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Additional data on post-Paleozoic sea-lilies (Crinoidea, Echinodermata) from the Outer Carpathians of the Czech Republic and Poland

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Abstract: Jurassic (Tithonian) and Lower Cretaceous (Berriasian/Valanginian-Hauterivian) strata of the Vendryně and Cieszyn Limestones formations in the Czech Republic and Poland are locally rich in crinoid remains, consisting of whole cups, isolated cup elements, brachial plates, columnals and pluricolumnals, cirrals, and holdfasts. They are assigned to isocrinids (Isocrinida: Isocrinus cf. amblyscalaris, Isocrinida indet.), cyrtocrinida (Cyrtocrinida: Eugeniacrinites sp., Phyllocrinus sp., Gammarocrinites sp., *Hemicrinus tithonicus*, *Plicatocrinus hexagonus*, Cyrtocrinida indet.), millericrinids (Millericrinida: Millericrinida indet.), and thiolliericrinids (Comatulida, Thiolliericrinidae: Thiolliericrinidae gen. et sp. Indet.). Late Cretaceous (Maastrichtian) and Paleogene (Paleocene-Oligocene) crinoids from the Subsilesian Unit are recorded as individual remains belonging to: Isocrinida indet., Cyrtocrinida indet., bourgueticrinids (Comatulida, Bourgueticrinina: Bourgueticrinina fam. et gen. indet.) and roveacrinids (Roveacrinida, Roveacrinidae gen. et sp. indet.). Roveacrinids were retrieved only from Maastrichtian samples. Despite the conclusions previously presented that isocrinids of the Outer Flysch Carpathians dominated around the Jurassic-Cretaceous boundary due to the very shallow sedimentary environment of these strata, we can now conclude that they were common and associated with cyrtocrinids in all types of environments. It is also worth mentioning that cyrtocrinids and isocrinids occur in Paleogene sediments that were deposited in extremely shallow environments. On the other hand, many literature data suggested that Cretaceous (by mid-Cretaceous) isocrinids migrated to deep-water areas, as a response to an increase in the number of predators during the so-called Mesozoic marine revolution.

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Résumé : Données complémentaires sur les lys de mer post-paléozoïques (crinoïdes ; Crinoidea, Echinodermata) des Carpathes externes de la République tchèque et de Pologne.- Les dépôts jurassiques (Tithonien) et crétacés inférieurs (Berriasien/Valanginien-Hauterivien) des formations de Vendryně et des Calcaires de Cieszyn de la République tchèque et de Pologne sont localement riches en restes crinoïdiques, représentés par des thèques entières, éléments isolés de thèque, pièces brachiales, columnales et pluri-columnales, de cirres et de crampons. Ils sont rapportés respectivement aux isocrinides (Isocrinida: Isocrinus cf. amblyscalaris, Isocrinida indet.), cyrtocrinides (Cyrtocrinida: Eugeniacrinites sp., Phyllocrinus sp., Gammarocrinites sp., Hemicrinus tithonicus, Plicatocrinus hexagonus, Cyrtocrinida indet.), millericrinides (Millericrinida : Millericrinida indet.) et aux thiolliericrinides (Comatulida, Thiolliericrinidae : Thiolliericrinidae gen. et sp. indet.). Ces crinoïdes du Crétacé supérieur (Maastrichtien) et du Paléogène (Paléocène-Oligocène) sont représentés par des restes isolés appartenant aux : Isocrinida indet., Cyrtocrinida indet., bourgueticrinides (Comatulida, Bourgueticrinina: Bourgueticrinina fam. et gen. indet.) et aux rovéacrinides (Roveacrinida, Roveacrinidae gen. et sp. indet.). Les rovéacrinides ont été récupérés uniquement dans les échantillons du Maastrichtien. Malgré les conclusions présentées préalablement que les isocrinides des Carpathes du Flysch externe dominaient aux alentours de la limite Jurassique-Crétacé en raison de l'environnement sédimentaire beaucoup moins profond de ces dépôts, nous pouvons maintenant conclure qu'ils furent communs et associés aux cyrtocrinides dans tous les types d'environnement. Il est également utile de préciser que les cyrtocrinides et les isocrinides sont présents dans les sediments paléogènes qui furent déposés dans les environnements extrêmement peu profonds. De nombreuses données suggèrent que les isocrinides crétacés (depuis le Crétacé moyen) ont migré dans les zones d'eaux profondes en réponse à l'accroisssement du nombre de prédateurs lors de la soi-disant révolution marine mésozoïque.

Mots-clefs:

- Carpathes occidentales ;
- Unité silésienne ;
- Unité sous-silésienne ;
- Jurassique ;
- · Crétacé ;
- Paléogène ;
- Crinoidea ;
- taxonomie ;
- République tchèque ;
- Pologne

1. Introduction

HOHENEGGER (1861) was the first to mention crinoid remains from the Outer Flysch Carpathians, namely *Pentacrinites annulatus* RÖMER from the Vendryně Formation and the upper member of the Cieszyn Limestone Formation. Ro-GALA (1909) and KOKOSZYŃSKA (1949) claimed that remains of *Pentacrinus* sp. (=*Isocrinus*?) and *Pentacrinus neocomiensis* (DESOR) (=*Isocrinus*? neocomiensis) are common in the Lower Cretaceous of the Outer Carpathians. However, such statements and taxonomic assignments raised our doubts and needed to be verified. Later, unspecified echinoderms were also mentioned from both the Czech and Polish sectors of the Outer Carpathians (Cieszyn Beds) (e.g., WAŚKOWSKA-

OLIWA et al., 2008). Crinoids from the Polish sector of the Outer Carpathians (Cieszyn Limestone Formation) were the sole topic of Salamon et al. (2020). These latter authors stated that the echinoderms are absent from the Vendryně and Hradiště formations (Tithonian and Berriasian/Valanginian-Hauterivian respectively). They added that Isocrinus cf. amblyscalaris (Thurmann) and Isocrinida indet. both occur in the Vendryně Formation (Tithonian), whereas crinoids are more diversified in the Cieszyn Limestone Formation (Berriasian) and are represented by isocrinids (Isocrinida) and cyrtocrinids (Cyrtocrinida) belonging to the following taxa: Isocrinus? annulatus (ROEMER), Balanocrinus subteres (MÜNSTER), B. cf. smithi HESS & GALE, and Hemicrinus sp.



