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Cyclocrinus, an enigmatic Jurassic–Cretaceous crinoid

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Key words: Crinoidea, *Cyclocrinus*, Bajocian–Oxfordian, Albian, Europe, taxonomy

ABSTRACT

Previously undescribed material in the Natural History Museum Basel provides the basis for a reappraisal of the enigmatic Middle Jurassic to Early Cretaceous genus *Cyclocrinus* D'ORBIGNY known only from mostly single columnals and attachment discs. Only one of the previously described Jurassic species, *C. rugosus*, is recognized despite wide variation in morphology of columnals ranging from Bajocian to Oxfordian in age. A small percentage of columnals are axillary, show facets for side branches or are arched, which has led to the assumption that *Cyclocrinus* columnals represent radicular cirrals and should be assigned to the Order Bourgueticrinida. Both hypotheses are rejected. The prevalence of single columnals is explained by the restriction of loose, galleried (α) stereom to an area near the facets and around the axial canal; through-going ligament fibres responsible for the preservation of pluricolumnals were thus largely absent from much of the stereom. *Cyclocrinus variolarius* (SEELEY) from the Albian of England hardly differs from the Jurassic *C. rugosus*. The ordinal position of *Cyclocrinus* and of the family Cyclocrinidae SIEVERTS-DORECK is left open though the form has some resemblance to the Early Jurassic millericrinid genus *Amaltheocrinus* KLIKUSHIN.

ZUSAMMENFASSUNG

Bislang nicht beschriebenes Material des Naturhistorischen Museums Basel dient als Basis für eine erneute Evaluation der rätselhaften Crinoidengattung *Cyclocrinus* D'ORBIGNY von der nur Stielglieder und Haftscheiben, aber keine Kelchteile bekannt sind. Nur die erstbeschriebene Art *C. rugosus* (D'ORBIGNY) wird anerkannt, da die Variabilität der morphologischen Merkmale eine Abgrenzung weiterer Arten trotz Vorkommens über einen Zeitraum vom Bajocium bis Oxfordium nicht erlaubt. Ein kleiner Prozentsatz der Stielglieder ist axillär, hat Sockel für Seitenzweige oder ist gekrümmt, was zur Vermutung führte, die Stielglieder als Teile von Wurzelzirren von Bourgueticriniden aufzufassen. Beide Hypothesen werden zurückgewiesen. Das Vorkommen weitgehend einzelner Stielglieder wird mit der Beschränkung von lockerem, regulärmaschigem (α) Stereom auf den Bereich der Gelenkflächen und des Axialkanals gedeutet; das weitgehende Fehlen von durchgehenden Kollagenfasern trägt offenbar zur Seltenheit von Stielfragmenten dieser Formen bei. *Cyclocrinus variolarius* (SEELEY) aus dem Albium von England unterscheidet sich kaum vom jurassischen *C. rugosus.* Die Zuweisung von *Cyclocrinus* bzw. der Familie Cyclocrinidae SIEVERTS-DORECK zu einer bestehenden Ordnung wird offen gelassen obgleich gewisse Aehnlichkeiten mit der Millericriniden-Gattung *Amaltheocrinus* KLIKUSHIN aus dem Lias bestehen.

Introduction

Large cylindrical columnals with peculiar tuberculate facets ascribed to the genus *Cyclocrinus* are found in sedimentary rocks ranging from Bajocian to Oxfordian, from Europe and Russia, and are thus represented in many collections, public and private. *Cyclocrinus* columnals also occur in the Albian of England though they are poorly known. Peculiar are axillary columnals with three or more facets indicative of column branching. Such developments and other features like the occurrence of arched pluricolumnals led Radwańska & Radwański (2003) to propose that the base of the column was branched to form a root-like attachment structure (radix). However, attachment discs found occasionally prove that the animals anchored to shells of molluscs. In an earlier paper, Klikushin (1984) reconstructed the attachment structure of these crinoids as branched and cemented.

In Bajocian to Callovian strata *Cyclocrinus* columnals mostly occur as single pieces wider than high, and pluricolumnals are rarely encountered, quite in contrast to cylindrical columnals of millericrinids and columnals of isocrinids that occur in the same rocks. No satisfactory explanation for this unusual phenomenon has so far been offered. Another riddle is the complete absence of parts of the crown from the strata in which the columnals are found. Nearly nothing is known about the ontogeny of the *Cyclocrinus* column and to which part of the column the morphologically different columnals may have belonged. It is the purpose of the present paper to discuss these questions, in particular the proposed models, based on a review of the different species mentioned in the literature and well preserved material from the Natural History Museum Basel. Descriptions include new material of the Early Cretaceous species C. *variolarius* (SEELEY). The systematic position will also be explored

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though the taxonomically important crown is still completely unknown. It is to be hoped that future finds or perhaps undescribed museum material will help to clarify this situation.

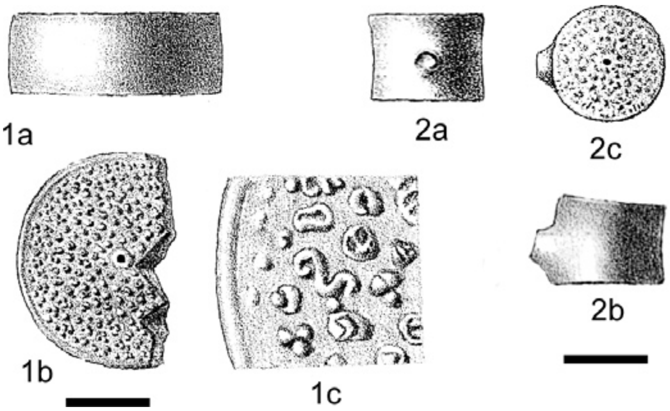
Institutional abbreviations: NMB, Natural History Museum Basel (Switzerland); JME, Jura-Museum, Eichstätt (Germany).

History of research

An overview on the history of the genus was recently given by Radwańska & Radwański (2003). In the following account, the most important papers pertinent to the present discussion are summarized.

Cyclocrinus was proposed by d'Orbigny (1850: 291) for his previously established *Bourgueticrinus rugosus* (1841: pl. 17, figs. 16–19) from the Bajocian of France. Quenstedt (1856: 514) described in some detail cylindrical, slightly convex columnals and an attachment disc from the Middle Jurassic (Bathonian and Callovian) of Germany as *Mespilocrinites macrocephalus*. In particular, he mentioned the fine marginal crenulae, the irregular tubercles or groups of tubercles on the facet and the narrow lumen.

Trautschold (1859) described a series of elements from the Oxfordian of the Moscow area. The material contained columnals and axillary columnals considered by the author to be radials supporting brachials (loc. cit.: pl. 1, fig. 5–7). Still other columnals carry a small socket on the latus (loc. cit.: pl. 1, fig. 8) and one was thought to be a topmost columnal (pl. 1, fig. 9) fused to a cup, not figured because of bad preservation. Trautschold compared his specimens to Quenstedt's *Mespilocrinus macrocephalus* with which they share a narrow lumen and a tuberculate facet, but differ in straight sides and the lack of marginal crenulae. On the basis of the differences in the columnals, but also by the supposed presence of radials, Trautschold erected for the remains a new genus *Acrochordocrinus* with the type species *insignis*. Interestingly, only the tuberculate facet of the



Figs. 1, 2. Syntypes of *Cyclocrinus rugosus* (d'Orbigny), Bajocian, France. 1) Large damaged columnal, lateral (a), facet (b) and facet enlarged (c) to show vermiculi (de Loriol 1886: pl. 124, fig. 1). 2) Columnal with lateral socket, lateral views (a, b) and facet (c) (de Loriol 1886: pl. 124, fig. 3). Scale bars: 10 mm.

columnals diagnosed the genus. *Acrochordocrinus* was not accepted by de Loriol (1878: 103; 1886: 3) and subsequent authors such as Klikushin (1984), but continued to be used in some of the Russian literature (see Radwańska & Radwański 2003: 308).

Moesch (1867) established a new species, *Mespilocrinus areolatus*, from the Middle Oxfordian Birmenstorf Member of the Aargauer Jura. The three columnals figured had facets that vary from uniform tuberculate (loc. cit.: pl. 7, fig. 2a) to irregular, sparsely tuberculate (loc. cit.: pl. 7, fig. 2b) to tubercles arranged in a ring around the lumen (pl. 7, fig. 2c). Moesch did not discuss any of the previously described species though his specimens are within their morphological range.

Quenstedt (1876: 382–394, pl. 104, figs. 138–157; pl. 105, figs. 1–4, 8–12) described many specimens of his *Mespilocrinites macrocephalus* that give a good indication of the variability of the species. Most of the specimens were from Bathonian and Callovian strata, but a very large and a small columnal are Bajocian. The small columnal has two sockets on the latus (loc. cit.: pl. 105, fig. 4); the facet is concave and smooth, and the lumen is narrow. Quenstedt (loc. cit.: 386) mentioned that such columnals were never found in younger strata. This columnal closely resembles one of d'Orbigny's *rugosus* specimens reproduced here (Fig. 2). Another specimen of *rugosus* figured by d'Orbigny (1850: pl. 17, fig. 17) showed a facet closely resembling Quenstedt's *macrocephalus* (1858: pl. 68, fig. 29). Based on these specimens, *C. macrocephalus* is conspecific with *C. rugosus*.

De Loriol (1878) confirmed *Cyclocrinus* as a valid genus, and described *C. macrocephalus* (Quenstedt) from Bathonian to Callovian and *C. areolatus* (Moesch) from Oxfordian strata. He proposed a third species, *C. renevieri*, from the Early Cretaceous (Valanginian) of the Pre-Alps of the Canton of Fribourg. He pointed out that *areolatus* is very similar to *macrocephalus* and considered his assignment of *renevieri* to *Cyclocrinus* as provisional. In fact, the columnals of *C. renevieri* resemble those of *Amaltheocrinus amalthei* from the Early Jurassic; assignment to *Cyclocrinus* seems problematic because the facets of the *renevieri* columnals are more strongly crenulate around the periphery. Rasmussen (1961: 163) referred *C. renevieri* to *Apiocrinites*. De Loriol (1886) described d'Orbigny's *C. rugosus* from the Bajocian in much detail (see Figs. 1, 2). He also described the French material of *C. macrocephalus* from the Callovian and *C. areolatus* from the Oxfordian, repeating his former (1878) view that *areolatus* is difficult to distinguish from *macrocephalus*. Of doubtful assignment to *Cyclocrinus* were considered *C.*? *socialis* (Quenstedt) from the Pliensbachian, *C.*? *strangulosus* d'Orbigny 1850 from the Bajocian, *C.*? *precatorius* d'Orbigny 1850 from the Bathonian and *C.*? *dumortieri* de Loriol 1885 from the Oxfordian. These species are based on small, barrel-shaped, rather high columnals that commonly preserved as pluricolumnals; the facets have marginal crenulae and lack the peculiar tubercles distinctive for *Cyclocrinus*. Assignment to this genus is therefore unjustified.

