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Crinoids from Svalbard in the aftermath of the end-Permian mass extinction

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Abstract: The end-Permian mass extinction constituted a major event in the history of crinoids. It led to the demise of the major Paleozoic crinoid groups including cladids, disparids, flexibles and camerates. It is widely accepted that a single lineage, derived from a late Paleozoic cladid ancestor (Ampelocrinidae), survived this mass extinction. Holocrinid crinoids (*Holocrinus*, Holocrinida) along with recently described genus *Baudicrinus* (Encrinida), the only crinoid groups known from the Early Triassic, are considered the stem groups for the post-Paleozoic monophyletic subclass Articulata. Here, we report preliminary data on unexpectedly diverse crinoid faunas comprising at least four orders from the Lower Triassic (Induan and Olenekian) of Svalbard, extending their stratigraphic ranges deeper into the early Mesozoic. These findings strongly imply that the recovery of crinoids in the aftermath of the end-Permian extinction began much earlier at higher palaeolatitudes than in the central Tethys.

Key words: Arctic, Svalbard, echinoderms, crinoids, P/T extinction, recovery.

Introduction

Recovery of most organisms from the end-Permian mass extinction, other than a few nekto-pelagic and reef taxa, is thought to have spanned the entire Early Triassic (*i.e.* ~5 million years; see *e.g.* Benton 2005; Brayard *et al.* 2009, 2011; Foster

and Twitchett 2014). Crinoids were suggested to re-diversify from a single holocrinid lineage achieving great morphological and behavioural innovations not before the Middle–Late Triassic (Simms and Sevastopulo 1993; Simms 1999; Baumiller *et al.* 2010; Hess and Messing 2011; Gorzelak *et al.* 2012).

Although several authors have proposed alternative evolutionary scenarios suggesting polyphyletic and Paleozoic origins of articulate crinoids, supporting evidence is lacking. Similarities between Paleozoic and Mesozoic crinoids have simply been attributed to convergent evolution (Simms and Sevastopulo 1993; Hess and Messing 2011). Notwithstanding the above, the fossil record of crinoids in the Lower Triassic is patchy. For instance, Oji and Twitchett (2015) based solely on columnal remains recently erected a new genus, *Baudicrinus* from the Lower Triassic of Oman. Such findings highlight that the low abundance of crinoids in the aftermath of the end-Permian extinction need not necessarily be attributable solely to extinction but may in part reflect the incompleteness of the fossil record, and the migration of taxa to refuges.

So far, only a few studies have been devoted to fossil crinoids from Svalbard (*e.g.* Høltedahl 1911; Rousseau and Nakrem 2012; Gorzelak *et al.* 2013) and the Triassic representatives have never been the subject of a thorough investigation. Here, we report preliminary data on unexpectedly diverse crinoid faunas from the upper Vardebukta Formation and the Tvillingodden Formation (Lower Triassic) at Mariaholmen (Svalbard).

Geological setting

The paleo-geographical reconstruction of the Early Triassic (Mørk *et al.* 1982) depicts a land area to the west of the southern part of Svalbard while the southwards-extending epi-continental basin delineates an extensive embayment of the Panthalassa Ocean into the northern margin of the Pangea supercontinent (Fig. 1; Riis *et al.* 2008; Worsley 2008). Within a Tertiary fold-thrust belt, the lithological succession at Mariaholmen dips steeply eastward; the Lower Triassic sequence is well exposed along the south and southeast coast of the island (Fig. 2). Due to strong tectonic disturbance and quaternary cover, only a 228 m-thick sequence comprising the upper part of the Vardebukta Formation and the Tvillingodden Formation was investigated (Fig. 3). The stratigraphy of these sediments was revised by Birkenmajer and Trammer (1975) and Mørk *et al.* (1982, 1999).

The Permian–Triassic boundary in Svalbard has usually been placed at the top of the Kapp Starostin Formation based on an abrupt sedimentary change (Mørk *et al.* 1982, 1989, 1999; Gruszczynski *et al.* 1989; Błażejowski 2004). However, palynology, organic chemo-stratigraphy and bio-magnetostratigraphy indicate that the Permian/Triassic boundary lies within the basal part of the Vardebukta Formation.

