

Origin and radiation of the comatulids (Crinoidea) in the Jurassic

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Abstract The early history of the comatulids is discussed based on recently described Jurassic specimens. Their centrodorsals suggest that the Order Comatulida is a monophyletic, synapomorphic clade that originated with *Palaeocomaster* from stem group pentacrinitids and not from a paracomatulid ancestor. A pentacrinitid is also considered ancestor to *Paracomatula*. As a result Paracomatulidae are classified with Pentacrinitina, making Paracomatuloidea redundant as a suborder of Comatulida. *Palaeocomaster paucicirrus* n. sp. from the Toarcian/Aalenian of Quedlinburg, northern Germany, and *Palaeocomaster benthuysi* n. sp. from the Pliensbachian of Sedan, France, are described as new.

Keywords Comatulids · Paracomatulids · Phylogeny · Taxonomy

Introduction

The present paper was initially part of a larger paper describing Early and Late Jurassic mudstone faunas with mainly remains of *Balanocrinus* species, but also some comatulids. Upon the advice of one of the reviewers (H. Hagdorn) it was divided into three parts (Hess 2013a, b, this paper). The comatulids from the Oxfordian sites of Andelot-Morval and Savigna are described in detail in one of the parallel papers (Hess 2013b). The present part is mainly concerned with the early history of the comatulids and the position of the paracomatulids, but also contains

descriptions of two new Early Jurassic comatulids. In combination with previously described material from the Early and Middle Jurassic (Hess 2006, 2012) the comatulids now available demonstrate that centrodorsals are essential to the classification of comatulid species in the Jurassic, even if cups with basals and radials are not available for additional information. Gislén (1924), though recognizing the importance of centrodorsals for comatulid classification, provisionally referred all species of which only the centrodorsal was known to the genus *Glenotremites* of Goldfuss (1829). This approach was rejected by Rasmussen (1961, p. 278), and his criticism is fully justified by the present state of knowledge. The previously described Bathonian forms (Hess 2012) and those from the Oxfordian (Hess 2013b, present paper) anticipate the diversity of centrodorsals found in living comatulids. Several different types are represented in the Jurassic (classification according to Hess and Messing 2011) and are discussed in the following, but not without first clarifying the status of the paracomatulids, also present in the Early Jurassic. Figure 1 shows a number of paracomatulids and comatulids from the Triassic to the Upper Jurassic in their stratigraphical sequence.

Suprafamilial taxa of Jurassic comatulids

Comatulids or feather stars are the dominant living crinoids. The Order Comatulida A.H. Clark of the *Treatise* (Hess and Messing 2011) includes three suborders: Comatulidina A.H. Clark with a number of superfamilies, Bourgueticrinina Sieverts-Doreck with four families and Guillecrinina Mironov & Sorokina with one family. In Comatulidina the superfamilies Paracomatuloidea Hess, Solanocrinitoidea Jaekel, Tropiometroidea A.H. Clark and

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Notocrinioidea Mortensen have Jurassic representatives. The Paracomatuloidea date to the Late Triassic (Norian). It will be shown in the present paper that the paracomatulids are not ancestral to the comatulids proper but have to be classified with Pentacrinina Gray, suborder of Isocrinida Sieverts-Doreck. Thus, the first true comatulids date to the Early Jurassic. Doubts that the Paracomatuloidea may not form part of the comatulid crown group have recently been expressed by Rouse et al. (2013); these authors also concluded from molecular data that Guillecrinina and Bourgueticrinina arose from within Comatulidina, rendering the latter group paraphyletic and its subordinal name redundant. As a consequence both Guillecrinina and Bourgueticrinina are also redundant, but are nested as families in the Comatulida.

