Title: The late Frasnian rhynchonellid genus Pammegetherhynchus (Brachiopoda) in Poland, and its relevance to the Kellwasser Crisis

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The late Frasnian rhynchonellid genus *Pammegetherhynchus* (Brachiopoda) in Poland, and its relevance to the Kellwasser Crisis

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The rhynchonellid species, *Pammegetherhynchus kowalaensis* sp. n., occurs in the late Frasnian (Early to Late *Palmatolepis rhenana*, and possibly early *Palmatolepis linguiformis* conodont zones) marly-bituminous succession at Kowala (various outcrops) in the Gałęzice Syncline, south of Kielce in the Holy Cross Mountains, Poland. The only other known species of this genus is the type species, *Pammegetherhynchus merodae* Sartenaer, 1977, from the late Frasnian (somewhere in the Early and Late *Palmatolepis rhenana* Zones) of the French Fagne (dark shales of 'Matagne' aspect), and, probably, of the Eifel ('Büdesheimer Goniatitenschiefer'). *P. kowalaensis* sp. n. occurred in level-bottom pioneer assemblages, thriving in reef downslope, mostly poorly-oxygenated habitats of the Kellwasser interval. The species finally disappeared near the Frasnian-Famennian boundary. The genus *Pammegetherhynchus* seems to be particularly suited to stressed deep-water shelf environments in the European part of the Laurussian shelf, widely distributed in this crisis time.

Key words: Brachiopoda, Rhynchonellida, taxonomy, biostratigraphy, palaeoecology, mass-extinction, Kellwasser Crisis, Frasnian, Devonian, Poland.

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Introduction

Pammegetherhynchus merodae Sartenaer, 1977, the type species of the genus *Pammegetherhynchus* Sartenaer, 1977, was until recently the sole representative of the genus. Therefore, it is useful to describe a second and closely related species from the southern Holy Cross Mountains, Central Poland (Fig. 1), collected by the authors between 1968 and 1995. The new species was first mentioned by Sartenaer (1977: pp. 67, 68, 74),

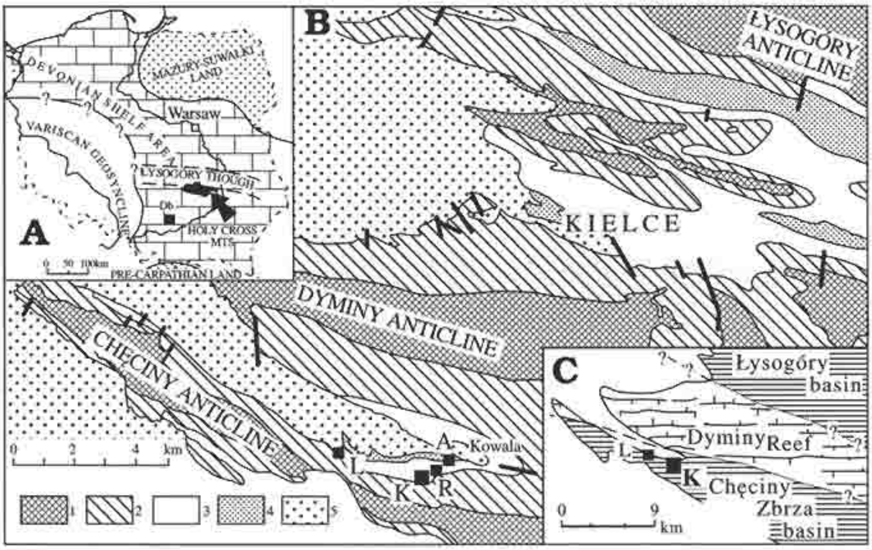

Fig. 1. Paleogeographic scheme of the Frasnian in Poland (**A**); Db – Dębnik area near Cracow, LJ – Łagów-Janczyce area in the eastern Holy Cross Mountains, and geological sketch map of the western part of the Holy Cross Mountains to show location of sites of *Pammegetherhynchus kowalaensis* sp. n. (**B**), and Frasnian facies pattern of the Holy Cross Mountains (**C**); after Racki *et al.* (1993: fig. 1, modified). L – Jaźwica quarry (Łgawa Hill), K – Kowala road cut, R – Kowala railroad cut, A – Kowala quarry; 1 – Cambrian–Silurian, 2 – Lower–Middle Devonian, 3 – Upper Devonian, 4 – Lower Carboniferous, 5 – Permian–Mesozoic cover.

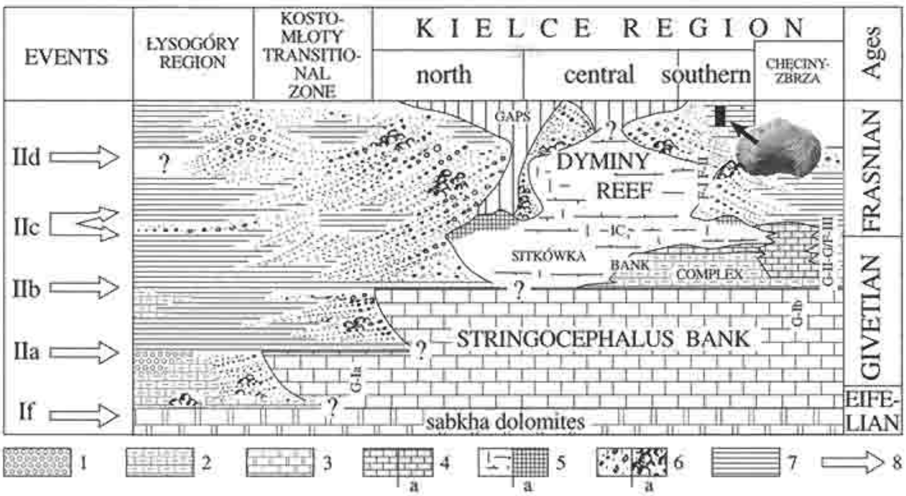

Fig. 2. Position of the rhynchonellid-bearing deposits under study (arrowed) against developmental stages of the Devonian bank-to-reef complex of the Holy Cross Mountains; stratigraphic-facies cross-section (after Racki 1993a: fig. 3, modified) shows eustatic rhythmic control of the depositional pattern; Ie–IId – transgressive-regressive cycles modified from Johnson *et al.* (1985), G-Ia to F-II – regional sedimentary units (Racki 1993a). 1 – siliciclastics; 2 – marls and limestones; 3 – dolomites (secondary dolomitisation omitted); 4 – biostromal bank facies (a – intershoal facies); 5 – reef facies (a – Kadzielnia-type bioherms); 6 – carbonate slope facies (a – organic buildups); 7 – marly limestones and shales (basin facies); 8 – main transgressive events; 9 – synsedimentary tectonic episodes.

and then by various authors (see 'Comments of synonymy'), including Sartenaer (1985: p. 320, fig. 1 *pro parte*, p. 322) and Mikłas (in Racki *et al.* 1993: p. 69). This locally abundant species has been known for some time in the Polish literature under the names *Liorhynchus rhomboideus*(?) (Phillips, 1836) by Sobolev (1909a: pp. 219, 221, not p. 223 as *L. rhomboideus*, not p. 367 as *L.* aff. *rhomboideus*), ?*Rhynchonella acuminata* Mart. by Sobolev (1909b: p. 91) and *Calvinaria* cf. *albertensis* (Warren, 1928) by Filonowicz (1973).