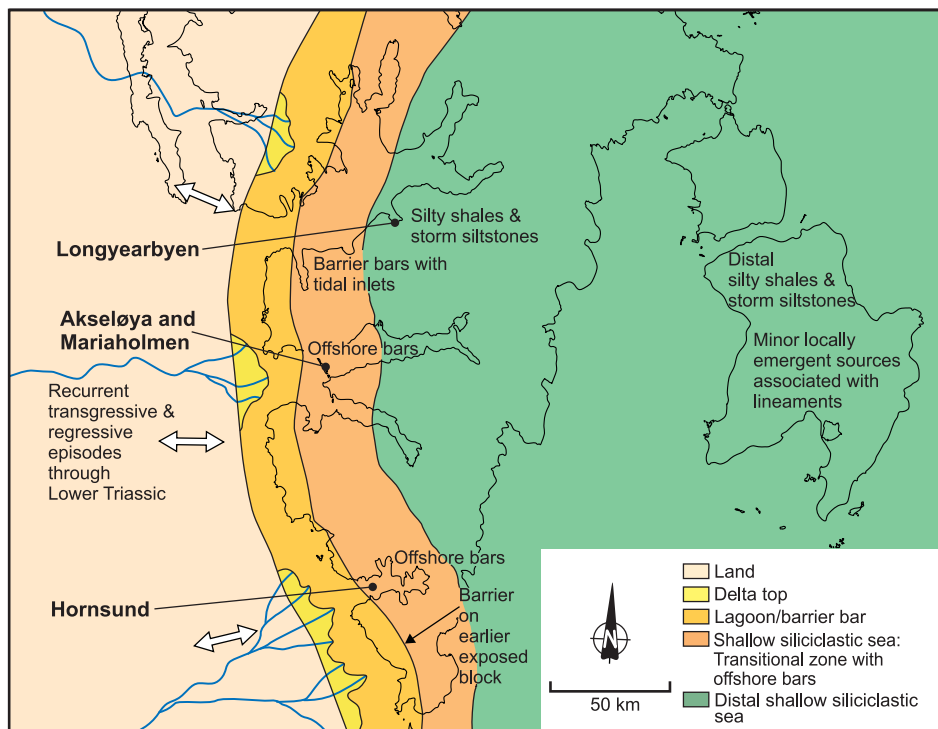


Fig. 1. Palaeogeographic map showing the Lower Triassic facies relationships in Svalbard (modified from Mørk *et al.* 1982). A land area is situated west of the southern part of Svalbard. Shallow siliciclastic marine deposits including lagoonal and barrier bars appear as coast-parallel facies belts adjacent to more distal fine-grained deposits further to the east.

The upper part of the Vardebukta Formation contains the so-called *Myalina* Bed yielding conodonts indicative of the late Griesbachian/early Dienerian (Induan) age (Nakrem *et al.* 2008), whereas bio-magnetostratigraphic analysis (Hounslow and Nawrocki 2008) suggests a late Griesbachian age. The boundary between the Vardebukta Formation and the overlying Tvillingodden Formation is usually regarded as the Induan/Olenekian boundary (see summary in Mørk *et al.* 1999). However, the magnetostratigraphic analysis of Hounslow and Nawrocki (2008) indicates that the Vardebukta Formation may well extend into the Olenekian rather than terminating close to the Induan–Olenekian boundary. Mørk *et al.* (1989, 1994) and Mørk (1994) showed the existence of a major early Olenekian transgression in the circum-Arctic area. Its age is based on a characteristic fossil assemblages (conodonts, ammonoids, bryozoans and bivalves) from the Tvillingodden Formation (Mørk *et al.* 1999; Nakrem *et al.* 2008; Hounslow *et al.* 2008). According to the palynological investigations of Vigran *et al.* (2014), the overlying Tvillingodden Formation corresponds to the *Naumovaspora striata* assemblage zone (early Olenekian/Smithian). In the upper part of the Tvillingodden Formation, the Skilisen Bed (a prominent unit of sandy biosparitic grainstone, formally defined by Mørk *et al.*



Fig. 2. A. Map of northern Europe with enlarged schematic geological map of Svalbard with investigated locality at Mariaholmen indicated (B). Triassic deposits in blue while the remaining areas are in brown.