3. Materials and methods

The crinoid collection from the Leszna Górna Quarry is housed at the University of Silesia in Katowice, Faculty of Natural Sciences, Institute of Earth Sciences, Poland, and recorded under catalogue number: GIUS 8-3693. The crinoids from the Czech localities (Vendryně and Dolní Líštná) are partly housed in the collections of the Czech Geological Survey in Brno, Czech Republic: CGS MB15 to 40.

Crinoids were retrieved from the following localities (see Figs. 1 - 2):

- 1. Olza River gorge in Vendryně (49°39' 51.2"N 18°41'38.5"E). Marly shales exposed in the river gorge are part of the Vendryně Formation. They are early Tithonian in age, based on the macrofauna with *Exogyra nana* (ŘEHOŘ *et al.*, 1978; VAŠÍČEK, 1972). Crinoid elements were obtained during 1979-1980 by washing weathered, easily disintegrating rock from marly paraconglomerate bodies. Marly shales and para-conglomerates are hemipelagites and slump masses deposited in the bathyal zone. Crinoids are very probably reworked from carbonate platforms together with other macrofauna, carbonate ooids, *etc.*
- Wopienka Quarry in Vendryně (49°40' 34.5"N 18°43'07.3"E). A few thick banks of detrital limestone formerly exposed in the quarry can be assigned to the upper member of the Cieszyn Limestone Formation. The crinoid remains were collected from weathered surfaces of siliciclastic-limestone banks in 1977. The presumed age of the strata is Berriasian-Valanginian as in the Dolní Líštná quarry. During the 2019 fieldtrip, the quarry wall was no longer accessible, being completely covered by slope debris and vegetation. The detrital limestones were deposited in the same sedimentary setting as identical strata of the Dolní Líštná Quarry.
- Dolní Líštná Quarry (49°41'17.3"N 18° 41'45.9"E). Thick-bedded marlstones interbedded with marly siltstones and marlstones are assigned to the upper member of the Cieszyn Limestone Formation. The lower part of the quarry wall is upper Berriasian and the upper part, lower Valanginian, based on dinocyst biostratigraphy (Boorová et al., 2003). Numerous isolated crinoid elements were retrieved during field seasons in 1979-1981 by washing rusty weathered residues from crevices in limestone banks. The common occurrence of crinoids was confirmed during summer 2019 by three of us (MB, MAS and TB). The detrital limestones were deposited by turbidity currents in a submarine fan in the bathyal zone. Contained crinoids, oysters,

- bryozoans, brachiopods, carbonate ooids, *etc.* are reworked from the carbonate platform.
- 4. Bystřice nad Olší (49°38'23.9"N 18°42' 17.1"E). The Maastrichtian to Selandian strata of the Frýdek Formation are exposed in the large meander of the Olše River (so-called Bouček locality). The section consists of grey marls with slumps and slides. Crinoid ossicles were picked from washed residues of the Maastrichtian strata. The marls with slumps were deposited in upper bathyal depths, and crinoids may either be reworked from the deeper sublittoral or even autochthonous.
- Jatný (49°37'35.0"N 18°43'06.9"E). Brown-grey pebbly mudstones and paraconglomerates exposed at Jatný Creek in Bystřice nad Olší can be assigned to the slumped facies of the Menilite Formation (Oligocene). Crinoid ossicles are a part of the reworked shelly macrofauna. The planktonic foraminiferal assemblage is composed of multiple taxa reworked from various Eocene levels and may indicate an Eocene age for the crinoid remains. The pebbly mudstones were deposited in the upper bathyal zone. The macrofauna is reworked from different sublittoral and upper bathyal habitats, so the original habitat of the crinoids is not known.
- 6. Hluchová (49°38'44.6"N 18°44'22.0"E). Oligocene strata similar to those of the Jatný section were exposed in the Hluchová River gorge. Brown-grey pebbly mudstones contain large foraminifers and a shelly macrofauna of diminutive size (bryozoans, molluscs, brachiopods, echinoderm ossicles, etc.). Crinoid remains were picked from washing residues. The fauna may be partly or completely reworked from the Eocene. The outcrops, now covered, are no longer accessible. The sedimentary setting was probably the same as that at Jatny.
- 7. Zaolší (49°38'07.2"N 18°42'22.9"E). Oligocene strata similar to those of the Jatný section are exposed in the left (southern) river bank of the Olše River at Bystřice and Olší. Faunal composition, age and sedimentary setting are nearly the same as those of the Jatný section.
- 8. Starý Jičín (49°34'39.5"N 17°58'10.2"E). Occasional excavation exposed dark-grey calcareous claystones with few turbiditic calcareous sandstones and fine-grained biodetritic conglomerates, up to 160 cm-thick. These strata are part of the Frýdek Formation. Planktonic foraminifers from the claystones indicate a Danian to Selandian age. Crinoid remains were retrieved from washed residues of the disaggregated conglomerate. The hemipelagic claystones



