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# ISOPOD AND LIMULID MARKS AND TRAILS IN TONGANOXIE SANDSTONE (UPPER PENNSYLVANIAN) OF KANSAS

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## ABSTRACT

Tracks and trails have not been described previously from Pennsylvanian rocks of Kansas, although they occur abundantly in almost every sandstone of this area examined by the author. Discovery of fossil animal remains of any kind in the Tonganoxie Sandstone Member is important because the paleoenvironment of this stratigraphic unit is not well understood. Tracks and trails found in considerable numbers in the basal part of the Tonganoxie Sandstone are here interpreted as being of isopod and limulid origin. Both arthropods are rare as fossils and not known from the Pennsylvanian of Kansas. No trails or tracks of other origin could be recognized. A comparison with Recent environments of limulids and isopods supports interpretation of the Tonganoxie Sandstone Member as probably estuarine in origin.

## INTRODUCTION

During the winter of 1965-66, when attending the University of Kansas, I had the opportunity to study the Pennsylvanian rocks in Kansas. On numerous excursions abundant and well-preserved trace fossils, mainly tracks and trails preserved in sandstones, were found. In many sandstones they are the only fossils seen. Surprisingly, no reports on their presence exist, although trace fossils often provide much paleoecologic information.

Trace fossils are tracks, trails, and burrows made by animals and preserved in sedimentary rocks. HÄNTZSCHEL (1962) included marks that are made by dead bodies in his definition of trace fossils. SEILACHER (1964) defined trace fossils as sedimentary structures resulting from biological activity. This excludes agglutinated tests, as well as marks left by dead bodies drifting or rolling over the ground.

Trace fossils are important for interpretation of paleoenvironments because they are always autochthonous. The origin of many tracks, trails, and burrows is hard to interpret, and resulting conclusions tend to be uncertain, and thus trace fossils never have been popular with paleontologists. Trace fossils occur in marine, lacustrine, and continental sedimentary rocks of all geological systems from Precambrian to Recent (HÄNTZSCHEL, 1962). A prerequisite for identification and interpretation of trace fossils is sufficient knowledge of Recent *"Lebensspuren"* of all biotopes.

Seilacher (1953, 1964) divided trace fossils into five ethological groups: dwelling burrows (Domichnia), feeding burrows (Fodichnia), feeding trails (Pascichnia), resting trails (Cubichnia), and crawling trails (Repichnia).

Representatives of only two groups are described in this paper, Repichnia and Cubichnia. According to Seilacher (1964), Repichnia (here called crawl trails) are trails or burrows left by vagile benthos during locomotion; Cubichnia are shallow rest marks left by vagile benthos hiding temporarily in the sediment, usually sand, and obtaining their food as scavengers or suspension feeders.

Trace fossils are deformations of the sediment or its bedding planes. Burrows may be preserved as hollows or fillings of hollows. Only part of the *"Lebensspuren"* are imprinted on the surface of the sediment. Surface tracks and trails are likely to be exposed to destruction by flooding or shifting of the topmost strata at the bottom of the sea, river, lake, or on land. Only a small fraction of them is preserved (Häntzschel, 1962).

## GEOLOGIC SETTING

The marks and trails described in this paper were found on 23 slabs of micaceous siltstone, each about 4 cm. thick, recovered from a shale pit 4 miles southwest of Ottawa, Franklin County, Kansas (NW¼ sec. 23, T. 17 S., R. 19 E.). The siltstone is part of the Tonganoxie Sandstone Member of the Stranger Formation, Douglas Group, Virgilian Stage of the Pennsylvanian System (Paper 18, Fig. 1). The Pennsylvanian of Kansas is well known for its excellent development of cyclothems each of which begins with continental sediments. The Tonganoxie Sandstone Member represents the basal part of such a cyclothem, the marine phase of which is represented by the Westphalia Limestone Member containing abundant fusulinids. The siltstone at the trace-fossil locality is underlain by the Ottawa coal, which also belongs to the Tonganoxie Sandstone Member. This very local coal lentil of probably autochthonous origin is quite thin and underlain by the Weston Shale Member.

