

# Crinoids from the Middle Liassic Rosso ammonitico beds

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With 6 figures and 2 tables in the text

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**Abstract:** Crinoids from the Rosso ammonitico beds of Bulgaria, Crimea and Caucasus include: *Chladocrinus basaltiformis* (MILLER) and „*Isocrinus*“ *schlumbergeri* (LORIOI) from the order Isocrinida; *Amaltheocrinus amalthei* (QUENSTEDT), Quenstedticrinidae n. fam., *Quenstedticrinus quenstedti* n. g. n. sp., Shroshaecrinidae n. fam., *Shroshaecrinus shroshaensis* n. g. n. sp. and *Cotylederma manchevi* n. sp. from the emended order Cyrtocrinida; Gutticrinidae n. fam. and *Gutticrinus guttiformis* n. g. n. sp. from the order Bourgueticrinida. Crinoid ecology bears upon the origin of the Lower Jurassic „olistoliths horizon“ in Crimea and Bulgaria.

**Key words:** Crinoidea, Articulata, Middle Liassic, taxonomy, paleoecology; Bulgaria, Crimea, Caucasus.

**Zusammenfassung:** Unter den Crinoiden des Ammonitico Rosse Bulgariens, der Krim und des Kaukasus finden sich folgende Taxa: *Chladocrinus basaltiformis* (MILLER) und „*Isocrinus*“ *schlumbergeri* (LORIOI) aus der Ordnung Isocrinida; *Amaltheocrinus amalthei* (QUENSTEDT), Quenstedticrinidae n. fam., *Quenstedticrinus quenstedti* n. g. n. sp., Shroshaecrinidae n. fam., *Shroshaecrinus shroshaensis* n. g. n. sp. and *Cotylederma manchevi* n. sp. aus der emendierten Ordnung Cyrtocrinida; Gutticrinidae n. fam. und *Gutticrinus guttiformis* n. g. n. sp., aus der Ordnung Bourgueticrinida. Die Ökologie dieser Crinoiden steht in Zusammenhang mit der Entstehung unterjurassischer Olistolith-Horizonte.

## 1. Introduction

The ammonitico rosso facies is characteristic for many Mesozoic deposits of southern Eurape. The red biogenic limestones commonly contain numerous ammonites. Such limestones occur at all levels of the Jurassic in Italy (DESIO, 1973; MARIOTTI et al., 1978), Yugoslavia (BESHICH, 1975), Czechoslovakia (ANDRUSOV, 1945), Hungary (PATAKY et al., 1982), Roumania (BĂRBULESCU, 1974), Bulgaria (KOHEN, 1938, 1946) and Turkey (PHILIPPSON, 1918). Within the U.S.S.R., ammonitico rosso facies is known from the Eastern Carpathians (SLAVIN, 1963), the Crimea and the Caucasus.

Middle Liassic ammonitico rosso rocks particularly are interesting, because they are commonly crinoidal limestones that yield a rich and peculiar crinoid complex from which many groups of Mesozoic and Cenozoic crinoids are derived.

## 2. Material

The type material for the present study is kept in the Structural and Marine Geology Section of the Leningrad Mining Institute; it comes from three localities.

1. Caucasus, South-Eastern Georgia. Large red crinoidal limestones are found in Middle Liassic vulcanogenic rocks. Such layers exposed at the outskirts of Shrosha contain a diverse Pliensbachian fauna including crinoids (Tables 1 and 2).

2. Crimea, Central Mountain part. Limestone olistoliths of 0.5 to 100 m in the middle of Taurian Formation in the Bodrak, Alma and Salgyr River valleys contain a Late Triassic, early or middle Liassic fauna (MURATOV, 1960; SHALIMOV, 1969; ASTAKHOVA, 1972). The Middle Liassic limestones are commonly crinoidal (MOISSEEV, 1925; FEDOROVICH, 1927; VASILIEVA, 1952; SOKRATOV, 1955; CHERNOV, 1981; SLAVIN et al., 1983; see Table 1). Liassic crinoids were found by the author in a pink limestone block in the Ammonitian Ravine at right bank of the Bodrak River („Bodrak-1“ in Table 2), in a yellowish-grey crinoidal limestone block on the northern slope of Patil Mountain south of Trudoliubovka, Bodrak Valley („Bodrak-2“ in Table 2) and in red biogenic limestone olistoliths near Petropavlovka south of Simferopol, Salgyr Valley („Salgyr“ in Table 2).

3. Bulgaria. Red argillaceous limestones with a rich Middle Liassic fauna are known from the sububs of Kotel, where crinoids have been found (Table 1) by T. S. MANCHEV („Kotel“ in Table 2).

## 3. Taxonomy

The order taxonomic scheme of the Pentacrinida used here corresponds to that supplemented by H. W. RASMUSSEN (1978) and KLIKUSHIN (1982).

Y. A. ARENDT's (1974) taxonomy for the order Cyrtocrinida is accepted with the suborders Cyrtocrinina SIEVERTS-DORECK, 1953 (short-stalked forms; theca consisting of radials); Holopodina ARENDT, 1974 (non-stalked forms; theca consisting of radials and an indivisible basis) and Hyocrinina RASMUSSEN, 1978 (long-stalked forms; theca consisting of radials and basals). Two superfamilies are distinguished in the latter suborder: Plicatocrinacea ZITTEL, 1879 (basal ring indivisible; three to eight radials; one or two primibrachials) and Hyocrinacea CARPENTER, 1884 (nom. transl. hic ex Hyocrinidae CARPENTER, 1884; basal ring consisting of three to five basals or indivisible; five radials; two or more primibrachials). The Plicatocrinacea include three families: Plicatocrinidae ZITTEL, 1879

Table 1. Distribution of sea-lilies in Shrosha (Caucasus), Salgyr (Crimea) and Kotel (Bulgaria) after previous investigations.

Localities	Names of species in the transcription of cited authors	References	Corrected names of species
Shrosha (Caucasus)	<i>Pentacrinus basaltiformis</i> MILLER	NEUMAYR & UHLIG (1892, p. 3) FOURNIER (1896, p. 92, 110) KUZNETSOV (1937, p. 30) MEFFERT (1941, p. 91) KAKHADZE (1947, p. 47) NUTSUBIDZE (1966, p. 9, pl. 1, fig. 8, 9) TOPCHIAHVILI (1969, p. 31) PAFFENHOLZ & MALKHASJAN (1983, p. 33)	<i>Chladocrinus basaltiformis</i> (MILLER)
	<i>Isocrinus cf. basaltiformis</i> GOLDFUSS	OSWALD (1906, p. 321)	<i>Chladocrinus basaltiformis</i> (MILLER)
	<i>Pentacrinus cf. scalaris</i> QUENSTEDT	FOURNIER (1896, p. 110) OSWALD (1906, p. 321)	<i>Chladocrinus basaltiformis</i> (MILLER)
	<i>Pentacrinus cf. scalaris</i> GOLDFUSS	NUTSUBIDZE (1966, p. 10, pl. 1, fig. 10, 11)	<i>Chladocrinus basaltiformis</i> (MILLER)
	<i>Pentacrinus subangularis</i> MILLER	NUTSUBIDZE (1966, p. 9, pl. 1, fig. 4)	<i>Seiocrinus laevisutus</i> (POMPECKJ)
	<i>Pentacrinus laevisutus</i> POMPECKJ	NUTSUBIDZE (1966, p. 7, pl. 1, fig. 1-3)	<i>Seiocrinus laevisutus</i> (POMPECKJ)
	<i>Pentacrinus goniogenos</i> POMPECKJ	NUTSUBIDZE (1966, p. 8, pl. 1, fig. 5-7)	<i>Seiocrinus laevisutus</i> (POMPECKJ)
	<i>Acrochordocrinus amalthei</i> QUENSTEDT	NEUMAYR & UHLIG (1892, p. 3) MEFFERT (1941, p. 91) KAKHADZE (1947, p. 47)	<i>Amaltheocrinus amalthei</i> (QUENSTEDT)
	<i>Acrochordocrinus cf. amalthei</i> QUENSTEDT	FOURNIER (1896, p. 110) OSWALD (1906, p. 321)	<i>Amaltheocrinus amalthei</i> (QUENSTEDT)
Salgyr (Crimea)	<i>Pentacrinus</i> sp.	MOISSEEV (1925, p. 988)	<i>Chladocrinus basaltiformis</i> (MILLER)
	<i>Millericrinus</i> sp.	MOISSEEV (1925, p. 988)	<i>Amaltheocrinus amalthei</i> (QUENSTEDT)
Kotel (Bulgaria)	<i>Pentacrinus basaltiformis</i> MILLER	BERNDT (1934, p. 67, 79, 85) BAKALOW (1942, p. 87; 1948, p. 111) NACHEV (1968, p. 193)	<i>Chladocrinus basaltiformis</i> (MILLER)
	<i>Pentacrinus basaltiformis nudus</i> QUENSTEDT	TOULA (1890, p. 329, 394; 1896, p. 287)	<i>Chladocrinus basaltiformis nudus</i> (QUENSTEDT)
	<i>Pentacrinus tuberculatus</i> MILLER	BAKALOW (1905, p. 483; 1948, p. 111)	<i>Chladocrinus basaltiformis</i> (MILLER)
	<i>Extracrinus subangularis</i> MILLER	BERNDT (1934, p. 67) NACHEV (1968, p. 193)	<i>Seiocrinus laevisutus</i> (POMPECKJ)
	<i>Extracrinus aff. subangularis</i> MILLER	BAKALOW (1905, p. 483)	<i>Seiocrinus laevisutus</i> (POMPECKJ)
	<i>Cyclocrinus aff. amalthei</i> QUENSTEDT	BERNDT (1934, p. 67)	<i>Amaltheicrinus amalthei</i> (QUENSTEDT)
	<i>Encrinus</i> sp.	KOHEN (1938, p. 7)	<i>Amaltheocrinus amalthei</i> (QUENSTEDT)

Table 2. Materials on eleven sea-lilies species from five Rosso ammonitico localities (the description of localities see in the text; the column „1“ is the collections numbers; the column „2“ is the quantity of specimens). The abbreviations (in the column „Skeleton part“) are following: C = stem fragments and columnals, B = basal rings, R = radials, IBr = primibrachials, T = thecae.

