

Article

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Death on “live broadcast”—fish mortichnia from the Upper Cretaceous plattenkalk of Lebanon

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Non-technical Summary

The trace fossils presented here belong to the category of animal behavior that Seilacher had defined and called “mortichnia.” However, Vallon and colleagues did not recommend the usage of this ethological category, because its recognition not only depends on trace fossil morphology, but also on tracemaker physiology and environmental interpretation. The two latter assumptions in particular cannot always be deduced correctly, rendering the whole interpretation false (especially when modern analogues of such environments or closely related organismal groups do not exist). Nevertheless, the category exists, and with the recently recovered specimens, a redefinition is attempted.

The specimens from Lebanon are all traces left by dying fish. At the beginning, the traces show the greatest physical strengths of the tracemakers, as their body movements were still relatively powerful. Over the course of the mortichnion, the traces reflect increasing exhaustion. The undulating movements of the tail fin decrease, and the resulting trail becomes more and more asymmetrical. Its depth becomes shallower. During last moments of the tracemakers’ lives, their movement was reduced to barely discernible movements. Finally, the trail ends with the death and the preserved corpse of the tracemaker.

In our redefinition of mortichnia, we argue that trace fossils included in this ethological group must contain the fossilized corpse of the tracemaker. The corpse must ideally show signs of illness or predation (the tracemaker body fossil, however, is neither part of the trace fossil nor is it to be regarded as the actual trace fossil). Other trails or trackways, especially from non-fish tracemakers like *Solemya* at the Solnhofen Lagerstätte (Kimmeridgian–Tithonian; Germany), may show signs of loss of orientation, or the tracemakers might try to avoid certain areas that impose hostile living conditions (e.g., ripples, crests) if the environment is drying out and the tracemakers breath via gills.

Abstract

Proper identification of behavioral patterns is an important prerequisite for the identification of any trace fossil and even more so for its interpretation. For the last 70 yr, the continually advancing state of ichnological knowledge has led to a gradual recognition of recurrent patterns of organismal behavior documented in the fossil record, which in turn gave rise to the ethological categories. “Mortichnia” was proposed for traces created during a death struggle of the tracemaker but has been reported only in a few cases. Fish mortichnia so far have only been reported in one specimen recovered from the Upper Jurassic Plattenkalk of Nusplingen (SW Germany). The category mortichnia is refined herein, but remains ambiguous. Eight newly discovered unique specimens of mortichnia from Upper Cretaceous marine sediments in central Lebanon (Haqil, En Nammoura) are preserved together with their tracemakers and described herein. In addition, 14 further incomplete specimens were collected where no tracemakers are present. However, morphology and close provenance allow them to be assigned to the same ichnotaxon.

The Lebanese mortichnia originate from fish that were subjected to significant environmental or individual stress leading to their deaths. During death convulsions, their bodies created sedimentary structures with a specific recurring morphology. The ichnogenus *Pinnichnus* n. igen. with ichnospecies *P. haqilensis* and *P. emmae* n. ispp. is proposed for these specimens.

Introduction

In most cases, the tracemaker of any specific trace fossil remains unknown, usually owing to preservational differences and the contrasting taphonomic path. However, any use of a trace in the description of paleoenvironmental characteristics requires that the behavior of its producer is correctly inferred. This is achieved by comparison with modern ethology (e.g., Martin and

Bateson 2021), although an incomplete fossil record necessarily calls for a certain level of simplification and generalization. In ichnology, this purpose is served by the ethological classification of Seilacher (1953), which was later significantly improved and extended (Vallon *et al.* 2016 and references therein). The latest amendment (sequestrichnia, or stowing traces) was proposed by Uchman and Wetzel (2016).

Mortichnia as a category was first proposed by Seilacher (2007) for distinct traces encountered at the Solnhofen Plattenkalk locations. In particular, trackways with arthropod fossils at their ends were interpreted as tracemakers that struggled with and finally succumbed to hostile environmental conditions (Vallon *et al.* 2015a). Most of these trackways have been proved to be traces of molting; thus, the number of specimens assigned to this category has plummeted significantly. Only very few genuine mortichnia remain, for example, looped trails with open, articulated shells of the bivalve *Solemya* at their ends (Röper *et al.* 1999); the last tail movements of the fatally injured shrimp *Telsonichnus* (Schweigert 1998; Schweigert and Dietl 2005); and a fish trace fossil identical to the ones described herein (Schweigert *et al.* 2016).

Threats to life with a possible lethal outcome can occur to any tracemaker. These can include predation by other animals, exposure to hostile environments, disease, rapid burial, or similar events. Vallon *et al.* (2016) recommended against the usage of the category mortichnia, because its recognition is to some extent more interpretive compared with others. Burrows, for example, may immediately be recognized through their morphology alone as pure living structures (domichnia), as feeding burrows (pascichnia), or if the tracemaker applied a combined living and feeding strategy, as fodinichnia. With mortichnia, the trace-making animal needs to be not only preserved, but also recovered, and for it to be proven without doubt that this body fossil is indeed a fossilized corpse rather than just an exuvia (in the case of arthropods). When the tracemaker is neither preserved nor recovered (e.g., in incomplete specimens), these locomotion traces cannot undoubtedly be recognized as mortichnia and should then be referred to as “repichnia” (or respectively), even if there is a possibility that mortichnia might occur at the investigated locality (see Supplementary Table S1).

Geological Settings

The origin of the Mesozoic sedimentary formations in Lebanon is associated with a distinct NNE-SSW trending fault line, which is dissected by secondary, subvertical faults, resulting in a series of discontinuous geological units with still unresolved stratigraphic correlation. This active fault system at the outer margin of the continental shelf of the Tethys Ocean created the grounds for several pull-apart basins in which plattenkalk were sedimented in a warm marine environment (Hüchel 1970). The oldest platy limestones in the area are from the Jurassic; the vast majority, however, were deposited during the Late Cretaceous (Cenomanian–Santonian; Walley 1997).

The rich paleontological sites of the Upper Cretaceous in the central part of Lebanon have been known for a long time. Among the most famous are En Nammoura, Haqil, Hgula, and Sahel Alma (see Fig. 1). The quality of the fossils is unique; the state of preservation, diversity and abundance of the local sedimentary basins being comparable to those of the Konservat-Lagerstätten at Monte Bolca (Italy) and the Solnhofen Archipelago (Germany) (e.g., Barthel 1978; Barthel

et al. 1994; Dalla Vecchia *et al.* 2002; Marramà *et al.* 2016; Pasini *et al.* 2019). Fish are most commonly recovered, but crustaceans are also present in addition to less frequently reported echinoderms, plants, reptiles, insects, and birds.

The sedimentary development of the local basins has not yet been studied and documented in detail, but it is preassumed that the individual sites represent different types of paleoenvironments. While the limestones around En Nammoura were formed at the margin of a relatively large basin and were influenced by eustatic sea-level movements, the other localities originated from tectonically induced local subsidence and were gradually filled with plattenkalk (Gayet *et al.* 2012).

The abundance of a well-preserved fossil fauna in these Upper Cretaceous Lebanese sites might result from periodic overgrowth by microbes (Gayet *et al.* 2012). The reason for such “algal blooms” could lie in heavy precipitation in the hinterlands on the nearby continent bringing in a large influx of nutrients while locally lowering the salinity, perhaps even resulting in so-called red tides (although, to our knowledge, dinoflagellates have not yet been investigated in the Lebanese plattenkalk). Such an increase in biomass in relatively small, confined marine basins may have led to an anoxic environment, as evidenced by locally elevated bituminous content (Ghalayini *et al.* 2018). The temporary deterioration of environmental conditions would then result in poisoning and suffocation of the marine fauna, which died off relatively quickly. The dead animals accumulated on the basin floors, where they were quickly overgrown by microbes and then buried by fine-grained material, mainly carbonate mud (Gayet *et al.* 2012).

