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A diverse crinoid fauna from the Middle Jurassic (Upper Bajocian–Callovian) of the Polish Jura Chain and Holy Cross Mountains (south-central Poland)

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Key words: crinoids, Middle Jurassic, Poland, palaeobiogeography, taphonomy, epibiontism

ABSTRACT

A systematic account of a diverse crinoid fauna from the Middle Jurassic (Upper Bajocian–Callovian) of the Polish Jura Chain and Holy Cross Mountains (south-central Poland) is presented. The description is supplemented with a list of all crinoid species found hitherto in the Tatra Mountains and the Pieniny Klippen Belt (Poland), which were a part of the northern margin of the Tethys during Middle Jurassic time. *Balanocrinus hessi* seems to be endemic and established its own population in the epicontinental sea. Other stalked crinoids entered from the Tethys through the East-Carpathian Gate or from a westerly way, and constitute a typical Mediterranean fauna. Stemless forms are regarded to be unsuccessful immigrants. The crinoid remains are preserved mostly as columnals and pluricolumnals, the majority of which are encrusted and bored by various epi- and endobionts. No encrustation or boring, however, occurred during the lifetime of these crinoids. The association of well-preserved columnals/pluricolumnals with the broken and abraded isolated columnals, may be the evidence of a within-habitat time-averaging of the crinoid assemblages.

ZUSAMMENFASSUNG

Aus mitteljurassischen (Bajocian–Callovian) Sedimenten des südlichen Zentralpolens (Krakow–Częstochowa Hochland und Heilig-Kreuz Gebirge) wird eine diverse Crinoidenfauna systematisch beschrieben und stratigraphisch eingestuft. Die Beschreibung wird durch eine Zusammenstellung sämtlicher Crinoiden-Spezies ergänzt, die bislang im Tatra-Gebirge und im Pieniny Klippen-Gürtel gefunden wurden. Beide Regionen waren während des Mittleren Jura Teil des Nordrandes der Tethys. *Balanocrinus hessi* bildete eigenständige Populationen in diesem epikontinentalen Meeresbereich und scheint endemisch gewesen zu sein. Andere gestielte Crinoiden drangen aus der Tethys durch die Ost-Karpaten-Pforte oder aus westlicher Richtung vor und stellen typische mediterrane Faunenelemente dar. Ungestielten tethyalen Formen gelang offensichtlich keine Einwanderung. Die Assoziation von gut erhaltenen Columnalien/Pluricolumnalien mit zerbrochenen und abgenutzten Columnalien könnte als 'time averaging' der Crinoidenvergesellschaftungen gesehen werden.

Introduction

Reviewing the rather scant literature describing the Middle Jurassic crinoids from epicratonic Poland, one may erroneously feel that these echinoderms are very rare and their findings are very incidental. In only one paper dealing with the taxonomic composition of crinoids from the Middle Jurassic (Dayczak-Calikowska 1980), we find information about the occurrences of seven species in the epicratonic Poland: (*Balanocrinus* aff. *subteroides*, *Cyclocrinus macrocephalus*, *Mespilocrinus macrocephali* [*sic*!], *Pentacrinus nodosus*, *P. cingulatus*, *P. pentagonalis* and *P. crista halli* [*sic*!]), but with neither descriptions nor illustrations. Currently, however, it has been observed that in each of the investigated areas, the crinoid fragments form the dominant faunistic component and are characterized by a quite important biodiversity. In the present study, seven localities have been investigated, from the Upper Bajocian to Callovian of the Polish Jura Chain and Holy Cross Mountains (south-central Poland). Seven isocrinid and two comatulid crinoid taxa, as well as the columnals of Millericrinidae (two morphotypes) have been documented. Although Głuchowski (1987) reported previously many of the discovered isocrinids from deposits of the same or slightly younger age in the Tethyan part of Poland (Pieniny Klippen Belt and the Tatra Mountains), comatulids and millericrinids are described for the first time. This new crinoid material gives the opportunity to show their diversity in epicontinental Polish Basin during the late Bajocian–Callovian, their palaeobiogeographic affinities with the Tethyan crinoid faunas and possible migration routes, as well as their taphonomic history.

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Fig. 1. Schematic geological map of Poland, with the investigated localities in the Polish Jura Chain and the southwestern margin of the Holy Cross Mountains (map modified after Radwańska & Radwański 2003).

Geographical and geological setting

The reported material comes from two main areas of the epicratonic Polish Basin: the Polish Jura Chain (belonging to the Cracow-Częstochowa Upland) and the southwestern margin of the Holy Cross Mountains (Fig. 1).

In the Polish Jura Chain, four localities were investigated: Zalas, Ogrodzieniec, Blanowice and Kawodrza/Gnaszyn (Fig. 1). The Polish Jura forms a monoclinally extended structure, spreading from southeast to northwest in south-central and central Poland (Fig. 1). In this area, the Upper Bajocian through Bathonian sediments are composed mainly of dark-grey clays, with many levels of massive siderites, as well as carbonate concretions. This complex in the Polish Jura is known as the Ore-Bearing Częstochowa Clay Formation (Dayczak-Calikowska et al. 1997; Kopik 1998; Matyja & Wierzbowski 2000; Zatoń & Marynowski 2006). The layers gently dip at an angle of no more than 2° in northeastern direction (Znosko 1960). These sediments are exposed in numerous active or non-active clay-pits. The samples were taken from six active clay-pits, embracing the following ammonite zones, established for Submediterranean Province (see Mangold & Rioult 1997): Parkinsoni Zone (uppermost Bajocian; Kawodrza), Zigzag Zone (Lower Bathonian; Kawodrza), Morrisi and Bremeri Zone (Middle Bathonian; Blanowice, Gnaszyn and Ogrodzieniec) and Retrocostatum Zone (Upper Bathonian; Gnaszyn and Ogrodzieniec). These sediments are capped by often condensed Callovian deposits, consisting of limestones, sandstones and sandy-limestones (Dayczak-Calikowska et al. 1997). The samples from the Zalas Quarry (Fig. 1) were taken from the Callovian sandstones, sandy limestones, as well as from the stromatolite layer (for details see Matyja 2006).

