

Early Cretaceous (Valanginian) sea lilies (Echinodermata, Crinoidea) from Poland

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Key words: Crinoidea, isocrinids, Early Cretaceous, Poland, taxonomy, palaeobiogeography

ABSTRACT

Valanginian strata in central epicratonic Poland have recently yielded crinoids, not previously recorded from the area. The fauna comprises isocrinids (*Balanocrinus subteres*, *B. gillieronii*, “*Isocrinus?*” *lissajouxi*), millericrinids (*Apiocrinites* sp.) and comatulids (Comatulida indet.). For comparison, a few samples of isocrinids from Valanginian strata of Hungary (Tethyan province) were also analysed. The isocrinids, cyrtocrinids and roveacrinids (*sensu* Rasmussen 1978 inclusive of *Saccocoma* sp.) were already known from the Valanginian of

the southernmost Tethyan regions of Poland (Pieniny Klippen Belt and Tatra Mountains). The current study demonstrates their occurrence in central epicratonic Poland, and suggests that many Jurassic to Cretaceous stalked crinoid taxa (mainly isocrinids) predominated in the shallow-water settings of this area. Thus, the hypothesis of migration (at least from mid-Cretaceous onwards) to deep-water areas, as a response to an increase of the number of predators during the Mesozoic marine revolution, seems not to be universally applicable.

Introduction

Current knowledge of the Early Cretaceous crinoids from extra-Carpathian Poland is very limited. Pisera (1984) recorded only roveacrinids (*Styracocrinus peracutus*) and comatulids (*Glenotremites* sp.) from the Barremian-Cenomanian of northern Poland. Unpublished data (M.A. Salamon) from Albian strata in southern Poland (for details see Marcinowski 1974), record representatives of isocrinids (columnals of *Balanocrinus* cf. *infrasilvensis*, “*Isocrinus?*” *arduennensis*) and roveacrinids (brachials), which are not common. Crinoids from the Pieniny Klippen Belt and Tatra Mountains in southern Poland, which formed part of the Tethys, are better studied. According to Głuchowski (1987 and literature cited therein) saccocomid remains associated with isolated isocrinids (*Balanocrinus* sp., *B. subteres*, *B. gillieronii*, and “*Isocrinus?*” sp.) are commonest in the Berriasian-Hauterivian. Amongst the cyrtocrinids, Głuchowski (1987) noted the following taxa from Early Cretaceous strata: Cyrtocrinida indet., *Gammarocrinites compressus* (= *Sclerocrinus*, see Hess 2004), *Phyllocrinus* sp., *P. belbekensis* and *Lonchocrinus staszici*. Late Cretaceous crinoids from extra-Carpathian Poland have received more attention recently, with Merta (1972), Remin (2004), Jagt & Salamon (2007 and literature cited therein), Salamon (2007), Salamon et al. (2007) and Sekuła et al. (2008), noting that all Mesozoic crinoid orders (*sensu* Rasmussen 1978) are common.

The present study documents Early Cretaceous crinoids from the Polish part of the Tethyan Realm, which are more numerous and taxonomically diverse than previously assumed. In particular this study 1) characterises the crinoid assemblages from epicratonic and Tethyan Poland, and 2) discusses their palaeobiogeography and palaeoecology.

Additionally, isocrinids from Valanginian strata in Hungary are described. Although at these Hungarian localities cyrtocrinids are the commonest, they have already been thoroughly described earlier (Szörényi 1959; see also Arendt 1974, table 2). Only *Balanocrinus subteres* is recorded from these Hungarian sections.

All described material is housed in the Laboratory of Paleontology and Biostratigraphy of the Department of Earth Sciences of the University of Silesia, Poland (institutional abbreviation GIUS).

Geological setting

Poland

Valanginian of epicratonic Poland

The abandoned brick-pit at Wąwał (Figs. 1a–b; 2a) is situated near the town of Tomaszów Mazowiecki (central Poland). Ac-

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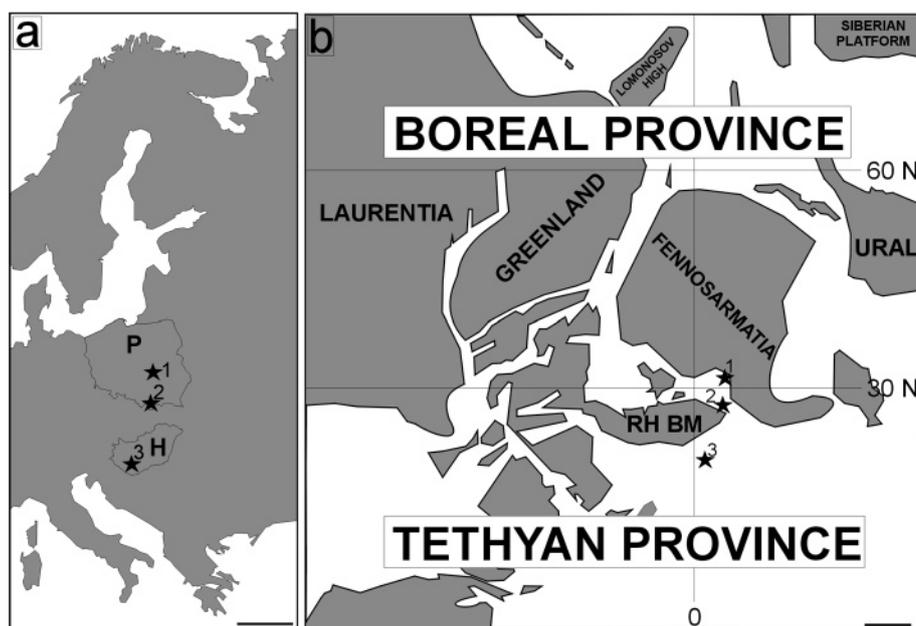


Fig. 1a) Map of Central Europe with localities in Poland (P) and Hungary (H) indicated with stars. 1: Wąwał (epicratonic Poland; Tethyan realm), 2: Czorsztyn (Tethyan Poland), 3: Kisújbánya and Hidas Valley (Hungary). b) Palaeogeographical map of Europe and adjacent areas during the Early Cretaceous. RH: Rhenish Massif, BM: Bohemian Massif. Map modified after: http://www.searchanddiscovery.com/documents/97020/plate_15.jpg. Scale bars are 500 km.

cording to Kutek et al. (1989; see also Kaim 2001), the exposed section starts with a calcareous pebble conglomerate overlying Jurassic limestones. Above follow clayey sands and silts with phosphatic nodules and ferruginous ooids. These sediments, as well as the overlying clays with phosphatic nodules, are assigned an Early Valanginian age (Kaim 2001). Early Late Valanginian strata are represented by clays with phosphatic nodules. The upper part of this sequence comprises silts intercalated by limestones. The crinoids were recorded only in the uppermost part of the section (for sampled interval see Fig. 2a).