1982; see also Dallmann 1999) contains conodont assemblages of late Smithian age (Nakrem *et al.* 2008). Early Triassic crinoids described herein were collected from the upper part of the Vardebukta Formation and the Tvillingodden Formation at Mariaholmen, Svalbard (70°41'30" N, 14°48'01" E; Fig. 1).

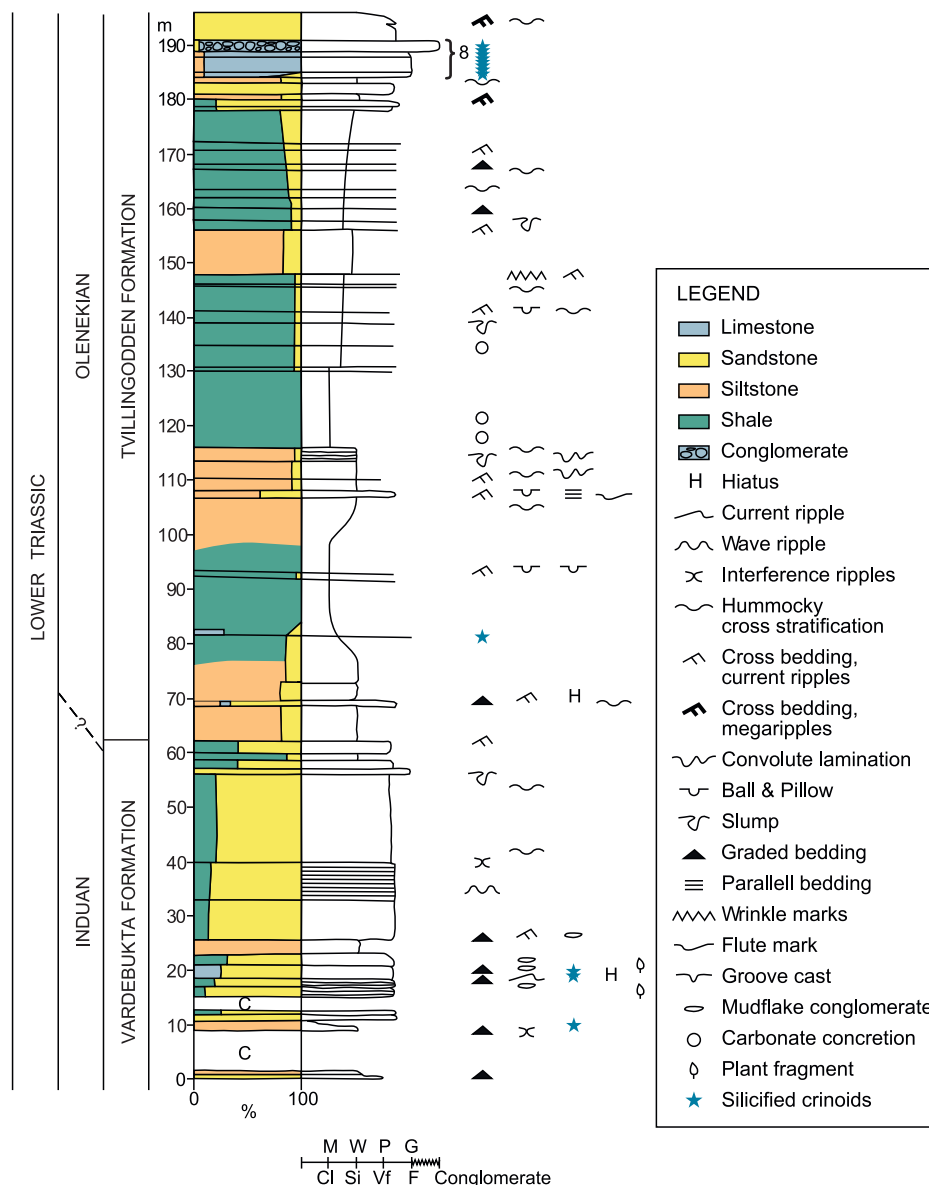


Fig. 3. Fragment (about 195 metres) of the investigated section along the south and southeast coast of Mariaholmen, Svalbard. About 90 meters of the lowermost part of the Vardebukta Formation is covered by Quaternary deposits. The upper part of the Vardebukta Formation consists of shallow-marine (including pro-delta) sediments. The overlying Tvillingodden Formation is characterized by a transgressive system tract in the lower part and a regressive system tract in the upper part. Abundant silicified crinoid ossicles were recovered from eight samples taken from a highly fossiliferous limestone (the Skilisen Bed). Carbonate classification following Dunham (M – mudstone, W – wackestone, P – packstone, G – grainstone) and the grain size of the clastic deposits is based on the Udden-Wentworth grade scale (Cl – clay, Si – silt, Vf – very fine sand, F – fine sand).

