Marine Biodiversity (2024) 54:3
https://doi.org/10.1007/s12526-023-01398-1

SENCKENBERG

SHORT COMMUNICATION

Neoichnological analysis of sea stars in the deep sea near the Aleutian Trench: behavioral insights from in situ observations

Olmo Miguez-Salas[1,2] · **Angelika Brandt**[1,3] · **Camille Moreau**[4]

Received: 8 September 2023 / Revised: 28 November 2023 / Accepted: 4 December 2023

Abstract

The study of biogenic structures (e.g., lebensspuren) produced by benthic fauna on the seafloor provides invaluable information about the behavior of their tracemakers. In the case of sea stars, most of the previous research has been focused on shallow-marine environments due to the extreme scarcity of data from deep-sea lebensspurens. Here, we examined sea star traces from six deep-sea stations (deeper than 4500 m) near the Aleutian Trench (North Pacific). A total of six families were identified from still images. The majority of them were not observed producing any lebensspuren or just pentameral impressions related to resting and feeding activities. Two members of the families Pterasteridae and Porcellanasteridae could be clearly characterized by a composite behavior resulting in contrasting lebensspuren morphotypes. A morphotype belonging to the genus *Hymenaster* undet. produced pentameral impressions (related to predation) and punctuated trails (related to podia locomotion). Members of the family Porcellanasteridae produced oval to circular impressions (that may be related to burrowing trails for the detection of organic matter), flat-shallow trails (related to podia locomotion), and irregular M-ridged trails (related to locomotion while feeding through the sediment interface). There is a severe scarcity of data related to the locomotion of past deep-sea Asteroidea (i.e., trace fossils) and their ichnotaxonomical classification. We discuss the implications of our results for the ichnofamily Biformitidae, as well as the importance of considering other features (e.g., podia impressions) rather than just hook-shaped traces related to arm locomotion.

Keywords Deep sea · Asteroidea · Lebensspuren · Behavior · Still images

Introduction

Ichnology deals with the study of biogenic sedimentary structures resulting from the interaction between benthic fauna and substrates (e.g., bioturbation, bioerosion) in past and modern environments as well as their final products, trace fossils and lebensspuren, respectively. Analyses of these biogenic structures provide valuable information about the behavior of the marine taxa that produce them (i.e., tracemakers) (Przeslawski et al. 2012; Miguez-Salas et al. 2020, 2022, 2023a; Brandt et al. 2023). The paleoichnology of sea stars has been mainly restricted to the so-called resting traces, the type ichnogenus *Asteriacites* von Schlotheim, 1820, which also has the brittle stars as possible tracemakers. *Asteriacites* is an important component of marginal marine and shallow marine trace-fossil assemblages but also occurs sometimes in the deep-sea realm (Mikuláš 1992; Knaust and Neumann 2016; Belaústegui et al. 2017). Thus, up to now, paleoichnological data from deep-sea environments is comparatively scarcer. It is known that asteroids produce motility traces that record their movement across the seafloor (Mángano et al. 1999; Gingras et al. 2008). The ichnofamily Biformitidae (Knaust and Neumann 2016) was erected for imprints resulting from locomotion using asterozoan arms, selected *Biformites* Linck, 1948, as its type ichnogenus, and included the other ichnogenera *Arcichnus*

Communicated by S. Stöhr

✉ Olmo Miguez-Salas
olmo.miguez-salas@senckenberg.de

[1] Department of Marine Zoology, Senckenberg Research Institute, 60325 Frankfurt, Germany

[2] Departamento de Estratigrafía y Paleontología, Universidad de Granada, Av. Fuentenueva 18002, Granada, Spain

[3] Department of Biological Sciences, Institute of Ecology, Evolution and Diversity, Johann Wolfgang Goethe University Frankfurt, Max-von-Laue-Str. 13, 60438 Frankfurt, Germany

[4] Marine Biology Lab, Université Libre de Bruxelles (ULB), 50 Av. FD Roosevelt, B-1050 Brussels, Belgium

Sutcliffe, 1997 and *Harpichnus* Vallon et al., 2015 under this family. Nevertheless, there is scarce documentation of locomotion ichnogenera in the deep-sea fossil record, and even more elusive are the traces of predation created by asteroids as they dig into shallow sediment for feeding (Gingras et al. 2008).

