Gastropod succession across the Early–Middle Frasnian transition in the Holy Cross Mountains, southern Poland

WOJCIECH KRAWCZYŃSKI

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Gastropod response to a marked carbon isotopic geochemical anomaly across the Early–Middle Frasnian transition (*Palmatolepis transitans–Palmatolepis punctata* conodont zones) has been analysed along the southern Laurussian shelf, mainly within the Dyminy Reef in the Holy Cross Mountains. Gastropods are represented by three reefal associations (*Kowalatrochus sanctacrucensis*, *Euryzone kielcensis*, and *Grabinopsis guerichi* associations), and an impoverished open-shelf *Straparollus laevis* assemblage. The most severe diversity crisis is connected to the disappearance of local low-energy muddy habitats, as a result of a transgressive pulse (Middlesex Event) and benthic habitat changes tied to strongly fluctuating carbon cycling; this has been observed at the highly diverse Kadzielnia-type assemblage. Fifteen taxa have been recognised in this distinctive Early Frasnian mud-mound association, including six (probably endemics), which are unknown from the Middle Frasnian. The disappearance of three relict Givetian species (*Euryzone delphinuloides*, *Straparollus laevis*, and *Goniasma*? *zarecznyi*) is also recorded. Other species probably migrated into the shallower water part of Dyminy Reef and persisted in the Middle and Late Frasnian. The Middlesex Event and the earlier major biogeochemical perturbation seem to have less serious effects for evolution of gastropods in the Polish-Moravian part of the Laurussia shelf than the catastrophic Frasnian–Famennian extinction. Two new taxa are described: *Frydiella kaimi* gen. et sp. nov. (Eotomariidae) and *Heidelbergeria czarnieckii* gen. et sp. nov. (Elasmonematidae).

Key words: Gastropoda, Eotomariidae, Elasmonematidae, bioevents, Frasnian, Devonian, Poland.

Wojciech Krawczyński [wojtekk@us.edu.pl], Uniwersytet Śląski, Wydział Nauk o Ziemi, ul. Będzińska 60, PL-41-200 Sosnowiec, Poland.

Introduction

Geochemical studies of Frasnian strata have shown a major biogeochemical perturbation in global carbon cycling across the Early–Middle Frasnian boundary (= *Palmatolepis transitans–Palmatolepis punctata* zonal boundary, as proposed by the Subcomission on Devonian Stratigraphy, http://www.geneseo.edu/~frasnian/index.htm; see Becker and House 1998; Ziegler and Sandberg 2001), which has a supraregional distribution (Yans et al. in press). That $\delta^{13}C$ anomaly has also been documented in carbonate facies across the Early and Middle Frasnian interval in the Polish-Moravian part of the epicontinental Laurussian shelf (Racki et al. 2004; Pisarzowska et al. 2006), best exposed in the Holy Cross Mountains, southern Poland (Fig. 1).

During the Early Frasnian, a near-symmetric reefal structure appeared in this part of Laurussian shelf (Dyminy Reef, Racki 1993b; see also Szulczewski 1995), inhabited mainly by stromatoporoids and corals (Kaźmierczak 1971; Nowiński 1993; Wrzołek 1988, 1993; Narkiewicz et al. 1990), and associated by benthic faunal elements such as brachiopods (Racki 1993a), crinoids (Głuchowski 1993), and more rarely, among others, trilobites (Chlupáč 1993) and gastropods (Krawczyński 2002).

Frasnian gastropods from the Holy Cross Mountains were first described in the nineteenth and at the beginning of the twentieth centuries by Pusch (1837), Gürich (1896), Siemiradzki (1909), and Sobolev (1909, 1912). In the 1980s, studies of Devonian gastropods were resumed by Karczewski (1980, 1989). Later Krawczyński (1999, 2002) revised some Devonian gastropods, and reanalysed their palaeoecological aspects as well as the impact of global bioevents on gastropod faunas during Frasnian time. New finds of Early Frasnian gastropods (Łukaszewicz 2001; Niemczyk 2003) have enabled an updated determination of the gastropod record of probably high environmental stress across the Early–Middle Frasnian boundary. The present work is a continuation of a study on gastropod faunas prior to the great collapse of reefal ecosystems at the Frasnian–Famennian boundary, in times characterised by significant biogeochemical disturbance (see Racki 2005; Yans et al. in press).

Institutional abbreviations.—GIUS, Faculty of Earth Sciences, University of Silesia, Sosnowiec, Poland; MGUWr, Geological Museum, University of Wrocław, Wrocław, Poland; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

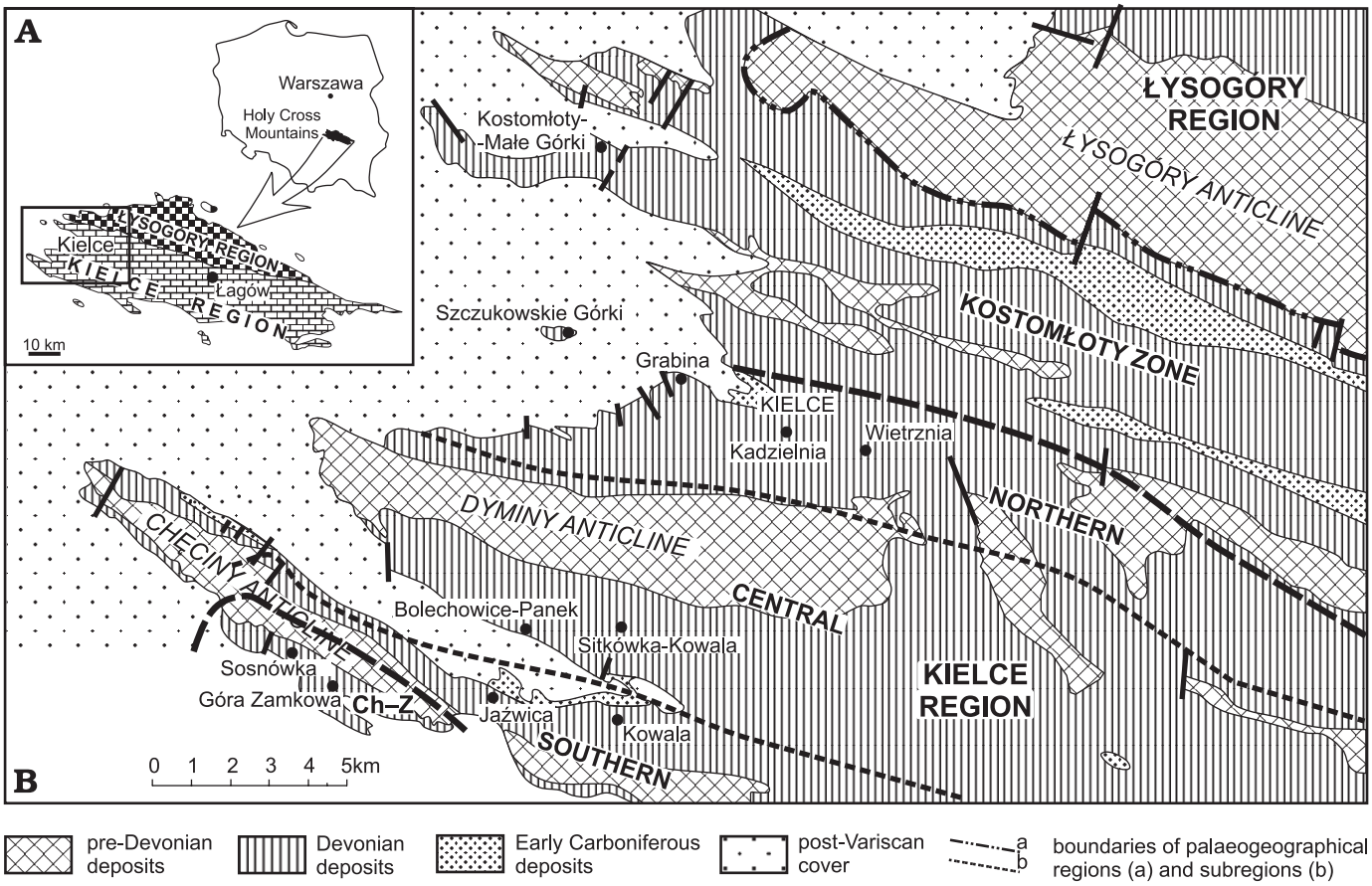

Fig. 1. **A**. Location of Holy Cross Mountains and palaeogeographic framework of the Devonian in Poland (modified after Racki 1993b: fig. 1). **B**. Locations of studied geological sections in the western part of the Holy Cross Mountains with division on palaeogeographical units (modified from Szulczewski 1971 and Racki 1993b). Abbreviation: Ch-Z, Chęciny-Zbrza subregion.

Geological setting

The Holy Cross Mountains constitute the best exposed and intensely studied portion of the Devonian Polish-Moravian epicontinental shelf of Laurussia (see Dadlez et al. 1994). The area of the Holy Cross Mountains is divided into two distinct palaeogeographic-tectonic regions (Szulczewski 1971, 1995; Racki 1993b): the Łysogóry palaeolow situated between the Małopolska Block and the East European platform, and the Kielce palaeohigh within the Małopolska Block. During the Middle and Late Devonian, a carbonate platform formed here, which, in the Early Frasnian, transformed into a near-symmetrical reef structure as a result of shelf drowning due to eustatic sea level rise (Johnson et al. 1985; Racki 1993b). The main part of that biogenic buildup, known as the Dyminy Reef, refers to the Central Kielce subregion, and its slopes occur in the northern and southern Kielce region. The Frasnian Dyminy Reef was surrounded by two intrashelf basins: the Chęciny-Zbrza subregion in the south and the Łysogóry-Kostomłoty subregion in the north (Fig. 1; Szulczewski 1971, 1995; Racki 1993b).

