ECDYSICHNIA – A NEW ETHOLOGICAL CATEGORY FOR TRACE FOSSILS PRODUCED BY MOULTING

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Abstract: The shedding of exoskeletons is an important aspect of the lifecycle of some invertebrates (mainly arthropods). To rid themselves of the old cuticula (= exuvia), these animals often have to thrash about, twist around or rub themselves against the sediment or other more or less solid objects. In softgrounds, this behaviour may create distinctive patterns that have to be regarded as trace fossils. Accordingly, some ichnospecies of *Rusophycus* have recently been interpreted as traces made during ecdysis. Most of the so-called "Schwoimarken" from the Solnhofen lithographic limestones (Upper Jurassic, SE Germany), usually interpreted as structures made by dead organisms swaying in response to water movements, must be understood as traces of arthropod ecdysis. In this context, we erect *Harpichnus bartheli* igen. et isp. nov. and propose the new ethological category, ecdysichnia, for moulting traces. In most "Schwoimarken" containing body-fossil remains other than arthropods, we see sediment displacement by scavenging arthropods rather than mortichnia (*sensu* Seilacher, 2007). We further propose inclusion of the recently erected category pupichnia for pupation chambers as a subcategory of ecdysichnia. In our opinion, pupation is a special form of moulting that does not justify the splitting of categories, as briefly noted by Vallon *et al.* (2013).

Key words: Animal behaviour, ecdysis, Solnhofen lithographic limestones, Schwoimarken.

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INTRODUCTION

Trace fossils are objectively divided into either morphological (Książkiewicz, 1977; Uchman, 1995, 1998; cf. also Knaust, 2012) or ethological groups (Seilacher, 1953; Bromley, 1996). In the following discussion, we focus on the ethological categories proposed by Seilacher (1953), who classified animal trace fossils according to different kinds of behaviour. During the past 60 years, his scheme has been modified and extended by various authors. The latest versions were published by Buatois and Mángano (2011) and Vallon *et al.* (2013, 2015) and the latter included the recognition of digestichnia (Vallon, 2012) as an ethological group for digestion traces, briefly defined by Vialov (1972).

Especially in arthropods, ecdysis or moulting is an important part of the lifecycle. Ecdysis occurs at intervals in order to exchange the rigid cuticula or durable exoskeleton for a new, larger one, allowing the animal to grow. Generally and especially in mature individuals, the replacement of

the cuticula is a difficult, rather violent exercise (e.g., Kaleemur Rahman and Subramoniam, 1989; observations on freshwater crayfish in aquaria). The more difficult it is to shed the firm exoskeleton, the more forceful the rubbing and twitching of the arthropod. Concurrently, more violent movements result in deeper penetration of the sediment, leading in turn to a higher preservation potential. Particularly in calm environments with a high sedimentation rate, these traces have a reasonable chance of being preserved in the fossil record.

Seilacher (2007) interpreted some rusophyciform trace fossils as traces made by trilobites during moulting. On the basis of sedimentary relationships, the trilobites were considered to have moulted while partly or completely buried (cf. Seilacher, 2007, pp. 34, 192). Similarly, the Upper Jurassic Solnhofen lithographic limestones have yielded examples of trace fossils produced during the ecdysis of arthro-

pods. For all of these examples, we propose the new ethological category ecdysichnia (moulting traces).

The specimens described and figured below are housed in the following collections (presented in alphabetical order): Bayerische Staatssammlung für Paläontologie und Geologie, München (BSPG), Bürgermeister-Müller-Museum, Solnhofen (BMMS), Jura-Museum Eichstätt, Eichstätt (JME), Staatliches Museum für Naturkunde, Stuttgart (SMNS) and the private collection of Roger Frattigiani in Laichingen (all in Germany).

ECDYSICHNIA

The term for the ethological group ecdysichnia is a Latin-based derivation from the ancient Greek *ekdysis* (= act of taking off), combined with the suffix *-ichnia* used since Seilacher (1953) for ethological categories of traces. It was already characterised by Abel (1935, pp. 280–287), although no ethological classification existed in his time. Nevertheless, Abel recognised that most arthropod fossils were exuviae, shed exoskeletons, rather than fossilised bodies, because they were mostly disarticulated or exhibited gaps resembling ecdysal breakage lines in modern arthropods. According to Abel's criteria, exuviae, shed feathers, hatched eggs or cocoons, etc., should be included within the ecdysichnia. In principle, we agree, because a substrate (e.g., eggshell, cocoon, or sediment) is altered and (actively) manipulated by the hatching or moulting process itself (cf. Bertling *et al.*, 2006). However, ecdysial suture lines in exoskeletons have to be excluded from ecdysichnia (not in the sense of Abel, 1935: 280) because they are (onto-)genetically programmed for each species. Intraspecific breakage patterns in eggshells of reptiles, mammals (Monotremata) and birds will always be ambiguous. Deciding whether a crack in an eggshell is an ecdysichnion, a praedichnion or the result of taphonomy probably will be an insuperable challenge. Furthermore, eggshells, cocoons, exuviae, etc., have to be treated as body fossils, and only the cracks in them represent the trace fossils. Naming all these traces would result in a flood of new names bearing only minimal useful information. Therefore, we recommend against naming ecdysichnia that are based on breakage lines.

Genise *et al.* (2007) introduced the ethological category pupichnia for pupation chambers created in terrestrial substrates. In contrast to calichnia, where the breeding structure (chamber or nest) is produced and used by at least two different individuals of the same species, pupichnia are produced by the same individual. The resulting structures function as protection during pupation for the tracemaker. Following Abel's guidelines (1935), we recommend including the pupichnia within the ecdysichnia. In our opinion, the difference between ecdysial and pupational behaviour does not justify the splitting of categories. This also avoids creating a huge range of ethological groups that will hardly ever be used, because they apply only to a narrow range of animals with special behaviour (e.g., natichnia included within repichnia by Bromley, 1996; see also Vallon *et al.*, 2015).

Within the new ethological category ecdysichnia we therefore include all traces left in or on any substrate by animals that are connected with moulting. This can be pupation (see Genise *et al.*, 2007 for the recognition of these traces), ecdysis (the latter mostly in arthropods) or shedding of the skin (e.g., a deer rubbing his newly grown antlers on a tree trunk, creating scratches in the bark). However, in the fossil record probably only insect pupation and arthropod ecdysis will be preserved or recognisable.

