WERE *MICRICHNUS SCOTTI* ABEL AND *ARTIODACTYLUS SINCLAIRI* ABEL OF THE NEWARK SERIES (TRIASSIC) MADE BY VERTEBRATES OR LIMULOIDS?

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ABSTRACT. Comparison between *Micrichnus scotti* Abel and *Artiodactylus sinclairi* Abel of the Newark series (Triassic) of New Jersey and the trails of modern and fossil *Limulus* yields convincing evidence of the xiphosurous origin of the Triassic trails rather than the vertebrate origin hitherto postulated. This conclusion supports the contention that estuarine conditions existed locally during Newark deposition.

INTRODUCTION AND ACKNOWLEDGMENTS.

As one phase of the investigation, 1938, of the origin of *Paramphibius* trails in the Upper Devonian of the Penn-York Embayment, the writer had occasion to survey most of the published accounts of small heteropodous trails in the fossil record. A few of these trails, especially those never assigned to vertebrates, were discussed in the comparative paleoichnology section of the 1938 paper. Several other trails which are remarkably similar to the trail record of the Xiphosura, but which have been customarily attributed to vertebrates, were intentionally omitted from that discussion lest an array of too many pseudo-vertebrate trails obscure the issue and weaken the arguments being developed to account for the origin of the Devonian trails. With the establishment of *Paramphibius* as the trail of a protolimuloid creature as the result of that study, the other so-called vertebrate trails of somewhat similar stamp will now bear reëxamination in this light. *Kouphichnium* of the Solnhofen Plattenkalke (Jurassic) of Germany and *Micrichnus* of the Newark Beds (Triassic) of New Jersey are the outstanding examples of this type of trail. A brief review of the *Kouphichnium* problem now awaits publication in the *Palaeontologische Zeitschrift*. There it will be shown that the German trail and its many named variants were in all likelihood made by the common *Limulus walchi* of the Solnhofen lagoon rather than by a pterodactyl (Winckler, 1886), an archeopteryx (Walther, 1904; Jaekel, 1929) or dinosaur (Abel, 1912, 1935; Wilfarth, 1937) as had been previously supposed. A few of the details of the basis for this new assignment will come out in the discussion of the *Micrichnus* problem, below.

In the discussion which follows the reader is referred to Caster's 1938 paper for the details of xiphosuran locomotion and illustrations of fossil and recent limuloid trails, a knowledge of which is essential for the development of the present hypothesis. By reference to these illustrations and the fine photographs of the trails of the Newark series shown in Abel's "Vorzeitliche Lebensspuren" (1935), duplication of illustrative material is spared this paper.

It is a pleasure at the outset to acknowledge the great debt all students of paleoichnology owe Dr. Othenio Abel for his stimulating works on the fossil evidences of life. In the present study his "Vorzeitliche Lebensspuren" has been an ever-present compendium of ichnological data. Specimens and data for this restudy were made available through Dr. Hermann Schmidt of Göttingen, Dr. Walter Häntzschel of Dresden, Drs. F. Broili and E. Dacqué of München, Dr. Eugène Dubois of Haarlem, Dr. Chas. W. Gilmore of the U. S. National Museum, Drs. B. F. Howell and J. B. Knight of Princeton University, Dr. Barnum Brown of the American Museum of Natural History, and Dr. C. O. Dunbar of Yale University. I am grateful to all of these colleagues for their cooperation and to Dr. Walter H. Bucher of the University of Cincinnati for much friendly advice.

THE TRAILS.

Micrichnus scotti was described by Abel in 1926, and discussed somewhat more fully by him, in 1935, in his "Vorzeitliche Lebensspuren." His material was collected from a quarry on the Princeton University Campus in the Stockton group of the Newark series (Upper Triassic). This remains the only known occurrence of the trails. *Artiodactylus sinclairi* was described by Abel at the same time, from the same locality, but from much less material. The descriptions which follow are based on Abel's originals and especially on his fine illustrations, with augmentation from extensive collections loaned me for study by the colleagues mentioned above. It appears after wide search that virtually the entire American collection of these Triassic trails is before me as I write. I understand that the original quarry has become overgrown and at the present time new materials can be recovered only by extensive excavations.

