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A RHYNCHONELLID-DOMINATED
LATE FAMENNIAN BRACHIOPOD ASSEMBLAGE
FROM THE HOLY CROSS MOUNTAINS (POLAND)

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Late Famennian brachiopods are described for the first time from the Holy Cross Mts. (Góry Świętokrzyskie), Poland. Six taxa belong to two families, the Rhynchonellidae and the Cranaenidae; the new genus *Pugnaria* and three new species (*Rozmanaria magna*, *Pugnaria plana* and *Cranaena lgaviensis*) are proposed. The brachiopods are dominated by the smooth and comparatively large sulcate *R. magna* and the uniplicate *P. plana*. This macrobenthic assemblage, called *Rozmanaria magna* assemblage, is interpreted here as having successfully colonized deep-water habitats typical of the Chęciny-Zbrza intrashelf basin on the rising slope of the submarine ridge in the Kielce region.

Key words: Brachiopoda, Articulata, Rhynchonellida, morphology, taxa, paleoecology, Famennian, Poland.

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INTRODUCTION

Brachiopods belong to the commonest elements of the Famennian faunas in the Holy Cross Mts., yet remain insufficiently known. There are only two modern palaeontological studies (Biernat 1970, 1983) dealing almost exclusively with early Famennian faunas from a few localities, particularly Kadzielnia at Kielce and Jabłonna (fig. 1).

The present paper contains the description of the late Famennian articulate brachiopods collected during the years 1979—1984 from the Gałęzice syncline. Previously only the sulcate (i.e. with dorsal sulcus and ventral fold) rhynchonellids, *Rozmanaria equitans* (Schmidt) and *Plecto-rhynchella* cf. *collinensis* (Frech) have been cited from strata of similar age, respectively, at Jabłonna (Biernat 1983), and the Bolechowice-1 bore-

hole (Żakowa 1967). In older literature the fauna is briefly mentioned, including a preliminary list of brachiopods by Czarnocki (1916) for the well-known sites at Gałęzice.

The new record constitutes a distinctive assemblage dominated by rhynchonellids characterized by their widely varying anterior commissural folds. This variability causes problems in the systematics. As to homeomorphy of these forms and the taxonomic value of sulcation, the discussion will be presented elsewhere (Biernat and Racki 1986).

The investigated material is housed at the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, for which abbreviation ZPAL is used.

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REGIONAL AND STRATIGRAPHICAL SETTING

The brachiopods were collected at the three localities in the southern limb of the Gałęzice syncline (fig. 1B). All of them are active quarries so that detailed study is difficult, and the material was gathered only from loose blocks and waste-heaps.

Almost the whole collection came from the higher part of a thick series of alternating, monotonous, marly limestones and shales (Marly Facies of Szulczewski 1971); the most fossiliferous sites being dumps located near the northern wall of the Wola Quarry, S. of Kowala and NE of the Łgawa Hill Quarry, and S. of Bolechowice. Cephalopods, trilobites, corals, and fish remains are frequently pyritized at Łgawa Hill Quarry and were collected with the brachiopods.

Only a single specimen of a rhynchonellid, *Rozmanaria magna*, came from the cephalopod limestones exposed in the northern wall of the Ostrówka Quarry near Gałęzice (Multifossiliferous Facies of Szulczewski 1971).

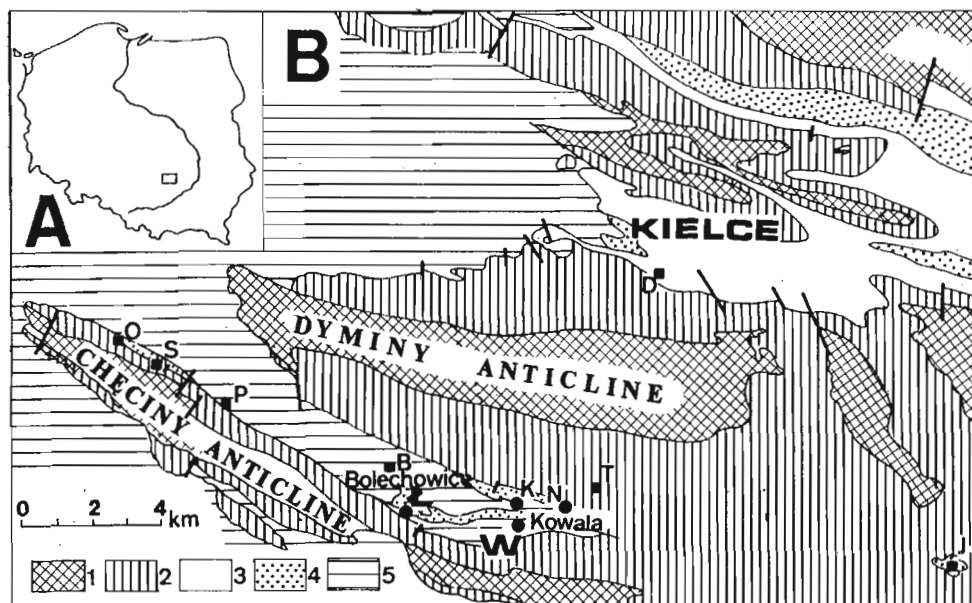


Fig. 1. Location of the discussed region (A) and Famennian localities (B) in the Holy Cross Mts. (after Szulczewski 1971, simplified). Outcrops of the Famennian basal facies are marked with circles and the condensed facies — with quadrangles (after Szulczewski 1978, 1981; Żakowa and Nehring-Lefeld 1983). 1 — Pre-Devonian deposits, 2 Lower and Middle Devonian, 3 Upper Devonian, 4 Lower Carboniferous, 5 Post-Variscan cover; B borehole Bolechowice, D Kadzielnia, J Jabłonna, K borehole Kowala, Ł Łgawa hill Quarry, N Kowala, northern Hill, O Ostrówka Hill, P Piekło, S Besówka, T Trzuskawica, W Wola Quarry.

Because of the collecting limitations the stratigraphical data could be established only on the basis of conodonts obtained from the rock matrix.

In the Wola Quarry, the brachiopods are accompanied by the conodonts *Palmatolepis glabra lepta* Ziegler et Huddle and *Polygnathus nodocostatus* Branson et Mehl (see Klapper and Ziegler 1979: text-fig. 6), indicating the undivided Upper crepida to Lower trachytera Zones. Because this fauna occurs above strata previously dated (Racki 1976) as representing the marginifera Zone it seems clear that the fauna studied is representative of that zone and/or Lower trachytera Zone.

It has been possible to age the fauna from the Łgawa Hill Quarry more precisely because *Scaphignathus* cf. *velifer* Helms and *Palmatolepis minuta* Branson et Mehl indicate the uppermost marginifera or trachytera Zone. Brachiopod bearing samples from the Ostrówka Quarry contains rich mixed conodont assemblages typical of almost the whole Famennian, but the results from the conodonts studied by Szulczewski (1978) indicate that the section cannot be older than the Upper marginifera Zone.

Consequently, the brachiopods described are mostly late, but not latest, Famennian (? do III to do IV) in age; restriction of their range to the trachytera Zone is possible.

MATERIAL

The collection of brachiopods comprises about 220 specimens which are relatively well preserved, thick-shelled, articulated, and mostly adult growth stages, although young shells are present. To a greater or lesser extent these specimens are exfoliated, some preserved as internal moulds and display traces of muscle scars and of pallial sinuses (fig. 7). No shells are broken, and few are damaged, including asymmetrical outlines probably resulting from sediment compaction. Some interiors are partly recrystallized, as shown by the peels of the ten sectioned specimens pl. 42—46.