Valanginian of the Tethys (Pieniny Klippen Belt)

The Czorsztyn Castle Klippe locality (Figs. 1a–b; 2b) presently exposes Berriasian to Valanginian sediments, even though Krobicki et al. (2006) described Aalenian to Albian-Cenomanian sediments from the same locality. The Valanginian is represented by red crinoidal limestones, which are partially flooded at present (compare Krobicki et al. 2006, figs. A13–A14; for sampled interval see Fig. 2b).

Hungary

According to Horváth (1968), the Kisújbánya section (Figs. 1a–b; 2c) exposes the Late Valanginian; the upper portion of the outcrop being of Hauterivian age is not currently visible. The lower part of the section comprises fining-up siliciclastic sediments overlain by marls. The middle part consists of conglomerates, sandstones and sandy marls. The uppermost part is characterized by the occurrence of unstratified marls, described in detail by Bujtor (1993). Crinoids were recorded only from conglomerates, which also commonly

yielded molluscs and brachiopods (for sampled intervals see Fig. 2c).

The Hidas Valley section (Figs. 1a–b; 2d) is dated as Valanginian (Bujtor 1993). The sequence exposes thinly laminated marls and massive limestones. According to Bujtor (1993), the whole section is cut by numerous lines of green tuff. Rare crinoids are confined to the limestones. No other fauna has been found; however, according to Bujtor (1993) ammonites and brachiopods also occur here (for sampled intervals see Fig. 2d).

Material and methods

A clay bulk sample of ca. 200 kg was taken from Wąwał. In the Pieniny Klippen Belt (Czorsztyn Castle Klippe section) a sample of ca. 50 kg was taken, and in Hungary eleven samples each of ca. 30 kg were collected (for details see Fig. 2).

The clay mass was left in water for 6 days and then washed and sieved using diameters of 1.0 mm, 0.5 mm and 0.315 mm mesh sizes. Samples were then dried at 200 °C and all crinoid material was picked from the residue using a binocular microscope.

The limestones and marls were treated with glauber salt (five times with a boiling – freezing procedure for limestones and two times for marls). The obtained residue was then washed in hot tap water; the next steps were as above.

Systematic palaeontology

Remarks. Systematics follow Rasmussen (1961, 1978). According to Rasmussen (1961), in most cases only the column of the Early Cretaceous isocrinids is known, and he therefore proposed to use “*Isocrinus?*” for species for which a definite

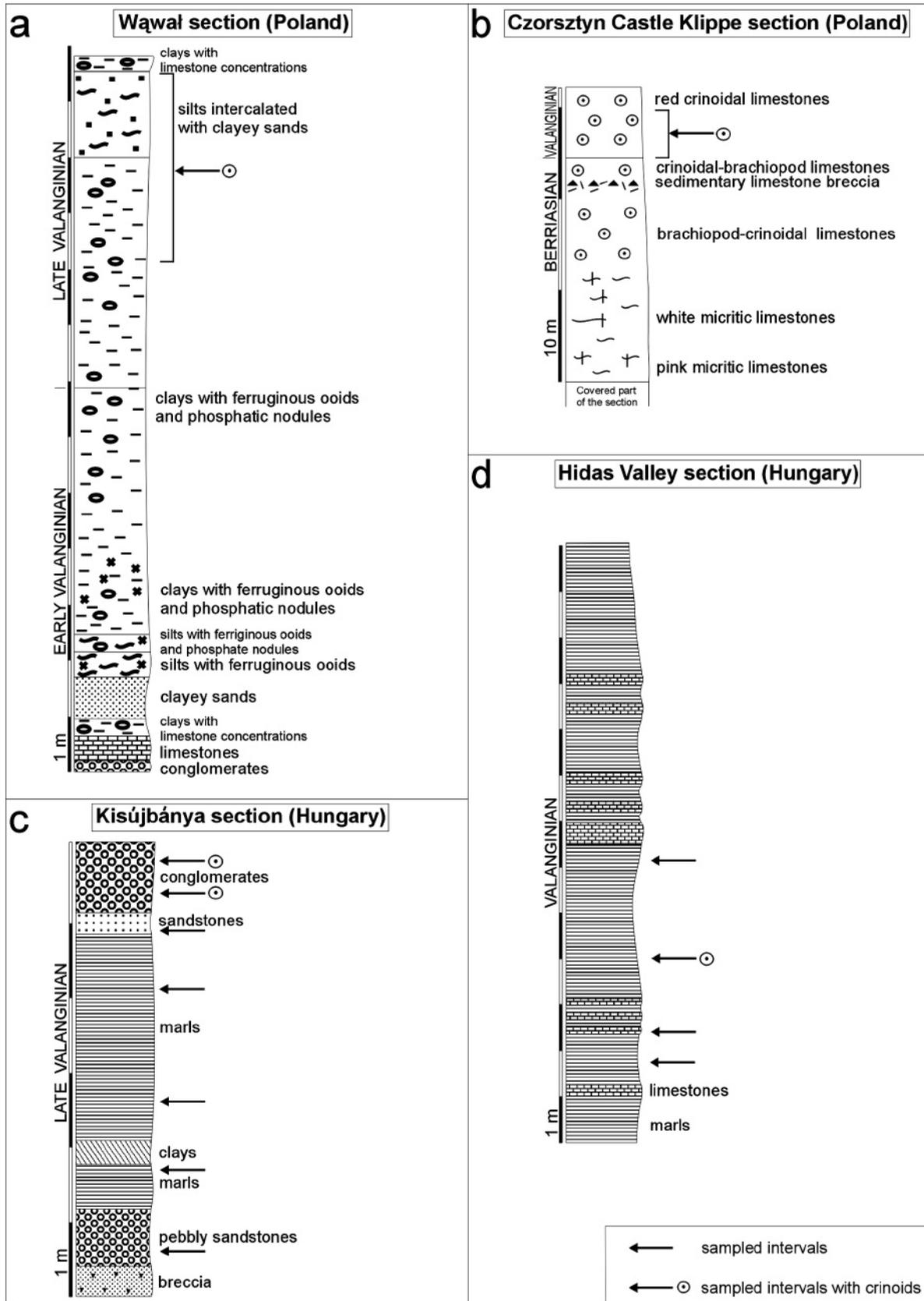


Fig. 2. Logs of the studied sections in Poland (a, b) and Hungary (c, d) with sampled intervals indicated.

generic identification was not possible. This view is adopted here.