In the western margin of the Holy Cross Mountains, three localities were investigated: Mnin, Wola Morawicka and Gumienice (Fig. 1). Mnin, where dark-grey sandy mudstones are intercalated with coquinas, limy sandstones and limestones, it is a few metres thick and latest Bajocian in age. Foraminiferal assemblages (Dayczak-Calikowska & Kopik 1973) confirm this stratigraphic position. Wola Morawicka, where 6 m of black clays of uppermost Bajocian (Parkinsoni Zone) through lowermost Middle Bathonian (Progracilis Zone) are exposed. The clays are underlain by conglomerates with quartzite sandstone pebbles, 40 cm of sandy limestones with oncolites and an upper stromatolitic layer (Siemiątkowska 1969; Barski 1999: fig. 2). The clays are overlain by 15 m of limy gaizes with flints, glauconites and sponge spicules and the lowermost part is filled with ammonites of early Callovian age (upper Herveyi through Calloviense Zone) (Siemiątkowska 1969; Siemiątkowska-Giżejewska 1974; Barski 1999). The rest of the middle and upper Bathonian, as well as the lowermost Callovian, are lacking and an erosional gap in the uppermost clays is suspected (Barski 1999). Gumienice, Lower Callovian, where organodetrital limy sandstones, sandy-marly limestones and marls of several metres of thickness are exposed (Siemiątkowska 1969).

Material and methods

The collection is housed at the Laboratory of Palaeontology and Biostratigraphy of the University of Silesia, Poland (Catalogue main numbers: GIUS 8–2510, 8–2569, 8–2571).

During the fieldwork, 11 samples (ca. 10 kg per sample) were obtained from seven localities of the Polish Jura Chain and the Holy Cross Mountains (Fig. 1). For comparison purposes, additional crinoids were obtained from Cloughton Wyke on the Yorkshire coast of northeastern England, where the sandy mudstones and mudstones of the Scarborough Formation, early Bajocian in age (Humphriesianum Zone), are well exposed (see Rawson & Wright 1995 for comprehensive informations). The clay sediments of Bajocian–Bathonian age, were left in hot tap water for 2 days and then washed and sieved using 1.0 mm, 0.5 mm and 0.315 mm mesh sizes. The resulting material was then dried at 140 °C and all the crinoid material was removed from the residue using a binocular.

The samples from the Callovian carbonates, locally slightly marly, were obtained mainly from the weathered surface. After washing, the samples were treated with glauber salt (three times of boiling – freezing procedure) during 3 days. The obtained residue was then washed using hot tap water; the next steps follow the same procedures as above.

Systematic palaeontology

Measurements used in this section (after Moore & Jeffords 1968):
KD: columnal diameter (in mm)
KH: columnal height (in mm)
KHi: KH/KD*100

Order Isocrinida Sieverts-Doreck 1952
Family Isocrinidae Gislén 1924
Genus *Isocrinus* Agassiz 1836
Type species. – Isocrinites pendulus von Meyer 1836

***Isocrinus* sp.**

(Fig. 2a)

Material. – 17 columnals (1 nodal), 3 pluricolumnals, 17 brachials, 25 cirrals; GIUS 8 – 2571/I.
Dimensions. – KD: 0.6-6.0; KH: 0.4-2.8; KHi: 47-67.
Description. – Stellate columnals. Articulum is flat and no ornamentation is visible. Latera is smooth. Lumen is very small and circular. Cirrals are of variable shape, mainly oval, but ellipsoidal and rhombic are also present. Brachials are small and smooth, with a single large thorn on the dorsal side.
Remarks. – Because the characterized stellate columnals of *Isocrinus* sp. did not co-occur with any other ossicles, it was assumed that the associated cirrals and brachials belong to one species.
Distribution in Poland. – Uppermost Bajocian (Holy Cross Mountains).

***Isocrinus nicoleti* (Desor 1845)**

(Fig. 2b)

1879 *Pentacrinus nicoleti* Desor; de Loriol: 139, pl. 15, fig. 34–36.
1987 *Isocrinus nicoleti* (Desor); Głuchowski: 46, pl. XXVI/1–6, pl. XXVII/1–6, XXVIII/1–5, text-fig. 16/1.
2000 *Isocrinus nicoleti* (Desor); Tang, Bottjer & Simms: 46–54, fig. 4, 5a, b.

Material. – 15 columnals; GIUS 8 – 2571/In.
Dimensions. – KD: 2.6-5.3; KH: 0.8-1.8; KHi: 31-34.
Description. – Stellate columnals. Petal floors are elongated with a well developed crenularium. Crenularium consists of numerous and fine culmina; 23 to 28 crenulae per petal. Crenulae of radial part nearly touch each other and leave narrow slits. Lumen is small and circular.
Distribution in Poland. – Aalenian–Bathonian (Tatra Mountains), Toarcian–Bathonian (Pieniny Klippen Belt), uppermost Bajocian (Polish Jura and Holy Cross Mountains).

***Isocrinus bajocensis* (d'Orbigny 1850)**

(Figs. 2c, d)

* 1850 *Pentacrinus bajocensis* n. sp.; d'Orbigny: 291.
1992 *Chladocrinus bajocensis* (d'Orbigny); Klikushin: 102–103, 105.

Material. – 6 pluricolumnals; GIUS 8 – 2571/Ib.
Dimensions. – KD: 0.6-4.8; KH: 0.6-2.1; KHi: 44-100.
Description. – Stellate columnals. Articulum is flat, with thin, drop-like, almost ellipsoidal petal floors. Petals are separated one from another by thin adradial crenulae; every petal is surrounded by 12 to 16 thin marginal crenulae. Marginal crenulae are of equal size, distinctly longer than adradial crenulae. Lumen is small and circular. Nodal columnals are larger than internodal columnals. Latera of columnals is cover by irregular, small tubercles. Internodal columnals with a sharp keel in the middle part of the latera. Cirrus scars are large, oval and directed upward.
Discussion. – Simms (1989) included the genus *Chladocrinus* Agassiz 1836 into the synonymy of *Isocrinus* Agassiz 1836 (for detailed discussion see Simms 1989: 35–36).
Distribution in Poland. – Uppermost Bajocian (Holy Cross Mountains), uppermost Bajocian–lowermost Bathonian (Polish Jura).

Family Pentacrinidae Gray 1842
Genus *Pentacrinites* Blumenbach 1804
Type species. – Pentacrinites fossilis Blumenbach 1804

***Pentacrinites dargniesi* Terquem & Jourdy 1869**

(Fig. 2e)

* 1869 *Pentacrinites dargniesi* n. sp.; Terquem & Jourdy: 146, pl. 15, fig. 1–7.

