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An intact Comatulid Crinoid from the Toarcian of southern Germany

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With 4 figures

Summary

A new comatulid crinoid, *Procomaster pentadactylus* gen. et sp. nov., is described on the basis of a single, virtually intact specimen from the south German Posidonienschiefer (Lower Toarcian). It is the second oldest true comatulid known but has a comparatively advanced morphology, with only five unbranched arms and robust, recurved cirri.

Its phylogenetic position is unknown but its morphology suggests that two distinct comatulid groups were already present in the early Toarcian, implying a common ancestry still earlier in the Jurassic or late Triassic.

The occurrence of an apparently benthic crinoid in the anoxic to dysaerobic facies of the Posidonienschiefer is remarkable. It may have accidentally drifted in on vesicular seaweed or some other floating substrate, or this may represent the extreme edge of its range during a brief period of higher oxygen levels in the Posidonienschiefer basin.

Zusammenfassung

Ein neuer comatulider Crinoide, *Procomaster pentadactylus* gen. et sp. nov., wird beschrieben aufgrund eines einzelnen, praktisch vollständigen Exemplars aus dem süddeutschen Posidonienschiefer (Unter-Toarcium). Es ist der zweitälteste bekanntgewordene echte Comatulide; gleichwohl hat er eine vergleichsweise fortgeschrittene Morphologie mit nur fünf unverzweigten Armen und kräftigen, zurückgebogenen Zirren.

Seine stammesgeschichtliche Stellung ist nicht bekannt, jedoch legt seine Morphologie nahe, daß es im frühen Toarcium bereits zwei verschiedene Gruppen der Comatuliden gegeben hat. Dies bedeutet, daß ein gemeinsamer Ursprung noch früher im Jura oder in der späten Trias gelegen hat.

Das Vorkommen eines offensichtlich benthonischen Crinoiden in der sauerstoffreien bis -armen Fazies des Posidonienschiefers ist bemerkenswert. Das Tier mag zufällig auf einem Blasentang oder irgendeinem anderen treibenden Substrat angetriftet sein, oder der Fund könnte auch den äußersten Rand seines Lebensraums während einer kurzen Zeit höheren Sauerstoffgehalts im Posidonienschiefer-Becken bezeichnen.

Acknowledgements

I should like to thank Mr A. Brune, of Aalen, who discovered the specimen, and Mr J. Fischer, in whose quarry it was found. I also thank Dr. Gerd Dietl, of the Staatliches Museum für Natur-

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Introduction

The suborder Comatulidina, in the articulate order Isocrinida (SIMMS, in press a), is the dominant extant crinoid group with a diversity exceeding all other extant crinoids together. They are characterised by the presence of a centrodorsal, usually cirriferous, in place of the stem characteristic of most other crinoids. By abandoning the stem during the larval stages comatulids achieve a much greater vagility than the comparatively sessile stalked isocrinids. Active locomotion over short distances may be achieved by crawling or even swimming and this is probably one of the reasons for their success (MEYER & MACURDA 1977).

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The evolutionary sequence of events leading from stalked isocrinids to stemless comatulids has been clarified by the discovery of a number of morphologically inter-mediate forms. In 1951 HANS HESS described a new crinoid, *Paracomatula helvetica*, from the Swiss Bathonian, which he considered to lie close to the line of ancestry of comatulids. The most significant feature of this 10-armed crinoid was the very short, tapered stem which could almost be regarded as a segmented centrodorsal. On the basis of similarities in the symplectial articula, HESS considered *Paracomatula* to have been derived from *Pentacrinites*, though in other respects, such as arm branching, their morphology was quite distinct. Almost three decades earlier GISLÉN (1924) had also suggested derivation of comatulids from the Pentacrinitidae on account of the reduction of the proximal pinnules in *Seirocrinus* and many comatulids.

