

Bathonian (Middle Jurassic) crinoids of the Hidas Valley (Mecsek Mountains, S Hungary) and their biogeographic significance

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Abstract The Bathonian crinoid fauna that occurs in red nodular limestone and argillaceous limestones from the Hidas Valley, Mecsek Mts (southern Hungary) consists of three isocrinid and six cyrtocrinid species. Isocrinids are represented by *Balanocrinus inornatus* (d’Orbigny), *B. berchteni* Hess and Pugin and *Balanocrinus* sp. Cyrtocrinids are represented by *Phyllocrinus stellaris* Zaręczny, *P. birkenmajeri* Głuchowski, *P. malbosianus* d’Orbigny, *Apsidocrinus* sp., *Lonchocrinus* sp., and the new species *Psalidocrinus hidasinus* sp. nov. This last species is the earliest occurrence of the genus *Psalidocrinus* previously known from the Early Tithonian to Valanginian. This is the first crinoid fauna described from the Middle Jurassic (Bathonian) of Hungary. The co-occurrence of isocrinids and cyrtocrinids indicates an environment subject to weak currents. The stratigraphical and geographical distribution of the identified cyrtocrinid genera and species suggests a Tethyan origin and subsequent migration to the northern Tethyan shelf.

Keywords Cyrtocrinida · Isocrinida · Middle Jurassic · Taxonomy · Palaeoecology · Tethys · Hungary

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Abbreviations

ZPAL Ca.8	Collection of the Institute of Paleobiology, Polish Academy of Sciences
Hc	Total cup height
Hd	Aboral part height
Wc	Cup diameter
KD	Columnal diameter
KH	Columnal height

1 Introduction

Jurassic crinoids are well known from Europe due to classical monographs by de Loriol (1877–1879, 1882–1884) and Quenstedt (1874–1876) (see also Arendt 1974; Hess 1975, 2006; Simms 1989). Middle Jurassic Tethyan crinoids from Europe are much less studied and described from Switzerland (Hess 1975, 1999), Italy (Manni and Nicosia 1984; Castellana et al. 1989) and recently from France (Charbonnier et al. 2007, 2009; Hess 2012). From Hungary, only Late Jurassic crinoids have been reported from the Bakony Mountains by Manni et al. (1992). On the other hand, Early Cretaceous crinoids have been briefly described from Hungary by Szörényi (1959), Sieverts-Doreck (1961) and Salamon (2009). The purpose of the current study is to describe the first crinoids from the Middle Jurassic (Bathonian) of the Hidas Valley (Mecsek Mountains) from southern Hungary and to analyse their palaeogeographical context.

2 Geological setting

According to Császár and Haas (1983); see also Galács (1984a), Middle Jurassic deposits of the Mecsek Mountains

(southern Hungary) belong to four formations: Pusztakisló Limestone Formation (Aalenian), Komló Marly Limestone Formation (Aalenian, Bajocian), Óbányai Limestone Formation (Bathonian) and Dorogói Marly Limestone Formation (Callovian). The Komló and Óbánya Formations are both rich in fossil crinoids (Bódy 2000).

The investigated material has been collected in the outcrops of Óbányai Formation in Hidas Valley in the Mecsek Mountains (Fig. 1). The exposed Bathonian section is about 10 m thick. The Bathonian age of the Óbánya Limestone Formation was established by Galácz (1984b, and literature cited therein) on the basis of ammonites. The Bathonian strata are capped by nearly 2 m thick Callovian deposits.

The Bathonian sequence exposed in the Hidas Valley (Fig. 2) begins with red ammonitic limestone about 4 m thick, which represents the Early Bathonian. The Middle Bathonian consists of two thin, 0.25 m thick layers of red argillaceous limestone, separated by the red, 0.25 m thick ammonitic limestone. The upper layer of the argillaceous limestone is overlain by a sequence of alternating red