En Nammoura Quarry

GPS coordinates: 34.0563889°N, 35.6886111°E

Stratigraphy: Late Cretaceous, middle Cenomanian (93 Ma, Sannine Formation)

Material: MIM/F1021

The village of Nammoura is located in the mountains on the south side of the Nahr Ibrahim Valley, in the district of Kersewan, governorate of Mount Lebanon. The first quarry there began business in 1915, and the present fossil sites were opened in the 1950s. The total exposure of the sedimentary layers now extends approximately 1 km along the valley and 500 m across it. The Nammoura Plattenkalk is a lithographic limestone: a pale, laminated micrite (Dalla Vecchia *et al.* 2002).

Fossils are less abundant than in the other localities and are generally recovered as single specimens. Layers with mass mortalities or overlapping skeletons are rarely encountered. However, the preservation of the specimens is extraordinary. Plants occur more abundantly in these sediments than at other Lebanese localities. The relative richness of both terrestrial fauna and flora suggests that Nammoura was close to a land area during the middle Cenomanian (Barale *et al.* 2004).

Haqil Quarry

(= also transcribed from Arabic as Haqel, Hakel, or Hakil)

GPS coordinates: 34.1646103°N, 35.7574225°E

Stratigraphy: Late Cretaceous, lower to middle Cenomanian (95 Ma, Sannine Formation)

Material: MIM/F1001–MIM/F1020

Haqil is a small village situated northeast of Beirut in the district of Jbeil, governorate of Mount Lebanon. It is located in a deep

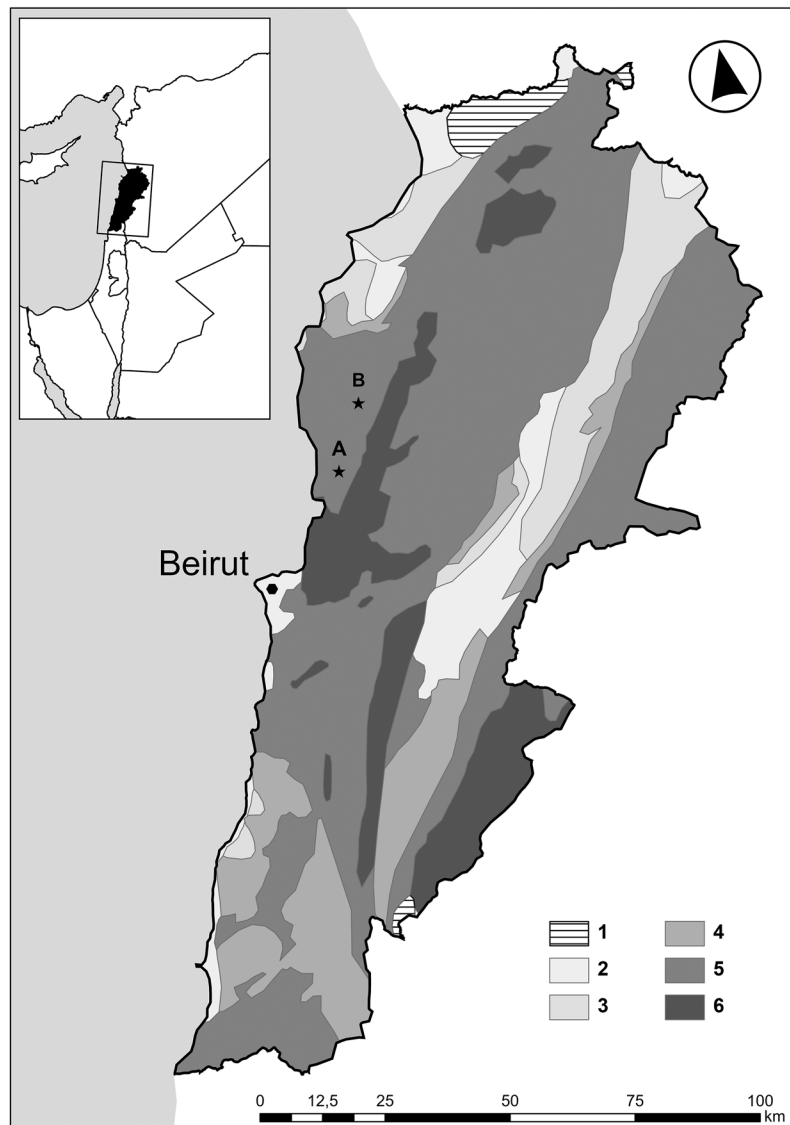


Figure 1. Simplified geological map of Lebanon. 1, Volcanic rocks (upper Cenozoic), 2, nonmarine sediments (Quaternary), 3, limestones, conglomerates (Miocene–Pliocene), 4, marine chalks and limestones (Late Cretaceous–Neogene), 5, fluvio-deltaic sandstones, marine limestones (Early–Late Cretaceous), 6, limestones, dolomites (Early–Late Jurassic). Sites with traces of *Pinnichnus* n. igen. are marked with an asterisk (A, Haqil; B, En Nammoura) (based on Walley 1997).

valley lying 700 m above sea level. The slightly siliceous plattenkalk of this small occurrence represents one of the richest deposits of fossil fish in the world. The site has been known since the time of the Crusades (Davis 1887) and is likely the oldest Lebanese locality yielding fossil fish.

The limestones are well stratified, with bedding in the centimeter range, and the strata are variably inclined, falling to the west. The color varies from pale yellow to a brownish gray, gray to almost black. The Haqil limestone is composed of ~75% CaCO_3 and ~20% SiO_2 , with the remaining ~5% consisting mostly of clay minerals.

The fish beds were deposited in small basins only a few hundred meters across, probably having a tectonic origin at the intersection of block fault systems. The fossiliferous layers are always accompanied by breccia-like deposits that rest unconformably on the basin slopes and represent the initial phase of the basin fillings probably resulting from small-scale turbidites released by earthquakes. The fossiliferous plattenkalk layers, on the other

hand, indicate slower deposition in a subsequent stagnant stage (Krings and Mayr 2004; Gayet et al. 2012).

Materials and Methods

Our study is based on 22 specimens (8 of them with a preserved tracemaker) collected by professional fossil collectors (coauthors R.N. and P.A.S.) in the Lebanese Upper Cretaceous Lagerstätten. These specimens display close similarity with the fish-made mortichnion described by Schweigert et al. (2016) from Nusplingen (Kimmeridgian, Germany).

As the abovementioned specimens were primarily collected for commercial purposes, they unfortunately lack information on the respective sampling sites and also on their stratigraphic positions. Their counterparts (imprints on the opposite slab) were discarded. Despite this, the specimens exhibit a sufficient amount of information due to their exceptional preservation in combination with their tracemakers.

Owing to the specific morphology of the traces described below, the new ichnogenus *Pinnichnus* with two new ichnospecies is proposed.

The reported specimen from Nusplingen (Upper Jurassic, Germany) is housed in the Staatliches Museum für Naturkunde in Stuttgart (SMNS; see Schweigert et al. 2016). The Lebanese specimens were originally housed in the private but publicly accessible collections of R.N. and P.A.S. To ensure their accessibility in the future, the best solution is to store them in public collections (ICZN §16C, §72F). Historically, important scientific specimens have been taken out of their countries of origin (some illegally) and brought to European or American institutions. We therefore committed to repositing the type material in Lebanon as part of its legacy of natural heritage. Unfortunately, at present, Lebanon has no publicly funded Natural History Museum. However, the MIM Museum in Beirut (متحف ميم in Arabic) comes close to this concept. Although this mineralogical–paleontological museum is also fully financed from private sources, due to close cooperation with Saint Joseph University of Beirut and membership in the International Council of Museums, it fully meets the criteria of a public museum. All specimens found in Lebanon and described in this article are therefore included in the MIM Museum’s collection on the basis of a contract with the original owners and are provided with official depository numbers (MIM/F1001–1021).

Results

Systematic Ichnology

Pinnichnus n. igen.

Derivation of Name. *pinna* = fin in Latin.

Type Ichnospecies. *Pinnichnus haqilensis* n. isp.