More recently a second, still more primitive, "protocomatulid" has been recognised. *Pentacrinus interbrachiatus* BLAKE, from the Pliensbachian of the Yorkshire coast, was described as a typical stalked isocrinid on the basis of a partial crown and an isolated pluricolumnal from the same locality (TATE & BLAKE 1876). The pluricolumnal has since been found to belong to an unrelated isocrinid, *Chladocrinus robustus* (WRIGHT), but the crown represents a distinct species. The discovery of a number of well preserved crowns of this species in museum collections has shown that the stem, broken off in the holotype, is actually very short and comprises only a few cirrinodals (SIMMS, in press b). *Pentacrinus interbrachiatus*, assigned to a new genus, *Eocomatula* (SIMMS, in press a), has weakly endotomous arms and cirri with a rhomboidal section. In these respects it resembles pentacrinitids. It resembles *Paracomatula* in the inflated latera of the radials and in the very short stem comprising only cirrinodals. However, unlike the stem of *Paracomatula*, that of *Eocomatula* does not taper distally. Thus *Eocomatula* represents an almost perfect morphological intermediate between the Pentacrinitidae and *Paracomatula* and demonstrates a possible evolutionary sequence from the long-stemmed pentacrinitids to the stemless comatulids through the loss of the distal part of the stem progressively earlier in ontogeny (SIMMS, in press c).

In this original discussion concerning the phylogenetic position of *Paracomatula helvetica* HESS (1951) considered that it did not lie on the direct line of descent of comatulids, this being evident from the presence of true comatulids in pre-Bathonian strata. Paracomatulids are now known from at least the early Toarcian (SIEVERTS-DORECK pers. comm.; SIMMS, in press b) and possibly even as early as the late Triassic

(SIMMS, in press a). True comatulids are very rare before the late Bajocian, the earliest being found in the basal Toarcian. LORIOL (1888) described two specimens, a centrodorsal and a radial circlet, from the "Couche à *Leptaena*" (*tenuicostatum* Zone) of Calvados, northern France. Although he ascribed distinct specific names to the two specimens (*Antedon morierei* and *A. caraboeufi*), it is highly probable that they represent a single species, since assigned to the genus *Palaeocomaster* (RASMUSSEN 1978).

Considering the great rarity of comatulid remains in pre-Bathonian strata, the discovery of an intact comatulid in the Toarcian Posidonienschiefer is especially remarkable and forms the subject of this paper. The specimen is important since it provides an insight into the early development of a group with a comparatively poor fossil record.

Systematic description

Class Crinoidea MILLER 1821
Subclass Articulata MILLER 1821
Order Isocrinida SIEVERTS-DORECK 1952
Suborder Comatulidina A. H. CLARK 1908
Family incertae sedis

Procomaster pentadactylus gen. et sp. nov.

Holotype: The holotype and only known specimen (fig. 1) is an exceptionally well preserved individual with the arms, pinnules and cirri largely intact. It was found in September 1983 by Mr A. Brune, of Aalen, who presented it to the Staatliches Museum für Naturkunde, Stuttgart (Specimen SMNS No. 26993).

Type locality: Zell u. A., Württemberg; quarry J. Fischer. Topogr. map 1 : 25000, sheet No. 7323 Weilheim a. d. Teck, r: 3541000/h:5390850.

Type horizon: Posidonienschiefer (Lower Toarcian) 25 cm below the top of Schwarzjura epsilon II, 4. This is equivalent to the lower part of the *exaratum* Subzone of the *falciferum* Zone.

Derivation of name: *Procomaster* – in reference to the very early occurrence of this comatulid; *pentadactylus* – after the five very slender arms.

Diagnosis. – A small, slender comatulid with five arms composed throughout of very low brachials. About 25 robust, strongly recurved cirri.

Stem/Centrodorsal. – The centrodorsal in this specimen is entirely concealed by the cirri. Hence it is not possible to positively determine whether it is a single ossicle, as in true comatulids, or is composed of several discrete nodal columnals as in paracomatulids. It is clearly less than 5 mm long since it is not visible between the cirri at this level. There is some indication from the preserved arrangement of the cirri that the cirral sockets are arranged in 10 or 15 vertical rows.

Cirri. – About 23 cirri are visible in the specimen. The most intact are about 25–30 mm long and comprise about 40–45 cirral ossicles. They curve gently in their proximal and medial region through about 50–60°, curving more sharply through a further 100–120° in their distal part. Cirral ossicles are rounded rhomboidal in section with the fulcral bar parallel to the minor axis. Articula are strongly sigmoidal in side view (figs. 2, 3). They are slightly shorter in the proximal region of the cirri than further distally, where length is about 70% of width. The terminal ossicle is short and bluntly conical (fig. 2). Cirral ossicle latera are smooth and unornamented.

