Acta Geologica Polonica, Vol. 53 (2003), No. 4, pp. 301-320

The Jurassic crinoid genus *Cyclocrinus* d'Orbigny, 1850: still an enigma

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ABSTRACT:

Radwańska, U. & Radwański, A. 2003. The Jurassic crinoid genus *Cyclocrinus* d'Orbigny, 1850: still an enigma. *Acta Geologica Polonica*, **53** (4), 301-320. Warszawa.

A rich collection of isolated columnals and fragmentary pluricolumnals, varying considerably in size, shape, and sculpture, from the Upper Oxfordian of the Couiavia region (northwestern Central Poland), is the basis for a critical discussion of the crinoid genus *Cyclocrinus* and its species. These are all based on dissociated columnals with tuberculate articular faces, and all with similar if not identical arrays of tubercles. The collection studied contains tuberculate columnals, as well as those with plain articular faces, which acquire tuberculation when etched with acids. This indicates the corrosional nature of tuberculation in the newly established species, *Cyclocrinus couiavianus* sp.nov., and in all other *Cyclocrinus* material. The structure of fragmentary pluricolumnals, whose arching and branching are reminiscent of root systems of some bourgueticrinids, would suggest that all *Cyclocrinus* material represents nothing else but modified radicular cirrals of unrecognizable members of the order Bourgueticrinida Sieverts-Doreck, 1953, rather than Cyrtocrinida or Millericrinida as previously assumed.

Key words: Articulate crinoids, *Cyclocrinus*, New species, Crinoid root systems, Upper Jurassic, Oxfordian, Poland.

INTRODUCTION

The subject of the present paper is the crinoid genus *Cyclocrinus*, established by d'Orbigny (1850). It is enigmatic in view of the fact that ever since its erection, based on three species of isolated columnals, relevant parts of the crowns have not been recorded. This explains why in the *Treatise on Invertebrate Paleontology* the genus is characterized solely by its columnals. Intriguing, however, is its listing in the basic systematic account (Wienberg Rasmussen 1978, p. *T*826), and not in the separate category of taxa based on disarticulated skeletal elements (Jeffords 1978, pp. *T*930-*T*937). Such special treatment has certainly been triggered by the peculiar tuberculate sculpture and remarkable size of columnals (up to 30 mm in diameter) which are not uncommon in various Middle to lower Upper Jurassic deposits of Europe. Even more intriguing is the fact that *Cyclocrinus* is the only genus contained in the family Cyclocrinidae Sieverts-Doreck, 1953, whose affinity still remains unclear (see Hess 1975; Ubaghs & *al*. 1978, p. *T*305), having been assigned either (Sieverts-Doreck 1953, followed by Hess 1975) to the order Cyrtocrinida, or (Ubaghs & *al*. 1978, p. *T*305, and Wienberg Rasmussen 1978, p. *T*826; earlier suggested by de Loriol 1878, p. 104) to the Millericrinida.

In the present paper, discussed are mass-aggregated isolated columnals of a unique shape, and longer stem(?) fragments of various size and structure, all previously unrecorded for the genus *Cyclocrinus*. Our analysis suggests that *Cyclocrinus*, and the Cyclocrinidae, should be reassigned at the order level. Moreover, the material collected comes from deposits of a late-Oxfordian age,

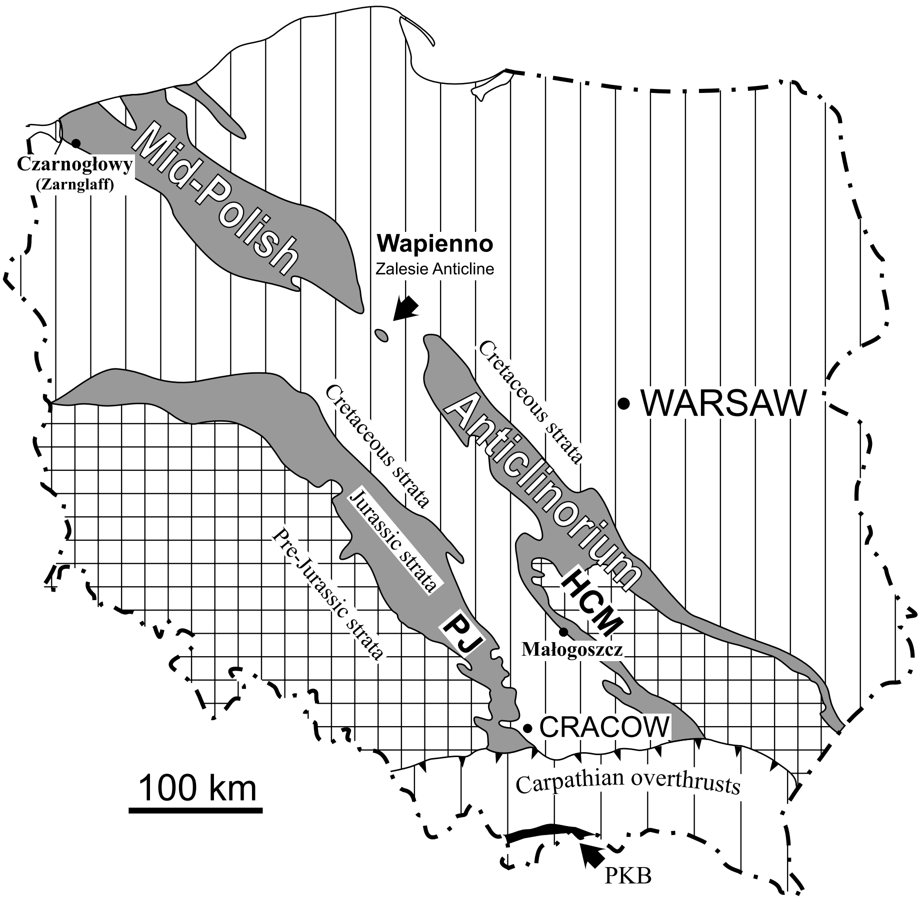

Fig. 1. Geological map of Poland, without Cenozoic cover, to show location of Wapienno Quarry in Zalesie Anticline, in the Couiavia region of the Polish Lowland (north-western Central Poland); **PJ** - Polish Jura, **HCM** - Holy Cross Mountains, **PKB** - Pieniny Klippen Belt in the Carpathians; indicated is also the locality Małogoszcz which has yielded numerous echinoderms (crinoids, echinoids, starfish) of Early Kimmeridgian age (adopted from MATYJA & WIERZBOWSKI 2000, fig. 1)

and thus represents the stratigraphically youngest members of these two taxa to date.

As our conclusions offer quite a new insight into the nature of *Cyclocrinus*, the present paper is divided into two parts, the first providing a description compatible with that of previous authors, whilst the second uses terminology conforming to the newly postulated nature of the genus.

PART 1. THE CURRENT STATUS OF *CYCLOCRINUS*

Provenance of material

Most of the material studied comes from the Wapienno Quarry, situated in the salt-domed anticline of Zalesie (Couiavia region) in the Polish Lowland, northwestern part of Central Poland (see Text-fig. 1). The whole area of the Polish Lowland bears an uneven cover of Palaeogene/Neogene (up to a few hundred metres thick) and Pleistocene (glacial) deposits upon degraded Alpine (Laramide) tectonic structures featuring the whole area of Poland beyond the Carpathian overthrusts (see Text-fig. 1; compare data by KUTEK & GŁAZEK 1972). Of these tectonic structures, the backbone is formed by the Mid-Polish Anticlinorium, along which Jurassic sequences are exposed in westernmost Pomerania in the northwest (the main locality being Czarnogłowy, see Text-fig. 1, and RADWAŃSKA 1999, pp. 291 and 298-299) and around the Holy Cross Mountains (HCM in Text-fig. 1) in the southeast. The Holy Cross structure, with its Variscan core, was uplifted as a result of the interference of the Mid-Polish Anticlinorium with the Carpathian fore-bulge arch external to the Carpathian fore-deep (see KUTEK & GŁAZEK 1972; MARCINOWSKI & RADWAŃSKI 1983, 1989). Along the Carpathian fore-bulge arch, Jurassic sequences are also exposed in the Polish Jura (PJ in Text-fig. 1) whose southernmost tip is the Cracow Upland, around and within the city of Cracow (see Text-fig. 1).

Comparative material comes from both the Holy Cross Mountains margins and the Polish Jura, including the Cracow Upland. A single report is from the Jurassic sequence of the Pieniny Klippen Belt (PKB in Text-fig. 1) in the Carpathians, discussed below.

The subsurface occurrence of Jurassic strata in the Couiavia region was first recorded by ZEUSCHNER (1847a,b), who studied a borehole section in the nearby anticline at Ciechocinek. In the Zalesie Anticline, Jurassic strata under a thin cover of Pleistocene deposits were recognized near Barcin/Krotoszyn as early as the 1850s (see RUNGE 1870, pp. 48-49). A limekiln and an adjacent quarry, soon called Wapienno Quarry, were established in 1858 (see JENTZSCH 1877, p. 162; 1884). Similar subsurface exposures at Bielawki (*Hansdorf* in the German literature), discovered in 1860, were first reported on by RUNGE (1870, pl. 2; see also JENTZSCH 1884, p. 41), and soon exposed at Bielawy Quarry. The easily accessible, ubiquitous fossils of various kinds have then attracted the attention of many specialists, amongst whom Ferdinand ROEMER (1878), GELHORN, DAMES, VON AMMON (*fide* JENTZSCH 1884, pp. 42-43), LANGENHAN (1890), and JAEKEL (1892), whose discoveries were summarized and complemented by GALLINEK (1895, and 1896, pp. 354-362; see also SCHMIDT 1905).

Little, if anything, was added to the above data until the early 1970s when the Couiavia Cement Plant was established, and its geological prospecting co-surveyed by the staff of the Faculty of Geology, University of Warsaw. The present-day picture of the tectonics and stratigraphical context of the Couiavian salt-domed anticlines and adjacent parts of the Mid-Polish Anticlinorium relies on these studies (MATYJA & *al.* 1985; MATYJA & WIERZBOWSKI 1985, 1998, 2000, 2002).

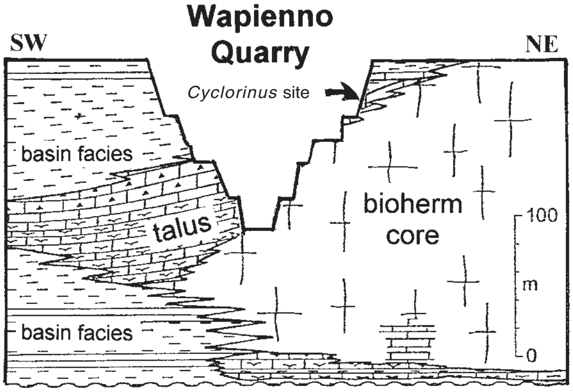

Fig. 2. Sketch of facies distribution of the Upper Jurassic (Oxfordian) sequence exposed at Wapienno Quarry, to show the provenance of mass-aggregated remains of *Cyclocrinus couiavianus* sp.nov. (adopted from MATYJA & *al*. 1985, fig. 4)

The Jurassic sequence of the Zalesie Anticline is composed of a sponge-cyanobacterial carbonate buildup of the biohermal type, surrounded by a kind of talus composed of detrital limestones, locally more or less intensively slumped. The sequence continues throughout the entire Oxfordian, with underlying Callovian deposits condensed, up to the Lower Kimmeridgian – Lower/Middle Volgian marly-silty basin facies indicative of drowning of the buildup (MATYJA & *al.*1985). Recognized thus was the halokinetic rise of the basement which favoured the existence and development of carbonate buildup on the seafloor, and its further growth up to, and/or above, wave base, to become supposedly capped by a reef-like community of hermatypic corals (see MATYJA & WIERZBOWSKI 1985, pp. 32-33 and fig. 1).

