

An Upper Jurassic Boreal echinoderm Lagerstätte from Janusfjellet, central Spitsbergen

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Rousseau, J. & Nakrem, H.A.: An Upper Jurassic Boreal echinoderm Lagerstätte from Janusfjellet, central Spitsbergen. *Norwegian Journal of Geology*, vol. 92, pp 133-161. Trondheim 2012. ISSN 029-196X.

A well-preserved, low-diversity assemblage of fossil echinoderms from the early Middle Volgian in the Slottsmøya Member (Agardhfjellet Formation) has been discovered at Janusfjellet, Sassenfjorden area, central Spitsbergen. Five species are recognised: the isocrinid *Chariocrinus* sp., the pedinoid *Hemipedina* sp., the forcipulate asteroid Asteriidae sp., the ophiacanthid Ophiacanthidae sp. and the ophiurid Ophiurinae sp. A depositional environment model reconciling autecologic, taphonomic and sedimentary evidence is presented. The Janusfjellet Lagerstätte was formed by a single, rapid burial event during a storm, entombing together autochthonous asteroids and ophiurids, and allochthonous crinoids and echinoids on a dysoxic muddy sea-floor. Comparable echinoderm material from the Boreal Late Jurassic-Early Cretaceous is scarce, outdated and usually poorly described and illustrated. The scarcity of reported occurrences probably results from a collector bias for rare complete specimens and does not reflect the true echinoderm composition of Mesozoic high-latitude communities.

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Introduction

Echinoderm ossicles have a high preservation potential as fossils. Their skeletons, however, disarticulate easily and rapidly after death, so they are relatively rare as articulated specimens. Because of the fragility of the echinoderm skeletons, preservation of complete specimens requires special conditions. Burial has to be rapid and effective enough to prevent subsequent disruption by currents or scavengers (Donovan 1991). Echinoderms are particularly sensitive to smothering by sediments, because this effectively blocks their water-vascular system. Following Seilacher (1970), the results of such events have been referred to as “obtrusion deposits”. Tempestites and turbidites have commonly been suggested as physical mechanisms for the creation of exceptionally well-preserved assemblages known as Lagerstätten. Late Jurassic examples in Europe include the Solnhofen Plattenkalk of Bavaria (Hess 1999) and the French lithographic limestones of Cerin (Breton et al. 1994) and Canjuers (Roman et al. 1991, 1993, 1994). However, very few echinoderm fossils have until now been reported from high-latitude deposits.

Well-preserved echinoderm fossils were discovered in the Upper Jurassic of central Spitsbergen, Arctic Norway, during fieldwork expeditions of the Spitsbergen Jurassic Research Group (Natural History Museum University of Oslo and University of Alaska, Fairbanks) between 2008 and 2010. The material contains one crinoid and one echinoid species identifiable to genus level, as well as new asteroids and ophiuroid species which are currently being described by, respectively, Rousseau & Gale (in prep.) and Rousseau

& Thuy (in prep.). These taxa are here referred to in open nomenclature. Using this exceptional material, the current contribution establishes the first paleoenvironmental interpretation of High-Boreal Mesozoic echinoderms.

The Late Jurassic Arctic

The Late Jurassic marine rocks that nowadays crop out in central Spitsbergen were deposited in a high-latitude, cold water setting (Fig. 1A).

Distinct Boreal (Arctic and northernmost Europe) and Tethyan (southernmost Europe and margins of the former Tethys seaway) marine faunal assemblages have been recognised through the Late Jurassic and Early Cretaceous, with the greatest faunal differentiation between Callovian and Aptian times (Gordon 1974). Changes in the distribution of ammonites and bivalves suggest episodes of faunal migration between the Boreal and Tethyan realms, coupled to the opening and closing of seaways between the north and the south (Zakharov & Rogov 2003, 2004). Difficulties in correlation of the Northwest European region (Tethyan) with both tropical and polar regions have resulted in the widespread use of regional stratigraphy for the uppermost Jurassic and lowermost Cretaceous (Fig. 1B; Ogg 2005). The latest Jurassic Volgian stage, established in western Russia by Nikitin in 1881, has since been extensively used and defended—after its withdrawal from the International Stratigraphic Scale in 1991—by Russians and Boreal region workers (see Zakharov 2003).

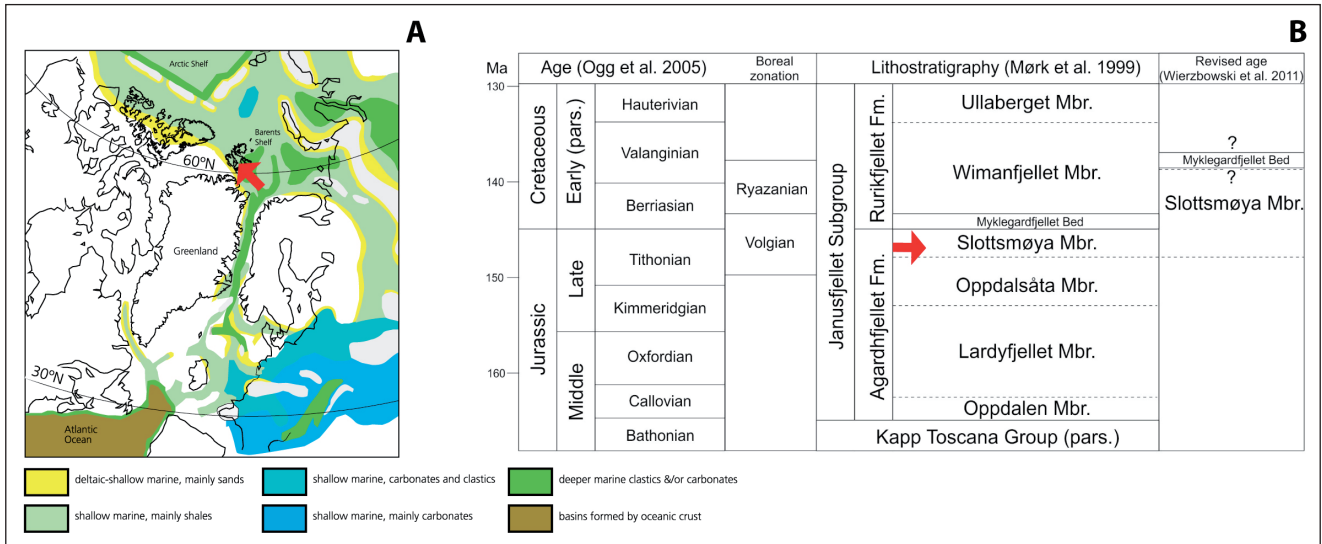


Figure 1. Palaeogeographic and stratigraphic setting. A. Paleogeographic map of the European North Atlantic and Boreal regions in the Late Jurassic. The position of Svalbard is indicated by an arrow. Modified from Torsvik et al. (2002: 27). B. Chrono- and lithostratigraphic correlation for the Late Jurassic – earliest Cretaceous interval of central Spistbergen. An arrow indicates the stratigraphic level of the Janusfjellet Lagerstätte.

High-Boreal water temperatures of 5-10°C (mean 8°C) have been proposed for the Tithonian–Valanginian by Ditchfield (1997) from a belemnite oxygen isotope study in Kong Karls Land (East Svalbard), whilst calculated water paleotemperatures are generally higher in Europe (Tithonian range = 13.9 to 19.8°C) (see Gröcke et al. 2003 table 4 and fig. 10 for a review). Seawater cooling in the latest Jurassic, initiated in the Early Tithonian and reaching a minimum temperature of 11°C (Scotland data) in the Mid Tithonian, has also been suggested from recent stable isotopes and Mg/Ca ratio data (Nunn & Price 2010).

Geological setting

The study area (Fig. 2), in central Spitsbergen, is stratigraphically situated in the well-known Agardhfjellet Formation (Fig. 1B), the lowermost unit of the Upper Jurassic–Lower Cretaceous Janusfjellet Subgroup (Dypvik et al. 1991a) of the Middle Jurassic–Lower Cretaceous Adventdalen Group (Parker 1967). The black shales of the Agardhfjellet Formation were deposited in a marine open shelf environment with periods of restricted water circulation (Mørk et al. 1999).

