

***Balanocrinus* (Crinoidea) from the Jurassic: species concept, reconstruction, ontogeny, taphonomy and ecology**

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Abstract Early and Late Jurassic mudstones of Europe are rich in remains of the isocrinid *Balanocrinus*. Recently collected material from the Early Pliensbachian of Sedan (France), from the Oxfordian of Andelot-Morval and Savigna (Département du Jura, France), and Les Rouges-Terres (Canton of Jura, Switzerland) adds significantly to the knowledge of the most important Jurassic species. The Oxfordian faunas that also include isocrinids, comatulids and a cyrtocrinid are the subject of a parallel publication. In the present paper intact specimens of *Balanocrinus gracilis* (CHARLESWORTH) from Sedan, including early growth stages, and early ontogenetic stages of *Balanocrinus brachiospina* HESS from Savigna are described. The material from Savigna allows reconstruction of the animal and a comparison with the type species, *Balanocrinus subteres* (MÜNSTER in GOLDFUSS), for which columnals from the Middle Oxfordian sponge facies of Holderbank (northern Switzerland) and cup plates previously described from Germany are used. The taphonomy and palaeoecology of *Balanocrinus* occurrences in mudstones of Early to Late Jurassic localities of England, France and Germany are discussed and compared with beds of *Chariocrinus* from the Early and Middle Jurassic of Switzerland.

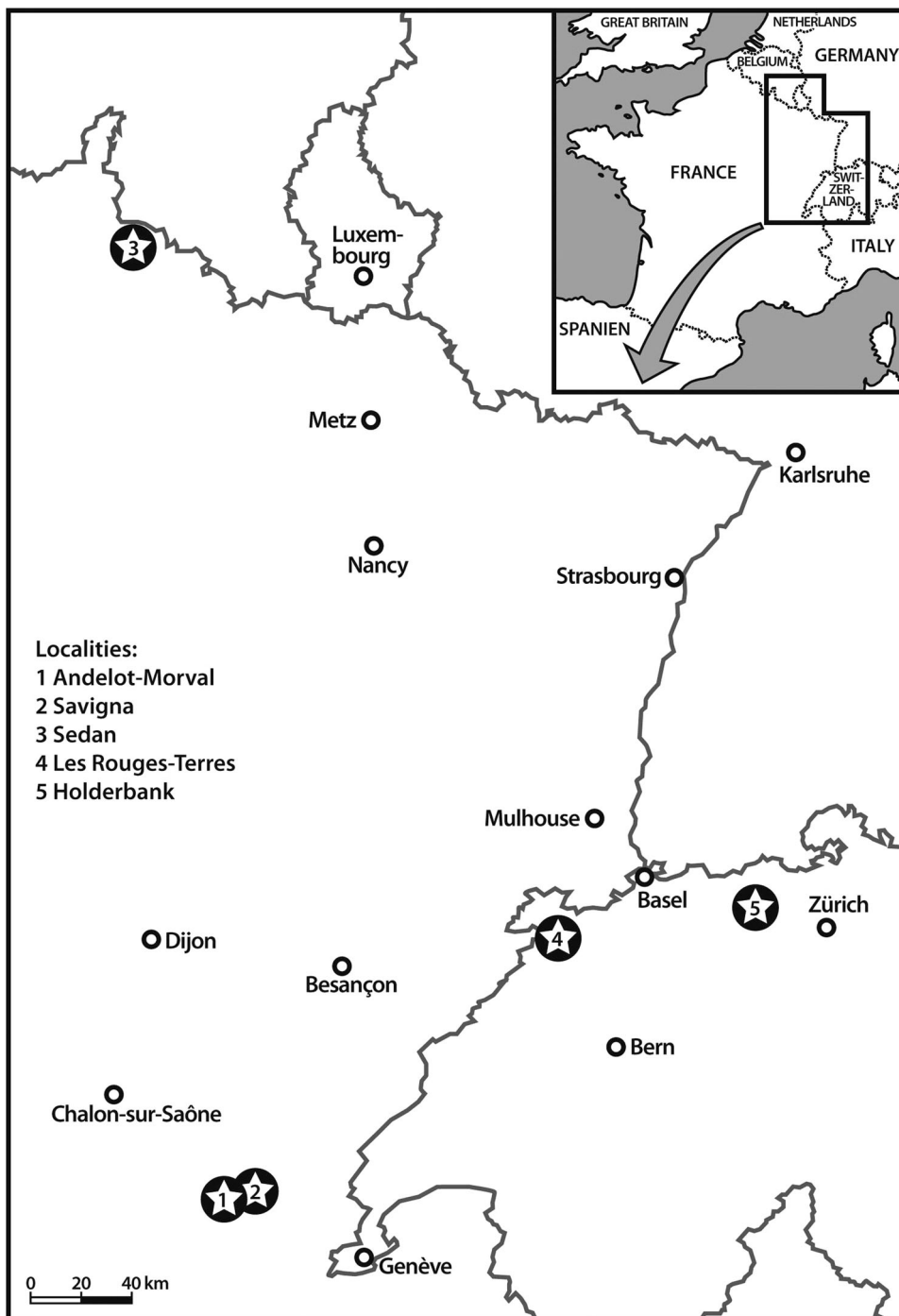
Keywords *Balanocrinus* · Jurassic · Reconstruction · Ontogeny · Taphonomy · Ecology