Two huge quarries, Wapienno Quarry and Bielawy Quarry, have been established along the southern limb of the Zalesie Anticline, for the exploitation of lime and crude material for Portland cement. Exposed at Wapienno Quarry, over 100 metres deep and about 1.5 km wide, are both the buildup and its talus (see Text-fig. 2). The Pleistocene cover (tills and glaciofluvial shingle) varies in thickness from almost nil to less than 10 metres.

Note that sections exposed at Wapienno and Bielawy quarries have in some papers been referred to as Barcin, or Piechcin-Barcin, in reference to small towns nearby (see COLLINS & WIERZBOWSKI 1985, RADWAŃSKI 2000).

Faunal content

The rich faunal spectrum of the Jurassic strata in the Couiavia region, and their echinoderm content, were already recognized by ZEUSCHNER (1847a, b), who recorded, among other fossils, a single species of crinoid ("*Pentacrinus angulatus* GOLDFUSS") and two species of the regular echinoid *Cidaris*.

The ubiquity of a highly diverse fauna, particularly crinoids at Bielawy Quarry, soon attracted the attention of Otto JAEKEL, whose classic monograph (JAEKEL 1892) was based on material from Solnhofen and other sections in Germany, as well as from this very quarry. From Bielawy Quarry he reported two microcrinoid species, *Plicatocrinus tetragonus* JAEKEL, 1892, and *Tetracrinus langenhani* JAEKEL, 1892. In the *Treatise on Invertebrate Paleontology*, the former is partly objected in the text (WIENBERG RASMUSSEN 1978, p. *T*829), but well re-illustrated (compare Jaekel 1892, pl. 25, figs 1, 6, 6b = Wienberg Rasmussen 1978, fig. 557/1h-1j).

Extensive collecting by Jentzsch (1877, 1884), Langenhan (1890), and Gallinek (1895, 1896) from Bielawy and Wapienno quarries has resulted in the recognition of almost all invertebrate phyla plus some fish and reptile teeth. Of crinoids, Gallinek (1896) reported the occurrence of two species, described as "*Pentacrinus pentagonalis* Goldfuss" and "*Pentacrinus cingulatus* Münster".

A sequel to the above recognitions has appeared as late as the 1980s when ammonite assemblages (Matyja & *al.* 1985), significant because of their Submediterranean *versus* Subboreal biogeographical affinities (Matyja & Wierzbowski 2000, 2002), were recognized. These appeared to co-occur with hermatypic corals (Matyja & Wierzbowski 1985), diverse brachiopods, locally mass-aggregated (Krawczyński 2003), mass-occurring sponges (Kołsut, in prep.), prosopid and homolid crabs (Collins & Wierzbowski 1985), rare large-sized *Rhabdocidaris nobilis* (Münster, 1826) associated with diverse cidaroids and other regular echinoids (Radwańska 2000, 2003a), disintegrated *Sphaeraster* and other starfish (Radwańska 2003b), as well as mass-aggregated remains of *Cyclocrinus*, first reported by Radwański (2000).

The present-day exposures at Wapienno and Bielawy quarries show all of these much varied and locally ubiquitous faunal elements to occur in some layers in the talus facies of the carbonate buildup (see Matyja & Wierzbowski 1985). They occur either as detrital elements, commonly in slump-originated layers, or in isolated blocks (olistholiths, up to over 1 metre in diameter) within the slump avalanches. This clearly indicates that all faunal assemblages in the talus deposits were derived from shallow depths, situated above the wave base, in the photic zone. All were destroyed by stormy(?) agitation when the salt-diapired basement led to a successive rise of the carbonate buildup (cf. Matyja & Wierzbowski 1985, fig. 1).

All the *Cyclocrinus* material studied comes from a set (arrowed in Text-fig. 2), about 15 metres thick, of detrital limestones belonging to the upper part of the talus fringing the buildup.

Stratigraphical age

The entire sequence exposed at Wapienno Quarry is of Oxfordian age, with the lowest Oxfordian overlying the condensed Callovian, and terminated at the highest Oxfordian (Matyja & *al.* 1985; Matyja & Wierzbowski 2000, 2002). The *Cyclocrinus* site, situated in the upper portion of the talus sequence at Wapienno Quarry (arrowed in Text-fig. 2), is thus aged as Upper Oxfordian, Bimammatum and/or Planula Zone (see Matyja & Wierzbowski 2002).

Previous Polish records of *Cyclocrinus*

The first unequivocal record of the genus *Cyclocrinus* in Poland is that by Wójcik (1910, p. 472), who listed "*Cyclocrinus macrocephalus* Lor." from the Callovian sands at Filipowice (Cracow Upland).

Escaped from recognition is an old record from the Polish Jura, repeated by Różycki (1953), who listed "*Cyclocrinus macrocephalus* de Lor." from the Callovian of Rudniki; he also listed "*Mespilocrinus macrocephali* Qu." from Poręba Mrzygłodzka (= Kierszula), the locality of F. Roemer (1870), whose determination is objected below.

The only illustration of *Cyclocrinus* is by Merta (1972, p. 37 and pl. 4, fig. 4a-4b), who, under the name of "*Cyclocrinus areolatus* (Moesch)", figured one of two large-sized, tuberculate specimens collected from the Upper Oxfordian of Opoczno (Holy Cross Mountains); these two specimens are re-studied herein (Text-fig. 6).

Unacceptable to us is the record of "*Cyclocrinus rugosus* (d'Orbigny)" and "*Cyclocrinus* sp." from the Jurassic sequence of the Pieniny Klippen Belt; neither sketches nor photographs of poorly preserved, small-sized specimens given by Głuchowski (1987, figs 13/1, 13/4 and pl. 1, figs 1-6) allow assigment to the genus *Cyclocrinus*.

Material studied

The talus lithologies at Wapienno Quarry, from which the material studied comes (see Text-fig. 2), are detrital limestones, poorly to indistinctly bedded, with a variable content of marl which gives a greyish colour to irregular layers or portions thereof. The frequency of *Cyclocrinus* remains varies from isolated and widely scattered columnals, to rock-building masses. In the latter case, layers composed of *Cyclocrinus* columnals, longer stem(?) fragments, referred herein as pluricolumnals, and abundant hash compose typical encrinites (see Text-fig. 3), usually devoid of a marly admixture, and thus whitish to even bright-white in colour. From such encrinites, *Cyclocrinus* remains are difficult to extract, as the rock seldom cracks along the surface of these remains, and usually fractures along cleavage planes $\{10\bar{1}1\}$ of composing calcite crystals. Columnals from marly layers are easy to extract, usually due to the presence of a thin marly (? diagenetic) film around particular specimens, which then are often more or less corroded, having a tuberculate pattern on their faces well visible

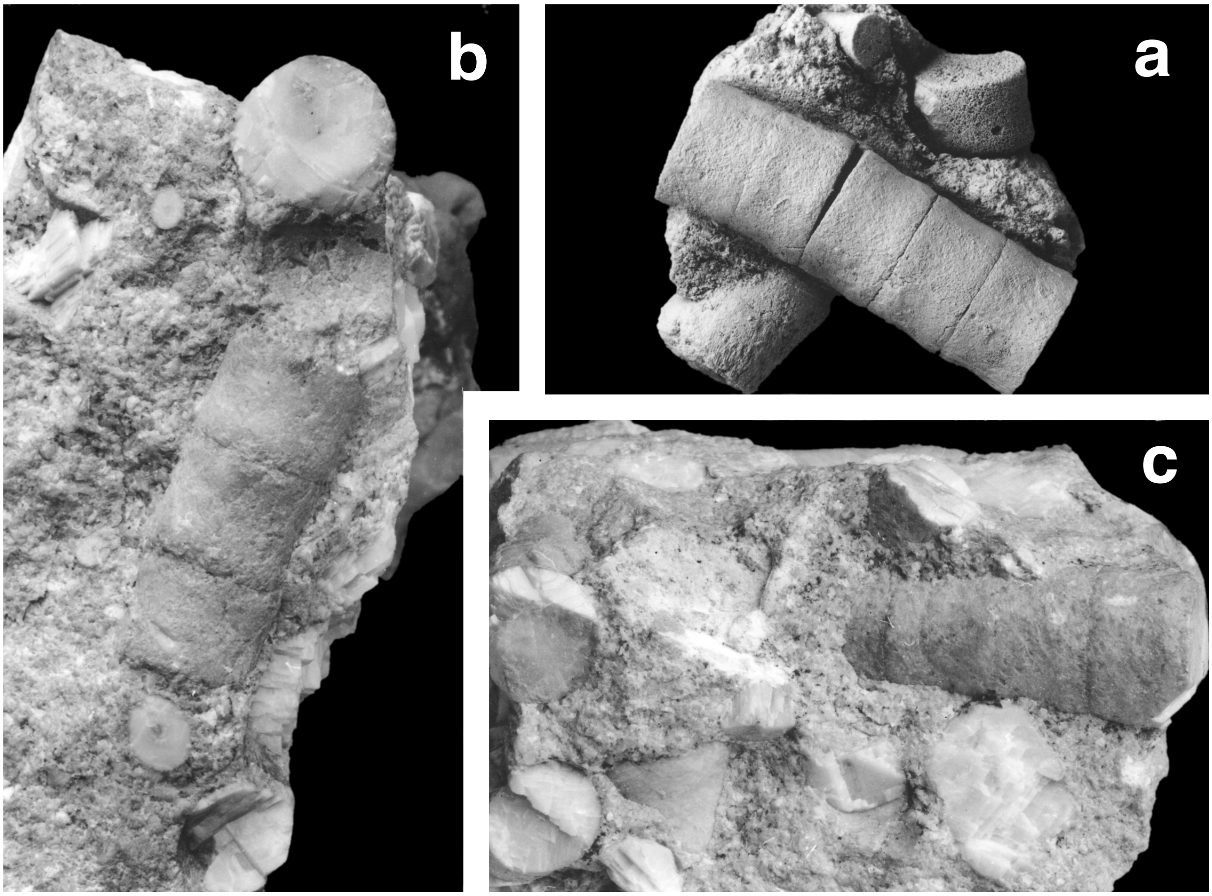

Fig. 3. Encrinites composed of isolated columnals, longer pluricolumnals, and abundant hash of *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry: **a** - Weathered surface, **b**-**c** - Hammered surface; all × 1.5

(see Text-fig. 8.7-8.13). Columnals obtained from encrinites look fresh, with almost glassy luster, but with articular faces usually plain (see Text-fig. 8.1-8.6).

Of the countless columnals observed, only some average-shaped forms, and all extremes in shape, size, or sculpture, have been collected.

In the taxonomic treatment below, all *Cyclocrinus* material collected from Wapienno Quarry is assumed to be conspecific.

The nature of tuberculation

The fact that the tuberculation on articular faces in *Cyclocrinus* columnals appears in corroded specimens (? diagenetically; possibly, by pressure-solution) has led the present authors to focus on comparative *Cyclocrinus* material from Middle and Upper Jurassic deposits in Poland. The most spectacular tuberculation is displayed by specimens from a condensed residual lag of Callovian age at Wola Morawicka (Holy Cross Mountains). This glauconitic lag, up to 10-15 cm thick, is replete with diverse fossils (e.g. ammonites of the Macrocephalus and the Calloviense zones, see SIEMIĄTKOWSKA-GIŻEJEWSKA 1974), more or less corroded and commonly overgrown by stromatolitic crusts (see SZULCZEWSKI 1967, figs 3-4). The presence, in such a deposit, of the most clearly tuberculate *Cyclocrinus* columnals (see Text-fig. 4) has reinforced our idea of the corrosional nature of tuberculation on articular faces in *Cyclocrinus* columnals.