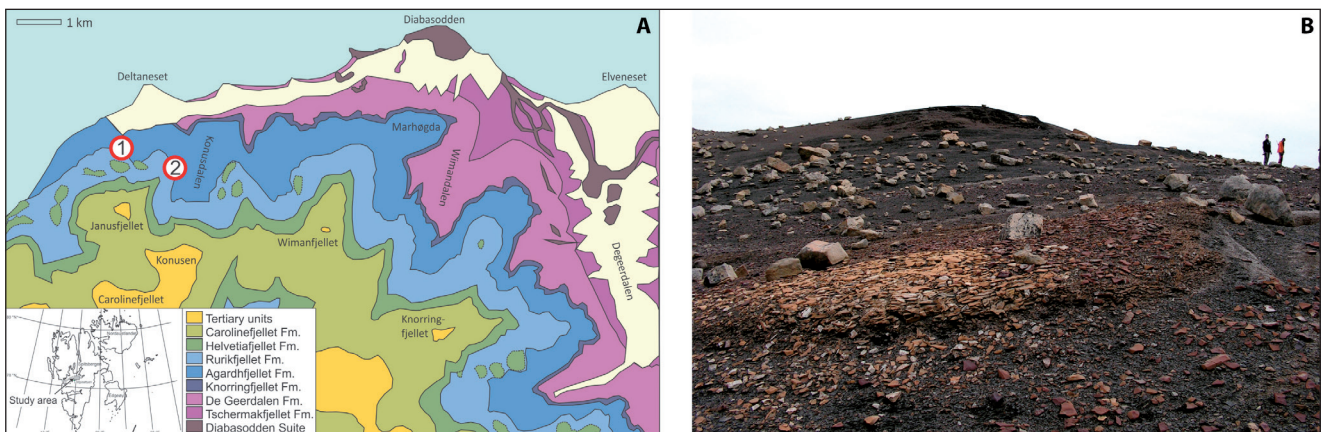


Figure 2. Field localities in Sassendfjorden, central Spitsbergen. A. Geological map of the study area with the different collection sites. Redrawn and adapted from Dallmann et al. (2001). 1 – Janusfjellet (N78°20'35.4", E15°49'85.2"), 2 – Konusdalen (N78°19'97.1", E15°52'15.5"). The bottom left corner map shows the position of the study area on Spitsbergen. B. The Janusfjellet site showing the layer of siderite concretion eroding at surface level.

Fossil echinoderms were found within the Slottsmøya Member (Fig. 1B), the uppermost unit of the Agardhfjellet Formation. This member is a succession of dark-grey to black silty mudstone weathering to paper shales and containing red to yellowish siderite concretions (Dypvik et al. 1991a; Hammer et al. 2011; Collignon & Hammer 2012). Sedimentological analyses suggest that it was deposited in an open marine environment with limited oxygenation (Dypvik 1991; Nagy et al. 2009). The local occurrence of sideritic lenses are interpreted as storm deposits below storm wave base on a muddy, poorly oxygenated sea bottom (Dypvik et al. 1991a). The Slottsmøya Member has been assigned a Volgian to Ryazanian age based on ammonites (Parker 1967; Birkenmajer et al. 1982; Ershova 1983; Wierzbowski et al. 2011), foraminifera (Nagy & Basov 1998) and palynomorph (Løfaldli & Thusu 1977; Bjærke 1978) biostratigraphy.

Apart from echinoderms, the Slottsmøya Member has yielded a considerable amount of micro- and macrofossils including foraminifera, bivalves, brachiopods, scaphopods, gastropods, belemnites, ammonites, and large skeletons of marine reptiles, both short- and long-necked plesiosaurs, and ichthyosaurs (see articles within this volume). Hydrocarbon seep carbonate bodies have also been found in the area (Hammer et al. 2011).

Material collection

The material for this study was collected during the paleontological expeditions of the Spitsbergen Jurassic Research Group to the Sassenfjorden area between 2008 and 2010. The material is deposited in the palaeontological collections of the Natural History Museum in Oslo (PMO). More than 120 rock samples have been collected from an exposed horizon of sideritic concretion lenses (Fig. 2B) naturally fractured by freezing and thawing. The horizon was intensively sampled at Janusfjellet (Janus mountain, Fig. 2A, site 1). Echinoderm fossils were also collected from

similar concretions found at the same stratigraphic level in the neighbouring Konusdalen (Konus valley, Fig. 2A, site 2). 227 specimens belonging to five species were recognised within the 121 processed samples from the Janusfjellet Lagerstätte (Table 1). The fossils were nicely revealed by natural erosion and very little preparation was necessary.

Autecology and palaeoenvironment

Crinoidea

All crinoids present in the Spitsbergen samples seemingly belong to a single species of the isocrinid genus *Chariocrinus* Hess, 1972. Abundant disarticulated columnal, brachial and cirral ossicles, articulated pluricolumnals with attached cirri, articulated arms with attached pinnules, as well as limited cup material have been found at the Janusfjellet and Konusdalen sites (Fig. 3A-E). These have noditaxis 8 to 10 columnals long (Fig. 3B) and low columnals varying in shape from pentagonal to pentalobate (Fig. 3C-E). They can be recognised as *Chariocrinus* by the sharpness of the columnal interradii, the columnal crenulation pattern and the strongly symplexial internodal articulations coupled with the completely synostial (*sensu* Hunter et al. 2011) articulations between the nodals and first internodals.

Recent isocrinids live attached to a hard substrate or anchored to the soft sea-floor with their cup elevated in the water column. They are rheophilic suspension feeders and deploy their arms as a net to catch food particles carried by currents. Arm branching and the presence of pinnules, as seen on the Spitsbergen specimens (Fig. 3A), increase the density of this filtration net. Accordingly, *Chariocrinus* sp. is interpreted as a sessile suspension-feeder, anchored to the sea-floor by cirri on the distal portion of the stem. The animals could have aggregated into colonies similar to the *Chariocrinus* “meadows” illustrated by Hess (1999) and Wetzel & Meyer (2006).

Table 1: Occurrence of the different echinoderm taxa in the Janusfjellet Lagerstätte.

Pluricolumnals specimens were at least one noditaxis long, shorter sections of articulated columnals were recorded as present. Arm sections consisted of a series of brachials with articulated cirri. Asterozoans preserving a portion of the disc with at least one articulated arm were counted as specimens. Articulated arm sections not attached to discs were recorded as present.

	Chariocrinus sp.			Hemipedina sp.		Asterozoans sp.	Ophiacanthidae sp.	Ophiurinae sp.	Total number of samples	Total number of specimens
	Pluricolumnals	Disarticulated columnals	Arm sections	Tests	Disarticulated plates					
Recorded presence	32	39	32	20	17	42	3	38	121	
A - Janusfjellet	27	33	29	20	17	42	2	33	110	
B - Konusdalen	5	4	3	0	0	0	1	5	11	
Specimens count	50	n/a	46	9	n/a	50	1	71		227
A - Janusfjellet	47		35	9		50	1	62		204
B - Konusdalen	3		11	0		0	0	9		23
Rel. abundance (%)			26.0	5.1		28.2	0.6	40.1		