Introduction

The present paper is the first of three dealing with Early and Late Jurassic mudstone faunas that contain mainly remains of *Balanocrinus*, but also isocrinids and rare comatulids; at one of the locations a new species of *Tetracrinus* was found. In the following, several aspects of the occurrences (Fig. 1) are discussed. In a second paper (Hess 2013a), the rich crinoid faunas from the Oxfordian localities of Savigna (French Jura), Andelot-Morval (French Jura), and Les Rouges-Terres (Swiss Jura) are described in detail. The third paper (Hess 2013b) treats the early history of the comatulids, based in part on the new material. The bulk of the crinoid ossicles at all sites belongs to *Balanocrinus*, a genus that dominates Jurassic mudstones (de Loriol 1882–1889; Hess 1975; Simms 1989a; Thuy et al. 2011), but also occurs in other types of rock. Thus, *Balanocrinus* may be regarded as the ecologically most successful genus of Jurassic stalked crinoids. The Savigna material is described as *B. brachiospina* HESS (2013a) and allows a detailed analysis and reconstruction of the species whose column resembles that of *B. subteres* (MÜNSTER in GOLDFUSS), the type species of the genus. The Middle Oxfordian *B. subteres* with a cylindrical column and the Early Oxfordian *B. pentagonalis* with a pentagonal column are easily distinguished by the column, but their crown is poorly known. New material from Switzerland significantly increases the knowledge of these popular species. Well preserved material of *Balanocrinus gracilis* from the Lower Jurassic (Pliensbachian, Thuy et al. 2011) further adds to the knowledge of Jurassic *Balanocrinus* and is described in the following. Bulk processing of large amounts of sediment (Gale 2011; Hess 2013a) at Savigna yielded numerous small postlarval ossicles that are described in the following. For information on the localities

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Fig. 1 Map with localities discussed in the present paper and in Hess (2013a, b)



of Savigna, Andelot and Les Rouges-Terres, and the material collected there, see Gale (2011), Hess (1960, 1966, 2013a); Gale, in preparation). The specimens of *B. subteres* are from the Chalch Quarry, Holderbank, northern Switzerland (Hess and Spichiger 2001). Taphonomy and palaeoecology of the various *Balanocrinus* occurrences are discussed and compared with those of *Chariocrinus*, a similarly gracile isocrinid from mud- or marlstones.

***Balanocrinus* species based on columnals and parts of the crown**

Balanocrininae ROUX (1981) constitute a subfamily of Isocrinidae GISLÉN (1924), the dominant family of Mesozoic stalked crinoids, see Hess and Messing (2011). The main genus of the subfamily is *Balanocrinus* AGASSIZ in DESOR (1845), with *B. subteres* (MÜNSTER in GOLDFUSS

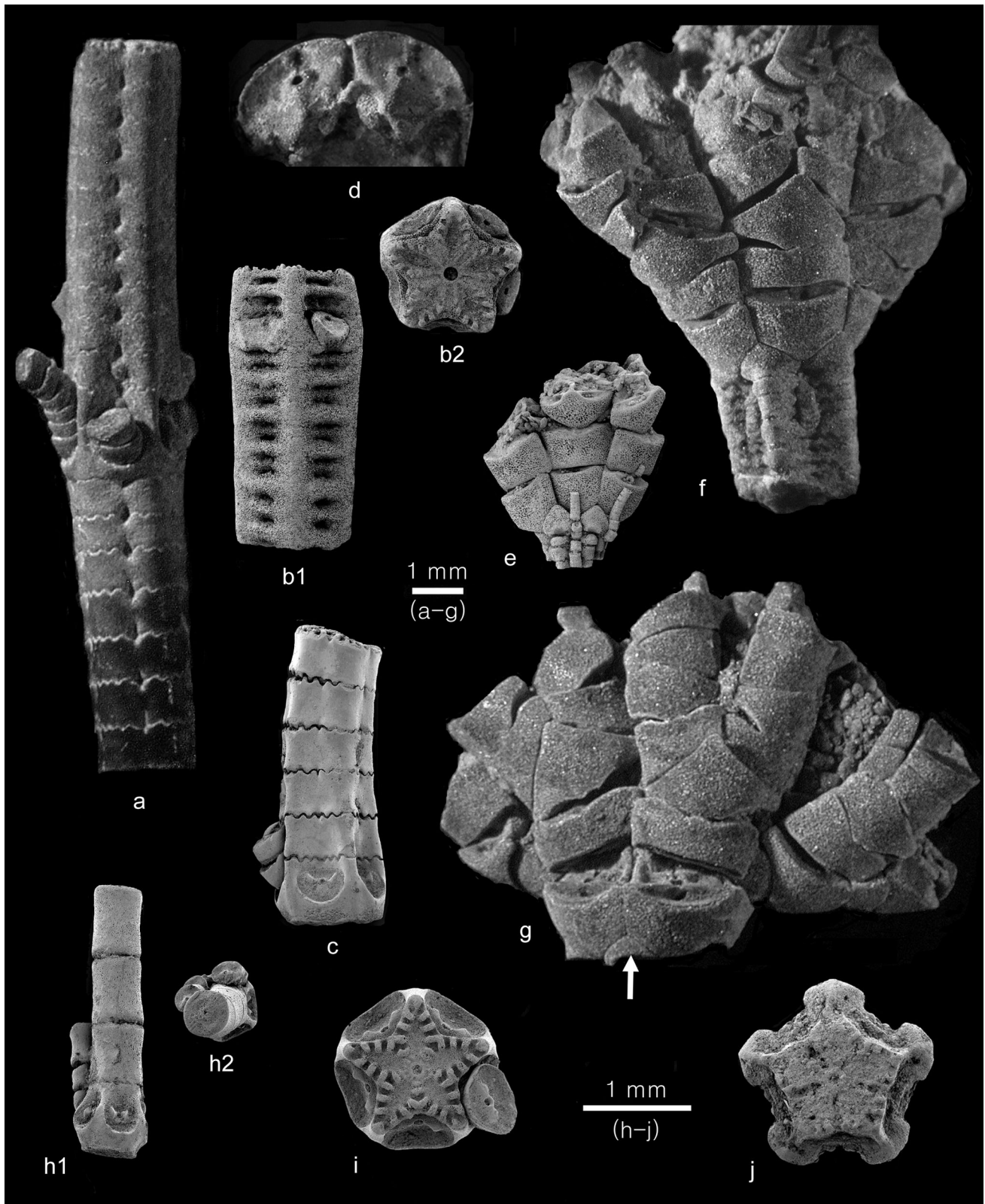
1831, p. 176) as type species. According to Quenstedt (1876, p. 245) Goldfuss' specimens are from Weisser Jura Alpha, Streitberg, and Weisser Jura Gamma, Hohenstaufen. Quenstedt noted the first mass occurrence at the upper limit of the Ornatenton, corresponding to the Lower Oxfordian Cordatum Zone, from e.g. Geislingen, and his figured specimens (1876, pl. 99, fig. 26–55) are from the Ornatenton Formation and Weisser Jura Alpha (Early Oxfordian) and Gamma (Lacunosamergel Formation, Platynota Zone, Lower Kimmeridgian), respectively. Among the localities are Lochen in the Swabian Alb and Birmensdorf (=Birmenstorf) in northern Switzerland, an area of sponge facies extending from the Middle Oxfordian Birmenstorf Member (Transversarium Zone) to the Lochen Formation of southern Germany (Weisser Jura Alpha and beyond to Gamma, Lower Kimmeridgian). The lower part of the Lochen Formation is interbedded with the Impressamergel Formation corresponding to the Effingen Member of Switzerland and eastern France (Couches d'Effingen, Enay 1966). The range of *B. subteres* is not clear although the occurrence in the Birmenstorf Member and the marly Impressamergel Formation seems certain; and this means that the species is not restricted to the sponge facies. The species is common in Middle Oxfordian marlstones (Transversarium Zone, "Marnes de Latrency") of the Département Haute-Marne (Courville and Villier 2003, pl. 1, fig. 10–11).

