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A new holocrinid (Articulata) from the Paris Biota (Bear Lake County, Idaho, USA) highlights the high diversity of Early Triassic crinoids ✡

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Abstract

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After the end-Permian crisis and the extinction of their four Paleozoic subclasses, crinoids rapidly recovered. This group is classically believed to have radiated from a small surviving clade and to have diversified during the Middle and Upper Triassic from two lineages. Nevertheless, recent findings suggested that several lineages of crinoids had already diversified during the Early Triassic, and that their diversity has been overlooked. Here we describe a new form of holocrinid, *Holocrinus* nov. sp., from the earliest Spathian (Early Triassic) of southeastern Idaho (USA). So far, the exceptional completeness of sampled specimens, with skeletal elements of arms and stem in connection, is unique for the Early Triassic. They show that derived morphological features had already evolved ~1.3 million years after the Permian-Triassic boundary, supporting the scenario of a rapid Early Triassic diversification of crinoids.

Keywords:
Articulata
Crinoidea
Holocrinus
Spathian
Paris Biota

1. Introduction

Originated in the Lower Ordovician, crinoids have a long and rich fossil record, with more than 6,000 species recorded so far (Pawson, 2007). They occupied an important place with key ecological positions in many Paleozoic and Mesozoic marine communities; their fossil remains are commonly found in abundance in geological exposures of that time (Rouse et al., 2013; Gorzelak et al., 2015). Like other echinoderms, crinoids have been profoundly affected by the end-Permian crisis when most Paleozoic subclasses went extinct, post-Paleozoic crinoids all belonging to the unique subclass Articulata that is considered monophyletic (Pawson, 2007; Hess and Messing, 2011; Rouse et al., 2013; Wright et al., 2017).

Supported by fossil and molecular evidences, a classic evolutionary scenario assumes that after the end-Permian crisis, the remaining crinoids radiated from a small clade probably differentiated from the Cladida at the end of the Permian (Hagdorn, 2011; Hess and Messing, 2011; Rouse et al., 2013). Then, they rapidly diversified from two distinct lineages in the

Middle or Upper Triassic (Simms, 1988; Hagdorn, 1995; Twitchett and Oji, 2005; Hess and Messing, 2011; Oji and Twitchett, 2015), the evolution of both passive and active motility (Baumiller et al., 2010; Hagdorn, 2011; Rouse et al., 2013) being triggered by predation during the so-called 'Mesozoic Marine Revolution' (Baumiller et al., 2010). They gave rise to all forms of post-Paleozoic crinoids including present-day comatulids and stem-crinoids (Rouse et al., 2013; Oji and Twitchett, 2015). This scenario implies that the Mesozoic diversification of crinoids occurred early and was rapid compared to other echinoderms (Twitchett and Oji, 2005), with all large modern clades represented at the end of the Triassic and early Jurassic. No basic innovation happened after the Triassic and no new crinoid habitat has been invaded since that time (Hagdorn, 2011). A peak in morphological disparity was reached as soon as the Middle Triassic (Baumiller et al., 2010).

Recent works have contributed to complement the established scenario, new findings suggesting that crinoids were already diversified as soon as the very Early Triassic (Kashiyama and Oji, 2004; Hagdorn and Göncüoglu, 2007; Oji, 2009; Hagdorn, 2011). Some authors even suggested that distinct lineages might have survived the end-Paleozoic extinction and that the stratigraphic range of certain articulates could extend deeper into the Paleozoic (Klikushin, 1987; Webster and Jell, 1999; Twitchett and Oji, 2005; Webster and Lane, 2007; Oji and Twitchett, 2015; Cohen and Pisera, 2017).

Most specimens of Early Triassic crinoids are represented by the genus *Holocrinus*, which has been extensively studied (Leonardi, 1968; Hagdorn, 1983, 1986, 2011; Mostler and Rossner, 1984; Schubert et al., 1992; Baumiller and Hagdorn, 1995; Kashiyama and Oji, 2004; Oji, 2009; Salamon et al. 2012, 2015, among others), although the predominance of fragmentary remains is a limiting factor to our knowledge of the genus earliest representatives (Hagdorn and Göncüoglu, 2007). Here we describe a new species of *Holocrinus* with most skeletal elements of stem and arms in connection, a feature documented for the first time in the Early Triassic (Leonardi, 1968; Mostler and Rossner, 1984; Schubert et al., 1992; Kashiyama and Oji, 2004; Oji, 2009; Hagdorn and Göncüoglu, 2007; Hagdorn, 2011; Salamon et al., 2015). The described specimens represent a unique opportunity to improve our knowledge of Early Triassic crinoids, all the more *Holocrinus* being central in the evolution of forms leading to isocrinids, a dominant group after the Carnian extinction whose origin remains poorly documented compared to encrinids (Hagdorn, 2011; Stiller, 2011).

2. Material and methods

2.1. Examined material

Four specimens of crinoids have been collected so far from the earliest Spathian strata containing the Paris Biota in southeastern Idaho (Brayard et al., 2017, 2019a, 2019b; Doguzhaeva et al., 2018; Botting et al., 2019; Charbonnier et al., 2019; Iniesto et al., 2019; Romano et al., 2019; Thuy et al., 2019). These specimens were found in an exceptional good state of preservation with ossicles of the proximal stem and isolated arms in connection. Their preservation state is unique for fossils of this age compared to crinoid remains from North America (Schubert et al., 1992), Svalbard (Salamon et al., 2015), Japan (Kashiyama and Oji, 2004) and Oman (Twitchett and Oji, 2015), composed of rare isolated ossicles, mainly columnals. In the present study, proximal stems and sub-complete arms were sampled. Neither cup nor distal stem were found.

