Caster 1944.
Limuloid trails in upper Triassic of Arizona.

COMPLIMENTS OF THE WRITER

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LIMULOID TRAILS FROM THE UPPER TRIASSIC (CHINLE) OF THE PETRIFIED FOREST NATIONAL MONUMENT, ARIZONA.

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ABSTRACT. The Newspaper Rock ("Pictograph") sandstone (Chinle: Upper Triassic) of the Petrified Forest National Monument, Arizona, yields a new type of limuloid trail (*Kouphichnium arizonae* Caster, new form) which is interesting for the perfection of the xiphosurous track detail; for exhibiting in the holotype trail two variations of the ectognath imprint, either of which in the past would have been the basis for correlating the trail with a bipedal vertebrate; and finally, for establishing quite certainly the direction in which the track-maker progressed,—a matter of previous divergent opinion. The presence of the Xiphosura in the Chinle poses ecologic problems not hitherto considered in evaluating these purportedly wholly continental deposits.

INTRODUCTION.

HETEROPOD trails are known from the record of nearly half a billion years (Cambrian to Recent), and are troublesome Problematica always. In recent years we have grown sufficiently familiar with the ichnology of existing organisms somewhat more satisfactorily to tackle the solution. The new Upper Triassic trails herein described are important evidence for the xiphosuran interpretation of one type of very ancient heteropod trail. These spoor are at the same time a synthesis of three kinds of track evidence, each of which in other years would probably have been evaluated as attributable to the Vertebrata. In fact, the new trails had been informally identified in this manner when first seen by the writer.

Mr. Howard Stagner, Park Naturalist (1939) at the Petrified Forest National Monument, called our attention to the trails on exhibition with Triassic vertebrate material in the Monument Museum. Through Mr. Stagner's kindness and coöperation, permission was secured from the National Park Service to borrow the trails for study in Cincinnati. He also generously provided stratigraphic data and searched with some success for additional materials. Stagner's description of the stratigraphy of the Newspaper Rock sandstone appears under his name in Daugherty's (1941) monograph on the Upper Triassic Flora of Arizona.

HETEROPOD TRAILS.

In order to present the clarifying data to be gleaned from the new Triassic trails, it seems advisable first briefly to summarize our knowledge of this general type of trail. Although formerly assigned to vertebrates, in the last few years trails such as this have been more successfully correlated with king crabs. The belated solution of the Problematica is due to the great variability of limulid trails, on the one hand, and general ignorance of their ichnology, on the other. Probably no organisms capable of making a trail of more than one kind of footprints, makes more mutable and misleading records than the Limulida. Their perplexing register goes back to early Paleozoic times, and out of it has grown a truly amazing lore.

In those few instances where limulid cadavers occur in the same beds as the trails, (*e.g.*, the remains of *Protolimulus* Williams (1885) and Packard's (1900) *Merostomichnites* trails occur together in the Upper Devonian of the Penn-York Embayment), or at the end of a "death-march" after the manner of the common occurrence of *Limulus walchi* in the Solnhofen Jurassic (Walther, 1904), the spoor have been, almost inescapably, rightly correlated. But, curiously, because such trails were accepted as limulid on the *prima facie* evidence of association, they were seldom, if ever, until recently, closely analyzed. Consequently, a surprising number of trails virtually identical to those associated with remains, but without direct carcass connection, have been interpreted, on the basis of first impression, and often with great pains and ingenuity, as vestiges of vertebrates.

