; 21, *Cyrtospirifer brodi* (Venjukov, 1886); 22, *Sentosia profunda* McKellar, 1970; 23, *Centrorhynchus* sp.; 24, *Cyrtospirifer wesgensis* Zheiba, 1980; 25, *Schizophoria* (*S.*) *shubarica* Martynova, 1961; 26, *Donallosia* sp.; 27, *Ptychomaletoechia* sp.; 28, *Athyris* aff. *area* Baliński, 1995b; 29, *Cyrtospirifer* cf. *acutus* Nalivkin, 1960; 30, *Rhytialosia* sp.; 31, *Coeloterorhynchus* sp.; 32, *Crinisarina* aff. *reticulata* (Gosselet, 1877); 33, *Eobrachythyris?* *palkowae* (Gürich, 1903); 34, *Dmitria gibbosa* Baliński, 1995b; 35, *Cyrtopsis famenniana* (Paeckelmann, 1942). All $\times 1$.

spiriferides, athyridides, and rhynchonellides. Adult shell dimensions vary widely from 2 mm length in micromorphic cardiariid *Loborina lobata* Baliński to more than 40 mm in spiriferid *Dmitria gibbosa* (Gürich).

Final remarks

The Latest Frasnian–Early Famennian brachiopod sequence in the Late Devonian of the Dębnik area record the benthic faunal dynamics during the F–F extinction, the post-extinction survival and recovery in southern Poland. The survival interval, which persisted during the basal Famennian Early *Pa. triangularis* Zone, was characterized by low diversity and low frequency cyrtospiriferid–rhynchonelloid or cyrtospiriferid–productoid assemblages (Baliński 1995a) frequently represented by stunted phenotypes characteristic for disturbed and stressed environments (the “Liliput” phenomenon of Urbanek 1993). The same pattern of expansion of cyrtospiriferids and productoids in the middle part of the *Pa. triangularis* Zone was observed in the Holly Cross Mountains (Racki 1990; Racki and Baliński 1998). During the *Pa. crepida* Zone, brachiopods, as well as a whole shelf ecosystem, seem to successfully recover after the serious disturbance at the F–F boundary. The post-extinction recovery of the shelf biota during the *Pa. crepida* Zone is also observed in the Holy Cross Mountains (Racki 1990, 1998; Racki and Baliński 1998).

The earliest Famennian survival fauna from the Dębnik anticline is similar in composition to the early Famennian survivor fauna described from the Hanover Shale of eastern North America by Day and Over (2002, this volume). The two survival faunas feature eight common taxa at the family or generic level, i.e., linguloid, chonetid, *Praewaagenoconcha*, rhipidomellid, *Schizophoria*, trigonirhynchid, leiorhynchid, and *Cyrtospirifer*. Other earliest Famennian survival brachiopod faunas from several localities of North America also feature similar species (Day, personal communication October 2000). The brachiopod assemblage revealed in the Early *Pa. triangularis* Zone in section at Šumbera near Brno, Czech Republic, similarly as that from Dębnik, consists of productoids, schizophorids, cyrtospiriferids, and costate rhynchonellid *Ripidiorhynchus* (Racki 1998: 400).

The post-extinction survival interval in the Dębnik area spans the entire *Pa. triangularis* Zone and probably the basal part of the *Pa. crepida* Zone. Sandberg and Ziegler (1996) suggested that the average duration of a Famennian conodont zone is 0.5 Ma. Assuming such a duration, the brachiopod fauna in Dębnik area rebounded after some 1.5–2.0 Ma. of the survival interval. Work by Kirchner and Weil (2000: 177) showed that extinctions do not trigger immediate evolutionary rebounds and that significant originations of new taxa following mass extinction took as long as 10 Ma. The post-extinction recovery of the brachiopod fauna following the F–F extinction was quite rapid in comparison, at least in the Dębnik area of southern Poland. According to Erwin (2000) survival intervals have highly variable durations. Similarly, McGhee (1996) no-

ticed that the timing of brachiopod recoveries after the F–F extinction varied from region to region. Jablonski (1998) documented similar geographic variation in patterns of biotic recovery of molluscs following the end-Cretaceous extinction. The delayed rebound and rediversification of echinoderms in the early Famennian of northwest China and Europe was discussed by Lane et al. (1997) and Erwin (1998) (see also Głuchowski 2002).

Systematic paleontology

Class Lingulata Gorjansky and Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1829

Family Lingulidae Menke, 1828

Genus *Barroisella* Hall and Clarke, 1892

Barroisella campbelli Cooper, 1942

Fig. 3A.

Barroisella campbelli new name; Cooper 1942: 228.

Barroisella campbelli Cooper, 1942; Baliński 1995a: 30, pl. 1: 10, 14, 16.

Material.—Fourteen more or less fragmentary specimens embedded in rock.

Remarks.—The available specimens are characterized by their small longitudinally elliptical shell that tapers posteriorly with poorly preserved internal markings. Internal markings of this species are well known from illustrated specimens from nearby localities (Baliński 1995a: pl. 1: 10, 14, 16). Of those, the most characteristic internal feature is the dorsal median ridge that bifurcates near mid-valve and enfolds a second short ridge (Baliński 1995a: pl. 1: 14, 16).

Occurrence.—*B. campbelli* is known from the Late Devonian of the USA (Indiana, New York). Studies by Baliński (1979, 1995a) indicate that in Poland (at Dębnik) this species ranges from the early Frasnian through the early Famennian (*Pa. crepida* Zone).

Class Strophomenata Williams et al., 1996

Order Productida Sarytcheva and Sokolskaya, 1959

Suborder Productidina Waagen, 1883

Superfamily Productoidea Gray, 1840

Family Productidae Gray, 1840

Subfamily Leioproductinae Muir-Wood and Cooper, 1960

Genus *Nigerinoplica* Lazarev, 1986

Nigerinoplica sp.

Fig. 3E–G.

Nigerinoplica sp.; Baliński 1995a: 34, fig. 6; pl. 2: 8, 10; pl. 5: 9.

Material.—Four fragmentary specimens from set II and three specimens from set III of trench Z-17.

Remarks.—This species was first described from slightly younger Early Famennian horizons in the Dębnik area by

Baliński (1995a). Those previously documented, as well its occurrence outlined here fall within the interval of the *Pa. triangularis* and lower part of *Pa. crepida* Zones. The poorly preserved specimens from trench Z-17 are medium sized, with a strongly convex ventral valve. Rare spines are scattered on the ventral valve, situated on elongated spine bases that arise anteriorly from short radial ribs.

The Dębnik specimens are probably conspecific with *Productella herminae* Frech that is a characteristic fossil from the Elets beds (lower Famennian) of the East European Platform (Markovski and Nalivkin 1934; Sarytcheva and Sokolskaya 1952). *Productella herminae* was also described by Żakowa (1965) from the lower Famennian of borehole Karniowice 3 situated approximately 6 km to the east of Dębnik. It is also reported by Kościelniakowska (1967) from the Frasnian of the Holy Cross Mountains. Lazarev (1986: 67) first suggested that specimens reported as *P. herminae* from Russia belong to his new genus *Nigerinoplica* Lazarev.

Superfamily Echinoconchoidea Stehli, 1954

Family Sentosiidae McKellar, 1970

Subfamily Caucasiproductinae Lazarev, 1987

Genus *Praewaagenoconcha* Sokolskaya, 1948

Praewaagenoconcha cf. *speciosa* (Hall, 1867)

Fig. 3B–D.

Praewaagenoconcha cf. *speciosa* (Hall, 1867); Baliński 1979: 31–32, pl. 3: 3, 6.

Material.—31 fragmentary specimens from trench Z-17. This species is rare in the most of the trench Z-17 section although it is quite common in the upper part of the set II being one of the characteristic brachiopods of the assemblage of the *Pampocilorhynchus geniculatus* interval.

Remarks.—Three specimens of the species reported in earlier studies were recovered from slightly younger strata of trench Z-16 and quarry Z-2 from the lower part of *Pa. triangularis* conodont Zone (Baliński 1979). The present collection, although rather poorly preserved, includes numerous specimens. This species is closely similar to *Productella speciosa* Hall from the Chemung Group, USA (Hall and Clarke 1892: pl. 17: 25, 26) in its general appearance. It has relatively fine spines, which occur on both valves. One specimen preserves ventral teeth and dorsal sockets. A spine bearing median ridge, a feature common to members of *Praewaagenoconcha*, is not observed on the ventral valves of available specimens.

Suborder Chonetidina Muir-Wood, 1955

Superfamily Chonetoidea Bronn, 1812

Family Chonetidae Bronn, 1862

Subfamily Dagnachonetinae Racheboeuf, 1981

Genus *Ryssochonetes* Johnson, 1970

?*Ryssochonetes* sp.

Fig. 3J.

Material.—One partially exfoliated specimen embedded in matrix from the lowest beds (set I) of trench Z-17 and six ad-

ditional fragmentary specimens etched using acetic acid from the limestone (upper part of the set II); one specimen from topmost layer of trench Z-17.

Remarks.—The species is characterized by its small shell with radial costellae crossed by concentric undulating fila. The internal shell structure of the species remains unknown because of the poor preservation of available specimens.

Occurrence.—This species was found in the highest Frasnian (set I) and in the lowest Famennian (the upper part of the set II, the Early *Pa. triangularis* Zone) of the section in trench Z-17. One fragmentary shell was recovered in the uppermost bed of the trench (set III, the Middle *Pa. triangularis* Zone).

Subfamily Devonochonetinae Muir-Wood, 1962

Genus *Longispina* Cooper, 1942

Longispina sp.

Fig. 3K.

Material.—One shell fragment embedded in rock.

Remarks.—The species is represented by a single poorly preserved and fragmentary specimen that has a row of hinge spines almost parallel to the cardinal margin of the ventral valve. The specimen occurs in the lowest bed of trench Z-17 (set I, highest Frasnian).

Order Orthida Schuchert and Cooper, 1932

Suborder Dalmanellidina Moore, 1952

Superfamily Dalmanelloidea Schuchert, 1913

Family Rhipidomellidae Schuchert, 1913

Rhipidomellid gen. et sp. indet.

Fig. 3I.

Material.—Two fragmentary specimens from the earliest Famennian (set II) of the trench Z-17.

Remarks.—This is one of the first brachiopods to appear immediately above the Frasnian–Famennian boundary in trench Z-17. Poor preservation of the specimen does not permit a more definite identification.