Valanginian crinoids of epicratonic Poland

Order Isocrinida SIEVERTS-DORECK IN UBAGHS 1953

Family Isocrinidae GISLÉN 1924

Genus *Balanocrinus* AGASSIZ IN DESOR 1845

Type species *Pentacrinites subteres* MÜNSTER IN GOLDFUSS 1826

Balanocrinus subteres (MÜNSTER IN GOLDFUSS 1826) (Figs. 3b, d–h)

- 1826 *Pentacrinites subteres* MÜNSTER IN GOLDFUSS: 176, pl. 53, fig. 5
1856 *Pentacrinites subteres* MÜNSTER; Quenstedt: 554, 586, 657, pl. 72, fig. 34, pl. 73, fig. 81, pl. 80, figs. 104–105
1870 *Balanocrinus subteres* MÜNSTER; von Zittel: 274, pl. 39, figs. 13–14
1879 *Pentacrinus (Balanocrinus) subteres* (MÜNSTER); de Loriol: 172, pl. 17, figs. 29–37
1884 *Balanocrinus subteres* (MÜNSTER); de Loriol: 348, pl. 192, figs. 7–12, pl. 193
1955 *Balanocrinus subteres* (MÜNSTER); Hess: 476, fig. 4
1975 *Balanocrinus subteres* (MÜNSTER); Hess: 58, pl. 20, fig. 8, pl. 24, figs. 2–3
1979 *Balanocrinus (Balanocrinus) subteres* (MÜNSTER); Klikushin: 92, fig. 3c
1982 *Balanocrinus subteres* (MÜNSTER); Klikushin: 302, pl. 2, fig. 6
1987 *Balanocrinus subteres* (MÜNSTER); Gluchowski: 52–55, pl. XXXVI/1, 3–6, pl. XXXVII/2–4, 7, 8, pl. XXXVIII/1–8, pl. XXXIX/6, text-fig. 17/8
1992 *Balanocrinus subteres* (MÜNSTER); Klikushin: 87–88, pl. 5, figs. 9–12
1996 *Balanocrinus subteres* (MÜNSTER); Klikushin: 118–120, pl. 8, figs. 7–10
For further synonyms see Klikushin (1996, p. 118)

Material: 332 columnals, 76 brachials, 89 cirrals (GIUS 9–3468Bs)

Description: Columnals circular to subpentagonal. Facet covered with large, wide triangular petal floors. Petal floors separated by very small and thin adradial crenulae; every petal floor surrounded by 5–8 marginal crenulae. Nodals higher than internodals. Nodals with five circular and upward directed cirrus scars; cirrus scars bordered by a thin rim. Latera smooth and straight, in some cases concave or convex. Lumen small and circular. Juvenile columnals very high, and with convex latera. Facet covered with short and thick crenulae. Cirrals elliptical to cylindrical in outline. Proximal cirrals low, wide and longer than distal cirrals. Facet concave, with high, relatively thin perilumen (especially in case of distal cirrals). Fulcral ridge of cirrals with paired pointed projections adorally. Latera smooth. Brachials V- or U-shaped, muscular, sometimes with a single thorn on the dorsal side.

Discussion: For a detailed discussion see “Resemblance of related taxa”.

Occurrence: Early Jurassic to Early Cretaceous of the Czech Republic, England, France, Germany, Hungary, Italy, Lebanon, Portugal, Romania, Russia, Slovakia, Spain, Switzerland, Syria, Tunisia, and North America. In Poland, the range is Bajocian to Valanginian.

Balanocrinus gillieronii (DE LORIO 1879) (Figs. 3a, c)

- 1879 *Pentacrinus (Balanocrinus) gillieronii* DE LORIO: 183, pl. 18, fig. 3
1961 *Balanocrinus gillieronii* (DE LORIO); Rasmussen: 83–84
1979 *Balanocrinus (Balanocrinus) gillieronii* (DE LORIO); Klikushin: 92, fig. 3g
1982 *Balanocrinus gillieronii* (DE LORIO); Klikushin: 302, pl. 2, figs. 3–4
1987 *Balanocrinus gillieronii* (DE LORIO); Gluchowski: 55, pl. XXXVI/2, text-fig. 17/7
1992 *Balanocrinus gillieronii* (DE LORIO); Klikushin: 87, pl. 5, figs. 4–5

Material: 372 columnals, 46 brachials, 59 cirrals (GIUS 9–3468 Bg).

Description: Columnals circular. Facet covered with triangular, large and wide petal floors. Petal floors separated by very small adradial crenulae; every petal floor surrounded with 5–8 marginal crenulae. Nodals higher than internodals. Nodals with five circular and upward directed cirrus scars. Latera smooth and straight. Lumen small and circular. Cirrals elliptical to cylindrical in outline. Facet concave, with high, relatively thin perilumen. Circular fulcral ridge of cirrals with paired pointed projections adorally. Latera smooth. Brachials V- or U-shaped, muscular.

Discussion: For a detailed discussion see “Resemblance of related taxa”.

Occurrence: Early Cretaceous of Switzerland, Ukraine (Crimea). In Poland, the range is Upper Jurassic to Valanginian.

Genus *Isocrinus* AGASSIZ 1836

Type species *Isocrinites pendulus* VON MEYER 1836

“Isocrinus?” lissajouxi (DE LORIO 1904) (Figs. 3i–l)

- 1904 *Pentacrinus lissajouxi* DE LORIO: 63, pl. 4, fig. 22
1961 *“Isocrinus?” lissajouxi* (DE LORIO); Rasmussen: 137–138, pl. 18, fig. 1
1992 *“Isocrinus?” lissajouxi* (DE LORIO); Klikushin: 114, pl. 12, figs. 4–8

Material: 4 pluricolumnals and 32 columnals (GIUS 9–3468II).

Description: Columnals pentalobate. Facet covered by elliptical or drop-like petal floors. Petal floors separated by relatively small and thin adradial crenulae up to 8 in number; every petal floor surrounded with 8–10 marginal crenulae. Small and smooth radial area visible at the facet edges. Nodals higher than internodals. Nodals with five circular and upward directed cirrus scars. Latera of median? and proximal columnals covered by prominent median ridge; in case of distal columnals it is straight and smooth. Lumen small and circular.

Discussion: According to Rasmussen (1961), the present taxon shows a broad, rounded and prominent median ridge on the columnal latera, distinguishing it from other Early Cretaceous Isocrinidae. This can only be confirmed in median? and proximal columnals (compare Fig. 3I), whereas lateral surfaces of distal columnals are straight and smooth (compare Fig. 3k). It should also be noted here that Klikushin (1992) illustrated columnals of *“I.?” lissajouxi* with rather straight or slightly convex lateral surfaces but covered by small and numerous granules (see Klikushin 1992, pl. 12, fig. 6). Such specimens were not observed in the present material.