To substantiate this observation, some of the columnals collected at Wapienno Quarry have been treated in a dilute acetic acid, others in citric acid. Analyzed were only columnals extracted from encrinites, *i.e.* those with plain, non-tuberculate articular faces.

After immersion in acetic or citric acid for a couple of days, tuberculation appeared to variable extents on both faces in most of the columnals treated. Specimens immersed in acid not fully, acquired tuberculation solely on their parts treated (see Text-fig. 5). Some specimens treated with acid reacted differently, not developing tuberculation, but producing a compact crust of cal-

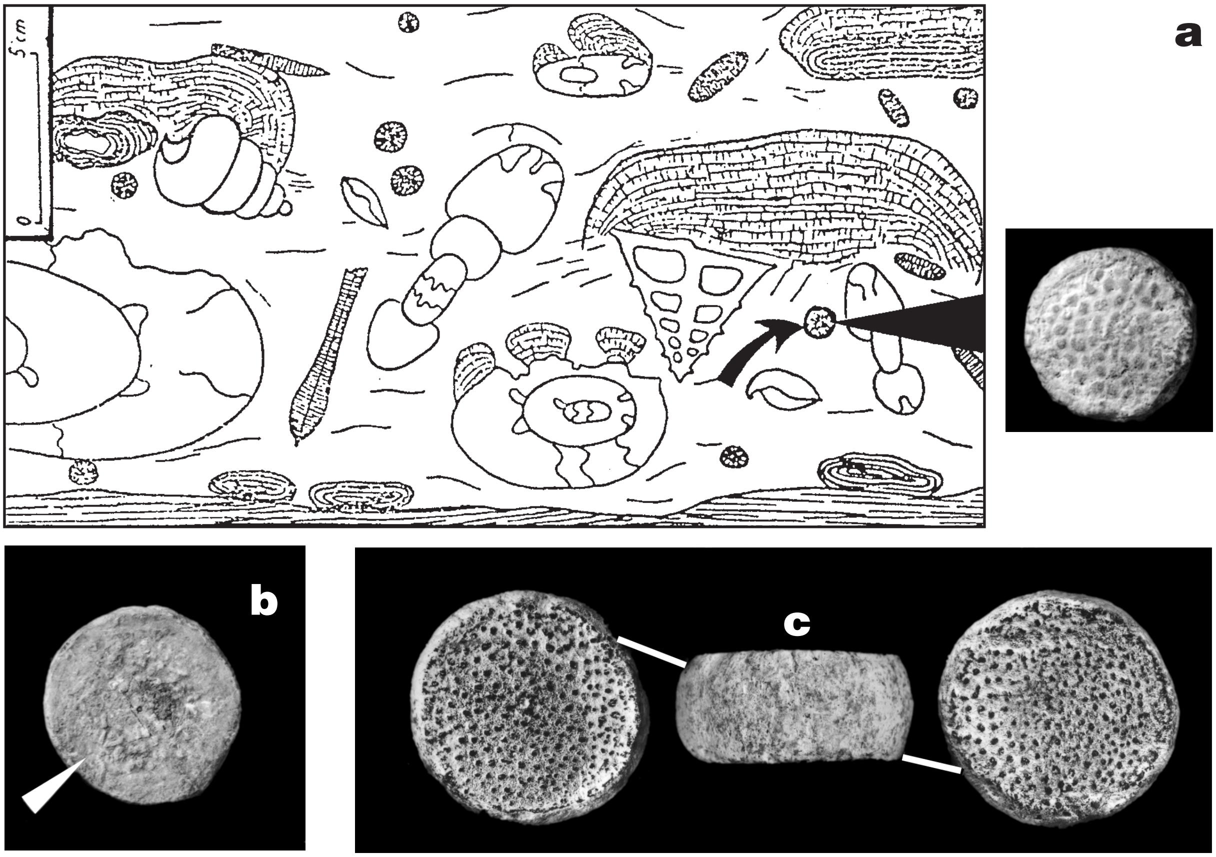

Fig. 4. **a** - Advanced tuberculation occurring in a *Cyclocrinus* columnal (× 1.5) from the condensed residual lag of Early Callovian age from Wola Morawicka, Holy Cross Mountains (adopted from SZULCZEWSKI 1967, fig. 4); **b**-**c** - Comparative specimens of tuberculate *Cyclocrinus* columnals from the condensed residual lag (the "Knobby Layer") of Callovian age at Kozłowiec/Czerwieniec, Cracow Upland (*b*, arrowed is a part with indistinct vermiculi) and at Wrzosowa, Polish Jura (*c*); all × 1.5

cium acetate, or citrate, respectively; the conditions of such differentiation remain as yet unclear.

In the present authors' interpretation, the tuberculation on articular faces of *Cyclocrinus* columnals is nothing else but a replica of the stereom meshwork (cf. MACURDA & *al*. 1978). Its structure may best be compared to that referred to by SMITH (1980, 1984) as *simple perforate* in echinoid plates (see SMITH 1980, fig. 1; 1984, fig. 3.2). The tubercles on the columnals studied are borne by the mineralised matter of the stroma, and are not a morphological feature of the calcite lattice.

To clarify the above, two conjoined columnals from the Upper Oxfordian of the Holy Cross Mountains (one of them was figured by MERTA 1972, pl. 4, fig. 4) have

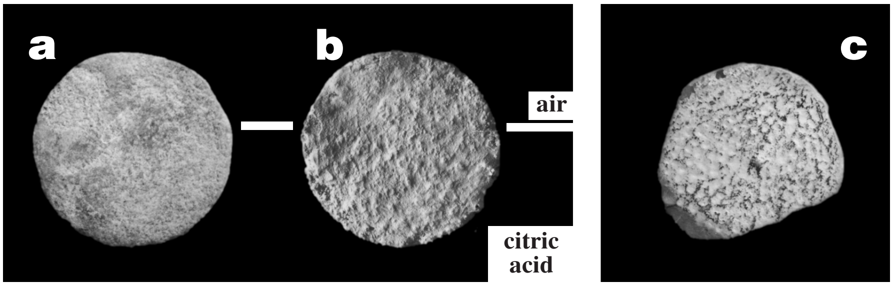

Fig. 5. **a**-**b** - Columnal of *Cyclocrinus couiavianus* sp.nov. (No. 5 *in* Text-fig. 8) from Wapienno Quarry, prior to (*a*) and subsequent to treatment with citric acid (*b*) when immersed with its lower portion only (white line indicates the level of immersion; slight tuberculation above is due to capillary fringing of acid); both × 1.5; **c** - Another columnal of *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry, after full immersion in citric acid; × 1.5

been separated mechanically and treated with citric acid. The result is that the tuberculation, *i.e.* the same stroma pattern, on one face mirrors that of the other (see Text-fig. 6). It is thus apparent that the definite stroma pattern continues throughout columnals in articulation.

The fact that etching turns the stroma into a positive relief, i.e. tuberculation, indicates that its fossilisation is stronger than that of the surrounding calcite lattice. A further study however is needed to determine the chemical product of this fossilisation, and its relationship with the primary organic tissue (collagenous fibres). Stronger mineralisation of the stroma is evident in all *Cyclocrinus* material which is typically tuberculate, although to variable extents.

When the corrosional nature of tuberculation and stronger mineralisation of the stroma are considered, it becomes clear why there is no previous report of *Cyclocrinus* columnals with articular faces sculptured by pits to oppose tubercles; nor any previous interpretation of how these tubercles could solely interlock two adjacent columnals (!).

In all *Cyclocrinus* columnals studied from Wapienno Quarry the pattern of tuberculation is practically identical, being composed of equally sized tubercles distributed regularly all over the faces. As such, it is regarded as a typical feature of the species. In other words, it confirms the conspecifity of the *Cyclocrinus* specimens from the Wapienno Quarry studied.

Comparative *Cyclocrinus* columnals from other Polish localities primarily originate from the condensed Callovian residual-lag deposits replete with corroded fossils (the so-called “Knobby Layer”, usually covered by the stromatolite). These specimens are all distinctly tuberculate and, as a rule, the stronger corrosion, the more advanced the tuberculation. This is illustrated by specimens coming from the “Knobby Layer” exposed at Wrzosowa in the Polish Jura (see Text-fig. 4c; cf. also SZULCZEWSKI 1968, fig. 17), Czerwieniec/Kozłowiec in the Cracow Upland (see Text-fig. 4b; cf. also WÓJCIK 1910, SZULCZEWSKI 1968, fig. 12), as well as Lasocin and Mnin in the Holy Cross Mountains (cf. SZULCZEWSKI 1968, fig. 22; SIEMIĄTKOWSKA-GIŻEJEWSKA 1974). Those from Wrzosowa are distinctly barrel-shaped, and those from Czerwieniec/Kozłowiec display locally indistinct vermiculi. On the other hand, weakly tuberculate are specimens from the less condensed Callovian sequence of Zalas in the Cracow Upland (cf. WÓJCIK 1910).

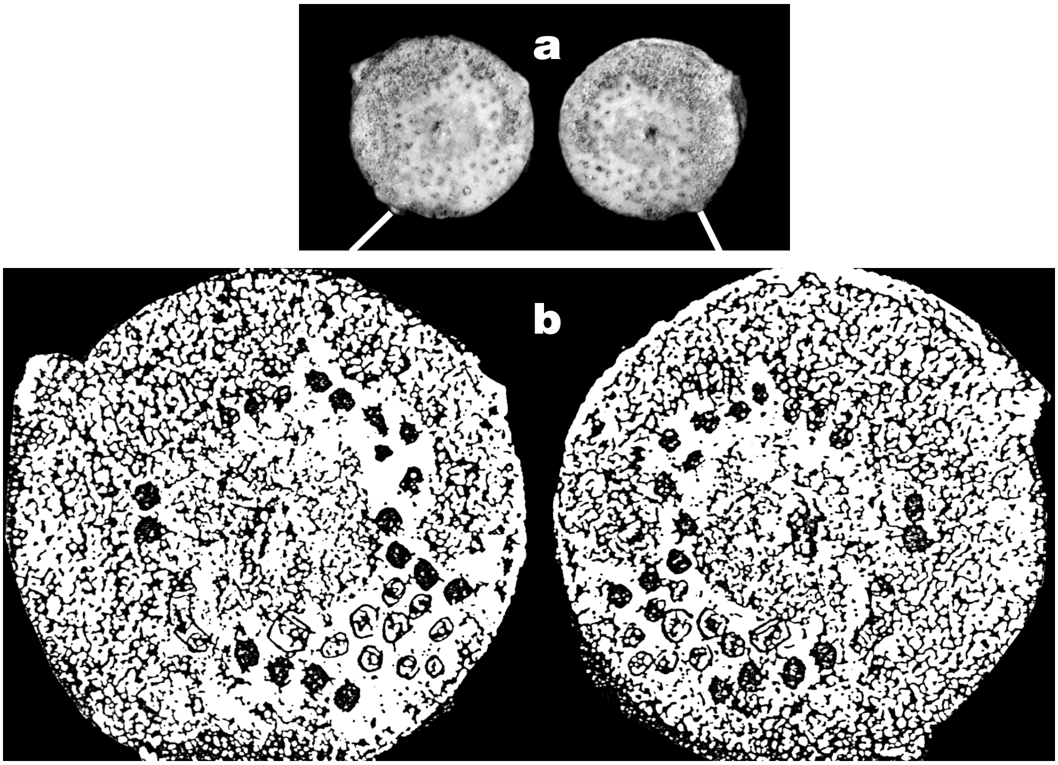

Fig. 6. Two originally conjoined columnals of *Cyclocrinus* separated, and treated with acetic acid, to show their mirrored tuberculation: **a** - General view, × 1.5; **b** - The same, magnified (× 5) and retouched. Comparative specimens from the Upper Oxfordian of Opoczno (Holy Cross Mountains); left-hand specimen is the one previously illustrated by MERTA (1972, pl. 4, fig. 4a-4b)