No.	Names of species	Skeleton part	Localities									Total quantity of specimens	
			Shrosha		Salgyr		Bodrak-1		Bodrak-2		Kotel		
			1	2	1	2	1	2	1	2	1		2
1	<i>Chladocrinus basaltiformis</i>	C	JB-1, 17	148	IK-29, 31	56	—	—	IK-26	77	IG-2	515	796
2	<i>„Isocrinus“ schlumbergeri</i>	C	JB-19	18	IK-31	15	—	—	—	—	—	—	33
3	<i>Seiocrinus laevisutus</i>	C	JB-3, 18	33	IK-28, 30	61	IK-3	38	IK-45	2	IG-3	5	139
4	<i>Pentacrinus ex gr. fossilis</i>	C	—	—	IK-52	10	—	—	—	—	—	—	10
5	<i>Amaltheocrinus amalthei</i>	B	JB-21	3	IK-33	1	—	—	—	—	—	—	4
		C	JB-21	121	IK-33, 34	46	IK-44	6	—	—	IG-5	8	181
6	<i>Amaltheocrinus bodrakensis</i>	C	—	—	IK-32	4	—	—	IK-17	23	—	—	27
7	<i>Quenstedticrinus quenstedti</i>	T	JB-2	6	—	—	—	—	—	—	—	—	6
		R	JB-23	61	IK-46	24	—	—	—	—	—	—	85
		IBr1	JB-24, 25	128	IK-46	49	—	—	—	—	—	—	177
		C	JB-22	150	IK-46	149	—	—	—	—	—	—	299
8	<i>Shroshaecrinus shroshaensis</i>	T	JB-26	2	—	—	—	—	—	—	—	—	2
		B	JB-26	3	IK-55	1	—	—	—	—	—	—	4
		R	JB-26	2	IK-55	2	—	—	—	—	—	—	4
		IBr1	—	—	IK-55	3	—	—	—	—	—	—	3
		C	JB-27	98	—	—	—	—	—	—	—	—	98
9	<i>Cotylederma manchevi</i>	T	—	—	—	—	—	—	—	IG-4	5	5	
10	<i>Cotylederma</i> sp.	T	JB-28	2	IK-47	1	—	—	—	—	IG-4	8	11
11	<i>Gutticrinus guttiformis</i>	T	JB-28	2	IK-47	2	—	—	—	—	—	—	4



(number of radials usually not equal to five; columnal articularia with radiating sculpture; Jurassic); Cyclocrinidae SIEVERTS-DORECK, 1953 (five unequal radials; columnal articularia with a warty sculpture in the centre; Lower Jurassic - Lower Cretaceous) and Quenstedticrinidae n. fam. (see below). The family Cyclocrinidae includes two genera: *Cyclocrinus* d'Orbigny, 1850 (= *Acrochordocrinus* TRAUTSCHOLD, 1859; non *Cyclocrinites* EICHWALD, 1840 = *Cyclocrinus* EICHWALD, 1860) (columnal articularia without peripheral radiating ribs; Middle Jurassic - Lower Cretaceous) and *Amaltheocrinus* KLIKUSHIN, 1984 (see below). Included in superfamily Hyocrinacea are: Hyocrinidae CARPENTER, 1884 (three basals; theca-column transition smooth; stem slender; columnal articularia with 6 to 7 radiating pairs of crenellae; Recent); Calamocrinidae A. M. CLARK, 1973 (nom. transl. hic ex Calamocrininae A. M. CLARK, 1973; basal ring consisting of three or five basals or rarely indivisible; theca-column transition smooth or sharp; stem with large diameter; columnal articularia with 8 or more radiating pairs of crenellae; Cretaceous - Recent) and Shroshaecrinidae n. fam. (see below).

The order Bourgueticrinida consists of five families (RASMUSSEN, 1978), namely: Bourgueticrinidae LORIOU, 1882; Bathyrcrinidae BATHER, 1899; Phrynocrinidae A. H. CLARK, 1907, Porphyrocrinidae A. M. CLARK, 1973 and Gutticrinidae n. fam.

#### 4. Taxonomic description

Class Crinoidea

Subclass Articulata MILLER, 1821

Order Pentacrinida TORTONESE, 1938

Family Isocrinidae GISLÉN, 1924

Subfamily Isocrininae GISLÉN, 1924

Genus *Chladocrinus* AGASSIZ, 1835 emend. SIEVERTS-DORECK, 1971

Type species: *Pentacrinites basaltiformis* MILLER, 1821.

Diagnosis: Two primibrachials (the second is axillar); IB1-2 junction synarthral; IIBr1-2 synarthral; IIBr2-3 muscular; IIBr3-4 synostosis. Basals small and disunited; stem proximally stellate and distally pentangular or round with nodals larger than internodals; large cirral sockets are directed outside and upwards; 5 to 20 internodals; petals lanceolar or drop-like; peripheral crenellae small but numerous.

Remarks: L. AGASSIZ, in establishing the diagnosis of *Pentacrinus*, included 17 species known by that time and noted that „on pourrait désigner sous le nom de *Chladocrinus* les espèces dont les rayons accessoires forment des verticilles plus ou moins distants“ (AGASSIZ, 1835, p. 195). Since the term „rayons accessoires“ remained ill defined, „*Chladocrinus*“ remained an invalid name until H. SIEVERTS-DORECK (1971) reestablished it, providing type species and diagnosis. Although it is disputable, whether AGASSIZ's phrase really referred to *Pentacrinus basaltiformis* and not to *P. subangularis* (type species of *Seirocrinus*; see below), whose whorls are still more parted, *Chladocrinus* AGASSIZ emend. SIEVERTS-

DORECK has now an established place in pentacrinid taxonomy (RASMUSSEN, 1978; ROUX, 1978).

Distribution: Upper Triassic - Middle Jurassic.

*Chladocrinus basaltiformis* (MILLER, 1821)

Fig. 1 A-C

1821 *Pentacrinites basaltiformis* n. sp. - MILLER, p. 62, pl. 2, fig. 1-6.

1971 *Chladocrinus basaltiformis* (MILLER). - SIEVERTS-DORECK, S. 316-317, Abb. 1,2.

Lectotype: specimen figured by J. S. MILLER (1821, pl. 2, fig. 1); Lower Jurassic, Pliensbachian of England.

**Description:** Stem pentangular, rounded-pentangular or rarely round. Columnal sides smooth, convex in proximal and straight in distal part of the stem; feebly pointed tubercles sometimes found on the interrarial corners of the small columnals; radial sutural pits common; sutures serrated proximally and smooth distally; large oval cirral sockets occupying the whole nodal height plus lower supranodal and upper infranodal margins; sockets slightly deepened in pentangular (proximal) nodals and strongly deepened in roundet (distal) ones; cirral canal and fulcral ridge situated above socket centre; 13 to 18 internodals (among 20 complete internodes there was one with 13 internodals, nine with 14, four with 15, one with 16, four with 17 and one with 18); the drop-like articular petals surrounded by crenellae, the largest of which are situated on the periphery-radius transition.

**Dimensions** (in mm): stem diameters 3.2 to 6.8 in Crimea, 3.5 to 9.7 in the Caucasus and 3.8 to 10.4 in Bulgaria; columnal height 1.0 to 2.0.

**Remarks:** All available stem fragments have smooth external surfaces, corresponding to the subspecies *Chladocrinus basaltiformis nudus* (QUENSTEDT, 1852) (= *Pentacrinus nudus* SCHLÖNBACH, 1863). The transversal row of small granules is characteristic for columnal of *Ch. basaltiformis*.

In addition to *Ch. basaltiformis*, other species of *Chladocrinus* have been mentioned from Middle Liassic ammonitico rosso beds: *Ch. tuberculatus* (MILLER), noted from the Kotel region (BAKALOW, 1905), is a Lower Sinemurian form (mainly *Caenites turneri* zone), while *Ch. jurensis* (QUENSTEDT), discovered in Italy (MENEGHINI, 1881), is characteristic for the Upper Toarcian. The occurrence of *Ch. cf. scalaris* (GOLDFUSS) in the Shroshian limestone would agree with the known stratigraphic range of this species. But none of the stem fragments in our material or in the literatures (NUTSUBIDZE, 1966) are comparable with *Ch. scalaris* (GOLDFUSS, 1833, pl. 52, fig. 3). In most probability we deal with only one, but very variable species, namely *Ch. basaltiformis*.