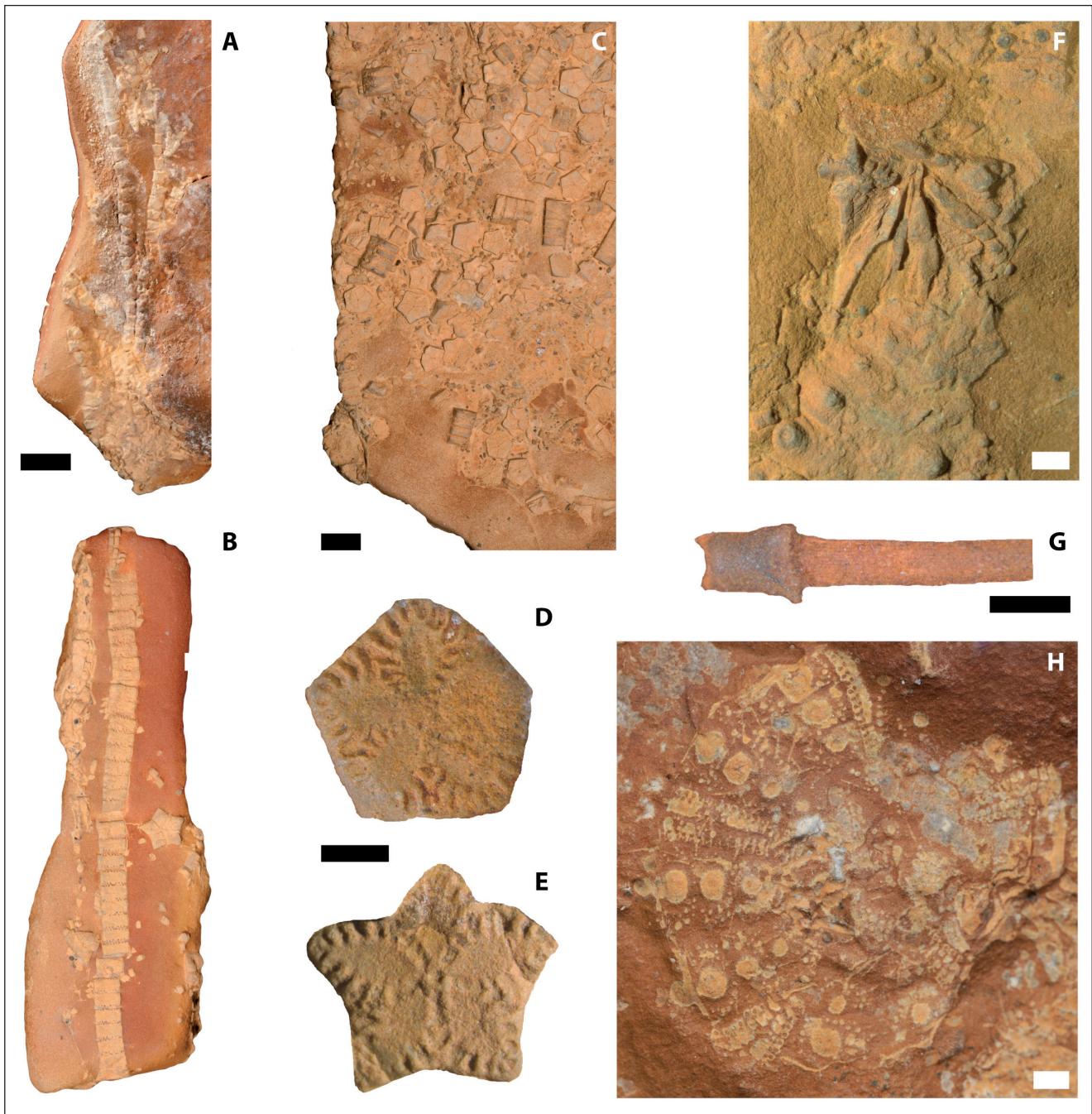


Figure 3. The Janusfjellet Lagerstätte allochthonous fauna. A-E: *Chariocrinus* sp. A. PMO 217.968. Partially articulated arms. B. PMO 217.906. Lateral view of a pluricolumnal with some partial cirri. B is to scale with A. C. PMO 217.903. Accumulation of disarticulated ossicles typical of the Janusfjellet Lagerstätte. D. PMO 217.958. Columnal in distal (aboral) view. E. PMO 217.914. Columnal in distal view. E is to scale with D. F-H: *Hemipedina* sp. F. PMO 217.997. Apical view of the oral region of a partial test. G. PMO 217.905. Details of spine. H. PMO 218.011b. Apical view of test. Scale bars are 1 mm across, except in C where it is 10 mm across.

Stalked crinoids are generally considered to be sessile, but extant isocrinids have been observed to “crawl” — by automising the distal part of their stem and re-attaching farther away on the seafloor (Messing et al. 1988; Baumiller & Messing 2007). Evidence from fossil stem morphology has led to the conclusion that ancient forms could do the same (Rasmussen 1977; Donovan 1990). There are no muscles along isocrinids stems, the ossicles being held together by two types of ligaments (Ausich et al. 1999). Short, intercolumnal

ligaments are found between each adjacent ossicle of the column. Supplementary, long, through-going ligaments run along each internode unit, from the infranodal (proximal) to the nodal (distal). Consequently, each nodal is linked distally to the next internode by only short ligaments across a synostosal articulation. Decay experiments have shown that synostoses are also the preferred plane of post-mortem disarticulation in isocrinids (Baumiller et al. 1993, 1995).

The multielement construction of both the stem and the arms gives flexibility to the crinoid body. Pentaradial columnals, like those of the Spitsbergen material, are better at resisting stress than circular ones because of the increased effective surface for the crenularium (Ausich et al. 1999). The well developed crenularium and symplexial articulations of *Chariocrinus* sp. furthermore indicate that it could withstand some strain.

Since no complete individual has been found, we can only speculate on the total length of the stem of *Chariocrinus* sp. A long stem provides a feeding advantage because the crinoid can elevate its cup higher above the sea bottom. A tiering of the suspension-feeding niche is thus often observed within high-diversity communities (Ausich et al. 1999). In the low-diversity Spitsbergen benthos, growing high above the sea-floor probably did not give a substantial competitive advantage. On a muddy substrate as in Spitsbergen, however, crinoids often develop a long, creeping stem which extends for several centimetres on the mud to provide better attachment (Ausich et al. 1999). Moreover, if a dysoxic bottom layer was present, it could have been essential for the animal to position its cup high above the sediment-water interface, as crinoids do not have any specialised respiratory organs and generally require well-oxygenated waters (e.g., Webster 1975; but see also LaBarbera 1982) to sustain their relatively high metabolic rate (Roman 1994; Ausich & Simms 1999).

Recent stalked crinoids are almost entirely confined to deep-water environments (Bottjer et al. 1988). However, Jurassic isocrinids lived in a wider range of environments and were common everywhere from the outer shelf to shallow waters (Bottjer & Jablonski 1988). Hunter & Underwood (2009) have proposed a paleoenvironmental scheme based on Bathonian crinoids from England and France. Within this analytical model, *Chariocrinus* has been associated with low-energy facies (Hunter & Underwood 2009: fig. 4). Their analysis also suggested a link between the number of cirri and the energy level of the environment, shorter internodes being functionally more successful in higher energy environments where there is a stronger need for attachment and stabilisation. *Chariocrinus* has noditaxis of intermediate length and thus relatively few cirri, a fact consistent with their occurrence in generally quieter and relatively deeper-water facies according to Hunter and Underwood's model. However, these conclusions were questioned by Salamon et al. (2010) who reported multiple contradicting examples from eastern Europe. The genus type species, *Chariocrinus andreae* Desor 1845, is widespread through the Middle Jurassic of Europe and generally occurs in shallow-water ooids shoals (Meyer 1988, 1990). Wetzel & Meyer (2006: 161), moreover, interpreted the life habitat of *Chariocrinus wurtembergicus* Opel 1856, another relatively common Middle Jurassic species in Europe, as an area "elevated slightly above a muddy seafloor, close to wave base, and affected by some turbulence". The interpretation of the water depth of palaeoenvironments is a thorny issue in paleontology. Nevertheless, the functional morphology evidence

presented above points to the occurrence of monospecific colonies of the rheophilic suspension feeder *Chariocrinus* sp. in areas of the Spitsbergen Late Jurassic sea, with aerobic waters and at least some current activity.

Echinoidea

Nine partially complete, flattened, small regular echinoid tests with elements of the coronal system and of the lantern preserved in place have been collected (Fig. 3F-H). Disarticulated plates and spines have also been found within the material. These echinoids are here assigned to the genus *Hemipedina* Wright, 1855 on the basis of its straight ambulacral columns with uniserial pore pairs throughout and ambulacral plates similar in shape and size all reaching the perradial suture. The following functional morphology analysis is based on the work of Smith (1984).

Echinoids are mobile, active animals and the great majority of regular taxa live as epifauna. *Hemipedina* sp. seemingly used its oral spines to travel on the sea-floor as do extant regular echinoids. Its aboral and oral interambulacral tubercles are not strongly differentiated. The tubercles are perforated, which means that the fixation of spines was helped by a central ligament running between the mamelon and the spine base. Areoles are circular and extend symmetrically around the boss (Fig. 3F), so it can be inferred that there was no preferred direction of spine stroke (Smith 1984: 34). The circular shape of the test also indicates that the animal could move in all directions with equal ease.

Hemipedina sp. belongs to the Pedinoida, which were common members of shallow-water faunas in the Mid and Late Jurassic. Contrastingly, *Caenopedina* Agassiz, 1869, the only extant pedinoid genus, is mostly found in deep waters (Anderson 2009). The distribution of echinoids appears to be strongly controlled by lithofacies and most are rare in clay substrates because of the danger of clogging of their water vascular system by fine suspended particles (Ernst & Seibert 1977). Yet, pedinoids and echinothuriids are adapted to inhabit softer bottom environments (Roman 1994), a fact consistent with the association of *Hemipedina* sp. with the fine-grained lithology of the Spitsbergen deposits.

In the North Sea, extant regular echinoids living on dark muddy bottoms have a diet composed of detritus, carcasses and small organisms whereas near-shore, rocky bottom inhabitants are grazers (Schäfer 1972). *Hemipedina* has a weak perignathic girdle (Smith & Kroh 2011) which suggests that the lantern apparatus was used for plucking food particles rather than for mechanically stressful rasping. Moreover, the basal euechinoid crescent-shaped teeth are not particularly strong (Smith 1984: 67). *Hemipedina* sp. is thus assumed to have been a generalist omnivore.

The nature and function of echinoid tube feet can be inferred from the shape and arrangement of the ambulacral pores. *Hemipedina* sp. had uniserial, suckered tube feet (Fig. 3H). The tube feet pores become slightly offset near

the peristome, but there is no food-gathering crowding of the tube feet. The absence of phyllodes on the oral side also indicates, by contraposition, a life in relatively quiet energy conditions. The species has double pores with relatively well-developed partition and rim, but without elongation of the adradial pore. The pores are uniformly rounded over the whole test, which accordingly lacked tube feet specialised for oxygen exchange. Cold water temperature considerably slows down the metabolic rate and oxygen consumption in echinoids. Moreover, colder water has a higher dissolved oxygen saturation level. Extant species living in cold, deep waters often lack specialised respiratory tube feet, whereas they are generally present in warm shallow-water species in reef environments (Smith 1984: 93). Evidently, oxygen acquisition in the cold Spitsbergen muddy sea bottom was not an important problem for the epifaunal *Hemipedina* sp.