Briefly to pursue this curious oversight with a few examples,—we find thousands of tracks and trails in the Solnhofen Plattenkalke all showing the same details as those which lead to dead crabs; yet, for three-quarters of a century these have been known under the name *Kouphichnium* (Oppel, 1862) and in all that time on only one occasion has a single specimen of the trails been correlated with the crab that made it (Abel, 1935). Even this trail, which preserves the very outline of the carapace, was relegated for half a century to the vertebrates! *Kouphichnium* has through the years been attributed by a long list of most eminent paleontologists to pterodactyls, bipedal dinosaurs, ancient birds and jumping mammals. Jaekel (1929) divided the Solnhofen spoor into four groupings, all of which he thought were made either by *Archaeopteryx* and *Archaeornis* or by three still more ancient and otherwise unknown "Urvogel". The *Limulus* features of these trails are so patent, when once those feature are understood, that it was really a very simple matter to make the necessary comparisons for establishing their relationship with the ubiquitous *Limulus walchi* of the Solnhofen deposits. It is more understandable that certain other limuloid trails, which occur in strata devoid of crab remains thus far, were at first misconstrued as evidence of tetrapods. The Upper Devonian trails in the Catskill beds of Pennsylvania, which Willard (1935) described as *Paramphibius*, are of this ilk. The hypothetical track-maker of the Devonian made a rather plausible bridge between the fishes and the amphibians ("Ichthyopoda") until the merostome possibilities of its spoor were investigated. The Triassic trails from New Jersey which Abel (1926, 1935) called *Micrichnus* and *Artiodactylus*, perfectly typical limulid trails though they are, still offer fewer ecological difficulties when interpreted as birds, dinosaurs or split-clawed mammals, than they do as what they are.

The principal reason for the error in evaluating limulid trails is the curious toed aspect of the imprints made by the fifth pair of walking legs (ectognaths). The basic plan of *Limulus* ichnology has been generalized in a previous paper by the writer (1938, Fig. 5). In essence, the walking-trail comprises forwardly-directed chevrons of round holes or bifid imprints or scratches made by the anterior three or four pairs of simple supporting feet (endognaths). The endognathic chevrons are in alternation with the imprints of the fifth pair of feet (ectognaths) which are modified by four or five movable blades at the termination of the antepenult segment for the function of pushing the animal forward. See Text Fig. 1. Since the anterior four pairs of feet act more or less as a unit in alternation with the pushers, a sort of tetrapodal gait is achieved by the limulids, and heteropody characterizes the trail.

The pusher has undergone minor evolutionary changes since it first appeared in the middle Paleozoic; there is also considerable ontogenetic modification of the organ which correlates rather well with the paleontologic changes (see Caster, 1938, Fig. 4). In addition to these biogenetic possibilities of variation, there is considerable variation in employment of the device at all stages. No matter what the variant, its track most strik-

