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RECENT ADVANCES IN ICHNOLOGY OF CRAWLING STALKED CRINOIDS

BY

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Abstract — Stalked crinoids have generally been overlooked when considering trace fossil makers — largely because they were long considered fully sessile. However, observations both in the field and in laboratory experiments revealed that some members of the order Isocrinida use their arms to actively move along the bottom, dragging the stalk behind. This activity leaves distinct traces on the sediment surface. Here, we re-examined time-lapse movies made in 2017 and crawling traces produced by stalked crinoids (the isocrinine *Metacrinus rotundus*) in previously published neoichnological experiments using new 3D digitization techniques (laser scanning and photogrammetry) in order to provide a more detailed 3D morphology of these traces. These data reveal some previously unnoticed crawling behavior and features of the traces of *M. rotundus*. We also demonstrate that crinoid-bearing beds are sometimes associated with ichnofossils that can be potentially interpreted as crinoid crawling traces. These data sources may provide more direct evidence of active locomotion in fossil crinoids.

“If I have seen further it is by standing on the shoulders of giants.” — Isaac Newton. We dedicate this paper to celebrate the scientific career of our mentor and friend Prof. Tomasz K. Baumiller who has recently retired. Our correspondence and meetings (usually accompanied with beer) guided us to the big-picture level.

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INTRODUCTION

Motility in Recent crinoids has long been known. In particular, the crawling, and in some taxa swimming abilities of feather stars – those members of order Comatulida that shed the postlarval stalk – are well documented (e.g., Clark, 1915; Meyer et al., 1984; Shaw and Fontaine, 1990). Since at least the middle 1980s, however, evidence began accumulating that some stalked sea lilies (isocrinids = order Isocrinida) can also relocate by crawling with their arms along the substrate, dragging the stalk behind them (Messing, 1985). During crinoid locomotion, the crawling arms and passively pulled stalk interact with the sediment surface. *Surprisingly, however, little attention* has been paid to the traces produced during this activity. Notably, deep sea distribution of post-Paleozoic stalked crinoids and specific substrate preference of some species (carbonate hardgrounds), make ichnological study rather difficult.

Messing (1985: p. 189) was probably the first who noticed isocrinid locomotion traces: "...a single isocrinid (*E. parrae*?) was observed detached and crawling along the substrate. Although it did not move during the 5 min of observation, there was an obvious drag mark behind...". This observation was subsequently reported by Messing et al. (1988: p. 481) in the following way: "During dive JSL-I-1362 (17 June 1983, off Grand Bahama I., 403 m), a single isocrinid [probably *Endoxocrinus parrae* (Gervais)] was found detached and lying on its side on open sediment with an obvious drag mark over 1 m long behind its stalk". In the same paper the latter authors also mentioned (p. 482) that: "In September 1986, one of us (CGM) observed a *C. asterius* in the crawling posture in 260 m, the sediment slope around its crown bearing short radiating scratch marks. An area of confused but similar marks scored the sediment surface behind the crinoid, between it and a boulder about 2 m away". Unfortunately, no photos or drawings of the traces were provided in these papers. More recently, Baumiller and Messing (2007: fig. 4) took a major step forward and provided the first video footage, which shows a displacement of the sediment surface left by the stalk of crawling *Neocrinus decorus*. However, these video footages were shot at too low an angle to recognize fine details of the traces. Instead, the latter authors provided a photo of distinct traces produced by a crawling stalkless crinoid (comatulid species *Davidaster rubiginosa*), which nicely illustrated the ichnological potential of crinoids (Baumiller and Messing, 2007: fig. 5).

Recently, Brom et al. (2018) illustrated and described the morphology of the locomotory traces produced by an isocrinine crinoid in detail via neoichnological experiments on the shallowest living stalked isocrinine, *Metacrinus rotundus*. They reported that the locomotory traces are generally comprised of wide, sometimes weakly sinuous median trails consisting of few semicircular and parallel or intersecting furrows left by the stalk and cirri dragged on the bottom, and lateral short tracks of various shapes made by

the crawling arms. Previously, Neto de Carvalho et al. (2016) illustrated an unidentified isocrinid fossil from the Middle Jurassic of Portugal that was found at the end of its trail, which they described as a new ichnospecies, *Krinodromos bentou*, interpreted as a mortichnial crawling trail. They diagnosed this new ichnotaxon as follows: "a narrow and flat central area with an irregular winding furrow, or almost no sedimentary disruption, bordered by shallow and large grooves externally limited by irregular piles of sediment" (p. 47).