Abel was impressed by the similarity in appearance between these trails of the red sandstone and the well-known *Kouphichnium* of the Solnhofen Plattenkalke of Bavaria, which have always been hitherto thought of as vertebrate trails. On the basis of this similarity he thought that the Triassic trails were unquestionably made by vertebrates also. He was inclined toward the idea that they might be the spoor of an incipient bird, but always kept his mind open to the possibility that they might have been made by a dinosaur of rather unusual design, or even by some unknown vertebrate. He recognized in evaluating the Triassic trails nearly all of the difficulties involved in the customary interpretations of the Jurassic trails.

As Abel mentioned, and as can be observed in slabs from the quarry, the trails occur on several laminae of one horizon consisting of thin-bedded and moderately fine-grained red sandstone of the usual Newark type. The sandstone tends to break into thin flags and occasionally has thin shale partings. No trails have been observed in the shale. No information is available at present on the total thickness of the track zone in the quarry, but that more than one layer is represented is clear from the material at hand. It is unfortunate that the grain of the track-bearing sediment is a little too coarse for optimum recording of the details of the trails, although the composite picture leaves little to be desired. On several of the laminae the trails are extremely abundant, and at first sight seem to criss-cross the surfaces in all directions. On one slab approximately 12 inches by 14 inches seven trails are seen. It is regrettable that no records have been kept of orientation of any of the slabs *in situ* or of the trends of the trails at the various laminae *in situ*. When one determines the direction in which the organisms moved on slabs showing these multiple records a general uniformity of direction of the trails on any one slab is clear. In the case of vertebrates such a record might be of relatively little significance, but any evidence pointing to the seasonal recurrence of the trails and constancy of general trend become important factors when dealing with limuloid ichnology. Shore trails of the Xiphosura seem under ordinary circumstances to be made chiefly during the shoreward migration for spawning, and barring untoward circumstances, reflect by their constancy of trend the pressing urge of the adult organisms. Most of the track-bearing laminae show evidences of wave rippling. No other types of fossils have been observed on the track slabs.

None of the trails which have thus far been described shows a natural beginning or end. All appear to be relatively long trails made by organisms walking on moist, muddy sand which only just previously had been beneath the water. This statement can be made on the basis of comparisons with experimental trails made by our existing *Limulus polyphemus* in the laboratory at Cincinnati. They suggest stranding at turn of tide. If this proves to be the circumstance under which they were made, then the direction of the trails probably reflects the general consensus as to the direction of the retreating water. Whatever the setting, no evidence is at hand as yet that any of the animals died while making tracks. Nor is there any evidence that any of them endeavored to burrow for moisture or protection after the manner of horseshoe crabs stranded nowadays. Obviously the environmental picture is incomplete.

The longest trail which I have seen is slightly over 15 inches long and about 2.5 inches wide. In this trail 13 steps or hitches are indicated. The width of the trails varies considerably; the widest seen is 2.75 inches wide, but the average is a little less than 2 inches in width, with some trails less than an inch wide. Not enough trails are now available to make a statistical study of their dimensions possible. The suggestion is offered, however, that seemingly there are two maxima and a wide variety of smaller sized trails. This may be wishful thinking conditioned by the knowledge that in *Limulus* and *Paramphibius* trails such is the situation. In those trails the mature sexual dimorphism is reflected by the variations in trail dimension and the fact also that during the nuptial migrations the adults are accompanied by immature animals of all sizes. Abel concluded from his material, and rightly so far as his material showed, that the length of the hitch (jump) was usually subequal to the width of the trail. The material at hand, however, fails to support this conclusion. Most of the trails show much shorter hitches than Abel thought, and only exceptionally is the condition which he illustrated attained.