Superfamily Enteletoidea Waagen, 1884

Family Schizophoriidae Schuchert and LeVene, 1929

Genus *Schizophoria* King, 1850

Subgenus *Schizophoria* (*Schizophoria*) King, 1850

Schizophoria (*Schizophoria*) sp.

Fig. 3H.

Remarks.—Two poorly preserved and fragmentary specimens were collected from set II of trench Z-17. They are similar to *Schizophoria schubarica* Martynova, 1961 reported from limestones in trenches Z.orb.-1 and 8 at Dębnik. According to Baliński (1995a: 31) those occurrences are within the interval of the *Pa. crepida* Zone and probably part of the Early *Pa. rhomboidea* conodont Zone. The poor state of preservation of the present specimens does not permit satisfactory comparison with other species.

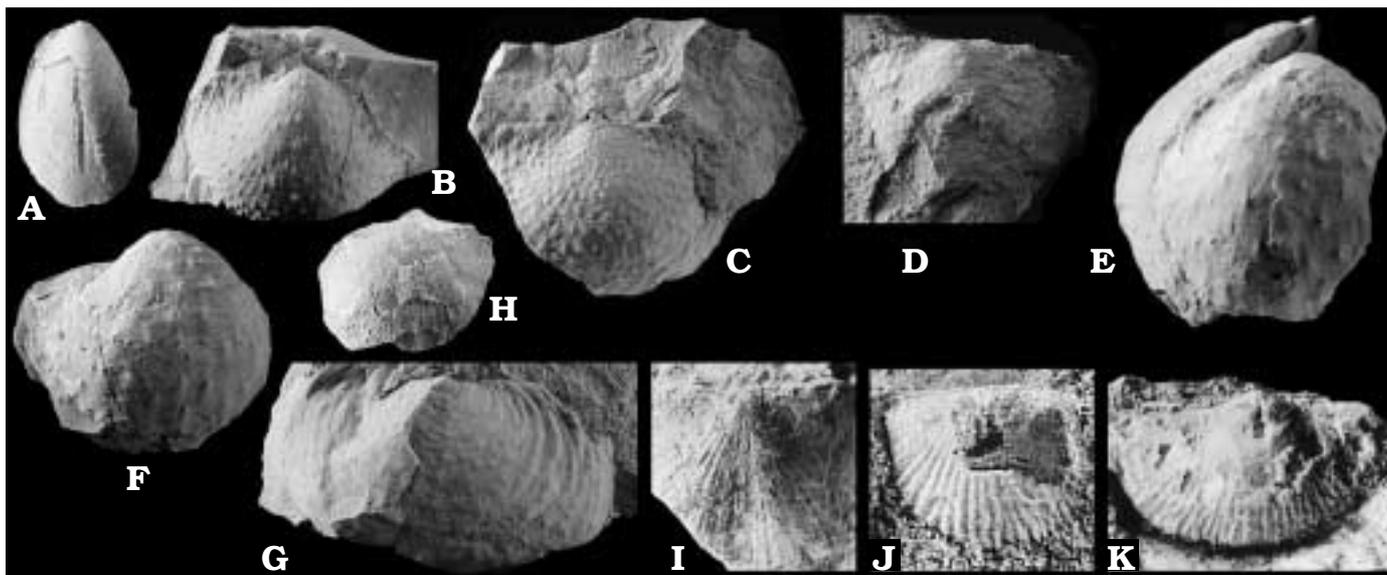


Fig. 3. Early Famennian brachiopods, trench Z-17, Dębnik anticline, Poland. **A.** *Barroisella campbelli* Cooper, 1942; partially exfoliated shell Bp 46/48a in dorsal view; $\times 3$. **B–D.** *Praewaaagenoconcha* cf. *speciosa* (Hall, 1867). **B.** Exterior of the ventral valve Bp 46/20a. **C, D.** Internal view of two partially exfoliated dorsal valves Bp 46/25a and Bp 46/25b; $\times 1.5$. **E–G.** *Nigerinoplica* sp. **E, F.** Side view of two shells Bp 46/24a and Bp 46/18a. **G.** Shell Bp 46/24b in dorsal view showing partially removed ventral valve and interior of the dorsal valve; $\times 1.5$. **H.** *Schizophoria* (*Schizophoria*) sp.; incomplete shell Bp 46/37a in dorsal view; $\times 1.5$. **I.** Rhipidomellid gen. et sp. indet; exterior of poorly preserved ventral valve Bp 46/40; $\times 1.5$. **J.** *?Ryssochonetes* sp.; incomplete shell Bp 46/15 in ventral view; $\times 15$. **K.** *Longispina* sp.; poorly preserved shell Bp 46/17z in ventral view; $\times 5$.

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Trigonirhychiidae Schmidt, 1965

Subfamily Hemitoechiinae Savage, 1996

Genus *Pampoecilorhynchus* Sartenaer, 1968

Pampoecilorhynchus geniculatus sp. nov.

Figs. 4, 5D–I.

Holotype: ZPAL Bp 46/52d, complete shell illustrated in Fig. 5G.

Type locality: Bed 12 of the set II, trench Z-17 near the village of Dębnik, Cracow Region, southern Poland.

Type horizon: Platy Limestone Unit, Lower Famennian, Early *Palmatolepis triangularis* Zone.

Etymology: After geniculation of the anterolateral shell margin.

Diagnosis.—Shell medium sized, rarely exceeds 21 mm in width, wider than long, dorsibiconvex, anterior commissure strongly uniplicate; costae rounded to slightly sharp, usually two to three on flanks, two in sulcus and three on fold; first two lateral costae bounding the ventral sulcus have a tendency to form spurs anteriorly; anterior and lateral margins of both valves always geniculate in large specimens. Differs from all other species of the genus by the character of the shell costation that is thicker and with costae confined to the anterior half of the shell only.

Material.—21 complete or slightly damaged and 53 fragmentary shells. Most specimens exfoliated to some degree. Large specimens make up most of the collection with the smallest 6.7 mm in length.

Description.—Shell medium sized, usually not exceeding 21

mm in width, wider than long, transversely elliptical to transversely subpentagonal in outline, dorsibiconvex, uniplicate with well defined sulcus and fold; hinge line angular, lateral margins arched, anterior margin truncated. In large shells (above 12–14 mm in length) the anterior and lateral margins are geniculate with a serrated commissure between the valves laying in the middle of the geniculation. Medial sector of geniculate part of the shell flat, slightly concave in adjacent lateral sectors. Postero-lateral commissure sticking out and sharp.

Ventral valve with moderately convex postero-median region and almost flat to even slightly concave flanks; beak small erect, deltidial plates small, disjunct. Sulcus clearly bounded by strong lateral costae that arise some distance from the umbo; the bottom of the sulcus usually slightly convex.

Brachial valve about twice as convex as the ventral one; in lateral profile the valve is gently arched to straight or even slightly concave in anterior half. Fold distinct, begins some distance from the umbo, separated laterally by deep troughs; when fold bears three or more costae the lateral costae are slightly higher than the medial costae.

Posterior region of shell with very delicate, low and rounded radial ribs; the median ribs are better marked and anteriorly they become very strong costae. The lateral ribs disappear in the middle of the shell, or, some of them continue anteriorly to give rise of strong lateral costae. This gives a general impression that both posterior and anterior regions of the shell display a different kind of ornamentation.

The majority of shells (64%) bear two costae in sulcus

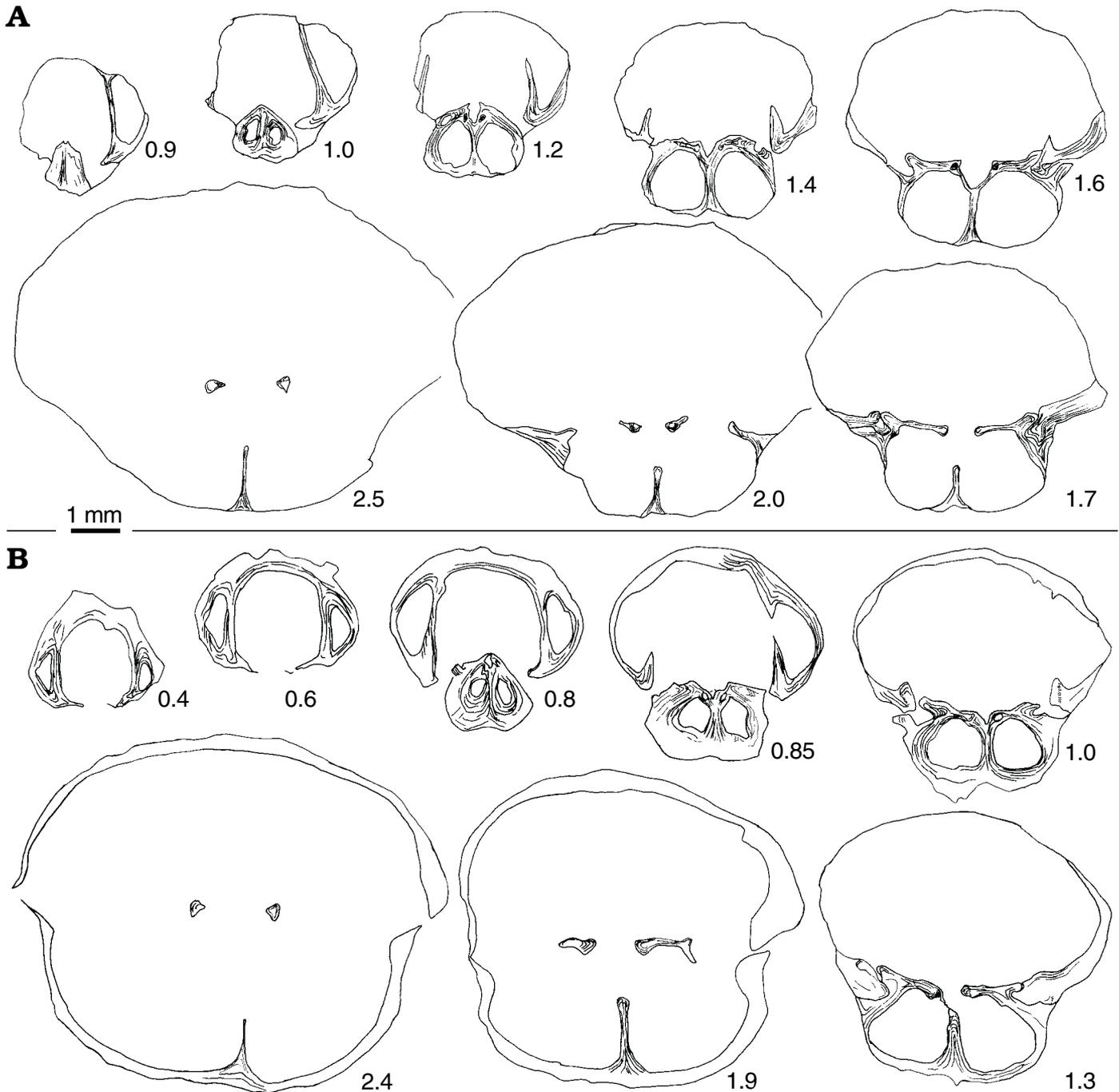


Fig. 4. Transverse serial sections of two shells Bp 46/52g (A) and Bp 46/52h (B) of *Pampoecilorhynchus geniculatus* sp. nov. Numbers refer to distances in mm from the ventral apex.

and three costae on the fold, 20% of shells have three and four costae, respectively. In 8% of shells there is a single plication in sulcus and two on the fold, and 4% of shells have four and five costae, respectively. There are two to three lateral costae; parietal costae usually absent, developed in a few specimens only. In cross-section costae are rounded to slightly angular, with tendency to being more angular anteriorly. Micro-ornament not observed.

