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Limulus: a Living Fossil

Horseshoe Crabs Aid Interpretation of an Upper Jurassic Environment (Solnhofen)

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The author presents some little-known and new information on Recent *Limulus*. He writes about changes from the dorsal sculpture and ciliation, mucus secretion and molting in the earliest forms, and foraging and reconnaissance trails, the increase in size of *Limulus* as compared with their Upper Jurassic ancestors, and the importance of the gill apparatus in locomotion. Such knowledge helps in the interpretation of the fossil *Limulus* trails in the Solnhofen lithographic limestone. The form of the tracks suggests a subaquatic origin and not walking on exposed tidal flats, as has often been assumed. The reason for the preservation of the tracks is explained.

Introduction

"The present is the key to the past." This statement by Charles Lyell (1797–1875) has proved very fertile for geology at large. But uniformitarian principles may also be applied to some degree in paleontological disciplines like biostratonomy and paleoecology. These deal respectively with the fate of animal remains until their ultimate burial or with the reconstruction of relationships between animals and their environment. Of course the further we go back into the past, the less reliable our results, because we encounter more animals that lack living counterparts. Even so, the observation of similar species in the present may help our understanding.

Biostratonomic and paleoecologic deductions play an important role in solving the puzzles of the Solnhofen lithographic limestone of southern Germany. This rock was used for centuries for building and paving. It became well known after the invention of lithography; in addition being ideal for this purpose, the homogeneous limestone is famous for its perfectly preserved fossil fauna. The best-known specimen, because of its evolutionary importance, is *Archaeopteryx*, the first bird. The bulk of the fossils, however, are of marine origin, and even between recrystallized sedimentary particles there are the microscopic remains of marine plankton. Undisturbed layers with ideal bedding planes and other criteria suggest deposition in a quiet lagoon bordered by a shore line in the north and a bar of coral reefs in the south [5]. The lagoon bottom consisted of a complex basin and ridge pattern that followed a pre-existing relief. Under these conditions reconstruction of the environment in Upper Jurassic times (about 145×10^6 a ago) is rather difficult.

For some time the excellent preservation of the fossils was thought to be due to episodes during which the water receded from the lagoon with subsequent mummification of the stranded animals [1, 15]. A re-evaluation of biostratonomic, paleoecologic, and sedimentologic criteria produced a model that requires persistent submarine conditions [3–6]. Assumptions about most of the animal groups used for interpretation must be checked against their living relatives with respect to behavior, anatomy and function. After their death, the different stages of decay under various conditions supply further information. We present an interpretation of the Solnhofen limulids based on such considerations.

The ancient group of xiphosurid arthropods includes three living genera: *Tachypleus* and *Carcinoscorpius* are restricted to the Indo-Pacific area whereas *Limulus* is widely distributed along the Atlantic shores of North and Central America. The morphology of Recent genera has hardly changed since the Devonian (360×10^6 a); change was not necessary because the coastal environment inhabited by the limulids did not shift. Their high resistance to salinity and temperature fluctuations further favored their survival. Among fossil forms, *L. (Mesolimulus) walchi* Desmarest from the Solnhofen beds is best known in preservation and from trails. The anatomy and many other features of Recent limulids are quite well known and have stimulated renewed interest during the last few decades [2, 18–21, 26, 34], but the interrelatedness of form and function is often neglected and it is this that is so essential to the paleontologist making paleoenvironmental studies.

Living Limulus

These beautifully constructed animals consist of three segments: the prosoma, the opisthosoma, and the sword-like telson. We will consider just a few features
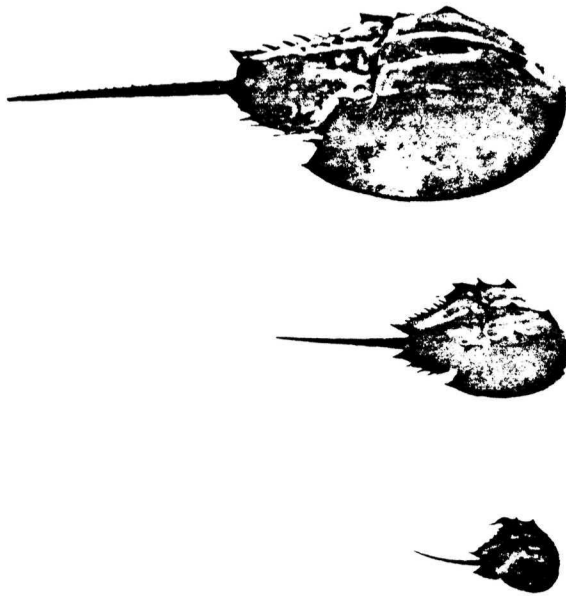
Fig. 1. Change in dorsal sculpture during ontogeny of *Limulus polyphemus* L. Three specimens from Florida. Length of adult ♂ (top) 370 mm.