Apart from the observations of Abel (1935), only a few examples of fossil ecdysis have been documented. Bishop (1986) described different ways of moulting in several Recent decapod groups and compared them with the fossil record. Brandt (2002) compared ecdysial patterns in different arthropod groups, also including further references for moulting patterns, and Tetlie *et al.* (2008) described the ecdysis of eurypterids in detail. But only Seilacher (2007, p. 34) described trace fossils made during arthropod moulting. He interpreted four ichnospecies of *Rusophycus* as possible ecdysichnia: *R. morgati* Baldwin, 1977, *R. carleyi* (James, 1885), *R. radialis* (Seilacher, 1991), and *R. polonicus* (Seilacher, 1970). Most *Rusophycus* ichnospecies are interpreted as cubichnia (e.g., Häntzschel, 1975; Bromley, 1996) or fodinichnia (e.g., Seilacher, 2007). According to Seilacher (2007), the moulting trilobites took advantage not only of the protection provided by the sediment during their ecdysis, but also of its coherence, which helped them to get out of their old cuticulae. In the case of moulting trilobites, these *Rusophycus*-like trace fossils do not show the filtration chamber that would have been left open underneath the trilobite body for combined detritus and suspension feeding (Seilacher, 2007) as in other ichnospecies of *Rusophycus*. Moreover, the trilobite's coxae and proximal podomeres of the endopodites left sharp impressions in the moulting traces. They originated from the trilobite pressing itself downwards into the sediment to provide leverage for the feet, easing the extraction of legs from their old cuticula (Seilacher, 2007, p. 34). Therefore, other ichnospecies, such as *Rusophycus moyensis* Mángano *et al.*, 2002, where imprints of the coxae are present, might be regarded as possible ecdysichnia as well. A revision of these ichnotaxa, however, would be beyond the scope of the present article.

As already indicated, a moulting arthropod remains within a rather small area. Modern decapods toss and turn to get rid of their old cuticulae during ecdysis (e.g., Kaleemur Rahman and Subramoniam, 1989). In contrast to trilobites, moulting traces of modern arthropods tend to be more complex. They commonly exhibit such a wide variety of movements that it is difficult to erect individual ichnotaxa for these structures.

Nevertheless, in a striking example from the Solnhofen lithographic limestones (Fig. 1), a compound trace fossil is preserved, showing the whole spectrum of processes linked to ecdysis. The arthropod, *Mecochirus longimanatus* (Schlotheim), plunged down through the water column, producing a landing trace (Fig. 1B). It crawled about 30 centimetres, mainly pushing itself forward with its outspread uropods, perhaps trying to find anchorage in the sediment for the forthcoming moulting. While thrashing about and twisting around during ecdysis (Fig. 1C), it created the bent, slightly indistinct furrows and ridges on the sediment surface. Parts of the ecdysis were executed while the individual
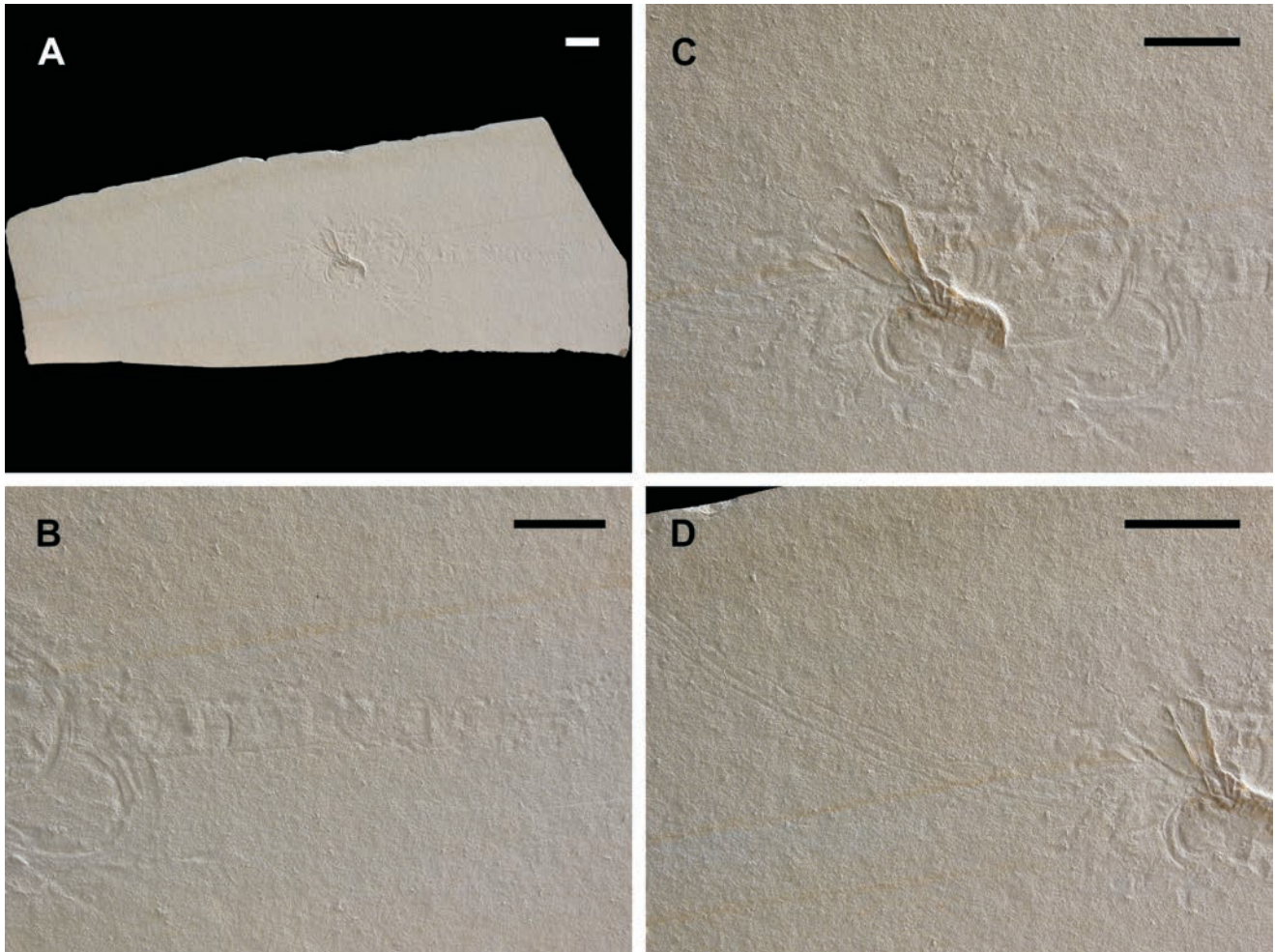
Fig. 1. Compound trace fossil produced by *Mecochirus longimanatus* (Schlotheim), showing landing structure, ecdysichnion and repichnion (SMNS 67538; ex coll. Roger Frattigiani); Langenaltheim, Solnhofen lithographic limestones, "Obere Schiefer". Scale 5 cm. **A.** Overview. **B–D.** Details of same slab. Landing structure and repichnion with repeated imprints of the tail fan in order to find anchorage for the forthcoming moulting (B). Ecdysichnion *Harpichnus bartheli* igen. et isp. nov. with the exuvia of *M. longimanatus* in its centre (C). Second repichnion recording the successful moulting of the tracemaker and its departure from the moulting site (D).

was lying on its side (two large crescentic scratches). Finally, the arthropod walked away (Fig. 1D), leaving its exuvia behind. Unfortunately, the adjacent slab was not collected, so the end of the story remains unknown.