Diagnosis. Uniserial trackway-like, unbranched, straight to bent linear arrangement of multiple segments, each consisting of a depression alternated with a mound. The individual segments may be connected by a wavelike furrow. Frequency of segments usually increases from distal to proximal end of the trace (and their lengths decrease respectively). Simultaneously, the amplitude of the wave decreases as well as the penetration depth of the depressions and height of the mounds.

Remarks. The new ichnogenus *Pinnichnus* belongs to the group of traces produced by fish while swimming close to the bottom. The only described representatives of this category so far are the repichnia *Broomichnium*, *Undichna*, and *Parundichna*.

Broomichnium can easily be distinguished by its bilaterally symmetrical, trackway-like imprints, formed probably by fins of small demersal fish (Benner et al. 2008). *Undichna* consists of one or multiple continuous or intermittent wavy lines, and *Parundichna* of bundles of subparallel sinuous scratches arranged in a chevron-like pattern. The three ichnogenera are made by healthy fish during normal locomotion with their bodies floating in the water column in a physiological position (sagittal plane view, lateral side up). Thus, the result is a highly symmetrical trail generated by the repetitive movement of the lower portions of the paired fins (mainly *Parundichna*) or the unpaired caudal fin (mainly *Undichna*; in the case of multiple rows in *Undichna*

pectoral, pelvic and anal fins may be involved respectively; Trewin 2000; Simon et al. 2003). All of these locomotion traces were created by fish swimming close to the substrate surface and therefore only created superficial structures. A thorough revision of the genus *Undichna*, together with a detailed geometric analysis of the trails of each species, was carried out by Minter and Braddy (2006).

Pinnichnus, on the other hand, was created while the fish swam in an oblique to horizontal side position, which (apart from Pleuronectiformes; e.g., Schreiber 2013) is a sign of intoxication, disease, or injury of the tracemaker, usually resulting in death (e.g., White 1981; Sharma 2019). As the fish touched the substrate, their still-existing survival instinct caused an escape-panic reaction. Consequently, the caudal fin imprint cannot be considered as the fish’s normal movement but a result of fading attempts to escape from the seabed (*P. haqilensis*), or even death throes (*P. emmae*), while listing or swimming on its side. These initially strong movements of the caudal fin disturbed the sediment surface in a larger depth than the above-described locomotion traces. During the course of the trace, the fish’s strength was fading and the produced segments of the traces became weaker, occurring at shorter intervals and, where present, the amplitude and wavelength decreased. We therefore interpret the specimens described here as mortichnia.

Both *Undichna* and *Pinnichnus* encompass broad morphological variation, which often is a result of only minor changes in tracemaker behavior (e.g., steering as adaptation to current changes) or is rooted in taphonomic processes. Minter and Braddy (2006) underscored in their revision of *Undichna* the importance of recognizing recurrent patterns in contrast to describing every minor variant as a new ichnospecies. Because the Lebanese finds come from depositories, usually without specific collection data, it is impossible to decide whether our morphotypes (described later) are of ethological origin or rather are caused by taphonomic effects such as rock splitting (MacNaughton and Pickerill 2003; “taphotaxa” sensu Lucas [2001]). Therefore, only two ichnospecies were distinguished based on clearly recurring diagnostic characteristics, and recurring variations were referred to as “morphotypes.”

The only other described and named mortichnion, *Telsonichnus*, especially *Telsonichnus speciosus*, is relatively similar to *Pinnichnus*. It mainly differs from the new ichnogenus in its parallel arrow-shaped depressions and ridges (Schweigert 1998; Schweigert and Diel 2005). Individual segments of *Telsonichnus* are connected by a median line that is never present in *Pinnichnus*.

Pinnichnus haqilensis n. isp.
(Fig. 2A–F)

Derivation of Name. Haqil = Lebanese locality yielding the type material of the ichnospecies.

Holotype. MIM/F1001 (Fig. 2D).

Paratypes. Six specimens (MIM/F1002 MIM/F1003 [Fig. 2E], MIM/F1008 [Fig. 2F], MIM/F1009, MIM/F1016 [Fig. 2A], MIM/F1017).

Other Material. Fourteen incomplete specimens, without the preserved tracemaker. Although these specimens belong to the same ichnotaxon, they therefore cannot be referred to as mortichnia in the sense redefined herein (MIM/F1004–MIM/F1007 [under the

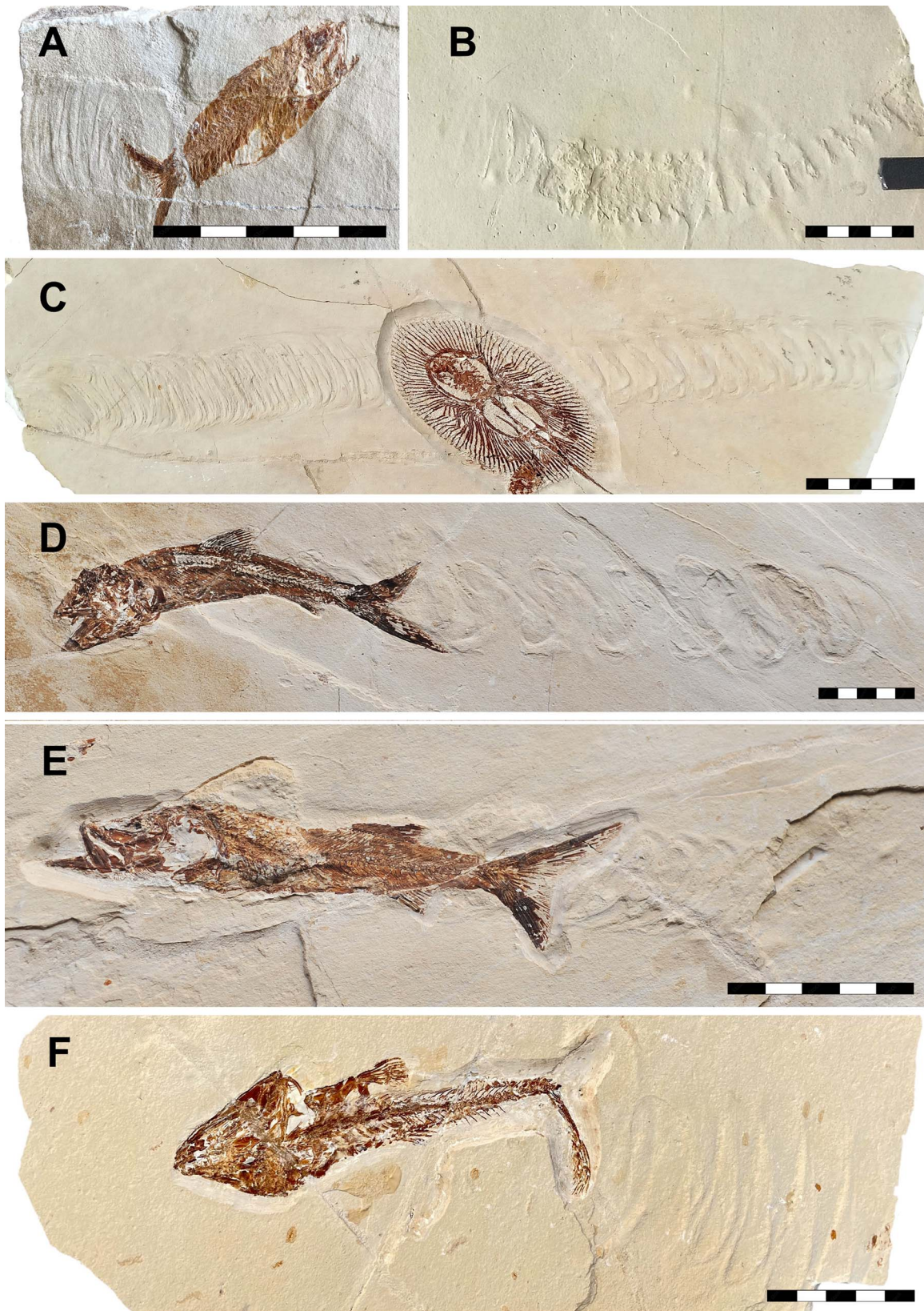


Figure 2. **A**, Bony fish *Acrognathus dodgei* with “arcuate” morphotype of *Pinnichnus haqilensis* n. isp. (MIM/F1016). **B**, “Curved ripple-like” morphotype of *P. haqilensis*, developed as the discontinuous, shallow arcs (MIM/F1005). **C**, A specimen showing the transition between “curved ripple-like” (right) and “arcuate” (left) morphotypes of *P. haqilensis*. The stingray *Cyclobatis oligodactylus* occurring in the middle is not related to the fossil trace (MIM/F1004). **D**, A fully developed shape of *P. haqilensis* combines deep “crescents” and ripples, in the presence of tracemaker, bony fish *Hakelia* sp. (MIM/F1001, holotype). **E**, *Pinnichnus haqilensis* in “curved ripple-like” shape, with the tracemaker, *Hakelia* sp. (MIM/F1003). **F**, *Pinnichnus haqilensis* in “curved ripple-like” shape, with the tracemaker, ray-finned fish *Eurypholis boissieri* (MIM/F1008). Scale bar, 5 cm.

