Crinoids from the Famennian of the Holy Cross Mountains, Poland

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Disarticulated crinoid columnals and pluricolumnals from the Famennian of the Holy Cross area were analysed. Sixteen crinoid taxa were distinguished, only one of which is based on stems attributed to a calyx-based genus, and the others are classified within artificial supraspecific units. Two of these are new: *Schyschcatocrinus levis* sp. nov. and *Cosmocrinus polonicus* sp. nov. The described crinoid fauna shows distinct extinction-recovery temporal pattern: the Frasnian–Famennian crisis affected 50% of stem-based families and 70% of late Frasnian stem-based genera. The succession of crinoid faunas represented by three faunal intervals has been identified and correlated to standard conodont zones: FIa, *Palmatolepis triangularis* Zone (relic "Frasnian" crinoid assemblage *Schyschcatocrinus delicatus–Calleocrinus kielcensis*), FIb, *Pa. crepida* to *Pa. marginifera* zones (crinoid assemblage *Calleocrinus kielcensis–Schyschcatocrinus levis*) and FIc, *Pa. trachytera* to *S. praesulcata* zones (crinoid assemblage *Cosmocrinus polonicus–Acbastaucrinus affectatus*). The succession was controlled mostly by eustatic factors.

Key words: Crinoidea, Famennian, Holy Cross Mountains, extinction, recovery.

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Introduction

Commonly crinoids are preserved as disarticulated skeletal elements, particularly stem ossicles which may be present in rock-forming abundance. Generally, dissociated stem remains of Paleozoic crinoids are neglected by paleontologists because of the inability of linking majority of them with crowns, making their classification within "natural" system possible. Therefore, only whenever it is possible columnals are classified within crown-based genera (only *Cosmocrinus* recognized herein), in remaining cases, higher rank units are used provisionally in the category of "Subclass and order uncertain". It must be remembered that such taxonomy concerning stem-based genera has a minimal chance to express true evolutionary relationships. Moreover, it is highly difficult to estimate a reality of the crinoid biological species recognition on the basis of stem morphology. It seems that in many cases stem-based species are sound biologically, but it is also plausible that similar stems from different geographically and stratigraphically localities may belong to completely unrelated species (Głuchowski 1993). However, since the occurrence of complete skeletons of crinoids is less common than the preservation of the stem ossicles, for taxonomic purposes it is necessary to use their stem remains, despite restrictions connected with stem-based taxonomy (for detailed discussion see Moore and Jeffords 1968; Donovan 2001).

Famennian crinoid faunas represented by more or less complete skeletons are known and documented in England, Germany, Belgium, China, the USA, Morocco, Argentina and Australia (Lane et al. 1997, 2001; Maples et al. 1997; Webster et al. 1999; Jell and Jell 1999). Moreover, disarticulated crinoid stem parts from Famennian of Kazakhstan (Sisova 1988) and Afghanistan (Stukalina 1997) have been described as well.

Famennian crinoids from Poland have not been described in detail so far. Earlier, on the basis of insufficient and poorly preserved crinoid columnals from the Holy Cross Mountains, only representatives of the following genera had been recognized: *Stenocrinus*, *Schyschcatocrinus*, *Anthinocrinus* and *Cosmocrinus* (Głuchowski 1981a, b). These assignments were later partly verified by Głuchowski (1993). The new material from the Holy Cross Mountains allows for further refinement and a more detailed taxonomic analysis of the fauna. Moreover, applying research procedures similar to those used for Givetian–Frasnian faunas (Głuchowski 1993) allow for a comparison of crinoid assemblages across this time interval.

Material

Famennian crinoids are documented mostly from the northern and southern parts of the Holy Cross pelagic ridge (Racki 1990; Szulczewski 1995). The examined crinoid material comes from nine localities (Fig. 1) and is represented exclusively by separate skeleton ossicles (mostly columnals). Crinoid remains built mostly allochtonous accumulations within facies differentiated sediments.