Taxonomic jungle

The original diagnosis of the genus *Cyclocrinus*, given by D'ORBIGNY (1850, p. 291), is very simple indeed: "*Ce sont des articles ronds sans rayons sur l'articulation*" [Columnals circular, devoid of crenulation]. When creating the genus, D'ORBIGNY assigned three species to it, namely *Cyclocrinus rugosus*, *C. annularis*, and *C. strangulatus*, as follows:

Cyclocrinus rugosus (D'ORBIGNY, 1841), which had earlier (1829; ? manuscript date, or a simple mistake), been referred to *Burgueticrinus*, but in fact first illustrated in D'ORBIGNY (1841, pl. 17, figs 16-19) as relatively large columnals with tuberculate articular faces, from the Middle Jurassic (Bajocian) of France;

Cyclocrinus annularis (F.A. ROEMER, 1839) = *Eugeniacrinites annularis* of F.A. ROEMER (1839, p. 17 and pl. 17, fig. 34a-b), a bead-like, small columnal with indistinct crenulation at the margin, and tuberculate around the central canal; the specimen came from the Middle Jurassic of Germany;

Cyclocrinus strangulatus D'ORBIGNY, 1850, indicated to be similar to the former, but having columnals more elongated (taller) and barrel-shaped.

Not matching the above diagnosis of the genus was thus the species *C. annularis* with its indistinct crenulation along the margin, as well as was *C. strangulatus*. With so few morphological features, it is understandable that the feature of tuberculation became decisive to DE LORIOL (1878, pp. 103-104; and 1886, pp. 1-3), who re-established the genus to comprise many forms illustrated under different generic names by authors such as QUENSTEDT (1858), TRAUTSCHOLD (1859), MOESCH (1867, 1874), GREPPIN (1870), and F. ROEMER (1870). To understand the taxonomic treatment by DE LORIOL (1878, 1886), previous studies are here briefly outlined.

In his monumental work *"Der Jura"*, QUENSTEDT (1858, pl. 68, figs 28-33) illustrated, under the name "*Mespilocrinites macrocephalus* QUENSTEDT, 1858", six tuberculate specimens differing from those of D'ORBIGNY (1841) by a more or less barrel-like shape. Of these, the smallest illustrated (QUENSTEDT 1858, pl. 68, fig. 31) is closely similar to the one figured by F.A. ROEMER (1839), that is *C. annularis*, whereas those illustrated in lateral view (QUENSTEDT 1858, pl. 68, figs 32-33), especially one much taller than wide (QUENSTEDT 1858, pl. 68, fig. 33) are reminiscent of *C. strangulatus* of D'ORBIGNY (1850). All these specimens are Callovian in age (*Macrocephalusschicht* of QUENSTEDT). Moreover, under the name "*Mespi1ocrinites amalthei*", QUENSTEDT (1858, pl. 24, figs 38-40) illustrated small-sized columnals, crenulated along the margin, from the Lower Jurassic of Germany. A very similar, if not identical, columnal was subsequently illustrated from the Middle Jurassic of the Polish Jura by F. ROEMER in 1870 (compare ROEMER's pl. 17, figs 9-10, with that of QUENSTEDT's pl. 24, fig. 40), who used the name "*Mespilocrinus macrocephalus* QUENST.". On the other hand, several years earlier, from the Aargauer Jura (*Birmensdorferschichten*), MOESCH (1867, pl. 7, figs 2*a*-2*c*) had illustrated, under the new name "*Mespilocrinus areolatus* MOESCH, 1867", three columnals identical to those of QUENSTEDT's *macrocephalus*, but of a different age (Late Jurassic, Oxfordian). MOESCH (1867) and F. ROEMER (1870), dealing with regional Jurassic faunas, overlooked or neglected the impressive report by TRAUTSCHOLD (1859).

TRAUTSCHOLD (1859) described a rich material of tuberculate, very large (diameters up to 30 mm, height to 9 mm) isolated columnals from the Lower Oxfordian (Cordatum Zone) of the Moscow region (Russia). After comparison with specimens presented by QUENSTEDT (1858), and a personal discussion with Friedrich August QUENSTEDT, he classified this material as the new genus and species, *Acrochordocrinus insignis* TRAUTSCHOLD, 1859.

The genus *Acrochordocrinus* was already synonymized with *Cyclocrinus* by DE LORIOL (1878, p. 103; and 1886, p. 3), a course of action accepted by both HESS (1975, p. 72) and by WIENBERG RASMUSSEN (1978, p. *T*826). Nevertheless, in the Russian literature it has long been regarded as separate (see e.g., GERASIMOV 1955, GERASIMOV & *al.* 1962, ARENDT & GEKKER 1964), and it still exists in a common use in the museum collections.

Of the specimens illustrated by TRAUTSCHOLD (1859, pl. 1, figs 1-11), the one which should be regarded as the type (fig. 1a-1c) is rectangular in lateral view, while two smaller ones are hourglass-like (fig. 3c-3d); some others (figs 5-10) are either ramified (figs 5, 7-9)

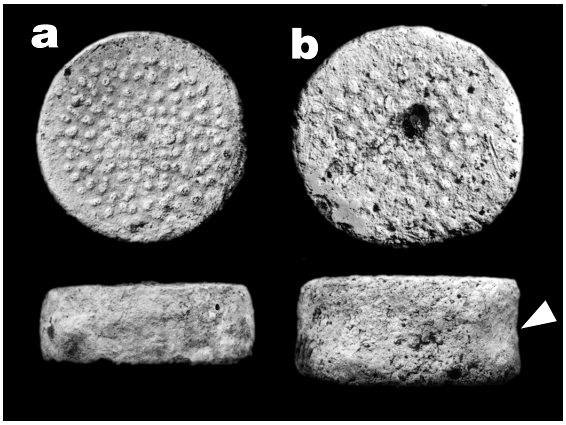

Fig. 7. Comparative columnals of "*Acrochordocrinus insignis* TRAUTSCHOLD, 1859" from the Lower Oxfordian (Cordatum Zone) of the Moscow region (Russia); arrowed is a slightly hourglass-like constriction of one columnal; × 1.5

or bifurcated (figs 6 and 10); none of the specimens illustrated is barrel-shaped. Topotypical material at the present authors' disposal contains (see Text-fig. 7a-7b) both rectangular and slightly barrel-shaped specimens; of the former, some are partially hourglass-like (arrowed in Text-fig. 7b).

TRAUTSCHOLD (1859, p. 111) suggested that the appearance and development of tuberculation was a result of weathering at exposure, but he considered this feature to be important in the diagnosis of his newly established genus, whose name referred to tuberculation (Greek *akrochordon* – a tubercle; see TRAUTSCHOLD 1859, p. 113). The generic diagnosis was thus very simple as well: "*Trochitae facie articulari plana verrucosa, verrucis irregulariter dispositis*" [Articular face of columnals flat, tuberculate, with the tubercles dispersed irregularly], and this certainly stimulated DE LORIOL (1878) to assign to the genus *Cyclocrinus* exclusively the tuberculate specimens.

Neither QUENSTEDT (1858) nor TRAUTSCHOLD (1859) referred to papers by D'ORBIGNY (1841, 1850) when creating the new taxa. Moreover, TRAUTSCHOLD (1859) was the only author who attributed the tuberculation to factors other than the original columnal morphology. In the present authors' interpretation, TRAUTSCHOLD's specimens acquired tuberculation either by synsedimentary or diagenetic corrosion.

DE LORIOL (1878, p. 103), with Swiss material at his disposal, suggested that *rugosus* of D'ORBIGNY (1841), *macrocephalus* of QUENSTEDT (1858), and *insignis* of TRAUTSCHOLD (1859), were conspecific although he differentiated these from *areolatus* of MOESCH (1867). As *rugosus* was absent from his material, DE LORIOL (1886) illustrated it later using French specimens. Nevertheless, the rich material illustrated by DE LORIOL (1878, pl. 14, figs 1-26; and 1886, pls 124-126) appears to have been classified very arbitrarily, which may be explained as follows.

A barrel-shaped columnal, finely crenulated along the margin and bearing papilla-like tubercles around the central canal (DE LORIOL 1878, pl. 14, fig. 2b), referred to as *C. macrocephalus*, does not differ from that reported as *C. rugosus* by DE LORIOL (1886, pl. 124, fig. 5b; re-figured by WIENBERG RASMUSSEN 1978, fig. 555/1c);

Of specimens assigned to *C. areolatus* by DE LORIOL (1878, pl. 14, figs 23-26), the three smaller ones match those presented by MOESCH (1867), but the fourth, being twice larger, and featuring an indistinct circular arrangement of tubercles (DE LORIOL 1878, pl. 14, fig. 23) does not differ from another specimen of *C. rugosus* of D'ORBIGNY (1841), reported by DE LORIOL (1886, pl. 124, fig. 7*a*; re-figured by WIENBERG RASMUSSEN 1978, fig. 555/1b).

A single specimen of *C. macrocephalus* presented by DE LORIOL (1878, pl. 14, fig. 21) bears very distinct worm-like tubercles (*vermiculi*), a feature noted in *C. rugosus* (D'ORBIGNY, 1841) by DE LORIOL (1886, pl. 124, fig. 1b; re-figured by WIENBERG RASMUSSEN 1978, fig. 555/1d).

Barrel-shaped specimens with papilla-like tubercles at the central canal occur both in *C. macrocephalus* and *C. areolatus* (compare DE LORIOL 1878, pl. 14, figs 14 and 25).

Of the specimens illustrated by DE LORIOL (1886, pls 124-126), columnals of identical morphology are present both in *rugosus* and *macrocephalus* (compare DE LORIOL's pl. 124, fig. 7-7a [Re-figured by WIENBERG RASMUSSEN 1978, fig. 555/1a-1b] and pl. 125, fig. 7; pl. 124, figs 5-6, 8 and pl. 125, figs 8-9 plus pl. 126, fig. 4). Into their variability range *areolatus* falls as well (see DE LORIOL 1886, pl. 126, figs 10-12).

It is apparent that sculptural features of *C. rugosus* (D'ORBIGNY, 1841), *C. macrocephalus* (QUENSTEDT, 1858), and *C. areolatus* (MOESCH 1867), overlap. Moreover, DE LORIOL's (1878, 1886) designations were evidently influenced by the stratigraphical age of the specimens, *rugosus* being Bajocian (see D'ORBIGNY 1841), *macrocephalus* Callovian or Late Bathonian, and *areolatus* Oxfordian (see DE LORIOL 1878, pp. 107, 109 and 111). Another species, distinguished by DE LORIOL (1878), as *Cyclocrinus renevieri* DE LORIOL, was of Neocomian age. The latter falls into the wide *amalthei* "group" of species (as noted by DE LORIOL 1878, p. 110), whose generic placement still remains a moot point (see WIENBERG RASMUSSEN 1978, p. *T*826 and *T*828; HESS 1975, p. 72; JÄGER 1993, pp. 75-87). Not discussed in the present paper are other species included with a query or not in the genus *Cyclocrinus* by DE LORIOL (1886, pp. 4-13, pls 122-123 and 127), which all belong to the *amalthei* "group".