**Distribution:** Lower Jurassic, Pliensbachian (mainly *Amaltheus margaritatus* zone) of Portugal, Spain, England, Sweden, France, Switzerland, Italy, Germany, Bulgaria and Turkey. Inside the U.S.S.R., the species is known from Crimea and the Caucasus in deposits of the same age. A similar form was noted in the Liassic of the Soviet North-East (TUCHKOV,

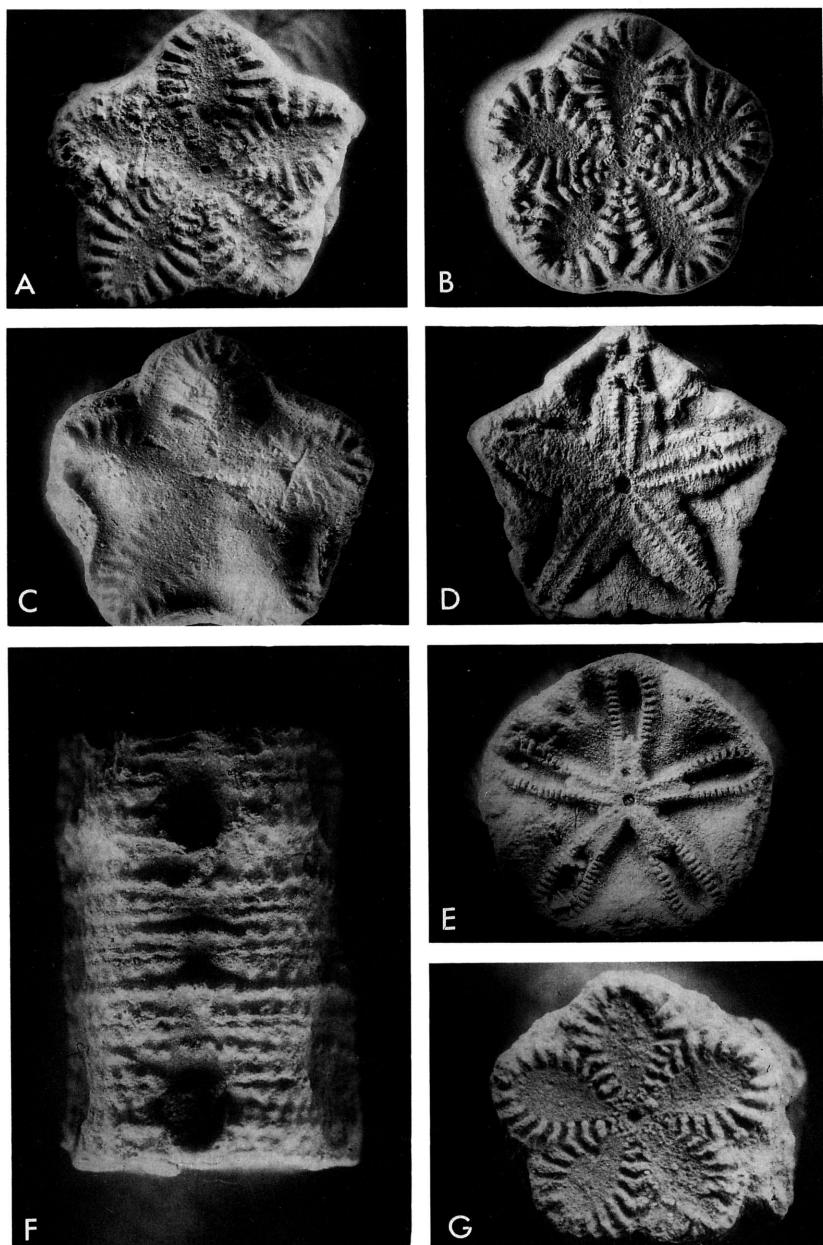


Fig. 1. A-C = *Chladocrinus basaltiformis* (A = JB-1-1, the articulum of a proximal columnal, x 5; B = JB-17-2, the articulum of a columnal from the middle stem part, x 5; C = JB-17-3, the upper articulum of an infranodal, x 5). D, E = *Seirocrinus laevisutus* (D = JB-18-2, the articulum of a proximal columnal, x 4; E = IG-3-1, the articulum of a distal columnal, x 4). F, G = „*Isocrinus*“ *schlumbergeri* (F = JB-19-1, the stem fragment with two nodals, x 12; G = JB-19-2, the articulum of a columnal, x 12).

1946, 1962; VORONOV & CHEREPANOV, 1953; SAKS et al., 1959; PARAKETSOV & POLUBOTKO, 1970; TUCHKOV et al., 1972).

Material: 796 stem fragments (see Table 2).

Genus *Isocrinus* MEYER in AGASSIZ, 1835

„*Isocrinus*“ *schlumbergeri* (LORIOI, 1886)

Fig. 1 F, G

1884-1889 *Pentacrinus schlumbergeri* n. sp. - LORIOI, p. 100, pl. 141, fig. 8-10.

Lectotype: specimen figured by P. DE LORIOI (1884-1889, pl. 141, fig. 8); Lower Jurassic, Pliensbachian of France.

Description: Stem pentangular or rarely stellate; columnal sides straight; transversal ridge bearing small granules in the middle of each columnal; rows of small tubercles also along lower and upper columnal margins; sutures crenellated; nodals larger than internodals; small round cirral sockets placed near the upper nodal margin, are directed outwards and not deepened; cirral canal and fulcral ridge placed in the centre of socket; only 2 to 4 internodals; lanceolar articular petals surrounded by short crenellae; some forked crenellae placed in the radial zones.

Dimensions (in mm): stem diameter 2.2 to 3.9; columnal height about 1.0.

Distribution: Lower Jurassic, Pliensbachian of France, Crimea and Caucasus.

Material: 33 stem fragments (see Table 2).

Family Pentacrinidae GRAY, 1842

Genus *Seiocrinus* GISLÉN, 1924

Type species: *Pentacrinites subangularis* MILLER, 1821.

Diagnosis: Two primibrachials, the second being axillar. Radials have shoots directed downwards along the stem. The stem is pentangular or rounded and very long (up to 20 m) and consists of columnals of several orders, which differ strongly in height but have almost constant diameters; short cirri pressed to the stem in an upward direction; internodals numerous. Petals narrow, groove-like or drop-like and surrounded by numerous small crenellae, with wide radial triangles being situated between the petals.

Remarks: AUSTIN & AUSTIN (1846) had established the genus *Extracrinus* for pentacrinids with repeatedly branching arms. Later F. A. BATHER (1898) has shown that the type species (*Pentacrinites briareus* MILLER, 1821) was a synonym of the *Pentacrinus*' type species (*Pentacrinites fossilis* BLUMENBACH, 1804) since both were based on the same specimen. P. DE LORIOI (1884-1889), however, considering *Extracrinus* as an independent genus, subdivided it into two groups: the *E. briareus* group (i. e. *Pentacrinus* s. s. according to the present view) and the *E. subangularis* group. T. GISLÉN (1924) established the genus *Seiocrinus* for the latter.

The species of the genus could be divided into two groups according to columnal articulum patterns. In the first group there are drop-like petals and radial triangles ornamented by tubercles or ribs; in the second, the petals are groove-like and the triangles are smooth. To the first group one can attribute four Middle

Liassic species: *S. acutipelvis* (QUENSTEDT, 1876); *S. colligatus* (QUENSTEDT, 1852); *S. biemeri* (KOENIG, 1825 emend. QUENSTEDT, 1876) and *S. subangularis* (MILLIER, 1821) (= *Pentacrinites bollensis* SCHLOTHEIM, 1813 nom. nud.; = *Pentacrinites fasciculosus* SCHLOTHEIM, 1813 nom. nud.; = *Pentacrinites lepidotus* AUSTIN & AUSTIN, 1842; = *Pentacrinites briaroides* QUENSTEDT, 1852) and one Norian species, namely *S. alaska* (SPRINGER, 1925). Only one Middle Liassic species — *S. laevisutus* (POMPECKJ, 1897) — may be attributed to the second group. It is known only from the Mediterranean province (see below), while all members of the first group are northern (North America, England, France, Switzerland, Germany). *S. subangularis* and *S. alaska* range to the North-East and Far East of the U.S.S.R.

Distribution: Upper Triassic — Lower (?Middle) Jurassic.

*Seiocrinus laevisutus* (POMPECKJ, 1897)

Fig. 1 D, E, 6

\* 1897 *Pentacrinus* (*Extracrinus*) *laevisutus* n. sp. — POMPECKJ, S. 718, Taf. 30, Fig. 1-15, Taf. 31, Fig. 1.

1897 *Pentacrinus* (*Extracrinus*) *goniogenos* n. sp. — POMPECKJ, S. 724, Taf. 30, Fig. 16-22.

1913 *Pentacrinus laevisutus* POMPECKJ — VADÁSZ, S. 64, Abb. 1-5.

1918 *Pentacrinus rotiensis* n. sp. — SPRINGER, p. 3, pl. 1, fig. 1,2.

1937 *Pentacrinus pompeckji* n. nom. — BIESE, S. 267.

Lectotype: specimen figured by J. F. POMPECKJ (1897, Taf. 30, Fig. 1); Lower Jurassic, Pliensbachian of Turkey.