Gorzela et al. (2020) further explored the ichnological potential of stalked crinoids by demonstrating that autotomized arms of *Metacrinus rotundus* display vigorous movements that may produce traces on the sediment surface. These traces are comprised of straight or arched grooves, usually arranged in radiating groups, and shallow furrows. They (Gorzela et al., 2020) also reported similar traces associated with detached arms of the oldest (Early Triassic) stem-group isocrinine (*Holocrinus*).

In this paper we re-examine our data collected during neoichnological experiments with *Metacrinus rotundus* conducted in 2017 (Brom et al., 2018). In particular, we provide unpublished time-lapse movies that reveal some previously unnoticed crawling behavior of isocrinine crinoids. We also illustrate for the first time some locomotion traces not illustrated in Brom et al. (2018) and apply a new 3D digitization techniques (laser scanning) to selected gypsum counterparts of the traces in order to provide a more detailed 3D morphology. We then show that similar traces are likely to be found at least as early as in the Triassic.

INSTITUTIONAL ABBREVIATIONS

ZPAL	—	Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland (ZPAL V.42ICH_N1-4) – 4 fragments of counterparts: gypsum casts of Recent traces.
GIUS	—	University of Silesia in Katowice, Faculty of Natural Sciences, Institute of Earth Sciences, Poland (GIUS 8-3696) – 1 counterpart: modeling clay cast of Triassic traces.

MATERIALS AND METHODS

Analyzed time-lapse movies (movies 1–6 in Supplementary Online Material; see also Fig. 1) and crawling traces were captured during neoichnological experiments performed in 2017 by one of us (KB). These data were published in part by Brom et al. (2018). For a detailed description of sampling and handling of crinoid specimens and movie acquisition see Brom et al. (2018). In these experiments light-gray, fine-grained sand from the Pacific coast (Nishiakazawa beach; 34.652660N, 137.363772E) was used. 3D models (.ply files