Ventral valve interior with distinct and subparallel to

slightly convergent dental plates. Dorsal valve interior with wide outer hinge plates and narrow crural plates supported by a long median septum forming Y-shaped septalium (Fig. 4). Connectivum not observed in all seven sectioned specimens.

Remarks.—The strongly costate shell with the interior dominated by the dental plates and strong uncovered septalium suggest that the specimens described here represent the Early Famennian genus *Pampoecilorhynchus* Sartenaer, 1968. The new species differs from other representatives of the genus

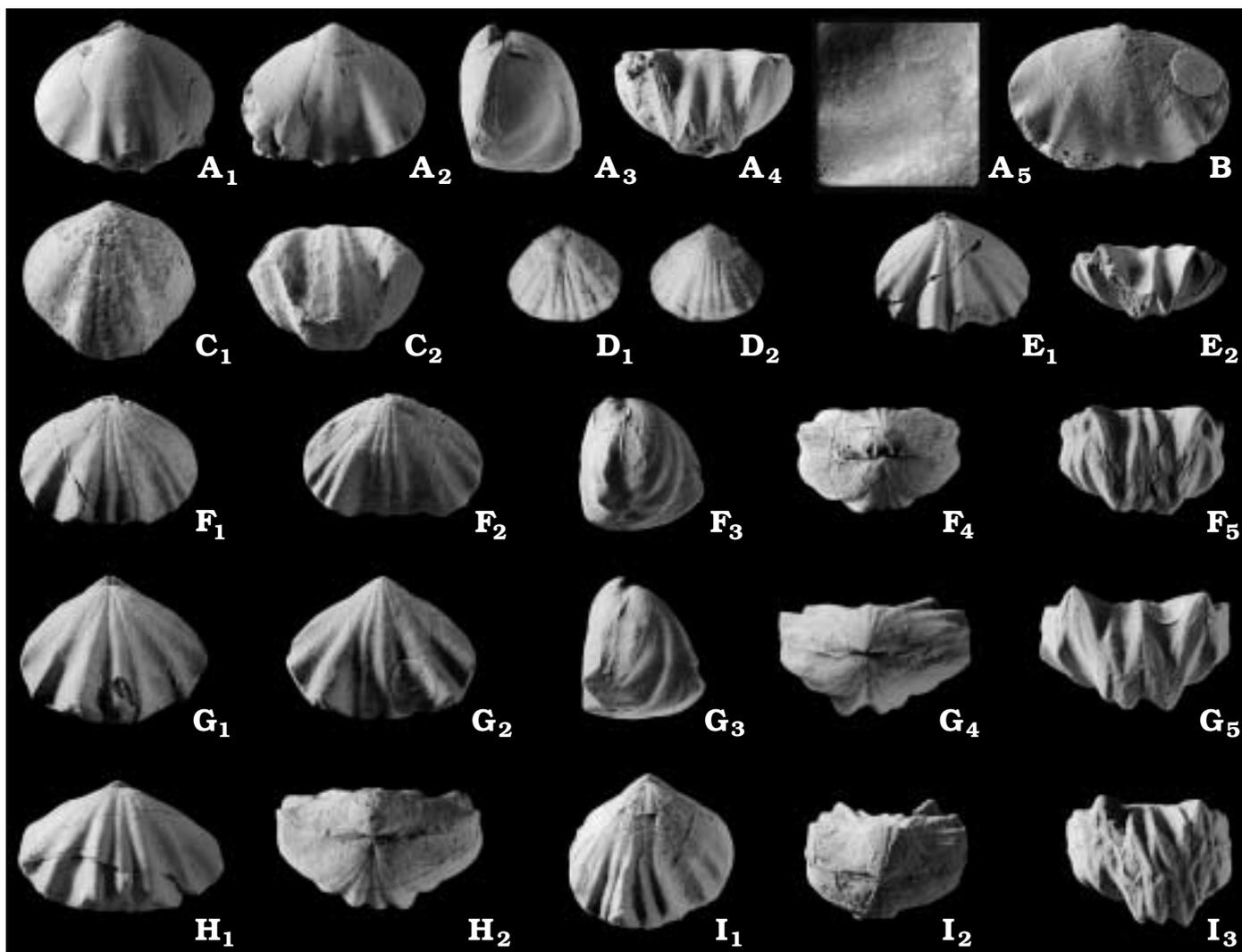


Fig. 5. Early Famennian brachiopods, trench Z-17, Dębnik anticline, Poland. **A, B.** *Chapinella striata* sp. nov. **A.** Holotype Bp 46/33a in dorsal, ventral, lateral, and anterior views; **A₅** shows surface microornamentation. **B.** Shell Bp 46/33b in ventral view. **C.** *Orbiculatisinuostrium laeve* (Gürich, 1903); shell Bp 46/28a in dorsal and anterior views. **D–J.** *Pampoecilorhynchus geniculatus* sp. nov. **D.** Juvenile shell Bp 46/52a in dorsal and ventral views. **E.** Shell Bp 46/52b in dorsal and anterior views. **F, G.** Two shells Bp 46/52c and Bp 46/52d in dorsal, ventral, lateral, posterior, and anterior views (**G**, holotype). **H.** Expanded laterally shell Bp 46/52e in dorsal and posterior views. **I.** Elongated shell Bp 46/52f in dorsal, posterior, and anterior views. All $\times 1.5$ except **A₅** $\times 4$.

by having fewer costae, with costae strongly developed on the anterior half of the shell only. From the type species *Pampoecilorhynchus nux* (Gosselet, 1887) the new species differs by its smaller and wider shell with distinctly geniculate antero-lateral shell margins. From *P. abellanus* Sartenaer, 1968 the new species differs by its more strongly globose shell. Shells of *P. lecomptei* (Sartenaer, 1954) and *P. arianus* Sartenaer, 1968 are also geniculated but differ from *P. geniculatus* sp. nov. by their strong costae originating at their umbones.

Externally the new species is closest to *Pampoecilorhynchus praenux* Sartenaer, 1958 described from the Early Famennian of the Dinant Basin and Vesdre Massif (Sartenaer 1958, 1968, 1985). The present species differs from the Belgian form by its fewer medial and lateral costae that are

smaller with rounded cross-sectional profiles in the posterior region of the shell and its distinct geniculation of the shell margins. *Pampoecilorhynchus praenux* is the index fossil for the brachiopod zone in Belgium, that there is associated with conodonts of the Middle *Pa. triangularis* Zone (Sartenaer 1985). *Pampoecilorhynchus* cf. *praenux* described by Matyja and Żbikowska 1974 from the *Pa. crepida* Zone of the Minkowice 1 borehole (Lublin Basin, Poland) was rejected from the species by Sartenaer (1985: 321). It is probable that *P. geniculatus* is the oldest representative of the genus.

Occurrence.—According to Sartenaer (1968: 31–33; 1985: 321) the genus *Pampoecilorhynchus* occurs in the Early Famennian (mainly *Pa. triangularis* conodont Zone) of USA, Germany, Belgium, France, Iran, and Afghanistan. *P. geniculatus* sp. nov. occurs in dark-grey micrites represent-

ing the Early and basal part of the Middle *Pa. triangularis* Zone in trench Z-17 near the village of Dębnik, Cracow Region, southern Poland.

Superfamily Pugnacoidea Rzhonsnitskaya, 1956

Family Pugnacidae Rzhonsnitskaya, 1956

Genus *Chapinella* Savage, Eberlein and Churkin, 1978

Chapinella striata sp. nov.

Figs. 5A, B, 6.

Colophragma? sp.; Baliński 1995a: 45–47, pl. 4: 6–7, fig. 11B.

Holotype: ZPAL Bp 46/33a, a complete shell illustrated in Fig. 5A.

Type locality: Trench Z-17 near the village of Dębnik, Cracow Region, southern Poland.

Type horizon: Platy Limestone Unit, Lower Famennian, the Early *Palmatolepis triangularis* Zone.

Etymology: After very delicate striae on the shell surface.

Diagnosis.—Shell medium sized, usually up to 21 mm in width, wider than long, strongly dorsibiconvex, the greatest thickness situated at two-third of the shell length from the umbo or slightly further anteriorly; anterior commissure strongly uniplicate; usually three costae in fold and two in sulcus, up to three costae on flanks; medial costae originate near mid-length of the shell, lateral costae are distinct near the anterior margin; shell surface weakly striate. Interior of the dorsal valve with extremely short medial myophragm that supports the base of the hinge plates. The new species differs from *C. bucareliensis* Savage et al., 1978 by the more inflated posterior region of its dorsal valve.

Material.—Ten complete or almost complete shells and 45 shell fragments, all from trench Z-17. In addition, 33 specimens were recovered and described by Baliński (1995) from slightly younger horizons at the Z-2 and Z-9 outcrops (see synonymy).

Description.—Shell medium sized for the genus, outline subelliptical, wider than long, width averages 102 to 139% of shell length, strongly dorsibiconvex; cardinal margin curved, lateral margins rounded, anterior margin truncate or gently arched; anterior commissure strongly uniplicate.

Ventral valve distinctly less convex than the dorsal one, with gently convex flanks; sulcus distinct, begins one-third to one-half of the valve length from umbo, deep, with concave to slightly convex bottom; beak suberect to erect, protuberant.

