Frasnian gastropod synecology and bio−events in the Dyminy reef complex of the Holy Cross Mountains, Poland

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Frasnian gastropods from the Kowala Formation (north−western part of the Holy Cross Mountains, Poland) form five reef associations and one lagoonal assemblage are described. The distinct influence of regional shallowing−upward cycles on the composition of gastropod fauna have been observed. Composition changes of this fauna were controlled by IIb/c, IIc, and IId cycles. Early Frasnian reef association appeared with predominantly thick−shell gastropods, which occur in the upper Sitkówka Beds. At the beginning of IIb/c cycle, Kadzielnia−type mud mounds with a high diversified gastropod association appeared. The next cycles caused the disappearance of mud mounds (IIc), the sinking of the Dyminy reef (IId), and extinction of the gastropod associations from the upper Sitkówka Beds. Two gastropod associations and one poorly diversified lagoonal assemblage predominated in the reef−cap stage. Frasnian reef gastropods have not been observed in the Famennian and Early Carboniferous series. Thus, they probably became extinct together with the collapse of the Frasnian reef ecosystem near the Frasnian−Famennian boundary. Twenty seven taxa have been recognized, among them three new species and two new genera are described: Kowalatrochus sanctacrucensis gen. et sp. nov., Grabinopsis guericchi gen. et sp. nov., and Loxoplocus (Donaldiella) karczewskii sp. nov. Two poorly known Gürich’s species have been also revised: Euryzone kielcensis and Orecopia kadzielniae.

Key words: Gastropoda, Devonian, taxonomy, palaeoecology, Frasnian−Famennian extinction, Poland.

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Introduction

Devonian gastropods, which mostly occur in reef and lagoonal facies, are very poorly known, especially from palaeoecological and evolutionary viewpoints. There is a lack of data regarding the history of this group during the major extinction time of reef ecosystems at the Frasnian−Famennian boundary (McGhee 1996). Extensive new material collected in Frasnian sequences of the Holy Cross Mountains allowed more detailed investigations of the gastropods.

Frasnian gastropods from the Holy Cross Mountains were first described by Pusch (1837). One of them is Buccinum vetustum which is from the Frasnian limestone at Karczówka hill in Kielce. Gürich (1896) presented more detailed descriptions of Frasnian gastropods. He has depicted eleven Frasnian species, including four new ones: Pleurotomaria kadzielniae, Pleurotomaria cardiolae, Polytropis kielcensis, and Loxonema polonicum. There are a lot of works with notices on the occurrence of Frasnian gastropods (e.g., Siemiradzki 1909; Sobolev 1909, 1912; Stasińska 1953; Kaźmierczak 1971; Szulczewski 1971; Różkowska 1980; Racki 1988, 1993b; Karczewski 1992). Karczewski (1980, 1989) published two papers about Devonian gastropods from the Holy Cross Mountains where he also took into account Frasnian taxa. In the present paper some of the Karczewski’s determinations are corrected. The history of development of gastropod fauna is studied in context of Frasnian global events.

Geological settings

The Holy Cross Mountains are divided into the three main palaeogeographical units: the Łysogóry region, Kielce region, and the Kostomłoty transitional zone between them (Szulczewski 1971, 1995; Racki 1993b, 1997). Frasnian gastropods occur mainly in the rocks of the Kielce region, which has been divided (Racki 1993b) into four subregions: Northern, Central, Southern, and Chęciny−Zbrza. The studied material was collected from the first three subregions: Northern (Kadzielnia, Karczówka, Grabinia, Szczukowskie Górki), Central (Sitkówka−Kowala, Sitkówka−Jaźwica, Panek), and Southern (Kowala, Jaźwica) (Fig. 1). That division is connected with a visually symmetric Frasnian reef structure, which is called the “Dyminy reef”. A shoal corresponding to the Central Kielce subregion is recognized, and the slopes are
consequently recognized in the Northern and Southern Kielce subregions (Fig. 2; see Racki 1993b).

The history of the reef evolution was scrutinized by Racki (1993b) and Szulczewski (1995). The middle Givetian aggraded *Stringocephalus* bank was drowned in the late Givetian (cycle IIb; *sensu* Johnson et al. 1985; see also Racki 1997; Fig. 2), and a stromatoporoid-coral biostromal complex appeared (lower Sitkówka Beds; see Kaźmierczak 1971; Szulczewski 1971; Racki 1993b, 1997; Fig. 2). A large transgressive pulse in the early Frasnian (Early *Palmatolepis punctata* Zone) caused the appearance of the symmetrical reef structure (the upper Sitkówka Beds) surrounded by Kadzielnia-type mud mounds and the Detrital Beds. The strongest transgressive pulse (IId *sensu* Johnson et al. 1985), connected with anoxic Kellwasser events (Walliser 1996), contributed to the disappearance of the reef structure (*Pa. rhenana* Zone) and its covering by the reef cap, as well as to its total extinction before the Frasnian–Famennian boundary (see Narkiewicz 1987; Racki 1990; Fig. 2).

The gastropods can be mostly found in biolithites and organodetrital limestones and less often in marly limestones (Fig. 3; for detailed lithostratigraphic terminology, including set definitions, see Racki 1993b). Locations with gastropod faunas are concentrated in the Frasnian Kowala Formation sets, detrital beds and lower Frasnian mud mounds (Fig. 2).

**Material**

Most of investigated material (about 300 specimens) was collected by the author during field trips in 1995–2000. Forty specimens were collected by Racki in 1976–1994 and later initially studied by Karczewski (1989). The gastropod collection from the Institute of Palaeobiology of the Polish Academy of Science, Warsaw (abbreviated ZPAL), and gastropods from the original collection of Gürich (1896) deposited at the Geological Museum of the Institute of Geological Sciences of Wroclaw University (abbreviated MGUWr), have also been studied. The author’s collection as well as Racki’s specimens are housed at the Faculty of Earth Sciences of Silesian University, Sosnowiec (abbreviated GIUS).
Taxonomic review of gastropods

Abbreviations used: H/W, height to width of the shell ratio; H_w/W_w, height to width of a whorl ratio; H_a/W_a, height to width of the aperture ratio.