Klikushin (1984) recognized five species: *C. areolatus* (Moesch 1867) from the Oxfordian of France and Switzerland; *C. insignis* (Trautschold 1859) from the Oxfordian of Poland, Lithuania and the surroundings of Moscow; *C. macrocephalus* (QUENSTEDT 1858) from the Callovian of France, Germany, Switzerland, the Moscow area and the Caucasus; *C. rugosus* (D'ORBIGNY 1840) from the Bajocian of France and Germany; and *C. variolarius* (SEELEY 1866, under ?*Torynocrinus*) from the Albian of England. Seeley did not figure this last species, but he mentioned that "the base is an expanded plate contracting conically to the size of the thick cylindrical cheese-like pieces forming the column". Columnal facets are "ornamented with concentric rows of pustules, generally very close together". Rasmussen (1961: 164, pl. 23, figs. 6, 7) figured two specimens from the Cambridge collection. He chose an attachment disc or root with apparently smooth columnal facet from the Hunstanton Red Chalk (loc. cit.: pl. 23, fig. 6) as the type of *C. variolarius* and also figured a columnal with a rugose facet from the same location. According to Rasmussen this species resembles the Jurassic *C. rugosus* and *C. insignis*, but differs from *C. rugosus* by the lack of crenulae along the edge. *Cyclocrinus variolarius* extends the range of the genus to the late Early Cretaceous.

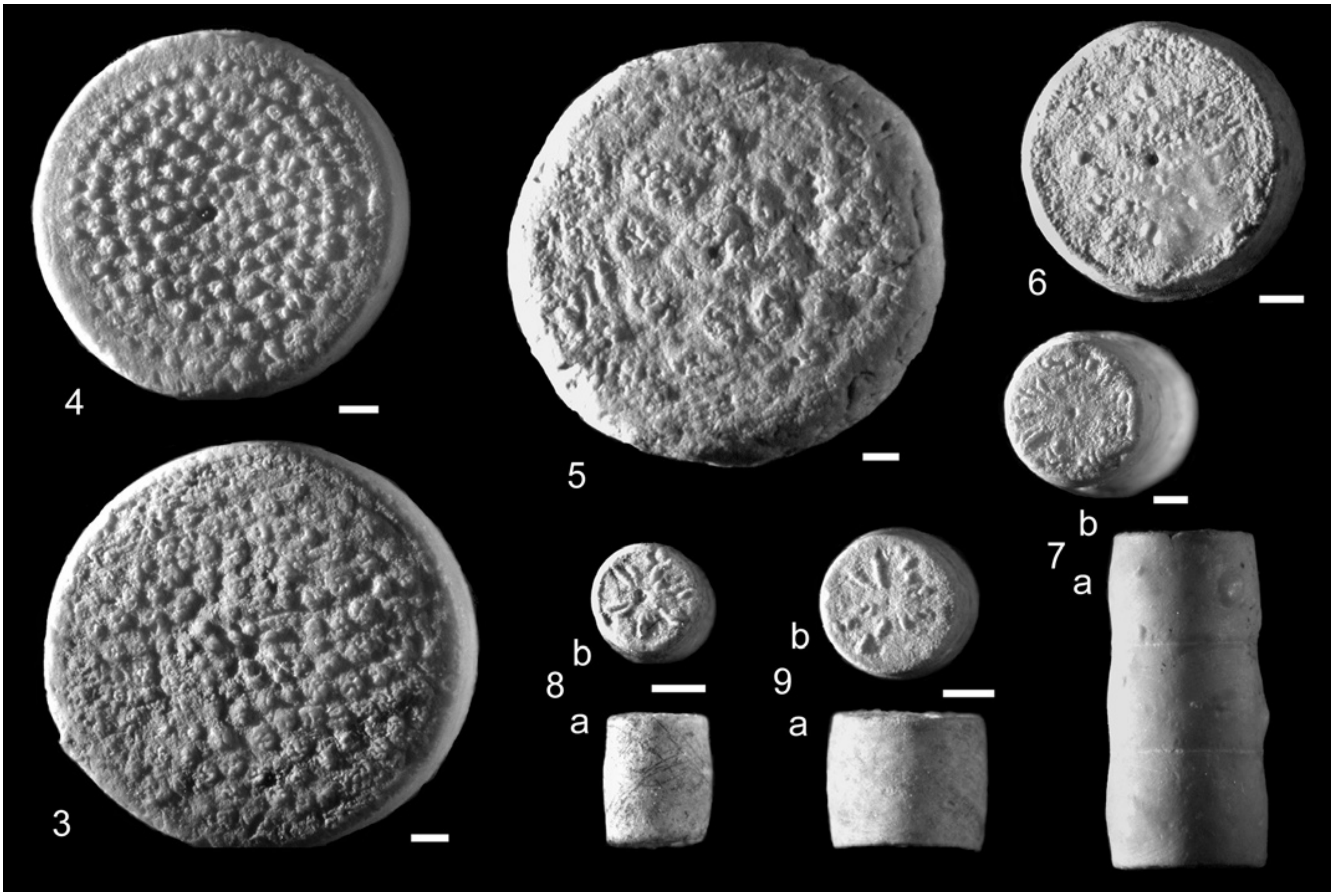
Gluchowski (1987) described columnals of *C. rugosus* from the Jurassic (Bajocian to Oxfordian) of the Pieniny Klippen Belt of Poland. He tentatively assigned some brachials and a low, millericrinid-like cup with bulging radials to *Cyclocrinus* and tried a reconstruction. The underside of the cup has a wide cavity, but the facet is unknown so that combination with the distinctive *Cyclocrinus* columnals is doubtful.

Radwańska & Radwański (2003), recognizing only d'Orbigny's *rugosus* (1841, under *Bourgueticrinus*), considered *macrocephalus* (QUENSTEDT 1858), *insignis* (TRAUTSCHOLD 1859) and *areolatus* (MOESCH 1867) to be within the variability of *rugosus*. Radwańska & Radwański suggested that assignment of the fossils to different species was influenced by their stratigraphical age; *rugosus* from the Bajocian (d'Orbigny 1841), *macrocephalus* from the Callovian and *areolatus* from the Oxfordian (Moesch 1867; de Loriol 1878). Salamon & Zatoń (2007) described columnals from the Callovian of the Polish Jura as *Cyclocrinus macrocephalus*, but with reference to Radwańska & Radwański (2003); these authors proposed the new species *C. couiavianus* from the Late Oxfordian of Poland. This species is characterized by cylindrical, low to relatively high columnals that may be somewhat constricted; the fresh facets are plain, but show the distinctive tuberculation when corroded. This tuberculation is similar to that of *C. rugosus*. Many columnals of *Cyclocrinus* are not well preserved or have calcareous deposits so that ornamentation may show up only upon weathering. It thus appears that the main distinctive character of *couiavianus* is the shape of the columnals and perhaps the common occurrence of pluricolumnals, though the Polish authors did not mention their percentage.

Occurrence

Columnals and attachment discs of *Cyclocrinus* are known from strata of Bajocian to Late Oxfordian and Albian age, but Callovian strata have furnished the majority of specimens reported in the literature. Strata that yield *Cyclocrinus* include the Bathonian Varians Member, composed of argillaceous limestones, and the Early Callovian "Macrocephalen-Oolith" (Brauner Jura ε) or "Macrocephalus-Schichten" (Macrocephalus Zone, now Herveyi Zone; see Callomon et al. 1992), partly composed of iron oolites. The occurrence in the Ornatenton Formation mentioned by Quenstedt appears to be doubtful (G. Dietl, G. Knittel, pers. comm. 2007). The Stuttgart Museum has a large specimen of the ammonite *Erymnoceras* with several attachment discs of *Cyclocrinus* from the Late Callovian Grenzkalk (Coronatum Zone) of the Wutach area (G. Dietl, pers. comm. 2007). These sedimentary rocks were laid down under conditions unsuitable for the preservation of intact crinoids, except in one special case, a lens of the isocrinid *Hispidocrinus leuthardti* in the Varians Member (Hess 1999). However, pluricolumnals of *Isocrinus*, *Balanocrinus* and *Millericrinus* occasionally occur in these strata. An interesting occurrence was described by Trautschold (1859) who found a large number of columnals in Callovian marlstones near Moscow, apparently without accompanying fossils. Radwańska & Radwański (2003) described a mass aggregation of *Cyclocrinus couiavianus* in detrital limestone forming the talus of a Late Oxfordian carbonate buildup, in places with crinoidal limestones. This is the latest Jurassic occurrence of *Cyclocrinus* and is the only locality where *Cyclocrinus* pluricolumnals apparently occur commonly. In the Bathonian of the Ardèche Department in France, *Cyclocrinus* columnals are accompanied by cups of the cyrtocrinids *Cyrtocrinus nutans*, *Dolichocrinus aberrans*, *Eugeniacrinites cariophilites*, *Lonchocrinus dumortieri* and *Phyllocrinus fenestratus* (Dumortier 1871; de Loriol 1886; Roman 1950: 46, 47; author's collection). In the Middle Oxfordian Birmenstorf Member of Switzerland, *Cyclocrinus* columnals are accompanied by cups of *Argoviacrinus rarissimus*, *Cyrtocrinus nutans*, *Eugeniacrinites cariophilites*, *Pilocrinus moussoni*, *Plicatocrinus hexagonus* and *Tetracrinus moniliformis* (Hess 1975; Hess & Spichiger 2001). These occurrences are hardground faunas preserved under reduced sedimentation. Interestingly, no *Cyclocrinus* holdfasts have been reported from Oxfordian strata with cyrtocrinids, perhaps because *Cyclocrinus* is rare in them.

Remains of *Cyclocrinus* from different strata and mainly Swiss localities are preserved in the Natural History Museum Basel. In particular, a series of columnals and attachment discs collected in the 19th century from the Callovian of Sangetel near Matzendorf (Canton Solothurn) by R. Cartier, a parish priest at Oberbuchsiten, serves to illustrate some of the aspects of these enigmatic crinoids. Unfortunately, this locality is not accessible any more and the exact location is unknown. The Sangetel farmhouse lies on the top of an anticline composed of Callovian limestones and marlstones. Recent Callovian outcrops 250 m NE of the farmhouse are locally rich in fossils such as ammonites (*Macrocephalites* sp.), bivalves (*Pholadomya*, *Ctenostreon*, *Lopha*, *Modiolus*), brachiopods (terebratulids) and irregular echinoids (*Pygomalus*), but I have not found any remains of crinoids. Pockets of marlstones that would be suitable for well preserved crinoids are largely devoid of fossils. The Swiss occurrences embracing at least five columnals are listed in Table 1.



