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Extraordinary diversity of feather stars (Echinodermata: Crinoidea: Comatulida) from a Lower Jurassic (Pliensbachian–Toarcian) rock reef of Feuguerolles (Normandy, France)

Hans Hess[1] · Ben Thuy[2]

Abstract Comatulid feather stars are rare fossils in the Early Jurassic, providing only patchy insights into the early evolution of the group. Here, we describe new finds of comatulids from the late Pliensbachian to late Toarcian of Feuguerolles, Calvados, France. They include new species belonging to four superfamilies. The dominant genus is *Palaeocomaster*, with *P. structus* n. sp. represented by centrodorsals. For *Palaeocomaster,* the family Palaeocomasteridae n. fam. is proposed; it is placed in the Superfamily Comatuloidea. *Solanocrinites* is represented by *S. jagti* n. sp. The new taxa *Andymetra toarcensis* n. sp. and *Spinimetra chesnieri* n. g. et n. sp. are Family incertae sedis. The diagnoses of Comatuloidea and Solanocrinitoidea are modified based on the new material. The paracomatulid *Singillatimetra truncata* n. sp. is represented by a columnal, as is *Forcipicrinus normannicus* n. g. et n. sp. tentatively assigned to Pentacrinitina, Family incertae sedis. The material indicates that an important early comatulid radiation took place prior to the Toarcian Oceanic Anoxic Event, creating some basic types of these free-living crinoids. Along with the stratigraphic distribution patterns of the co-occurring stalked crinoids including the isocrinids *Pentacrinites collenoti*, *Isocrinus* (*Chladocrinus*) *basaltiformis*, the millericrinid *Amaltheocrinus amalthei*, and the cyrtocrinids *Cotylederma docens*, *Eudesicrinus mayalis*, *Praetetracrinus inornatus*, *Sacariacrinus* n. sp. and *Tetracrinus* n. sp., the new feather star finds suggest that the Toarcian Oceanic Anoxic Event was not of major influence to crinoid diversity.

Keywords Comatulids · Crinoidea · Early Jurassic · Normandy · Toarcian oceanic anoxic event

✉ Hans Hess
hans.hess@bluewin.ch

Ben Thuy
bthuy@mnhn.lu

1 Naturhistorisches Museum Basel, Augustinergass 2, 4001 Basel, Switzerland

2 Natural History Museum Luxembourg, 25, rue Münster, 2160 Luxembourg, Luxembourg

Introduction

Feather stars, those members of order Comatulida that shed the postlarval stalk (Hemery et al. 2013; Rouse et al. 2013), are the dominant living crinoids, especially in shallow marine environments. During much of their early evolutionary history, however, feather stars (comatulids in the following) were rare actors in shallow marine environments dominated by various groups of stalked crinoids, in particular isocrinids, cyrtocrinids and millericrinids. The Lower Jurassic comatulid fossil record is particularly meagre, with only five currently known species belonging to two genera: *Procomaster pentadactylus* Simms (1988), and four species of *Palaeocomaster* (Hess 2014a). The current state of knowledge indicates that the first significant increase in morphological disparity and taxonomic diversity of the comatulids started in the Middle Jurassic (Hess 2014b).

Jurassic comatulids are rare fossils and mostly too small to be commonly detected by field collectors. A significant share of the currently known Jurassic comatulid fossil record was discovered by careful picking of bulk sieving residues (Hess 2014a). Here, we describe new comatulids from the Early Jurassic of Normandy, France, which on the

one hand dramatically illustrate just how rare comatulid fossils are in the Early Jurassic and, on the other hand, demonstrate that micropalaeontological samples are the most promising source for new discoveries of Jurassic comatulids. In fact, the material described herein was recovered from the washing residues of 220 individual sediment samples collected bed by bed. Thorough picking of echinoderm microfossils produced several hundreds of thousands of crinoid fragments including 18 comatulid centrodorsals and 2 paracomatulid/pentacrinine columnals.

Although they constitute only a very minor part of the crinoid fauna dominated by Isocrinida (large numbers of Isocrinidae and small numbers of Pentacrinitidae), Cyrtocrinida (Cotyledermatidae, Eudesicrinidae, Tetracrinidae), and Millericrinida (*Amaltheocrinus*), the comatulid remains described in the present paper significantly increase the meagre number of forms known from the Early Jurassic, a critical time for the evolution of these crinoids that dominate today's seas (Hess 2014a; Hess and Messing 2011).

Geological context

The material described herein was collected in the now disused Guérin quarry on the left bank of the river Orne near Feuguerolles, southwest of Caen, Calvados Department in Normandy, France (Fig. 1). The Ordovician Armorican quartzites which were formerly mined in the

quarry are unconformably overlain by a highly condensed succession of Lower to Middle Jurassic marls and limestones. The oldest Jurassic sediments represent transgressive deposits and infillings of the eroded surface of the tilted quartzites which, at the time of deposition, formed near-shore rock reefs with numerous decimetre- to metre-scale cavities and depressions (Rioult 1968). Some of these cavities are filled by strongly indurated gastropod-rich limestones (the so-called 'poches à gastéropodes' of Rioult 1968), others by poorly lithified, clayey skeletal sands rich in echinoderm debris. These infillings are overlain by a succession of thin marl and limestone beds, which show considerable, small-scale spatial variation in thickness and lateral extent as a result of the complex palaeo-topography.

In spite of their obvious interest as deposits of an exceptional palaeo-environmental setting, regrettably few studies have dealt with the Lower Jurassic sediments of Feuguerolles so far (Rioult 1968; Dugué et al. 1998; Vernhet et al. 2002; Weis et al. 2015). To date, no comprehensive biostratigraphic framework has been published. Thanks to meticulous bed-by-bed collecting of ammonites and thecid brachiopods by Marc Chesnier (Cresserons, Calvados, France), the strata that yielded the crinoid remains described herein can be stratigraphically subdivided in detail following the chronozone concept of Page (2003). The transgressive infillings within and on top of the Palaeozoic quartzite cavities are mostly dated to the Late Pliensbachian Margaritatus Chronozone, although some are slightly older (Early Pliensbachian Ibex and Davoei

Fig. 1 Location map of the Guérin quarry (marked by a *star*) in Feuguerolles, Calvados, France. Modified after Dommergues et al. (2008)
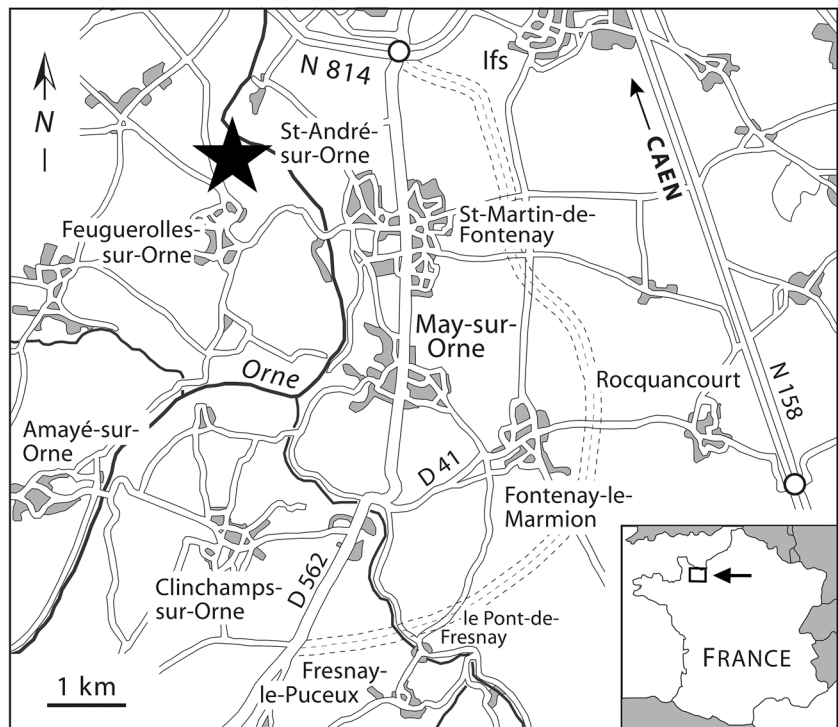
Chronozones). Evidence for the Spinatum Chronozone is sparse and as yet insufficiently documented. The overlying succession of marls and limestones yielded ammonite and thecid evidence for the Early Toarcian Tenuicostatum Chronozone (Semicelatum Subchronozone), Serpentinum Chronozone (Exaratum and Falciferum Subchronozones) and Bifrons Chronozone (no data on Subchronozones yet). The youngest crinoid material described herein was recovered from sediments dated to the Late Toarcian Variabilis Chronozone.

The stratigraphic completeness of the successions is difficult to assess due to the scarcity of ammonites and other index fossils, the lateral variability of most beds and the strong stratigraphic condensation of the succession. The biostratigraphic evidence at hand suggests Subchronozone—level depositional gaps at least in the Uppermost Pliensbachian to Lowermost Toarcian part of the succession.

Materials and methods

The specimens described herein were extracted from the washed residues of bulk sediment samples taken by Marc Chesnier (Cresserons, Calvados, France) at various places, here called loci, in the Pliensbachian to Toarcian succession of the Feuguerolles outcrop. Processing of the samples consisted in several cycles of soaking in water and decantation of the suspended mud fraction. No sieve was used. Every sample or locus was assigned a number and precisely located both stratigraphically and spatially to account for the high lateral variability of the various beds.

Selected specimens were mounted on aluminium stubs and gold coated for scanning electron microscopy using a Jeol Neoscope JCM-5000. All specimens figured and/or described herein are housed at the Natural History Museum of Le Mans (France) (collection acronym MHNLM).

Overview of crinoid material

The Feuguerolles crinoid fauna supplements the Toarcian fauna of May-sur-Orne described by de Loriol (1882 in 1882–1889) and discussed by Hess (2006). The crinoid material examined in the context of the present paper was recovered from 220 samples ('loci'). In spite of the large number of samples, richness in species is small, e.g. compared to the Arzo assemblage (Late Pliensbachian) with more than 30 species (Hess 2006). Similar to Arzo (Hess 2006, fig. 6), the remains are poorly sorted in most cases as demonstrated by the presence of all sizes, including juvenile specimens. In contrast to the Arzo material which included a number of intact cups and many pluricolumnals, the Feuguerolles material is highly disarticulated although mostly well preserved. The richness and preservation of crinoids at Arzo may be explained by their accumulation under conditions of reduced sedimentation on hardgrounds in the subphotic zone. In contrast, the Feuguerolles material was deposited under near-shore reefal conditions. The comatulid remains are dissociated centrodorsals but with basal circlets attached in three *Palaeocomaster structus* n. sp. specimens. The following beds [see Fig. 2 (coupe no. 15)] have furnished the comatulids: **D1** (Domerian, locus 355, sandy marlstones with siliceous nodules): *Solanocrinites jagti* n. sp. **T1a** (Toarcian, Tenuicostatum Zone, 354 and 358, sandstones): *Spinimetra chesnieri* n. g. et n. sp. **T1bc** (Toarcian, Tenuicostatum Zone, 425, marlstones): *Andymetra toarcensis* n. sp. **T6** (Toarcian, Serpentinum Zone, 211, marlstones): *Palaeocomaster structus* n. sp. **T8** (Toarcian, Bifrons Zone, 314, 325, 397, 489, 490, marlstones): *Palaeocomaster structus* n. sp. **T9** (Toarcian, Variabilis Zone, 293, 307, marlstones): *Palaeocomaster structus* n. sp.