If we reject *renevieri* from *Cyclocrinus*, then the hitherto known stratigraphical age of the genus should have been abridged down to the Lower Oxfordian (see MOESCH 1867; DE LORIOL 1878, 1886; GERASIMOV & *al.* 1962; HESS 1975, p. 72). The stratigraphical range of the genus *Cyclocrinus*, and the family Cyclocrinidae, is thus corrected as Middle to Upper Jurassic, more precisely Bajocian to Upper Oxfordian as here documented, rather than Lower Jurassic – Lower Cretaceous as indicated by UBAGHS (1978, p. *T*395) and WIENBERG RASMUSSEN (1978, p. *T*826).

The species content of the genus *Cyclocrinus* thus remains very poor indeed. HESS (1975, pl. 20, fig. 12), when illustrating a large-sized, tuberculate specimen from the Callovian of Switzerland, synonymized *areolatus* with *macrocephalus*. As indicated above, these two species cannot be properly distinguished from *rugosus*, which represents the only well-established species, indicated as the type already by DE LORIOL (1886, p. 2), and so accepted by WIENBERG RASMUSSEN (1978, p. *T*826).

Of note is that DE LORIOL (1878, p. 106 and pl. 14, fig. 20) was the only author who recorded and illustrated for *Cyclocrinus* skeletal elements other than columnals, namely an anchor-like fragment (holdfast) featured by small tubercles over its entire surface.

To conclude, all kinds of ornament features which may be seen on *Cyclocrinus* columnals, are such as slight crenulation at the margin, papilla-like tubercles oriented radially along the central canal, circular arrangement of tubercles, worm-like tubercles (*vermiculi*), and these appear in all species reported by earlier authors regardless of the age of particular specimens (Middle, or Late Jurassic).

The tuberculation, the nature of which is evidently corrosional, is more or less clearly developed in all species or specimens reviewed. As may be seen in illustrations in older literature items, the pronouncedness of tuberculation on *Cyclocrinus* columnals varies markedly, from distinct warts of various sizes in specimens of comparable size (see DE LORIOL 1878, pl. 14, figs 12 and 18), to those occurring as darker spots against a lighter background (see DE LORIOL 1878, pl. 14, fig. 1). In the present authors' opinion, this range of variation results from the variably advanced corrosion which progressed either during sedimentation, prior to the final burial of specimens, or during diagenesis.

Another feature should be commented on. This is the cylindrical shape, *i.e.* rectangular lateral profile, which in almost all the hitherto reported specimens is more or less flat barrel-like, with a tendency to form columnals taller than wide, and even distinctly elongated (see e.g. QUENSTEDT 1858, pl. 68, fig. 33). Exceptions are *C. rugosus* specimens some of which are flat-cylindrical, i.e. almost rectangular in lateral profile (see D'ORBIGNY 1841, pl. 17, fig. 16; DE LORIOL 1886, pl. 124, fig. 7 = WIENBERG RASMUSSEN 1978, fig. 555/1a), and *C. macrocephalus* figured by HESS (1975, pl. 20, fig. 12). Such flat-cylindrical, very large columnals are also those distinguished by TRAUTSCHOLD (1859) as *Acrochordocrinus insignis* from the Oxfordian of Russia. It is thus apparent that even the feature of cylindrical shape occurs throughout the stratigraphical range.

Our conclusion is that the material collected in Wapienno Quarry bears the closest similarities to the comprehensively documented "*Acrochordocrinus insignis* TRAUTSCHOLD, 1859", a species later reassigned by DE LORIOL (1878) to *Cyclocrinus*, and synonymized with *macrocephalus* QUENSTEDT, 1858. If all of these in fact represent *rugosus* D'ORBIGNY, 1841, it should be noted that the material collected shows features not reported by previous authors. To avoid possible confusion, the material collected is thus referred here to a new species, *Cyclocrinus couiavianus* sp.nov.

Systematic account

Genus *Cyclocrinus* D'ORBIGNY, 1850

TYPE SPECIES: *Bourgueticrinus rugosus* D'ORBIGNY, 1841; *SD* DE LORIOL (1886, p. 2)

DIAGNOSIS (WIENBERG RASMUSSEN 1978, p. *T*826), emended: Columnals large, more or less cylindrical with narrow central canal and with plain articular faces displaying variable tuberculation when corroded.

SPECIES INCLUDED: *Cyclocrinus rugosus* (D'ORBIGNY, 1841), *Cyclocrinus couiavianus* sp.nov.

Cyclocrinus couiavianus sp.nov.
(Text-figs 3, 5, 8-10)

HOLOTYPE: The columnal presented as item 5 in Text-fig. 8.

PARATYPES: Columnals presented as items 1-4 and 6-9 in Text-fig. 8.

TYPE LOCALITY: Wapienno Quarry, Couiavia region, north-central Poland.

TYPE HORIZON: Upper Oxfordian, Bimammatum and/or Planula Zone.

DERIVATION OF THE NAME: Neo-Latinized adjective *couiavianus*, to indicate the Couiavia region in north-central Poland.

DIAGNOSIS: Columnals cylindrical, tending to become elongate vertically, to become tall, or even taller than wide, and to constrict medially; articular faces plain when fresh, but furnished with fine, equally sized tubercles regularly distributed throughout when corroded.

DESCRIPTION: The columnals vary considerably in size and shape (see Text-fig. 8), ranging from minute ossicles to those of 16.0-16.5 mm in diameter (item 6 in Text-fig. 8), as well as from those relatively thin, cylindrical and thus rectangular in lateral profile (item 4) to those almost as tall as wide (items 1-3), or even taller than wide (items 13a, 13c), either cylindrical to slightly barrel-shaped (items 2, 10-11) or constricted medially to a variable extent (items 1, 3, 5-6, 9, 12-13). The holotype (item 5) is large (16.0 mm in diameter) and more strongly constricted on one side (left in Text-fig. 8.5). Generally, the constriction varies in its advance in particular columnals, or in their parts, to give a more or less distinct hourglass shape. The central canal is very narrow, well visible in some specimens (item 8), obscured by calcite overgrowths in others.

The tuberculation appears solely on articular faces. In specimens from encrinites (items 1-6 in Text-fig. 8), the equally sized, evenly distributed, wart-like tubercles may either hardly be visible (item 5, the holotype; after etching see Text-fig. 5), exposed patchily (item 3), or undetectable (items 1-2 and 4). In specimens from marly lenses (items 7-13 in Text-fig. 8), the tuberculation as a rule is well pronounced (see items 7-8).

The pluricolumnals (column segments) illustrate both the above variables of their successive columnals, as well as diverse height/width ratio in successive columnals (item 11), or in columnals of comparable size from various segments (item 12).

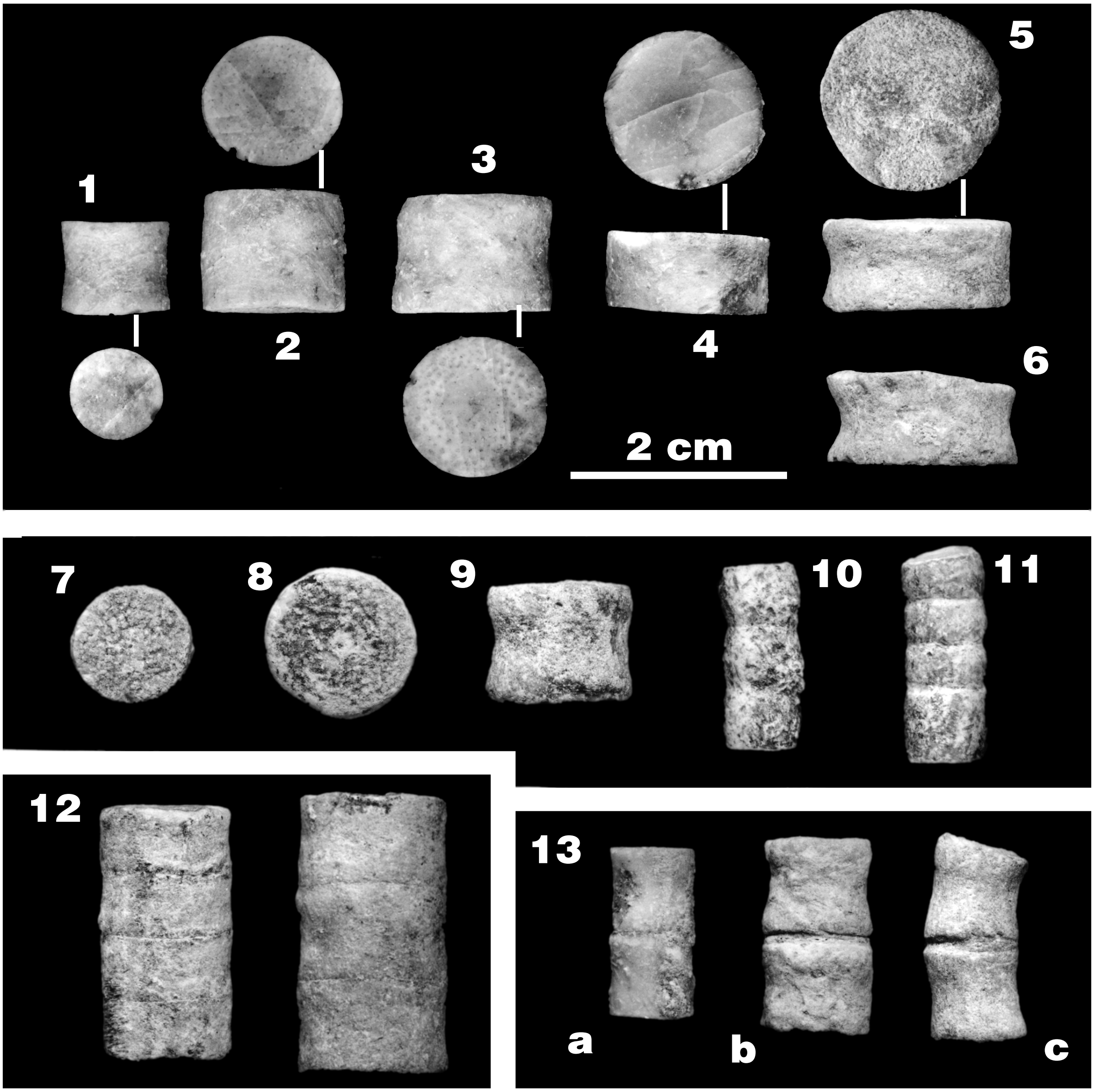

Fig. 8. *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry; all × 1.5; **1-6** - Columnals from encrinites: the type series, to show variation in shape (of lateral outline, and height/width ratio); Fig. 5 represents the holotype in articular and lateral views; **7-13** - Columnals and pluricolumnals from marly limestones: **7-8** - Isolated columnals, to show well-developed tuberculation; **9** - Isolated columnal in lateral view; **10** - Pluricolumnal composed of barrel-shaped columnals; **11** - Pluricolumnal with columnals of variable height/width ratio; **12** - Pluricolumnals of comparable size, but composed of a variable number of columnals; **13** - Specimens of two conjoined columnals of variable lateral outline, taller than wide, to show their either straightline (Figs 13a-13b) or arched jointing (Fig. 13c)

To note, every columnal forms a separate crystal of calcite, whose cleavage planes of the rhombohedron $\{10\bar{1}1\}$ are well pronounced in some specimens (see items 1-4 in Text-fig. 8; especially, articular view of item 4).

