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REGULAR RESEARCH ARTICLE

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Experimental neoichnology of crawling stalked crinoids

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Abstract

Stalked crinoids have long been considered sessile. In the 1980s, however, observations both in the field and of laboratory experiments proved that some of them (isocrinids) can actively relocate by crawling with their arms on the substrate, and dragging the stalk behind them. Although it has been argued that this activity may leave traces on the sediment surface, no photographs or images of the traces produced by crawling crinoids have been available. Herein, we present results of neoichnological experiments using the shallowest species of living stalked crinoid, *Metacrinus rotundus*, dredged from Suruga Bay (near the town of Numazu, Shizuoka Prefecture, ∼ 140 m depth). Our results demonstrate that isocrinids produce characteristic locomotion traces, which have some preservation potential. They are composed of rather deep and wide, sometimes weakly sinuous, central drag marks left by the stalk and cirri, and short, shallow scratch marks made by the arms. Based on the functional morphology and taphonomy, it has been argued that the ability to autotomize the stalk and relocate had already evolved in the oldest stem-group isocrinids (holocrinids), likely in response to increased benthic predation pressure during the so-called Mesozoic marine revolution. Our data show that this hypothesis may be corroborated in the future by ichnological findings, which may provide more direct proof of active locomotion in Triassic holocrinids.

Keywords Sea lilies · Traces · Locomotion · Experiments · Triassic

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We dedicate this paper to the memory of our mentor and friend Dr. Hans Hess who recently passed away. Our joint meetings and correspondence fired up our interests in crinoids (which Hans used to call: "masterpieces of nature and the most beautiful of fossils"… We fully agree with him).

Editorial handling: C. Meyer.

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Introduction

One of the most fascinating and surprising traits of some Recent stalked crinoids, the isocrinids, is their locomotion ability. Although most isocrinids anchor only via hook-like cirri rather than a cemented holdfast or roots, no evidence existed that they could relocate. It was therefore assumed that they were sessile (e.g., Lawrence 1987). Although isocrinids include the most shallow dwelling of any extant stalked crinoids (in as little as 100 m depth off Japan, e.g., Oji 1986), in situ observations had to await the development of submersible technology (e.g., Macurda and Meyer

1974), and locomotion was not observed for another decade (Messing 1985; Messing et al. 1988; Baumiller and Messing 2007; Baumiller et al. 2008). Results obtained from these deep-sea explorations, as well as from laboratory flow-tank experiments (Baumiller et al. 1991; Birenheide and Motokawa 1994), revealed that isocrinids may actively (at a speed of up to about ~ 30 mm/s) relocate by crawling with their arms and dragging the stalk behind them. Two basic types of isocrinid locomotion have been distinguished: (1) the so-called finger-tip pull, where the crawling involves a repeating sequence of movements by the proximal portions of the leading arms only, bending sharply away from the substrate; and (2) the so-called elbow-crawl, where traction with the substrate is provided by the pinnule-covered oral side of the middle third to distal half of the arms that remain strongly flexed aborally (Baumiller and Messing 2007). In both modes of locomotion, the stalk, which remains nearly straight with only the proximal portion being bent away from the bottom, is pulled passively by the crawling arms. It has been argued that this activity generates traces on the substrate. Unfortunately, due to low angles at which the video footages were shot, no detailed photos of such locomotion traces were available (Baumiller and Messing 2007). Notably, it has been only mentioned that crawling isocrinids produce two types of traces: (1) a drag mark left by the stalk, and (2) short radiating scratch marks around the central drag (Messing et al. 1988).

The aim of this study is thus to document for the first time the morphology of the traces produced by Recent isocrinids. This has been achieved by neoichnological experiments, which were carried out on the shallowest living stalked crinoid *Metacrinus rotundus* under controlled laboratory conditions. The detailed description of the traces made by this stalked crinoid may potentially be used for detecting isocrinid and holocrinid moving traces on bedding surfaces in the geologic record, giving evidence of crinoid motility in the past.