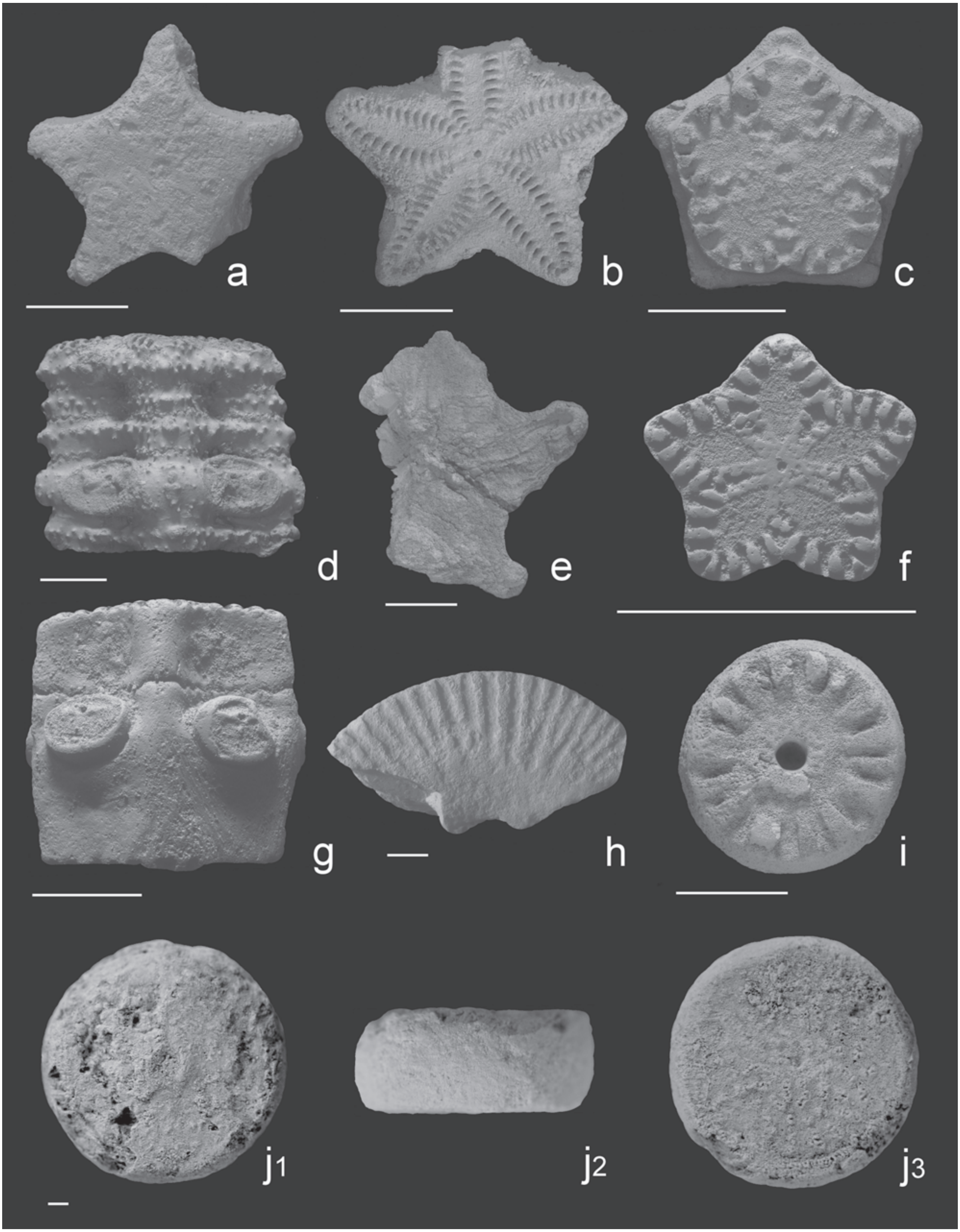
Material. – 3 columnals, 1 pluricolumnal; GIUS 8 – 2571/Pd.
Dimensions. – KD: 2.4-6.8; KH: 1.0-2.1; KHi: 31-42.
Description. – Stellate columnals with strongly bent edges. Petal floors are narrow and very long, marked by very distinct symmetric depressions. Crenulation pattern is not preserved. Lumen is large and circular.
Distribution in Poland. – Aalenian–Bathonian (Tatra Mountains), Toarcian–Bathonian (Pieniny Klippen Belt), uppermost Bajocian (Polish Jura).

Genus *Balanocrinus* Agassiz, in Desor 1845
Type species. – Pentacrinites subteres Münster, in Goldfuss 1826

***Balanocrinus berchteni* Hess & Pugin 1983**

(Figs. 5b, d–g)

Material. – Over 1000 columnals and pluricolumnals; GIUS 8 – 2570; 2571/Bb.
Dimensions. – KD: 0.9-5.8; KH: 0.6-2.5; KHi: 43-66; see also the Figure 4.
Description. – Columnals are circular to pentalobate. Articulum is flat, with triangular, very large petal floors. Petal floors are separated one from another by thin adradial crenulae; every petal is surrounded by 6 to 8 marginal crenulae. Marginal crenulae are of equal size, distinctly thicker than adradial. Nodal columnals are higher and wider than internodal columnals. Cryptosymplectial articulation is visible between nodal columnals and infranodal columnals. Juvenile specimen columnals much higher than adult ones and with less frequent marginal crenulae. Lumen is very small and circular. Latera of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nodal columnals is convex; in internodal columnals latera is smooth and straight. Five cirrus scars per each nodal columnal deflected upward; they are large and oval or circular.

Discussion. – Klikushin (1979), giving many arguments (e.g. the shape of the stalk, ornamentation of the articulation facet, position of the cirral sockets), distinguished the genera *Margocrinus* and *Terocrinus*, the representatives of which were earlier assigned to *Balanocrinus*. According to Simms (1989), the features given by Klikushin (1979) are rather unimportant for indication of the phylogenetic relationships. Therefore, Simms (1989) included *Margocrinus* and *Terocrinus* into the synonymy of genus *Balanocrinus*.

Distribution in Poland. – Bajocian (Pieniny Klippen Belt), uppermost Bajocian–Bathonian (Holy Cross Mountains), uppermost Bajocian–Bathonian (Polish Jura).

Balanocrinus hessi **SALAMON & ZATOŃ 2006**

For a detailed description and photo plates, see Salamon & Zatoń (2006: 7, fig. 3)

Genus *Chariocrinus* HESS 1972
Type species. – Isocrinus andreae DESOR 1845

Chariocrinus andreae **(DESOR 1845)**

(Figs. 2f, g)

* 1845 *Isocrinus andreae* n. sp.; Desor: 213.
1879 *Cainocrinus andreae* (DESOR); de Loriol: 112, pl. 14, fig. 31–38.
1972 *Chariocrinus andreae* (DESOR); Hess: 197, fig. 15–20, 22.

Material. – 103 isolated columnals (8 nodals), 12 pluricolumnals; GIUS 8 – 2510, 8 – 2571/Ca.

Dimensions. – KD: 1.0-3.8; KH: 0.3-1.5; KHi: 20-71; see also the Figure 4.

Description. – Pentalobate to stellate columnals. Articulum is flat with a distinct crenulation pattern. Petal floors are elongated with a well developed crenularium consisting up to 15 crenulae. Crenularia of neighbouring petal floors nearly touch each other in the radial part of the articulum. Lumen is small and circular. Radial pores are visible on the latera. Internodal columnals and nodal columnals are almost equal in diameter, however, nodal columnals are slightly higher and with elliptical cirrus scars. Cryptosymplectial articulation is visible beetwen nodal and infranodal columnals. Cirri socket is small, with a depressed elliptical outline, and directed outwards.