A characteristic of the collection is the smoothness of the shells and rather poor taxonomical differentiation. Rhynchonellids prevail of which more than a hundred are sulcate (*Rozmanaria* Weyer), seventy uniplicate (*Pugnaria* n. gen.), five somewhat medially incised (? *Pugnaria* sp.) and

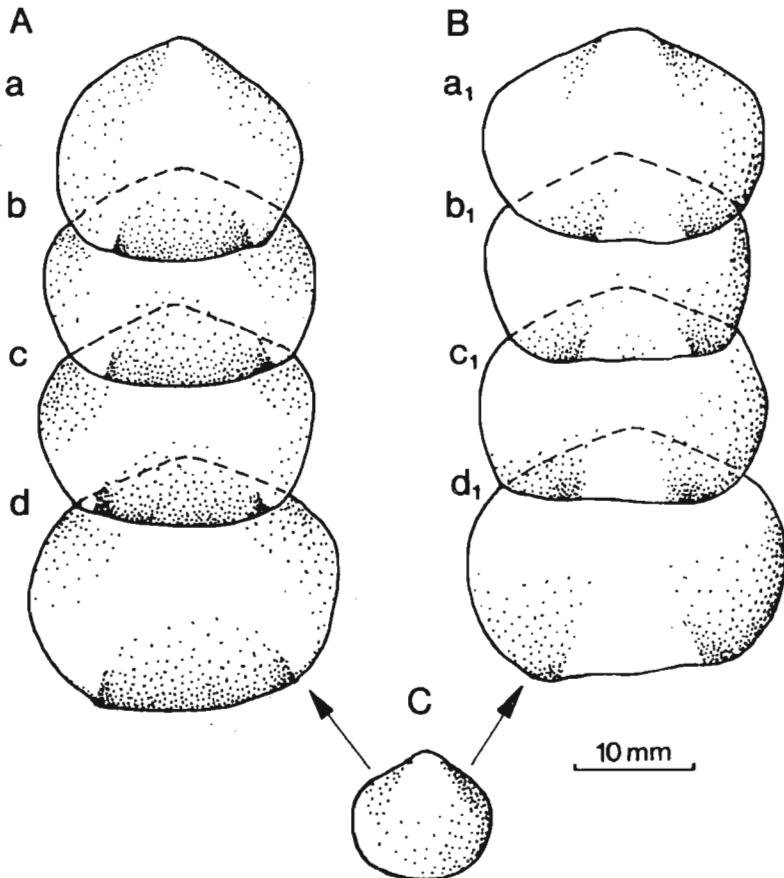


Fig. 2. Ventral view of A uniplicate (*Pugnaria plana*) and B sulcate (*Rozmanaria magna*) forms and C young, rectimarginate form, probably common for both groups.

a few radially undulated (*Planovatiostrum* Sartenaer). Cranaenids are quite numerous, and the fauna is completed by a badly preserved, single specimen of a thick-ribbed rhynchonellid (pl. 41: 4) and an orthid.

The range in species from sulcate to uniplicate to medially notched is of much interest; their shell morphology and internal structure (pls. 35—37, 39, 42—45) are all very similar. Possibly the main external difference is the appearance of their anterior commissures (fig. 2). The notched form (a member of ? *Pugnaria*) may be a link uniting the sulcate and uniplicate forms.

When comparing samples from the Wola and Łgawa Hill quarries one can recognize some differences in the state of preservation of specimens and, to some extent, in their taxonomic compositions (see p. 102). Shells from the Wola Quarry are better preserved; those from the Łgawa Hill Quarry more often being crushed, more exfoliated, with thinner shells and with more highly recrystallized interiors.

SYSTEMATIC PALAEOLOGY

Family ?**Pugnacidae** Rzhonsnitskaya, 1956

Subfamily **Rozmanariinae** Havlicěk, 1982

Diagnosis (emend.) — Smooth to somewhat radially undulated, sulcate, uniplicate or medially notched hinge plates divided, slightly varying in thickness; cardinal process, dorsal median septum and dental plates lacking or very thin to rudimentary.

Genera included: *Rozmanaria* Weyer 1972, *Pugnaria* n. gen., *Planovatiostrum* Sartenaer, 1970, ?*Hadyrhynchia* Havlicěk, 1979, *Errhynx* Havlicěk, 1982.

Remarks. — The above genera are not rare, are widely distributed geographically but stratigraphically restricted, till now, to the Late Famennian except the Eifelian *Errhynx* (Havlicěk, 1982: 112). They are all rather similar internally, but vary somewhat externally, especially in the appearance of their anterior commissures (pls. 36: 1c—5c; 37: 1c—5c; 39: 1c—4c; 40: 3c). They constitute a distinctive group of subfamily rank within the family Pugnacidae, according to the diagnosis of the family (according to Ager *et al.*, 1965: Treatise H572). This supports the opinion of Weyer (1972: 85) who included, although provisionally, his genus *Rozmanaria* in the Pugnacidae.

Stratigraphical range. — Middle Devonian (Eifelian); Upper Devonian (Late Famennian), Clymenia and Wocklumeria stages.

Genus *Rozmanaria* Weyer, 1972

Type species. — *Leiorhynchus? equitans* H. Schmidt, 1924: pl. 7: 16a, b, 17.

Diagnosis (emended). — Small to medium sized, smooth, nonstrophic, sulcate rhynchonellids of almost equal biconvexity, deltidial plates extremely small; dorsal adductors elongate; sometimes a weak myophragm present; hinge plates disjunct; crural plates, dorsal median septum and dental plates absent.

Species assigned: *Rozmanaria equitans* (H. Schmidt), *R. magna* sp. n., ?*R. krestovnikovi* (Rozman).

Remarks. — The characteristics of the above diagnosis are considered as the main generic criteria common both to *L.? equitans*, the type species of the genus, and the

newly described *R. magna* (comp. the present diagnosis and that given by Weyer 1972: 85). These "identical" characteristics evolved in these two, short-living (Famennian) forms, seem to reflect a natural relationship between them. It might be possible that another Famennian form, "*Plectorhynchella*" *krestovnikovi*, a member of small *Plectorhynchella equitans* group (*sensu* Rozman 1960, 1962) may belong to that genus. However, a lack of detailed information about the interior of "*P.*" *krestovnikovi* (Rozman 1960, 1962; Żakowa 1967) make its generic status very uncertain (Ferrari and Vai 1973). Peels of two recently sectioned shells of this species from the South Ural Mts. and from the Holy Cross Mts., which unfortunately are badly recrystallized, show no traces of internal structure. Therefore, the species is provisionally included in the genus *Rozmanaria*. Interiors of shells from the type locality need careful study.

Rozmanaria magna sp.n.

(pls. 35, 36; pl. 37: 3—5; pl. 41: 4; pls. 42, 43; figs. 2—5)

Type specimen: ZPAL Bp. XXXI/54, pl. 35: 5a—c; *paratypes*: ZPAL Bp. XXXI/50, pl. 35: 2a—c; ZPAL Bp. XXXI/66, pl. 35: 3a—c (Wola Quarry, Kowala); ZPAL Bp. XXXI/10, pl. 41: 4 (Łgawa Hill Quarry).

Type locality: Kowala (Wola Quarry), Holy Cross Mts.

Type horizon: Famennian (? do III to do IV).

Derivation of name: Lat. *magnus*—large for the genus.

Diagnosis.—Rhynchonellids in general subquadrate in outline, sulcation confined to the anterior half of the shell and commonly of moderate development with a tendency to be flattened and incipiently intraplicated.

Material.—One hundred and twenty shells, the majority from Wola Quarry, about twenty from Łgawa Hill Quarry, and one from Ostrówka Hill Quarry near Gałęzice. All shells are articulated, many badly decorticated, some damaged and deformed, and in most cases the interiors are recrystallized.

Dimensions (in mm):

Specimen No.	length	width	thickness	length/width	length/thickness
ZPAL Bp. XXXI/10	15.5	11.5	6.3	1.3	2.4
ZPAL Bp. XXXI/43	22.0	27.8	11.0	0.7	1.0
ZPAL Bp. XXXI/54 (Holotype)	16.5	19.5	8.7	0.8	1.8
ZPAL Bp. XXXI/56	16.0	19.4	8.3	0.8	1.9
ZPAL Bp. XXXI/66	17.0	12.3	9.0	1.3	1.8

Description.—Shell of medium size, varying in outline from subquadrate to transversely elliptical, moderately biconvex posteriorly with the ventral beak only slightly more elevated than the dorsal one; shell of maximum width near its midlength, width variable, about one-third more than the maximum shell length; cardinal angles sufficiently well pronounced, rounded; lateral commissure to a variable degree arcuate; anterior commissure moderately sulcate to gently intraplicate (pls. 35, 36).

Pedicle valve: Evenly convex, deepest in the posterior half or third; beak small, somewhat incurved; pedicle foramen small, circular and hypothyridid, in old specimens often reduced; deltidial plates small, disjunct, barely discernible; median fold wide, low and flat originating on the anterior half of the valve, bounded by two lateral rib-like elevations (pl. 36: 2c, 4c).

Brachial valve: Normally regularly convex, deepest at midlength, only rarely more posteriorly; sulcus wide and shallow, confined to the anterior half of the valve, sometimes somewhat linguiform (pl. 36: 5c).

Ornament: Concentric thickened growth bands are densely and regularly packed over the whole shell surface, usually 3 per mm, as in *Plectorhynchella collinensis* (Frech) from the Carnic Alps (Ferrari and Vai 1973: pl. 22: 1, 2).