In the modern deep sea, the star-shaped resting impressions are also one of the most common lebensspuren and are usually named star-shaped traces. They have been documented in many areas worldwide, but mainly superficially or as anecdotal descriptions of the whole lebensspuren assemblage (Ewing and Davis 1967; Hollister et al. 1975; Kitchell et al. 1978; Young et al. 1985; Wheatcroft et al. 1989; Gaillard 1991; Jones et al. 2007; Bell et al. 2013; Durden et al. 2020; Miguez-Salas et al. 2020). However, several studies demonstrated that asteroids create motility traces that evidence their motion across the seafloor (e.g., perforated trail *sensu* Przeslawski et al. 2012) and that predation/scavenging traces produced by these tracemakers digging into shallow sediment to feed on organisms can be observed (Howell et al. 2003; Gingras et al. 2008). However, none of these behaviors and traces has been characterized in detail from deep-sea environments.

Undoubtedly, sea star traces are a frequent component of deep-seafloor landscapes. However, most behavioral interpretations are retrieved from shallow-marine species. Therefore, new discoveries in the modern deep seafloor are necessary in order to facilitate our understanding of their fossil counterparts, and in particular to decipher the relationship with the specific behaviors of their tracemakers. Here, we examine sea star traces from six deep-sea stations above 50°N latitude in a subarctic (North Pacific) environment at over 4500 m depth that were sampled during the AleutBio expedition. The aims of this research are (1) to describe sea star lebensspuren morphotypes, (2) to study variations in their morphological patterns, and (3) to evaluate these new morphotypes and what roles they might play in trace fossil research.

Material and methods

This study is based on data acquired during the “AleutBio” expedition aboard the German research vessel *R/V SONNE* (cruise SO293; July–September 2022), whose overall objective was to investigate the biogeography and biodiversity of deep-sea biota across the Bering Sea and Aleutian Trench region. Seafloor imaging analyses were conducted utilizing the Ocean Floor Observation System (OFOS), a towed camera integrated into the R/V SONNE’s onboard equipment. This system features a Full-HD video camera and a 45-megapixel mirrorless camera (Canon EOS R5; resolution of 8192 × 5464 pixels). A triangular configuration of three laser points, spaced 40 cm apart, provides a calibrated scale for the still camera. Six OFOS transects were performed, sampling the abyssal seafloor near the Aleutian Trench at depths ranging from 4299 to 5327 m (Fig. 1). Each camera transect spanned over 1 km with an average visible width of 1.5 m, resulting in a survey of more than 15,000 m^2 of the seafloor. The seafloor sediment predominantly consisted of diatoms and radiolarians mixed with muddy terrigenous clay. Approximately one still image was captured every 10 s along the transect, generating a total of over 5000 still images (refer to Miguez-Salas et al. 2023b for additional details). The still images utilized in this study have been deposited on Zenodo (Miguez-Salas 2023).

The sea stars’ family or genus ranks were aimed at the discrimination of taxa in the still images. A conservative identification approach was followed in the majority of our image-based observations for reasons of limitation in the image quality and the general difficulty of observing diagnostic characters in in situ photographs. Therefore, an open nomenclature was used, following the recommendations for marine image identifications (Horton et al. 2021). Sea star size was measured by calculating the maximum distance between opposite arms. Sea star lebensspuren morphotypes were described based on morphological features (e.g., size, sinuosity, spacing). Sea star impression areas were calculated by drawing around individual pentameral impressions on scaled images (scaled using the 40 cm distance between laser dots on the seabed) with the free-hand tool from Fiji software (Schindelin et al. 2012). All continuous sea star trails were measured as far as could be seen in the image with the free-hand tool. Additionally, trail sinuosity (total trail length divided by the minimum distance between the beginning and end of the trail) as well as spacing between impressions (when possible) were measured for each trail type.

Results

A total of 71 sea star specimens belonging to six families and associated lebensspuren were identified on the still images (Fig. 2, Supplementary File 1). Among the identified sea stars families: two families including three genera (Solasteridae: *Lophaster* and *Paralophaster*; Pedicellasteridae) did not register any traces, two genera from two families produced pentameral impressions (Astropectinidae: *Dytaster* and Pterasteridae: *Hymenaster*), and two families (Pterasteridae: *Hymenaster*; Porcellanasteridae) were observed doing a composite behavior with different lebensspuren morphotypes. The genus *Freyella* (family: Freyellidae), which is a suspension-feeding sea star, did not leave any visible trace. Two specimens were not possible to classify at any rank. Station 4 showed the highest diversity (Supplementary File 1).