During analyses of Early Frasnian gastropod faunas, all sites which represent Kielce facies subregions have been carefully studied (Fig. 2; for section and lithological unit terminology see "Register of localities" in Racki 1993b). The central portion of the Dyminy Reef is represented by the Sitkówka-Kowala section, with the set B representing reefal facies with gastropods (upper Sitkówka Beds; see Kaźmierczak 1971; Narkiewicz et al. 1990; Racki 1993b). The same reefal facies appeared along the southern slope at Jaźwica (sets H, I, and K; see Racki 1993b; Łukaszewicz 2001) and Kowala (set A; see Krawczyński 2002). The most important biofacies feature of the Early Frasnian was the wide appearance of Kadzielnia-type mud mounds (Kadzielnia Limestone Member of Narkiewicz et al. 1990), formed below wave base (Szulczewski and Racki 1981). The bioherms with rich gastropod faunas occurred along the northern (e.g., Kadzielnia, set A) and southern slopes (e.g., Jaźwica, set J) of the Dyminy Reef. Gastropods are also known from some levels in the Wietrznia quarry section within biodetrital Frasnian strata (set B) along the northern side of the Dyminy Reef (lower Wietrznia Beds; see Racki 1993b).

Highly peculiar is the occurrence of a low species richness Givetian–Frasnian gastropod assemblage within the Chęciny-Zbrza intrashelf basin at Góra Zamkowa (Chęciny Beds, sets F and H; Racki 1993a, b). An unique assemblage is known from the Goniatite Level (the uppermost Szydłówek Beds; *Pa.*

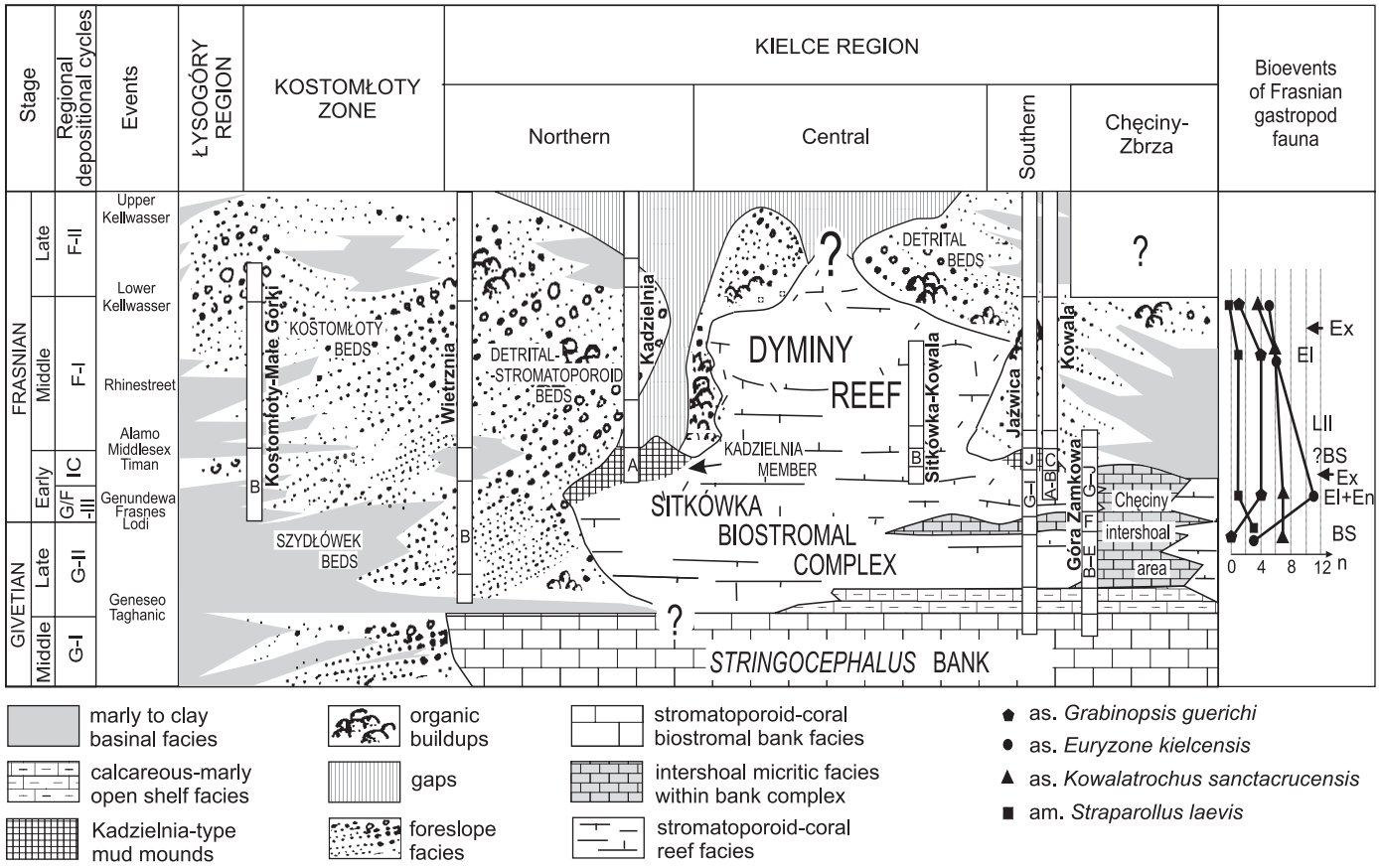

Fig. 2. Studied Devonian sections, with subdivision on sets (letters mean sets with gastropods) against stratigraphic-facies cross-section of the Late Givetian and Frasnian strata of the Holy Cross Mountains (after Racki 1993b, modified) as well as bioevents of Frasnian gastropod fauna study; n, number of taxa; BS, biotic stagnation; El, extraregional immigration; En, endemics; Ex, extinction; LII, limited intraregional imigration; as., association; am., assemblage (see Racki 1993a, b). Regional depositional cycles after Racki (1993b); global events after House (2002).

transitans Zone) at the Kostomłoty-Małe Górki section (see Racki et al. 2004), which has also yielded a strongly pyritised, redeposited gastropod fauna (Jagt-Yazykova et al. 2006).

Material and methods

The material studied was partly collected by Grzegorz Racki between 1976 and 1994; a preliminary study was carried out by Karczewski (1989). The majority of Frasnian gastropods was collected by the author between 1995 and 2005 (some 300 specimens) and these have in part been described (Krawczyński 2002). In addition to this material, collections of Early Frasnian gastropods of Łukaszewicz (2001) and Niemczyk (2003) have been included as well. All these collections are housed at the Faculty of Earth Sciences of the University of Silesia in Sosnowiec. For comparison, the original Georg Gürich's collection (1896) at the Geological Museum of University of Wrocław has also been consulted, as has material contained in the collections of the Institute of Paleobiology of the Polish Academy of Sciences at Warsaw.

The majority of the specimens studied originates from various limestone and marly limestone lithologies, and usually were found on erosion surfaces or karst/sinkholes, which accounts for the fairly good preservation of diagnostic features of the shell surface. Specimens from the Goniatite Level are represented mainly by pyritised internal moulds, but there also are some with well-preserved outer ornament (see Jagt-Yazykova et al. 2006).

Only Early Frasnian gastropod shells which are identifiable to the genus level have been taken into account as well as some indeterminate specimens which show typical features that differentiate them from similar taxa which appear later.

Review of Frasnian gastropods from the Holy Cross Mountains

The Early Frasnian gastropods studied belong to the non-reef *Straparollus laevis* assemblage (see Krawczyński 1998), from the deeper intrashelf basin of the Chęciny-Zbrza subregion (see Racki 1993b), and to three reef-dwelling associations described by Krawczyński (2002): *Kowalatrochus sanctacrucensis* (in the *Actinostroma* assemblage; see also Racki

1993b), *Euryzone kielcensis*, and *Grabinopsis guerichi* (in the Kadzielnia-type mud-mound assemblage, Table 1; see also Kaźmierczak 1971; Szulczewski 1971; Szulczewski and Racki 1981; Racki 1993b).

The gastropod classification of Bouchet et al. (2005) is used in a review below and in systematical part of this paper.

Euomphaloidea

***Straparollus laevis* (d'Archiac and Verneuil, 1842)** (Fig. 3B, C).—Five well-preserved shells and about 40 fragments from the abandoned Góra Zamkowa quarry (sets F and H). These shells are common in the Late Givetian set D at Chęciny, and occur also, but are less numerous there, in sets F and H (Chęciny Beds, Givetian–Frasnian boundary beds; Racki 1993b: 149). This species has been described from Givetian deposits at numerous localities in the Rhenish Slate Mountains area (d'Archiac and Verneuil 1842; Sandberger and Sandberger 1856; Holzapfel 1895; Heidelberger 2001) and in England (Phillips 1841; Whidborne 1891).

***Straparollus serpens* Phillips, 1841** (Fig. 3D, E).—Four near-complete shells from the Kadzielnia Member along the southern and northern slopes of the Dyminy Reef (Jaźwica, set J; Kadzielnia, set A) and from younger Frasnian rocks at Grabina (sets A and C) and at Bolechowice-Panek (set B). This taxon occurs in stromatoporoid-detrital facies and Kadzielnia-type mud mounds; *S. serpens* was described from some localities exposing Givetian strata in England (Phillips 1841; Whidborne 1891).