Materials and methods

Living specimens of the shallowest isocrinid, *Metacrinus rotundus* (Fig. 1), were dredged from northeastern Suruga Bay (near the town of Numazu, Shizuoka Prefecture) in June and August of 2017 (~ 35°3′N, ~ 138°48′E,

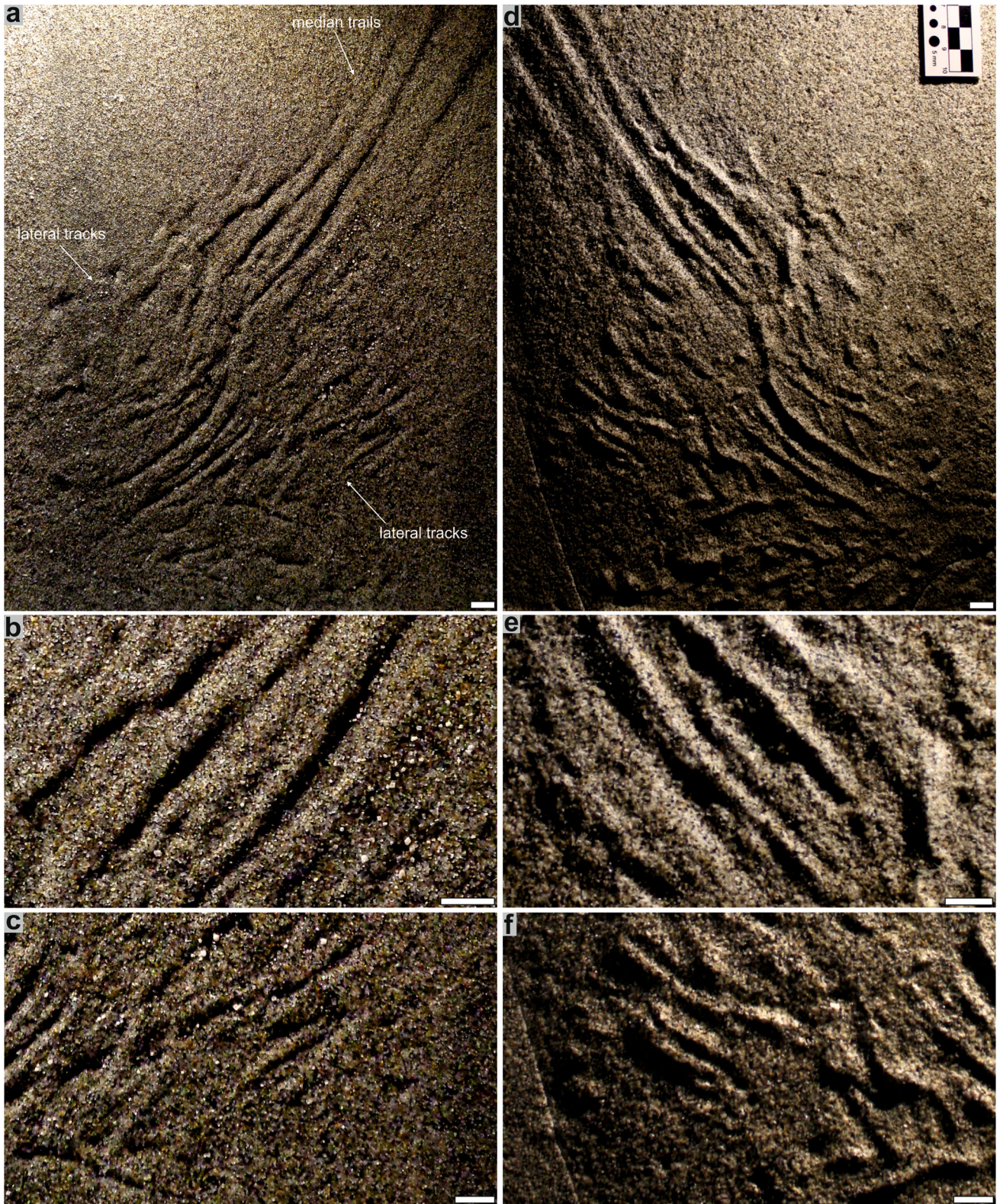**Fig. 1** *Metacrinus rotundus* during locomotion
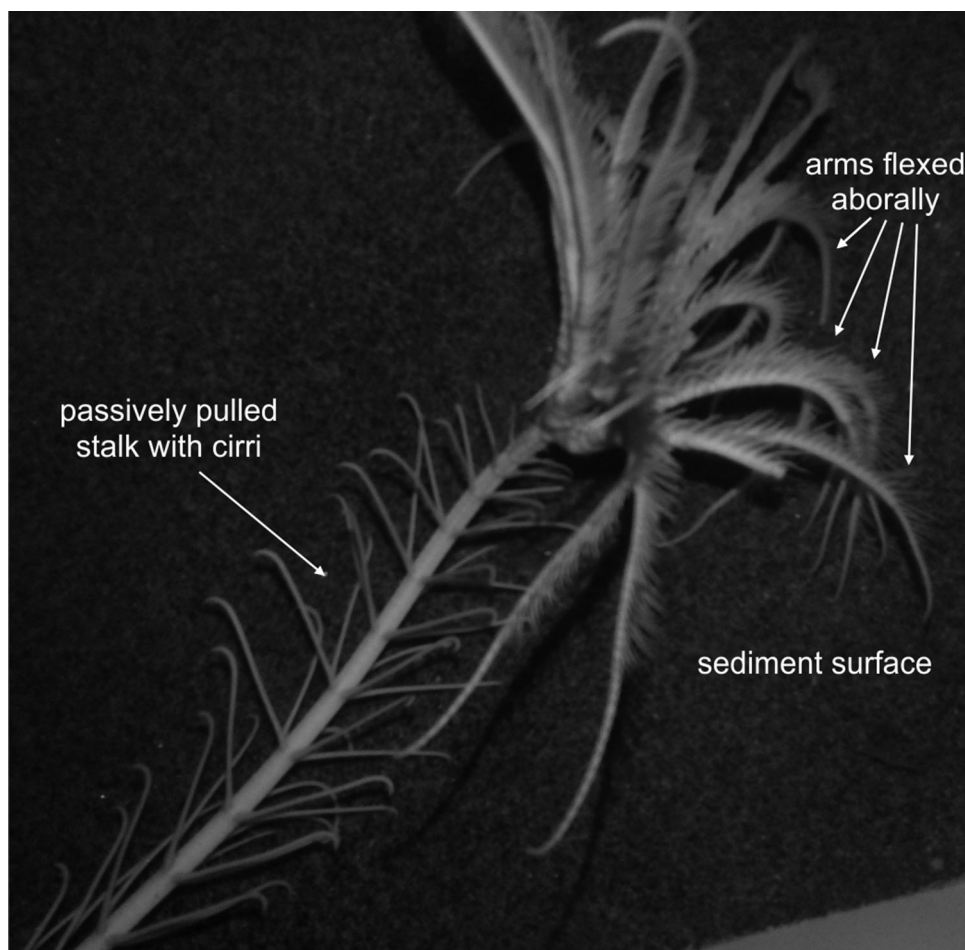
Fig. 2 Surface features produced by *Metacrinus rotundus*. **a** General view of median trails and lateral tracks left by cirriferous stalk and arms, respectively. **b** Close up of median trails. **c** Close up of lateral tracks. **d–f**. Gypsum casts (hypichnia) of the above illustrated traces (**a–c**; correspondingly). Scale bars 1 cm