The trails and tracks are preserved on the underside of siltstone as molds of markings that were made on the surface of thin clay laminae below. They occur in a sequence, 1 m. thick, of about 20 thin-bedded siltstone and claystone strata overlying the Ottawa coal. Each siltstone bed grades upward from coarser silt at the base to claystone above. The siltstone strata are cross-laminated, the laminae variable in thickness. Marks made by drifting and rolling dead material are present in appreciable numbers on the surface of the strata indicating presence of water currents (Pl. 1, Fig. 1). Ripples were seen on some of the siltstone layers. Above this sequence the siltstone is coarser grained and clay beds are absent.

The local Ottawa coal lentil, which can only be recognized in the vicinity of Ottawa, is defined as the base of the Tonganoxie Sandstone Member (Ball *et al.*, 1963). Siltstone was deposited rapidly on the coal swamp and tree trunks rooted in the Ottawa coal were buried in upright position

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### EXPLANATION OF PLATE 1

Drag marks and isopod trails on siltstone bedding planes in Tonganoxie Sandstone near Ottawa, Kansas.

FIGURE

*1.* Straight, curved, and parallel drag marks preserved in hyporelief on the underside of silty sandstone bed, providing evidence of strong current action, KUMIP no. 25125, ×0.9.

*2-6.* Isopod marks and trails.

*2.* Rest marks with well-preserved leg impressions, at anterior end two grooves parallel to axis of pit (e) possibly indicating presence of antennae or modified maxillipeds, KUMIP no. 25138, ×2.7.

*3.* Rest mark with well-developed leg impressions and anterior grooves (a) and short crawl trail leading into rest mark, KUMIP no. 25138, ×4.5.

FIGURE

*4.* Two rest marks connected by crawl trail, with parallel axes, indicating rheotactic orientation pointing anteriorly against current, leg imprints (a) indicating articulated segments, KUMP no. 25126, ×1.2.

*5.* Crawl trail showing overlap caused by current action, tracks straight to cuneiform, KUMIP no. 25123, ×0.5.

*6.* Lightly imprinted crawl trail showing two slight curves and intermittent straight course, curving believed to have been caused by current action, tracks cuneiform, KUMIP no. 25123, ×0.9.

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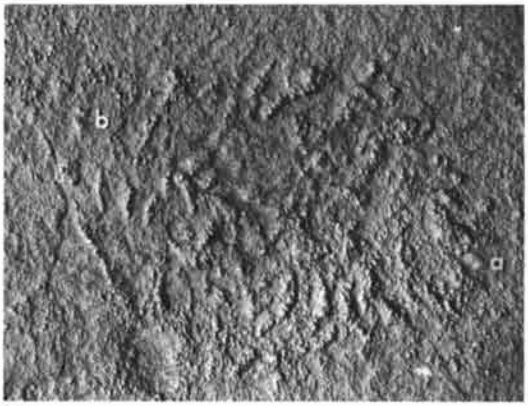

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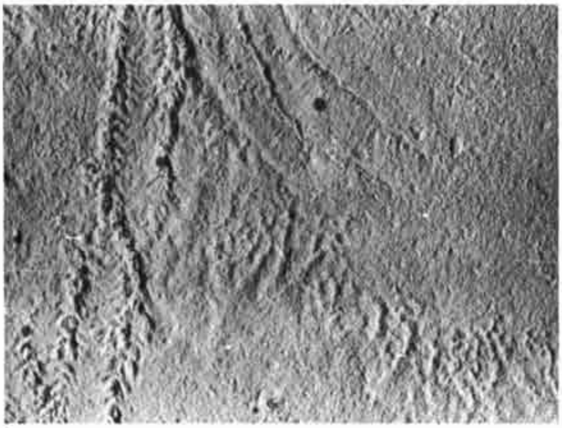