***Euomphalus* aff. *pulcher* Paeckelmann, 1913** (Fig. 3A).—A single, very well-preserved basal portion of shell from the Kadzielnia Member. This specimen is closer to the Givetian *Euomphalus pulcher* described by Paeckelmann (1913) (Dorper Kalk, Rhenish Slate Mountains) but has more distinct spines on the umbilical margin. Because the upper part of the whorl is not preserved, it is impossible to assign this material to species level; *E.* aff. *pulcher* is connected to the reefal *Euryzone kielcensis* association within the Kadzielnia-type assemblage.

***Orecopia kadzielniae* (Gürich, 1896)** (Fig. 3F–H).—A single internal mould and two well-preserved basal portions of shells. This species is known only from the Holy Cross Mountains area, where it occurs in Early Frasnian strata at Kowala (set A, the upper Sitkówka Beds), as well as Kadzielnia (set A) and Jaźwica (set J; the Kadzielnia Member). It is more common in Middle Frasnian stromatoporoid-coral limestones at Grabina (set A; upper Sitkówka Beds). *Orecopia kadzielniae* is also known from the *Kowalatrochus sanctacrucensis* association, within the *Actinostroma* assemblage, as well as from the *Euryzone kielcensis* association belonging to the Kadzielnia-type assemblage (see Krawczyński 2002).

Eotomarioidea

***Lahnospira taeniata* (Sandberger, 1842)** (Fig. 4D, E).—Seven pyritised specimens with well-preserved external surface and about 170 internal moulds with the position of selenizone visible. *Lahnospira taeniata* is the commonest species of gastropod at the Goniatite Level (uppermost Szydłówek Beds; Early Frasnian) at the active quarry Kostomłoty II (= Małe Górki), forming part of a molluscan thanatocoenosis (see Jagt-Yazykova et al. 2006). This species also appears in the Late Frasnian biodetrital limestones at Grabina (set C), and has been recognised in Givetian strata at Villmar (Rhenish Slate Mountains; Sandberger 1842; Goldfuss 1844; Heidelberger 2001).

***Euryzone kielcensis* (Gürich, 1896)** (Fig. 4L, M).—Two near-complete shells (one of them juvenile) and two fragments from the Early Frasnian Kadzielnia limestone along the southern (Jaźwica, set J) and northern (Kadzielnia, set A) slopes of the Dyminy Reef. This species is index gastropod element of a highly diverse Kadzielnia-type assemblage. A revised diagnosis and description were presented by Krawczyński (2002).

***Euryzone delphinuloides* (Schlotheim, 1820)** (Fig. 4F–H).—Two well-preserved fragments. This species occurs in Early Frasnian limestones at Kowala (set A) and also in Middle Givetian strata at Jaźwica (set A). *Euryzone delphinuloides* characterises complexes of lagoon and reef basins and is widely distributed in the Givetian of the Rhenish Slate Mountains and of England (d'Archiac and Verneuil 1842; Lotz 1900; Paeckelmann 1922; Heidelberger 2001).

Fig. 3. Early Frasnian Euomphaloidea, Subulitoidea, Palaeostyloidea, and Codonocheilidae from the Holy Cross Mountains. **A**. *Euomphalus* aff. *pulcher* Paeckelmann, 1913, GIUS 4-1658 Jaź-139, Jaźwica quarry (set J); basal (A_1) and lateral (A_2) views of shell. **B**, **C**. *Straparollus laevis* (d'Archiac and Verneuil, 1842), Góra Zamkowa (set F). **B**. GIUS 4-1763 GZ-90/1; apertural (B_1) and apical (B_2) views of shell. **C**. GIUS 4-1423 GZ-80/1, lateral view of shell. **D**, **E**. *Straparollus serpens* (Phillips, 1841), GIUS 4-1635 Jaź-117 (**D**) and GIUS 4-1642 Jaź-124 (**E**), Jaźwica quarry (set J); lateral views of shells. **F–H**. *Orecopia kadzielniae* (Gürich, 1896). **F**. MGUWr.1939s, holotype (internal mould) from the original Gürich's collection, Kadzielnia (set A), apical (F_1) and apertural (F_2) views. **G**. GIUS 4-1232 Ko-19, Kowala quarry (set A), apertural (G_1) and basal (G_2) views of shell. **H**. GIUS 4-1669 Jaź-150, Jaźwica quarry (set J), basal view of shell. **I**. *Macrochilina ventricosa* (Goldfuss, 1844), GIUS 4-1190 GZ-11, Góra Zamkowa (set F), apertural (I_1) and lateral (I_2) views of shell. **J–T**. *Westerna subcostata* (Schlotheim, 1820). **J**, **K**. MGUWr.338s-1 (**J**) and MGUWr.338s-2 (**K**), Kadzielnia (set A), lateral views of internal moulds from the original Gürich's collection. **L–O**. Sitkówka-Kowala (set B). **L**. GIUS 4-851 SKo-6, apertural (L_1) and lateral (L_2) views of shell. **M**. GIUS 4-852 SKo-7, apertural view of shell. **N**. GIUS 4-850 SKo-5, apertural view of teleoconch fragment. **O**. GIUS 4-847 SKo-2, apertural view of shell. **P**. GIUS 4-866 Ko-1, Kowala quarry (set A), lateral view of shell. **Q–S**. Kadzielnia (set A). **Q**. ZPAL Ga-VI/47, lateral view of shell. **R–S**. ZPAL Ga-VI/31 (**R**) and ZPAL Ga-VI/34 (**S**), lateral views of teleoconch fragments. **T**. GIUS 4-1603 Jaź-85, Jaźwica quarry (set J), teleoconch fragment. **U**. *Dihelice* cf. *dathei* Schmidt, 1905, ZPAL Ga-VI/45, Wietrznia (set B), lateral view of teleoconch fragment. **V**. *Goniasma*? cf. *zarecznyi* (Gürich, 1903). GIUS 4-1763 GZ-90/2, Góra Zamkowa (set F), lateral view of shell. →

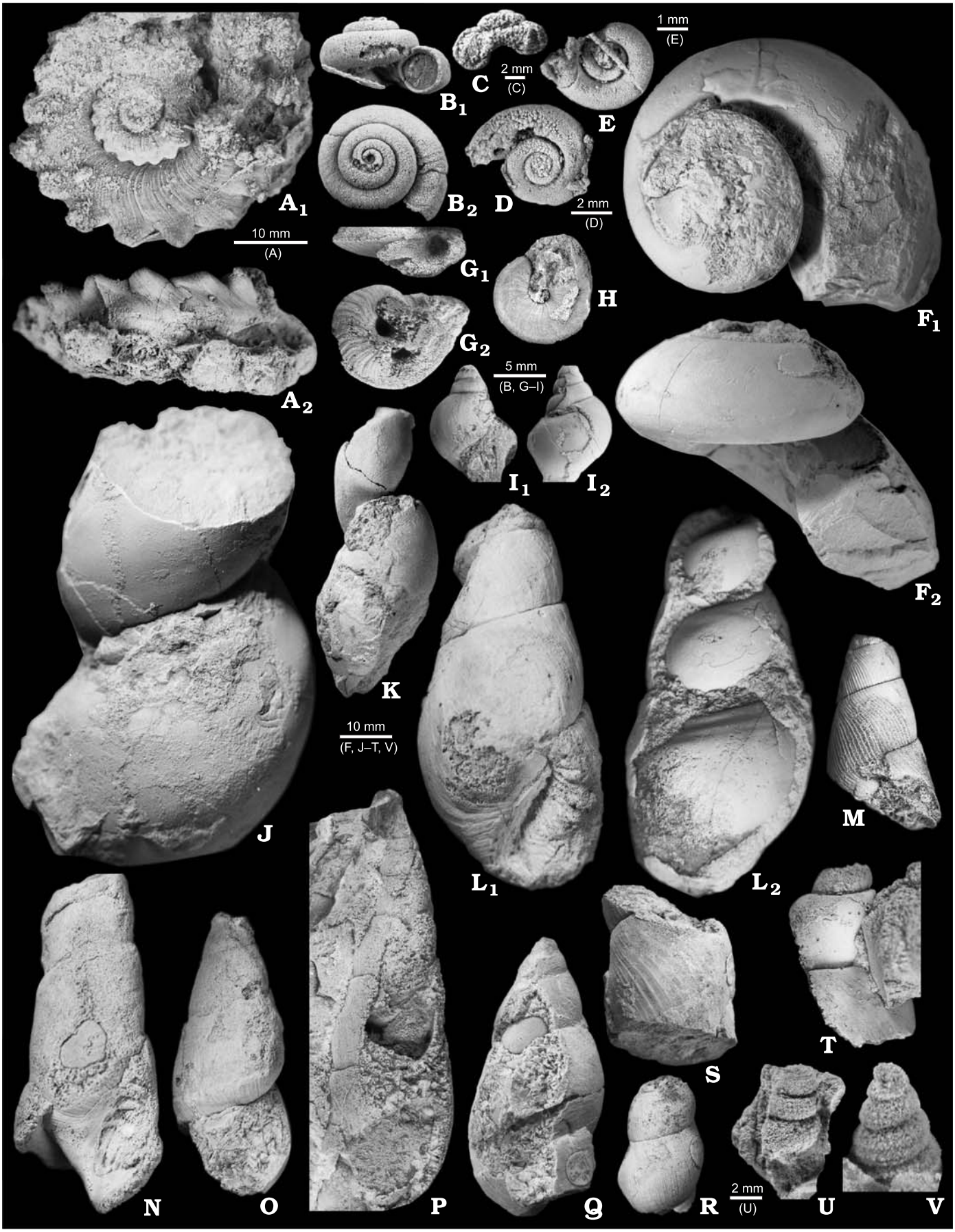
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Table 1. Occurrence of Frasnian gastropods in the Holy Cross Mountains. Abbreviations: l, lower; *Pa.*, *Palmatolepis*; u, upper; *, occurs also in the *Grabinopsis guerichi* association.