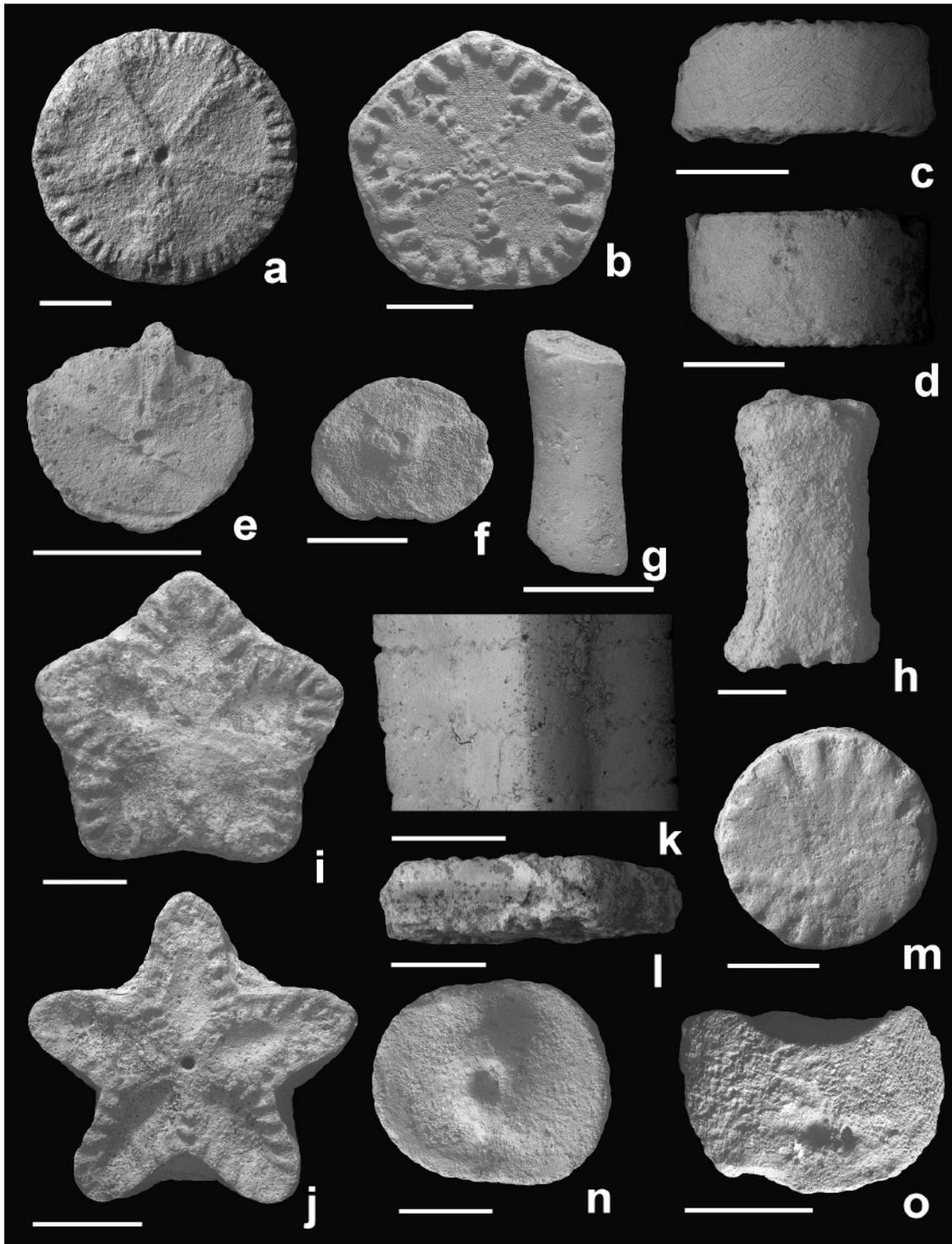


Fig. 3. Early Cretaceous (Valanginian) crinoids from the epicratonic Poland. Scale bars equal 1 mm. a) *Balanocrinus gillieroni* (de Loriol) (GIUS 9-3468Bg/1), facet of columnal. b) *Balanocrinus subteres* (Münster in Goldfuss) (GIUS 9-3468Bs/1), facet of proximal? columnal. c) *Balanocrinus gillieroni* (de Loriol) (GIUS 9-3468Bg/2), latera of columnal. d) *Balanocrinus subteres* (Münster in Goldfuss) (GIUS 9-3468Bs/100), latera of columnal. e) *Balanocrinus subteres* (Münster in Goldfuss) (GIUS 9-3468Bs/390), facet of brachial. f) *Balanocrinus subteres* (Münster in Goldfuss) (GIUS 9-3468Bs/430), facet of cirral. g) *Balanocrinus subteres* (Münster in Goldfuss) (GIUS 9-3468Bs/431), latera of cirral. h) *Balanocrinus subteres* (Münster in Goldfuss) (GIUS 9-3468Bs/102), latera of juvenile columnal. i) “*Isocrinus?*” *lissajouxi* (de Loriol) (GIUS 9-3468II/5), facet of distal/median? columnal. j) “*Isocrinus?*” *lissajouxi* (de Loriol) (GIUS 9-3468II/6), facet of proximal columnal. k) “*Isocrinus?*” *lissajouxi* (de Loriol) (GIUS 9-3468II/1), latera of pluricolumnal. l) “*Isocrinus?*” *lissajouxi* (de Loriol) (GIUS 9-3468II/7), latera of proximal columnal. m) *Apiocrinites* sp. (GIUS 9-3468As/1), facet of columnal. n) Comatulida (GIUS 9-3468Ci/1), facet of cirral. o) Comatulida (GIUS 9-3468Ci/2), latera of cirral.

Occurrence: Early Cretaceous of France, Switzerland, and Ukraine (Crimea). In Poland, the range is Valanginian. According to Jäger (1981a, b) “*I.*?” cf. *lissajouxii* is also known from the Hauterivian of Germany.

Order Millericrinida SIEVERTS-DORECK IN UBAGHS 1953

Suborder Millericrinina SIEVERTS-DORECK IN UBAGHS 1953

Family Apiocrinitidae D’ORBIGNY 1840

Genus *Apiocrinites* MILLER 1821

Type species *Apiocrinites rotundus* MILLER 1821 = *Encrinites parkinsoni* SCHLOTHEIM 1820.

