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Argoviacrinus rarissimus n. g. n. sp., a new crinoid (Echinodermata) from the Middle Oxfordian of northern Switzerland

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Key words: Crinoid, *Argoviacrinus rarissimus* n. g. n. sp., Middle Oxfordian, Switzerland, description, affinities, palaeoecology

ZUSAMMENFASSUNG

Aus den Birmenstorf Schichten (mittleres Oxford) von Holderbank (Kt. Aargau) wird eine neue Crinoiden-Art, *Argoviacrinus rarissimus* n. g. n. sp., beschrieben. Der Einzelfund ist ein kleiner Kelch aus Radialkranz, Basalia und stielartigem Centrodorsale mit Zirren; die Gelenkfläche zum Stiel ist eine unbewegliche Krypto-Symplexie mit Randwulst und Körnerbelag, die eine ursprüngliche Synarthrie überlagert. Die Aehnlichkeit der Gelenkfläche mit Stielgliedern der sessilen Cyrtocriniden, die dominierenden Crinoiden der Birmenstorf Schichten, dürfte eine Konvergenzerscheinung sein. Die Form wird als Weiterentwicklung der Thiolliericrinidae und somit als aberrantes Mitglied der Ordnung Comatulida angesehen.

ABSTRACT

The unique specimen of a new crinoid, *Argoviacrinus rarissimus* n. g. n. sp., from the Middle Oxfordian Birmenstorf Member of Holderbank (Canton Aargau) is a small cup with radials, basals and a stem-like cirriferous centrodorsal. The articular facet to the stem is a circular inflexible cryptosymplexy with rim and granules, transformed from a cryptosynarthry during development. The morphological similarity to the stems of cyrtocrinids, the dominant crinoids of these strata, is considered to be due to convergence. The form is thought to be related to the Thiolliericrinidae and, thus, is an aberrant member of the Order Comatulida.

1. Introduction

The Middle Oxfordian sponge facies of northern Switzerland ("Argovian" Birmenstorf Beds) is popular with fossil collectors for its rich fauna of ammonites, sponges, bryozoans and brachiopods but, perhaps, even more for its echinoderms (echinoids, crinoids). Indeed, the clove-like cups of *Eugeniacrinites cariophilites* were first figured by Scheuchzer in 1702. Of special interest is the rich fauna of peculiar and at times bizarre crinoids of the Order Cyrtocrinida that were extensively described in the classic monographs of Loriol (1877–1879; 1882–1889) and Quenstedt (1874–1876) (see also Hess 1975). It came as a big surprise that a completely new type of crinoid has been found in these extensively searched strata by the junior author during her diploma work.

2. Geological setting

During the Late Jurassic the study area was situated in an epicontinental sea structured into local basins and swells. Coeval platform deposits are found toward the northwest. In the northern part of the large Chalch (also called "Schümel") quarry at Holderbank (coordinates: 655.900/253.500), the Birmenstorf Member is exposed along a length of about 150 m as a roughly 30 m high inclined wall with vegetation at the top. The beds strike roughly NW-SE with a 30–60° dip. The stratigraphically higher Effingen Member is exposed in other parts of the quarry. The Birmenstorf Member has been characterized as a basinal spongolite (Gygi 2000a) with siliceous sponges making up as much as 30 % of the rock volume. It is a succession of micritic limestones, marly limestones and marls with a thickness of 4 to 4.5 m at the Chalch quarry. The Effingen Member, a basinal argillaceous mudstone, is a succession of blue-grey marls with interbedded marly limestones and pure limestones; it reaches a thickness of about 240 m in the Holderbank area (R. Allenbach, pers. comm., 2001). The Birmenstorf Member was deposited during the Transversarium Zone; the Effingen Member includes the Bifurcatus and the lower part of the Bimammatum Zones (Gygi 2000b).

The fossils were collected from the surface at the foot of the eastern part of the wall and the talus below. They all belong to the Birmenstorf Member as the situation at the outcrop prevents contamination by fossils from the Effingen Beds. In the lower Effingen Beds, about 5 m above the top of the Birmenstorf Member (a bed covered with sponges), a 25 mm

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thick lens occurs packed with crinoid ossicles from species that occur in the underlying Birmenstorf Beds. Their relatively small size (the largest elements are less than 5 mm in diameter) suggests that they were well sorted before they accumulated, possibly during a tempestite event. The echinoderm species in the lower parts of the Effingen Member also occur in the Birmenstorf Member, but species diversity and number of specimens in the Effingen Member is lower.