of the modern animals. Observations of living specimens and interpretations gained from them and from motion pictures should add to the general store of knowledge.

Dorsal Sculpture

Limulus exhibits a marked change in shell sculpture during ontogeny (cf. [26]). In many animals such a change implies an alteration in the mode of life. The dorsal spines, which are so prominent in young and intermediate specimens (Fig. 1), are blunted or reduced in adults. What benefits do prominent spines confer upon adolescents? Small limuli are easily toppled over by currents or other accidents; once on their backs they try to turn over by arching body and telson [20, 34]. Under these conditions strong spines are useful to prevent skidding on the prosoma. They are also functional in digging as they prevent back-slip in the sediment while the prosoma is bulldozing ahead. Two anterolateral spines of the opisthosoma protect the tops of the water inlets at the lateral slits of the main body joint (Fig. 2).

The sculpture is reduced when the animal's life changes from almost continous burrowing and hiding to more frequent roaming on the surface and shallow digging. A smooth shell exerts less friction against currents. A decrease in prosoma vaulting accompanies this change; in young animals it is highly domed to make the thin shells more resistant. The low-vaulted adults have acquired very thick shells; a hydrodynamically positive shape is more adaptive (Fig. 1).

Opisthosoma spines

The opisthosoma is laterally armed by fixed and mobile spines. The fixed spines point dorsally, while the tips of the mobile ones are directed ventrally. When resting on the bottom (see Fig. in [29]) and when burrowing, *Limulus* swings its mobile spines down to brace itself in the sediment. Their mobility allows prosoma to be lifted and lowered slightly, which gives an additional advantage in digging (film supplied with [20]).

Cilation

The development of marginal ciliation in immature limuli seems to be linked with the decline in sculp-
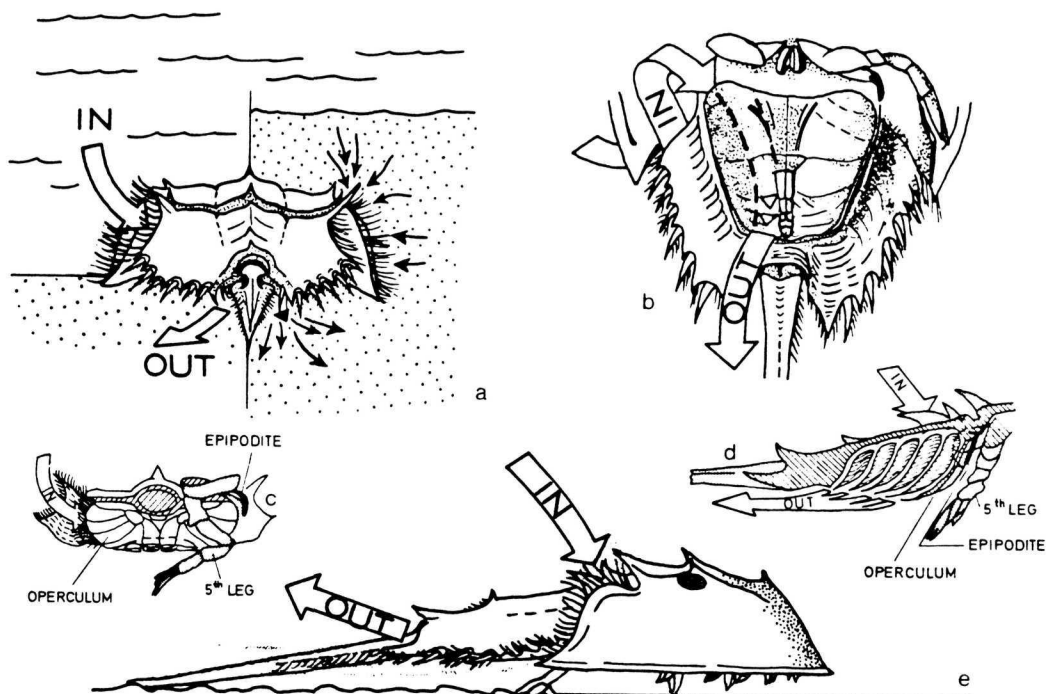