Dorsal valve regularly convex in lateral profile, with swollen posterior region and slightly concave near both ends of the cardinal margin; the valve thickness from 51 to 71% of the total shell thickness; fold originates at mid-valve, moderately elevated, with rounded top in transverse profile.

Eighty-one per cent of the specimens with three costae on fold and two costae in sulcus. Four and five costae, respectively, occur in 15% of the specimens. One shell with two costae on fold and two shells with five costae. Lateral costae are shorter and markedly weaker than the medial costae; with

one to as many as three lateral costae on each flank of the dorsal valve and two to four costae on the ventral valve. Very weak and fine radial striae are observed on well preserved specimens; their number averages 8 to 9 per mm.

Ventral interior with distinct subparallel dental plates and distinct umbonal chambers (Fig. 6). Dorsal interior with thin hinge plates unsupported by median septum; in umbonal region a very short median thickening or myophragm occurs in sectioned specimens (Fig. 6), although it cannot be regarded as a true median septum.

Remarks.—The new species characterizes the earliest Famennian brachiopod assemblage found in trench Z-17. This species was identified earlier as *Colophragma?* sp. in nearby Z-2 and Z-9 outcrops with limestones that represent slightly younger horizons of *Pa. triangularis* Zone (Baliński 1995a: 45–47, pl. 4: 4–5, fig. 11B). *Chapinella striata* sp. nov. shares many external characters with the type species *C. bucareliensis* Savage et al., 1978. The latter was described from the Middle to Late Famennian of Port Refugio Formation, southeastern Alaska (Savage et al. 1978). The Polish species differs mainly by having more inflated posterior region of the dorsal valve as it is seen in a lateral profile of the shell. Small individuals of *C. striata* resemble very much "*Pugnax*" *rara* Sartenaer, 1969 (= *Chapinella rara*, according to Savage et al. 1978) from the Lower Famennian of western Canada (Sartenaer 1969). The main difference between these species is in the position of the greatest thickness of the shell that in the latter is situated at the top of always recurved posteriorly tongue. The Polish species differs from *Chapinella kovalevi* Cherksova, 1997 of the Late Famennian of Taimyr (Cherksova 1997) by having weaker costae, more convex ventral valve, shorter tongue, and lower dorsal fold.

Savage et al. (1978) attributed *Parapugnax bactriense* Johnson et al., 1969 from the Famennian West Range Limestone of Nevada, USA, to *Chapinella*. The holotype and the three of the illustrated paratypes of the Nevada species differ markedly from *C. striata*. The fourth paratype (Johnson et al. 1969, pl. 157: 14–18) externally is close to the Polish species on one hand, and to *Colophragma ellipticum* Cooper and Dutro, 1982 on the other. It is possible that all three species are closely related although systematically they are currently attributed to different genera. The differences between *Chapinella* and *Colophragma* are not great, if not problematic, and the presence of a short median septum in the latter genus seems to be overemphasized.

Occurrence.—*Chapinella striata* sp. nov. occurs in dark-grey micrites in trench Z-17 near the village of Dębnik, Cracow Region, southern Poland. It was described earlier as *Colophragma?* sp. in slightly younger horizons sampled in exposures in quarry Z-2 and trench Z-9 (Baliński 1995a).

Superfamily Camarotoechioidea Schuchert and LeVene, 1929

Family Leiorhynchidae Stainbrook, 1945

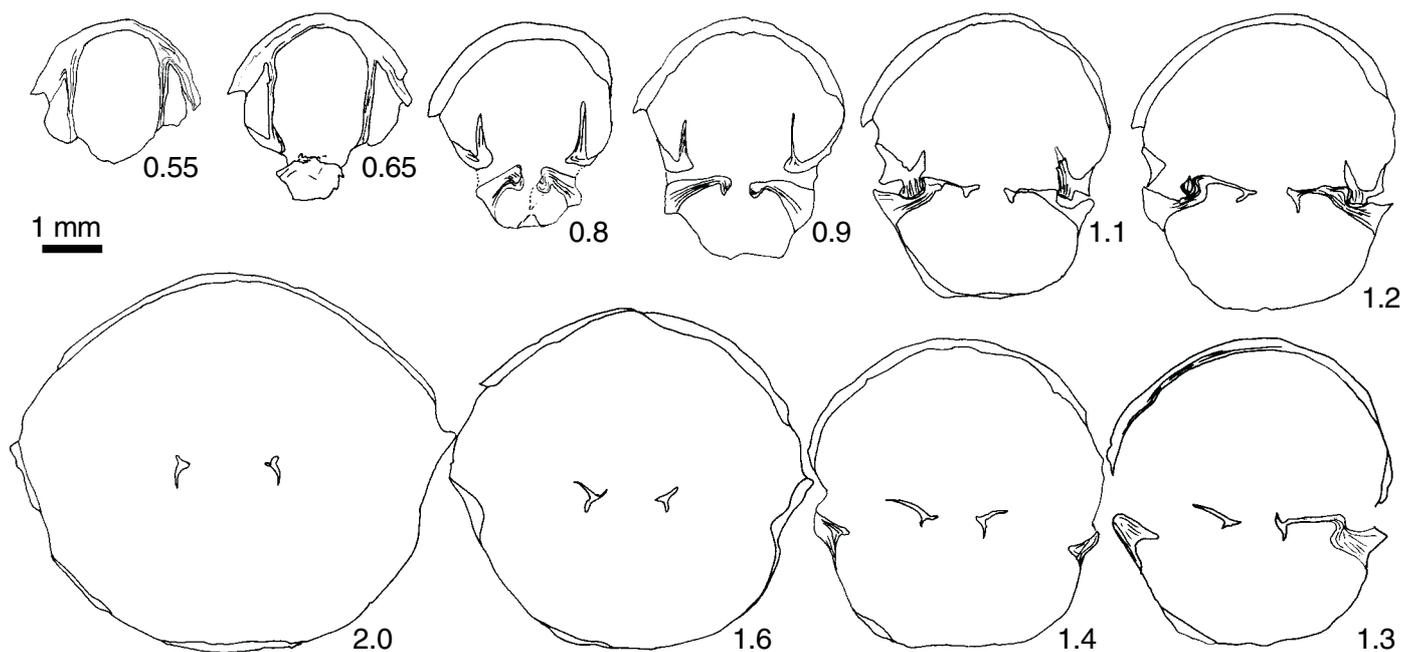


Fig. 6. Transverse serial sections of shell Bp 46/33c of *Chapinella striata* sp. nov. Numbers refer to distances in mm from the ventral apex.

Subfamily Leiorhynchinae Stainbrook, 1945

Genus *Orbiculatisinurostrum* Sartenaer, 1984

Orbiculatisinurostrum laeve (Gürich, 1903)

Fig. 5C.

Leiorhynchus laevis Gür.; Gürich 1903: 150, pl. 2: 12, 15.

Leiorhynchus laevis Gürich; Baliński 1979: 47–49; pl. 9: 1–7, fig. 16.

Orbiculatisinurostrum laeve (Gürich); Baliński and Racki 1999: fig. 1.7.

Material.—The material coming from trench Z-17 includes 2 complete shells and 68 fragmentary specimens.

Description.—Gürich's species was re-described under its original generic name by Baliński (1979). In 1984 Sartenaer erected the new genus *Orbiculatisinurostrum* and designated *L. laevis* from Dębnik as the type species.

Remarks.—In trench Z-17 *Orbiculatisinurostrum laeve* appears at the base of the Middle *Pa. triangularis* Zone, i.e. about 1.3 m above the F–F boundary. It is one of the most abundant brachiopods in this part of the section. It was described earlier by Baliński (1979) from several neighboring outcrops of the Lower Famennian beds: Z-2, Z-3, Z-13, Z-15, and Z-16.

Order Athyridida Boucot, Johnson, and Staton, 1964

Suborder Athyrididina Boucot, Johnson, and Staton, 1964

Superfamily Athyridoidea Davidson, 1881

Family Athyrididae Davidson, 1881

Family ?Didymothyridinae Modzalevskaya, 1979

Genus *Pygmis* gen. nov.

Type species: *Nucleospira jablonensis* Biernat, 1983.

Etymology: Combination of letters of Gr. *pygmaios* (a dwarf) and *Athyris*.

Diagnosis.—Shell small, smooth, ventribiconvex to almost biconvex, weakly uniplicate; dorsal fold very low, begins at anterior third of shell, or absent; ventral sulcus shallow to very shallow; ventral beak erect; small concave ventral area present, delthyrium open; dental plates distinct, subparallel; cardinal plate short, partly embedded in the shell substance; spiralia directed laterally with at least of four volutions; jugum well developed. *Pygmis* differs from majority of athyridoids by its small, smooth shell. From equally small helenathyrids it differs by the absence of diplospirium.

Remarks.—Biernat (1983) described the type species of *Pygmis* gen. nov. as a species of *Nucleospira* Hall, 1859. *Nucleospira jablonensis* Biernat, 1983 from Jabłonna and Dębnik lacks the microspinose shell ornament, dorsal median septum and the cardinal process characteristic of *Nucleospira*. *Pygmis jablonensis* (Biernat, 1983) has distinct dental plates, that are lacking in *Nucleospira*.

Pygmis gen. nov. is easily distinguished from majority of the athyridoids by its very small shell (rarely exceeds 8 mm in length) and smooth shell surface lacking growth lamellae. Externally the new genus is most similar to the Upper Devonian (Frasnian) helenathyridin *Biernatella* Baliński, 1977. Both forms are characterized by smooth and small to very small rostrate shells. *Biernatella* differs from *Pygmis* by its well developed diplospirium not observed in *Pygmis* (Fig. 7). *Pygmis* also lacks the densely spaced growth lamellae characteristic of *Biernatella* (Baliński 1995: 138, figs. 4N, 7S, 9U).