Numerous *Balanocrinus* species have been described from mudstones to hardgrounds of Early Jurassic (Sinemurian) to Lower Cretaceous (Albian) age; Triassic and Upper Cretaceous occurrences are questionable. Pluricolumnals (stem fragments) and columnals of this genus have been known for a long time and were described in the important monographs (de Loriol 1877–1879, 1882–1889; Quenstedt 1876). However, elements of cup and arms were described only more recently (Sieverts-Doreck 1967; Hess 1975, 2006; Simms 1989a; Hess and Gale 2010). More or less intact specimens are restricted to Pliensbachian (Simms 1989a, 1999; Thuy et al. 2011) and Kimmeridgian localities (Bourseau et al. 1998). Assignment of the elements from Savigna to a named species has proved difficult although there is no lack in taxa. In the *Paléontologie française* 23 species of *Balanocrinus* were described, 13 of which from the Oxfordian (de Loriol 1882–1889, p. 381), but all are based on columnals only. A large number of finds of cylindrical columnals and pluricolumnals from Lower to Upper Jurassic strata were ascribed to *Balanocrinus subteres* (see Biese 1935–1937). Salamon (2009) described the species from the Valanginian of Poland and discussed a Bajocian occurrence. It seems inconceivable that a single-stalked crinoid species has such a wide horizontal and vertical distribution. The smooth, predominantly cylindrical columns of *Balanocrinus* species may appear to

lack distinctive characters suitable for specific classification. That this is not generally the case is demonstrated in the parallel paper (Hess 2013a), in which additional information from parts of the crown helps to properly define nominal species. Hess (2013a) compares the Middle Oxfordian material from Savigna with ossicles of *B. pentagonalis* from the Lower Oxfordian of Les Rouges-Terres and with columnals of *B. subteres* from the Middle Oxfordian Birmenstorf Member of Holderbank, but also with cup plates from the Impressamergel Formation of the Swabian Alb described by Sieverts-Doreck (1967). Intact specimens of *Balanocrinus gracilis* (CHARLESWORTH) from the Pliensbachian of Sedan (Thuy et al. 2011) complement the comparison with *B. brachiospina* HESS and are described in the following.

***Balanocrinus gracilis* (CHARLESWORTH), the most completely preserved species of the genus (Fig. 2)**

The remains of *B. gracilis* from Sedan are partly pyritised and include parts of the column, partial crowns, arm fragments and isolated ossicles. Some of the arm fragments are deformed by a myzostome (Hess 2010). Thuy et al. (2011, fig. 3a) figured a specimen with proximal column, cup and base of arms; the basals are barely in contact. These authors also figured an isolated cup that has a pentalobate columnal on its lower (aboral) side (loc. cit., fig. 3b–c). Relative to the radials the basals diminish in size with age of the animal (Fig. 2e–g). The juvenile specimen (Fig. 2e) also shows that radials and primibrachials are relatively higher than in adult individuals; such allometric growth in width with respect to height is common with brachials of isocrinids, and indeed typical with most crinoids (Ausich and Wood 2012). The primibrachials are joined by an embayed synarthry (Fig. 2f, g, d). The first pinnule is on the second secundibrachial (Fig. 2g). Secundibrachials 3 and 4 are articulated by synostosis (Fig. 2f, arm at left). The first nodal with cirri is the fourth columnal below the cup (Fig. 2f). The proximal column shows distinct, narrow grooves (fossulae) between the columnals, expressed as radial pores on the latera (Fig. 2b). As already noted by Carpenter (1884, p. 18) these "interarticular pores" do not reach the lumen, and their role is unclear. Latera of columnals from this part of the column are inflated between the margins. More distally, the radial pores diminish in size, and the column becomes pentalobate (Fig. 2c) to cylindrical (Fig. 2a). The proximal facet of nodals is pentastellate (Fig. 2i); a nodal from the proximal part of the column has interradian extensions, and the proximal facet is nearly pentagonal and has fossulae (Fig. 2j). A postlarval pluricolumnal of four with a nodal is figured in Fig. 2h. It is rounded pentagonal to circular in