- were deposited at upper or middle bathyal depths. The crinoids and other macrofauna, including bryozoans, bivalves and echinoids, are reworked from the sublittoral zone.
- 9. Ženklava (49°33'17.0"N 18°06'52.1"E). Dark brown-grey pebbly mudstones with calcareous sandstone layers exposed in a small stream can be assigned to the lower Oligocene pebbly mudstone facies of the Menilite Fm. Rare crinoid ossicles were picked up from the washing residues of microfauna. The sedimentary setting was probably the same as that at Jatný.
- 10. Leszna Górna Quarry (49°42'14.5"N 18° 44'07.5"E). This active quarry in Poland exposes the upper member of the Cieszyn Limestone Formation. Medium- to thick-bedded, coarse-grained detrital limestones, interbedded with black silty shales and marly shales, prevail. The stratigraphy of these strata is complicated by the overthrusting of tectonic slices, each one subdivided internally into blocks by strike-slip faults (e.g., KOPRIANIUK, 2007). The thinning of the limestone banks and the growing proportion of shales in the top of the quarry indicate the transition to the overlying Hradiště Formation (upper Valanginian according to its foraminiferal content). Thus the detrital limestones of the Cieszyn Limestone Formation are most probably also Valanginian. The occurrence of a crinoid fauna was confirmed previously. A specimen of Plicatocrinus hexagonus Sieverts-Doreck, now lost, was found (BP in 2004) in debris covering the northern wall of the Leszna Górna Quarry. A new collection was made in the quarry (MB, MAS and TB in August 2019), and crinoids were found at the eastern end of the first operating level of the quarry.

Crinoid remains occurring on the surface of slabs were photographed in the field using an iPhone S. In addition, seven carbonate samples, each weighing from 5 to 7 kg, were collected and taken back to the Laboratory of the Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia, in Katowice. Five samples were selected at random, and a series of thin sections (TS) and polished slabs (PS) were prepared. TS and PS were then investigated and interpreted (BF). The next step consisted in treating the rock samples with GLAUBER's salt (up to five cycles of boiling-thawing). The mixture was then washed using running hot tap water and screened on a sieve column (Ø 1.0, 0.315 and 0.1mm mesh, respectively). Finally all macerated samples were dried at 180°C. Residues were hand-picked using a microscope. Some specimens were cleaned with hot hydrogen peroxide and then rinsed under running hot tap water. All crinoids recovered from maceration were photographed using a Canon Eos 350D digital camera.

4. Results

As a result of our new investigations during 2019, numerous remains consisting of crinoid cups, isolated cup elements, brachial plates, columnals, and pluricolumnals were collected. The following taxa were identified:

- Isocrinus cf. amblyscalaris (THURMANN, in THURMANN & ÉTALLON), represented by more than 200 isolated columnals and pluricolumnals, and columnals and pluricolumnals visible on PS. I. cf. amblyscalaris was collected in the Leszna Górna Quarry (Valanginian; Poland), Olza River gorge (Tithonian; Czech Republic), the Dolní Líštná Quarry (Berriasian-Valanginian; Czech Republic), and the Wopienka Quarry (Berriasian-Valanginian; Czech Republic).
- Isocrinida indet., represented by more than 300 isolated columnals and pluricolumnals, numerous brachials and cirrals, and columnals, pluricolumnals and brachials visible on PS and in TS. Isocrinida indet. was collected in the Leszna Górna Quarry (Valanginian; Poland), Olza River gorge (Tithonian; Czech Republic), the Dolní (Berriasian-Valanginian; Líštná Quarry Czech Republic), the Wopienka Quarry (Berriasian-Valanginian; Czech Republic), Bystřice nad Olší (Maastrichtian; Czech Republic), Starý Jičín (Paleocene; Czech Republic), and Jatný (Eocene/Oligocene; Czech Republic).
- Eugeniacrinites sp., represented by a single cup collected in the Leszna Górna Quarry (Valanginian; Poland).
- *Phyllocrinus* sp., represented by two cups from the Leszna Górna Quarry (Valanginian; Poland).
- Gammarocrinites sp., represented by six isolated columnals and seven brachial plates. Gammarocrinites sp. was collected in the Leszna Górna Quarry (Valanginian; Poland).
- Hemicrinus tithonicus PISERA & DZIK, represented by three cups. H. tithonicus was collected in the Leszna Górna Quarry (Valanginian; Poland).
- Cyrtocrinida indet., represented by one partly preserved cup, several isolated cup remains, brachial plates, and columnals visible on PS and in TS. Cyrtocrinida indet. was collected in the Leszna Górna Quarry (Valanginian; Poland), the Dolní Líštná Quarry (Berriasian-Valanginian; Czech Republic), Hluchová, and Ženklava (Eocene/Oligocene; Czech Republic).
- Millericrinida indet., represented by 27 columnals. Millericrinida indet. was collected in the Leszna Górna Quarry (Valanginian; Poland), Olza River gorge (Tithonian; Czech



Republic), the Dolní Líštná Quarry (Berriasian-Valanginian; Czech Republic), and the Wopienka Quarry (Berriasian-Valanginian; Czech Republic).

- Thiolliericrinidae gen. et sp. indet., represented by 50 columnals. Thiolliericrinidae gen. et sp. indet. was collected in the Leszna Górna Quarry (Valanginian; Poland), Olza River gorge (Tithonian; Czech Republic), the Dolní Líštná Quarry (Berriasian-Valanginian; Czech Republic), and the Wopienka Quarry (Berriasian-Valanginian; Czech Republic).
- Roveacrinida gen. et sp. indet., represented by a single brachial plate. Roveacrinida was collected in Bystřice nad Olší (Maastrichtian; Czech Republic).
- Bourgueticrinina gen. et sp. indet., represented by three columnals. Bourgueticrinina was collected in Starý Jičín (Paleocene; Czech Republic), Jatný and Zaolší (Eocene/Oligocene; Czech Republic).

5. Taphonomy

Only Jurassic and Lower Cretaceous crinoid ossicles (ca. 700 ossicles) were used for taphonomic analyses. Upper Cretaceous-Paleogene individuals were too few. Investigated specimens were scrutinised in search of: 1) epibionts, 2) predation traces, 3) signs of abrasion, chemical alteration of ossicle structure and bioerosion traces, and 4) disarticulation gradient sensu BRETT et al. (1997).