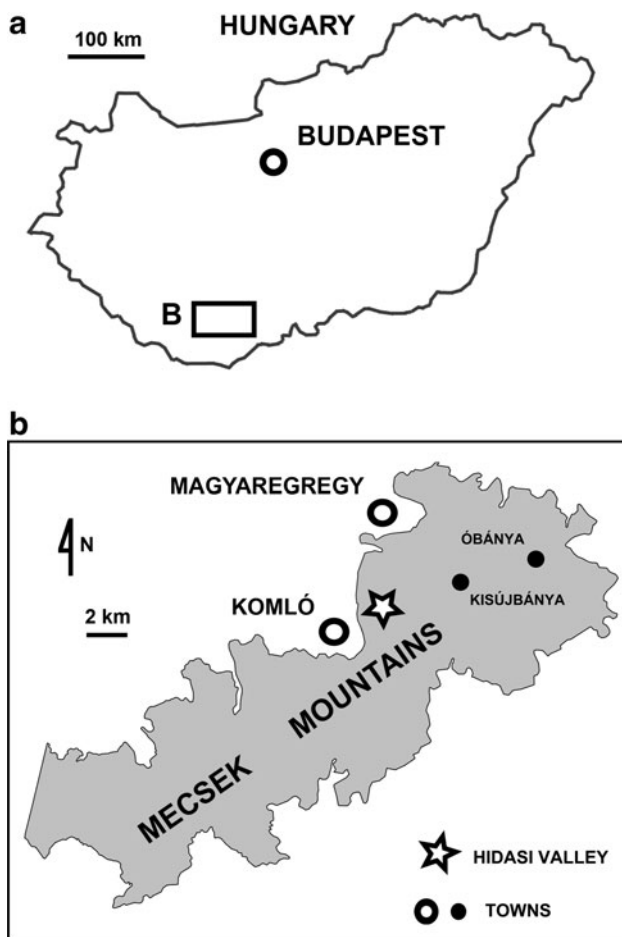


Fig. 1 Schematic map of Mecsek Mountains with investigated section indicated

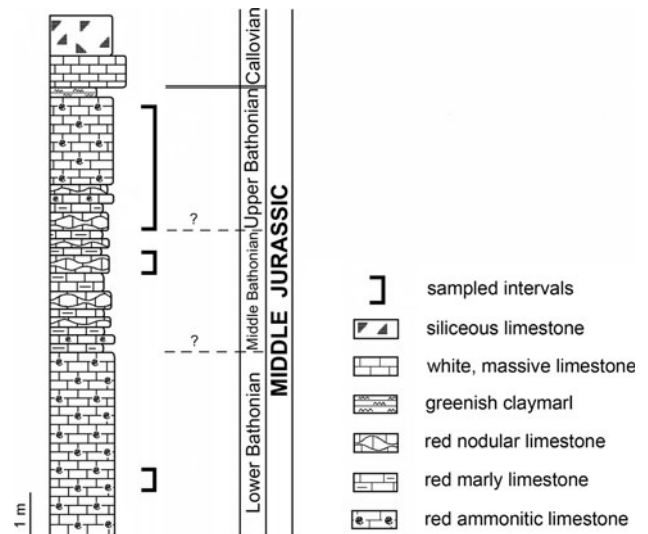


Fig. 2 Stratigraphical sequence exposed in Hidas Valley and the interval sampled

nodular limestone and red argillaceous limestone with individual layers between 0.25 and 0.5 m in thickness. The Middle Bathonian strata are about 2.5 m thick. The Upper Bathonian, that is over 3 m thick, starts with red, about 0.5 m thick nodular limestone, which is overlain by 0.25 m thick, red clayey limestone. The red argillaceous limestone is overlain by 2 m thick, red ammonite-bearing limestone with a 0.25 m thick, red nodular limestone in its lower part. The uppermost part of the Bathonian sequence consists of thin layers of about 0.25 m thick, greenish clayish marl. The capping Callovian deposits consist of 1 m thick, white massive limestone overlain by a 1 m thick, siliceous limestone.

3 Materials and methods

The larger specimens were collected directly from the outcrop by Andras Galácz and Andrzej Pisera, whereas the microrests were collected by Adrien Bódy and were the subject of his unpublished MSc Thesis. 29 limestone samples were recovered from the section from three different intervals of the Bathonian strata (Fig. 2). All limestone samples were boiled in water with glauber salt and frozen (five times). Then, they were washed in warm water and sieved using 0.65 and 0.45 mm mesh. After washing, the samples were dried at 160 °C. The obtained residues were picked by hand under a binocular microscope for skeletal elements of crinoids (Bódy 2000). Smaller specimens were photographed under SEM (Institute of Paleobiology, Warsaw). All specimens have been studied and measured under a binocular microscope and all measurements given are in mm. Crinoid terminology

follows Moore and Jeffords (1968). All described material is housed in the collection of the Institute of Paleobiology, Polish Academy of Sciences (ZPAL Ca.8), Warsaw, Poland (Fig. 3).

4 Systematic palaeontology

Class Crinoidea MILLER, 1821

Subclass Articulata MILLER, 1821

Order Isocrinida SIEVERTS-DORECK, 1952

Family Isocrinidae GISLÉN, 1924

Genus *Balanocrinus* AGASSIZ IN DESOR, 1845

Type species Pentacrinites subteres MÜNSTER IN GOLDFUSS, 1826

Balanocrinus inornatus (D'ORBIGNY, 1850) (Fig. 4i–j)

1850. *Pentacrinus inornatus* D'ORBIGNY, p. 891.

1887. *Balanocrinus inornatus* D'ORBIGNY; de Loriol, p.311, pl. 184, figs. 3–9.

1911. *Balanocrinus inornatus* D'ORBIGNY; Boule, p. 111, pl. 22, fig. 12.

1912. *Balanocrinus inornatus* D'ORBIGNY; Lissajous, p. 173, pl. 18, fig. 32.

1927. *Balanocrinus inornatus* (D'ORBIGNY); Valette, p. 27.

2012. *Balanocrinus inornatus* D'ORBIGNY; HESS, p. 223, fig. 7a–c.

Material. 100 columnals and 22 pluricolumnals.

Measurements. KD: 1.3–8.8 mm; KH: 0.8–3.5 mm.