The dominant Feuguerolles species is *Isocrinus* (*Chladocrinus*) *basaltiformis* (Miller). The presence of a species of *Balanocrinus* whose columnals resemble juvenile *Isocrinus* cannot be excluded, but the genus is a very minor part of the fauna in any case. Other conspicuous and common components of the assemblages are the distinct *Cotylederma docens* Deslongchamps in Deslongchamps and Deslongchamps, represented by disarticulated plates and two specimens with the cup attached to the basal element; *Eudesicrinus mayalis* (Deslongchamps in Deslongchamps and Deslongchamps) and *Amaltheocrinus amalthei* (Quenstedt), both represented by attachment structures, columnals, cup plates and brachials; *Praetetracrinus inornatus* (Simms), represented by attachment disks, columnals, basal circlets, radials and primibrachials, and *Sacariacrinus* n. sp., represented by three radial circlets, radials and primibrachials. Minor constituents are columnals of *Pentacrinites collenoti* (de Loriol) and of *Millericrinus? adneticus* (Quenstedt). The comatulids and paracomatulids scattered in different samples seem to be chance findings. The cyrtocrinids that include the cup of a new species of *Tetracrinus* (von Münster) and remains of a new species of *Sacariacrinus* Nicosia will be described in a separate paper.

Three loci with comatulids (298, 358, and 425) lack remains of *Praetetracinus*, but contain *Cotylederma docens* or *Eudesicrinus mayalis*, both attached to the substrate by a basal element. Of special interest are scratch marks and peculiar concentric rings on many swollen first and some second primibrachials of *Cotylederma docens*. Furrows present on many columnals of *Praetetracrinus inornatus* were also reported from *Praetetracrinus doreckae* by Jäger (1995, pl. 1, fig. 17–20). Some ossicles bear bite marks,
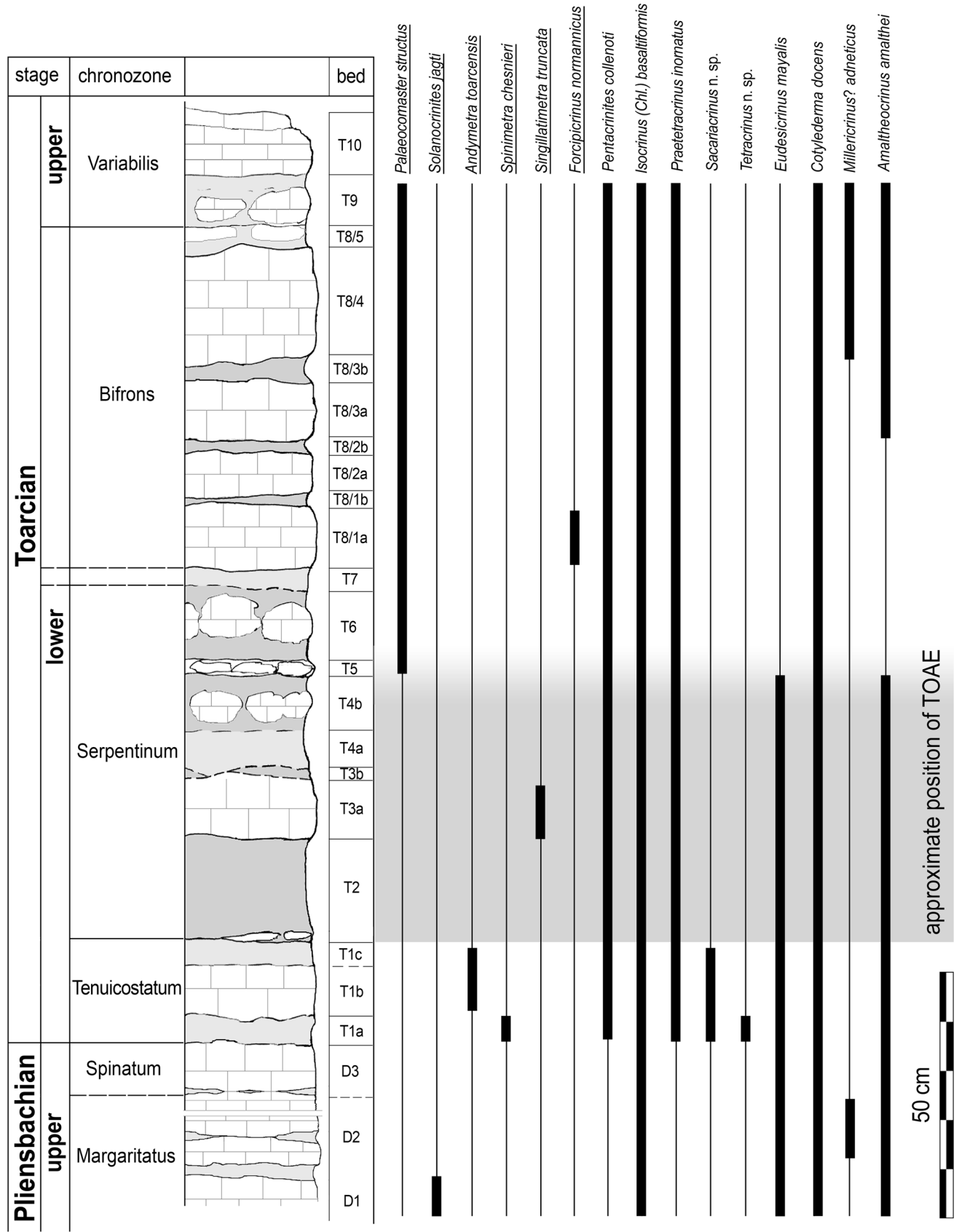
◄**Fig. 2** Stratigraphic log of one part of the Guérin quarry in Feuguerolles, Calvados, France, considered as one of the most complete and representative within the laterally highly variable succession. *Thick black lines* on the *right side* indicate the stratigraphic distribution of the crinoid taxa identified in the studied material. *Underlined species* are described in the present report

and similar marks occur on columnals of *Amaltheocrinus* that also include other deformities.

Described material

With three exceptions (Figs. 3c, 5a, 8b), only centrodorsals or parts thereof are available from the different loci. The Pliensbachian (Domerian, locus 355) furnished one specimen; all the other specimens were from Toarcian loci (082, 211, 243, 293, 298, 307, 314, 325, 354, 358, 397, 418, 425, 489, and 490). Three loci (358, 418, and 425) included two specimens of one species.

Most centrodorsals are very small and some are fragile. Those of *Palaeocomaster structus* n. sp. have a through-going centrodorsal cavity seen as adoral and aboral openings, presumably the result of post-mortem disarticulation. Centrodorsals are suitable for taxonomy and phylogenetic analyses (Hess 2014a) and are classified in several genera. Three centrodorsals (Figs. 3c, 5a, 8b) are preserved with attached basal circlet, but none with a radial circlet.

Systematic palaeontology

Note As explained in the section *Discussion,* the present material indicates that *Palaeocomaster* should be assigned to a separate family Palaeocomasteridae n. fam. in the Superfamily Comatuloidea rather than in Solanocrinitoidea. Summers et al. (2014) restored Comatulidae Fleming (1828) in place of Comasteridae Clark (1908), in accordance with ICZN Article 23.9. The corrected name has since been used in at least one other paper (Messing and Tay 2016). Correspondingly, diagnosis of Comasteroidea of the *Revised Treatise* (Hess and Messing 2011) is modified in the following.

Order Comatulida A. H. Clark 1908.

Superfamily Comatuloidea Fleming 1828.