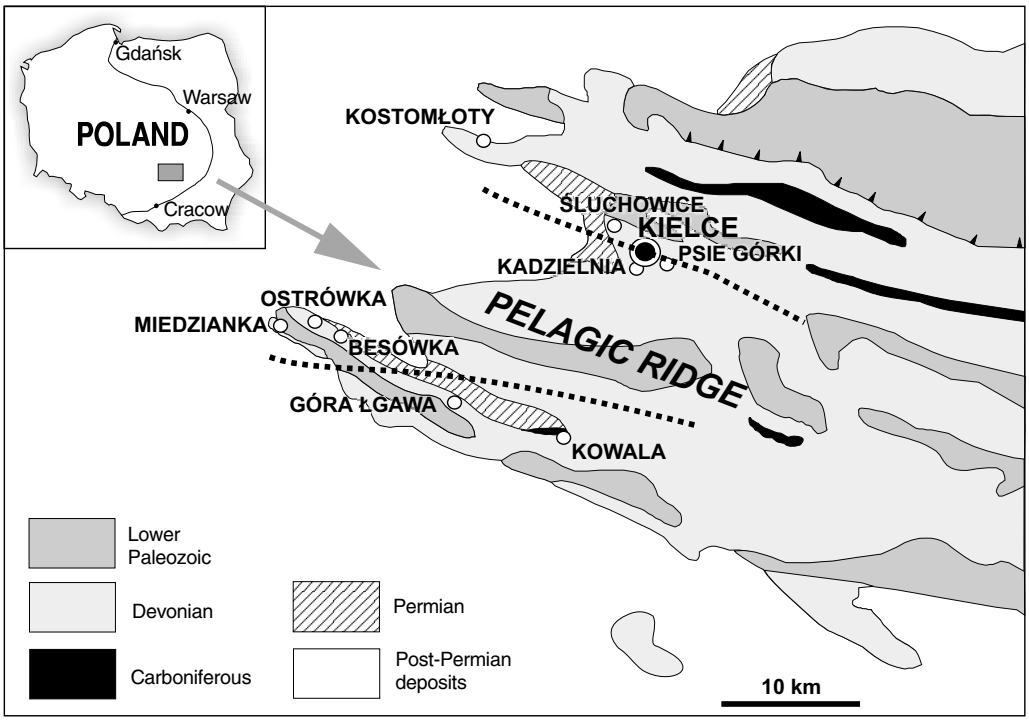

Fig.1. Location of the Famennian crinoid sites in the Holy Cross area. Simplified geological map after Marynowski et al. (2000).

Crinoid localities from Psie Górki (sample PG-A), Kowala (sample Ko-A) and Miedzianka (sample Mi-A; *Palmatolepis triangularis* Zone) and from Śluchowice and Kostomłoty (*Pa. crepida* Zone) represent various bioclastic facies (Szulczewski 1971, 1979, 1989; Racki 1990; Racki et al. 1993; Racki and Baliński 1998). However, crinoid localities from Psie Górki (sample PG-B; *Pa. crepida* Zone), Kowala (sample Ko-B; mostly *Pa. crepida* Zone), Kowala (sample Ko-C; *Siphonodella praesulcata* Zone), Kadzielnia (*Pa. rhomboidea* to *Pa. marginifera* zones) and Góra Łgawa (*Pa. postera* to *Pa. expansa* zones), represent crinoid-rich partings within marly deposits (debris flows, Biernat and Szulczewski 1993; see also Szulczewski 1971; Racki 1990; Żakowa and Radlicz 1990; Racki et al. 1993). The remaining localities, Miedzianka (sample Mi-B; *Pa. crepida* Zone), Ostrówka and Besówka (*Pa. trachytera* to *S. praesulcata* zones), represent a complex of condensed crinoid-cephalopod limestones (Szulczewski 1978, 1989; Szulczewski et al. 1996; Racki personal communication May 1998). Crinoid material from Cracow Region (Dębnik) and Moravia (Mokrá quarry at Brno), Czech Republic, which was made available by Professor Grzegorz Racki, was used for comparative purposes.

The collection comprises more than thousand columnals and pluricolumnals obtained by washing the marly samples and from acetic acid residues of limestones. Some specimens were studied only on the weathered rock slab surfaces. The material is housed in the Department of Paleontology and Biostratigraphy of the University of Silesia in Sosnowiec, abbreviated GIUS.

Systematic paleontology

Subclass Inadunata Wachsmuth and Springer, 1885
Order Cladida Moore and Laudon, 1943
Family Botryocrinidae Wachsmuth and Springer, 1886
Genus *Cosmocrinus* Jaekel, 1898

Type species: *Cosmocrinus holzapfeli* Jaekel, 1898

Cosmocrinus polonicus sp. nov.

Fig. 2O–U.

Cosmocrinus distinctus Stukalina, 1977; Głuchowski 1981a: 49, pl. 3: 12.
Cosmocrinus distinctus Stukalina, 1977; Głuchowski 1981b: 89–110.

Holotype: GIUS-4-91/3, Fig. 2S.

Type locality: Kadzielnia quarry, Kielce, Holy Cross Mountains.

Type horizon: Marly limestones, *Palmatolepis rhomboidea* to *Palmatolepis marginifera* zones.

Derivation of the name: From Latin *polonicus,* Polish.

Diagnosis.—*Cosmocrinus* species with ornamented xenomorphic and non-cirriferous stem.

Material.—235 columnals and pluricolumnals.

Dimension of the holotype (in mm).—Columnal diameter (KD) 6.6; luminal diameter (LD) 0.9; crenularial diameter (CD) 5.7; columnal height (KH) 2.2.

Description.—The stem is medium-sized (diameter 2.9–7.0 mm), xenomorphic and lacking cirri. Three sorts of columnals forming the stem are differentiated in height, shape and ornamentation. Lateral side of the lowest, flat columnals (proxistele?) is covered with distinct, numerous outgrowths or tubercles (Fig. 2Q, R). Relatively higher and