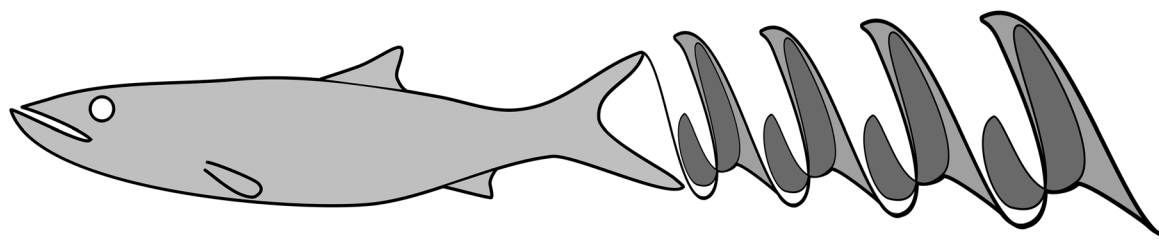


Figure 3. A schematic illustration of the “curved ripple-like” morphotype (morphotype 1) of *Pinnichnus haqilensis*, together with one of its tracemakers, *Hakelia* sp. (Teleostei). The dark gray areas resemble the deepest depressions; mounds are present in the areas between. The changes in wave height and segment spacing are exaggerated in this sketch. In reality, they are subtler and extend over much longer distances.

number F1007, there are two specimens on one slab], MIM/F1010–MIM/F1015, MIM/F1018–MIM/F1020).

Type Locality and Stratigraphy. Active limestone quarry near Haqil, NW Lebanon (34.1646103°N, 35.7574225°E), Upper Cretaceous, lower to middle Cenomanian

Known Tracemakers. *Acrognathus dodgei*, *Eurypholis boissieri*, *Hakelia* sp., *Sardinoides* cf. *minimus*

Diagnosis. *Pinnichnus* initially with an asymmetrical wavelike furrow that may be looped or with sharp bends. Segments uniformly curved, often crescentic ripples and depressions, commonly asymmetrical with one side having sharper bends, deeper depressions, and higher mounds. Spacing of segments at first wide and strongly asymmetrical (morphotype 1), later more closely spaced and more symmetrical until the mounds resemble closely spaced, thin, linear to crescentic ribs (morphotype 2).

Description. *Pinnichnus haqilensis* occurs in two morphotypes of slightly different appearance; still, these merely represent variants of the same kind of movement of the tracemaker, depending on its velocity, orientation, exhaustion, and height above the sediment surface. The two morphotypes can merge into each other. In all morphotypes, the fish sank toward the bottom. When touching the seafloor, the tracemakers attempted to swim free again, often while listing or lying on their sides. In the complete specimens, the animals did not succeed and their corpses were preserved at the end of their traces. In incomplete specimens, where the tracemakers’ bodies have not been preserved (owing to different circumstances such as erosion, slab size, etc.), the chances are high that a corpse was preserved at the end of a trail. However, there also is a chance of a lucky escape, making it impossible to assign them to an ethological category other than repichnia.

Pinnichnus haqilensis was observed to be made by different fish genera (*Hakelia*, *Eurypholis*, *Acrognathus* etc.) that touched the sediment with their caudal fins. Relief generated by the swinging caudal fin upon its penetration in the sediment always shows a typical pattern of recurrent loops, sharp bends, pointed ends, and so on. Although different body plans create slight variations, we do not deem them sufficient to split *P. haqilensis* into several ichnospecies.

Morphotype 1 (“curved ripple-like”: MIM/F1001–MIM/F1003; MIM/F1004, partially; MIM/F1005; MIM/F1006; MIM/F1007, partially; MIM/F1008–MIM/F1011; MIM/F1013–MIM/F1015; MIM/F1018–MIM/F1020). Individual segments are relatively wide compared with morphotype 2. Their shapes range from shallow arcs only weakly defined by their outlines, often discontinuous (e.g., specimen MIM/F1005, Fig. 2B), to a more deeply outlined series of crescentic forms with a recurrent J-shaped pattern, especially when the tracemaker fish was listing (e.g., specimen MIM/F1004, Fig. 2C). A fully developed shape of the trace combines “crescentic” depressions and ripples, which correspond to a periodic motion of the caudal fin. This form is exemplified by well-developed specimen MIM/F1001 (Fig. 2D), which preserves the tracemaker (fish: *Hakelia* sp.) and six repetitions of trace segments having a total length of 19.5 cm. The individual ripples are 45–50 mm in width and 30–40 mm in length (Fig. 3).

Morphotype 2 (“arcuate”: MIM/F1004, partially; MIM/F1007, partially; MIM/F1012; MIM/F1016; MIM/F1017). In this morphotype, the individual segments are so closely spaced that neither trail nor depression-mound segments can be recognized. The trace rather consists of slightly elevated bow-shaped ribs or wrinkles.

A typical example, preserved together with its tracemaker (*Acrognathus dodgei*), is specimen MIM/F1016. In this specimen, nine pairs of crescentic ripples are preserved immediately behind the tail of the fish, having an average width of 25 mm and a total length of the trace of 35 mm (Fig. 4).

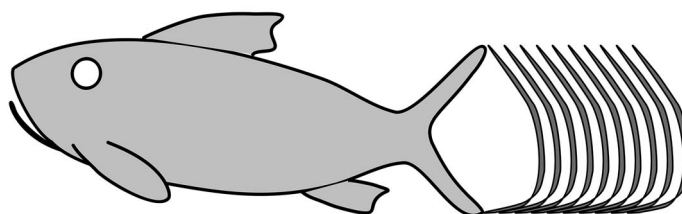


Figure 4. A schematic illustration of the “arcuate” morphotype of *Pinnichnus haqilensis*, together with one of its tracemakers, *Acrognathus*.

Remarks. Both morphotypes were created mainly by movements of the caudal fin. The depth of the traces was the result of the penetration depth of the caudal fins and ultimately reflects the fish’s ability to move. In this scenario of a dying fish, caudal movements would still have been relatively strong at the beginning of the trace and would have resulted in deep sediment penetration at a relatively high velocity. Therefore, the single segments consisting of depressions and mounds of pushed-away sediment are broadly spaced. In normal swimming position, these movements would resemble the ichnotaxon *Undichna unisulca*. With increasing effects of toxication or exhaustion, the fish started to swim more and more obliquely, creating an increasingly asymmetrical repichnion. When the fish was listing to one side, the caudal fin now started to create a more and more asymmetrical line with sharp bends or loops. With each movement, sediment was pushed away, and the crescentic depressions and mounds were formed (curved ripple-like morphotype, morphotype 1). Over time, the swimming movements became less and less powerful, resulting in decreasing penetration depths, reduced swimming speed, and with it, more closely spaced segments. Simultaneously, the depressions became shallower and the mounds flatter.