Asteroidea

Abundant asteroid remains, both nearly complete specimens and detached but complete arms, with spines and pedicellariae clearly visible in section along the sides of the arms, have been found at Janusfjellet (Fig. 4A-B).

These are all attributed to a single new taxon which is currently being described (Rousseau & Gale, in prep.) and will here be identified as *Asteriidae* sp. This forcipulatid neoasteroid shows elongated arms, a small disc, very broad ambulacral grooves with narrow adambulacrals and weakly developed or absent actinals and strongly quadriserial tube feet. The shape of the basal pieces of pedicellariae (ϵ -shaped in cross-section, see bp in Fig. 4B and 5B) and the morphology of the terminal and oral ossicles are typical of the *Asteriidae*.

Modern members of the *Asteriidae* family are slow-moving, mobile carnivores living epifaunally on the sea bottom. The relatively large body size, small disc size, multi-element arms, quadriserial tube feet and adoral carina present in *Asteriidae* sp. are all features which favour a predatory mode of feeding (Blake 1987, 1990). The wide ambulacral groove, covered with numerous tube feet, provided a strong adhesion force which helped *Asteriidae* sp. to grab and hold its prey. Modern predatory asteroids feed mostly on bivalves, gastropods and other echinoderms, including other asteroids, ophiuroids and echinoids, and are known to form large feeding groups (Spencer & Wright 1966). Thus, *Asteriidae* sp. lived gregariously as an epifauna on the Spitsbergen muddy sea-floor and hunted for bivalve, gastropod and echinoderm preys.

Ophiuroidea

Two species of ophiuroids have been found in the Janusfjellet Lagerstätte (Fig. 4C-F). Specimens of the most common species, represented by more than 70 partial articulated discs (Fig. 4E-F) and a large number of arm fragments, have often been found clustered together in the Spitsbergen samples. These specimens can be unequivocally assigned to *Ophiurinae* Lyman, 1865 by the presence of an arm comb

(Fig. 4F) and by the superficial nature of the second tentacle pores. This new ophiurid species is here referred to as *Ophiurinae* sp. and will be described in a later publication (Rousseau & Thuy, in prep.). The second species is much more rare and has been recognised from one relatively complete articulated disc (Fig. 4C) as well as three arm fragments. These can be confidently placed within the *Ophiacanthidae* Perrier, 1891 on the basis of their long, erected arm spines and of the noded aspect of the arms (Fig. 4D), combined with the presence of disc spines, ear-shaped arm spine articulations and oral plates without lateral wings. It is currently being described (Rousseau & Thuy, in prep.) and will here be referred to as *Ophiacanthidae* sp.

Both species are moderately large, with mean disc diameters around 15 mm, and are interpreted as epifaunal surface dwellers. Ophiuroids inhabit all types of sedimentary environments and all depths, but prefer low-energy waters with a low sedimentation rate (Roman 1994). Gregarious behaviour is known in both infaunal and epifaunal modern ophiuroids (Spencer & Wright 1966; Zatoń et al. 2008), in particular in environments with low predation pressures (Aronson 1989). At Janusfjellet, specimens of *Ophiurinae* sp. are commonly found stacked up in multiple layers within the siderite concretion level. These must have originated from large monospecific aggregates of living individuals.

Ophiurinae sp. resembles the extant genera *Ophiura* Lamarck, 1801 and *Ophioplinthus* Lyman, 1878. It most probably lived with the dorsal disc up and the mouth directed down to the sea-floor. Its relatively long, flexible arms were used for locomotion, while the short arm spines might have been used to gather carrion, detritus or prey (Hess & Meyer 2008).

Ophiacanthidae sp. was probably a suspension feeder and used its long, robust, erected arm spines to trap food particles, as do some modern suspension-feeding ophiacanthids (O'Hara & Stöhr 2006; Hess & Meyer 2008).

Hess & Meyer (2008) suggested that, based on extant ophiuroid ecology, taxa inhabiting high-energy environments would have relatively short and blunt arms. In that view, the relatively long arms of both species are in accordance with the low-energy environment of the central Spitsbergen sea during the Late Jurassic.

Depositional environment

The multielement skeletons of echinoderms are highly sensitive to post-mortem depositional processes. Experimental taphonomy has shown that disarticulation of echinoderm carcasses exposed on the sea-floor occurs on a day time scale (e.g., Kidwell & Baumiller 1990; Allison 1990; Baumiller et al. 1995; Oji & Amemiya 1998; Kerr & Twitchett 2004). Kroh & Nebelsick (2010) provided a good overview of echinoderm taphonomy, with focus on diagenesis and the use of disarticulated material in palaeoenvironment interpretation. Under normal conditions of slow to moderate

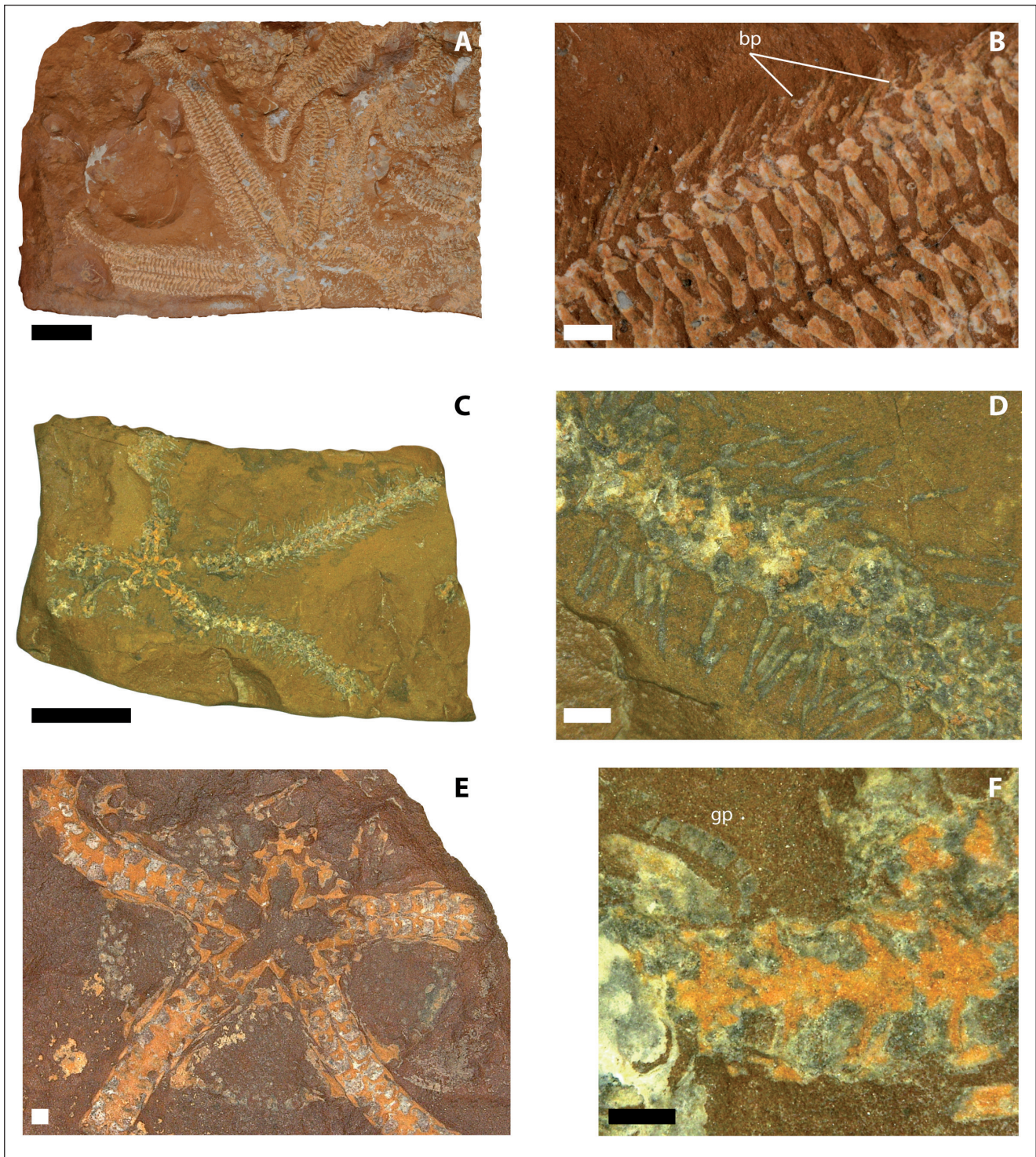


Figure 4. The Janusfjellet Lagerstätte autochthonous fauna. A-B: *Asteriidae* sp. PMO 218.011a. A. Specimen eroded in a cut-through fashion, abactinal view of the actinal ossicles. B. Close-up of a portion of the arm from A, basal pieces (bp) of straight pedicellariae visible in cross-section. C-D: *Ophiacanthidae* sp. PMO 217.899a. C. Articulated disc exposing the oral side. D. Close-up of a section of the arm from C. E-F: *Ophiurinae* sp. E. PMO 218.010a. Oral view of disc with 4 articulated arms. F. PMO 217.960. Oral view of base of the arm with arm comb (gp - genital papillae) preserved in place. Scale bars in A and C are 10 mm across; B, D, E, and F are 1 mm across.