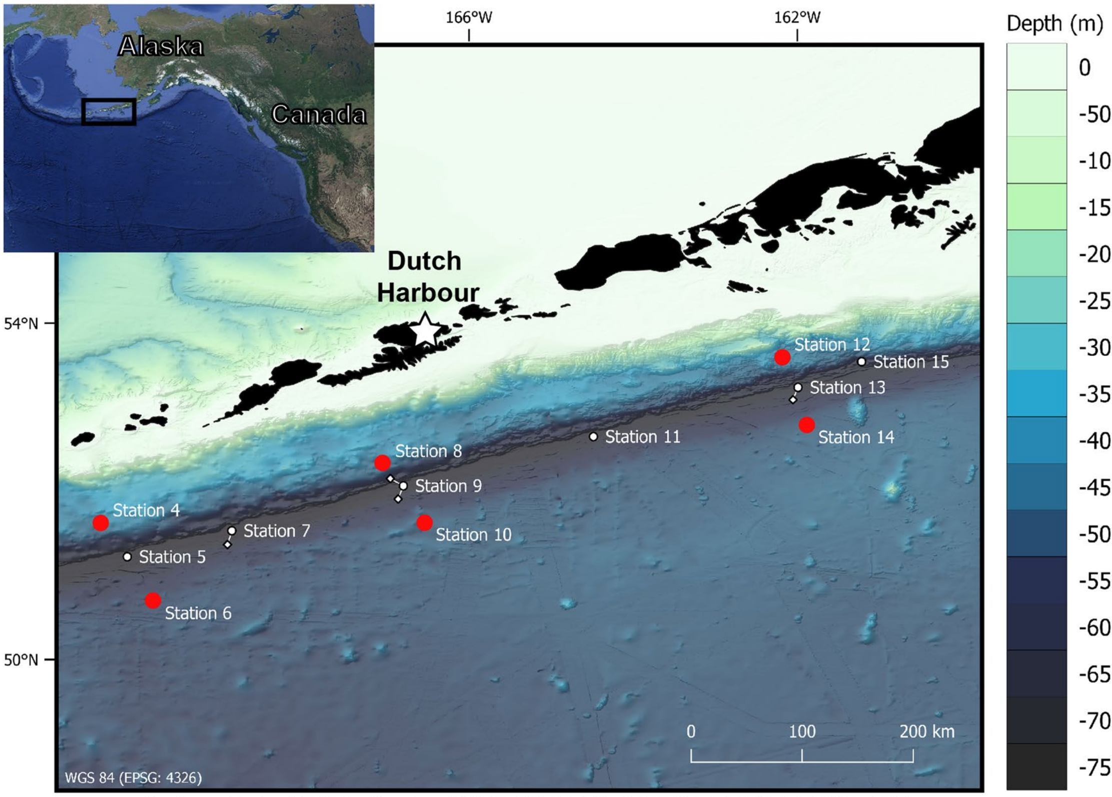

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Fig. 1 Simplified bathymetric map of the study area near the Aleutian Trench with the locations of the stations where the OFOS was deployed (red thick dots), and sea stars lebensspuren were characterized (courtesy of Dr. Anne-Cathrin Wölfl and Kevin Kess)