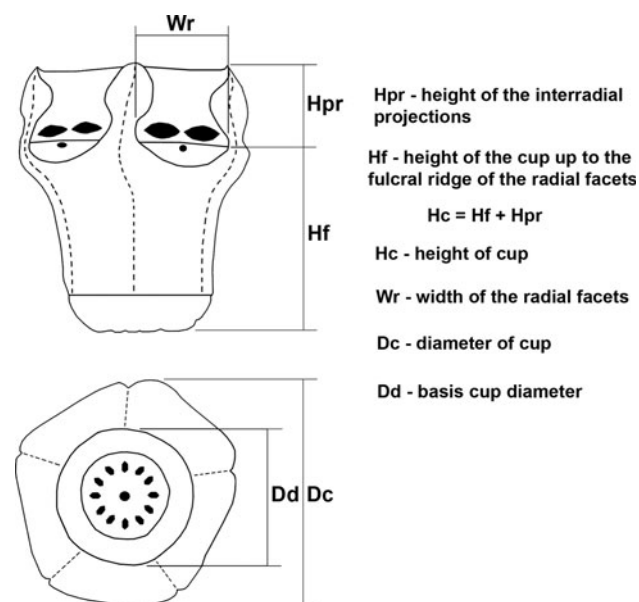


Fig. 3 Measured parameters of *Psalidocrinus hidasinus* sp. nov. (modified after Žitt 1978b, p. 119, Table 2 and Manni and Nicosia 1985, p. 81, Table 1)

Description. Columnals circular, high and sometimes with slightly concave lateral surface. Articulation surface flat with large, triangular petals. Each petal separated from one another by thin adradial crenulae. Marginal crenulae of the same size, 9–12 per petal, thicker and larger than adradial crenulae. Lumen small, circular.

Discussion. *Balanocrinus inornatus* (D'Orbigny) is slightly similar to *Balanocrinus subteres* (Münster in Goldfuss), which is the most common isocrinid species in the Jurassic and Early Cretaceous, but *B. subteres* have larger marginal crenulae. In addition, Hess (written communication 2012) suggest, that the stratigraphic range of *B. subteres* has been overestimated.

Occurrence. Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary. Bajocian of France and Spain (Lissajous 1912, Valette 1927), Bathonian of France (Loriol 1877; Boule 1911) and Late Bajocian–Early Bathonian of France (Hess 2012).

Balanocrinus berchteni HESS AND PUGIN, 1983 (Fig. 4m)

1983. *Balanocrinus berchteni* HESS AND PUGIN, p. 696, figs. 2, 3.

1987. *Margocrinus berchteni* HESS AND PUGIN; Głuchowski, p. 56, pl. 41, figs. 3, 4; text-fig. 17/4.

2006. *Balanocrinus berchteni* HESS AND PUGIN; Salamon and Zatoń, p. 6, fig. 5a–c.

2012. *Balanocrinus berchteni* HESS AND PUGIN; Boczarowski, p. 356, text-fig. 4c–d.

Material. 16 columnals and 1 pluricolumnal.

Measurements. KD: 1.9–3.8 mm; KH: 1.2–1.8 mm.

Description. Columnals circular, pentagonal to pentalobate. Articulation surface flat with triangular large petals. Petals separated one from another by thin adradial crenulae. Each petal surrounded by 6–8 marginal crenulae. Marginal crenulae are of the same size and thicker than adradial. Lumen is very small, circular and poorly visible.

Discussion. The Bajocian species *Balanocrinus moeschi* de Loriol from France is slightly similar to *B. berchteni* Hess and Pugin, but it differs regarding the columnal shape, that is thinner and often with sharp edges in *B. moeschi*. More similar to *B. berchteni* are the Oxfordian *B. campichei* de Loriol and the Kimmeridgian *B. maritimus* Bourseau, David, Roux, Bertrand and Clochard from France (Bourseau et al. 1998). The species *B. campichei* has similar average height of columnals to *B. berchteni* and the articulation surface of columnals is smooth, so they may be even conspecific. *B. maritimus* has similarly shaped columnals that are circular to pentalobate but marginal crenulae are thicker, and petals floors drop-like in shape; in some case petal floors are rhombic.

Occurrence. Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary. Bajocian of Switzerland (Hess and