Description: The stem is proximally pentagonal, rounded-pentagonal and becomes rarely round in distal sections of the stem. The columnals are of variable height. Columnals of the first and second orders reach the greatest height radially, while those of the third and fourth orders are thickest in the interradian sectors and often do not reach the external stem surface in the radial sectors. Columnal sides are smooth, flat or rarely convex. Feeble roundet knobs are sometimes developed on the interradian faces of large columnals. Nodals are equal to the columnals of the first and second orders in size. Small slit-like cirral sockets are considerably deepened and extend from the lower to the upper margin of the nodal. In the proximal stem part, cirri were fitted into deep furrows extending from the sockets upwards. Distally these furrows are less pronounced. Internodal numbers increase from zero (near the theca) to some dozens distally. Articular petals are narrow, slit-like; they slightly widen towards the periphery and are lined by a narrow, but high row of tiny teeth. The radial triangles are convex, smooth and sometimes slightly rough.

Dimensions (in mm): stem diameters 3.7 to 14.2 (Crimea), 5.7 to 12.5 (Caucasus) and 7.5 to 13.5 (Bulgaria); columnal height up to 6.5.

Remarks: *Pentacrinus goniogenos* represents proximal stem parts of *S. laevisutus*. *P. rotiensis* is analogous to *P. goniogenos* (i.e. = *S. laevisutus*). P. DE LORIO (1884-1889) had described the species *Pentacrinus levisutus* (= *Chladocrinus*?) before J. F. POMPECKJ (1897) described *Pentacrinus laevisutus* (= *Seiocrinus*).

nus). W. BIESE (1937) renamed the latter as „*P. pompeckji*“, which was unnecessary because LORIOLO's and POMPECKJ's species belong to different genera.

The so-called „*Pentacrinus* (or *Extracrinus*) *subangularis*“ (“cf. *subangularis*“ or „aff. *subangularis*“) with smooth radial triangles from Portugal (LORIOLO, 1890-1891), from Bulgaria (BAKALOW, 1905; BERNDT, 1934; NACHEV, 1968) and from Caucasus (NUTSUBIDZE, 1966) belong to this species.

Distribution: Lower Jurassic, Pliensbachian (the *Amaltheus margaritatus* zone mainly) of Portugal, Roumania, Bulgaria, Turkey, Crimea, Caucasus and Indonesia.

Material: 139 stem fragments (see Table 2).

Order Cyrtocrinida SIEVERTS-DORECK, 1953

Suborder Hyocrinina RASMUSSEN, 1978

Superfamily Plicatocrinacea ZITTEL, 1879

Family Cyclocrinidae SIEVERTS-DORECK, 1953

Genus *Amaltheocrinus* KLIKUSHIN, 1984

Type species: *Apiocrinites amalthei* QUENSTEDT, 1852.

Diagnosis: Columnal articular covered by radiating ridges in the periphery and by weak knobs, short ridges or ringlets in the central part.

Distribution: Lower Jurassic.

### *Amaltheocrinus amalthei* (QUENSTEDT, 1852)

Fig. 2 A-D, 3 A-C

\* 1852 *Apiocrinites amalthei* n. sp. — QUENSTEDT, S. 612, Taf. 53, Fig. 25-28 (non Fig. 29-31 = *Quenstedticrinus quenstedti* n. g., n. sp.).

1858 *Mespilocrinites amalthei* QUENSTEDT. — QUENSTEDT, s. 198, Taf. 24, Fig. 38-40 and 41 (basal ring) (non Fig. 41 upper part = *Quenstedticrinus quenstedti* n. g., n. sp.).

1876 *Apiocrinus amalthei* QUENSTEDT. — QUENSTEDT, S. 373, Taf. 104, Fig. 88-100, 105s (basal ring) (non Fig. 101-104, 105 upper part, 106-110 = *Quenstedticrinus quenstedti* n. g. n. sp.).

1884-1889 *Cyclocrinus amalthei* QUENSTEDT. — LORIOLO, p. 4, pl. 122, fig. 1-23.

1892 *Acrochordocrinus amalthei* QUENSTEDT. — NEUMAYR & UHLIG, S. 3.

1936 *Millericrinus amalthei* QUENSTEDT. — KUHN, S. 239, Taf. 9, Fig. 14, 16.

1958 *Cyclocrinus amalthei* (QUENSTEDT). — SIEVERTS-DORECK, S. 445 and copies of QUENSTEDT's figures.

1984 *Amaltheocrinus amalthei* (QUENSTEDT). — KLIKUSHIN, p. 79.

Lectotype: specimen figured by F. A. QUENSTEDT (1852, Taf. 53, Fig. 27 and 1858, Taf. 24, Fig. 40); Lower Jurassic (Pliensbachian) of Germany.

Description: The basal ring is fairly low with a smooth and convex external surface. The base of this ring is round, flat and smooth. There are five depressions for the rasials on the upper side of the basal ring. These depressions are separated by several sharp ridges extending from the axial canal to the periphery. The small axial canal has a pentagonal outline (the angles are interradian). The first columnal is high, bulbous and enlarged upwards. Other columnals are high, smooth and sometimes slightly curved. Articular of the small proximal columnals are ornamented by a few, coarse, irregularly situated radiating ridges. One notices short radiating ridges at the periphery and sparse ring-like ridges or tubercu-

les in the middle of articula of the larger proximal columnals. Articula of the larger distal columnals are covered by irregular, often interrupted radial ridges. The axial canal is round. The root has a crust-like form.

Dimensions: basal ring 3.0 to 8.6 mm in diameter, 0.6 to 4.6 mm high; stem diameter 2.1 to 9.5 mm; columnal height (without the proximal one) 1.0 to 6.5 mm.

Remarks: Some authors (SCHLÖNBACH, 1863 and others) considered *Amaltheocrinus amalthei* (QUENSTEDT, 1852) as a synonym of *A. hausmanni* (RÖMER, 1836).

*A. amalthei* is often found together with *Quenstedticrinus quenstedti* n. g. n. sp. (see below). Therefore F. A. QUENSTEDT (1852, 1858) erroneously combined both forms into one reconstruction. He placed the first and second primibrachials of the present *Q. quenstedti* on the enclosed basal ring (considering it radial) of *A. amalthei*. Then he placed two radials of *Q. quenstedti* on the second (axillar) primibrachials of the same species. Later (QUENSTEDT, 1876) he made another and again incorrect reconstruction: he placed the radials and then the primibrachials of *Q. quenstedti* on the basal ring of *A. amalthei*. H. SIEVERTS-DÖRCK (1958) rightly delimited QUENSTEDT's reconstructions, having found a resemblance between the radials and primibrachials figured by him and *Eugeniocrinus deslangchampsii* LORIOU (= *Quenstedticrinus*). She erroneously attributed QUENSTEDT's and LORIOU's forms to the genus *Eudesicrinus*, whose theca is attached with its basis whereas *Quenstedticrinus* had a long stem.

*A. bodrakensis* KLIKUSHIN, from the Upper Sinemurian limestones of Crimea (see „Bodrak-2“ in Table 2), older than *A. amalthei* and has only radial ridges without supplementary sculptures near the axial canal on the articula.

Distribution: Lower Jurassic, Pliensbachian (mainly *Amaltheus margaritatus* zone) of Italy, France, Switzerland, Germany, Bulgaria, Crimea and Caucasus.

Material: 8 basal rings, 181 stem fragments and columnals (see Table 2).

#### Family Quenstedticrinidae n. fam.

Diagnosis: The basals form a small merged ring placed within the radial ring. There are five large divided radials and two primibrachials (the second is axillar).

Comparison: This family differs from the Plicatocrinidae by having a five-rayed theca, a hidden basal ring and two primibrachials, and from the Cyclocrinidae by the symmetrical theca and a hidden basal ring.

Composition: One genus *Quenstedticrinus* n. g.

Distribution: Lower Jurassic.

#### Genus *Quenstedticrinus* n. g.

Type species: *Quenstedticrinus quenstedti* n. g. n. sp.

Diagnosis: Theca wide and conical; radials equal or slightly different; IBr1-2 junction synostosomal; stem depression deep; columnals cylindrical, with irregular radiating ridges on the articular faces.