Gastropod assemblages and associations (Krawczyński 1998, 2002)	Geochronology	Frasnian										
		Early			Middle						Late	
	Conodont biozones (Ziegler and Sandberg 1990)	*Pa. falsiovalis*		*Pa. transitans*	*Pa. punctata*	*Pa. hassi*		*Pa. jamieae*	*Pa. rhenana*			*Pa. linguiformis*
		l	u			l	u		l	u		
	Sea-level cycles (Johnson et al. 1985)	IIb		IIb/c	IIc						IId	
	Regional shallowing-upward cycles (Racki 1993b) / Taxonomy	G/F-III		IC	F-I						F-II	
Straparollus laevis Assemblage	*Straparollus laevis* (d'Archiac and Verneuil, 1842)	■	■	■								
	Goniasma? cf. *zarecznyi* (Gürich, 1903)	■										
Kowalatrochus sanctacrucensis Association	*Macrochilina ventricosa* (Goldfuss, 1844)	■	■	■	■	■	■	■	■			
	Kowalatrochus sanctacrucensis Krawczyński, 2002	■	■	■	■	■	■	■	■			
	Lahnospira taeniata (Sandberger, 1842)			■	■	■	■	■	■	■	■	■
	Euryzone delphinuloides (Schlotheim, 1820)	■	■	■								
	Naticopsis protogaea (Goldfuss, 1844)	■	■								■	■
	Orecopia kadzielniae (Gürich, 1896)	■	■	■	■	■	■	■	■			
	Westerna subcostata (Schlotheim, 1820)	■	■	■	■	■	■	■	■	■	■	■
	Naticopsis inflata (Roemer, 1843)*	■	■	■	■	■	■	■	■	■	■	■
Euryzone kielcensis Association	*Euryzone kielcensis* (Gürich, 1896)			■								
	Euomphalus aff. *pulcher* Paeckelmann, 1913			■								
	Straparollus serpens (Phillips, 1841)			■	■	■	■	■	■	■	■	■
	Frydiella kaimi gen. et sp. nov.			■								
	Porcellia bifida (Sandberger and Sandberger, 1856)			■							■	■
	Heidelbergeria czarnieckii gen. et sp. nov.			■								
	Spanionema scalaroides (Whidborne, 1889)			■	■	■	■	■	■			
Grabinopsis guerichi Association	*Roemeriella octocincta* (Roemer, 1843)			■	■	■	■	■	■	■	■	■
	Grabinopsis guerichi Krawczyński, 2002			■	■	■	■	■	■			
	Palaeozygopleura (*Rhenozyga*) sp.			■	■	■	■	■	■			
	?loxonematoid indet.			■								
Unrecognised associations	*Dihelice* cf. *dathei* Schmidt, 1905			■								
	Palaeozygopleura (*Bohemozyga*) *pyritica* Krawczyński, 2006 in Jagt-Yazykova et al. 2006			■								
	Naticopsis aff. *kayseri* Holzapfel, 1895			■								

***Frydiella kaimi* gen. et sp. nov.** (Fig. 4A–C).—See description on p. 689.

Trochoidea

***Kowalatrochus sanctacrucensis* Krawczyński, 2002** (Fig. 5F–L).—One excellently preserved specimen, 76 near-complete shells and 19 fragments with ornament well visible. This species occurs quite commonly in the Early Frasnian at Kowala (set A), Sitkówka-Kowala (set B) and Jaźwica (sets I, K), and also in the Middle Frasnian at Grabina (set A; upper Sitkówka Beds). It is connected with the reefal *Actinostroma* assemblage and characteristic of the *K. sanctacrucensis* association, known to date from the Devonian of the Holy Cross Mountains only.

***Roemeriella octocincta* (Roemer, 1843)** (Figs. 5D, E, 6M: r).—Two near-complete shells and three fragments with well-preserved ornament. Coeloconoidal, trochiform shells with typical ornament consisting of four spiral cords with small tubercles on the platform of juvenile whorls, are known from the Early Frasnian Kadzielnia Member (Jaźwica, set J), from lower Wietrznia Beds at Wietrznia (set B) as well as from Middle and Late Frasnian Detrital Beds at Grabina (set C) and

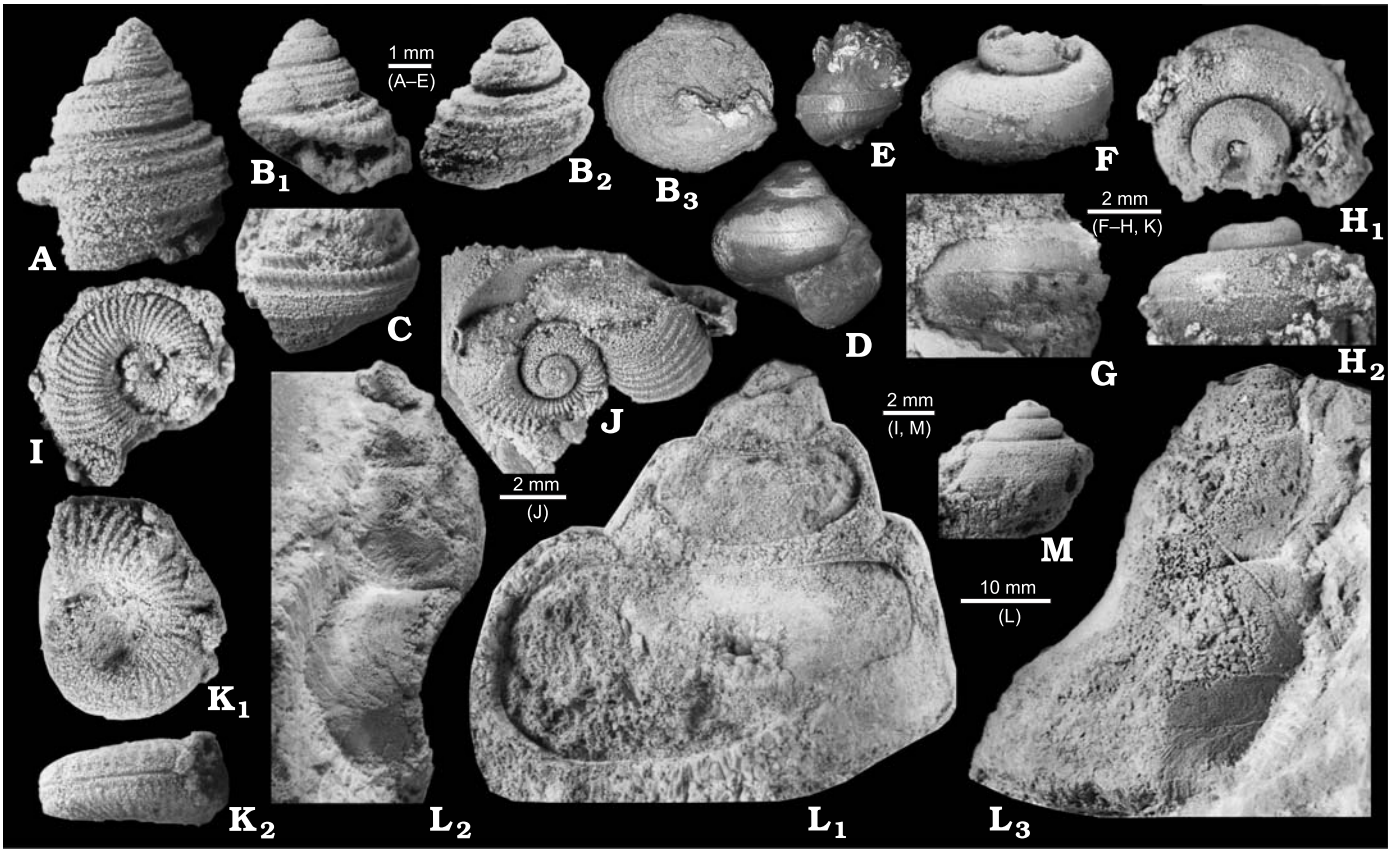

Fig. 4. Early Frasnian Eotomarioidea and Porcellioidea (Vetigastropoda) from the Holy Cross Mountains. **A**–**C**. *Frydiella kaimi* gen. et sp. nov., Jaźwica quarry (set J). **A**. Holotype, GIUS 4-1136 Jaź-31, lateral view. **B**. GIUS 4-1137 Jaź-32, apertural (B_1), lateral (B_2), and basal (B_3) views of shell. **C**. GIUS 4-1135 Jaź-30, fragment of last whorl with well preserved ornamentation. **D**, **E**. *Lahnospira taeniata* (Goldfuss, 1844), Kostomłoty II (Małe Górki) quarry (set B_3). **D**. GIUS 4-2282 Kos-12, apertural view of pyritised shell. **E**. GIUS 4-2277 Kos-7, lateral view of pyritised shell. **F–H**. *Euryzone delphinuloides* (Schlotheim, 1820). **F**, **G**. GIUS 4-1237 Ko-24 (**F**) and GIUS 4-1239 Ko-26 (**G**), Kowala quarry (set A), lateral views of shells. **H**. GIUS 4-1637 Jaź-119, Jaźwica quarry (set J), apical (H_1) and lateral (H_2) views of shell. **I–K**. *Porcellia bifida* (Sandberger and Sandberger, 1856), Jaźwica quarry (set J). **I**, **J**. GIUS 4-1629 Jaź-111 (**I**) and GIUS 4-1628 Jaź-110 (**J**), apical views of shells. **K**. GIUS 4-1140 Jaź-35, apical (K_1) and lateral (K_2) views of shell. **L**, **M**. *Euryzone kielcensis* (Gürich, 1896). **L**. GIUS 4-1467 Kd-3, Kadzielnia (set A), lateral views of neotype shell. **M**. GIUS 4-1134 Jaź-29, Jaźwica quarry (set J), lateral view of juvenile shell.