The problematic small and smooth shelled *Glassia drever-*

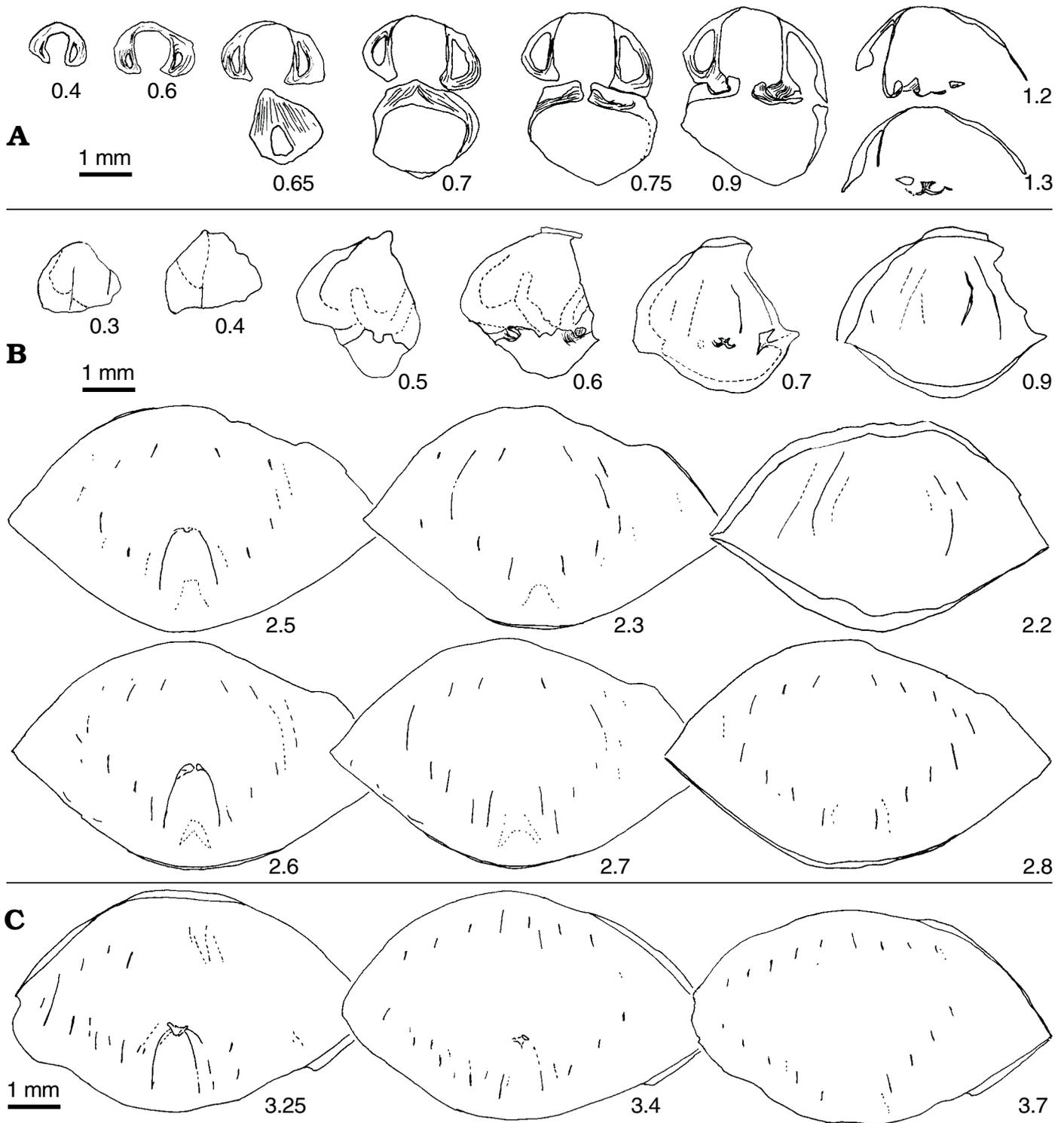


Fig. 7. Transverse serial sections of three shells Bp 46/57e, 46/58, and 46/57f of *Pygmis jablonensis* (Biernat, 1983). Numbers refer to distances in mm from the ventral apex.

manni Maillieux (1936) from the Late Frasnian Matagne Formation tentatively assigned to *Peratos* Copper, 1986 by Copper (1986: 858) has been demonstrated to represent immature shells of the rhynchonellide *Ryocarhynchus tumidus* (Kayser, 1872) by Godefroid and Helsen (1998: 263–264, fig. 17). Several small poorly known Late Devonian athyridids may belong

to the new genus, including: *Athyris(?) meristelloidea* Nalivkin, 1930 from the Late Devonian of Turkestan (Nalivkin 1930: 146–147, pl. 8: 12, 13); and *Athyris minuta* Klähn, 1912 from the Frasnian of Germany (Klähn 1912). The latter species most likely represents a species of *Biernatella*.

Pygmis differs from *Leptathyris* Siehl, 1962 by the ab-

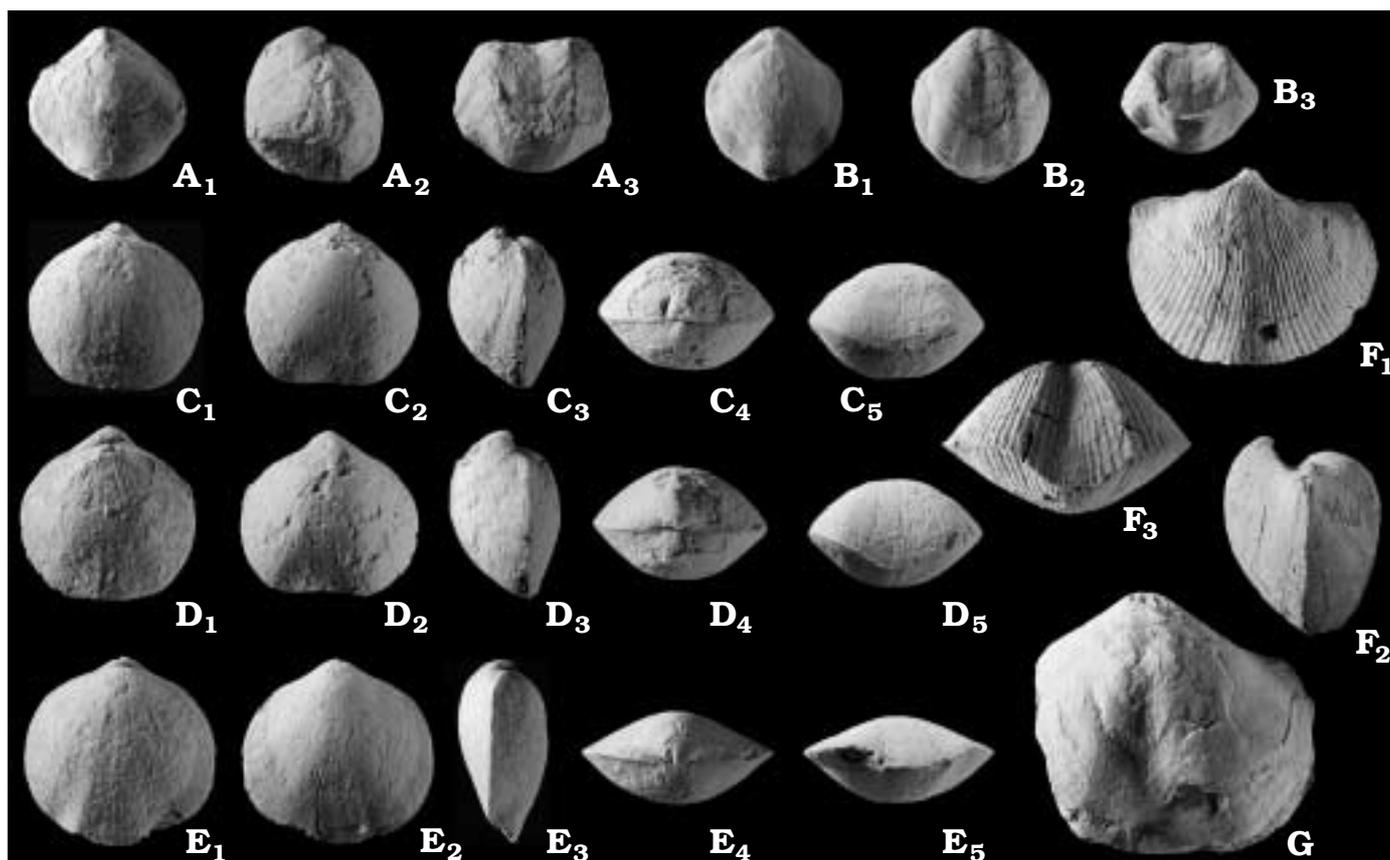


Fig. 8. Early Famennian brachiopods, trench Z-17, Dębnik anticline, Poland. **A, B.** *Crinisarina angelicoides* (Merriam, 1940). **A.** Complete shell Bp 46/49a in dorsal, lateral, and anterior views. **B.** Complete shell Bp 46/49b in dorsal, ventral and anterior views. **C–E.** *Pygmis jablonensis* (Biernat, 1983); three shells Bp 46/57a, b, and c in dorsal, ventral, lateral, posterior, and anterior views. **F.** *Cyrtospirifer minor* (Gürich, 1903); adult shell Bp 46/1a in dorsal, lateral, and anterior views. **G.** *Warrenella* sp.; incomplete shell Bp 46/16 in ventral view. All $\times 1.5$.

sence of a bisulcate shell, its less pronounced dorsal umbo, and lack of a depressed cardinal plate. Externally *Pygmis* resembles the small Famennian athyridid *Johnsonathyris* Savage, Eberlein, and Churkin, 1978, although the shells of the former are less convex and feature concentric growth lamellae and radial costellae lacking in *Pygmis*.

Stratigraphic and geographic range.—As for the type species given below.

Pygmis jablonensis (Biernat, 1983)

Figs. 7, 8C–E.

Nuclespira jablonensis n. sp.; Biernat 1983: 142, 149–150, pl. 4: 1, pl. 5: 1, pl. 6: 1–2.

Emended diagnosis.—Shell small (rarely exceeding 8 mm in length), as wide as long, widest at midlength, subcircular to subpentagonal in outline, rather thick, ventribiconvex to subequal, weakly uniplicate, fold and sulcus poorly developed.

Material.—Three complete and one slightly damaged shell, and 25 shell fragments. All shells interiors infilled by sparry calcite that conceals some details of internal shell structures.

Dimensions in mm:

Cat. No. ZPAL Bp	L	W	T	Tvv	Tdv	T/L %
46/58	7.8	7.8	4.4	2.3	2.1	56
46/57a	7.8	8	5.4	2.8	2.7	69
46/57b	7.8	8	5.0	3.8	2.2	64
46/57c	8.6	8.6	4.0	2.5	1.5	47

Description.—Shell rarely exceeds 8 mm in length, about as wide as long, shell thickness averages 45–69% of the shell length, ventral valve slightly more or equally convex as the dorsal valve; hinge line short, slightly angular; lateral margins regularly arched, anterior margin almost straight, anterior commissure weakly uniplicate.