Composition: Four species: *Q. deslangchampsii* (LORIOU, 1882 sub *Eugeniocrinus*) and *Q. marginatus* (ORBIGNY, 1840 sub *Millericrinus*) from the Pliensbachian of France; *Q.?*

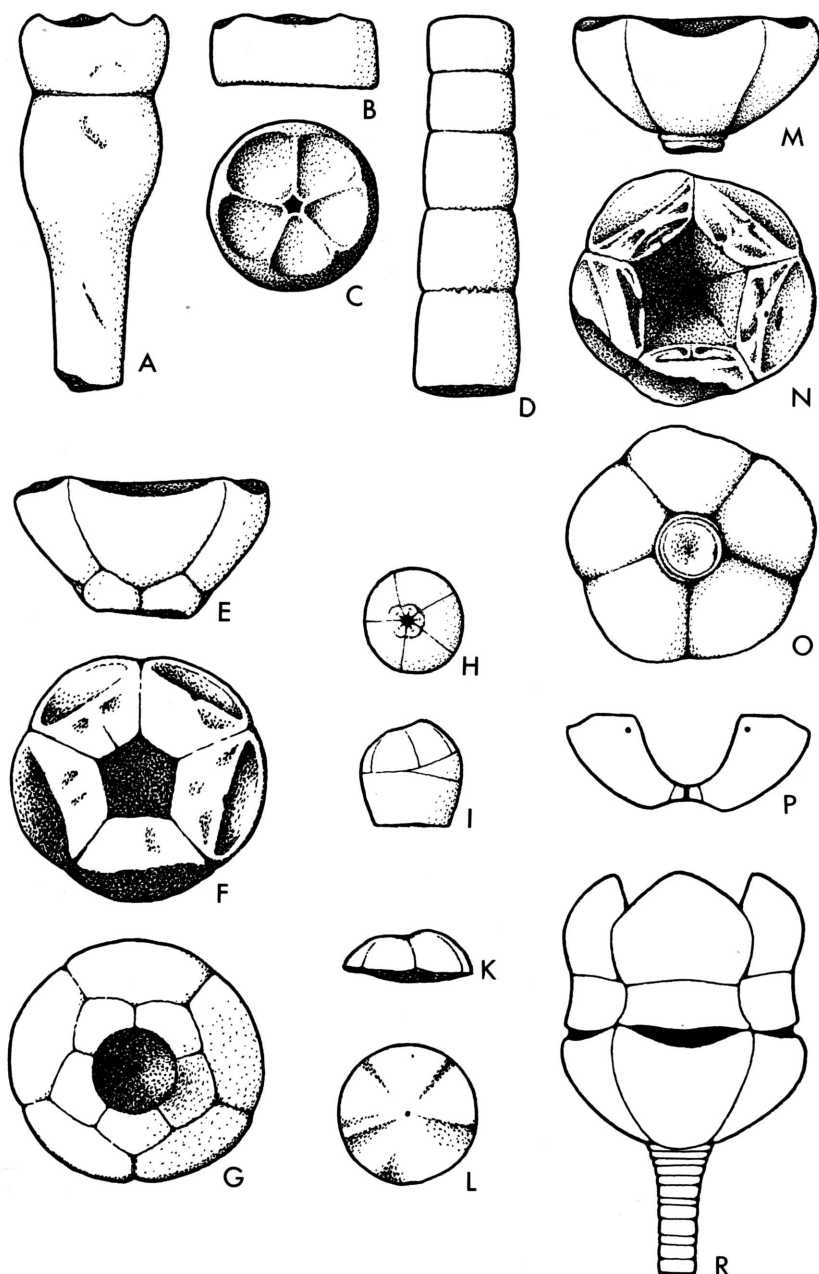


Fig. 2. A-D = *Amaltheocrinus amalthei* (A = JB-21-1, the basal ring with the first columnal; B = JB-21-3, the basal ring from one side; C = the same specimen from above; D = JB-21-4, the stem fragment). E-G = the holotype JB-26-1 of *Shroshaecrinus shroshaensis*, the



*liasinus* (QUENSTEDT, 1852 sub *Plicatocrinus*) from the Pliensbachian of Germany; *Q. quenstedti* n. sp. from the Pliensbachian of Germany, Crimea and Caucasus.

Remarks: *Q. deslongchampsii* is known from thecae and primibrachials, while *Q. marginatus* is based on stems. Since both were found in beds of the same age and from the same locality (LORIO, 1882-1884), one may suppose that they represent a single species. Attribution of „*Plicatocrinus*“ *liasinus* to the present genus is uncertain, since its theca had a slightly asymmetrical construction (QUENSTEDT, 1876). However the presence of a stem depression does not permit to attribute it to the Holopodina, as proposed by Y. A. ARENDT (1974).

Distribution: Lower Jurassic.

*Quenstedticrinus quenstedti* n. sp.

Fig. 2 M-R, Fig. 3 D-H

1852 *Apiocrinites amalthei* n. sp. — QUENSTEDT (pars), S. 612, Taf. 53, Fig. 29-31.

1858 *Mespilocrinites amalthei* QUENSTEDT. — QUENSTEDT (pars), S. 198, Taf. 24, Fig. 41 upper part.

1876 *Apiocrinus amalthei* QUENSTEDT. — QUENSTEDT (pars), S. 373, Taf. 104, Fig. 101-104, 105 upper part, 106-110.

1958 *Eudesicrinus* n. sp. — SIEVERTS-DORECK, S. 442.

See also synonymy for *Amaltheocrinus amalthei*.

The species is named in honour of FRIEDRICH AUGUST QUENSTEDT (1809-1899), a German stratigrapher and paleontologist.

Holotype: theca No. JB-2-1 (Leningrad Mining Institute), fig. 2 M-O.

Type locality: Southern Caucasus, South-Eastern Georgia, settl. Shrosha.

Type bed: Lower Jurassic, Upper Pliensbachian, *Amaltheus margaritatus* zone.

Description: The basal ring forms the bottom of the dorsal cup, being covered from below by the first columnal. The radials are large and convex. They have a triangular outline on the external theca surface and lean upon the first columnal with their lower slightly cut angles. The radial external surface is smooth and rarely covered by indistinct granules or irregular tubercles. The upper radial faces are horizontal and have obvious muscular construction. The cup cavity on the upper radial margin level measures one third of the thecal diameter. The first primibrachial is muscular below (towards the radial) and synostiosal above (towards the second primibrachial). The synostiosal face is smooth, with hardly visible ribbing near the outer margin. The external surface of IBr1 is convex, smooth or rarely granulated, while its side faces have flat parts where these plates were laterally adjoined to each other. The IBr2 is axillar, with a synostiosal lower face (towards a IBr1), while the upper side bears two muscular faces for the se-

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theca (E = from one side, F = from above, G = from below). H - L = *Gutticrinus guttiformis* (H = the holotype JB-28-1, the theca from above; I = the same specimen from one side; K = IK-47-1, the radial ring from one side; L = the same specimen from below). M - R = *Quenstedticrinus quenstedti* (M = the holotype JB-2-1, the theca from one side; N = the same specimen from above; O = from below; P = a schematic section through a basal ring and two adjacent radials; R = a reconstruction of the theca with the closed primibrachials). All the figures are given in 2.5 magnification.

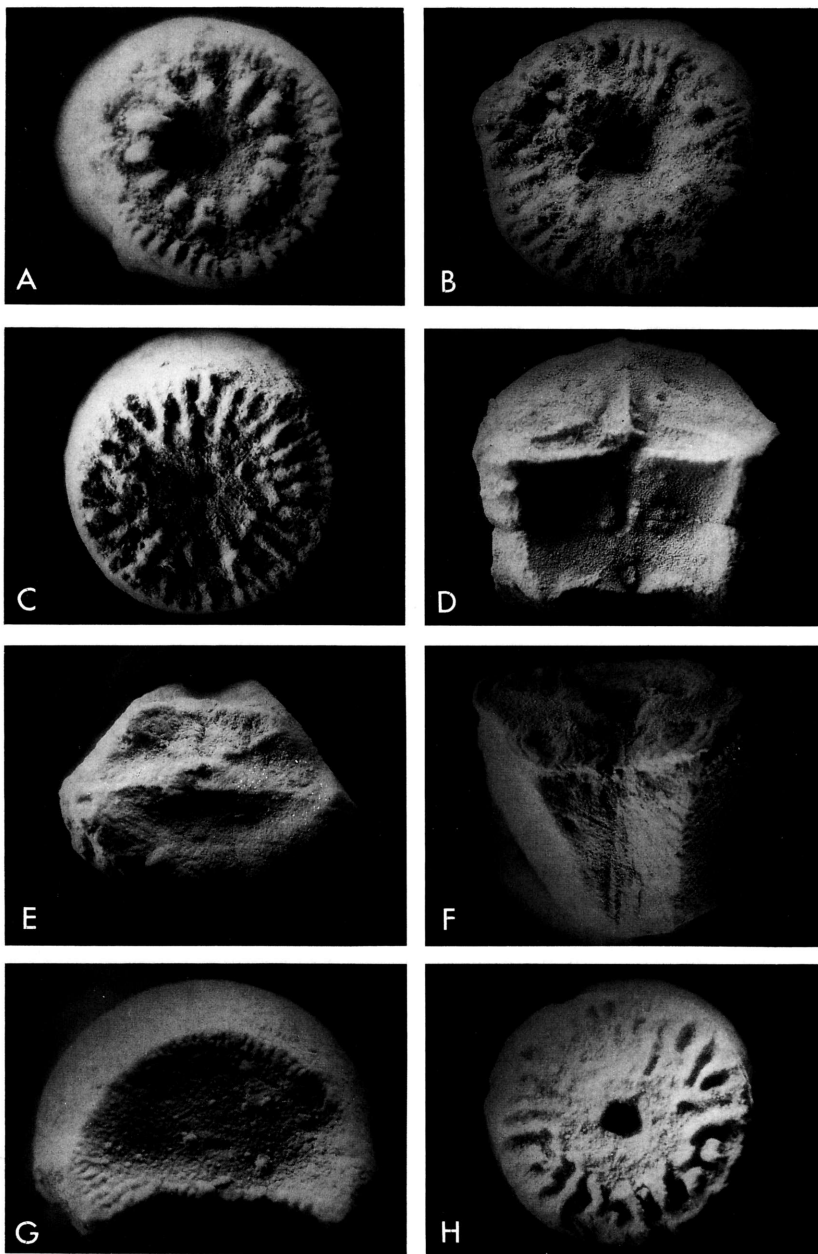


Fig. 3. A - C = *Amaltheocrinus amalthei* (A = JB-21-7, the articulum of a proximal columnal, x 10; B = JB-21-5, the articulum of a columnal from the middle stem part, x 9; C = JB-21-6, the articulum of a distal columnal, x 7). D - H = *Quenstedticrinus quenstedti* (D = JB-25-1, the first and the second primibrachials from inside, x 7; E = JB-23-4, the radial from above, x 8; F = JB-23-3, the radial from inside, x 8; G = JB-25-2, the lower articulum of a second primibrachial, x 8; H = JB-22-1, the articulum of a proximal columnal, x 11).

cond brachials. These upper muscular faces are directed upwards in small specimens and obliquely into the theca in larger ones. The external surface of IBr2 is strongly convex, smooth or rarely weakly granulated, in contrast to the flat side faces. The stem is round, with columnals having different heights and diameters and convex or smooth external surface near the theca, where the sutures are denticulated. Distally columnals become cylindrical with equal heights and smooth sutures. The radiating ridges on the articular reach to the periphery (proximally) or cover nearly the whole joint face (distally) and are bent, forked, fused and pass at unequal distances. The axial canal is narrow and round. The root has an irregular cylindrical form.