Szczukowskie Górki. This species occurs within the *Euryzone kielcensis* (Kadzielnia-type assemblage) and *Grabinopsis guerichi* (*Stachyodes* assemblage; see Racki 1993b) associations, as well as in the Late Frasnian "*Naticopsis*" *excentrica* association (the *Frechastraea pentagona* assemblage; see Wrzołek 1988). *Roemeriella octocincta* was first described from Frasnian deposits of the Harz Mountains (Roemer 1843; see also Blodgett and Frýda 1999).

***Heidelbergeria czarnieckii* gen. et sp. nov.** (Fig. 5A–C).—See description on p. 690.

Porcellioidea

***Porcellia bifida* (Sandberger and Sandberger, 1856)** (Fig. 4I–K).—Six near-complete quasi-planispiral shells and a single fragment from the Early Frasnian Kadzielnia Member (Jaźwica, set J). In the Holy Cross Mountains this species is also known from the Late Frasnian Detrital Beds (Grabina, set C). *Porcellia bifida* rather preferred fore-reef habitats, e.g., in the *Euryzone kielcensis* and the "*Naticopsis*" *excentrica* associations (see Krawczyński 2002). This species is also known from the Givetian of the Rhenish Slate Mountains (Sandberger and Sandberger 1856; Heidelberger 2001) and of England (Whidborne 1892).

Codonocheilidae

***Dihelice* cf. *dathei* Schmidt, 1905** (Fig. 3U).—A single shell lacking early whorls of the spire, from set B at Wietrznia (Early Frasnian). The pupiform evolute shell with typical ornament of 5–6 noded, spiral cords. Closely similar material was described by Schmidt (1905) from the Givetian of the Rhenish Slate Mountains.

Neritimorpha

***Grabinopsis guerichi* Krawczyński, 2002** (Fig. 6L, M: g).—About 140 near-complete shells, all from multi-species clusters formed by small-sized shells of *G. guerichi* association (Krawczyński 2002), characteristic of reefal settings. This species occurs in the Early Frasnian Kadzielnia Member

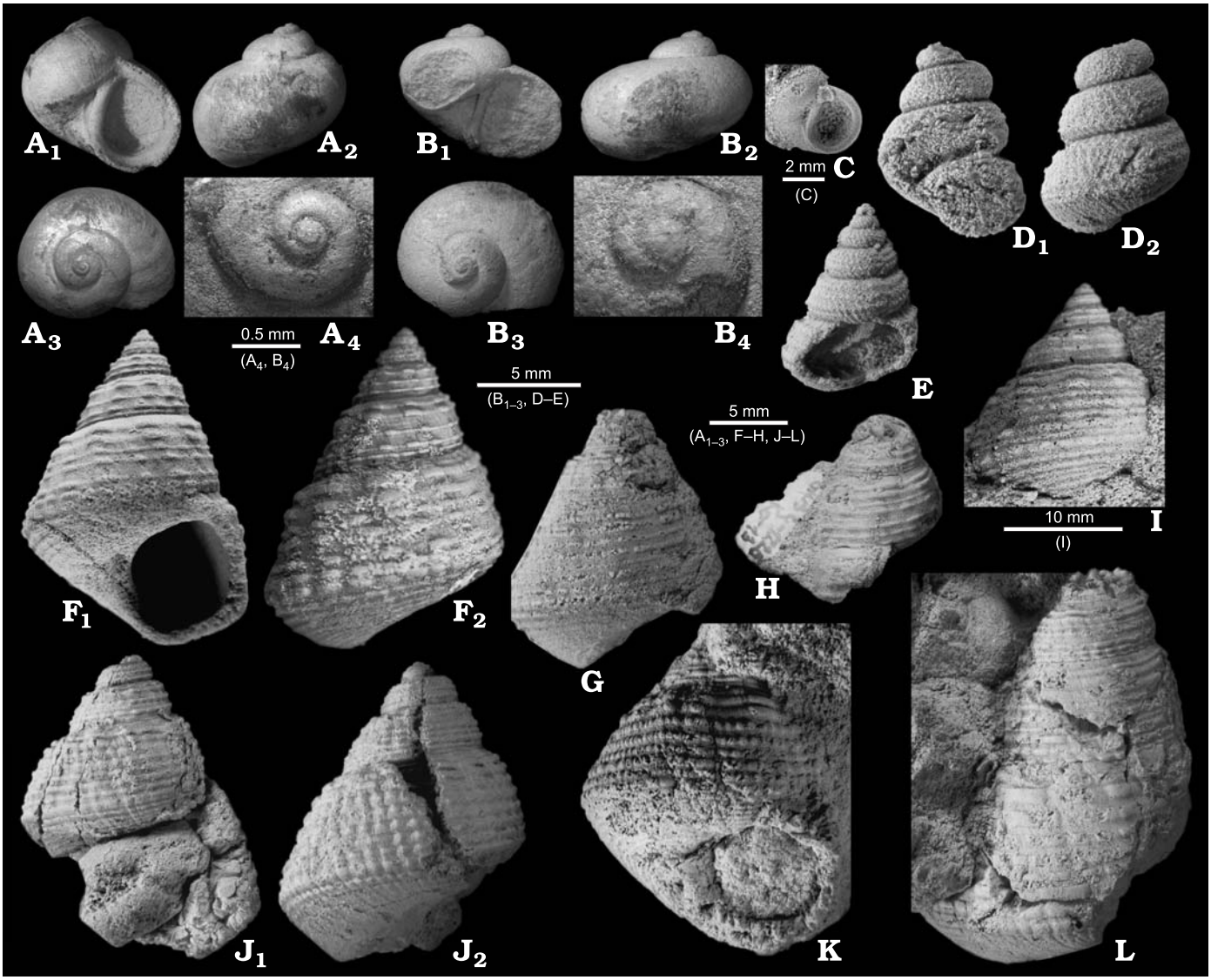

Fig. 5. Early Frasnian Trochoidea (Vetigastropoda) from the Holy Cross Mountains. **A**–**C**. *Heidelbergeria czarnieckii* gen. et sp. nov. A. **A**. ZPAL Ga-VI/29, Kadzielnia (set A), apertural (A_1), lateral (A_2), apical (A_3) views, and apical view of protoconch (A_4) of the holotype. **B**, **C**. Jaźwica quarry (set J). **B**. GIUS 4-1109 Jaź-4, apertural (B_1), lateral (B_2), apical (B_3) views, and apical view of protoconch (B_4). **C**. GIUS 4-1146 Jaź-41, apertural view. **D**, **E**. *Roemeriella octocincta* (Roemer, 1843), Jaźwica quarry (set J). **D**. GIUS 4-1130 Jaź-25, apertural (D_1) and lateral (D_2) views. **E**. GIUS 4-1129 Jaź-24, lateral view. **F**–**L**. *Kowalatrochus sanctacrucensis* Krawczyński, 2002. **F**. GIUS 4-1569 Ko-81, apertural (F_1) and lateral (F_2) views of holotype. **G**–**I**, **L**. GIUS 4-1219 Ko-6 (**G**), GIUS 4-1226 Ko-13 (**H**), GIUS 4-1614 Jaź-96 (**I**), and ZPAL Ga-VI/58 (**L**), lateral views. **J**. ZPAL Ga-VI/59, apertural (J_1) and lateral (J_2) views. **K**. GIUS 4-1223 Ko-10, apertural view. **F**–**H**, **J**–**L**. Kowala quarry (set A). **I**. Jaźwica quarry (set I).

(Jaźwica, set J; see Fig. 6L: g) and in the Wietrznia Beds at Wietrznia (set B; see Fig. 6M: g). It was first described from the upper Sitkówka Beds of Grabina (set B; Middle Frasnian).

***Naticopsis inflata* (Roemer, 1843)** (Fig. 6A–K, L_1: n).—22 near-complete shells and 12 fragments with well-preserved external surface. In the Holy Cross Mountains, *Naticopsis inflata* occurs commonly in the Early Frasnian of Kowala (upper Sitkówka Beds, set A), at the Kadzielnia Member (Kadzielnia, set A; Jaźwica, set J), and has also been recognised from the younger Frasnian of Grabina (sets B and C), at Sitkówka-Jaźwica (set B), Szczukowskie Górki and Łagów (Krawczyński 2002; see also Siemiradzki 1909; Sobolev 1912). *N. inflata* occurs in reefal and fore-reef associations: *Kowalatrochus sanctacrucensis*, *Euryzone kielcensis*, *Grabinopsis guerichi*, and "*Naticopsis*" *excentrica*. This species is widely distributed on the Laurussian shelf and, in addition to the Harz Mountains, has been reported from the Frasnian of the Erzgebirge (Gallwitz and Gothan 1939), the Sudetes (Tietze 1871) and the Main Devonian Field in Russia (Nalivkin 1941).

