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Authors: Salamon, Mariusz A., Gorzelak, Przemysław, and Zatoń, Michał

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Brief report

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In quest of cyrtocrinid origins: Evidence from Late Triassic ossicles from the Tatra Mountains

MARIUSZ A. SALAMON, PRZEMYSŁAW GORZELAK, and MICHAŁ ZATOŃ

We report cyrtocrinid (Crinoidea) ossicles from the Rhaetian (Late Triassic) of the Tatra Mountains (southern Poland). The columnals are high, the facets are covered with thick crenulae and the latera are concave. Such features of symplectial articulation and latera distinguish them from the columnals of other Triassic crinoids (i.e., millericrinids and encrinids) and therefore we consider they belong to Cyrtocrinida. The oldest representatives of cyrtocrinids were known from the Early Jurassic, therefore the presented material constitutes the oldest world record of these crinoids to date. We speculate that perturbations related to the global mid-Carnian extinction combined with predation intensity observed in the Middle–Late Triassic have been involved in early origin of Cyrtocrinida.

Introduction

To date, no Triassic crinoids have been identified as belonging to the order Cyrtocrinida. This fact is surprising because the cyrtocrinids are considered the most diverse and numerous of Early Jurassic crinoids. The present discovery of columnals from the Tatra Mountains suggests that the cyrtocrinid fossil record stretches back to at least the Rhaetian. Furthermore, according to Hans Hagdorn personal communication 2004 to Hess (2006) undescribed crinoids resembling cyrtocrinids (eudesicrinids with *Dinardocrinus*) are present in the Carnian Hanwang Formation of central China.

It is widely accepted that the Late Triassic was a crucial phase of articulate crinoid phylogeny (Simms and Ruffell 1990; Hagdorn and Campbell 1993; Simms 1999). Of special interest is the influence of the global mid-Carnian extinction event. According to Simms and Ruffell (1990), this event was caused by elevated average temperature, which may have been caused by rising atmospheric CO_2 released during enhanced volcanic activity associated with the dispersal of Pangea. These processes affected many marine invertebrates including disappearance of as many as 80% of the Early Carnian crinoid genera. Among these, all encrinids, ainigmacrinids, traumatocrinids, and probably all holocrinids went extinct (see also Hagdorn et al. 2007). Re-occupation of new niches probably occurred after this event. Also, paracomatulids probably originated after mid-Carnian extinction (Hagdorn and Campbell 1993). Presumably, based on the comment in Hess (2006), also cyrtocrinids may have appeared at that time.

Institutional abbreviation.—GIUS, Faculty of Earth Sciences, University of Silesia, Sosnowiec, Poland.

Geological setting

The investigated Rhaetian sediments crop out in the Lejowa Valley of the Tatra Mountains, southern Poland. The crinoid-rich interval consists of sandy limestones, black on the fresh surface or brownish when weathered, ca. 1 m thick, belonging to the so-called transitional beds of the Fatra Formation (Gaździcki 1974, 2006). The crinoidal sandy limestones are underlain by shales, marls with bivalves and dolomites. Above the sandy limestones, a bed of shales ends the Rhaetian Fatra Formation in this area, and the sandy limestones of the Kopieniec Formation begin the Lower Jurassic (Hettangian–?Sinemurian) sequence.

The crinoidal sandy limestones of the Fatra Formation are from the *Glomospirella friedli* and *Triasina hantkeni* foraminiferal Assemblage Zone (see Gaździcki 2006).

Material and methods

We examined crinoid remains from the Lejowa Valley sandy crinoidal limestones from new field-collected samples and existing museum collections. The crinoids were recovered using glauber salt solution (several cycles of freezing and melting). The residue was then washed, dried at 180°C and handpicked under a binocular microscope. 64 crinoid remains were collected, among which undeterminable isocrinid ossicles dominated (52 specimens of columnals and brachials). Twelve isolated ossicles and several ossicles on the slab surface were identified as cyrtocrinid columnals.

All identified cyrtocrinid columnals have been measured and compared to columnals of Early Jurassic cyrtocrinids as well as to the Middle Triassic encrinids, silesiacrinids, and dadocrinids. Simple statistical analyses were performed and the results are provided in Table 1.

Description

Material.—12 isolated columnals and several columnals on the slab surface. GIUS 7-3474.

Description.—Columnals are cylindrical and high. Articular

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facet covered with very thick and rather short crenulae. Lumen is large and circular. Latera are smooth and concave.