Few of the trails which I have seen show all of the track details, but from a comparative study three essential parts of a complete trail are certain. A median tail groove, and simple paired footprints of varying number which were formed in alternation with small digitate impressions are the fundamentals. Some trails show also lateral grooves parallel to the tail groove and just outside the footprints. All of these characters are subject to considerable variation and degree of omission in the trails.

Most of the Newark trails show signs of a median tail groove. I shall discuss the trails as a whole, without reference to *Micrichnus* or *Artiodactylus*, which I will show are synonymous. The tail groove of both trails may be either continuous or interrupted. In continuous trails the groove shows periodic waxing and waning of the depth of its incision and of its width. In subsurface laminae only the deeper portions of the tail groove are recorded, and many of the trails which seem to show a disjunct condition of the groove can be interpreted in this manner. Some of the surface trails, however, do show that the tail was only periodically dragged at one phase of each step, as judged by the relation of the drag marks to the position of the digitate footprints. In such trails the nature of the organ which made the grooves is best shown. The grooves begin and end evanescently in a long drawn out taper; in the middle of each marking the groove widens out considerably but is widest toward the front, and may actually be so truncated toward the front as to appear cuneiform. Usually a central bladelike furrow continues from the posterior end through the widest part of the drag-mark. Seemingly from this evidence the tail must have been a long, tapering organ with a sharp point which dragged in a bladelike manner through the trail when the body was being uplifted. On curves the tail was usually lifted, reoriented at a slight angle from its previous position, and reset on the surface, thus illustrating its rigid condition. Usually the tail groove shows the direction of movement by a slight piling up of the mud or sand in front of the tail each time it is on the surface. The absence of the tail groove in some trails leads one to suppose that the animal walked occasionally with the tail uplifted. Identical tail grooves, continuous or discontinuous, are made by Limuloids from the Devonian to the recent.

On either side of the median tail groove are the relatively regular impressions of the paired appendages of which evidence of five pairs is seemingly present in the trails, or else one pair was placed four times in the mud prior to the emplacement of the fifth pair! Not many trails show the impressions of all of the feet at one time. From the nature of the multiple footprints they are referred to as simple imprints and from the fact that they occasionally have the fifth pair superposed upon them it appears that they were made by one or four pairs of fore feet. The position of the simple imprints in the trail varies a great deal, but a few tracks show them in what appears to be their anatomical position in relation to the rest of the trail. Here the imprints occur in opposite pairs, the most forward set being nearest to the median line, and the rear set being relatively far from the median line, and in most cases constituting the lateral bounds of the trail. Such complete track records form anteriorly-directed chevrons of simple imprints. The actual tracks themselves vary fully as much as their pattern in the trail. Usually only one or two pairs of simple tracks are present, and these may be unequally developed on the two sides of the trail. This is especially true on curves. The usual condition of the simple footprints is mere dimples or tiny pricks in the surface. Sometimes they occur as elongate ovoid impressions, and commonly as elongate arcuate impressions. Occasionally the material at hand shows that these long imprints split toward the front. The feet were apparently terminally split or chelate. In many trails the simple feet are represented by long scratches only, and in some instances the scratches are double, reflecting the terminal bifidy. In other trails the simple prints are represented only by a cluster of pricks in the mud apparently made by the dancing movement of the ends of the split feet. Abel saw on his material only evidence for a single pair of dimple-like impressions in alternation with the digitate imprints. He thought of them as the impressions of the middle finger of dangling fore feet used in a crutchlike manner similar to that described for the Jurassic *Kouphichnium.* Probably had he noted several pairs of impressions he would have postulated exploratory placement of the forefeet each time before a hitch (jump) was made after the manner which he (1935), Wilfarth (1937), and others, postulated for the *Kouphichnium* vertebrate. As a matter of fact, here again, the pattern and details observed in the Triassic trails so closely conform to the ichnology of the endognaths of the limuloids that other comparisons now seem fatuous. Some of the comparable variations of such tracks are shown in the *Paramphibius* paper.