Another example (also produced by *Mecochirus longimanatus*) from the Solnhofen lithographic limestones of the Hardtbuck locality near the village Mörnsheim shows very similar behaviour (Fig. 3). In this specimen, the trace of the animal's departure after moulting is not recorded, but the landing trace is present along with the indistinct, crescentic grooves and ridges plus a clearly defined half-circle of scratches (Fig. 3B).

Both of these ecdysichnia resemble the moulting process of the Recent sand lobster *Thenus orientalis* (Lund), which was described by Kaleemur Rahman and Subramoniam (1989) in great detail. *Thenus orientalis*, as it begins moulting, remains upright with its appendages firmly buried in sand. The thoracic region swells as the arthropod imbibes water through its mouth and soft cuticle. Owing to this increase in pressure underneath the old cuticula, the carapace is lifted up and pushed forward. The abdomen remains un-

changed until the animal twitches after about 5 minutes and then usually rolls on its side. By twitching and wriggling, the lobster now slowly pulls its antennules and antennae out of the carapace. Such movements probably created the numerous indistinct grooves and ridges in the fossil examples (Figs 1C, 3A). The carapace swings forward and the legs are pulled out, which takes about 25–30 min. Finally, the abdomen and tail leave the exuvia by flipping movements and jerks that correspond to the distinct semicircular scratches of the trace fossils made by *Mecochirus* (Figs 1C, 3C). Within 10–20 minutes after ecdysis, *T. orientalis* regains mobility. This lobster has not been reported to consume its own exuvia as a few other taxa do to reabsorb some of the calcium that was lost during the shedding of the old skin (Hammond *et al.,* 2006). Obviously, neither did the fossil *Mecochirus* lobsters consume their exuvia.

In another specimen from the Solnhofen lithographic limestones, both repichnion and exuvia are preserved (Fig. 2). This *Mecochirus longimanatus* evidently was buried during moulting, because on the stratinomically upper side of the slab a collapsed tunnel connects this surface to the exuvia
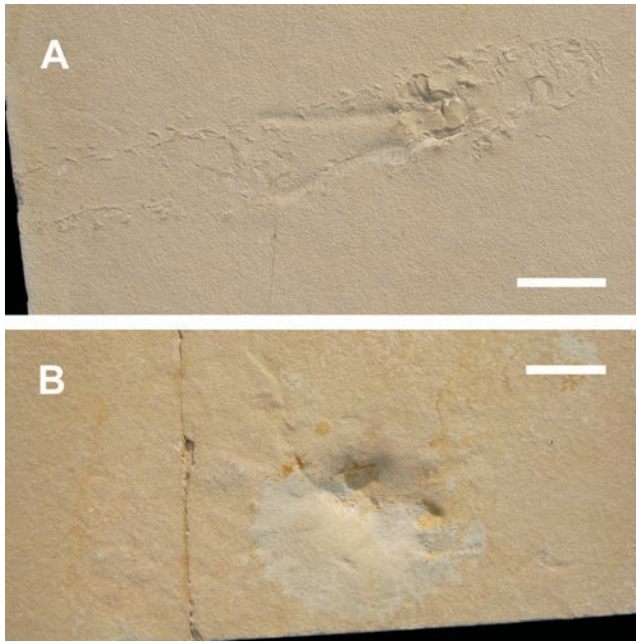
Fig. 2. Compound trace fossil made by *Mecochirus longimanatus* (Schlotheim), showing repichnion, exuvia and fugichnion; Langenaltheim, Solnhofen lithographic limestones, "Obere Schiefer". Scale 5 cm. Private collection of Roger Frattigiani, Laichingen, Germany.

preserved on the stratinomically lower surface (Fig. 2B; Schweigert and Frattigiani, 2004). Although the characteristic traces left by moving in an irregular manner are not visible in this specimen, it has to be regarded as a compound trace fossil, consisting of a repichnion, ecdysichnion and fugichnion. In this particular specimen, ecdysis was quite smooth, maybe eased by the rapid burial holding the old cuticula in place, while the arthropod retracted its body out of it (similar to the trilobite ecdysis described by Seilacher, 2007: 34).

A NEW INTERPRETATION OF THE SO-CALLED "SCHWOIMARKEN"

Barthel (1978: 191) used the German term "Schwoimarke" for a special type of sedimentary structure occurring in the Solnhofen lithographic limestones, mainly in the Solnhofen and Langenaltheim basins (at the Obere Haardt, Hummelberg and Schrandel localities). The term *Schwoimarke* derives from the nautical German word *schwoien* (English "to swing [at anchor]") and *Marke* (English "mark"). Barthel (1978, 1964, 1966) used this term for sedimentary structures produced by dead animals that are fixed at one end of their body and dangle around this mooring in unidirectional or changing currents. Because of this movement, the dead bodies are presumed to leave scars and grooves on the sediment surface. The producing body is almost always preserved within this area of sedimentary disturbance, being to some extent disarticulated. This feature is usually interpreted as a sign of decay. Fish, for example, have lost their scales and in most cases the head is detached

from the rest of the body (Fig. 6; cf. Mayr, 1964; Barthel, 1966, 1978; Viohl, 1983, 1998; Barthel *et al.*, 1990). The most commonly known producers of "Schwoimarken" are arthropods and fish. However, plants (Barthel, 1978), cephalopods and even terrestrial vertebrates (e.g., the sphenodont described by Barthel, 1964 as *Homoeosaurus*; Fig. 7) do occur. "Schwoimarken" in association with fossil insects have so far not been reported, although fossils of insects are quite common.

Dead animals produce decomposition gasses during decay. If these gasses cannot escape through the skin or body openings, they buoy up the carcass (e.g., Schäfer, 1962; Reisdorf *et al.*, 2012). Such light bodies are able to leave sedimentary structures, such as scars and grooves on softground surfaces, but in most cases the bedding planes of the Solnhofen lithographic limestones were stabilised by microbial mats (Keupp, 1977a, b; Röper *et al.*, 2000). Such microbial covers made the sediment more resistant to pressure, which hampered the development of sedimentary disturbances. Hence, a dead body bobbing up could hardly cause a disturbance on this consolidated seafloor. To leave recognisable grooves that could be preserved in the fossil record, it would have to be thrust into it by strong currents.