REMARKS: The newly proposed species, *Cyclocrinus couiavianus* sp.nov., differs from *C. rugosus* (D'ORBIGNY, 1841) by its tendency to acquire a regularly distributed tuberculation when columnals are corroded (syndepositionally, diagenetically, or artificially as treated with acids), the tuberculation then being the only morphological feature of the articular faces. Furthermore, there is a general tendency to form tall columnals, even taller than wide, and to acquire a medially constricted (hourglass-like) shape.

A tendency to form elongate columnals, almost as tall as wide, is rather uncomon in other *Cyclocrinus* specimens previously reported (see QUENSTEDT 1858, pl. 68, figs 32-33; MOESCH 1867, pl. 7, fig. 2c; DE LORIOL 1878, pl. 14, fig. 8; and 1886, pl. 125, figs 12-14, and pl. 126, fig. 9).

An hourglass-like shape has first been noted by TRAUTSCHOLD (1859) in his Early Oxfordian specimens. A very slight constriction medially in *Cyclocrinus rugosus* was reported by DE LORIOL (1886, p. 14 and pl. 124, figs 3, 6, 9), but it is also seen in one specimen of *Cyclocrinus macrocephalus* illustrated by that author (DE LORIOL 1886, pl. 125, fig. 11).

Never reported was the presence of pluricolumnals (column segments), whose variable structure is discussed below.

STRATIGRAPHICAL RANGE: Middle Jurassic (Bajocian – Callovian) to Upper Oxfordian, as here documented.

Regeneration of pluricolumnals

Some of the pluricolumnals of *Cyclocrinus couiavianus* sp.nov. show a drastic change in the diameter of two successsive columnals, one of which is distinctly narrower than the preceding one (see Text-fig. 9). As reviewed by OJI (2001), such a feature is typical of many extinct and/or extant echinoderms, not just crinoids, in which a body part either injured (e.g., by predatory attack; *sublethal predation* of LAWRENCE & VASQUEZ 1996) or autotomized through stress (see MÜLLER 1969, DONOVAN 1991, AMEMIYA & OJI 1992, LAWRENCE 1992, OJI & OKAMATO 1994, OJI 2001), was successfully regenerated. Regeneration has thus been recognized in some crinoid parts, albeit other than columnals, viz. crowns of stalked crinoids (AMEMIYA & OJI 1992); crinoid arms (NEUMANN & KOHRING 1998, OJI 2001); crinoid spines (HATTIN 1958), as well as in ophiuroid and asteroid arms (HESS 1960; MÜLLER 1969; MEYER 1984; BOMWER & MEYER 1987; ARONSON 1987, 1992; see also reviews by HOTCHKISS 1979, 2000, and LAWRENCE & VASQUEZ 1996). It is also commonly known to produce comet-like specimens of starfish. All the illustrated cases are typified by a drastically smaller size of the body part regenerated, well observable in fossil crinoids (see HATTIN 1958, pl. 98, figs 1-2; NEUMANN & KOHRING 1998, fig. 1; OJI 2001, figs 1A-1B). Excepted is a case of deformation of an injured stem, that is of its several successive columnals, presented by AUSICH & BAUMILLER (1993), and interpreted as imperfect regeneration ("overgrowth") by OJI (2001). Supposedly, of the same nature are also pathologies in pluricolumnals illustrated by JAGT (1999, pl. 8, figs 1-3 and 7-8).

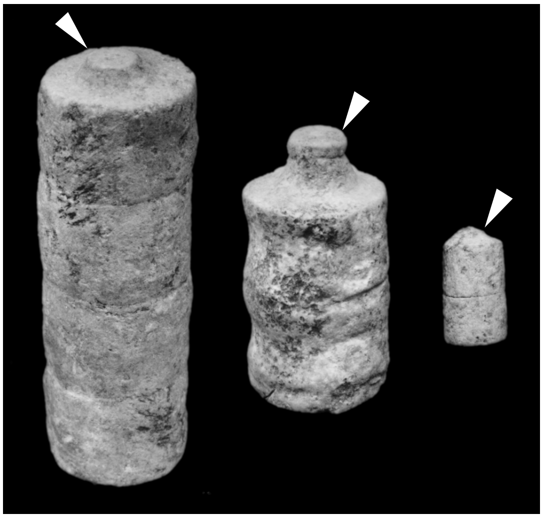

Fig. 9. Pluricolumnals of *Cyclocrinus couiavianus* sp.nov. of various size, showing regenerated columnals (*arrowed*); Wapienno Quarry, taken × 1.5

The pluricolumnals of *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry discussed, both larger and smaller (see Text-fig. 9), are consequently thought to have been regenerated after damage caused by an unknown agent.

PART 2. JUST WHAT IS *CYCLOCRINUS*?

In the material of *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry, several features of isolated columnals, or of pluricolumnals, are very peculiar. These are so peculiar that we, inspired by a report of MESSING (2001), dare provoke a question: Just what is *Cyclocrinus*?

In some isolated columnals studied, there appear large sockets that could hardly be interpreted as of cirrals. Within pluricolumnals, there are some arched to a variable extent, while others have one columnal bearing two large sockets, tuberculate and opposing each other laterally (see Text-figs 10-11). None of these features indicative of ramification, or bifurcation, are known in stalks of articulate crinoids, but they are typical (see Moore 1967; Klikushin 1982; Jagt 1999; Jagt & *al.* 1994, 1998) of radicular systems of some bourgueticrinids. For this reason, we here propose that all *Cyclocrinus* columnals studied do not represent disintegrated columns, but disarticulated root systems, *i.e.* modified radicular cirrals. Regarding this, one may easily compare features of the material studied with those illustrated by previous authors for bourgueticrinid root systems and their radicles, as follows:

– large sockets in isolated columnals (Text-fig. 10c) with those presented by Klikushin (1982), and reproduced herein (Text-fig. 12.1a); the same concerns smaller-sized sockets (see Text-figs 10a-b and 12.1b, 1e);

– columnals with two opposed, tuberculate sockets (Text-fig. 10d-10g; see also Text-fig. 11b) with those recognizable in a specimen illustrated by Klikushin (1982), and reproduced herein (Text-fig. 12.1a);

– arched pluricolumnals (Text-fig. 11a) with those presented by Moore (1967, pl. 6, fig. 13; reproduced herein as Text-fig. 12.2a), and by Jagt & *al.* (1994, fig. 1).

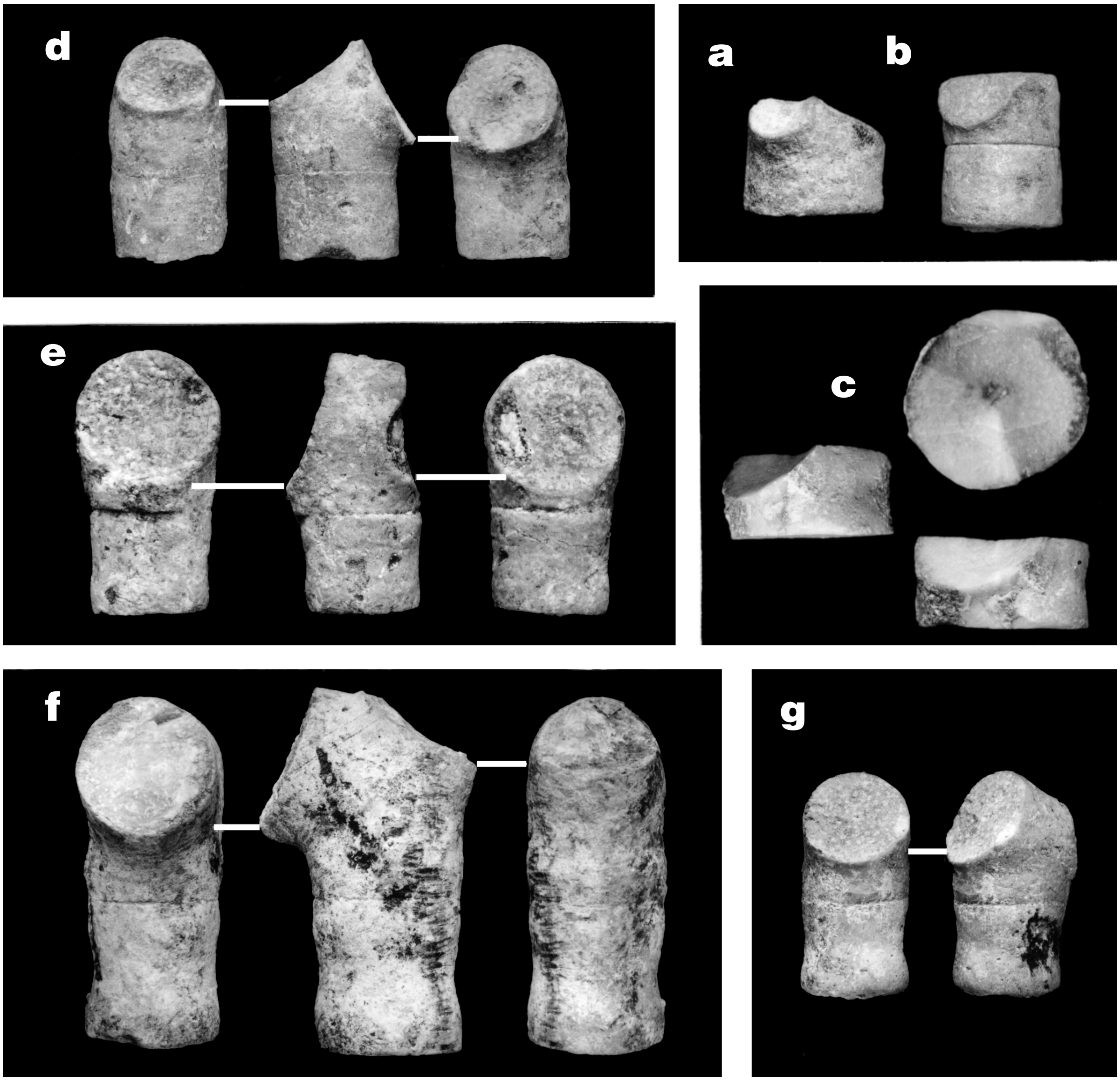

Fig. 10. Branched columnals/pluricolumnals of *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry; all × 1.5; **a**-**b** - Columnals with a small-sized socket; **c** - Columnal with a socket of the size of the parent columnal; **d**-**f** - Pluricolumnals with one columnal forked into two branches of the size of the parent columnal; **g** - Another pluricolumnal, to show one of the forked articular faces distinctly tuberculate

A few other details of pluricolumnals of *C. couiavianus* sp.nov., comparable to those of radicular systems of bourgueticrinids, comprise: (*i*) Variable height of subsequent columnals (see Text-fig. 8.11), and (ii) Variable height of columnals of comparable diameter (see Text-fig. 8.12). These two features correspond exactly to those presented by MOORE (1967, pl. 6, fig. 15; reproduced herein as Text-fig. 12.2b) for bourgueticrinid radicles.