**Euomphaloideans**

*Straparollus (Straparollus) serpens* (Phillips, 1841) (Fig. 4E).—Eleven specimens of the discoidal shell of this species and some fragments of its spire have been found in the middle Frasnian upper Sitkówka Beds of Grabina (set A) and in the late Frasnian Detrital Beds of Panek (set B) and Grabina (set C).

*Straparollus (Straparollus) circularis* (Phillips, 1841) (Fig. 4A, B).—Relatively large shells (diameter to 5 cm) with a distinct peripheral ridge on the last whorl and with septation in the older part of spire occur in the Kadzielnia Member (Kadzielnia, set A) and in the Detrital Beds (Panek, set B); Grabina, set C).

**Pleurotomarioideans**

*Liospira* sp. (Fig. 5G, H).—A fragment of a discoidal shell with a selenizone at the periphery of the whorl has been found in the middle Frasnian upper Sitkówka Beds (Grabina, set B).

*Villmaria ventricosa* Heidelberger, 2001 (Fig. 4G).—Species of recently erected genus *Villmaria* Heidelberger, 2001. Five well preserved turbiniform shells and six shell fragments are present, which are characterized by a gradate spire with a gently projecting selenizone just above the whorl periphery. The shells have spiral ornamentation on the inclined ramp and a rounded convex base (see also Heidelberger 2001). *V. ventricosa* was recognized in the upper Sitkowa Beds (Grabina, set B; Kowala, set A) as well as in the Kadzielnia Member (Kadzielnia, set A) and the Detrital Beds of Grabina (set C).

*Loxoplocus* (Donaldiella) karczewskii sp. nov. (Fig. 6A–E).—See description on p. 273.

*Laehnospira taeniatia* (Sandberger, 1842) (Fig. 4M).—Species of recently erected genus *Laehnospira* Heidelberger, 2001. A few specimens of *L. taeniatia*, the shell having a turbiniform shape with a wide protruding selenizone (see also Heidelberger 2001), were found in the middle Frasnian of the upper Sitkowa Beds (Grabina, set B).

*Euryzone kielcensis* (Gürich, 1896) comb. nov. (Fig. 7G–L).—See description on p. 274.

*Coelozo* sp. (Fig. 8N).—Two fragments of a shell with a wide selenizone just above the suture have been established in the upper Sitkowa Beds at “Kowala” quarry (lower Frasnian, set A).

**Cirroideans**

*Porcellia bifida* (Sandberger and Sandberger, 1850–1856) (Figs. 4L, 7A–C).—Four relatively well preserved pseudo-
Fig. 3. Correlation of reference sections representing the Northern (Grabina), the Central (Panek), and the Southern (Kowala) Kielce Region with faunal composition, and lithology (after Kaźmierczak 1971; Szulczewski 1971; Coen-Aubert and Wrzołek 1991; Racki 1993b; Krawczyński 1998).
isostrophic shells were identified from the middle to late Frasnian in the Kadzielnia Member (Kadzielnia, set A; Jaźwica, set J) and in the Detrital Beds of Grabina (set C).

Trochoideans

*Kowalatrochus sanctacrucensis* gen. et sp. nov. (Fig. 8A–K).—See description on p. 276.

*Roemeriella octocincta* (Roemer, 1843) (Figs. 4H–I, 7F).—Species of recently erected genus *Roemeriella* Blodgett and Frýda, 1999. Eighteen rather well preserved specimens and 5 fragments of turbiniform shells were collected from the early to middle Frasnian in the Kadzielnia Member (Jaźwica, set J) as well as in the Detrital Beds (Grabina, set C; Szczukowskie Górkı).

Teleoconchs have prosoclinal costa on the first 2–3 whors without spiral ornamentation and four distinct spiral cords with small tubercles appearing on the next 4–6 whors. The next whors of the coeloconoidal shell have equal development of both spiral and prosoclinal elements forming a cancellate ornamentation (see also Blodgett and Frýda 1999).

*Roemeriella cyclostomoides* (Roemer, 1854) (Fig. 5L).—One well preserved specimen and 2 shell fragments were found in the middle Frasnian at Grabina, set B.

Murchisonioideans

*Murchisonia nerinea* (Sandberger and Sandberger, 1850–1856) (Figs. 4F, 5K).—Two fragments of the spire of *M. nerinea* were found in the upper Sítkówka Beds and the Detrital Beds of Grabina (middle and late Frasnian; set B and C).

*Murchisonia* sp. (Fig. 4D).—A few specimens with a turriculate spire and a selenizone at the periphery of the whorl have been found in the Kadzielnia Member (Kadzielnia, set A; middle Frasnian) as well as in the Detrital Beds of Panek (set B2; late Frasnian).

Neritoideans

*Grabinopsis guerichi* gen. et sp. nov. (Fig. 5A–F).—See description on p. 278.

*Naticopsis (Naticopsis) inflata* (Roemer, 1843) (Figs. 4O,
7D, E, 8O).—The most common specimens in Frasnian deposits exhibit naticiform shells with a large morphological variation within the species. *N. inflata* has been recognized from early to late Frasnian in the upper Sitkówka Beds (Kowala, set A2; Grabina, set B; Szczukowskie Górkı); in the Kadzielnia Member (Kadzielnia, set A; Jaźwica, set J), and in the Detrital Beds (Grabina, set C; Sitkówka-Jaźwica, set B).

*Naticopsis* (*Naticopsis*) *protogaea* (Goldfuss, 1844) (Figs. 4P, 8P).—Two fragments of shell with poorly preserved external surface have been found in the upper Sitkówka Beds (Kowala, set A2; Grabina, set B; Szczukowskie Górkı), in the Kadzielnia Member (Kadzielnia, set A; Jaźwica, set J), and in the Detrital Beds (Grabina, set C; Sitkówka-Jaźwica, set B).

*Naticopsis* (*Naticopsis*) *excentrica* (Roemer, 1843) (Fig. 4N).—Twenty shells of *N. excentrica* with typical ornamentation, consisting of zigzag costa on the older whorls and moderately collabral cords on later whorls, have been identified from the late Frasnian of Grabina (set C).

Omphalotrochoideans

*Orecopia kadzielniae* (Gürich, 1896) comb. nov. (Fig. 9A–I).—See description on p. 279.