Methods

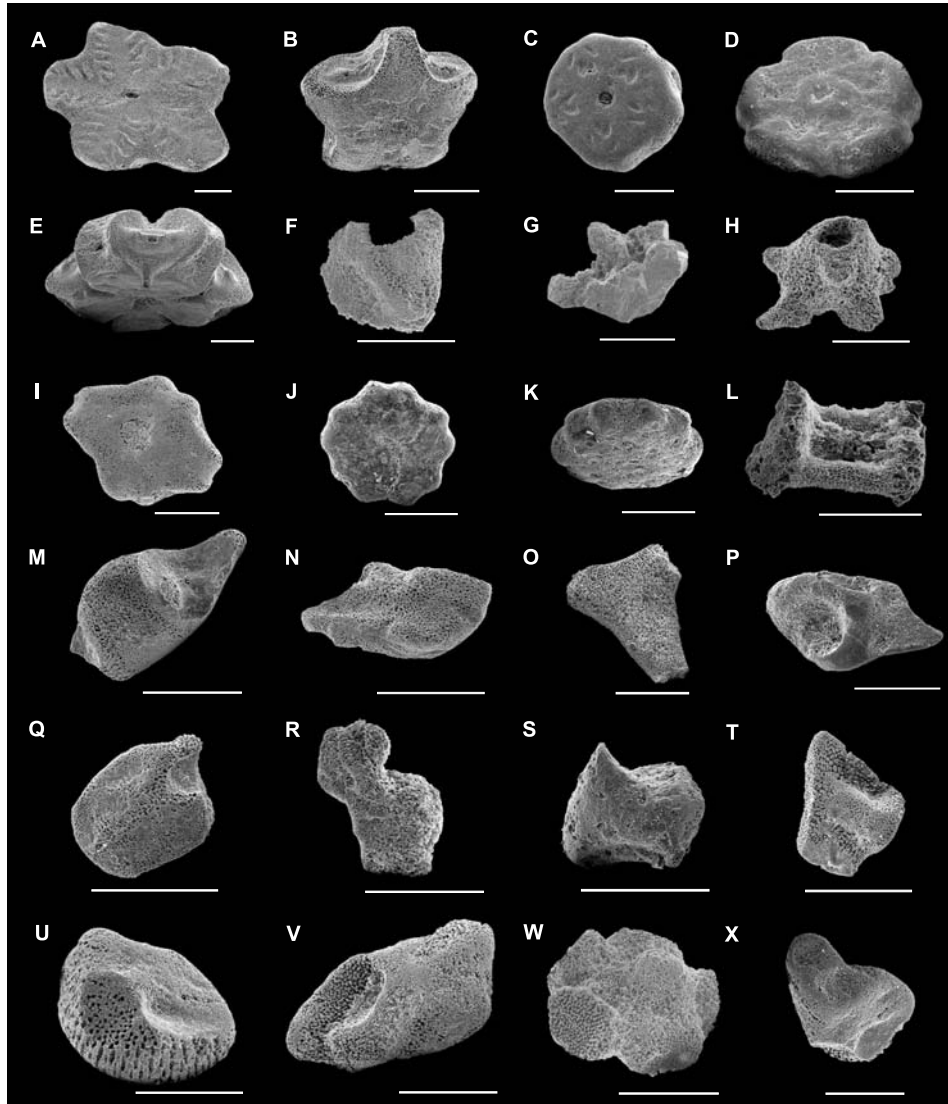
Samples, ranging from 0.4 to 10.5 kg, were collected from different levels of the section with most of the material from the calcareous Skilisen Bed. To optimize the subsequent dissolution process, after weighing the broken samples, rock fragments were placed in a net (mesh size 1.4 mm) over a plastic tank in order to retrieve both silicified and phosphatic fossils (inarticulate brachiopods, conodonts, fish teeth and scales) from the limestone and carbonate cemented sandy deposit. To prevent the destruction of phosphatic material, buffered acetic acid was used following Jeppsson's procedure (Jeppsson *et al.* 1999).