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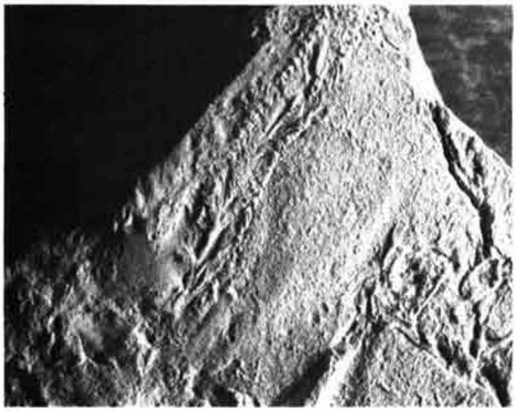

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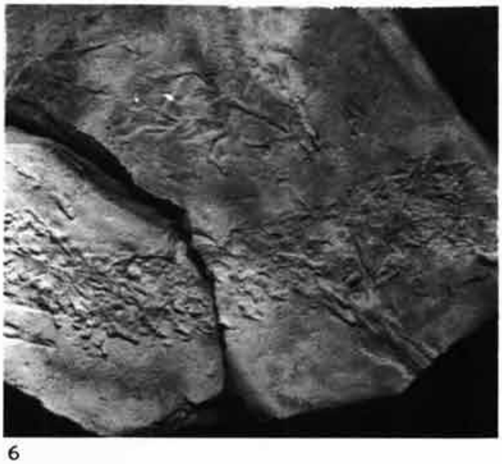

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(Bowsher & Jewett, 1943, p. 28). With the marks and trails a cluster of *Sphenophyllum cuneifolium* Zeiller in upright position was found in the siltstone. The cluster consists of about 50 adjacent stalks that cut across three overlying siltstone beds. The smaller stalks were buried in the second bed and had not rotted away when the third bed was deposited around the taller plants. The tops of the beds show current grooves on the downstream side of the plants. The fact that the thin multileaved *Sphenophyllum* stalks were not pushed over indicates that currents were weak. The continuance of the plants through three successive beds demonstrates rapid sedimentation of the siltstone. The whole sequence might have been laid down during one flood period which could have been brought about either by change of a river channel or by tidal influx. Mud cracks suggest temporary fluctuations of water level. Yet sedimentation was completed before the plants could die or rot away. This kind of environment seems to be perfectly fitted for preservation of delicate surface tracks.

Lins (1950) gave a very detailed description of the origin and environment of the Tonganoxie Sandstone just northeast of Franklin County. Sanders (1959) extended its study into the Franklin County area. Both workers agree that the Tonganoxie sandstone represents the filling of a shallow southwest-trending valley. Lins stated that a southwest-flowing river transported fine-grained micaceous sand, silt, and clay derived from the east and deposited them in channels and on the flood plain of a valley that was 12 to 20 miles wide. This valley was very shallow, compared with its width, indicating that the river was nearly at grade. The thin-bedded, fine-grained siltstone presumably was deposited along channel margins in calmer water. The lower part of the Tonganoxie Sandstone shows no indication of marine influence; it is therefore interpreted to be fluviatile in origin (Lins, 1950, p. 131-136). Ball (1964, p. 310) interpreted the sandstones of the Douglas Group as deposits of a mixed environment and stated that they are part of the complex record of the shore zone and probably contain marine as well as nonmarine deposits.

Plant remains at the trace-fossil locality are abundant and well preserved. Lists of plant species in the Tonganoxie are given by Cridland & Morris (1963) and Cridland, Morris, & Baxter (1963, p. 59).

All illustrated specimens and type specimens are deposited in the University of Kansas Museum of Invertebrate Paleontology (KUMIP). The catalog numbers are given in the figure explanations.

## EXPLANATION OF PLATE 2

Isopod and limulid trails on siltstone bedding planes in Tonganoxie Sandstone near Ottawa, Kansas.