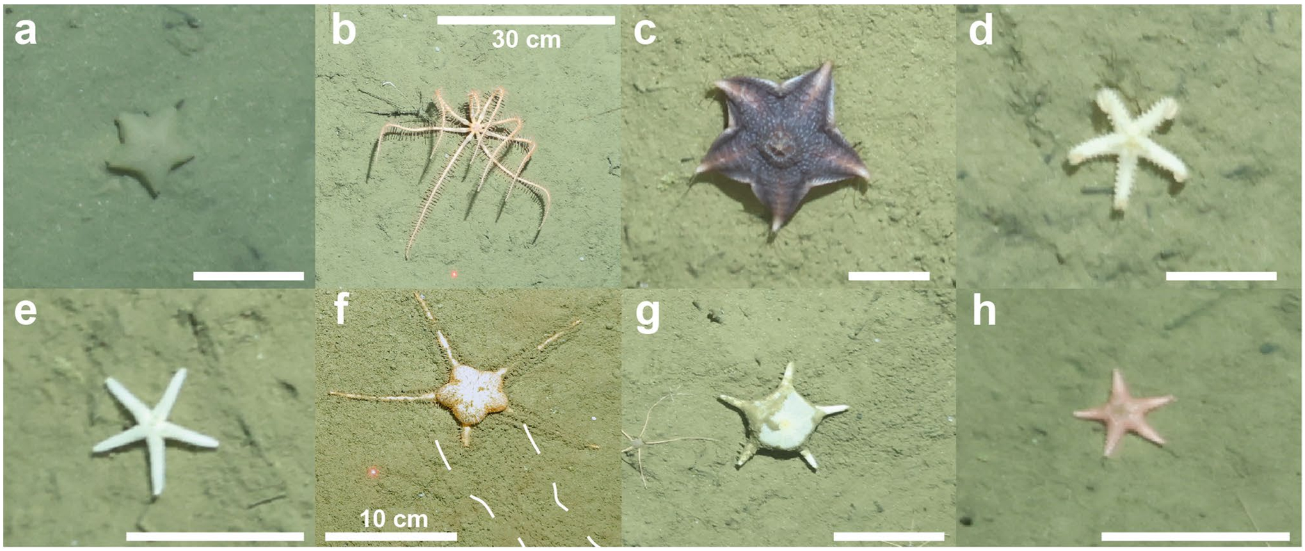

Fig. 2 Observed sea star specimens (OFOS images) included in this study. **a** *Pteraster* undet; **b** *Freyalla* undet; **c** *Hymenaster* undet; **d** *Paralophaster* undet.; **e** *Pedicellasteridae* undet; **f** *Dytaster* undet. with punctuated trail (white dashed lines); **g** Porcellanasteridae undet.; **h** *Lophaster* undet. Scale bars = 5 cm

Table 1 Lebensspuren morphological measurements of *Hymenaster* specimens. In bold are the characterized morphotypes

Station_image code	Sea star size (cm)	Punctuated tail			Pentameral impression (cm^2)	Spacing (cm)
		T. length (cm)	S. length (cm)	Sinuosity		
12_IMG_0143	7.3	109.22	79.17	1.37		
14_IMG_0244		107.73	98.68	1.09	12.1	
4_IMG_0556	7.2				7.2	
4_IMG_0653	7.3				7.3	
4_IMG_0688	7.8	167.43	71.09	2.35	7.2	132.67
6_IMG_0324					12.7	
6_IMG_0552					13.7	
6_IMG_1147					13.2	
6_IMG_1171	12.2				12.6	20.7
					9.5	30.58
8_IMG_0242	9.7	52.83	36.61	1.44	9.7	
8_IMG_0461	9.9	46.65	41.8	1.11		
8_IMG_0479	8.5				8.5	
8_IMG_0518	8.9	160.3	105.41	1.52		
8_IMG_0556	15.3	130.94	86.79	1.50	15.3	42.32
8_IMG_0580	9.4				14	
8_IMG_0673	7.5	45.02	43.75	1.02	8	
8_IMG_0749	10	32.84	18.86	1.74	10.9	
8_IMG_0768		230.66	209.98	1.09		
8_IMG_0825		219.57	174.02	1.26		
8_IMG_0829	7.6	155.34	120.25	1.29		

Two lebensspuren morphotypes have been observed in relation to *Hymenaster* (Table 1). The first one was the pentameral impression ($n = 15$) where the five arms were clearly preserved (black triangles in Fig. 3a, b, and f). Around this impression, a thin sediment ridge (1 to 2 cm) was developed due to sediment remobilization and compaction (Fig. 3b and e). The pentameral impressions have an average area of 10.8 cm^2. The average spacing ($n = 4$) between impressions was 56.7 cm (Fig. 3f). The second one was a punctuated trail ($n = 12$) related to podia locomotion (i.e., tube feet) (white dashed line in Fig. 3c–e and g). The podia imprints were usually elongated, randomly distributed, and parallel to the direction of movements. The average sinuosity value of these trails was 1.4. In the case of *Dytaster*, only two specimens were observed (Supplementary File 1). However, in one of them, a punctuated trail seems to occur with similar features (see Fig. 2f).

Three lebensspuren morphotypes have been observed in relation to Porcellanasteridae (Table 2). The first one was a circular to oval impression ($n = 4$), where the pentameral symmetry of the arms was poorly preserved (black triangles in Fig. 4). These impressions were the result of Porcellanasteridae burrowing before beginning their feeding or locomotion activities (Fig. 4). This morphotype has an average area of 6.4 cm^2. The second one was a flat-shallow trail characterized by a slightly disrupted upper sediment layer; podia impressions were occasionally preserved (white dashed line in Fig. 4), probably depending on the sediment consolidation and characteristics. The average length and sinuosity value of these trails were 58 cm and 1.32, respectively. The third one was an irregular M-ridged trail produced by the tracemaker movement through the sediment-water interface (black dashed line in Fig. 4). This morphotype was composed of two irregular sediment ridges. The "shaky" movement of the tracemaker—not strictly linear and straight—resulted in two sediment ridges at the sides of the trail that are commonly irregular rather than continuous and parallel. The average length and sinuosity value of these trails were 79.3 cm and 1.36, respectively.