Carbonate dissolution resulted in the fine-grained insoluble residue sinking through the net to the bottom of the container preventing fragments from being smeared with the insoluble residue and allowing the acid to be in contact with the rock surface, increasing the dissolution rate. The dissolution of calcium carbonate usually took between 6 to 7 weeks. Once the reaction ceased, the acid was filtered out, the insoluble residues washed with tap water and wet sieved (standard mesh set from 16 down to 0.25 mm). All fractions >0.5 mm were screened for fossils. Most crinoid elements were found in the 0.5–1 mm and 1–2 mm fractions; they were mostly disarticulated but relatively well preserved implying para-autochthonous assemblages. Only a small portion of ossicles were broken by this procedure.

Morphological description

The upper part of the Vardebukta Formation yielded crinoid plate molds occurring as replacement ghosts after dissolution of calcitic ossicles; only two levels contained a few silicified ossicles of different morphology (Fig. 4A, F, G). Some of them are pentagonal and sub-stellate in outline and can be assigned to those observed in Early Triassic holocrinids (Holocrinida) and/or Middle Triassic iso-

Fig. 4. Early Triassic crinoids from the Vardebukta Formation (Induan: A, F, G) and Tvillingodden Formation (Olenekian: B–E, H–X) of Svalbard. Scale bars equal 0.5 mm. **A.** Medial/proximal? internodal of *Holocrinus*, articular facet ZPALV.42/P-T/h1, sample no. 2. **B.** Proximal nodal of *Isocrinus*, articular facet ZPALV.42/P-T/i1, sample no. 2. **C.** Proximal? nodal of Encrinida, articular facet ZPALV.42/P-T/e1, sample no. 5. **D.** Proximal internodal of Encrinida, articular facet ZPALV.42/P-T/e2, sample no. 5. **E.** Calyconodal of Encrinida (Ainigmacrinidae), lateral and oblique view view ZPALV.42/P-T/e3, sample no. 5. **F.** Broken fragment of roveacrinid brachial, lateral view ZPALV.42/P-T/r01, sample no. 1. **G.** Broken fragment of roveacrinid? theca, lateral view ZPALV.42/P-T/r00, sample no. 1. **H.** Holdfast of unknown crinoid, lateral view ZPALV.42/P-T/c1, sample no. 6. **I.** Unassignable columnal?, articular facets view ZPALV.42/P-T/c2. **J–K.** Centrodorsal? of Comatulida?, upper view (J) and lateral and oblique view (K) ZPALV.42/P-T/cc1, sample no. 5. **L–X.** Roveacrinida ossicles. **L.** Distal brachial plate (NBrn) of Roveacrinida, lateral view ZPALV.42/P-T/r1, sample no. 5. **M.** Secundibrachial plate (IIBrn) of *Osteocrinus*, oblique upper view of outer side ZPALV.42/P-T/r3, sample no. 6. **N.** Primibrachial plate (IBr1) of *Osteocrinus*, oblique →



adradial view from above of inner side ZPALV.42/P-T/r4, sample no. 5. **O.** Brachial plate of *Somphocrinus*, lateral view ZPALV.42/P-T/r5, sample no. 9. **P.** Primibrachial plate (IBr2) of *Osteocrinus*, oblique adradial view of outer side ZPALV.42/P-T/r2, sample no. 7. **Q.** First primibrachial plate (IBr1) of *Osteocrinus*, oblique upper view of outer side ZPALV.42/P-T/r6, sample no. 4. **R.** Radial plate (Rad) of *Osteocrinus*, lateral view ZPALV.42/P-T/r7, sample no. 5. **S.** Distal plate (IIBrn) of *Somphocrinus*, abradial outer lateral view ZPALV.42/P-T/r8, sample no. 5. **T.** Primibrachial plate (IBr1) of *Osteocrinus*, oblique abradial view from below of inner side ZPALV.42/P-T/r9, sample no. 7. **U.** Thecal plate of ?juvenile *Osteocrinus*, tilted lateral view slightly from above ZPALV.42/P-T/r10, sample no. 6. **V.** First primibrachial plate (IBr1) of *Osteocrinus* ZPALV.42/P-T/r11, sample no. 6. **W.** Thecal plate of juvenile *Osteocrinus*, tilted lateral view slightly from above ZPALV.42/P-T/r12, sample no. 9. **X.** Broken thecal plate of *Somphocrinus*, lateral view ZPALV.42/P-T/r13, sample no. 12. Number of sample refers to profile from Fig. 3.