Diagnosis Centrodorsal thick to thin discoidal or pentagonal, rarely stellate; aboral apex broad, cirrus-free, flat or slightly convex or concave, sometimes with narrow radiating interradial impressions (also in fossil Notocrinoidea); dorsal star absent, but center of aboral apex sometimes depressed; central cavity less than 40 % of centrodorsal diameter, larger in very small specimens; adoral surface with interradial furrows for basals, but no radial pits or coelomic impressions. Cirrus sockets generally rather large, without distinct ornament, crowded around centrodorsal margin in one to three irregular tiers, never forming vertical columns. Basis of cirrus sockets loosely connected in *Palaeocomaster*. Some species of *Comatula, Comanthus, Comaster, Phanogenia* and *Capillaster* with centrodorsal thin, reduced, commonly not projecting over exposed aboral surface of radials and bearing few or no cirri. Basal rosette unknown in *Palaeocomaster* but present in other genera; basals rod-shaped, with tips commonly exposed interradially. Subradial clefts may be present, especially in large specimens. Radials typically with short exposed surface, commonly concealed midradially or barely exposed interradially; rarely completely concealed; well exposed and trapezoidal in species with reduced centrodorsal; well exposed with tongue-like extensions separating bases of adjacent rays in paedomorphic *Comatilia*. Radial articular facet parallel to oral–aboral axis or nearly so and with shallow fossae. Interarticular ligament fossae large, high and wide, generally higher than aboral ligament fossa, and separated by broad and shallow midradial furrow, which is commonly constricted between muscle fossae. Adoral border of interarticular fossae straight or slightly curved, horizontal or slightly sloping. Adoral muscle fossae high in *Palaeocomaster*, low in other genera and forming narrow bands along horizontal adoral edge. Radial cavity large, with a spongy calcareous filling in living species. Rays divided at least at primibrachial 2, commonly up to several times more producing as many as 200 undivided arms. Synarthry or modified synarthry between primibrachials 1 and 2 and secundibrachials 1 and 2, either relatively featureless or resembling syzygies. True syzygies present only in *Comatula*. First pinnule on secundibrachial 2 (when series composed of 4 ossicles). Pinnulation incomplete only in *Comatilia*, which lacks several pinnules after the first pair. Oral pinnules slender, flagellate, of numerous short pinnulars. Distal pinnulars of at least some oral pinnules bearing a comb formed by peg- or blade-like teeth, one or two per pinnular. Similar combs present elsewhere only in some Heliometrinae (Antedonoidea). Middle and distal pinnules commonly extremely spiny. Arms arising farthest away from the eccentrically placed mouth (=posterior) commonly shorter than those arising closest to mouth, sometimes lacking ambulacral groove but with better developed gonads. Mouth typically displaced off center or marginal and anal papilla central or subcentral on disk (commonly less so in juveniles); mouth central or subcentral in *Phanogenia, Palaeocomatella, Aphanocomaster, Comissia, Rowemissia* and *Comatilia*.
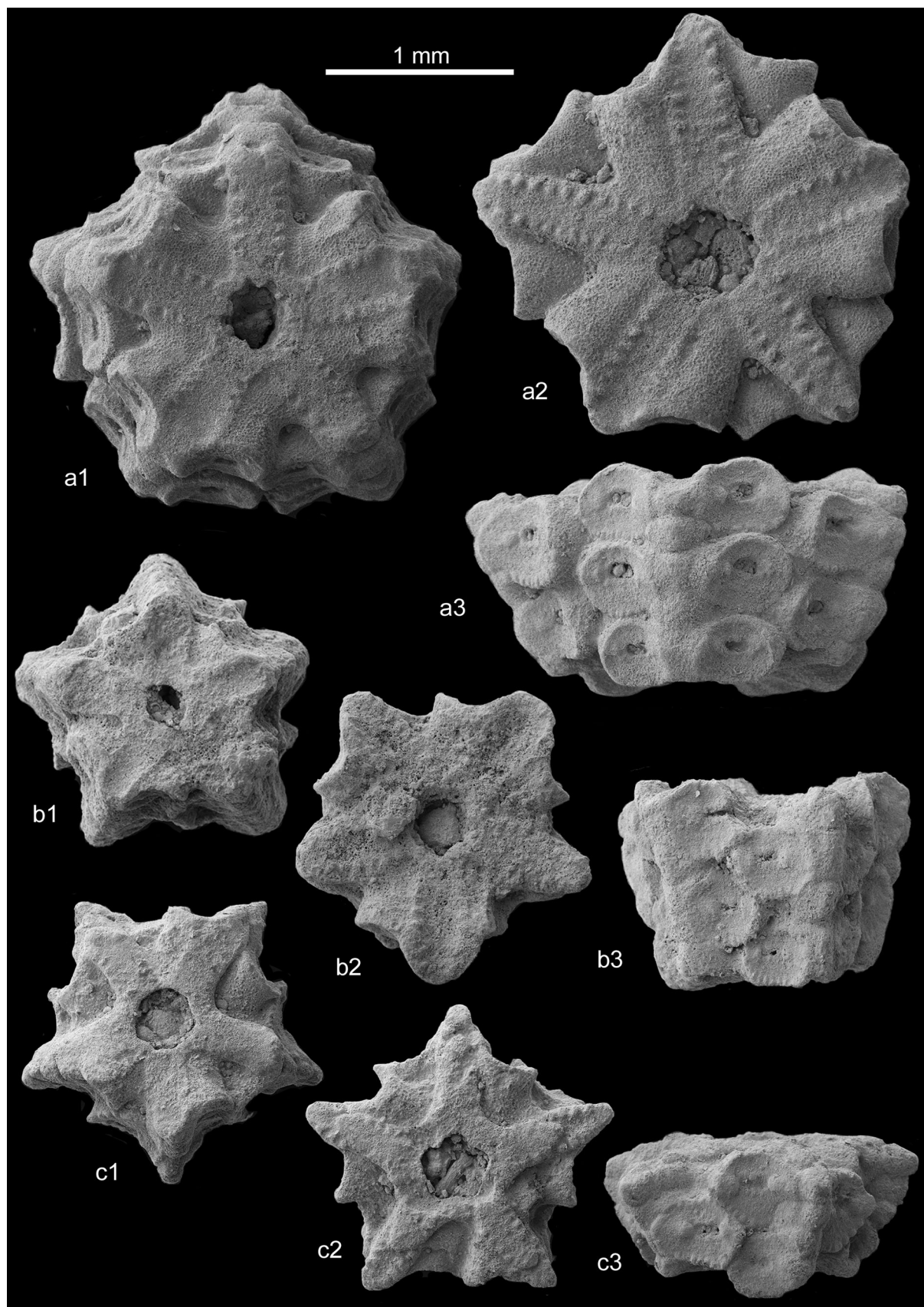
◀**Fig. 3** *Palaeocomaster structus* n. sp., centrodorsals (**a**, **b**); centrodorsal with attached basal circlet (**c**), Feuguerolles (Normandy, France). **a** MHNLM 2015.1.12, holotype, locus 489, early Toarcian (Bifrons Chronozone); **a1** aboral, **a2** adoral, **a3** lateral. **b** MHNLM 2015.1.16 locus 418-A, early Toarcian (Serpentinum Chronozone); **b1** aboral, **b2** adoral, **b3** lateral. **c** MHNLM 2015.1.13, paratype, locus 490, early Toarcian (Bifrons Chronozone); **c1** aboral, **c2** adoral, **c3** lateral

Early Jurassic (Hettangian)—Holocene.

Palaeocomasteridae n. fam.

Diagnosis Centrodorsal with rather loosely aggregated tube-like bases of smooth cirrus sockets, sockets arranged in one to three irregular rows, interradial ridges not developed; centrodorsal cavity deep and sealed aborally by a thin plate, but open in less well-preserved specimens; width of cavity 15–25 % of centrodorsal diameter. Basals united in a star-shaped ring around the centrodorsal cavity, with narrow petals marginally crenulated; petals distinct or more or less fused to the centrodorsal.

Early Jurassic (Hettangian)—Late Jurassic (Kimmeridgian).

Palaeocomaster is the only genus of the family. Included species: *P.styriacus* Kristan-Tollmann 1988, Hettangian; *P. morierei* (de Loriol 1889 in 1882–1889), Pliensbachian; *P. benthuyi* Hess 2014a, Pliensbachian; *P. paucicirrus* Hess 2014a, Toarcian/Aalenian; *P. schlumbergeri* (de Loriol 1889 in 1882–1889), Bathonian; *P. messingi* Hess (2012), Bathonian; *P. stellatus* Gislén (1924), Bathonian; *P. latiradius* (Carpenter 1882), Bathonian; *P. calloviensis* (Carpenter 1882), Callovian; *P. guirandi* (de Loriol 1889 in 1882–1889), Oxfordian; *P. musculosus* Hess (2014b), Oxfordian; *P. wurtembergicus* (Carpenter 1881), Kimmeridgian.

Palaeocomaster Gislén 1924

Diagnosis See family

Palaeocomaster structus n. sp., Figs. 3, 4, 5, and 6a.

Material Twelve centrodorsals or parts thereof were examined, two with attached basal circlet. Their diameter varies from about 2.5 mm (Fig. 3a) to 1 mm (Fig. 5c), and their height from 1.2 mm (Fig. 3a, b) to 0.4 mm (Figs. 5c, 6a). They range from the Serpentinum Chronozone (three specimens) to the Variabilis Chronozone (two specimens); seven specimens are from the Bifrons Chronozone. Apart from the type specimens, the material includes specimens MHNLM 2015.1.16 to 2015.1.23.

Holotype MHNLM 2015.1.12; centrodorsal, Fig. 3a.

*Paratypes* Centrodorsals with attached basal circlet, MHNLM 2015.1.13, fig. 3c (locus 490, Bifrons Chronozone), MHNLM 2015.1.14, fig. 5a, locus 293 (Variabilis Chronozone), MHNLM 2015.1.15, fig. 5b, locus 325 (Bifrons Chronozone).

Etymology Latin, struo, structus; for the stacked elements making up the centrodorsals.

Type locality and horizon Guérin quarry, Feuguerolles, Calvados, France, locus 489 of Marc Chesnier, bed T8/2, Bifrons Chronozone, early Toarcian, Early Jurassic.

Diagnosis Centrodorsal slightly conical, rounded pentagonal in outline, composed of several layers (nodals) that may be fused or preserved as one- to three-layered disks with through-going cavity and crenulated petals on each facet; adoral centrodorsal cavity roughly 20 % of centrodorsal diameter, up to 30 % in smaller specimens, aborally sealed in a juvenile specimen and probably also in intact adults. Adoral surface of individual disks with slightly concave impressions with weakly crenulated interradial petals; aboral surface similar, but petals may be less developed, with edges slightly crenulated. Basal circlet stellate, fused to centrodorsal; petals crenulated and broadly united around cavity. Depending on centrodorsal height, 2–5 elliptical cirrus sockets on each side; axial canal rectangular; cirral scars smooth or with slightly ornamented transverse ridge, part of rim weakly crenulated.

Description Of the twelve specimens described, all but one (Fig. 5b) have aboral opening only slightly smaller than adoral opening. The two best preserved specimens are also the largest (Figs. 3a, 5a). In the holotype (Fig. 3a), adoral and aboral sides appear similar, but centrodorsal is slightly conical (the aboral end is narrower). One centrodorsal is more or less intact (Fig. 5b) with aboral facet closed and irregular; adoral facet has three narrow, slightly concave petals fused to neighbouring bases of cirrus sockets. The second largest centrodorsal (Fig. 5a) bears basal circlet adorally, with only two rows of cirrus sockets and open aborally, suggesting that it is incomplete. Holotype centrodorsal (Fig. 3a) appears intact adorally, as indicated by regular petal structure, but not sealed aborally. However, aboral diameter of centrodorsal cavity is only about half that on adoral surface, as in relatively high centrodorsal (Fig. 3b), indicating that both centrodorsals are almost complete. Cirral scars are mostly smooth; axial canal is elliptical to rectangular and may be flanked by weak knobs (Figs. 3a3; 5a3) but no distinct transverse ridge. Two centrodorsals have basal circlet attached (Figs. 3c, 5a). In the paratype (Fig. 5a), petal-shaped basals are united interiorly, forming stellate circlet around central cavity. Basal circlet is fused here with centrodorsal, and standing out from its surface. Figure 3c illustrates similar situation but with three basal petals somewhat shorter and two much shorter than those on centrodorsal. The aboral surface commonly has interradial petals that may have crenulated
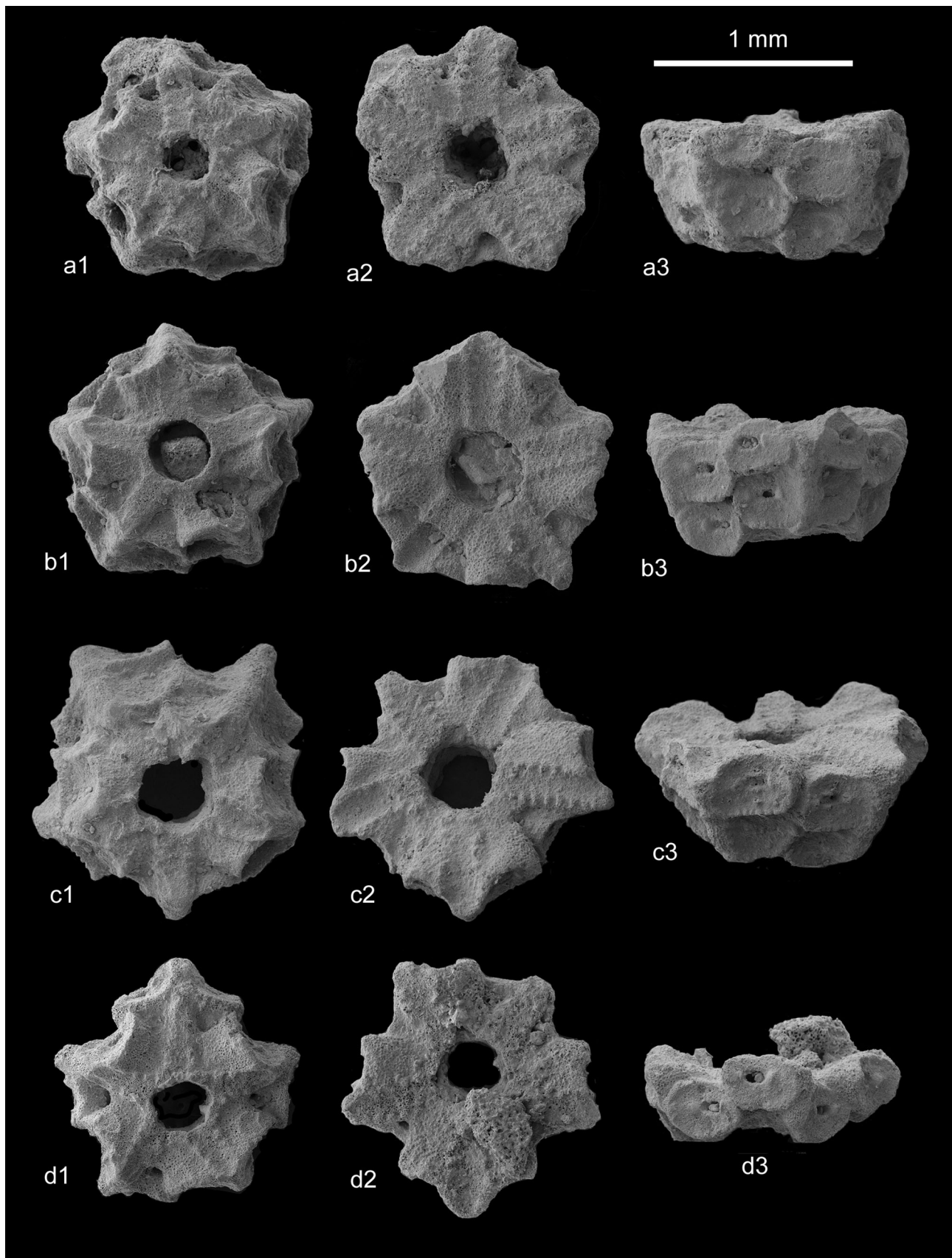
◄ **Fig. 4** *Palaeocomaster structus* n. sp., centrodorsals, Feuguerolles (Normandy, France). **a** MHNLM 2015.1.17, locus 243, early Toarcian (Bifrons Chronozone); **a1** aboral, **a2** adoral, **a3** lateral. **b** MHNLM 2015.1.18, locus 211, early Toarcian (Serpentinum Chronozone); **b1** aboral, **b2** adoral, **b3** lateral. **c** MHNLM 2015.1.19, locus 397, early Toarcian (Bifrons Chronozone); **c1** aboral, **c2** adoral, **c3** lateral. **d** MHNLM 2015.1.20, locus 307, late Toarcian (Variabilis Chronozone); **d1** aboral, **d2** adoral, **d3** lateral