Loxonematoideans

*Loxonema* sp.—Two poorly preserved turriculate shells were found in the upper Sitkówka Beds and the Detrital Beds of Grabina (middle and late Frasnian; set B and C).

*Palaeozygopleura* (*Rhenozyga*) cf. *retrostriata* (Kirchner, 1915) (Figs. 5M, 7H).—Species of recently erected subgenus *Palaeozygopleura* (*Rhenozyga*) Frýda, 2000. Near 20 fragments of small turriculate shells with minute collabral cords on the whors (see also Frýda 2000) were recognized in the upper Sitkówka Beds (Kowala, set A2; Grabina, set B; Szczukowskie Górkı) and also in the Kadzielnia Member (Jaźwica, set J).

*Palaeozygopleura* (*Rhenozyga*) sp. A (Figs. 4K, 5I).—Four specimens without protoconchs and some fragments of spire with collabral cords were collected from the Kadzielnia Member (Jaźwica, set J) and also from the upper Sitkówka Beds and the Detrital Beds of Grabina (set B and C).

*Palaeozygopleura* (*Rhenozyga*) sp. B (Fig. 4J).—This species consists of eight shell fragments lacking protoconchs with a more slightly rounded whorl profile and more densely spaced collabral ribs than *Palaeozygopleura* (*Rhenozyga*) sp. A. This taxon was found in the middle to upper Frasnian in the the upper Sitkówka Beds and the Detrital Beds of Grabina (set B and C).

Subulitoideans

*Macrochilina ventricosa* (Goldfuss, 1844).—Two complete subulate shells without ornamentation and five fragments of spire were identified from the middle to late Frasnian in the upper Sitkówka Beds of Szczukowskie Górkı and the Detrital Beds of Grabina (set C).

*Westerna subcostata* (Schlotheim, 1820) comb. nov. (Figs. 4C, 8L–M; see also Figs. 14A, 15B, C).—The largest gastropod of the Polish Devonian, whose turriculate shells can reach even 20 cm in height, was collected from the lower to upper Frasnian in the upper Sitkówka Beds (Kowala, set A2; Sitkówka-Kowala, set B), the Kadzielnia Member (Kadzielnia, set A), and the Detrital Beds of Panek (set B2). The material includes 68 specimens.
Earlier this species was assigned to *Macrocheilus* Phil¬
lips, 1841 or *Macrochilina* Bayle, 1880. However, the high
turriculate shell with a rounded base, as well as the initial
prosclinal shape of the labrum (and growth lines) that sub-
sequently becomes orthoclinal, and the weakly developed
siphonal notch due to the absence of the columellar fold are
typical features for the Frasnian genus *Westerna*.

*S. scalaroides* (Whidborne, 1889) (Fig. 7G).—One well
preserved shell and a fragment of a spire with the
typical varices have been found in the Kadzielnia limestone
at Kadzielnia (set A) and in the upper Sitkówka Beds of
Szczukowskie Górki.

**Description of new and poorly
known species**

Superfamily Pleurotomarioidea Swainson, 1840
Family Lophospiridae Wenz, 1938
Subfamily Lophospirinae Wenz, 1938
Genus *Loxoplocus* Fischer, 1885

**Remarks.**—Turriculate shells with V−shaped notch forming a
narrow convex selenizone at the middle of whorl belong to
genus *Loxoplocus*. Three subgenera are distinguished ac-
cording to their spire height and the disjunction of their
whorls. The protoconch of *Loxoplocus* is not known. Onto-
genic development of teleoconch is equal except for the sub-
genus *Loxoplocus* (*Loxoplocus*) Fischer, 1885, which is
marked by the disjunct whorls in the gerontic stage.

Subgenus *Loxoplocus* (*Donaldiella*) Cossmann, 1903

**Type species:** *Loxoplocus* (*Donaldiella*) *filosa* (Donald, 1902); the Late
Ordovician, Scotland.

**Remarks.**—*Loxoplocus* (*Donaldiella*) is distinguished by its
distinctly turriculate spire, whilst the similar *L.* (*Lophospira*)
Whitfield, 1886 has a relatively lower turbiniform shell. The
shell of *L.* (*Loxoplocus*) differs from both *L.* (*Lophospira*)
and *L.* (*Donaldiella*) by its disjunct whorls. Species of *L.* (*Donaldiella*) are singled out on the basis of its relative spire
height, apertural shape, and depth of the notch.

*Loxoplocus* (*Donaldiella*) karczewskii sp. nov.

Fig. 6A–E.


**Holotype:** GIUS 4−1293/Pan−21 (Fig. 6A).

**Type horizon and locality:** Active quarry “Panek”, set B3, the Detrital Beds; late Frasnian.

**Derivation of the name:** In memory of Dr. Leon Karczewski—investi-
gator of fossil snails.

**Material.**—Fourteen spire fragments without a preserved ap-
erture or older part of the shell (GIUS 4−1285−1288/P13−16,
4−1292−1301/Pan−20−29).

**Diagnosis.**—High turriculate shell with rounded aperture;
narrow distinctly prominent selenizone at the periphery of the
whorl. Septation present in the older part of the spire. *Loxoplocus* (*Donaldiella*) karczewskii sp. nov. differs from the type species *L.* (*Donaldiella*) *filosa* (Donald, 1902) by its
more slender spire and more prominent selenizone. The Late
Silurian *L.* (*Donaldiella*) *morinensis* Horny, 1952 has an oval
aperture and a differing whorl profile.

**Description.**—Shell turriculate (about 10 cm in height),
number of whorls unknown; shape of whorls distinctly angular; deep notch in center of outer lip, forming a narrow convex
selenizone at the periphery of the whorl; growth lines prosocinal above selenizone and opisthoclinal below it, base
with orthocinal growth lines; ornamentation consists of a
strong spiral cord midway between the suture and periphery
on the sutural ramp, anomphalous base with two spiral cords:
the first one of which is just above suture and the weak sec-
ond cord is situated between the periphery and lower suture;
aperture rounded; protoconch unknown; septation common
in the older part of the spire (see Fig. 15A); pleural angle con-

stant (about 12°), variability of the translation index \((H_w/W_w)\) low (Fig. 10).