Sulcation: Young shells are very rare. Judging from the preserved growth-lines of adults, juveniles to about 25 mm long show the rectimarginate shell (fig. 2C). Sulcation, as a slight ventral deflection, is recognizable at about midlength of the fully grown shell (fig. 2B) and anteriorly is bordered by two marginal slight local elevations (fig. 3). This phase of growth may correspond to the start of the geniculate biconvexity (vertical growth) of *Uncinulus* or *Kransia* (comp. Westbroek 1967: 37) and is considered here as an indicator of early adulthood (? adolescent). As growth proceeded the anterior commissure became more strongly developed medially. The sulcus and fold became broader in relation to the general shell width, widening anteriorly, and becoming better defined. In general sulcation remains moderate in relation to the general shell size. Late in ontogeny some individuals developed additional deflections in the middle of the sulcus and fold (fig. 3), producing an ?intracommisured commissure.

Variability (fig. 3, 5) effects the shell outline (although the general subquadrate outline is maintained), thickness (biconvexity) and the adult stage of sulcation. Of the forty-seven shells measured sixteen have a length/width ratio of 1.0 or 0.9 indicating almost equal length and width, and thirty-one have greater widths than lengths, a length/width ratio of about 0.6—1.0. Some variation occurs in the shell thickness within the posterior half of the shell as well as slight differences in the convexity of the individual valves (fig. 5).

Two morphotypes of sulcation (A and B) are recognized:

A — sulcation well defined, relatively deep and narrow, sometimes additionally intracommisured or slightly linguiform (fig. 3Af—Aj). Shells are commonly subquadrate of smaller size with a length/width ratio of 0.9—1.0, and more biconvex with a length/thickness ratio of 1.6—2.0; the lateral commissures are long and moderately arcuate (pl. 36: 3a).

B — sulcation shallower, with a straight to weakly waved anterior margin (fig. 3Aa—Ae; Ba—Bd); ventral fold may be depressed medially. Shell outlines are variable, subtransverse and generally larger than A and wider than long with a length/width ratio of 0.6—0.8; less convex with a length/thickness ratio of 1.9—1.2; lateral commissures shorter and more arcuate than A (pl. 35: 3, 5; fig. 3Ab—Ae, B).

The differences observed are associated with the speed of growth, members of the A Group grew faster than those of the B Group.

Interior (pl. 42, 43; fig. 4). Pedicle valve: dental plates absent; teeth solid, cyrtomatodont; muscle field varying in length, myophragm very weak to absent; diductor scars distinct, enclosing small, elongate adductors; in some specimens ovarian markings present; impressions of main pallial sinuses divergent anteriorly giving off secondary lateral branches near the valve margin.

Brachial valve: hinge plate divided, thickened and supported at the valve margins; relatively large dental sockets have ventro-laterally directed thickened inner socket ridges; crural bases variable, robust; median septum absent; muscle field distinct with elongate posterior and anterior adductor scars; thread-like myophragm

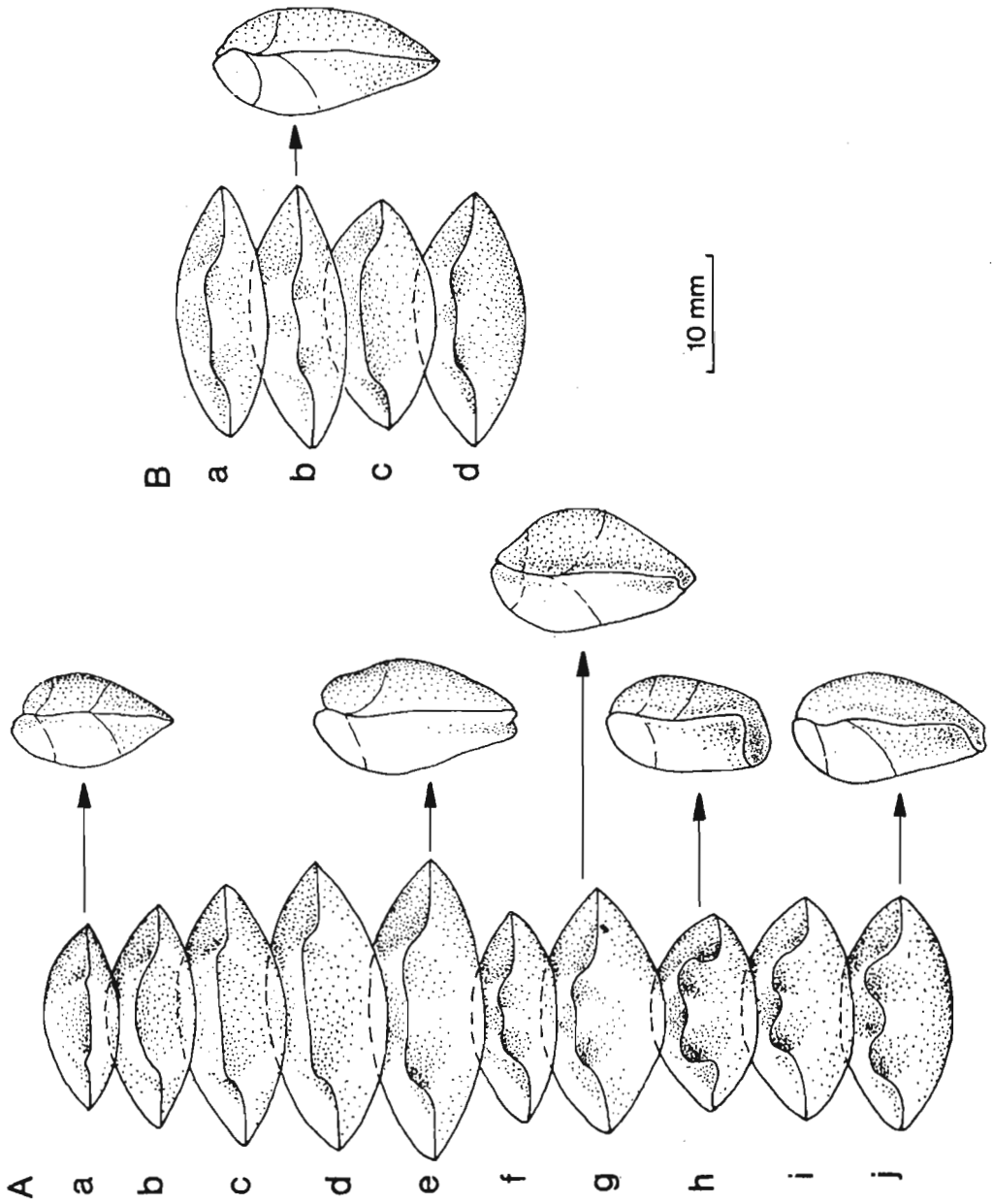


Fig. 3. *Rozmanaria magna* sp. n. Variability of the sulcate anterior commissure. A specimens from Wola Quarry, B specimens from Łgawa Hill Quarry.

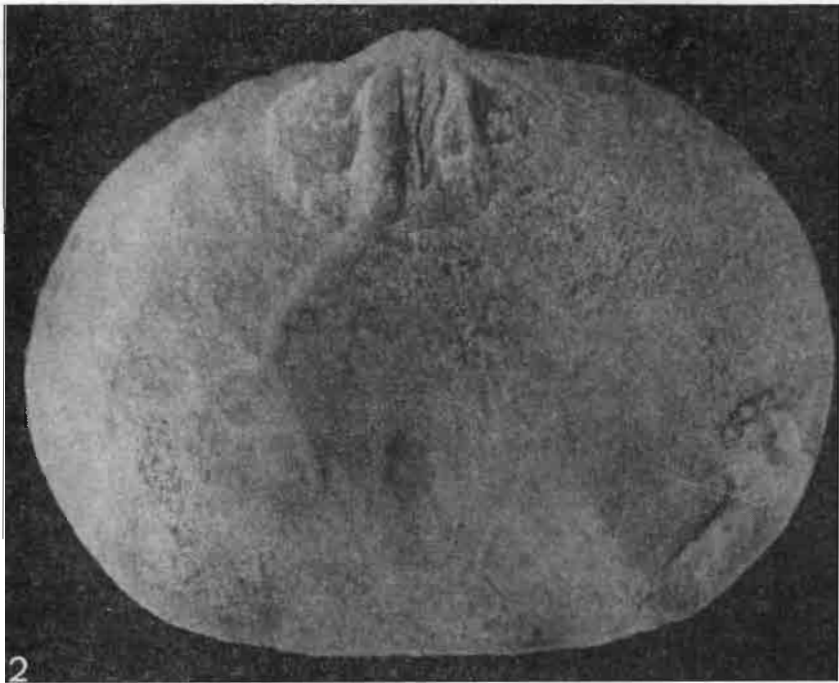
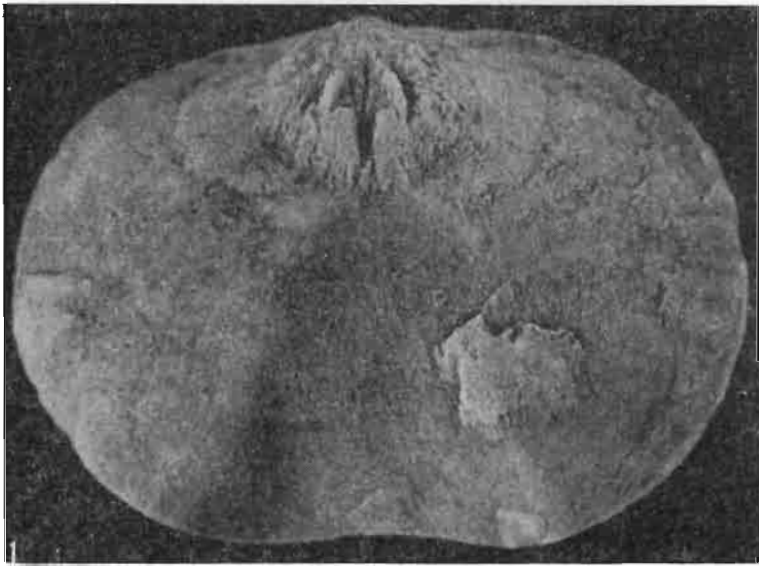


