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very best wishes
Kenneth E. Caster

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Trails of Limulus and Supposed Vertebrates from Solnhofen Lithographic Limestone

BY

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TRAILS OF LIMULUS AND SUPPOSED VERTEBRATES FROM SOLNHOFEN LITHOGRAPHIC LIMESTONE

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The heteropodous tracks and trails from the lithographic limestone of the Solnhofen vicinity, Bavaria, *Koupichnium lithographicum* Oppel, *Protornis bavarica* Jaekel, *Ornichnites caudata* Jaekel, *Hypernithes jurassica* Jaekel, and related forms, appear to have been made by the ubiquitous *Limulus walchi* of the deposits, or a close relative, rather than by vertebrates, to which they have usually been attributed.[1]

The tracks and trails of the Jurassic Plattenkalke, from the region around Solnhofen, Bavaria, have been studied and interpreted by many writers since they were first made known by Oppel in 1862. The fact that the trails embrace two kinds of tracks made them Problematica of outstanding interest from the start. Several variations of Oppel's original trails have subsequently been described, including the spoor of *Limulus walchi*, with which apparently the heteropodous trails have not been hitherto compared in published accounts, since they were considered from the very first as having been made by vertebrates. It is the object of this article to see where this omitted comparison may lead us.

These observations on European trails are an outgrowth of

[1] See, also Pal. Zeitschr., XXII Bd., S. 12-19, 1940.

studies pursued in conjunction with a reinterpretation (Caster, 1938) of *Paramphibius* Willard (1935) from the Upper Devonic rocks of Pennsylvania. In the course of that work it became necessary to make a rather thorough comparative paleoichnological survey of heteropod trails, especially those which are demonstrably xiphosuran. It soon became clear that many heteropodous trails in the Solnhofen Plattenkalke, which have always been referred to vertebrates, should be subjected to closer scrutiny with a limuloid interpretation in mind. Only those Solnhofen trails, however, which had been assigned unquestionably to *L. walchi* by other students were discussed in the *Paramphibius* paper, lest the attack on too many supposed vertebrates, so far apart in time, should seriously weaken the argument as a whole.

Since Limulus is a stranger to-day to the shores of Europe, its anatomy and ichnology have not been commonly well known there. It is curious that although the general ichnological features of Limulus have been described in ichnological literature for many years, the fact that it leaves a heteropodous trail has, until very recently, been almost universally forgotten by ichnologists. A review of limuloid ichnology was given in Caster's 1938, paper, to which of necessity reference must be made in the progress of this comparison.

Most Xiphosura, and apparently all representatives of Limulus, possess, in addition to an anterior pair of chelicerae, four pairs of chelate, walking or "simple," feet (endognaths) and a sixth pair of modified walking feet (ectognaths) which serve principally as pushers. As was brought out in the 1938 paper, the simple feet are placed on the ground essentially as a unit in alternation with the pushing feet. The imprints of the latter are often superposed on the tracks of the simple feet.

To one not familiar with the walking Limulus it is rather surprising to discover the curious construction of the pushing feet. They possess each four (or five) posteriorly concave blades which are articulated to the distal end and dorsal side of the propodos (penult) segment of the leg. They are also connected by muscles to the proximal end of the dactylus (distal) segment. In repose the concave blades lie upon the dorsal surface of the dactylus which they overhang, and are quite inconspicuous when the animal moves about in the water. When, however, the animal crawls on the bottom, the dactylus is bent so that its end is directed posteriorly, and its dorsal surface lies on or in the bottom mud. The flexing of the distal joint causes the blades to rise and radiate fanwise from one another. This explains the term flabellum which is occasionally applied to them. The concave under surfaces of the blades are then pressed on the bottom material, and are a very effective pushing organ. When fully distended and flatly impressed, the flabellum leaves four (or five) toe-like impressions anteriorly radiating from the heel-like mold of the dorsal surface of the dactylus. At the end of the dactylus there are sometimes imprinted the markings of two movable terminal spines. When impressed in this manner the flabellar impression is rather startlingly like the foot-print of a small vertebrate. Caster (1938) brought out some of the ontogenetic variations in the form of the flabellum, and the correlary changes in its mode of implacement which modern horseshoe crabs exhibit. These variations are of considerable ichnological, as well as evolutionary, importance.