Remarks.—The first specimens of this new species were described by Karczewski (1980) as *Stegocoelia* (*Hypergonia*) sp. However, the narrow convex selenizone at the periphery proves assignment his specimens to family Lophospiridae. The genus *Loxoplocus* has been recognized from the Ordovician and Silurian as well as from the Early Devonian (Horný 1952; Linsley 1968). The location of investigated specimens has allowed extension of the stratigraphic distribution of the genus *Loxoplocus* from the Ordovician to the late Frasnian.

**Distribution.**—Holy Cross Mountains: Panek, set B3 (the Detrital Beds; late Frasnian).

Family Gosseletinidae Wenz, 1938
Subfamily Coelozonidae Knight, 1956
Genus *Euryzone* Koken, 1896

*Type species:* *Euryzone delphinuloides* (Schlotheim, 1820); Middle Devonian, Germany.

Remarks.—The genus *Euryzone* contains species with trochiform shells and a wide, gently concave selenizone not bordered by spiral cords at the centre of the whorl ramp. The ontogenetic development of the spire is equal or with an increasing pleural angle.

**Euryzone kielcensis** (Gürich, 1896) comb. nov.

Fig. 7l–L.

*Polytopis kielcensis* sp. nov.; Gürich 1896: 310.

**Neotype:** GIUS 4-1134/Kad-3 (Fig. 7l–K).

**Type horizon and locality:** Kadzielnia in Kielce, set A—the biohermal Kadzielnia Member; middle Frasnian.

**Material.**—Two almost complete shells and two spire fragments (ZPAL Ga-VI/28, 33; GIUS 4-1134/Kad-3, 4-1174/ Kad-3).

**Revised diagnosis.**—Large-sized trochiform shell, narrowly phaneromphalous with a flattened base. Whorl profile with two distinctly rounded angulations: the first just below the suture and the second at the periphery. A steep inclined ramp with wide selenizone at middle of whorl is present between the angulations. The species differs from *E. delphinuloides* by its distinctly higher spire.

**Description.**—The trochiform shell is large (measurements of neotype: height 55 mm, width 56.5 mm) and slightly

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gradate with 5–6 whorls. Surface of the whorl flattened near suture and below strongly bent to form a weak, convex angulation. The ramp below this angulation is strongly inclined and becomes flattened on the narrow, phaneromphalous base. Rounded periphery at the border of the ramp and base. The selenizone is wide, flat and gently concaves, not bordered by spiral threads at the middle of the whorl ramp. Sutures are canalicate. Aperture rounded.

Ornamentation consists of spiral cords at ramp and base, but in gerontic stage consist only of growth lines. Growth lines are orthocline near suture and become prosocline below with a small sinus at the ramp above the selenizone. Growth lines below selenizone are opisthocline. Protoconch unknown. Pleural angle is 82°.

Remarks.—This species has been described by Gürich (1896) on the basis of specimens from Kadzielnia. However, its illustration is absent in the Gürich’s work. This is a relatively rare species, but a complete specimen has been found at the type locality. It has been designated as the neotype (GIUS 4-1478/ Kad-3; Fig. 6F–H).
Distribution.—Holy Cross Mountains: Kadzielnia, set A and Jaźwica, set J (the Kadzielnia Member, early Frasnian).

Superfamily Trochoidea Rafinesque, 1815
Family Holopeidae Wenz, 1938
Genus *Kowalatrochus* gen. nov.

*Type species:* *Kowalatrochus sanctacrucensis* gen. et sp. nov.

*Type horizon and locality:* Active quarry “Kowala” near Kielce, set A₂, the upper Sitkówka Beds, early Frasnian.

*Derivation of the name:* From type locality Kowala and trochus from trochiform shell.

*Diagnosis.*—*Kowalatrochus* gen. nov. differs from similar *Yunnania* Mansuy, 1912 by the shape of its shell. *Yunnania* has a turbiniform shell with an anomphalous base. **Compso−nema** Gordon and Yochelson, 1983 has a narrow phaneromphalous base with a circumumbilical ridge. The relatively large trochiform shell and cryptomphalous base of *Kowalatrochus* distinguishes it from other representatives of the family Holopeidae (see Knight 1941; Knight et al. 1960; Gordon and Yochelson 1983). Protoconch unknown. Teleoconch has a stable ontogenic development.

*Species assigned.*—Only the type species.

*Kowalatrochus sanctacrucensis* sp. nov.

*Holotype:* GIUS 4-1569/Ko-81 (Fig. 8A).

Fig. 10. Distribution of translation index (Hₜ/Wₘ) of *Loxoplocus (Donaldiella) karczewskii* sp. nov. from the late Frasnian of Panek (set B₃).
**Type horizon and locality:** As for the genus.

**Derivation of name:** From Latin name of the Holy Cross Mountains.

**Material.**—Thirty two almost completely preserved shells and about 60 fragments with well preserved ornamentation (ZPAL Ga-VI/49–55, 57–59; GIUS 4-1017/Gr-149, 4-1019–1020/Gr-151–152, 4-1022–1028/Gr-154–160, 4-1030–1034/Gr-162–166, 4-1045/Gr-177/2, 4-1115/Jaź-10, 4-1119–1128/Jaź-14–23, 4-1213–1214/SKo-9–10, 4-1217–1227/Ko-4–14, 4-1257–1258/Ko-44–45, 4-1336/Ko-58, 4-1348/Ko-70/8, 4-1351–1352/Ko-73–74).

**Diagnosis.**—Ornamentation consists of nine spiral cords on the whorl ramp and 10–11 spiral cords below the periphery.

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Fig. 11. Distribution of translation (H/W) and of apertural shape (H_a/W_a) indexes of *Kowatrocklus sanctacrucensis* gen. et sp. nov. from the early to middle Frasnian of the upper Sitkówka Beds.

Fig. 12. Distribution of translation (H/W) and of apertural shape (H_a/W_a) indexes of *Grabinopsis guerichi* gen. et sp. nov. from the middle Frasnian of the upper Sitkówka Beds.

Fig. 13. Distribution of translation (H/W) and of apertural shape (H_a/W_a) indexes of *Orecopia kadzielniae* (Gürich, 1896) comb. nov. from the early and middle Frasnian of the upper Sitkówka Beds.

on the base. Wide collabral undulations are also visible on the ramp.