3. Fauna

The richly fossiliferous Birmenstorf Member is characterized by abundant siliceous sponges, ammonites, echinoderms and brachiopods. The fauna is similar to the somewhat younger Lochen Beds (Bimammatum Zone) of the Swabian Alb, deposited at the margins of sponge-algal bioherms (Ziegler 1977). The crinoids listed below have been collected at Holderbank during a time period of 200–250 hours by the junior author. A relatively large number (several hundreds) of mostly very small brachials and columnals is not listed because of doubtful assignment. A list of the total fauna collected will be reported elsewhere (Spichiger, in preparation).

List of crinoids from the Birmenstorf Member of the Chalch quarry, Holderbank (assignment based on Hess 1975).

Isocrinida	
Isocrinus cingulatus (MÜNSTER in GOLDFUSS)	
Pluricolumnals (stem fragments) and columnals	66
Brachials (including 6 with aboral spine)	7
Balanocrinus subteres (MÜNSTER in GOLDFUSS)	
Pluricolumnals and columnals	324
Brachials	1
Cyrtocrinida	
Cyrtocrinus nutans (GOLDFUSS)	

Remarks: Cups of this species have great variation in height, ornamentation and in the ratio of radial cavity diameter to cup diameter, which is between 0.8 and 0.2 (a ratio of 0.4 to 0.5 being the most common). Correspondingly, the radial articular facets vary considerably in size. Brachials with granulated surface, previously assigned to *Sclerocrinus compressus* (= *Gammarocrinites compressus* in the *Treatise on Invertebrate Paleontology*, Rasmussen 1978, T831) (Hess 1975, Pl.25, figs. 2 and 3) are here assigned to *Cyrtocrinus nutans*. As already discussed by Jaekel (1891, p. 622), the two forms are linked by intermediates and may at most be distinguished by their surface structure, a character that we now regard as part of the intraspecific variation, an opinion shared by Loriol (1877–1879, p. 209 and 1882–1889, p.115).