Fig. 4. *Rozmanaria magna* sp. n.: 1—2 two brachial valve interiors (moulds) showing preserved muscle scars and pallial sinuses (2); ZPAL Bp. XXXI/4, Wola Quarry, $\times 4$.

Pugnaria plana

Rozmanaria magna

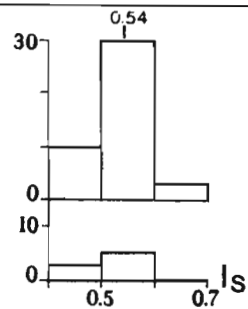
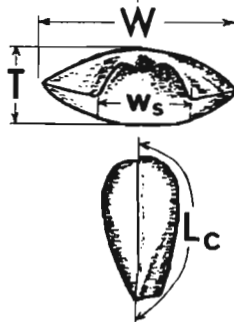
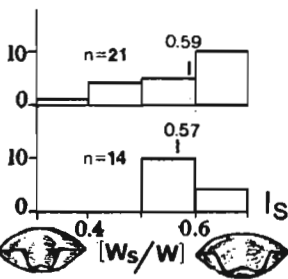
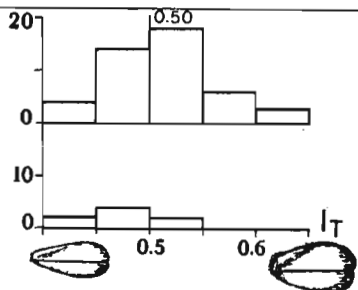
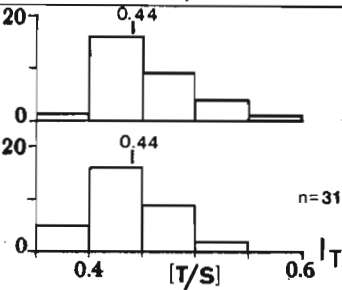
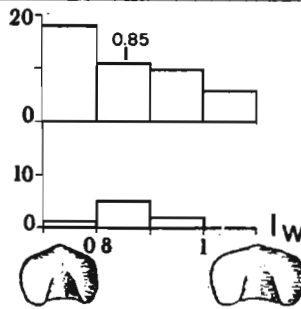
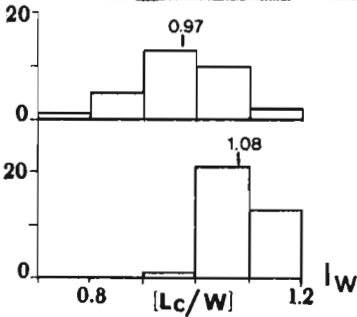
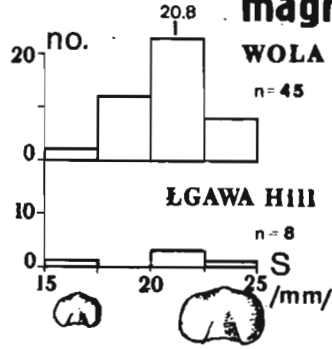
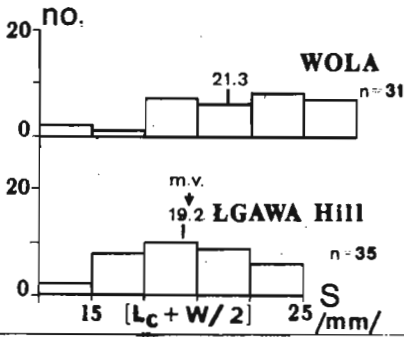


Fig. 5. Variability of the most important external features in *Rozmanaria magna* sp. n. and *Pugnaria plana* gen. et. sp. n. from the Wola and Łgawa Hill Quarries. I_S index of sinus size, I_T index of shell thickness, I_W index of shell width, $m. v.$ median value, L_c length along pedicle valve curvature, $L_c + W/2$ average value of the shell length and width, n number of measurements, $no.$ number of specimens, S shell size, T shell thickness, W shell width, W_s width of sulcus.

sometimes present; ovaria, if present, large; pallial sinuses divergent anteriorly, branching additional ones near the valve margin (fig. 4: 2).

Remarks.—*R. magna* possesses few distinct features separating it from *Rozmanaria equitans* (H. Schmidt). Externally it differs by being about two and a half times larger, by being strongly transverse but without any tendency to develop the lateral lobes so characteristic of the German species (H. Schmidt 1924: pl. 7: 16a, 16b; Weyer 1972: pls 1, 2; this paper, pl. 36). The sulcus and fold are less developed, starting near the midlength of the shell. Internally, both species are much alike and they are judged to be congeneric.

Occurrence.—Poland, Upper Famennian (? do III to do IV); Wola Quarry, Łgawa Hill Quarry, Ostrówka Quarry, Holy Cross Mts.

Genus *Pugnaria* gen. n.

Type species: *Pugnaria plana* sp. n.

Derivation of name: resembling in general shell morphology *Pugnax* as well as *Rozmanaria*—like forms.

Diagnosis.—Medium sized, smooth, moderately biconvex, uniplicate to slightly medially notched; cardinal process, dorsal median septum and dental plates absent; traces of dental nuclei may occur; hinge plates divided, thin, horizontal.

Species assigned: *Pugnaria plana* sp. n.

Remarks.—Specimens of the type species attain about 26 mm in length. They are like members of *Planovatiostrum* Sartenaer, but are smooth and have no dental plates, a feature commonly used as a generic criterion (e.g. Cooper 1969: 221). Internally they resemble *Isopoma* Torley, especially in having thin hinge and crural plates in relation to the general shell size. They also resemble *Rozmanaria*, particularly in their internal structures (e.g. divided hinge plate and lack of dental plates, cardinal process and dorsal median septum) differing by having hinge plates which are thinner and horizontal, smaller muscle fields, an uniplicate anterior commissure with rounded margins, a more elongate and flatter shape and concentric growth-lines which are widely and irregularly distributed. The differences in these features are rather slight, but in view of the great internal and external variability in these species they offer a sufficient number of character combinations to define the genus and species well (Biernat and Racki 1986).

Pugnaria plana sp. n.

(pls. 38, 39, pl. 44: 2 a—g; 45; figs. 2, 5—7)

?1856. *Terebratula Llw* Richter: 40, fig. 156—159.

Type specimen: ZPAL Bp. XXXXI/108, pl. 38: 3a—d; paratypes: ZPAL Bp. XXXI/113, pl. 38: 2a—d (Wola Quarry, Kowala); ZPAL Bp. XXXI/80, pl. 39: 1a—e; ZPAL Bp. XXXI/81, pl. 39: 2a—e (Łgawa Hill Quarry).

Type locality: Kowala, Wola Quarry, Holy Cross Mts.

Type horizon: Famennian (? do III to do IV).

Derivation of name: *Lat. planus*—flat—shell of limited biconvexity.

Diagnosis.—Smooth, medium sized, subcircular to subtransverse rhynchonellids; uniplicate, sulcus and fold elements moderately developed.

Material.—About seventy shells, of which the majority came from Łgawa Hill Quarry and about twenty from Wola Quarry. All shells are articulated, almost all are seriously decorticated, many (especially those from Łgawa Hill Quarry) are damaged and recrystallized internally.