Dimensions (in mm): theca with an upper diameter of 10.6 to 12.8 and a height of 3.8 to 5.0; upper width of the radial is 4.5 to 8.9; height is 3.8 to 7.1; IBr1 width 4.7 to 8.2 and height 2.5 to 3.6; IBr2 width 4.8 to 9.1 and height 2.9 to 6.4; stem diameter 2.4 to 5.5, columnals height up to 3.8.

Comparison: This species differs from *Q. marginatus* by smaller size and relatively lower columnals. It also differs from *Q. deslongchampsii* by greater size and a considerable convexity of the radial and primibrachial plates, and from *Q. ? lia-sinus* by greater size and a symmetrical theca.

Distribution: Lower Jurassic, Pliensbachian of Germany, Crimea and Caucasus.

Material: 6 thecae, 85 radials, 177 primibrachials and 299 stem fragments and columnals (see Table 2).

#### Superfamily Hyocrinacea CARPENTER, 1884

##### Family Shroshaecrinidae n. fam.

Diagnosis: Theca wide and conical with 5 basals and 5 radials, in which muscular facets occupy nearly all upper faces. The number of the primibrachials is unknown (two?). The stem depression is deep. The columnals are cylindrical, relatively low and ornamented by some regularly radiating ribbing on the articular. The stem-theca transition is morphologically accentuated.

Comparison: This family differs from the Hyocrinidae by having five basals and a sharp separation of stem and theca. It differs from Calamocrinidae and Hyocrinidae by wider muscular facets on the upper radial sides and coarse articular ribbing.

Composition: One genus, *Shroshaecrinus* n. g.

Distribution: Lower Jurassic.

##### Genus *Shroshaecrinus* n. g.

Type species: *Shroshaecrinus shroshaensis* n. sp.

Diagnosis: See the family diagnosis.

Remarks: *Shroshaecrinus* resembles *Orbignycrinus* BIESE, 1935 and other genera of the order Millericrinida, but differs from them by lacking an enlarged proximal stem joint as a basis for the theca. In *Shroshaecrinus* this basis is a concave stem facet and its very thin proximal columnals do not take part in the theca construction.

Composition: Only the type species.

Distribution: Lower Jurassic.

*Shroshaecrinus shroshaensis* n. sp.

Fig. 2 E-G, Fig. 4 A-E

The species has been named after the type locality.

Holotype: theca No. JB-26-1 (Leningrad Mining Institute), Fig. 2 E-G.

Type locality: village Shrosha, Southern Caucasus, South-Eastern Georgia.

Type bed: Lower Jurassic, Upper Pliensbachian, *Amaltheus margaritatus* zone.

**Description:** The theca is smooth or finely granulated. The basals are pentagonal, but sometimes have a rather irregular outline and are slightly convex in small specimens and flat in larger ones. The basis of the basal ring is horizontal and round or slightly oval. The stem depression is shallow in small specimens and deep in larger ones. The radials are pentagonal and rather convex. The upper radial faces are horizontal and have a strongly pronounced muscular articulation. The cup cavity diameter on the upper radial margin level is equal to a quarter of the theca diameter. The stem is round or slightly oval in its upper part, with a smooth external surface. Columnals are thin, with varying heights near the theca. They are monotonous and do not become higher in the lower part of the stem. The columnal articulation bears on the periphery short, but coarse radiating ribs separated from the margin by a narrow smooth border, while a five-rayed symmetry is expressed on the articulation of the most proximal columnals by the presence of five longer ribs corresponding to the interbasal sutures. The stem axial canal is round and narrow. The root is crust-like.

**Dimensions** (in mm): upper theca diameter 11.9 to 13.0; theca height 7.2 to 8.5; upper width of the radials about 7.0, height about 5.0; upper diameter of the basal ring 4.7 to 9.5; stem diameter 2.0 to 4.2; columnal height up to 3.0.

**Distribution:** Lower Jurassic, Pliensbachian of Caucasus.

**Material:** two thecae, 4 basal rings, 4 radials, 3 primibrachials and 98 stem fragments and columnals (see Table 2).

Suborder Holopodina ARENDT, 1974  
Superfamily Holopodacea ROEMER, 1856  
Family Eudesicrinidae BATHER, 1899

Genus *Cotylederma* QUENSTEDT, 1852*Cotylederma manchevi* n. sp.

Fig. 4F

The species has been named in honour of TRUDOLIUB STEFANOV MANCHEV, a Bulgarian geologist.

Holotype: theca No. IG-4-1 (Leningrad Mining Institute), Fig. 4 F.

Type locality: Kotel, North-Eastern Bulgaria.

Type bed: Pliensbachian, Lower Jurassic.

**Description:** The theca is irregular and conical, with the basis being much more slender than the top. Accordingly, the cup cavity is wide and funnel-shaped, with unknown radial construction. The external surface of the theca is smooth, but sometimes shows weak concentric growth lines. Extremely fine

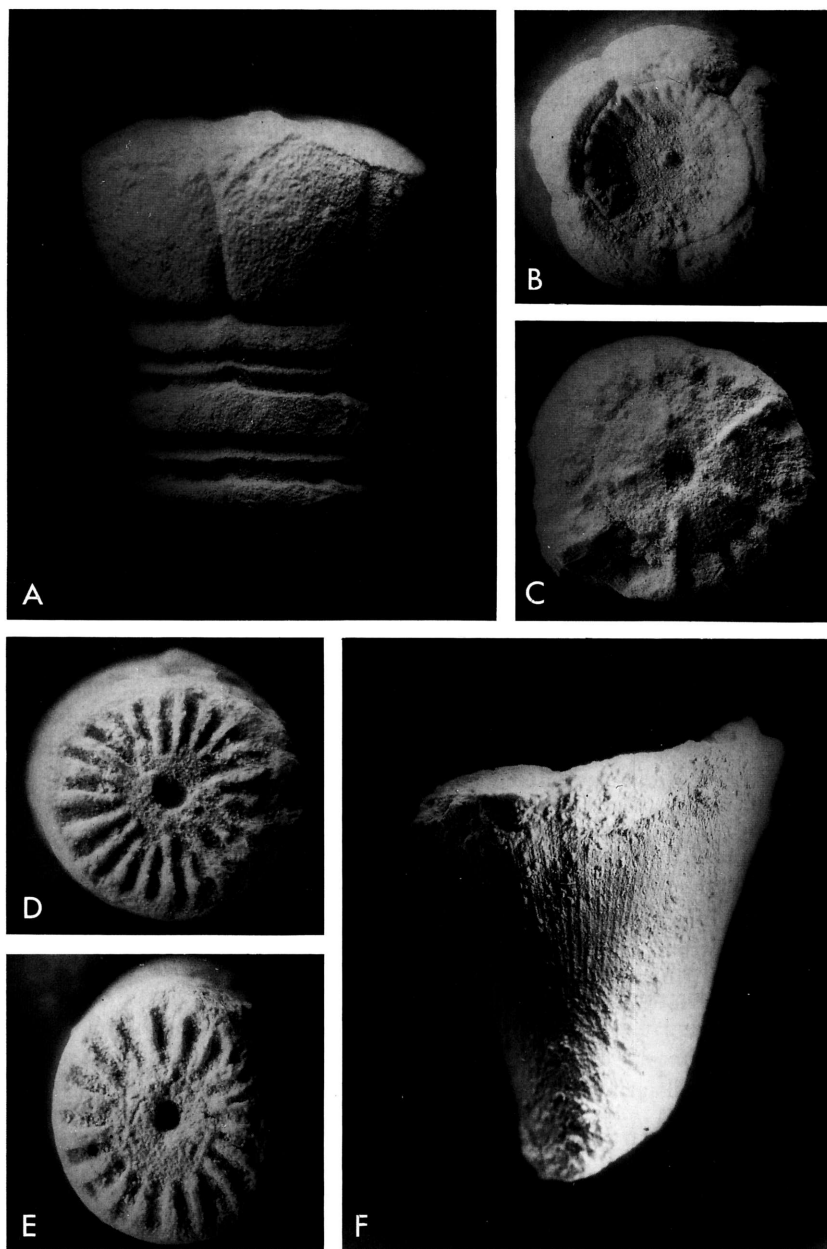


Fig. 4. A- E = *Shroshaecrinus shroshaensis* (A = JB-26-3, the basal ring on the proximal stem fragment, x 9; B = JB-26-4, the basal ring with the first columnal from below, x 7; C = JB-27-1, the articularium of a proximal columnal, x 12; D = JB-27-2, the articularium of a columnal, x 11; E = JB-27-3, the same, x 11). F = the holotype of *Cotylederma manchevi* IG-4-1, the theca, x 5.

vertical hatching is observed on some specimens. The attaching disc is small and flattened.