Description.—Large-sized shell (to 5 cm of height), trochiform with 7–8 whorls and thick walls of the spire. The height of the spire is a little larger than the height of the aperture. The ramps of the whorl are relatively steeply sloping and weakly arched. A small callus is present on the cryptophalous base. Small funicles surround the umbilicus. Sutures shallower, poorly demarcated. Aperture rounded, outer lip narrow along its edges. Protoconch is unknown. Pleural ture shallow, poorly demarcated. Aperture rounded, outer lip with the basal wall. A very prominent columellar fold present at the middle of the columellar lip. There is a distinct concave notch below the columellar fold. Aperture is hemispherical. Lower part of the labrum is elongated. Ornamenation consists of two spiral ridges on the upper part of the whorl. Growth lines and protoconch are unknown. Pleural angle is stable (100–135°).

Variability.—The shells of Kowalatrochus sanctacrucensis show moderate differences of the translation index H/W (1.15–1.65) and the index of apertural shape H/Wa (1.1–1.5) (Fig. 11).

Distribution.—Holy Cross Mountains: Kowala, set A2, Jażwica, set I–K, and Sitkówka-Kowala, set B (the upper Sitkówka Beds; early Frasnian); Grabina, set A (the upper Sitkówka Beds; middle Frasnian).

Superfamily Neritoidea Rafinesque, 1815
Family ?Plagiothyridae Knight, 1956
Genus Grabinopsis gen. nov.

Type species: Grabinopsis guerichi sp. nov.

Type horizon and locality: the inactive quarry “Grabina” (W part of Kielce), set B, the upper Sitkówka Beds, middle Frasnian.

Diagnosis.—Grabinopsis gen. nov. is characterized by a rounded small shell with a low spire. Columellar lip with one prominent columellar fold. Ornamenation contains of two spiral angular ridges just below the suture. Grabinopsis gen. nov. differs from Dirachis Whidborne, 1891 by its lower spire and the single columellar fold. Other genera from the family Plagiothyridae (Plagiothyra Whidborne, 1892 and Littorinides Knight, 1937) have much higher turbiniform shells, anomphalous bases, and more developed spiral ornamentation. The almost sphaerical shell is similar to the shell of Naticopsis M'Coy, 1844 but the last whorl of Grabinopsis has a higher an aperture as well as aperture expanded in a direction perpendicular to the axis of the shell. Grabinopsis has a minutely phaneromphalous base and a spiral ornamenation not known in Naticopsis.

Remarks.—The naticiform shell, the presence of spiral ridges, and the prominent columellar fold suggest affinities with the family Plagiothyridae. However, some doubts are raised because of the absence of a well preserved last whorl, growth lines, and due to unknown nature of the protoconch.

Species assigned.—Only the type species.

Grabinopsis guerichi sp. nov.

Fig. 5A–F.


Holotype: GIUS 4-981/Gr-113 (Fig. 5A).

Type horizon and locality: As for the genus.

Derivation of the name: In memory of Dr. Georg Gürich who found first specimens of this gastropod.

Material.—Eighteen almost complete shells and 9 fragments (GIUS 4-974–981/Gr-106–113, 4-1207/SzG-12/2).

Diagnosis.—The spire has deep and nearly canaliculate sutures. Ornamenation consists of two spiral ridges on the upper part of the whorl.

Description.—Small-sized naticiform shell (maximum height 4 mm), with a low spire and having 5–6 whorls. Whorls strongly embrace one another. Profile of the last whorl is rounded with a weak angulation formed by a prominent spiral ridge in the upper part of the labrum. A second weak spiral ridge runs just below the first one. Surfaces between the suture and first ridge, as well as between the spiral ridges, are slightly concave. Sutures are deep and nearly canaliculate. Whorls join just below the lower weak spiral ridge.

Base rounded, narrowly phaneromphalous. Umbilicus surrounded by a ridge which is formed at the contact of outer lip with the basal wall. A very prominent columellar fold present at the middle of the colomellar lip. There is a distinct concave notch below the columellar fold. Aperture is hemispherical. Lower part of the labrum is elongated. Ornamenation consists of two spiral ridges on the upper part of the whorl. Growth lines and protoconch are unknown. Pleural angle is stable (100–135°).

Variability.—Shells of Grabinopsis guerichi gen. et sp. nov. is characterized by few changes of the relative shell height as well as by a more variable apertural shape (Fig. 12).

Remarks.—The first shells of this species were found by Gürich in Frasnian limestones at Karczówka hill. However, these shells had not been determined because of their poorly preserved character. Specimens from the original Gürich’s collection have been lost.

Distribution.—Holy Cross Mountains: Szczukowskie Góriki, Grabina, set B (the upper Sitkówka Beds; middle Frasnian).

Suborder uncertain

Family Omphalotrochidae Knight, 1945
Genus Orecopia Knight, 1945

Type species: Orecopia mccoyi (Walcott, 1884); Frasnian, North America.

Remarks.—Genus Orecopia Knight, 1945 is characterized by a trochiform, narrowly phaneromphalous shells with a wide rounded sinus on the upper part of the labrum. The similar genus Omphalotrochus Meek, 1864 has a spiral ridge at the upper part of outer lip. Labroculus Heidecker, 1959 differs from Orecopia by its cryptophalous base with a wide callus. Orecopia displays an archaeogastropod-type proto-
conch and cyrtococonoid teleoconch. Older whorls are sometime closed by septa.

Orecopia kadzielniae (Gürich, 1896) comb. nov.

Fig. 9A–I.

Pleurotomaria kadzielniae sp. nov.; Gürich 1896: 306, pl. 11: 3.

Straparollus (Straparollus) grabinensis sp. nov.; Karczewski 1989: 110, pl. 3: 1.

Holotype: MGUWr.1939.s (Fig 9A, B).

Type horizon and locality: Inactive quarry “Kadzielnia” (S part of Kielce), set A, the Kadzielnia Member, early Frasnian.