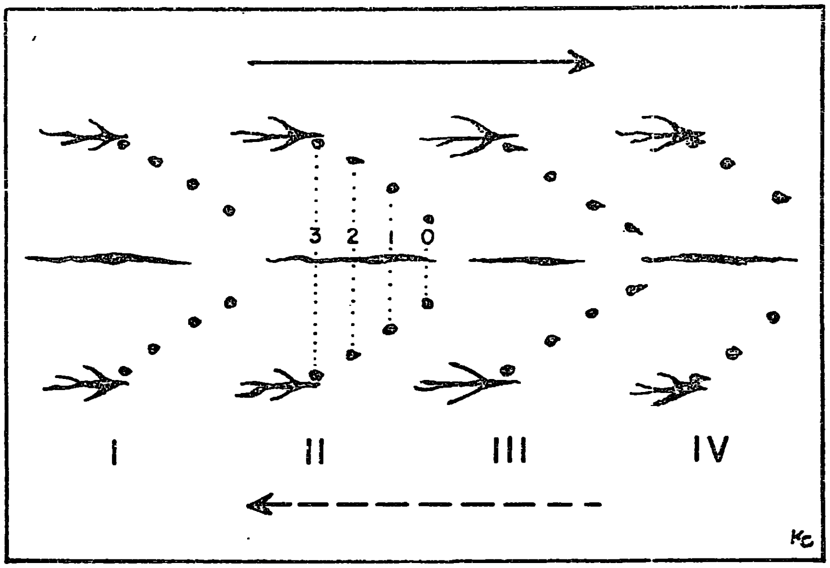

Fig. 1. Diagram of an adult *Limulus* trail. This illustrates the contrast between reality and the vertebrate hypothesis[1] usually offered to account for such spoor. Solid arrow points the direction in which the crab walked; dash-line arrow shows the orientation necessary for the vertebrate interpretation. I-IV, successive steps or hitches of the king crab; 0-3, imprints of the four anterior pairs of simple feet (endognaths); the first pair (0) are seldom recorded; 4, tracks of the fifth pair of feet (ectognaths) or pushers. Figure 2 demonstrates the variations in ectognathic function and tracks. An analysis of *Limulus* locomotion is given as Fig. 5 in the writer's 1938 paper.

[1] In contrast to the limulid analysis of such a trail, we have the various vertebrate theories, all of which are perhaps epitomized by that of Wilfarth (1937). He accounted for the very similar *Kouphichnium* trail in the Solnhofen Jurassic as follows: first, after a careful survey of vertebrate possibilities, he "imported" the American bipedal dinosaur, *Ornitholestes*, the only vertebrate known to him, as he said, precisely capable of making the trail. He imagined that the little dinosaur hobbled along by "trial and error"; sitting on its haunches at track III, it reached forward to position *1* with its short dangling fore-feet and pressed its longest digits in the mud; this was apparently not far enough; it then lifted its arms, and spreading them a little further apart, implanted them further forward at position *2*; still not far enough; for a third time, it reached forward, with wider spreading arms, to implant its middle digits at station *3*; only after this preliminary exploration did the dinosaur move forward by the wholly ingenuous device of using its implanted fore-feet and longest fingers in the manner of "crutches" by which to swing its hind-feet "through its arm-pits," thus to stand at last at the new position II; whereupon, the "trial and error" skirmish was renewed before the next "jump" was made!

ingly simulates the hind-foot print of a vertebrate. Some of the best-known variations in the flabellar (pusher) imprint are shown, together with their mode of origin, in Text Fig. 2. As