Specimens were found in two close, coeval earliest Spathian exposures composed of grey-blue to orange, thin-bedded silty limestones of the Thaynes Group reflecting deposition within the relatively shallow western U.S. basin (Brayard et al., 2017, 2019b). During the Early Triassic, it was located at a near-equatorial position on the western margin of Pangea. Deposits overlie the middle Smithian Lower Limestone unit and lie beneath the Middle Limestone unit dated from the early Spathian based on the occurrence of, e.g., the ammonoid species *Tirolites harti* (Brayard et al., 2017, 2019b). It is coeval or slightly older than the *Tirolites*/*Columbites* beds of South China which yield a radiometric age of ~250.6 Ma (Galfetti et al., 2007).

2.2. Methods

Part of the anatomy of examined specimens is hidden under a fine layer of sediment, which requires very delicate and risky manual preparation. Instead, we applied synchrotron X-ray fluorescence (XRF) major-to-trace elemental mapping to reveal additional features. While the commonly used 3D X-ray tomography suffers from a physical limitation for the study of such flattened fossils (due to the extremely high difference in X-ray absorbance along the flat and long dimension of the sample, respectively), synchrotron XRF mapping of heavy elements such as strontium and yttrium has shown great promise to reveal slightly buried fossil remains, as signal from these elements can escape from a depth of a few hundred µm in fossils (Gueriau et al., 2014, 2018). This 2D imaging technique relies on a similar principle as elemental mapping under a scanning electron microscope (SEM-EDX), but instead of electrons (under the SEM), the emitted XRF photons (element-specific) are produced by bombarding the fossil with X-rays generated by a synchrotron light source. The main advantages are that synchrotron setups can accommodate large fossils (Bergmann et al.,

2012) and are sensitive to trace elements up to the part per million level (Bergmann et al., 2010; Gueriau et al., 2014, 2015). For more information about the XRF principle, advantages of using the synchrotron light, data collection parameters and properties, see Gueriau et al. (2018).

Synchrotron micro X-ray fluorescence (µXRF) maps were collected at the DiffAbs beamline of the SOLEIL synchrotron (Gif-sur-Yvette, France), using a monochromatic beam of 18 keV, selected for excitation of K-lines from phosphorus to yttrium and L-lines from cadmium to uranium. The beam was reduced down to a diameter of 50 µm using a molybdenum pinhole, allowing high resolution mapping of the specimens. The sample was mounted on a scanner stage allowing 90 mm movements with micrometer accuracy, and orientated at 45° to the incident beam and at 45° to the XRF detector, a four-element silicon drift detector (Vortex ME4, Hitachi High-Technologies Science America, Inc., total active area: 170 mm^2) placed in the horizontal plane. µXRF elemental maps were then produced through the collection of integrated intensities (sum of the four elements of the XRF detector) in selected spectral regions of interest corresponding to emission from elements showing contrast between the fossil and its encasing matrix. See Brayard et al. (2019a) for additional information and examples of synchrotron µXRF imaging of Paris Biota fossil specimens.

Specimens were also examined under luminescence. The imaging system used to record the luminescence images is a home-made set-up which consists of a low-noise 1 megapixel Si EM-CCD camera (Qimaging Rolera EMC2) which sensitivity ranges between 200 and 1100 nm. The camera is fitted with a UV-VIS-IR 60 mm 1:4 Apo Macro lens (CoastalOptics) in front of which is positioned a filter wheel holding 8 Interference band-pass filters (Semrock) to collect images in specific spectral ranges. Illumination was provided by 16 LED lights ranging from 365 to 700 nm (CoolLED pE-4000), coupled to a liquid light-guide fiber fitted with a fiber-optic ring light guide, allowing homogeneous illumination of the region of interest (see Brayard et al., 2019a for additional information and examples).

3. Systematic paleontology

Systematics and terminology for morphological descriptions follow the revised version of the Treatise of Invertebrate Paleontology, Crinoidea, volume 3 (Hess and Messing 2011). The proposed open nomenclature follows Bengtson's (1988) recommendations.

Specimen repositories. Figured specimens are all deposited in collections of university of Burgundy in Dijon abbreviated UBGD (Université de Bourgogne, Géologie Dijon, France).

Phylum Echinodermata Klein, 1754

Class Crinoidea Miller, 1821

Subclass Articulata Zittel, 1879

Order Holocrinida Jaekel, 1918

Family Holocrinidae Jaekel, 1918

Genus ***Holocrinus*** Wachsmuth et Spinger, 1887

Holocrinus nov. sp.

Figs. 1-3

1968. Non *Holocrinus* nov. sp. - Leonardi.

2004. Non *Holocrinus* nov. sp. - Kashiyama and Oji.

Syntypes: UBGD 30563 and UBGD 30564.

Material: UBGD 30563, UBGD 30564, UBGD 30611, UBGD 30612.

Type locality: Earliest Spathian exposures of the Paris Canyon, west of the city of Paris, Idaho (USA).

Stratigraphic position: Earliest Spathian (Early Triassic, ~250.6 Ma), Lower Shale unit of the Thaynes Group.

Diagnosis: Small columnals 1.8 mm wide. Cryptosymplexy between nodals and infranodals. Long cirri with over 20 cirrals. Arms with pinnules regularly developed on alternate sides of successive brachials except on every third brachial (hypozygal) that lack pinnule. In pinnules, first and second pinnulars of identical size.