Measurements.—See Table 1.

Discussion

Resemblance to millericrinids.—The morphology of the specimens under discussion most resemble that observed in the representatives of the family Dadocrinidae (sensu Lowenstam 1942). Although the representatives of Dadocrinidae were differently interpreted (encrinids or holocrinids, Hess 1975; Simms 1988), they were ultimately classified as millericrinids (Hagdorn 1995, 1996). The latter author discussed the similarity of these crinoids with the encrinids; however, they have uniserial arms and in most cases dicyclic cups as adult animals. Therefore, they should be treated as an independent family of Millericrinida.

Dadocrinid facets may be covered by thick and short crenulae, and their lateral surfaces are commonly flat and convex, but may also be concave (see e.g., Głuchowski 1986; Hagdorn 1996; Salamon 2003; Głuchowski and Salamon 2005) as in the Rhaetian specimens from Tatra Mountains (Fig. 1). On the other hand, the stratigraphic range of dadocrinids known from the Tethys and its northern branch (Germanic Basin) is limited only to the Anisian. This circumstance, as well as our statistical analyses (measurements) require to rule out the assignment of the documented specimens to the family Dadocrinidae.

Additionally, in the Triassic deposits there was documented another family of Millericrinida, called Bangtoupocrinidae, which encompasses two genera: *Silesiacrinus* and *Bangtoupocrinus*. In this case, the assignment of the Tatra specimens to the genera mentioned above should also be excluded. *Silesiacrinus* was a common crinoid both in the Germanic Basin and Alpine Anisian (Illyrian; e.g., Hagdorn et al. 1996). Moreover, its facets are covered by rather thin and long crenulae, resembling those in the large Jurassic millericrinids (e.g., *Millericrinus*), but they are significantly shorter (especially the proximal columnals) than the columnals of the Rhaetian specimens described here.

Bangtoupocrinus is known from the Upper Anisian of China, as well. However, the morphological features of its columnals distinguish this genus from the present finds. In this case, the stem is built by columnals without cirri and facets were covered by thin or thick, long crenulae, in many cases similar to those in *Silesiacrinus*. Latera were straight or convex, commonly covered with fine tubercles (see Stiller 2000: figs. 7–9). It is worth mentioning that even the distal columnals, generally much higher than the proximal ones, are significantly shorter in *Silesiacrinus* and *Bangtoupocrinus* than in the Rhaetian forms from the Tatra Mountains (compare Hagdorn et al. 1996; Stiller 2000).

The only remains of millericrinids occurring in Late Triassic (Norian and Rhaetian) deposits are represented by brachials, columnals and terminal stalks acting as holdfasts known from the Hallstatt Limestones and the Zlambach Beds of Salzkammergent in Austria. However, according to Hagdorn (1995) they have strong similarity with Jurassic millericrinids. The latter information, despite of lack of illustrations, seems to be sufficient to exclude their similarity to the Rhaetian specimens reported here.

It must also be stated that the Triassic columnals of cyrtocrinids from the Tatra Mountains, differ from the majority of Early Jurassic millericrinids (details in Klikushin 1987; Simms 1989; Jäger 1993, 1995; Hess 2006). The only certain representatives of the genus is *Shroshaecrinus* (Millericrinidae sensu Simms 1989; see also comments in Hess 2006), already known from the Sinemurian, resemble the forms reported in the present paper. Especially the specimens presented by Jäger (1995: pl. 6: 2, 7) are very similar to the Late Triassic cyrtocrinids. The columnals from Jäger (1995) are high, may possess concave lateral surfaces, and their facet could have been covered with thick and sparse crenulae. However, we share the opinion of Nicosia (1991) that *Shroshaecrinus* should be treated as a tetracrinid, not as a millericrinid (detailed discussion in Nicosia 1991; Salamon et al. 2007).

Resemblance to encrinids.—Some of the encrinid (Encrinidae) columnals, especially those from the distal part of the stem, may be high, commonly with concave latera and their facets covered with thick and short crenulae. However, despite this morphological similarity, the assignment of the Rhaetian specimens from Poland to Encrinidae is excluded— the last occurrences of encrinids are confined to the Middle Carnian (Hagdorn 1995: fig. 1).