Dorsal Cup and Tegmen. – The dorsal cup is entirely concealed by the cirri but it must be very small and low since the combined height of the centrodorsal and dorsal cup is no more than 5 mm. No trace of the tegmen is visible.

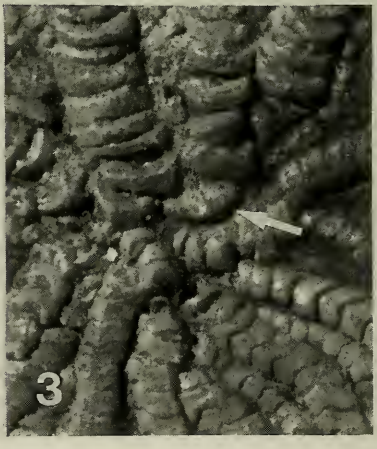

Fig. 1. Holotype and only known specimen of *Procomaster pentadactylus* gen. et sp. nov. Found 25 cm below the top of Schwarzjura epsilon II,4 (lower part of the *exaratum* Subzone) in the quarry of J. Fischer in Zell u. A., Württemberg. Specimen SMNS No. 26993. – x1.

Fig. 2. Detail of cirri showing sigmoidal articula and conical terminal ossicle (arrowed). – x3.

Fig. 3. Detail of cup region showing synarthrial articulation at IBr1–2 (arrowed). – x5.

Fig. 4. Medial region of arms with intact pinnules. The positions of consecutive syzygial articulations are indicated by the small arrows. – x4.

Arms. – Only five arms are visible in this specimen and, since there is no trace of any further arms, it seems probable that they do not branch at IBr2 as is typical of most articulate crinoids. All but one, which lacks the distal portion, are apparently intact. They are long and slender, with a length of 56 mm and diameter near the arm base of 2.35 mm. There are more than 120 brachials in each arm. They are very low throughout its length with a height/width ratio of less than 0.4 in proximal brachials. Brachial latera appear smooth and unornamented. The articulation at IBr 1-2 is synarthrial, with a faintly granular fulcral ridge (fig 3). All other brachial articula appear to be either muscular or syzygial. Syzygies occur at about every third to fifth articulation (fig. 4), though the form of the articulum has not been seen. Muscular articula have a moderately large aboral ligament fossa covering about 40° of the total articulum area.

Pinnules. – Pinnules are present throughout the preserved portions of the arms. They reach a maximum length of about 14 mm about midway along the arm, decreasing in length both proximally and distally from this point. The longest pinnules comprise about 30 unornamented, roughly equidimensional pinnular ossicles. The ambulacral groove is about 0.2 mm wide. The form of the pinnules is less easy to make out in the proximal region of the arms although there does not appear to be any clear differentiation of pinnule type along the arm.

Discussion

The discovery of this comatulid is remarkable for several reasons, aside from the general rarity of intact fossil comatulids. Firstly, it is important as representing one of the earliest comatulids known, being only slightly younger than *Palaeocomaster morierei/caraboeufi* (Loriol 1888) from the basal Toarcian. Secondly, assuming it was a benthic form, like all other known comatulids, then it is unique among the Posidonienschiefer crinoid fauna which otherwise consists exclusively of the pseudopelagic pentacrinitids *Seirocrinus subangularis* (Miller) and *Pentacrinites dichotomus* (M'Coy) (Seilacher et al. 1968; Simms 1986). Finally, its distinctive morphology indicates that even in the early Toarcian there may already have been at least two distinct comatulid lineages, implying an even earlier origin for the group.

The presence of a benthic echinoderm in the Posidonienschiefer is not, in itself, especially remarkable since a variety of benthic faunal elements, including echinoids and ophiuroids, are known from a number of levels. However, although these forms occur at the more oxygenated horizons (Seilacher 1982) they appear to be generally tolerant of low oxygen levels whereas this is not the case for crinoids. Hence, benthic crinoids were effectively excluded from the Posidonienschiefer which consequently is dominated by pseudopelagic forms which inhabited the better oxygenated surface waters. This comatulid therefore clearly represents an exotic element of the Posidonienschiefer fauna, comparable with some of the nonmarine elements such as pterosaurs or sphenodontids. However, whereas these may have flown or been drifted into the area on debris rafts this cannot have been the case for benthic crinoids. The delicate construction of crinoids, their rapid rates of disarticulation after death (Meyer & Meyer 1986) and the intact nature of this specimen precludes any possibility of it having been swept by currents into the basin from shallower water since the projected distances are too great. The possibility of it having passively drifted in attached to vesicular seaweed which became detached from its holdfast in shallow water is a more plausible explanation. However, it is perhaps significant that a comparatively diverse benthic fauna,