crinids (Isocrinida; see Hess and Messing 2011). The most noticeable ossicles of this upper part of the Vardebukta Formation are a partially broken and recrystallized thecal plate resembling *Osteocrinus* sp. and three other ossicles, possibly of the pelagic roveacrinids (Roveacrinida; Fig. 4F, G). The Tvillingodden Formation revealed an unexpectedly high number of diversified silicified crinoid ossicles, dominated by columnals and brachial plates of holocrinids (*Holocrinus*) – this difference in the abundance of crinoids throughout the section is most likely related to fossil preservation (extension of diagenetic silicification). The distal internodal plates of these crinoids are sub-circular, sub-pentagonal (basaltiform) and pentagonal whereas the medial and proximal internodals are sub-stellate. The larger columnals have a distinct petaloid pattern. The nodal columnals are higher and wider than the internodals. All nodals display symplectial lower facets. Cirrus scars are deeply depressed and elliptical in outline. They may have a lip at their lower margin. The transverse ridge is inflated on both sides of lumen. Cirrus scar facets are horizontal. Brachials are muscular and small, V- or U-shaped. These holocrinid plates were accompanied by other crinoid ossicles including two holdfasts of unknown crinoids (Fig. 4H).

Among other crinoid elements discovered were strongly stellate columnals with petals (Fig. 4B): their articular facets are smooth, the lumen is large and the lower nodal articular facet is either cryptosymplectial or synostiosial which is indicative of isocrinids. Within a single layer of the upper part of the section (sample no. 5 in Table 1), two extremely enlarged and modified nodals are also present (Fig. 4E). These ossicles strongly resemble the so-called calyconodal, a synapomorphic ossicle, of the highly specialized *Ainigmacrinus* (Encrinida) previously known exclusively from the early Late Triassic (Hagdorn 1988). The Svalbard calyconodals have five very deep cirrus sockets with longitudinally depressed latera separated by five protruding and strongly concave lateral surfaces of interradial. The cirrus sockets are cordate and display an inflated transverse ridge with a relatively large lumen. Deep furrows (on both sides of the facet) extend from each socket toward the lumen. Low and subpentagonal columnals with a reduced epifacets may belong to encrinids (Fig. 4C–D; Hagdorn *et al.* 1996). They are of similar diameter and height as holocrinid and isocrinid columnals, but their morphology is different. Similar columnals are known from the Middle Triassic and have been ascribed to immature encrinid columnals (Hagdorn *et al.* 1996).

The Tvillingodden Formation in Svalbard contains possible pelagic roveacrinids (Roveacrinida) similar to those described by Kristan-Tollmann (1975) from the Upper Triassic limestones of Austria. Generic determination is nearly impossible for isolated brachial plates. All brachial ossicles are rather smooth, devoid of any coarse or reticulate ornamentation. Thecal, radial and brachial plates from the upper part of the section have only genera-level features; we assign them to juvenile specimens and/or to new species (to be described elsewhere). These specimens display smooth low aboral projections with short interrational edges and radial

Table 1
 Weight of limestone samples used and major crinoid groups identified in each sample. The stratigraphic level refers to profile from Fig. 3.