The genus *Naticopsis* McCoy, 1844 has a trapezoidal on the inside and concentric on the outside operculum in comparison to similar shells of *Hessonia* Heidelberger, 2001, which has a paucispiral operculum (Bandel and Heidelberger 2001). In the absence of an operculum it is very dificult to recognise

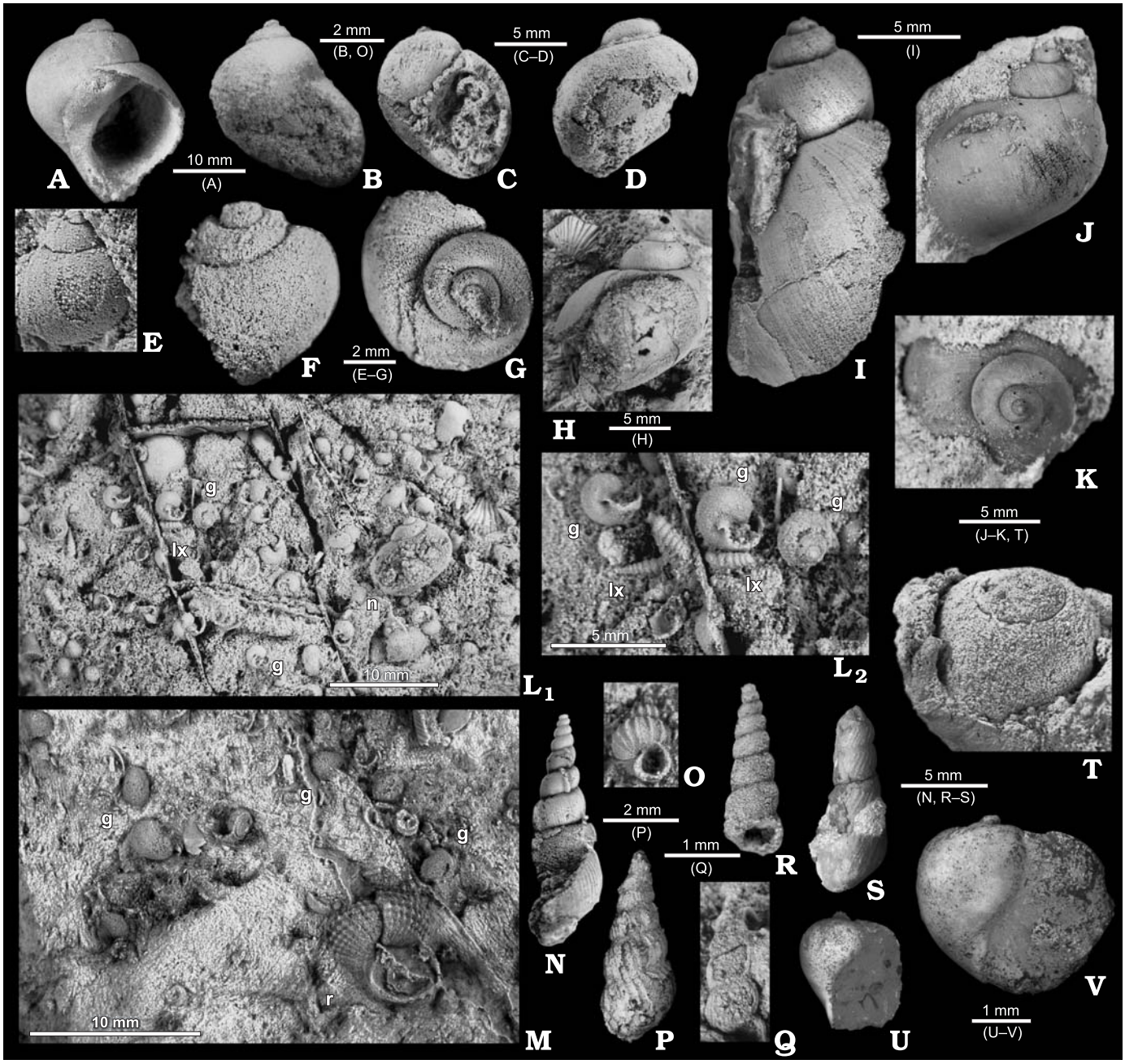

Fig. 6. Early Frasnian Neritopsoidea and Loxonematoidea from the Holy Cross Mountains. **A**–**K**. *Naticopsis inflata* (Roemer, 1843). **A**. ZPAL Ga-VI/30, Kadzielnia (set A), apertural view of shell with well preserved ornamentation. **B**, **C**. GIUS 4-1238 Ko-25 (**B**) and GIUS 4-1230 Ko-17 (**C**), Kowala quarry (set A), apertural views of shells. **D**–**F**, **H**–**J**. GIUS 4-1148 Jaź-43 (**D**), GIUS 4-1145 Jaź-40 (**E**), GIUS 4-1623 Jaź-105 (**F**), GIUS 4-1648 Jaź-130 (**H**), GIUS 4-1631 Jaź-113 (**I**), and GIUS 4-1640 Jaź-122 (**J**), Jaźwica quarry (set J), lateral views of shells. **G**, **K**. GIUS 4-1636 Jaź-118 (**G**) and GIUS 4-1630 Jaź-112 (**K**), Jaźwica quarry (set J), apical views of shells. **L**, **M**. *Grabinopsis guerichi* association: g, *Grabinopsis guerichi* Krawczyński, 2002; r, *Roemeriella octocincta* (Roemer, 1843); n, *Natocopsis inflata* (Roemer, 1843); lx, ?loxonematoid indet. **L**. GIUS 4-1645 Jaź-127, Jaźwica (set J), weathered surface with gastropods (L_1) and increased surface fragment with unrecognized ?loxonematoid shells (L_2). **M**. GIUS 4-2388 Wt-1, Wietrznia (set B), well preserved gastropod shells on weathered surface. **N**. *Spanionema scalaroides* (Whidborne, 1889), GIUS 4-1193 Kd-1 Kadzielnia (set A), lateral view of shell. **O**–**Q**. *Palaeozygopleura* (*Rhenozyga*) sp. **O**, **P**. Jaźwica quarry (set J). **O**. GIUS 4-1634 Jaź-116, apertural view of shell. **P**. GIUS 4-1837 Jaź-208, lateral view of shell. **Q**. GIUS 4-1348 Ko-70/22, Kowala quarry (set A), apertural view of shell fragment. **R–S**. *Palaeozygopleura* (*Bohemozyga*) *pyritica* Krawczyński, 2006 in Jagt-Yazykova et al. 2006. **R**. GIUS 4-1627 Jaź-109, Jaźwica quarry (set J), apical view of shell. **S**. GIUS 4-2284 Kos-14, Kostomłoty II (Małe Górki) quarry (set B_3), lateral view of pyritised holotype shell. **T**. *Naticopsis protogaea* (Goldfuss, 1844), GIUS 4-1353 Ko-75, Kowala quarry (set A), lateral view of shell. **U**, **V**. *Naticopsis* aff. *kayseri* Holzapfel, 1895, GIUS 4-2288 Kos-18 (**U**) and GIUS 4-1164 Kos-2 (**V**), Kostomłoty II (Małe Górki) quarry (set B_3), apertural views of pyritised shells.

the genus. *Hessonia piligera* (Sandberger and Sandberger, 1856), recorded from Givetian deposits of the Rhenish Slate Mountains (Sandberger and Sandberger 1856; Holzapfel 1895; see also Heidelberger 2001), is morphologically identical to *N.*

inflata from the Frasnian of the Harz Mountains (Roemer 1843; Clarke 1895), but *Hessonia piligera* has two grooves at the parietal part of the inner lip, which enabled precise fitting of paucispiral operculum, in difference to *Naticopsis inflata*. These details of aperture structure are the sole differences among the two taxa, similarly as in some other neritimorphs (e.g., *Neritopsis* and *Nerita*; see Kaim and Sztajner 2005).

***Naticopsis protogaea* (Goldfuss, 1844)** (Fig. 6T).—Only a single teleoconch, lacking the aperture. As with *N. inflata*, the operculum of this taxon is unknown, leaving generic assignment doubtful (see Heidelberger 2001). This species occurs at some levels with the Early Frasnian upper Sitkówka Beds at Kowala (set A) within the *Kowalatrochus sanctacrucensis* association. The rounded shell with comparatively low whorls of *N. protogaea* was found also in the Stromatoporoid-Detrital Beds at Grabina (set C; see Krawczyński 2002), and is also known from the Givetian and Frasnian of the Rhenish Slate Mountains (Goldfuss 1844; Paeckelmann 1922; Heidelberger and Koch 2005).

***Naticopsis* aff. *kayseri* Holzapfel, 1895** (Fig. 6U, V).— Two well-preserved pyritised shells lacking protoconchs from the Goniatite Level (Early Frasnian Szydłówek Beds) at Kostomłoty. An almost rounded shell with nearly flat sides, protruding apex and strongly developed last whorl similar to *N. kayseri* from Givetian limestone at Martenberg (Rhenish Slate Mountains; Holzapfel 1895). The form from the Holy Cross Mountains has a better developed ultimate whorl and the aperture occupies two thirds of shell width (Krawczyński in Jagt-Yazykova et al. 2006). The same type of shell was described by Heidelberger and Koch (2005) from the Givetian of Schwelm (Rhenish Slate Mountains).