Table 1. Quantitative and qualitative data of cyrtocrinids and other Triassic crinoids; SD, standard deviation, CV, coefficient of variation. Middle Triassic encrinids: Encrinidae gen. et sp. indet. (Pelsonian–Illyrian, Holy Cross Mountains, southern Poland, coll. no. GIUS 7-2225/48a-51w); Middle Triassic silesiacrinids: *Silesiacrinus silesiacus* (Pelsonian–Illyrian, Holy Cross Mountains, southern Poland, coll. no. GIUS 7-1724/34a-c/34ss); Middle Triassic dadocrinids: *Dadocrinus* sp. (Lower Anisian, Holy Cross Mountains, southern Poland, coll. no. GIUS 7-2225/1a-8h, 10, 23-26).

Crinoid group	Total numeber of columnals	Mean height (H) [mm]	Mean diameter (D) [mm]	Mean H/D	SD of H/D	CV of H/D (%)	Articular faces	Lateral faces
Late Triassic cyrtocrinids	12	2.658	1.817	1.49	0.13	8.72	covered with thick and short crenulae	flat or concave
Early Jurassic cyrtocrinids	32	2.728	1.956	1.42	0.26	18.3	covered with thick and short crenulae	flat or concave
Middle Triassic encrinids	100	2.819	5.234	0.6	0.25	41.7	covered with thick and short crenulae	flat or convex
Middle Triassic silesiacrinids	100	1.748	5.585	0.32	0.11	34.4	covered with thin and long crenulae	flat, convex or bearing tubercles
Middle Triassic dadocrinids	100	1.625	2.655	0.63	0.18	28.6	covered by thick and short crenulae	flat, convex or rarely concave

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Resemblance to Early Jurassic (Hettangian) cyrtocrinid columnals.—The Jurassic cyrtocrinids known so far were noted from sediments no older than the Sinemurian (e.g., Arendt 1974; Hess 2006 and literature cited therein). For the current study, 32 cyrtocrinid columnals from the Hettangian of Kopieniec Wielki, Tatra Mts. (details in Głuchowski 1987) were used for comparison. Either, their sizes and morphology (Table 1, Fig. 1E, F) are similar or even identical to the Late Triassic cyrtocrinid columnals reported here. Only the coefficient of variation of H/D of Late Triassic cyrtocrinids is slightly lower (8.72%) than that those from Early Jurassic (18.3%). This, however, may only be a result of a larger sample size of the latter. Moreover, the coefficient of variation of H/D of Late Triassic cyrtocrinid columnals is closer to those of Early Jurassic than to any of the Middle Triassic crinoids (see Table 1). Thus, it is most plausible that the Late Triassic and Early Jurassic ossicles belong to the same cyrtocrinid taxon.

Concluding remarks

It is commonly accepted that Cyrtocrinida branched from the Millericrinida during the Late Triassic by reduction of stem and basal plates (e.g., Simms 1989). However, Pisera and Dzik (1979) suggested that the morphology of cyrtocrinid columnals, as well as their uniserial arms, point to their origin from the Middle Triassic dadocrinids (Dadocrinidae). A similar opinion was put forward by Manni and Nicosia (1999), who stated that the oldest representative of cyrtocrinids is *Nerocrinus petri*, the representative of the family Nerocrinidae, known from the Pliensbachian of Italy.

By comparison with millericrinids, cyrtocrinids are strongly specialised and have several morphological and behavioural features that can be interpreted as anti-predatory adaptations. They had a crown and arms structure that could be enrolled in a cavity formed by large median prolongation of the second primibrachials or by interradial processes of the radials (Hess 1999). Furthermore, they were smaller, comparing to the millericrinids, which suggests that paedomorphosis was involved. Also cyrtocrinids seemingly inhabited deeper settings. They have been documented mainly in association with sponge-brachiopod reefs that formed at considerably depths (e.g., Hess 1999; Salamon 2008; Zatoń et al. 2008). It is presumed that some species occupied quiet areas in the shelter of larger crinoids, such as isocrinids (see e.g., Głuchowski 1987). It is also worth stressing that modern cyrtocrinids occur at depths exceeding 200 m (Hess 1999). By analogy with the modern examples, this can be considered as an anti-predatory response, because Oji (1996) has shown that predation intensity is higher in shallow than deeper waters.