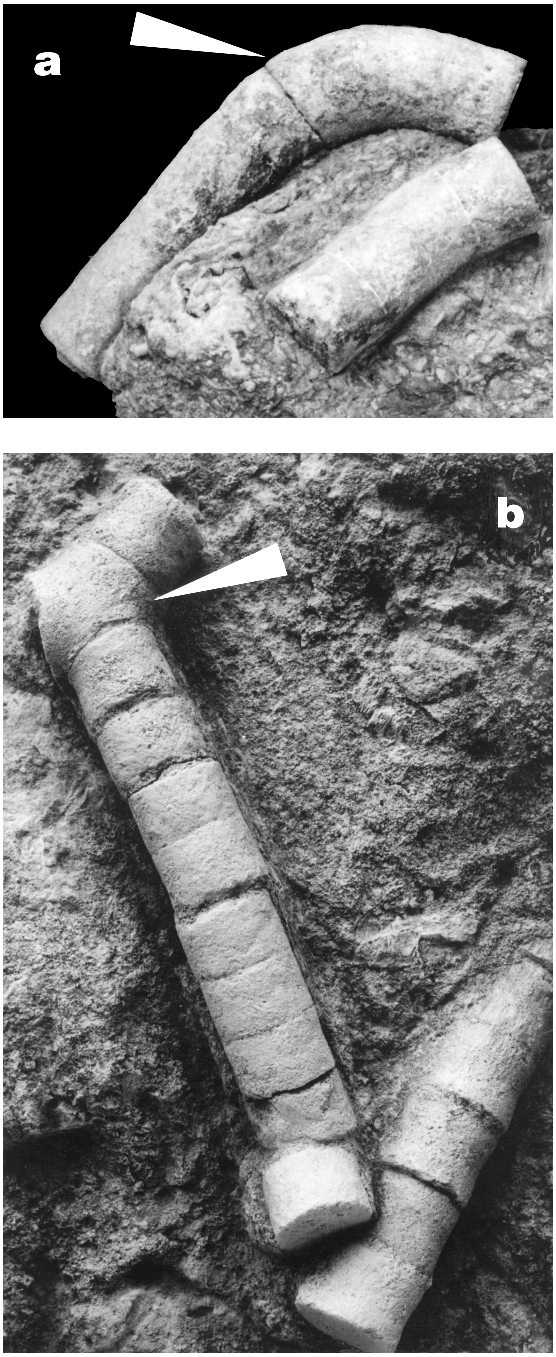

Fig. 11. Pluricolumnals of *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry: **a** - Arched; **b** - Bifurcated; × 1.5

The bourgueticrinid root systems under comparison are very extensive, to form a maze of variously shaped rootlets, and the total number of their ossicles much exceeds that of the column of a single animal (see JAGT 1999; JAGT & *al*. 1994, 1998 – of that latter, its pl. 7, fig. 7 is reproduced herein as Text-fig. 13). This may be the reason for the ubiquitous material in the Wapienno sequence where encrinites of *C. couiavianus* sp.nov. have formed (see Text-fig. 3), although the number of crinoid individuals may not have been significant in that environment. The posture of these crinoids cannot be determined. When all *Cyclocrinus* ossicles were interpreted as columnals, the stem was thought to have been long, rigid and stout (as suggested by DE LORIOL 1878, p. 104; repeated by WIENBERG RASMUSSEN 1978, p. *T*826). In our new interpretation of the ossicles of *C. couiavianus* sp.nov. as radicular, evolved to stabilize and anchor the animal in unstable bottom sediment, the stem may alternatively be postulated as relatively much thinner and flexible, contrary to that recognized in Late Cretaceous (Maastrichtian) bourgueticrinids (see MOORE 1967, JAGT & *al*. 1998).

In other *Cyclocrinus* specimens, presented by previous authors, identical peculiar features are recognizable, as follows:

- columnals with small ramification (see D'ORBIGNY 1841, pl. 17, figs 18-19; TRAUTSCHOLD 1859, p. 112, pl. 1, figs 5 and 7-8; DE LORIOL 1878, pl. 14, figs 10-11; pl. 124, figs 3 and 8);
- columnals bifurcated (*see* TRAUTSCHOLD 1859, p. 112, pl. 1, figs 6 and 9-10; DE LORIOL 1886, pl. 125, fig. 10; GERASIMOW 1955, pl. 2, fig. 10); that such 'roof-shaped' columnals might have belonged to a radix was indicated by WIENBERG RASMUSSEN (1978, p. *T*826).

In consequence of the above, it is assumed that all the *Cyclocrinus* species distinguished by earlier authors also represent nothing else but the fragmentarized root systems of some bourgueticrinid species ranging from the Bajocian/Bathonian through to the Lower/Middle Oxfordian.

If accepted, one problem remains: the variability of the tuberculation pattern in the *Cyclocrinus* specimens reported by earlier authors, *i.e.* the presence of such particular features as circular array of tubercles, radial tubercles at the central canal, vermiculi, and marginal crenulation. Do these diverse patterns correspond to diverse "biological" species of bourgueticrinids other than *C. couiavianus* sp.nov., whose ornamentation consists solely of regularly distributed tubercles?

Beyond the scope of the present paper is the problem of morphological similarity of the root systems of the suggested bourgueticrinids (i.e. articulate crinoids) to root systems (see BRETT 1981) of diverse Palaeozoic crinoids and other pelmatozoans.

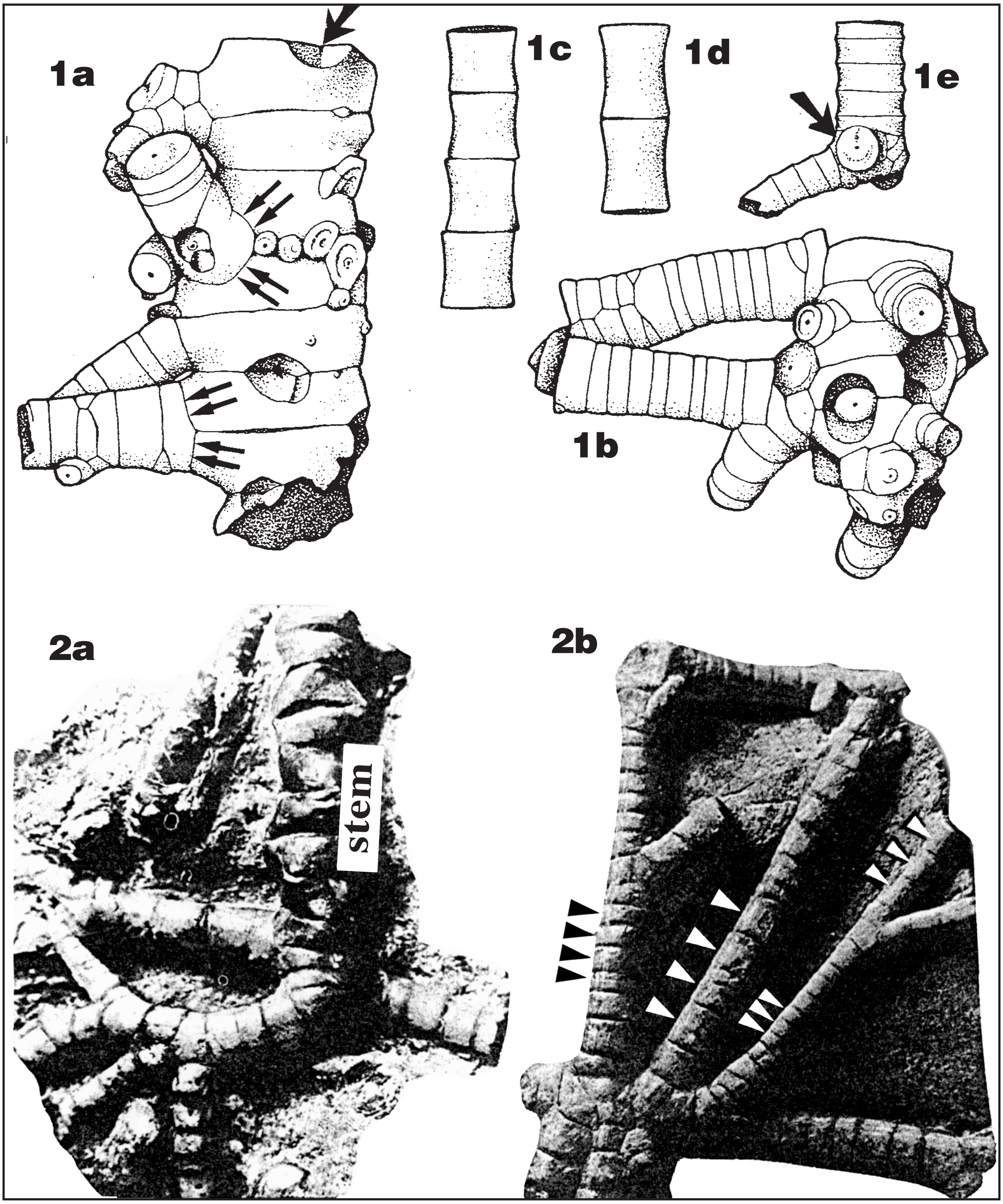

Fig. 12. Selected fragments of root systems in Bourgueticrinidae (*adopted from* Moore 1967, *and* Klikushin 1982), for comparison with material of *Cyclocrinus couiavianus* sp.nov. from Wapienno Quarry; **1a-1b** - *Dunnicrinus aequalis* (d'Orbigny, 1841): "distal stem ends" (× 3) of Klikushin (1982, figs 1*G*-1*H*); **1c-1e** - *Bourgueticrinus baculatus* Klikushin, 1982: 1c-1d - "fragments from the stem parts" (× 3), and 1e - "distal radicular part of a stem" of Klikushin (1982, figs 6*G*, 6*H*, 6*I*); indicated are large-sized sockets, either exposed (*single arrows*) or unexposed (*doubled arrows*), to compare with Text-fig. 10a-10c; **2a-2b** - *Dunnicrinus mississippiensis* Moore, 1967: 2a - "distal end of stem with attached branching radicular cirri" of Moore (1967, pl. 6, fig. 13), *c*. × 3; 2b - "bottom of radicular cirri" of Moore (1967, pl. 6, fig. 15), × 3; indicated are fragments of adjacent cirri bearing ossicles (cirrals) of different height/width ratio (*four larger arrows*) and such very cirrals within one cirrus (*three smaller arrows*), to compare with Text-fig. 8.11-12

Taxonomic consequences

The interpretation of all *Cyclocrinus* ossicles as bourgueticrinid radicular cirrals, involves an evident taxonomic confusion. Until the present authors' suggestion is verified and a definite genus/species of bourgueticrinids is identified, it is proposed to keep the above discussed species name *Cyclocrinus rugosus* (D'ORBIGNY, 1841) for all hitherto described *Cyclocrinus* remains other than *Cyclocrinus couiavianus* sp.nov. The name *Cyclocrinus rugosus* is thus to be kept also for all other specimens from Poland, exemplified by these of Wola Morawicka (see Text-fig. 4a), Kozłowiec/Czerwieniec (see Text-fig. 4b), Wrzosowa (see Text-fig. 4c) and Opoczno (see MERTA 1972, pl. 4, fig. 4a-4b; and Text-fig. 6 herein).

Eco-taphonomy of *Cyclocrinus*

The occurrence of *C. couiavianus* sp.nov. in the Wapienno sequence at levels lacking other macrofauna suggests an opportunistic nature of the newly established species. Its life habitat would have been a limy or marly bottom, not firmly stabilized, and located either at the top, or on gently sloping flanks, of the biohermal buildup. Such bottom conditions have been established for the final stages of formation of the sequence exposed at Wapienno Quarry (cf. Text-fig. 2 and MATYJA & WIERZBOWSKI 1985, fig. 1).