Discussion

The impact of sea stars on benthic communities is contingent upon their feeding strategy (such as opportunistic omnivores, predators, herbivores, detritus feeders) and the trophic level of their prey within the community (Howell et al. 2003; Mironov et al. 2016; Motti et al. 2018; Garrido et al. 2021). Thus, lebensspuren features are expected to depend on their feeding strategies, since asteroids typically transit the seabed

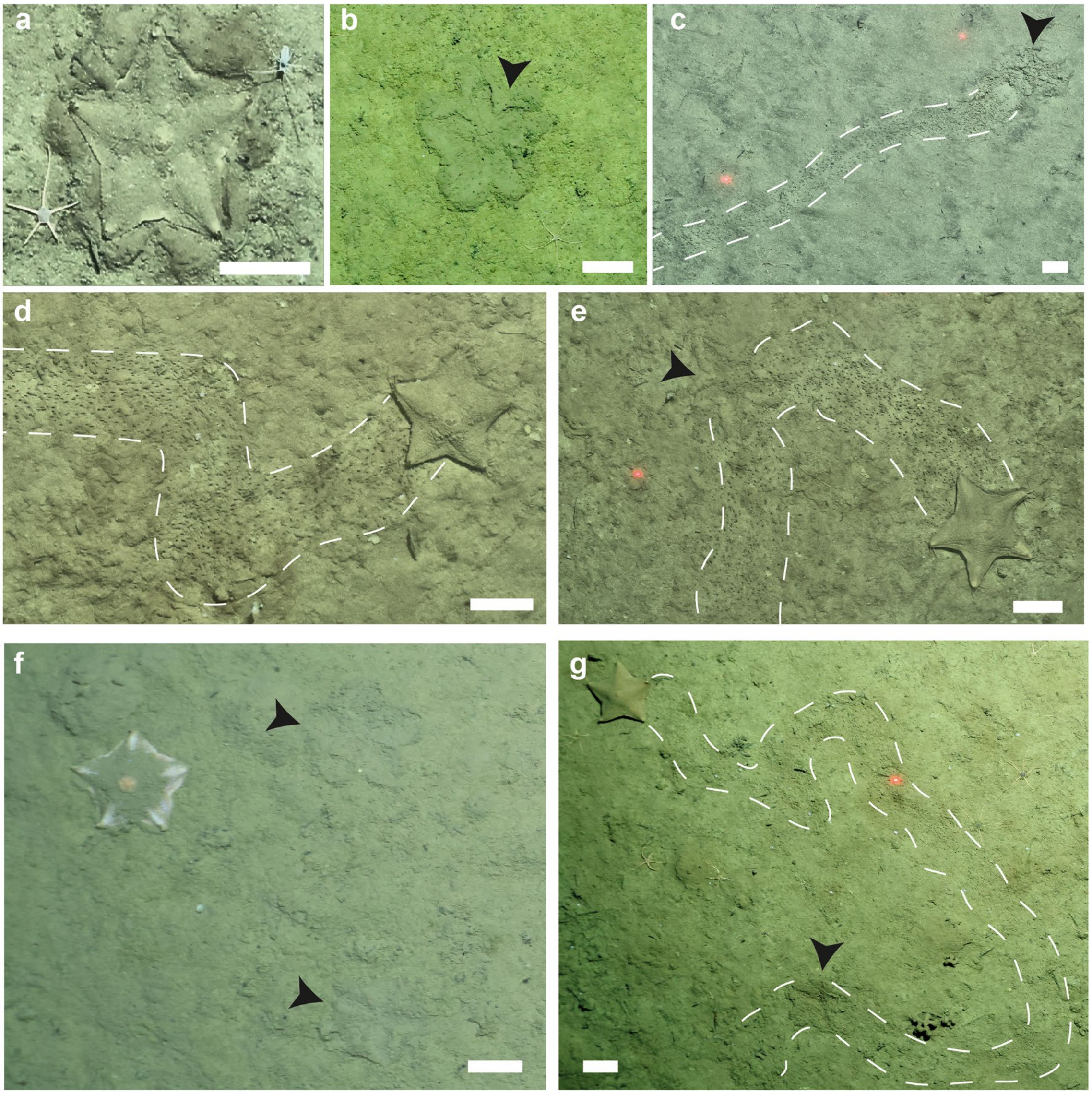

Fig. 3 *Hymenaster* specimens (**a**, **d–g**) producing the different lebensspuren morphotypes: (1) pentameral impression (black triangles; **b**, **c**, **e–g**) and (2) punctuated trail (white dashed lines; **c–e**, **g**). Scale bars = 5 cm

rapidly between feeding locations (Durden et al. 2020). In the present study, we observed that most of the identified sea stars did not produce multiple lebensspuren morphotypes besides the pentameral impressions related to resting or feeding (digestion) (e.g., *Dytaster* and *Hymenaster*). However, we noted that some sea stars (*Hymenaster*, Porcellanasteridae) produced various lebensspuren morphotypes associated with different behaviors.