Ventral valve with erect beak and very shallow medial sulcus, which appears about midvalve; area high but narrow and concave; delthyrium open. Dorsal valve with slightly swollen posterior region; median fold lacking or weakly developed at the anterior margin only.

Interior of the ventral valve with distinct subparallel dental plates and cavities, teeth massive. Dorsal valve interior with massive cardinal plate, posteriorly embedded in shell

substance, expanded anteriorly as thin, conjunct inner hinge plates (Fig. 7A, B). Spiralia with at least four volutions; lateral branches of jugum long, arise in posterior one-third to two-fifths of the shell length. Other details of the internal shell structure are difficult to study due to recrystallization of the shell interior.

Shell surface smooth except very faint growth lines.

Remarks.—The Dębnik specimens are identical externally with *Pygmis jablonensis* (Biernat, 1983) described from the early part of the Famennian of Jabłonna. At Dębnik, *P. jablonensis* occurs a few meters above the last occurrence of helenathyrid *Biernatella polonica*. The similar general appearance of the shell of both forms raises the question whether they are phylogenetically related. On close comparison it is found that externally *P. jablonensis* differs from all species of *Biernatella* in having a smooth uniplicate shell lacking concentric lamellae. Careful sectioning of several specimens did not confirm the presence of diplospirium found in all of the helenathyrids.

Occurrence.—The species is uncommon in the topmost 3 m of dark-grey micrites (set III, Middle *Pa. triangularis* Zone) in trench Z-17 near the village of Dębnik, Cracow Region, southern Poland. It occurs here usually in small nest-like groupings composed of a few complete shells. The species was described originally by Biernat (1983) from the early part of the Famennian of Jabłonna (Holy Cross Mountains, Central Poland) where it is documented in trench III in the intervals of the Middle *Pa. triangularis*, Late *Pa. crepida* or Early *Pa. rhomboidea* to Early *Pa. marginifera* Zones.

Subfamily Cleiothyridininae Alvarez, Rong, and Boucot, 1998

Genus *Crinisarina* Cooper and Dutro, 1982

Crinisarina angelicoides (Merriam, 1940)

Figs. 8A, B, 9.

Athyris angelicoides n. sp.; C.W. Merriam 1940: 84–85, pl. 10: 1

Material.—Twelve complete or slightly damaged shells and nine fragments. Although the specimens are frequently exfoliated, three of them preserve well the characteristic lamello-spinose ornament in small weathered patches.

Remarks.—The specimens from Dębnik closely correspond in shell shape, dimensions and parasulcation to those of *Athyris angelicoides* Merriam, 1940 from the Early Famennian of the Upper Devils Gate Formation of Nevada (Merriam 1940). Cooper and Dutro (1982: 92) placed this species in their new genus *Crinisarina*. Two other specimens described from a slightly younger horizon from the Dębnik anticline (*Pa. crepida* conodont Zone) by Baliński (1995a) as “*Athyris*” aff. *reticulata* (Gosselet, 1877) are very similar externally to the present specimens. The younger specimens, however, differ by having deeper and more angular ventral sulcus distinctly bounded laterally by folds. Their ventral valves also differ by having concave antero-lateral flanks. They most probably represent another species related to *C. angelicoides* on one hand, and to *Spirigera reticulata* Gosselet on the other. Although the specimens from the interval of the *Pa. crepida* Zone are completely exfoliated and thus devoid of original shell ornamentation, they almost certainly represent the genus *Crinisarina*. Recent examination by the present author of the topotype material of *Spirigera reticulata* var. *carinata* Gosselet, 1877 from Senzeilles (Belgium) revealed that the variety possesses characteristic angular ventral sulcus and angular summit of the dorsal fold and the shell ornamentation, which consists of concentric growth lamellae bearing a fringe of spines (see also Gosselet 1877,

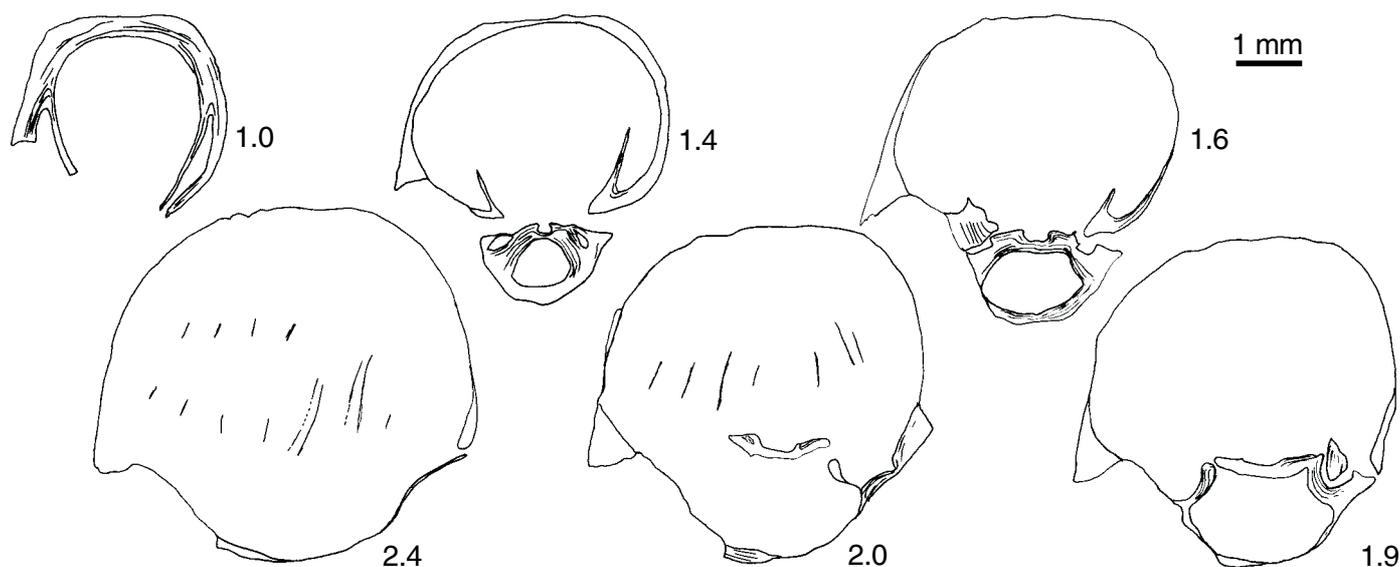


Fig. 9. Transverse serial sections of shell Bp 46/49q of *Crinisarina angelicoides* (Merriam, 1940). Numbers refer to distances in mm from the ventral apex.

pl. 3: 3f). Thus, most probably Gosselet's species also belongs to the genus *Crinisarina*. If it is so, there is a homonymy between *Spirigera reticulata* Gosselet, 1877 and *Cleiothyridina reticulata* Stainbrook, 1947. The later is a type species of the genus *Crinisarina* Cooper and Dutro, 1982. Unfortunately, the details of the internal shell structure of these two forms remains unknown.

Occurrence.—*Crinisarina angelicoides* occurs in the early Famennian in the *Cyrtospirifer* Zone of the Upper Devils Gate Formation of Nevada (Merriam 1940). In Poland the species occurs in dark-grey micrites in trench Z-17 near the village of Dębnik, Cracow Region, southern Poland. It was also found in the early Famennian set F at Psie Górki, Holy Cross Mountains.

Suborder Spiriferidina Waagen, 1883
 Superfamily Cyrtospiriferoidea Termier and Termier, 1949
 Family Cyrtospiriferidae Termier and Termier, 1949
 Subfamily Cyrtospiriferinae Termier and Termier, 1949
 Genus *Cyrtospirifer* Nalivkin in Frederiks, 1929
Cyrtospirifer minor (Gürich, 1903)

Fig. 8F.

Spirifer Archiaci Vern. var. *minor* Gürich; Gürich 1903: 142–143, pl. 1: 4–7.

Spirifer Archiaci Vern. var. *minor* Gür.; Jarosz 1919: pl. 8: 23.

Cyrtospirifer minor (Gürich, 1903); Baliński 1979: 67–69, fig. 22, pl. 17: 1–11.

Material.—Two complete, 11 slightly damaged and 69 fragments of shells and valves.

Remarks.—This small *Cyrtospirifer* species is one of the commonest brachiopods in the lowermost Famennian beds exposed in trench Z-17 near Dębnik. It is most abundant in set II where it dominates (together with *Pamphocylorhynchus geniculatus* sp. nov.) the assemblage. *Cyrtospirifer minor* was described by Baliński (1979) from slightly younger horizons, but still representing *Pa. triangularis* conodont Zone. The oldest occurrence of the species is in trench Z-6 and the basal set I of trench Z-17 (about 0.7 m below Frasnian–Famennian boundary) in the highest Frasnian *Ryocarhynchus tumidus* brachiopod zone. *C. minor* is very rare in this horizon, however, being represented exclusively by single broken valves.

Genus *Tenticospirifer* Tien, 1938

?*Tenticospirifer* sp.

Material.—One fragment of the conical ventral valve from the lowest bed (set I) of trench Z-17.

Remarks.—The species is probably conspecific with the Middle and Late Frasnian specimens of the Dębnik anticline described earlier by Baliński (1979) as *T. cyrtiniformis* (Hall and Whitfield, 1872). According to the recent revision of *Tenticospirifer* by Ma and Day (2000) the American spe-

cies *Spirifera cyrtiniformis* Hall and Whitfield belongs to the genus *Conispirifer* Lyashenko. The American species as well as other members of *Conispirifer* differ from *Tenticospirifer* by having poorly defined to obsolescent fold and sulcus (Ma and Day 2000: 456). The catacline ventral interarea, well-defined fold and sulcus and fewer medial plications of the specimens from Dębnik may represent a species of *Tenticospirifer*.

Suborder Delthyridina Ivanova, 1972
 Superfamily Reticularioidea Waagen, 1883
 Family Reticulariidae Waagen, 1883
 Subfamily Rhenothyridinae Gourvanec, 1994
 Genus *Warrenella* Crickmay, 1953
Warrenella sp.

Fig. 8G.

Material.—One incomplete, strongly deformed shell from the lowest bed (set I) of trench Z-17 (the latest Frasnian).

Remarks.—The material is insufficient to allow a reliable specific determination.