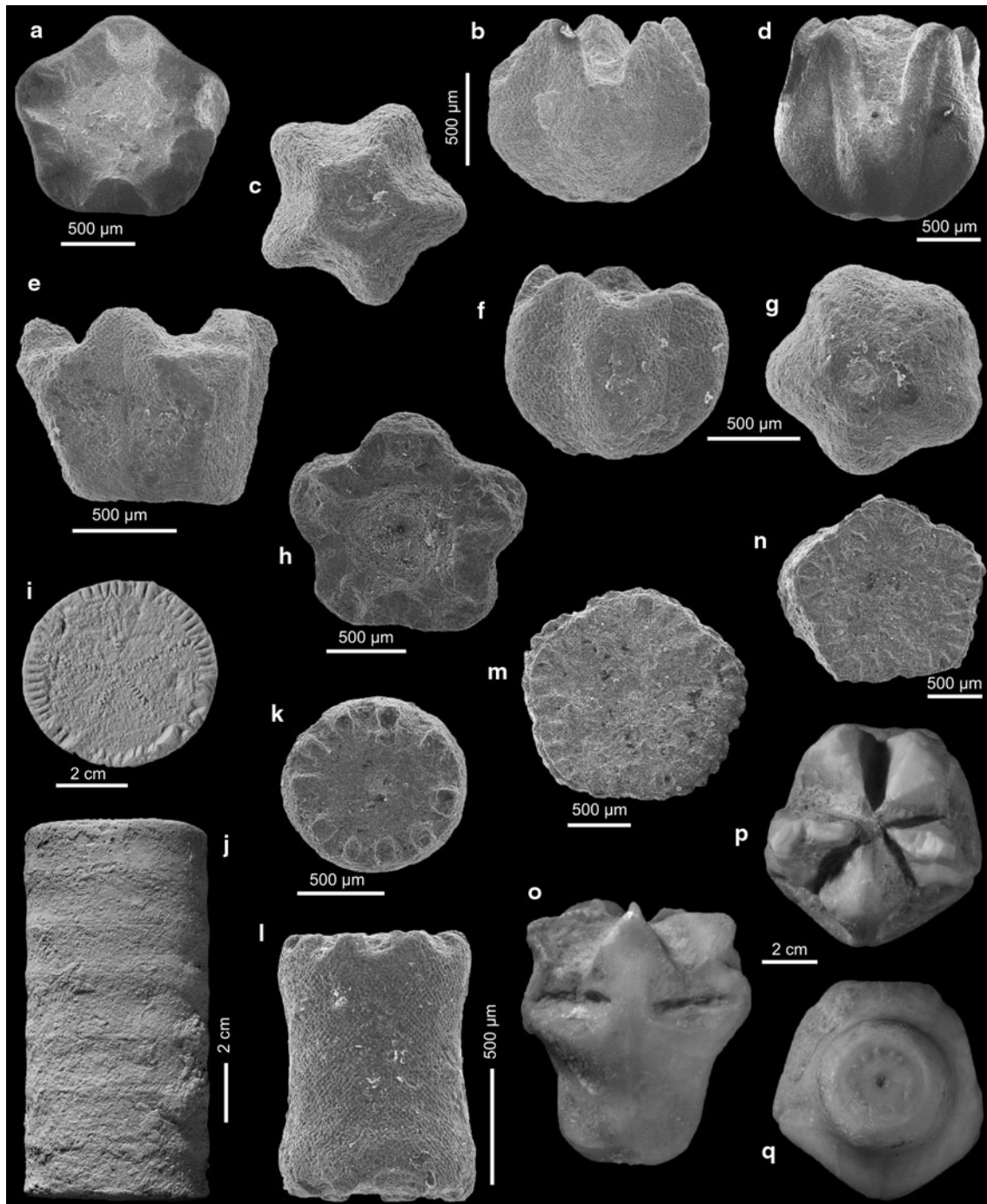


Fig. 4 Middle Jurassic (Bathonian) crinoids of the Hidas Valley, Mecsek Mountains. *Phyllocrinus stellaris* Zaręczny, cup; distal view (a), lateral view (b), proximal view (c); ZPAL Ca.8/1 (a), ZPAL Ca.8/2 (b), ZPAL Ca.8/3 (c). *d* *Phyllocrinus malbosianus* d'Orbigny, cup; lateral view; ZPAL Ca.8/4. *e* *Lonchocrinus* sp., cup; lateral view; ZPAL Ca.8/5. *Phyllocrinus birkenmajeri* Głuchowski, cup; lateral view (f), proximal view (g), and distal view (h), ZPAL Ca.8/6 (f, g), ZPAL Ca.8/7 (h). *Balanocrinus inornatus* (d'Orbigny), articular face

of the columnal (i), lateral view of the pluricolumnal (j); ZPAL Ca.8/8 (i), ZPAL Ca.8/9 (j). *Apsidocrinus* sp., articular face of the columnal (k), lateral view of the columnal (l); ZPAL Ca.8/10 (k), ZPAL Ca.8/11 (l). *m* *Balanocrinus berchteni* (Hess and Pugin) articular face of the columnal; ZPAL Ca.8/12. *n* *Balanocrinus* sp. articular face of the columnal; ZPAL Ca.8/13. *Psolidocrinus hidasinus* sp. nov., cup, holotype; lateral view (o), distal view (p), proximal view (q); ZPAL Ca.8/14

Pugin 1983) and Bajocian–Bathonian of Poland (Głuchowski 1987; Salamon and Zatoń 2006, 2007, Bożczarowski 2012).

***Balanocrinus* sp.** (Fig. 4n)

Material. 30 columnals.

Measurements. KD: 0.8–2.0 mm; KH: 1.0–5.0 mm.

Description. Columnals pentagonal in outline, sometime with sharp edge. Lateral surface slightly concave. Articular surface flat with rhombic and sharply terminated petals. Every petal is surrounded by 6–8 marginal crenulae and separated by thin adradial crenulae. Lumen circular, small and poorly visible.