Figs. 3–9. *Cyclocrinus variolarius* (SEELEY) from the Albian of England (collected by A.S. Gale).
3, 4) Columnal facets, Red Chalk, Hunstanton (Norfolk), middle or early late Albian (3: height 5.8 mm, NMB M10697; 4: height 4.9 mm, NMB M10698). 5–9) Shenley Limestone, Double Arches Pit, Leighton Buzzard, Bedfordshire (Early Albian, Leymeriella tardefurcata Zone, L. regularis Subzone): 5, facet of slightly weathered columnal (height 4.2 mm, NMB M10699); 6, columnal with slight marginal crenulation (height 5 mm, NMB M10700); 7, pluricolumnal, lateral (a) and upper facet (b) (NMB M10701); 8, small columnal with paired radial crenulae, lateral (a) and facet (b) (NMB M10702); 9, small columnal with irregular crenulae, lateral (a) and facet (b) (NMB M10703). Photographs Hess. Scale bars: 1 mm.

In the Albian of England, *Cyclocrinus* occurs in the fossiliferous Red Chalk of Hunstanton (Norfolk) and in the Shenley Limestone of Double Arches Pit, Leighton Buzzard (Bedfordshire). According to Rasmussen (1961), the Red Chalk contains the cyrtocrinid *Hemicrinus canon* and the isocrinids *Nielsenicrinus cretaceus* and *Isocrinus*? *legeri*. *Cyclocrinus* columnals are very well preserved in marly parts of the Shenley Limestone, and the fine-grained sedimentary rocks also contain *Isocrinus legeri*, a new species of *Balanocrinus*, *Apiocrinites gillieroni*, *Torynocrinus canon* and cups of a new roveacrinid (Hess & Gale in prep.) as well as a large variety of other fossils, especially brachiopods. These mud-derived sedimentary rocks are notable for the presence of crinoids, which differ in their mode of attachment, cirri and discs or roots, and even include a pelagic roveacrinid. The sediment filled preformed cavities in ironstone in a high-energy, shallow, subtidal environment (Eyers 1992). A. S. Gale collected material at two localities. One is the Red Chalk of Hunstanton (Norfolk), Seeley's (1866) original locality, mid or early late Albian age, the other is the Shenley Limestone of Double Arches Pit, Leighton Buzzard, Bedfordshire (early Albian, Leymeriella tardefurcata Zone, L. regularis Subzone; see Eyers 1992). The figured material (Figs. 3–9) shows similar variability in column shape and facets as the Callovian material. Some facets are densely tuberculate (Figs. 3, 4), similar to the specimens in Plate II (figs. 12, 14). A facet with groups of tubercles arranged around a central "rosette" (Fig. 5) compares well with facets of Callovian columnals (Pl. I: figs. 1, 15; Pl. II: fig. 14). The small, high columnals show paired or irregular radial crenulae (Figs. 7–9), quite similar to those from the Callovian (Pl. II: figs. 9, 11, 15, 16). Even the marginal crenulation, thought by Rasmussen (1961: 164) to be absent from the Albian species, is developed in some of the Albian columnals (Fig. 6). There are no axillary columnals or columnals with side branches. On purely morphological grounds, *Cyclocrinus variolarius* cannot be distinguished from *C. rugosus*.

Table 1. Columnals and attachment discs of the crinoid *Cyclocrinus rugosus*, for specimens housed in the Natural History Museum Basel.

Stratum, locality, collection number	Unbranched	Axillary or lateral socket	Attachment disc	Pluricolumnal (2 columnals)
Bathonian (Varians-Schichten), Lostorf (M5354, 5355)	81	0	0	3
Bathonian (Varians-Schichten), Lostorf (M1373, 1377)	63	1	0	1
Bathonian (Varians-Schichten), Lostorf (M5112)	7	0	0	0
Bathonian (Varians-Schichten),Trimbach (M3014)	14	0	0	0
Bathonian, La Pouza (Ardèche) (M3013)	43	0	0	0
Callovian (Macrocephalus-Schichten), Hornussen (C124)	7	1	0	0
Callovian (Macrocephalus-Schichten), Lostorf (M1364)	6	0	0	0
Callovian (Macrocephalus-Schichten), Ramiswil (2687)	18	1 + 1 lateral socket	1	1
Callovian (Macrocephalus-Schichten), Sangetel (M3000, 3017, 3106)	238	10 + 2 lateral socket	6	0
Callovian (Anceps-Athleta-Schichten), Schleitheim (M1372)	32	0	0	0
Oxfordian (Cordatus-Schichten), Hägendorf (Homberg)	14	0	0	0
Total	**523**	**13 + 3 lateral socket**	**7**	**5**

Descriptive morphology

Column shape

Most of the columnals are cylindrical with straight or slightly convex and smooth sides. Large columnals are low and may reach a diameter of up to 30 mm; the smaller ones are higher and may be barrel-shaped. An exception is provided by the columnals described by Radwańska & Radwański (2003) as *Cyclocrinus couiavianus*, which are relatively higher and may have weakly concave sides.

The Sangetel material includes numerous small columnals (Pl. II: figs. 8, 9, 11, 13, 15, 16). These are cylindrical or slightly barrel-shaped; their height is roughly equal to the diameter (except Pl. II: fig. 11). Facets show radial crenulae that may be paired (Pl. II: figs. 15, 16). The columnal in Plate II (fig. 9), demonstrates the early development of a central "rosette" and that in Plate II (fig. 13), a transition from crenulae to grouped tubercles. There can be no doubt that these columnals are from juvenile specimens and they demonstrate that the distinctive tuberculation of the large columnals appears at a later, adult stage (Pl. I: figs. 4, 15; Pl. II: fig. 10, 12, 17). Some rather large columnals may retain the radial crenulae (Pl. II: fig. 3) and tubercles may be radially arranged, similar to the crenulae of the smaller specimens (Pl. II: fig. 5). The majority of the Sangetel columnals have slightly convex latera. Arched columnals are assumed to be from the distal part of the column, near the attachment disc or articulating with it (Pl. II: fig. 17). They are mostly rather thin.

Branching

Axillary columnals are found occasionally. They were not reported from the Bajocian of France by de Loriol (1886), but do not seem to be very rare in Callovian and Oxfordian strata (Trautschold 1859: pl. 1, figs. 5–10; Quenstedt 1876: pl. 104, figs. 147, 157; de Loriol 1876: pl. 14, fig. 11; de Loriol 1886: pl.125, fig, 10; l. 126, fig. 8; Radwańska & Radwański 2003: fig. 10); see also Table 1. In Poland, the oldest remains of *Cyclocrinus* occur in Callovian limy sandstones and limestones; axillary columnals are found in these and in Oxfordian strata (Salamon, pers. comm. 2007). Most axillary columnals have three facets, two of them at an angle of about 45°, but Quenstedt (1876: pl. 104, fig. 157) figured an elliptical columnal with four facets, two of them lateral and all pierced by an axial canal.

The Sangetel material contains axillary columnals that vary widely in the mode of branching (Pl. I: figs. 9, 11–14, 16, 17; Pl. II: fig. 10). Some specimens are axillary with two facets at an angle of about 45° (Pl. I: figs. 12, 17), but a few have much steeper facets that may become nearly vertical (Pl. I: figs. 9, 13, 14). In most cases the facets have a similar narrow lumen (Pl. I: figs. 9, 14), but in two cases (one figured in Pl. I: fig. 17) the lumen is slit-like, combining the two adjoining facets. In another case one facet has no lumen at all, but there is a stereomic thickening at the crest separating the facets (Pl. I: fig. 12). The specimen in Plate I (fig. 11), demonstrates a nascent branching facet not pierced by an axial canal. The large columnal in Plate II (fig. 10) has four facets without lumen of an axial canal: the axial canal is visible only in the centre of the upper and lower facets (Pl. II: figs. 10b, c). A wedge-shaped, arched columnal has four facets (Pl. I: fig. 16), and none of the two vertical facets is pierced by an axial canal (Pl. I: fig. 16a).

Holdfasts

Attachment discs were described by Quenstedt (1876: 386; pl. 105, figs. 8, 12). He mentioned that they commonly embraced on their lower side the piece of a bivalve or were attached to the "thick shell of *Ammonites laeviplex*". De Loriol (1878: pl. 14, fig. 20) figured a rather high root with granular surface found together with columnals of "*C. macrocephalus*", but his assignment is doubtful because no facet is preserved. Russian specimens were described by Gerasimov (1955: pl. 1, figs. 1, 5; pl. 2, fig. 1 – a large elongate specimen). The rich material of *C. couiavianus* collected by Radwańska & Radwański (2003) from the Oxfordian at Wapienno does not contain any holdfasts (Radwańska, pers. comm. 2004).

The attachment discs from Sangetel were anchored to bivalve shells as demonstrated by corresponding impressions (Pl. II: fig. 1b); the specimen in Plate II (fig. 2) is fused with a vertical shell. There are up to three column facets per disc, the facets are concave and have fine tubercles. A small disc has a facet with distinct perilumen (Pl. II: fig. 2).

Articular facets

Three articulation types are known from the crinoid column: the symplexy, the synostosis sensu lato and the synarthry (Donovan 1988, 1989, 1990; Ausich et al. 1999). The symplexy is by far the most common type. A symplexy is characterized by ridges (culmina) on one joint face interlocking with grooves (crenellae) on the opposite joint face, marked externally by a crenulate suture. The combination of ridge and adjacent groove is called crenula (pl. crenulae). Crenulae may be radially arranged as in encrinids, millericrinids and the extant hyocrinids; in isocrinids the crenularium (entire area of columnal articular facet bearing crenulae) is arranged in a petaloid pattern. A petal is formed by a loop of crenulae that enclose an areola of mostly drop-like or elliptical shape. Cryptosymplexies are tight articulations of symplectial pattern but with much lower relief. They are developed between nodals and internodals of isocrinids. Breaking of the column at this point guarantees that segments always end with a whorl of cirri for better attachment.

Synostoses are rigid and united by short ligament fibres; opposed facets are flat or shallow concave, seen externally as a straight suture. They confer only limited movement between different columnals which separate relatively easily after death of the animal (Moore et al. 1968). True synostoses, as defined in the *Treatise* (Moore 1978: T242), appear to be exceptional in columnals of articulate crinoids where even flat facets have some kind of weak relief (Hess 2006). Such articulations have been called zygosynostoses and the calcareous deposits reduce mobility nearly or completely (Moore et al. 1968). *Cyclocrinus* columnals may be ranged in this group though facets with a narrow band of marginal crenulae are uncommon; however, marginal crenulae are weak or lacking altogether in most specimens. The externally visible sutures of *Cyclocrinus* columns are thus straight (Quenstedt 1876: pl. 104, fig. 138; de Loriol 1886: pl. 126, fig. 5; Radwańska & Radwański 2003: fig. 11).

Synarthries are restricted to juvenile isocrinids, thiolliericrinids and bourgueticrinids. The synarthry is characterized by two opposing bundles of long ligaments that are separated by a fulcral ridge.