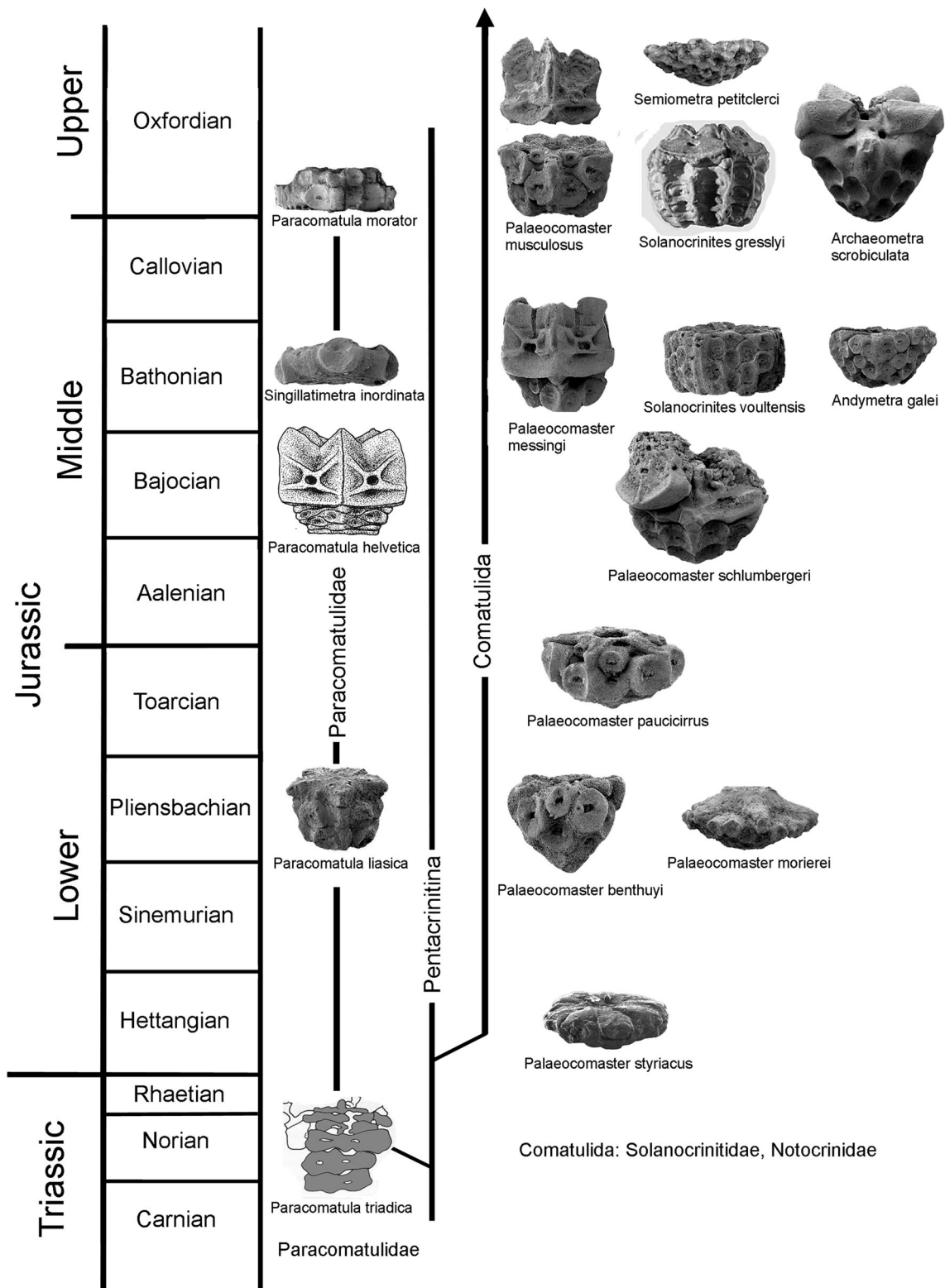
Comatulids from Hettangian to Oxfordian

Comatulids are rare fossils in Jurassic sediments. Because of their mostly small size, especially in the Lower Jurassic, the remains are not usually found by field collectors, and they are exceptional fossils even in residues of processed bulk sediments. The Early Jurassic species all belong to the genus *Palaeocomaster* Gislén (1924), with *P. styriacus* Kristan-Tollmann (1988) from the Hettangian, *P. morierei* (Loriol, 1888) and the presumably conspecific *P. caraboeufi* (Loriol, 1888), *P. benthuyi* n. sp. from the Pliensbachian, and *P. paucicirrus* n. sp. from the Toarcian/Aalenian. In the Middle Jurassic the number of described genera and species increases significantly. *Palaeocomaster* is represented by the Bathonian *P. schlumbergeri* (Loriol, 1888), *P. stellatus* Gislén (1924), *P. latiradius* (Carpenter, 1882), and *P. messingi* Hess (2012); from the Callovian is *P. calloviensis* (Carpenter 1882). Also present in the Bathonian is *Andymetra*, with *A. galei* Hess (2012) and *A. ladoixensis* (Loriol, 1888; see Hess 2012); and the superficially similar genus *Semiometra* Gislén (1924) makes its first appearance with *S. muelleri* (Carpenter 1880). The genus *Solanocrinites* (Goldfuss, 1829) is first recorded from the Bajocien/Bathonian with *S. ooliticus* Gislén (1924) and *S. voutensis* Hess (2012). In the Late Jurassic the number of species increases even further, and some species become larger. In the Oxfordian *Palaeocomaster* is represented by *P. guirandi* (Loriol, 1889) and *P. musculosus* Hess (2013b), *Andymetra* by *A. donovani* Hess (2013b), and *Semiometra* by *S. petitclerci* (Caillet, 1923; see Hess 2013b). The genus *Solanocrinites* is prominent, with approximately 7 species in the French and Swiss Jura (Loriol 1879, 1888); *Archaeometra* Gislén (1924) includes the large and sturdy *A. scrobiculata* (Münster in Goldfuss, 1831; see Carpenter 1881 and Hess 2013b).

Fig. 1 Phylogeny of paracomatulids and comatulids from Late Triassic to early Upper Jurassic. Geological ages and specimens not to scale. Sources of the figured representative specimens: *Paracomatula triadica* Hagdorn and Campbell (1993, part of fig. 6; the segmented centrodorsal is shadowed); *Paracomatula liasica* Hess, new SEM photograph; *Paracomatula helvetica* Hess (Hess and Messing 2011, from Rasmussen 1978; this is a composite picture); *Singillatimetra inordinata* Hess (2012); *Palaeocomaster styriacus* Kristan-Tollmann (1988); *Palaeocomaster benthuyi* n. sp., this paper; *Palaeocomaster morierei* (Loriol), new SEM photograph, this paper; *Palaeocomaster paucicirrus* n. sp., this paper; *Palaeocomaster schlumbergeri* Loriol, this paper; *Palaeocomaster messingi* Hess (2012); *Solanocrinites voutensis* Hess (2012); *Andymetra galei* Hess (2012); *Palaeocomaster musculosus* Hess 2013b, centrodorsal and cup in lateral view); *Solanocrinites gresslyi* (Étallon), Hess and Messing (2011); *Archaeometra scrobiculata* (Münster in Goldfuss), Hess (2013b); *Semiometra petitclerci* (Caillet), Hess (2013b)

The position of the paracomatulids

Paracomatulids have a discoidal, compact, functional centrodorsal composed of closely fitting individual columnals. The group is classified in the Family Paracomatulidae Hess and includes *Paracomatula* Hess and *Singillatimetra* Hess. Species of *Paracomatula* have centrodorsals composed of a variable number of columnals. The centrodorsal of *P. triadica* Hagdorn and Campbell (1993) from the Norian has three low columnals proximally and three higher, aborally sealed nodals distally (Fig. 1). *P. liasica* Hess (2006) from the Pliensbachian has two nodals sealed aborally (Fig. 2); the presence of a number of isolated columnals indicate that they were not tightly connected. *Paracomatula* sp. from the Late Sinemurian–Early Pliensbachian (Nicosia 1991, fig. 42) has seven nodals; an open axial canal distally suggests an unfinished stage of development or incomplete preservation. *P. helvetica* Hess (1951) from the Bajocian has three nodals proximally and two low, aborally sealed elements distally (Fig. 1). *P. morator* Hess from the Oxfordian (Hess 2013b) has two closely united nodals with a moderately wide centrodorsal cavity proximally and an open, narrow cavity or axial canal distally where the pronounced symplexy is quite unusual for the genus. This rather complex picture is corroborated by the Bathonian *Singillatimetra inordinata* Hess (2012) with only one aborally sealed nodal (Fig. 1). Common to all these forms is a five-sided centrodorsal of coalesced elements articulated by a more or less distinct pattern of crenulae and cirrus sockets offset to either side of radial midline. Internodals are never developed. The adoral (upper) facet of the centrodorsals shows impressions for the stellate cirlet of basals and resembles symplectial facets of *Pentacrinites* and *Eocomatula* nodals, with narrow interradian petals bordered by short, uniform crenulae. The basal cirlet of the Bajocian *P. helvetica* consists of narrow pieces (see Hess and Messing, 2011, fig. 371b), but the cirlet is much more developed in the



Pliensbachian *P. liasica* where the upper facet resembles the facet of a pentacrinitid columnal (Fig. 2b). Unfortunately, the basal cirlet is hardly visible in the Norian *P. triadica* Hagdorn and Campbell (1993), and the corresponding facets are not exposed, making a direct comparison impossible. In contrast to the thick column of *Eocomatula* the tapered column of *Pentacrinites dargniesi* has a sealed axial canal in the distal-most columnal.