Apiocrinites sp. (Fig. 3 m)

Material: 18 columnals (GIUS 9–3468As).

Description: Columnals circular. Facet covered with relatively short crenulae; occasionally with small tubercles surrounding the perilumen. Latera smooth.

Discussion: According to Rasmussen (1961), several species of *Apiocrinites* occurred in the Early Cretaceous of Europe. At present, based on columnals of this genus, it is difficult to state which of the species is involved. However, it is probable that columnals with smooth latera from the Valanginian of Poland may either belong to *A. renevieri* (known of Berriasian of western Europe), *A. oosteri* (known of Valanginian of western Europe) or *A. valangiensis* (known from the Valanginian of western Europe). Latera of all these are covered with distinct granules or a characteristic keel (compare e.g., Rasmussen 1961, pl. 22, figs. 1–4) and their stratigraphic distributions concern the Middle rather than Early Cretaceous. On the other hand, assignment to a particular species (or even genus) of millericrinids is invariably difficult. Morphology of different columnals (e.g., Jurassic millericrinids) indicate that they are almost identical (see Radwańska 2005a; Salamon & Zatoń 2005, 2007; Schweigert et al. 2008). Following Salamon & Zatoń (2005), a systematic placement of these crinoids is only possible when cups are available.

Occurrence: Early Jurassic–Upper Cretaceous (Cenomanian) of Europe, Asia, northern Africa and North America.

Order Comatulida CLARK 1908 (Figs. 3n–o)

Material: 67 cirrals (GIUS 9–3468Ci).

Description: Cirrals cylindrical laterally. Distal cirrals long, proximal cirrals low and wider than distal ones. Facet strongly concave, with relatively high perilumen. Lumen trapezoidal. Latera smooth.

Discussion: It is plausible that some cirrals currently assigned to comatulids, may belong to isocrinids. This statement especially concerns comatulid distal cirrals that are relatively long. On the other hand, the possibility of misidentifying comatulid proximal cirrals is small. Proximal cirrals of comatulids are very low (similarly as in isocrinids), but exhibit strongly concave facet. Finally, and most important, in the lateral view the margins of facets have

a form of upside-down ‘S’ (compare Fig. 3o). Cirrals bearing such a shape of margins are unknown among isocrinids.

Occurrence: According to available literature (Carpenter 1880; de Loriol 1879; Gislén 1924; Rasmussen 1961; Hess 1975; Pisera 1984), only three comatulid genera are known from the Early Cretaceous of Europe (*Solanocrinites*, *Glenotremites*, *Palaeocomaster*). The next representative, *Roiometra* with the sole species, *R. columbiana*, has been described only from the Colombia to date (Clark 1944). It seems, however, that a representative of *Solanocrinites* may be present in the material currently studied. Rasmussen (1961) described several species of this genus which are common in the Valanginian of western Europe (details in Rasmussen 1961, table on pp. 413–414).

Valanginian crinoids of Tethyan Poland

Balanocrinus subteres (MÜNSTER IN GOLDFUSS 1826)

Description and discussion in “Resemblance of related taxa”.

Balanocrinus gillieronii (DE LORIO 1879)

Description and discussion in “Resemblance of related taxa”.

Order Cyrtocrinida SIEVERTS-DORECK IN UBAGHS 1953

Suborder Cyrtocrinina SIEVERTS-DORECK IN UBAGHS 1953

Family Sclerocrinidae JAEKEL 1918

Genus *Cyrtocrinus* JAEKEL 1891

Type species *Eugeniocrinites nutans* GOLDFUSS 1829

Cyrtocrinus cf. *remesi* (Figs. 4a–b; but see also Figs. 4a1–b2 and comments in captions)

Material: 27 brachials (GIUS 9–3468Cr).

Description: Brachials stout, with strongly flattened sides. Secundibrachials may be hyperpinnulate (two pinnules per brachial).

Discussion: Of a dozen or so representatives of the genus (review in Arendt 1974), only two are known from the Early Cretaceous (*C. remesi* and *C. variabilis*). However, *C. variabilis* was mentioned by Arendt (1974) only from the Valanginian of the Crimea, whereas *C. remesi* is common in the Czech Republic (Szörényi 1959). Based on this fact only, *Cyrtocrinus* remains are here referred to as *Cyrtocrinus* cf. *remesi*.

Occurrence: *Cyrtocrinus remesi* was so far only known from the Valanginian of the Czech Republic.

Genus *Sclerocrinus* JAEKEL 1891

Type species *Eugeniocrinites compressus* GOLDFUSS 1829

Sclerocrinus cf. *strambergensis* (Figs. 4c–e)

Material: 15 brachials (GIUS 9–3468Sc). However, numerous abraded brachials and columnals coming from macerated limestones may also belong to this taxon.

Description: Primibrachials mainly rectangular in outline. Secundibrachials low and with deep ambulacral grooves. Muscular articulation and pinnula socket visible on one side. The