Discussion. – Hess (1972) suggested the new genus *Chariocrinus* for *Isocrinus andreae* DESOR, but this genus also embraced *Pentacrinus leuthardti* DE LORIOL, *P. cristagalli* QUENSTEDT, *P. württembergicus* OPPEL, *Balanocrinus bathonicus* DE LORIOL and *B. mosensis* DE LORIOL. Quite recently, Eagle & Hikuroa (2003) created the species *Chariocrinus latadiensis* EAGLE & HIKUROA, from the Middle Jurassic of Antarctica. Simms (1989), despite a considerable morphological similarity between *Chariocrinus* and *Hispidocrinus*, assigned *Chariocrinus leuthardti* (DE LORIOL) to *Hispidocrinus*. He explained it by the fact that axillaries of *C. leuthardti* bear large conical spines, typical for *Hispidocrinus*. Moreover, the differences among the species of *Chariocrinus*, mentioned by Hess (1972), were shown many times (e.g. Hess 1972, 1999; Klikushin 1979, 1992; Głuchowski 1987; Eagle & Hikuroa 2003). Simms (1989), on the other hand, claimed that such deliberations are rather unsupported, because we still know very little about the representatives of *Chariocrinus*. He pointed out that the only possibility is the indication of differences between the type species and *Chariocrinus württembergicus* (OPPEL), possessing the largest basals relative to the overall cup size. *Chariocrinus württembergicus* (OPPEL) basals also differ from the other Liassic isocrinids, by their markedly pentagonal outline and large contact area.

Distribution in Poland. – Aalenian and Bajocian (Pieniny Klippen Belt), Bathonian–Callovian (Polish Jura and the Holy Cross Mountains).

Order Comatulida CLARK 1908
Superfamily Paracomatulacea HESS 1951
Family Paracomatulidae HESS 1951
Genus *Paracomatula* HESS 1951
Type species. – Paracomatula helvetica HESS 1951

Paracomatula helvetica **HESS 1951**

(Figs. 3b–d)

* 1951 *Paracomatula helvetica* n. sp.; Hess: 208–216, pl. 11, text-fig. 1–12.

Material. – 8 brachials; GIUS 8 – 2571/Ph.

Description. – Primibrachs composed of 2 ossicles per ray; synarthry between these ossicles. Proximal side with a straight muscular articulation; subellipsoidal synarthry on distal side. Distal brachials are low disc to wedge shaped, with a muscular articulation on the proximal and syzygial on distal side.

Distribution in Poland. – Bathonian (Holy Cross Mountains), Middle Bathonian (Polish Jura).

Fig. 2. Middle Jurassic (Bajocian–Callovian) crinoids of Poland (Polish Jura Chain and Holy Cross Mountains). a) *Isocrinus* sp. (GIUS 8 – 2571/I$_1$), articular face of the proximal columnal (Uppermost Bajocian, Holy Cross Mountains, Wola Morawicka). b) *Isocrinus nicoleti* (DESOR) (GIUS 8 – 2571/In$_1$), articular face of the ?proximal columnal (Uppermost Bajocian, Polish Jura, Kawodrza). c, d) *Isocrinus bajocensis* (D'ORBIGNY) (GIUS 8 – 2571/Ib$_{1, 2}$), articular face of the distal (?medial) columnal (c) and pluricolumnal in lateral view (d) (c, Uppermost Bajocian, Holy Cross Mountains, Wola Morawicka; d, Polish Jura, Kawodrza). e) *Pentacrinites dargniesi* TERQUEM & JOURDY (GIUS 8 – 2571/Pd$_1$), articular face of the ?proximal columnal (Uppermost Bajocian, Polish Jura, Kawodrza). f, g) *Chariocrinus andreae* (DESOR) (GIUS 8 – 2571/Ca$_{1, 2}$), articular face of the proximal columnal (f) and pluricolumnal in lateral view (g) (Bathonian, Holy Cross Mountains, Wola Morawicka). h) Millericrinina – Ist morphotype (GIUS 8 – 2571/M$_1$), articular face of the columnal (Callovian, Polish Jura, Zalas). i) Millericrinina – IInd morphotype (GIUS 8 – 2571/M$_2$), articular face of the distal columnal (Middle Bathonian, Polish Jura, Gnaszyn). j) *Cyclocrinus macrocephalus* (QUENSTEDT) (GIUS 8 – 2571/Cm), columnal in lateral view (j$_1$) and articular face of the columnal (j$_2$, j$_3$) (Callovian, Polish Jura, Zalas). Scale bars: 1 mm.