$\sim$ 140 m depth). Crinoids were collected from the sea bottom using a 90-cm-wide naturalist dredge with a net. Collected individuals ($\sim$ 20) were transferred to an experimental seawater tank in Nagoya University Museum within several hours after capture. The aquarium was maintained at a constant seawater temperature of $\sim$ 16 °C, in darkness and under circulation provided by a water pump. The seawater used in the experimental tank was obtained from the sea surface of the dredging site. In general, sampling and handling methodology followed Kitazawa and Oji (2010, 2014).

After 2 weeks of acclimatizing the crinoids, the experimental tank was divided into two zones ("breeding" and experimental) separated from each other by a plastic net. Within the experimental zone, we placed a $\sim$ 40 $\times$ 30 cm box floored with fine-grained sand, which was smoothed before crinoid was introduced. The behavior of crawling crinoids was observed using a self-made underwater camera that was constructed on the basis of small single-board computer—Raspberry Pi 3 device with connected V2 Camera Module. These parts were placed into a commercially available, small transparent container with a power bank. The container box was secured with insulating tape to prevent any leaks. Raspberry Pi 3 board was combined with the source of red light that is generally less stressful for crinoids. Also, to avoid exposing crinoids to permanent light, the Raspberry Pi device was programmed to switch on the light source for only about 3 s while taking a picture. The camera was set to take one photograph per minute. All photographs were captured overnight for about 10–11 h (until the battery became dead). The following day, the images were downloaded and subsequently combined in time-lapse video files. At the same time, the traces on the sediment were photographed, and gypsum casts were made. These neoichnological experiments were repeated 12 times using different individuals.