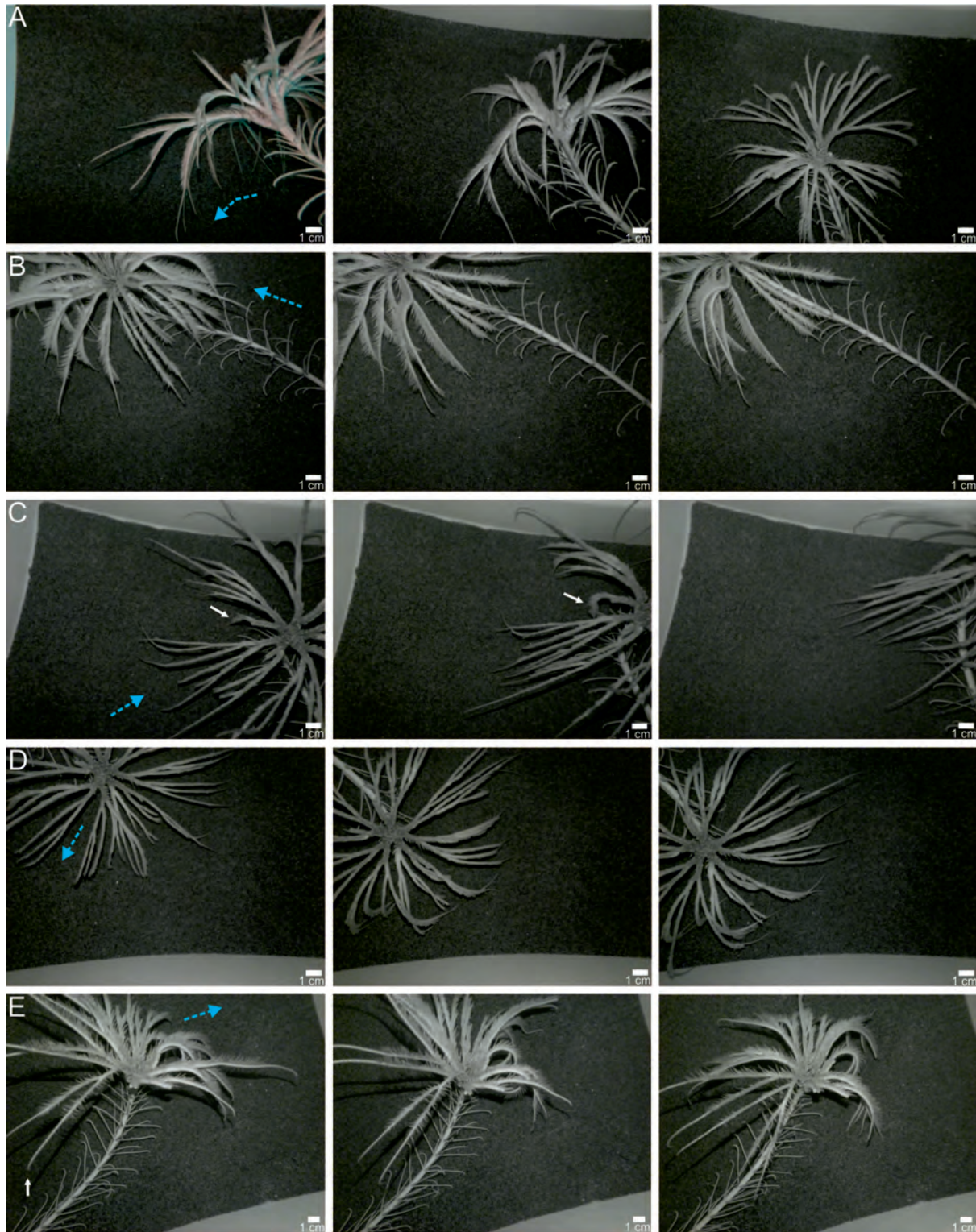


FIGURE 1— Still frames showing different crawling movements of *Metacrinus rotundus*. Rows A–E each represent a separate trial. The direction of movement is indicated by dotted blue arrows. Note that nearly all the arms can be involved in locomotion; the animal can be pulled with the leading arms and pushed with the trailing arms (e.g., white arrows).