- Strongly abraded epibionts, most probably serpulids, are detected on the lateral surface of three isocrinid pluricolumnals. They were found only on specimens from the Polish locality (Leszna Górna Quarry). As suggested by SALAMON and GORZELAK (2010), the low frequency of epibionts probably implies that pauses in sedimentation or omission were rare during the deposition of these sediments.
- 2. Some of the studied ossicles (9%) revealed a large variety of indentations, such as scratches and pits. They are rather shallow and measure 0.3 mm in width and up to 1.2 mm in length. All indentations are located on lateral surfaces. They may represent bite marks or barnacle borings; however, it their production during transport cannot be excluded.
- Eighty percent of Jurassic and 50% of Cretaceous ossicles have evidence of mechanical abrasion. This is consistent with their transport in gravitational flows. The associated macrofauna consists of thecideid brachiopods, oysters and bryozoans, all indicating shallow-marine, peri-reefal habitats. Some columnals are strongly abraded and rounded, and their articular surfaces

are not visible. Similarly, pluricolumnals consisting of several columnals are heavily rounded. According to Gorzelak and Sala-MON (2013), such features can arise from transportation over a distance in excess of 100 km (see GORZELAK & SALAMON, 2013: Fig. 2.c-d). Alternatively, the abrasion of crinoid ossicles may be a side effect of sediment reworking (or transport plus sediment reworking). On the other hand, 20% of remains display no such signs. Their co-occurrence (abraded ossicles and well-preserved columnals, pluricolumnals, plus cups) indicates that crinoids may represent a mixture of remains from different environments.

Almost 30% of the Jurassic and 30% of the Cretaceous ossicles have dissolution traces and their stereom mesh is poorly visible. Additionally, many columnals and pluricolumnals are overgrown by epitaxial calcite. Cretaceous ossicles are brown, yellowbrown and sometimes red from a stain resulting from an iron-oxide coating.

As suggested above, crinoid remains represent a mixed assemblage of allochthonous and parautochthonous elements, as supported by the co-occurrence of strongly abraded ossicles, and less abraded, articulated ossicles (e.g., cyrtocrinid cups). The presence of cyrtocrinid cups may be explained by their cups being massive with tightly sutured plates, and, therefore, classified as Taphonomic type III sensu Brett et al. (1997; see also Zaтoń et al., 2008). Bourgueticrinid cups also belong to this type. Isocrinids, millericrinids and thiolliericrinids possessed much more weakly sutured calyx plates and, therefore, are prone to rapid post-mortem disarticulation. They are classified as Taphonomic type II (BRETT et al., 1997), and their most common ossicles are columnals, pluricolumnals and brachials.

6. Palaeoecology

While the palaeoecology of bourgueticrinids, millericrinids, and thiolliericrinids is relatively well known (e.g., KLIKUSHIN, 1987; AUSICH et al., 1999, and references therein), the way of life, especially bathymetric preferences, of cyrtocrinids and isocrinids, should be revised. In the recent years, several studies showed that stalked cyrtocrinids commonly lived in both shallow- (SALAMON & GOR-ZELAK, 2007; ZAMORA et al., 2018; SALAMON, 2019; KRAJEWSKI et al., 2020) and deep-water environments (e.g., Zатоń et al., 2008; and literature cited therein). Ausich et al. (1999) stated that cyrtocrinids preferred deeper habitats, typically below 100 m depth. Extant cyrtocrinids have been documented only at considerable depths (e.g., Ausich et al., 1999; and literature cited therein; DONOVAN & JAKOBSEN, 2004; for detailed discussion see Krajewski et al., 2020).



Some authors (e.g., BOTTJER & JABLONSKI, 1988; OJI, 1996; GORZELAK et al., 2012) have suggested that isocrinids disappeared from shallow water to take refuge in deep-water settings. Ол (1996) added that isocrinids settled in new and deep-water areas by the Early Jurassic. Earlier Oil (1985) concluded that, during the Mesozoic, a lot of isocrinids migrated to deep zones where they were not subject to predatory attacks. However, he also stated that some isocrinids still preferred shallow seas, e.g., Chariocrinus andreae (DESOR). According to Oji (1985), the last shallow-water representatives of the order Isocrinida are known from the upper Aptian of Japan [Isocrinus hanaii Oji and Isocrinus? neocomiensis (DESOR)]. SALAMON (2007, 2008a, 2008b, 2008c, 2009; see also e.g., JAGT, 1999; HESS & GALE, 2010; LACH, 2016; ZAMORA et al., 2018; SALAMON et al., 2019) compiled a list of shallow-water Jurassic and Cretaceous (also post-Aptian) sections containing common isocrinids. AMÉZIANE and ROUX (1997) stated that the absence of stalked crinoids from shallow-water settings is a consequence of their functional morphology. They observed that, among Recent stalked crinoids, some forms are also known from relatively shallow-water settings (60 m). HESS (1999) noted that isocrinids are few after the Cretaceous, but we regard this as a sampling bias resulting from palaeogeography (most marine sediments were deposited in shallow waters close to current coastlines). WHITTLE et al. (2018) concluded either that migration of less mobile invertebrates (e.g., isocrinids) into deeper zones was globally asynchronous or that post-Mesozoic isocrinid occurrences from both Antarctica and South America were "retrograde reversions" to Paleozoic-type communities in cool waters. In fact, post-Mesozoic isocrinid are not as rare as claimed, and they are equally common in shallowand deep-water sediments (see data in: e.g., MOORE & VOKES, 1953; RASMUSSEN, 1972; OJI, 1990; MEYER & OJI, 1993; DONOVAN, 1995; BAUMIL-LER & GAŹDZICKI, 1996; DONOVAN & VELTKAMP, 2001; SALAMON, 2009; DONOVAN et al., 2015, 2019; SALAMON et al., 2019; WHITTLE et al., 2018; and references therein).