Discussion. The studied material comprises a few dozens of isolated columnals, that are not well enough preserved for a precise determination. They may belong either to *Balanocrinus hessi* Salamon and Zatoń, known from the Callovian of southern Poland, or to *B. pentagonalis* (Goldfuss), known from the Jurassic of Europe and Asia (Salamon and Zatoń 2006).

Occurrence. Late Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary. The genus *Balanocrinus* is known from Jurassic and Cretaceous sediments from all over the world.

Order Cyrtocrinida SIEVERTS-DORECK in UBAGHS, 1952
Suborder Cyrtocrinina SIEVERTS-DORECK in UBAGHS, 1952
Family Phyllocrinidae JAEKEL, 1907

Genus *Phyllocrinus* D'ORBIGNY, 1850

Type species *Phyllocrinus malbosianus* D'ORBIGNY, 1850

Phyllocrinus stellaris ZARĘCZNY, 1876 (Fig. 4a–c)

1876. *Phyllocrinus stellaris* ZARĘCZNY, p. 213, pl. 1, fig. 9.
1979. *Phyllocrinus stellaris* ZARĘCZNY; Pisera and Dzik, p. 823, pl. 4, figs. 2–4, text-figs. 11a, b, 13e–f.

1987. *Phyllocrinus stellaris* ZARĘCZNY; Głuchowski, p. 32, pl. 11, figs. 1–6, pl. 12, figs. 1–6, pl. 13, figs. 1–4, text-fig. 15/3.

2008. *Phyllocrinus stellaris* ZARĘCZNY; Salamon, p. 84, fig. 3b–d.

Material. 37 cups and 3 incomplete cups.

Measurements. Hc 1.2–1.4 mm, Hd 0.5–0.9 mm, Wc 1.6–2.0 mm.

Description. Cups small and low, pentalobate in outline. Radial cavity shallow. Radials are bulging with rib. Interradial processes triangular in outline, short. Cup base wide. Suture lines poorly visible, in furrows.

Discussion. Arendt (1974), Pisera and Dzik (1979) and Głuchowski (1987) consider that *P. stellaris* Zareczny differs from *P. belbekensis* Arendt in shape of the cup, stem facet and interradian processes. On the other hand, Salamon (2008) and Hess et al. (2011) suggested that *P. stellaris* and *P. belbekensis* are just different developmental stages, and thus conspecific, but left this question unstudied and open to further detailed analysis, which is, however, not possible with the herein described material.

Occurrence. Late Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary. Late Callovian, Early-

Middle Oxfordian (?) to Tithonian of Poland (Pisera and Dzik 1979; Salamon 2008).

Phyllocrinus malbosianus D'ORBIGNY 1850 (Fig. 4d)

1850. *Phyllocrinus malbosianus* D'ORBIGNY, p. 110.

1961. *Phyllocrinus malbosianus* D'ORBIGNY; Rasmussen, p. 229, pl. 33, figs. 1, 2.

1978a. *Phyllocrinus malbosianus* D'ORBIGNY; Žitt, p. 41, pl. 1, figs. 1–13, pl. 2, figs. 1–7, pl. 5, figs. 13, 14.

1987. *Phyllocrinus malbosianus* D'ORBIGNY; Głuchowski, p. 34, pl. 15, figs. 1, 2, text-fig. 15/1.

2010. *Phyllocrinus malbosianus* D'ORBIGNY; Salamon and Gorzelak, p. 874, text-figs. 2b–d, 6a.

Material. 11 complete and 3 incomplete cups.

Measurements. Hc 1.6–1.9 mm, Hd 1.0–1.3 mm, Wc 2.0–2.3 mm.

Description. Cups hemispherical in shape, pentalobate in outline. Basal part of cup flattened with circular stem facet. Radials bulging with rim. Interradial processes triangular in outline, high (often broken). Suture lines in furrows, distinctly visible.

Discussion. The investigated material consists cups whose total height and diameter suggest that they represent juvenile development stage and have non-deformed interradian processes, case often observed by other authors (Žitt 1978a; Głuchowski 1987; Salamon and Gorzelak 2010).

Occurrence. Late Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary. Oxfordian and Tithonian of Poland (Głuchowski 1987; Salamon and Gorzelak 2010). Tithonian to Hauterivian of Austria, France, Germany, Italy, Portugal, Russia, Spain and Switzerland (Arendt 1974) and Valanginian of the Czech Republic (Žitt 1978a).

Phyllocrinus birkenmajeri GŁUCHOWSKI, 1987 (Fig. 4f–h)

1987. *Phyllocrinus birkenmajeri* GŁUCHOWSKI, p. 35, pl. 15, figs. 6–10, text-fig. 15/8.

Material. 36 cups.

Measurements. Hc 0.7–1.0 mm, Hd 0.4–0.5 mm, Wc 1.0–1.2 mm.

Description. Cups small, conical and slightly rounded in aboral part. Basal part of the cup flattened with large round cavity for stem. Radials convex. Interradial processes short and damaged in most specimens. Suture lines on interradians well visible.