edges, similar to those on the adoral surface, but less produced in most cases; the specimen in Fig. 6a has nearly equal petals. Almost all facets bear petals, indicating that the centrodorsal was formed by fusion of several nodals during ontogeny. Number of cirrus sockets on each nodal side depends on centrodorsal height and varies from five (holotype, Fig. 3a) to two in specimens preserved as a nodal (Figs. 4d, 5c–d, 6a). Centrodorsals with only one or two rows of cirrus sockets have similarly sized adoral and aboral openings (Figs. 3c; 4b–d; 5a, c–d; 6a), suggesting that they are incomplete. Presumably, one or more nodals making up the centrodorsal were lost post-mortem, indicating that they were not tightly fused in life. The cirral scars are mostly smooth; the axial canal is elliptical to rectangular, and it may be flanked by weak knobs (Figs. 3a3; 5 a3). However, a distinct transverse ridge is not developed. The rims of the scars may be weakly crenulated (Figs. 3b3, c3; 4b3, c3). The centrodorsals have a flat adoral surface with petals that are merged with adjoining bases of cirrus sockets on two opposing sides; on the other sides, the petals are free in two cases and partly free in another one. Thus, the petals are either embedded in produced bases of cirrus sockets or stand out against the bases (Fig. 3a2). Such a situation is also seen in other specimens (e.g. Fig. 4c). Petals that are slightly convex (Fig. 3c1) may match concave petals (Fig. 3b1) of presumably adjoining disks. Petals assumed to be from an interior surface of the centrodorsal all reach the central cavity. Two centrodorsals are preserved with attached basal circlet (Figs. 3c and 5a). In the paratype Fig. 5a, the petals are united around the central cavity in a closed basal ring. The basal circlet is here fused with the centrodorsal, and stands out from the surface. Such a situation also occurs in the specimen in Fig. 3c, but in this case three of the petals on the circlet are somewhat shorter than those on the centrodorsal, and two of them are much shorter.

Remarks The 12 specimens are thought to belong to a single species, although there are some differences, especially in the shape and crenulation of the petals. However, overall morphology, including the presence of one to three stacked nodals making up the slightly conical centrodorsal, is not in favour of the presence of several distinct species. Similar variability also occurs in other species of *Palaeocomaster*, e.g. in *P. paucicirrus* (Hess 2014a, fig. 5). The present species is similar to *P. paucicirrus* Hess (2014a)
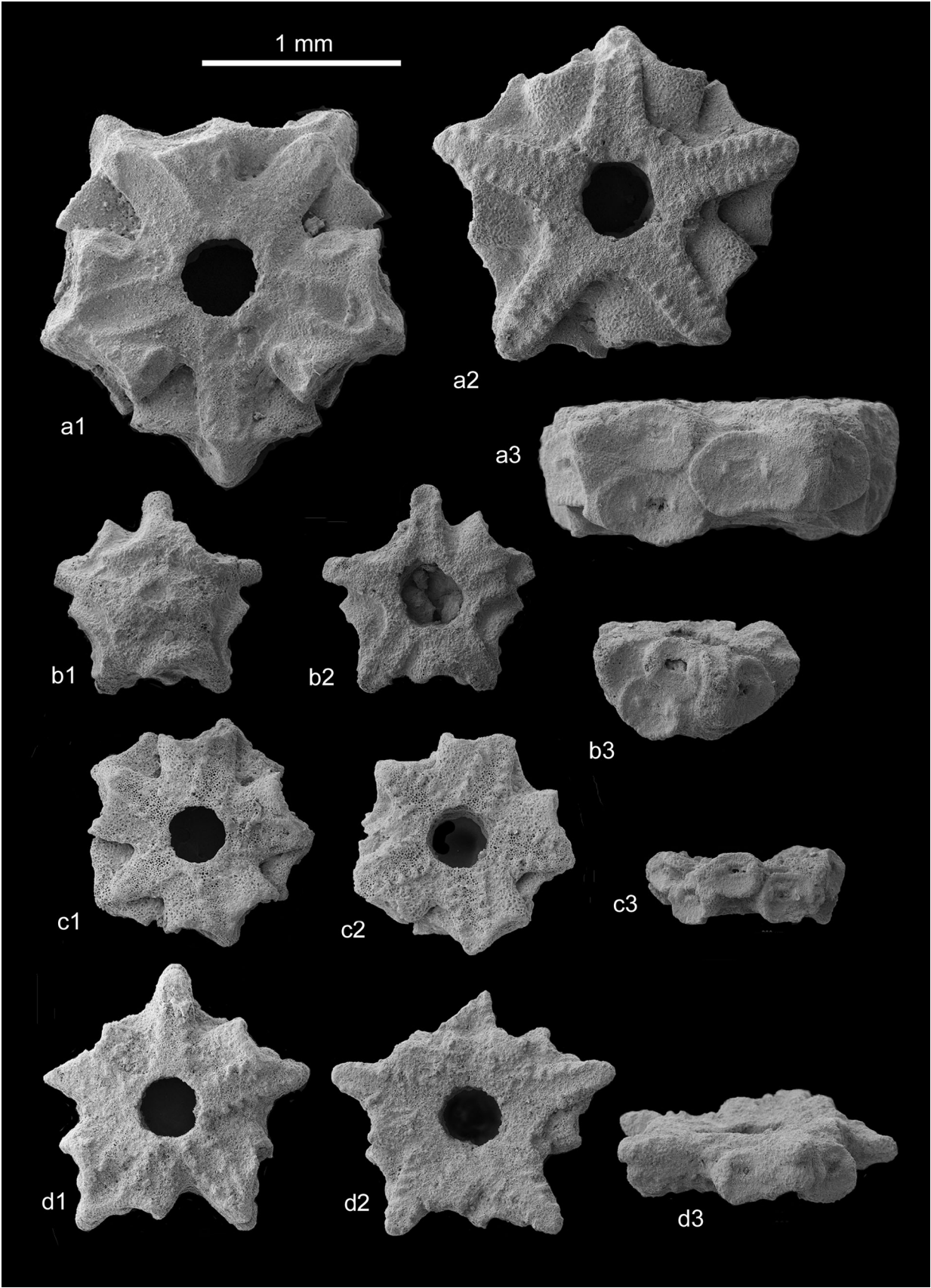
from the Toarcian/Aalenian of Quedlinburg. In the well-preserved specimens of *P. paucicirrus,* the aboral apex is closed and concave (Hess 2014a, fig. 5a–c). The attached basal circlet is superimposed on the centrodorsal and its petals are equally long; they also lack the crenulated margins of *P. structus* n. sp. The width of the cavity in the Quedlinburg specimens is 25 % of centrodorsal diameter in the holotype, but larger in another specimen; the number of cirrus sockets is two or three on each side of centrodorsal; they are more prominent and circular than those of *P. structus* n. sp. Specimens assigned to *Palaeocomaster* were described by Nicosia (1991) from the Late Sinemurian-Early Pliensbachian of Turkey. The material includes three conical centrodorsals with closely set cirrus sockets, a narrow axial canal and a closed aboral apex. The finds were not named, and this is also true of a pentagonal, low cup without centrodorsal. Simms (1988) described an intact five armed comatulid as *Procomaster pentadactylus* from the German Posidonienschiefer (Early Toarcian). Because the centrodorsal is concealed by roughly 25 robust cirri, the arrangement and scars of the cirrus sockets cannot be ascertained, although Simms assumed that they are arranged in 10 or 15 vertical rows. Since the cirrus sockets of the most complete specimen of the present species total 25 (holotype, Fig. 3a), it cannot be excluded that the forms are conspecific. However, *P. pentadactylus* with its centrodorsal diameter of perhaps 5 mm is larger than the holotype of *P. structus* n. sp., with only about half that diameter. *P. pentadactylus* has a crown height of 6 cm, and one may assume by analogy that *P. structus* n. sp. was smaller. Because the centrodorsal is not exposed, *P. pentadactylus* cannot be assigned to family, although Simms discussed a possible relationship with Atelecrinidae (*note*: at the time this family included five armed *Atopocrinus* now excluded from the family) and Solanocrinitidae in which unbranched arms also occur.

Superfamily Solanocrinitoidea Jaekel 1918.

Diagnosis Centrodorsal truncated conical to discoidal or columnar with cirrus-free aboral apex. Postlarval column with synarthrial articulations retained in adults of Thiolliericrinidae. Cirrus sockets arranged in 10–20 vertical columns or in a few irregular, marginal circles, reduced or obliterated in Thiolliericrinidae. Centrodorsal cavity very narrow. Basals stout, generally united, in Decameridae forming large rhombic plates surrounded by the radial circlet and forming bottom of large shallow radial cavity. In other families, basals rod-shaped, visible interradially or concealed. Radial cavity large. Arms undivided or divided at first or second primibrachial.

Early Jurassic (Pliensbachian)—Late Cretaceous (Coniacian).

Family Solanocrinitidae Jaekel 1918.