Fig. 2a–e. Schematic presentation of water flow through the gill system of *Limulus*: a) on sea bottom (left); under sediment (right); b) ventral view of opisthosoma and pusher leg with flabellum (upper right-hand side); c) as in b, but frontal view with prosoma removed; d) longitudinal section of opisthosoma to show gill chamber, gill positions, and flabellum; e) "reconnaissance swimming" by gill-jet.

tural prominence. Ciliation almost disappears in mature specimens. The bristles can be aligned to perform at least two functions. The long bristles flanking slits in the prosoma and opisthosoma (Fig. 2) provide a screen to exclude particles, while water can flow freely (Fig. 2a). The bristles also help to strip off mucus as the animal 'greases' its path through the sediment (see below).

Mucus secretion

Slime buds have long been reported to be associated with the nervous system of *Limulus*: "They are scattered over the whole surface of the body..." [16]. Their purpose, however, was not clear and various explanations have been offered [16]. Watching early ontogenetic stages (second and third molts) for several weeks led us to a reasonable interpretation. The small burrowing *Limulus*, when removed from the sediment and put into sea water, was dragging slime shreds behind itself, but quickly shed the slime because it impeded progress in the water. Since slime was always found when the animal was burrowing, its secretion was obviously associated with this activity. The reasons could be: (1) the tender shell is liable to suffer damage during movement within the sediment and the greasing effect of the slime removes the sediment particles in conveyor fashion as the animal digs ahead; (2) the mucus creates some stability in the sediment, an advantage that is known to aid various burrowers in the animal kingdom; (3) the slime makes the sediment adhere to the shell, so that animals surfacing on a exposed tidal flat remain well camouflaged. Mucus secretion vanishes at least on the dorsal side of the shell. In full grown *Limulus* many specimens show epibionts (Fig. in [29] and cover).

Molting

Limulids molt to reach their consecutive growth stages. The exact number of these stages is still uncertain [17, 24, 26]. Published data combined with our own show that after the earliest tailed stage (length 6 mm) five to six moltings occur during the first year, but only two in the second and third years [17]. Thereafter one molt per annum is recorded [25, 26]. *Limulus* takes 9 to 12 years to reach maturity [29] at a prosomal width of 200 mm (comp. Fig. 3b). We add a few words on the two molts following the first tailed stage because there seem to be no published data. The animal observed was kept in confinement under natural conditions. The specimen (length 6.2 mm) molted 10 days after capture. Now 9 mm long, the animal had its next molt 23 days later. It rested for 5 to 6 days before molts (pre-ecdysic rest), but postecdysic inactivity lasted for less than one day (Fig. 3a). During these inert phases *Limulus* stayed under the sediment and its feeding activities were much reduced or suspended. Molting was effected on the surface [20, 24].