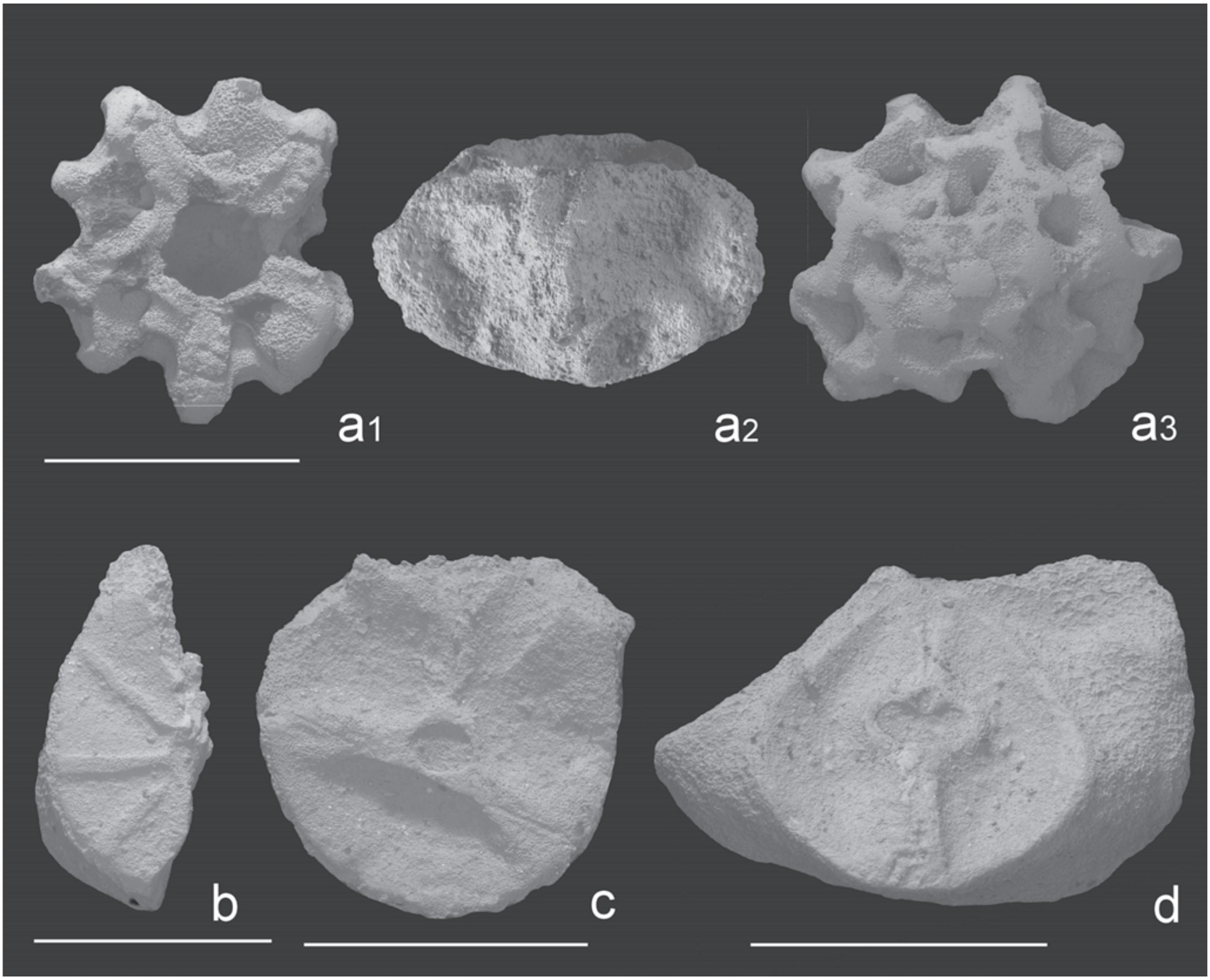


Fig. 3. Middle Jurassic (Bathonian) crinoids of Poland (Polish Jura Chain and Holy Cross Mountains). a) *Palaeocomaster* sp. (GIUS 8 – 2571/P), centrodorsal ventral face (a_1), lateral view (a_2) and dorsal side (a_3) (Middle Bathonian, Polish Jura, Gnaszyn). b–d) *Paracomatula helvetica* Hess (GIUS 8 – 2571/Ph$_{1, 2, 3}$), syzygy of distal brachial (b), muscular articulation (c), and distal face of primibrach (d) (Bathonian, Holy Cross Mountains, Wola Morawicka). Scale bars: 0.5 mm (a); 1 mm (b–d).

Superfamily Solanocrinitacea Jaekel 1918
Family Solanocrinitidae Jaekel 1918
Genus *Palaeocomaster* Gislén 1924
Type species. – Actinometra guirandi de Loriol 1889

***Palaeocomaster* sp.**
(Fig. 3a)

Material. – 1 centrodorsal; GIUS 8 – 2571/P.
Dimensions. – Centrodorsal diameter equals to 1.3 mm, theca height equals to 0.65 mm.
Description. – Centrodorsal is low and circular, with a large cirrus-free on the dorsal area. Radial cavity is rather wide and circular. Articulum is high and steep, with triangular interarticular ligament fossae. Dorsal side is slightly convex, with 3 irregular marginal circles (12 cirrus sockets) of cirrus sockets. Cirrus sockets are rather large; an elevated margin around the nerve lumen is visible. Ventral side with a deep cavity, ca. 0.4 the centrodorsal diameter. Basal rays are rod-shaped and exposed in the interradial point.
Distribution in Poland. – Middle Bathonian (Polish Jura).

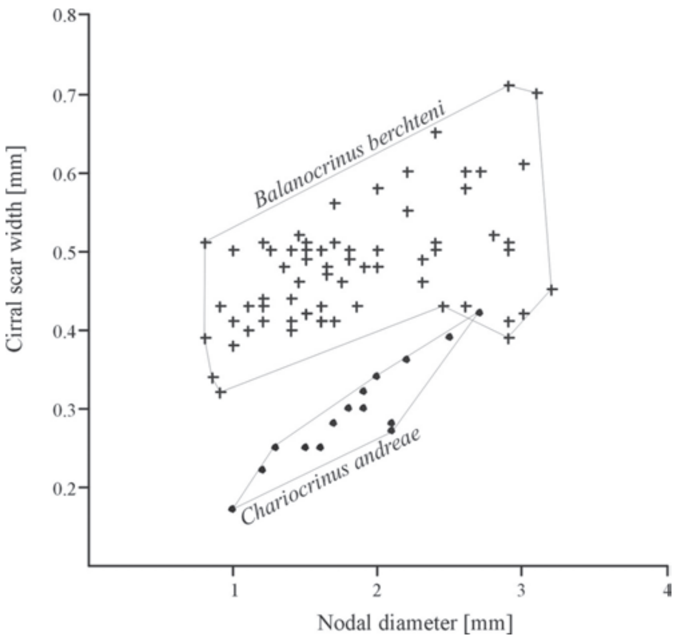


Fig. 4. Plot of cirral scar width vs. nodal diameter, for *Balanocrinus berchteni* Hess & Pugin (crosses) and *Chariocrinus andreae* (Desor) (points). The plot was made using the PAST software (Hammer et al. 2001).

Order Millericrinida Sieverts-Doreck 1952
Suborder Millericrinina Sieverts-Doreck 1952
(Figs. 2h, i)

Material. – 1 very large columnal of the Ist morphotype and 3 small columnals of the IInd; GIUS 8 – 2571/M.
Description. – Morphotype I: very large and circular columnals; articulum with radiating, rather long and thin crenulae; lumen is probably very large and circular. Morphotype II: very small and circular columnals; articulum with thick and short crenulae; lumen is relatively large and circular.
Distribution in Poland. – Middle Bathonian (Polish Jura, morphotype II), Callovian (Polish Jura, morphotype I).

Family Cyclocrinidae Sieverts-Doreck 1952
Genus *Cyclocrinus* d'Orbigny 1850
Type species. – Bourgueticrinus rugosus d'Orbigny 1841

Cyclocrinus macrocephalus **(Quenstedt 1858)**
(Fig. 2j)

1975 *Cyclocrinus macrocephalus* (Quenstedt); Hess: 72, pl. 20, fig. 12.

Material. – 8 columnals; GIUS 8 – 2571/Cm.
Dimensions. – KD: 10-10.85; KH: 6-8; KHi: 60-74.
Description. – Columnals are large and cylindrical in outline. Articular surfaces covered by numerous and irregular tubercles. Lumen is small and circular.
Discussion. – For a detailed discussion, see Radwańska & Radwański (2003).
Distribution in Poland. – Callovian (Polish Jura).