Near the death of the tracemaker, the fish might have assumed a horizontal position. Exhaustion and toxication would have progressed to a point where the fish was only able to make tiny movements with its caudal fin. At this point, the thrust provided and the sediment penetration of the fin would have been at a minimum. The produced individual segments now have rather symmetrical shape and are very closely spaced (arcuate morphotype, morphotype 2). At the end of the traces, the tracemaker died, and its body fossil may be preserved.

Pinnichnus emmae n. isp.

(Fig. 5A,B)

2016 mortichnium Schweigert et al., Fig. 3 [specimen SMNS 96078/35].

Derivation of Name. Emma = first name of R.P.’s daughter, who was born during the preparation of the manuscript of this article.

Holotype. MIM/F1021 (Fig. 5A,B).

Paratype. SMNS 96078/35 (Schweigert et al. 2016: fig. 3).

Type Locality and Stratigraphy. Active limestone quarry near En Nammoura, district of Kersewan, governorate of Mount Lebanon, Lebanon (34.0563889°N, 35.6886111°E), Upper Cretaceous, middle Cenomanian.

Known Tracemakers. *Caturus* cf. *furcatus*, *Dercetis* sp.

Diagnosis. *Pinnichnus* with segments of isolated subtriangular to crescentic depressions on sediment surfaces alternating with similarly shaped mounds. Both depressions and mounds slant toward one side.

Description. Specimen MIM/F1021 displays almost straight series of 15 individual segments, with a total length of 19 cm. The sizes of the triangular segments are nearly constant, 25–27 mm by 7–9 mm, at intervals of 10–12 mm. The trail ends with the body fossil of the tracemaker, the fish *Dercetis* sp.



Figure 5. A, Ray-finned fish *Dercetis* sp. with associated mortichnium *Pinnichnus emmae* n. isp. (MIM/F1021, holotype). B, Detail of the same sample with well-developed triangular segments of the trace. Scale bar, 5 cm.

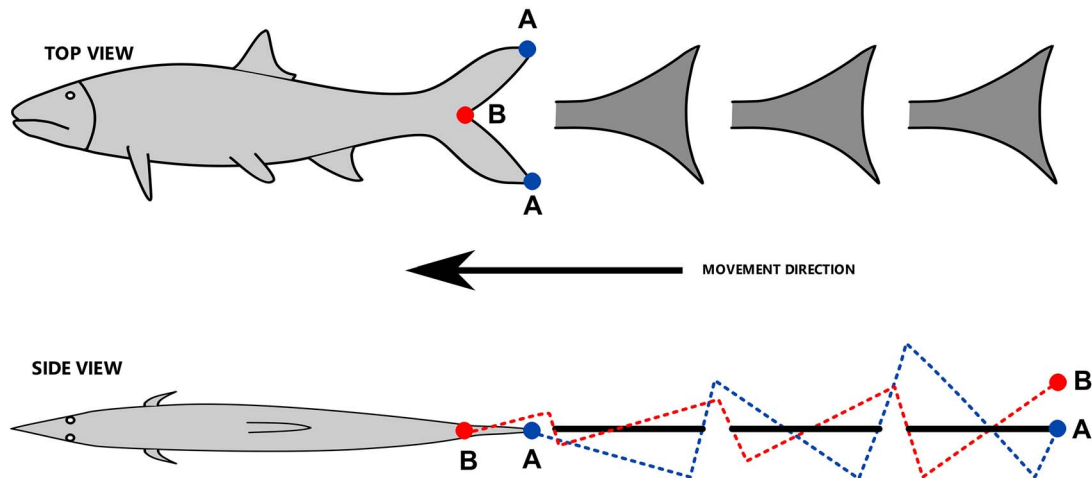


Figure 6. Origin of trace *Pinnichnus emmae*, produced by a fish of the genus *Caturus* (“German morphotype”). The principle of motion of the caudal fin described with the aid of three reference points. First sediment contact was made by both tips of the caudal fin (A, A) and thereafter by the caudal peduncle (B). The latter contact lifted the fish back up and interrupted the trace, and the cycle started over until the fish succumbed its lethal injuries. The dashed black line represents the level of the seabed.

Remarks. The described trace shows a striking similarity with the specimen reported by Schweigert *et al.* (2016) from the Upper Jurassic Nusplingen Plattenkalk, Germany. Their trace, ~29 cm long, is also preserved together with the tracemaking fish (*Caturus cf. furcatus*, specimen SMNS 96078/35) and reveals a distinct recurrent pattern of triangular forms of concave/convex character. The only difference is the orientation of the triangles, the apices of which point to the tail of the fish, hence in the direction of the movement of the tracemaker. In the case of the newly recovered Lebanese specimen MIM/F1021, they are oriented in the opposite direction.

These differences can be explained by two modes of movement of the tracemaker, which, however, merely pose two variants of the same style, typical for the origin of *P. emmae*. In specimen SMNS 96078/35 from the German Upper Jurassic, the dying fish, slowly sinking to the bottom, always touched the sediment

with both tips (marked A in Fig. 6) of the caudal fin first, and only then with the whole of the tail including the caudal peduncle (marked B in Fig. 6). The fish then leaped up above the seabed for a short time and shifted slightly forward to start sinking back to the bottom again. This produced a series of triangular depressions whose broad bases are orientated away from the fish body (“German morphotype”; see Fig. 6).

In the “Lebanese morphotype,” the fish, upon sinking, touched the seafloor first with its caudal peduncle (specimen MIM/F1021). Combined with a forward movement of the whole fish, the caudal fin dragged sediment with it until the two fin tips touched the bottom, creating the triangular depressions with their bases orientated toward the fish’s body. Much like in the previously described specimen, the fish then leaped above the bottom for a short time, shifted slightly forward, and then produced another segment of the same shape (Fig. 7).

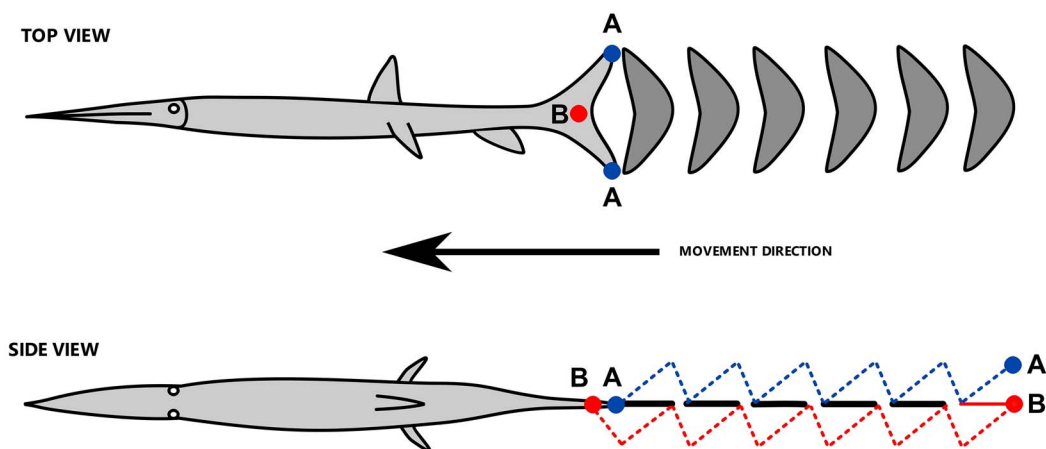


Figure 7. Origin of trace *Pinnichnus emmae*, produced by a fish of the genus *Dercetis* (“Lebanese morphotype”). In this morphotype, sediment contact was first made by the caudal peduncle (B) and thereafter by the two tips of the caudal fin (A, A).

Discussion

Mortichnia—A Valid Category Worth Re-establishing?

The trace fossils described herein clearly belong to a category of animal behavior that Seilacher (2007) had defined and called *mortichnia*. However, Vallon et al. (2016) recommended against the use of this ethological category because its recognition depends not only on trace fossil morphology, but also on tracemaker physiology and environmental interpretation. The two latter assumptions in particular cannot always be deduced correctly, rendering the whole interpretation dubious, especially when modern analogues of such environments or closely related organismal groups no longer exist.