Material.—Seven almost complete specimens, 3 internal moulds, 1 well preserved base as well as 6 fragments of the spire and 7 axial sections (M.G.U. Wr. 1939.s.: ZPAL Ga-VI/14, 16–22; GIUS 4-1021/Gr-153, 4-1024/Gr-156/2, 4-1028/Gr-160/2, 4-1036/Gr-168, 4-1038–1043/Gr-170–175, 4-1045/Gr-177/1, 4-1046/Gr-178, 4-1191/Gr-179, 4-1232/Ko-19, 4-1284/Gr-181).

Diagnosis.—Orecopia kadzielniae differs from O. mccoyi (Walcott, 1884) by narrowly planeromphalous base. O. cotei Pedder, 1966 has a carina at the periphery of the whorl. O. kirchholmiensis (Keyserling, 1846) has more rounded whorls and deeper sutures (see Chernychev 1884, 1887).

Description.—Large, high to low trochiform shell (maximum width 6.5 cm) with 6–7 whorls. First two whorls are flattened, next one abuts just below rounded periphery. Sutures are relatively flat. Ramp of the whorl is almost flat from suture to about half of the distance between suture and periphery. Wide sinus developed on the flat part of the ramp. Lower part of the ramp has a concave spiral belt with a breadth equal to about ¼ of ramp width. Base is rounded, narrowly planeromphalous. Columellar lip is strongly thickened. Umbilicus deep, surrounded by thick funicles. Growth lines form a wide, insignificant sinus on the base. Abandoned whorls are closed by septa (see Fig. 16A). Aperture rounded, protoconch and outer lip are not preserved. Pleural angle decreasing during ontogenic development from 100 to 170°.

Variability.—The population of the species O. kadzielniae shows sufficiently high variability of the translation index H/W (0.45–0.85). It is caused by changes of the spire height and the relatively stable values of the aperture shape index Hₜ/Wₜ (Fig. 13).

Remarks.—This species was described by Gürich (1896) from the Frasian of Kadzielnia. The holotype of Pleurotomaria kadzielniae is an internal mould and it is housed in Gürich’s collection at the Geological Museum of Wroclaw University. The concave belt at the ramp of the whorl had been identified as a selenizone in the original description.
Shape and biometrical measures clearly indicate the resemblance of Gürich’s specimen to the specimens collected by the author at Grabina. That allows revision of this species.

**Distribution.**—Holy Cross Mountains: Kedzielnia, set A (the Kedzielnia Member), Kowala, set A₂ and Grabina, set A (the upper Sitkówka Beds; from early to middle Frasnian).

**Frasnian gastropod faunas from the Kowala Formation**

An *assemblage* is defined as a community of various organic group taxa, living in the same environment, with prominent role of gastropods. An *association* is defined as part of an assemblage containing only one organic group. All these syn-ecological units are linked with facies types described by Racki (1993b) for Frasnian faunal assemblages. Five associations of gastropods and one assemblage were analysed in the context of field observations, microfacies, and accompanying fauna (Fig. 2).

**Lagoonal habitats**

*Loxoplocus (Donaldiella) karczewskii Assemblage.***—Typical site: the “Panek” quarry, set B₃ (Detrital-Stromatoporoid Beds; late Frasnian). The biota is connected with the light gray wackestone and packstone (facies L-1; Fig. 15A), containing amphilopoids, massive stromatoporoids and calcispheres. The uncommon species *Loxoplocus (Donaldiella) karczewskii* (Table 1) and also the very rare unidentified pleurotomarids are the dominant macrofaunal taxa. Those molluscs lived in the calm, shallow waters of back-reef and lagoon (Fig. 17C).

**Reef habitats**

*Euryzone kielcensis Association* of the Kedzielnia-type Assemblage (Fig. 7).—Typical site: Kedzielnia, set A (the Kedzielnia Member; early–middle Frasnian). Other locations:
Jaźwica (set J), Kowala (set C). The Kadzielnia–type Assemblage, representing the very diverse biocoenosis of mud mounds, has been derived from the stromatoporoid bindstone (facies R–3b; Fig. 14C). Mud mounds were created below the wave base. The community contains (Fig. 17A; Kaźmierczak 1971; Szulczewski 1971; Szulczewski and Racki 1981): massive stromatoporoids, massive and branched tabulates, branched and solitary rugosans (the Macgeea–Thamnophyllum Assemblage; Wrzołek 1988, 1993), brachiopods (the Fitzroyella alata–Parapugnax breccie Association; Racki 1993a), trilobites (Chlupač 1993), ostracods (Malec and Racki 1993), crinoids (the Schyschcatocrinus Assemblage; Racki and Soboń-Podgórska 1993), and microproblematiques: moravaminids and labyrintoconids (Racki and Soboń-Podgórska 1993). The diverse association contains at least 11 taxa of gastropods (see Table 1): Euryzone kielcensis, Westerna subcostata, Naticopsis (Naticopsis) inflata, Spanionema scalaroides, Orecopia kadzielniae, Roeremiella octocincta, Porcellia bifida, Villmaria ventricosa, as well as unidentified murchisonids and holopeids.

Kowalatrochus sanctacruensis Association of the Actinostroma Assemblage (Figs. 8, 17A, B).—Typical site: the “Kowala” quarry, set A (Fig. 3; the upper Sitkówka Beds; early Frasnian). Other locations: Jaźwica (set I), Sitkówka-Kowala (set B), Grabina (set A). The association is present in floatstones and rudstones, characteristic for the early Frasnian reef environment (facies R-3fr or R-3r; Figs. 14A, B, 16A). Fauna in those environments are comprised mostly of massive and branched stromatoporoids (the Actinostroma Assemblage; Racki 1993b) and tabulates, branched rugosans, and less often massive rugosans (Macgeea–Thamnophyllum and Hexagonaria hexagona Assemblages; Wrzołek 1988, 1993), brachiopods (Desquamatia macroumbonata association; Racki 1993a), calciisponges (Hurcewicz 1993), crinoids (the Schyschcatocrinus Assemblage; Gluchowski 1993), isissellids and calcispheres (see Racki and Soboń-Podgórska 1993), and ostracods (Fig. 17A, B). The associa-
tion consists of: *Kowalatrochus sanctacrucensis*, Westerna subcostata, Oreocopia kadziezielae, Coelozone sp., Straparollus (Straparollus) serpens, Naticopsis (Naticopsis) inflata, Naticopsis (Naticopsis) protogaea, and Lahnospira taeniata (see Table 1).