Diagnosis Aboral side of centrodorsal flat or concave, commonly rugose or with irregular furrows. Cirrus sockets closely placed, commonly large, arranged in 10–15 columns (exceptionally as many as 20). Stout rod-shaped basals commonly exposed interradially, meeting centrally without forming large plates in bottom of radial cavity. Adoral side of centrodorsal with radiating, commonly short coelomic furrows in at least some species of *Comatulina* but not in other genera, although secondary furrows along each side of the basal rods may occur in corroded specimens. Exposed surface of radials rather large to short or concealed. Interarticular ligament fossae and adoral muscle fossae generally low and wide, forming narrow bands in *Solanocrinites* and *Comatulina* but may be higher and triangular in *Archaeometra*. Rays undivided or divided at first or second primibrachial, exceptionally at second secundibrachial or more distally.

Early Jurassic (Pliensbachian)—Late Cretaceous (Coniacian). Genera: *Solanocrinites* Goldfuss 1829 in 1826–1833, *Archaeometra* Gislén 1924, *Comatulina* d'Orbigny 1852 in 1850–1852, *Pachyantedon* Jaekel 1891.

Solanocrinites Goldfuss 1829 (in 1826–1833).

Diagnosis See Hess and Messing 2011.

Solanocrinites jagti n. sp., Fig. 6b.

Material Only the holotype.
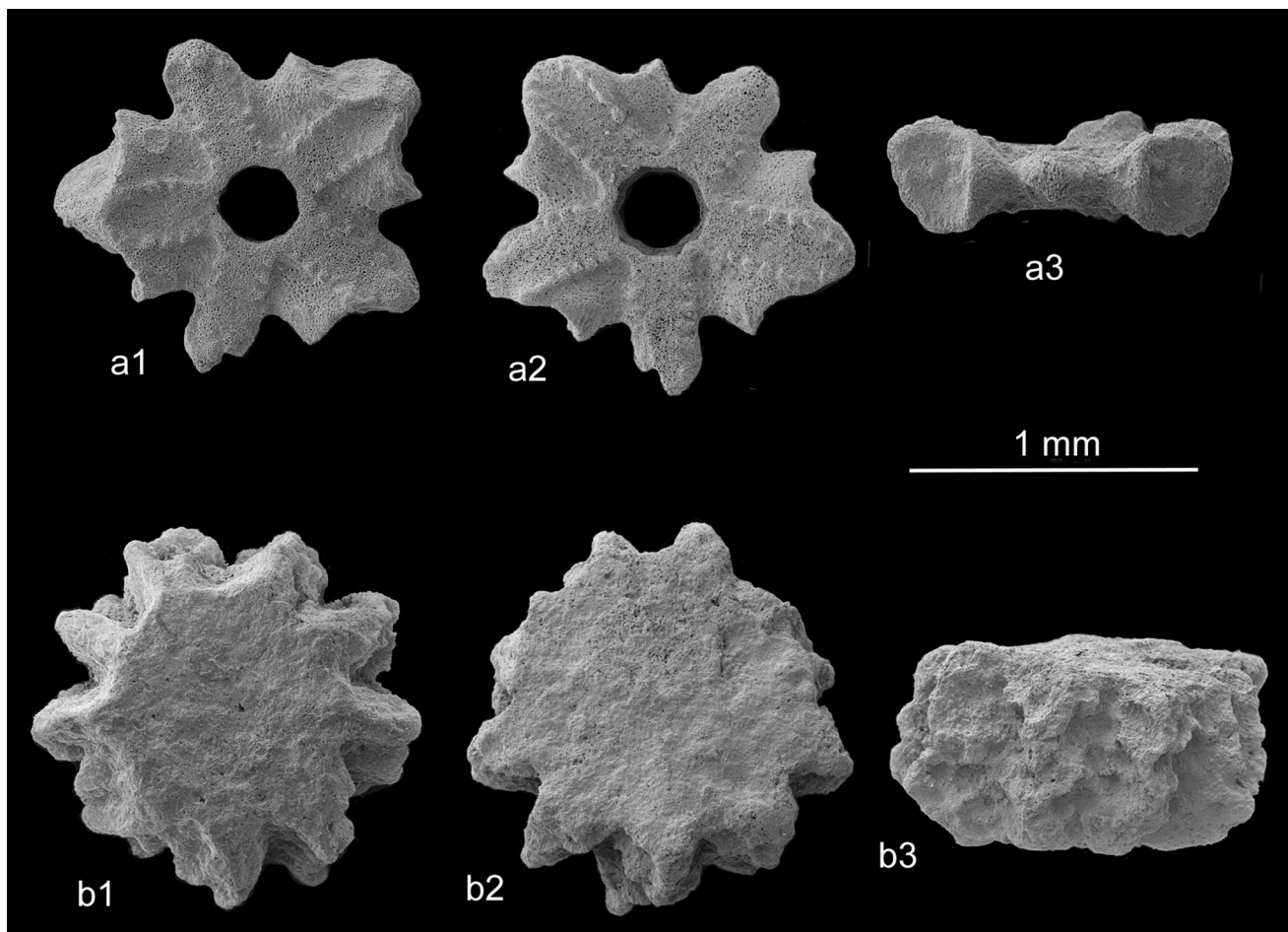
Holotype MHNLM 2015.1.24; centrodorsal, Fig. 6b.

Fig. 6 **a** *Palaeocomaster structus* n. sp., centrodorsal, MHNLM 2015.1.23, locus 314, early Toarcian (Bifrons Chronozone), Feuguerolles (Normandy); **a1** aboral, **a2** adoral, **a3** lateral. **b** *Solanocrinites jagti* n. sp., centrodorsal, MHNLM 2015.1.24, holotype, locus 355, late Pliensbachian (Margaritatus Chronozone), Feuguerolles (Normandy); **b1** aboral view, **b2** adoral, **b3** lateral

Etymology Dedicated to John W. M. Jagt for his work on echinoderms, particularly crinoids.

Type locality and horizon Guérin quarry, Feuguerolles, Calvados, France, locus 355 of Marc Chesnier, bed D1, Margaritatus Chronozone, late Pliensbachian, Early Jurassic.

Diagnosis Centrodorsal columnar, slightly conical, wider than tall and circular in cross section; central cavity narrow; sides with five interradial and five radial vertical ridges; cirrus sockets sunken, lacking any distinct articular features, in two irregular columns of 2–3 sockets per radial area; adoral side nearly flat, petals indistinct, fused with radial parts, and not produced; aboral apex slightly concave, unsculptured.

Remarks The ten projecting ridges are better seen from the aboral side because of the slightly conical shape of the centrodorsal. The centrodorsal cavity is filled by sediment but narrow; the adoral facet lacks produced interradial petals which seem to be fused with the radial parts. Available information supports assignment of the centrodorsal to *Solanocrinites*, making it the oldest representative of the genus. It differs from the Middle Jurassic *S. voultensis* Hess (2012) in having 10 distinct vertical ridges, 5 interradial and 5 radial. Similar ridges occur in the Upper Jurassic *S. costatus* Goldfuss and *S. gresslyi* (Étallon), see Hess and Messing (2011, fig. 38), and are characteristics of the genus.

Superfamily incertae sedis.

Family incertae sedis.

Andymetra Hess 2012.

Diagnosis See Hess 2012.

Andymetra toarcensis n. sp., Fig. 7.

Material The holotype and specimen MHNLM 2015.1.31.

Holotype MHNLM 2015.1.25, centrodorsal, Fig. 7a.

Etymology Name formed in reference to the Toarcian age of the species.

Type locality and horizon Guérin quarry, Feuguerolles, Calvados, France, locus 425 of Marc Chesnier, bed T1bc, Tenuicostatum Chronozone, early Toarcian, Early Jurassic.

Diagnosis Centrodorsal low bowl-shaped, irregularly circular with strongly projecting cirrus sockets; adoral surface with crenulated interradial petals, narrow and flat to concave, partly fused medially with tubular bases of neighbouring, nascent cirrus sockets; cirrus sockets about 50, circular, deeply sunken, largely unsculptured, with small axial canal surrounded by faint rim; upper cirrus sockets developed as strongly outward-projecting tubes; width of

cavity 16 % of centrodorsal diameter; aboral apex small, lacking cirrus sockets.

Description The two centrodorsals are of similar size and morphology. The better preserved holotype has a jagged outline due to some cirrus sockets projecting strongly outward. Sockets diminish in diameter aborally and are deeply sunken, except those in the uppermost (adoral) row. Second specimen (Fig. 7b) similar, but adoral side partly covered by sediment and not well preserved.

Remarks *Andymetra toarcensis* n. sp. differs from the Bathonian *A. galei* Hess (2012, fig. 10b) mainly by the jagged outline caused by the more strongly projecting cirrus sockets. *A. galei* also has larger and less sunken cirrus sockets. Upper Oxfordian *A. donovani* Hess (2014b) has an outline approaching that of *Andymetra toarcensis*, but bears only 2–3 rows of sockets, despite its somewhat larger size (3 mm diameter vs. 2.4 mm in *A. toarcensis* n. sp.). In addition, the petals in *A. donovani* do not form a stellate ring fused to bases of flanking nascent cirrus sockets. The centrodorsal of Upper Oxfordian *Semiometra petitclerci* (Caillet 1923) shares deeply sunken cirrus sockets with *A. toarcensis* n. sp., but is lower, with more numerous sockets, and without the individualized adoral side sockets. The adoral surface of the present species is similar to that of *S. petitclerci* (see Caillet 1923, fig. 1b), but latter has narrow petals similar to those of *A. donovani*. *Semiometra petitclerci* is known from specimens with the distinctive radial circlet attached to the centrodorsal (Radwańska 2007, fig. 3); the aboral pole bears a dorsal star (see Radwańska 2007, pl. 1, fig. 1e–f). Because the radial circlet is so far unknown in the three species assigned to *Andymetra*, the relationship between the two genera must remain open. However, the occurrence of a hemispherical, bowl-shaped and densely cirrated centrodorsal in the Early Jurassic shows that an increase in the number of cirri was one of the main trends in comatulid radiation. This is confirmed by *Spinimetra chesnieri* n. g. et n. sp. described below.

Superfamily incertae sedis.

Family incertae sedis.

Spinimetra n. g.