Changes in studied foraminiferal assemblages were strongly influenced by sedimentary conditions. During the late Tithonian, benthonic forms displaying calcite-cemented agglutinating tests (Ataxophragmiidae) and also those secreting calcium-carbonate walls (Involutinidae) became the dominant foraminifers colonizing the shelf area. The Involutinidae especially preferred reef-like environments during the time interval during which the lower part of the Cieszyn Limestone Formation was deposited (Nescieruk & Szydło, 2001). The following foraminiferal assemblages previously mentioned, also noticed in the Lesznianka stream (Poland), evidence drastic changes in sedimentary regime during the Berriasian. During that time shallow-water sedimentation was

replaced by deposition dominated by high-energy gravity flows (including turbidity currents) and resulted in the formation of a carbonate complex with interbedded marly shales (upper part of the Cieszyn Limestones Formation). Hemipelagic sedimentation was also a feature of the Berriasian and predominated during the Valanginian during tectonic quiescence. In that time of decreasing availability of calcium carbonate, sediments were colonised by deep-infaunal detritus- and bacteria-feeders under low-oxygen conditions. They record changes in trophic conditions, leading to the dominance of siliceous agglutinated taxa in foraminiferal assemblages (GEROCH & KAMIŃSKI, 1995; SZYDŁO, 2004, 2005).

When the crinoid fauna is included in this picture, it is clear that isocrinids, millericrinids and thiolliericrinids occur in Jurassic and Cretaceous deposits. They are accompanied by numerous cyrtocrinids. Though these rocks are deep-water (bathyal), they contain a shallow-water reworked macrofauna including crinoids. KLIKUSHIN (1987) described the largest collection of thiolliericrinids from Crimea to date, where these crinoids lived within the coral reefs. In addition to thiolliericrinids, Klikushin (1987) often referred to oysters, nerineid gastropods, 'true' (unstalked) comatulids, and echinoids, which all co-occur with them. Similarly, millericrinids occurring in the Upper Jurassic deposits are usually associated with shallow-water environments (e.g., Salamon & Zatoń, 2005; RADWAŃSKA & RADWAŃSKI, 2005). On the other hand, deep-water discoveries of millericrinids are known, although most of these are Early Jurassic in age (e.g., Hess, 2006). Late Jurassic and post-Jurassic sedimentation, as indicated above, changed its character from slope hemipelagites and slumps in the Tithonian to turbidites in the Berriasian and Valanginian (with a deepening trend). Also in these much deeper (>200 m) environments, isocrinids and cyrtocrinids, together with millericrinids and thiolliericrinids (Berriasian-Valanginian sections in the Czech Republic: Dolní Líštná Quarry, Wopienka Quarry), were widely distributed. It is also worth mentioning that cyrtocrinids and isocrinids occur in the Paleogene sediments of the Czech Republic (Bystřice nad Olší, Hluchová, Jatný, Starý Jičín, Zaolší, and Żenklava). These deposits are bathyal (upper slope) according to microfossil and lithofacies characteristics. The crinoid remains may be shallowwater but also bathyal. The accompanying fauna is derived from a mix of all these habitats.

We should remember, on one hand, that, in these environments, some invertebrates were redeposited from deeper parts of the sublittoral zone. Therefore, it is possible that some crinoids originally inhabited these zones. On the other hand, the state of preservation of the post-Mesozoic crinoids is quite good, with no signs of abrasion clearly visible on facets, etc. (compare e.g., Fig. 3.J, T-U). It seems unlikely that they underwent vigorous and extended transport.



7. Systematics

The systematics of crinoids follows the scheme proposed by Hess and Messing (2011).

Order Isocrinida SIEVERTS-DORECK, in Moore et al., 1952

Suborder Isocrinina SIEVERTS-DORECK, in UBAGHS, 1953

Family Isocrinidae GISLÉN, 1924

Subfamily Isocrininae GISLÉN, 1924

Genus Isocrinus
MEYER, in AGASSIZ, 1836

Type species: *Isocrinites pendulus* MEYER, in AGASSIZ, 1836

Isocrinus cf. amblyscalaris (Thurmann, in Thurmann & Éttalon, 1861)

(Fig. 3.I, L)

1861 ? Pentacrinus amblyscalaris Thurmann, in Thurmann & ÉTTALON, p. 351.

Material. More than 200 isolated columnals and pluricolumnals, and columnals and pluricolumnals visible on PS; catalogue numbers: GIUS 8-3693Ica, CGS MB25.

Description. Columnals are stellate, and medium to large in size. Their diameter is 4.40 mm, and their height varies between 1.45 and 2.60 mm. Crenularium is well developed and consists of a maximum of 18 crenulae per petal. Petal floors are relatively thin, sometimes long. Interradial areas are well developed. Latera ornamented by knobby ridges situated radially or by an interradial knob. Lumen is very small and circular.

Detailed discussion in Salamon et al. (2020).

Range in Outer Carpathians: Tithonian-Valanginian.

Isocrinidae indet.

(Fig. 3.H, J-K)

Material. More than 300 isolated columnals and pluricolumnals, numerous brachials, cirrals, columnals, pluricolumnals, and brachials visible on PS and in TS; catalogue numbers: GIUS 8-3693Iin, CGS MB15, MB16, MB21, MB24, MB26, MB27, MB28, MB32, MB38, MB39.

Description. Columnals are very small to extremely large, with diameter ranging from 0.55 to 10.40 mm. Shape varies from circular to pentagonal or pentalobate, sub-pentagonal and subpentalobate, or stellate. Articular facets are commonly not visible; in some cases only relics of crenulae are visible. It seems that crenulae are thin. Latera is smooth or ornamented by knobby ridges situated radially or by an interradial knob. Lumen is very small and circular. Cirrals are small to medium in size, smooth, and elliptical or circu-

lar in section. Brachials are rather small, V- or rarely U-shaped. Proximal facets of primibrachials are muscular. They have large muscle fields; other facets display an embayed synarthry or a cryptosynarthry. Secundibrachials are smooth. They have deeply incised adoral furrows and oblique muscular facets with large muscle fields. Proximal brachials are wide. Distal brachials are higher than wide.