The segmented centrodorsals of paracomatulids and the centrodorsals of comatulids *s. str.* are homologous structures descended from a pentacrinitid stem group. A common origin of the two clades is supported by characters of the cup. *Paracomatula helvetica* has narrow basals with crenulated margins, united centrally and embedded in the proximal side of the radial cirlet (Hess and Messing, fig. 371d). The stellate basal cirlet with narrow interradial petals bordered by short, uniform crenulae, or its impression on the centrodorsal (Hess 1951, fig. 7), closely resembles the respective structure of *Pentacrinites* (Hess and Messing 2011, fig. 21d,f) or *Eocomatula* (loc. cit., fig. 232b). Steep radial articular facets occur in *Paracomatula* and *Pentacrinites* (Hess and Messing 2011, fig. 21e and 371c), although the muscle fossae are less developed in the latter genus. Simms (1988, p. 275) somewhat arbitrarily classified Eocomatulidae with Paracomatuloidea, although “they might equally well be placed with the Pentacrinitidae on other characters”, and he considered them “an almost perfect intermediate stage between the Pentacrinitidae and Paracomatulidae”. However, Hess and Messing (2011), following Hagdorn and Campbell (1993), placed *Eocomatula* in the Pentacrinitina because of several apomorphic characters, such as radials with pyramidal projection, rhomboidal cirrals and endotomous arm branching, not found in *Paracomatula*. Gislén (1924, p. 204) discussed *Pentacrinites* as a possible precursor to the comatulids. Rasmussen (1978, p. T311) expanded the discussion by the

inclusion of *Paracomatula*, although he mentioned that in the original description (Hess 1951) it was postulated that *Paracomatula* was not directly involved in the evolution of comatulids. The early evolution of the comatulids was not further discussed by Hess and Messing (2011). The centrodorsal of *Palaeocomaster* is synapomorphic, making the Comatulida a monophyletic clade. As a consequence, Paracomatulidae must be transferred from Comatulida to Isocrinida, Suborder Pentacrinitina; and the Superfamily Paracomatuloidea in Hess and Messing (2011) becomes redundant. *Eocomatula* has a column of five nodals articulated symplectically and cirrus sockets offset to either side. Cirrals are more rounded than in *Pentacrinites*, and they become rhomboidal only distally. Arm branching is feebly endotomous beyond tetrabrachials (see Simms 1989, pl. 6, fig. 3). Thus, pentacrinitine characters are rather weakly expressed in *Eocomatula*; and this approaches the genus to *Paracomatula*, although placement of the genera in separate families seems justified. Transfer of Paracomatulidae to Pentacrinitina necessitates modifications in suborder diagnosis in Hess and Messing (2011), see section “Systematic palaeontology”.

Centrodorsal types

In the Jurassic several types of comatulid centrodorsals occur. They may be classified as follows (see also Fig. 1).

1. The centrodorsal is five-sided, but rather irregular in shape, without distinct interradial angles; and it is composed of more or less fused but still distinct tubes that widen outwards to the cirrus sockets. The aboral side is rugose or smooth and, if flat, devoid of cirrus sockets. The basals are united centrally to form a cirlet, and they articulate with the centrodorsal via narrow petals, similar to the paracomatulids. The

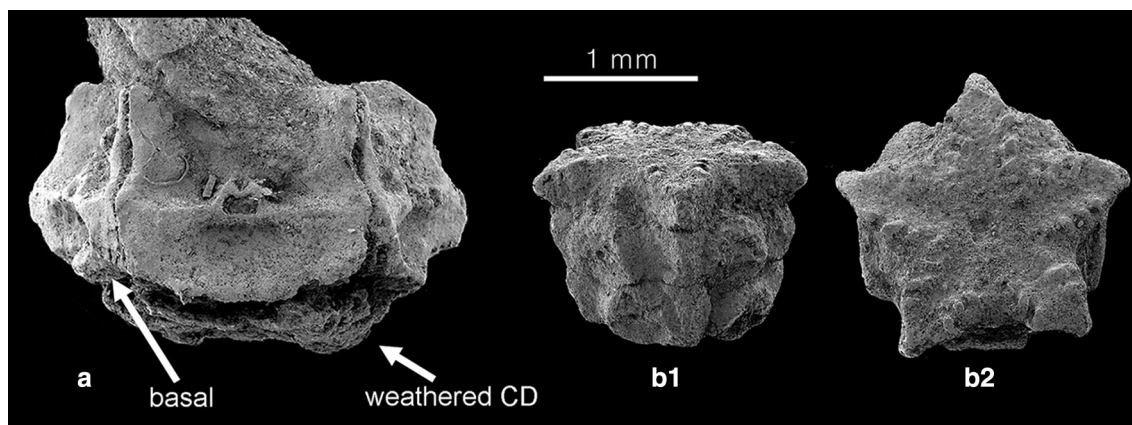


Fig. 2 *Paracomatula liasica* Hess, Pliensbachian, Arzo, Switzerland. **a** Lateral view of cup with partly weathered centrodorsal, paratype (Hess 2006, pl. 23, fig. 3), M10360; **b** centrodorsal with basal cirlet,

holotype (Hess 2006, pl. 23, fig. 4), M10361; **b1** lateral view, **b2** adoral view, note resemblance of basal cirlet to facet of *Pentacrinites*

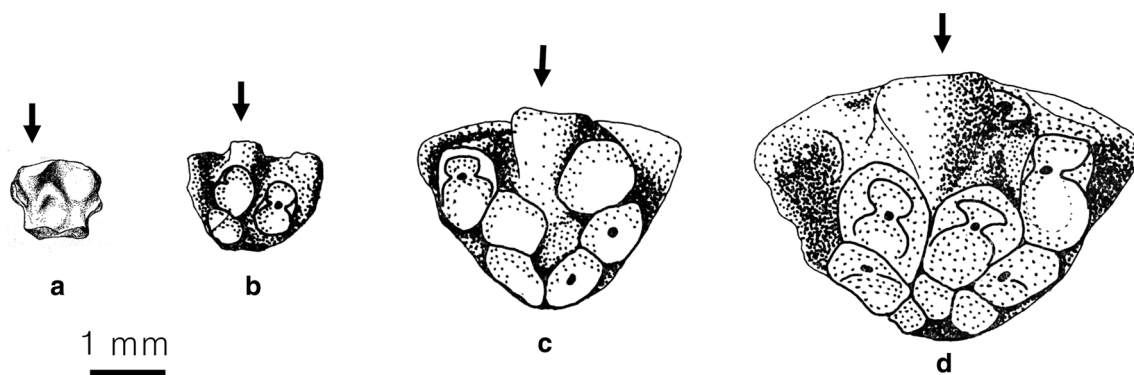


Fig. 3 Growth stages of centrodorsals of *Archaeometra koprivnicensis* (Remeš) from the Lower Cretaceous of Štramberk (from Žitt 1980). Arrows indicate interradian position

radials, where preserved, have large and steep articular facets with high muscle fossae; consequently, the radial cavity is rather wide. This group includes *Palaeocomaster* Gislén. In contrast to the paracomatulids the centrodorsal of *Palaeocomaster* species is assembled from individual “cirrus tubes” that can still be recognized in part. This feature is present already in the first species, *P. styriacus* Kristan-Tollmann (1988) from the Hettangian.