Knowledge of late Frasnian brachiopod faunas in the Holy Cross Mountains is still poor, with the exception of gypidulids (Godefroid & Racki 1990), athyridids (e.g., Baliński 1995), and atrypids (Racki & Baliński 1998). *Pammegetherhynchus kowalaensis* sp. n. is characteristic of a late Frasnian decline episode in the Middle–Late Devonian, when backstepping bank-to-reef changes were occurring (Fig. 2). An accurate estimation of the stratigraphic range of the species has some significance in discussions of the record of the hypoxic Kellwasser Events and faunal characters of the Frasnian-Famennian (F–F) crisis in this part of the Laurussian shelf (see Fig. 1A).

Institutional abbreviation: IGP – Institut of Geology of the University of Warsaw.

Other abbreviations: l – length of the pedicle valve, w – width of the shell, t – thickness of the shell, bv – brachial valve, pv – pedicle valve.

Systematic palaeontology

(P. SARTENAER)

The material (490 well preserved specimens) is stored in the University of Warsaw (Szulczewski's collection, containing the holotype and paratypes), Silesian University at Sosnowiec and in the Institute Royal des Sciences Naturelles de Belgique in Brussels.

Genus *Pammegetherhynchus* Sartenaer, 1977

Type species: *Pammegetherhynchus merodae* Sartenaer, 1977; late Frasnian, shales of 'Matagne' aspect, Ardennes, Dinant Basin, France

Remarks. — As a result of the assignment of the new species from the Holy Cross Mountains to *Pammegetherhynchus*, two slight modifications have to be introduced in the definition of the genus: 'median costae exceptionally present; lateral costae absent' must be replaced by: 'median costae either exceptionally or commonly (around 50% of the specimens) present; lateral costae absent or exceptionally present'.

Pammegetherhynchus kowalaensis sp. n.

Figs 3A–T, 4A–Y and 5.

non *Pammegetherhynchus*; Mikłas in Racki *et al.* 1993: pl. 2: 1, 3, p. 73, pl. 5: 1, 2, 3a–c, 4a–c, 6a–b, 10.
Pammegetherhynchus sp. A; Mikłas in Racki *et al.* 1993: pl. 2: 2, p. 70, pl. 5:5a–b, 7a–b, 8a–b, 9a–b.

Holotype: IGP/S-1, complete shell, illustrated in Fig. 3K–O.

Type locality: Road section at about 300 m west of the railroad cut of the Kielce-Busko line at Kowala (Fig. 1B).

Type horizon: Dark to black (weathering grey and greyish-reddish to greyish-yellowish) bedded to subnodular marly limestones and shales, and mostly fine-grained detrital deposits with brachiopod shell clumps and coquinite intercalations (= upper part of set III and basal part of set IV in Mikłas (in Racki *et al.* 1993: pp. 68–73); Late *Palmatolepis rhenana* Zone (see Szulczewski 1990: p. 332).

Derivation of the name: From Kowala, locality in the Gałęzice Syncline, Holy Cross Mountains, Poland.

Diagnosis. — *Pammegetherhynchus kowalaensis* sp. n. differs from *P. merodae*, the only other species of the genus, in having a smaller shell size (only few specimens of *P. kowalaensis* reach the size of specimens of *P. merodae*) and a smaller shell thickness, lower tongue, and more frequently present median costae.

Material. — The 490 specimens comprise 272 specimens in a good state, 105 in a satisfactory state of preservation, and 113 specimens that are fragmentary.

Dimensions. — Dimensions of eleven specimens, of which nine are photographed, are given on Table 1 (columns 1–8 are adult specimens, columns 9–10 are ephebic, and column 11 is a juvenile).

Width is clearly the largest dimension. Maximum width of shell occurs at a point between 53 and 67% of the length of shell anterior to the ventral beak. Length and thickness have similar values. Greatest thickness of the shell is at the front. The wide apical angle varies from 123 to 136°.

Table 1. Measurements (in mm) of eleven specimens of *Pammegetherhynchus kowalaensis* sp. n. Abbreviations: l – tength, t – thickness, w – width, bv – brachial valve, pv – pedicle valve. Measurements shown in parentheses indicate a reasonable estimate on a damaged specimen.

in mm	IGP/ S-2	IGP/ S-3	IGP/ S-4	IGP/ S-1	IGP/ S-5	IGP/ S-7	IGP/ S-8	IGP/ S-6	IGP/ S-9	IGP/ S-10	IGP/ S-11
l	19.6	19.1	17.9	17.6	16.9	16.2	16.1	15.5	14.8	14.2	11.4
w	24.8	23.6	24.9	23.7	22.8	22.6	21.6	23.3	19.6	18.8	15
lpv unrolled	35.5	33	32.5	30	32	27.5	26	30.5	24	25	18
t	19.7	17.4	17.9	17.7	17.2	15.5	14.6	18.1	14.3	12.9	8.5
tpv	5.5	6.1	5.2	5.2	5.6	5.2	6.2	4.7	4.5	4.6	2.5
tbv	14.2	11.3	12.7	12.5	11.6	10.3	8.4	13.4	9.8	8.3	6
l/w	0.79	0.81	0.72	0.74	0.74	0.72	0.75	0.67	0.76	0.76	0.76
t/w	0.79	0.74	0.72	0.75	0.75	0.69	0.68	0.78	0.73	0.69	0.57
t/l	1	0.91	1	1	1.01	0.96	0.91	1.17	0.97	0.91	0.75
apical angle	123°	124°	136°	134°	133°	134°	129°	136°	127°	126°	126°

Description. — Front margin uniplicate. Strongly inequivalve, the brachial valve being clearly higher than the pedicle valve. Contour of shell, in ventral view, is an irregular pentagon with rounded angles, deeply depressed by the sulcus. Commissure sharp. Lateral commissures are very rarely undulated by costae which are almost always absent. Top of shell coincides with top of tongue. Valves convexo-concave near postero-lateral commissures. Cardinal line short. Inflated umbonal regions. Dorsal flanks steep.