(1-10 cm per 100 years) burial rates, almost all echinoderm remains, even the tightly sutured thecae of some blastoids and camerate crinoids, will be exposed on the sea-floor for several years and suffer complete disarticulation (Brett & Baird 1986). Thus, the preservation of the articulated multi-element skeletons of echinoderms provides unequivocal

evidence of a fast and effective burial event (Brett & Baird 1986; Brett 1990; Nebelsick 2004).

Obrution events (*sensu* Seilacher et al. (1985): “rapid burial event”) usually happen within a few hours to a few days (Brett 1990). Storms (tempestites) and submarine slides

(turbidites) are the most common causes of obrution deposits. Smothering is a common cause of death for echinoderms since their water-vascular system is susceptible to clogging by sedimentary particles (Rosenkranz 1971; Schäfer 1972). Nearly all “starfish beds” are thought to be derived from an episode of rapid sedimentation in the habitat of the organisms, thus effectively burying them alive (e.g., Goldring & Stephenson 1972; Donovan 1991).

The Janusfjellet echinoderm Lagerstätte occurs as a layer of siderite concretions within a thick succession of grey to black shales indicative of a fine-grained, hemipelagic background deposition. These shales have been interpreted as a distal shallow shelf environment with low sedimentary input except under storm conditions (Dypvik 1985; Dypvik et al. 1991a; 1991b).

The Slottsmøya Member has further been identified by Nagy et al. (2009) as a transgressive period with a dysaerobic sea bottom. The echinoderm fossils are preserved within a c. 20 cm-thick layer of easily recognisable siderite concretions (Fig. 2B) at both the Janusfjellet and the Konusdalen sites. Assuming some post-burial compaction, this is more than thick enough to smother echinoderms effectively. No break in sedimentation can be recognised within the layer, which is assumed to represent a single burial event.

Brett (1990) described typical obrution burial layers as structureless mudstone or siltstone with fossils preserved only in the lower part. This is consistent with field observations from the Spitsbergen sites. Extensive surface search for fossils within and around the sideritic layer had been performed in the area in 2006 without success (M. Høyberget, pers. comm., 2010). As the area is highly subject to erosion, it took only a few years to uncover the fossil-rich lower part of the layer, which lay at the surface when the sites were revisited in 2010.

When observed in thin-sections (Fig. 5), the sideritic layer consists of fine-grained material with some coarser quartz grains (compare the bottom and top halves of Fig. 5A). The coarser material constitutes most of the matrix between the disarticulated crinoid ossicles observed from Konusdalen (compare Fig. 5C-D with the top part of Fig. 5A) whilst thin-sections of slabs preserving articulated asteroid material show a matrix composed of the smaller fraction (compare Fig. 5B with the bottom part of Fig. 5A). It is important to note that Figure 5A is an horizontal section and does not represent a purely vertical succession in grain size as the picture might suggest. The coarser fraction can be interpreted as reworked material transported by the storm event into the muddy sea bottom.

Thus, the Janusfjellet Lagerstätte was formed by a single, fast storm event in an otherwise calm offshore shelf environment. Such background conditions, moreover, prevented the reworking of the obrution deposit (Brett et al. 1997a). As mentioned earlier, the Spitsbergen sea-water was relatively cold during the Late Jurassic. This also favoured the

preservation of articulated echinoderm skeletons by slowing down the rate of decay of soft tissue (Kidwell & Baumiller 1990).

Interestingly, within this single deposition event, the material shows different states of disarticulation. The preservation quality of fossil echinoderms reflects both the depositional processes associated with burial and the differential influence of taphonomy on different morphotypes (Meyer et al. 1989). Both field and laboratory studies (Lewis 1986, 1987; Allison 1990; Kidwell & Baumiller 1990) led to the recognition of a taxonomic bias in echinoderm taphonomy, as highly different rates of disarticulation have been observed for different taxa, even within classes. Accordingly, Brett et al. (1997b) have classified echinoderms into three taphonomic grades. Type 1 echinoderms, such as asteroid and ophiuroids, have skeletal plates held together by soft tissues and are thus very unlikely to remain articulated after death. Type 2 echinoderms have skeletons with some loosely and some tightly articulated parts and consequently exhibit variable preservation of different portions of their skeletons. Some crinoids (including isocrinids) and most regular echinoids fall within this category. Type 3 echinoderms have tightly articulated or sutured skeletal plates and are the least susceptible to disarticulation. Examples include irregular echinoids, blastoids and some crinoids. Thus, crinoid units (pluricolumnals, arm sections, calyce) and echinoid tests can resist disarticulation for much longer periods than the loosely articulated ossicles of asteroids and ophiuroids. Variation in decay rates between taxa can usually explain how different preservation grades can be found together in an apparently uniform depositional environment (Allison 1990).

In the Janusfjellet Lagerstätte, crinoids are represented by abundant arm sections and disarticulated ossicles, pluricolumnals not exceeding four noditaxis in length, and rare calyces. No complete or near-complete specimens have been found despite an intensive search effort. Crinoid pluricolumnals can survive on the sea-floor without disarticulating for extended periods (Oji & Amemiya 1998). The presence of individual disarticulated columnals (e.g., Fig. 3C) thus indicates that some specimens of *Chariocrinus* sp. had spent a considerable amount of decay time on the sea-floor before being buried. These ossicles could have been part of distal stem fragments shed by the crinoids during growth or as a defence mechanism, and have accumulated on the sea-floor over several years. They could also have been transported within the burial sediments and broken down to small units and individual columnals during the high-energy storm event.

The echinoid tests are relatively uncommon and mostly preserved as compressed half-tests with lantern elements in place but without attached spines (e.g., Fig. 3F). As compared to other echinoids, pedinid tests disintegrate relatively easily since there is very limited interlocking of stereom across plate sutures (Smith 1984; Kidwell & Baumiller 1990). Although being more sensitive to post-mortem damage than other echinoids, fossil pedinids with very good