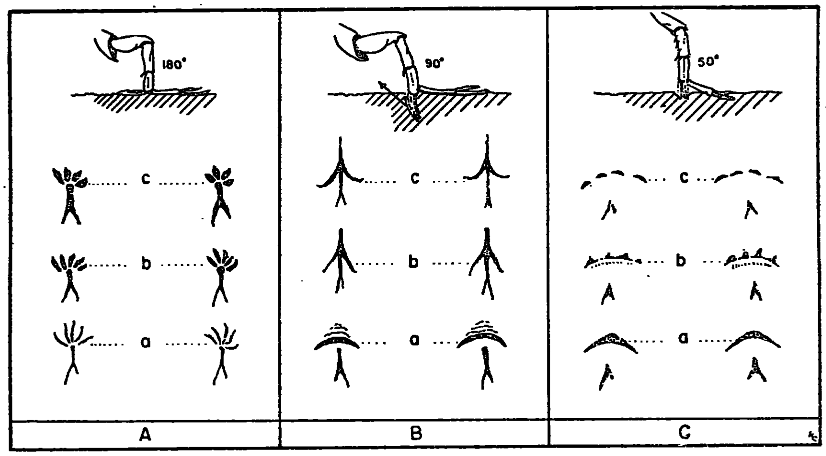

Fig. 2. Vertebrate-like tracks made by the pusher (flabellum) of the Xiphosura. In all examples the crabs walked up the page. A. Immature and ancestral Xiphosura; tracks made by a flatly impressed five-bladed flabellum which was fully expanded; the fan makes an 180° with the underbent ectognath segments; *a*, *Paramphibius* condition in the Upper Devonian; first interpreted as a fish-amphibian ("Ichthyopod"); *b*, four or five-bladed pusher, likewise flatly imprinted; Permian tracks of this type have been interpreted as the earliest bird tracks, and the rather similar *Artiodactylus* of the Triassic was interpreted as either mammal or reptile; *c*, immature flabellar imprint of a modern king crab; very similar to certain aspects of *Kouphichnium* of the Jurassic. B. Variations in the adult imprints of the limulid flabellum, the pusher being in these examples completely inserted in the mud during the forward push; the blades make an angle of only 90°, or a little less, with the distal ectognath segments. *a*, vertically inserted blades; distal segments flat on the ground; some forward drag and distortion of the bottom upon withdrawal of the blades preparatory to the next step; *Micrichnus* from the Triassic and variations of *Kouphichnium* in the Jurassic are of this type; both were formerly interpreted as vertebrate spoor; this type of track is commonly seen on modern beaches and very well shown in *Micrichnus paleocenus* Russell (1940) from the Paskapoo Paleocene of Alberta; *b*, similarly inserted blade, but the semicircle of blades becoming forwardly concave to form a chevron-shape insertion; considerable forward gouge formed at time of withdrawal; described as reptile and bird tracks from the Triassic and Jurassic; correctly identified in the Paleocene; *c*, still greater flexibility of the arc of the pusher to form chevrons of inverted quarter-circles; common today; described as ancient bird tracks (*Ornichnites* and *Protornis*) in the Solnhofen Jurassic. This is the flabellar condition to be seen on the left side of the holotype of the new Triassic trail. C. Incomplete semicircular imprints of flabellum; variants of B, *a*; blades make less than 90° angle

the legend of this figure indicates, many of these flabellar mutations have been the basis for form-genera and species. Since in most instances the ichnological categories correlate with morphologic differences of the known or unknown track-maker, they are in a sense justified, and are often very useful. The flabellum originally contained five blades, but there has been a recurring tendency to lose one, thus changing the aspect from an asymmetrical semicircle, to a bipartite arrangement of parts. The angle made by the blades and the underbent terminal segments of the pushing leg decreases both paleontologically and ontogenetically; the amount of lateral or fanwise spread of the blades is another variable matter.

Certain of the flabellar imprints create a tetrapod illusion when oriented in the limulid manner, as seen in Text Fig. 2, A and C, whilst others have such an aspect only when viewed in a contrary manner, as for example, Text Fig. 2, B. Since any adult *Limulus* or limulid can make both sorts of tracks at will, possibly with certain ecologic contingencies as determinants, and since these tracks are so very different in appearance, it is not surprising to find two form-genera of supposedly vertebrate ichnites in several of the limulid track localities. Text Fig. 2 illustrates many of these features and cites examples.

In the holotype slab of the new trail from the Arizona Triassic, we find the interesting association of both types of trails in a single record. The right and left sides of this trail, if not associated as we see them here, would have been almost certainly assigned in former times to two different form-genera and species of vertebrate. Furthermore, the two genera would have been imagined to have walked in opposite directions. In other words, according to the seventy-five-year-old ichnological custom, the right side of the trail would have been viewed as made by an animal walking up Plate 1, whereas the left side

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with underbent terminal segments and are incompletely inserted so as to make a disjunct track; *a*, common condition today in rather soft mud; *b*, broadly expanded blades; after insertion the backward push distorts the mud so as to simulate a sole-print of a vertebrate; terminal spine prints often obscure in this type of track; such tracks have been interpreted as mammalian; this is the condition to be seen on the right side of the new Triassic trail, plate 1; *c*, "tip-toe" track made by the vertically imbedded blades and the tip of ectognath; a somewhat rarer modern track; also known from the Newark Series and the Solnhofen beds.

corresponds to a hypothetical animal walking down the page! By the accident of uniting both sorts of perfectly normal adult *Limulus* tracks in one trail this holotype becomes a sort of minor "Rosetta stone" in heteropod ichnology. There is no question of the limulid origin of the new trail, and it differs only in minor features from the famous *Kouphichnium* trails of *Limulus walchi* in the Jurassic. Those minor features seem adequate, in view of the years separating the records, to warrant a separate specific name for the Arizona trail.