Contour of pedicle valve is an half-ellipse or even half-circumference in longitudinal median sections, and a very flat half-ellipse depressed by the sulcus in transverse median sections. Flanks regularly convex, but slope is more abrupt in the postero-lateral region. Sulcus beginning imperceptibly at a distance from the beak varying between 26 and 50 % of the length of the shell, or between 23 and 36% of the unrolled length of the valve. Sulcus, which is already wide at point of origin, widens anteriorly either progressively and rapidly or considerably in its posterior part and minimally in its anterior part; in the latter case the contour of the depression of the sulcus has a horseshoe shape. Sulcus reaches its maximum width, which is large (60 to 85% of width of shell), at junction of frontal and lateral commissures. Bottom of sulcus is either flat or slightly concave, rarely slightly convex. Sulcus deep at front, and, although its borders are rounded, it is clearly separated from the flanks, with which it forms, in most specimens, a right angle in its anterior part. Tongue with sharp

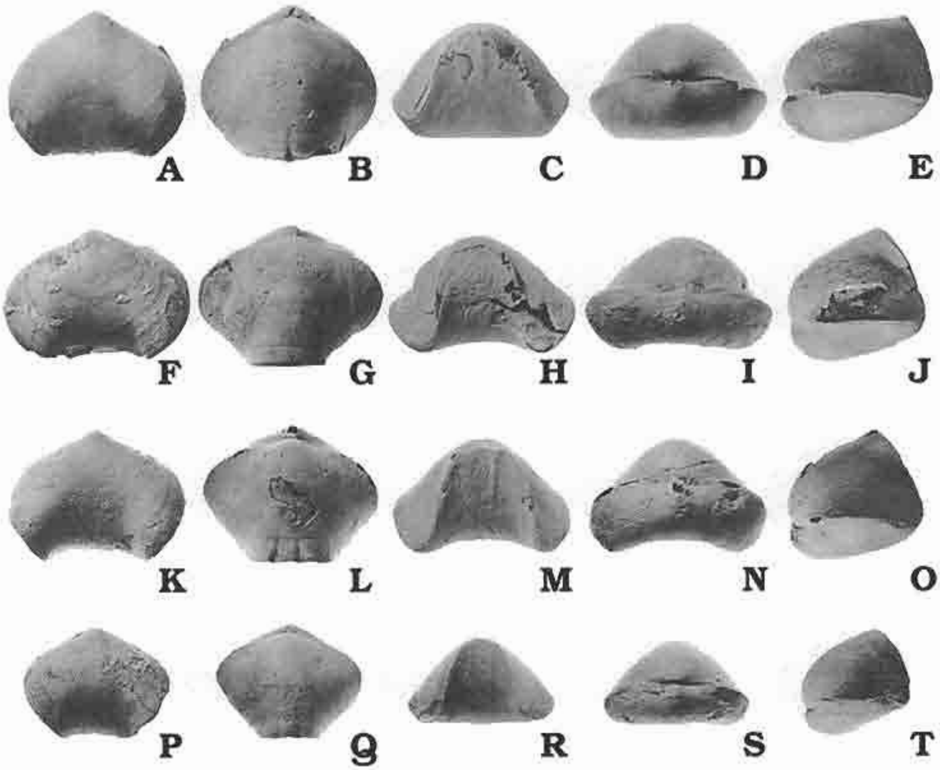

Fig. 3. *Pammegetherhynchus kowalaensis* sp. n. from road cut at Kowala (late Frasnian), Holy Cross Mountains, Poland. Ventral, dorsal, frontal, apical, and lateral views. **A–E**. IGP/S-3; costal formula: 2/1; 0; 0; see also Fig. 5. **F–J**. IGP/S-4; costal formula: 0; 0; 0. **K–O**. Holotype IGP/S-1; costal formula: 3/2; 0; 0. P–T, IGP/S-9; costal formula: 3/2; 0; 0. All figures are natural size.

borders, always standing out clearly. Top of tongue forming an elliptical arch, and exceptionally an ogival one. Upper part of tongue almost always more or less recurved posteriorly, and, exceptionally, tangent to a vertical plane. Top of valve located at a point between 20 and 30% of the length of the shell anterior to the beak. Beak small, erect to slightly incurved, sometimes strongly incurved. The beak comes often close to the brachial valve, and sometimes is applied on it; therefore, the foramen has not been observed in any specimen. Ventral interarea long (43 to 60% of width of shell), concave, usually around one millimetre high, and generally poorly delimited. Deltidial plates may be observed in transverse serial sections. Flanks are narrow and at the same level as the umbonal region in their posterior part, but their borders are more or less steep.

Brachial valve moderately high to high. Curve of the valve is one quarter of an ellipse or one quarter of a circumference, sometimes inflected in its posterior part, in longitudinal median sections. Contour is an half-ellipse in transverse median sections. Flanks slope steeply towards commissure and are generally separated from the fold, in the anterior part of the shell, by a clear inflexion, which is sometimes feeble or even absent. The inflated umbonal region generally extending slightly posteriorly beyond pedicle beak. Height of valve increases uninterruptedly in direction of front. Fold high with arched elliptical (exceptionally ogival) top in its anterior part; it begins imperceptibly at a variable distance from the beak.

Shell costellate. Costae low, wide, simple, blunt, and restricted to the most anterior part of the shell. The general costal formula, which is a grouping of at least 75% of the specimens in median, parietal and lateral categories, is: 0-3/0-3; 0; 0. In 321 specimens in which median costae could be