FIGURE

*1.* Isopod crawl trail running at 90 degrees to current direction, composed of several elongate grooves which indicate shoving movement of animal over sediment and imprinting hard margins of animal's exoskeleton, an overlapping crawl trail at right, KUMIP no. 25126, ×0.9.

*2.* Limulid crawl trail showing along sides two grooves made by outer edges of cephalothorax, KUMIP no. 25122, ×0.9.

*3.* Isopod crawl trail with track made by telson or pointed end of posterior shield, animal crawled over an irregularity of ground, imprinting its posterior end into the sediment, KUMIP no. 25124, ×0.45.

*4.* Very strongly imprinted isopod trail in which the hard chitinous exoskeleton of the animal obliterated the outer bar of crossing cuneiform tracks believed to be of limulid origin, KUMIP no. 25126, ×0.9.

*5,6.* Meeting of two limulid trails with straight groove made by telson of female continuing as feather-like groove in lower part of 5, struggle of male limulid to attach himself to female is seen in tracks made by lashing telson (a) and groove imprinted with edge of cephalothorax (b), isopod crawl trail at left, KUMP no. 25132, *5*, ×0.22, *6*, ×0.45.

## ISOPOD MARKS AND TRAILS

### REST MARKS (CUBICHNIA)

Thirteen imprints found on five slabs are here interpreted as isopod rest marks. The structures are indistinctly U-shaped, shallow pits about 8 to 10 mm. wide and 11 to 15 mm. long. The open end of the **U** is called posterior, the other end anterior. On either side of the shallow pits six or seven straight leg imprints join the pit at an angle of less than 90 degrees and are directed anteriorly (Pl. 1, fig. 2-4). Some of the leg imprints show articulated segments at an angle slightly less than 180 degrees (Pl. 1, fig. 4a). Some of the rest marks, in addition, have two anterior grooves parallel to the length of the pit (Pl. 1, fig. 2a, 3a). These grooves are either slightly deeper or longer than the leg imprints or they may be absent. However, they are different from the leg imprints which are equally deep. These imprints could have been made by the antennae or by the first pair of thoracic limbs modified as maxillipeds.

One imprint consists of a crawl trail leading into the posterior end of a rest mark (Pl. 1, fig. 3b). In another imprint two rest marks are connected by a crawl trail (Pl. 1, fig. 4). The longitudinal axes of both rest marks are parallel to each other and the crawl trail is placed at an angle. Very shallow tracks between the second and the third rest marks in this imprint indicate that the animal moved from the second to the third place more swimming than walking.

On all slabs with multiple rest marks the anterior ends are oriented in more or less the same direction. Thus the heads of the animals were turned against the water current. Abundant current marks on the bedding plane also indicate relatively strong water flow. Schäfer (1962, p. 438) drew attention to the rheotactic orientation of resting tracks (arranged parallel to each other as a result of like orientation) made by *Cragon*, a crustacean, on intertidal flats of the North Sea. On silty clayey intertidal flats he noticed a few hundred oriented tracks of this crustacean. Rheotactic behavior is not restricted to marine animals. In streams the swimming and bottom-dwelling organisms often show the same behavior (Richter, 1926, p. 223).

On North Sea intertidal flats *Cragon* digs into the sediment until only the antennae, antennulae, eyes, and carapace are exposed (Schäfer, 1962, pp. 437-438). The long antennae are constantly moving, causing scratch circles and radially oriented linear tracks. The arthropods from the Tonganoxie Sandstone did not do any significant digging as indicated by the flat rest marks and by the lack of disturbed sediment. The linear imprints on the side of the rest marks are not oriented radially, as if imprinted by one appendage, but rather reflect the position of the legs on the body. There is no evidence of burrowing, but the animal probably pressed itself tightly to the bottom or pushed slightly into the surface of the sediment. Seilacher (1953, p. 88) stated that an animal resting under water usually leaves tracks that can not be distinguished from marks of dead

## EXPLANATION OF PLATE 3

Limulid trails and tracks on siltstone bedding planes in Tonganoxie Sandstone near Ottawa, Kansas.