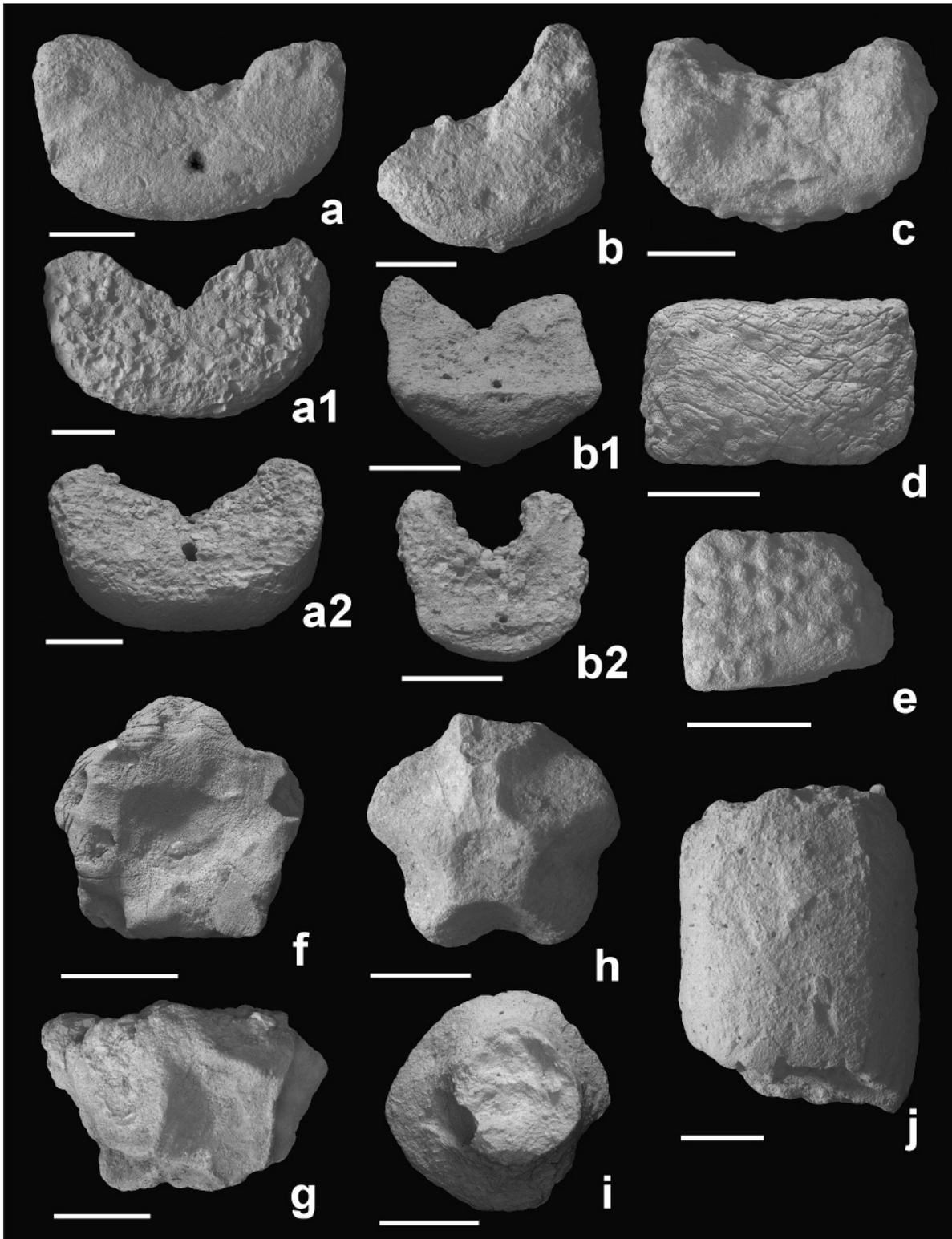


Fig. 4. Early Cretaceous (Valanginian) crinoids from the Tethyan of Poland. Scale bars equal 1 mm. a) *Cyrtocrinus* cf. *remesi* (GIUS 9-3468Cr/1), IBr1 in proximal? view. Examples of Jurassic *Cyrtocrinus* sp. primibrachials are shown in a₁) and a₂) for comparison (details in Salamon 2008b); IBr1 in proximal view (a₁) and IBr1 in distal view (a₂). b) *Cyrtocrinus* cf. *remesi* (GIUS 9-3468Cr/2), IBr2 in distal? View. Examples of Jurassic *Cyrtocrinus* sp. primibrachials are shown in proximal views in b₁) and b₂) for comparison (details in Salamon 2008b). c) *Sclerocrinus* cf. *strambergensis* (GIUS 9-3468Sc/1), IBr1 proximal view. d–e) *Sclerocrinus* cf. *strambergensis* (GIUS 9-3468Sc/2, 3), latera of brachials. f–h) *Phyllocrinus belbekensis* Arendt (GIUS 9-3468Pb/1-3), cup, upper side (distal; f), lateral (g), lower side (proximal; h). i–j) *Cyrtocrinina* (GIUS 9-3468Cyi/88, 2), terminal disc (i) and latera of columnal (j).

second side is syzygial, with radiating crenulae 4 to 7 in number. All brachials covered by rounded tubercles.

Discussion: Among Late Jurassic – Early Cretaceous species of *Sclerocrinus*, only very few have granulated ossicles (compare Jaekel 1891; Pisera & Dzik 1979; Žitt 1982 and literature cited therein; Głuchowski 1987). There is a close similarity of the presently documented brachials to *Gammacrinites compressus* (= *Sclerocrinus*; see Hess 2004) recorded by Głuchowski (1987) from the Callovian – Berriasian of the Pieniny Klippen Belt in southern Poland. The latter author described cups, as well as primibrachials and secundibrachials with dorsal surfaces covered by tubercles. Similar elements were described previously by Jaekel (1891) from the Valanginian of the Czech Republic as *Gammacrinites strambergensis*. At present, based on the Valanginian age of the present material, it is decided to refer to these elements as *S. cf. strambergensis*. On the other hand, I know of granulated ossicles from Berriasian sediments of the Pieniny Klippen Belt (details in e.g., Krobicki 2006) which certainly belong to *Sclerocrinus*. In the light of Głuchowski's (1987) research these should be classified as *S. compressus*; however, they do not show any differences with respect to *S. strambergensis*. Therefore, it is probable that these taxa are conspecific.

Occurrence: Early Cretaceous (Valanginian) of the Czech Republic and Poland?

Family Phyllocrinidae JAEKEL 1907

Genus *Phyllocrinus* D'ORBIGNY 1850

Type species Phyllocrinus malbosianus D'ORBIGNY 1850

Phyllocrinus belbekensis ARENDT 1974 (Figs. 4f–h)

1974 *Phyllocrinus belbekensis* ARENDT: 118, pl. 14, figs. 1–21, 14d–k

Material: 5 cups (GIUS 9–3468Pb).

Description: Cups small and low (max. height 1.3 mm, max. width 2.6 mm), pentagonal in outline. Radial cavity shallow (ca. 30% of height) and wide (45–50% of width). Radials bulging outwards. Interradial processes triangular in outline, rather narrow and long. Cup base wide, with round facet for stem. Suture lines very distinct.

Discussion: For detailed discussion see Salamon (2008b).

Occurrence: Late Jurassic–Early Cretaceous of central and eastern Europe.

Suborder Cyrtocrinina SIEVERTS-DORECK IN UBAGHS 1953 (Figs. 4i–j)

Material: 87 columnals and four terminal discs (GIUS 9–3468Cy).

Description: Different columnals. Some of them very high, cylindrical or barrel-shaped and slightly conical. Facet of most columnals abraded, covered by thick marginal crenulae in some cases. Latera smooth. Lumen relatively large and circular. Terminal discs with irregular base.

Valanginian crinoids of Hungary

Balanocrinus subteres (MÜNSTER IN GOLDFUSS 1826)

Description and discussion in “Resemblance of related taxa”.

Resemblance of related taxa

The majority of species of *Balanocrinus* are known exclusively from isolated ossicles. However, Hess (1972) reconstructed a specimen of *B. pentagonalis*, based on isolated radials and brachials, derived from the same strata as columnals of this form. According to Hess, this fulfilled to ascribe all these elements to a single taxon. However, recently, Simms (1989) assembled a very rich collection of complete or near-complete ‘balanocrinid’ specimens from the British Liassic (but see also Hess 2006).