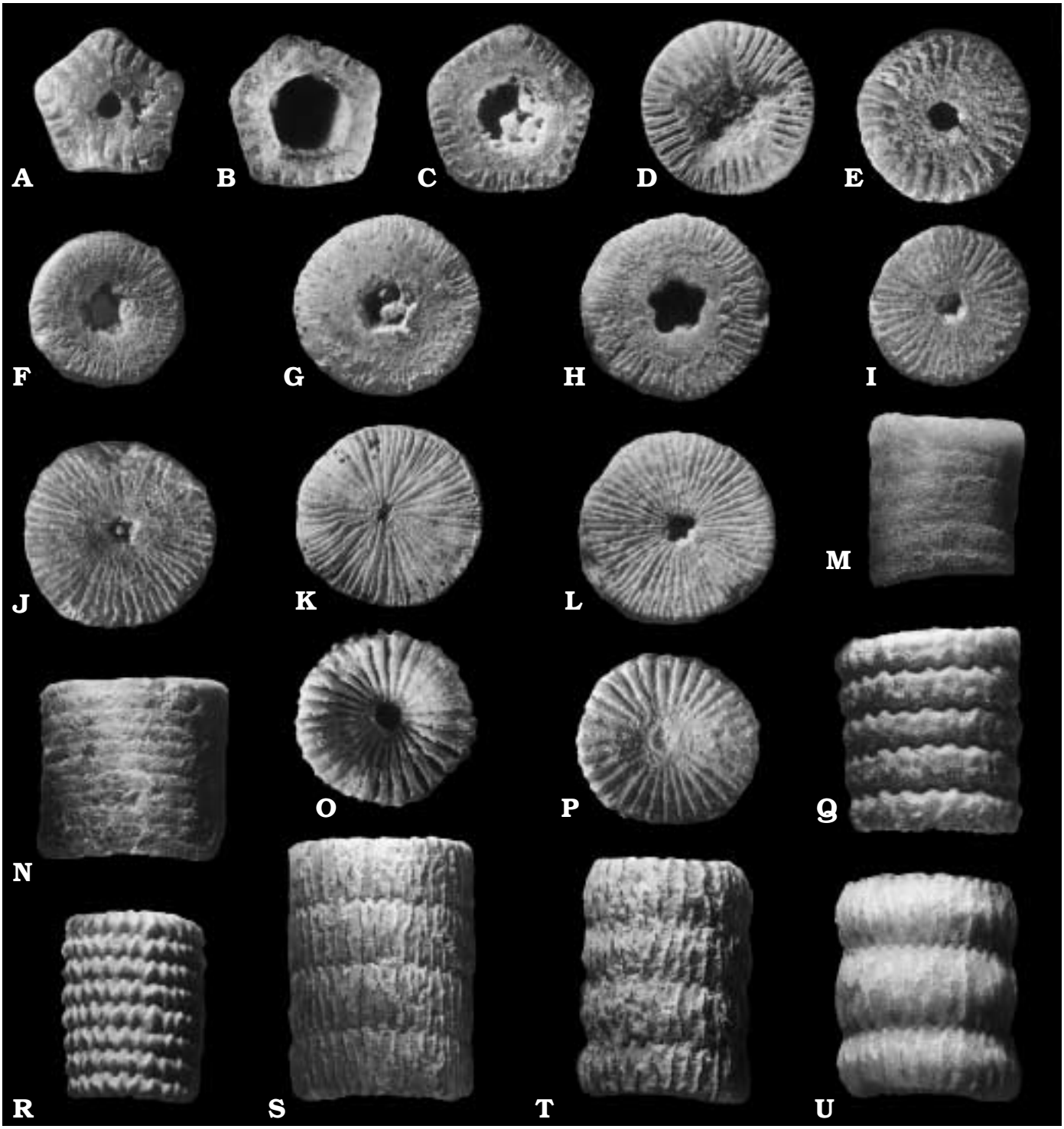

Fig. 2. **A**. *Kasachstanocrinus* sp., GIUS-4-445/4, Kostomłoty, × 20. **B**, **C**. *Urushicrinus* sp., GIUS-4-455/1-2, Psie Górki, sample PG-A, × 15. **D**. *Anthinocrinus* sp., GIUS-4-91/33, Kadzielnia, × 12. **E**. *Schyschcatocrinus delicatus* Głuchowski, 1993, GIUS-4-455/8, Psie Górki sample PG-A, × 15. **F**–**H**. *Schyschcatocrinus levis* sp. nov., GIUS-4-91/11-13, Kadzielnia; **F**, **G** × 15, **H** (holotype GIUS-4-91/13) × 12. **I**–**J**. *Stenocrinus altus* Sisova, 1988, GIUS-4-91/15-16, Kadzielnia, × 10. **K**–**N**. *Calleocrinus kielcensis* Głuchowski, 1993, GIUS-4-91/45-52, Kadzielnia, × 10. **O**–**W**. *Cosmocrinus polonicus* sp. nov., GIUS-4-91/3-9, Kadzielnia; **O**–**Q** × 7, **R** and **S** (holotype GIUS-4-91/3) × 5; **T**, **U** × 10.

barrel-shaped columnals (mesistele?) have on their lateral side numerous ridges (Fig. 2T, U), arranged more or less regularly. However, lateral side of cylinder-like columnals (dististele?) is covered with more delicate, sometimes bifurcated, ridges (Fig. 2S). Articular facet is flat (proxistele) to more or less concave (mesi- to dististele). Small lumen is

pentagonal, strongly rounded. Crenularium is composed of rather coarse and long culmina, sometimes dichotomous at the columnal edge (Fig. 2O, P).

Remarks.—The species differs from the most similar *C. distinctus* Stukalina, 1977 from the Late Devonian of Eastern Kasakhstan in lacking cirri. Few specimens from some localities were previously (Głuchowski 1981a, b) treated as non-cirriferous stem sectors of *C. distinctus*. However, the new abundant material does not contain any cirriferous nodals and shows that the stalk of the Polish species really lacks cirri.

Occurrence.—This species has been documented from *Pa. crepida* to *S. praesulcata* zones: Kadzielnia, Kowala (samples Ko-B and C), Ostrówka, Besówka.