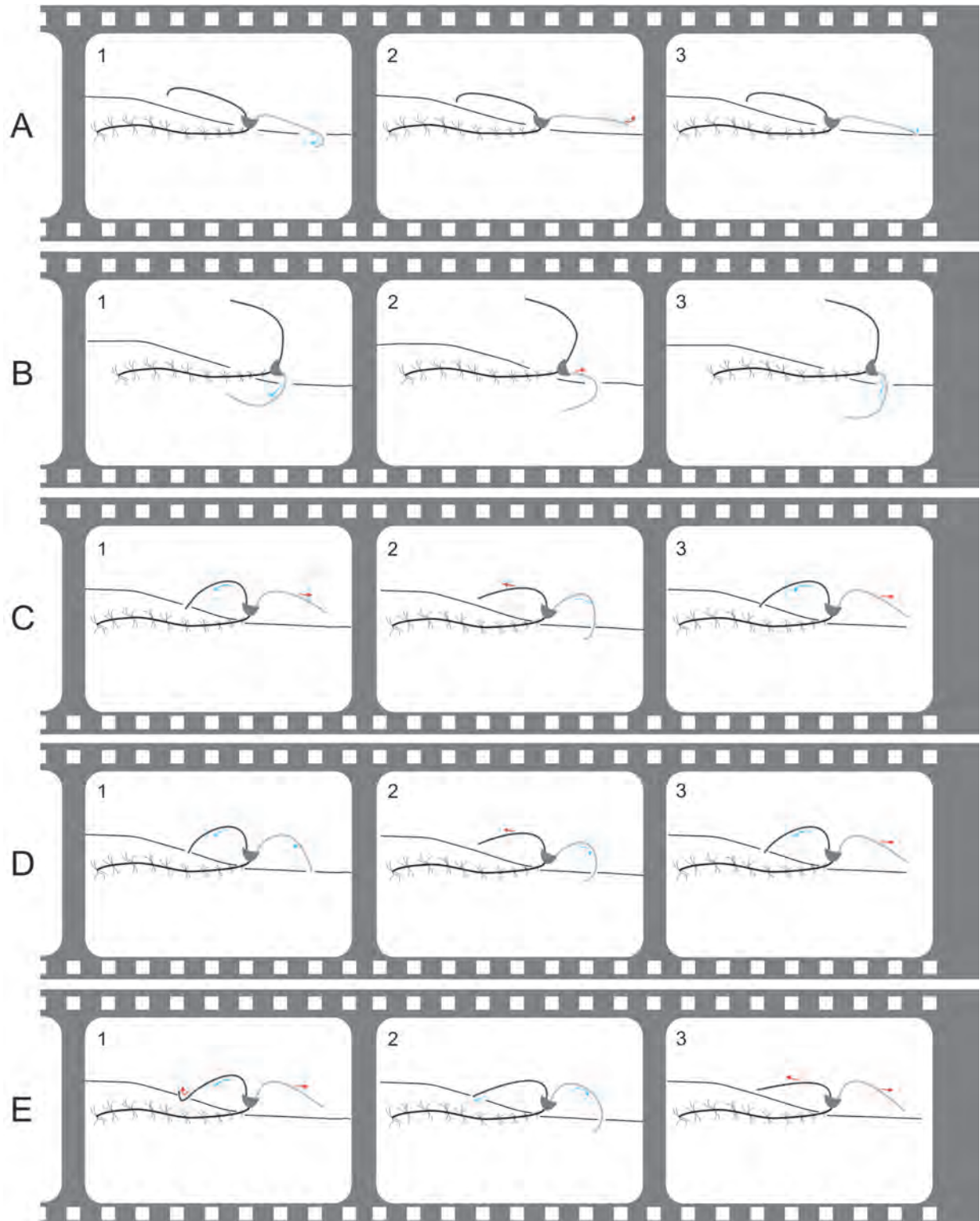


FIGURE 2— Schematic diagrams of the three major types of isocrinine locomotion (A and B modified after Baumiller and Messing, 2007: fig. 2; C and D modified after Birenheide and Motokawa, 1994: fig. 1). **A**, the finger-tip pull. **B**, the elbow-crawl. **C–E**, the pole push & pull. Blue arrows indicate aboral arm flexure; red arrows indicate oral arm flexure.

1–4 in Supplementary Online Material) of selected traces were acquired with a Shining 3D EinScan Pro 2X 3D scanner fixed on a tripod, EXScan Pro 3.2.0.2 software, and then processed with Meshlab 1.3.3, Blender 2.82 and ParaView 5.8.0 to get the false-color depth maps (see Gorzelak et al., 2020).

A set of photographs of trace fossils associated with the holocrinid stem fragments was taken at different angles. A 3D model (.ply file 5 in Supplementary Online Material) and false-color depth map were acquired by means of photogrammetric technique using Visual SFM 0.5.26 and the MeshLab 1.3.3 or Agisoft Photoscan 1.2.0. These traces were found on the surface of a large (ca. 1 m) limestone block belonging to the so-called Karchowice Fm. (Middle Triassic, middle Anisian) of Tarnów Opolski (Poland) (Szulc et al., 2015).

Quantitative data of the traces (widths, lengths, intersection angle — in map view — between the primary median trail and the grooves flanking the axial trail on both sides) were obtained using ImageJ (Rasband, 1997–2018).