Description:

Stem (Fig. 1). Shape of columnals substellate in cross section. Internodes short, noditaxes composed of seven columnals. Nodals higher than internodals: nodals *ca.* 0.6 mm thick, internodals *ca*. 0.45 mm thick. All columnals 1.8 mm wide; nodals not wider than internodals. Articular facets symplectial between columnals of a same nodotaxis, forming crenulate sutures in lateral view. Articulation cryptosymplectial between distal facet of nodals and infranodals, visible as a straight line in lateral view. Nodals with at least three elliptical cirrus sockets; total number of cirrus sockets present per nodal not visible on any preserved specimens. Proximal cirrals with synarthrial articulation, elliptical in cross section. Cirri very long with over 20 cirrals.

Arms (Figs. 2, 3). Arms long, flexible, uniserial throughout, even distally. Brachials short, never wedge-shaped even distally. Pinnules regularly developed on alternate sides of

successive brachials except on every third brachial (hypozygal) that lack pinnule. In pinnules, first and second pinnulars exhibit the same size. Cup not preserved in the available specimens. **Remarks**: Only arms and proximal stems were available for study. The cup and the distal end of stems (dististeles) remain unknown. In addition, articular facets of columnals could neither be properly observed nor fully described. Considering the lack of knowledge of cup and articulation morphologies, two imperative features for crinoid species identification, no species name was attributed to the present taxon, formal species designation pending for further findings. However, the specimens present a unique combination of both derived and ancestral morphological features that had never been described so far, suggesting that the taxon is new to science.

The studied specimens show two diagnostic characters of the family Holocrinidae: (*i*) long, highly flexible (Fig. 3) and uniserial arms (Fig. 2), and (*ii*) stem with few long cirri attached to cirrinodals (Fig. 1(C, D); Hess and Messing, 2011). In addition, the stem is composed of short internodes. Long cirri are connected to nodales with elliptical and synarthrial articular facets between proximal cirrals, two typical characters found in the genus *Holocrinus* (Hess and Messing, 2011).

Besides these diagnostic features of the Holocrinidae, specimens also show derived characters that are commonly found in Isocrinidae. The substellate shape of columnals in cross section is more common in Isocrinidae than in Holocrinidae, although it has already been reported in certain *Holocrinus* (Hagdorn et al., 1996). The presence of cryptosymplectial articulations between nodals and infranodals (Fig. 1(B)) is typical of the genus *Isocrinus*. However, cryptosymplexy has already been reported in *Holocrinus* specimens of the Smithian Hiraiso Fm. of Japan (Kashiyama and Oji, 2004; Hess and Messing, 2011). Kashiyama and Oji (2004) considered their assignation of columnals with cryptosymplexies to *Holocrinus* as tentative considering the low stratigraphic position of these fossils. Indeed, no reliable record of *Isocrinus* representatives had been reported from the Early Triassic in 2004. Kashiyama an Oji (2004) were followed by Hess and Messing (2011) who considered that cryptosymplexy may be present in holocrinids as soon as the Early Triassic. On the contrary, Salamon et al. (2015) collected crinoid nodals in the Early Triassic of Svalbard and assigned them either to the genus *Holocrinus* or *Isocrinus*, depending on the presence of symplectial (*Holocrinus*) or cryptosymplectial and synostosial (*Isocrinus*) articulations between nodals and infranodals. Major differences between morphological features of holocrinids and isocrinids were reviewed by Hagdorn (2011). The two groups mainly differ in the morphology of arms and cups. Considering the typical holocrinid features found in the sampled specimens from Idaho,

we follow Hess and Messing (2011) and consider that cryptosymplexies can occur in some *Holocrinus*.

While proximal arms are uniserial in holocrinids, arms are supposed to distally become biserial with wedge-shaped brachials in hypothetical forms ancestral to Articulata (Hagdorn, 2011). In specimens from the Paris Biota, the presence of short, not wedge-shaped brachials and uniserial arms even distally are derived characters (Fig. 2). While in ancestral holocrinids the second pinnular is longer than the first one (Hagdorn, 2011), first and second pinnulars are the same size in Paris Biota specimens (Fig. 2(C, D)). Finally, in the present specimens, every third brachial lack a pinnule and arm branching is regular. These two derived characters contrast with other *Holocrinus* representatives in which arm branching is irregular (Hess and Messing, 2011).

The new species exhibits obvious morphological similarities with other *Holocrinus* species described from Early and Middle Triassic deposits worldwide (Hagdorn, 1986, 2011; Hagdorn et al., 1996, 1997; Schubert et al., 1992; Kashiyama and Oji, 2004; Niedzwiedzki and Salamon, 2006; Salamon et al., 2015). As in most *Holocrinus* species, the stem is composed of short internodes (between 5 and 9 internodals), nodals are higher than internodals, and cirri are very long (Hess and Messing, 2011; Fig. 1). However, *Holocrinus* nov. sp. can be distinguished from most other *Holocrinus* representatives by its relative small size, the stellate shape of columnals in cross section (also reported in *Holocrinus dubius* and *Holocrinus meyeri*; Hagdorn et al., 1996), which may be partly due to their proximal position in the stem and the small size of specimens, and the presence of cryptosymplexies between nodals and infranodals (Fig. 1(B)). Svalbard crinoid remains described by Salamon et al. (2015) differ from the new species by the absence of cryptosymplexy, and by the subcircular to subpentagonal shape of columnals in cross section. Specimens of *Holocrinus* nov. sp. described from the Smithian of Japan (Kashiyama and Oji, 2004) and Russia (Oji, 2009) differ by the inflated lateral surface of internodals, and by very high nodals compared to internodals (nodals are 1.7 higher than internodals against 1.3 in the new American species). Specimens of *Holocrinus* nov. sp. from the Olenekian of Italy (Leonardi, 1968), Austria (Mostler and Rossner, 1984) and Turkey (Hagdorn and Göncüoglu, 2007) differ by the circular to pentagonal shape of columnals. *Holocrinus smithi* Clark, 1908 from the Spathian of North America differs by the absence of cryptosymplexy, more rounded shape of columnals in cross section, and wider nodals (up to 5.3 mm in diameter). *Holocrinus acutangulus* (Meyer, 1847) from the Anisian of Germany, Poland, Austria, and Hungary (Niedzwiedzki and Salamon 2006; Hagdorn et al. 1996, 1997; Salamon et al., 2012) is