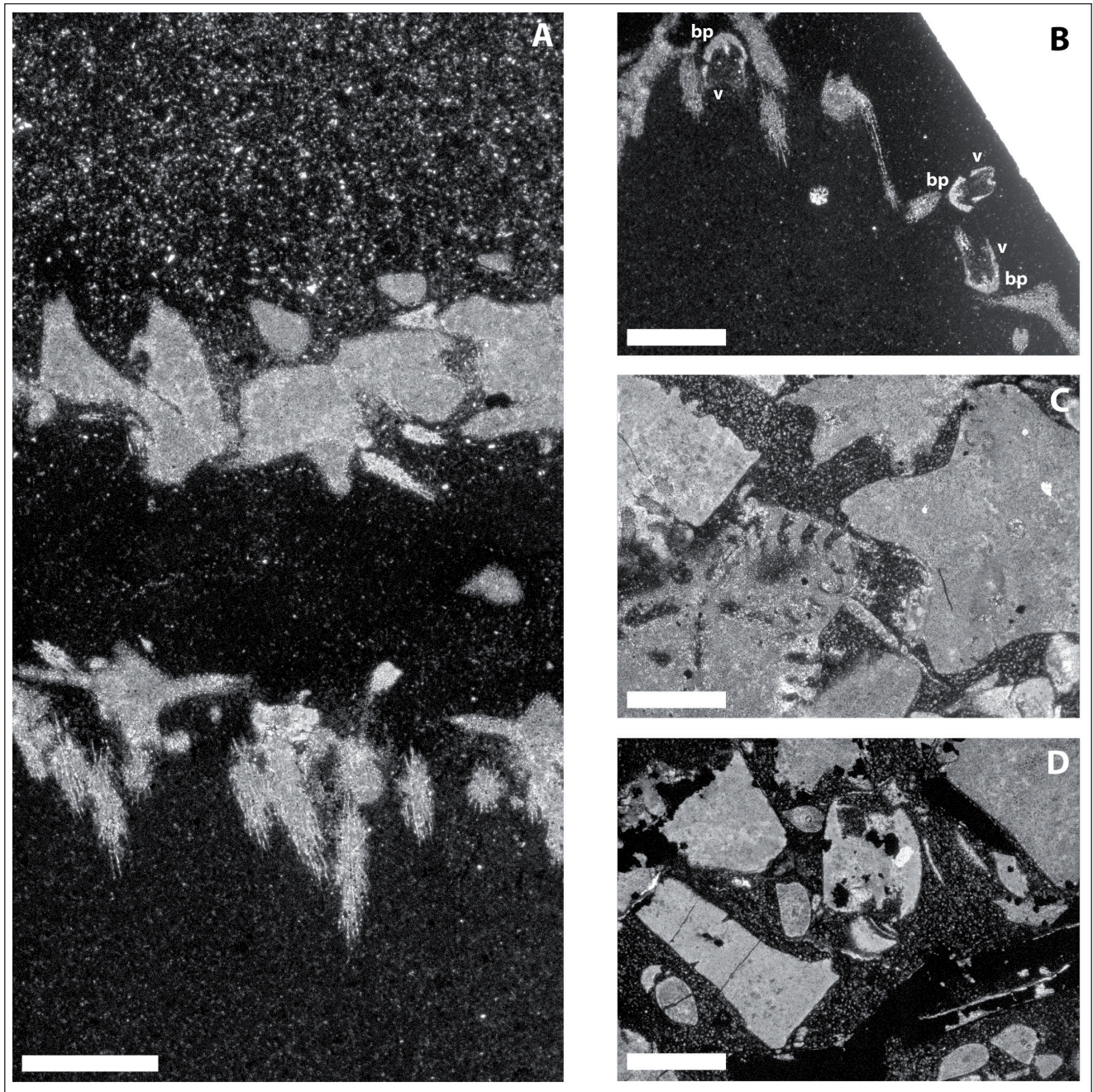


Figure 5. Photomicrographs of thin-sections A-B: Material from Janusfjellet, both transverse sections of PMO 217.988. A. Transverse section through the arm of an Asteriidae sp. B. Three pedicellariae from Asteriidae sp. Note also a planispiral benthic foraminifera near the centre of the image. bp – basal piece of pedicellariae, v – valve of pedicellariae. C-D: Material from Konusdalen. C. Transverse section of PMO 217.985. Articular facets of two Chariocrinus sp. columnals. D. Cross-section of PMO 217.983. Disarticulated crinoid ossicles. All scale bars are 1 mm across.

preservation are relatively common (e.g., compare pictures of Pedinidae genera within *The Echinoid Directory*, Smith & Kroh 2011). Consequently, the quite damaged state of the Janusfjellet *Hemipedita* sp. specimens implies that they either have spent a long time on the sea-floor before being buried or that they have suffered high-energy transport.

The best preserved taxa in the Janusfjellet Lagerstätte are, bemusedly, those most prone to post-mortem disarticulation. The three species of asteroids and ophiuroids preserve fragile details such as pedicellariae (Fig. 4B), articulated

spines (Fig. 4D), arm comb (Fig. 4F) and mouth papillae, which are highly susceptible to decay. A majority (88%) of the Ophiurinae sp. specimens are preserved with the oral side up. Zatoń et al. (2008) suggested that this indicates current-driven disturbance, as ophiuroid discs are heavier on the dorsal side. However, since articulated skeletons are preserved, this small-scale disturbance and transport must have happened while the individuals were alive or very shortly after their death, within the “window of invulnerability” discussed by Kidwell & Baumiller (1990).

Counterintuitive to the Brett et al. (1997b) classification, the Janusfjellet Lagerstätte Type 1 echinoderms are better preserved than Type 2 echinoderms found in the same layer. Hence, a morphology-related decay bias cannot here explain the occurrence of disarticulated crinoids, spineless half-echinoids and well articulated asteroids and ophiuroids preserved by the same burial event. Two hypotheses are here considered to resolve the issue.

The first hypothesis assumes that all five species found in the Janusfjellet Lagerstätte are autochthonous and were preserved in their life environment. According to this model, a low-diversity community with a colony of *Chariocrinus* sp., gregarious patches of Ophiurinae sp. and Asteroidea sp., and rare *Hemipedina* sp. and Ophiacanthidae sp. inhabited the Late Jurassic Spitsbergen distal shallow shelf, and there became entombed by an exceptional storm event. Living asteroids and ophiuroids were trapped and killed by the sediment deposition. Crinoids were able to escape by automising parts of their stem and arms, which became trapped in the sediments, along with ossicles of stems naturally shed during growth and which had been lying on the sea-floor for years. This could explain the absence of complete *Chariocrinus* sp. specimens and their preservation as relatively short pluricolumnals and numerous disarticulated ossicles. Similarly, assuming that the small number of echinoids found in the Lagerstätte represent a true low density within in the community, it is not impossible that no living *Hemipedina* sp. individual was trapped by the burial layer and that only test fragments from long dead individuals lying on the sea-floor became preserved.

Another possibility is that the Janusfjellet Lagerstätte preserved both autochthonous and allochthonous specimens. According to this second hypothesis, the storm current itself would have transported partially disarticulated crinoids and, possibly, echinoids downslope to a dysaerobic bottom inhabited by gregarious ophiuroid and asteroids. These were killed by smothering and trapped by the deposition associated with a thick waning flow. The differential disarticulation of the taxa is here explained by the preservation of allochthonous crinoids and, maybe, echinoids within the living environment of asteroids and ophiuroids.

This second model is supported by evidence suggesting that the Spitsbergen sea bottom was dysoxic during the Late Jurassic (see Introduction). Foraminiferans of the epifaunal to shallow-infaunal D2 morphotype described by Nagy et al. (2009) have been observed within the echinoderm-rich sideritic concretions (e.g., in Fig. 5B), a further indication of a low benthic oxygen level. Crinoids have relatively high oxygen demands, while some asteroids and ophiuroids can tolerate a lower level of oxygen (Ausich & Simms 1999). This suggests that while gregarious Ophiurinae sp. and Asteroidea sp., and rare Ophiacanthidae sp. inhabited the dysaerobic sea bottom, colonies of *Chariocrinus* sp. could not survive on this oxygen-reduced sea-floor and must have inhabited better oxygenated, more agitated and presumably shallower waters. This second hypothesis is also consistent with the

observation of a coarser-grained matrix between the crinoid debris than within the articulated asteroids (Fig. 5).

The position of *Hemipedina* sp. within this second model is somewhat problematic. The species does not show well-developed specialisation for oxygen intake which could mean it also inhabited a more oxygen-rich environment and is allochthonous in the Janusfjellet Lagerstätte. However, *Hemipedina* sp. could also have lived autochthonously under dysaerobic conditions as echinoids can have very low metabolic rate in cold water environments. The small size of the species is also somewhat consistent with a low metabolic rate. As a possible evidence for transport, it is worth noting that, despite being quite rare, four echinoid specimens were found in close vicinity of each other on a single, small concretion slab (PMO 217.912).

Similar hypotheses of mixed faunas composed of autochthonous and allochthonous species have been presented for other echinoderm Lagerstätten. Different Triassic ophiuroid beds (Twitchett et al. 2005; Zatoń et al. 2008) and Middle Jurassic crinoid assemblages (Łuków area, eastern Poland: Salamon 2008a; Villier 2008; northern Lithuania: Salamon 2008b) are thought to preserve together an assemblage of taxa from different environments. Taphonomic arguments for faunal mixing have been forwarded by Twitchett et al. (2005) and Zatoń et al. (2008). At Łuków, where a rich echinoderm fauna of Boreal affinity has been found in Callovian erratic clays, the transport hypothesis is also supported by the high ecological diversity of the fauna (Villier 2008).

Another interesting example is the Lower Callovian La Voulte Lagerstätte (Fischer 2003) and adjacent Chénier Ravine (Charbonnier et al. 2007), Southeast France. The diverse fauna is there attributed to heterogeneous bottom conditions preserving together parautochthonous and autochthonous taxa. Charbonnier et al. (2007) placed the La Voulte Lagerstätte around the slope-basin transition, a palaeoenvironmental setting involving a distinctive bottom topography comprising fault-generated steep blocks and prone to sediment slides. This hypothesis is used to explain the presence of cyrtocrinid crinoids and siliceous sponges with a preference for hard substrates in the muddy sea bottom dominated by ophiuroids and crustaceans. The Janusfjellet Lagerstätte differs in the fact that all species present, including *Chariocrinus* sp. and *Hemipedina* sp., could live on a muddy substrate. On Spitsbergen, it is the different tolerance to low oxygen conditions of the different species, rather than their substrate preferences, that suggests mixed origins for the fauna.

Combining evidence from sedimentology, species morphology and taphonomy, we conclude that the Janusfjellet Lagerstätte preserves a high Boreal, low-diversity, mixed echinoderm fauna. Ophiuroids and asteroids were buried on the dysaerobic sea-floor where they lived by a single storm event carrying sediments and remains of crinoids and echinoids living in better oxygenated areas.