CRAWLING BEHAVIOUR

Baumiller and Messing (2007) distinguished two major types of crinoid crawling: the so-called finger-tip pull (Fig. 2A) and elbow crawl (Fig. 2B). In the first type, the arms are arranged more or less radially and oriented sub-parallel to the substrate (with ambulacra facing up) (Fig. 2A1–3). The movement is generated via aboral flexure of the distal tips of the leading arms only, which press against the bottom and displace the crinoid forward (power phase) (Fig. 2A1). In the subsequent recovery phase the distalmost parts of the leading arms lift off the bottom and extend orally (Fig. 2A2). On the other hand, in the elbow crawl, movement is generated by aboral flexure of proximal articulations of the leading arms, which undergo a sequence of power and recovery strokes (Fig. 2B1–3). During this locomotion, all the arms are strongly flexed aborally and point their distal tips toward the stalk but only the pinnule-bearing oral side of the middle third to distal half of the arm adjacent to the substrate creates traction with the bottom (Fig. 2B1, 3).

Birenheide and Motokawa (1994) first briefly described a rather different mode of locomotion in *Metacrinus rotundus* during incubation in aquaria. They observed movement via pulling with the leading arms and, from time to time, via pushing with the back arms. More specifically, during pulling, the leading arms straighten by extending orally, anchor with the distal tips on the substrate, and then strongly bend aborally. This locomotion strategy was sometimes supplemented by trailing arms, which flex aborally, anchor with the distal tips on the bottom, and straighten by oral bending. Herein, we supplement these previous observations on *M. rotundus* and provide further direct proof (time-lapse movies) for its mode of locomotion, which reveal some previously unnoticed crawling behavior (Figs. 1, 2C–E, movies 1–6 in Supplementary Online Material).

The crawling pattern observed by us in *M. rotundus* is somewhat intermediate between the finger-tip pull and elbow crawl (herein referred to as the “pole pull and push” strategy). However, the movement of the leading arms seems to be mostly generated by aboral flexure at median articulations (although distal and proximal articulations may also be involved). The ambulacral pinnule-bearing surfaces of the arms during the power phase are not entirely oriented upward and sub-parallel to the substrate, as in the case of finger-tip pull; rather, some of them (from the more distal side) are more flexed aborally, though not as much as in the elbow-crawl (Fig. 2C vs. 2B). The distal arm tips point more toward the substrate (Figs. 2C2, D2) rather than toward the stalk. As a result, the distal arms still generate most of the traction against the bottom. However, both the non-pinnulate arm tips and the pinnule-bearing oral side of the distal arm contact the substrate (Fig. 2C2). Pulling with the leading arms via aboral flexure may alternate with pushing by the orally flexing trailing arms (Figs. 2C1–3), or both leading and trailing arms may flex simultaneously (Figs. 2D1–3). For the pushing power stroke, the trailing arms, which anchor to the substrate by their tips (Figs. 2C1, D1), straighten orally, while the recovery involves lifting the arm tips off the substrate and aboral arm flexure (Figs. 2C2, D2). The distalmost parts of the trailing arms may also curl orally while still against the substrate (Fig. 2E1); they suddenly straighten as they push off the bottom (Figs. 2E2–3; see movie 6 in Supplementary Online Material).

In our experiments, *Metacrinus* specimens commonly turned left or right during locomotion (Fig. 1, movies 3–6 in Supplementary Online Material). In such cases, nearly all the arms are arranged radially, and could be involved in “pole pull and push” locomotion.

CRAWLING TRACES

The crawling arms passively pull the cirriferous stalk, which leaves similar traces on the sediment surface in all types of locomotion. 3D digitization techniques applied to the traces produced in neoichnological experiments (Brom et al., 2018) provided more detailed morphologic data on these traces. Their revised description is given below.

Description (slightly emended after Brom et al. 2018).—The most common trail architecture, produced during locomotion on a more or less straight path, are horizontal traces comprised of median trails left by the cirriferous stalk dragged on the bottom (fig. 2a, b, d, e in Brom et al., 2018, see also Fig. 4B, C), and lateral short tracks made by the crawling arms (fig. 2a, c, d, f in Brom et al., 2018, see also Fig. 4B, C). Median trails can be long, rather smooth, and comprised of up to four semicircular and parallel furrows, ~ 3–8 mm (mean: 5 mm) wide. However, the width and depth of each furrow may vary along the course of the trace. Likewise, transitions between single-, double-, triple-, and four-lobed trails are present.