somewhat similar but can be distinguished by its wider columnals (up to 3.1 mm), subpentagonal in cross section (Niedzwiedzki and Salamon, 2006). *Holocrinus wagneri* (Benecke, 1887) from the Anisian of Germany clearly distinguishes by the presence of only two to three cirrals per nodal. *Holocrinus beyrichi* (Picard, 1883) from the Anisian of Germany is characterized by very short cirri. In *Holocrinus dubius* (Goldfuss, 1831) from the Anisian of Germany, Austria, Poland, Hungary, Italy, and Caucasus (Hagdorn, 1986; Niedzwiedzki and Salamon, 2006; Salamon et al., 2012), the stem is composed of wide nodals (up to 4.6 mm) and more rounded columnals subpentagonal to substellate in shape, and by symplectial articulations between nodals and infranodals. Columnals of *Holocrinus meyeri* Hagdorn et Gluchowski, 1993, from the Anisian of Poland, are much wider (up to 7.7 mm in diameter) and are subpentalobate to circular in shape with symplectial articulations (Hagdorn and Gluchowski, 1993, Hagdorn et al., 1996). *Holocrinus doreckae* Hagdorn, 1983 from the Anisian and Ladinian of Germany has also large columnals (up to 4.8 mm in diameter), more rounded in cross section (subcircular to sublobate), and shows no cryptosemplexy. Specimens of *Holocrinus* sp. indet. were reported from the Early or Middle Triassic of Turkey (Hagdorn and Göncüoglu, 2007); they mostly differ from *Holocrinus* nov. sp. by their subcircular to subpentagonal shape in cross section.

4. Discussion

4.1. Preservation of Early Triassic crinoids

Despite the many new findings published over the last decades (Kashiyama and Oji, 2004; Hagdorn and Göncüoglu, 2007; Oji, 2009; Hagdorn, 2011; Salamon et al., 2012, 2015), the morphology of early representatives of holocrinids remains poorly known. The preservation of their skeleton is always highly fragmentary and Early Triassic holocrinids were exclusively known by isolated columnals, pluricolumnals, and cirrals so far (Hagdorn and Göncüoglu, 2007). In holocrinids as in isocrinids, it is believed that new columnals were constantly generated below the infrabasal circle while distal elements gradually moved towards the distal end of the stem and were ultimately shed off at the rupture point below nodals (Oji and Shonan, 1992; Shonan and Oji, 1998; Hagdorn and Göncüoglu, 2007; Hagdorn, 2011). This permanent shedding of distal stem parts in cirrus-attached crinoids can account for the overrepresentation of distal columnals and cirrals in holocrinid concentration beds during the Early Triassic, a common conservation pattern in Mesozoic isocrinids as well. Conversely, it can also account for the extremely rare occurrence of proximal columnals, brachials and cups with all elements in connection. In the specimens described here, the

substellate shape of columnals with cirri in connection suggests that proximal stem parts (proxistele) are preserved (Hagdorn, 2011).

Such a rare preservation has been already encountered in the Middle Triassic *Konservat lagerstätten* of the Germanic Basin (Hagdorn, 2011), but is exceptional for the Early Triassic, as the present specimens constitute the earliest post-Paleozoic crinoids with skeletal elements in connection recorded so far. This is certainly because such crinoid *Konservat lagerstätten* had not been discovered before due to the scarcity of Early Triassic shallow water environments required for this type of preservation. In the Muschelkalk *Konservat lagerstätten* of the Germanic Basin, subsequent stages in holocrinid decay were described by Hagdorn and Baumiller (1998). Interestingly, complete and articulated specimens were typically found smothered with mud (Hagdorn and Baumiller, 1998). Kashiyama and Oji (2004) also reported that isolated columnals of the Smithian Hiraiso Fm. were well preserved in siltstones, while similar remains were just preserved as molds in sandstones. In the present case study, the exceptional preservation state of specimens has probably been facilitated by the occurrence of silt deposits.

4.2. The diversity of Holocrinus

Recent studies have significantly renewed our knowledge of the first post-Paleozoic crinoids, which appear more diversified than previously assumed (Kashiyama and Oji, 2004; Hagdorn and Göncüoglu, 2007; Oji, 2009; Hagdorn, 2011; Salamon et al., 2012). Several works also indicate that distinct crinoid lineages might have survived the end-Permian mass extinction and that Articulata have originated very soon after this event or even before, during the Permian (Klikushin, 1987; Twitchett and Oji, 2005; Oji and Twitchett, 2015; Cohen and Pisera, 2017). Due to its wide stratigraphic range and central phylogenetic position, the genus *Holocrinus* has been extensively studied, especially in the 1980s and 1990s (Hagdorn 1983, 1986; Schubert et al., 1992; Baumiller and Hagdorn, 1995), although it remains poorly known because of its fragmentary preservation (Hagdorn and Göncüoglu, 2007). It is not until the last decade that new findings from the northern hemisphere increased our knowledge of this genus.