The fossil record of Boreal echinoderms

Fossil echinoderms from the Boreal realm have a very fragmentary record, mostly concealed within studies on bivalves and ammonites and accounts of geological expeditions from the early 20th century. Although an extensive list of echinoderms reported from the Boreal Jurassic and Early Cretaceous is compiled in Table 2, only the Late Jurassic–Early Cretaceous specimens with sufficient published description will be considered in the following discussion.

Greenland

Possibly the best account of Late Jurassic–Early Cretaceous echinoderms from the Boreal region to date was given by Spath (1947), who described one asteroid and one crinoid from the Ryazanian of Southwest Jameson Land, Greenland. The asteroid material was provisionally referred to *Astropecten* (?) Gray 1840 sp. indet., as Spath noted that it had relatively small marginals. Spath's material is certainly not comparable to *Asteriidae* sp., which does not possess the characteristic paxillosidae marginal plates. Stalked crinoids from the same locality with pentagonal to star-shaped columnals, 0.75 mm thick for a diameter of two millimetres, are described as "*Pentacrinus*" cf. *tenellus* Eichwald, 1868 but Spath recognised the tentative nature of this assignment. "*Pentacrinus*" Miller, 1821, a commonly used generic name for stalked crinoids with pentagonal columnals during most of the 19th century, is now invalid and fossils previously identified as such are mostly assigned to the accepted genus *Pentacrinites* Blumenbach, 1804. Upon re-examination of the material, some early accounts of "*Pentacrinus*" have also been reassigned to other isocrinid genera (e.g., Hunter et al. 2011). Similarly, the material from Southwest Jameson Land could belong to Isocrinida. However, the description is insufficient and the illustrations (Spath 1947: pl. V, figs. 10–11) too poor to here allow further comparison with the Spitsbergen *Chariocrinus* sp.

Spath (1935) had also previously reported an ophiurid specimen from the Upper Oxfordian of the Kap Leslie Formation, Milne Land. This specimen (Spath 1935: pl. 11, fig. 2) is one of the few Boreal echinoderms comparable with the Spitsbergen material. The single, articulated ophiuroid from the Upper Oxfordian *Pecten* Sandstone, was assigned to *Ophiurites* Leriche, 1931 sp. ind. It consists of an articulated disc with four attached arms which superficially resembles the Spitsbergen Ophiurinae sp. The scarcity of information and poor illustration of the Greenland material prevent a better comparison at present. It would nevertheless be very interesting to compare the original specimen to the new Spitsbergen material.

The Upper Jurassic of Milne Land has also yielded crinoid and echinoid material reported within paleoecological studies of macroinvertebrates by Fürsich (1984a, 1984b) and Fürsich & Heinberg (1983). The majority of the microfossil associations and assemblages (composed mainly

of bivalves, brachiopods and serpulid worms) recognised by Fürsich (1984a, 1984b) are devoid of echinoderm fossils. When they occur, their relative abundance is between 0.1 and 0.2%. Such a rarity of echinoderms in the fossiliferous Upper Jurassic succession of Milne Land is surprising. The abundant benthic fauna has been extensively studied so it is unlikely that the fossils were simply unnoticed. Gastropods and bivalves with aragonitic shells are preserved, often as recrystallised shells. This suggests that diagenetic dissolution cannot explain the scarcity of echinoderm fossils, since the high-Mg calcite of their ossicles is more resistant to dissolution than aragonite. The fossil associations and assemblages show relatively low diversity, a fact attributed to dysoxic benthic conditions or an unstable, shifting substrate. According to Fürsich (1984b: 332), all "high level suspension feeders such as crinoids are extremely rare" in the Kap Leslie Formation.

Russia

Early work by Lahusen and Trautschold and later work by Gerasimov (see Table 2 for detailed references) on the Russian Platform led to multiple reports of Jurassic echinoderms from central Russia. Crinoids, cidaroid echinoids and the irregular echinoid "*Echinobrissus*" (= *Nucleolites* Lamarck, 1801) *scutatus* Lamarck, 1816 are commonly reported. With the exception of a few species of *Cyclocrinus* D'Orbigny, 1850, all crinoids are referred to "*Pentacrinus*" although some clearly show isocrinid affinities. Their identification is probably a mere reflection of 19th century crinoid taxonomy. Published descriptions and illustrations are poor, but confident reassignment to different genera might be possible by observation of the original material.

In a review of fossil isocrinids from the former U.S.S.R., Klikushin (1982) described two species, *Percevalicrinus beaugrandi* Klikushin, 1982 and "*Pentacrinus*" ?*shastensis* Klikushin, 1982, from Volgian deposits in the Arctic Urals and the Taymyr Peninsula. The absence of illustration of the material referred to as *Percevalicrinus beaugrandi* does not allow for comparison. *Percevalicrinus* Klikushin, 1981 is a Late Jurassic–Early Cretaceous genus considered by Klikushin (1981) as a sister genus to *Margocrinus* Klikushin, 1979, a genus which might itself be a synonym of *Balanocrinus* Agassiz, 1847 (Simms 1989). Moreover, some columnals illustrated by Klikushin as *Percevalicrinus tenellus* Eichwald, 1868 (Klikushin 1987: pl. 2, figs. 2–3) clearly appear to belong to two different species. With its lancet-shaped petals and separate adradial crenulae in the interradial, "*Pentacrinus*" ?*shastensis* (Klikushin 1987: pl. 7, fig. 1), the second species reported from the Taymyr region is clearly different from the Spitsbergen material.

Arctic Canada and Alaska

The Upper Jurassic Ringnes Formation of the Sverdrup Basin has been widely studied by petroleum geologists and often compared to other Boreal sequences. Jeletzky (1973) considered the Canadian Arctic marine fauna as extremely

Table 2: Jurassic—Cretaceous Boreal echinoderms.

Taxa names are given according to the original publication, although the taxonomic placement of some specimens is in need of revision (see discussion in text). Quotation marks are used for doubtful names.