Results

Behavior

Each individual displayed similar crawling behavior leaving distinct traces on the sediment surface. A crinoid usually began moving with the aid of its arms using the so-called elbow-crawl within a few hours after being introduced into the experimental zone (i.e., during the night) at a maximum speed of $\sim$ 1 mm/s (Fig. 1; Supplementary Movies 1, 2). In this mode of locomotion, a repeated sequence of arm movements generated power strokes against the bottom and recovery strokes adjacent to the bottom, passively pulling the stalk along the substrate, but without active involvement of cirri. The direction of

Fig. 3 Surface features produced by *Metacrinus rotundus*. **a** General ▶ view of median trails and lateral tracks left by distalmost cirri and arms, respectively. **b** Close up of median trails. **c** Close up of lateral tracks. **d**–**f** Gypsum casts (hypichnia) of the above illustrated traces (**a**–**c**; correspondingly). Scale bars 1 cm

locomotion commonly consisted of one straight path towards the edge of the sand box, although the turning of a crinoid leading to a change in direction, was also observed. No backwards movements were observed. In the morning, individuals were commonly found outside the box with spread crowns and were attached to the plastic net by their cirri.

Traces

Crinoids used in this study produced two different trail architectures. The most common, produced during locomotion on a more or less straight path, were horizontal traces composed of median trails left by the stalk and cirri dragged on the bottom (Fig. 2a, b, d, e), and lateral short tracks made by the crawling arms (Fig. 2a, c, d, f). Observed median trails were long, smooth and composed of up to 3 semicircular and parallel furrows, $\sim$ 3–7 mm wide. However, the width and depth of each furrows sometimes varied along the course of the trace. Likewise, transitions between trilobate to bilobate or unilobate trails were observed. The lateral depressions or grooves were commonly inclined at a low angle (5°–25°) with respect to the median trails and started from the edge of the median trails or a few centimeters away. They were straight, sometimes oval or slightly curved, short (up to about few cm long), rather shallow ($\sim$ 0.2–2 mm) and narrow ($\sim$ 1–5 mm) (Fig. 2c, f).

A rather different trail architecture was produced by individuals which were turning during locomotion (Fig. 3). In this case, the median trail was often sinuous and composed of two smooth, semicircular parallel or intersecting furrows, $\sim$ 4 mm wide, only left by the two distalmost cirri elevating the distal part of the stalk (Fig. 3a, b, d, e). In this situation, the lateral depressions (Fig. 3c, f) made by the arms were usually inclined at a considerable angle (90°) with respect to the median trail and started more than a few centimeters away. These tracks were commonly distributed asymmetrically, that is, they were present on only one side.

Discussion

The end-Permian extinction profoundly influenced the evolutionary history of crinoids, not only through a drastic decline in their diversity (Simms 1999; Twitchett and Oji