Subclass and order uncertain
Group Pentameri Moore and Jeffords, 1968
Family Anthinocrinidae Yeltyschewa and Sisova in Schewtschenko, 1966

***Anthinocrinus* sp.** (Fig. 2D).—The material contains 29 poorly preserved medium-sized, circular to slightly pentagonal columnals. The areola is pentalobate, lowered and bordered by straight and rather thick culmina. The lumen is wide, pentagonal. The latus is smooth and slightly concave. Some specimens were previously (Głuchowski 1981a, b) classified as *A. wenjukowi* (Yeltyschewa in Yeltyschewa and Stukalina, 1977). Occurs in the *Pa. triangularis* to *Pa. marginifera* zones: Psie Górki (sample PG-A), Miedzianka (samples Mi-A and B), Kowala (samples Ko-A and B), Kostomłoty, Kadzielnia.

***Urushicrinus* sp.** (Fig. 2B, C).—The material contains 32 very poorly preserved small, pentagonal columnals with large strongly rounded lumen. The areola is flat and bordered by 4–5 short culmina grouped solely in the radial zones. The latus is smooth and gently concave. Occurs in the *Pa. triangularis* to *Pa. marginifera* zones: Psie Górki (sample PG-A), Śluchowice, Kowala (sample Ko-B), Kadzielnia.

***Kasachstanocrinus* sp.** (Fig. 2A).—The material contains 51 very poorly preserved small, pentagonal columnals with strongly marked angles and smooth latus. The lumen is small, rounded. Areola is flattened, medium-sized bordered by straight and thick culmina. Occurs in the *Pa. triangularis* to *S. praesulcata* zones: Kowala (samples Ko-A, B, and C), Kostomłoty, Miedzianka (sample Mi-B), Śluchowice, Ostrówka, Besówka.

Group Cyclici Moore and Jeffords, 1968
Family Schyschcatocrinidae Dubatolova, 1971
Genus *Schyschcatocrinus* Dubatolova, 1971

Type species: *Pentagonocyclicus astericus* Schewtschenko, 1966.

Schyschcatocrinus levis sp. nov.

Fig. 2F–H.

Schyschcatocrinus creber Dubatolova, 1975; Głuchowski 1981a: 41, pl. 3: 19 (partim).

Schyschcatocrinus creber Dubatolova, 1975; Głuchowski 1981b: 98–99, fig. 2 (partim).

Holotype: GIUS-4-91/13, Fig. 2H.

Type locality: Kadzielnia quarry, Kielce, Holy Cross Mountains.

Type horizon: Marly limestones, *Palmatolepis rhomboidea* to *Palmatolepis marginifera* zones.

Derivation of the name: From Latin *levis*, smooth.

Diagnosis.—*Schyschcatocrinus* species with flattened articular facet, smooth areola and very delicate culmina.

Material.—129 columnals.

Dimension of the holotype (in mm).—columnal diameter (KD) 2.8; luminal diameter (LD) 0.8; crenularial diameter (CD) 1.0; columnal height (KH) 1.5.

Description.—The columnals are medium-sized (2.5–4.0 mm) with smooth and gently convex latus. The articular facet is flattened with pentagonal to pentalobate lumen. Well-developed areola is smooth, bordered by crenularium composed of numerous (70–80) very delicate, sometimes dichotomous culmina.

Remarks.—The species differs from *S. delicatus* Głuchowski, 1993 from Givetian and Frasnian of Southern Poland in having a thicker stem composed of columnals with a wider and smooth areola, very delicate culmina and relatively wider lumen. Poorly preserved specimens from some localities were previously (Głuchowski 1981a, b) classified as *S. creber* Dubatolova, 1975.

Occurrence.—This species have been documented from *Pa. crepida* to *S. praesulcata* zones: Kadzielnia, Kostomłoty, Śluchowice, Miedzianka (sample Mi-B), Psie Górki (sample PG-B), Kowala (samples Ko-B and C), Ostrówka, Besówka and in the *Pa. crepida* to *Pa. marginifera* zones of the Moravia, Czech Republic (Mokrá quarry).

Schyschcatocrinus delicatus Głuchowski, 1993 (Fig. 2E).—The material contains 186 minute columnals with flattened articular facet. The areola is rather broad, bordered by crenularium composed of straight and relatively coarse culmina. Occurs in the Givetian–Frasnian of Southern Poland (Głuchowski 1993) and also in the Famennian *Pa. triangularis* Zone of the Holy Cross Mts: Psie Górki (sample PG-A), Miedzianka (sample Mi-A), Kowala (sample Ko-A) and Cracow Region (Dębnik).

Family Stenocrinidae Dubatolova, 1971

Stenocrinus altus Sisova, 1988 (Fig. 2I, J).—The material contains 27 rather high columnals with flattened articular facet perforated by small pentagonal to pentalobate lumen. The areola is narrow bordered by wide crenularium composed of long, dichotomous culmina. The latus is weakly convex with minute tubercles and small cirrus scars on nodals. Poorly preserved specimens from some localities were previously (Głuchowski 1981a, b) classified as *S. degratus* Dubatolova, 1975. Occurs in the *Pa. triangularis* to

S. praesulcata zones: Kowala (samples Ko-A, B, and C), Psie Górki (sample PG-B), Kadzielnia, Ostrówka and in the *Pa. crepida* to *Pa. marginifera* zones of the Moravia, Czech Republic (Mokrá quarry). The species was initially described from late Famennian of Central Kasakhstan (Sisova 1988).