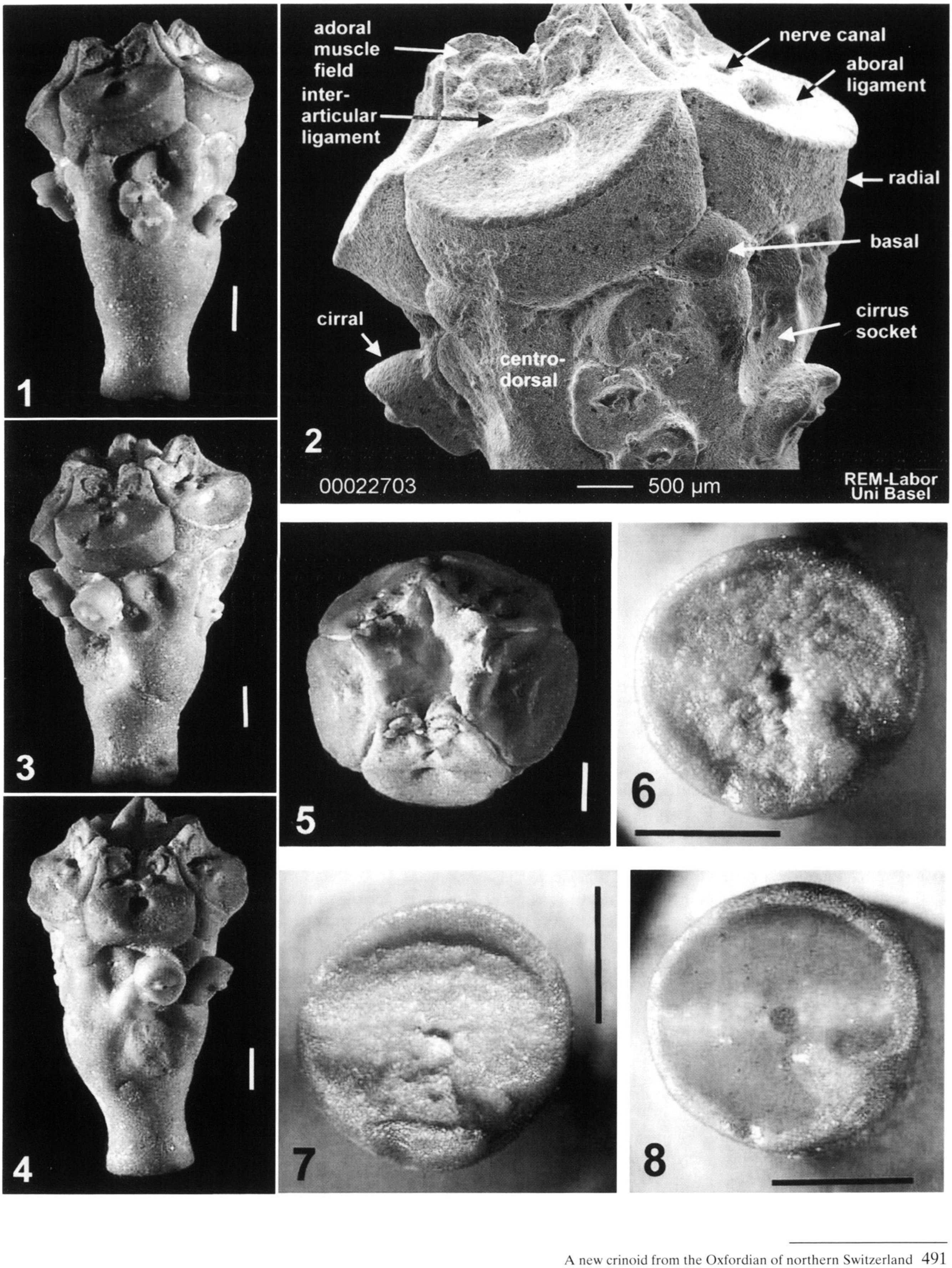
Cups attached to proximal columnal	27
Cups (isolated)	144
Proximal columnals (with facet to cup)	382
Columnals (including 28 pluricolumnals)	707
Brachials	118
Eugeniacrinites cariophilites (*caryophyllatus*) (V. SCHLOTHEIM)	
Cups attached to proximal columnal	2
Cups (isolated)	57
Second primibrachials (IBr2 = primaxillary)	19
Columnals	395
Pilocrinus moussoni (DESOR)	
Cups	23
Brachials	89
Columnals (including 4 pluricolumnals)	98
Gymnocrinus moeschi DE LORIOL	

Remark: These brachials may belong to *Pilocrinus moussoni*, the taxonomic position of *Gymnocrinus* will be discussed in the forthcoming revision of the *Treatise on Invertebrate Paleontology, Pt. T Crinoidea*)

Second primibrachials (IBr2 = primaxillary)	9
Tetracrinus moniliformis GOLDFUSS	
Basal circlets	5
Radials (isolated)	12
Brachials	584
Pinnulars (fused, dagger-like)	3
Columnals	1
Plicatocrinus hexagonus MÜNSTER	
Cups	1
Comatulida	
Archaeometra scrobiculata (MÜNSTER)	
Cups with centrodorsal	2
Brachials ("*Archaeometra aspera* [QUENSTEDT]")	399
Undetermined ossicles	
Isocrinid cirrals (*Isocrinus cingulatus* or *Balanocrinus subteres*)	197
Attachment discs of cyrtocrinids	19

Fig. 1–8. Holotype of *Argoviacrinus rarissimus* n. g. n. sp, Birmenstorf Member, Holderbank. Natural History Museum Basel, M 9995. Scale bars (except Fig. 2) = 1 mm. (Photographs 1 and 3–8 by H. Hess.)

1. Lateral view.
2. SEM photograph of upper part (same position as Fig. 1). (Photograph by K. Duffner.)
3. Another lateral view, note circular pit on the left side caused by unknown parasite.
4. View with pit in front.
5. Oral view with radial articular facets.
6. Distal articular facet to stem, note somewhat irregular rim and areola with scattered granules, calcareous deposit at lower right.
7. Distal articular facet to stem with lighting to show rim and areola in upper part.
8. Wet distal articular facet to show weak horizontal synarthrial ridge.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4. Systematics

Class Crinoidea
Order Comatulida A. H. CLARK, 1908
Family Thiolliericrinidae A. H. CLARK, 1908

Genus *Argoviacrinus* n. g.
Type species: *Argoviacrinus rarissimus* n. sp., by monotypy.
Derivation of name: After the occurrence in Canton Aargau (lat. argovia).