Foraging

The small animal that provided our information on molting and slime secretion revealed its foraging pattern too. It was confined within a tank containing sediment and sea water; these were changed frequently.
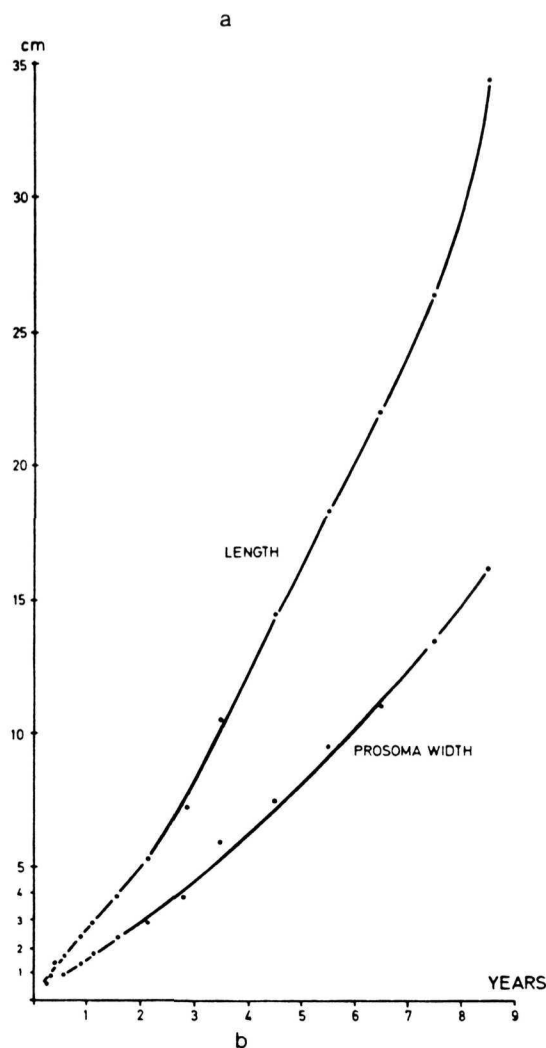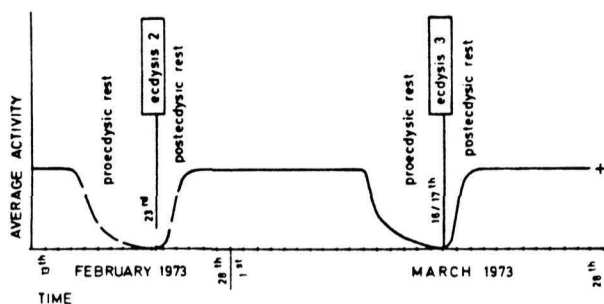

a

b

Fig. 3a and b. Growth in *Limulus*: a) molting (ecdysis) phases in a young specimen, starting with the "first tailed stage"; b) growth curves of total length and prosoma width based on three individuals, compiled from [17, 25] and own observations (earliest stages). Curves represent growth to early adult stage only.

The limulid "mined" half the bottom surface initially, then two thirds, and finally the entire surface per day. To obtain food, limulids use their prosomata in bulldozer fashion to plow into and dig under the sediment [20, 34]. The young limulid never started to dig at once on new sediment. It followed the tank walls and then returned toward the center in irregular trails (Fig. 4a). During this "reconnaissance" the fifth pair of legs (pushers) made the dominant tracks (Fig. 5a). The resulting "reconnaissance trail" is of considerable importance for the interpretation of the fossil trails of the lithographic limestone.
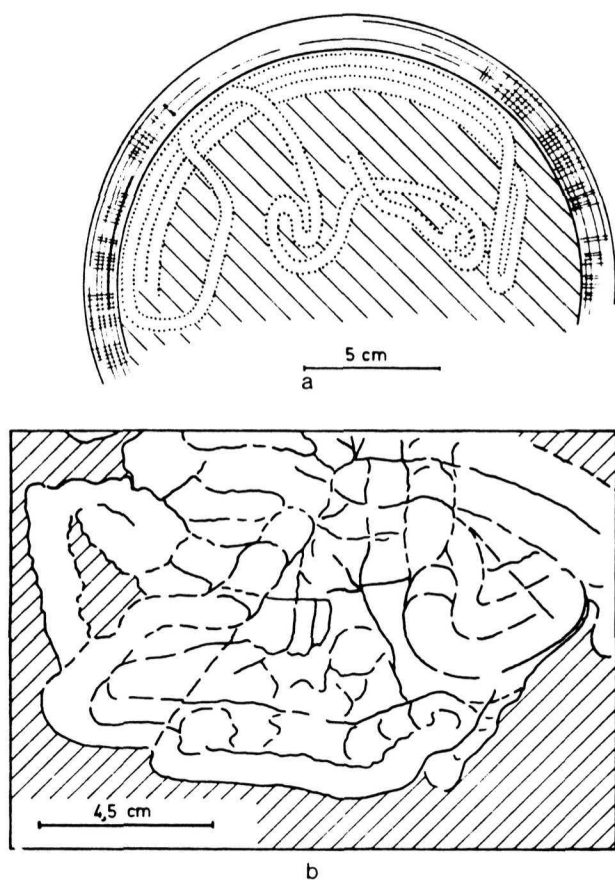
Fig. 4a and b. Trails of Recent young *Limulus*: a) reconnaissance trail; b) foraging trail.
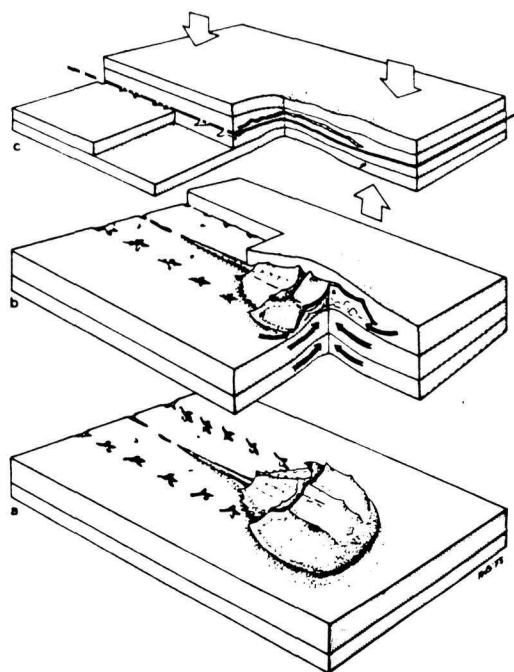