2. The centrodorsal is columnar with cirrus sockets in regular columns separated by ridges; the interradian angles are produced and the aboral apex flat and cirrus-free. The narrow, rod-shaped basals lack crenulae and form a closed circlet. The radial articular facets are outward-sloping and relatively low, the radial cavity is moderately wide. The group includes *Solanocrinites* Goldfuss. Centrodorsals of this type first appear in the Bathonian, and there are many Late Jurassic forms.
3. The centrodorsal is hemispherical in juveniles to conical in adults, roughly five-sided but without sharp interradian angles; the cirrus sockets are irregularly distributed, large and facing downwards; the radial area is not divided by a ridge. The basals are rod-like and produced, they lie on prominent ledges of the centrodorsal and meet around the central cavity. The radial circlet is mostly lower than the centrodorsal, but the radials have a large free aboral surface. The radial facets are outward-sloping in the lower part; in the upper part nearly vertical muscle fossae result in a rather narrow radial cavity. This group includes *Archaeometra* Gislén. In this mainly Late Jurassic group large conical centrodorsals appear for the first time in comatulid history.
4. The centrodorsal is low hemispherical and lacks distinct interradian angles; the cirrus sockets are crowded and form irregular rows, the aboral apex has only a small cirrus-free area. The centrodorsal cavity is narrow. The radial articular facets are outward-sloping in most forms. Jurassic members of

the group are *Andymetra* Hess and *Semiometra* Gislén. The oldest fossil ascribed to *Semiometra* is *S. abnormis* (Carpenter 1880) from the Bathonian, and the youngest fossils are the Maastrichtian *S. impressa* (Carpenter), *S. lenticularis* (Schlüter), see Rasmussen (1961), and *S. saskiae* Jagt (1999). *S. petittclerci* (Caillet 1923) has been recorded from the Oxfordian of France, Poland and northwestern Germany, see Hess (2013b). This wide range makes the genus, or at least its type of centrodorsal, the most successful in comatulid history. Similar centrodorsals dominate the largest family of extant comatulids, the Antedonidae (Hess and Messing 2011). The success of such centrodorsals may be due to their capacity to accommodate the largest number of cirri on the smallest surface.

Centrodorsal formation

The segmented centrodorsal of *Paracomatula* may be regarded as a much shortened column with the function of a comatulid centrodorsal composed of a single ossicle. Centrodorsals composed of several fused, preformed columnals are unknown in extant comatulids, even in forms with a very high five-sided centrodorsal such as *Zenometra* (see Hess and Messing 2011, fig. 703a). During the pentacrinoid larval stage living comatulids have a column without cirri, and they are attached by a disc. Subsequently, cirri are formed in the uppermost columnal, and the rest of the column is discarded; additional columnals never form below the cup. In contrast, paracomatulids formed a variable number of columnals, those below the cup mostly with cirri; subsequently, column growth was stopped. It never came to the addition of cirri on a growing, single element as in the true comatulids. *Palaeocomaster* species are the first comatulids with cirrus bases assembled on a single centrodorsal during growth. This is demonstrated by the rather loose structure and the presence of smaller sockets at

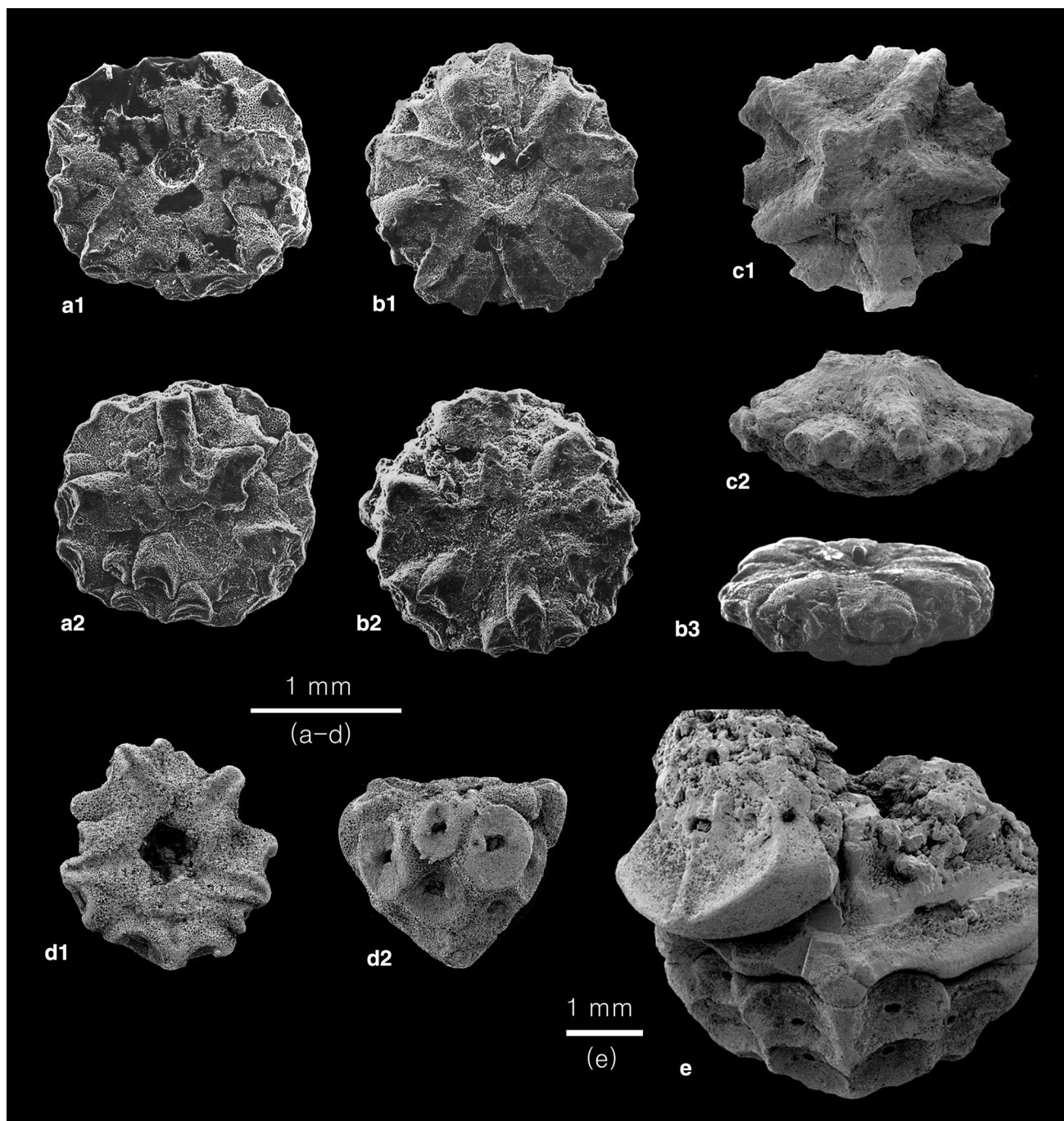


Fig. 4 Jurassic comatulids. **a–b** Centrodorsals of *Palaeocomaster styriacus* Kristan-Tollmann (1988), Hettangian, Salzkammergut, Austria; **a1** adoral, **a2** aboral; **b1** adoral, **b2** aboral, **b3** lateral, holotype (from Kristan-Tollmann 1988). **c** Centrodorsal with basal circling of *Palaeocomaster morierei* (Loriol, 1888), Pliensbachian, Arzo, NMB M10358; **c1** proximal, **c2** lateral. **d** Centrodorsal of