Calleocrinus kielcensis Głuchowski, 1993 (Fig. 2K–N).—The material contains 192 columnals and pluricolumnals. The heteromorphic stem is composed of low columnals with straight or weakly convex latus. The articular facet is flat and covered with numerous dichotomous culmina. The lumen is very small, stellate to circular. Poorly preserved specimens from some localities were previously (Głuchowski 1981a, b) classified as *Salairocrinus humilis* (Dubatolova, 1971). Occurs in the Frasnian of Southern Poland and probably Dinant Basin, Belgium (Głuchowski 1993) and also in the Famennian *Pa. triangularis* to *Pa. marginifera* zones: Psie Górki (samples PG-A and B), Kowala (samples Ko-A and B), Kostomłoty, Kadzielnia.

Family Taranshicrinidae Sisova, 1988

Taranshicrinus vulgaris Sisova, 1988 (Fig. 3T, U).—The material contains 19 columnals and short pluricolumnals. The heteromorphic stem is composed of relatively high columnals with gently convex latus, sometimes covered with minute tubercles, and with large cirrus scars on nodals. The articular facet is flat with medium-sized, pentagonal to circular lumen surrounded by perilumen. The crenularium is narrow, composed of short, straight and rather coarse culmina. Poorly preserved specimens from some localities were previously (Głuchowski 1981a, b) classified as *Hexacrinites*? sp. Occurs in the *Pa. crepida* to *S. praesulcata* zones: Kowala (samples Ko-B and C), Kadzielnia, Góra Łgawa. The species was first described from the late Famennian of Central Kasakhstan (Sisova 1988).

Family Floricyclidae Moore and Jeffords, 1968

Acbastaucrinus affectatus Sisova, 1988 (Fig. 3F–K).—The material contains 107 columnals and short pluricolumnals. The thin heteromorphic stem is composed of circular, high and strongly convex columnals. The lumen is large, pentalobate bordered by weakly marked perilumen. The areola is flat and smooth, surrounded by extremely narrow crenularium composed of minute culmina. Poorly preserved specimens from some localities were previously (Racki et al. 1989) classified as *Glyphidocrinus*. Occurs in the *Pa. crepida* to *S. praesulcata* zones: Kowala (samples Ko-B and C), Psie Górki (sample PG-B), Śluchowice, Miedzianka (sample Mi-B), Ostrówka, Besówka. The species was first described from late Famennian of Central Kasakhstan (Sisova 1988).

***Cyclocion* sp.** (Fig. 3O–Q).—The material contains 14 poorly preserved minute, circular columnals having a convex and smooth latus. The lumen is large, strongly pentastellate. Areola is wide and smooth bordered by very short culmina. The columnals were previously (Racki et al. 1989) classified as *Tomeocrinus*. In general, the articular facet morphology seems to correspond to *C. distinctus primus* Sisova, 1988 from the late Famennian of Central Kasakhstan (Sisova 1988), in spite of weakly marked (damaged?) crenularium. Occurs in the *Pa. crepida* to *S. praesulcata* zones: Kowala (samples Ko-B and C), Psie Górki (sample PG-B), Ostrówka.

Family Leptocarphiidae Moore and Jeffords, 1968

Cyclocaudiculus longus Głuchowski, 1986 (Fig. 3A–E).—The material contains 59 very high, circular columnals with smooth and distinctly concave latus. Lumen is pentalobate to circular. The crenularium is narrow composed of straight and thick culmina. Occurs in the *Pa. crepida* to *S. praesulcata* zones: Kowala (samples Ko-B and C), Kadzielnia, Ostrówka, Besówka and in the *Pa. crepida* to *Pa. marginifera* zones of the Moravia, Czech Republic (Mokrá quarry). The species was initially described from late Tournaisian of Ostrówka (Głuchowski 1986).

Family Salairocrinidae Dubatolova, 1971

Tjeecrinus insectus (Yeltyschewa in Dubatolova, 1964) (Fig. 3V, W).—The material contains 39 circular columnals with articular facet covered with rather thick, straight and dichotomous culmina. The lumen is small, pentalobate. The latus is straight and smooth. Occurs in the late Frasnian of the Southern Poland, Kuznieck Basin, Russia and Dinant Basin, Belgium (see Głuchowski 1993) and also in the Famennian *Pa. triangularis* to *Pa. marginifera* zones: Psie Górki (samples PG-A and B), Miedzianka (sample Mi-A), Śluchowice, Kadzielnia.

Family Kstutocrinidae Schewtschenko, 1966

***Kstutocrinus* sp.** (Fig. 3L–N).—The material contains 37 poorly preserved minute, high, barrel-like columnals with small, pentagonal lumen. The crenularium is very narrow composed of rather thick culmina. The latus is smooth, sometimes with minute tubercles at mid-height. Occurs in the *Pa. triangularis* to *Pa. marginifera* zones: Kowala (samples Ko-A and B), Psie Górki (samples PG-A and B), Miedzianka (samples Mi-A and B), Kostomłoty, Śluchowice, Kadzielnia.

Family Exaesiodiscidae Moore and Jeffords, 1968

***Cyclostelechus*? sp.** (Fig. 3X).—The material contains 7 very poorly preserved discoidal columnals with pointed epifacet. The lumen is very small, pentagonal? surrounded by depressed, smooth areola. The crenularium is very narrow, extremely weakly marked (damaged?). The shape of some columnals is somewhat convergent with *Exaesiodiscus* Moore and Jeffords. Occurs in the *Pa. crepida* to *S. praesulcata* zones: Kowala (samples Ko-B and C), Kadzielnia and also in the latest Famennian of Dębnik, Cracow Region.