Sample number	Stratigraphic level [m]	Weight of sample [kg]	Crinoid groups, number and types of ossicle
1	10.65	0.6	roveacrinids (1 incomplete theca and 3 brachials)
2	19.6	1.6	holocrinids (3), isocrinids (2), Crinoidea indet. (2 cirrals)
3	20.3	1.7	–
4	83.7	10.5	holocrinids (3), roveacrinids (1 brachial), Crinoidea indet. (1 columnal, 2 brachials, 3 cirrals)
5	184.4	0.4	holocrinids (9), isocrinids (4), encrinids (2 calyconodals, 10 columnals, 3 brachials), roveacrinids (7 thecae/theal plates, 10 brachials), Crinoidea indet. (13 columnals, 4 brachials, 9 cirrals)
6	185.0	2.2	holocrinids (41 columnals), isocrinids (6 columnals), encrinids (13 columnals), roveacrinids (8 brachials and 2 thecae/theal plates), Crinoidea indet. (27 columnals, 3 centrodorsals?, 2 holdfasts, 4 cirrals, 7 brachials)
7	186.9	0.8	holocrinids (7 columnals), isocrinids (1 columnal), roveacrinids (2 theca/theal plate and 2 brachials), Crinoidea indet. (5 cirrals)
8	187.4	0.5	holocrinids (8 columnals), isocrinids (2 columnals), encrinids (5 columnals)
9	189.2	2.1	holocrinids (3), isocrinids (1), roveacrinids (3 theca/theal plates and 7 brachials), Crinoidea indet. (12 columnals, 4 cirrals)
10	190.5	2.2	holocrinids (3 columnals), isocrinids (1 columnal)
11	191.9	7.9	holocrinids (9 columnals), isocrinids (3 columnals), roveacrinids (1 brachial), Crinoidea indet. (6 columnals, 2 cirrals, 2 brachials)
12	193.85	2.6	holocrinids (21 columnals), isocrinids (3 columnals) encrinids (2 columnals), Crinoidea indet. (5 columnals, 1 centrodorsal?, 2 cirrals, 6 brachials)

plates with vertical articular facets, weak ridges and prominent edges, both typical of *Osteocrinus* sp. (Fig. 4M–N, P–R, T–W). Individual radials and scarce thecae were found with isolated brachials. Some brachials, triangular in outline (conical to cylindrical, with comminutive articular facets), resemble those of *Somphocrinus* (Fig. 4O, S, X). Distal brachials (NBrn; see Fig. 4L) correspond to those of the saccocomid, *Saccocoma quendstedti* Sieverts-Doreck *et* Hess, 2002 (Hess 2002), known from the Upper Jurassic (Lower Kimmeridgian) of Germany. Their articular facets display spinose extensions on both sides of the food groove. On the whole, the Svalbard somphocrinid (roveacrinid) assemblages show a fairly high level of species diversity. Most could be assigned to three genera: *Somphocrinus* sp. (one species), *Osteocrinus* sp. (at least three species) and a few “saccocomid-

-like” brachial remains here assigned to Roveacrinida (gen. indet., one species). The full taxonomic description will be published elsewhere.

Other echinoderm plates are hard to diagnose and we leave them unassigned. For instance, low and slightly conical ossicles, irregularly pentagonal in outline and devoid of lumen, are present (Fig. 4J–K). On one side they possess irregularly placed depressions and, on the other, they are smooth but slightly depressed in the centre. Such ossicles resemble centrodorsals of stalkless comatulids (Comatulida, *cf.* Hess and Messing 2011, fig. 582e). Intriguing irregular four-sided columnals? with a large lumen, atypical of any post-Paleozoic crinoid taxa, also occur (Fig. 4I).

Discussion

Although it has been suggested that the range of various groups of articulates should be extended down to the Paleozoic and/or Early Triassic (Webster and Jell 1999; Twitchett and Oji 2005; Webster and Lane 2007), this idea has not been widely accepted. For instance, according to the latest edition of the Treatise on Invertebrate Paleontology, the Articulata is retained as a monophyletic, post-Paleozoic clade (Hess and Messing 2011). In accordance with this, recent molecular clocks suggest that articulate crinoids have roots in the Middle–Late Triassic (Rouse *et al.* 2013). The latter study suggested that articulate crinoids likely radiated from a small clade that passed through the end-Permian extinction rather than from several surviving lineages. However, it should be pointed out that the 95% confidence limits on the Beast analyses extend into the Permian (Rouse *et al.* 2013). Indeed, as highlighted by Roux *et al.* (2013), molecular data of extant crinoids need to be treated with caution because they can only support the monophyly of the class Crinoidea, not that of the subclass Articulata.