Crinoid columnals are pierced by an axial canal; the corresponding lumen varies in width and shape. The lumen may be surrounded by an empty space, the areola**,** or by a ring of smooth, granular or vermicular surface (perilumen). A perilumen is developed in quite a few *Cyclocrinus* columnals (Pl. II: figs. 6, 7). While all *Cyclocrinus* columnals are cylindrical with more or less tuberculate facets and a very narrow lumen the facets show considerable differences, not just between the different "species", but also within a species from a single location. In the following section the sculpture on facets described by a number of authors is compiled to find out whether these are distinctive enough for separation on the species level.

Bajocian. *Cyclocrinus rugosus* columnals have facets that vary between uniform tuberculate (d'Orbigny 1841: pl. 17, figs. 17, 19; de Loriol 1886: pl. 124, figs. 4a, 6a, 7a; Quenstedt 1876: pl. 105, fig. 3), tubercles arranged in radial groups (de Loriol 1886: pl. 125, fig. 1b), vermicular or ringlets (de Loriol 1886: pl. 124, figs. 1b, 5b), or tubercles may be arranged in a flower-like pattern with a central "rosette" (de Loriol 1886: pl. 124, fig. 5b; pl. 125, fig. 4b). On facets with grouped tubercles the periphery may be more distinctly crenulate compared to facets with uniform tuberculation (de Loriol 1886: pl. 124, fig. 5).

Bathonian. Cylindrical *Cyclocrinus* columnals were described by Dumortier (1871: pl. 5, figs. 7–11) as *Millericrinus*; these columnals from the Ardèche Department show facets with irregular, somewhat radially arranged tubercles that may be confluent. I have found similar columnals at the original locality, though preservation is not very good; they resemble de Loriol's *C. macrocephalus* (1886: pl. 126, fig. 4).

Callovian. "*Cyclocrinus macrocephalus*" columnals have facets which vary between uniform tuberculate (Quenstedt 1856: pl. 68, fig. 29; Quenstedt 1876: pl. 104, fig. 151, pl. 105, figs. 1–3, 6, 7; de Loriol 1877–79: pl. 14, figs. 1, 12, 16–19; de Loriol 1886; pl. 125, fig. 7), grouped tuberculate (de Loriol 1877–79: pl. 14, figs. 2–7; de Loriol, 1886: pl. 125, fig. 7), radially arranged tubercles (Quenstedt 1856: pl. 68, fig. 31; de Loriol 1877–79: pl. 14, fig. 3; de Loriol 1886: pl. 125, fig. 8), or the tubercles show a concentric arrangement with a central "rosette" (Quenstedt 1856: pl. 68, fig. 31; de Loriol, 1886: pl. 125, figs. 11–13). Sculpture may be reduced to a "rosette" (Quenstedt 1876: pl. 104, figs. 145, 156) or a raised perilumen (Quenstedt 1876: pl. 104, fig. 150; pl. 105, figs. 18, 27). Some facets show irregular radial ridges or crenulae that may be fused tubercles (de Loriol 1886: pl. 126, fig. 6). On facets with grouped tubercles, the periphery may be more distinctly crenulate compared to facets with uniform tuberculation.

Oxfordian. The facets of the three columnals figured by Moesch (1867: pl. 7, figs. 2a-c) as "*Mespilocinus areolatus*" have (a) rather uniform tubercles, (b) more irregular, sparse tubercles and, (c) a ring of tubercles around the narrow lumen. Further facets figured as "*C. areolatus*" are uniformly tuberculate (de Loriol 1877–79: pl. 14, figs. 23, 24) or tubercles are sparse and more or less radially grouped (de Loriol 1877–79: pl. 14, figs. 25, 26; de Loriol 1886: pl. 126, figs. 10, 11). The periphery is crenulate on most of these facets. "*Acrochordocrinus insignis*" has facets densely to sparsely covered by tubercles or groups of tubercles, distinct marginal crenulae are lacking in the Russian material (Trautschold 1859: pl. 1; Quenstedt 1876: pl. 105, figs. 5, 6; Radwańska & Radwański 2003: fig. 7). Columnals of this species were also described by Klikushin (1984); they include facets with grouped tubercles (pl. 6, figs. 2–4; pl. 7, fig. 1), sparse tubercles (pl. 7, figs. 2, 5), radially arranged tubercles (pl. 7, fig. 3), irregular radial ridges or crenulae (pl. 7, fig. 4) similar to those of "*C. macrocephalus*" mentioned above (de Loriol 1886: pl. 126, fig. 6). *Cyclocrinus couiavianus* has facets that are plain when fresh, but show fine, regularly spaced tubercles when corroded (Radwańska & Radwański 2003: figs. 5, 8), marginal crenulae seem to be lacking.

It is obvious from the above compilation that ornamentation of the facets overlaps between the different forms so that species cannot be properly diagnosed on the base of the facets alone. This conclusion is in accordance with Radwańska & Radwański (2003) whose *C. couiavianus* is diagnosed mainly by the shape of the columnals. It seems astonishing that a single species, *C. rugosus*, ranged from the Bajocian to the Oxfordian, but perhaps species differed in characters of the still unknown crown.

As in the columnals described in the literature, our material displays a wide variety of sculpture. As discussed above, small columnals mostly have a few radial crenulae. Most of the larger columnals have groups of tubercles. Rarely, tubercles are sparse or even absent (Pl. I: fig. 11; Pl. II: fig. 7). Groups of tubercles may be more or less concentric; in the specimen in Plate II (fig. 14) the tubercles stand out as a result of weathering that also reveals growth lines around the periphery. Large, low columnals may be covered by single tubercles (Pl. II: figs. 12, 17). A cluster of tubercles arranged in a flower-like ("rosette") pattern is not uncommon around the lumen (P1. I: fig. 15; Pl. II: figs. 4b, 10b, 14). Some columnals have a more or less raised perilumen (Pl. II: figs. 6, 7, 12b, 17); the perilumen is exceptionally developed in the columnal in Plate II (fig. 7), which lacks tubercles and is distinctly crenulate around the periphery. Marginal crenulae may be developed to various extents (Pl. I: figs. 1, 11, 15; Pl. II: figs. 4, 6, 7), but commonly are indistinct, lacking altogether or are fused into a rim (Pl. I: figs. 12, 14, 16, 17; Pl. II: figs. 3, 10, 12, 17).

Lateral sockets

A number of columnals have small, protruding lateral sockets, appropriately called *bourgeon* (= bud) by de Loriol (1886: 15). Among d'Orbigny's original columnals is one with a socket (1841: pl. 17, fig. 19); it was re-figured by de Loriol (1886: pl. 124, fig. 3) and is reproduced in Figure 2. Additional such columnals were figured by de Loriol (1886: pl. 125, figs. 1–6), two of them with two sockets. According to this author (1886: 15), such sockets are restricted to columnals of the Bajocian *C. rugosus*. Quenstedt (1876: pl. 105, fig. 4) figured a columnal with two lateral sockets from the Bajocian ("Sowerbyi Bank") of Giengen. However, such columnals have also been found in later strata as documented by a columnal from the Callovian of Ramiswil, Switzerland described below (Pl. I: fig. 1). A columnal of "*Acrochordocrinus insignis*" from the Oxfordian of Moscow figured by Trautschold (1859: pl. 1, fig. 8) also showed a protruding lateral socket. All these sockets are circular and do not have a synarthrial facet distinctive for "true" cirri of the isocrinid type. Such sockets have to my knowledge not been reported from cylindrical columnals of Jurassic millericrinids, but are reminiscent of the Triassic *Qingyanocrinus* of uncertain ordinal affinity (Stiller 2000). They are easily distinguished from the facets of axillary columnals that are larger and commonly at an angle of about 45° to each other.

A small columnal from Sangetel with a relatively small concave socket (Pl. I, fig. 8) resembles those described in the literature from Bajocian sites. The most interesting columnal with a lateral socket comes from the Callovian of Ramiswil (Pl. I: fig. 1). In contrast to the Bajocian material, where the facets of the sockets are concave without notable sculpture, the socket figured here is straight and has tubercles similar to those on the upper and lower facets, suggesting that branching may also start from a latus. A somewhat elliptical columnal from the Callovian of Hornussen (Canton Aargau) has a budding, very small socket at the narrow end (Pl. I: fig. 4). It may represent an early stage of a budding branch of an elliptical columnal described by Trautschold (1859: pl. 1, fig. 5).

Regeneration

Lissajous (1900: pl. 3, fig. 10) described a columnal of "*Cyclocrinus macrocephalus*" from the Callovian, narrowing on one side to less than half its diameter. He suggested that perhaps this columnal supported a cup. Pluricolumnals with a drastic change in the diameter of two successive columnals were thought by Radwańska & Radwański (2003: fig. 9) to be regenerated. But is this really regeneration? Regeneration is rather common in crinoid arms, both in extant and fossil forms, but it seems exceedingly rare in columns. An example is the Ordovician *Lichenocrinus dubius* Miller described by Ausich & Baumiller (1998). Columns of extant crownless isocrinids may remain alive; they help to regenerate the crown, provided that the most proximal part of the column with basals and the aboral nerve centre is present (Amemiya & Oji 1992). Without this proximal part the column can regenerate cirri but not the column. Donovan & Pawson (1997) presented evidence of column regeneration from museum specimens of the extant bourgueticrinid *Democrinus*. The authors concluded from stereomic calcite overgrowth sealing the axial canal that the column continued to live without the crown, presumably absorbing dissolved nutrient through the ectoderm. Donovan & Schmidt (2001) described Ordovician *Cincinnaticrinus* columns with rounded ends that they ascribed to overgrowths of the column following decapitation. A number of mostly small columnals have a raised perilumen around the axial canal (e.g. Quenstedt 1876: pl. 104, fig. 150). Such columnals resemble those of *Eugeniacrinites hoferi* (Quenstedt 1876: pl. 105, figs. 15, 18, 27).

In our material, some columnals show a moderate (Pl. I: figs. 2, 5) or drastic (Pl. I: fig. 3) change in diameter. This occurs in pluricolumnals (Pl. I: figs. 3, 5) and in single columnals (Pl. I: fig. 2). The lower, non-figured facets of the convex columnals which narrow upward (Pl. I: figs. 2, 5) have flat tuberculate facets on the lower, wider side. The upper side of the columnal in Pl. I (fig. 2), has a small rosette around the lumen. A convex and a cylindrical columnal have facets with teat-like stereomic calcite overgrowth sealing the axial canal (Pl. I: figs. 6, 7).