including crustacea and echinoids, occurs together with the comatulid in Lias epsilon II, 4 (HAUFF & HAUFF 1981). This suggest that oxygen levels were relatively high at this time enabling the benthic fauna of surrounding areas to briefly extend their ranges further into the Posidonienschiefer basin. Hence the distance that this benthic crinoid was transported could have been considerably reduced.

The phylogenetic position of *Procomaster* is particularly interesting and problematic. Despite its very early stratigraphic position it appears to be a comparatively advanced form barely distinguishable at first glance from some extant comatulids. Although the centrodorsal is not visible, the advanced morphology of this crinoid suggests it is a true comatulid rather than a paracomatulid. The most significant feature is the presence of only five arms. Although quite a number of fossil and extant crinoids are known in which the five arms remain undivided, the primitive condition for articulate crinoids is for the arms to branch at IBr2. They may often branch further distally as well. Reduction to a simple five-armed condition is an advanced trait unknown among post-Palaeozoic crinoids prior to this early Toarcian form. In the unbranched and delicate nature of these arms, it differs significantly from *Eocomatula*, with its robust, endotomously branched arms, and also *Paracomatula* which has long arms dividing once, at IBr2, and composed of relatively tall brachials. The strongly recurved cirri also appear more advanced than those of either *Eocomatula* or *Paracomatula*.

Clearly *Procomaster* represents a considerable advance upon either of these two "proto-comatulid" genera though it cannot readily be placed in any existing comatulid phylogeny. This can be attributed al least in part to the poor fossil record of early comatulids although the issue es further complicated by an inadequate classification for the group. Only five comatulid families are known to include forms with unbranched arms; the Atelecrinidae, Solanocrinitidae, Decameridae, Eudiocrinidae, and Pentametrocrinidae. *Procomaster* does not resemble any of these particularly closely. The Pentametrocrinidae have longer cirral ossicles, from 2.5 to 5 times their width. *Eudiocrinus* has a syzygy rather than synarthry at IBr1–2. In *Decameros* and *Pseudoantedon* (Decameridae) there is no indication of synarthrial or syzygial articula in the arms. This leaves only the Atelecrinidae and Solanocrinitidae.

The Atelecrinidae have a comparatively primitive comatulid morphology, with the persistence of prominant basals in the cup. However, known species differ in the greater relative height of the brachials, though it is not clear how diagnostic this character is. The Solanocrinitidae show a considerable range of variation and include some of the earliest known comatulids. However, the synarthrial articula are apparently very flat and have only been seen at IBr1–2 in forms with the arms branching at IBr2, thus differing from *Procomaster*. Thus *Procomaster* cannot unequivocally be assigned to any of these five comatulid groups, though the possibility must still remain that it has closer affinities with some group not otherwise known to have any 5-armed representatives. However, with the present inadequate classification scheme for the comatulids it is very difficult to assess the phylogenetic position of this specimen.

Conclusions

The discovery of an intact, 5-armed comatulid crinoid in the Posidonienschiefer poses many problems, both for the systematist and the palaeoecologist. It is clearly distinct from any other Mesozoic comatulid but the present, inadequate classification of the group hinders attempts to determine its phylogenetic position. It bears similarities

both to the Atelecrinidae and the Solanocrinitidae, though it cannot uneqivocally be linked with either on the limited data available. This problem can probably only be resolved by the discovery of further material, in which the precise form of the centrodorsal can be seen, and, more fundamentally, through a major revision of comatulid systematics.

The presence of an obviously benthic crinoid in the predominantly anoxic to dysaerobic facies of the Posidonienschiefer is equally puzzling. It may represent the extreme limit of this species' range during a transient period of relatively high oxygen levels, but more probably it represents an example of "accidental pseudoplankton", being inadvertently carried into the basin after attaching to a fixed but buoyant substrate which was subsequently cast adrift.

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