Hymenaster species are known predator/scavengers that feed on small benthic invertebrates including foraminifers and crustaceans, as well as surface-derived matter, in particular pteropod molts and planktonic foraminifers (Mortensen 1927; Howell et al. 2003; Courtene-Jones et al. 2017). Howell et al. (2003) stated that photographs of this species depict it effortlessly moving across the sediment surface, leaving barely a trace and suggesting that H. membranaceus feeds on epifauna and planktonic detritus at the sediment surface. However, the images of that study show a poor quality, and the oblique field view of the camera may have inhibited the observation of biogenic structures on the seafloor. We might not have the same species of *Hymenaster* but they seem to have similar behaviors. Here, we observed that *Hymenaster* transited the seafloor leaving a punctuated trail behind until it pushes into the sediment producing a pentameral impression, probably for feeding purposes. It is difficult to estimate whether this morphotype corresponds solely to predation, since the organism would most likely carry out digestion during resting in the same place (Blake 1989). In other words, the lebensspuren morphotypes of this tracemaker

Table 2 Lebensspuren morphological measurements of Porcellanasteridae specimens. In bold are the characterized morphotypes

		Flat-shallow tail			M-ridged trail			Circular to oval impression (cm^2)
Station_image code	Sea star size (cm)	T. length (cm)	S. length (cm)	Sinuosity	T. length (cm)	S. length (cm)	Sinuosity	
10_IMG_0435	6.4				68.44	45.11	1.52	
10_IMG_0577	7.2	80.47	48.19	1.67				11.3
12_IMG_0294	4.8				35.92	28.1	1.28	
14_IMG_0200	4.7				51.4	43.22	1.19	5.3
14_IMG_0470	9.8	40.65	34.12	1.19				12.3
14_IMG_0498	6.2				179.37	130.84	1.37	5.9
4_IMG_0090	5.2	61.47	45.96	1.34				
4_IMG_0291	4.6	67.45	59.72	1.13				
4_IMG_0297	4				20.23	16.16	1.25	
4_IMG_0325	4.9	36.72	22.15	1.66				4.9
4_IMG_0405	4.1							
4_IMG_0431	6.6	63.39	50.81	1.25				
4_IMG_0555	4.3				35.53	29.52	1.20	4.3
4_IMG_0578	6.1							
4_IMG_0626	5.4	59.87	57.92	1.03				4.6
6_IMG_0148	5				124.5	84.28	1.48	
6_IMG_1318	5.5				156.14	101.37	1.54	6.5
8_IMG_0390	2.3				42.97	30.38	1.41	2.9
Mean	5.2	58.57	45.55	1.32	79.39	56.55	1.36	6.4

represent a combination of locomotion and predation (Fig. 3). Analyzing whether this foraging behavior is systematic or not based on the current data is complicated. In this study, we only have four impressions in which we can accurately measure the spacing between them and the values vary from 123 to 20 cm. Also, the sinuosity values have a wide variability going from 2.35 to 1.09 (Table 1). Thus, we cannot accurately measure if *Hymenaster* is a generalist or selective feeding predators. A wider database and morphological measurements on both lebensspuren morphotypes are necessary to shed light on these questions. These interrogations also apply to *Dytaster*, which is a predator as well (Howell et al. 2003). Unfortunately, only two specimens were observed producing pentameral impressions and punctuated trails, suggesting a locomotion and predatory behavior similar to *Hymenaster* (Fig. 2f).