Fig. 5. Diagram of limulid preservation and formation of pseudo-undertracks in the Solnhofen lithographic limestone (Upper Jurassic) based on track sections. Note: the trail consists almost entirely of pusher leg imprints.

"Foraging trails" originate during intensive search for food by burrowing. A roughly meandering pattern is produced. Meanders usually touch but do not inter-

sect, except when sediment is exploited at different levels (Fig. 4b). Surface reconnaissance sometimes led to the limulid staking out an area which was subsequently foraged. A larger specimen (70 mm) burrowed so deeply that its foraging actions were not visible at the surface. Still larger specimens apparently do not dig continously. Adult foraging trails in general resemble those of juveniles. Digging sites, however, leave crateriform impressions (written communication of C. N. Shuster). Continuous burrowing is apparently abandoned by the adult.

Size

Shell size may provide some valuable criteria for comparisons of fossil with living limulids. The literature contains rather sparse data [17, 24, 26] that may be combined with our own observations to give a growth curve from first molt to an early mature stage (Fig. 3b). There are fuller data on the size range of adults relative to the geographic distribution of limulids [26, 27]; according to these, the largest female reached a prosomal width of 350 mm. A shell in our collection measures 750 mm in length and 380 mm in prosomal width. The fact that only small specimens of Solnhofen limuli are preserved in collections has passed almost unnoticed [5]. Hardly an individual exceeds 150 mm in overall length. They were assumed to be stray specimens which had been lost on the way to the coast to mate there [23]. Straying is a correct assumption. Mating, on the other hand, is unlikely unless these species matured at a much smaller size than Recent *Limulus*. Recovery of a limulid trail spanning 220 mm was reported from one of the quarry districts not long ago [13]. A 630/330 mm length/width ratio can be reconstructed for the animal [13]. Mature individuals from the Upper Jurassic must therefore have been at least equal in size to living *Limulus*.

Why, then, are finds of immature limulids so dominant? We many safely assume that fully grown specimens were more resistant and experienced enough to escape from the lethal lagoons. Small individuals, after losing their orientation, were too weak to find their way out and hence were preserved.

Locomotion

Limulus seems to achieve locomotion by two modes, walking and swimming [18, 19, 34]. Closer inspection shows that a third mode can occur in special conditions under water. The fifth pair of legs is again involved. The chelate legs hardly touch the bottom, so all support to the body has gone once the pushers leave the ground. Apparently other organs are involved. A simple glance at the general morphology of *Limulus* will help to explain at least some of the problems.