FIGURE

*1.* Crawl trail leading away from meeting place (lower part of trail illustrated in Pl. 2, fig. 6), with digitate tracks superimposed on all other tracks (a) and two sets of median grooves (b) made by telsons, indicating that trail was made by two animals attached to each other, KUMIP no. 25133, ×0.7.

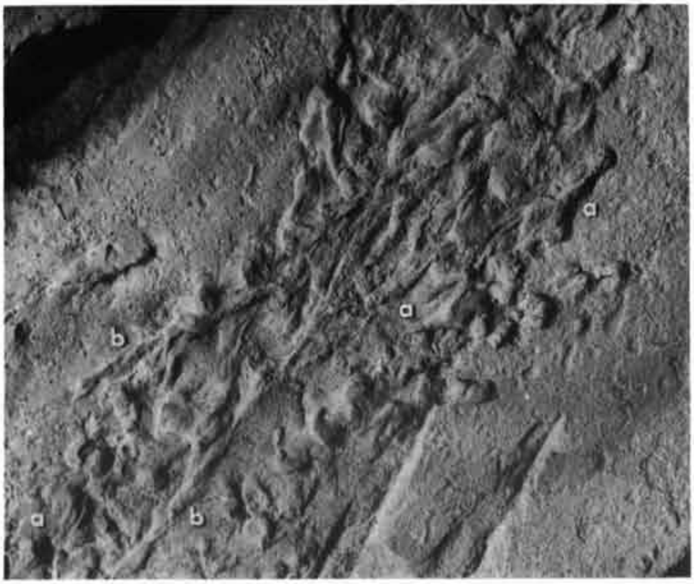
*2.* Very regular straight feather-like drag mark made by telson of swimming young limulid, KUMIP no. 25140, ×0.9.

*3.* Crawl trail with discontinuous lateral grooves made by edge of cephalothorax (a) and series of transverse impressions (b) ending on both sides in longitudinal grooves (c) made by inner edge of underside of cephalothorax, KUMIP no. 25131, ×0.45.

*4.* Trail made by half walking, half swimming limulid, with well-preserved feather-like marks at left (b, c) made by dragging appendages and at right (a) with walking or balancing imprints of appendages (see fig. 5), KUMIP no. 25121, ×0.9.

*5.* Chelicerous marks made by limulid walking on long legs (part of trail illustrated in fig. 4), KUMIP no. 25121, ×2.7.

*6.* Irregular drag mark made by telson of large limulid while swimming close to ground, KUMIP no. 25143, ×0.9.



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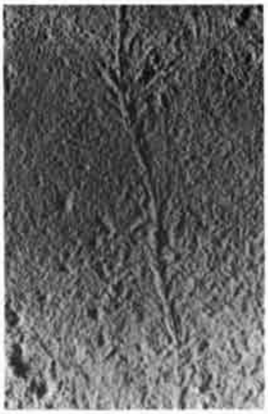

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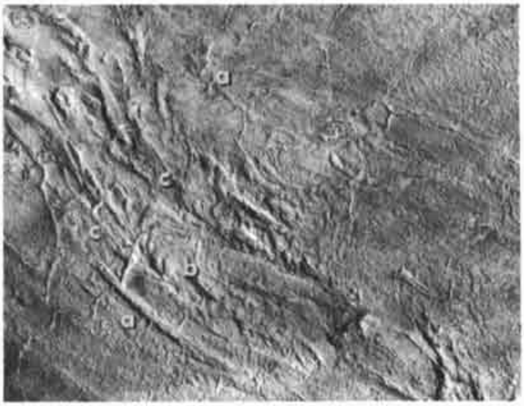