Porcellanasterids are non-selective mud deposit feeders (Mironov et al. 2016). Here, we observed impressions with a poorly preserved pentameral shape. This suggests that the Porcellanasteridae pushed into the sediment and then scooped the mud with lateral movements. We were not able to identify various impressions within the same trail (i.e., no spacing measurements). Thus, these impressions may be attempts of the tracemaker to identify buried organic matter resources. Then, if not enough organic matter was detected within the sediment, a locomotion period would start (i.e., flat-shallow trail) (Fig. 4). Pushing into the sediment and then contract pulling the body forward to feed on buried resources is a process that demands much more energy than transiting the surface. Therefore, if Porcellanasteridae detects that the organic matter quantity is not worthy, a flat-shallow trail will be produced and the tracemaker would move to another location. In the case of "suitable" sediment, an irregular M-ridged trail will start. In other words, these trails produced by Porcellanasteridae are feeding lebensspuren associated with an active movement in the substrate and removal of fecal material that was buried within the top centimeters of sediment. The similar sinuosity values between these two morphotypes reveal that the tracemaker is not able to develop a more complex foraging pattern when a food resource is found (i.e., a meandering pattern to exploit these resources more efficiently) (Miguez-Salas et al. 2022). This result seems to corroborate that members of the family Porcellanasteridae are non-selective deposit feeders. In any case, the present study shows the usefulness of neoichnological analyses to characterize deep sea star behaviors based on still images.

Implications for the fossil record

The ichnogenus *Asteriacites* von Schlotheim, 1820 results from the resting activity of sea stars (Asteroidea) and brittle stars (Ophiuroidea) (Knaust and Neumann 2016). However,