The digitate impressions which alternate with, and are occasionally superposed upon, the simple impressions are the chief basis, of course, for the trails having been thought of as vertebrate. These prints do resemble rather amazingly the tracks of small vertebrates. The digitate impressions are usually most deeply impressed of all the track structures, and in many trails are all that remains of the spoor. From the depth of their impression it would appear that they at their phase of the stride bore nearly the entire weight of the animal whereas the weight was distributed over several pairs of simple feet at the next phase of the stride. In straight-away trails the digitate imprints are opposite one another, lending support thereby to Abel's idea of a jumping creature. On turns, however, the outer foot tends to assume a more forward position, thus giving a staggered trail. The length of the stride (hitch or jump) in these trails is judged as the distance between two consecutive imprints of a digitate foot. In a trail 15 inches long and on the average 2.5 inches wide the width of the stride is rather constantly just under an inch. This proportion appears to be average for the essentially straight trails. A complete digitate impression is made up of three elements: an anteriorly radiating semicircle of four elongate-ovoid toelike impressions, behind which is a long, narrow impression, somewhat longer than any of the radiating imprints, and at the opposite end of which are the imprints of two short, mutually movable structures. The entire digitate impression is usually just about equal to the longest simple impression of the same trail. The digitate tracks vary in their position in the trail nearly as much as the simple ones, but are usually directed with the radiating toelike marks forward or anteromesiad. This means that they are usually at an angle to the trend of the individual simple prints. In the same trail, and from trail to trail the details of the digitate impressions can be seen to vary a great deal. None of the original material studied apparently showed the details well enough to make a synthesis possible. Much of the present collection is of the same calibre, but fortunately a few slabs are exceptionally well preserved and from them it has been possible to derive with certainty the details of these impressions, already presented. As was brought out in the *Paramphibius* paper, digitate impressions showing these features must have been made by a xiphosuran. So far as known these are the only many-footed organisms having a pair of digitate feet. *Limulus* and the limuloids have been thus endowed from the very beginning of their geological record, apparently. In these animals, behind the chelicera and the four pairs of walking legs, or endognaths, the sixth pair of appendages, the ectognaths, are modified into pushing organs. The presence of these pushers has been known for a long time by zoölogists, but ichnologists and vertebrate paleontologists have usually overlooked them in searching out the makers of digitate trails. Most ichnological work on heteropodous trails has been done in Europe where the living *Limulus* is a stranger. This is undoubtedly the principal reason for the oversight. Figs. 2 and 3 in Caster, 1938, show details of the pushing apparatus of *Limulus*.

The toelike impressions of digitate tracks of the sort seen in the Newark beds were presumably made by the expanded blades of the flabellum of the pusher. This is a circlet of concave, lanceolate blades which are attached to the dorsal surface of the penult segment (propodos) of the ectognath. In repose the blades overhang and snugly hug the terminal segment (the dactylus). The blades are so articulated with the propodos and dactylus that when the latter is underbent and pressed, dorsal surface down, in the mud, the flabellum opens fanwise and upward. In racial youth and more recent individual juvenescence the expanded blades make nearly 180 degrees with the underbent dactylus, and could at best be thought of as possibly serving a snowshoe-like supporting function. In later ontogenetic and phylogenetic stages the articulation is less extensive, and the blades make more nearly 90 degrees with the underbent dactylus. In this condition the ectognath is a very effective pushing apparatus, for now the blades of the flabellum are inserted in a spadelike manner nearly vertically in the mud and serve effectively to propel the animal. Obviously, the flabellar impression made at various phylogenetic stages of the limuloids or at various growth stages of an individual species will differ greatly. Truth is, that they resemble each other so little that trails of the two stages have usually been not only attributed to quite different vertebrates, but have been studied in opposite orientation.