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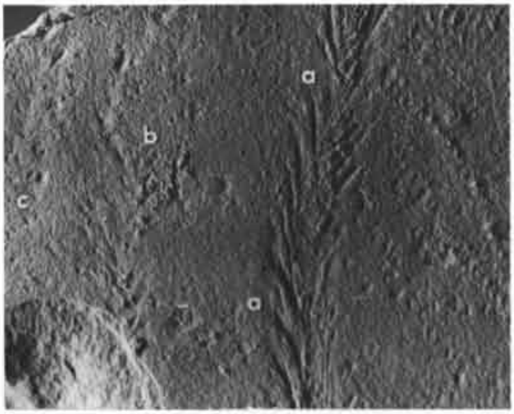

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bodies because of the buoyancy of the water. Thus, usually a rest mark indicates digging into the sediment. This possibly happened here too. The animal probably used some method to sink into the sediment, but it was probably quite small and light so that its weight alone was not sufficient.

The well-preserved rest marks show six or seven pairs of leg impressions, indicating that they were made by an animal with six or seven pairs of legs. The body was elongate, and its height probably small, and, therefore, it did not have to dig into the sediment in order to withstand the current. Antennae or a modified first pair of limbs or both were present. The rest marks are connected with the crawl trails now to be described.

## CRAWL TRAILS (REPICHNIA)

Almost all siltstone slabs with trace fossils show crawl trails, which were made by the same animal that made the rest marks described above. In conformity with current American usage the individual imprints of organs of locomotion are here referred to as tracks, while a series of tracks made by one individual is called a trail.

Individual tracks have a variety of forms, more or less straight (Pl. 1, fig. 5), crescentic, or cuneiform (Pl. 1, fig. 6; Pl. 2, fig. 1). The inside bar of the cuneiform track is usually longer than the outside bar. The tracks are about 1 mm. apart. If curved or cuneiform, the convex side points in the direction of movement. The trails must have been formed under water. The few trails that trend at 90 degrees to the water-current direction show definite effects of current action (Pl. 2, fig. 1). The appendages of the crawling animal have stirred up sediment that has been carried by the current. The direction of movement of most trails is against the current as indicated by current marks. The trails show certain differences that must either be due to different sizes of animals or to different conditions of the stream, such as variation of water cover causing the same type of animal to move about in a different manner. The same type of trails may have both deep or shallow tracks. Trails with the shallowest tracks often are 1 or 2 mm. narrower than those with more deeply imprinted tracks. Considering the fact that the tracks in both types of trails are made by the same kind of animal, a different setting of feet due to change of environmental or behavioral factors is probable. Because the oldest tracks are the most lightly imprinted, it seems possible that either the current became stronger or that the water became shallower.

One lightly imprinted trail (Pl. 1, fig. 6) shows that the animal first moved in a straight line, then went into a slight curve after which it resumed a straight direction. Other trails are similar but stop abruptly and are overlapped (about 6 to 12 pairs of tracks) by a new trail (Pl. 1, fig. 5; Pl. 2, fig. 1). These overlaps in a straight direction of the trail could have been caused by action of the current on the crawling animal. The result was either a short change in direction or a small sideway setback.

One very strongly imprinted trail (Pl. 2, fig. 4) is bordered on both sides by continuous grooves which appear to obliterate the outside bars of the cuneiform tracks. Only the inside bars are preserved. The grooves are believed to have been imprinted by the edge of the hard chitinous exoskeleton of the animal.

One trail, at 90 degrees to the direction of the current, consists of a number of elongate grooves

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## EXPLANATION OF PLATE 4

Limulid trails and tracks on siltstone bedding planes in Tonganoxie Sandstone near Ottawa, Kansas.

FIGURE

*1.* Curved feather-like trail to which, after turn of 90 degrees, a second feather-like trail and several scratchlike tracks are added interpreted to show that swimming limulid made a turn and current action brought it out of balance, so that appendages of one side of animal dragged on ground, KUMIP no. 25137, ×0.9.

*2.* Feather-like tracks made by telson and appendages (note mudcracks), KUMIP no. 25136, ×1.3.

FIGURE

*3.* Trail made by limulid sliding close to bottom, probably swimming and making drag marks and Y-shaped imprints with its endognaths, KUMIP no. 25122, ×0.9.