Our preliminary findings document at least four crinoid orders from the Early Triassic, earlier hypothesized by Twitchett and Oji (2005). This either implies that the recovery of crinoids in the aftermath of the P/T extinction was rapid or that more than a single taxon survived the end-Permian. However, it seems rather unlikely that such a rapid rate of morphological divergence from a single holocrinid lineage could have taken place within a few Myrs following the P/T boundary. More probably at least a few crinoid taxa, survived the end-Permian mass extinction. Consequently, the crown-group divergence of articulate crinoids extends deeper in time. This is consistent with recent data suggesting the presence of crinoids referred to as a new genus *Baudicrinus* (Encrinida) in the Lower Triassic of Oman (Oji and Twitchett 2015; see also Twitchett *et al.* 2004). However, Oji and Twitchett (2015) erected this new genus based on limited and poorly preserved type material. For example, they used symplexial articulation of the crinoid column as a diagnostic feature, but the feature is widely distributed among post-Pa-

leozoic taxa (e.g. *Dadocrinus*, see Salamon and Niedźwiedzki 2005, fig. 2b–d), *Qingyanocrinus* (see Stiller 2000, fig. 4.21, 4.23) and *Silesiacrinus* (see Stiller 2000, fig. 11.14–16), *Lonchocrinus* (see Głuchowski 1987, pl. 3, fig. 1b), *Apsidocrinus* (see Głuchowski 1987, pl. 9, fig. 5) and many Paleozoic taxa (e.g. Głuchowski 2002, fig. 2E; Głuchowski and Racki 2005, fig. 4c–f). Furthermore, Oji and Twitchett (2015) illustrated isolated ossicles displaying clear evidence of abrasion and post-diagenetic fracturing; therefore, redeposition from Paleozoic rocks cannot be excluded since highly fossiliferous Permian beds with crinoids are actually known in Oman (e.g. Webster *et al.* 2009).

The occurrence of at least four major crinoid clades in the Lower Triassic may have important implications for their phylogenetic relationships, especially with regard to the so-called microcrinoids known from the Paleozoic. From a palaeogeographic perspective, the Svalbard roveacrinid occurrence is consistent with the circum-Tethyan distribution of this crinoid order, extending far north into the Arctic realm due to surface water circulation that allowed the dispersal of somphocrinid larvae as well as of adults during the Late Triassic. The most intriguing discovery may be that of the comatulid-like plates: if these prove to be centrodorsals, they will force a reassessment of previous hypotheses of their Late Triassic origins and imply that the crinoid stalk might have been lost multiple times as previously suggested by molecular data (Rouse *et al.* 2013). Furthermore, discovery of encrinid-like ossicles in the Lower Triassic may solve a long-standing problem concerning the similarities between the late Paleozoic cladid Erisocrinidae and the Triassic encrinids that were long attributable to convergent evolution. Future analysis combining morphological and new temporal data of late Paleozoic and early Mesozoic crinoid taxa (such as in stratocladistics; see Holterhoff and Baumiller 1996) may answer important phylogenetic questions (for instance whether post-Paleozoic crinoids indeed represent descendants of several of the major Paleozoic clades rather than just one).

Conclusions

On the whole, the Svalbard materials are crucial for a number of reasons. Most importantly, it considerably extends the ranges of at least four major crinoid clades back to the Early Triassic, which may radically reassess the previous hypothesis about the timing of post-Paleozoic crinoid radiation. Previous studies suggested that crinoids underwent a major radiation during the Middle–Late Triassic which led to the appearance of many taxa displaying both active and passive mobility (Baumiller *et al.* 2010; Hagdorn 2011; Gorzelak *et al.* 2012). This major morphological and behavioural radiation of crinoids was likely triggered by their interactions with benthic predators during the so-called Mesozoic marine revolution (Baumiller *et al.* 2010). However, our data suggest that the Triassic radiation of crinoids began earlier and was certainly a far more prolonged evolutionary event than previously thought.

The question concerning why crinoid faunas from Svalbard were able to recover so rapidly after the end-Permian extinction is now open. Despite the timing and nature of extinction crisis in higher palaeolatitudes closely resembling those from lower latitude Tethyan settings, previous data also implied a noteworthy rapid recovery in boreal settings (Wignall *et al.* 1998). Strikingly, a recent study also revealed that the Svalbard Archipelago yields one of the most diverse Early Triassic ichthyopterygian assemblages known worldwide (Maxwell and Kear 2013).

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