Loxonematoidea

***Palaeozygopleura* (*Rhenozyga*) sp.** (Fig. 6O–Q).—Ten shells with partially visible ornament; The earlier whorls are not preserved and therefore, it is impossible to identify this material to species level. These small gastropods are common in reefal facies within the *Grabinopsis guerichi* association of the Early Frasnian Kadzielnia-type assemblage (Jaźwica, set J), and appear also in the same association in the Middle Frasnian *Stachyodes* assemblage (Grabina, set B).

***Palaeozygopleura* (*Bohemozyga*) *pyritica* Krawczyński, 2006 in Jagt-Yazykova et al. 2006** (Fig. 6R, S).—Five pyritised fragments with well-preserved ornament and a single poorly preserved non-pyritised shell. They occur in the Goniatite Level (the uppermost part of Szydłówek Beds; Early Frasnian, *Palmatolepis transitans* conodont Zone), being part of the thanatocoenosis preserved there (see Jagt-Yazykova et al. 2006). Representatives of this species have also been found in the coeval Kadzielnia Member (Jaźwica, set J; see correlations in Pisarzowska et al. 2006).

?loxonematoid indet. (Fig. 6L: lx).—Ten poorly preserved, small (ca. 5 mm height) turriculate shells with unusual, uncoiled ultimate whorl in gerontic stadium, and similar to representatives of the superfamily Loxonematoidea Koken, 1889. However, because of poor preservation (of both proto- and teleoconchs), it is almost impossible to identify this taxon in more detail; it is probably new. These gastropods are assigned to the *Grabinopsis guerichi* association, appearing in the Kadzielnia-type assemblage (Jaźwica, set J).

***Spanionema scalaroides* (Whidborne, 1889)** (Fig. 6N).—A single complete turriculate shell with typical collabral swellings, irregularly distributed on the whorl surface, from Kadzielnia (set A). This species is included in the *Euryzone kielcensis* association, and is also known from the upper Sitkówka Beds of Szczukowskie Górki (Krawczyński 2002) as well as from the Givetian of England (Whidborne 1891) and the Rhenish Slate Mountains, Germany (Holzapfel 1895; Heidelberger 2001).

Subulitoidea

***Macrochilina ventricosa* (Goldfuss, 1844)** (Fig. 3I).—Two well-preserved shells from the Early Frasnian at a quarry on Góra Zamkowa, Chęciny (set F; the *Straparollus laevis* assemblage) and from the upper Sitkówka Beds at Kowala (set A; the *Kowalatrochus sanctacrucensis* association within the *Actinostroma* assemblage). This species has previously been recorded from the Middle and Late Frasnian successions of the northern slope of the Dyminy Reef (Szczukowskie Górki and Grabina; see Krawczyński 2002), and is also known from the Givetian of the Rhenish Slate Mountains (Goldfuss 1844; Sandberger and Sandberger 1856) and of England (Whidborne 1891).

***Westerna subcostata* (Schlotheim, 1820)** (Fig. 3J–T).—Four near-complete shells, 30 fragments of teleoconchs with well-preserved outer surface and two internal moulds. Shells large (up to 200 mm in height), turriculate and known from different reefal settings representing the *Kowalatrochus sanctacrucensis* association (Kowala, set A; Sitkówka-Kowala, set B) and of the *Euryzone kielcensis* association (Kadzielnia, set A; Jaźwica, set J) within the Kadzielnia-type assemblage. Moreover, they commonly appear in the Late Frasnian *Straparollus circularis* association (Bolechowice- Panek, set B; see Krawczyński 2002) and in Frasnian strata at Łagów (Siemiradzki 1909). This Frasnian species is fairly widely distributed in the Eifel and Rhenish Slate Mountains (Goldfuss 1844; Paeckelmann 1912), the Harz Mountains (Roemer 1843) and England (Phillips 1841; Whidborne 1891).

Palaeostyloidea

***Goniasma*? cf. *zarecznyi* (Gürich, 1903)** (Fig. 3V).—Nine poorly preserved, small turriculate shells with poorly visible selenizone just below the whorl periphery, from the Givetian–Frasnian transition (the Chęciny Beds) in the western quarry at Góra Zamkowa (set F), occurring within the open marine *Straparollus laevis* assemblage. This species is also

known from Late Givetian strata of the Dębnik Anticline (Cracow Upland; Gürich 1903).

Systematic palaeontology of the new gastropod taxa

Superfamily Eotomarioidea Wenz, 1938
Family Eotomariidae Wenz, 1938
Genus *Frydiella* nov.

Type species: *Frydiella kaimi* gen. et sp. nov.; monotypic.

Derivation of the name: In honour of Dr. Jiří Frýda—Palaeozoic gastropod specialist from Prague (Czech Republic).

Diagnosis.—*Frydiella* gen. nov. is characterised by a turbiniform, anomphalous shell with a moderately high spire and a protruding selenizone, on the periphery of the whorl, with an additional, weak spiral cord. *Frydiella* gen. nov. differs from *Bembexia* Oehlert, 1888, *Clavibembexia* Blodgett, Frýda, and Racheboeuf, 1999, *Dictyobembix* Tyler, 1965, and *Breizospira* Blodgett, Frýda, and Racheboeuf, 1999 in having a higher spire and more distinct selenizone. The genus *Quadricarina* Blodgett and Johnson, 1992 has a lower whorl and a concave selenizone with an additional pair of spiral cords. The genera *Kersadiella* Blodgett, Frýda, and Racheboeuf, 1999 and *Balbinipleura* Bandel and Frýda, 1996 closely resemble each other as far as shell shape is concerned, but their selenizones are more concave and delimited by strong spiral cords and lack an additional spiral thread inside the selenizone. A selenizone with an additional cord is known in *Ruedemannia* Foerste, 1914 (family Lophospiridae Wenz, 1938), but the selenizone is wider and does not protrude; in addition, the spiral cord is stronger than in *Frydiella* gen. nov.

Frydiella kaimi gen. et sp. nov.

Fig. 4A–C.

Holotype: GIUS 4-1136 Jaź-31 (Fig. 4A).

Type locality: Active quarry "Jaźwica" near Kielce, Holy Cross Mountains, Poland.

Type horizon: Kadzielnia Member, Early Frasnian (Late Devonian).

Derivation of the name: In honour of Dr. Andrzej Kaim—Mesozoic gastropod specialist from Warsaw (Poland).

Material.—Two near-complete shells, a single fragment, and a single mould of external shell surface (GIUS 4-1135 Jaź-30, 4-1136 Jaź-31, 4-1137 Jaź-32, 4-1168 Sn-1).

Diagnosis.—Convex subsutural ramp with three tubercle spiral cords one of which is weaker below the upper suture. There are six nodular spiral cords on the anomphalous base.

Description.—Shell small, dextral and turbiniform of moderate whorl height, consisting of five whorls (size of the holotype: height 6.4 mm, width 5.5 mm), convex ramp, ornamentation on ramp consists of three strong spiral cords, and counting from the upper suture, the second and third of these strongly protrude. Prosocline growth lines cross spiral cords and form small tubercles at cross points. Base slightly flattened, anomphalous with six distinct spiral cords and tubercles appearing as a result of crossing with growth lines. Aperture with a shallow slit in the middle of the outer lip; this slit forms a rather wide selenizone which protrudes slightly above the surface of the whorl. The selenizone is also delimited by two spiral cords and shows an additional less distinct spiral thread in the center. The inner lip is weakly thickened and poorly preserved. Sutures are deep and slightly grooved, the lower being situated just below the first spiral cord under the selenizone. Protoconch poorly preserved. Pleural angle is 68°.

Discussion.—*Frydiella kaimi* sp. nov. is a rare, probably endemic, species encountered in the *Euryzone kielcensis* association within the the Kadzielnia-type mud mound assemblage (see Szulczewski and Racki 1981).

Occurrence.— At the type locality, Jaźwica (the Kadzielnia Member, set J; Early Frasnian) and in marly limestones at Sosnówka (*Phlogoiderhynchus* Level, set D) in Holy Cross Mountains, Poland (the bottom of *Phlogoiderhynchus* Level at Sosnówka is probably Early Frasnian in age; see Pisarzowska et al. 2006: fig. 16).

Superfamily Trochoidea Rafinesque, 1815
Family Elasmonematidae Knight, 1956
Genus *Heidelbergeria* nov.

Type species: *Heidelbergeria czarnieckii* gen. et sp. nov.; monotypic.

Derivation of the name: In honour of Dr. Doris Heidelberger—Palaeozoic gastropod specialist from Oberursel (Germany).

Diagnosis.—This genus is characterised by a turbiniform shell with low whorls and narrow phaneromphalous base and thick columellar lip; it differs from the Silurian *Discordichilus* Cossmann, 1918 in having a narrow phaneromphalous base, a straighter columellar lip with a thicker parietal part. The genus *Elasmonema* Fischer, 1885 has shallower sutures, distinctly higher whorl and collabral ornament. *Heidelbergeria* differs from *Anematina* Knight, 1933 by a thicker columellar lip and a lower whorl. The genus *Holopea* Hall, 1847 (family Holopeidae Wenz, 1938) is similar in shell shape but has a thinner and more arched inner lip and only prosocline growth lines. *Archaeosphera* Heidelberger and Bandel, 1999 resembles the new genus very closely in shell shape, but *Heidelbergeria* has a thicker and straighter inner lip, a narrower umbilicus and whorls embrace each other distinctly below the periphery. The turbiniform shell with thick columellar lip is also similar to that of genera of the family Anomphalidae Wenz, 1938. *Heidelbergeria* differs from the Permian *Sosiolytes* Gemmellaro, 1889 in showing a narrow phaneromphalous base and thick inner lip. The Carboniferous *Turbinilopsis* Koninck, 1881 has a longitudinal groove on the columellar lip and the umbilicus is covered by callus. *Anomphalus* Meek and Worthen, 1867 and *Isonema* Meek and Worthen, 1866 have cryptomphalous shells.