Diagnosis: Cup composed of circlet of 5 radials and basals that are exposed in the interradial angles; radial articular facets well developed, outward sloping, radial cavity moderately deep; uppermost columnal or centrodorsal high, with 3 cirri in each radius, distally cylindrical and tapered; articular facet to stem a cryptosymplexy with rim and secondary deposit of granules on shallow areola, superimposed on a cryptosynarthry.

Argoviacrinus rarissimus n. g. n. sp.
Holotype: Natural History Museum Basel, M 9995.
Derivation of name: After the extreme rarity.
Type locality and horizon: Chalch quarry, Holderbank (Aargau), coordinates: 655.900/253.500. Birmenstorf Member (Middle Oxfordian).

Diagnosis: see genus (monotypy).

5. Description

The perfectly preserved holotype is a cup with radial circlet and basals, attached to the topmost columnal or centrodorsal (Figs. 1–4). It has a total height of 9 mm; the largest diameter (radial circlet) is 5.3 mm and the distal diameter (stem facet) 2 mm.

The radials have a relatively low free, unsculptured lateral surface and are laterally contiguous. The diameter of the radial cavity (centrodorsal lumen) is about one fourth of the diameter of the cup (Fig. 5). The basals are exposed in the interradial angles as small, convex, triangular plates. The radial articular facets are large, almost quadratic, with rounded lower part and outward sloping at an angle of about 45°. The nerve canal (central lumen) is nearly circular and rather small. The aboral ligament fossa occupies nearly half of the facet, the ligament pit is deeply sunk. The shallow interarticular ligament fossae are roughly triangular. The muscular fossae are well developed, with two sculptured muscular areas.

The centrodorsal or proximal columnal is high (nearly 6 mm), broad and subcircular at the top and tapered distally. In the uppermost part, just below the radial circlet, are five groups of three confluent cirrus scars or sockets in irregular arrangement with a weak sculpture around the central canal. In each group of three sockets one or two cirrals are preserved in situ; they have a short, but prominent, transverse fulcral ridge. Some sockets are protruding, but others are more or less fused to the surface of the centrodorsal (Fig. 2). Beneath one group of cirrals is a circular pit (caused by an unknown parasite), with a small drop-like opening in the centre (Figs. 3, 4).

The articular facet to the stem is circular and nearly flat; it has a distinct articular rim surrounding a shallow depressed space (areola) with scattered granules (Fig. 6). This type of union may be called a cryptosymplexy (weak or hidden symplexy) in which the crenularium (ridges and grooves on the rim) is indistinct. According to the terminology of the *Treatise on Invertebrate Paleontology* (Moore 1978, p. T242), it may also be called a zygosynostosis ("ligamentary articulation in which opposed joint faces are nearly flat areas for attachment of short ligament fibres combined with moderate calcareous deposits"). The rim is somewhat irregular; on one side the edge seems to have been damaged during life and a calcareous deposit extends from the rim to the center of the facet. This swelling would have prevented close contact between the centrodorsal and the columnal below and may have been produced only after the animal became detached from the stem. When the surface is wet a weak longitudinal ridge (fulcrum) extending from one side of the rim to the other and separating a pair of semicircular fossae is visible (Fig. 8). This indicates that a juvenile flexible synarthry has been transformed during development into a rigid articulation by deposition of stereom (Fig. 7). It is appropriate to call the underlying structure a cryptopsynarthry.

Synarthries have two opposing bundles of ligament that are separated by a fulcral ridge (for a discussion of stem articulations see Hess et al. 1999). Such unions are best known in the Order Bourgueticrinida, Upper Cretaceous to Recent crinoids, which presumably descended from thiolliericrinids (Simms 1988). The articular facets are more or less circular and have rather deep bifascial pits, a feature that makes the stem flexible. However, columnals in certain regions may be inflexible and such articulations have been described as synostoses (rigidly jointed, flat articular facets) or as syzygies (ridges of one side oppose ridges of the other) by Roux (1977). Roux (1974) mentioned the occurrence of syzygies in Bathycrinidae (= Bourgueticrinidae) in the proximal part of the stem where one of the ridges of the syzygial crenularium developed to a fulcrum. In the distal part of the column of these crinoids syzygies are also present; the original synarthrial articulation (still visible in the center of the facet) secondarily evolved to a syzygy. (It should be noted that most authors restrict the use of the term "syzygy" to arm articulations.) Synarthrial stem articulations of these extant forms may pass through different stages during development. The same seems true of *Argoviacrinus*, with a facet showing characters of both cryptosynarthry and cryptosymplexy (or zygosynostosis).