The setting of *Cyclocrinus* remains in irregular, more or less slumped, layers indicates that catastrophic events were responsible for the demise of *Cyclocrinus* biotopes resulted from the total damage of their inhabitants. These could either have been heavy storms, or slope overloading which triggered mass movements along the buildup's slopes, or both. Under such environmental conditions influenced by catastrophic (lethal) events, the complex root system in *C. couiavianus* sp.nov. was an ecological response to facilitate anchorage and guarantee the survivorship of crinoids in their habitats. This root system is assumed to have been extensive, to yield much detritus after crinoids died, disintegrated, and/or were totally crushed. Locally, their detritus led to rock-building, the *Cyclocrinus* encrinites lithology.

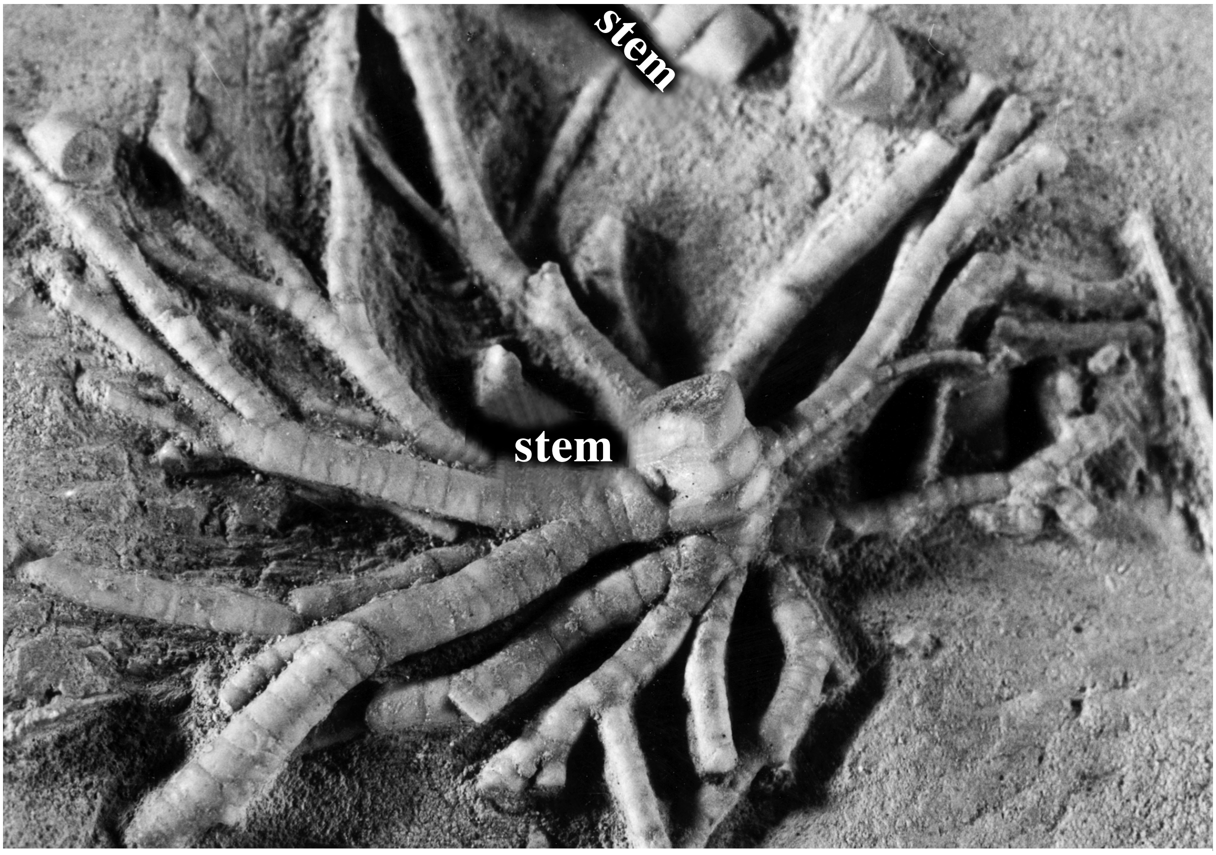

Fig. 13. Complete root system of the bourgueticrinid *Dunnicrinus aequalis* (D'ORBIGNY, 1841) from the Late Maastrichtian (Maastricht Formation) of The Netherlands, to show the archings and branchings of radicular cirri, as well their total bulk (maze) *versus* the distal stem fragment; re-figured from JAGT & *al*. (1998, pl. 7, fig. 7); *c*. × 2

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Cases of regeneration in the root system in *Cyclocrinus* studied (see Text-fig. 9) indicate that some events caused only partial disruption and damage, *i.e.* sublethal injury (*sensu* OJI 2001) to the crinoids. Biogenic damage of the crinoids studied appears to have been of limited importance, if at all. The swimming activity and/or foraging of large sharks, i.a. *Orthacodus longidens* (AGASSIZ, 1843) and crocodile-like reptiles *Dakosaurus maximus* QUENSTEDT, 1858, whose teeth have long been known (see JENTZSCH 1884; GALLINEK 1895, 1896) and still are easy to be found in the Wapienno sequence, may have caused only local damage of crinoid biotopes.

Recurring storm agitation is consequently postulated as the main agent acting in the shallow-marine portions of the Wapienno buildup. The proposed scenario of life, death, and burial conditions for the crinoid *C. couiavianus* sp.nov. agrees well with, and supplements, environmental factors inferred by MATYJA & WIERZBOWSKI (1985) for the higher and/or final stages of development of the Wapienno biohermal buildup, supposedly stimulated by successive rise of the salt-diapiric basement.

FINAL REMARKS

A cirral interpretation of *Cyclocrinus* ossicles (“columnals”) may explain the presence, in the material studied, of a reasonable number of pluricolumnals, unknown from previous reports. It is presumed that these could be formed and preserved when *Cyclocrinus* root systems had violently been eradicated and transported in a bulk of parent sediment, *e.g.* slumped, as in the case of the Wapienno sequence (see Text-fig. 14).

In the presented study of the still enigmatic crinoid genus *Cyclocrinus* D’ORBIGNY, 1850, its basic problem stands unanswered: to which genus/species the *Cyclocrinus* “columnals”/roots have belonged? Neither the sequence of Wapienno nor other localities in Poland delivered any crinoid remains which could be referred to as congeneric/conspecific with *Cyclocrinus*. At Wapienno, a scanty material of microcrinoids (see JAEKEL 1892) and pentacrinids (see GALLINEK 1896) is rather beyond consideration. In other localities, *Cyclocrinus* “columnals” are the only crinoid remains. Should the heavy root system, called *Cyclocrinus*, be ascribed to any of the small-sized delicate crinoids?

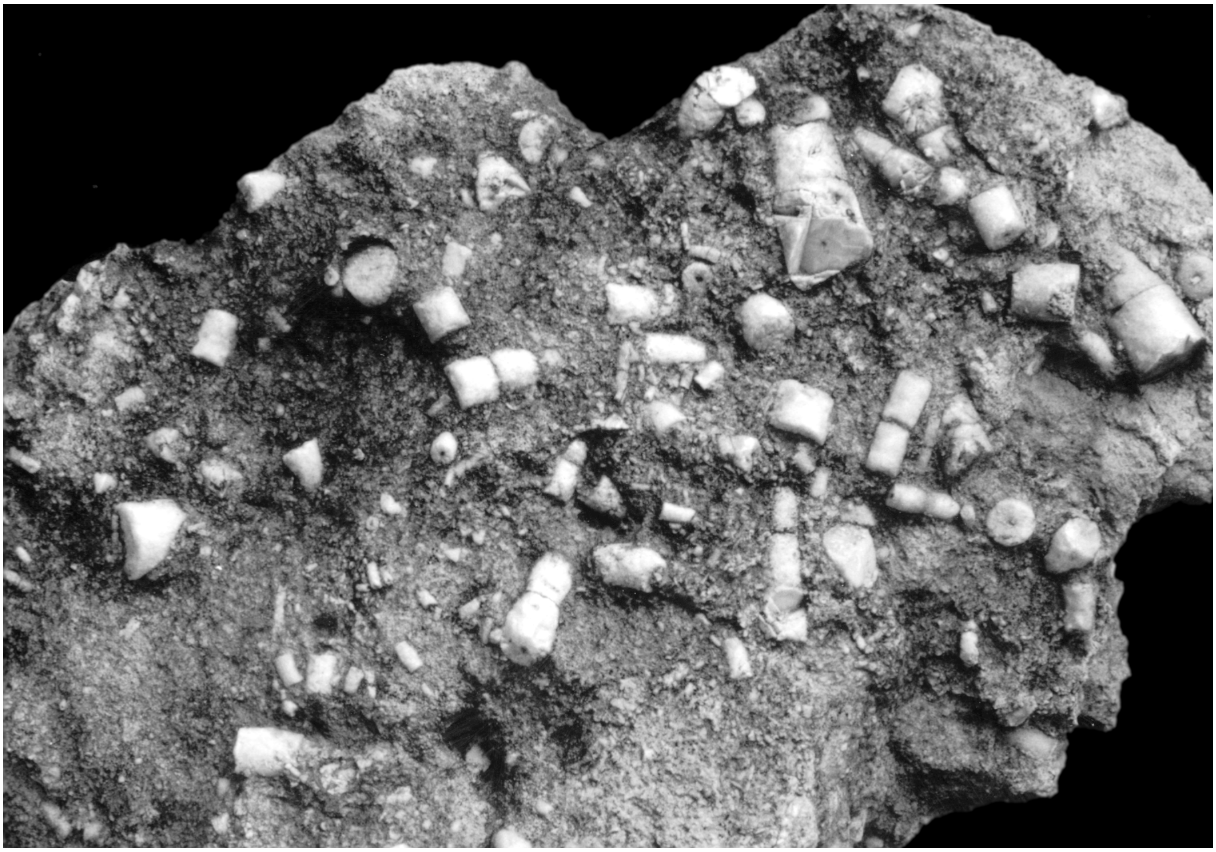

Fig. 14. Radicular cirrals of *Cyclocrinus couiavianus* sp.nov. scattered abundantly throughout a marly mass slumped along flanks of the biohermal buildup exposed in Wapienno Quarry; nat size

Acknowledgements

Heartfelt thanks are addressed to Dr. John W.M. JAGT, Natuurhistorisch Museum Maastricht (The Netherlands), for his kindness in supplying a photo, permission of its use in this paper, and a constructive review of the manuscript, as well as for access to his library. Other bibliographic assistance was given by Dr. Ortwin SCHULTZ (Vienna, Austria), Dr. Manfred JÄGER (Dotternhausen, Germany), Dr. Gérard BRETON (Le Havre, France), Dr. René-Pierre CARRIOL (Paris, France), Mr. Roland REBOUL (Saint Chinian, France), and Mr. Rinus LANGEVELD (Eindhoven, The Netherlands), to whom cordial thanks are offered. Some comparative specimens of *Cyclocrinus* have generously been donated by Mr. Roman GAD of Łopuszno (Poland), Dr. Vladimir G. KLIKUSHIN of St. Petersburg (Russia), Dr. Vasily MITTA (Vernadsky State Geological Museum, Moscow, Russia), and Dr. Ewa GŁOWNIAK, of our Institute.

Ing. Krzysztof MĄCZKA, M.Sc., The Director of Lafarge Cement Polska S.A., to which Wapienno and Bielawy quarries belong, is acknowledged for making easy access to the quarries, and for kindly offered logistic help during the fieldworks.

Last but not least, thanks to Mike RADWAŃSKI for careful computer setting of the manuscript, and Marcin GÓRKA, M.Sc., for processing Text-fig. 1.

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Manuscript submitted: 10th October 2002
Revised version accepted: 20th September 2003