Dimensions (in mm):

Specimen No.	length	width	thickness	length/width	length/thickness
ZPAL Bp. XXXI/108 (Holotype)	22.1	26.5	10.0	0.9	2.0
ZPAL Bp. XXXI/80	19.0	21.0	10.1	0.9	2.2
ZPAL Bp. XXXI/81	19.0	20.5	9.0	0.9	2.2

Description. — Shell of medium size, varying in outline from almost circular to, exceptionally, subquadrate; biconvex to moderately ventribiconvex posteriorly; the greatest width being at about midlength of the shell and usually exceeding its length; ventral beak slightly elevated, covering the dorsal one in adults; lateral commissures are well arched, relatively long in relation to the general shell length; the anterior commissure has a rounded outline, with moderately developed sulcus and fold elements and slight uniplication.

Pedicle valve: Convexity fairly even with the greatest depth variously positioned, but commonly anterior to the hinge line; beak small, slightly incurved.

Brachial valve: Regularly convex, the greatest depth in younger (smaller) shells at about midlength but moving posteriorly with growth.

Ornament: Growth-lines thickened, linear, widely and rather irregularly spaced (1—2 per mm) all over the shell surface but usually more dense (2—3 per mm) on the anterior part of shell.

Uniplication: As with the sulcate condition it is an adult feature. It is a moderate undulation, ill-defined laterally, and having a rounded anterior margin (fig. 5). The disposition of growth lines, limited shell wall thickness, marked shell flattening, and weak uniplication may indicate a regular shell growth, which may have been controlled environmentally (see p. 24).

Variability (figs. 5, 6): Variation is mostly expressed in the shell outline, shape and, to some extent, in the appearance of uniplication. Of the forty-five specimens measured, twenty seven have length/width ratios of 1.0—1.1, indicating lengths greater than widths; eighteen specimens with length/width ratios ranging from 0.7—1.1 have shells wider than long. Greater variation occurs in the length/thickness ratios, which range from 1.2—2.8. In general, more biconvex shells (twenty four measured) have length/thickness ratios ranging from 2.3—2.8. Their length, to some extent, exceeds shell width and the specimens are more or less ovate in outline, with more accentuated uniplications and almost straight anterior margins (pl. 39: 2; fig. 5). Twenty one of the forty five specimens are moderately biconvex with length/thickness ratios ranging from 1.2—2.2. They are wider than long, subcircular to nearly subtransverse in outline, with a moderate uniplication having a rounded anterior margin.

Interior (fig. 7; pl. 44: 2a—g). Pedicle valve: dental plates lacking, teeth somewhat elongated, cyrtomatodont, as in *Rozmanaria magna* sp. n. (pl. 43: 1e); muscle field with small diductors, adductors a little elongated, myophragm very weak, two main vascula media well divergent anteriorly.

Brachial valve: Dental sockets correspondingly deep; divided hinge plates thin, horizontal; inner and outer socket ridges thin; crural bases rounded; crura correspondingly thin, divergent dorsally; adductors ovate; myophragm absent or very slight; pallial sinuses lemniscate, main vascula media divergent anteriorly branching laterally and anteriorly (fig. 7).

Remarks. — This is a characteristic form, distinctive from the known smooth, uniplicate rhynchonellids. It is quite probable that it includes a rhynchonellid briefly described and figured, as *Terebratula Llw.* from the Upper Devonian *Wocklumeria*

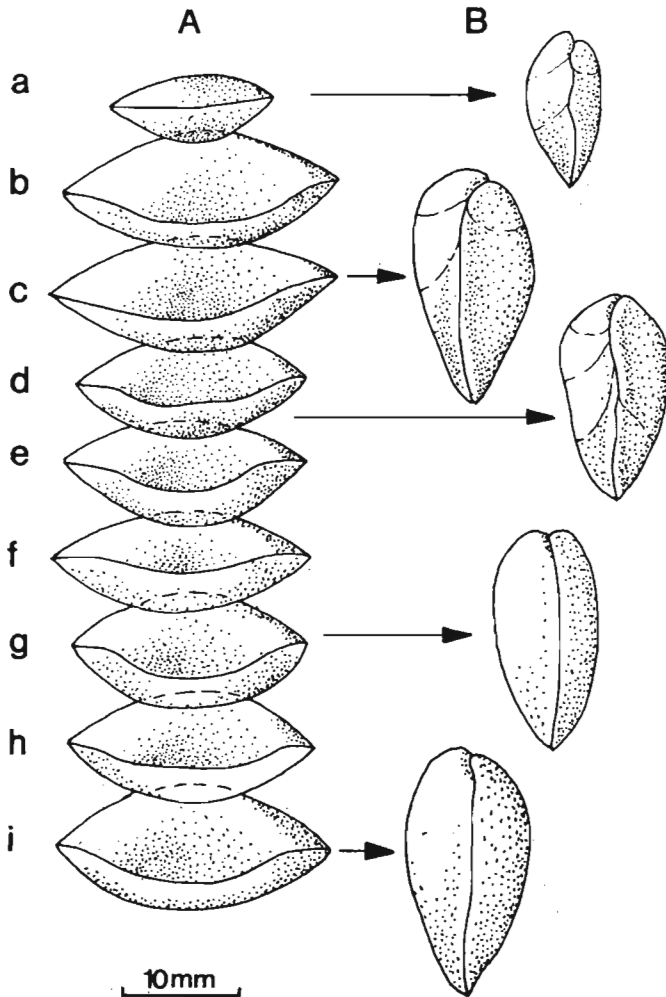


Fig. 6. *Pugnaria plana* gen. et sp. n. Variability of uniplicate specimens from Łgawa Hill Quarry in a anterior commissure and b side views; some variation occurs in the appearance of the uniplication and biconvexity of shells.

layer of the Rhin region (Richter 1856; Weyer 1972). The exteriors are similar, but unfortunately the interior of the Richter form is not known, preventing a more precise taxonomy.

Occurrence.—Poland, Famennian (? do III to do IV or older; Wola Quarry and Łgawa Hill Quarry, Holy Cross Mts.). F. R. G. ? Famennian (do VI) Rhenish Slate Mts.

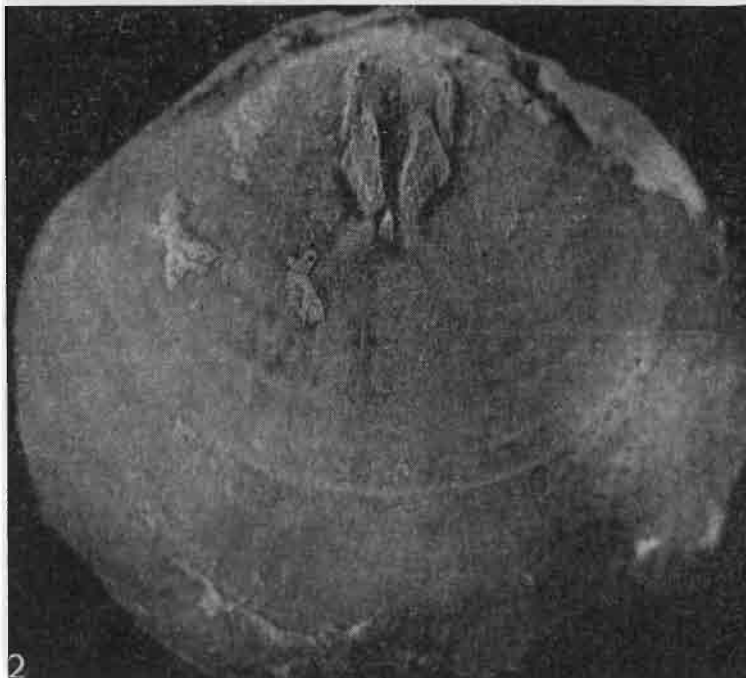
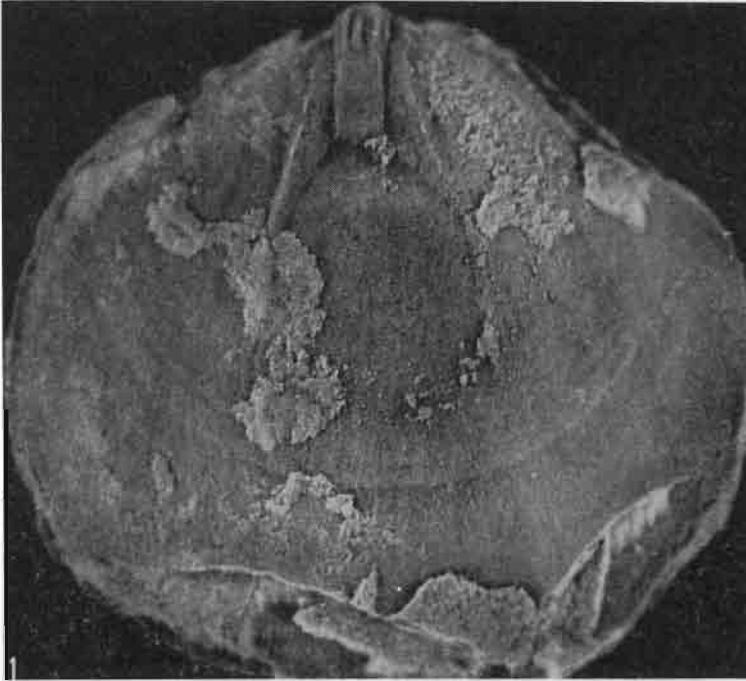
?*Pugnaria* sp.