The young Limulus walks after the manner of the antecedent form, Paramphibius, with the flabellar blades pressed flatly on the ground, more as a support for the body than as a pushing apparatus. The resultant foot-print is very similar to that of a small amphibian or reptile. Such trails recall the vertebrates in their original orientation. An example of a properly oriented Limuloid trail which was wrongly interpreted is Willard's *Paramphibius* (1935) or *Artiodactylus* Abel (1926). When the crab approaches maturity the flabellar blades are considerably strengthened and grow less movable. It then becomes virtually impossible for the blades to be flatly pressed in the mud. The angle between them and the underbent dactylus then tends to approach more nearly 90 degrees than the 180 degrees of immaturity. This means that the ephebic blades are pressed spadelike in the mud in a nearly vertical semi-circle. The pushing efficiency of the ectognath therefore improves with age. When withdrawn, the blades fold together and even overlap medially. In relatively soft mud they usually cause a slight deformation, or even a drag-mark, toward the front in the process of removal. The uninitiated worker examining the mature flabellar imprint inevitably concludes, like many before him, that a small vertebrate, possibly bird or reptile, made the track. But note the difference: the uninitiated would have supposed that paper by the present author (1938). Many illustrations of a wide variety of normal limulid trails and also the trails of the Devonic Paramphibius were shown at that time. It so happens that not a single Solnhofen trail in either European or American collections shows anywhere near the perfection of detail so commonly exhibited by the Devonic Paramphibius material, or by induced trails made by Limulus in the laboratory. It seems inevitable that comparable trails do occur in the Plattenkalke, but they must have been cast aside or overlooked. Renewed search in the classic localities may still prove fruitful.

Diagnostic of the accepted trails of *L. walchi* are the size and general trend, the presence of chelate simple foot-prints, and indistinct flabellar impressions; thus establishing primary heteropody. A median drag-mark of the telson is usually present, and may be continuous or interrupted. The size of the trails varies considerably, although they have apparently two maxima, which suggests a slight ephebic sexual discrepancy. This is similar to the condition in existing forms, where the female is quite a bit larger than the male. The trails are normally undulatory, but toward the cadaver usually become straighter. No records have been made of the trend of the trails *in situ*. It seems safe to predict that when such records are made, most of them will lead in a shoreward direction, for it is presumable that in Solnhofen, as is usual elsewhere, the crabs approached shore primarily on their nuptial errand and were of relatively direct purpose. Certainly at Solnhofen, as at the present time, immature animals accompanied the adults on this seasonal excursion. Evidence of any periodicity in the trail layers in the Plattenkalke would be of great corroborative interest. As yet we have none. Subaereal trails probably trend in general toward the water, with the possible exception of those that end in a dead animal, for most crabs to-day, when stranded at turn of tide, manage to find their way to the water again with considerable directness.

When the king-crab walks in its most usual manner over regular terrane and under optimum conditions, either in very shallow water or subaerially, the simple feet are placed on the ground with their distal ends forward. When the chelæ leave their record they serve as excellent indicators of the direction in which the animal walked. Furthermore, when the complete complement of simple feet is impressed in any one hitch or stride, the front pair of foot-prints is nearest the median line, and the distance of the tracks from the line increases progressively posteriorly. Complete sets of simple tracks made in this manner are in the form of anteriorly directed chevrons, and help, even when incomplete, to point the direction of movement. No complete suites of simple tracks have been observed in the Solnhofen material. When the chelate feet are used in a scratching manner, rather than for mere support, the scratch-lines usually tend to form chevrons, or partial chevrons, posteriorly directed, since the feet are in this process pulled backward in the mud in an effort to move ahead. There are exceptions to this, however. Backwardly directed chevrons of scratches are not uncommon in the death-throe trails at Solnhofen.