Family *incertae sedis*

Dronovicrinus notabilis Stukalina, 1977 (Fig. 3R, S).—The material contains 5 circular, relatively high columnals with

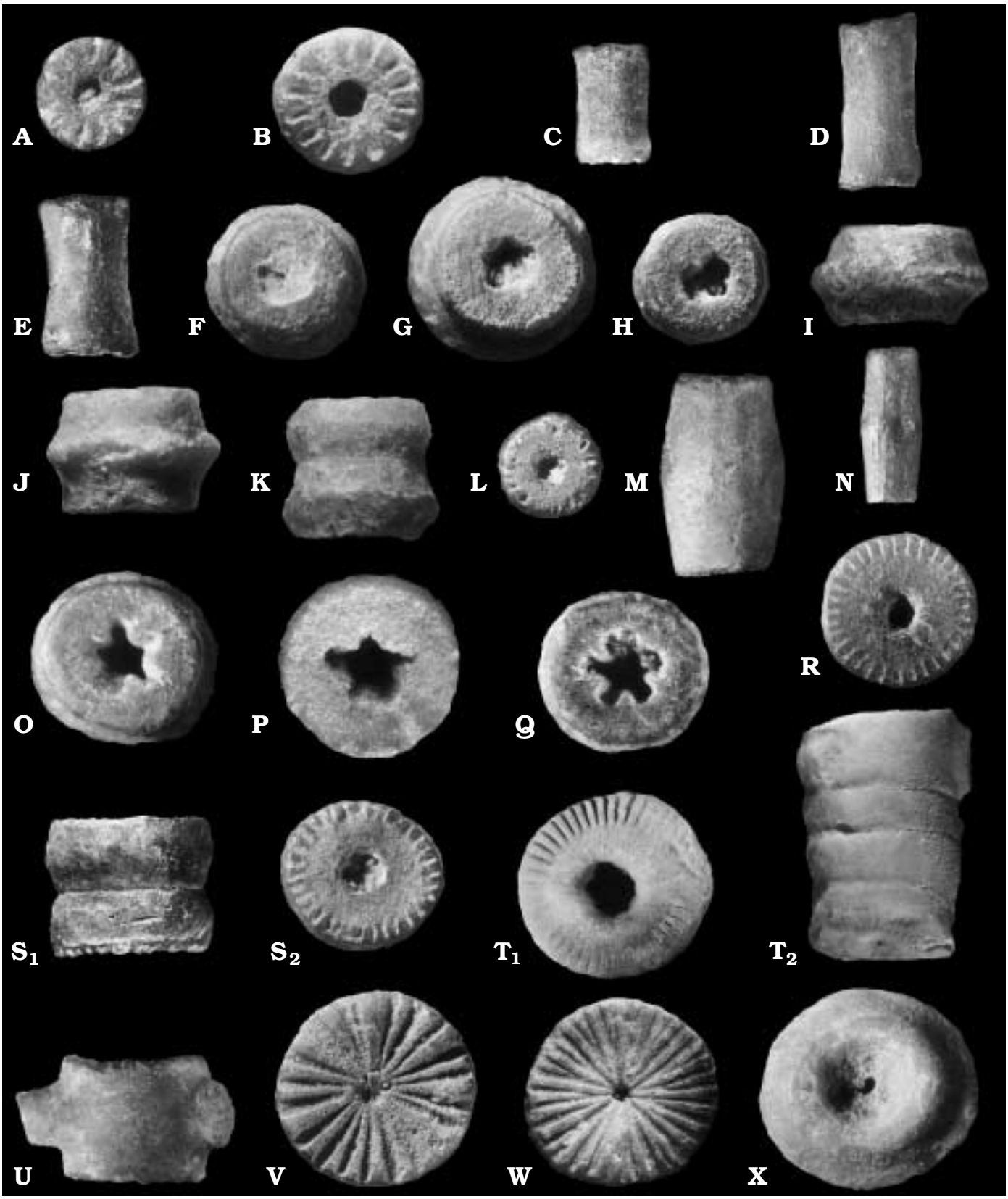

Fig. 3. **A–E**. *Cyclocaudiculus longus* Głuchowski, 1986, GIUS-4-504/1-5, Besówka, × 10. **F–K**. *Acbastaucrinus affectatus* Sisova, 1988, GIUS-4-149/1-6, Ostrówka, × 20. **L–N**. *Kstutocrinus* sp., GIUS-4-455/10-12, Psie Górki, sample PG-A, × 10. **O–Q**. *Cyclocion* sp., GIUS-4-428/1-3, Kowala, sample Ko-B, × 10. **R**, **S**. *Dronovicrinus notabilis* Stukalina, 1997. **R**. GIUS-4-445/9, Kostomłoty, × 10. **S**. GIUS-4-91/20-21, Kadzielnia, × 7. **T**, **U**. *Taranshicrinus vulgaris* Sisova, 1988. **T**. GIUS-4-11/1-2, Góra Łgawa, × 7. **U**. GIUS-4-431/1, Psie Górki, sample PG-B, × 10. **V**, **W**. *Tjeecrinus insectus* (Yeltyschewa in Dubatolova, 1964), GIUS-4-91/37-38, Kadzielnia, × 10. **X**. *Cyclostelechus*? sp., GIUS-4-149/10, Ostrówka, × 15.

convex, smooth latus. The articular facet is flat with pentagonal lumen. The areola is smooth and bordered by narrow crenularium composed of straight, coarse and rarely dichotomous culmina. Occurs in the *Pa. crepida* to *Pa. marginifera* zones: Kowala (sample Ko-B), Kadzielnia. The species was first described from the late Famennian of the Middle Afghanistan (Stukalina 1997).