Sedimentary structures originating from water movements are common at some localities within the Solnhofen area. Janicke (1969) described oscillation ripples from the localities at Haunsfeld and Daiting. Other ripple types (mostly current ripples) were mentioned from the localities at Pfalzpaint, northeast of Eichstätt (Walther, 1904; Röper *et al.*, 1999; Vallon and Röper, 2006), Painten (Barthel, 1964) and from the Kelheim region (Schairer, 1968). However, in the central basins of Solnhofen and Eichstätt, where the "Schwoimarken" mostly occur, only one layer shows current structures (roll marks of ammonites). It is situated at the base of the lithographic limestone facies (Seilacher, 1963; Röper, 2005, fig. 5). In the remainder of the section, no current structures have been reported or were observed during our fieldwork. They also would be unexpected because water depths between 20 and 50 m are assumed for the lithographic limestone facies of both central basins of the Solnhofen lagoonal environment (Keupp, 1977a; Wings, 2000). Unidirectional currents at these depths are rather unlikely unless of turbidity-current origin. Oscillatory water movement could hardly occur, since the central parts of the basins were deeper than the storm wave base.

To understand the origin of a "Schwoimarke" that was originally published by Mayr (1964) and recently reillustrated by Seilacher (2007, pl. 75), several palaeontological studies have been carried out. Janicke (1969) showed how carcasses act within currents or oscillating water movements. He demonstrated that long objects, such as fish and logs, are oriented parallel to the current direction. Their centre of gravity points up-current and their longitudinal axis is oriented parallel to the current.

Once the objects acquire a stable rheotactical position, they generally retain it. In such cases, they flip over before regaining stability with their centre of gravity against the current. As they turn over, carcasses must leave some marks in a softground that are similar to the "Schwoimarken", but resemble roll marks even more (cf. Pavoni, 1959). Janicke
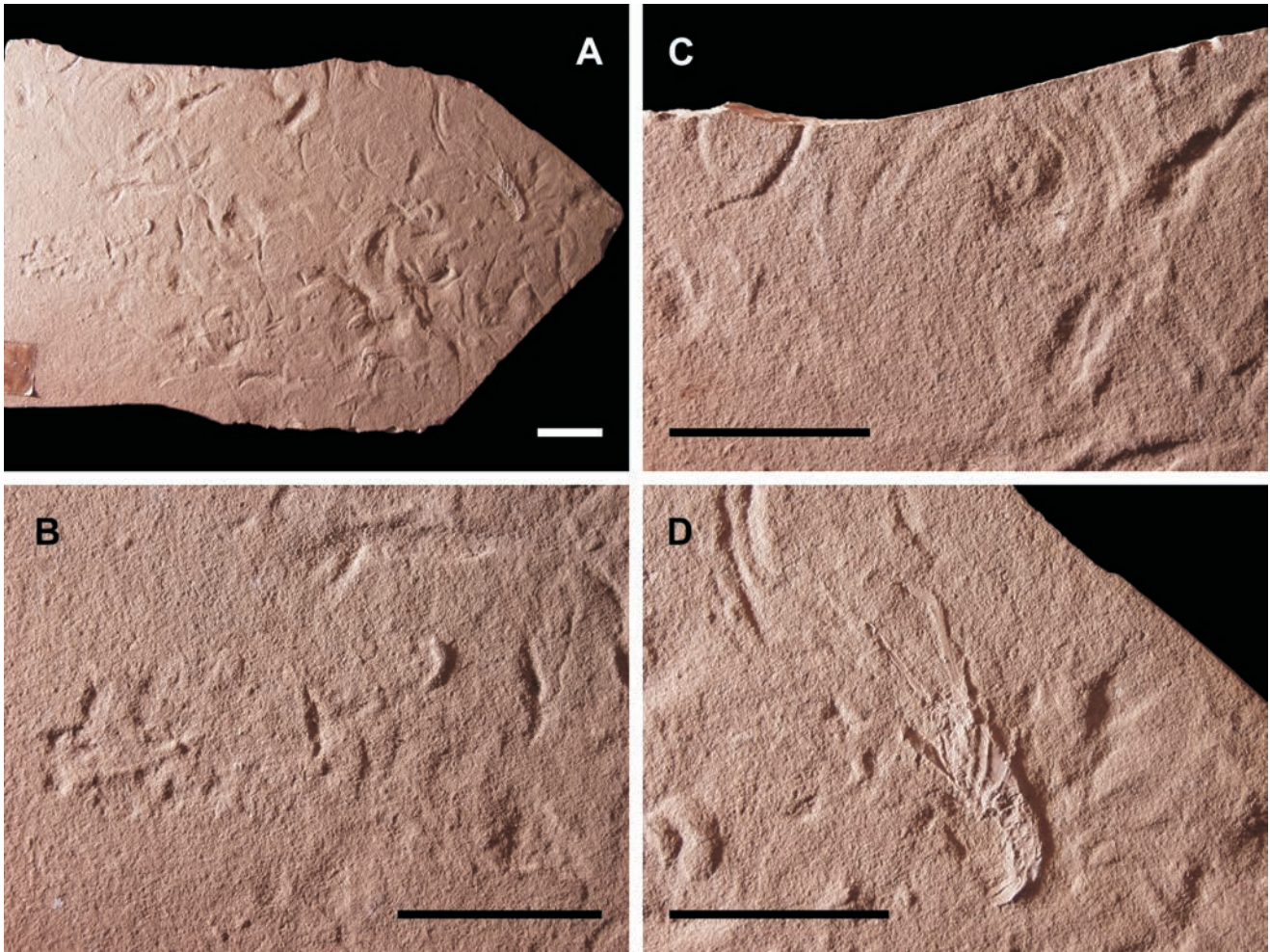
Fig. 3. *Harpichnus bartheli* igen. et isp. nov. (JME-SOS 6357) from the Hardtbuck locality near Mörnsheim, Solnhofen lithographic limestones, "Obere Schiefer"; preserved as mainly negative epirelief. Scale 5 cm. **A.** Overview of the ecdysichnion. **B–D.** Details of the same slab. Landing trace and repichnion with imprints of tail fan (B). Scratch-semicircle probably produced by the tail fan, while the tracemaker was lying on its side (C). Tracemaker; exuvia(?) of *Mecochirus longimanatus* (D).

(1969) recognized only very weak marks, because he used sand as sediment instead of carbonate mud. The marks he observed were orientated in a line parallel to the current, rather than spread two-dimensionally on a sediment surface, as documented by Mayr (1964) in the fossil record or in experiments by Barthel (1966). Therefore, the "Schwoimarken" of the Solnhofen area were not caused by unidirectional water currents.

Barthel (1966) did experiments with living fish, which he tossed onto carbonate mud to compare their traces with the fossil examples from the Solnhofen lithographic limestones. Indeed, the traces showed some similarity to fossil sedimentary structures, but the concordance was insufficient. In detail, they were not arranged in a more or less circular pattern and imprints of the fish's body and tail fin were produced, rather than single grooves and ridges. Barthel (1966), in order to reproduce the fossil "Schwoimarke" published by Mayr (1964; also amongst others, Barthel, 1978, pl. 61, fig. 1; Barthel *et al.*, 1990, fig. 6.2; and this paper, Fig. 6), took a dead fish and fixed it by its head on the bottom of a sediment-free flume. The posterior part of the fish started to twist and flip up and down, swinging in a three-quarter cir-

cle. After he put the dead fish onto carbonate mud, he simulated current movements of the fish, using pincers. Since he could not produce a "ring-shaped mound" around the surface disturbances as in the original specimen of Mayr (1964), he repeated the experiment with a viscous layer of carbonate mud below and a freshly deposited, less dense layer on top. Finally, he was able to reproduce the ring-shaped mound around the fish's body.