6. Affinities

Argoviacrinus rarissimus n. g. n. sp. is a crinoid that has the cup of a comatulid (radial articular facets and development of basals), the centrodorsal (although considerably higher) of a thiolliericrinid (presence of cirri) and the circular column of a cyrtocrinid (rimmed, granulose symplectial facet). Somewhat similar stem facets also occur in the Cyclocrinidae, a group of uncertain affinities represented by columnals only. Thiollieri-crinids typically have a truncated conical or discoidal centrodorsal with a distinct synarthrial facet. In contrast, *Argoviacrinus* has a high, stem-like centrodorsal with a cryptosymplectial facet superimposed on a cryptosynarthry. The presence of a cryptosynarthry is crucial for classification and indicates that this peculiar crinoid may well be a sister taxon of Thiolliericrinidae, sharing with them the cirriferous centrodorsal. However, it differs in the later development of an immovable column. In cladistic terms the synarthry on the centrodorsal of Thiolliericrinidae and of *Argoviacrinus* is considered a symplesiomorphy, the modified facet of *Argoviacrinus* producing an immovable stem an autapomorphy. The immovable stem is thus considered to be a character convergent with the cyrtocrinids that share the same habitat. In view of the availability of only a single specimen and the lack of corresponding columnals we provisionally classify this form as an aberrant member of the Thiolliericrinidae within the Order Comatulida.

The Upper Jurassic and Lower Cretaceous Thiolliericrinidae combine characters of comatulids (a centrodorsal, in most of the Jurassic forms bearing cirri) and bourgueticrinids (a stem with synarthrial articulations but lacking cirri). Thiolliericrinids were cemented to the bottom or to some object by a basal disc that synarthrially articulated to the stem. An attachment disc with synarthrial articulation from the Birmenstorf Beds of Trimbach was figured by Hess (1975, Pl. 25, fig. 1) who assigned it to *Thiolliericrinus* or possibly *Burdigalocrinus*. In articulate crinoids new columnals are formed below the cup so that the oldest columnals are in the distal part of the stem. One could argue that the most distal columnal of *Argoviacrinus rarissimus* might have had a synarthrial facet (mirrored by the synarthry of the attachment disc). However, columnals and attachment discs found together with thiolliericrinid cups invariably have synarthrial articular facets (Klikushin 1987). Typical thiolliericrinid cups have so far not been found in the Birmenstorf Beds.

It may be assumed that thiolliericrinids retained synarthrial columnals through paedomorphosis from a larval, comatulid-like ancestor. Early Cretaceous Thiolliericrinidae are considered to lie near the ancestry of the bourgueticrinids. A close relationship between the two groups is also supported by their stratigraphic distribution; bourgueticrinids appeared only after the last known and morphologically similar thiolliericrinids that had centrodorsals lacking cirri (Simms 1988). The relationship was already recognized by Loriol (1882–1889, p. 544): "En réalité le *Thiolliericrinus* est un *Antedon* qui a conservé une tige, comme dans l'état larvaire, composée d'articles dont les facettes articulaires sont analogues à celles de l'état Pentacrinoïde de l'*Antedon*, et, on peut le dire aussi, un *Antedon*, avec la tige d'un *Bourgeticrinus*." *Argoviacrinus*, a thiolliericrinid design with immovable stem, seems to have been a short-lived, singular experiment.