The 1938 paper demonstrated the ichnologically important fact that Limulus is responsible for a wide variety of trails. From youth to maturity the mode of locomotion as well as the size of the trails and detail of the tracks change greatly. Then too, the depth of water, or absence of it, the slope of the bottom, the wetness of the mud in subaerial locomotion, consistency of the bottom, fatigue of the organism, etc., are all factors materially altering the record of locomotion at all life stages. Some variations which were induced experimentally were shown in the aforementioned paper. Many variations of trail and track, sufficiently different to have been the basis for distinct form-genera, are the rule with these creatures. Many of these variations, some of which are almost the precise counterparts of those experimentally produced, occur in the Solnhofen records, but have been hidden under the mantle of Problematica attributed to vertebrates.

There are problematica which seem to be varietal trails of *Limulus walchi.* Most of the Solnhofen trails which show heteropodous features have at some time or other been assigned to Oppel's Ichnites (or Kouphichnium) *lithographicum,* (1862). Oppel imagined that the trail was made by an Archeöpteryx, a new and amazing discovery in the Plattenkalke at that time. This trail, more than any other perhaps, has been the indirect basis for the familiar reconstructions of the lagoonal scene, dominated by either small numbers or hordes of ancient birds, pterodactyls or tiny dinosaurs walking the mud-flats, for ever since Oppel's time all these creatures, and others, have been conjured up as the makers of the heteropod trails. In mind are such reconstructions as Figuier's illustration (1866) of Rhamphorhynchus on the Solnhofen tidal flats (in Abel, 1935, fig. 127), or Rudloff's reconstruction (1907) for Walther of both Archeopteryx and Rhamphorynchus on the strand (Abel, 1935, fig. 128). It is not impossible that the ecological implications of this customary picture may be utterly without factual basis.

Oppel (1862) gave the essential features of the trails; details were added by Walther (1904) in the Festschrift for Ernst Hæckel (p. 147, 203, 211, and fig. 5). Abel (1935, and elsewhere) has added more data as well as interesting interpretations. Walther reported that he had seen whole slabs covered with the trails, running in all directions. This convinced him that flocks of ancient birds "hopped around happily on the mud surface at Solnhofen." He described the trails as mostly of a quiescent sort, trending now in straight lines, now in wavy courses, and occasionally in narrow curves.

According to all writers on the subject, the typical Kouphichnium trails are comprised of tetraradiate "toe" impressions which alternate with single pairs of roundish impressions. A discontinuous groove usually runs along the median line of the trail. The foot-prints are usually oppositely implanted. At a distance of about 2 cm. from the radiate trails Walther reported "claw impressions." The radiate imprints were usually spaced 6 cm. apart, and the length of what was termed the "jump" was usually about 5 cm. in a straight line, but on curves the outer tracks might be as much as 9 cm. apart. In his drawings and description Walther intimated that the short outer toe-prints turned back at approximately right angles to the middle toe. It was his impression, as also Oppel's before him, that the radiate tracks were made by the hind feet, whereas the simple rounded imprints were made by the crutchlike use of the carpal bones of the wing. Walther (p. 203) reported seeing elsewhere slabs covered with similar tracks of smaller size in which the "crutch-marks" were absent. Abel (1912) was less prone to accept the trails as those of ancient birds, the while concurring in the opinion that they were of vertebrate origin, a view which he still held in his 1935 work. Abel favored a small dinosaur of the Compsognathus type.