Acknowledgements

Sincere thanks are extended to Dr. Jed Day (Illinois State University, Normal) for many critical comments and improvement of English of the manuscript. This work was partially supported by the State Committee for Scientific Research in Poland (KBN; grant P04D 024 13 to G. Racki).

References

- Alekseeva, R.E. 1969. New and unusual lower Devonian spiriferids (suborder Athyrididina) [in Russian]. *Doklady AN SSSR* 187: 1157–1159.
- Alvarez, F., Rong Jia-Yu, and Boucot, A.J. 1998. The classification of athyridid brachiopods. *Journal of Paleontology* 72: 827–855.
- Baliński, A. 1977. *Biernatella*—a new Devonian double-spired brachiopod. *Acta Palaeontologica Polonica* 22: 175–186.
- Baliński A. 1979. Brachiopods and conodonts from the Frasnian of the Dębnik anticline, southern Poland. *Palaeontologia Polonica* 39: 1–95.
- Baliński A. 1995a. Brachiopods and conodont biostratigraphy of the Famennian from the Dębnik Anticline, southern Poland. *Palaeontologia Polonica* 54: 1–85.
- Baliński A. 1995b. Devonian athyridoid brachiopods with double spiralia. *Acta Palaeontologica Polonica* 40: 129–148.
- Baliński, A. 1996. Frasnian–Famennian brachiopod faunal extinction dynamics: an example from southern Poland. In: P. Copper and J. Jin (eds.), *Proceedings of the Third International Brachiopod Congress, Sudbury–Ontario–Canada, 2–5 September 1995*, 319–324. Balkema, Rotterdam–Brookfield.
- Baliński, A. and Racki, G. 1999. Wymieranie i odradzanie się faun ramienionogowych a kryzys na granicy fran–famen. *Przegląd Geologiczny* 47: 373–378.
- Biernat, G. 1983. Ramienionogi z utworów famenu Jabłonnej, Góry Świętokrzyskie. *Biuletyn Instytutu Geologicznego* 345: 135–154.
- Bouckaert, J., Mouravieff, A., Streef, M., Thorez, J., and Ziegler, W. 1972.

- The Frasnian–Famennian boundary in Belgium. *Geologica et Palaeontologica* 6: 87–92.
- Boucot, A.J., Johnson, J.G., and Staton, R.D. 1964. On some Atrypoid, Retzioid, and Athyridoid Brachiopoda. *Journal of Paleontology* 38: 805–822.
- Bowen, Z.P., Rhoads, D.C., and McAlester, A.L. 1974. Marine benthic communities in the Upper Devonian of New York. *Lethaia* 7: 93–120.
- Brice, D., Carls, P., Cocks, L., Copper, P., Garcia-Alcalde, J.L., Godefroid, J., and Racheboeuf, P.R. 2000. Brachiopoda. In: P. Bultynck (ed.), Subcommission on Devonian Stratigraphy. Fossil Groups Important for Boundary Definition. *Courier Forschungsinstitut Senckenberg* 220: 65–86.
- Bronn, H.G. 1862. *Die Klassen und Ordnungen der Weichthiere (Malacozoa)*, vol. 3 (1). 518 pp. C.F. Winter'sche Verlagshandlung, Leipzig.
- Cherkesova, S.V. [Čerkesova, S.V.] 1997. New species of the Famennian Pugnacidae (Brachiopoda) from Central Taimyr [in Russian]. *Paleontologičeskij žurnal* 1997: 59–62.
- Cooper, G.A. 1942. New genera of north American brachiopods. *Journal of the Washington Academy of Sciences* 32: 228–235.
- Cooper, G.A. and Dutro, J.T. 1982. Devonian Brachiopods of New Mexico. *Bulletins of American Paleontology* 82–83: 1–215.
- Copper, P. 1986. Evolution of the earliest smooth spire-bearing atrypoids (Brachiopoda: Lissatrypidae, Ordovician–Silurian). *Palaeontology* 29: 827–866.
- Crickmay, C.H. 1953. *Warrenella*, a new genus of Devonian brachiopods. *Journal of Paleontology* 27: 596–600.
- Dadlez, R., Kowalczewski, Z., and Znosko, J. 1994. Some key problems of the pre-Permian tectonics of Poland. *Geological Quarterly* 38: 169–190.
- Day, J. and Over, D.J. 2002. Post mass extinction survival fauna from the lowermost Famennian (Lower *triangularis* Zone) of eastern North America. *Acta Palaeontologica Polonica* 47: 189–202.
- Davidson, T. 1881. On genera and species of spiral-bearing Brachiopoda, from specimens developed by the Rev. Norman Glass. *Geological Magazine* 8: 1–13.
- Erwin, D.H. 1998. The end and the beginning: recoveries from mass extinctions. *Trends in Ecology and Evolution* 13: 344–349.
- Erwin, D. 2000. Life's downs and ups. *Nature* 404: 129–130.
- Ginter, M. 2000. Chondrictyan fauna of the Frasnian–Famennian boundary beds in Poland. *Acta Palaeontologica Polonica* 47: 329–338.
- Głuchowski, E. 2002. Crinoids from the Famennian of the Holy Cross Mountains, Central Poland. *Acta Palaeontologica Polonica* 47: 319–328.
- Godefroid, J. and Helsen, S. 1998. The last Frasnian Atrypida (Brachiopoda) in southern Belgium. *Acta Palaeontologica Polonica* 43: 241–272.
- Gorjansky, V.Iu. (Gorānskij, V.Ū.) and Popov, L.E. 1985. Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells [in Russian]. *Paleontologičeskij žurnal* 1985: 3–14.
- Gosselet, J. 1877. Note sur le Famennien. Quelques documents pour l'étude des schistes de Famenne. *Annales de la Société Géologique du Nord* 4: 303–320.
- Gosselet, J. 1887. Note sur quelques Rhynchonelles du terrain Dévonique supérieur. *Annales de la Société Géologique du Nord* 14: 188–221.
- Gourvennec, R. 1994. In: J.L. Carter, J.G. Johnson, R. Gourvennec, and Hong-Fei Hou: A revised classification of the spiriferid brachiopods. *Carnegie Museum, Annals* 63: 327–374.
- Gray, J.E. 1840. *Synopsis of the Contents of the British Museum*, 42nd edition. 370 pp. British Museum, London.
- Gürich, G. 1903. Das Devon von Dębnik bei Krakau. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 15: 127–164.
- Hall, J. 1867. *Descriptions and Figures of Fossil Brachiopoda of the Upper Helderburg, Hamilton, Portage and Chemung Groups*. *Natural History of New York, Palaeontology*, vol. 4, part. 1. 428 pp. New York State Geological Survey, Albany.
- Hall, J. and Clarke, J.M. 1892. An introduction to the study of the genera of Paleozoic Brachiopoda. *Geological Survey of the State of New York, Palaeontology* 8: 1–394.
- Hałas, S., Baliński, A., Gruszczyński, M., Hoffman, A., Małkowski, K., and Narkiewicz, M. 1992. Stable isotope record at the Frasnian/Famennian boundary in southern Poland. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1992: 129–138.
- Harries, P.J. and Kauffman, E.G. 1992. Patterns of survival and recovery following the Cenomanian–Turonian (Late Cretaceous) mass extinction in the Western Interior Basin, United States. Fifth International Conference on Global Bioevents Göttingen, 278–298.
- Ivanova, E.A. 1972. Main features of spiriferid evolution (Brachiopoda) [in Russian]. *Paleontologičeskij žurnal* 1972: 28–42.
- Jablonski, D. 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. *Science* 279: 1327–1330.
- Jaroszyński, J. 1919. Studien über das Krakauer Devon. I-Teil: Das obere Famennian in der Umgebung von Dębnik. *Bulletin International de l'Académie des Sciences, Serie B* 1918: 85–130.
- Johnson, J.G. 1970. Taghanic Onlap and the End of North American Devonian Provinciality. *Bulletin of the Geological Society of America* 81: 2077–2105.
- Johnson, J.G., Reso, A., and Stephens, M. 1969. Late Upper Devonian brachiopods from the West Range Limestone of Nevada. *Journal of Paleontology* 43: 1351–1368.
- Kauffman, E.G. and Hart, M.B. 1996. Cretaceous bio-events. In: O.H. Walliser (ed.), *Global Events and Event Stratigraphy in the Phanerozoic* 285–311. Springer, Berlin.
- King, W. 1850. A monograph of the Permian fossils of England. *Palaeontographical Society, Monograph* 3: 1–258.
- Kirchner, J.W. and Weil, A. 2000. Delayed biological recovery from extinctions throughout the fossil record. *Nature* 404: 177–180.
- Klähn, H. 1912. Die Brachiopoden der Frasn-Stufe bei Aachen. *Jahrbuch der Königlich Preussischen Landesanstalt und Bergakademie zu Berlin* 33: 1–39.
- Kościelniakowska, O. 1967. Dewon górny w północnej części Gór Świętokrzyskich. *Biuletyn Geologiczny Uniwersytetu Warszawskiego* 8: 54–118.
- Kuhn, O. 1949. *Lehrbuch der Paläozoologie*. 326 pp. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Lane, N.G., Waters, J.A., and Maples, C.G. 1997. Echinoderm faunas of the Hongguleleng Formation, Late Devonian (Famennian), Xinjiang-Uyghur Autonomous Region, People's Republic of China. *Journal of Paleontology* 71 (2: Supplement): 1–43.
- Lazarev, S.S. 1986. Productacea with and without articulation: an evolutionary phenomenon at the end of the Devonian [in Russian]. *Paleontologičeskij žurnal* 1986: 61–69.
- Lazarev, S.S. 1987. Origin and systematic position of the main groups of Productida (brachiopods) [in Russian]. *Paleontologičeskij žurnal* 1987: 41–52.
- Ma, X. and Day, J. 2000. Revision of *Tenticospirifer* Tien, 1938, and similar spiriferid brachiopod genera from the Late Devonian (Frasnian) of Eurasia, North America, and Australia. *Journal of Paleontology* 74: 444–463.
- Markowskii, B.P. and Nalivkin, D.V. 1934. The Zadonsk and the Eletz Beds [in Russian]. *Trudy Glavnogo Geologo-Razvedočnogo Upravleniä* 313: 1–38.
- Matyja, H. and Żbikowska, B. 1974. Stratygrafia dewonu górnego profilu wiercenia Minkowice 1 (basen lubelski). *Acta Geologica Polonica* 24: 663–694.
- McGhee, G.R. 1996. *The Late Devonian Mass Extinction. The Frasnian/Famennian Crisis*. i–xi + 303 pp. Columbia University Press, New York.
- McKellar, R.G. 1970. The Devonian productoid brachiopod faunas of Queensland. *Geological Survey of Queensland (Palaeontological Paper)* 342: 1–40.
- Menke, C.T. 1828. *Synopsis methodica molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur; cum synonymis critica et novarum specierum diagnosisibus*. 91 pp. G. Uslar, Pyramonti.
- Merriam, C.W. 1940. Devonian Stratigraphy and Paleontology of the Roberts Mountains Region, Nevada. *Geological Society of America, Special Papers* 25: 1–114.