(pl. 37: 1a–d, 2a–d, pl. 44: 1a–e)

Material.—Five adult shells, articulated, slightly damaged posteriorly and decorticated; one shell has been sectioned. Kowala (Wola Quarry). Approximate dimensions (in mm:)

Specimen No.	length	width	thickness	length/width	length/thickness
ZPAL Bp. XXXI/2	18.8	19.9	0.9	1.0	2.0

Description. — Shell of medium size, subcircular in outline; biconvex, the greatest



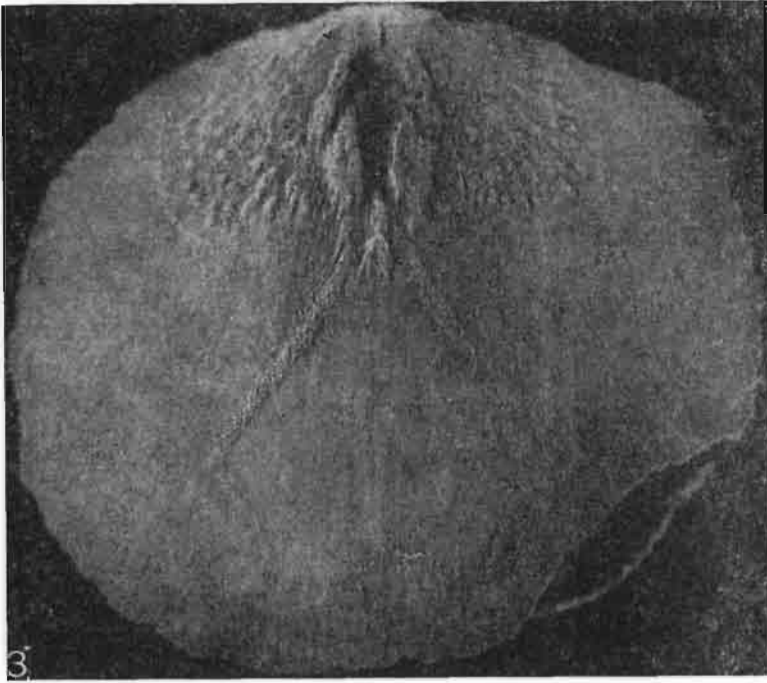


Fig. 7. *Pugnaria plana* gen. et sp. n.: interiors of 1 pedicle and 2 brachial valves of the specimen preserved as a mould, ZPAL Bp. XXXI/37; 3 brachial valve interior (mould) with traces of muscle scars, gonads and pallial sinuses, ZPAL Bp. XXXI/36. All from Lgawa Hill Quarry; $\times 6$.

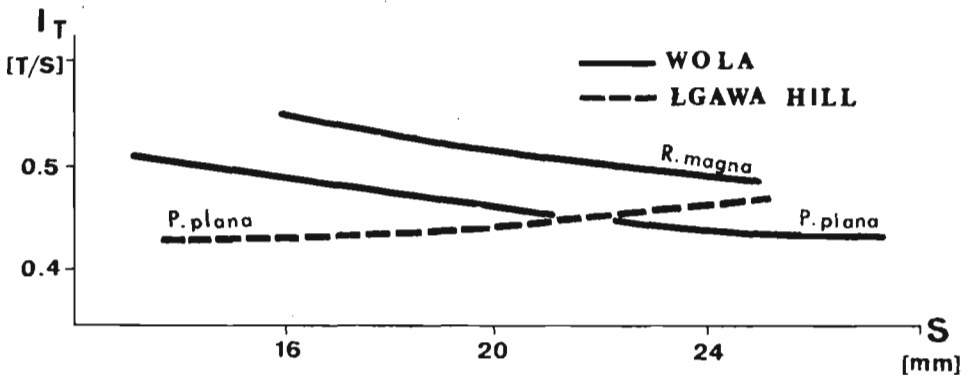


Fig. 8. Correlation between thickness index (I_T) and shell size (S) in *Rozmanaria magna* sp. n. and *Pugnaria plana* gen. et sp. n. from the Wola and Lgawa Hill Quarries; note some differences between the mentioned species reflecting different conditions and mode of the brachiopod growth (cf. Worsley and Broadhurst 1975). See also fig. 5.

convexity of the pedicle valve at about the hinge margin, that of the brachial valve anterior of the hinge; the greatest width at about midlength; lateral margins much arcuate; anterior commissure medially incised, and the front of the shell showing a slight bisulcation (pl. 37: 1ab, 2a-d).

Interior. Pedicle valve: dental plates rudimentary?; muscle field quite strongly marked, as in *Rozmanaria magna* (fig. 4). Brachial valve: dental sockets correspondingly deep; divided hinge plates thin, evenly arcuate; crural bases somewhat thickened, median septum absent.

Remarks.—The specimens are uncertainly placed because of possessing features of both *Rozmanaria magna* and *Pugnaria plana*. Internally they are more like the former in having similar ventral muscle fields and somewhat arcuate hinge plates. External differences in comparison to *R. magna* and *P. plana* are minimal, the main distinguishing feature being the incised anterior commissure and slight median bisulcation (pl. 37: 1c, 2c). Although these features may be very variable the incision and bisulcation appear late in life, much later than the sulcation in *Rozmanaria magna* or uniplication in *P. plana*. Cooper (1983; 27) noted that notches of this sort may be developed instead of sulcation or uniplication.

Genus *Planovatiostrum* Sartenaer, 1970

Type species: Leiorhynchus planoovalis, D. V. Nalivkin, 1937: 76, pl. 12: 12.

Planovatiostrum planoovalis (Nalivkin, 1937)

(pl. 40: 1a—d, 2a—d, 3a—d)

1962. *Pseudoleiorhynchus planoovalis* (Nalivkin) Rozman: 127—129, pl. 17: 1—9, figs 33—34.

?1972. *Plectorhynchella* ? nov. sp. Weyer: 89, pl. 2: 7—8.

Material.—Four specimens, articulated, slightly damaged posteriorly, very flattened. Kowala (Wola Quarry).

Dimensions (in mm):

Specimen No.	length	width	thickness	length/width	length/thickness
ZPAL Bp. XXXI/ 155	13.4	18.6	6.9	0.7	1.9
156	12.9	15.7	6.3	0.7	2.0
157	11.9	15.3	6.2	0.7	1.9

Description.—Shells are transversely oval in outline, much flattened, evenly biconvex; slight radial rib-like undulations, three to four, being confined to the evenly marked dorsal fold and ventral sulcus. Interior not studied.

Remarks.—Although rather rare and insufficiently known, the specimens are assigned to *Planovatiostrum*, principally on account of their exterior, and they are thought to be conspecific with *P. planoovalis* (Nalivkin). They correspond with this species, occurring in the Famennian of Kazakhstan (sulcifer layer) and Mugodzhary (Kurgandzhary layer) (Rozman 1962: pl. 17: 1—9), but differ somewhat in being more flattened and in having a less well pronounced sulcus and fold, and radial ribs. It also resembles the Moroccan *P. undulatus* (G. et H. Termier) from the Famennian (do IV and V) (Drot 1964: pl. 23: 8a—8c, 9a—9c), but differs in the same characteristics as the two former species. These three forms are undoubtedly closely related. It is possible that *Plectorhynchella* sp., from *Wocklumeria* layer, Rhin region, Hön-

netalbahneinschnitt at Oberrödinghausen (Weyer 1972: pl. 2: 7a—d; 8a—e) may belong to *P. planovalis*. The former is smaller, but its posterior edges are acute, its ventral beak protruding a little beyond the dorsal one, and it possesses a few slight, irregular ribs in the dorsal sulcus. Unfortunately, the interior of ?*Plectorhynchella* sp. is unknown so its generic assignment remains unclear.

Occurrence.—USSR, Late Famennian, North-eastern part of Kazachstan (sulcifer layer), Mugodzhary (Kurgandzhary layer). Poland, Famennian (? do III to do IV, Wola Quarry, Holy Cross Mts). F. R. G., Famennian (do VI), Rhenish Slate Mts.

?Planovatiostrum cf. *undulatus* (Termier et Termier, 1950)

(pl. 40: 5a—d)

Material.—One well preserved specimen but with a slightly damaged ventral beak, articulated and somewhat decorticated. Found in the Wola Quarry.