Diagnosis Centrodorsal circular and cone shaped in the adult specimen, hemispherical in the juvenile specimen; adoral surface with basal circlet of narrow, marginally crenulated petals, merged with the five adjoining, nascent bases of cirrus sockets around centrodorsal cavity; width of cavity 16 % of centrodorsal diameter; cirrus sockets numerous, small, crowded and deeply sunken, with pronounced horseshoe-shaped rim, each side projecting
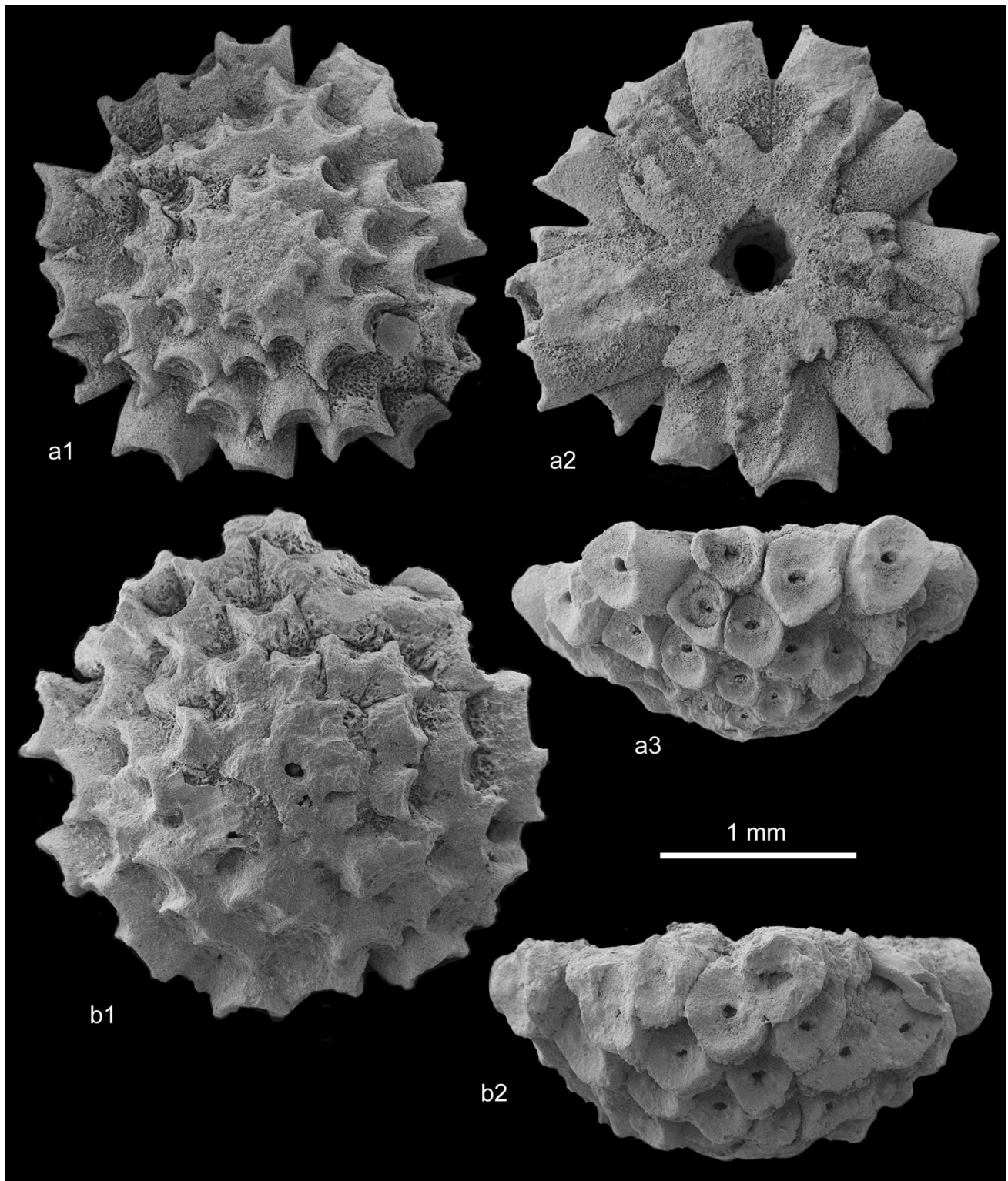
Fig. 7 *Andymetra toarcensis* n. sp., centrodorsals, locus 425, early Toarcian (Serpentinum Chronozone), Feuguerolles (Normandy); **a** MHNLM 2015.1.25, holotype; **a1** aboral, **a2** adoral, **a3** lateral. **b** MHNLM 2015.1.31; **b1** aboral, **b2** lateral

outward and downward as a blunt triangular spine. Aboral apex nearly flat, about 20 % of centrodorsal diameter in holotype, with small opening on the aboral pole.

Etymology Latin, *spina*, spine or thorn, for the spiny appearance of the centrodorsal; *metra* is a suffix commonly used for comatulids.

Type species *Spinimetra chesnieri* n. sp.

Remarks Morphology of the densely cirrated, conical, spiny centrodorsal of *Spinimetra* is unique among Lower Jurassic comatulids and, indeed, among later fossil forms. Similar cirrus sockets are known from the extant *Atopocrinus* A. H. Clark, Family Atopocrinidae Messing 2011 in Hess and Messing 2011, and Superfamily uncertain (Hess and Messing 2011, fig. 37, 2b). An undescribed species of *Atopocrinus* shares with *Spinimetra* several potential synapomorphies (Messing, pers. comm. 2016). These include cirrus socket structure, pores between sockets connecting to centrodorsal cavity, and tube-shaped rudimentary sockets on the aboral surface flanking the narrow basals. Differences include the strong interradial ridges, unitary construction, and apparent lack of basal crenulae in the living *Atopocrinus*. The construction of the *Spinimetra* centrodorsal from multiple 'nodals' versus the unitary construction in *Atopocrinus* (with interradial ridges) seems a major evolutionary distinction above family level. Extant Atelecrinidae also share with *Spinimetra* and *Atopocrinus* a conical centrodorsal with similar sockets, but lack the pores and tube-shaped rudimentary sockets. Atelecrinidae also differ in having wedge-shaped basals that form an externally visible ring (Messing 2003, 2013).

Spinimetra chesnieri n. sp., Fig. 8.

Material Three centrodorsals, holotype and two additional, juvenile specimens MHNLM 2015.1.27 and 2015.1.28.

Holotype MHNLM 2015.1.26, centrodorsal, Fig. 8b.

Etymology Dedicated to Marc Chesnier who collected and carefully recorded the material.

Type locality and horizon Guérin quarry, Feuguerolles, Calvados, France, locus 358 of Marc Chesnier, bed T1a, Tenuicostatum Chronozone, early Toarcian, Early Jurassic.

Diagnosis See genus (monotypic).

Description of holotype. Outline in aboral view is regularly circular but jagged due to protruding socket spines; profile is conical with flattened apex. Sockets are crowded, about 100, with approximately 10 around aboral apex, increasing as irregular columns to 20 around adoral margin. Radial and interradial areas not differentiated. Adoral surface with five regular, rather narrow and marginally crenulated interradial petals that protrude, like the socket spines, beyond centrodorsal margin. Petals fused with adjacent bases of nascent cirrus sockets around centrodorsal cavity. Symplectial articulation between a petal and the underlying cirrus socket (Fig. 8 b3; arrow) suggests that petals are part of a basal circlet. From the two bases of cirrus sockets emerging in each radius between the petals, one is much smaller and superimposed on the larger one. Sockets are

Fig. 8 *Spinimetra chesnieri* n. g. and sp., locus 358 (**a**, **b**), early ▶ Toarcian (Tenuicostatum Chronozone), Feuguerolles (Normandy). **a** MHNL 2015.1.27, juvenile centrodorsal; **a1** aboral, **a2** adoral, **a3** lateral. **b** MHNLM 2015.1.26, holotype, centrodorsal with attached basal circlet; **b1** aboral, **b2** adoral, **b3** lateral (*arrow* indicates symplectial articulation between basal circlet and centrodorsal). **c** Juvenile centrodorsal, MHNLM 2015.1.28, locus 354, early Toarcian (Tenuicostatum Chronozone), Feuguerolles (Normandy); **c1** aboral, **c2** adoral, **c3** lateral

hourglass-shaped between angular lateral processes of centrodorsal rim, with small axial canal at narrowest point. Aboral apex is nearly flat, with small central orifice.

Description of smaller (juvenile) individuals. Centrodorsal outlines and profiles are irregular. Cirrus sockets number about 20 in two rows (Fig. 8c) or about 30 in four rows (Fig. 8a). Adoral petals are indistinct, especially in the smaller specimen.

Remarks *Andymetra* differs from *Spinimetra* by larger, circular and shallow cirrus sockets. The Oxfordian *Semiometra petitclerci* (Caillet 1923) has a low, bowl-shaped centrodorsal; cirrus sockets have lateral tubercles but lack a horseshoe-shaped rim with spiny extensions (see Hess 2014b, fig. 11b; Radwańska 2007, pl. 1, fig. 1d). In contrast to the juvenile specimens (Fig. 8a, c), the aboral apex of the holotype has only a small opening. The smaller of the juvenile specimens (Fig. 8c) has only two rows of cirrus sockets and the openings are similar on both sides. The larger centrodorsal (Fig. 8a) has four rows of sockets and a smaller opening aborally. This suggests that the centrodorsal of *Spinimetra* was built from stacked parts, similar to *Palaeocomaster structus* n. sp. However, petals are less produced on the adoral side of the juveniles indicating a more coherent stereom. Apart from overall shape and arrangement of the cirrus sockets, the adoral side is basically similar in *S. chesnieri* n. sp., *A. toarcensis* n. sp. and *Semiometra petitclerci*.

Order Isocrinida Sieverts-Doreck 1952 in Moore, Lalicker & Fischer.

Diagnosis See Hess and Messing 2011.

Suborder Pentacrinitina Gray 1842.

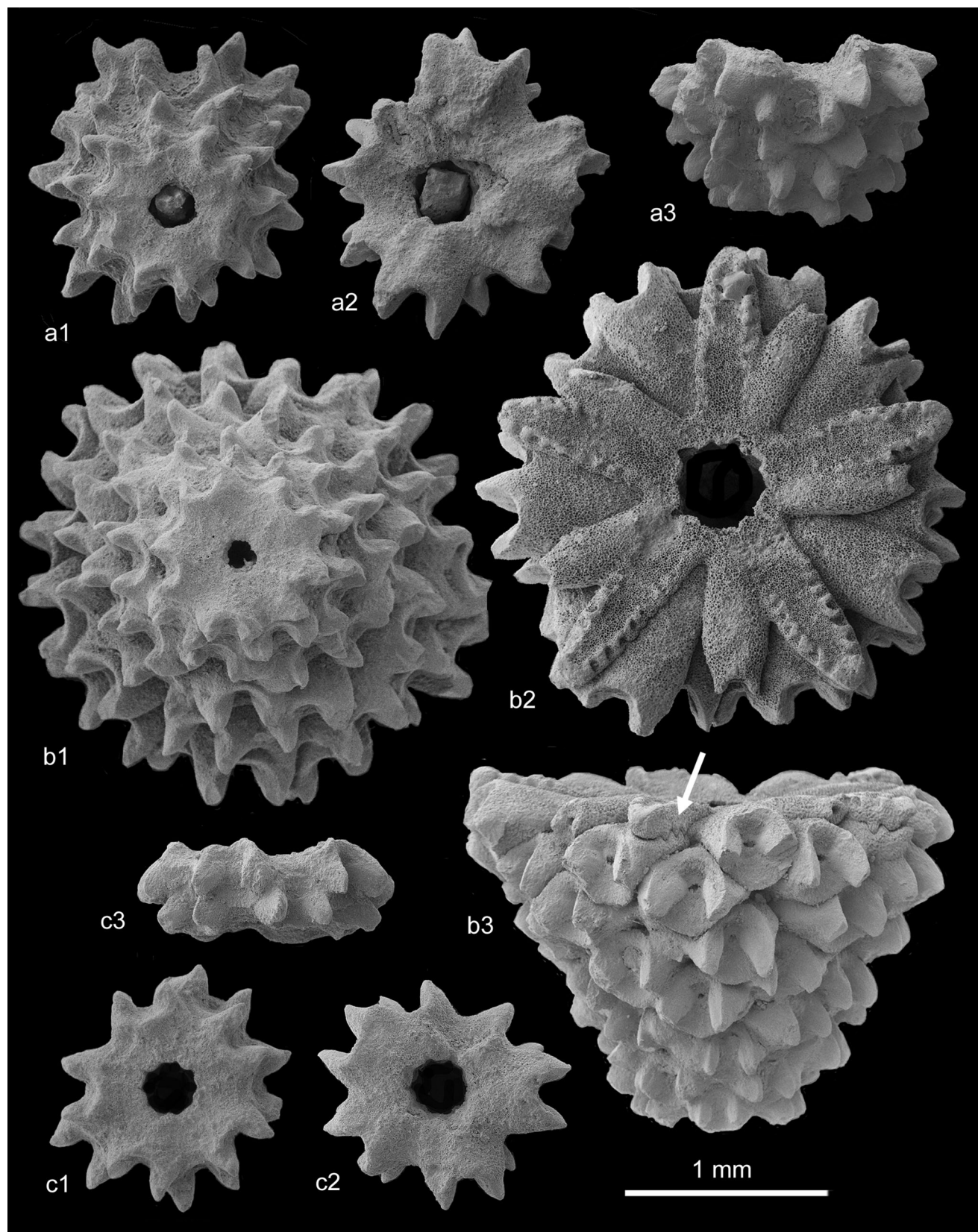*Diagnosis* See Hess 2014a.