Discussion. The investigated specimens are similar to the holotype described by Głuchowski (1987; pl. 15, fig. 7) in the outline of the cup and shape of arm facets. However, dimensions of our specimens are smaller than those of the holotype and this may suggest that the herein described specimens represent juvenile development stages.

Occurrence. Late Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary; Bajocian of Poland (Głuchowski 1987)

Genus *Apsidocrinus* JAEKEL, 1907

Type species *Apsidocrinus remesi* JAEKEL, 1907.

Apsidocrinus sp. (Fig. 4k–l)

Material. Nine columnals.

Measurements. KD 1.4–2.4 mm; KH 1.7–4.0 mm.

Description. Columnals circular in outline and variable in height (from 1.5 to 4.0 mm). Lateral surface slightly concave. Articular surface covered with 10–11 thick and short marginal crenulae. Lumen large, circular and poorly visible.

Discussion. The studied material comprises a few isolated elements. Some of the features i.e. marginal crenulae and shape of columnals may indicate that those elements belong to *Apsidocrinus moeschi* (Zittel).

Occurrence. Late Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary. The genus *Apsidocrinus* is known from the Late Jurassic to Early Cretaceous (Early Kimmeridgian–Valanginian) (Arendt 1974; Rasmussen 1978; Žitt 1978b; Manni and Tinozzi 2001) of Europe.

Genus *Lonchocrinus* JAEKEL, 1907

Type species *Eugeniocrinus dumortieri* DE LORIO, 1882.

Lonchocrinus sp. (Fig. 4e)

Material. Three incomplete cups.

Measurements. Hc 0.9–1.1 mm, Hd 0.6–0.8 mm, Wc 1.3–1.5 mm.

Description. Cup pentagonal in outline, lower part rounded. Radial cavity shallow. Interradial processes narrow and massive, triangular in outline. Suture lines on interradians distinctly visible.

Discussion. Material only comprises three cup fragments but these are well enough preserved in order to assign them to *Lonchocrinus dumortieri* (de Loriol).

Occurrence. Late Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary. Various species of the genus *Lonchocrinus* are known from Middle Jurassic (Callovian) to Early Cretaceous (Valanginian) of France, Switzerland, Russia and Czech Republic (Arendt 1974; Rasmussen 1978); Bajocian and Callovian of Poland (Głuchowski 1987).

Family Psalidocrinidae ŽITT, 1978b

Genus *Psalidocrinus* REMEŠ AND BATHER, 1913

Type species *Psalidocrinus remesi* BATHER, 1913 in REMEŠ AND BATHER (1913).

Psalidocrinus hidasinus sp. nov. (Fig. 4o–q; Table 1)

Holotype. ZPAL Ca.8/14, Fig. 4o–q.

Type locality and stratigraphic level. Hidas Valley, Mecsek Mountains, southern Hungary; Bathonian.

Etymology. Named after the Hidas Valley, Mecsek Mts, type locality of the species.

Material. Four cups.

Measurements. See Table 1

Diagnosis. *Psalidocrinus* with large massive cup that is pentagonal in outline; radials separated by distinct sutures. Interradial processes very small and triangular.

Description. Cup large, massive and pentagonal in outline. Interradial processes triangular in outline and concave. Interradials high and massive. Suture lines on interradians distinctly visible. Each radial plate separated from another by distinct suture. Radial facet large and wide. Muscle fossae large and deep. Basal part of cup circular in outline with articulation surface. Short, thin marginal crenulae with small and circular lumen.

Discussion. Generally, three cups are well-preserved and in the biggest of them the upper part of the interradian processes is poorly visible. *P. hidasinus* sp. nov. differs from other species of the genus *Psalidocrinus* in the shape of the cup and interradian processes (see Table 2). All Jurassic species of the genus *Psalidocrinus* have similar height of the cup. Regarding its outline, the cup of *P. hidasinus* sp. nov. is somewhat similar to *P. armatus* (Zittel) (see Pisera and Dzik 1979, p. 849) but the aboral part of the cup of *P. armatus* is more slender than in the new species. Basal part of the cup of *P. hidasinus* is similar to *P. zitti* Manni and Nicosia (see Manni and Nicosia 1985, p. 83) but has smooth surface in contrast to *P. zitti* that is granulate. The Early Cretaceous (Valanginian) *P. strambergensis* Remeš and *P. remesi* Bather have funnel-shaped cups. Interradial processes of *P. hidasinus* are the smallest among all species of the genus. The new species, in contrast to *P. zitti* and *P. dalpiazzi* Manni and Nicosia, has somewhat elongated interradian processes. *P. hidasinus*, *P. armatus*, *P. zitti*, *P. strambergensis* and *P. remesi* all display suture lines between radial plates, in opposition to *P. dalpiazzi* that has ridges between radial plates and under the radial facet instead (see Manni and Nicosia 1987, p. 268). *P. hidasinus*

Table 1 Cup measurements of *Psalidocrinus hidasinus* sp. nov.