By quoting and modifying the four questions raised by Tinbergen (1963) about animal behavior, Vallon et al. (2016) outlined the criteria upon which ethological categories of trace fossils should be based. Seilacher (2007) based his category on holistic interpretation rather than on trace fossil morphology alone. Thus, classification of trace fossils as *mortichnia* is not as intuitive as for other categories and does not make them easily recognizable. Specifically, incomplete specimens lacking a preserved corpse cannot undoubtedly be interpreted as *mortichnia*. Moreover, even when a body fossil is present, it needs to be proved beyond any doubt that it indeed is a fossilized corpse and not, for example, an exuvia, as is commonly encountered in the Solnhofen Plattenkalk. Vallon et al. (2015a) therefore needed to reinterpret many proposed death-struggle traces from the Solnhofen Archipelago (e.g., Seilacher 2007) as traces left during arthropod molting (ecdysichnia).

Genuine *mortichnia* remain scarce and, so far, are only known from rare examples, for example, *Telsonichnus* (Schweigert 1998; Schweigert and Diel 2005; Schweigert et al. 2016), the spiral or looped trails produced by the bivalve *Solemya* (Röper et al. 1999), or the specimens from Lebanon described herein.

When referring trace fossils to the category *mortichnia*, the list of Tinbergen’s questions modified by Vallon et al. (2016) needs to be answered and evaluated.

The first question (What was the function of the behavior that was recorded as a trace? What did the tracemaker try to achieve?) is easy to answer: No tracemaker wants to die. All fight against death as long as they can and on some occasions might even succeed. In incomplete specimens, which are the rule rather than the exception, recognition of a successful or an unsuccessful escape will not be possible. Traces then should be referred to *repichnia*, or in the case of burial, *fugichnia*.

The second question (What external factors controlled or were controlled by this behavior?) can be difficult to answer, especially when environmental interpretation of the locality is unsure. In the cases described herein, environmental stress, for example, fluctuations in salinity, oxygen levels, toxication caused by algal blooms (such as red tides), is probable but, as in the Solnhofen area, cannot easily be proven. The basins between the Solnhofen Archipelago were thought to be hostile environments (e.g., Viohl 1998), mainly owing to exquisite fossil preservation and lack of trace fossils. However, that interpretation is being challenged as new material of poorly preserved trace and body fossils is more frequently recorded (e.g., Röper and Rothgaenger 1998). The former collection bias of recording only exquisite specimens and disregarding most trace fossils has led to the misinterpretation of these sedimentary environments as hostile, and many of the recovered trace fossils have wrongly been referred to as *mortichnia*. The described specimens of *Telsonichnus* and the German

morphotype of *Pinnichnus emmae*, however, are related to lethal injuries during predation and undoubtedly belong in the category *mortichnia*. So, of course, do our specimens described herein with their tracemakers preserved at the end of the traces, although the animals did not die due to predator attacks. Nevertheless, no systematic excavation, where everything is recorded, has been carried out at the Lebanese localities. As in the Solnhofen quarries of yesteryear, trace fossils and poorly preserved specimens do not sell for high prices; if existing, they are usually discarded. The known fossils from Lebanon are all exquisitely preserved and come to scientists via fossil traders largely without ecological or stratigraphic context, rendering environmental interpretations similar to those undertaken for the Solnhofen Archipelago questionable.

The third question (How did the trace develop during the ontogeny of an individual tracemaker?) needs to be modified slightly and adjusted to the creation of the trace, because these traces captured only a few moments of the tracemaker’s lifetime. During the death struggle, the physical strength of the tracemaker decreases with time. With progressing exhaustion, the produced traces will be most powerful at the beginning until they completely fade away with the death of the tracemaker. In the specimens of *P. haqilensis* described earlier, this is recognizable in the decreasing interval between single segments, the decreasing penetration depth of the tail trail, and the flattening of depressions and mounds. Similarly, the triangular depressions of *P. emmae* became flatter with proceeding exhaustion. This aspect might be recognizable in most *mortichnia*, perhaps even if the tracemaker corpse is not preserved.

Question four (How did this behavior originate during the phylogeny of the tracemaker?) has the same answer for any tracemaker. Nobody wants to die, and every tracemaker will fight against pending death. This behavior is probably as old as life on Earth.

The answer to the final question (added by Vallon et al. 2016), of how the trace fossil was created (ichnogeny; Belaústegui et al. 2016), always starts with a death threat imposed to the tracemaker that affects it either suddenly or slowly. Examples of a sudden death threat include a possible lethal injury, whereas intoxication may progress relatively slowly. After a certain time, the tracemaker’s body will not be able to maintain normal metabolism and instead will focus on fighting off impending death. Death-struggle traces, however, start with the contact between the tracemaker’s body and the substrate where the death throes are recorded (cf. Bertling et al. 2006, 2022). Creation of the trace usually involves the main body parts used for locomotion, because the tracemakers will literally try to escape impending death by moving away. Main body parts would be the caudal fin in the specimens described in this article, feet or hands in land vertebrates, a muscular foot in mollusks will use, and so.

However, the *mortichnia* described herein are all horizontal trace fossils. If bivalves are rapidly covered with sediment, they create vertical escape structures, commonly regarded as *fugichnia* (Vallon et al. 2016). An unsuccessful escape leaving the clam’s shell at the top of the trace would have to be regarded simultaneously as a *mortichnia* and a *fugichnia*. In escape traces that do not contain the tracemaker’s body, we must assume either that the escape was successful or that the body was not preserved. Here an overlap of behavioral categories cannot be avoided, if *mortichnia* are to be reinstated.

Nevertheless, can we perhaps find criteria to redefine the category *mortichnia* in order to re-establish it? The first attempt was made by Sarjeant (1975) with his definition of “taphoglyphs” (not to be mistaken for aboriginal ritual carvings in trees in eastern

Australia; see Etheridge 1918). However, this group did not particularly include traces, but rather body (fossil) positions that were reached during the last moments of the animal's life or were taken on by the dead body immediately after death (e.g., through desiccation) or during transportation of the dead body by a predator, scavenger, or abiotic medium (similar observations have been made by Weigelt [1927]). Sarjeant's definition was very broad and also integrated soft tissue imprints (e.g., feathers and wing membranes) and rather horrifying examples of casts of writhing dogs and people in volcanic tuff at Pompeii from the time of the Roman Empire. Even posthumously trampled skeletons would fall within Sarjeant's taphoglyphs (e.g., Plio-Pleistocene remains of a young flamingo that was stepped upon by a llama-like camelid; Cabral-Perdomo 1996).

As Sarjeant's taphoglyphs are based on taphonomic concepts, his definition cannot be incorporated within the ethological system created by Seilacher (1953), as it completely neglects any animal behavior recorded in substrates. An exception is the modern repichnion created by a moth fallen onto wet beach sand (Howard 1976).

Fortey and Seilacher (1997) defined a relatively broad category of trace-body fossil co-occurrences, calling them "close associations." The ichnotaxon and the animal are usually preserved on the same bedding plane and are mutually compatible in their morphology and their size. Close associations are exemplified by upper Cambrian traces of *Raaschichnus gundersoni* in connection with an aglaspid arthropod (Hesselbo 1988), Upper Ordovician brittlestars *Taeniaster bohemicus* that often occur near the resting trace of *Asteracites lumbricalis* (Mikuláš 1990), and an Upper Cretaceous tetradactyl digitigrade footprint that was associated with a nearby protoceratopsid dinosaur (Niedźwiedzki et al. 2012). Winding *Solemya* trails with their tracemakers' bodies at the ends are reported from the plattenkalk of the Solnhofen Archipelago (Barthel 1978; Röper et al. 1999).