**Straparollus (Straparollus) circularis** Association of the Actinostroma Assemblage (Fig. 4).—Typical site: the “Panek” quarry, set B; (Fig. 3; the Detrital-Stromatoporoid Beds, late Frasnian). Other locations: Sitkówka-Jaźwica (set B). The association occurs in stromatoporoid-coral rudstones (facies R-3r; Fig. 15B, C). It is associated with stromatoporoids, tabulates, as well as massive and branched rugosans (the Frechastraea smithi Assemblage; Wrzolek 1988, 1993), thick-shell bivalves of the genus *Megalodon* (see Fig. 15B; Karczewski 1992), and rarer brachiopods and crinoids (the *Calleocrinus* Assemblage; Wrzolek 1988, 1993), trochospongias of the genus *Rhenozyga* sp. A, *Palaeozygoopleura* (Rhenzygo) sp. B and undetermined microdomatids, murchisonids and loxonemats.

**Grabinopsis guerichi** Association of the Stachyodes Assemblage (Fig. 5).—Typical site: Grabina, set B (Fig. 3; the upper Sitkówka Beds; middle Frasnian). The association is derived from the Stachyodes–Renalcis build up with a wackestone matrix (facies R-2b; Fig. 16B). There are large fragments of crinoid columns and sometimes even complete preserved calices of crinoids (the *Calleocrinus* Assemblage; Gluchowski 1993), numerous ostracods, tiny brachiopods, and bellerophontid gastropods dispersed among the branches of the giant *Stachyodes* and *Renalcis* build up (Fig. 17B). This gastropod fauna includes: *Grabinopsis guerichi*, *Naticopsis* (Naticopsis) inflata, *Palaeozygoopleura* (Rhenzygo) sp. A, *Palaeozygoopleura* (Rhenzygo) cf. *retrostriata*, *Roemeriella cyclostomoides*, *Villmaria ventricosa*, *Murchisonia* (Murchisonia) *nerinea*, *Liospira* sp., as well as unidentified loxonemids and subulitids (see Table 1).

**Naticopsis (Naticopsis) excentrica** Association of the Frechastraea pentagona Assemblage (Fig. 4).—Typical site: Grabina, set C (Fig. 3; the Detrital Beds; late Frasnian). The association is linked with rudstone (facies R-1; Fig. 16C) built with fragments of reef-building organisms: massive stromatoporoids, tabulates, massive and branched rugosans (the *Frechastraea pentagona* Assemblage; Wrzolek 1988), and also brachiopods, remains of crinoids (the *Calleocrinus* Assemblage; Gluchowski 1993), plates of echinoids and ophiuroids, nautiloids, bivalves, bellerophonts, fish remains, and fragments of trilobites (see Coen-Aubert and Wrzolek 1991) (Fig. 17B). The strongly diversified association consists of following taxa (see Table 1): *Straparollus* (Straparollus) *serpens*, *Liospira* sp., *Villmaria ventricosa*, *Lahnospira taeniata*, *Roemeriella bifida*, *Naticopsis* (Naticopsis) inflata, *Naticopsis* (Naticopsis) *excentrica*, *Naticopsis* (Naticopsis) protogaea, *Palaeozygoopleura* (Rhenzygo) sp. A, *Palaeozygoopleura* (Rhenzygo) sp. B and undetermined microdomatids, murchisonids and loxonemats.

### Syenological interpretation

There are a couple of widespread eurytopic gastropod species among the recognized groups and associations, for example: *Naticopsis* (Naticopsis) *inflata*, *Roemeriella octocincta*, *Villmaria ventricosa*, *Macrochilina ventricosa*, and *Palaeozygoopleura* (Rhenzygo) cf. *retrostriata*. Sometimes they are known from different environments (reef or open shelf). There are also some stenotypic species connected only with a specific type of habitat, for example: *Kowalatrochus sanctacrucensis*, *Grabinopsis guerichi*, *Euryzone kielcensis*.

The gastropod associations of the lagoon facies are quite typical. The dominant element among them is the turritulate species *Loxoplocus* (Donaldiella) *karczewskii*. It is very hard to find any specimens with discoidal shells among this association. Turritulate shells could be adapted for life among the branched corals or stromatoporoids, which often dominated this environment (Fig. 16C).

There are numerous large thick-shell gastropods in the reef associations, exemplified by *Kowalatrochus sanctacrucensis*, *Westerna subcostata*, and *Oreocopia kadziezielae*, adapted for existence in high energy conditions (Fig. 17A–C). A separate group is an association with small, thin-shelled gastropods, often dwelled (?) in the reef slots and among the colonies of the reef-building organisms (Fig. 17B). Possibly, they used the protective function of the colonial skeletons against enemies or strong waving, e.g., *Palaeozygoopleura* (Rhenzygo) sp., *Grabinopsis guerichi* gen. et sp. nov., *Spanionema scalaroides* (Whidborne, 1889). The similar taxa to gastropods from the *Grabinopsis guerichi* and *Naticopsis (Naticopsis) excentrica* associations (i.e., *Straparollus*, *Murchisonia*, *Loxonema*) also exist in Frasnian reef facies of Western Canada (see Leavitt 1968). Similar ecologi-
Table 1. Occurrence of Frasnian gastropods in the Holy Cross Mountains (after Krawczyński 1998, 1999); l, lower, u, upper.