Range in Outer Carpathians: Tithonian-Valanginian, Maastrichtian, Paleocene, Eocene/Oligocene.

Order Cyrtocrinida SIEVERTS-DORECK, 1952

Suborder Cyrtocrinina SIEVERTS-DORECK, 1952

Superfamily Eugeniacrinitoidea ROEMER, 1855

Family Eugeniacrinitidae ROEMER, 1855

Genus Eugeniacrinites MILLER, 1821

Type species: *Eugeniacrinites quinquangularis* MILLER, 1821

Eugeniacrinites sp.

(Fig. 3.A)

Material. One cup; catalogue number: GIUS 8-3693Fs.

Description. Cup is smooth, funnel-shaped and slightly pentagonal in outline. Radial articular facets are moderately low and very wide. They have small aboral ligament fossae, deeply excavated inter-articular fossae, and relatively low adoral muscle fossae. Radial articular facets are separated by rather large interradial projections; interradial projections are blunt. Radial cavity is shallow, probably due to matrix infilling. Suture lines are clearly visible. Facet to stem is circular and wide.

Discussion. The generic type species, *Eugenia-crinites cariophilites* (SCHLOTHEIM), is similar to the cup at hand with its smooth, funnel-shaped and pentagonal in outline cup (cf. Hess, 1975: Tab. 23, fig. 1; Hess & Messing, 2011: Fig. 88/1a). However, the stratigraphic range of the type species is restricted to the Middle Oxfordian. There is also some similarity between the specimen at hand and *Eugeniacrinites zitteli* JAEKEL (blunt interradial projections). This character distinguishes *E. cariophilites* from *E. zitteli*, as already pointed out by Hess et al. (2011). The latter authors described *E. zitteli* from the Tithonian and Berriasian of eastern Poland. *E. zitteli zitteli* and *E. zitteli moravicus* are considered separate species.

For more detailed discussion see HESS *et al.* (2011).

Range in Outer Carpathians: Valanginian.



◀ Figure 3: Post-Paleozoic crinoids from Outer Flysch Carpathians of the Czech Republic and Poland. Scale bar equals 1 mm. A. Eugeniacrinites sp., cup, lateral view. Leszna Górna Quarry (Valanginian). GIUS 8-3693Es. **B.** Phyllocrinus sp., cup, lateral view. Leszna Górna Quarry (Valanginian). GIUS 8-3693Pm. C-D. Gammarocrinites sp., columnals, articular face (C) and lateral view (D). Leszna Górna Quarry (Valanginian). GIUS 8-3693Gs. **E.** Cyrtocrinida indet., cup, lateral view. Leszna Górna Quarry (Valanginian). GIUS 8-3693Ci. F-G. Hemicrinus tithonicus PISERA & DZIK, cups, adoral (F) and aboral views (G). Leszna Górna Quarry (Valanginian). GIUS 8-3693Ht. H, J-K. Isocrinidae indet., pluricolumnal, lateral view (H), columnal, articular face (J, K). Leszna Górna Quarry for H (Valanginian), GIUS 8-3693Iin, Starý J (Paleocene), CGS MB38, and Olza River gorge for K (Berriasian/Valanginian), CGS MB15. I, L. Isocrinus cf. amblyscalaris (THURMANN, in THURMANN & ÉTTALON), pluricolumnal, lateral view (I), columnal, articular face (L). Leszna Górna Quarry (Valanginian). GIUS 8-3693Ica. M-N. Bourgueticrinina fam. and gen. indet., columnals, articular face (M) and lateral view (N). Starý Jičín (Paleocene). CGS MB37. O-Q. Thiolliericrinidae gen. et sp. indet., columnals, articular face (O, P) and lateral view (Q). Wopienka Quarry for O (Berriasian/Valanginian), CGS MB19, Dolní Líštná Quarry for P, (Berriasian/Valanginian), CGS MB22, and Leszna Górna Quarry for Q (Tithonian/Berriasian), GIUS 8-3693Th. R-S. Millericrinida indet., columnals, articular faces. Leszna Górna Quarry for R (Tithonian/Berriasian), GIUS 8-3693Mi, and Wopienka Quarry for S (Berriasian/Valanginian), CGS MB20. T-U. Roveacrinida indet., brachial. Bystřice nad Olší (Maastrichtian), CGS MB31.

Figure 3 : Crinoïdes post-paléozoïques des Carpathes externes du Flysch de la République tchèque et de Pologne. Barre d'échelle : 1 mm. A. Eugeniacrinites sp., thèque, vue latérale. Carrière de Leszna Górna (Valanginien). GIUS 8-3693Es. B. Phyllocrinus sp., thèque, vue latérale. Carrière de Leszna Górna (Valanginien). GIUS 8-3693Pm. C-D. Gammarocrinites sp., columnales, face articulaire (C) et vue latérale (D). Carrière de Leszna Górna (Valanginien). GIUS 8-3693Gs. E. Cyrtocrinida indet., thèque, vue latérale. Carrière de Leszna Górna (Valanginien). GIUS 8-3693Ci. F-G. Hemicrinus tithonicus PISERA & DZIK, thèques, vues adorale (F) et aborale (G). Carrière de Leszna Górna (Valanginien). GIUS 8-3693Ht. H, J-K. Isocrinidae indet., pluricolumnale, vue latérale (H), columnale, face articulaire (J, K). Carrière de Leszna Górna pour H (Valanginien), GIUS 8-3693Iin, Starý Jičín (Paléocène), CGS MB38, et talus de la rivière Olza pour K (Berriasien/Valanginien), CGS MB15. I, L. Isocrinus cf. amblyscalaris (THURMANN, in THURMANN & ÉTTALON), pluricolumnale, vue latérale (I), columnale, face articulaire (L). Carrière de Leszna Górna (Valanginien). GIUS 8-3693Ica. M-N. Bourgueticrinina fam. et gen. indet., columnales, face articulaire (M) et vue latérale (N). Starý Jičín (Paléocène). CGS MB37. **O-Q.** Thiolliericrinidae gen. et sp. indet., columnales, face articulaire (O, P) et vue latérale (Q). Carrière de Wopienka pour O (Berriasien/Valanginien), CGS MB19, carrière de Dolní Líštná pour P, (Berriasien/Valanginien), CGS MB22, et carrière de Leszna Górna pour Q (Valanginien), GIUS 8-3693Th. R-S. Millericrinida indet., columnales, faces articulaires. Carrière de Leszna Górna pour R (Valanginien), GIUS 8-3693Mi, et carrière de Wopienka pour S (Berriasien/Valanginien), CGS MB20. T-U. Roveacrinida indet., brachiale. Bystřice nad Olší (Maastrichtien), CGS MB31.