Kouphichnium arizonae Caster, new form.

Plate 1

All details of this new trail are to be seen on the original and best (holotype) example of the spoor which is illustrated on Plate 1. This specimen is on exhibition in the Museum of the Petrified Forest National Monument, near Holbrook, Arizona. A rubber mold of the holotype slab is in the University of Cincinnati type collection (No. 24300), and plaster molds will be gladly furnished those who are interested.

The type sandstone trail shows on either side of a nearly continuous middle groove (telson drag-mark) six serial imprints of three pairs of endognathic limulid feet and five serial repetitions of the ectognathic pushers. The average width of the trail is 65 mm. and of the endognathic portion only, about 35 mm. The braces of tracks are about 35 mm. apart. The endognath imprints apparently correspond to tracks 1-3 of Text. Fig. 1; the ectognathic ones correspond to No. 4 in that figure. At the place marked "g" on the photograph, a single

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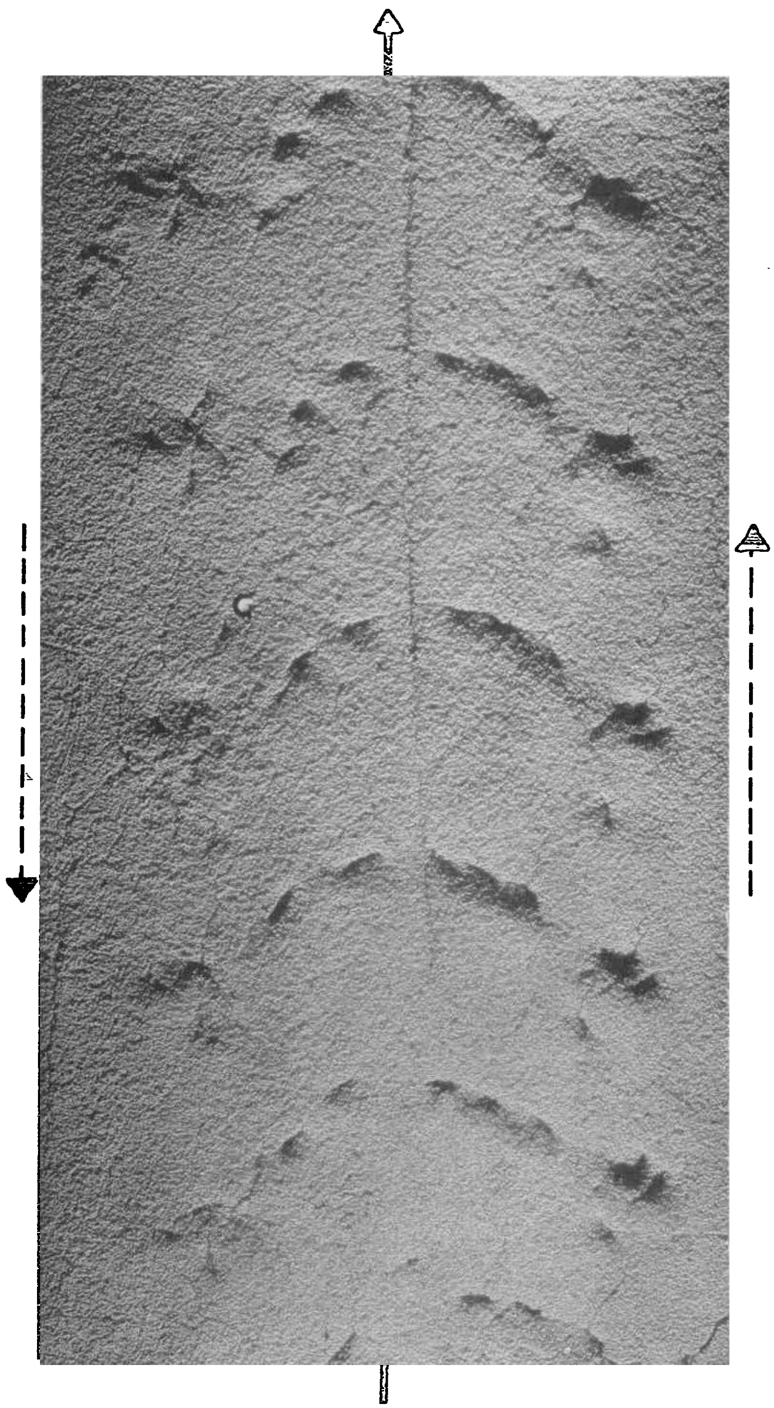
Plate 1