Succession of the crinoid faunas

Mid-Late Devonian crisis in crinoid evolution was one of the greatest in Phanerozoic (Moore 1948; Roux 1987). It was first manifested by global drastic impoverishment of crinoid paleobiocenoses in the early Famennian. Despite later revival of crinoid faunas (Maples et al. 1997), their differentiation remained at the lowest level in whole Devonian. The relatively low diversity of the Holy Cross Mountain Famennian crinoid assemblages, defined by means of stem-based taxa may be a consequence of Frasnian–Famennian mass extinction. This most significant in Devonian extinction event is well documented among diverse marine biota (see Sepkoski 1996; Walliser 1996). However, some studies of the calyx-based crinoid taxa diversity have shown that the major declines appear to coincide with the end of the Givetian (Baumiller 1994), and Frasnian–Famennian extinction was a non-event for crinoids (Webster et al. 1998). This peculiar pattern, however, may be nothing more than a consequence of a preservational and/or regional bias (see McIntosh 2001).

The analysis of available sections from the Frasnian–Famennian boundary in the Holy Cross Mountains shows the disappearance of stromatoporoid-coral reefs and reduction in shallow-water reef-related biota, including crinoids (Racki et al. 1989; Racki 1990; Racki and Baliński 1998). Paleogeography of the Holy Cross Mountains during Famennian was dominated by the central pelagic carbonate platform which separated two intra-shelf basins (Fig. 1). The later evolution of Famennian biota was related to transgression and levelling of sea bottom morphology to the central swell level, i.e., generally with shallowing up (Szulczewski 1992, 1995).

The Famennian crinoid fauna in this area (Fig. 4) is less than one half diverse taxonomically as that of the Frasnian, and represents two crinoid zones: *Tjeecrinus insectus* (Racki et al. 1989; Głuchowski 1993) and *Cosmocrinus polonicus* (Głuchowski 1981b; Racki et al. 1989). Varying frequencies of stem-based crinoid taxa from the Holy Cross Mountains allow the identification of three crinoid assemblages: *Schyschcatocrinus delicatus–Calleocrinus kielcensis* (SdCk), *Schyschcatocrinus levis–Calleocrinus kielcensis* (SlCk), *Cosmocrinus polonicus–Acbastaucrinus affectatus* (CpAa) (Table 1). Their succession comprises three faunal intervals (FI). The nature of this succession in diversity sense is of eustatic origin and corresponds to transgressive-regressive cycles (T–R) of Johnson et al. 1985 (see also Racki 1997).

Table 1. General characteristics of the crinoid assemblages from Famennian of the Holy Cross area. Diversity index (DI) counted according to the E.H. Simpson's (1949) formula.

Assemblage	Dominant taxa	Average percentage	Number of taxa	Average diversity index
CpAa	*C. polonicus* *A. affectatus*	28.9 26.1	9	4.34
SlCk	*S. levis* *C. kielcensis*	29.2 19.8	15	6.75
SdCk	*S. delicatus* *C. kielcensis*	55.1 24.7	8	2.76

Faunal interval FIa.—It represents the earliest Famennian (*Pa. triangularis* Zone) and most strongly mirrors the effects of the F–F event. It is characterized by a very significant decrease in diversity among crinoids. Breakdown in the development of crinoid faunas at the Frasnian–Famennian boundary (Late *Pa. linguiformis* Zone) is the effect of drastic drop in sea level in the regressive phase of T–R cycle IId and extremely anoxic conditions (Kellwasser event) (Racki 1998). The crisis affected as many as 50% of families and 70% of late Frasnian genera (Głuchowski 1999). The surviving crinoid fauna documented here (crinoid assemblage SdCk) is represented only by 8 taxa and has a definitely relic "Frasnian" character, additionally emphasised by the presence of index species *Tjeecrinus insectus*, which appeared in the Holy Cross Mountains area already in late Frasnian (Głuchowski 1993).

Faunal interval FIb.— It represents early Famennian (*Pa. crepida* to *Pa. marginifera* zones) and is characterized by the strong recovery and diversification of crinoid paleobiocenoses, exemplified by a near doubling of their diversity (Głuchowski 1999). Recovery of crinoid faunas is registered outside the Holy Cross Mountains area as well (Maples et al. 1997) and occurred in transgressive pulses of T–R cycle IIe. Significant recovery of other biota also occured at that time (Racki 1990). Among the crinoids described here, except for still dominant "Frasnian" genera (crinoid assemblage SlCk) some new "Famennian" genera appeared as well: *Cosmocrinus, Acbastaucrinus, Dronovicrinus, Taranshicrinus*. The presence of the first of the mentioned genera is particularly distinct in the crinoid faunas of the Holy Cross Mountains (crinoid *Cosmocrinus polonicus* Zone) (Głuchowski 1981b; Racki et al. 1989). Among the genera reported here for the first time, *Cyclocaudiculus*, *Cyclocion* and probably *Cyclostelechus* have ranges extending into the Carboniferous of Southern Poland (Głuchowski 1981a b, 1986). Some "Carboniferous" elements repopulating Famennian faunas are documented also in echinoderm localities from Northern China (Maples et al. 1992, 1994, 1997), Kazakhstan (Sisova 1988), Afghanistan (Stukalina 1997), England (Lane et al. 2001), and Czech Republic (*Cyclocaudiculus longus* described herein).