Palaeocomaster benthuvi n. sp., Early Pliensbachian, Sedan, holotype, M11416; **d1** adoral, **d2** lateral. **e** Centrodorsal with cup and first primibrachial (note synarthrial distal facet) of *Palaeocomaster schlumbergeri* (Loriol, 1888), Bathonian, Luc-sur-Mer, Calvados (see Bigot 1938). NMB M11034

the zone of growth near the adoral side (see Hess 2012, fig. 11a2, b2; and Figs. 4a1, d1, 5a in the present paper). Žítt (1980, Fig. 3) described growth stages in centrodorsals of *Archaeometra koprivnicensis* (Remeš) from the Lower Cretaceous of Štramberk; the smallest centrodorsal with a

height of 1 mm has a column-like lower part with five cirrus sockets (Žítt 1980, fig. 3; Fig. 3a). The aboral pole of Žítt's smallest specimens (not figured by Žítt) shows distinct traces of a column with a pentagonal outline and a trace of the axial canal. This confirms that the larval

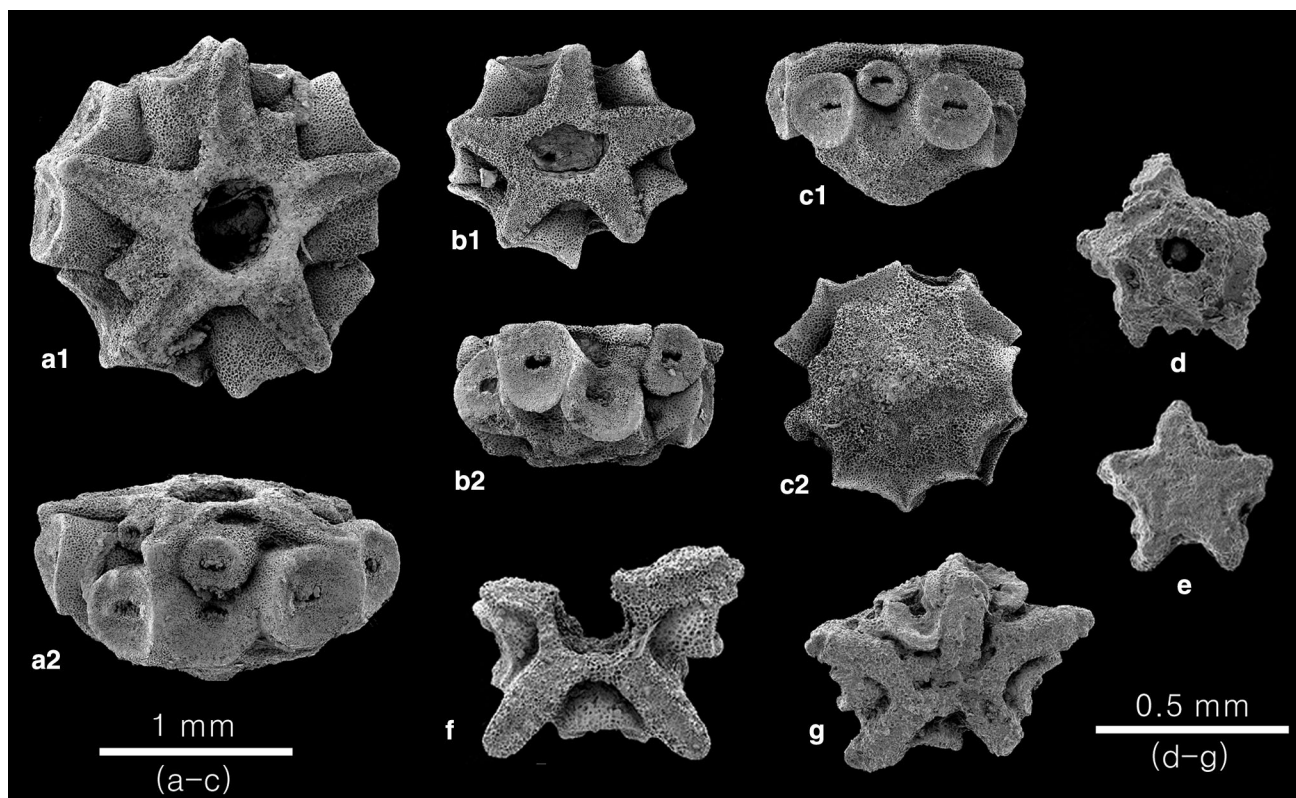


Fig. 5 *Palaeocomaster paucicirrus* n. sp., centrodorsals with basal circlings, Toarcian/Aalenian, Quedlinburg, northern Germany. **a1** Adoral, **a2** lateral, holotype, SMNS 70107/1; **b1** adoral, **b2** lateral, SMNS 70107/2; **c1** lateral, **c2** aboral with convex apex, SMNS 70107/3; **d** aboral view of small centrodorsal with closed centrodorsal cavity, SMNS 70107/4; **e** aboral view of small centrodorsal with open centrodorsal

cavity, SMNS 70107/4; **e** aboral view of small centrodorsal with open centrodorsal cavity, SMNS 70107/6; **f** adoral view of partly broken centrodorsal with basal circling, SMNS 70107/6; **g** adoral view of deformed centrodorsal with basal circling, SMNS 70107/7

column was cast off after formation of the first five cirri, as in extant comatulids. During further growth the aboral pole was partly resorbed, and the earliest cirrus sockets nearly disappeared. Growth of additional cirri started as small knobs between imprints of basals near the centrodorsal cavity, followed by gradual lengthening towards the periphery. In a specimen of *Glenotremites pulcher* Žižka (1980) described the growth of cirrus sockets as finger-like processes starting near the margin of the centrodorsal cavity. The small processes have a marked axial canal even before reaching the periphery of the centrodorsal. Such growth is also seen in our material (Figs. 4d, 5a; Hess 2013b, fig. 11c2–3; 12b2).