From new Kouphichnium trails collected at Solnhofen and additional material recovered in 1923, at Pfalzpainter, near Eichstätt, Bavaria, Abel was able (1927) to amplify previous accounts. He concurred with Oppel and Walther that most of the trails showed simultaneous implacement of the digitate feet and, like them, concluded that the animal must have jumped or hopped. He continued to think of the forefeet as having been used in a crutch-like manner, but the new material showed three pairs of roundish impressions between each two pairs of radiate ones. The pair of impressions which he interpreted as posteriormost were closest together, *i.e.*, nearest the median line; the second pair was a little more widely spaced and the third pair widest apart. The dimensions for the original Solnhofen material given by Abel (1927) were: length of jump 81 mm.; width of track 61 mm.; the hind pair of foot-prints were 42 mm. apart; the second pair were 58 mm. apart, and the third pair 80 mm. apart. The new Solnhofen trail recorded no tail impression. In new material from Pfalzpainter, the spacing of the "crutch impressions" was 42 mm., 52 mm., and 62 mm. In this material the tail-drag is preserved. Abel discovered that in many of the new trails the structure attributed to the middle toe of the radiate impression showed terminal splitting. He suggested at first syndactyly of two toes to account for this curious condition. Later he suggested that this was a double impression of the middle toe due to a slight wavering of the animal and shifting of the foot on the off-jump. Still later he suggested the possibility of explaining the anomaly by an epidermal formation of the middle toe such as one finds in desert jumping mice. Abel also mentioned the existence of very delicate radiating impressions, so fine that they were inevitably destroyed on prepared material, which extended forward from all of the toe-marks. These he suggested (1927) could have been made by hairs, were it possible to connect the trails with some as yet unknown mammal. In 1926 he pointed out that such marks could also have been made by feathers. With the new material before him, Abel (1926, 1927, 1935) caught and developed the idea of a small hopping vertebrate, preferably a dinosaur (Compsognathus?) which placed its hind feet simultaneously on the ground, and raised them in the same manner. Between every jump the two very small dangling hands, or at least the middle fingers of them, were set on the ground: first, close together; then after a moment's hesitation, a little further forward and a little further apart; finally for a third time, still further apart and further forward. Only after this preliminary exploratory shifting did the jump occur. Abel thought that a slab from Mörnsheim, which he examined while writing his 1935 book, preserved the indistinct impression of three toes on some of the "crutch-prints," although ordinarily even here simple roundish imprints were the rule. The Mörnsheim trails show only single pairs of the simple "crutch-prints" in alternation with the digitate "hind foot-prints."

Jaekel (1929) gave the name *Hypernithes jurassica* to trails similar to those discussed by Abel, which show several crutch-like impressions, and *Ornichnites caudatus* to those showing only two "crutch-prints." Jaekel's trails are considered somewhat later in this report.

Wilfarth (1937) took up the interpretation of the Jurassic trails where Abel left off. He leaned with Abel toward a reptilian track-maker, strong of leg and weak of arm, having one digit far longer than the rest so that only its claw left an imprint during the crutch-like propulsion, which Oppel and Walther before them had subscribed to. By endeavoring to eliminate possibilities, Wilfarth rejected birds, mammals, pterodactyls, and Compsognathus, finally to require a dinosaur of the American Ornitholestes type. This he forthwith imported by a sweep of the pen to the Solnhofen lagoon. He offered painstaking diagrams of a skeletal restoration of Ornitholestes superimposed on Kouphichnium trails of the same proportional enlargement to show the feasibility of his idea. He would thus relegate to a hesitant, limping, progression, the little dinosaur whose very name, as well as anatomy, had hitherto implied quite different mode of existence! Both Wilfarth and Jaekel (as seen below) illustrate the danger of carrying assumption too far beyond fact. So much, by way of review, of the varying interpretations of these particular trails.