A similar situation is posed by finds of body fossils inside trace fossils where the respective animal cannot be safely identified as the tracemaker. These include, for example, tunnels of "*Thalassinoides*" isp. that contain fragmentary bodies of middle Silurian calymenid trilobites. These were probably dwelling in the burrows as commensals but did not participate in their construction (Watkins and Coorough 1997). A fossil record of prey remains in a den of a bigger carnivore has been also reported, as interpreted from the find of fragmented bones of Lower Triassic dicynodont *Lystrosaurus* sp. in the burrows of *Scoyenia* isp. (Modesto and Botha-Brink 2010).

The category taphichnia was briefly defined by Pemberton et al. (1992) for trace fossils related to the end of a tracemaker's lifetime, especially representing traces connected to unsuccessful attempts of escaping rapid burial by sediment. Nevertheless, escape traces (fugichnia) had been already defined by Frey (1973) as a separate category. Taphichnia differ from fugichnia only by the preservation of the producer at the end of the trace. Whether the escape attempt was successful or not is not relevant for the tracemaker in that context, and Vallon et al. (2016), following Bromley (1996), incorporated taphichnia into fugichnia. In this respect, fugichnia, especially taphichnia, are very similar to mortichnia. However, the time passed between death struggle and ultimate fate is rather sudden in taphichnia by a rapid worsening of living conditions through burial. Mortichnia, on the other hand, represent a gradual transition other than sedimentation clearly reflected by the traces.

Seilacher's (2007) ethological group mortichnia was based on the study of specimens from the German Upper Jurassic plattenkalk areas of Solnhofen and Nusplingen and was defined as traces reflecting the last movements of their producers. Because they are preserved together, these traces can be unequivocally attributed to their tracemakers. Within mortichnia, Seilacher (2007) further distinguished traces that originated from:

- *death convulsions*: traces resulting from movements that differ from the usual locomotion of the tracemakers, ending with their death induced by other than peaceful processes;
- "*death marches*" (*sic* Seilacher [2007]; better called "last trails/trackways"): traces documenting the "last steps in life," terminated by the body fossils of their tracemakers; and
- *landing marks*: structures formed by the fall of the dead body onto the bottom.

In contrast, Seilacher strictly excluded structures formed by dead bodies or their shells under the influence of an abiogenic medium, such as roll and drag marks produced by empty ammonite shells, fish vertebrae, or plant remains due to flowing water or wind (e.g., Seilacher 1953, 1963; Pavoni 1959; Vallon et al. 2015b; Lomax et al. 2017). In this context, it is puzzling, why he included landing marks of animals that had died while afloat in the water column as "postmortem traces." These clearly represent marks and not traces *sensu stricto* (cf. Seilacher 1953; Bertling et al. 2006, 2022; Jacobsen and Bromley 2009; Vallon et al. 2015b).

Death convulsions are caused by movements that are largely controlled by the neural networks in the spinal cord (or similar) and even function when the central nervous system has been removed from the body. These are surprisingly rare in the fossil record, and so far have only been recorded in traces of the ichnogenus *Telsonichnus*, in which the shrimp producing the traces was lethally injured by a predator (Schweigert 1998; Schweigert et al. 2016).

The ill-named "death marches" (better called "death trails" or "death trackways" in order to avoid Nazi jargon; Seilacher [2007] used "death marches" based on older German literature and colloquial German, probably unaware of its negative connotation), seem to be preserved somewhat more frequently. The best-known examples were recovered at the Upper Jurassic sedimentary basins in Germany in the vicinity of Solnhofen. Their most common feature is the preservation of a body fossil at the end of the trackway, for example, *Kouphichnium* spp., with its tracemaker, the horseshoe crab *Mesolimulus walchii* (e.g., Malz 1964; Barthel 1978; Frickhinger 1994; Lomax and Racay 2012) or the repichnia associated with *Mecochirus longimanatus*, *Eryon* sp., and other crustaceans (e.g., Mayr 1967; Leich 1993; Barthel et al. 1994; Viohl 1998). Vallon et al. (2015a), however, saw in many of these traces of molting (ecdysichnia), as the preserved body fossils are exuviae rather than actual corpses.

Supplementary Table S2 shows a summary of about 60 published "death convulsions" and "final journeys" produced by macroscopic organisms, together with several dozen other occurrences whose producers belong to the meiofauna. However, the total number of fossil traces preserved together with their tracemakers must be significantly higher—for example, more than 50 such finds are known for the genus *Telsonichnus* alone (G. Schweigert personal communication 2023).

In that context, it is necessary to mention one more specific category that at least has a connection to mortichnia, which we

call here “death in resting.” In contrast to the death convulsions or death trackways, these fossils testify to a peaceful, or at least a sudden, death of their producers, as these animals were not moving at their last moments. Their bodies are preserved in their usual resting position, commonly within their burrows (for a review, see Supplementary Table S2). Compared with death convulsions and death trackways, vertebrates are the most common body fossils encountered in this category (e.g., therapsids in their burrows from Permo-Triassic sediments of the Karoo Basin in southern Africa; e.g., Groenewald 1991; Groenewald et al. 2001; Damiani et al. 2003). The reason for this is probably a preservational advantage for body fossils within their burrows. However, as no substrate was actively changed during the animals’ passing, they cannot be regarded as trace fossils, and must be disregarded as possible mortichnia (cf. Bertling et al. 2006, 2022; Vallon et al. 2015a).

Schweigert et al. (2016) conducted a detailed study of mortichnia from the Upper Jurassic Nusplingen Plattenkalk (Germany), concluding that their key feature is the preservation of the body fossil of the tracemaker, often bearing clear signs of lethal wounds.

Most recovered *Telsonichnus* specimens are made by the shrimp *Antrimpos undenarius*. Although these “true mortichnia” are rare, *Antrimpos* body fossils with signs of predation are recovered frequently. Schweigert (2007) reported that up to 50% of the recovered *Antrimpos* specimens are “half-eaten.”

To date, the only “true mortichnion” (sensu Schweigert et al. 2016) produced by a vertebrate, specifically the fish *Caturus cf. furcatus*, was recovered at the Nusplingen Plattenkalk locality. As in the case of the Nusplingen *Telsonichnus*, the authors

pointed to a lethal injury inflicted on the fish’s body by a predator.

Redefinition of the Category Mortichnia

As mentioned earlier, mortichnia are almost unrecognizable as such when they are incomplete, because they always have the character of repichnia or fugichnia or, in some cases, even fodinichnia or pascichnia. Tracemaker behavior often cannot be deduced from the trace morphology alone, and other characteristics, for example, pathology of the tracemakers’ body fossils or sedimentary environments, must be closely investigated. Overlap with other categories is much larger than in other groups, where mere transitions exist, and renders the category mortichnia difficult if not impossible to define (see Table 1). Vallon et al. (2016) therefore did not recommend its use. Nevertheless, as exemplified here, death struggle or death throes represent a form of living behavior that may be useful to recognize in connection with worsening environmental conditions, rendering mortichnia a useful category. However, the greatest caution should be applied when trace fossils are referred to as mortichnia or when new ichnotaxa are established, because wrong conclusions are easily drawn.

Schweigert et al. (2016; based on Seilacher [2007]) have already redefined characteristics of this ethological group. However, with our numerous additional material, we would like to adjust and modify these observations. Finally, we would like to take a look onto possible ichnotaxobases for future ichnotaxa.