Morphology of the cup (basals and radials)

The earliest Comatulida belong to the genus *Palaeocomaster*, classified in the Solanocrinitoidea. The earliest specimen with basals preserved is *P. morierei* (Loriot) from the Pliensbachian of Arzo; and it is here refigured at a larger scale (Fig. 4c). The basals are prominent, the stellate center is raised and its diameter is only approximately

40 % of centrodorsal diameter; the facet to the radial circling is cryptosymplectical. Correspondingly, the diameter of the radial circling attached to this structure must have been small, or the aboral surface of the radials must have been strongly overhanging. A raised center of basals with reduced diameter is not seen in other Jurassic forms, although the radials are also overhanging in *P. messingi* (see Hess 2012, fig. 11b1). The basals of *P. messingi* Hess (2012) and *P. musculosus* Hess (2013b) form a low basal circling that seems to be fused with the centrodorsal. *P. styriacus* Kristan-Tollmann (1988), the earliest species of the genus, was described as having a centrally united, low basal circling with narrow, shallow and crenulated extensions (“Rinnen”). However, the corresponding drawing (Kristan-Tollmann, 1988, text-fig. 1; also reproduced in Hess and Messing 2011, fig. 404f) does not really match the photograph (loc. cit. pl. 1, fig. 1b; Fig. 4a1), which in fact shows impressions of part of the basals on the adoral side of the centrodorsal. The better preserved holotype (loc. cit. pl. 1, fig. 2b; Fig. 4b1) does not show a distinct basal circling at all. Thus, Kristan-Tollmann’s “basal circling” or part thereof seems to be just an interradial imprint of a non-preserved circling of similar outline. The basal circling may

have resembled those of *Palaeocomaster messingi* (Hess 2012, fig. 11a3), *P. paucicirrus* n. sp. (Fig. 5), and *P. musculosus* Hess 2013b, fig. 11c3 and 12b3), which are all similar. In the latter species the basal cirlet may also be fused with the radial cirlet (see Hess 2013b; fig. 12a1). Stellate basal cirlets with narrow interradial petals bordered by short, uniform crenulae, or their impression on the centrodorsal, closely resemble the respective structures in *Pentacrinites*, *Eocomatula* and *Paracomatula*.

The oldest forms with preserved radial cirlet are of Bathonian age. They include *Palaeocomaster messingi* Hess (2012), *P. schlumbergeri* (Loriol 1888), and *P. stellatus* Gislén (1924). The Bathonian *P. latiradius* (Carpenter 1882) and the Callovian *P. calloviensis* (Carpenter 1882) are large forms and are preserved with the base of the crown of 10 arms. The Oxfordian *P. musculosus* (Hess 2013b) is known from two centrodorsals and a cup. In *P. messingi* and *P. musculosus* the radial articular facets are steep, with high muscle fossae (see Hess 2012, fig. 11b2; Hess 2013b, fig. 12a2) The muscle fossae are somewhat less developed in *P. schlumbergeri* (Fig. 4e) and *P. latiradius* (see Carpenter 1882, fig. 1b), and they are rather small in *P. stellatus* (see Gislén 1924, fig. 206). Radials with steep facets and high muscle fossae of most *Palaeocomaster* species are thus similar to *Paracomatula helvetica* and *P. liasica* Hess (2006; Fig. 2a); steep facets also occur in other comatulids, such as comasterids, but the muscle fossae are low in this group. In contrast, most comatulids have more or less outward-sloping facets. Centrodorsals composed of partly uncoalesced “cirrus tubes” are found in Early Jurassic forms and in the later *P. messingi*, *P. schlumbergeri* and *P. musculosus* n. sp., which have cups with steep radial articular facets.

Comatulid radiation

A *Palaeocomaster*-type centrodorsal may have been a precursor to the densely cirrated, hemispherical centrodorsals so common in later fossil and extant comatulids. Transition forms are the Bathonian *Andymetra galei* Hess (2012, fig. 10b) and the Oxfordian *A. donovani* Hess (2013b). Both species possess centrodorsals with partly uncoalesced “cirrus tubes” and imprints of narrow, crenulated basals. In contrast, the Oxfordian *Semiometra petioleri* (Caillet) is more advanced, as shown by a compact centrodorsal with fused cirrus bases and an aboral apex with a dorsal star (Hess 2013b, Fig. 11b; Radwańska 2007, pl. 1–2); correspondingly, it is placed in the Superfamily Notocrinoidea. *Semiometra* appeared as early as the Bathonian with *S. abnormis* (Carpenter 1880), based on a single, flat centrodorsal with two rows of cirrus sockets; it has a distinct dorsal star and radial pits on the adoral side.

Rouse et al. (2013) mentioned the species as the oldest crown group fossil comatulid, and they proposed a date of 165 mya for the minimum age of the crown Comatulidina. Taking *Palaeocomaster styriacus* from the Hettangian as the oldest crown group comatulid, followed by *P. morierei* and *P. benthuyi* n. sp. from the Pliensbachian, a minimum age of 196–199 mya seems more adequate for the crown group Comatulida.

Hess and Messing (2011) classified *Palaeocomaster* in the Family Solanocrinitidae (Suborder Solanocrinitoidea), which also includes *Archaeometra*, *Solanocrinites* and *Comatulina*, forms with a compact centrodorsal and more or less inclined radial articular facets. In *Solanocrinites* and the closely related *Comatulina* the cirrus sockets occur in regular columns separated by vertical ridges; and the basal cirlet is tightly joined to the radial cirlet (see Hess and Messing 2011, fig. 38a,e,f). In contrast, *Archaeometra* has a conical centrodorsal with irregularly arranged cirrus sockets and high, prismatic basals that are less tightly connected with the centrodorsal and the radial cirlet. With *Andymetra* included, the Solanocrinitidae embrace forms that mirror the Jurassic radiation of the comatulids, when the major types of centrodorsals appeared.

Several Superfamilies of Comatulida (Hess and Messing 2011) are represented in the Jurassic, Solanocrinitoidea (four genera in Solanocrinitidae and several genera in Thiolliericrinidae), Tropiometroidea (*Rhodanometra*, *Comaturella*), Notocrinoidea (*Semiometra*), and *Procomaster* of uncertain suprafamilial assignment. This rather high diversity is contrasted with the rarity of fossil specimens. Simms (1990) discussed the various hypotheses put forward by different authors on the apparently poor fossil record of the group during the Jurassic. He concluded that comatulid diversity remained relatively low until at least the start of the Upper Jurassic and that, although they are now the most successful single crinoid group, their diversification was far from an “explosive radiation”. Their greater ecological flexibility as postulated by Simms led to a noteworthy increase in number of specimens only with the appearance of suitable habitats such as sponge and coral reefs. However, even in such environments comatulids remained a minor component of the crinoid fauna during the Jurassic and Early Cretaceous. This is exemplified by the Bathonian of the Ardèche (Hess 2012), the Oxfordian sponge facies of the Swiss and Swabian Jura, and the Valanginian of Štramperk (Žižt 1980), all dominated by cyrtocrinids. A notable exception is the Early Cretaceous (Berriasian-Valanginian) reefal facies of the Crimea, rich in genera and specimens of thiolliericrinids (Klikushin 1987); however, these are not free-moving but neotenusly derived comatulids, reverting to attachment by a column. Despite their present success, the fossil record of the comatulids remains scattered throughout much of their