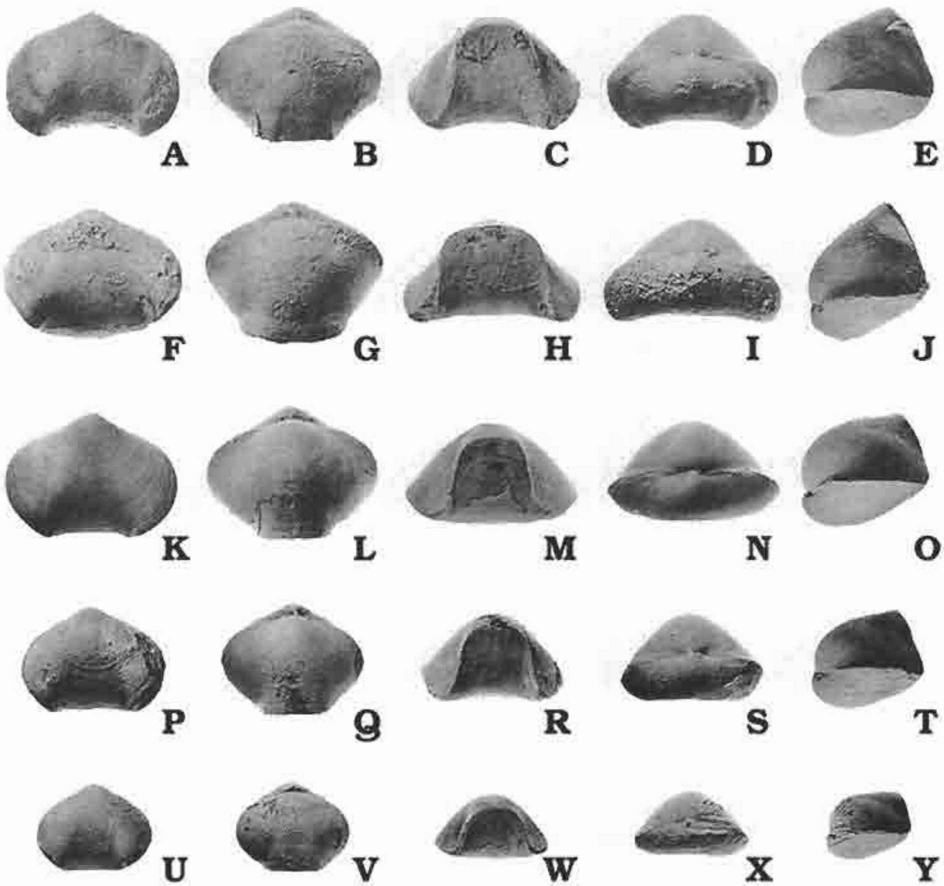

Fig. 4. *Pammegetherhynchus kowalaensis* sp. n. from road cut at Kowala (late Frasnian), Holy Cross Mountains, Poland. Ventral, dorsal, frontal, apical, and lateral views. **A–E**. IGP/S-5; costal formula: 3/2; 0; 0. **F–J**. IGP/S-6; costal formula: 0; 0; 0. K–O, IGP/S-7; costal formula: 3/2; 0; 0. **P–T**. IGP/S-10; costal formula: 0; 0; 0. **U–Y**. IGP/S-11; costal formula: 3/2; 0; 0. All figures are natural size.

counted, the distribution is as follows: 0: 171 sp. (53%); 2/1: 51 sp. (16%); 3/2: 64 sp. (20%); 4/3: 32 sp. (10%); 5/4: 2 sp. (0.65%); 6/5: 1 sp. (0.35%). Lateral costae have been observed in 7 specimens: 1/2: 1 sp.; 2/3: 4 sp.; 3/4: 1 sp.; 2/3 on one side and 4/5 on the other: 1 sp. No parietal costae.

Surface covered with costellae, 7 to 9 per mm at front; they are separated by striae approximately equivalent to 1/5th to 1/6th their width. Costellae are commonly divided. Growth lines are commonly observable.

The characteristic internal features of the genus can easily be recognized on Fig. 6, among others: thick dental plates, short and stout teeth, no septum, no septalium, thick hinge plates, stout and relatively long crura.

Comments of synonymy. — This species of *Pammegetherhynchus* has not been found in coeval strata at Łgawa Hill (= eastern Jaźwica) near Bolechowice in the same syncline, as supposed earlier by Racki (1981: p. 174 *pro parte*), Rigby *et al.* (1981: p. 165), Racki *et al.* (1989: fig. 2, p. 548 *pro parte*), Racki (1990: p. 177 *pro parte*), Godefroid & Racki (1990, pp. 47, 64), Mikłas (in Racki *et al.* 1993: table 1, p. 72 *pro parte*), Racki *et al.* (1993: p. 89 *pro parte*, p. 90 *pro parte*, p. 91 *pro parte*, fig. 14, p. 94 *pro parte*) and Racki (in Racki *et al.* 1993: p. 100 *pro parte*). The abundant specimens

Fig. 5. *Pammegetherhynchus kowalaensis* sp. n. IGP/S-3; fine radial striation (× 6) on tongue of specimen figured on Fig. 3A–E.

from the Łgawa Hill locality belong to a new genus, characterized by a smaller size, a more transverse outline, and a still more invaginated sulcus, starting nearer to the beak (Sartenaer & Racki in preparation).

Comparisons. — More detailed comparison of both species of *Pammegetherhynchus* shows that smaller-sized *P. kowalaensis* sp. n. has a less developed tongue and fold on account of a proportionally smaller thickness as indicated by the t/w [0.68 to 0.79 (0.75 for holotype) for *P. kowalaensis*, 0.70 to 0.92 (0.92 for holotype) for *P. merodae*] and t/l [0.91 to 1.17, most values between 0.91 and 1.01 (1 for holotype) for *P. kowalaensis*, 0.90 to 1.24 (1.24 for holotype) for *P. merodae*] ratios; top of tongue forming almost always an elliptical arch (in *P. merodae* the arch is elliptical in 71% of specimens, and ogival in 29%), this arch being commonly flattened; median costae present in almost 50% of specimens (they are usually absent in *P. merodae*); lateral costae extremely rarely present (they are never present in *P. merodae*).

Geographical location and stratigraphical position. — Three localities in the Holy Cross Mountains in the eastern part of the Gałęzice Syncline near Kowala within a radius of 1 km (Fig. 1B; for details see Racki 1993a: pp. 177–179): (1) railroad cut of the Kielce-Busko line at Kowala in the uppermost part of set H in Szulczewski (1971: fig. 5, p. 75 = unit H-2b in the present sense; see Fig. 7); (2) road section at about 300 m west of this railroad cut in the upper part of set III and in the basal part of set IV in Mikłas (in Racki *et al*. 1993: p. 70); (3) eastern wall of Kowala (formerly Wola) quarry south of Kowala in equivalents of set H in Szulczewski (1971: p. 75, pl. 33: 1); in Units I and II in Racki (1993b,: fig. 3, p. 7, p. 8; = units H-2a–H-2b in the present sense, see Fig. 7).