Trace fossils that may undoubtedly be included into mortichnia, must:

Table 1. Compilation of different categories for trace fossils and sedimentary structures encountered together with body fossils, and their interpretation (with related references).

| Category | | Original name | Description |
|---------------|---|------------------------------------|---|
| Not traces | Physical sedimentary structures | Taphoglyphs (partim Sarjeant 1975) | Imprints after deposition or transport of dead bodies |
| | | Schwoimarken (partim Barthel 1978) | Imprints after deposition or transport of dead bodies |
| | | Mortichnia (partim Seilacher 2007) | Landing marks, dead bodies sinking from the water column impacting on the seafloor |
| | Body fossils | Taphoglyphs (partim Sarjeant 1975) | Imprints of soft tissues (skin, feathers, etc.) |
| Trace fossils | Fodinichnia, fugichnia, pascichnia, repichnia | Taphoglyphs (partim Sarjeant 1975) | Traces of “last steps” |
| | | mortichnia (partim Seilacher 2007) | Traces of “last steps” (“death trackways”) |
| | Ecdysichnia | Schwoimarken (partim Barthel 1978) | Traces of molting, originally interpreted as traces during dying or marks after dying |
| | Praedichnia | Schwoimarken (partim Barthel 1978) | Traces of scavengers, originally interpreted as marks after dying |
| | Fugichnia | Taphichnia (Pemberton et al. 1992) | Traces of unsuccessful escapes from burial by sediment |
| | Domichnia | Mortichnia (Groenewald 1991, 1996) | Proof of “death in resting” in burrows of their producers (no sediment has been changed during dying, no traces) |
| | Mortichnia | Mortichnia (new definition) | Traces showing gradual exhaustion before death, death convulsion (sensu Seilacher 2007); associated with body fossils that may show signs of predation |

- Ideally contain the fossilized corpse of the tracemaker. The tracemaker, however, is *neither* part of the trace fossil *nor* is it to be regarded as the actual trace fossil. (Note we do not write “must contain a body fossil.” This has caused misinterpretation, as many arthropod body fossils, especially in the Solnhofen Archipelago, were proven to be exuviae and not actual corpses [Vallon et al. 2015a].)
- The corpse should ideally contain signs of what caused its death. In many cases, that would be a lethal injury, often effected by a predator. However, in the examples from Lebanon described herein, no injuries have been detected, and death must have been a result of illness, poisoning, parasites, environmental stress (e.g., oxygenation, salinity), or similar.
- At the beginning, the traces show the greatest physical strength of the tracemakers, as body movements were still powerful. Traces created at the beginning (distally from a tracemaker’s corpse) therefore show, for example, in the case of fish, deepest penetration into the sediment, the most widely spaced individual segments or similar, the highest amplitude of caudal fin movements. (Note: In the case of *Telsonichnus*, the severed telson often dug itself into the sediment.) Toward death, movements of the tracemaker will almost fade away due to exhaustion, and the resulting traces show, for example, lower penetration, shorter segment intervals, or lower amplitude.
- Some trails or trackways may show signs of loss of orientation. However, caution must be applied, as looping, spiral courses might also be signs of food source exploitation or signs that the tracemaker has lost body symmetry (loss of limbs during molting or similar).
- Tracemakers might try to avoid certain areas that impose hostile living conditions, for example, ripple crests if the environment was drying out and the tracemakers breathe via gills.

Ideally, most if not all of these features should be present in trace fossil specimens assigned to the ethological group mortichnia. The fewer of these characters that are recognized in particular specimens, the more unlikely it is that the specimens in question are death-struggle traces. In such cases, the traces will probably still show dominance of other behaviors and then should be categorized in their respective ethological groups. Most of the above-mentioned criteria are based on our observations of fish and shrimp mortichnia. The last two criteria are mainly valid for invertebrate tracemakers and are based on theoretical assumptions and the *Solemya* mortichnia from the Solnhofen Plattenkalk. We hope that with the publication of this list, more mortichnion specimens will be recognized and the list of mortichnia criteria can be further adjusted and refined.

Ichnotaxobases are the characteristics defining ichnotaxa (Bromley 1996; Bertling et al. 2006, 2022). Bertling et al. (2022) suggested seven valid features: overall shape, orientation, ornamentation, internal structure, wall structure/lining, composition (mainly for digestichnia), and arrangement of subunits. Owing to the nature of mortichnia, internal structure, wall structure/lining, and composition are not available. Other features *not available* as possible ichnotaxobases for mortichnia are discussed here:

- Although the tracemaker’s corpse is a necessary requirement for mortichnia, the tracemaker’s taxonomy is not (see Bertling et al. 2006).
- If there are signs of predation on the tracemaker’s body, these are also unimportant for the mortichnion itself (although they may be regarded as praedichnia themselves, for example,

Caedichnus), other than relating to the cause of death. Significant, however, are the movements the injured tracemaker recorded in the sedimentary substrate after being attacked.

- Certain ratios may vary significantly during the ichnogeny of mortichnia as exemplified earlier. This has its reasons in the nature of the traces. With impending death, the created traces will resemble less and less powerful movements of the tracemaker, changing the segment ratios of a trace (e.g., width to length to penetration depth (height) of each segment).
- Orientation is not regarded as an important ichnotaxobase when applied to mortichnia. All so far described ichnogenera (including *Pinnichnus*) have a horizontal orientation. Vertical forms are better placed into the ethological category fugichnia.

Remaining as *possible* ichnotaxobases are therefore only the following:

- Overall morphology is highly dependent on tracemaker anatomy, substrate, and behavior (Minter et al. 2007). A mortichnion will look significantly different when produced by an arthropod, mollusk, or fish. Then, different ichnogenera should be applied. However, morphological differences within one of the mentioned higher tracemaker taxa may be applied for differentiation at the ichnospecies level (cf. Rindsberg 2018).
- Ornamentation might be important at the ichnogeneric level, but certainly at the ichnospecific level, if certain appendices of the tracemaker create a distinctive pattern.
- Although we only refer to two morphotypes in *P. emmae*, Bertling et al. (2022) suggested the arrangement of subunits to be an ichnotaxobase. We agree that this might be important to catch a pattern of arrangements in other ichnotaxa, such as biting traces or trackways. However, the behavioral difference expressed in the two morphotypes of *P. emmae* is minute and, in our opinion, does not justify splitting, although slight differences might be of importance in other mortichnia.

Conclusions

For more than a century, trace fossils have occasionally been recovered with their makers (e.g., Abel 1922). With the development of paleoenvironmental and ethological approaches to trace fossils, several attempts to characterize death-struggle traces have been made, and various terms and categories have gradually been defined, such as taphoglyphs (Sarjeant 1975), *Schwoimarken* (Barthel 1978), taphichnia (Pemberton et al. 1992), and mortichnia (Seilacher 2007).

Although such finds are without any doubt unique and rare, these traces usually do not differ significantly from normal behaviors in the tracemaker’s life (repichnia, fodinichnia, fugichnia, domichnia, etc.).

However, there are also traces that indicate a completely different behavior. The first such specimens were described from the Upper Jurassic plattenkalk of Nusplingen (Germany). These are *Telsonichnus speciosus* and *T. minutus*, interpreted as evidence of death convulsions of lethally injured shrimp shortly before their death (Schweigert 1998). Several dozen traces were recovered in direct association with the tracemaker. Two decades later, a so far unique find of a trace of the same ethological character, but in association with a fish of the genus *Caturus*, was described from the same sedimentary basin (Schweigert et al. 2016).

In addition, the newly recovered specimens from the Upper Cretaceous plattenkalk basins at Haqil and En Nammoura in

Lebanon reported herein can also be interpreted as death-struggle traces. As in the case of the Nusplingen specimen, the traces from Lebanon are often encountered in association with their trace-makers. However, the fish from Lebanon show no signs of predation and must have died from toxication, environmental stress, or parasite infestation.

Based on the specific morphology of the traces, the new ichnogenus *Pinnichnus* has been erected, including two ichnospecies *P. haqilensis* n. isp. and *P. emmae* n. isp. At the same time, the ethological category mortichnia is revised and redefined as traces left by unsuccessful fading attempts of a dying tracemaker to escape impending death.

Currently, traces from three sedimentary basins of marine origin meet the above definition of mortichnia: Solnhofen Archipelago (Upper Jurassic, Germany; unnamed looping *Solemya* trails), Nusplingen (Upper Jurassic, Germany; *Telsonichnus speciosus*, *T. minutus*, and *Pinnichnus emmae* igen. et n. isp.), and Haqil, En Nammoura (Upper Cretaceous, Lebanon; *Pinnichnus haqilensis* n. isp. and *P. emmae* n. isp.).

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Data Availability Statement. Data and Supplementary Material (Supplementary File: Supplementary Tables S1 and S2) are available from the Zenodo Digital Repository: <https://zenodo.org/records/11142868>.

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