The lateral depressions or grooves radiate forward at different, generally low angles (5°–53°) relative to the median

trails and start from the edge of the median trails or a few centimeters away. They are straight, sometimes triangular, oval or slightly curved, short (0.5–4.8 cm long; mean: 1.9 cm), rather shallow (~ 0.2–2 mm) and narrow (~ 1–9 mm) (fig. 2c, f in Brom et al., 2018; see also Fig. 4B, C). The length-to-width ratio of these tracks ranges from 2.5 to 8.9 (mean: 6.8). They may intersect each other at different angles (forming check marks or cross marks) (Fig. 4B, C).

The median trails produced by turning individuals are similar. They are commonly sinuous and comprised of two to four smooth, semicircular parallel or intersecting furrows, 3–9 mm wide (mean: 6.2 mm), left by the cirriferous stalk (fig. 3a, b, d, e in Brom et al., 2018, see also Figs. 3, 4A, D). However, the lateral depressions (fig. 3c, f in Brom et al., 2018, see also Fig. 3) made by the arms may orient up to about 90° relative to the median trail and may start more than a few centimeters away. These tracks are commonly distributed asymmetrically and are sometimes present on only one side. Their morphology and size are virtually the same as the lateral tracks produced during locomotion on a more or less straight path.

DISCUSSION

Re-examination of our time-lapse movies made in 2017 revealed some previously unnoticed crawling behavior of stalked crinoids. More specifically, we show that crawling *M. rotundus* may display a complex moving behavior, herein referred to as the pole pull and push pattern, that takes a variety of forms. As this movement may form distinct traces on the sediment surface, it has some ichnological potential. Indeed, Neto de Carvalho et al. (2016) ascribed similar traces from the Middle Jurassic to crawling activity of a crinoid (referred to the ichnospecies *Krinodromos bentou*), and Brom et al. (2018) suggested that similar ichnofossils are likely to be present as early as in the Triassic. Notably, following the end-Permian mass extinction, crinoids underwent major functional changes, i.e., the predominantly sessile forms of the Paleozoic were largely replaced by highly motile taxa (Baumiller and Messing, 2007, Gorzelak et al., 2016). This change is thought to be related to increased predation pressure during the so-called Mesozoic Marine Revolution (Baumiller et al., 2010; Gorzelak et al., 2012). Thus, especially post-Paleozoic forms were certainly able to produce traces on the sediment surface, although some Paleozoic taxa such as advanced eucladids may have also possessed crawling abilities (e.g., Baumiller and Messing, 2007; Donovan, 2012).

Holocrinids (order Holocrinida sensu Jaekel, 1918), which were among the first crinoids to appear following the end-Permian extinction, developed highly flexible muscular arms and specialized autotomy planes at the distal nodal facets in their stalk, which allowed them to detach from the substrate and crawl (Baumiller and Hagdorn, 1995; Hagdorn, 2011; Gorzelak, 2018). Early Triassic holocrinids also likely displayed another anti-predatory trait—post-autotomy arm thrashing—as inferred from characteristic traces found