So far, *Holocrinus* includes eleven nominal species reported from the Griesbachian to the Ladinian (and possibly up to the Rhaetian), in Europe, Asia, and North America. The richness of its fossil record gradually increases with time from the Early Triassic to the Middle Triassic and declines in the Late Triassic. Very early putative representatives of the genus *Holocrinus* have been reported from the Induan of Svalbard (Salamon et al., 2015), but

this occurrence needs to be confirmed. Two species were reported from the Smithian of Svalbard, North Japan, and eastern Russia, and three species were described in the Spathian of Italy, Austria, Hungary, and North America. Most species are present in the Middle Triassic, with seven species for the Anisian of Germany, Poland, Austria, Hungary, Italy, Caucasus and Turkey, and two species for the Ladinian of Germany and Spain. Species were mainly reported from the Anisian and Ladinian of the Germanic Basin and are particularly common in the Anisian (Salamon et al., 2012). One species was also reported from the Anisian of Caucasus and one from the Ladinian of Spain (Alicante Basin), the only one to be known from outside the Germanic Basin in the Middle Triassic. In the Upper Triassic, holocrinids were exclusively represented by the genus *Tollmannicrinus* Kiklushin, 1992, which is recorded from the late Anisian to the Rhaetian in Europe, Asia, Timor, and New Zealand (Hagdorn, 2011). However, one *Holocrinus* species was recently reported from the Rhaetian of Iran; if confirmed, this would extend the stratigraphic range of the genus to almost the entire Triassic (Salamon et al., 2012). To conclude, the genus *Holocrinus* shows an exceptionally long stratigraphic record and survived the mid-Carnian extinction when a major turnover took place in Triassic crinoid diversity including the extinction of encrinids (Hagdorn, 2011; Salamon et al., 2012). Currently, the genus *Holocrinus* includes the following species and records:

- *Holocrinus?* sp. from the Griesbachian/Dienerian of the Vardebukta Fm. and from the Smithian Tvillingodden Fm., Svalbard (Salamon et al., 2015);
- *Holocrinus* nov. sp. from the Smithian Hiraiso Fm., North Japan (Kashiyama and Oji, 2004) and Smithian Zhitkov Fm., South Primorye, eastern Russia (Oji, 2009);
- *Holocrinus* nov. sp. from the earliest Spathian of the Thaynes Fm., Idaho (this study);
- *Holocrinus* nov. sp. from the Spathian Werfen Fm., Southern Alps, Italy (Leonardi, 1968), Northern Alps of Austria (Mostler and Rossner, 1984), and Czopak Marl Fm. of Hungary (Hagdorn and Göncüoglu, 2007);
- *Holocrinus smithi* Clark, 1908 from the Spathian part of the Moenkopi Group, Nevada and Arizona, and Thaynes Group, Idaho (Hagdorn, 1986; Schubert et al., 1992);
- *Holocrinus acutangulus* (v. Meyer, 1847) from the early Anisian of Germany, Poland, Austria, and Hungary (Niedzwiedzki and Salamon, 2006; Hagdorn et al., 1996, 1997, Salamon et al., 2012);
- *Holocrinus wagneri* (Benecke, 1887) from the early Anisian of Germany;
- *Holocrinus beyrichi* (Picard, 1883) from the middle Anisian of Germany;

- *Holocrinus dubius* (Goldfuss, 1831) from middle-late Anisian of Austria, Poland, Hungary, Italy, and Caucasus (Hagdorn, 1986; Niedzwiedzki and Salamon, 2006; Salamon et al., 2012);
- *Holocrinus meyeri* Hagdorn et Gluchowski, 1993, from the late Anisian of Poland (Hagdorn and Gluchowski, 1993; Hagdorn et al., 1996);
- *Holocrinus doreckae* Hagdorn, 1983 from the upper Anisian and Ladinian of Germany (Hagdorn, 1983);
- *Holocrinus* sp. indet. from the Early or Middle Triassic of Turkey (Hagdorn and Göncüoglu, 2007);
- *Holocrinus cisnerosi* Schmidt, 1935, from the Ladinian of Spain (Hagdorn, 2011);
- *Holocrinus?* sp. from the Rhaetian Nayband Fm., Central Iran (Salamon et al., 2012).

From this updated checklist, it turns out that our knowledge of *Holocrinus* is biased by the overrepresentation of *Konservat lagerstätten* from the Middle Triassic of the Germanic Basin. *Holocrinus* is assumed to occur worldwide during the Early and Middle Triassic (Hagdorn, 1995; Hagdorn and Göncüoglu, 2007; Salamon et al., 2012) but it appears to be mainly limited to the Northern Hemisphere – from North America, Europe, eastern Russia and North Japan. However, the diversity of the genus remains under-estimated, considering for example the new findings from the Carnian of Italy and China who are still awaiting for a formal description and publication (Hagdorn, 2011).

4.3. The Early Triassic diversification of crinoids

In the recent version of the Treatise of Invertebrate Paleontology, Crinoidea, volume 3 (Hess and Messing, 2011), the sub-class Articulata is regarded as monophyletic and exclusively post-Paleozoic. This is supported by recent molecular results (Rouse et al., 2013, Wright et al., 2017) suggesting that the Articulata stemmed in the Middle or Upper Triassic and radiated from a small clade that survived the end-Paleozoic crisis. This is also in agreement with former evolutionary scenarios that assumed that post-Paleozoic crinoids diversified during the Middle and Late Triassic with both passive and active motility (Baumiller et al., 2010; Hagdorn, 2011) being triggered by benthic predators during the so-called ‘Mesozoic Marine Revolution’ (Baumiller et al., 2010). However, molecular results should be taken with caution because analyses of extant crinoids can only support the monophyly of the entire class Crinoidea (Roux et al., 2013) and confidence limits of the molecular clock cannot exclude a Permian origin of the sub-class Articulata (Rouse et al., 2013; Salomon et al., 2015, Cohen and Pisera, 2017).