Dimensions (in mm): upper theca diameter 6.4 to 19.1; lower theca diameter 3.0 to 5.7; thecal height without radials 11.6 to 17.5.

Comparison: The new species resembles *C. miliaris* DESLONGCHAMPS & DESLONGCHAMPS from the Middle Liassic of France, but differs from it by having smooth external surfaces and a more regularly conical theca.

Remarks: On large pentacrinid stem fragments several other settling places of *Cotylederma* sp. have been found (see Table 2), but due to their fragmentary nature, they have not been specifically determined. *Cotylederma* sp. was also found in the Rosso ammonitico of Turkey (VADASZ, 1913).

Distribution: Lower Jurassic, Pliensbachian of Bulgaria.

Material: 5 thecae (see Table 2).

#### Order Bourgueticrinida SIEVERTS-DORECK, 1953

##### Family Gutticrinidae n. fam.

Diagnosis: The theca is drop-like or ball-shaped and consists of radials and a proximal. The radial facettes are very small. The stem is round or slightly elliptical in cross section. Columnal articula are covered by weak radiating ribs near their periphery.

Comparison: This family differs from Bourgueticrinidae and Bathycrinidae by articula with radial ribbing and from all other families of the order by the absence of a basal ring.

Composition: One genus, *Gutticrinus* n. g.

Distribution: Lower Jurassic.

##### Genus *Gutticrinus* n. g.

Type species: *Gutticrinus guttiformis* n. g., n. sp.

Diagnosis: See the family diagnosis.

Remarks: Radially ribbed articula are known in the proximal stem part of Recent Porphyrocrinidae (ROUX, 1977). This ribbing can be the primitive articulum construction type for the order Bourgueticrinida.

Composition: The type species only.

Distribution: Lower Jurassic.

##### *Gutticrinus guttiformis* n. sp.

Fig. 2 H-L

The species name has been derived from „gutta“ (Latin) = drop.

Holotype: theca No. JB-28-1 (Leningrad Mining Institute), Fig. 2 H, I.

Type locality: village Shrosha, Southern Caucasus, South-Eastern Georgia.

Type bed: Lower Jurassic, Upper Pliensbachian, *Amaltheus margaritatus* zone.

Description: The theca is drop-like, widening upwards, with a rounded upper part and a smooth external surface. The triangular radials are large with slightly unequal sizes and narrow upwards. The radial cavity is very narrow and pentagonal (with radial angles). Small upper radial facettes form the pentalobate ring; they are muscular with a weak filcral ridge. The base of each radial is slightly

curved downwards. The radial ring base is convex. The proximal narrows downwards. The proximal base is horizontal, nearly oval and concave. Several weak, short radiating ribs go towards the periphery and are separated by sizeable intervals seen on the lower proximal face. The axial canal is round and very narrow, with rare tubercles being placed around it. The stem has not been identified.

**Dimensions** (in mm): greatest theca diameter 5.2 to 6.7; proximal base diameter 3.8 to 4.4; diameter of the upper radial facettes ring (in the holotype) 1.8; theca height 5.3 to 5.7.

**Remarks:** Remains of this species were found together with those of *Q. quenstedti* and *S. shroshaensis*. Stem construction is similar in all three forms, which makes their identification difficult. *Millericrinus* sp. from Crimea (MOISEEV, 1925) and *Encrinus* sp. from Kotel (KOHEN, 1938) are possible stem groups.

**Distribution:** Lower Jurassic, Plensbachian of Crimea and Caucasus.

**Material:** 4 thecae (see Table 2).

## 5. Paleobiogeography and paleoecology

Crinoid faunas of the Middle Liassic Ammonitico Rosso are surprisingly similar in all known regions, including three main ecological elements, namely: temporarily attached stalked Isocrinidae, firmly attached stalked Hyocrinina and encrusting unstalked Holopodina (Fig. 5).

There are, nevertheless, regional differences. *Chladocrinus*, for example, is prevalent in most localities known to us (see Table 2) and in many sections of Southern European countries, but has not been found in the „Bodrak-1“ locality. Other pentacrinids are rare everywhere, while *Seiocrinus* dominates in „Bodrak-1“. The remains of this crinoid genus are also the main component of Middle Liassic crinoidal limestone in Northern Turkey (POMPECKJ, 1897; VADASZ, 1913). Hyocrinina form minor elements in most faunas, but as common as other groups in Georgia and some Crimean localities.

It is necessary to note that the crinoid complex under discussion developed in northern regions, where ammonitico rosso facies is not found (Central France, Northern Switzerland, Germany etc.) and where forms absent in the Rosso ammonitico (e. g. various species of the genus *Terocrinus*) are also associated.

Isocrinids are represented in Middle Liassic biocoenoses mainly by the large genus *Chladocrinus*, whose stems reach 1 to 2 metres in length and more than 10 mm in diameter. Cirri in this genus are widely spaced and small in comparison with the stem. The following ecological model would account for this: the distal stem part lay on the bottom attaching itself by cirri, while proximal parts of it raised vertically, elevating the crown into the upper near-bottom water layers, most favourable for getting foot (fourth tier in Fig. 5), in which *Chladocrinus* had no rivals. Therefore the *Chladocrinus* remains prevale (mass-wise) in almost all localities.

In contrast, „*Isocrinus*“ *schlumbergeri* had a slender (2 to 4 mm) and short stem. Its cirri were closely spaced and very long in relation to stem diameter. This crinoid sat on a „pillow“ of cirri anchored to hard objects on the bottom, while

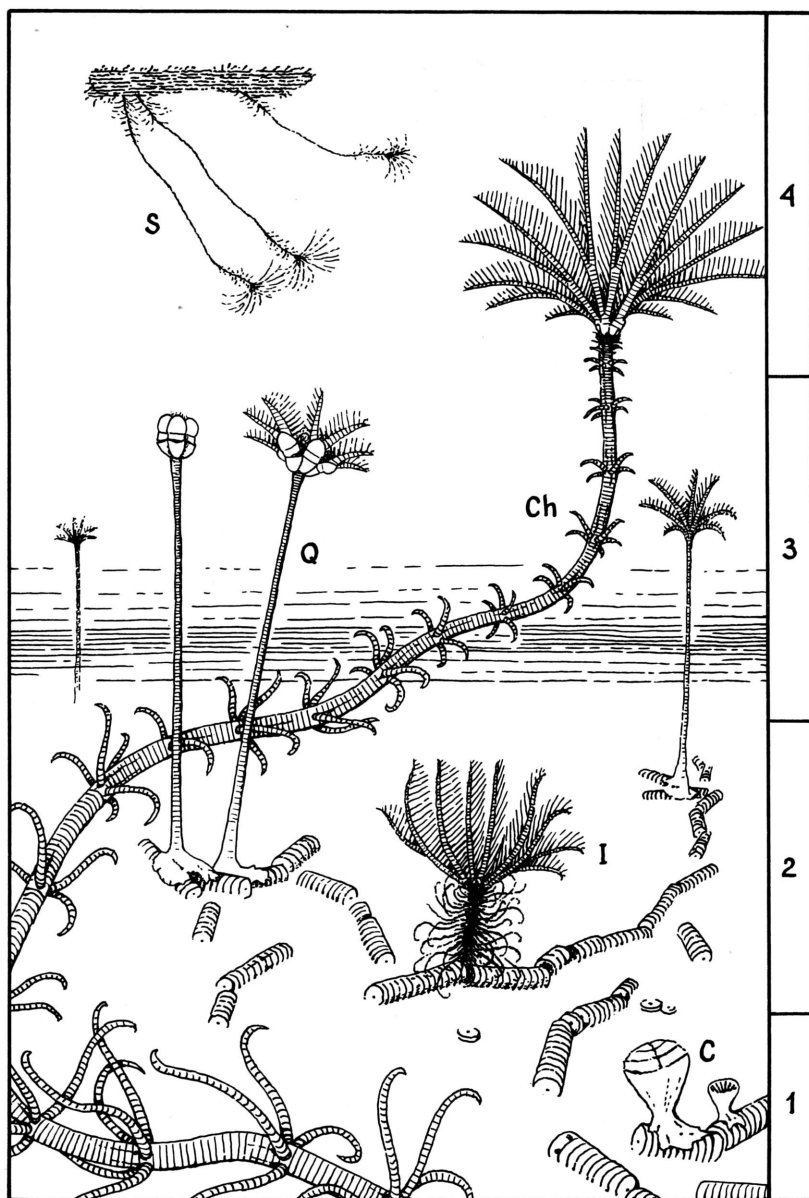


Fig. 5. Reconstruction of a crinoid community in the Ammonitico Rosso facies (the figures to the right are the ecological tiers).