Specimen no.	Hc (mm)	Hf (mm)	Hpr (mm)	Dc (mm)	Dd (mm)
1	10.8	7.0	3.8	8.3	6.4
2	11.2	7.3	3.9	7.6	6.1
3	8.7	6.1	3.5	6.8	4.6
4	14.6	9.1	5.5	9.8	7.6

Table 2 Cup measurements of various *Psalidocrinus* species (for abbreviations see Fig. 3)

Species	Age	Hc (mm)	Hf (mm)	Hpr (mm)	Dc (mm)	Dd (mm)	Wr (mm)
<i>Psalidocrinus hidasinus</i> n. sp.	Bathonian	8.7–14.6	7.0–9.1	3.8–5.5	7.4–10.0	5.3–7.1	2.4–4.3
<i>Psalidocrinus armatus</i> (Zittel, 1870)	Tithonian	2.5–8.0	1.5–6.0	–	2.3–10.1	1.0–3.8	0.7–3.5
<i>Psalidocrinus zitti</i> Manni and Nicosia, 1985	Early Tithonian	4.4–11.8	1.8–5.5	1.4–8.2	4.6–11.0	3.8–7.4	1.1–5.7
<i>Psalidocrinus dalpiazii</i> Manni and Nicosia, 1987	Tithonian	12.5	5	7.5	13.1	4	6.2
<i>Psalidocrinus strambergensis</i> Remeš, 1912	Valanginian	–	6.2–8.4	–	10.5–16.5	4.3–7.6	4.6–9.0
<i>Psalidocrinus remesi</i> Bather, 1913	Valanginian	11.3–20.9	3.8–8.3	7.5–12.9	9.2–16.1	5.5–7.5	5.1–9.0

sp. nov. is the oldest representative of the genus *Psalidocrinus*.

Occurrence. Late Bathonian, Hidas Valley, Mecsek Mountains, southern Hungary.

5 Palaeoecology

The Bathonian crinoids from the Hidas Valley, Mecsek Mountains comprise three species of isocrinids and six species of cyrtocrinids. All crinoids are represented by isolated elements and cups. In our material, 85 % of 146 columnals of isocrinids belong to *B. inornatus*. Cyrtocrinids, on the other hand are represented mainly by cups (106 complete cups), except *Apsidocrinus*, which is represented only by nine columnals. Cyrtocrinids dominate the Hidas Valley crinoid fauna, while isocrinids are subordinate. Isocrinid and cyrtocrinid associations from the Tethys were recently described from the Middle Jurassic (Bathonian-Early Callovian) of France by Charbonnier et al. (2007), Charbonnier (2009) and by Hess (2012). This French Bajocian-Early Callovian crinoid assemblage is very rich and much more diversified with six species of isocrinids, seven species of cyrtocrinids (that dominate the fauna), five comatulid species, one apiocrinid species and one cyclocrinid species. Its taxonomic composition is totally different from the Bathonian Hungarian crinoid fauna, and only two genera *Balanocrinus* and *Lonchocrinus* are in common. Analyses of the bathymetric range of recent crinoids and their morphology and distribution by Charbonnier et al. (2007 and references therein) have shown that associations of cyrtocrinids and isocrinids suggest depths greater than 200 m. Judging from the preferences of recent cyrtocrinids (Hess 1999), their dominance may also indicate that the water depth was even exceeding 200 m, even though stalked crinoids have changed their bathymetric range since the Jurassic (Donovan and Jakobsen 2004 and references therein). Recent isocrinids live at 200–300 m water depth or more (Macurda and Meyer 1974; Baumiller et al. 1991; Hess 1999). However, Hess (2012) suggested that dominant number of the ossicles of cyrtocrinids indicate moderately-deep water with minimal transport of skeletal elements. On

the other hand, stalked crinoids with strong, long stems with cirri may have lived in more dynamic palaeoenvironments characterized by rather shallow and turbulent water. *B. inornatus*, *B. berchteni* and *Balanocrinus* sp. are common both in shallow- and deep-water palaeoenvironments. It should be noted, however, that the Middle and Late Mesozoic was the time when isocrinids began to occupy new deep-water habitats in response to increasing predation related to the Mesozoic marine revolution (Vermeij 1977; Meyer 1985; Oji 1996). All cyrtocrinid species known (both fossil and recent) live attached to hard substrate, usually rock. No hard bottom was observed in the investigated rocks, but for attachment they may have used ammonite shells, and other skeletal elements, which are common in these rocks. However, no direct evidence for this has been found, because all aragonitic shells are dissolved in the studied section.