However, moving the dead fish with pincers instead of a current probably affected the experiment towards a desired outcome. Furthermore, the grooves and ridges should be at more or less the same distance from the fixed head and arranged in a three-quarter circle (Barthel, 1966), rather than evenly spread in a full circle around the body fossil. In addition, a decomposing fish should not only have fallen apart faster in the area where it was continually bent and stretched (decomposed part close to its head), but also in the tail fin region, which would repeatedly impact the sediment surface, as Barthel (1966) pointed out. Since the tail part is the most intact section of the body, it could not have produced the sediment disturbance (see also Seilacher, 2007). Therefore, in contrast to Barthel (1966), we do not see a sat-
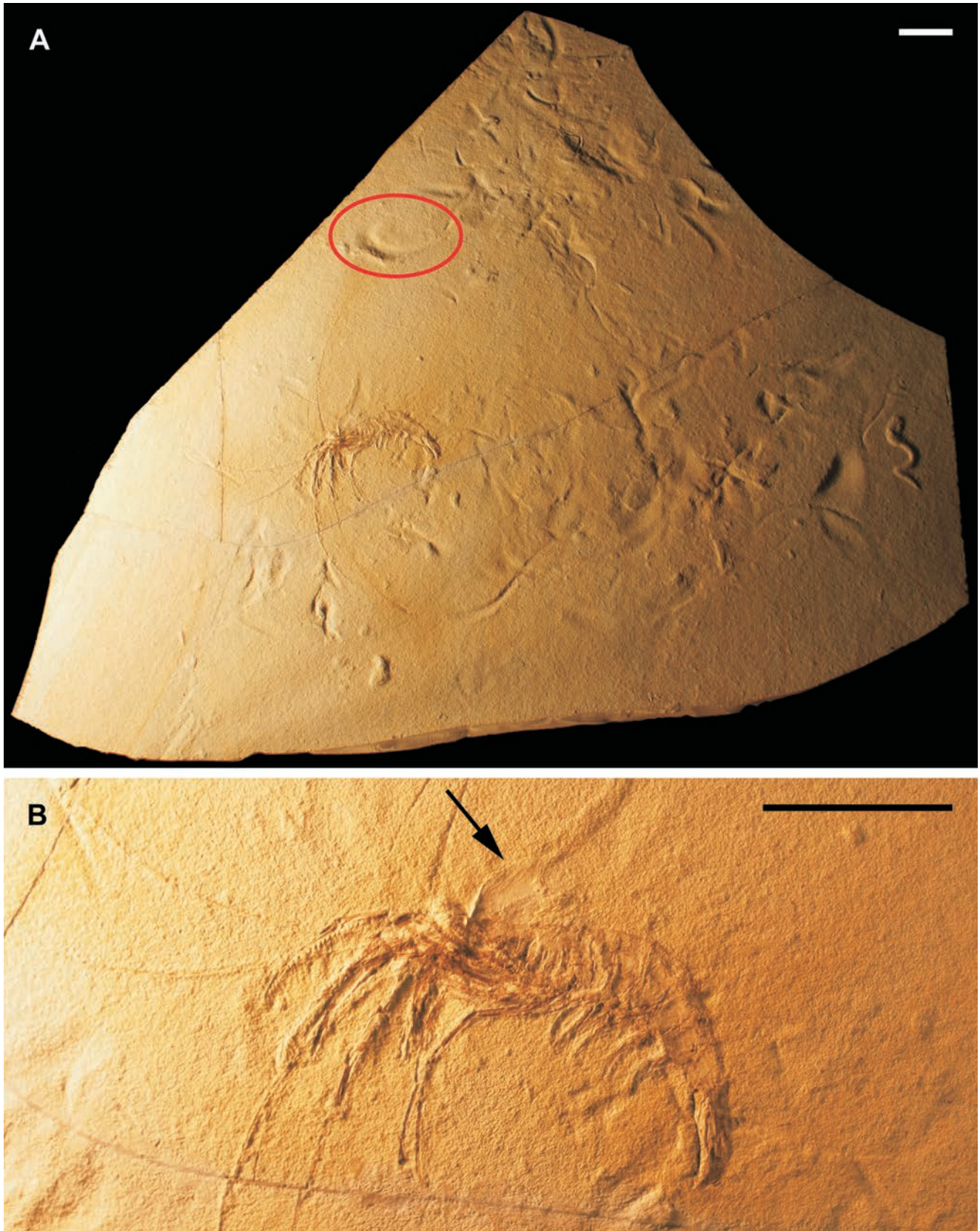
Fig. 4.   Lying slab with the holotype (circle) of *Harpichnus bartheli* igen. et isp. nov. (BMMS 721 b) produced by *?Aeger* sp.;
Solnhofen, Schwarzberg locality, Solnhofen Formation ("Malm zeta 2b", "Obere Schiefer"). Scale 5 cm. **A.** Overview of the slab. **B.** De-
tail of A, carapax (arrow) of ?*Aeger* sp. swung forward, indicating that the body fossil of the tracemaker is an exuvia and not an actual car-
cass.

isfactory conformity between (1) the sedimentary structures created in his experiment and (2) the original fossil sedimentary structure from the Solnhofen lithographic limestones (republished here in Fig. 6).

The interpretation of swaying fish bodies in a current as producers of at least some "Schwoimarken" might still be plausible for some of the ridges and grooves on a sediment surface. The body mass of a bigger fish, buoyed up by gases of decomposition, might be able to produce sedimentary structures similar to the "Schwoimarken", even in a carbonate mud partly consolidated by microbes. But, as Barthel (1966) himself noted, if they were moved by a unidirectional current, they should be arranged in a three-quarter circle around the carcass and not in a full circle.

Oscillatory currents can produce markings similar to "Schwoimarken". In German literature, these are called *Scharrkreise* (sing. *Scharrkreis*; see Jurasky, 1933; Barthel, 1978; Müller, 1983; Bromley and Jakobsen, 2011; Bromley *et al.*, 2014). These "scratch circles" consist of concentric grooves and ridges that are produced by a fixed object (usually plants), moved by wind or water. In contrast to the "Schwoimarken", which never show only circular scratches, but rather have hook-shaped or crescentic grooves and ridges, these sedimentary structures are far more symmetrical. Marks produced by oscillation should have two clusters of impact marks directly opposite each other (Janicke, 1969; cf. Collinson *et al.,* 2006). Also, if oscillation is responsible for the "Schwoimarken", they should be more common in the same beds, and all fossils obtained from the same strata should show similar structures. Furthermore, elongate remains of organisms should have a rheotactic orientation perpendicular to the oscillation movements in these beds (cf. Janicke, 1969) and oscillation ripples are to be expected nearby. However, since neither such sedimentary structures nor alignments are reported (or known from our fieldwork) surrounding the "Schwoimarken", they must have originated from other mechanisms.