Faunal interval FIc.—It represents late Famennian (*Pa. trachytera* to *S. praesulcata* zones) and is initially character-

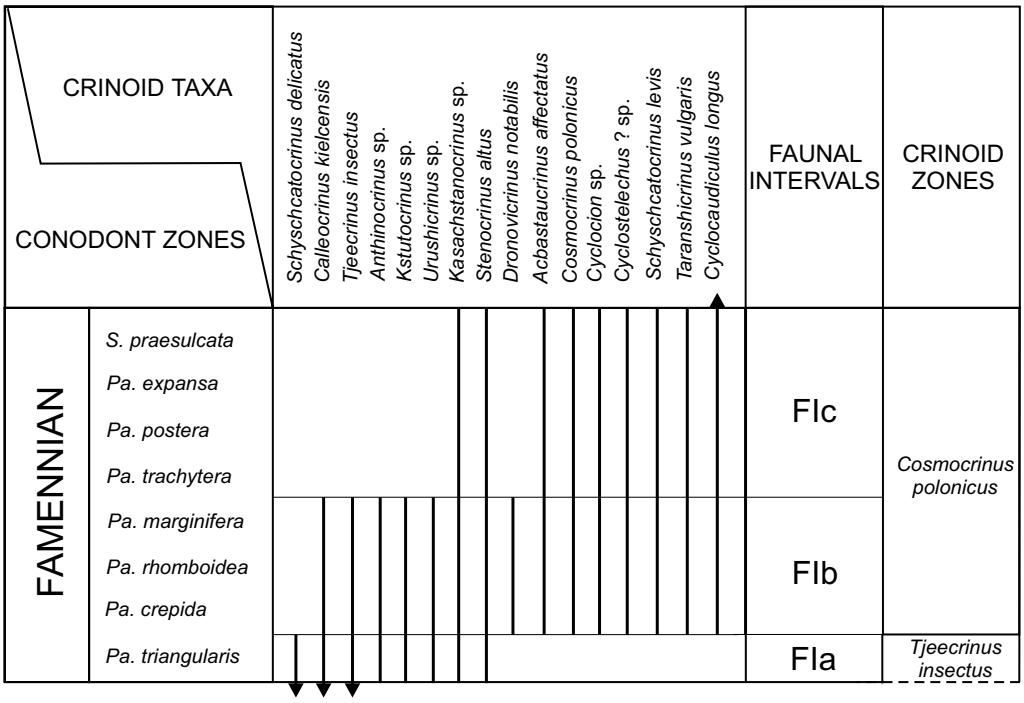

Fig. 4. Stratigraphic distribution of the Famennian crinoid taxa in the Holy Cross Mts.

ized by impoverishment of crinoid paleobiocenoses, and later their disappearance (Głuchowski 1999). Despite the reduction in the number of genera (mainly "Frasnian"), "Famennian" character of crinoid faunas documented with "Carboniferous" accent, was preserved (crinoid assemblage CpAa). Decrease of taxonomic crinoid diversity may be connected with glacieustatic regressive phase of T–R cycle IIe. However, the influence of T–R eustatic changes of cycle IIf on crinoid faunas of the Holy Cross Mountains area is marked in a different way. It is highly probable that this time the next transgression (*Pa. expansa* Zone and Lower *S. praesulcata* Zone) and successive significant decrease of sea level (Middle *S. praesulcata* Zone), turned out to be more destructive for crinoids settled on the pelagic ridge. Only the remains of the crinoid fauna are still registered here near the Devonian–Carboniferous boundary in Kowala (sample Ko-C). In the meantime, rich echinoderm faunas from the latest Famennian were documented in England (Lane et al. 2001), Kazakhstan (Sisova 1988), Afghanistan (Stukalina 1997), and China (Maples et al. 1992, 1994), means in the regions where reef-building organisms were much less affected by F–F extinction event (Webb 1998). Crinoids appeared once again in great numbers in the Holy Cross Mountains (Ostrówka) not till the late Tournaisian (*S. anchoralis* Zone) (Głuchowski 1986). This suggests that the turning point of Devonian–Carboniferous (Hankenberg crisis) had a much greater impact on echinoderm habitats in the Holy Cross Mountains than did the F–F event. The stromatoporoid-dominated reefs declined globally at the same time but their recovery during Tournaisian was more rapid (Webb 1998). This shows that the crisis was profound not only in pelagic biota (see Walliser 1996).

Biogeographic remarks

The postulated disappearance of endemism in the Famennian is unusual for echinoderms. It is reflected in the similarity between paleogeographically distant crinoid faunas of China, North America and Western Europe (Waters et al. 1992; Lane et al. 2001). The reasons for this phenomenon can be seen both in drastic decline in diversity and drop of endemism as a result of F–F event, as well as in later anomalous climatic changes and global cooling (Maples et al. 1992; Waters et al. 1992). The presence of crinoid species known from Kazakhstan and Afghanistan in the Holy Cross Mountains and Moravia can be seen as an indirect proof of suggested decline in provincialism. As many as 80% of the Famennian species recognized herein were cosmopolitan, whereas among Givetian–Frasanian faunas their part was only less than 70%. However, such comparison based on crinoid stems taxonomy may be not fully correct. The small number of known Famennian crinoid faunas worldwide and the use of a varied taxonomic procedures make it difficult to provide a meaningful comparisons at this time.

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