Heidelbergeria czarnieckii sp. nov.

Fig. 5A–C.

Holotype: ZPAL Ga-VI/29 (Fig. 5A).

Type locality: Abandoned quarry Kadzielnia in Kielce, Holy Cross Mountains, Poland.

Type horizon: The Kadzielnia Member, Early Frasnian (Late Devonian).

Derivation of the name: In honour of Dr. Stanisław Czarniecki—a scholar of Carboniferous fossils from Cracow (Poland).

Material.—Two near-complete shells, a single fragment, and one mould of external shell surface (ZPAL Ga-VI/29; GIUS 4-1109 Jaź-4, 4-1146 Jaź-41).

Diagnosis.—H. czarnieckii is characterised by a turbiniform shell with low whorls; whorls embrace each other at one third of whorl height; profile of whorls distinctly rounded; no ornament.

Description.—Shell small, dextral, turbiniform with four whorls (size of holotype: height 9 mm, width 9 mm). Whorl height less than that of aperture. Profile of whorls is distinctly rounded. Sutures are deep, situated somewhat below the whorl periphery. Growth line is almost orthocline just below suture and then arches to strongly prosocline. Base is rounded and narrowly phaneromphalous. Outer lip is rounded and thin. Columellar lip is thick and slightly convex and expanded into the umbilicus, and at an angle of ca. 30° with respect to shell axis. Columellar lip connected to shell wall at two-thirds of height of aperture and forming delicate thickening at the parietal part. Aperture is oval, teardrop-shaped holostomatous with angulation at contact of outer lip with shell wall; almost no ornament, except of delicate growth lines. Archaeogastropod-like protoconch with a diameter of 200 μm (see Fig. $5A_4$ and B_4). Pleural angle is 90°.

Discussion.—*Heidelbergeria czarnieckii* sp. nov. is probably endemic, and is encountered in the *Euryzone kielcensis* association within the Kadzielnia-type reefal assemblage.

Occurrence.—At the type locality Kadzielnia (set A) and at the active quarry "Jaźwica" near Kielce (set J; Kadzielnia Member; Early Frasnian), Holy Cross Mountains, Poland.

Discussion

As a result of the transgression during the Middle Devonian, carbonate platforms appeared in the Polish-Moravian part of the southern shelf of Laurussia, developing, amongst other structural elements, on the Małopolska Block (Racki 1993b; Szulczewski 1995). First, the *Stringocephalus* biostromal bank developed during inundation in earliest Late Givetian time (cycle IIb *sensu* Johnson et al. 1985). Meanwhile, the Chęciny-Zbrza intrashelf basin formed in the southern part (Szulczewski 1971; Racki 1993b), which hosted the low-diversity *Straparollus laevis* assemblage as a result of extra-regional immigration (Racki 1988) (Table 1; see also Krawczyński 1998). That bottom-level assemblage persisted into the Early Frasnian and occurs there in the open shelf macrofossil-poor calcilutites and calcarenites (upper Chęciny Beds; see Racki 1993b).

The next strong transgressive pulse (IIb/c *sensu* Racki 1993b; see discussion in Pisarzowska et al. 2006) caused flooding of the platform and the Dyminy Reef grew (see also Szulczewski 1995). This was a time of additional extra-regional immigratory events (Racki 1988) and, linked with it, the appearance of typically Frasnian gastropod species. The reefal rim (barrier) was inhabited by the *Actinostroma* assemblage together with the *Kowalatrochus sanctacrucensis* association (Table 1) and characteristically large and thick shells of the following gastropods are encountered: *Kowalatrochus sanctacrucensis*, *Orecopia kadzielniae*, and *Westerna subcostata*. Along the southern and northern slopes of the reef, below wave base, mud mounds formed with a rich and diverse Kadzielnia-type fauna (Szulczewski and Racki 1981; Racki 1993b). Two gastropod associations occur here: (1) *Euryzone kielcensis*, comprising thick-shelled gastropods, in part linked to the *K. sanctacrucensis* association, as well as some probably endemics restricted to specific mud mound settings (see Table 1); (2) *Grabinopsis guerichi* (Table 1), comprising small gastropods, numerous and appearing in clusters (see Fig. 6L–M), and connected with fore-reefal facies: Kadzielnia-type and *Stachyodes* assemblages (Łukaszewicz 2001; Krawczyński 2002).

Along the northern slope of the Dyminy Reef (northern Kielce subregion; see Fig. 1), probably better developed detrital fore-reef facies occurred, enriched with massive stromatoporoids (Wietrznia Beds; Racki 1993b), occasionally attaining gigantic sizes (Racki and Sobstel 2004). These Early Frasnian rough-water habitats are characterised also by the occasional occurrence of gastropods assigned to the *G. guerichi* association (see Fig. 6M). A particular case of a pyritised gastropod association has been documented from the Goniatite Level of the Kostomłoty facies zone, formed as a result of expanding hypoxic conditions in the intrashelf Kostomłoty basin (Racki et al. 2004). This *post mortem* gastropod complex was formed by transportation of shells from reefal and fore-reef environments, probably as a result of quasi-estuarine circulation of water masses during storms (Jagt-Yazykova et al. 2006).

The next Middle Frasnian deepening pulse (IIc *sensu* Johnson et al. 1985; Middlesex Event, e.g., Becker and House 1998, House 2002), which probably coincided with a major biogeochemical perturbation in global carbon cycling (Yans et al. in press; see also Pisarzowska et al. 2006), reflected by disappearance of Kadzielnia-type mud mounds. As a result of environmental changes (e.g., fluctuating redox regimes and/or eutrophication; Leszek Marynowski, personal communication 2006), gastropods from the *Straparollus laevis* assemblage (*Straparollus laevis*, *Goniasma*? cf. *zarecznyi*) and a minimum of six endemics in the *Euryzone kielcensis* association [*Euryzone kielcensis*, *Euomphalus* aff. *pulcher*, *Frydiella kaimi*, *Heidelbergeria czarnieckii*, *Palaeozygopleura* (*Bohemozyga*) *pyritica* and an indeterminate loxonematid with un-

usual uncoiled shell in the gerontic stage (see Table 1, see also Fig. 2)] became extinct. The most taxa from that benthos (e.g., *Westerna subcostata, Orecopia kadzielniae, Porcellia bifida, Spanionema scalaroides*) migrated into reefal habitats (see Fig. 2). Only a single species, *Euryzone delphinuloides*, occurring as a relict from the Givetian *Stringocephalus* biostromal bank fauna from the *Kowalatrochus sanctacrucensis* association, became extinct (see Fig. 2; Krawczyński 1998).

From the start of the Middle Frasnian, no new gastropod species occur in any of the studied sections (biotic stagnation phase; see summary in Pisarzowska et al. 2006). New taxa occur only at the Middle–Late Frasnian transition, marking the next wave of extra-regional immigration connected with transgressive pulse IId (*sensu* Johnson et al. 1985) and the lower Kellwasser Event (Krawczyński 2002; see also Racki 1993b).

Conclusions

Due to the severe environmental stress, probably reflected in a major biogeochemical perturbation in global carbon cycling (*Palmatolepis punctata* event of Yans et al. in press), and connected with a transgressive pulse (IIc; see Johnson et al. 1985; Pisarzowska et al. 2006), the following regional bioevents in gastropod succession have been observed within the southern Polish shelf: (1) the probable extinction of three relict species from the Givetian *Stringocephalus* bank phase and demise of the low-diversity *Straparollus laevis* assemblage, inhabiting the Late Givetian Chęciny-Zbrza intrashelf basin; (2) disappearance (extinction or migration) of six probably endemic species, belonging to the highly diverse Kadzielnia-type biota (containing at least 15 gastropod taxa from the *Euryzone kielcensis* association and, in part, the *Grabinopsis guerichi* association), linked to submergence of the mud mounds, formed just below wave base; (3) interregional migration of gastropods, connected to high-energy environments of barrier reef (*Kowalatrochus sanctacrucensis* association and, in part, *Euryzone kielcensis* association), and also small gastropods from the *Grabinopsis guerichi* association, which occupied fore-reef environments; (4) lack of biotic reaction among eurytopic (cosmopolitan) gastropods connected with different reef associations (e.g., *Naticopsis inflata*).

Amongst the twenty-four typical taxa occurring in the Early Frasnian at least eleven could not survive environmental changes across the Early–Middle Frasnian transition. Mainly endemic species from highly diverse Kadzielnia-type benthic assemblage, developing locally, vanished (see also diversity analysis in Krawczyński 2002: fig. 18). All other species migrated into the shallower parts of Dyminy Reef complex and re-appeared in the Middle and Late Frasnian. Thus, neither the Middlesex Event nor the major biogeochemical perturbation did play a significant role in the evolution of gastropods in the Polish-Moravian part of the shelf (possibly like the whole biosphere; see Sepkoski 1996: fig. 6), in contrast to the catastrophic Frasnian–Famennian extinction (Krawczyński 2002). However, for the general determination of impact of that Middle Frasnian global bioevent it is necessary to conduct additional studies (see House 2002), particularly comparisons of gastropod development in other regions of the southern shelf of Laurussia.

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