There are slight discrepancies in the literature: *Palmatolepis gigas* Zone in the railroad cut of the Kielce-Busko line at Kowala (Sartenaer 1977: p. 74; 1985: p. 320, fig. 1, p. 322); probable Uppermost *P. gigas* Zone (*Palmatolepis linguiformis* Zone in recent terminology of Ziegler & Sandberg 1990) at Kowala (Racki 1990: p. 177); upper part of *P. rhenana* Zone in the road section about 300 m west of the railroad cut at Kowala (Mikłas in Racki *et al*. 1993: p. 70). These slight discrepancies are due to the refinement in conodont studies as well as to the difficulty of assessing the lower and upper boundaries of the Upper *P. gigas* Zone (approximately Late *P. rhenana* Zone

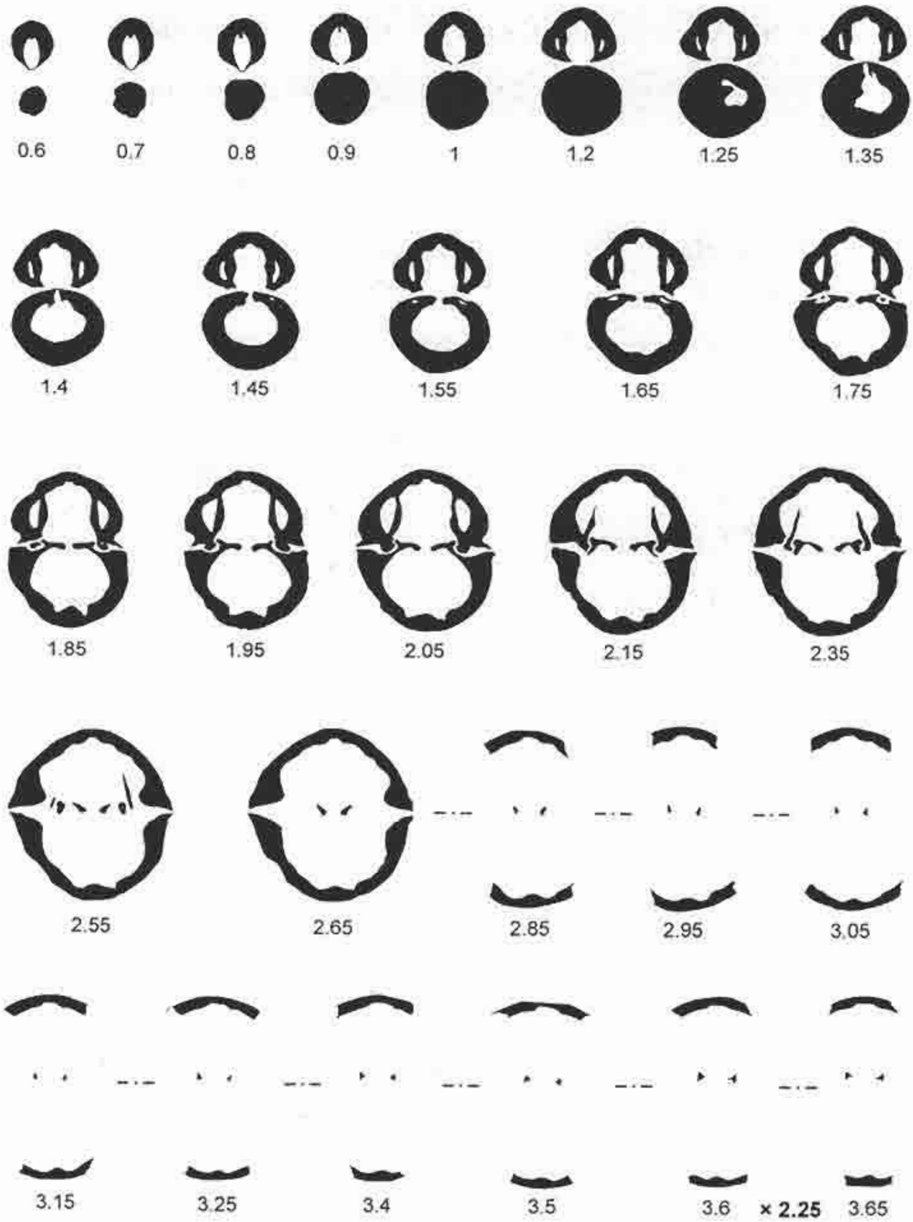

Fig. 6. *Pammegetherhynchus kowalaensis* sp. n. IGP/S-12 [l – 17 mm, w – 21.2 mm, t – 14.2 mm]. Camera lucida drawings of transverse serial sections; numbers refer to distances in mm from the ventral apex.

in recent terminology) in the Holy Cross Mountains sections, marked by low-frequency conodont faunas in the marly strata.

The species is not found outside the Gałęzice Syncline, as suggested by Filonowicz (1973), who mentioned *Calvinaria* cf. *albertensis* in the trenches N of the village of Skrzelczyce, and, questionably, in the Chęciny vicinity. Kościelniakowska (1967: p. 64, p. 72, p. 74) has indicated that

Liorhynchus rhomboidea (Phillips) was the most abundant fossil in the late Frasnian limestones (her beds C) of the Łysogóry region (Trzcianki ravine near Nieczulice). It is not believed that it refers to the species described in the present paper.

The Polish species is common in the Late *Palmatolepis rhenana* Zone, but it certainly occurs in the Early *P. rhenana* Zone (? late part only), and possibly in the early part of the *P. linguiformis* Zone.

Pammegetherhynchus ecology and record of the Kellwasser Crisis in the Holy Cross Mountains

(G. RACKI and M. SZULCZEWSKI)