Microstructure

The crinoid endoskeleton is a porous lattice of high-magnesium calcite called stereom. The columnals of living isocrinids are bound by two types of ligamentary tissue, intercolumnal ligaments and through-going ligaments (Grimmer et al. 1985). This arrangement has been called the two-ligament organization by Ausich & Baumiller (1998) who considered it to be a primitive feature of crinoids going back to Ordovician time. Through-going ligaments are long and penetrate a series of columnals (Ausich et al. 1999: fig. 12). They connect internodals and nodal with supranodal (the internodal situated proximally), and these articulations are called symplexies. Intercolumnal ligaments are short fibres that penetrate only superficially into a columnal; they connect the infranodals of isocrinids with nodals to which the cirri attach. Breakage between infranodals and nodals guarantees that the column always ends with a whorl of cirri for better attachment. It is the preferred breaking point for autotomy when the animal discards the distal part of the column. Fragmentation of columns before burial also occurs preferentially at this position and not at random. This has been demonstrated by Baumiller et al. (1995) in both living and fossil isocrinids. The articulation between nodals and infranodals of isocrinids is derived from the symplexy. Because it has a weak relief of symplectial pattern it should be called a cryptosymplexy, rather than a synostosis. Columnals with symplexies connected by through-going ligaments may be expected to be preserved more often as pluricolumnals.

The three articulation types, symplexies, cryptosymplexies and synostoses, have a morphology expressed in the microstructure of the stereom. Isocrinids thus show two main types of microstructural features (Roux 1977a; Macurda et al. 1978; Smith 1980). The so-called labyrinthic (or β) stereom is an irregular lattice of calcite with a thin meshwork of collagen microfibres. In contrast, the galleried (or α) stereom is a regular lattice with paraxial galleries where collagen fibres penetretate through the ossicle along the galleries of aligned pores and thus join several ossicles (Roux 1981: pl. 1, fig. 7). Galleried stereom typically forms the floor of petaloid zones while interpetaloid zones are composed of labyrinthic stereom. Smith (1984) distinguished a

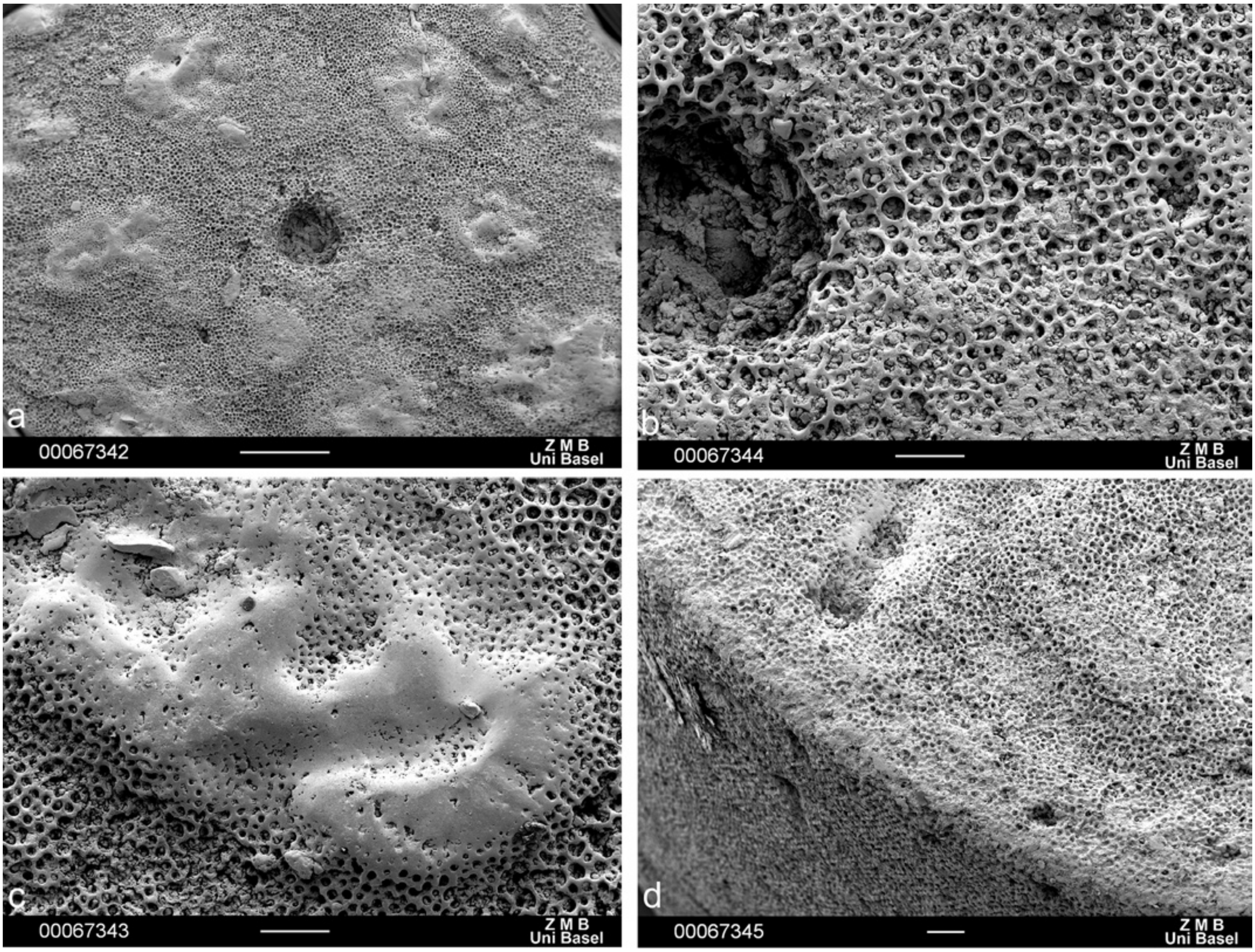


Fig. 10. *Cyclocrinus rugosus* (d'Orbigny) (NMB M10667, R. Cartier), Macrocephalus-Schichten, Sangetel. Facet with axial canal (a), area near axial canal enlarged (b), tubercle enlarged (c), edge (d). SEM photographs. Scale bars: 100 µm (b–d), 500 µm (a).

number of different stereom types in echinoid plates. Galleried stereom is developed wherever collagen has to attach on to an actively growing surface. Labyrinthic stereom is developed as a "filler". However, the distinction between galleried and labyrinthic stereom may at times be rather difficult as demonstrated by columnals of the extant bourgueticrinid *Democrinus* figured by Donovan (1997: 6; pl. 1, figs. 2, 4, 6; pl. 2, figs. 5, 7).

During diagenesis, the original structure of the stereom may be obliterated and this is especially true of many of the *Cyclocrinus* columnals. Well-preserved columnals from the Sangetel material were examined by scanning electron microscopy (SEM) and in thin sections. The microstructure of the facet shows a network of mostly round meshes in a thickened stereom that becomes imperforate in places, especially at the tubercles (Fig. 10c). Such a stereom has been called synostosial by Roux (1977a: fig. 3B). The stereom appears to be mostly galleried at the surface, especially around the lumen (Fig. 10b) but also on a broken surface (specimen not figured). However, the galleried structure is not so obvious as in the example of a columnal of *Balanocrinus pentagonalis* from the Oxfordian figured by Roux (1975: pl. 2, figs. 2, 3). On the latus the stereom is relatively fine-meshed and dense. Longitudinal thin sections show the presence of rather loose and thus probably galleried stereom near the surface and along the lumen (Fig. 11), while most of the inner body of the columnal has a dense, presumably labyrinthic, stereom which is also apparent in the horizontal cross-section. The sections also reveal the presence of microcavities. The common occurrence of patches with nearly or completely imperforate stereom on the facets and especially on the tubercles further contributes to weaken intercolumnal articulation. Roux (1975: pl. 1, fig. 2) figured similar dense stereom on the facet of a columnal of the Eocene bourgueticrinid *Conocrinus thorenti*, considered by that author to be an "external calcitic crust". However, the imperforate stereom on the raised tubercles of the *Cyclocrinus* columnals is considered to be a genuine development. Such imperforate stereom is typical of bearing surfaces in echinoids (Smith 1984: 29) and also of fulcral ridges on synarthrial articulations of crinoid columnals (Macurda & Meyer 1975: pl. 2, fig. 6; Macurda et al. 1978: fig. 186,6; Donovan & Pawson 1994: fig. 4 Donovan 1997: pl. 7, figs. 5, 6). The tubercles or other prominent structures on the facets of *Cyclocrinus* columnals may have served as pivotal elements; separation of columnals to a certain degree would have prevented lateral shear in turbulent water habitats. The prominent culmina on the symplectial facets of isocrinids have a galleried stereom (Donovan 1984: pl. 75, fig. 3). Culmina on cylindrical columnals of extant hyocrinids and bourgueticrinids show comparable meshed stereom (Roux 1980, 1990, 2002, 2004). In the proximal, cylindrical column of the extant bourgueticrinid *Democrinus parfaiti* the first columnals are joined by synostosial articulation with labyrinthic stereom. Starting from the third columnal the *Democrinus* stereom thickens on opposing sites to later become the fulcral ridge, and a galleried stereom develops around the lumen (Roux 1977b: 49, pl. 5, figs. 2–6). Such ontogenetic development may also have occurred in the column

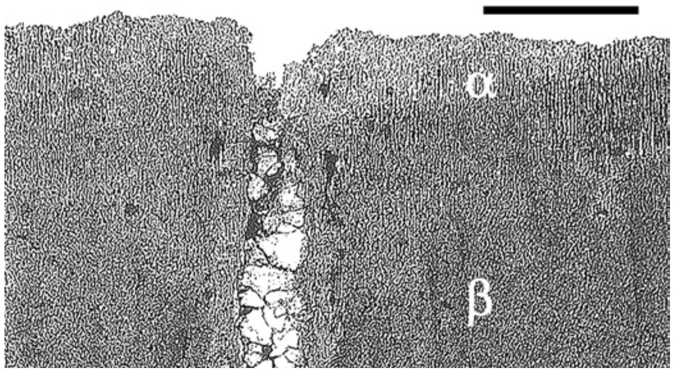


Fig. 11. *Cyclocrinus rugosus* (d'Orbigny) (NMB M10668, R. Cartier), Macrocephalus-Schichten, Sangetel. Longitudinal thin section through median part of columnal with facet and axial canal; loose, galleried (α) stereom in upper part and around lumen; dense, labyrinthic (β) stereom in lower part. Photograph Wetzel. Scale bar: 1 mm.

of *Cyclocrinus*. Columns of extant Hyocrinida which also are attached by a disc and lack cirri invite comparison. The circular facets are symplectial, with marginal crenulae that may be arranged in units of 1–3 and possess a wide lumen surrounded by an areola of variable width. The inner part is occupied by a galleried stereom with rather large meshes while the peripheral part around the crenular units is occupied by smaller-meshed, labyrinthic stereom (Roux 1990, 2002, 2004). The microstructure of the hyocrinid column with loose stereom around the lumen is thus comparable to other articulates with similar columns and may be a common characteristic of cylindrical columns firmly attached to the substrate. Articulations "made to break" as they occur in *Cyclocrinus* seem very unusual for crinoids whose column integrity must have been important for survival. Additional information on the influence of microstructure on the taphonomic behaviour of fossil and extant forms with cylindrical columns may help to solve this riddle.