- Modzalevskaja, T.L. (Modzalevskaâ, T.L.) 1979. Systematics of Paleozoic Athyrididae [in Russian]. *Paleontologičeskij žurnal* 1979: 48–63.
- Moore, R.C. 1952. *Brachiopods*. In: R.C. Moore, C.G. Lalicker, and A.G. Fischer (eds.), *Invertebrate Fossils*, 197–267. McGraw-Hill, New York.
- Muir-Wood, H.M. 1955. *A History of the Classification of the Phylum Brachiopoda*. 124 pp. British Museum (Natural History), London.
- Muir-Wood, H.M. 1962. *On the Morphology and Classification of the Brachiopod Suborder Chonetoida*. 132 pp. British Museum (Natural History), London.
- Muir-Wood, H.M. and Cooper, G.A. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *Memoir of the Geological Society of America* 81: 1–447.
- Nalivkin, D.V. 1924. In: G.N. Fredericks, *Paleontological études* 2. On Upper Carboniferous Spiriferids from the Urals [in Russian]. *Izvestiâ Geologičeskogo Komiteta* 38: 295–324.
- Nalivkin, D.V. 1930. Brachiopods from the Upper and Middle Devonian of Turkestan. *Trudy Geologičeskogo Komiteta* 180: 1–221.
- Narkiewicz, M. 1985. Badania dewońskiego szelfu węglanowego południowej Polski. *Przegląd Geologiczny* 5: 253–258.
- Narkiewicz, M. 1996. Devonian stratigraphy and depositional environments in proximity of the Sub-Carpathian Arch: Lachowice 7 well, southern Poland. *Kwartalnik Geologiczny* 40: 65–87.
- Narkiewicz, M. and Hoffman, A. 1989. The Frasnian/Famennian transition: the sequence of events in southern Poland and its implications. *Acta Geologica Polonica* 39: 13–28.
- Racheboeuf, P.R. 1981. Chonetacés (Brachiopodes) siluriens et dévoniens du Sud-ouest de l'Europe (Systématique–Phylogénie–Biostratigraphie–Paléobiogéographie). *Société Géologique et Minéralogique de Bretagne, Mémoires* 27: 1–294.
- Racki, G. 1990. Frasnian/Famennian event in the Holy Cross Mts, central Poland: stratigraphic and ecologic aspects. In: E.G. Kauffman and O.H. Walliser (eds.), *Extinction Events in Earth History. Lecture Notes in Earth Sciences* 30: 169–181.
- Racki, G. 1998. The Frasnian–Famennian brachiopod extinction events: A preliminary review. *Acta Palaeontologica Polonica* 43: 395–411.
- Racki, G. and Baliński, A. 1998. Late Frasnian Atrypida (Brachiopoda) from Poland and the Frasnian–Famennian biotic crisis. *Acta Palaeontologica Polonica* 43: 273–304.
- Racki, G., Racka, M., Matyja, H., and Devleeschouwer, X. (in press). The Frasnian/Famennian boundary interval in the South Polish-Moravian shelf basins: integrated event-stratigraphical approach. *Palaeogeography, Palaeoclimatology, Palaeoecology*.
- Rzonsnitzkaja, M.A. (Ržonsnickaâ, M.A.) 1956. Family Pentameridae and family Camarotoechiidae [in Russian]. In: L.L. Khalfin (ed.), *Atlas rukovodâših form iskopaemyh fauny i flory zapadnoj Sibiri*, 53–55. Gosgeoltehzdat, Moskva.
- Sandberg, C.S. and Ziegler, W. 1996. Devonian biochronology in geologic time calibration. *Senckenbergiana Lethaea* 76: 259–265.
- Sartenaer, P. 1954. *Deux Camarotoechia de la base de l'Assise de Senzeille. (Famennien inférieur)*. Volume Jubilaire Victor Van Straelen 1, 195–214.
- Sartenaer, P. 1958. De l'importance stratigraphique des rhynchonelles Famenniennes situées sous la zone *Camarotoechia omaliusi* (Gosselet, J., 1877). Troisième note: Le groupe de la *Camarotoechia nux*. *Bulletin l'Institut Royal des Sciences Naturelles de Belgique* 34: 1–32.
- Sartenaer, P. 1968. De l'importance stratigraphique des rhynchonelles Famenniennes situées sous la zone *Ptychomaletoechia omaliusi* (Gosselet, J., 1877). Sixième note: *Pampoecilorhynchus* n. gen. *Bulletin l'Institut Royal des Sciences Naturelles de Belgique* 44: 1–36.
- Sartenaer, P. 1969. Late Upper Devonian (Famennian) rhynchonellid brachiopods from Western Canada. *Bulletin Geological Survey of Canada* 169: 1–269.
- Sartenaer, P. 1984. Deux genres rhynchonellides nouveaux de la fin du Frasnien. *Bulletin l'Institut Royal des Sciences Naturelles de Belgique* 55: 1–16.
- Sartenaer, P. 1985. The stratigraphic significance of rhynchonellid genera at the Frasnian–Famennian boundary. *Courier Forschungsinstitut Senckenberg* 75: 319–329.
- Sarytcheva, T.G. (Saryčeva, T.G.) and Sokolskaya, A.N. (Sokol'skaâ, A.N.) 1952. A description of the Palaeozoic Brachiopoda of the Moscow Basin [in Russian]. *Trudy Paleontologičeskogo Instituta Akademii Nauk SSSR* 38: 1–307.
- Sarytcheva, T.G. (Saryčeva, T.G.) and Sokolskaya, A.N. (Sokol'skaâ, A.N.) 1959. On classification of pseudopunctate brachiopods [in Russian]. *Doklady Akademii Nauk SSSR* 125: 181–184.
- Savage, N.M., Eberlein, G.D., and Churkin, M. 1978. Upper Devonian Brachiopods from the Port Refugio Formation, Suemez Island, Southeastern Alaska. *Journal of Paleontology* 52: 370–393.
- Savage, N.M. 1996. Classification of Paleozoic rhynchonellid brachiopods. In: P. Copper and J. Jin (eds.), *Proceedings of the Third International Brachiopod Congress, Sudbury–Ontario–Canada, 2–5 September 1995*, 319–324. Balkema, Rotterdam.
- Schmidt, H. 1965. Neue Befunde an paläozoischen Rhynchonellacea (Brachiopoda). *Senckenbergiana Lethaea* 46: 1–25.
- Schuchert, C. 1913. Class 2. Brachiopoda. In: K.A. Von Zittel (ed.), *Textbook of Palaeontology*. Vol. 1 (2nd edition), 355–420. MacMillan & Co. London.
- Schuchert, C. and Cooper, G.A. 1932. Brachiopod Genera of the Suborders Orthoidea and Pentamerioidea. *Peabody Museum of Natural History, Memoirs* 4: 1–270.
- Schuchert, C. and LeVene, C.M. 1929. Brachiopoda (Generum et Genotyporum Index et Bibliographia). In: J.F. Pompeckj (ed.), *Fossilium Catalogus. I: Animalia, Pars* 42: 1–140. W. Junk, Berlin.
- Sokolskaya, A.N. (Sokol'skaâ, A.N.) 1948. Evolution of the genus *Productella* Hall and related forms in the Palaeozoic of the Moscow region [in Russian]. *Trudy Paleontologičeskogo Instituta Akademii Nauk SSSR* 14: 1–168.
- Stainbrook, M.A. 1945. Brachiopoda of the Independence Shale of Iowa. *Geological Society of America, Memoir* 14: 1–74.
- Stainbrook, M.A. 1947. Brachiopoda of the Percha Shale of New Mexico and Arizona. *Journal of Paleontology* 21: 297–328.
- Stehli, F.G. 1954. Lower Leonardian Brachiopoda of the Sierra Diablo. *Bulletin of the American Museum of Natural History* 105: 257–358.
- Termier, H. and Termier, G. 1949. Essai sur l'évolution des Spiriferidés. *Service Géologique du Maroc, Notes et Mémoires* 74: 85–112.
- Tien, C.C. 1938. Devonian Brachiopoda of Hunan. *Palaeontologia Sinica, Ser. B* 4: 1–192.
- Urbanek, A. 1993. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. *Historical Biology* 7: 29–50.
- Urbanek, A. 1997. Late Ludfordian and early Přidoli monograptids from the Polish Lowland. In: A. Urbanek and L. Teller (eds.), *Silurian Graptolite Faunas in the East European Platform: Stratigraphy and Evolution*. *Palaeontologia Polonica* 56: 87–231.
- Urbanek, A. 1998. Oligophyly and evolutionary parallelism: A case study of Silurian graptolites. *Acta Palaeontologica Polonica* 43: 549–572.
- Waagen, W. 1883. Salt Range Fossils, vol. I, part 4. *Productus-Limestone Fossils, Brachiopoda*. *Geological Survey of India, Memoirs, Palaeontologia Indica (Series 13)* 3–4: 391–546.
- Waagen, W. 1884. Salt Range Fossils, vol. I, part 4. *Productus-Limestone Fossils, Brachiopoda*. *Geological Survey of India, Memoirs, Palaeontologia Indica (Series 13)* 3–4: 547–610.
- Waagen, W. 1885. Salt Range fossils, vol. 1, part 4. *Productus Limestone fossils, Brachiopoda*. *Memoirs of the Geological Society of India, Palaeontologia Indica (series 13)* 5: 729–770.
- Walliser, O.H. 1996. Global events in the Devonian and Carboniferous. In: O.H. Walliser (ed.), *Global Events and Event Stratigraphy in the Phanerozoic*, 225–250. Springer, Berlin.
- Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E., and Popov, L.E. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London (series B)* 351: 1171–1193.
- Żakowa, H. 1965. Nowa fauna górno dewonu okolic Krakowa. *Kwartalnik Geologiczny* 9: 527–549.