Before turning to these differences, it should be noted that the so-called imprint of the sole of the foot in those trails showing the radial toelike impressions is made by the dorsal surface of the dactylus segment. In some trails the imprints of the two mutually movable spines at the end of the dactylus are shown, although they have ordinarily been overlooked in such trails, and are often not present. The spines more often leave their imprints in mature trails than immature, and in such trails have been the basis for a great deal of curious speculation, e.g. the "split toe" problem which is discussed by Abel and others.

We have seen that in older limuloids (*Paramphibius* for example) and in immature ones of more recent times the impressions of the pushers ordinarily show the flat imprints of the four (or five) flabellar blades, pressed with the concave side down in the mud. When the dactylus print is clearly shown this track simulates the footprint of a small reptile or amphibian. Trails of this stage of development are usually properly oriented, since the blade-prints are oriented in the same manner as toe-prints. When, however, the next stage is reached, the spadelike use of the adult flabellum leaves quite another type of track. Now the circlet of essentially vertical blades is pressed downward into the mud and a semicircular incision or gouge results. The termini of the semicircle lie well back along the imprint of the dactylus, and the illusion of a three-toed footprint is nearly perfect, the blades of the flabellum making the lateral toes, and the dactylus the middle toe. When the terminal spines leave their imprint at the end of the dactylus, the problem of a split or median toe arises. The place where the mud is disturbed by the removal of the flabellum, if not extensive, becomes the sole of the foot, and if a rather extensive dragmark is made, becomes the print of a "posterior toe" or "hallux." The illusion is so complete that it is not surprising at all that birds or dinosaurs have always been conjured up to explain such adult limuloid trails. Clearly, the tracks thus interpreted are oriented in reverse of their actual condition of making. In the Jurassic of Bavaria most of the limuloid trails are of this type, and have been consistently misoriented, and, unless accompanied by a *Limulus* cadaver, misinterpreted. In the Triassic trails before us, on the other hand, not many of the trails show the trifid condition very clearly. The average condition is approximately intermediate between the planate, juvenescent, condition seen in virtually all of the Devonian trails of *Paramphibius* and the right-angled, adult, condition seen commonly in Jurassic trails of *Kouphichnium* (*Limulus walchi*) and recent trails of *Limulus polyphemus*. Abel noted the two trends of the Newark trails, and being somewhat conditioned by his knowledge of the more advanced but comparable trails of *Kouphichnium* of the Jurassic, proposed for them the form-genera *Micrichnus* and *Artiodactylus*. There is a curious conflict of ideas and data in Abel's original description of them.

Micrichnus was thought of as being much like *Kouphichnium*, and therefore was consistently oriented in reverse for a limuloid. Abel was uncertain if there were three or four toes, but noted that the middle of the forward three at any rate was commonly split. He thought there was only one pair of dimple-like impressions of forefeet in alternation with the three or four-toed hind foot. *Artiodactylus* was clearly a more uncertain trail. He thought of it as having four toes all of which were forwardly directed, and apparently sans heel or rear toe, and in the only specimen illustrated, in spite of the name, shows no split toe. This trail Abel properly oriented, since the four toes he thought he saw correspond to the pusher blades. Even a casual examination of Abel's original figures shows a strange paradox. The trails which are commonest in the Princeton quarry he illustrates as *Micrichnus*, but most of his figures show clearly the planate imprints of the flabellar blades, and should by definition be assigned to his *Artiodactylus*. Furthermore, it is only on these *Micrichnus* trails that the so-called split median toe shows. The specimen illustrated as *Artiodactylus* on the other hand shows an adult flabellar impression, made clearly by an organ which opened only about 90 degrees, yet was so placed that in pushing backwards the four blades left their impression very clearly. Under normal conditions of locomotion this organism would have made most convincing trifid impressions of the sort postulated for *Micrichnus*.