Discussion

Palaeobiogeography

During the Middle Jurassic, the sediments of the Epicratonic Polish Basin had a transgressive character with two short regressive episodes during the early and late Bajocian (Subfurcatum Zone) and in the earliest Callovian (Herveyi Zone) (see Dayczak-Calikowska et al. 1997). According to Dayczak-Calikowska (1980) and Dayczak-Calikowska et al. (1997), the analysis of faunal assemblages and palaeogeographical development of the Polish Epicratonic Basin, as well as the European basins, has shown that from the Aalenian through late Bathonian, all the transgressive pulses were related to the Tethys Ocean. Their main paths, however, are still not clear (see Feldman-Olszewska 1997). Dayczak-Calikowska & Moryc (1988) suggested the East-Carpathian Gate via the Mid-Polish Trough as the main transgression route. Świdrowska (1994), on the other hand, claimed that at least the Aalenian transgression entered the Polish Basin from the west. The recent ammonite data (see Zatoń & Marynowski 2006) indicate, however, that a free marine connection between the Polish Basin and the Tethyan Ocean existed at least since the late Bajocian times. According to Dayczak-Calikowska (1980), the radical change of ecological conditions and the arrival of Boreal ammonites in the early Callovian, lead to the isolation of the Polish Basin from Mediterranean influences. The later transgression path, in the early Callovian, also changed to a northwestern direction (Dayczak-Calikowska et al. 1997). However, the most recent research (e.g. Dromart et al. 2003) indicates that the boreal ammonites could have migrated from the north, because of the severe cooling over the Middle–late Jurassic transition in the Northern Hemisphere.

Nearly all currently documented stalked crinoids, are known from coeval or slightly younger deposits occurring in the Tethyan areas (Alps, Pieniny Klippen Belt and Tatra Mountains; Rasmussen 1978; Głuchowski 1987; Hess 1999), suggesting an immigration from the south. According to Dayczak-Calikowska & Moryc (1988), the main path of Tethyan transgressions during Bajocian–Bathonian times was the East-Carpathian Gate. It is assumed here, that this gate also acted as a main path of immigration of late Bajocian–Bathonian crinoids from Tethys into the epicratonic Polish Basin.

The case of the immigration of the free-moving taxa (*Paracomatula helvetica* Hess and *Palaeocomaster*) remains unresolved. Neither of these taxa has been documented in the oceanic areas of southern Poland (see Pisera & Dzik 1979; Głuchowski 1987). Additionally, *P. helvetica* Hess has been noted so far only in the Middle Jurassic of Switzerland (Hess 1951; Rasmussen 1978). The situation is simultaneously complicated by the information about the occurrences of the genus *Palaeocomaster*. Its representatives are known from the Lower Jurassic (Pliensbachian) of France, Middle Jurassic (Bathonian–Callovian) of England and Upper Jurassic (Oxfordian–Tithonian) of England and France (de Loriol 1879; Gislén 1924; Rasmussen 1978; Klikushin 1992). Although these taxa are unknown from Germany, it cannot be excluded definitely that they could not have immigrated from the west. The particular ammonite taxa from the coeval Middle Bathonian deposits, for instance, are known to occur either in Germany and Poland (cf. Matyja & Wierzbowski 2006). It can be stressed that other stemless forms (saccocomids) were noted in the Bajocian deposits of the Pieniny Klippen Belt (Głuchowski 1987; for data concerning Tatra Mountains see Lefeld & Radwański 1960) and the Oxfordian–Kimmeridgian deposits of the Polish Jura (Matyszkiewicz 1997).

The only currently documented stalked form, *Balanocrinus hessi* Salamon & Zatoń, seems to be the endemic element. The current, excellent state of recognition of the Middle and Upper Jurassic isocrinids known from Europe and Asia attests that this taxon does not occur anywhere except the Polish Jura area (compare Hess 1955, 1972, 1975; Pisera & Dzik 1979; Hess & Pugin 1983; Głuchowski et al. 1983, 1986; Głuchowski 1987; Simms 1989; Klikushin 1992). The endemism phenomenon among Mesozoic crinoids is not surprising. In Triassic deposits, many of the characteristic forms of shallow epicratonic environments were reported (e.g. Hagdorn 1983; Głuchowski 1986; Hagdorn & Głuchowski 1993; cf. Salamon 2005). Similarly, in the Jurassic succession, Simms (1985, 1989) mentioned taxa occurring exclusively in the British Isles (i.e. *Balanocrinus solenotis* Simms). It is noteworthy that the degree of endemism of the crinoid fauna in the Muschelkalk (epicontinental Middle Triassic) is several times lower than the degree of endemism of the rest of the benthonic macrofauna. It probably results from a huge number of crinoids forming '*crinoid gardens*', that produced large number of larvae. This increased the chance of successful geographical expansion of crinoids (see Salamon & Niedźwiedzki 2005 for details).

The rest of the mentioned stalked crinoid taxa is characteristic of a relatively wide palaegeographical distribution, although their occurrence is actually restricted to Europe (Hess 1955, 1972, 1975, 1999; Rasmussen 1978; Simms 1989; Klikushin 1992). The exception is *Isocrinus nicoleti* (Desor), which is common in the Middle Jurassic of England, France, Switzerland and Iran (e.g. Klikushin 1992; Hess 1999; pers. obs. of MZ in north-eastern England). Recently, Tang et al. (2000) documented its mass-occurrences in shallow-water encrinites from the Middle Jurassic (Upper Bajocian or Lower Bathonian) of the United States Western Interior. It is noteworthy that in the light of Głuchowski's (1987) observations, the oldest findings of this species come from the Toarcian (Lower Jurassic) of the Pieniny Klippen Belt (Tethyan Poland). Therefore, its immigration must have occurred towards western (Switzerland, France, England and North America), eastern (Iran) and northern directions, to Polish epicontinental sea. The occurrence of *I. nicoleti* (Desor) has already been proven in the oldest investigated sediments (latest Bajocian). However, its occurrence cannot be excluded in the Aalenian deposits.