Ecology of the *Pammegetherhynchus*-dominated benthic fauna was described as *P.* sp. A Assemblage by Racki *et al.* (1993: fig. 14, p. 94; see also Racki 1981: p. 174 and Godefroid & Racki 1990: p. 47). *P. kowalaensis* sp. n. occurs in level-bottom, frequently low-diversity (even monospecific?) brachiopod biota, abundantly colonizing some downslope, mostly poorly-oxygenated and muddy habitats (see Fig. 8). This is a prominent example of non-reef rhynchonellid biofacies (Racki *et al.* 1993: p. 89). The brachiopods lie unattached to the sea bottom, because the pedicle foramen tends to be quickly reduced in adults. A relatively large-sized and more biconvex variety of *P. kowalaensis* sp. n. probably dwelled mostly in slightly more upslope and firm bottom environments, as exemplified by the sequence in the Kowala road cut (see Mikłas in Racki *et al.* 1993: fig. 3). Nevertheless, the overall hemipelagic environmental setting (Basin Facies of Szulczewski 1971: pp. 96–100) is well evidenced by a mostly low-energy sedimentary matrix (bituminous marly mudstones and wackestones) and associated biotas (sparse benthos as siliceous sponges, lingulids and soft-bodied infauna, and possibly also other brachiopods and corals, several pelagic elements: cephalopods, tentaculitoids, fishes, abundant palmatolepid conodonts), markedly coupled with apparently autochtonous brachiopod shell nests and clumps. This stagnant-water environment was episodically interrupted by transported biota and sediment from higher-energy events (storms?, tsunamis?, turbidites?) recorded in more or less reworked and ecologically mixed shelly intercalations including, besides *P. kowalaensis* sp. n., diverse upslope brachiopod associations comprising at least 25 species, mainly atrypids, athyrids, other rhynchonellids (*Coeloterorhynchus*, *Hypothyridina*, and some undescribed genera), spiriferids, and gypidulids. These last infrequent articulates have been described by Godefroid & Racki (1990: p. 51) as *Neometabolipa duponti* Godefroid, 1974. Preliminary lists of common genera are presented by Racki (1981: p. 174), and accompanied by frequency data and illustrations by Mikłas (in Racki *et al.* 1993: pls 2–9; table 1).

The expansion of such stressed oxygen-deficient habitats in the southern (Chęciny-Zbrza) intrashelf basin of the Holy Cross Mountains area is related to a late Frasnian sedimentary cycle (Figs 1C and 2). Similar depositional regimes appeared earlier on the southern slope of the backstepping Dyminy Reef during deepening pulses, as manifested in the Kowala-Bolechowice transect by marly-calcareous hemipelagic sets D, F and H (*sensu* Szulczewski 1971: p. 75) alternating with more shallow-water, mostly detrital deposits (Figs 2 and 7; see also Rigby *et al.* 1981: fig. 2). Each of the

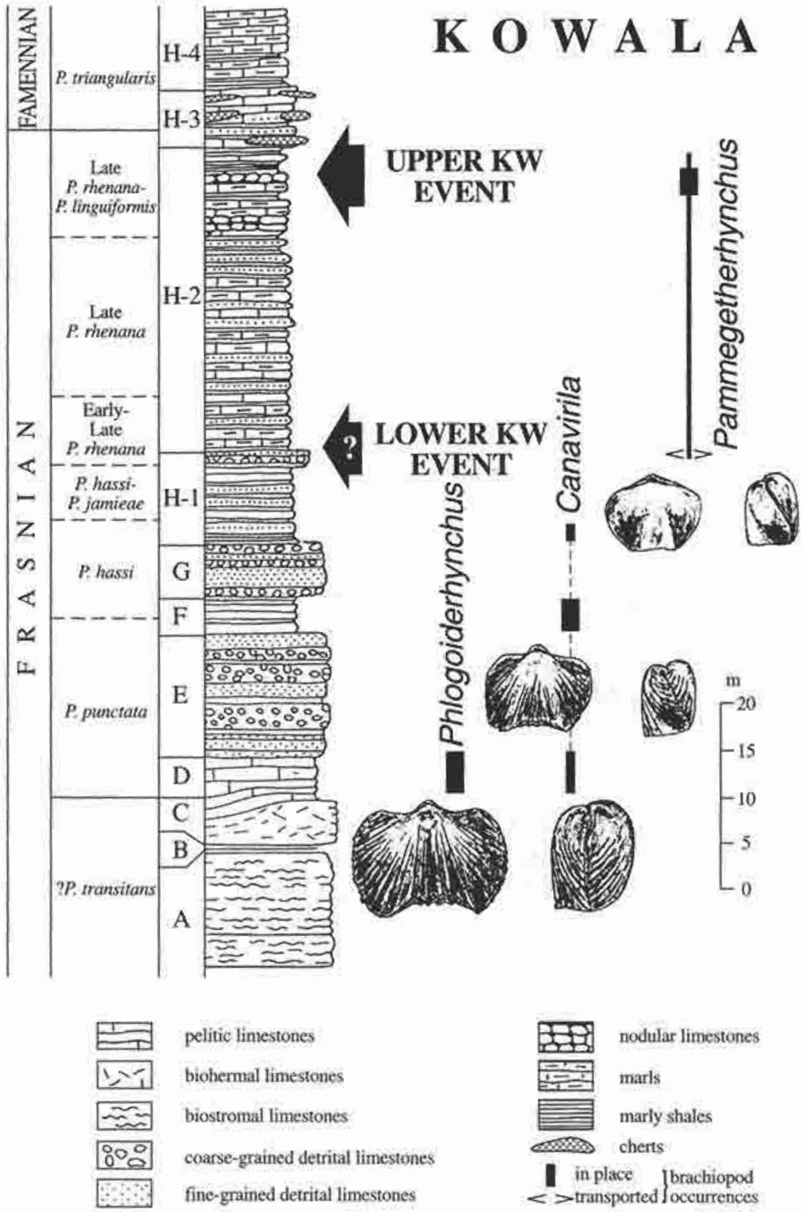

Fig. 7. Composite lithologic section of the Frasnian to early Famennian limestone to marly succession at Kowala, based on railroad cut (cf. Szulczewski & Skompski 1994: fig. 27) and western walls of quarry, and *simplified* distribution scheme of the most abundant rhynchonellid genera against supposed levels of the Kellwasser transgression/anoxic events in the late Frasnian sea-level highstand (e.g., Sandberg *et al.* 1992; Joachimski & Buggish 1993; Schindler 1993). Set terminology after Szulczewski (1971: p. 75), with new subdivision of the set H, and revised conodont datings (see also Racki 1993a: p. 15; Racki 1993b). Pronounced lateral variability within the micritic/marly unit H-2 from platy and partly detrital lithologies (unit H-2a) into more shaly and nodular varieties (unit H-2b; see e.g. Rigby *et al.* 1981: fig. 2) is signalized only. *P.* – *Palmatolepis.*

units is marked by a distinctive level-bottom rhynchonellid assemblage, starting from the middle Frasnian (*Palmatolepis punctata* Zone) *Phlogoiderhynchus polonicus* fauna (Biernat & Szulczewski 1975: p. 211; Racki 1993a: p. 132). Sartenaer & Racki (in preparation) will describe a species of the genus *Canavirila* Sartenaer, 1994, occurring in sets F (in abundance) and D, and probably also in the basal part of set H (*Palmatolepis punctata* to ?*P. jamieae* Zones). *Pammegetherhynchus kowalaensis* sp. n. is the last member of this rhynchonellid succession, and its appearance is linked with the final lithologic transition from detrital slope (fore-reef) calcareous facies to more argillaceous and bituminous, rhythmic basin sequence, i.e. sets G and H of Szulczewski (1971), respectively (see fig. 27 in Szulczewski & Skompski 1994, for the whole Frasnian-Famennian basin succession). Narkiewicz (1988: p. 629, fig. 7; see also Racki 1993b: p. 9) considered this depositional turning point as a record of the IId basal eustatic rise in the scheme of Johnson *et al.* (1985). The rapid deepening pulse in turn may have induced maximum formation of warm saline waters on the flooded shelf, creating anoxic conditions in stratified intrashelf basins (Lower Kellwasser Event), as proposed lastly by Joachimski & Buggisch (1993: p. 677).