Discussion

Microstructure and functional morphology

One of the most curious features of *Cyclocrinus* is that its remains occur mainly as single columnals: the rare pluricolumnals are mostly of smaller diameter. The Sangetel material includes two remains of a millericrinid with symplectial articulation, but these are pluricolumnals with their characteristic crenulate suture seen externally (Pl. I: fig. 18). The junction between *Cyclocrinus* columnals must have been particularly weak, assuming a similar residence time on the sea floor as the millericrinids. What could be the reason for this? In contrast to other cylindrical columnals, such as those of millericrinids, the facets of the *Cyclocrinus* columnals are not symplectial. The tubercles, if present, did not interlock but were opposed. In fact, Radwańska & Radwański (2003: fig. 6) figured the fractured, etched surfaces of two conjoined columnals displaying perfectly mirrored tuberculation. Incidentally, Radwańska & Radwański (2003: 310) considered differences in tuberculation to have resulted from "variably advanced corrosion which progressed either during sedimentation, prior to the final burial of specimens, or during the diagenesis". Such an assumption cannot be presumed to be general as demonstrated by the material described in the present paper. The synostosial nature of articulations in the column of *Cyclocrinus* would explain the predominance of single columnals. As shown by Baumiller et al. (1995), intercolumnal ligaments decay more readily than through-going ligaments. If burial occurred prior to complete disarticulation, the number of pluricolumnals vs. single columnals may indicate different tissue arrangements. The presence of pluricolumnals of isocrinids and millericrinids in sedimentary rocks where columnals of *Cyclocrinus* are single suggests that the *Cyclocrinus* column largely lacked through-going ligaments. The absence of galleried stereom and thus of through-going ligament fibres in *Cyclocrinus* columnals would explain their exceptional taphonomic behaviour.

The following conclusions can be made from the material described in this paper. Columns of *Cyclocrinus* probably were rather long and xenomorphic because of the presence of dissimilar columnals (at least in their facets) in material from a given location. Columnals attached to the basal disc are low and arched, with a convex lower and a concave upper facet (Pl. II: fig. 17). Columnals with additional facets, lacking the lumen of an axial canal, may have been from the distal part of the column, because the specimen figured in Plate II (fig. 10c), has a slightly convex, presumed lower facet; the wedge-shaped columnal in Plate I (fig. 16), may also be from this part of the column despite its considerable height. Away from the attachment disc columnals are cylindrical and increase in height. Small, juvenile columnals are relatively high and their facets have radially arranged crenulae (Pl. II: figs. 8, 11, 15, 16), which are being transformed into tubercles in some specimens (Pl. II: figs. 9, 13). High columnals are probably not from the proximal part below the cup where newly formed columnals tend to be low in most crinoid species. Growth lines in several specimens (Pl. II: figs. 12, 14) indicate successive widening of the columnals during a considerable timespan. Density of tubercles, whether grouped or not, tends to increase with column diameter and thus age in most cases; however, position in the column of columnals with sparse ornamentation (Pl. II: figs. 4, 6, 7) is unclear. Development of marginal crenulae appears to occur in columnals from different parts of the column (Pl. I: figs. 11, 15; Pl. II: figs. 4, 6, 7, 10) and the reason for this is unknown. The same is true for the axillary columnals (Pl. I: figs. 9, 12–14, 17) and those with sockets for presumed side branches (Pl. I: figs. 1, 4, 8). Why some axillary columnals have facets which are not pierced by an axial canal is a mystery (Pl. I: figs. 11, 12, 16a; Pl. II: fig. 10a). The absence of a lumen on otherwise well developed and well preserved facets (Pl. I: fig. 16a) has not been described before for any crinoid, except in terminal cryptosymplexies of isocrinid columns, with the lumen infilled by stereom following autotomy. Narrowing of the diameter of some columals (Pl. I: figs. 2, 3, 5) is probably not due to regeneration, but the reasons are unclear. In some columnals axial canals are sealed by stereomic overgrowth (Pl. I: figs. 6, 7, 12) and this may be due to continued growth after isolation as in an extant example (Donovan & Pawson 1997). The strange columal figured in Plate I (fig. 10), with its tetrameral symmetry, defies explanation at this point; it may not even belong to *Cyclocrinus* because of the rather large lumen.

Root or radix

Radwańska & Radwański (2003) interpreted the columnals of *C. couiavianus* and *C. rugosus* as radicles or radicular cirrals and thus as root parts. As a consequence, they placed *Cyclocrinus* in the Order Bourgueticrinida. They based this assignment on the presence of arched and axillary columnals in the Polish material. However, bourgueticrinids have columnals with mostly synarthrial articulations where the facet shows a pair of ligament pits separated by a fulcral ridge and the cross-section is elliptical. The earliest bourgueticrinids have been reported from the Late Cretaceous and their appearance in Mid-Jurassic times thus seems highly unlikely. Attachment discs of *Cyclocrinus* with impressions of bivalve shells at the base (Pl. II: fig. 1) demonstrate that attachment was not achieved by branched structures in soft sediment. This is substantiated by Quenstedt (1876: 386, pl. 105, fig. 8) who wrote that "roots with completely preserved margins commonly embrace a piece of a bivalve on their flat side, or preferably were attached to the thick shells of *Ammonites laeviplex*.". Similar attachment discs ascribed to "*Acrochordocrinus insignis*" were described from the Oxfordian of Russia by Gerasimov (1955: pl. 1, figs. 1, 5).

Klikushin (1984) reconstructed the attachment structure with "branches" of column emanating from an attachment disc and reuniting into a single column close to the basal disc (Fig. 12). Is there any fossil evidence for such a "mangrove" model? Branching columns are occasionally found in Late Jurassic millericrinids, large crinoids anchored by roots in soft sediment or by root-like holdfasts to pieces of coral (Ausich et al. 1999: fig. 8). Simple branching of columns of *Apiocrinites roissyanus* occurs away from the root, suggesting the formation of an additional column to perhaps carry a crown (de Loriol 1879: pl. 5, fig. 8; pl. 6, figs. 10–12); and such an assumption can also be made for cases of multiple branching (de Loriol 1879: pl. 6, fig. 9). In *A. roissyanus* there is no evidence that bifurcate columns were directed downward, toward the root, instead of upward, as in a tree. A curious pluricolumnal with multiple branching and buds was figured by de Loriol (1884: pl. 99, fig. 3) and is reproduced here (Fig. 13). One of the branches faces downward, similar to the Klikushin model, and thus could not have carried a crown. While this branch may have emanated from the root it could also have been formed on the column lying horizontally on the sea floor. The specimen was found in the Terrain à chailles, a marlstone notable for the occurrence of creeping columns of millericrinids. Some *Cyclocrinus* columnals indicate branching near the attachment disc (Pl. II: fig. 10). It cannot be proven whether the axillary facets of *Cyclocrinus* columnals away from the disc were directed downward, as in the Klikushin model, or upward. Attachment discs with facets

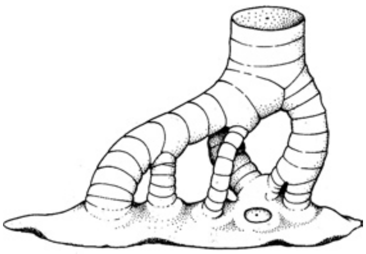


Fig. 12. Reconstruction of the attachment of "*Cyclocrinus insignis*" (TRAUTSCHOLD) (Klikushin 1984). No scale.

pointing in different directions (Pl. II: fig. 1) and columnals with side branches at a right angle (Pl. I: fig. 1) are not in favour of such a model. It seems difficult to understand why *Cyclocrinus* should first develop an attachment disc carrying several branches that would reunite to a single column.

Among the material listed in Table 1, the percentage of axillary *Cyclocrinus* columnals is 2.5 per cent, rising to 4 per cent in the Sangetel specimens. Axillary columns very rarely occur in Oxfordian millericrinids and cyrtocrinids. They have been found in the Middle Oxfordian *Liliocrinus* (de Loriol 1884: pl. 99, fig. 3; pl. 102, fig. 7), but seem to be somewhat more common in Late Oxfordian *Apiocrinites* (de Loriol 1878: pl. 6, figs. 11, 12; Hess 1975: pl. 22, fig. 15). Axillary columnals have also been described in the early Oxfordian cyrtocrinid *Eugeniacrinus astralis*, a name given because of the radial crenulae ("Strahlenrippen") on the facets (Quenstedt 1876: 430; pl. 106, figs. 34–37). Jaekel (1892: pl. 26, fig. 11) figured a branching column of the same form that he thought to belong to *Plicatocrinus hexagonus* and mentioned this to be a distal part of the column ("a lower branching of the column which suggests a *Rhizocrinus*-like root", caption to pl. 26, fig. 11). Branching in Jaekel's specimen is similar to branching seen in some *Cyclocrinus* columnals, while in Quenstedt's specimens branches are at a right angle to the axis of the column, similar to the larger lateral sockets of *Cyclocrinus*. Interestingly, a good number of Quenstedt's columnals show a narrowing of the diameter comparable to the "regenerated" columnals of *Cyclocrinus couiavianus* (Radwańska & Radwański 2003: fig. 9) and in the present study. The Middle Triassic *Eckicrinus radiatus* (SCHAUROTH), assigned by Hagdorn et al. (1996) to the Holocrinidae, has round cirrus sockets, which are usually very small, but may include both infranodals and supranodals and then show a multiradiate articulation pattern. Some of the smaller sockets of the Triassic form are quite similar to the lateral sockets of *Cyclocrinus* columnals and cirrus sockets of *Eckicrinus* may be greatly enlarged to suggest column branching (see Hagdorn et al. 1996: fig. 6a). Branching thus occurs in columns of millericrinids with symplectial articulation and is also found in columns of cyrtocrinids with synostosial articulations. The proposal that columnals of *Cyclocrinus* are part of a root system is rejected and *Cyclocrinus* clearly was attached by cementation.

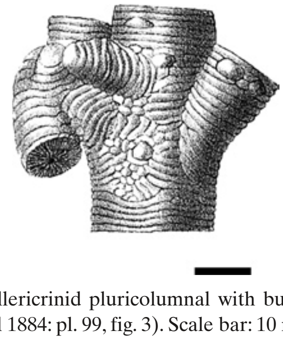


Fig. 13. Branched millericrinid pluricolumnal with buds, Middle Oxfordian, Besonvaux (de Loriol 1884: pl. 99, fig. 3). Scale bar: 10 mm.

Systematic placement

Cylindrical columnals are difficult to classify. This is especially true of forms where the crown or its parts are unknown. As a result, *Cyclocrinus* has been classified in the order Millericrinida, family Apiocrinidae by Biese (1935–37), or as a separate family Cyclocrinidae in the Cyrtocrinida by Sieverts-Doreck (1953) and Hess (1975). Rasmussen (1978) assigned the Cyclocrinidae to the Millericrinida. De Loriol (1886) left assignment of *Cyclocrinus* to a higher taxon open.