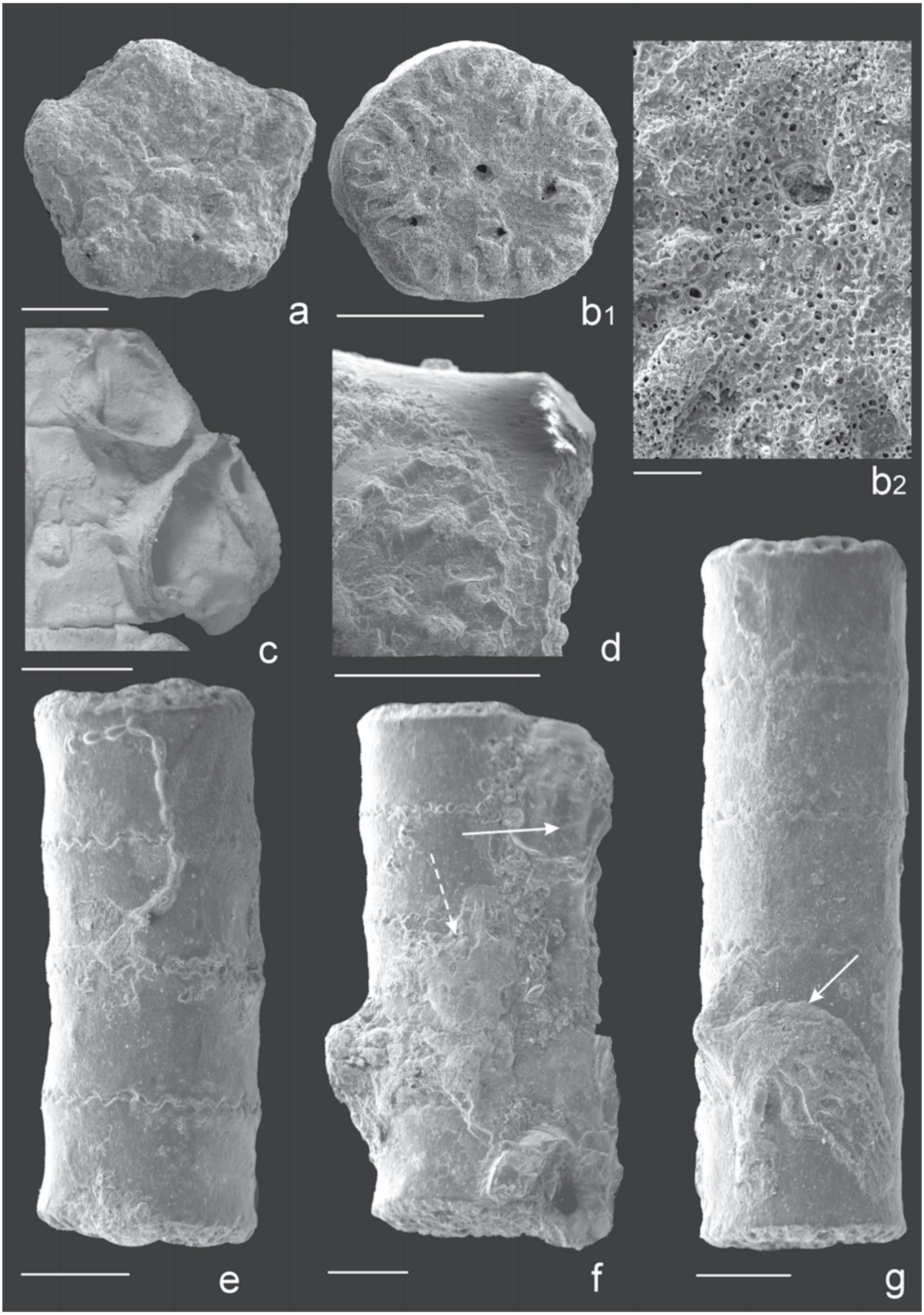
Taphonomy

Disarticulation pattern of crinoid stalks

It is well-known that crinoids, as well as other echinoderms, are very susceptible to disarticulation following death and are therefore rarely preserved as complete specimens (e.g. Donovan 1991; Brett et al. 1997; Ausich et al. 1999; Ausich 2001). Taking into account that under normal aerobic conditions, and especially if the remains experienced initial decay before further physical disturbances (Kidwell & Baumiller 1990; Brett et al. 1997), the complete disarticulation of crinoids into isolated ossicles usually takes place within one to two weeks (Donovan 1991; Brett et al. 1997; Ausich et al. 1999). These fossils can be very useful for delineating the relative sedimentation rates.

The investigated crinoids consist either of single columnals and pluricolumnals. Generally, ca. 70 % of crinoid elements consist of columnals and pluricolumnals, while cirrals, as well as brachial, basal and radial plates represent only a minority. Only one centrodorsal of comatulid was found. For the taphonomic observations, 100 pluricolumnals were randomly selected (mainly from the Middle Bathonian sample, Gnaszyn locality; see Fig. 1). They are mainly dark- to light brown in colour. The pluricolumnals consist of 2-8 connected columnals (mean value: 4.01). Only 15 noditaxes (the nodals connected with internodals) were found in the investigated material. They consist of 2-6 connected columnals (mean value: 4.13). Only five of them possess a single cirral ossicles still attached. The sides show some fractures but are not abraded. The articulation facets, on the other hand, may bear some signs of dissolution

Fig. 5. Epi- and endobionts on Middle Jurassic crinoids of Poland [Polish Jura Chain, Gnaszyn and Zalas (only "c")]. a) Abraded isocrinid columnal (GIUS 8 – 2571/I_u). b_1) Small pits on *Balanocrinus berchteni* Hess & Pugin (GIUS 8 – 2571/Bb_{e1}), probably made by algae. b_2) Close-up of one of the pit lying in the left side on the columnal shown on b_1. c) Tiny oysters on *Balanocrinus hessi* Salamon & Zatoń (GIUS 8 – 2569_{e1}). d) Poorly preserved cyclostomous bereniciform bryozoan, attached to *Balanocrinus berchteni* Hess & Pugin (GIUS 8 – 2571/Bb_{e2}). e) *Balanocrinus berchteni* Hess & Pugin (GIUS 8 – 2571/Bb_{e3}) occupied by adherent foraminifer *Bullopora*. f) *Balanocrinus berchteni* Hess & Pugin (GIUS 8 – 2571/Bb_{e4}) occupied by *Dorsoserpula* (solid arrow) and cyclostomous bryozoan (abraded; dotted arrow). g) Cyclostomous bryozoan (arrow) attached to *Balanocrinus berchteni* Hess & Pugin (GIUS 8 – 2571/Bb_{e5}). Scale bars: 0.1 mm (b_2); 1 mm (a, b_1, c–g)


a
b1
b2
c
d
e
f
g

and/or abrasion. Some of the columnals are broken with the surface coated by pyrite. The majority of them are encrusted, and few possess tiny borings (see below).

The disarticulation pattern of investigated crinoids appears to have been caused by a variable time of exposure of the stalks on the sea floor. The crinoids preserved as pluricolumnals and single columnals fall within taphonomic type 2 sensu Brett et al. (1997). This type includes echinoderms whose bodies contain portions in which the skeletal ossicles are more tightly sutured, as well as portions in which the modules are more delicately bound (see Brett et al. 1997). According to some authors (Baumiller & Ausich 1992; Brett et al. 1997), the pluricolumnals are the most resistant of all portions of pelmatozoan echinoderms to disarticulation. This is caused by the presence of through-going ligaments connecting the internodals and some portion of the neighbouring nodal within the stem (see Baumiller & Ausich 1992: fig. 3b). Indeed, the experiments of Baumiller & Ausich (1992) and Baumiller et al. (1995) have shown that the isocrinid stalks disarticulate at synostoses first, the articulation where the portion of the nodal (cirri-bearing columnal) is connected with the rest of the internodals (columnals without cirri) by only short ligament fibers (intercolumnal ligaments). Thus, the pattern of the stem disarticulation consists of pluricolumnals with the terminal end being a nodal (see Baumiller & Ausich 1992; Baumiller et al. 1995).