What are the limuloid aspects, if any, of these problematical trails? One should note, first of all, that though they vary greatly in dimension, they never surpass the width of known cadavers of *Limulus walchi* from the same strata. The variability in the size of the trails is very much the same as that shown by unquestionable trails of *L. walchi* and like them recalls the trails left on the western Atlantic seaboard every springtime when the large females of *Limulus polyphemus* come in toward shore either towing or accompanied by the somewhat smaller males. It has been already noted that in this vernal progress the ripe and the unripe mingle; trails of wide variety in size and detail result when this motley horde is marooned on mud-flats by tide or storm. One should bear in mind in evaluating the Solnhofen trails that *L. walchi* was on the average somewhat smaller than the existing *L. polyphemus*, a giant among limuloids.

The general aspect of the trails is much like those that the modern Limulus makes on mud in shallow water, or on wet mud subaerially whilst in search of water, having been stranded on the shore or mud-flat at low tide. Although no record of the trend of these trails *in situ* has been made, it would be as valuable here as for the unquestioned trails of *L. walchi.* From the general nature of Kouphichnium trails when compared with experimental trails made by limuli under varying laboratory conditions, it seems likely that most of these problematical Jurassic trails were made in an environment somewhat seaward from most of the recorded trails of *L. walchi, sensu stricto.* The Problematica exhibit, richer detail, which correlates with their appearance of having been made on wetter mud (if not occasionally in shallow water), than the "death marches" of *L. walchi, s.s.* This is in logical keeping with the fact that apparently never has a dead Limulus been found at the end of a Kouphichnium trail, whereas one is almost inevitably found at the end of the conventional trail of *Limulus walchi.* Kouphichnium trails were often made, apparently, under much the same conditions as Winkler's puzzling trail, mentioned above, which was for so long described as the "seat-place" of an archeopteryx, or dinosaur: the lime mud had been only recently exposed at low tide, or for other causes, and was still wet, and in fact may well still have had a little water lying on it. Under such conditions limuloid foot-prints are best recorded to-day, as Caster (1938) brought out experimentally. Enough water for a slight amount of lubrication, but insufficient for actual support of the animal on a mud of the proper consistency assures a trail of maximum detail. In view of the fact that Limulus carries a considerable amount of water in its gill-book chamber for some time after exposure to air, it can supply aqueous lubricant for quite a distance of subaerial walking on moist mud, the record of which will often be rich in detail. If the quest for water is unsuccessful and the branchial

Munich, very kindly prepared photographs of Kouphichnium in their care, and prepared casts of material for my use, which unfortunately current hostilities precluded my receiving. I am happy to acknowledge the kind services of Drs. B. F. Howell and J. B. Knight, of Princeton University, Dr. C. W. Gilmore, of the U. S. National Museum, and Dr. C. O. Dunbar, of Yale University, for the loan of comparative material of the American Triassic trail *Micrichnus scotti* and *Artiodactylus sinclairi*, on which a separate note has already appeared in print (Caster, 1939).

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CHART OF GEOLOGICAL PERIODS

CENOZOIC ERA	**Quaternic Period** *Planation Interval* **Tertic Period** *Planation Interval*
MESOZOIC ERA	**Cretacic Period** *Planation Interval* **Jurassic Period** *Planation Interval* **Triassic Period** *Planation Interval*
PALEOZOIC ERA	**Carbonic Period** *Planation Interval* **Yorkic Period** *Planation Interval* **Siluric Period** *Planation Interval* **Cambric Period** *Planation Interval*
PROTOZOIC ERA	**Taconic Period** *Planation Interval* **Keweenawic Period** *Planation Interval* **Animikic Period** *Planation Interval* **Selkirkic Period** *Planation Interval* **Nisconlithic Period** *Planation Interval* **Connaughtic Period** *Planation Interval* **Anianic Period** *Planation Interval*
ARCHEOZOIC ERA	**Algomic Period** *Planation Interval* **Huronic Period** *Planation Interval* **Laurencic Period** *Planation Interval* **Varennesic Period** *Planation Interval*
EOZOIC ERA	
AZOIC ERA	

CHARLES KEYES