Conversely, other authors have suggested that the stratigraphic range of some articulates could extend deeper into the Paleozoic or into the earliest Triassic (Webster and Jell, 1999; Twitchett and Oji, 2005; Webster and Lane, 2007; Salamon et al., 2015; Cohen and Pisera, 2017), including an intense morphological diversification early in the Triassic. Along with other results (Twitchett et al., 2004; Oji and Twitchett, 2015), this advocates for a rapid evolution of crinoids as soon as the Early Triassic, possibly from several articulate lineages that survived the end-Permian crisis.

4.4. Morphological evolution

Compared to the order Encrinida, the evolution of holocrinids, which is believed to lead to isocrinids, is less continuously documented (Hagdorn, 2011). Here, the newly described specimens of *Holocrinus* constitute an opportunity to better document evolutionary forms of crinoids leading to the emergence of isocrinids.

4.4.1. Evolution of size

The new species is characterized by its relative small size. Larger columnals (up to 4 mm) are for instance known from the slightly younger Spathian Virgin Limestone of Nevada (unpubl. specimen Muschelkalkmuseum MHI 1806; H. Hagdorn, pers. comm. 2018) and Utah (unpubl. field observation from the authors). However, it is unlikely that the studied specimens are juveniles of these larger forms because the stem shows derived morphological features (see above) while ancestral characters are usually preserved in juvenile stages of holocrinids (Hagdorn, 2011). This small size is similar to the size of several Early Triassic specimens previously described by Leonardi (1968), Mostler and Rossner (1984), Kashiyama and Oji (2004), Hagdorn and Göncüoglu (2007), Oji (2009), and Salamon et al. (2015). Many Early Triassic echinoderms have been reported to be small-sized animals (Twitchett and Oji, 2005; Twitchett, 2006), but recent discoveries of large-sized specimens of asteroids (Villier et al., 2018) and ophiuroids (Brayard et al., 2017; Thuy et al., 2019) contradict this view. The size of *Holocrinus* gradually increased during the Middle Triassic. Hagdorn et al. (1996) and Hagdorn and Göncüoglu (2007) specifically noticed a gradual increase in size of *Holocrinus* species from the lower Anisian (*H. acutangulatus*) to the late Anisian (*H. dubius* and *H. meyeri*) of the Germanic Basin.

4.4.2. Evolution of motility

During the Mesozoic, the diversification of crinoids was marked by morphological and ecological innovations that are mainly linked to the evolution of mobile forms. Autotomy and active motility are believed to have played a determinant anti-predatory role in the evolution of post-Paleozoic crinoids, and to have favored the diversification of motile crinoids represented by stem-crinoids with cirri and comatulids in Modern seas (Baumiller, 2008). Like their closest relatives isocrinids and comatulids, species of *Holocrinus* probably lived attached to either hard or soft bottom sediments by their cirri, a successful strategy also present in isocrinids (Hagdorn, 2011). This contrasts with encrinids, which were permanently cemented to hard substrates by means of a holdfast. There are taphonomic evidences (e.g., fragmentation patterns with segments terminating with a nodal, secondary secretion of calcite on the distal nodal facet) that holocrinids were also capable of autotomy (Baumiller and Hagdorn, 1995). This is supported by recent microstructural analyses of the stereom in holocrinid columnals from the Middle Triassic (Gorzelak, 2018). They could shed off the distal stem parts, move actively, then re-attach themselves to the substrate in a similar way to isocrinids. Such an innovation was made possible by the morphological evolution of the stem and the development of a preformed rupture point located below the nodal, and automatically positioning a cirriferous nodal at the very end of the stem for attachment (Hagdorn, 1983; Baumiller and Hagdorn, 1995; Hagdorn et al., 2007).

In isocrinids, the evolution of cryptosymplexies indicates a functional differentiation of the distal articulation of nodals associated to autotomy. This innovation was believed to first occur during the Anisian (Hagdorn, 1983, 2011). Here we document an earlier, Early Triassic occurrence of cryptosymplexies in holocrinids, in agreement with some previous observations (Kashiyama and Oji, 2004, Hess and Messing, 2011). It shows that a functional differentiation of the stem occurred very early in the evolution of holocrinids and was subsequently inherited by the isocrinids. This is not necessarily contradictory with the persistence of symplexies in other *Holocrinus* species during the entire Triassic. The evolution of cryptosymplexies could be regarded as a convergent feature present in crinoids living in marine habitats made of soft bottom sediments (Hagdorn, 1983).