Dimensions (in mm):

Specimen No.	length	width	thickness	radial ribs		
				pedicle v.	brachial v.	v.
ZPAL						
Bp. XXXI/106	19.8	28.2	8.1	3+2+3	2+3+2	

Description.—Medium sized; subtransverse in outline; lateral margins short, circular; anterior commissure with zig-zag deflections; ventral beak slightly elevated; anterior half of shell bearing short but distinct radial ribs. Interior unknown.

Remarks.—The external appearance suggests an affinity of the Holy Cross Mts. shell to the Famennian (do IV and V) species of Drot from Morocco (1964: 169—172, pl. 23: 8a—8c; 9a—9c; fig. 69). The differences are few and concern mainly the radial ribs which are thicker, ?shorter and ? more acute in our form.

Occurrence.—Poland, Famennian (? do III to do IV, Wola Quarry, Holy Cross Mts.).

Family *Cranaenida*, 1942

Genus *Cranaena* Hall et Clarks, 1893

Type species: *Terebratula romingeri* Hall, 1863: 48.

Cranaena lgaviensis sp. n.

(pl. 41: 1—3, pl. 46)

Type specimen: ZPAL Bp. XXXI/20, pl. 41: 2a—c.

Type locality: Łgawa Hill Quarry, Holy Cross Mts.

Type horizon: Famennian (? do III to do IV)—velifer zone.

Derivation of name: coming from the Łgawa Hill Quarry.

Diagnosis.—Smooth, medium sized, suboval in outline; ventral beak of moderate height; cardinal plate distinctly concave medially.

Material.—Twenty five specimens, articulated, much decorticated, and with damaged ventral breaks; three shells from Wola Hill Quarry, twenty two from Łgawa Hill Quarry.

Dimensions (in mm):

Specimen No.	length	width	thickness	length/width	length/thickness
ZPAL Bp. XXXI/					
58	17.2	11.2	7.6	1.5	2.1
10	12.9	6.4	6.2	2.0	2.0
20	18.4	15.3	8.8	1.2	2.0
26	19.9	16.0	10.3	1.2	2.0

Description.— Shell of medium size, subequally biconvex; suboval to oval in outline with the greatest width at about midlength of shell; lateral margins well arched, anteriorly convergent, anterior commissure straight to somewhat undulate?, cardinal margin terebratulid; ventral beak of moderate length, suberect; ventral palintrope indistinct; deltidial plates conjunct.

Interior (pl. 46). Pedicle valve: Dental plates straight and almost parallel, hinge teeth elongate, no median septum. Brachial valve: Cardinal plate free, perforate, medially deeply dorsally concave (? acutely); dental sockets comparatively wide and shallow; crural bases as short ridges discernible on both surfaces of the cardinal plate (pl. 46: *g*, *h*) and merging into short crura; loop shorter than half of the valve length; median septum absent.

Remarks.— The species appears to be much like *Cranaena* aff. *C. romingeri* (Hall) from the Potter Farm formation, Traverse group of Alpena County, Michigan (Cloud 1942: pl. 24: 13). However, this similarity concerns only the shell outline and moderate-ventral beak; the interior is insufficiently known. In comparison with *C. schucherti* Cloud, the German species from the Frasnian Iberg limestone, Harz (Cloud 1942: pl. 24: 1) our form differs in being much wider with lateral margins distinctly arched (comp. pl.: 1a, 2a, 3a), just like *C.* aff. *C. lincklaeni* (Hall) from the Hamilton group, New York (Cloud 1942: pl. 24: 20).

Occurrence.— Poland, Famennian (? do III to do IV, Łgawa Hill Quarry and Wola Quarry, Holy Cross Mts.).

REMARKS ON ECOLOGY

These Late Famennian brachiopods came from the thick, rhythmically-bedded marly series of the Kowala-Bolechowice area (fig. 1). As a matter of fact they represent a rare example of a richer benthos in this, generally non-fossiliferous, pelagic strata. According to Szulczewski (1971: 105) "the profile of Kowala corresponds to the deepest part of the Marly Facies, located below the photic zone". A deeper-water aspect of this brachiopod biotope is also shown by its biofacies setting, i.e. an association of various pelagic groups, chiefly planktic entomozoid ostracods and *Palmatolepis*-dominated conodont faunas. Recent analysis of this common Famennian deposit indicates a depth of a few hundred metres (Krebs 1979; Franke and Walliser 1983).

Sulcate *Rozmanaria magna* sp. n. is a predominant element (up to 60%) of the Wola Quarry collection that also contains seven other taxa. Some clear changes, both in the assemblage composition and in the morphology of particular forms, can be distinguished along the southern limb of the Gałęzice syncline. The collection from the Łgawa Hill Quarry is characterized by a rather high dominance (almost 70%) of uniplicate *Pugnaria plana* sp. n., as well as a relative richness of cranaenids (*Cranaena*

lgaviensis sp. n.). In this locality *P. plana* is smaller, thinner-shelled (with many "juvenile" shells), more elongate and comparatively flatter (figs. 5, 8) than those at Wola Quarry. These variations are presumably records of slight habitat differences, undetectable from the litho-facies, may be exclusively due to the weak, up to now, recognition of the Łgawa Hill section (see Racki and Zapaśnik 1979).

These biotope changes are explained by shallower-water facies (with more numerous cephalopods) in the Łgawa Hill area, i.e. in closer proximity to the submarine rise (Kielce facies region, Szulczewski 1977, 1981) marked by strongly condensed, fossiliferous (cephalopod-rich) limestones (Multifossiliferous Facies of Szulczewski 1971). As can be seen from its geographical situation, the Łgawa Hill section lies only about 1 km south of the nearest condensed sequence (Bolechowice — 1 borehole), whereas basin facies occur further north of the Wola Quarry (e.g. Kowala — 1 borehole), and nearest locality (Trzuskawica Quarry) of Kielce facies, situated 2 km to the NE (fig. 1B).

This hypothetical concept agree well with the brachiopods data. The faunas of the condensed Famennian sequences in the Holy Cross Mts. are very poorly known. However, literature data (Sobolev 1912; Czarnocki 1916; Zakowa 1967; Biernat 1983) and the observations of the author indicate their impoverished (quantitatively) nature and dominance of small rhynchonellids including *Rozmanaria equitans* Schmidt) (and *R. magna* np. sp.), as well as noting their greater diversity. Czarnocki (1916) listed in addition from Gałęzice some orthids, productellids, cyrtospiriferids, athyrids and smooth "atrypids". It is notable, that in the Late Famennian cephalopod facies of Rhenish, Thuringian and the Ural Mts. there occur also low diversity faunas of small rhynchonellid-dominated associations (Weyer 1972) characterized by *Planovatirostrum*, and the rarer *Rozmanaria equitans* (Schmidt) (see also Rozman 1962).

In conclusion, rather low-diversity macrobenthic assemblages with significant number of sulcate rhynchonellids, called here the *Rozmanaria magna* assemblage, is considered to flourish in the deeper-waters typical of the Chęciny-Zbrza intrashelf basin (cf. Szulczewski 1977, 1981), i.e. in habitats on the rising slope of the submarine ridge. The westernward shallowing resulted in a reduction in the brachiopod habitats, as is shown by the above mentioned differentiation of the *Pugnaria plana* populations. The gradual exclusion of the sulcate *R. magna* is conspicuous, although the geographical co-occurrence of uniplicate and sulcate rhynchonellids is rather unusual, especially in the light of data from the European Pliensbachian suggesting that they are mutually exclusive (Ager 1963: 101, and others).

Thus rhynchonellid sulcation may be a phenomenon linked with deeper-water biotopes, as has already been emphasized by, for example, Ager (1963, 1965), Vogel (1980) and Zezina (1985) (see also Cooper 1972).

It is suggested that the sulcate forms could live with their brachial valves down, so that the sulcation, together with a tendency for the shell to develop lateral lobes like the Mesozoic *Nucleata* (Ager 1965), gave an advantage in raising the median exhalant current above the sea floor (Ager 1965; Fürsich and Hurst 1974; Vogel 1980). The biomicritic, pyritiferous and marly rock matrices containing these fossils, together with bioturbation, are representative of soft, muddy substrates and very weak to stagnant hydrodynamic conditions. In such conditions an efficient separation of feeding currents was of primary importance for these brachiopods. Furthermore, quite intensive muscle activity might be deduced from the comparatively large and deeply impressed muscle scars. These characteristics seem to imply frequent shell openings for collecting food and respiration, activities which were probably of vital importance in resource-poor habitats.