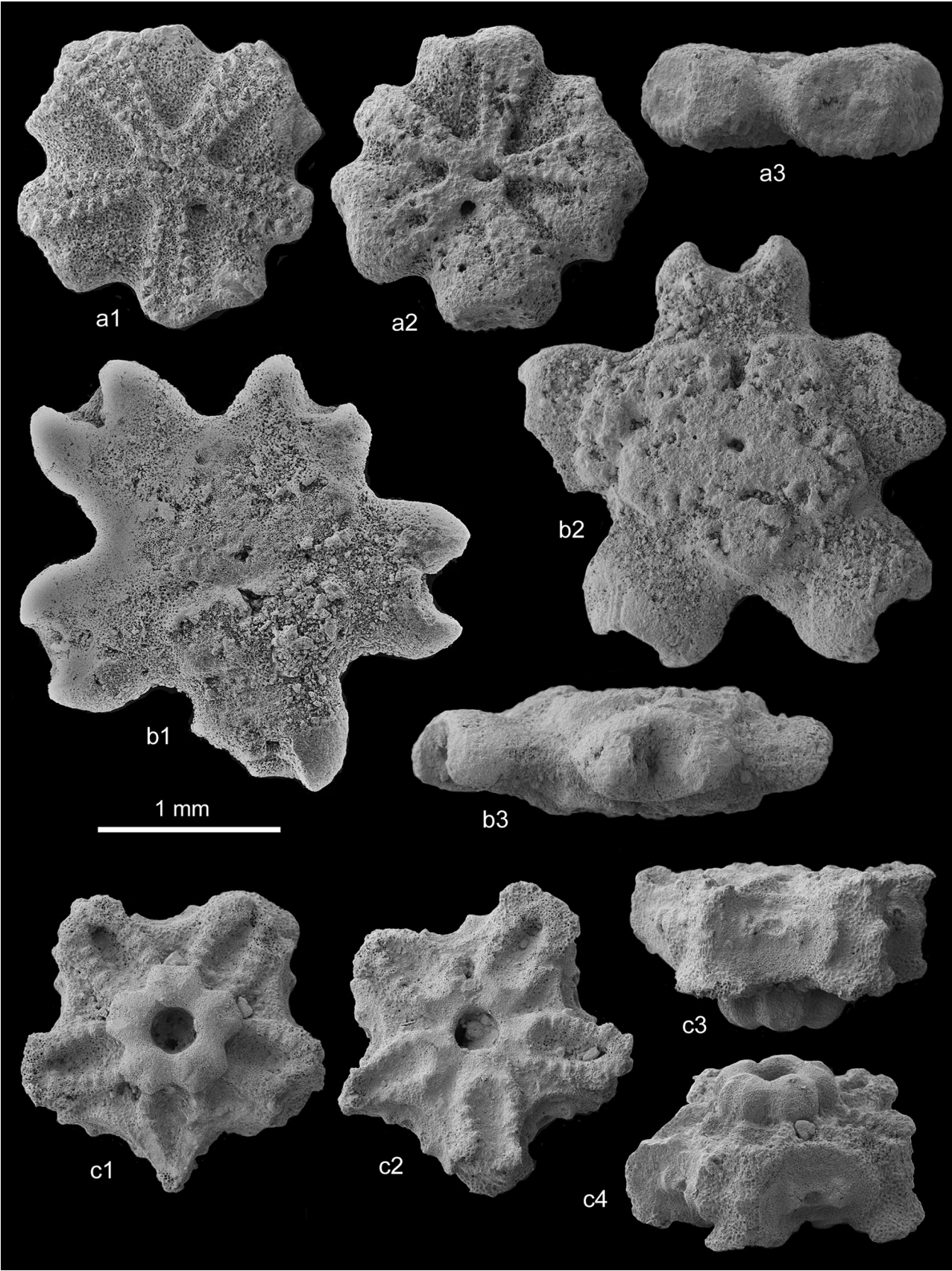Family Paracomatulidae Hess 1951.

Diagnosis See Hess 2014a.

Singillatimetra Hess 2012.

Diagnosis See Hess 2014a.

Singillatimetra truncata n. sp., Fig. 9a.

Material Only the holotype.

◀**Fig. 9 a** *Singillatimetra truncata* n. sp., MHNLM 2015.1.29, holotype, columnal, locus 298, early Toarcian (Serpentinum Chronozone), Feuguerolles; **a1** aboral, **a2** adoral, **a3** lateral. **b** *Forcipicrinus normannicus* n. g. and sp., MHNL.1.2015.30, holotype, columnal, locus 397, early Toarcian (Bifrons Chronozone), Feuguerolles; **b1** adoral, **b2** aboral, **b3** lateral (b1 is at the bottom). **c** *Pentacrinites collenoti* (de Loriol 1888 in 1882–1889), MHNL.2015.1.32, nodal with internodal attached, locus 397, early Toarcian (Bifrons Chronozone), Feuguerolles; **c1** aboral, **c2** adoral, **c3** lateral **c4** oblique lateral-aboral

Diagnosis Columnal centrodorsal-like, rather thick; axial canal narrow, interradial area star shaped, with coarsely crenulated petals widening outward; five cirrus sockets irregular, bulging and smooth, occupying whole height of ossicle, offset from radial midlines except in one ray. Cirral scars slightly concave, smooth. Both columnal facets similar.

Holotype MHNLM 2015.1.29, columnal, Fig. 9a.

Etymology truncata, Latin, for the truncated interradial petals.

Type locality and horizon Guérin quarry, Feuguerolles, Calvados, France, locus 298 of Marc Chesnier, bed T3, Serpentinum Chronozone, early Toarcian, Early Jurassic.

Description Interradial petals are star shaped, widening outward and with coarsely crenulated margins. Radial areas between the petals are truncated, ending with a large cirrus socket offset from midline. Sockets are separated by cleft. One socket is conspicuously smaller. Both facets are similar; sockets pointing slightly upward toward one facet likely indicate it as proximal facet.

Remarks This columnal differs from that of *S. inordinata* Hess (2012) in having a star-shaped outline with truncated endings interrupted by clefts. The interradial petals are strongly produced on both facets. Assignment to *Singillatimetra* is based on the presence of large, bulging cirrus sockets offset from the radial midline, and a narrow axial canal on both facets. The columnal is somewhat similar to nodals of *Pentacrinites*, such as *P. collenoti* (de Loriol 1888 in 1882–1889), here figured for comparison (Fig. 9c). However, nodals of the latter have elliptical, protruding petals; and the area between the crenulated margins is strongly concave. The cirral scar has a transverse ridge thickened at both ends. In addition, *P. collenoti* has small internodals found mostly as single ossicles, but may also be attached to nodals (Fig. 9c).

Pentacrinitina Gray 1842.

Family incertae sedis.

Forcipicrinus n. g.

Etymology Latin, *forceps*, after the forceps-like aspect of the cirrus socket bases.

Diagnosis Columnal moderately thick, with five claw-like radial processes harbouring smooth, deeply sunken circular cirrus sockets; axial canal very narrow; one facet with raised, star-shaped interior part showing short blunted interradial petals bordered by some scattered crenulae; other facet flat and largely unsculptured.

Type species Forcipicrinus normannicus n. sp.

Forcipicrinus normannicus n. sp., Fig. 9b.

Material Only the holotype.

Holotype MHNLM 2015.1.30, columnal, Fig. 9b.

Etymology Latin, *normannicus*, for the occurrence in Normandy.

Type locality and horizon Guérin quarry, Feuguerolles, Calvados, France, locus 397 of Marc Chesnier, bed T8/1, Bifrons Chronozone, early Toarcian, Early Jurassic.

Diagnosis See genus (monotypic).

Description Columnal is dominated by five claw-like radial extensions supporting circular, sunken cirrus sockets. One facet (Figs. 9b, 2) slightly convex with rounded petals that do not reach clefts between processes; petals are bordered by few scattered granules. Other facet (Figs. 9b, 1) flat, with a few scattered granules; three sockets projecting slightly upward suggest this as adoral. Axial canal is very narrow on both facets.

Remarks The narrow axial canal and the similar aboral and adoral facets of the ossicle suggest that it is not a centrodorsal belonging to Comatulida but rather a columnal of Pentacrinitina. In contrast to *Singillatimetra truncata* n. sp. and *S. inordinata* Hess 2012, the cirrus sockets are not offset from the radial midlines, a character of Paracomatulidae and Pentacrinitidae (see Hess and Messing 2011). Thus, assignment to Pentacrinitina is tentative and to a specific family uncertain. Some columnals of *Pentacrinites collenoti* (de Loriol 1888 in 1882–1889) were also found in the same bed. Figure 9c shows a nodal with attached internodal, illustrating slightly offset cirrus sockets and a cirral scar with transverse ridge thickened at the ends, characteristic of *Pentacrinites* (Hess and Messing 2011, fig. 21i–k).

Family Pentacrinitidae Gray, 1842.

Pentacrinites collenoti (de Loriol, 1888 in 1882–1889), Fig. 9c.

Material Three isolated nodals and two nodals with attached internodals from locus 397.

Description Small nodal and attached internodal having star-shaped outline with well-developed interradial petals (Fig. 9c), internodal visible laterally. Petals concave, surrounded by crenulated rim, and leaving some space around the axial canal for an internodal. One petal somewhat smaller, with acute tip. Axial canal is rather wide, 12 % of nodal diameter. Internodal small; diameter and height about half those of nodal.

Remarks The small size and the prominent internodal suggest that the two specimens are juvenile. Similarly, small specimens were figured by de Loriol (1888, pl. 200, figs. 2 and 3). In adult columns of the species, internodals are not visible (de Loriol 1888, pl. 200, fig. 1). Species of *Pentacrinites* vary in internodal development. They are small and not visible on the outside of the column in Bajocian *P. dargniesi* Terquem and Jourdy 1869 (see Hess and Messing 2011, fig. 21j,k); in the Bajocian/Bathonian *P. ausichi* Hess 2012, nodals and internodals are of similar diameter although the internodals are lower.