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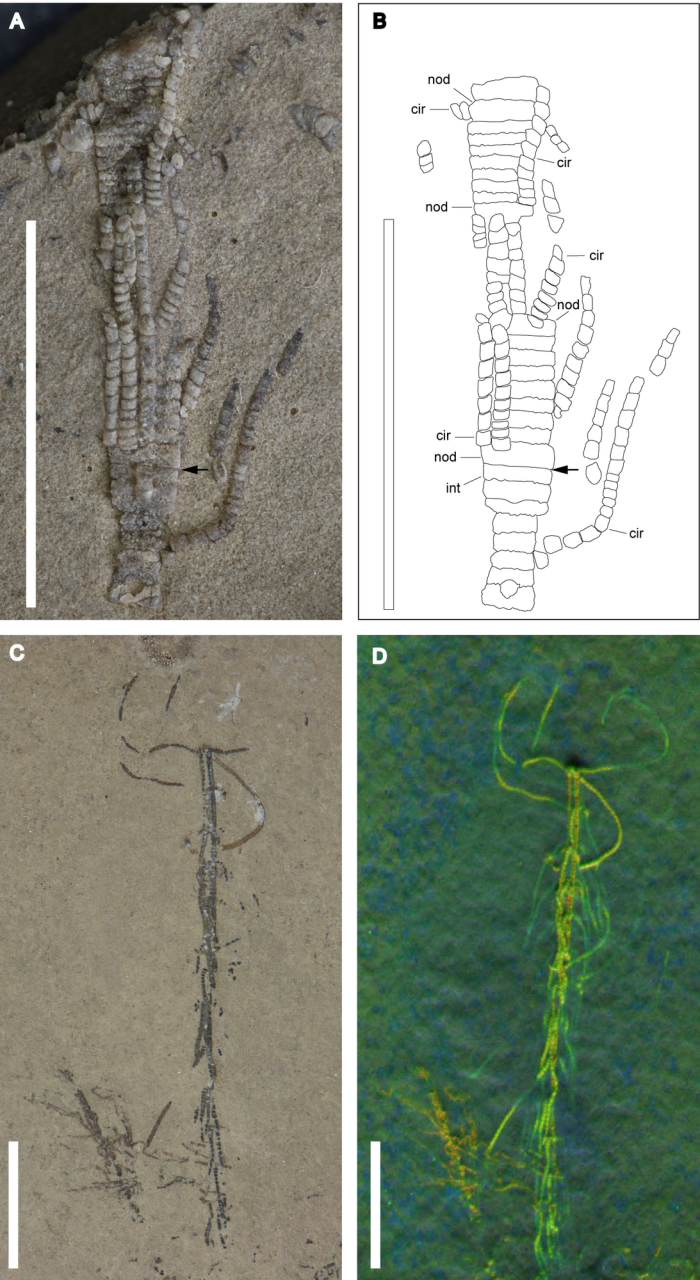
Figure captions

Figure 1. A, B. Close-up view of the proximal stem with cirri of specimen UBGD 30563 (syntype) in lateral view (A) and redrawn (B). Nod: nodal, int: internodal, cir: cirrus. The arrow indicates a cryptosymplectial articulation between the nodal distal facet and an internodal. **C, D**. Proximal stem of specimen UBGD 30612 (see also Brayard et al., 2019a: fig. 4(B)). C: optical photograph; D: Synchrotron XRF-mapping image (scanned at the DiffAbs beamline, SOLEIL; scan step: 60×60 μm^2, dwell time: 20 ms). Scale bars: 10 mm.

Figure 2. Isolated arms. **A**. Entire arm of specimen UBGD 30564 (syntype); black and white image resulting from illumination at 365 nm and detection at 650 nm. **B**. Close-up view of specimen UBGD 30611. **C, D**. Close-up view of specimen UBGD 30564 in lateral view (C) and redrawn (D). Br. p.: brachial plate with pinnule, Pi: pinnular plate, Br. no p: brachial with no pinnule. Scale bars: 5 mm.