7. Palaeoenvironment and palaeoecology

According to Gygi (1986) the facies of the Birmenstorf Member with siliceous sponge assemblages was deposited in relatively deep water (between 100 and 150 m) at a rather low sedimentation rate. Newer data, however, suggest a water depth near storm wave-base. During the Late Callovian, the Holderbank quarry was situated on a submarine swell (Bitterli 1977) that persisted into Oxfordian times (Allenbach 2001). The richness and diversity of the fauna also indicates rather shallow water and the presence of a local swell surrounded by deeper basins. Non-deposition during the Early Oxfordian and initially moderate deposition during the Middle Oxfordian suggest sediment by-passing on a swell rather than starvation. As discussed by Gygi (2000a) sponges became fossilized at an intermediate rate of sedimentation of mud. If the rate was too low, they were not fossilized but if it was too high (as in the lower Effingen Member), the sponges were smothered and disappeared in an inhospitable environment. Widespread, densely populated sponge biostromes characterize the Birmenstorf Beds. Sponges occur partly in life position but are mostly overturned or broken. The reason for this is unclear. Gygi (2000a) thought that sponges were overturned by the activity of animals such as fishes because the sediments were not influenced by tempestites. However, the sediments around the sponges are so deeply bioturbated that any evidence for or against the influence of tempestites has been lost (Allenbach 2001). Ammonites and echinoids such as *Paracidaris laeviuscula* and *Polydiadema langi* are mostly poorly preserved on one (their upper) side. This indicates that they corroded while lying exposed on the bottom. In contrast, the small, spherical echinoid *Magnosia decorata* and spines of regular echinoids as well as the large majority of the crinoid remains are well preserved and commonly need to be cleaned from the marly sediment. They may have been more easily accumulated in low spots on the sea floor or became trapped and protected by mud in low-energy pockets during local transport. Thus, the crinoids of the Birmenstorf Beds lived in an environment characterized by the presence of hardgrounds and other attachment sites (broken or overturned sponges, ammonite shells etc) and by a low sedimentation rate. The common occurrence of *Balanocrinus subteres* and *Isocrinus cingulatus* indicates that these long-stemmed isocrinids occupied a higher tier for feeding and were, thus, less susceptible to benthic predators or parasites than the host of cyrtocrinids cemented to the bottom. Most cups of *Cyrtocrinus nutans*, the most common species at Holderbank, are moderately asymmetric but some are spoon-like, with the articular facets for the arms at a right angle to the stem. In such cases the radials may be fused with the proximal columnal. The presence, at Holderbank, of species with mostly symmetric cups (*Eugeniacrinites*, *Pilocrinus*) and spoon-like cups indicates different niches. Asymmetry appears to have been an adaptation to constant unidirectional current, with the oral side of the crinoid directed downcurrent (Hess et al. 1999). This dependency on currents further substantiates an environment located on a swell where constant unidirectional currents can be expected.

Argoviacrinus is a thiolliericrinid-like crinoid; it has a centrodorsal with well developed cirri but, as judged by the distal articular facet of the centrodorsal, lost the flexibility of a synarthrial stem. Why would *Argoviacrinus* modify its juvenile synarthrial stem (presumably in a process of peramorphosis) during development in favour of a more rigid column? Thiolliericrinidae probably had rather short stems composed of maybe 5, mostly elliptical columnals (Klikushin 1987). The presence of synarthries with their bifascial ligament bundles must have made the stems quite flexible, and it may be assumed that such flexible stems were not easily broken in a reefal setting where water currents varied. In theory, thiolliericrinid crowns with their cirriferous centrodorsal could become detached from the stem (Hess et al. 1999), but it is not kown if or to what degree this occurred. Stem fragments (pluricolumnals) of thiolliericrinids that might give a clue have not been recorded so far, including the Lower Cretaceous of the Crimea, the richest reported site for these crinoids (Klikushin 1987). Crinoids with synarthrial stem articulations lacking a cirriferous centrodorsal are the Bourgueticrinida that occur from the Upper Cretaceous to Recent and include a number of extant forms living mostly in deeper waters (Hess et al. 1999). There is no report of a living bourgueticrinid having autotomized its stem, but individuals are commonly incomplete when captured. Dredged specimens rarely have intact stems (Rasmussen 1978). The modified cryptosynarthry of *Argoviacrinus* made the stem inflexible so that it may have broken at the centrodorsal. Unfortunately, more distal columnals and their articulation are unknown or unrecognized in the Birmenstorf Beds. In any case, cyrtocrinids with circular columns and cemented discs were the most abundant crinoids in the Birmenstorf sea. Strong attachments and immovable stems must have been one of the keys for their success; short, synarthrial and, therefore, flexible stems were not in demand, as demonstrated by the extreme rarity of - thiolliericrinids in these strata. The combination, in *Argoviacrinus*, of cirri and an immovable articulation to the stem may have contributed to survival of the animal by autotomy below the centrodorsal under stress conditions, separating the centrodorsal with cup and crown from the stem. Crinoids cemented to the bottom and occupying a very low tier, such as the very common cyrtocrinids, exhibit an extremely high degree of morphological plasticity. Such plasticity also seems to have formed *Argoviacrinus*.

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