	Area	Stratigraphic unit		Taxa	Reference
Greenland	Jameson Land	U. Volgian	Raukelv Fm	Crinoidea	Surlyk et al. 1973
		Ryazanian	Hesteelv Fm		
		Ryazanian	Crinoid Bjerg Mb	" <i>Pentacrinus</i> " cf. <i>tenellus</i>	Spath 1947
		Ryazanian	Crinoid Bjerg Mb	<i>Astropecten</i> sp. indet.	Spath 1947
	Milne Lanad	U. Callovian-Volgian	Kap Leslie Fm		
		U. Oxfordian	Kap Leslie Fm	<i>Ophiurites</i> sp. indet.	Spath 1935
		U. Oxfordian	Aldinger Elv Mb	<i>Pentacrinites</i> sp.	Fürsich & Heinberg 1983
L. Volgian		Krebsedal Mb	Cidaroidea	Fürsich 1984a, b	
	M. Volgian	Pernaryggen Mb	<i>Pentacrinites</i> sp.	Fürsich 1984a, b	
Russia	Ryazan region	Jurassic		" <i>Pentacrinus</i> " <i>pentagonalis</i>	Lahusen 1883
		Jurassic		<i>Cidaris elegans</i>	Lahusen 1883
		Jurassic		<i>Echinobrissus</i> (= <i>Nucleolites</i>) <i>scutatus</i>	Lahusen 1883
	Ryazan region	Jurassic		<i>Pentacrinites basaltiformis</i>	Trautschold 1859
		Jurassic		<i>Acrochordocrinus</i> (= <i>Cyclocrinus</i>) <i>insignis</i>	Trautschold 1859
		Jurassic		Cidaroidea	Trautschold 1859
		Jurassic		<i>Echinobrissus</i> (= <i>Nucleolites</i>) <i>scutatus</i>	Trautschold 1862
		Jurassic		<i>Cidaris</i> sp.	Trautschold 1862
		Jurassic		" <i>Pentacrinus</i> " <i>cingulatus</i>	Trautschold 1866
		Jurassic		<i>Cidaris</i> sp.	Trautschold 1866
		Jurassic		<i>Asterias jurensis</i>	Trautschold 1866
		Oxfordian		" <i>Pentacrinus</i> " <i>cingulatus</i>	Trautschold 1877
		Oxfordian		" <i>Pentacrinus</i> " <i>pentagonalis</i>	Trautschold 1877
	Central Russia	Callovian		" <i>Pentacrinus</i> " spp.	Gerasimov et al. 1996
		Callovian		<i>Cyclocrinus macrocephalus</i>	Gerasimov et al. 1996
		Callovian		<i>Echinobrissus</i> (= <i>Nucleolites</i>) spp.	Gerasimov et al. 1996
		Callovian		<i>Holectypus</i> spp	Gerasimov et al. 1996
		Callovian		<i>Plegiocidaris</i> spp.	Gerasimov et al. 1996
		Callovian		<i>Goniaster</i> cf. <i>jurensis</i>	Gerasimov et al. 1996
		Volgian		" <i>Pentacrinus</i> " cf. <i>crisagalli</i>	Gerasimov et al. 1995
		Volgian		<i>Echinobrissus</i> (= <i>Nucleolites</i>) <i>volgensis</i>	Gerasimov et al. 1995
		Volgian		<i>Rhabdocidaris</i> spp.	Gerasimov et al. 1995
		Volgian		<i>Pentacrinus</i> cf. <i>tenellus</i>	Gerasimov 1969
		Volgian		<i>Rhabdocidaris</i> spp.	Gerasimov 1969
		Volgian		<i>Plegiocidaris</i> spp.	Gerasimov 1969
	S-E Urals	Kimmeridgian		" <i>Pentacrinus</i> " <i>astralis</i>	Trautschold 1863
Northern Russia	L. Lias		" <i>Pentacrinus</i> " <i>basaltiformis</i>	Koschelkina 1962	
	Toarcian		" <i>Pentacrinus</i> " <i>subangularis</i>	Koschelkina 1962	
	L. and M. Lias		" <i>Pentacrinus</i> " ex. gr. <i>subangularis</i>	Efimova et al. 1968	
	Volgian		<i>Percevalicrinus beaugrandi</i>	Klikushin 1982	
	Volgian		<i>Percevalicrinus beaugrandi</i>	Klikushin 1982	
	Volgian		" <i>Pentacrinus</i> " ? <i>shastensis</i>	Klikushin 1982	
Arctic North America	Sverdrup Basin	Bathonian	Hiccles Cove Fm	<i>Isocrinus</i> sp.	Strimple 1973, Hunter and Zonneveld 2008
		U. Jurassic	Ringnes Fm	Crinoidea	Balkwill et al. 1977
		U. Jurassic	Ringnes Fm	Echinoidea	Balkwill et al. 1977
	Yukon-Alaska	Sinemurian	Murray Ridge Fm	Crinoidea	Poulton 1991
		U. Sinemurian-L. Toarcian	Almstrom Creek Fm	Crinoidea	Poulton 1991
		U. Pliensbachian	Kingak Fm	<i>Seiocrinus</i> sp. aff. <i>S. subangularis</i>	Poulton 1991
		U. Pliensbachian	Kingak Fm	" <i>Pentacrinus</i> " sp.	Springer 1926
	Berriasian or Valanginian		<i>Ophiura</i> sp.	Corgan 1962	
Svalbard	Spitsbergen	U. Jurassic	Agardhfjellet Fm	<i>Chariocrinus</i> sp.	Rousseau 2011, This study
		Volgian	Slottsmøya Mb	<i>Chariocrinus</i> sp.	Rousseau 2011, This study
		Volgian	Slottsmøya Mb	<i>Hemipedina</i> sp.	Rousseau 2011, This study
		Volgian	Slottsmøya Mb	Asteriidae sp.	Rousseau 2011, This study
		Volgian	Slottsmøya Mb	Ophiacanthidae sp.	Rousseau 2011, This study
		Volgian	Slottsmøya Mb	Ophiurinae sp.	Rousseau 2011, This study
		Volgian	Slottsmøya Mb	<i>Savignaster</i> sp.	Rousseau 2011
		L. Cretaceous	Helvetiafjellet Fm	Asteroidea	Rousseau 2011
		Aptian-Albian	Carolinefjellet Fm	Isocrinidae	Nagy 1963
		Aptian-Albian	Carolinefjellet Fm	Asteroidea	Nagy 1963
		Aptian-Albian	Carolinefjellet Fm	Ophiuroidea	Nagy 1963
		Aptian-Albian	Carolinefjellet Fm	Asteroidea	Rousseau 2011
		Aptian-Albian	Carolinefjellet Fm	Ophiuroidea	Rousseau 2011

impoverished when compared to those from equivalent horizons of northern Europe and northern Siberia. Macrofossil groups other than ammonites and bivalves are “too rare to be of any practical use” (Jeletzky 1973: 44) and, accordingly, their report and description have been neglected.

In the Yukon–Alaska region, the best known echinoderm specimen is the the Early Cretaceous *Ophiura* sp. described by Corgan (1962). It is preserved as a siltstone cast within a thick shale succession in the Old Crow area, northern Yukon. The specimen shows an articulated disc preserving a portion of five arms showing no sign of spinosity. As the specimen is seen in dorsal aspect only, it is impossible to assess the arrangement of the tentacle pores, an important characteristic distinguishing Ophiurinae sp. from the genus *Ophiura*. The original illustration is poor, making this *Ophiura* sp. difficult to compare with other material.

Svalbard

Fürsich (1984a: 70) considered the Late Jurassic fauna of Spitsbergen, dominated by species of *Buchia* (Bivalvia), as “impoverished” compared to the central East Greenland one. Nevertheless, the Spitsbergen echinoderm fauna is so far the richest encountered within the Boreal realm. In addition to the Janusfjellet Lagerstätte described here, asteroids, ophiuroids and crinoids have been found in other Upper Jurassic and Lower Cretaceous deposits on Spitsbergen (Nagy 1963; Rousseau 2011; Rousseau & Gale, in prep.).

Crinoid ossicles assigned to “*Pentacrinus*” sp., unidentified asteroids and ophiuroids reported by Nagy (1963) from the Lower Cretaceous of Spitsbergen were until recently the only other published echinoderm fossils from Svalbard. The crinoid columnal photographed by Nagy (1963: fig. 1) is most certainly an isocrinid and should be reassigned as Isocrinidae sp. until a more precise taxonomic placement can be made.

Nagy’s (1963: fig. 2) Early Cretaceous ophiuroid specimen from Kjellströmdalen is an articulated disc seen from the dorsal side with five arms attached. The disc is small and the arms are short and taper rapidly. Ophiurinae sp. is much larger and has a different overall body shape. Unless Nagy’s (1963) specimen is a juvenile, a fact impossible to assess from the photograph, it most likely belongs to a different species.

Conclusions

The well preserved fossils collected at Janusfjellet constitute the first Boreal echinoderm Lagerstätte and the northernmost occurrence of Mesozoic echinoderms to have ever been reported. As with most echinoderm Lagerstätten preserving articulated asterozoans, it was formed by sudden burial during a storm event. The material shows different grades of preservation with, surprisingly, the taxa most

sensitive to taphonomic stresses being the best preserved. A depositional environment model is suggested to explain this counterintuitive situation. Reworked sediments including crinoid and echinoid skeletal remains were transported to a dysoxic shelf environment. This sudden sediment input on a muddy sea-floor smothered and trapped the autochthonous benthic epifaunal Asteroiidae sp., Ophiurinae sp. and Ophiacanthidae sp. The isocrinid *Chariocrinus* sp. occupied a more agitated, better oxygenated environment and its skeletal fragments were transported with the sediment flow. Taphonomic evidence suggests that *Hemipedina* sp. was similarly allochthonous. The cold water temperatures of this high-latitude marine shelf promoted a good preservation quality by significantly slowing down decay processes. Dysoxicity of the sea bottom also prevented major post-burial disturbance by scavengers.

The five species of the high Boreal Janusfjellet Lagerstätte represent a unique window into the evolutionary history of echinoderms in high-latitude environments. Despite being of relatively low diversity, the fauna comprises interesting specimens which differ from previously described forms from the Boreal realm and from more thoroughly described lower latitude faunas.

The known Boreal realm fauna is generally echinoderm-poor as bivalves and ammonites have traditionally been the focus of marine, macro-invertebrate, palaeontological investigations in the Arctic. This study therefore constitutes a substantial addition to the limited records of Mesozoic Boreal echinoderms and a step towards the recognition of the phylum as an important member of high-latitude palaeocommunities.

Acknowledgments. - Fieldwork at Svalbard (2007-2010) was financed by the Norwegian Research Council, Norwegian Petroleum Directorate, Spitsbergen Travel, ExxonMobil, Fugro, Statoil, OMV, Powercontrols and Hydro, by grants nos. EC0425-09 and EC0435-09 from the National Geographic Society. FQRNT and NSERC PGS-M grants were also awarded to J.R. in 2010-2011.

The authors are grateful to all the volunteers and students who have contributed weeks of fieldwork for free on the project and helped collecting specimens. A special thanks to Magne Høyberget who collected an important part of the echinoderm specimens. Marine Collignon and Krzysztof Hryniewicz shared information on the profile investigated.

Tim A. Ewin, Aaron Hunter, Andrew S. Gale, Andrew B. Smith, and Ben Thuy greatly contributed to the identification of the material. Robert B. Blodgett, Mikhail A. Rogov and Matthew J. Vavrek helped with the review of Boreal echinoderm material.

Special thanks to David L. Bruton and Øyvind Hammer who carefully reviewed earlier versions of the manuscript and suggested helpful improvements, and to journal referees Christian A. Meyer and Loïc Villier for their valuable comments which were beneficial to the final version of the manuscript.

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