earlier history. Richer assemblages occur from the late Early Cretaceous (Aptian) onwards to the Late Cretaceous, see Rasmussen (1961). Fortunately, new discoveries add to our knowledge, although most of the forms belong to established genera. For example, Radwańska (2005) described seven taxa, including new species of *Palaeocomaster*, *Solanocrinites* and *Comatulina* from shrimp burrows of the Lower Kimmeridgian of Poland. Jäger (2010) described a diverse crinoid fauna dominated by comatulids from the Barremian of the Serre de Bleyton (France); *Comatulina* and *Semiometra* are represented by two species described as new, and *Decameros* by a previously described taxon. In the Cenozoic the door to the present richness was finally opened (e.g., Ciampaglio and Weaver 2004; Gislén 1924; Jagt 1999; Paul 1992; Shibata and Oji 2007, Sieverts-Doreck 1961).

Conclusions

During their Late Triassic/Jurassic radiation articulate crinoids made several attempts to get free from a potentially cumbersome column. Severe shortening as in *Eocomatula* and *Paracomatula* produced a number of species, but this development eventually came to an end with *Paracomatula morator* Hess (2013b) in the Late Jurassic. The reason may have been insufficient plasticity for the attachment of the cirri on individual nodals in these “trial centrodorsals”. Extreme column shortening to just a small stump took also place in the Middle Jurassic millericrinid *Ailsacrinus abbreviatus* Taylor (1983), the only and last of its kind in this order. At first glance the form is very similar to *Paracomatula helvetica*; both species have ten long, narrow arms with well-developed muscle fossae and numerous syzygies; cirri of *P. helvetica* are slender and lack altogether in *A. abbreviatus*. The analogy goes even further by the formation of dense colonies (see Taylor 1983; Hess 1999). In fact, the assemblage of *P. helvetica* at the type locality is unique by the occurrence of a thick bed of intact individuals of several generations; such a Lagerstätte is not known from any fossil comatulid. One cannot avoid to hypothesize that these animals were able to swim and, thus, to aggregate in large numbers under suitable ecological conditions. Swimming is of course a notable capability of comatulids with similar radial articular facets and arms (Janevski and Baumiller 2010). However, the breakthrough came only with the synapomorphy of the comatulid centrodorsal, which proved to be a lasting and smashing success. Well-developed muscle fossae on steep articular facets are seen in species of *Palaeocomaster*, notably *P. messingi* Hess (2012) from the Bathonian and *P. musculosus* Hess (2013b) from the Oxfordian. Was perhaps such development connected with the ability to swim? If so, it may have been an

impetus for the compact, highly versatile centrodorsal, suited to different lifestyles.

Systematic palaeontology

Remark The following nomenclatural revisions and diagnoses refer to the *Revised Crinoid Treatise* (Hess and Messing 2011).

Repositories NMB Natural History Museum Basel (Switzerland), SMNS Staatliches Museum für Naturkunde, Stuttgart (Germany).

Order Isocrinida Sieverts-Doreck, 1952

Diagnosis See Hess and Messing (2011).

Suborder Pentacrinitina Gray, 1842

Diagnosis Cup with radials projecting downwards and basals overhanging the top of the column; in *Paracomatula* radials without projection and large exposed surface, basal cirlet flat. Stellate cirlet of basals articulating with column with pattern of narrow interradial petals bordered by short, uniform crenulae. Arms divided at primibrachial 2 and further divided several times; division at primibrachials and secundibrachials isotomous, succeeding divisions endotomous; in *Paracomatula* 10 undivided, long arms after primibrachial 2. Interradial plates present in Pentacrinitidae and continuing in numerous plates of high tegmen, or absent in Eocomatulidae and Paracomatulidae. Synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2. Syzygies absent in Pentacrinitidae, but cryptosyzygies present in Eocomatulidae and Paracomatulidae where syzygies also occur. Highly cirriferous juvenile column with intercalated internodals in adults in Pentacrinitidae. Articular facet of columnals with narrow or elliptical to pyriform petals surrounded by a slightly crenulated edge and separated by large, more or less triangular, smooth or rugose radial areas. Column of *Eocomatula* and *Paracomatula* short, with at most a few columnals, some of which may be low and without cirri in *Paracomatula*; column of *Eocomatula* with nodals articulated by symplexy, in *Paracomatula* mostly by synostosis. Cirri commonly laterally compressed and long in *Pentacrinites* but shorter and more circular in *Seirocrinus*, thin and circular throughout in *Paracomatula*. Late Triassic (Norian)–Late Jurassic (Oxfordian).

Family Pentacrinitidae Gray, 1842

Diagnosis Radials large and projected outwards or downwards, lower edge of basals more or less curved downwards, overhanging the top of the column. Arms divided at primibrachial 2 and further divided several times; division at primibrachials and secundibrachials isotomous, succeeding

divisions endotomous. Interradial plates present and continuing in numerous plates of high tegmen. Brachials with weakly developed muscle fossae in pseudoplanktonic species. Ligamentary brachial articulations absent or restricted to secundibrachials 6 and 7, additional ligamentary articulations present in *Pentacrinites dargniesi*. Highly cirriferous juvenile column that may become very long with intercalated internodals in adults, reaching more than 20 m in *Seirocrinus*. Cirri commonly laterally compressed and long in *Pentacrinites* but shorter and more circular in *Seirocrinus* although differences are smaller in juvenile specimens. Column with persistent alternation and indefinite intercalation of columnals, small intercolumnals may be concealed by nodals. Upper Triassic (Norian)—Upper Jurassic (Oxfordian).

Family Eocomatulidae Simms, 1988

Diagnosis Interradial plates absent. Cryptosyzygies common throughout arm, facets with numerous fine marginal culmina. Short, untapered column of nodals, retaining distinct symplectial articulum on terminal columnal with open axial canal. Upper Triassic (Norian)—Lower Jurassic (Pliensbachian).

Family Paracomatulidae Hess, 1951

Diagnosis Column centrodorsal-like, composed of closely united five-sided columnals, terminal columnal with sealed axial canal; single columnal in *Singillatimetra*. Cirrus sockets without profile, offset to either side of the radial midline and arranged in 5 or 10 columns. Stellate cirlet of basals articulating with centrodorsal with pattern of narrow interradianal petals bordered by short, uniform crenulae (as in column of *Pentacrinites*). Radials with large exposed surface, commonly recumbent or overhanging. Radial articular facet large and steep to almost vertical; adoral muscle fossae high. Rays divided once at primibrachial 2; synrthry between primibrachials 1 and 2 and secundibrachials 1 and 2; cryptosyzygy with numerous fine ridges between secundibrachials 3 and 4. Syzygies after secundibrachials 11 or 12 on approximately every fifth brachial and with a few coarse ridges. First pinnule on secundibrachial 2. Upper Triassic (Norian)—Upper Jurassic Oxfordian).