A reduction in the size of the pedicle foramen during shell growth indicates a tendency, typical of many Palaeozoic rhynchonellids, towards a free-lying habit (e.g. Ivanova 1962), but even most adult specimens in this study display an aperture possibly for a thin pedicle. Thickened umbonal areas of the shell and a somewhat laterally expanded hinge margin in *Rozmanaria magna*, assisted in retaining a posterior downwards growth position, tethered upstream by the pedicle; much as in the Recent deep-water rhynchonellid *Cryptopora* (Curry 1983). Relative flattening during growth (fig. 8) of shells occurred in both the sulcate and in the uniplicate to medially incised species. Also the rather moderate biconvexity of the remaining species is another indication of soft-bottom conditions at the Wola Quarry area (cf. Walker 1974). These rather atypical conditions for brachiopods seem to be lost in the case of the Łgawa Hill assemblage, which perhaps lived on a firmer bottom.

The density of occurrences of specimens is rather low (up to one specimen per dcm^2) and there is no evidence for a gregarious mode of life for the rhynchonellids studied.

The comparatively large size of *Rozmanaria magna*, as compared to the other species of the genus, supposedly living in shallower-water, is surprising for a deep-water context. Although suggestive of a sufficient food supply, it is believed, on the contrary, as an indication of the good adaptation of these brachiopods, which lived in unfavourable conditions of very quiet and food-poor waters. This interpretation is partly supported by the more rapid attainment of maturity, as compared with *Pugnaria plana* (fig. 6). On the other hand, such deeper-water biotope appears to be distinctly expressed in the general shell morphology of these Famennian brachiopods (see Ager 1965, Fürsich and Hurst 1974; Vogel 1980) as well as by some degree of homeomorphy for uniplicate and sulcate species in the Wola assemblage. Homeomorphy is well documented for several deep-water Recent (Cooper 1972, 1980) and fossil (Ager 1965; Cooper 1983) brachiopods.

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GERTRUDA BIERNAT i GRZEGORZ RACKI

PÓZNOFAMEŃSKI, ZDOMINOWANY PRZEZ RHYNCHONELLIDA
ZESPÓŁ RAMIENIONOGÓW Z GÓR ŚWIĘTOKRZYSKICH*Streszczenie*

Późnofameńskie ramienionogi Gór Świętokrzyskich są niezbyt liczne i stosunkowo słabo poznane. W niniejszej pracy po raz pierwszy opisano ramienionogi późnofameńskie (? do III—IV) z synkliny gałęzickiej (głównie rejon Kowala—Bolechowice; fig. 1—8, pl. 35—46. Opracowana kolekcja jest liczna (220 okazów) a zespół zróżnicowany taksonomicznie. Udokumentowano występowanie sześciu taksonów należących do dwóch rodzin, Rhynchonellidae i Cranaenidae, przy czym zaproponowano jeden nowy rodzaj *Pugnaria*, i trzy nowe gatunki: *Rozmanaria magna*, *Pugnaria plana* i *Cranaena lgaviensis*.

Zdecydowanie dominującymi elementami opisanej fauny są gładkie i stosunkowo duże rynchonellidy o zmiennie wykształconym fałdzie brzegu przedniego, *R. magna* (sinus w skorupce grzbietowej!) i *P. plana* (sinus w skorupce brzusznej). Występowanie form „prześciowych” tj. o prostym brzegu przednim (*Pugnaria* (?) sp.) świadczy, że sposobowi wykształcenia fałdu przedniego nie można przypisywać dużej wartości taksonomicznej.

Opisana fauna została zinterpretowana jako zespół makrobentosu (zespół *Rozmanaria magna*) sukcesywnie zasiedlający stosunkowo głębokomorskie biotopy typowe dla chęcińsko-zbrzańskiego basenu wewnątrzszelfowego. W miarę spłylenia się basenu ku zachodowi, na skłonie podmorskiego grzbietu należącego do regionu kieleckiego, następowało pogarszanie się warunków rozwoju ramienionogów, wyrażone m.in. ich mniejszymi frekwencjami i spadkiem średniej wielkości skoruppek.

EXPLANATION OF PLATES 35—46

(a — brachial valve view, b — side view, c — anterior commissure view, d — pedicle valve view, e — umbonal part view)

Plate 35

1—5. *Rozmanaria magna* sp. n. variability of the shell outline, shell biconvexity and appearance of the anterior commissure in adult specimens from Wola Quarry: ZPAL Bp. XXXI/156; ZPAL Bp. XXXI/50; ZPAL Bp. XXXI/66; ZPAL Bp. XXXI/56; ZPAL Bp. XXXI/54 (holotype); $\times 2$.

Plate 36

- 1—5. *Rozmanaria magna* sp. n.: specimens from Wola Quarry: ZPAL Bp. XXXI/67; ZPAL Bp. XXXI/85; ZPAL Bp. XXXI/104; ZPAL Bp. XXXI/95 and from Łgawa Hill Quarry: ZPAL Bp. XXXI/82; specimens 2—5 slightly asymmetrical; $\times 2$.

Plate 37

- 1—2. ?*Pugnaria* sp.: traceable bisulcation at the anterior commissure of adult specimens from Wola Quarry: ZPAL Bp. XXXI/2, ZPAL Bp. XXXI/158; $\times 2$.
 3—5. *Rozmanaria magna* sp. n.: variability in shell size and appearance of the anterior commissure of adult shells from Wola Quarry: ZPAL Bp. XXXI/16; ZPAL Bp. XXXI/24; ZPAL Bp. XXXI/103; $\times 2$.

Plate 38

- 1—4. *Pugnaria plana* gen. et sp. n.: variability in shell size and outline of specimens from Wola Quarry: ZPAL Bp. XXXI/112; ZPAL Bp. XXXI/113; ZPAL Bp. XXXI/108 (holotype); ZPAL Bp. XXXI/110; $\times 2$.

Plate 39

- 1—4. *Pugnaria plana* gen. et sp. n.: variability in shell outline and appearance of the anterior commissure of 1, 2, 4 adult specimens from Łgawa Hill Quarry: ZPAL Bp. XXXI/80; ZPAL Bp. XXXI/81; ZPAL Bp. XXXI/89; and 3 adult shell from Wola Quarry, ZPAL Bp. XXXI/115; $\times 2$.

Plate 40

- 1—3. *Planovatiostrum planovalis* (Nalivkin, 1937): specimens from Wola Quarry: ZPAL Bp. XXXI/157; ZPAL Bp. XXXI/155; ZPAL Bp. XXXI/159; 3 a mould presenting traces of the dorsal (3a) and ventral (3d) muscle scars; $\times 2$.
 4. A mould of an unidentified rhynchonellid (from Wola Quarry) resembling *Eoparaphorhynchus*: ZPAL Bp. XXXI/160; $\times 2$.
 5. ?*Planovatiostrum* cf. *undulatus* (Termier et Termier, 1950): incomplete and exfoliated adult shell from Wola Quarry: ZPAL Bp. XXXI/106; $\times 2$.

Plate 41

- 1—3. *Cranaena lgaviensis* sp. n.: adult shells from Łgawa Hill Quarry: ZPAL Bp. XXXI/10; ZPAL Bp. XXXI/26; ZPAL Bp. XXXI/20; 3 holotype; all slightly damaged including ventral beak; $\times 2$.
 4. *Rozmanaria magna* sp. n.: adult specimen of asymmetrical outline from Wola Quarry: ZPAL Bp. XXXI/10; $\times 2$.

Plate 42

- 1a—1g. *Rozmanaria magna* sp. n.: cross sections of adult specimen, badly recrystallized from Wola Quarry, 18.4 mm long and 22.9 mm wide: ZPAL Bp. XXXI/145; crural bases and crura showed; \times approx. 7.

Plate 43

1. *Rozmanaria magna* sp. n.: a—h cross sections of adult shell from Wola Quarry, 17.4 mm long and 24.0 mm wide: ZPAL Bp. XXXI/146; teeth, dental sockets, crural bases and crura preserved; \times approx. 7.

Plate 44

1. ?*Pugnaria* sp.: a—e cross sections of adult shell from Wola Quarry, 17.5 mm long and 16.9 mm wide: ZPAL Bp. XXXI/121; crural bases preserved; \times approx. 7.
2. *Pugnaria plana* sp. n.: a—g cross sections of adult shell from Wola Quarry, 22.6 mm long and 24.0 mm wide: ZPAL Bp. XXXI/107; thin crura present; \times approx. 7 (continued in Pl. 45).

Plate 45

- Pugnaria plana* sp. n.: h—k continued from plate of cross sections showing crura; ZPAL Bp. XXXI/107; \times approx. 7.

Plate 46

- Cranaena lgaviensis* sp. n.: a—i cross sections of adult specimen from Egawa Hill Quarry: ZPAL Bp. XXXI/30; preserved dental plates, cardinal plate free; \times approx. 7.
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