section, the nodal is larger than the internodals and has cirrus sockets with a distinct aboral lip, but a cupule is hardly developed. The proximal (upper) facet of the

pluricolumnal is synarthrial. The postlarval elements are similar to the corresponding elements of *B. brachiospina* described in the following; and they present another

◀**Fig. 2** *Balanocrinus gracilis* (CHARLESWORTH), Early Pliensbachian, Sedan. **a** Pluricolumnal with nodal and cirri, showing the transition of proxistele to mesistele, grooves and radial pores diminish towards the distal (lower) end; M11348. **b** Proximal pluricolumnal with nodal (second element from top), M11350; **b1** lateral, **b2** proximal facet of supranodal at top; note fossulae on the facet leading to the radial pores. **c** Subpentalobate pluricolumnal of 6 with nodal, M11351. **d** Part of upper facet of cup showing synarthrial distal facets of two first primibrachials, M11347. **e** Juvenile cup and proximal brachials with base of column, M11345. **f** Proximal column and base of crown, the first nodal with cirri is in the position of the fourth columnal, note distal synostiosal facet of third secundibrachial at upper left; M11346. **g** Basal part of crown with tegmen at right and first pinnule on second secundibrachial, arrow indicates basal, M11349. **h** Postlarval, prejuvenile pluricolumnal with nodal and cirrus, M11352; **h1** lateral, **h2** upper synarthrial facet. **i** Distal, stellate facet of juvenile nodal with cirral, M11353. **j** Distal facet of juvenile nodal with fossulae and interrachial bulges, M11354

example of columnal width growing with positive allometry with respect to height. In contrast to *B. brachiospina*, *B. gracilis* has lower basals, an embayed synarthry between the two primibrachials, and aborally rounded brachials throughout the arm. Fossulae and radial pores are more common in the proximal column, and such columnals have an inflated latus, but are all of similar height.

Columnal ontogeny in *Balanocrinus brachiospina* HESS (Fig. 3)

Ontogenetic changes in isocrinids are particularly obvious in columnals. Prejuvenile columnals are high and slender, and they may have a median ring of irregular granules or knobs on the latus (Fig. 3d1); the facets are synarthrial and have a mostly weak ridge with crenulae at both ends (Fig. 3f, h, i). Short marginal crenulae are seen in a somewhat later, presumably juvenile phase (Fig. 3d2). The material from Savigna includes one pluricolumnal of 5 (Fig. 3c), three pluricolumnals of 3 (Fig. 3a), 10 pluricolumnals of 2 (Fig. 3b, d) and 65 single prejuvenile and early juvenile columnals of less than 1 mm diameter (Fig. 3e–i). Among them are both internodals and nodals; and the internodals have one or both articular facets synarthrial. The two smallest internodals without synarthrial facet have a diameter of 0.4 mm, comparable to internodals with synarthrial facet. The shape is commonly angular-oval at one end (Fig. 3h), but some columnals, both nodals and internodals, are pentagonal with sharp edges (Fig. 3e–f, i). Nodals are mostly higher than internodals, and their distal facet is synostiosal, as in adult specimens.

Synarthrial facets of small columnals of *Isocrinus* and *Balanocrinus* species have previously been recorded:

Rasmussen 1961, pl. 10, fig. 5, *Neocrinus tenellus* (EICHWALD); Jäger 1981, pl. 1, fig. 1–2, *Isocrinus annulatus* (ROEMER); and pl. 7, fig. 1–3, *Isocrinus acutus* JÄGER; Jäger 1985, pl. 11, fig. 1–3, *Balanocrinus subsulcatus* (MÜNSTER in GOLDFUSS); Jäger 2010, pl. 3, fig. 1, *Percevalicrinus* sp.; Simms 1989a, pl. 10, fig. 29–30, *Balanocrinus subteroides* (QUENSTEDT); Simms, 1989b, Fig. 2d–e, *Balanocrinus subteroides* and *B. quiaiosensis* LORIOI. Another example is a nearly circular internodal of *Balanocrinus smithi* HESS from the Albian with a diameter of 1 mm (Hess & Gale 2010, fig. 6i–j). The material from Savigna does not include any elliptical columnal with a crenulated fulcral ridge and devoid of marginal crenulae, such as figured by Simms (1989b, fig. 2d). Simms' fig. 2e shows a columnal facet with two culmina at one end of the transverse ridge and four culmina at the other end; similar to the present material (Fig. 3f, h–i). Very young individuals of the extant *Isocrinus decorus* (THOMSON) have elliptical columnal facets with some marginal crenulae at the poles of the fulcral ridge (Clark 1908, fig. 4), and this demonstrates that columnal ontogeny progressed similarly in extant and fossil isocrinids. A synarthrial articulation is not developed between nodal and infranodal at any growth stage.