It seems that many so-called anti-predatory adaptations among cyrtocrinids are related to co-evolving carnivorous groups. It is highly probable that perturbations related to the global mid-Carnian extinction combined with increased predation intensity on crinoids in the Middle-to-Late Triassic (diversification of durophagous predators such as sharks, basal actinopterygii, and placodonts, see Walker and Brett 2002) have involved in the early origin of Cyrtocrinida. It is worth mentioning that the first appearance of teleost fish that fed on calcareous prey appeared at this time (see Walker and Brett 2002: 131, fig. 4). However, it should be clearly stressed that teleost's diverification has occurred in Late Mesozoic. The influence of benthic predators (e.g., cidaroids) on crinoid evolution should also be taken into account (Baumiller et al. 2008; Gorzelak and Salamon 2009).

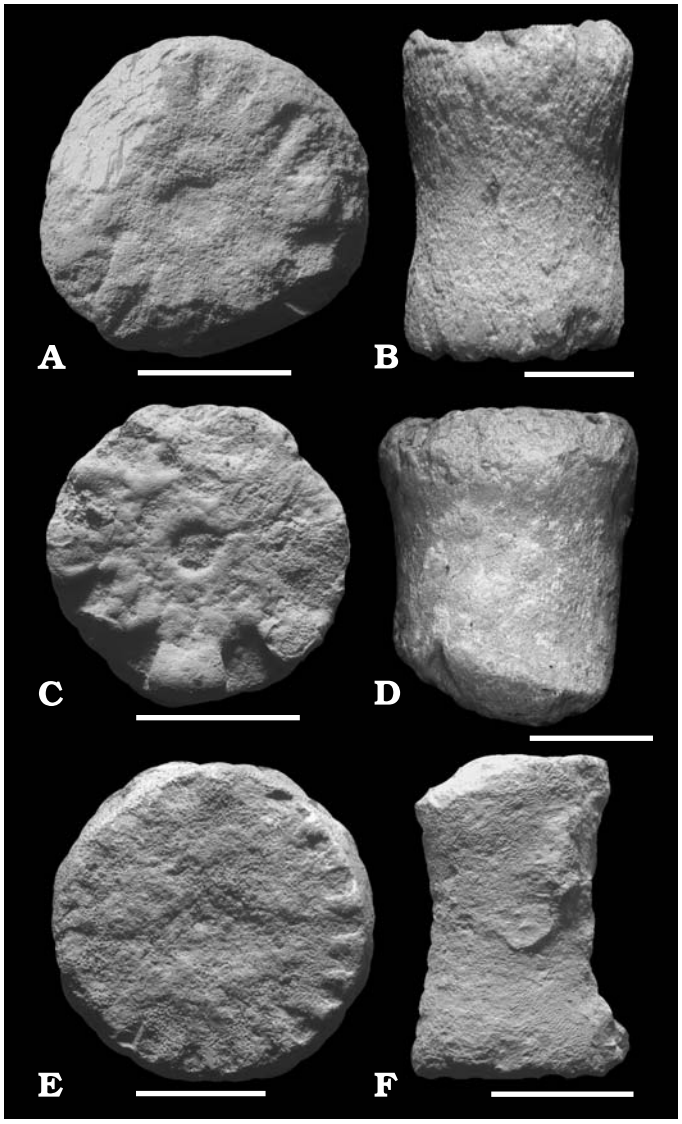


Fig. 1. Cyrtocrinid columnals from Lejowa Valley in Tatra Mountains, Poland. **A**–**D**. Rhaetian, Upper Triassic. **A**. Latera, GIUS 7-3474/1. **B**. Latera, GIUS 7-3474/2. **C**. Facet, GIUS 7-3474/3. **D**. Latera, GIUS 7-3474/4. **E**, **F**. Hettangian, Lower Jurassic. **E**. Facet, GIUS 8-3472/1. **F**. Latera, GIUS 7-3472/2. Scale bars 1 mm.

The Middle Triassic columnals from Poland yield certain traces of predation (own data) suggesting high predation pressure. On the contrary, McRoberts (2001) argued that durophagous predators may not have been sufficiently abundant or widespread during the Triassic. Furthermore, Schneider (1988) pointed out that predation on crinoids is deemed to have been relatively low at this time. However, discovery of columnals from the Middle Triassic of Poland with bite-marks, may strengthen the hypothesis that predation intensity may have exerted considerable influence on crinoid evolution including early origin of cyrtocrinids.

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Mariusz A. Salamon [paleo.crinoids@poczta.fm] and Michał Zatoń [mzaton@wnoz.us.edu.pl], Wydział Nauk o Ziemi, Uniwersytet Śląski, ul. Będzińska 60, PL-41-200 Sosnowiec, Poland;
Przemysław Gorzelak [pgorzelak@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

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