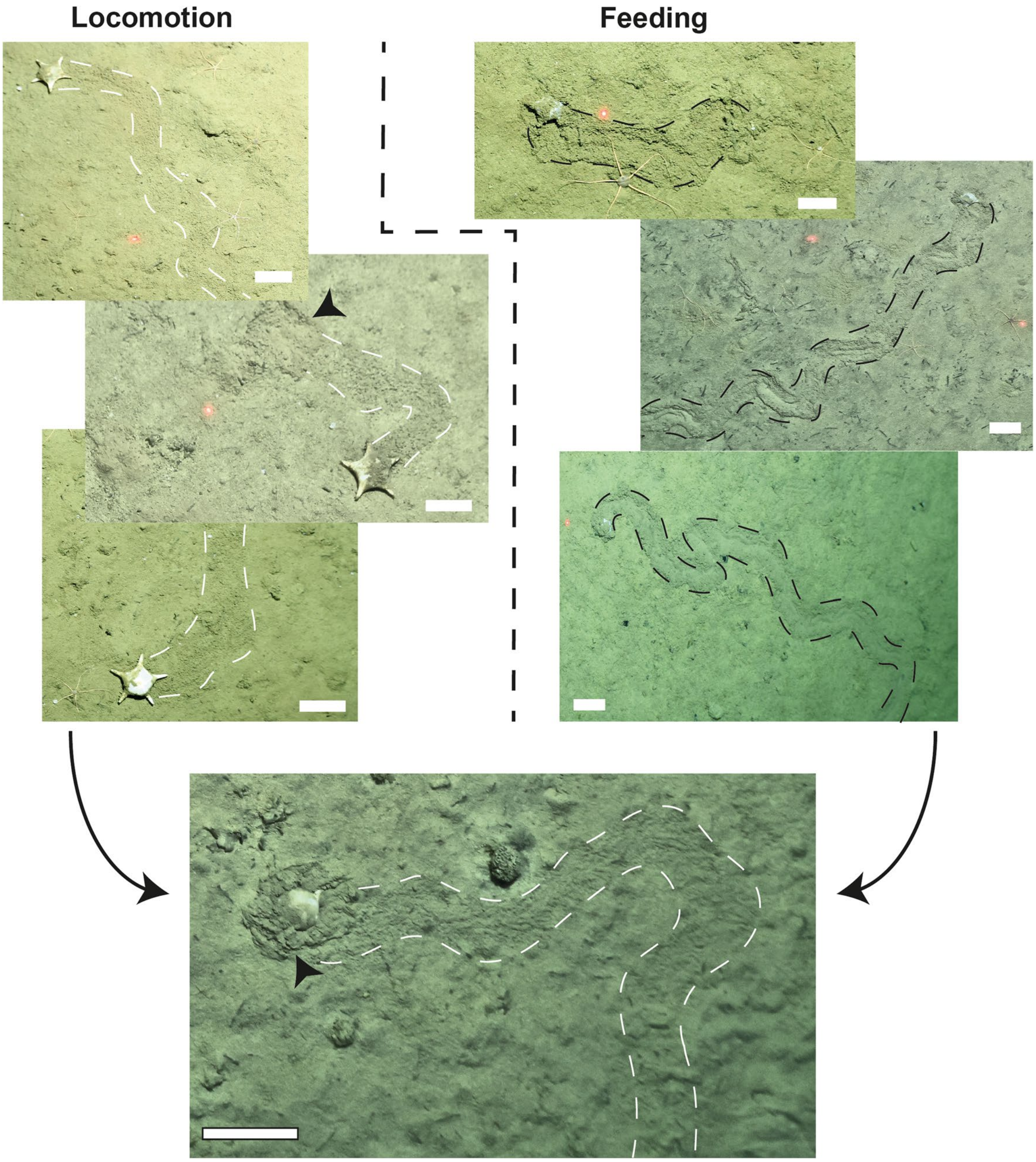

Fig. 4 Porcellanasteridae specimens producing the different lebensspuren morphotypes: (1) oval to circular impression (black triangles); (2) flat-shallow trail (white dashed lines); and (3) irregular M-ridged trail (black dashed lines). Scale bars = 5 cm

few tracemakers actually rest, and some of these traces are associated with feeding purposes (e.g., predation) or represent intergradations with locomotion traces (Buatois and Mángano 2011). Here, the majority of the lebensspuren can be correlated to the *Asteriacites* ichnogenus but they represent a combination of resting and feeding rather than just resting and digestion. For example, in the case of *Hymenaster*, the pentameral impressions can be attributed to a predatory behavior.

Knaust and Neumann (2016) stated that "The new ichnofamily Biformitidae is established for arc- or hookshaped imprints occurring isolated or clustered (e.g. trackways), which are mainly (but not exclusively) interpreted to be produced by ophiuroids and asteroids by means of locomotion on the sediment surface." The diagnosis of this ichnofamily is as follows: *arcuate or hook-shaped imprints occurring either isolated or clustered* (Knaust and Neumann 2016). Yet, the movement of asteroids primarily involves cyclic motions of the tube feet, whereas brittle-star locomotion is defined by undulating movements of the arms (Heddle 1967; Blake 1989; Mángano et al. 1999). Thus, arcuate or hook-shaped imprints would be mostly related to brittle stars' locomotion at deep sea. In the present study, the locomotion lebensspuren did not record any morphological features that resemble the ichnogenus diagnosis included within this new ichnofamily (e.g., *Biformites* Linck, 1948, *Arcichnus* Sutcliffe, 1997, *Harpichnus*, Vallon et al., 2015). In fact, our morphotypes are more similar to the sea star locomotion traces exposed in Mángano et al. (1999) and interpreted as tube feet impressions (see Fig. 3d, f in Mángano et al. 1999).

The aforementioned ichnogenera included within the ichnofamily Biformitidae have brittle stars as the most plausible tracemakers, while asteroids seem to take a backseat (see Knaust and Neumann 2016 and reference therein). We are not aware of any ichnogenus that can be correlated with the three described trail morphotypes associated with the locomotion and feeding activities of both *Hymenaster* and Porcellanasteridae. The residence lebensspuren time of trail morphotypes related to podia locomotion is low and its preservation in the fossil record will be scarce and strongly dependent on substrate properties. However, we open the question, based on the current observations, if the inclusion of unnamed trace fossils produced by sea star podia locomotion as the ones exposed by Mángano et al. (1999), should be included within Biformitidae ichnofamily by erecting new ichnogenera that embrace these asterozoan locomotion traces (i.e., not arcuate or hook-shaped imprints), or if they should be assigned to other established ichnofamily with similar morphological features and add asterozoan as possible tracemakers.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-023-01398-1.

Acknowledgements This is a publication of the "AleutBio" expedition onboard *R/V SONNE* (cruise SO293). The master and crew of *R/V SONNE*, especially Matthias Großmann, Heinz Voigt-Wenzel, and Wolfgang Borchert, are gratefully acknowledged for their support during OFOS deployments. The data were collected in the framework of the AleutBio project of BMBF grant 03G0293A to Prof. Dr. Angelika Brandt, Senckenberg Research Institute and Natural History Museum Frankfurt, Germany. This is AleutBio publication #6. We are most grateful for the constructive comments of two anonymous referees who helped us to improve the clarity of the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. The research of O. Miguez-Salas was funded by a Margarita Salas Fellowship from the Ministry of Spain and EU Next Generations projects.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval This study complies with ethical standards, according to the rules and guidelines of the journal.

Sampling and field studies All necessary permits for observations have been obtained by the author or contributors mentioned in the acknowledgments.

Data availability All data relevant to this study are included in this article.

Author contribution OMS and CM conceived and designed the research. OMS, AB, and CM carried out the fieldwork and observation. OMS and AB performed the data acquisition. CM conducted the sea star taxonomy. All authors gave final approval for the submission and publication of the manuscript.

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