lateral tracks

median trails
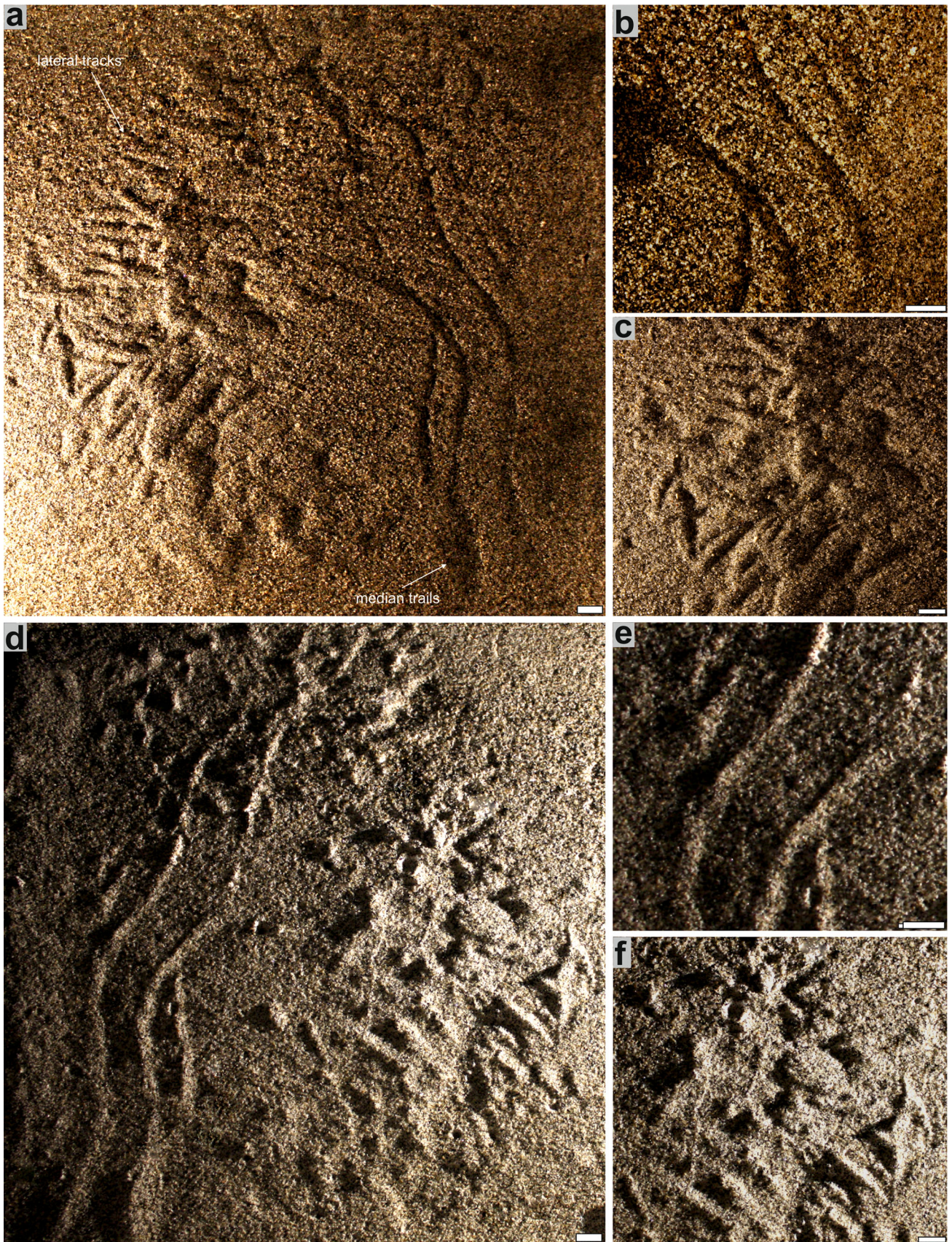
2005), but also through major functional changes (Baumiller et al. 2008, 2010). More specifically, Paleozoic crinoids, dominated by sessile forms, were replaced by predominantly motile taxa displaying many morphological and behavioral novelties (e.g., Gorzelak et al. 2012, 2016). Among these traits, autotomy planes and crawling abilities, which probably originated in the Triassic holocrinids and isocrinids (but see also Donovan 2012), are two of the best known textbook examples of dramatic functional changes in the evolutionary history of crinoids (e.g., Hagdorn 2011). Baumiller et al. (2010) argued that this novelty evolved as an effective escape strategy from echinoid predators during the so-called Mesozoic marine revolution. The ability to shed the stalk, which allowed active relocation, in the oldest post-Paleozoic stem-group isocrinids has been supported by taphonomic data (preferential disarticulation at the distal facets of nodals; see Baumiller and Hagdorn 1995), functional morphology (occurrence of highly flexible muscular arms, lack of holdfast; see, e.g., Hagdorn 2011) and micromorphology (occurrence of synostosial stereom in the distal facets of nodals, Gorzelak 2018). Our neoichnological experiment proved that isocrinids produce distinct traces on the sediment surface, which may have potential to be preserved as trace fossils. Interestingly, traces interpreted as a crawling trail of a crinoid have been recently discovered in the Middle Jurassic of Portugal (Neto de Carvalho et al. 2016). Similar trace fossils are likely to be found as early as in the Triassic. Indeed, *Holocrinus*-bearing beds commonly yield a wide range of trace fossils (e.g., Senkowiczowa 1982; Salamon 2003; Chrząstek 2013; MAS, personal observations), including trails, which are, however, commonly interpreted as arthropod traces. However, our neoichnological data suggest that holocrinids could be a tracemaker candidate of some of the ichnofossils observed in the Muschelkalk. We hope that our data provide a stimulus for a line of in-depth investigation of trace fossils from this age. Documenting such ichnological evidence may be particularly important, because it may provide more direct proof of active locomotion in the stem-group isocrinids.

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