This conflict of ideas and materials can be seen if one examines the illustrations of *Micrichnus* and *Artiodactylus* in Abel's Vorzeitliche Lebensspuren (1935), Figs. 109-113. All of the slabs here shown which are attributed to *Micrichnus scotti* are found to be oriented in reverse when analysed from the limuloid angle. In all of the figures the animal making the tracks walked down the page rather than up as the discussion and orientation would imply. In Fig. 109 the chief trail was made by an immature individual which implanted the flabellar blades nearly flatly at nearly 180 degrees from the underbent dactylus. This would fit the general scheme imagined for the *Artiodactylus* prints. The slab in Fig. 110 is one of the really rare examples in the Triassic material of the adult type of trail such as were made by *Limulus walchi* of the Jurassic under the name of *Kouphichnium* or by modern horseshoe crabs. The flabellar blades were impressed nearly vertically, and at essentially a right angle to the underbent dactylus. This creates a trifid trail, but under very similar circumstances the same animal could have made a trail like that illustrated in Fig. 113 as *Artiodactylus*. On the crest of the middle ripple of the slab in Fig. 110 an illusion of a footprint with several toes is created by the superposition of the digitate imprint of the main trail on a track from an earlier trail. When Fig. 111 is reoriented it shows the presence of at least two pairs of simple feet, the imprints of which are not particularly regularly distributed. Fig. 112 is an unusual trail, of which I have seen only one other example in the Triassic material. The elongate lateral imprints which Abel thought of as possible hand impressions, are precisely similar to the lateral grooves made by modern *Limulus* (and *Paramphibius* too) when the front part of the cephalothorax is uplifted while the simple feet are being placed in a forward position, and then held tilted aloft while the pushers force the body forward. If the head has not been elevated enough posteriorly the postlateral ("genal") spines drag in the mud. Such lateral drag-marks are largely accidental, but are quite unmistakable. These gouges show very clearly the direction in which the animal was moving. The trail in Fig. 113 which is referred to *Artiodactylus* is properly oriented, as was pointed out above, where its paradoxical qualities were mentioned. The condition of growth of the foot that made this track comes much closer to the condition necessary to make a typical *Micrichnus* trail, as typified by Fig. 110, than most of the feet which made the trails assigned to *Micrichnus* by its describer.

On the basis of this reinterpretation it would appear that *Micrichnus scotti* Abel and *Artiodactylus sinclairi* Abel were made by the same organism. Certainly the two types of trails are thoroughly gradational. All of the ichnological data of both trails conforms so perfectly to the xiphosuran pattern that it seems profitless, without some striking primary evidence in support, to pursue the hypothesis that the trails were made by a vertebrate of any sort. The name *Micrichnus scotti* for the Newark trails seems quite satisfactory, since no other limuloid trails thus far described are precisely of their stamp. The real quest from now on should be for further evidence of the Xiphosura in these red beds.

The environmental evidence is a militant factor against the present interpretation of the trails. The usual palecology of the Newark series would leave little place for marine, or essentially marine limuloids to make trails. Fortunately for the present interpretation, Bryant, 1934, described what appear to be marine coelacanth and elasmobranch fishes from the Lockatong formation of the Newark series in the Norristown region of Pennsylvania. While the fish horizon is distinct from the one in which we are concerned, it does open up very forcefully the possibility of estuarine conditions in some parts of Pennsylvania and New Jersey during Upper Triassic times. This does not necessarily mean that these regions must have been immediately adjacent to the sea, but certainly there must have been brackish connection through Appalachia. Elasmobranchs and limuloids will venture into only slightly brackish or even fresh water on occasion. During the nuptial migration at the present time *Limulus* ventures with no hesitancy into brackish water, and will live for a considerable time in entirely fresh water*. The evidence points to this mode of existence as very old for the group.

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* During the spring of 1939 an adult *Limulus polyphemus* was shipped in a wet moss packing from Florida to the Cincinnati Museum of Natural History. Mr. Ralph Dury, Director of the Museum, reports that the crab lived there for over three weeks in a fresh water aquarium, and was finally killed and preserved before showing any deleterious effects from the fresh water.

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