A swaying body is certainly not a convincing mode of origin for "Schwoimarken" of arthropod origin. Arthropods have much more delicate bodies than fish. Furthermore, the remains of arthropods within the sedimentary disturbances are never decayed as much as fish bodies. They rarely show decomposition in individual parts, but instead are at least partially articulated. In most cases, the telson is isolated or semidetached from the cephalothorax (Fig. 5). This implies that the preserved body fossils are more likely to be exuviae than fossilised carcasses (cf. Schweigert and Frattigiani, 2004). Additionally, these arthropod remains are usually not filled with the pale pink phosphoritic material that makes up the fossilised organic substance of the arthropods (Dietl and Schweigert, 2001; Schweigert, 2001; Briggs *et al.*, 2005). Exuvial sutures very often close again after ecdysis (Glaessner, 1969; Bishop, 1986), which may imply that a specimen was a carcass rather than an exuvia, although in reality the opposite is the case. A detailed discussion of how to distinguish dead bodies from exuviae can be found in Bishop (1986). For modern marine arthropod exuviae, Mikulic (1990) observed that even brief transport by the least perceptible degrees of water movement can produce some disarticulation in the moults. In order to produce the

deep grooves and sharp ridges of a "Schwoimarke", an exuvia agitated by oscillating currents should therefore be much more disarticulated than the specimens recovered. A light, paper-like exuvia floating above the seafloor, especially over a consolidated matground, would hardly leave any kind of sediment disturbance. However, an arthropod that is violently moving in an irregular manner during moulting, especially one using the substrate for traction, would clearly leave traces in relatively high relief during its attempts to leave the old cuticula. Furthermore, no "Schwoimarken" have been reported in association with fossils of land insects. If these sedimentary structures had been produced by dead bodies moved by currents, "Schwoimarken" whould also be expected at least around the larger insect fossils. For these (e.g., Ensifera), similar specific body weights to those of the smaller arthropods can be assumed (cf. Tischlinger, 2001).

Therefore, we regard the "Schwoimarken" of presumed arthropod origin as trace fossils, left during the moulting process. "Schwoimarken" that have another animal body fossil (e.g., the fish *Aspidorhynchus acutirostris* in Viohl, 1998: fig. 2, JME-SOS 4249) in their centre also most likely can be related to arthropods, because the crescentic grooves and ridges in the sediment surrounding the body fossil are identical in shape and size to those found around arthropod exuviae. Many arthropods are scavengers. While feeding on a carcass, crustaceans often clap their tail fans, either to retreat from rivals (aquarium observations) or perhaps also to break pieces out of the dead body to feed on them. These uropod movements can create grooves and ridges resembling the "Schwoimarken" from the Solnhofen lithographic limestones, since it is the same movement that allows them to shed their old cuticula. Barthel (1978, pl. 12) figured a true "Schwoimarke" that was produced by physical processes and not by the activity of organisms. This sphenodont (reproduced in Fig. 7) left an impression in the sediment and the anterior part of its body was then swayed about 20 millimetres to the side. Thus, genuine "Schwoimarken" only show a slight shifting of the producing object. The resulting sediment depressions are restricted to rather small areas where the producing object was only swung through a very short distance. Imprints are weak and not as deep and clearly outlined as the traces left during arthropod moulting or scavenging. Because they are produced by currents, the sedimentary disturbances also show more regular patterns than the traces left by arthropods.

Returning to the fish "Schwoimarke" described and illustrated by Mayr (1964), Barthel (1966) and Seilacher (2007), our interpretation is that the ring-like structure around the fish carcass is the remaining part of a microbial mat (cf. Seilacher, 2007), which probably was punctured as the fish carcass touched the substrate. After that, it either rolled up by itself, owing to internal tension, or more likely was rolled over in a more or less concentric pattern around the fish carcass by some kind of water movement working radially. This water movement was most likely produced by a group of decapods fighting over the fish carcass, feeding on it and evading rivals during feeding. The clapping of their tail fans synchronously produced the grooves and ridges close to the fish carcass (see also Seilacher 2007).
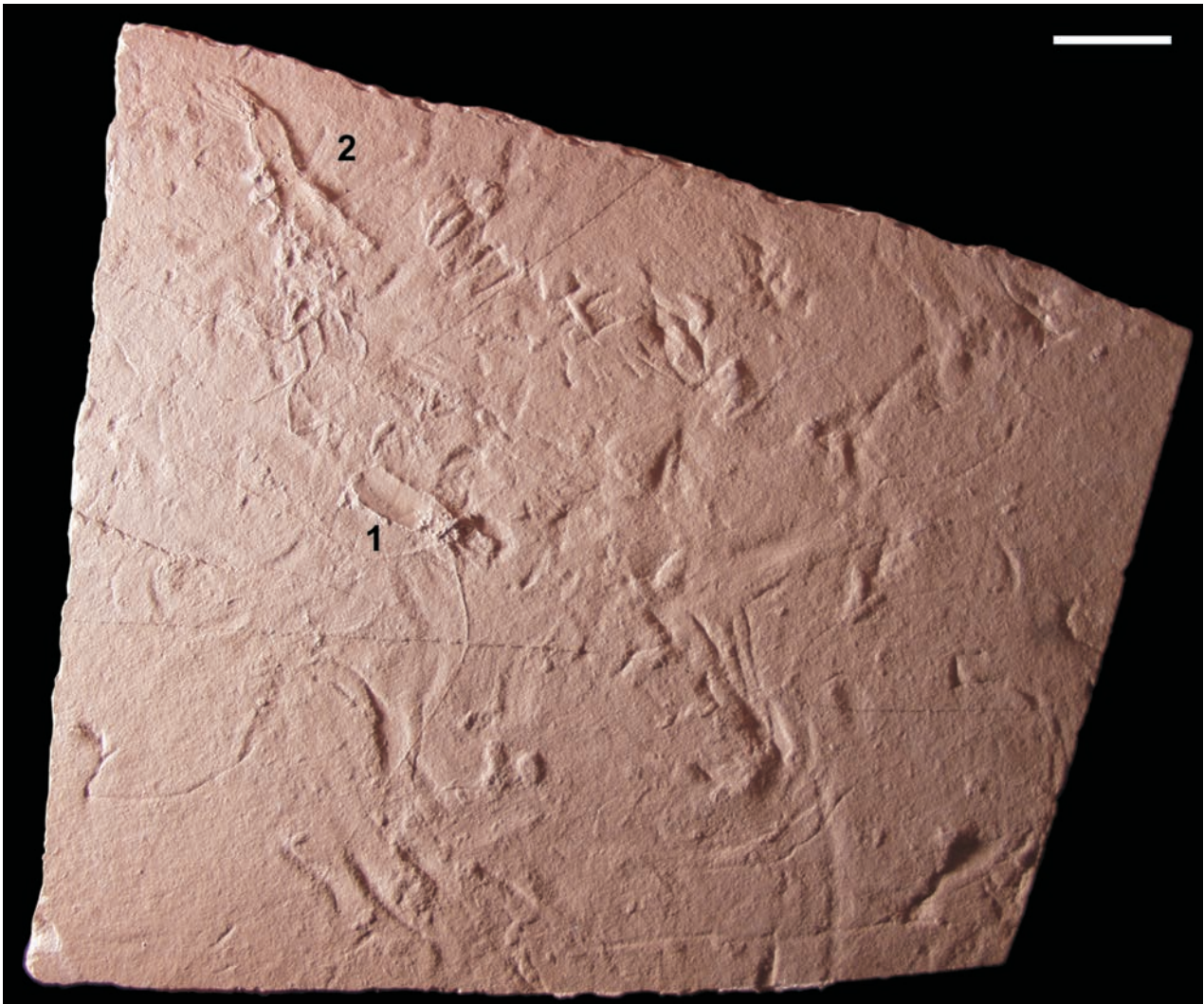
Fig. 5. *Harpichnus bartheli* igen. et isp. nov. (JME-SOS 6358) produced by *Aeger* sp. mainly preserved as negative epirelief. The cephalothorax (1) is separated from the telson (2) indicating an exuvia rather than a carcass; Solnhofen, Hummelberg locality; Solnhofen lithographic limestones, "Obere Schiefer". Scale 5 cm.