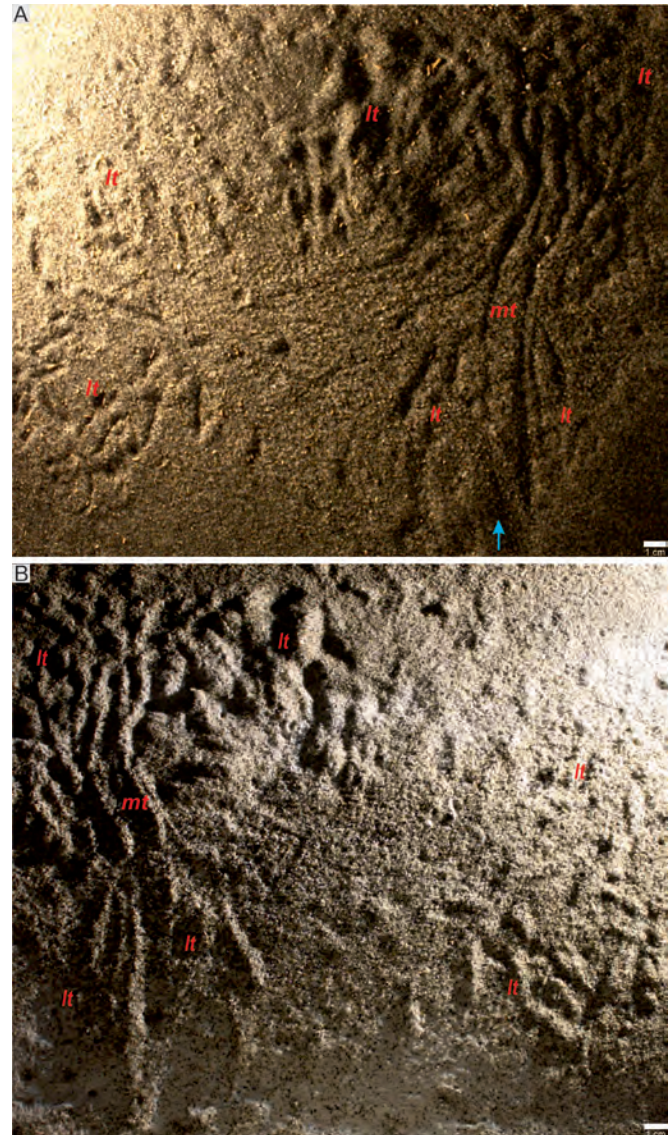


FIGURE 3— Surface features produced during locomotion of a Recent crinoid *Metacrinus rotundus*. Photographs of traces impression **A** and a positive gypsum cast taken from it **B**. Lighting is from the upper left in **A** and upper right in **B**. Blue arrow indicates direction of locomotion, lt - lateral tracks, mt - median trail.

associated with their detached arms that are similar to those produced by autotomized arms of Recent crinoids (Gorzelak et al., 2020).

Herein, we illustrate one example of a trail that can be potentially interpreted as a putative holocrinid crawling trail (Fig. 4E–G). It is comprised of median trails and some indistinct lateral short tracks. This median trail is ~25 cm long, rather smooth, and comprised of up to three semicircular and parallel furrows 2–5 mm wide (mean: 4 mm). A clear transition is visible between triple- and double-lobed trails (Fig. 4E). The lateral depressions or grooves (7–14 mm long;