Kouphichnium arizonae **Caster, new form. A *Limulus* trail from the Upper Triassic of Arizona: Newspaper rock ("Pictograph") sandstone member of the Chinle terrane. This holotype slab came from the Blue Forest area of the Petrified Forest National Monument, near Holbrook, Arizona. Type specimen in the Petrified Forest Museum. × 1.**

Compare with the track diagram given as Text Figs. 1 and 2; as will be seen, the crab walked up the page, as indicated by the central solid arrow; the dash-line arrows indicate directions in which the hypothetical vertebrates have been assumed to walk in order to account for tracks such as seen on either the left or right side of the trail. The crab apparently careened to the left while walking diagonally up a sloping sand surface. *G* indicates a gouge made by the left cephalic spine during the precarious climb up the slope.



gouge mark is shown; this apparently corresponds to the occasional mark left by the genal-spines of modern *Limulus*. (See Caster, 1938). The chevrons of simple tracks are unusual in being mere slits, rather than the usual oval or bifid ectognath imprints. This apparently reflects backward and lateral pushing or scratching with the simple feet and may correlate with the strenuous work of walking up a sloping beach. By forcing horseshoe crabs to walk up a sloping mud surface, somewhat comparable trails have been made experimentally. None of the Triassic trails show the bifid nature of the endognaths, but this is not unusual.

As we have already anticipated, the pusher tracks of the holotype slab are unique in their asymmetry. The tracks on the left side are normal for an adult walking crab. The condition is that shown diagrammatically in Text Fig. 2 *B, c*. The ones on the right are ordinarily made by a half-walking, half-swimming crab, since they are what might be termed "tiptoe" tracks which record only part of the flabellar anatomy. In this case the animal was apparently having a difficult passage up the sloping wet sand beach, and apparently proceeded careening toward the left side, thus to leave the occasional record of its left cheek-spine, and always barely able to keep its right pusher functioning. The strand-line probably was parallel to a diagonal from the upper left to the lower right of the picture; the slope to the lower left.

If the trail were symmetrical, with either type of pusher track duplicated to the exclusion of the other, the result would be very much like the Jurassic *Kouphichnium*. In the new trail the chevons of simple imprints are much more obtuse than in the Jurassic ichnite. The "jump" of the Triassic crab is slightly greater than in the Jurassic one, and the flabellar legs were apparently somewhat longer, for the pusher tracks are not superimposed upon the simple chevrons as they usually are in the Jurassic. It is doubtful if more than three of the Jurassic simple feet ever left their imprint, whereas here we see the regular record of four. Of the various mutations of the Solnhofen trail, those termed *Ornichnites caudatum* by Jaekel (1929) show ectognath records most similar to the left side of the present one. Somewhat similar trails have been described by Russell (1940) from the Paskapoo Paleocene of Alberta under the name *Micrichnus paleocenus*, and recognized as limulid trails. Russell was wisely reluctant to propose a new form-genus for his ichnites, and consequently referred them to Abel's Triassic form-genus, apparently not knowing of the true nature of the much more similar Jurassic *Kouphichnium*, to which the trails could with greater felicity be referred. The points of difference between the new Triassic trails and those from the Paskapoo are in details of the flabellar print, as can be seen by reference to Text Fig. 2 B, *a*, and the sparsity of endognathic imprints in the Paleocene trails. Most of the few simple imprints recorded show the bifid nature of the feet. Probably there was really very little change in the foot plan of the Limulids from Chinle to Paskapoo time, although there were undoubtedly carapace changes of specific importance; however, those characters are yet to be discovered in both terranes.