Synarthrial columnal facets are common to sessile isocrinids and free-living comatulids in the prejuvenile, pentacrinoid stage. Columnal skeletal structures in the early stages of development are also similar in isocrinids and comatulids, and those of the comatulid *Antedon bifida* as described by Lahaye and Jangoux (1987) may be used for a comparison with the present material. Swimming larvae of *A. bifida* are short-lived and become attached after a few days by a disc, transforming into cystideans. After about a week they progress to the pentacrinoid stage. This lasts about 15 weeks; and a larger, pentagonal proximale with a first set of cirri develops towards the end of this stage, after which the young comatulid detaches from the column. Pentacrinoid columnals differ to some extent according to their position. They are shortest below the cup where new columnals are formed. These have a median ring (see Lahaye and Jangoux 1987, fig. 12–13), which eventually disappears in older columnals towards the base of the column (loc. cit., fig. 12, 14). Such a ring-like structure is observed in the specimen in Fig. 3d, but it lacks in others. The ridge of the synarthrial articulations at opposite facets of a columnal is offset by about 60° (Lahaye and Jangoux 1987, fig. 21), and this is also seen in the columnals of *B. brachiospina*. In comparison with the prejuvenile, pentacrinoid columns described in *A. bifida*, the majority of present columnals may have belonged to a postpentacrinoid, early juvenile stage.

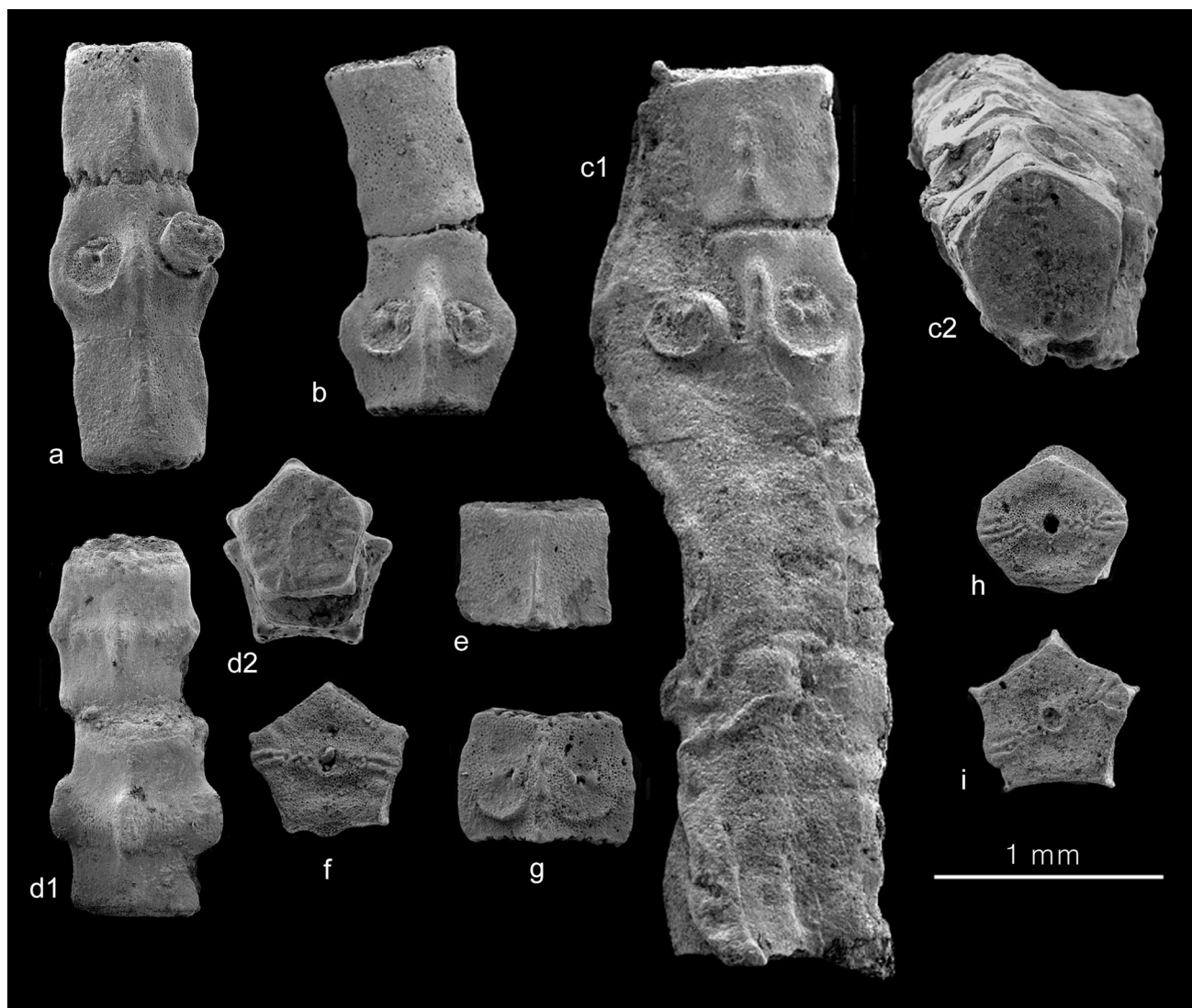


Fig. 3 *Balanocrinus brachiospina* HESS, early Late Oxfordian, Savigna 2b (see Hess 2013a). Postlarval (pentacrinoid stage), prejuvenile columnals and pluricolumnals. **a** Pluricolumnal of 3, nodal with cirral, connected by synostosis to infranodal below and by symplexy to supranodal above, upper and lower facets synarthrial, M11232. **b** Pluricolumnal of 2 with nodal and supranodal, upper facet synarthrial, M11233. **c** Pluricolumnal of 5 with nodal and cirral, with serpulid epizoan partly overgrown by bryozoan “*Berenicea*”, M11234; **c1** lateral, **c2** upper facet synarthrial and slightly angular.