Attachment discs with more than one columnal facet occur in Millericrinida (especially *Amaltheocrinus*) and in Cyrtocrinida. Branched columns also occur in these orders, though very rarely. Jurassic cyrtocrinids are mostly small and columns are short. Cups commonly are composed of fused ossicles that may also be fused to the uppermost columnal. Such development argues against assignment of *Cyclocrinus* to the Cyrtocrinida. However, synostosial articulation of columnals is common in cyrtocrinids though the microstructure is not known in most fossil forms. A detailed microstructural analysis of the column of the extant *Neogymnocrinus richeri* composed of two columnals (Bourseau et al. 1991) shows a complex organisation, with rather loose stereom around the axial canal and dense stereom toward the periphery. Columnals of this species also contain microcavities. Millericrinid columnals are connected by symplexies with through-going ligaments as inferred from the taphonomy.

The closest affinity of *Cyclocrinus* appears to be with the Early Jurassic (Pliensbachian) *Amaltheocrinus*. *Amaltheocrinus* was established by Klikushin (1984) for *Apiocrinites amalthei* QUENSTEDT (Quenstedt 1852). Quenstedt assigned the form to *Mespilocrinites* in 1856 and again to *Apiocrinus* in 1876. Sieverts-Doreck (1958) placed the species in *Cyclocrinus*. *Amaltheocrinus* is known from attachment discs, columnals and pluricolumnals as well as parts of cup and crown (Jäger 1985, 1993). It is a large form with a cylindrical column, known from mostly disarticulated elements. Jäger (1993: 77) found only 16 pluricolumnals (mostly composed of two elements) among 1000 columnals of *A. amalthei*, a situation similar to *Cyclocrinus*. The microstructure of *A. amalthei* columnals is comparable to that of *Cyclocrinus* and galleried stereom is developed around the axial canal and near the facet as shown by thin sections of columnals of *A. amalthei* from the Pliensbachian of southern Germany (NMB M5383). Columnals of *A. amalthei* are mostly low with straight sides, but occasionally sides may be somewhat convex or concave. Articular facets are quite variable (Figs. 14, 15). In the exterior part are short crenulae, which do not reach the latus resulting in straight sutures of pluricolumnals in lateral view. The central part is smooth or covered by irregular knobs or short crenulae, but around the axial canal an areola is developed in most cases. The lumen is somewhat variable, but in any case wider than in *Cyclocrinus*. The cup is pear-shaped and composed of mostly massive radials (Fig. 16), which may be fused (Fig. 19). The radial cavity is deep. Proximally, below the radial circlet, a basal circlet may be developed. The proximal brachials (primibrachials) are massive and connected by a smooth synostosis (Figs. 17, 18). The genus is represented in the Lower Jurassic of Germany by two species, *amalthei* (QUENSTEDT) and *hausmanni* (ROEMER) (Jäger 1985, 1993). *Amaltheocrinus* was assigned to the Cyclocrinidae, Order Millericrinida, by Klikushin (1987) and Jäger (1985). Because of the development of the cup, Jäger (1993) later thought *Amaltheocrinus* to be intermediate between cyrtocrinids and millericrinids, and he subsequently (pers. comm. 2002) considered *Amaltheocrinus* to constitute a family of its own with mixed characters of Millericrinida and Cyrtocrinida, leaving assignment to an existing order open. One of the main reasons for such treatment is the presence or absence of a basal circlet in cups of *Amaltheocrinus*; basals are well developed in millericrinids, but only exceptionally in cyrtocrinids (see also Hess 2006). In the forthcoming revision of the *Treatise* (Hess in prep.), *Amaltheocrinus* will be placed in the Millericrinida leaving assignment to a given family open. As long as elements of the cup are unknown, assignment of Cyclocrinidae and *Cyclocrinus* to an order is not possible. Columnal facets of *Amaltheocrinus* partly resemble those of Triassic crinoids such as *Qingyanocrinus* (Stiller 2000), but the Triassic form has circular cirrus sockets. Stiller (2000) proposed the family Qingyanocrinidae for the genus, but left assignment to a higher taxon open. In the *Treatise* (Hess, in prep.) the following diagnosis is foreseen.

Order uncertain
Family Cyclocrinidae SIEVERTS-DORECK 1953
[Cyclocrinidae SIEVERTS-DORECK in Ubaghs 1953: 764]

Crown unknown. Columnals cylindrical, mostly large and low, latera may be weakly convex; rarely axillary columnals or columnals with additional facets indicating branching, lateral sockets for small side branch also occur. Pluricolumnals exceptional. Lumen of central canal very narrow. Facets with numerous tubercles that may be uniformly distributed or arranged in groups, rarely ringlets or vermiculi or a smooth surface. There may be a fine marginal crenulation. Small columnals may have a few, mostly paired, radial crenulae. Attachment by disc with one to multiple concave column facets. Loose stereom near articular facets and around the lumen. Middle Jurassic–Early Cretaceous.

Cyclocrinus D'ORBIGNY 1850: 291 [**Bourgueticrinus rugosus* D'ORBIGNY 1841: 96; SD de Loriol 1886: 2] [= *Acrochordocrinus* TRAUTSCHOLD 1859: 112 (type, *A. insignis*; M]. Characters of family. Middle Jurassic (Bajocian)–Late Jurassic (Oxfordian): Europe (France, Germany, Poland, Russia, Switzerland); Early Cretaceous (Albian): England.

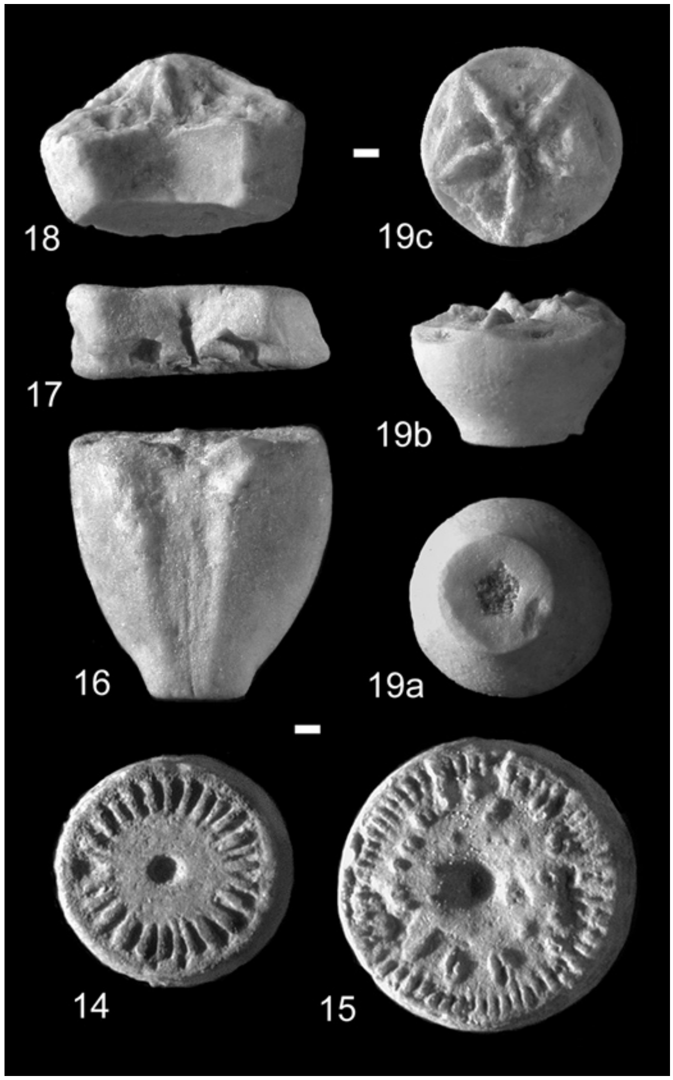


Fig. 14–19. *Amaltheocrinus amalthei* (QUENSTEDT), Pliensbachian, Germany. 14) Columnal facet, Etzelsdorf nr. Neumarkt. (NMB M10492). 15) Columnal facet, Etzelsdorf nr. Neumarkt (NMB M10490). 16) Adoral view of radial, Sulzkirchen (JME PL 1993/34) (Jäger 1993: Fig. 32b). 17) Adoral view of first primibrachial (IBr1), Sulzkirchen (JME PL 1993/49) (Jäger 1993). 18) Adoral view of axillary second primibrachial (IBr2), Sulzkirchen (JME PL 1993/51) (Jäger 1993). 19) Cup of fused radials, proximal (lower) (a), lateral (b) and distal with facets (c) for IBr1, Sulzkirchen (JME PL 1993/40) (Jäger 1993: Fig. 38). Photographs Hess. Scale bars: 1 mm.

Conclusions

Cyclocrinus is a very unusual crinoid in several aspects. It is the only post-Palaeozoic form which combines the following characters: axillary columnals, columnals with "unfinished" facets, well-developed facets lacking a lumen, columnals with sockets for side branches and columnals from the same location widely varying in shape and ornamentation of facets. Despite more than one and a half century of intense collection in the well-researched Jurassic and Cretaceous strata of Europe and Russia, it is the only large crinoid from which parts of cup or crown are still unknown. This is also the reason why the systematic position of *Cyclocrinus* remains enigmatic, though affinities exist with both millericrinids and cyrtocrinids.

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Plate I

Columnals of *Cyclocrinus rugosus* (d'Orbigny) (1–17) and *Millericrinus* sp. (18) from Bathonian and Callovian locations. Photographs Hess. h: height. Scale bars: 1 mm.

1) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Ramiswil (NMB M10639, R. Cartier): columnal, lateral with socket (a) and facets (b, c). 2) *Cyclocrinus rugosus*, Anceps-Athleta-Schichten, Schleitheim (NMB M10640): oblique view of columnal with flat lower facet and small, concave upper facet (h: 8.8 mm). 3) *Cyclocrinus rugosus*, Varians-Schichten, Lostorf (NMB M10641, A. Erni): pluricolumnal with very small and concave upper facet, oblique lateral (a) and upper facet (b). 4) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Hornussen (Wolftel) (NMB M10642, H. Hess): oval columnal with very small socket at narrow end (h: 4.4 mm). 5) *Cyclocrinus rugosus*, Varians-Schichten, Lostorf (NMB M10643, A. Erni): oblique lateral view of pluricolumnal composed of two unequal columnals. 6) *Cyclocrinus rugosus*, Varians-Schichten, Lostorf (NMB M10644, A. Erni): oblique lateral view of cup-shaped columnal with closed axial canal. 7) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10645, R. Cartier): small high columnal with closed axial canal on upper facet, oblique lateral (a) and lower facet (b). 8) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10646, R. Cartier): small high columnal, lateral with small socket (a) and upper facet (b). 9) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10647, R. Cartier): oblique lateral view of axillary columnal. 10) ?*Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10648, R. Cartier): small columnal with relatively wide lumen and facets with tetrameric symmetry, lateral (a) and facets (b, c); assignment doubtful. 11) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10649, R. Cartier): facet of irregular axillary columnal, smaller facet without axial canal (h: 6.3 mm). 12) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10650, R. Cartier): axillary columnal, smaller facet without axial canal, crest with stereomic thickening (h: 3.9 mm). 13) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10651, R. Cartier): axillary columnal with nearly vertical facet. 14) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10652, R. Cartier): axillary columnal with nearly vertical facet, lateral (a), oblique upper (b). 15) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M9586, R. Cartier): facet of columnal with grouped tubercles and crenulate periphery (h: 4 mm). 16) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10485, R. Cartier): wedge-shaped columnal with four facets, lateral (a), lower concave facet (b) and upper convex facet (c). 17) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10653, R. Cartier): axillary columnal with slit-like axial, canal across crest, lateral (a), upper (b). 18) *Millericrinus* sp., Macrocephalus-Schichten, Sangetel (NMB M10654, R. Cartier): pluricolumnal, lateral (a) and facet (b).