The only Triassic trails known to be limulid are those previously mentioned in the Newark series of New Jersey, of approximately the same age as the new ones. Both the *Micrichnus* and *Artiodactylus* forms of the Newark trails are much smaller and apparently reflect smaller adult crabs. They bear fewer simple imprints in alternation with the flabellar prints, and frequently show the terminal spines of the simple feet. The nature of the flabellar prints of the Newark crabs is shown in Fig. 2. We seem to be dealing with clues to two distinct species of limulid in the North American Trias. Both need to be verified by actual remains.

Occurrence.—According to data supplied by Mr. Howard Stagner, the new trails occur only in the "Pictograph" (Newspaper Rock, Stagner, 1941) sandstone member of the Upper Triassic, Chinle terrane, in the Blue Forest area of the Petrified Forest National Monument, near Holbrook, Arizona. This is in Sec. 22, T. 18 N., R. 24 E. of the Petrified Forest topographic quadrangle map. The sandstone interfingers with the shale from which Daugherty (1941) secured most of the excellent leaf imprints for his monograph. The sandstone is somewhat cross-bedded, and the tracks apparently occur on sloping foresets. Other tracks, none of which are comparable, and some of which are apparently of vertebrate origin, occur in the Newspaper Rock layer.

The Triassic setting of the Chinle sandstone terrane appears to have been formed on a plains area not far removed from the Triassic embayment of the sea. The flora described by Daugherty (1941) and the vertebrates described by Camp (1930) seemingly indicate the same general setting which Camp described as follows: "The Chinle was presumably deposited on a great low-lying floodplain near the seacoast, traversed by slow-moving streams subject to occasional overflows and freshets, and interspersed with large swampy areas and shallow lakes with scattered stands of conifers on the higher ground." With this picture of a low-lying coastal plain it is not difficult to think of the track-layers as a strand deposit on a dissected coast, perhaps merely a deposit formed in a deep embayment, or possibly during a temporary submergence of the coastal area. We need not even postulate wholly marine conditions, since crabs can live for long periods if subjected by urge or accident to brackish or even fresh water.[2]

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[2] There will be those who urge that this new record is added proof of the erstwhile fresh water invasion of certain members of the Limulida. Russell (1941) suggested this possibility to account for the limulid trails in the Paleocene Paskapoo some 800 miles from the nearest known occurrence of the marine Paleocene (Midway: Cannonball). The *Micrichnus* and *Artiodactylus* trails of the Newark terrane of New Jersey likewise occur in beds always judged to be wholly continental, intermontane deposits. Bucher (1940) was prone to consider favorably an argument posed by the writer (1940) that the "continent" of Appalachia may have been very tenuous in Upper Triassic times and that the deeper Atlantic estuaries may have penetrated the "intermontane" region thus opening the mud-flats to the nuptial conquest of limulids. It is unfortunate that our knowledge of Paleocene paleogeography is so meager as yet that we cannot in truth say how close the Paskapoo site really lay to the Midway embayment. There may be subsurface marine equivalents of the Paskapoo beds much nearer than the 800 miles cited by Russell to the nearest outcrop. The physiographic setting of the Paskapoo locale in Paleocene time was apparently in many respects similar to that of the Chinle of Arizona in the Upper Trias. It would seem premature, at this state of knowledge, to postulate, from uncertain ecological data alone, that any of the Limulida ever lived their course in a setting wherein never a single carcass has yet been found; their skeletal record is wholly marine.

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