The longitudinal section of the *Limulus* body resembles that of an aircraft wing profile. Forces similar to those acting on the latter in a current must become effective in *Limulus* also. The interplay of body shape and pusher action would cause a rather jerky movement so that we have to look for a stabilizing agent. The dorsal side offers little help. Ventrally we may disregard the prosoma, but the opisthosoma is worth consideration. In ventral view, with gill appendages removed, the gill chamber may be described as a

wedge-shaped concavity (Figs. 2b, d): its front and top are open and it narrows and tapers toward the telson; the lateral walls curve smoothly into the bottom of the depression. This shape is hydrodynamically very efficient. What is described as the bottom is actually the dorsal side of the gill chamber. All the *opisthosomatic* appendages are attached there and extend, obliquely pendant, into the chamber cavity. Five of these appendages each carry a pair of gill stacks [2, 26, 31] (Fig. 2d). The appendages are able to close the front and ventral side of the gill chamber almost completely. Small gaps remain at either side between the operculum (cover plate) and chamber walls (Fig. 2c); these gaps are the frontal water inlets which maintain inflow while the distal ends of the appendages control the outflow. The shape of the posterior margins (Fig. 2b) of the appendages allow laminar, median, and consecutive water expulsion to be accomplished. Thus a certain degree of maneuverability provides the stability we were looking for.

The shape of the gill chamber and the position of the gills presuppose a front-to-back waterflow. Observations of *Limulus* in shallow murky water are in accord with this. The animal exhales at either side of the telson (Fig. 2a). Suspended particles make the currents visible as small puffs to the rear and as slight whirls above the prosoma-opisthosoma notches. This can also be seen in a motion picture of *Limulus*, produced and generously loaned by the Institut für den Wissenschaftlichen Film (Göttingen) [20]. It would not be necessary to place such stress on this feature, were it not for the assumption in textbooks of rear-to-front water flow [12].

The function of the "gill-jet" would not be complete without the flabellum or epipodite [2, 26, 31, 33]. These small, spoon-shaped angular structures attached to the coxal elements of the pusher legs (Fig. 2b–d) exactly fit to close the anterior gill inlets. It is strange that such a striking organ as the flabellum could have remained without a reasonable explanation for so long [2, 35]. A series of slow-motion pictures in the film mentioned show that when the pusher legs are stretched, the epipodite moves backward to resume its position at the gill inlets. According to its location on the coxa, this precedes the movement of the more distal portion of the leg. As the gill chamber is closed in front, water can be forcefully discharged backward between the laminate abdominal appendages without any loss of thrust. The thrust in fact aids the pushers in locomotion. The backward stroke of the legs while swimming brings the epipodites into the closing position just at the moment when leg pairs 1 to 4 start to swing forward again and the gill apparatus flaps to continue the stroke (see [18, 34]). As forward expulsion of water is prevented by the flabella, progress in locomotion will not be impeded.

Two more functions may safely be ascribed to the flabella: the inlets are closed to prevent large particles from entering the gill chamber as the pushers stretch in digging actions. Also, while the animal rests under sediment, the mobile flabellum is useful in driving a slow but constant current into the gill chamber. This current would guarantee sufficient new water for the gills without demanding strong agitation of the gill apparatus, so that minimum effort is required. In addition, the flabella certainly have a sensory function

[35]. Comprehension of the collateral role of the gill apparatus leads to an understanding of the third mode of limulid locomotion. The combined use of the pusher legs and gill-jet may be called "reconnaissance swimming" (Fig. 2e), being largely exercised during reconnaissance. Most trails preserved in the lithographic limestone are of this kind; the animals did not wish to contact the treacherous sediment too closely but stayed near the bottom for orientation.