Family Phyllocrinidae JAEKEL, 1907

Genus *Phyllocrinus*ORBIGNY, 1850, in 1850-1852

Type species: *Phyllocrinus malbosianus* Orbigny, 1850, in 1850-1852

Phyllocrinus sp.

(Fig. 3.B)

Material. Two cups; catalogue number: GIUS 8-3693Pm.

Description. Cups are small, pentagonal in outline and display very short interradial processes that are triangular in outline. Radial articular facets are low and shallow with a flat triangular surface. Radial cavity is circular, moderately wide and rather shallow. Cups are narrow at lower part, and gradually expanding up to radial facets. Suture lines between radials are clearly visible. Facet to stem is small and pentagonal.

Discussion. There are numerous phyllocrinid taxa in Jurassic and Cretaceous strata worldwide (for review see ZARĘCZNY, 1876; REMEŠ, 1905; ARENDT, 1974; ŽÍTT, 1978a, 1978b, 1978c; PISERA & Dzik, 1979; Głuchowski, 1987; Zatoń et al., 2008; SALAMON & GORZELAK, 2010; HESS et al., 2011; ZAMORA et al., 2018). Some opinions suggest there are significant differences in the structure of phyllocrinid taxa (e.g., Konieczyński et al., 2016). On the other hand, MANNI et al. (1992) concluded that Phyllocrinus furcillatus Spenden includes closely related and morphologically inseparable forms (e.g., Phyllocrinus belbekensis Arendt; Phyllocrinus pieninensis Głuchow-SKI; Phyllocrinus stellaris ZARĘCZNY) that probably constitute a lineage. We agree, but decided to classify our specimens as Phyllocrinus sp. due to the small number of available individuals.

Range in Outer Carpathians: Valanginian.

Family Sclerocrinidae JAEKEL, 1918

Genus Gammarocrinites QUENSTEDT, 1858

Type species: *Eugeniacrinites compressus* Goldfuss, 1829

Gammarocrinites sp.

(Fig. 3.C-D)

Material. Six columnals and seven brachial plates; catalogue number: GIUS 8-3693Gs.

Description. Columnals are generally circular, with some barrel-shaped. Facet may be covered by as many as 14 long, thick crenulae. Latera covered by large and circular tubercles, the latter sometimes irregular. Lumen is rounded and moderately large. Secundibrachials are low and joined by muscular or syzygial articulation. Ambulacral grooves are deep and possess large facet for pinnules.



Discussion. There are many reports mentioning that cyrtocrinid elements covered with granules are classified as *Eugeniacrinites*, *Sclerocrinus* or other (*cf.* ARENDT, 1974; PISERA & DZIK, 1979; GŁUCHOWSKI, 1987; SALAMON & GORZELAK, 2010). Here, granulated elements are provisionally assigned to *Gammarocrinites*. In *Gammarocrinites*, granules appear to be larger than those of the other taxa mentioned above. Moreover, they cover both columnals and cup elements (*e.g.*, GŁUCHOWSKI, 1987: Fig. 14/7, 8; HESS & MESSING, 2011: Fig. 90/4).

Range in Outer Carpathians: Valanginian.

Genus *Hemicrinus*ORBIGNY, 1850, in 1850-1852

Type species: *Hemicrinus asterianus =Cyrto-crinus granulatus* JAEKEL, 1891

Hemicrinus tithonicus PISERA & DZIK, 1979

(Fig. 3.F-G)

1979. *Hemicrinus tithonicus* - PISERA & DZIK, p. 815-816, Fig. 6, Pl. 3, figs. 6-7.

Material. Three cups; catalogue number: GIUS 8-3693Ht.

Description. Cups are sub-pentagonal, low and moderately wide. Stem parts are well differentiated from spoon elements. Spoon elements are smooth. Radial facets are rather wide and equal in size. Radial aboral surface is crescentic and bears wide ligament fossae with small ligament pit. Radial adoral surface is triangular and wider than the aboral one. It bears two small, circular muscular fossae, both separated by a radial groove. Both surfaces are separated by a transverse fulcral ridge. Central cavity is rather shallow. Suture lines are visible. Facet to stem is concave. Stem part is long and circular in outline.

For detailed discussion see PISERA & DZIK (1979), and MANNI *et al.* (1992).

Range in Outer Carpathians: Valanginian.

Cyrtocrinida indet.