d Pluricolumnal of 2 pentagonal internodals with ornamented latera, M11235; **d1** lateral, **d2** upper, synarthrial facet. **e** Lateral view of internodal, upper facet symplectial, M11236. **f** Synarthrial facet of pentagonal internodal, M11237. **g** Lateral view of nodal, proximal (upper) facet symplectial with marginal crenulae, M11238. **h** Synarthrial facet of somewhat elliptical internodal, M11239. **i** Synarthrial facet of pentagonal internodal with sharp angles, other facet synostiosial, M11240

Reconstruction of *Balanocrinus brachiospina* HESS (Fig. 4)

The material from Savigna 2b, the richest section of the site (Gale 2011; Hess 2013a), includes 61 basals, one basal pair and seven basal circlets, suggesting 20 individuals. In addition are 228 radials (corresponding to 46 individuals), 168 first primibrachials with synostiosial distal facet (corresponding to 34 individuals), and 187 second primibrachials with synostiosial proximal facet (corresponding to 37 individuals). The numbers do not match exactly, but the

easily recognised and robust radials indicate a total number of 46 individuals. Secondary axillaries with proximal muscular facet number 743, and this suggests that the arms branched not only once at the second primibrachial, but rather once again. The proximal-most secundibrachials were in lateral contact and are aborally rounded. Many proximal secundibrachials are skew, suggesting that they were crowded in the proximal part of the crown. Progressing distally, the secundibrachials carry an aboral crest that develops into a thorn. The majority of the secundibrachials carry a thorn directed distally.

Secundibrachials number some ten thousand, and this may be compared with intact specimens of the Bajocian *Chariocrinus andreae* Hess of similar size. In adult individuals from different locations, the arms branch two or three times beyond the second primibrachial (Hess 1955, pl. 18, fig. 1; Hess 1972, fig. 22), with somewhat variable brachitaxes of 13–20 secundibrachials; the number of tertibrachials and tetrabrachials is 14–17; and the final, unbranched part may have as many as 75 brachials, especially in specimens with only two branchings, but usually less. Assuming 15 secundi- and tertibrachials each as well as 20 tetrabrachials in the final, unbranched part the numbers add to 1,250 brachials per individual. With such arm branching, the estimated 46 individuals of *B. brachiospina* from Savigna 2b would have produced 57,500 brachials, a reasonable number. *Chariocrinus andreae* is thus an acceptable model for *B. brachiospina*.

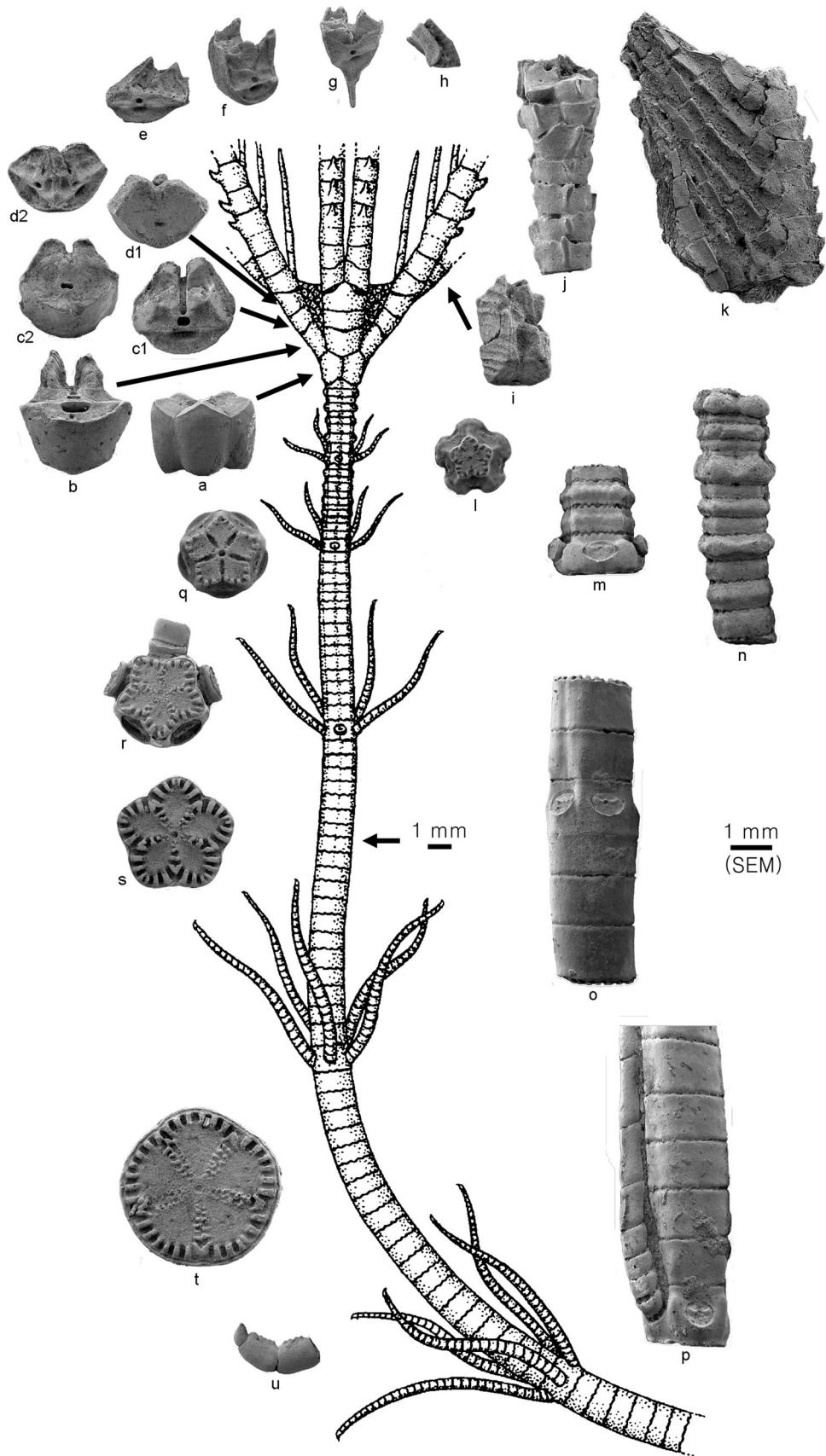
No complete noditaxis is present in the material. The longest pluricolumnal has 13 internodals, so that noditaxes must have been at least 14. Proximal columnals are generally lower and stellate to pentalobate, and they alternate in thickness. Nodals are more crowded below the cup than further distally (see Hess 2013a, fig. 6i). Columnals from the median part of the column, but especially from the distal part, are circular. The column is similar to that of a juvenile specimen of the living *Neocrinus decorus* (THOMSON) that has been used for projecting the various ossicles of *B. brachiospina* in Fig. 4. The number of columnals and pluricolumnals (Hess 2013a) also seems compatible with *C. andreae* as a model crinoid.