Discussion

Systematic considerations

The material includes a number of centrodorsals of *Palaeocomaster*, the most common comatulid genus in the Early Jurassic. A dominant character of *Palaeocomaster* species is a centrodorsal composed of more or less fused tubes widening outward to smooth cirrus sockets. *P. structus* n. sp. demonstrates that the centrodorsal was assembled by fusion of a few individual columnals during ontogeny and not by cirral growth on a single proximal nodal as in living forms (Lahaye and Jangoux 1987). In the pentacrinoid stage of living comatulids, a column without cirri is first formed. In *Antedon bifida*, an enlarged columnal (proximale) appears on top of the column after about 65 days, and further columnal growth ceases. Shortly thereafter, the first cirri develop radially on the proximale, followed by a second set in interradial position (Lahaye and Jangoux 1987); the proximale is the only nodal in the pentacrinoid column and is now called the centrodorsal. Somewhat later, the crinoid breaks away from the column with its support and starts a free-swimming life. In *Palaeocomaster*, the centrodorsal is assembled from several nodals with a rather wide axial canal, and distally sealed by a thin plate. Such morphology is reminiscent of *Paracomatula* Hess 1951 (see Hess and Messing 2011), which originated in the Late Triassic with *P. triadica* Hagdorn and Campbell 1993. Intact specimens are remarkably similar to *P. helvetica* Hess 1951; and both species have a short segmented column with rather narrow axial canal. The parts making up the centrodorsal-like column of *P. helvetica* lack

the pronounced, individualized bases of cirrus sockets of *Palaeocomaster*. The basal circlet of *Paracomatula* with its narrow petals is also pentacrinine-like (Hess and Messing 2011, fig. 37, 1d). Hess (2014a, p. 27) previously described *Palaeocomaster* species as the first comatulids with cirrus bases assembled on a single centrodorsal during growth. The material of *P. structus* n. sp. indicates that several columnal elements were involved in the formation of the centrodorsal. Another distinct character of *P. structus* n. sp. is a deep centrodorsal cavity sealed aborally by a thin plate. Such a structure is also seen in *Palaeocomaster styriacus* Kristan-Tollmann (1988), the earliest true comatulid. Gislén (1924, p. 142) did not discuss these characters in his diagnosis of the genus. In fact, Gislén included two species with only rudimentary cirri in the genus, *P. formae* Noelli 1900 from the Miocene, placed by Hess and Messing (2011) in *Comaster*, and *P. loveni* (Carpenter 1880) from the Early Cretaceous, which appears to lack cirri. Including the Hettangian *P. styriacus Palaeocomaster* is now represented in the Early Jurassic by five distinct species, all of them small with a centrodorsal not exceeding 1–2 mm in diameter. These species share the circular to five-sided centrodorsal composed of tube-like cirrus socket bases still recognizable individually. The cirral sockets are smooth. The centrodorsal cavity is deep and sealed aborally in well-preserved specimens by a thin plate; however, it may appear at the aboral apex in less well-preserved specimens. The radial circlet, preserved in specimens of some later species, is higher than the centrodorsal, with steep facets and large muscle fossae, and is thus similar to those of *Paracomatula helvetica* and *P. liasica* Hess 2014a. Interradial ridges are not developed. The basals are united in a star-shaped ring around the centrodorsal cavity, with marginally crenulated petals. The petals of the basal circlet may be distinct or more or less fused with the centrodorsal. Gislén (1924, p. 142) assigned *Palaeocomaster* to the family Comasteridae A. H. Clark 1908 (corrected to Comatulidae Fleming 1828; see Summers et al. 2014) as its sole fossil representative. At the time, the oldest species assigned to the genus were *P. schlumbergeri* (de Loriol 1889 in 1882–1889) and *P. stellatus* Gislén 1924, both from the Middle Jurassic. In the *Revised Treatise*, Hess and Messing (2011) established the Superfamily Comasteroidea A. H. Clark (pro Comasterida Gislén 1924, p. 229), now corrected to Comatuloidea Fleming 1828 (see above where an amended diagnosis is given). A basal rosette (see Hess and Messing, figs. 3,4 and 5,2) has so far not been observed in fossil specimens, but other characters agree well with the diagnosis for the centrodorsals of comasterids. However, Hess and Messing (2011) followed Rasmussen (1978) in assigning *Palaeocomaster* to the Superfamily Solanocrinitoidea Jaekel (1918), Family Solanocrinitidae Jaekel (1918). According to the *Revised Treatise* (Hess and Messing 2011, p. 76), the

Solanocrinitoidea has compact centrodorsals with sockets in 10–20 vertical columns separated by ridges, or in a few irregular marginal cycles in *Palaeocomaster*. On the basis of the newly described Early Jurassic species of *Palaeocomaster* (Hess 2012, 2014a, b; and present paper) that have centrodorsals composed of fused individual nodals and rather loosely aggregated bases of cirrus sockets, assignment to Solanocrinitoidea is no longer warranted. *Palaeocomaster* is better placed in Comatuloidea Fleming as a family of its own, Palaeocomasteridae n. fam., as indicated above. The first appearance of the predominantly Upper Jurassic genus *Solanocrinites* with the Pliensbachian *S. jagti* n. sp. is surprising. *Andymetra*, so far known from the Bathonian *A. galei* Hess and the Oxfordian *A. donovani* Hess, also appears at Feuguerolles with the distinctive *A. toarcensis* n. sp. This varied picture is rounded off by *Spinimetra chesnieri* n. g. and sp. Morphology of its densely cirrated and spiny centrodorsal seems to be derived, but the juvenile specimens (Fig. 8a, c) suggest that the centrodorsal was built from stacked layers, a primitive trait. *Andymetra* and *Spinimetra* cannot at present be assigned to given families, although *Andymetra* has some resemblance to *Semiometra* (Family Notocrinidae) and *Spinimetra* to *Atopocrinus* (Family Atopocrinidae).

Singillatimetra (Pentacrinitina), previously known only from the Bathonian, is represented by *S. truncata* n. sp., and to this group the new genus *Forcipicrinus* with *F. normannicus* n. sp. is added, although the radial position of the cirrus sockets makes its exact position within the Pentacrinitina unclear. The presence of a true *Pentacrinites* species, *P. collenoti* (de Loriol), at the locus of *F. normannicus* as well as the presence of *P. collenoti* at loci with comatulids (082, 233, 304, 325, 418) indicates that *Singillatimetra* and *Forcipicrinus* species are not just malformed columnals of *Pentacrinites*. No columnals similar to those of *Singillatimetra* and *Forcipicrinus* have been described under *Pentacrinites* species in the literature (Quenstedt 1876; de Loriol 1888 in 1882–1889; Jäger 1985; Simms 1989).

Palaeoecological considerations

The crinoid material described herein originates from deposits ranging from the late Pliensbachian to the late Toarcian, a time interval that witnessed profound global climatic and oceanographic fluctuations (Nikitenko 2008; Danise et al. 2013; Krencker et al. 2015; Danise et al. 2015; Gómez et al. 2016). Most notable are the upper Pliensbachian cooling followed by a rapid and vigorous warming at the onset of the Toarcian, which culminated in the so-called Toarcian Oceanic Anoxic Event (TOAE) (Jenkyns 1988; Gómez et al. 2016).

In spite of the minute share they contribute to the Feuguerolles crinoid assemblages, the comatulids provide some intriguing insights in terms of their occurrence patterns with respect to the upper Pliensbachian to lower Toarcian palaeoenvironmental perturbations. In fact, *Solanocrinites jagti* n. sp. belongs to a group which was previously assumed to have originated in Middle to Late Jurassic times (Hess and Messing 2011; Hess 2014a). *Andymetra* of unknown affinity is the first representative of an otherwise Middle to Upper Jurassic genus, while *Spinimetra* n. g. is surprisingly similar to the living feather star *Atopocrinus*. In Feuguerolles, they all occur in sediments predating the TOAE. Our new finds, thus, imply that the palaeoenvironmental perturbations in the context of the TOAE obviously played no major role, neither in hampering nor in promoting the early evolutionary history of the comatulids. The non-comatulid share of the Feuguerolles crinoid fauna corroborates the pattern (Fig. 2): the most abundant components occur throughout the upper Pliensbachian to upper Toarcian succession (*Isocrinus* [*Chladocrinus*] *basaltiformis* and *Cotylederma docens*) or at least throughout the Toarcian succession (*Praetetracrinus inornatus*), while the distribution patterns of *Eudesicrinus mayalis*, *Sacariacrinus* n. sp. and the millericrinids seem to be more related to temporary facies change than faunal turnover as a result of the TOAE.

The diversity of the comatulids and paracomatulids in the Feuguerolles material is extraordinary by Early Jurassic standards and can be explained at least in part by the palaeoenvironmental setting. In fact, ancient near-shore rock reefs are relatively rare in the geological record, and only in exceptional cases is the associated fauna well preserved (e.g. Surlyk and Sørensen 2010). Another very important factor, however, is sampling bias: the material at hand is unusually rich, with more than 100,000 crinoid ossicles available thanks to a combination of careful and thorough sampling and highly condensed and fossiliferous sampling beds. Lower Jurassic comatulids are exceedingly rare in general, and larger sample volumes are indeed likely to unearth comatulid remains in crinoid assemblages dominated by stalked forms as exemplified by the single specimen of *Procomaster pentadactylus* from the disproportionately well-sampled Toarcian Posidonia Shale.

The material described herein clearly demonstrates that the exhaustiveness of taxonomic surveys representing the basis for evolutionary studies depends on careful sampling and the inclusion of rare and untypical palaeoenvironments.

Conclusions

The comatulid material described in the present work significantly adds to the meagre Lower Jurassic fossil record of the group. From the Early Jurassic (Hettangian—Toarcian/Aalenian), four species of *Palaeocomaster* were

previously known from the Early Jurassic (Hettangian—Toarcian/Aalenian): the Hettangian *P. styriacus*, the Pliensbachian *P. morierei* and *P. benthuyi*, and the Toarcian/Aalenian *P. paucicirrus*, see Hess (2014a). The new comatulids from Feuguerolles belong to four superfamilies (Solanocrinitoidea, Comatuloidea, and two uncertain) and four genera (*Palaeocomaster*, *Solanocrinites*, *Andymetra* and *Spinimetra*) that make the Pliensbachian/Toarcian a hotspot of comatulid radiation. The small size of these early forms and their extreme rarity among the bulk of larger crinoids such as e.g. *Isocrinus*, *Amaltheocrinus* and *Cotylederma* indicate that they led a niche existence and are detected only by careful collection of large amounts of material. This has also furnished two species of Pentacrinitina, quite different from the common *Pentacrinites* species. They contribute to a scenario of 'explorative radiation', seemingly a testing ground for unattached life after the end-Triassic extinction event. Morphology of these early comatulid centrodorsals reinforces the notion of their derivation from pentacrinine ancestors (Hess 2014a). During this experimental phase, the multi-cirrated comatulid centrodorsal was victorious over its competitors, as demonstrated by four rather different results, represented by *Palaeocomaster*, *Solanocrinites*, *Andymetra*, and *Spinimetra*.

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