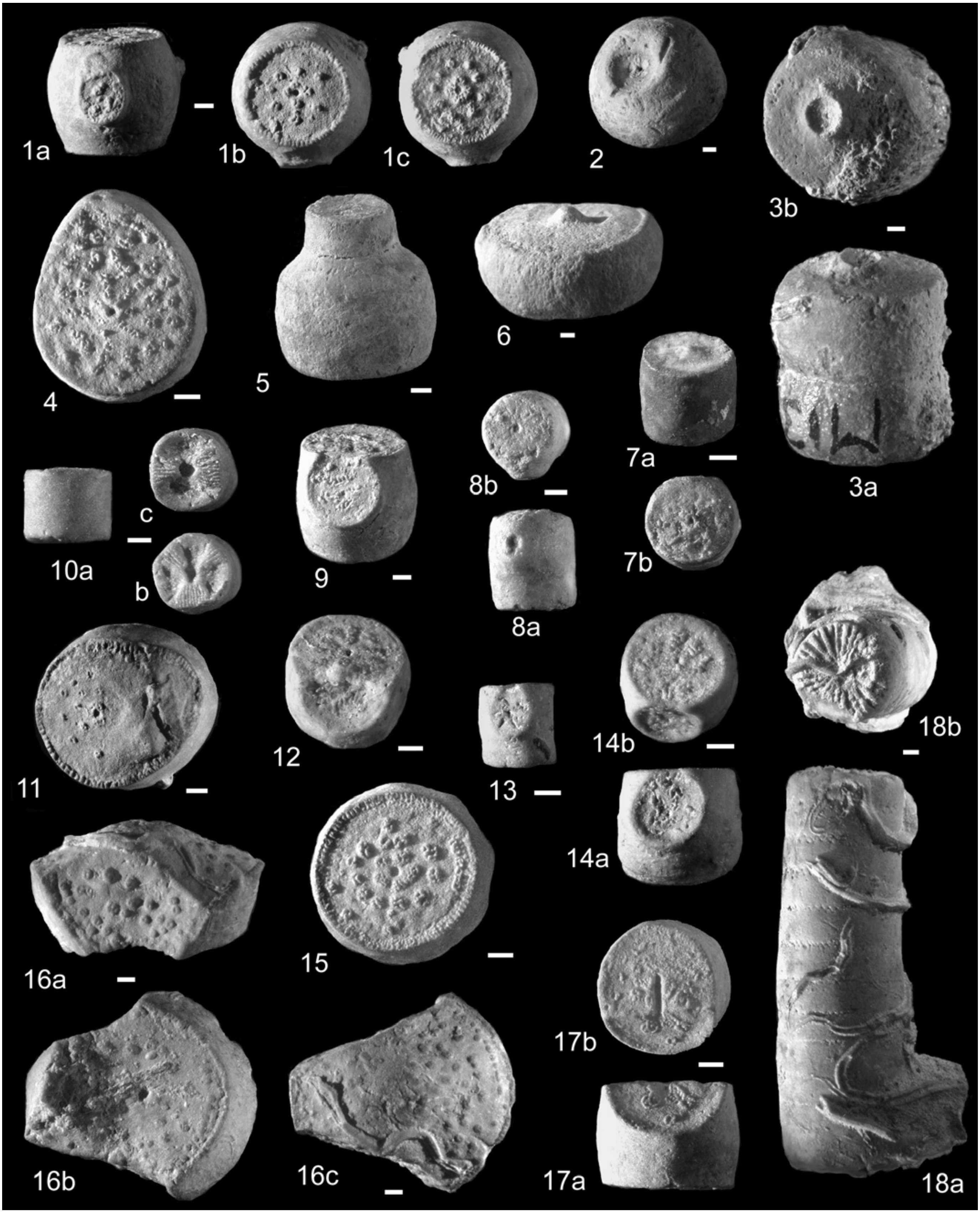
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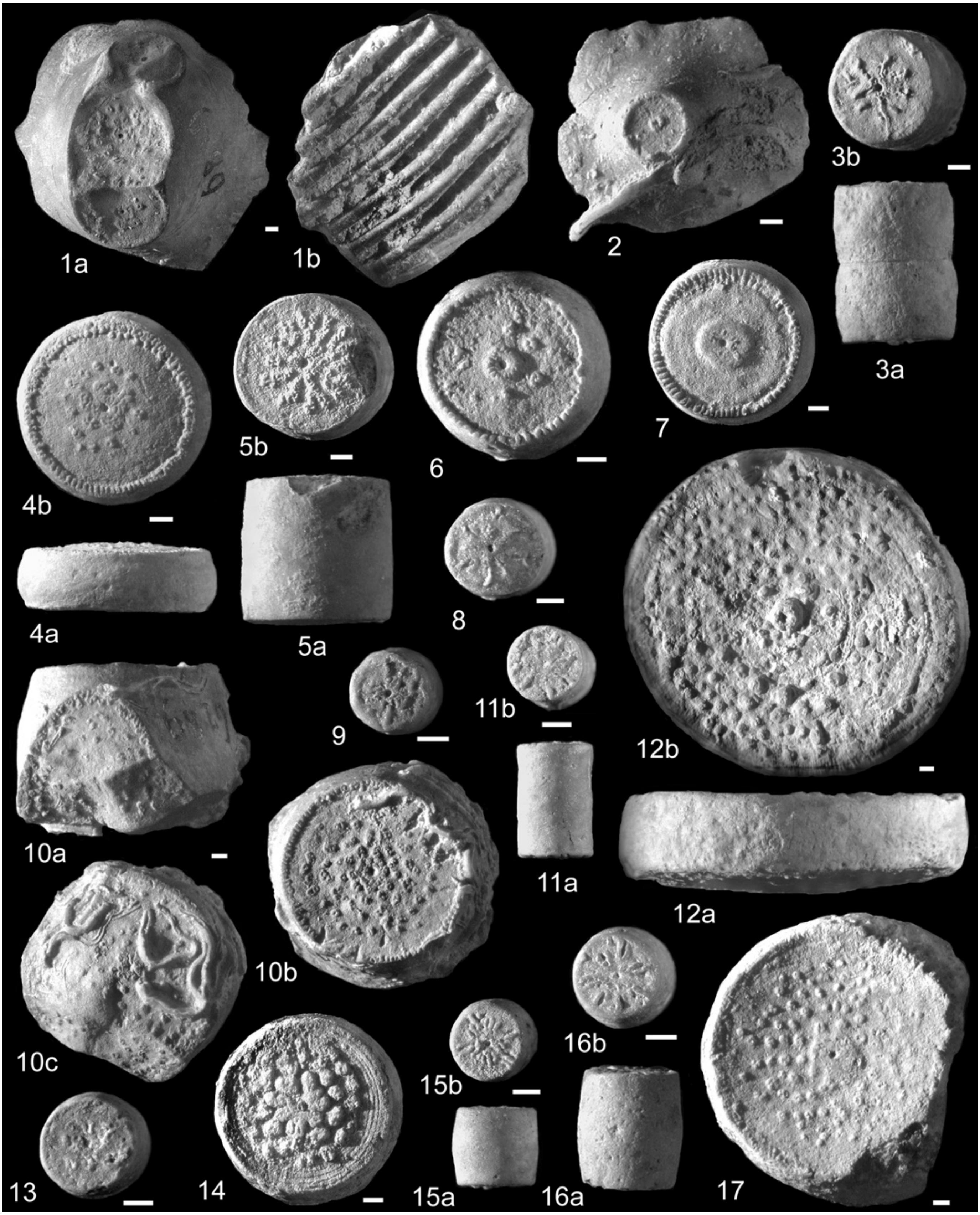
Plate II

Attachment discs (1, 2) and columnals (3–17) of *Cyclocrinus rugosus* (D'ORBIGNY) from Bathonian to Oxfordian locations. Photographs Hess. h: height. Scale bars: 1 mm.

1) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10482, R. Cartier): attachment disc with three facets, upper side (a) and lower side with impression of bivalve shell (b). 2) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10481, R. Cartier): small attachment disc grown into bivalve. 3) *Cyclocrinus rugosus*, Varians-Schichten, Lostorf (NMB M10655, A. Erni): pluricolumnal, lateral (a) and upper facet (b). 4) *Cyclocrinus rugosus*, Anceps-Athleta-Schichten, Schleitheim (NMB M10656): columnal, lateral (a) and upper facet (b). 5) *Cyclocrinus rugosus*, Anceps-Athleta-Schichten, Schleitheim (NMB M10657): high columnal, lateral (edge damaged) (a) and upper facet with tubercles in radial rows (b). 6) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10483, R. Cartier): facet of columnal with raised perilumen and sparse, grouped tubercles (h: 5.8 mm). 7) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10484, R. Cartier): facet of columnal with raised perilumen and crenulate periphery, tubercles lacking (h: 6.6 mm). 8) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10658, R. Cartier): facet of small columnal (h: 3.7 mm). 9) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10659, R. Cartier): facet of small columnal with small rosette and radial crenulae (h: 3 mm). 10) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10660, R. Cartier): large columnal with four lateral facets lacking lumen, lateral (a), upper facet (b) and lower facet (c). 11) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10661, R. Cartier): small high columnal, lateral (a) and facet (b). 12) *Cyclocrinus rugosus*, Cordatus-Schichten, Elfingen (NMB M10662, H. Hess): large columnal, lateral (a) and facet (b). 13) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10663, R. Cartier): facet of columnal with crenulae changing to tubercles (h: 3.3 mm). 14) *Cyclocrinus rugosus*, Anceps-Athleta-Schichten, Schleitheim (NMB M10664): facet of somewhat weathered columnal with grouped tubercles and growth lines (h: 5.5 mm). 15) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10665, R. Cartier): barrel-shaped columnal, lateral (a) and facet with radial crenulae (b). 16) *Cyclocrinus rugosus*, Macrocephalus-Schichten, Sangetel (NMB M10486, R. Cartier): barrel-shaped columnal, lateral (a) and facet with paired radial crenulae (b). 17) *Cyclocrinus rugosus*, Anceps-Athleta-Schichten, Schleitheim (NMB M10666): presumed upper facet of distal columnal near attachment disc, lower facet is convex (h: 4.8 mm).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