<table>
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<tr>
<th>Geochronology</th>
<th>Frasnian biozones (Ziegler and Sandberg 1990)</th>
<th>Sea-level cycles (Johnson et al. 1985)</th>
<th>Regional shallowing-upward cycles (Racki 1993b, 1997)</th>
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<td>gen. et sp. ex fam. Subulitidae indet.</td>
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cal differentiation into large- and small-sized groups have been observed in Kadzielnia-type brachiopods (Szułczewski and Racki 1981). Gastropods are a group that existed in each type of habitat of the Devonian shelf. They showed very high tolerance to changes in salinity, temperature and water depth (Murray 1966; Jamieson 1971). In the Frasnian carbonate complex of the Holy Cross Mountains, the huge majority of reef habitat associations (i.e., five associations) over the groups of lagoonal habitat (only one) was stated (Fig. 2). A similar synecological differentiation is observed in the Givetian reef complex of the North-East Australia (Cook 1995) as well as Frasnian reef complexes of the West Australia (Playford 1980), and Canada (Murray 1966). Slightly different patterns of gastropod associations are observed in Givetian reefs of Western Canada, where uncommon specimens can be found equally in all facies (Vopni and Lerbekmo 1972). Moreover, completely different patterns can be found in some reef complexes of Alberta, where gastropods mainly lived in fore-reef environments (Coppold 1976). The taxonomical composition of studied gastropods from the Holy Cross Mountains (see Table 1) is similar to Givetian and Frasnian gastropod faunas from the Harz Mountains and the Rheinish Slate Mountains (Roemer 1843, 1854; Blodgett and Fryda 1999; Fryda 2000; Heidelberger 2001). In the Rheinish Slate Mountains reefs, gastropods are reported mostly from back- and fore-reef facies (Krebs 1974; Burchette 1981; see also Wilson 1975). The taxonomic diversity of the assemblage and associations changed during the Frasnian of the Holy Cross Mountains. At the beginning of Frasnian, there was a remarkable increase in the significance of trochoids and subulitids caused by the general development of the Dyminy reef. In the middle and late Frasnian the contribution of trochoids decreased, on the other hand, the role of euomphaloids, neritoids, and omphalotrochoids increased greatly. The percentage of the representatives of Pleurotomarioidea and Loxonematoidea was greater in the middle Frasnian associations than in the early and late Frasnian ones (Fig. 18).

Gastropod faunas in the Kowala Formation and global events

The evolution of Frasnian gastropod fauna, dwelling on the southern Laurussian shelf, indicates a certain similarity of taxonomic diversity to other benthic groups like brachiopods, rugosans and tabulates (see Racki 1988, 1993a; Nowiński 1993; Wrzołek 1993). The most important element controlling the changes in the carbonate environments were regional depositional cycles caused mainly by eustatic changes of sea level (Racki 1993b; see also McGhee et al. 1991). Mostly, the reef-lagoonal gastropod faunas of the Kowala Formation were very sensitive to bathymetric changes. Practically at the beginning of almost each regional depositional cycle, there was a turnover in the taxonomic composition of the gastropod fauna. The extinction (or emigration) of many species was mainly observed in the middle Givetian and at the beginning of late Givetian in the Stringocephalus bank habitats. Biogeographic immigration of new species started from the early Frasnian to the beginning of late Frasnian (Krawczyński 1999; Fig. 2 herein).

Generally, the late Givetian gastropod fauna was poorly diversified. Assemblages of euomphalids, pleurotomarids, and murchisonids, for example Straparollus (Straparollus) laevis from Góra Zamkowa, were developed in the deeper shelf in the late Givetian and at the Givetian–Frasnian bound-

ary interval. There were no changes in the gastropod fauna of the Sitkówka Beds connected with global sea-level rise during the cycle G II (= T–R cycle IIb) and local epeirogenic event G/F III cycle (see Racki 1993b). The following colonization and immigration of the widespread Frasnian species (Orecopia kadzielniae, Westerna subcostata) appeared together with the evolution of Dynmy reef. Kadzielnia-type mud mounds, with the highly diverse Eurynoe kielcensis association, were developed below the wave base as a consequence of the transgressive pulse in the Pa. transitsans Zone (= cycle IIb/c sensu Racki 1997). As a result of the next transgressive pulse (= cycle IIC sensu Johnson et al. 1985) at the beginning of the Pa. punctata Zone, the mud mounds progressively sank and the unique Kadzielnia-type fauna became extinct. In the middle Frasnian, in the north part of the Dynmy reef, the organic buildups were built by large Stachyodes–Renalcius colonies, among which flourished the small gastropods of the Grabinopsis guerichi association. The transgressive pulse at the beginning of the late Frasnian (= cycle IId sensu Johnson et al. 1985), marked by anoxic lower Kellwasser event in later Pa. rhenana Zone, contributed to considerable facies changes and the gradual collapse of the Dynmy reef (see Narkiewicz 1987). Two gastropod associations were developed in the reef-cap phase: Strapa−rollus (Straparollus) circularis and Naticopsis (Naticopsis) excentrica, and also the poorly diversified assemblage Loxoplocus (Donaldiella) karczewskii. The ecosystems of the Dynmy reef finally collapsed at the end of Frasnian as a consequence of the strongest transgressive pulse and the anoxic upper Kellwasser event (Racki and Bąński 1998). The history of gastropods during the Frasnian–Famennian boundary event in the Polish part of the South Laurussia shelf is not exactly known. There is some interruption in the transition to Famennian pelagic sequences in the central part of the Kielce region (stratigraphic gap; see Szulczewski 1995), being probably a last gastropod refugium connected with the central part of the former Dynmy reef. Continuous sequences of the uppermost Frasnian at Kowala and Psie Górkí are poor in gastropods. The last Frasnian microdomatid gastropods have been found in silicified brachiopod−crinoid coquinas just below the Frasnian−Famennian boundary at the “Kowala” quarry (see Racki and Bąński 1998). Famennian gastropods from the Holy Cross Mountains occur in cephalopod limestones of Gałęzice and Łagów, for example, cosmopolitan species Naticopsis (Naticopsis) inflata and euomphalids, pleurotomarids as well as luxonemids known from the Famennian (see Sobolev 1911; Dzik 1994). Gastropods are also rare in marly facies at the “Kowala” quarry. Generally, the Famennian gastropods are very poorly investigated, especially the species connected with an impoverished reef environment. Only a few of the Frasnian genera (for example Naticopsis) have re−appeared again in the Visean coral−crinoid limestones from Gałęzice (Gromczakiewicz−Lomnicka 1973). The data concerning the Frasnian gastropods of the reef complex, as well as the Famennian gastropods from another parts of the World, have too superficial character (for example, from reef complexes of Canada; see Leavitt 1968; Jamieson 1971; Coppold 1976). Frasnian reef gastropods have not been observed in the Famennian and Early Carboniferous series. Thus, they probably became extinct together with the collapse of the Frasnian reef ecosystem near the Frasnian–Famennian boundary.

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References