Solnhofen Limulid Trails

In the preceding sections our study of Recent limuli has been related to data on their fossil counterparts from Bavaria. We will continue to use our results in considering the Solnhofen limuli and their trails. The frequency of finds is moderate: they are relatively more abundant in the north and east (Eichstätt to Kelheim) in areas closer to the supposed coastline [5]. A recent corollary of Solnhofen limulid trail history [14] differentiates subaerial and subaquatic trails by quality of tracks. Differences in leg imprints have been explained also by "undertracks," i.e. tracks initiated by the same leg may look different, depending on which of several superimposed bedding planes they were preserved in [10]. This implies that the sediments on and near the bottom surface were soft, and because of the preservation, remained in a subaquatic environment. There is evidence of differences in viscosity in successive layers at Solnhofen [3, 4]. Very soft mud will hold recognizable tracks only under water. Therefore it is difficult to accept that such trails originated on tidal flats at "low tide". It is striking that in the Solnhofen trails pusher leg imprints (Fig. 5a) predominate while those of chelate legs (pairs 1 to 4) are generally solitary or absent. Under normal conditions the latter effectively aid the pushers in walking [7, 19], even under water. In both aerial and aquatic environments there is a triple trail caused by geneal spines and telson [7, 32]. These facts contradict the hypothesis of walking on subaerially exposed lagoon bottoms and indicate the special mode of locomotion described as reconnaissance swimming. It is only when the animal is exhausted or near death that tracks of the chelate leg series occur clearly in trails (see also [8]). It is not very probable that all Solnhofen trails represent undertracks [10] with chelate imprints on a capping bed. This becomes quite evident in the final phases of "disorientation trails". It was pointed out [5] that, beside limulids that had simply stopped dead in their tracks, others had left variable trail patterns before death. Disorientation due to murky waters, lack of oxygen, hypersalinity, and/or presence of H_2S are held responsible for the strange behavior of the animals. Two such impressive trails are illustrated here (Fig. 6). In one instance the *Limulus* spiralled until death; in the second the animal dragged along, leaving consecutive and overlapping series of body imprints.

A further argument against intertidal exposure of the Solnhofen lagoons is the general absence of *Limulus* burrowings. Recent animals dig for food or protection into the tidal flats and beaches [7, 24]. The Jurassic limuli certainly would have tried to bury themselves and to wait in the moist sediment for the next "tide". The one possible burrow reported [11] rather indicates

Fig. 6a and b. *Limulus* (*Mesolimulus*). a) Disorientation trail. Bottom of slab (prosoma width 92 mm); b) Disorientation trail of an utterly exhausted animal. Full body imprints overlap. Top of slab (length 843 mm). Lithographic limestone, Maxberg, Solnhofen area (Courtesy of Dr. Th. Kress, Solenhofer Aktien Verein).

subaquatic origin: no trails lead to or from the digging site, which means that the animal must have been swimming to reach it and leave it. The state of preservation can make track interpretation difficult. The undertrack explanation (see above) requires badly preserved tracks in the bed the *Limulus* was actually walking on. Layers below that should show better imprints. This seems consistent with the experience that tracks are found on one bed surface while the shells of the animals are very often entombed in the capping layer. Since the lithographic limestone does not preserve internal structures, it is hard to decipher the facts, and there may be other processes involved which could complicate matters.

Many entirely embedded, unprepared specimens show slight sediment depression above and upward below the fossil. In Solnhofen ammonites this is a common phenomenon. It may be termed the Rothpletz effect after the scientist who first explained it [22]. As modified [3], this means that water in or under suitable shells may give them buoyancy and they become lighter than the embedding sediment. Since the dehydrating sediment had not yet lost its plasticity, sediment flow from below compensated for the uplift. The shell became part of the capping bed and, as in most Solnhofen fossils, was found sticking to the bottom of the slab. Continued dehydration, sediment overload, and frequently collapse of the shell are responsible for the depression on top of the fossil (Fig. 5). As the shell is buried, the track imprints are filled in too, but the body will be separated from the

trail by the Rothpletz effect. On recovery the slab will split open at the former bedding plane and the fill-in stubs of the tracks will break along this plane. The fractures resemble blurred tracks which seem to come out of the capping bed. Since these are not undertracks proper, we refer to them as "pseudo-undertracks". Thus, each limulid track from the lithographic limestone has to be checked by cutting the slabs to resolve the ambiguity.

Our attempt to reconstruct the paleo-environment of the Solnhofen area in Upper Jurassic times by means of functional analysis of the fossils found in relation to the sediment demonstrates the possibilities of the method and also the fallacies a paleontologist may encounter in such a venture.

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