However, the postulated event pattern remains equivocal in regard to weak biostratigraphic control, as emphasised by Szulczewski (1990: p. 332). The hard problem is reinvestigated herein because the appearance of the *Pammegetherhynchus* fauna is evidently associated with the lower part of set H. Conodont data and revision of previous determinations of faunas from Kowala, using the Ziegler & Sandberg (1990) taxonomy and zonal scheme, allow the emendation of the age interpretation of the newly subdivided Frasnian marly succession (of the set H) into three units (H-1 to H-3; Fig. 7), as proposed previously for the Jaźwica section (see fig. 3 in Racki & Zapaśnik 1979: p. 154). In fact, the definitive onset of basin regime and the flourishing of pelagic faunas, cephalopods including, in this area is associated with the deposition of the middle subset H-2, whilst largely detrital, coarsening-upward deposits characterized the underlying unit H-1. This facies turnover happened near the boundary between *Palmatolepis jamieae* and *P. rhenana* zones, and in a broad sense is linked with the first Frasnian highstand initiated by the *Palmatolepis semichatovae* transgression, as interpreted by Sandberg *et al.* (1992: pp. 46, 48). According to Schindler (1993: p. 117), the Kellwasser Crisis also starts probably in the Early *P. rhenana* Zone. The Lower Kellwasser Event is difficult to recognize accurately in the basin succession on the basis of lithology only, complicated in addition by distinctive lateral variation. According to available conodont datings, this event is recorded in the basal, marly-micritic part of the unit H-2 at the railroad cut (see Fig. 7), but possibly as high as the middle interval of this unit at the eastern part of the quarry. On the other hand, a permanent and even increasing detritus influx from adjoining organic shoals, including amphiporid branches, is still evidently recorded in western Kowala successions, i.e. road and railroad cut sections, within the subset H-2a (see Szulczewski 1971: pp. 99–100; Racki *et al.* 1993: pp. 95–96). The intermittent shallowings recorded in the G to H-2a set segment, resulted in complex lateral facies relationships. These might reflect both eustatic (see e.g., Narkiewicz 1988: p. 632; Sandberg *et al.* 1992: pp. 46, 48) and tectonic effects on this flanking zone of the submerging Dyminy Reef. Monotonous thin-bedded, partly wavy-bedded to nodular deposits (up to 17 m thick) are essentially

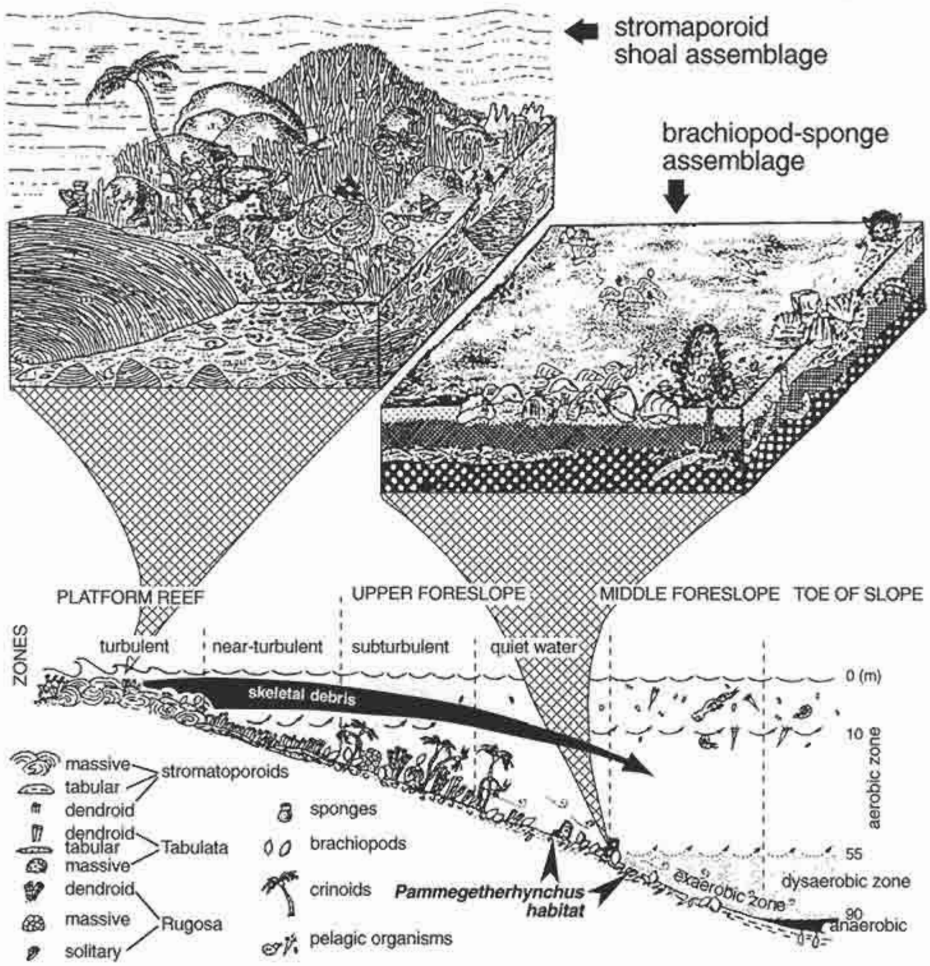

Fig. 8. Habitat of *Pammegetherhynchus* against overall biofacies model of the Frasnian reef of the Holy Cross Mountains (adapted from Racki *et al.* 1993: fig. 14; see also Racki & Baliński 1998); atrypid and rhynchonellid brachiopods are shown as dominant element of two different communities developed in contrasting environmental settings.

the only lithology of the unit H-2b, bearing the most abundant, largely in place accumulations of the rhynchonellid shells.