The reported crinoids belong to assemblages in which components underwent a different biostratinomical history following death. The investigated noditaxes and connected internodals may well be included within a 'taphonomic window' of 1-3 weeks following death (see Baumiller & Ausich 1992). Those noditaxes, with some cirral plates still attached, are considered here to be experienced the shortest duration of exposure on the sea-floor. After 3 weeks, the stalks can be disarticulated into segments of variable length and finally into individual columnals (Baumiller & Ausich 1992). This pattern is seen in very short pluricolumnals without preserved nodals, as well as in completely isolated ossicles. The lack of the complete isocrinid calyces is not surprising because this part of most crinoids is very prone to disarticulation on single plates just after death (see Donovan 1991; Brett et al. 1997; Ausich 2001). The dominance of columnals and pluricolumnals in the samples points to the winnowing of other crinoid elements mentioned above. The fact that well-preserved columnals/pluricolumnals are associated with broken and abraded isolated columnals may be the evidence that the assemblage is a within-habitat time-averaged (sensu Kidwell 1998) accumulation.

Epibiontism on crinoid stalks

In such siliclastic, muddy soft-bottom environments as the investigated Middle Jurassic clays, the only hard substrates to be colonized by various encrusters are various biological and nonbiological compounds exposed on the sea floor. The investigated crinoid remains, to lesser or greater degree, are also settled by various epi- and endobionts. The pattern of epi- and endobiontism of crinoids has a profound influence on taphonomical, as well as palaeoecological interpretations (see e.g. Feldman & Brett 1998; Głuchowski 2005; Radwańska & Radwański 2005). Many examples of epi- and endobionts on Jurassic crinoid remains were presented by Feldman & Brett (1998) from the Callovian of Israel, and Radwańska & Radwański (2005) recently described Oxfordian and Kimmeridgian crinoid stems infested by myzostomids and copepods from Poland. Radwańska (1999) showed also the millericrinid holdfast with echinoid scratch-marks. Upper Bajocian-Bathonian epi- or endobionts on crinoid stems have not been mentioned from Poland to date. Although Taylor & Wilson (2002, 2003) proposed a new terminology for hard-substrate encrusting biota, the general term *epibionts* is used here, as the case concerns only the biological remains.

Twenty-one, of all 100 studied pluricolumnals, do not possess epibionts at all. The rest of pluricolumnals are settled in a variable degree by rather undiverse assemblages characterized by a low number of specimens (Fig. 5), consisting mainly of adherent foraminifers (*Bullopora*), tubes of serpulids (*Dorsoserpula* morpho-subgenus), cyclostomous bereniciform bryozoans and undeterminable bivalves (probably oyster or oyster-like bivalve attachments). The majority of epibionts occur on the lateral side of pluricolumnals, but some (18 cases) also occur on the articular facets. Isolated columnals are mostly barren of epibionts, and when they sporadically occur, they belong to foraminifers. Some epibionts occur in successive generations on each other; foraminifers foul mainly the serpulids. Only on the lateral side of one pluricolumnal, with 6 ossicles, three groups of epibionts occur together. Normally, only two groups occur together, mainly foraminifers with serpulids. Some of the epibionts are abraded, thus a determination of bryozoans is impossible (even to the genus level) due to the lack of preserved gonozooids (Figs. 5d, f–g). A few isolated columnals bear tiny pits on their articulation facets, which could have been made by boring activity of algae (Fig. 5b). Only one pluricolumnal belonging to the Callovian *Balanocrinus hessi* bears a whole population of oysters (*Liostrea*), consisting of specimens of different ontogenetic growth stages (Fig. 5c).

The first important question concerning epibiontism phenomena on crinoid stalks, is whether they occurred during the life or post-mortem. However, in the investigated material, the epibiontism pattern clearly points to a post-mortem colonisation on already disarticulated specimens. This is indicated by the presence of epibionts on the articular facets and, more importantly, by the complete lack of characteristic swellings of stereom around the periphery of epibionts (see Feldman & Brett 1998). As well, the complete lack of deformation of pluricolumnals, resulting from natural reaction of crinoid stereom against the encruster, leads to its embedment (bioclaustration, see Palmer & Wilson 1988). Additionally, on any pluricolumnals encrusters such as serpulids do not show their spiralling tubes around the crinoid stem, the sign that the crinoid could have been fouled during lifetime (Feldman & Brett 1998). Instead, they are mostly longitudinally aligned along the pluricolumnals. The presence of encrusters on different sides of the stem fragments could have resulted from its transport-mediated rolling on the sea floor.

In the studied soft-bottom siliclastic environment of Middle Jurassic sea, the crinoid remains, as well as other biological remains (bivalves, ammonites, wood fragments, MZ pers. obs.), played a major role as secondary hard-substrates for various encrusters. The encrustation of such substrates, and later development of encrusters, must have occurred during pauses of sedimentation and/or omission, at least at the sites with the crinoid remains. Sometimes, the pauses may have been prolonged, what is well seen in the successive generation of encrusters. During this time, the dead crinoids lying upon the sea-floor were subjected to disarticulation, encrusted, bored and some of the stalks ossicles were prone to transportation and resulting abrasion (Fig. 5a).

Conclusions

Eleven crinoid taxa have been documented in the uppermost Bajocian–Callovian epicontinental deposits of the Polish Jura Chain and Holy Cross Mountains (Poland). The crinoid fauna consists of isocrinids [*Isocrinus* sp., *I. bajocensis* (d'Orbigny), *I. nicoleti* (Desor), *Pentacrinites dargniesi* Terquem & Jourdy, *Balanocrinus berchteni* Hess & Pugin, *B. hessi* Salamon & Zatoń, *Chariocrinus andreae* (Desor)], comatulids (*Palaeocomaster* sp., *Paracomatula helvetica* Hess) and millericrinids (Millericrinina fam. et sp. indet., *Cyclocrinus macrocephalus* (Quenstedt)]. Although some of the isocrinids have previously been reported from the investigated sediments, comatulids and millericrinids have been described for the first time. The crinoid fauna indicates that they migrated from the Tethys Ocean into epicontinental areas. The state of preservation of the reported crinoids (isolated columnals/pluricolumnals) attests that the assemblages are within-habitat time-averaged. During their residence on the sea floor, their remains were subjected to rapid disarticulation and encrustation/boring by various epi- and endobionts. However, there is no indication that the crinoids were infested during their lifetime.

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