MORTICHNIA *SENSU* SEILACHER (2007)

Apart from the "Schwoimarken", other trace fossils from the Solnhofen lithographic limestones can be explained as traces left during arthropod moulting. Some of them constitute traces that were recently described as mortichnia by Seilacher (2007, p. 212). Body fossils at the end of repichnia made by *Mecochirus* are usually turned the "wrong way" (e.g., Fig 2; Barthel, 1978, p. 324; pl. 42; Viohl, 1998, fig. 6; Seilacher, 2007, pl. 75), so they imply that the trace-maker was walking backwards. Another specimen shows a trackway of *Mesolimulus* walking in a spiral (Barthel, 1978, p. 334, pl. 47; Viohl, 1983, fig. 3). These and similar findings as well as the scarcity, but excellent preservation of body fossils, have led to the interpretation that the Solnhofen lithographic limestones were deposited under hostile, mostly hypersaline conditions (e.g., Mundlos, 1966; Janicke, 1969; Barthel, 1978; Viohl, 1983, 1998; cf. Seilacher, 2007; Wellnhofer, 2008). However, Schäfer (1962, 1964) already showed that a hostile environment near the basin floor is not necessary to preserve an articulated skeleton.

This hostile environmental model was developed for the Eichstätt Basin and later uncritically applied to the other basins of the Solnhofen lithographic limestones, although each basin is characterised by its own sedimentary features and fossil content. Each basin must have had its unique environmental and depositional conditions. Regardless, the above mentioned trackways have been interpreted as traces left by animals that could survive, at least briefly, in these hostile conditions (Caster, 1940; Mundlos, 1966; Barthel, 1964, 1978). Since *Mecochirus* has very long first pereiopods, previous authors (e.g., Barthel, 1978, p. 324) regarded them as being too heavy for a dying specimen to carry forwards, so the arthropod turned around and dragged them behind in its attempt to escape the hostile environment. The spirally arranged *Mesolimulus* repichnion was interpreted as having been made by an individual that had lost its orientation in the presumably hostile conditions of the Solnhofen lagoons (e.g., Barthel, 1978, p. 334; in contrast to Zeiss, 1975).

These interpretations seem plausible, but are not the only possible explanations. Pulling the extremely long first

Fig. 6. Feeding traces produced by arthropods around a carcass of *Ophiopsis* sp. (preserved as positive hyporelief; JME-SOS 4034 b). Scale 5 cm.

pereiopods out of an exuvia was surely rather difficult for *Mecochirus*. Walking backwards and trailing the long limbs behind creates friction, which renders it easier to pull the pereiopods out of the old cuticula. For example, specimen JME 1937/21a does not show any of the pale pink phosphatic substance, characteristic for the fossilised organic substance inside the cuticula and therefore needs to be re-interpreted as an exuvia.

The spiral traces of a *Mesolimulus* might have been caused by the loss of some legs or problems with pulling its legs out of the cuticula, thus losing the symmetry of the body. This condition tends to leave spiral traces (cf. Zeiss, 1975). In both cases, the freshly moulted arthropods departed, not on the sediment surface (which would have left repichnia), but upward into the water column. Leaving the exuvia by swimming away would not only not leave no further evidence of the lucky escape, but might also close eventually open sutures as the parts fell back into their old position (Glaessner, 1969; Bishop, 1986). Therefore, body fossils at the end of these tracks have to be regarded as fossilised exuviae, rather than carcasses. This implies that the overall depositional environment of the lithographic limestones of Solnhofen probably was not as hostile as usually

Fig. 7. Genuine "Schwoimarke" produced by a *Kallimodon pulchellus* ("*Homoeosaurus*")-carcass (BSPG 1887-VI-2); Painten near Kelheim. Scale 5 cm.

has been assumed. However, ecdysis may have ended fatally in some unlucky cases, leaving both ecdysial traces and a fossilised body, thus illustrating a direct link between ecdysichnia and mortichnia.

NEW ICHNOTAXA

Harpichnus igen. nov.

Type ichnospecies: *Harpichnus bartheli* isp. nov.

Etymology: According to the shape of most furrows and ridges, from the Ancient Greek ἅρπη [*harpē*] = a mythological sword (depicted in Ancient Greek and Roman artworks) with a straight blade that ends in a sickle-like bent tip, and the latinised Greek *ichnus* = trace.

Diagnosis: Surface imprints parallel to the bedding plane. Imprints are slightly to sharply bent, more or less hook- to crescent-shaped and developed as negative epirelief (furrow) with adjacent corresponding positive epirelief (ridge), similar in shape, but not as distinct as the furrow. The ridge may be on the convex or the concave side of the furrow, rarely on both sides. Usually the single elements, consisting of furrow and ridge each, occur together as irregular clusters, in which the single furrow-ridge elements are scattered.