(Fig. 3.E)

Material. One partly preserved cup, several isolated cup remains, brachial plates, and columnals visible on PS and in TS. All elements are more or less abraded; catalogue number: GIUS 8-3693Ci

Description. Only the lower part of the cup is preserved. It is slightly circular, with large, circular, rather shallow facet on stem. All radials assigned to Cyrtocrinida indet. are smooth and compact. Their surface is covered by relatively large pustules. Proximal facets are flat and small; distal facets have distinct muscular fields and very narrow aboral ligament area with a pronounced pit. First primibrachials are low. Second primibrachials are compact. Most of the secundibrachials are uniform in size, with convex aboral si

de. All brachials with convex surface are of muscular type. Columnals are stick-like or barrel-shaped. Latera is smooth or granulated, and may be straight or convex. Lumen is circular and rather small.

Range in Outer Carpathians: Tithonian-Valanginian, Eocene/Oligocene.

Order Millericrinida SIEVERTS-DORECK, 1952

Millericrinida indet.

(Fig. 3.R-S)

Material. 27 columnals; catalogue numbers: GIUS 8-3693Mi, GCS MB17, MB20, MB30.

Description. Columnals are low and circular. Articular facet is covered by thick crenulae that are mainly short. Lumen is circular and large. Latera is straight and smooth.

For detailed discussion see Salamon $et\ al.$ (2020).

Range in Outer Carpathians: Tithonian-Valanainian.

Order Comatulida A.H. CLARK, 1908 Suborder Comatulidina A.H. CLARK, 1908

Superfamily Solanocrinitoidea JAEKEL, 1918

Family Thiolliericrinidae A.H. CLARK, 1908

Thiolliericrinidae gen. et sp. indet.

(Fig. 3.O-Q)

Material. 50 columnals; catalogue numbers: GIUS 8-3693Th, CGS MB18, MB22, MB23.

Description. Columnals are of varying size, from 1.5 mm-diameter in small, low, discoidal forms to 7 mm-diameter in large, tall types. Columnals are barrel-shaped, sub-cylindrical or hourglass-shaped. Articular facet is circular or ellipsoidal. Fulcral ridge is serrated in some columnals. Marginal ridge is twinned, with twins almost perpendicular to each other on both sides of columnal. Lumen is very small and circular.

Discussion. KLIKUSHIN (1987) strived to attribute isolated columnals to different thiollericrinid cups. He concluded that columnals of *Loriolicrinus asper* KLIKUSHIN are low, parallel, hourglass-shaped, or oblique. Their latera could be smooth or tubercular. In another place he also stated that the columnals of *L. laevis* KLIKUSHIN may be parallel and not tall. Likewise concerning *Umbocrinus umbonatus* KLIKUSHIN with its low, parallel or oblique columnals that could be smooth or granulated (for more details see KLIKUSHIN, 1987: p. 633-651). However, in our opinion, associating thiolliericrinid cups with isolated columnals is dubious, especially in levels containing cups assigned to different taxa.



Range in Outer Carpathians: Tithonian-Valanginian.

Suborder Bourgueticrinina SIEVERTS-DORECK, in UBAGHS, 1953

Bourgueticrinina fam. and gen. indet.

(Fig. 3.M-N)

Material. Two columnals and one pluricolumnal; catalogue numbers: GIUS 8-3693Th, CGS MB33, MB37.

Description. Columnals are relatively high with elliptical ends constricted medially and have a fulcral ridge divided by a furrow; rhizocrinid pattern is clearly visible. The lateral surface is smooth and concave. The lumen is very small and circular

Range in Outer Carpathians: Paleocene, Eocene/Oligocene.

Order Roveacrinida SIEVERTS-DORECK, 1952

Family Roveacrinidae (PECK, 1943) GALE, 2019

Roveacrinidae gen. et sp. indet.

(Fig. 3.T-U)

Material. 1 brachial; catalogue number: CGS MB31.

Description. Single brachial is identified as an isolated second primibrachial plate (IBr2), quite uniform in size and outer features, most likely belonging to an individual that was disarticulated shortly after death. It is tall, elongate ('pin-like' or stick-like), nearly cylindrical in section and terminated by two slightly swollen, or bulbous, ends. The outer surface appears nearly smooth but displays a feebly pitted random (reticulate?) ornamentation on the plate body and a weak keel running along the radial edge. On their inner side is a continuous, narrow, and faint shallow furrow (feeding groove) with rounded side edges. The abradial extremity is cut obliquely to the plate length and bears a sloping crypto-synarthrial facet to the first secundibrachial. This proximal muscular facet is slightly rimmed. The adradial extremity is bulbous and bears two distal muscular facets to the next distal first secundibrachial. These muscular facets are directed outward with strong relief, marked ligament fossa and axial canal, and pronounced ligament fossae. The muscle fossae display outer narrow processes.

Discussion. All described morphological features recall the subfamily Roveacrininae or an early relative of the subfamily Hessicrininae (see GALE, 2019). Such roveacrinoidal plates usually occur either in quite large number in marker beds or rarely as scattered elements (current transport, bioturbation). The plate at hand suggests some scattering during transport and/or current winnowing. In any event, this is an allochthonous or a

parautochthonous element within an otherwise microfaunal assemblage.

Range in Outer Carpathians: Maastrichtian.

8. Conclusions

In the Czech sections of the Vendryně and Cieszyn formations (Outer Carpathians) of Tithonian and Berriasian-Valanginian age, remains (cups, isolated cup remains, brachials, columnals, pluricolumnals, and holdfasts), not previously described, of isocrinids, cyrtocrinids, millericrinids, and thiolliericrinids were found. In Maastrichtian sediments isocrinids and roveacrinids were documented. Paleocene to Oligocene strata yielded isocrinids, bourgueticrinids and cyrtocrinids. Isocrinids, cyrtocrinids, millericrinids, and thiolliericrinids were found in the only Polish location where crinoids had not been characterised before. The documented crinoid remains represent a mixed assemblage of allochthonous and parautochthonous elements. Jurassic and Cretaceous forms are equally common in deep- and shallow-water sediments, while cyrtocrinids and isocrinids present in post-Mesozoic strata occur only in extremely shallow environments.

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