Taphonomy and palaeoecology of *Balanocrinus* occurrences

Living stalked crinoids preferentially attach to hard or firm bottoms (see Hess et al. 1999). In contrast, members of the extinct genus *Balanocrinus* have successfully colonised muddy bottoms. The following examples of intact specimens from mudstone successions may help to elucidate the conditions of living. Simms (1989a, 1999) described specimens of *Balanocrinus gracilis* (CHARLESWORTH) from Lower Jurassic mudstones of England. The same species occurs in a Pliensbachian echinoderm Lagerstätte in the French Ardennes, where it is accompanied by articulated remains of asteroids and ophiuroids and also holothurian sclerites (Thuy et al. 2011). The echinoderms almost exclusively occur in shelly beds with the bivalve *Modiolus* as the dominant component, and the locally limited shelly layers helped to support a rich assemblage of echinoderms. These were disrupted by major, recurrent obrution events. The formation of the *Modiolus* beds appears to have been triggered by reduced sediment supply and improved water

conditions. Sieverts-Doreck (1981) described an occurrence of *Balanocrinus subteroides* (QUENSTEDT) from the Pliensbachian of Bielefeld. A crown with attached column, pluricolumnals and pluricirrals lies on the surface of a limestone bed from the clay pit. The interior of the bed also contains remains of the crinoid. The author did not discuss the palaeoecology of the find, but the well-preserved remains are of interest for comparison with the Savigna material. Intact specimens of the Kimmeridgian *Balanocrinus maritimus* BOURSEAU et al. (1998) were found within beds of marly limestones together with other echinoderms, such as the echinoid *Disaster*. The authors concluded that the crinoids lived at a water depth that may have reached several hundred metres and were rapidly killed and buried by pulses of muddy sediment. In other beds of this locality the crinoids are more or less disarticulated, similar to the Savigna occurrence.

The small isocrinid *Chariocrinus* HESS is another genus with occurrences of intact specimens in mudstones. Size and overall morphology are similar to *Balanocrinus brachiospina*, although internodes are shorter (Hess and Messing 2011). Sieverts-Doreck (1983) described crowns of *Chariocrinus wuerttembergicus* (OPPEL) from the Aalenian Opalinuston of Esslingen, a mudstone succession. Wetzel and Meyer (2006) discussed an occurrence of the same species from the Opalinuston Formation of northern Switzerland. Their detailed analysis shows that the animals lived on a temporary swell of the muddy seafloor, close to wave base, and were killed by a storm-induced suspension of mud. This autochthonous occurrence proves that the crinoids were able to live on a muddy bottom, given an oxygenated palaeoenvironment and sufficient food supply. Autochthonous occurrences of articulated, dense colonies of *Chariocrinus andreae* (DESOR) from the subtidal base of the Middle Jurassic Hauptrogenstein Formation support such a lifestyle (Meyer 1989; Hess 1999; Thuy and Meyer 2013). At certain localities thin layers of mudstone include intact specimens, although thicker lenses of several generations forming a crinoidal limestone resting on marl are more common. Such colonies must have existed for some time, with new generations of animals growing on the debris of their ancestors. Intact specimens in thin lenses may have been killed by a suspension of mud, similar to the *C. wuerttembergicus* occurrence. In longer-lasting colonies the animals may have met their death by unfavourable environmental conditions, but death through toxins from red tides has also been advocated (Meyer 1989). Subsequent preservation was guaranteed by a sediment cover from advancing sand waves (Hess 1999). In contrast to the *Balanocrinus* species, *C. andreae* has short noditaxes of commonly less than ten columnals, and more densely spaced cirri would have been favourable to life in a shallow environment.