Paracomatula Hess, 1951

Diagnosis Centrodorsal-like column of variable segments, distal or proximal segments may be lower and without cirri, in *P. morator* two fused columnals with symplectial upper and lower facets. Upper Triassic (Norian)—Upper Jurassic (Oxfordian).

Singillatimetra Hess, 2012

Diagnosis (after Hess 2012). Centrodorsal of single element, asymmetrical in outline; 5 bulging cirrus sockets arranged irregularly; no radial cavity or axial canal visible;

aboral and adoral sides similar, weakly sculptured, on aboral side irregular tubercles and weak radial impressions without crenulae, on adoral side narrow interradianal bands with short crenulae for articulation to basals. Middle Jurassic (Bathonian).

Order Comatulida A.H. Clark, 1908

Superfamily Solanocrinitoidea Jaekel, 1918

Family Solanocrinitidae Jaekel, 1918

Palaeocomaster Gislén, 1924

Palaeocomaster paucicirrus n. sp., Fig. 5

Material Seven centrodorsals with basal cirlet, ranging in diameter from 0.4 to 2 mm, are figured in Fig. 5a–g (SMNS 70107/1–7). Two postlarval centrodorsals and a broken small centrodorsal with basal cirlet, similar to the specimen in Fig. 5f, are not figured. The comatulid material from Quedlinburg is part of a large collection of crinoids dominated by plicatocrinids (Cyrtocrinida) with the following species: *Praetetacrinus inornatus* Simms), *P. doreckae* Jäger and *P. kutscheri* Jäger; the millericrinid *Shroshaecrinus? quedinburgensis* Jäger is also present; see Jäger 1995. Ophiuroids are common and were described by Kutscher (1996) who also collected the comatulid material.

Holotype Centrodorsal with basal cirlet, Fig. 5a, SMNS 70107/1.

Etymology *paucus*, L, for the few cirrus sockets on the centrodorsal.

Type locality and horizon. Quedlinburg, Upper Toarcian/Lower Aalenian (probably Aalensis Subzone), see Jäger (1995) and Kutscher (1996).

Diagnosis Small species. Centrodorsal with wide cavity, surrounded by stellate, prominent basal cirlet fused to the centrodorsal; aboral apex flat and slightly rugose to convex and smooth; two or three circular and smooth cirrus sockets on each side, axial canal rectangular, nascent sockets not reaching periphery.

Description The centrodorsals are discoidal to slightly hemispherical in shape, the apex may be somewhat rugose, but is smooth and convex in one specimen (Fig. 5c). Two specimens are somewhat oval in outline; and the specimen in Fig. 5g seems to be distorted by some physical influence. The centrodorsal cavity is circular in the holotype and in specimen Fig. 5f, but oval in specimens Fig. 5b, c. The width of the cavity is 25 % of centrodorsal diameter in the holotype; in specimen Fig. 5c with roughly circular outline it is 45 % along one axis and 35 % along the other. The cavity is surrounded by the prominent stellate basal cirlet that is fused with the centrodorsal. Weak sutures between centrodorsal and basal cirlet are still seen in the specimens in Fig. 5b2, c1. The interradianal extensions of the

basals have weak furrows with finely crenulated margin. They extend to the periphery of the centrodorsal or beyond. Four juvenile specimens have a diameter of <0.5 mm, in three of them the centrodorsal cavity is sealed aborally (Fig. 5e), but in one (Fig. 5d) it is still open. The cirrus sockets are large, circular and smooth, with rectangular axial canal. Arrangement of the sockets is somewhat irregular, and they are displaced against each other. The holotype has three sockets on each side, one of them smaller, except in one radius with only two large sockets; the sides are separated by an interradial ridge. The facet of the smallest sockets reaches only halfway to the periphery. The other centrodorsals have only two sockets on each side, and one of them may be smaller; they lack interradial ridges.

Remarks The new species differs from the other Early Jurassic species of the genus (*P. styriacus*, *P. morierei*, and *P. benthuyi* n. sp.) by a different shape and a prominent basal circling fused with the adoral facet of the centrodorsal. The Bathonian *P. messingi* has a narrower centrodorsal cavity and more numerous cirrus sockets, but the basal circling is similarly fused with the centrodorsal. In the Oxfordian *P. musculosus* (see Hess 2013b) the centrodorsal cavity is wide, but the cirrus sockets are more numerous, and the aboral apex is distinctly sculptured. This species shares with *P. paucicirrus* a stellate basal circling extending beyond the periphery, although the basals may also be embedded in the radial circling. *P. paucicirrus* n. sp. seems to be more closely related to the Bathonian *P. messingi* and the Oxfordian *P. musculosus* than to the other Early Jurassic forms.

Palaeocomaster benthuyi n. sp., Fig. 4d

Material Only the holotype, a centrodorsal, is available.

Holotype Centrodorsal, NMB M10416, Fig. 4d.

Etymology Dedicated to Ben Thuy, for his recognition of the Sedan Lagerstätte and his work on ophiuroids.

Type locality and horizon Sedan, French Ardennes; late Early Pliensbachian, Davoei Zone, see Thuy et al. (2011).

Diagnosis Small species. Centrodorsal conical, without interradial ridges; adoral surface with concave, slightly crenulated interradial extensions for reception of the basals; diameter of centrodorsal cavity 25 % of centrodorsal diameter. Cirrus sockets large and smooth, slightly oval and protruding, arranged in two to three rows, without interradial ridges; axial canal rectangular.

Description The centrodorsal is conical, with protruding cirrus sockets extending to the apex. The largest sockets occur in the middle, smaller ones are close to the adoral side and around the apex. The centrodorsal cavity is wide;

the adoral side is somewhat rugose and has interradial, concave extensions with slightly crenulated margins for attachment of the basals. The extensions are hardly demarcated from the base of the cirrus sockets; and they are interpreted as support for the basals.

Remarks The present centrodorsal has some resemblance with *Palaeocomaster* sp. from the Late Sinemurian/Early Pliensbachian of Turkey, represented by two small and a larger specimen (Nicosia 1991, fig. 43–44). In the figured Turkish specimen the cirrus sockets are also crowded and extend to the apex, but the shape is less conical and the cirrus sockets are more numerous, presumably the result of the larger size of the specimen that has a diameter of approximately 3 mm. However, the centrodorsal cavity is wider in *P. benthuyi* n. sp.

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