Figure 3. Three isolated arms of specimen UBGD 30564 (syntype). **A**. Optical photograph. **B**. Synchrotron XRF-mapping image (scanned at the DiffAbs beamline, SOLEIL; scan step: 100×100 μm^2, dwell time: 15 ms). Scale bars: 5 mm.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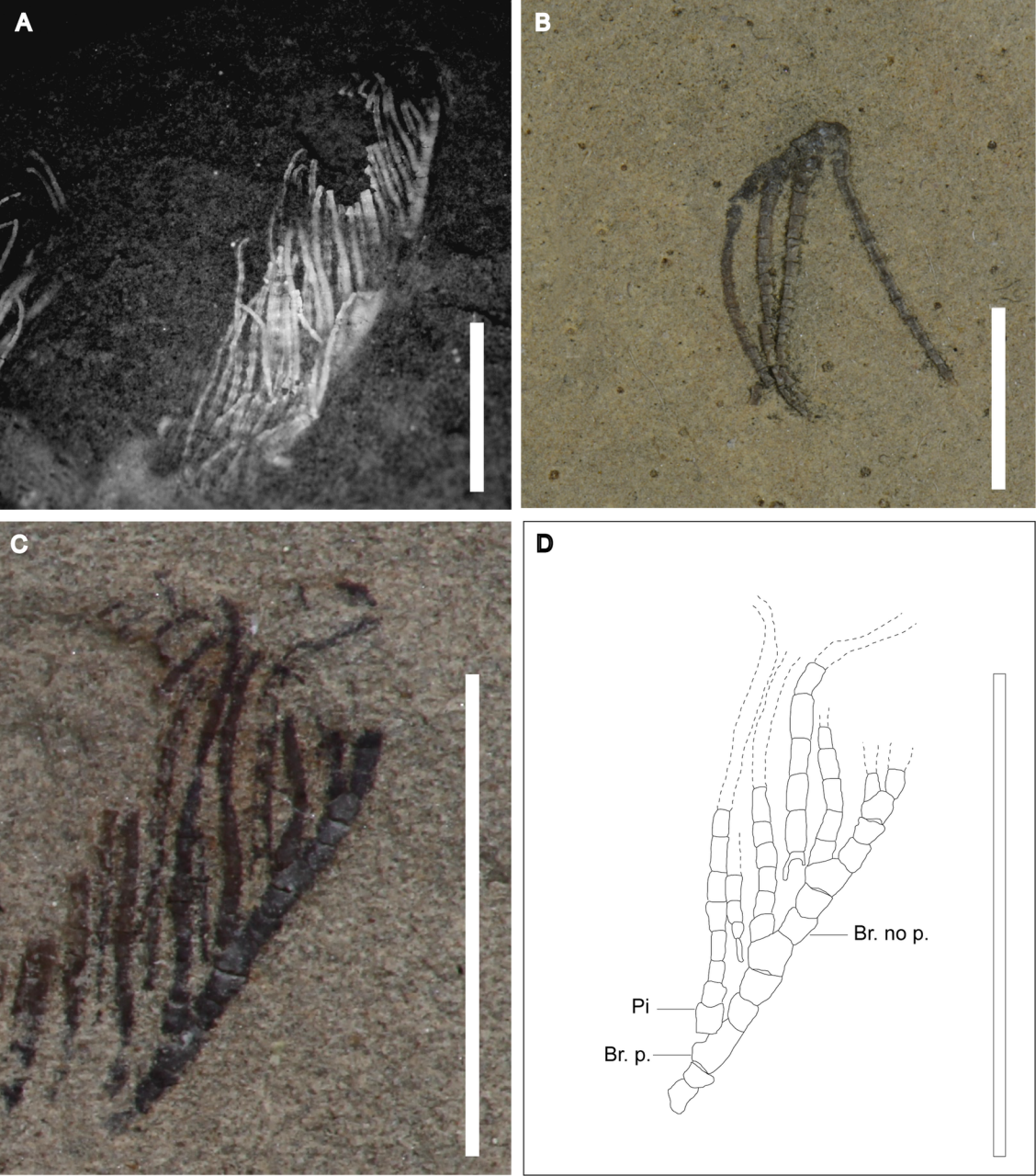
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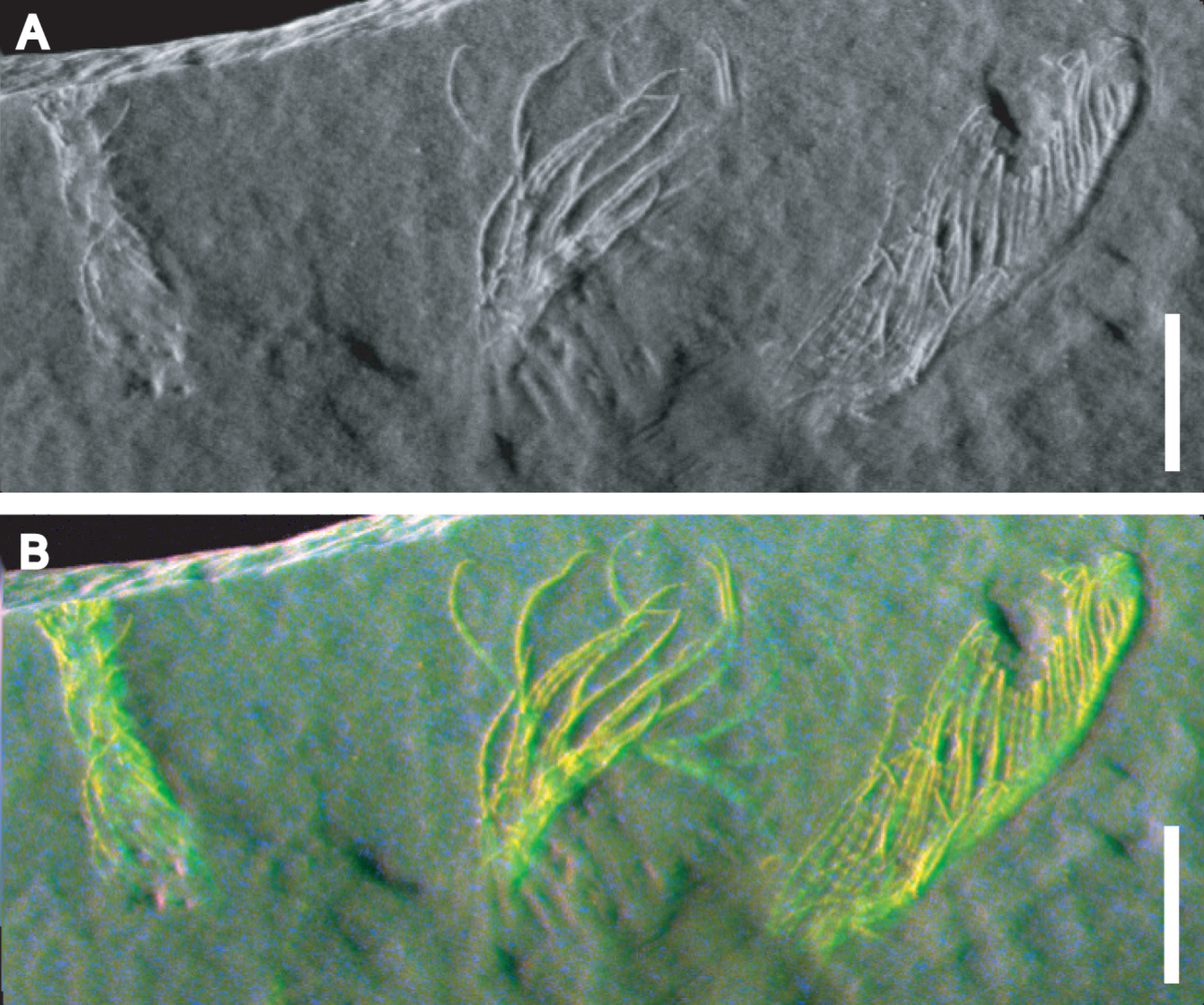
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