Harpichnus bartheli isp. nov.
Figs 1, 3–5

1966	Marks of tail tips – Barthel, fig. 1.
1966	Circle of bottom marks – Barthel, p. 1157.
1967	Ganoidfisch cf. *Ophiopsis* mit Spuren des Todeskampfes, stark verwest, aus einer restlichen Pfütze ablaufenden Wassers [Ganoid fish, cf. *Ophiopsis*, with traces of its death struggle, heavily decayed, from a remaining puddle of receding water] – Mayr, pl. 7, fig. 1.
1967	*Gyrodus hexagonus* Blainv, in Verwesung, mit Spuren, wahrscheinlich Zeichen seines Todeskampfes [*Gyrodus hexagonus* Blainv, in decay, with traces, probably signs of its death struggle] – Mayr, pl. 7, fig. 3.
1967	Reste eines stark verwesten *Aspidorhynchus*. Mit Spuren wahrscheinlich von seinem Todeskampf herrührend [Remains of a heavily decayed *Aspidorhynuchus*. With traces probably left by its death struggle] – Mayr, pl. 8, fig. 1.
1978	Schwoimarken – Barthel, p. 191
non 1978	[Unnamed] – Barthel, pp. 264–265, pl. 12.
1978	Scharrkreis – Barthel, p. 362, pl. 61, fig. 1.
1983	Schwoimarken – Viohl, pp. 12, 16.
v 1983	Zerfallener *Ophiopsis* mit Marken der Schwanzflosse [decayed *Ophiopsis* with marks left by the tail fin] – Viohl, fig. 4.
1987	Schwoimarken – Viohl, p. 8.
1990	Circular dragmark around fish – Barthel *et al.*, fig. 6.2.
? 1994	Schwemmarke eines *Antrimpos*/impression left by an *Antrimpos* – Frickhinger, p. 297, fig. 583.
1998	Schwoimarken – Viohl, p. 40, fig. 2.
? 1999	*Gyrodus* sp. mit Aufsetzspuren/*Gyrodus* sp. with land marks – Frickhinger, p. 152, fig. 269.
2011	*Eryon* mit Häutungsspuren [*Eryon* with ecdysial traces] – Leich, pp. 70–71, figs 1, 2.

Holotype: Specimen on the lower slab (BMMS 721b), illustrated in Fig. 4A (encircled).

Type locality: Solnhofen, Schwarzberg.

Type horizon: Lower Tithonian (Hybonotum Zone; Solnhofen Formation ("Malm Zeta 2b", "Obere Schiefer"). As the slab with the holotype was acquired from quarry workers by Friedrich Müller and later sold to the Bürgermeister-Müller-Museum, it is not possible to give a more precise stratigraphic position of the type horizon.

Occurrence: Solnhofen lithographic limestones, mainly in the Solnhofen-Langenaltheim Basin.

Etymology: After Karl Werner Barthel (1928–1981), German

geologist and palaeontologist. His main fields of study were the Nördlinger Ries impact crater, the regional stratigraphy of the Franconian Alb and the sedimentology and palaeontology of the Solnhofen lithographic limestones.

Diagnosis: *Harpichnus* where the negative epirelief (furrow) is shallow and the corresponding positive epirelief (ridge) is flat. The ratio between length, width and furrow depth is about 36:6:1.

Ichnotaxonomic distinctions: *Harpichnus bartheli* igen. et isp. nov. somewhat resembles *Telsonichnus* Schweigert, 1998 (*T. speciosus* Schweigert, 1998 and *T. minutus* Schweigert and Dietl, 2005) since both ichnogenera are mainly produced by uropod movements (Schweigert, 1998; Schweigert and Dietl, 2005). *Telsonichnus* is dominated by positive epirelief, whereas *Harpichnus* mainly exhibits negative epirelief. Furthermore, the furrows and ridges in *Harpichnus* are more irregular and by far not as arrow-like as in *Telsonichnus*. *Telsonichnus* is repetitive within short distances and these single specimens can be connected with a median line. *Harpichnus* specimens are instead spread over a distinct surface area without orientation towards each other. *Telsonichnus* is a surface trace fossil, created by the final movements of a lethally injured shrimp. In contrast to the ecdysichnion *Harpichnus*, *Telsonichnus* has to be regarded as a mortichnion (*sensu* Seilacher, 2007) that was produced in close relation to a praedichnion (*sensu* Ekdale, 1985).

Description: The holotype (circled on Fig. 4A) is located on the lower of two counter-slabs (BMMS 721 b = lower slab and BMMS 721 a = upper slab). The furrow has a length of 72 mm, a width of 14 mm and a depth of about 1.8 mm. The ridge lies on the convex side of the furrow. The outline of the latter is indistinct and the border to the surrounding sediment is fluent.

On the slab bearing the holotype, two clusters of the typically bent furrows and ridges are present. One of the clusters is lying at the edge of the slabs and extended into adjacent, unrecovered parts of the limestone bed. It contains an isolated pereiopod that was evidently detached during moulting. The other cluster appears to be completely recovered and extends over an area of about 740 × 320 mm. This area contains the body fossil of the ecdysichnion-producing ?*Aeger* sp. The furrows have a length of about 55 mm and a width of about 8 mm. Their maximum penetration into the sediment lies between 1 and 2.3 mm (usually around 1.5 mm). The ridges show similar sizes, but are not as clearly defined.

The producing arthropod, ?*Aeger* sp., is preserved on the edge of the larger cluster of furrows and ridges. The body fossil, preserved in almost dorsal position, can clearly be recognised as an exuvia because the carapace is swung open (Fig. 4B).

In other specimens (Figs 1C, 3C), sharply defined scratch circles produced by appendages of the tracemakers may locally be present. The furrows may cross one another. In the near surroundings or within the cluster of furrows and ridges, there usually is a body fossil (mostly an exuvia of a crustacean) preserved. The exuvia might show typical cracked ecdysial sutures. Other body fossils (e.g., fish) usually show traces of scavenging ("signs of decay" in older literature, e.g., Barthel, 1966).

Remarks: *Harpichnus bartheli* is mainly produced during the ecdysis of arthropods. However, it might also occur around incompletely eaten corpses and then has to be interpreted as a feeding trace, made by scavenging arthropods. Therefore, the existence of a body fossil will give an important clue, if the trace fossil has to be interpreted as an ecdysichnion or as a praedichnion (*sensu lato*).

During the moulting process, abdominal contractions, combined with the search for anchorage in the soft sediment, will lead to excavation of the *harpe-* to crescent-shaped furrows and may pile up this sediment in equally shaped ridges. However, the ridges will never be as distinct as the furrows, because the twitching may distribute the excavated sediment over a broader area. Negative epireliefs therefore dominate in *Harpichnus bartheli*.

On the edge of the slab with the holotype, posterior to the *Aeger?* body fossil, a serpentine trace fossil in positive epirelief is preserved. Wave-like movements may occur during ecdysis, but the preservation of the serpentine trace fossil as a positive epirelief does not comply with the majority of negative epireliefs. Thus this trace fossil does not belong to the cluster of *Harpichnus bartheli* and is either a digestichnion or an endichnion, made perhaps much later by an unknown producer.

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