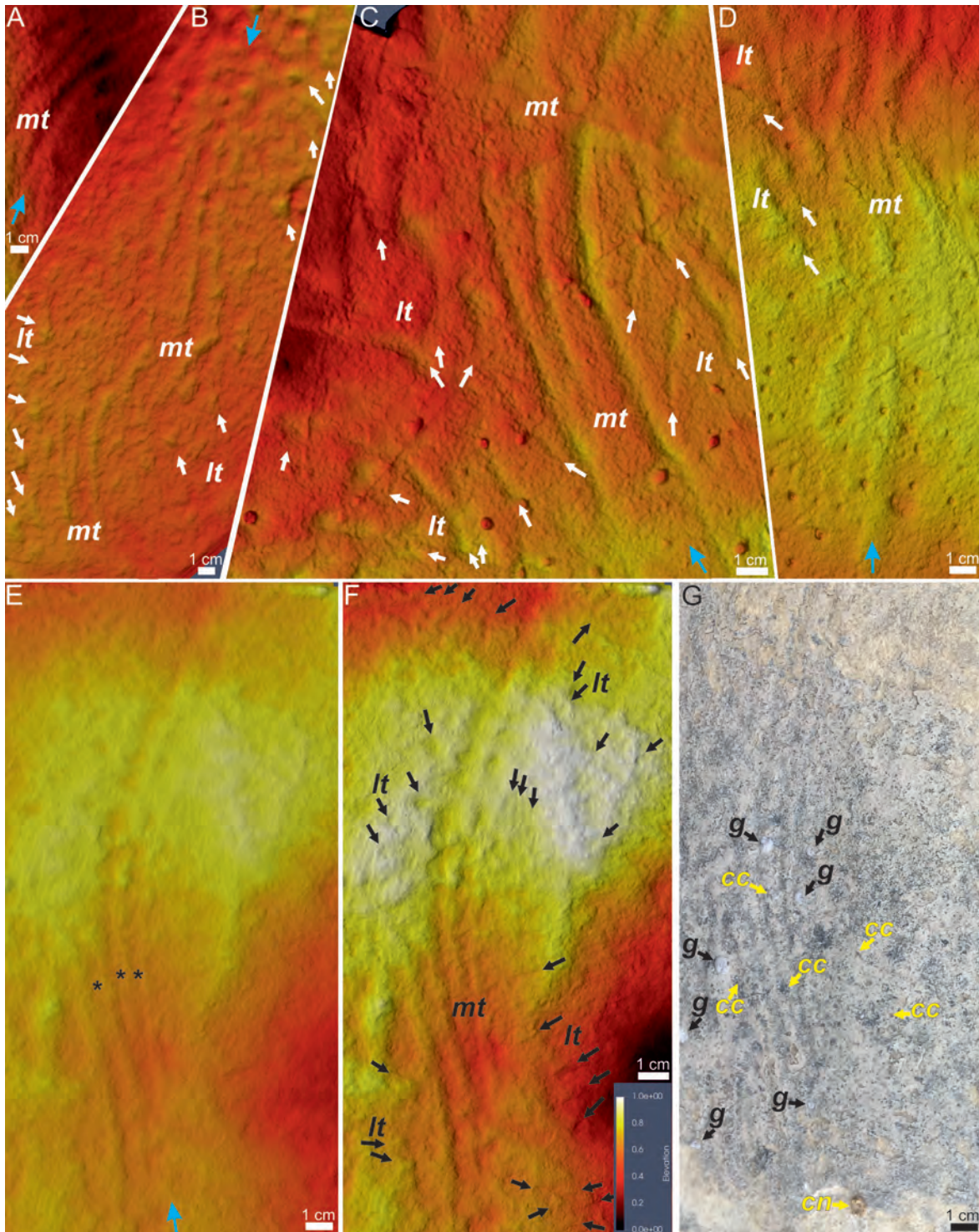


FIGURE 4 — Recent (A–D) and fossil (E–G) crinoid traces. A–D, false-color depth maps obtained from three-dimensional scans of gypsum casts of traces produced by a Recent crinoid *Metacrinus rotundus* (white arrows). E, F, false-color depth maps based on photogrammetry of the Middle Triassic traces (black arrows), GIUS 8-3696. Elevation in F has been increased ($\times 2$) to enhance depth contrast. G, photograph of the Middle Triassic slab (Karchowice Fm., Tarnów Opolski, GIUS 8-3696) containing crinoid traces and body fossils (red arrows) and *Coelostylinia*-like gastropods (black arrows). Abbreviations: cc, crinoid cirrals; cn, crinoid nodal; g, gastropods; lt, lateral tracks; mt, middle trail.

mean: 11 mm) spread at angles ranging from 16° to 81° relative to the median trails. Notably, this trace was found on a bedding surface containing some holocrinid ossicles (one nodal and few isolated cirrals). Although the surface also includes a few small and poorly preserved *Coelostylin*-like gastropods, and although gastropods do produce roughly similar traces (ascribed to the ichnogenus *Archaeonassa* Fenton and Fenton, 1937; see Buckman, 1994: fig. 2, Baucon and Felletti, 2013: fig. 9a), their trails typically consist of a median furrow (which can be variably ornamented by oblique or transverse elements) flanked by just two regular lateral ridges. Unlike typical *Archaeonassa* traces, the putative holocrinid Triassic traces are more irregular and display transitions between double- and triple-lobed trails, as well as some lateral depressions or grooves, just like the crawling traces of Recent crinoids.

CONCLUSIONS

In this paper we describe some previously unnoticed crinoid crawling behavior and features of the traces produced during this activity. Crinoid locomotory traces have the potential to be preserved as ichnofossils. Thus, rock slabs preserving trace fossils associated with crinoid remains certainly *deserve in-depth investigation*. Such ichnological evidence may be particularly valuable, because it may provide more direct proof of crawling activities in fossil crinoids.

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