C = *Cotylederma*, Ch = *Chladocrinus*, I = „*Isocrinus*“, Q = *Quenstedticrinus*, S = *Seirocrinus*.



the crown reached only slightly above the bottom (second tier in Fig. 5). *Pentacrinus* ex gr. *fossilis* BLUMENBACH, whose remains were found in the „Salgyr“ locality (see Table 2), belonged to the same ecological type. Unfavourable conditions near the sea bottom prevented further development of these forms.

The mentioned isocrinids were able to change their position, if needed, by autotomizing distal parts of the quickly growing stem along one of the cryptosymplectial sutures below the nodals. Development of monolithic stereome on the lower nodal surface overgrowing the axial canal (distally almost completely) also contributed. The animal, freed from its anchor, could drift along the bottom in the current, assisted by slow flaps of its arms (KIRK, 1911; ROUX, 1978). A semi-free mode of life was probably more usual in short-stalked forms (HAUFF, 1984).

The compact crown of the Hyocrinina was attached by a long and slender vertical stem to hard objects on the bottom. Spontaneous tearing off was impossible; but the crown was quite safe from casual attacks, because their massive primibrachials were able to cover the whole tegmen and the arms (see Fig. 2 R and Fig. 5). The immobility of the stem and the impossibility to throw off a „spoiled“ stem part promoted parasites to settle analogous to what has been described from many immovably attached crinoids (YAKOVLEV, 1939; ARENDT, 1961; BRETT, 1978). Hyocrinids occupied the third tier above the bottom (see Fig. 5).

Holopodina had no stem, but were attached by the basis of their theca. The crown was compact and the flattened primibrachials were able to cover it. They were usually anchored to crinoid stem debris, bivalve shells etc. *Cotylederma* settled preferably on ammonoid shells (VADÁSZ, 1913; SIEVERTS, 1932). Holopodina occupied the lowermost tier (see Fig. 5).

Crinoids of three ecological guilds constituted „meadows“ with high population density, with hard objects (ammonoid or bivalves shells) on the bottom providing initial substrates for colony development. Subsequently the community spread and new individuals could settle on skeletons of their own dead predecessors. In the end a biostrome with a considerable lateral extension but limited height could develop. Its bulk was made of crinoidal ossicles. Such a colony could exist only in the presence of near-bottom currents which not only provided food and oxygen to the passive filter feeders, but also washed up again the remains of dead organisms. Therefore the evident roundness of plates are observed in many cases. Occasional winnowing by storm events also resulted in condensation, so that Liassic and Triassic faunas may co-occur in some localities. For example, remains of the Pfliebsbachian *Seiocrinus laevisutus* (POMPECKJ) were found together with those of the Carnian *Laevigatocrinus subcrenatus* (LÄUBE) in the „Bodrak-1“ locality.

The calcareous bioherms litified quickly and without compaction, while the pelitic around was condensed and compacted (PETTIJOHN, 1974). This led to the formation of a „hard island“ rising above soft pelitic sediments. Such „islands“ could slip down paleo-slopes to allochthonous positions in the geosynclinal trough, where the primary bioherm bedding had no relation to the bedding of the surrounding rocks, which may also have a younger age than the bioherm. Active

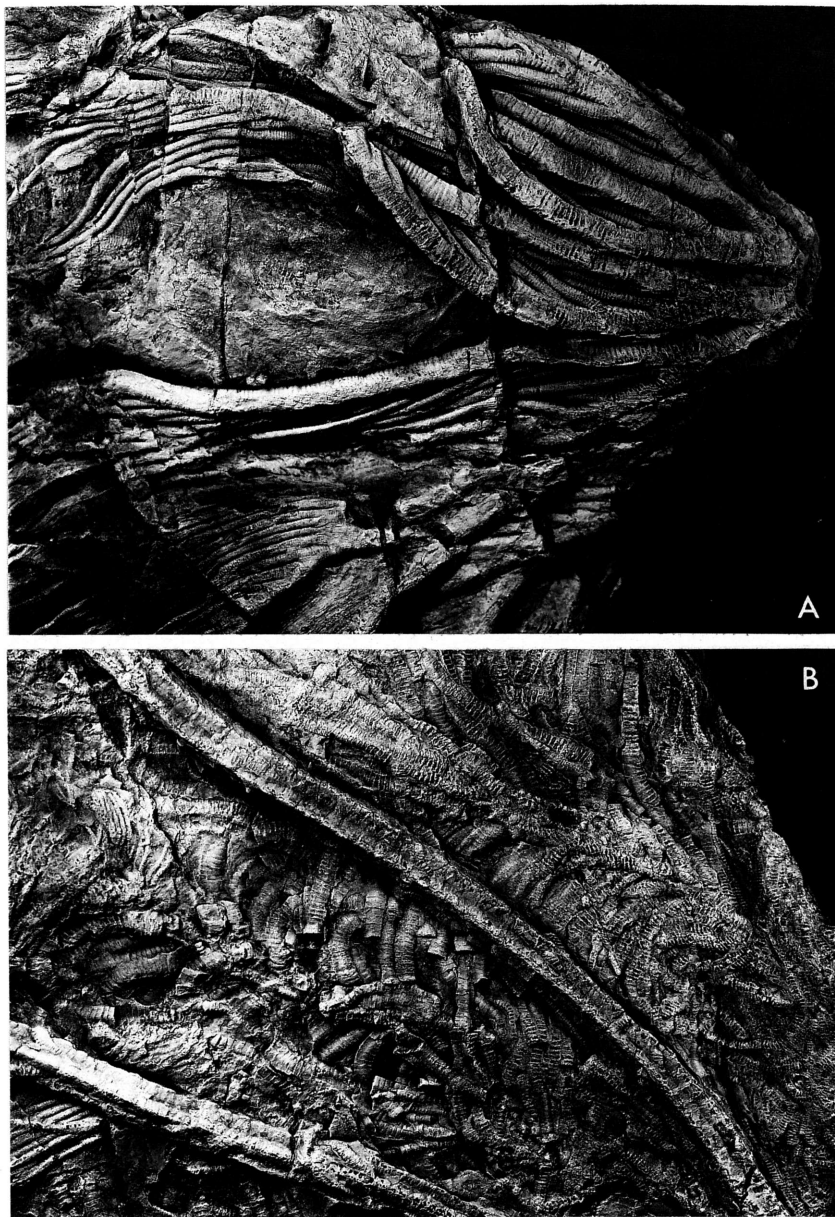


Fig. 6. A, B = Remains of *Seirocrinus laevisutus* from the Tautian black shales (A = IK-16-1, the crown, x 0,6; B = IK-16-2, stems with cirri, x 0,6). Coll. V. A. PROSOROVSKY (Leningrad University). Foto by B. S. POGREBOV.

tectonic movements in geosynclinal regions have contributed to the destruction and „redeposition“ of such crinoidal limestone „klippen“.

The mechanism by which limestone olistoliths formed in pelitic-schistose rocks (e. g. in the Crimea and the Kotel environs in Bulgaria) corresponds to existing models (SHALIMOV, 1960, 1962, 1969).

Crinoidal bioherms also provided convenient settling places for calcareous sponges, corals, bivalves, gastropods, brachiopods, bryozoans and sea-urchins (SHALIMOV, 1969; ASTAKHOVA, 1972) and numerous predatory ammonites and belemnites dwelt near them.

A crinoid alien to the described biocoenosis is represented as a minor element in crinoidal limestones of all localities. The species in question is *Seirocrinus laevisutus* (see Table 2). Long stems and even the crowns of this species are commonly presented in dark shales of Crimea (MUKHIN, 1917), Caucasus (AMMON, 1901; ZESSASHVILI, 1967) and in other localities, while one can find only small stem fragments in organogenic rocks. *Seirocrinus* led the pseudoplanktonic life i. e. it migrated as small colonies attached to floating objects, mainly wood fragments (QUENSTEDT, 1876; BERINGER, 1926; KLÄHN, 1929; HAUFF, 1960; SEILACHER et al., 1968; HAUDE, 1981 and others), to become drowned when the „raft“ lost its buoyancy. Colonies that sank to silty bottoms found there favourable conditions for preservation (Fig. 6), while those landing on crinoidal bioherms quickly disintegrated.

## 6. Acknowledgements

The present work was completed in the Structural and Marine Geology Chair of the Leningrad Mining Institute. The collection of Liassic crinoids from Bulgaria have been supplied by T. S. MANCHEV. A part of the collection from Georgia was received from A. S. GORSHKOV (Marine Geology Institute, Gelengik). The manuscript was critically reviewed by Dr. G. A. STUKALINA (All-Union Geological Institution, Leningrad). The English version of the paper was checked by I. F. NAFTUL'EFF. The author thanks Prof. A. SEILACHER for his help in supervising the manuscript.

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## Postscript

The manuscript of the paper had been prepared for the press before I received from Dr. MANFRED JÄGER a copy of his very interesting paper „Die Crinoiden aus dem Pliensbachium (mittlerer Lias) von Rottendorf am Klei und Empelde (Süd-Niedersachsen)“ — Ber. naturhist. Ges. Hannover, 128: 71-151 (1985). This work contains important data about the morphology, the taxonomy and the stratigraphical distribution of the crinoid genera *Amaltheocrinus*, *Chladocrinus* and *Seirocrinus*.