Length of stem and density of filtration fan determine the trophic tier occupied by crinoids (Ausich 1980; Ausich and Bottjer 1982; Bottjer and Ausich 1986). Accordingly, the herein described crinoids represent three trophic tier levels. Short-stalked cyrtocrinids such as *P. stellaris*, *P. malbosianus*, and *P. birkenmajeri*, which have crowns elevated up to 4 cm above the sea-floor and attach to hard objects on the bottom by a holdfast, belong to the first, lowest trophic tier. Cyrtocrinids with crowns from a few to a dozen cm above the bottom (*Apsidocrinus* sp., *Lonchocrinus* sp. and *P. hidasinus*) belong to the middle trophic tier. Isocrinids (*B. inornatus*, *B. berchteni* and *Balanocrinus* sp.), that have long stems, up to 1 m above sea-floor with cirri and large crowns with long, branched arms that could be effective filtration fans represent the highest trophic tier. The co-occurrence of cyrtocrinids and isocrinids suggests an environment subjected to weak currents, if the described crinoids really lived together. Under stronger currents, isocrinids dominate, because their long stems with cirri are a better adaptation to stronger currents (Rasmussen 1977; Roux 1987).

6 Palaeobiogeography

The Hidas Valley, Mecsek Mountains, (southern Hungary) was a part of the Tisia terrane, belonging to a

Mediterranean microcontinent during the Middle Jurassic (see Vörös 1993). This microcontinent was situated in the western part of Tethys Ocean and isolated from the European and African shelves by deep oceans (Vörös 1993). The southern marginal segment of the stable European plate, with the Mecsek Mountains, detached from the stable Europe in the Middle Jurassic, with the formation of the Magura Ocean. This is recorded by the thick hemipelagic, turbiditic marl sequence of the Bajocian, followed by the pelagic, red nodular limestone of reduced thickness in the Bathonian. From the Bathonian onward, this oceanic trough could have served as an alternative connecting route for faunal elements, such as Tethyan phylloceratids, which show a high proportional representation in the Mecsek ammonite faunas (Csontos and Vörös 2004).

The studied isocrinids, i.e. *B. inornatus*, *B. berchteni* and *Balanocrinus* sp. are widely distributed, both in shallow and deep water Jurassic rocks. It is worth mentioning that so far *B. inornatus* is only known from the western part of Tethys Ocean, from the Middle Jurassic of France and Spain (Hess 2012 and references therein). Cyrtocrinids described here, in contrast, have a more diverse palaeogeographical distribution.

Psalidocrinus hidasinus sp. nov. is a potential endemic species, as are other species of this genus that are known from small areas in the eastern part of the Tethys. *Phyllocrinus malbosianus* is until now known from the Tithonian to Hauterivian of Western Europe (Arendt 1974), from the Valanginian to Hauterivian of Crimea, the Valanginian of the Czech Republic (Žítt 1978a), and from the Tithonian of Poland (Głuchowski 1987). *P. stellaris* is known from the epicontinental deposits of Poland (Polish Jura Chain, Late Callovian and Early-Middle Oxfordian?, Salamon 2008), and from the Carpathians (Tethys) in Poland and Slovakia (Pieniny Klippen Belt, Oxfordian and Tithonian, Žítt and Michalík 1984; Głuchowski 1987). On the other hand, *P. birkenmajeri* is only known from the Bajocian of Poland (Głuchowski 1987). Besides, various species of the genera *Apsidocrinus* and *Lonchocrinus* are typical for the Jurassic of the European part of the Tethyan Ocean (Manni and Tinozzi 2001). The observed distribution of cyrtocrinid species in space and time suggests in most cases an origin in the Tethys and a later migration to the north to neighbouring shelf areas (Salamon 2008; Salamon and Zatoń 2006, 2007; Zatoń et al. 2008).

According to Vörös (1993) migration was not possible from the Tethys to the epicontinental sea during the Middle Jurassic because of the oceanic Alboran-Ligurian Penninic barrier and a related specific eastward oceanic current system, that (up to Callovian) prevailed in the western part of Tethys. The westward currents established close to the end of the Middle Jurassic (Callovian), as a result of the opening of the connection between the oceanic basins of

the western Tethys and the Central Atlantic, so called Hesperian Strait (see details in Vörös 1993), allowing for faunal migrations. This explanation coincides well with the observed distribution pattern of most studied cyrtocrinids, exception being only *Phyllocrinus birkenmajeri* with an oldest occurrence on the northern edge of Tethys Ocean (Bajocian of Poland, Pieniny Klippen Belt, Głuchowski 1987). However, this may be an artefact of preservation/collecting, as the species is rare.

7 Conclusions

The described isocrinid and cyrtocrinid fauna is a typical Tethyan crinoid association. While the studied isocrinids were already known from the Bathonian, the cyrtocrinids such as *P. stellaris*, *P. malbosianus* and *Apsidocrinus* sp. (that may belong to *A. moeschi*) are described here for the first time from the Bathonian. These are also the oldest occurrences of these genera and species. On the other hand, *P. birkenmajeri* from the Bathonian of the Hidas Valley is the youngest occurrence of this species. The herein described new species *P. hidasinus* represents the oldest occurrence of the genus *Psalidocrinus*, and possibly is an endemic species.

The described crinoid fauna most probably lived in palaeoenvironments with a water depth of 200 m or more, that were subjected to weak currents.

The oldest occurrence of most of the described crinoid species is located in the Tethyan area. Therefore their origin was suggested to be in the Tethyan region, and accordingly their migration to northern shelf areas of the Tethys occurred later, due to palaeogeographical changes and establishment of new current systems.

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