Among the currently recognised species, *B. subteres* and *B. gillieronii* have several morphological features which make them similar and, in my view, conspecific. De Loriol (1879) also stated that *B. gillieronii* was nearly identical to *B. subteres*.

According to most researchers distal and medial? columnals of *B. subteres* are circular, whereas those from the proximal part of the stem are pentalobate in outline (e.g., Münster in Goldfuss 1826; von Zittel 1870; Hess 1975; Klikushin 1982; Głuchowski 1987). However, *B. gillieronii* has only circular columnals (e.g., de Loriol 1879; Klikushin 1979, 1982; Głuchowski 1987), which fact makes them appear to be distal columnals of *B. subteres*. Głuchowski (1987) suggested previously that columnals of *B. gillieronii* show morphological features resembling those of *Balanocrinus subteres*. However, that author stated that in case of *B. gillieronii* 5–7 marginal crenulae per petal are invariably developed. In contrast, in case of *B. subteres*, they are shorter and thinner, and number 6–8. It seems, however, that this is a rather subjective observation since length and thickness of crenulae on articular surfaces depend on the position of the columnal in the stem. Comparing the morphology of the facets of both mentioned taxa available in the literature data, it can be clearly seen that forms with longer and shorter as well as thinner and thicker crenulae which are referred to both species, are present (compare e.g., Hess 1975, pl. 20, fig. 8 and pl. 24, fig. 2; Klikushin 1992, pl. 5/5 vs. pl. 5/11, 12). This is also the case in columnals derived from different environments and age of extra-Carpathian Poland, which are also deposited in GIUS collections. Among several elements which according to present knowledge should be assigned to *B. subteres* and *B. gillieronii*, at random 400 columnals were collected and measured. All measured parameters are similar (see Fig. 5), which may indicate that only one taxon is represented. It must be noted, however, that as long as *B. subteres* (and/or *B. gillieronii*) is known only from isolated ossicles (mainly columnals), there can not be certainty whether these elements only represent one taxon or eventually two.

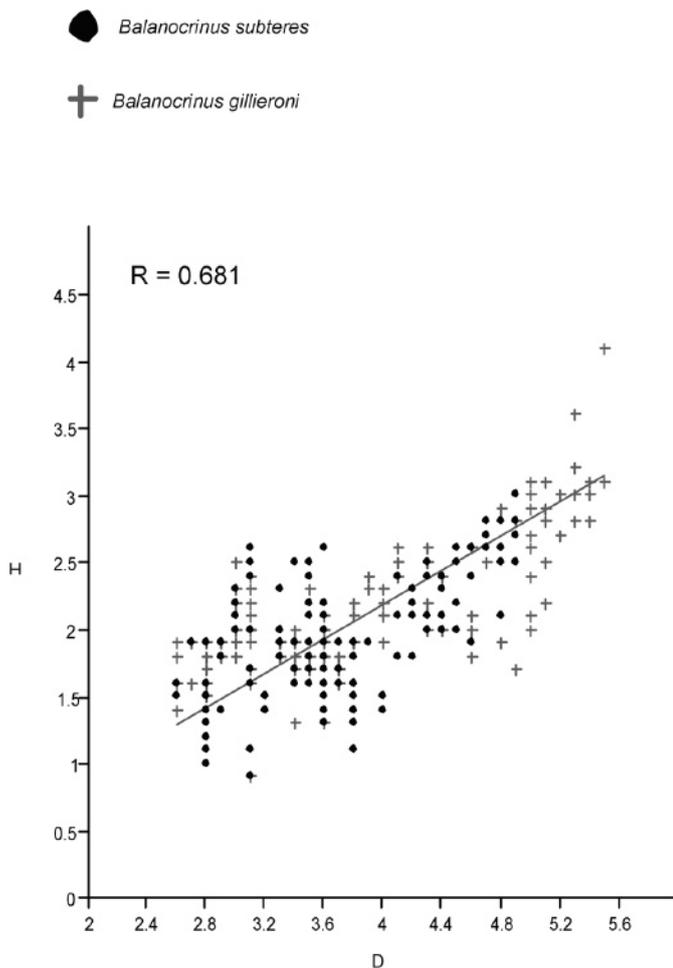


Fig. 5. Plot of columnar diameter (D) versus height (H) for data of *Balanocrinus subteres* and *B. gillieroni*. The plot was made using PAST (Paleontological Statistics Software Package for Education and Data Analysis, Hammer et al. 2001).

Discussion

Palaeobiogeography and palaeoecology

According to Kutek et al. (1989; see also Kaim 2001), present-day Poland was situated between the Boreal and Tethyan realms during the Valanginian (see Fig. 1b). The area of Poland was linked by the German Basin with the North Sea Basin in the north-west as well as with the Tethys in the south (e.g., Der-court et al. 1993).

The sample collected at Wąwał is from the uppermost (ca. 3 m; Fig. 2a) part of the Valanginian sequence exposed there. According to Kaim (2001, fig. 6) this part of lithological section corresponds to the boreal *Dichotomites* Zone (= ? upper *verrucosum* according to Tethyan zonation), which indicates a Late Valanginian age. In Hoedemaeker's opinion (1984), this time slice was characterised by a global regression. It is reflected also in the lithology of the Late Valanginian sediments in central Poland. Clay sedimentation was replaced in the ?upper *verru-*

cosum Zone by silty deposits. This change is seen in changes in taxonomical composition of certain invertebrate assemblages (details in Kaim 2001, fig. 10). It should be noted that the typical Tethyan ammonite *Saynoceras* was replaced by the typical Boreal *Dichotomites* (see comments in Płoch 1999). In relation to crinoid faunas, no differences among taxa were noted from Tethyan and Boreal provinces (compare Rasmussen 1961, table on pp. 410–416). On the other hand, it is difficult to ascertain which crinoids were unequivocally typically Tethyan and which were Boreal. Almost all Early Cretaceous crinoids appeared simultaneously in northern Africa, Asia as well as southern and northern Europe. In contrast, there is a marked taxonomic diversification among crinoids in the epicratonic and Tethyan sediments of Poland. However, this results from the fact that while the sea which covered central Poland was not very deep, the basin situated in southern Poland was deeper (see comments in Salamon & Zatoń 2007 and literature cited therein; presently Czorsztyn Castle Klippe, Fig. 2b). According to Kaim (2001), the lithological section exposed at Wąwał suggests shallow-water conditions near the photic zone. This observation is confirmed by the crinoid assemblage from this locality. Except for isocrinids (see comments below), millericrinids and comatulids (*sensu* Rasmussen 1978) preferring shallow-water conditions were very common (detailed discussion in Hess et al. 1999; Salamon & Zatoń 2005; Salamon 2008a). On the other hand, in the deep-water basin of Pieniny which was part of the Tethys, a different (both qualitatively and quantitatively) crinoid assemblage was documented. Except for isocrinid taxa (cosmopolitan *B. subteres*), cyrtocrinids considered as indicators of deep-water seas were common (details in Hess et al. 1999; Zatoń et al. 2008). It is possible that the variability among crinoids was related to a preferred mode of life rather than attachment. A similar observation is true for crinoids present in Jurassic sediments of Poland (review in Salamon 2008a). Similarly, as in the case of the Cretaceous, certain crinoids (e.g. cyrtocrinids) were connected to deep-water settings, whereas millericrinids and comatulids preferred shallow seas.