◀**Fig. 4** Position of ossicles of *Balanocrinus brachiospina* HESS, early Late Oxfordian of Savigna, on hypothetical isocrinid, redrawn from the figure of a young *Neocrinus decorus* (THOMSON) in Carpenter (1884, pl. 35, fig. 2). The extant specimen has a similar column, although with less crowded nodals proximally, but differs by small basals and high, symmetric proximal secundibrachials not in lateral contact. The projected figures of *B. brachiospina* ossicles are copied at half the scale from Hess (2013a), Fig. 5 (cup plates and primibrachials), 6–7 (columnals), and 8–9 (brachials and arm fragments). **a** Basal cirlet, M11343. **b** Radial, aboral-distal facet, M11253. **c** First primibrachial, M11251; **c1** proximal facet, **c2** distal facet. **d** Second primibrachial, M11247; **d1** proximal facet, **d2** distal facet. **e** Proximal facet of skew, hyposynostosal secundibrachial from proximal part of arm, M11292. **f** Distal facet of skew, aborally rounded secundibrachial from proximal part of arm, M11290. **g** Distal facet of thorned secundibrachial from median to distal part of arm, M11294. **h** Oblique adoral view of pinnular, M11305. **i** Oblique adoral view of two proximal brachials, straight sides with grooves indicate lateral contact, M11298. **j** Arm fragment of secundibrachials with axillary, distal facets of tertibrachial 2 are synostosal, M11301. **k** Part of median to distal arm with pinnules, M11369. **l** Proximal facet of pentalobate nodal, M11259. **m** Pluricolumnal with three internodals (two with crest) and nodal with cirrals, M11263. **n** Proximal pluricolumnal with three nodals, M11266. **o** Pluricolumnal with nodal, M11277. **p** Pluricolumnal with cirrus, M11281. **q** Proximal facet of nodal with fossulae, M11270. **r** Proximal facet of nodal with cirrals, M11267. **s** Facet of subpentilobate internodal, M11271. **t** Facet of large circular internodal, M11275. **u** Terminal cirrus, M11285

Most mass occurrences of *Balanocrinus* and *Chariocrinus* species are monospecific, and the animals lived in dense aggregations. At Savigna, some remains of an *Isocrinus* species occur rarely, while comatulids are exceptional. In contrast, ossicles of ophiuroids and, to a lesser degree, of asteroids are common. Early Oxfordian occurrences with *Balanocrinus pentagonalis*, e.g. at Les Rouges-Terres and Andelot-Morval, are similar in overall faunal composition. It may be concluded that muddy bottoms offered good conditions for dense stands of small crinoids. Such soft bottoms were equally suitable for a diverse fauna of ophiuroids and asteroids, but also holothurians and small echinoids (Hess 1965, 1966; Gale 2011; Thuy et al. 2011). At the Early Jurassic Sedan locality, shelly beds within the clay succession of otherwise low fossil content are thought to represent phases of more favourable bottom water conditions and/or reduced sedimentation rate (Thuy et al. 2011). Such environments offered opportunities for small species of *Balanocrinus* and *Chariocrinus*. In addition to muddy bottoms, *Balanocrinus* species also settled on hardgrounds of the Upper Jurassic sponge facies. The best-known example is *B. subteres*, the largest species of the genus. The fauna of the Birmenstorf Member of the Chalch Quarry with *B. subteres*, but also the similarly sized *Isocrinus cingulatus* (MÜNSTER in GOLDFUSS) and numerous rather large cyrtocrinids, lived on a swell at a water depth near storm wave base (Hess and Spichiger 2001). Moderate sediment deposition and extensive bioturbation prevented preservation of more or less intact crinoids, so that the find

of a pluricolumnal with an intact noditaxis (Hess 2013a, fig. 3a) is exceptional.

At Savigna, all remains of *Balanocrinus* were picked from washings of the mudstone. In addition to pluricolumnals and pluricirrals, some basal cirlets and a number of arm fragments and clusters of small ossicles (brachials and pinnulars) were isolated, but no slab of marlstone with attached, more or less intact crinoid remains was found. The material includes all ossicle types and all sizes, without any indication of grading or abrasion due to transport. Because of bioturbation it cannot be decided if the occurrence is autochthonous or parautochthonous. The clay grade of the sediment, total bioturbation and the lack of coarser debris suggest deposition below storm wave base (50 m), but the abundance of suspension-feeding crinoids and other fossils would support a somewhat shallower water depth of 40–60 m (Gale 2011). The asteroid fauna of Savigna is dominated by small taxa whose present relatives are characteristically found in the deep sea (Gale 2011). Asteroids from other localities of muddy shelf environments are also of small size. This is in line with the generally small size of *Balanocrinus*, the dominant crinoid in such soft-bottom environments. However, crinoids need a current to feed with their filtration fan, and they could not have persisted in quiet water. This is in favour of a current-induced parautochthonous deposit.

The crinoid fauna of Andelot-Morval is unusual in comparison with other Oxfordian mudstone occurrences. *Balanocrinus brachiospina* is rare in comparison with Savigna. The presence of the spectacular, large comatulid *Archaeometra scrobiculata* (GOLDFUSS) and the cyrtocrinid *Tetracrinus galei* HESS (2013a) is suggestive of the hard-bottom faunas of Jurassic sponge facies. These two significant elements of the fauna indicate the presence of harder bottoms within the mudstone sequence.

Conclusions

Many fossil isocrinid species are known from parts of the column and from a few specimens only. They have been named despite only small morphological differences and unknown position along the column. The result is a plethora of names and a record of similar-looking forms in geological formations of widely different age. As discussed herein and in the parallel paper (Hess 2013a), this unsatisfactory situation may be resolved through additional information from ossicles of the crown and columnals of different ontogenetic stages obtained from washed sediment samples.

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