The first occurrence of *P. kowalaensis* was found in the Kowala quarry within the lowermost part of unit H-2, and dated as the Early *Palmatolepis rhenana* Zone. Distribution of this species in particular sections exhibits a highly diachronous pattern, probably related to variable pioneer colonization history by specialized benthos of the stratified basin floor. In the eastern Kowala section, the rhynchonellid shells are abundantly present in several coquinite intercalations dispersed in the subset H-2a, but in the Kowala railroad cut locality the undoubted entry of this species is established as high as in the topmost part of this suite.

The last developmental phase of *P. kowalaensis* is clearly influenced by increasing anoxic conditions of the Upper (Main) Kellwasser Event, paired with assumed oceanic overturn within the late *Palmatolepis linguiformis* Zone (Schindler 1993: p. 118). Irregularly decreasing shell frequency is documented toward top of the subset H-2, ca. 18 m thick, in the eastern Kowala site: the last known occurrence of the less-biconvex variety is 2.0 m below the unit top within the more argillaceous (shaly) and assumed exaerobic portion of the sequence, and probably within the above mentioned conodont zone. This lithological trend is associated with overall biotic changes in benthic and pelagic fauna composition in the latest Frasnian interval (Racki 1993b: p. 9), comprising first order extermination of shelly benthos, paired with a bloom of siliceous biota (radiolarians and sponges). The low-density mode of occurrences may show that the final demise of this rhynchonellid species was coupled with the onset of episodic calcareous deposition of the unit H-3, and reflects a severe eustatic fall in the Frasnian-Famennian passage (Event 6 in Sandberg *et al.* 1988: p. 296) and/or local epeirogenic uplifts (Szulczewski 1971: p. 115). Pre-extinction, transported brachiopod faunas without *P. kowalaensis* have been found in a few crinoid-lumachelle lenticular streaks in the lower part of unit H-3; they comprise many biernatellids (*Biernatella polonica* Baliński, 1977; Baliński 1995: p. 147) and other athyridids, spiriferids (mainly cyrtospiriferids), orthids, and sporadic last atrypids and *Hypothyridina* (see Racki & Baliński 1998). The black medium-bedded, partly neomorphozed and chert-bearing limestones correspond apparently to a higher part of the Upper Kellwasser Limestone (Racki 1993b: p. 9).

There are only ambiguous data (Kościelniakowska 1967; Filonowicz 1973) concerning the possible occurrence of *Pammegetherhynchus* outside the Kowala-Bolechowice area. A few incomplete smooth rhynchonellid shells from the late Frasnian fossiliferous limestone intercalations of Sosnówka hill, 1 km W of Chęciny (Racki 1993a: p. 178), found in waste, may be representatives of the undescribed genus from the Łgawa Hill site (see 'Remarks' in 'Systematic palaeontology'). Thus, at the regional scale, the restricted distribution of *P. kowalaensis* within only the Chęciny-Zbrza basin (see Fig. 1C) is a remarkable feature, but it is well-known for this unique brachiopod-sponge association (Sobolev 1909b; Rigby *et al.* 1981: p. 165). This somewhat surprising biogeographical pattern might in part reflect a positive biological interaction between both groups of benthic organisms, and/or some ecological hindrances such as competition from other rhynchonellid species within the level-bottom niche (see Racki in Racki *et al.* 1993: p. 100). In general, this seems to be the case with *Ryocarhynchus tumidus* (Kayser, 1872), this being the prominent species in the age-equivalent brachiopod assemblage in nearby Cracow area (Dębnik; see Fig. 1A), southern Poland (Baliński 1979: pp. 14, 21). Similar species of *Ryocarhynchus* is commonly known also from monospecific shell clumps in coeval strata of the eastern Holy Cross Mountains (Łagów-Płucki and Janczyce sites). Infrequent small representatives of this widespread genus were detected by one of the co-authors (P.S.) at Jaźwica and Kowala. Comparable close affinities of the Cracow and eastern Holy Cross Mountains benthic biotas are recognizable among Givetian and Frasnian crinoid faunas (Głuchowski 1993: figs 18–19), and the subtle biogeographic zonation of the south Polish shelf becomes more and more apparent.

Geographical distribution and stratigraphical position of the genus *Pammegetherhynchus* in the Kellwasser Crisis interval

(P. SARTENAER and G. RACKI)

The geographical distribution and the stratigraphical position of *Pammegetherhynchus kowalaensis* sp. n. have been discussed above. The other species of the genus, *P. merodae*, is present in the dark shales of 'Matagne' aspect deposited mostly during late Frasnian time (Early and Late *Palmatolepis rhenana* Zones; a more precise position within these zones cannot be given) near the western margin of the southern border of the Dinant Basin in the French Fagne. The 'Matagne' aspect has been defined in the following way by Sartenaer (1970: p. 346): very finely laminated shales with olive to green fracture, breaking into fine scales, and containing some flattened nodules, rare calcareous lenses (some of them showing a cone-in-cone structure), and a mostly dwarfed fauna. Sartenaer (1977: p. 74) found ten specimens in the collections of various German institutions; they all derive from the 'Büdesheimer Goniatitenschiefer' (Early *P. rhenana*) of Büdesheim (Eifel) and belong to the genus *Pammegetherhynchus*. The restricted number of specimens does not allow the separation of the Eifel region specimens from the French species.

In summary, *Pammegetherhynchus* is restricted in range to the late Frasnian *Palmatolepis rhenana* Zone of Western and Central Europe, with the Polish representative likely extending up to the *P. linguiformis* Zone. Remarkably, the *Pammegetherhynchus*-bearing black marly suite of the Holy Cross Mountains, and both the 'Matagne' aspect and 'Büdesheimer Goniatitenschiefer', were at least partially deposited during the Kellwasser hypoxic interval in the global sea-level highstand (Transgressive–Regressive Cycle IId of Johnson *et al.* 1985: p. 577; Sandberg *et al.* 1992), especially in light of the eustatic scheme modified by Becker *et al.* (1993: p. 317, fig. 9).

Thus, *Pammegetherhynchus* might be considered as an example of brachiopods adapted to deteriorating low-oxygen conditions during the late Frasnian crisis. Data from the Holy Cross Mountains succession reveal that this genus apparently belonged to victims of the mass extinction event near the F–F boundary, being a culmination point of the stepwise marine ecosystem collapse (Sandberg *et al.* 1988: pp. 296–297; Schindler 1993: p. 117). Even so this major biotic turnover was generally insignificant for the deeper-water rhynchonellid biofacies (Racki *et al.* 1993: p. 103).

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