Post-Palaeozoic isocrinids from shallow-water settings of Poland

According to Oji (1985; but see also Hess 1999 and literature cited therein), extant isocrinids are distributed in relatively deep water (200–1000 m). The latter stressed that these crinoids disappeared from shallow water to take refuge in deep-water settings, and also suggested that the oldest representatives of isocrinids had settled in new, deep-water areas by the Early Jurassic. Oji (1985), for example, pointed out that *Seiocrinus subangularis* was supposed to inhabit depths of 100–600 m. On the other hand, he indicated that isocrinids preferred shallow seas (e.g., *Chariocrinus andreae* described by Hess 1972), and concluded that during the Mesozoic several isocrinids migrated to new, deep sea areas where they were not subject to predatory attacks (see also definition of Mesozoic marine revolution; details in Vermeij 1977; Oji 1996; Kelley & Han-

sen 2001). The last shallow-water isocrinids, according to Oji (1985), are from the mid-Cretaceous (Late Aptian) of Japan, from where *Isocrinus hanaii* and *Isocrinus? cf. neocomiensis* were described (but see also comments on Late Maastrichtian isocrinids by Jagt 1999).

Recent observations on crinoid faunas from Mesozoic and post-Mesozoic sediments of extra-Carpathian epicontinental Poland suggest that the hypothesis of Oji (1985, 1996) should be tested. It turns out that even in case of the southernmost part of Poland (Tatra Mountains and Pieniny Klippen Belt) of the Tethyan province, isocrinids lived in deep-sea areas (e.g., Głuchowski 1987; see also comments in Salamon & Zatoń 2007), but within the Tethys Realm (epicontinental Poland) isocrinids from shallow-water settings predominate. This also refers to Jurassic-Cretaceous as well as post-Mesozoic strata. Shallow-sea environments, presented below, are documented not only by palaeontological, but also sedimentological data. It should be clearly stressed, however, that there are many Jurassic-Cretaceous and post-Mesozoic localities (not mentioned below) in extra-Carpathian Poland, from where isocrinids and other crinoids associated, within shallow-water sediments are known. These are in part described in Salamon (2008b), however, most observations still await publication.

Examples

Jurassic

Zalas: a quarry in southern Poland, exposing Middle-Late Jurassic sediments (Early Callovian – Middle Oxfordian; e.g., Matyja 2006). In shallow-water (shallow sublittoral environment) sandy crinoid limestones of Early Callovian age the following isocrinid taxa have been recognised: *Balanocrinus hessi*, *B. subteres*, *Ch. adreae*, *Ch. cf. andreae* (Gorzela & Salamon 2006; Salamon & Zatoń 2006). Other crinoids represented are cyclocrinids and cyrtocrinids (Radwańska 2005b; Salamon & Gorzelak 2007; Salamon 2008b).

Małogoszcz: a quarry in southern Poland, exposing Late Jurassic (Kimmeridgian) and Early Cretaceous (Albian) sediments. In shallow-water sediments of the Kimmeridgian Upper Oolite unit (e.g., Kutek et al. 1992) the following stalked crinoid taxa have been noted: *Isocrinus pendulus*, *Balanocrinus subteres*, *Balanocrinus* sp. and *Pomatocrinus mespiliformis* (Radwańska 2005a; Salamon & Zatoń 2005). Other crinoids represented are free-swimming comatulids described in detail by Radwańska (2005a).

Julianka: a quarry in southern Poland, exposing deep-water Oxfordian and shallow-water Kimmeridgian limestones with common corals (Ostrowski 2005); the following stalked crinoid taxa (isocrinids and millericrinids respectively) have been seen: *Isocrinus pendulus*, *Balanocrinus subteres*, *Balanocrinus* sp. and *Millericrinina* indet. Other crinoids represented are numerous free-swimming comatulids (Salamon, unpublished data).

Owadów: a quarry in central Poland, exposing shallow-water, thick-bedded limestones of Tithonian age (details in Salamon et al. 2006). The following stalked crinoid taxa were recorded: *Isocrinus* sp., *Balanocrinus subteres*, *Balanocrinus* sp. and *Millericrinina* indet. Other crinoids represented are stalked comatulids (Thiollicerininidae; details in Klikushin 1987).

Cretaceous

Glanów: an outcrop in southern Poland, exposing shallow-water, coarse-grained sandstones, conglomerates and gravels of Late Cretaceous age (Cenomanian; e.g., Marcinowski 1974). The following stalked crinoid taxa were recorded: *Isocrinus* sp., *Millericrinina* indet. resembling *Apiocrinites* sp. and *Bourgueticrinus* sp. (Gorzela & Salamon 2006; Salamon 2007). Other crinoids represented are free-swimming comatulids (Salamon 2007).

Post-Cretaceous

Nasiłów: a quarry in eastern Poland, exposing Late Cretaceous (Maastrichtian) and shallow-water sediments of Danian (Świerczewska-Gładysz & Olszewska-Nejbert 2006). The following stalked crinoid taxa were recorded: *Isocrinus* sp., *Nielsenicrinus* sp. and *Bathyrinus* sp. (Sekuła et al. 2008).

These data indicate that Mesozoic and Cenozoic stalked crinoids were common in shallow-water settings (at least in epicontinental areas). Thus, the hypothesis of migration (at least from mid-Cretaceous onwards) to deep-water areas, as a response to an increase of the number of predators during the Mesozoic marine revolution, is not universally applicable. A similar opinion was expressed by Améziane & Roux (1997), who stated that the absence of stalked crinoids in shallow-water settings is a consequence of their functional morphology. They also noted that among the recent stalked crinoids, forms from relatively shallow-water settings are known. As a result, the hypothesis that modern isocrinids lived only in deep-water areas, is not well supported.

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