*4.* Trails consisting of chelicerous marks made by swimming and settling animal, possibly of limulid origin, KUMIP no. 25126, ×0.45.

(Pl. 2, fig. 1); as the trail trends into the current, the tracks become more like foot imprints. It appears that as the animal moved across the current, the margin of the exoskeleton was imprinted on the sediment several times, but the tracks of the feet were either destroyed subsequently by the current or by the shoving movement of the animal itself.

Another trail gives a more detailed picture of the ventral part of this arthropod (Pl. 2, fig. 3). Here it had to crawl over an irregularity of the ground and left a definite track of what was probably a posterior shield with a pointed end or a telson. As a rule this posterior feature must have been held up by the animal, because no other trails show imprints of it.

## DISCUSSION AND CONCLUSIONS

From the analysis of the rest marks and crawl trails a good deal of information can be derived about the animals that made them. It was between 6 and 10 mm. wide and about 15 mm. long. The height of the body must have been small. The exoskeleton was made of hard material. It had six or seven pairs of legs, and possibly a modified first pair of thoracic appendages, and antennae. It was able to swim and to crawl. This information points to only a very few known groups of animals. It seems certain that the animals were arthropods. The only group of arthropods fitting the description are the Isopoda. These are low-slung animals with six or seven pairs of feet, thick antennae, clawlike first thoracic appendages, a telson or a fused shieldlike area at the posterior end of the abdomen, and they have the right size.

Today, isopods can be found in all environments. The largest number of species are marine, many occur in brackish water, and quite a few in fresh water and on land. Wesenberg-Lund (1939, p. 530) stated that many originally marine species have become adapted to fresh water in Recent times. Trails and marks of Isopoda thus provide no evidence as to whether the Tonganoxie was deposited under marine, brackish, or fresh-water conditions.

The *Isopodichnus* trails which Glaessner (1953, p. 105) described from the Carboniferous of New South Wales do not show many similarities to the Tonganoxie specimens. A much closer resemblance exists with Pleistocene trails from Silesia described by Schwarzbach (1935, p. 143-152), formed on the bottom of a fresh-water lake. He related them to the isopod *Asellus aquaticus*. In experiments this species made trails similar to the fossil trails on the same kind of sediment. Abel (1935, p. 256-263) figured and described a number of superficially similar trails. Only two of them show close similarities. Abel (1935, fig. 237) illustrated a crawl trail from mudstone of the Permian *Tapinocephalus Beds* of the Great Karroo Basin in South Africa, and, in figure 238, showed arthropod trails from the Permian Dwyka Tillite of Aiais, Warmbad, South Africa. Both trails are somewhat larger than the Tonganoxie trails. It is to be expected that quite a number of arthropods make similar kinds of trails, so that the animal forming the simple crawl trail can be identified only to the order.

## LIMULID TRAILS AND TRACKS

Eleven different kinds of trails have been collected that can be compared with trails made by *Limulus* today and also with trails described from the Upper Devonian near Lanesboro, Pa., as *Paramphibius* by Willard (1935) and by Caster (1938). Six trails give evidence of crawling activity of the animal, the other trails show swimming activity rather than walking. Caster described Recent *Limulus* trails, especially trails made by young specimens. His descriptions and illustrations are of great importance for the interpretation of the origin of some of the Tonganoxie trails. In spring and summer 1965 I had opportunity to study and become well acquainted with the behavior of *Limulus polyphemus* on the intertidal flats of Barnstaple Harbor and other coastal areas of Cape Cod, where it is rather common.

Each of the 11 trails are described separately. Their width ranges from 13 to 55 mm.

### CRAWL TRAILS

The trail illustrated in Plate 2, figure 6 is one that identifies its originator most clearly. It is a composite type made by two animals.

Digitate tracks seem to be superimposed on the tracks of an earlier made trail (Pl. 3, fig. 1 at a). These "digitate" tracks are characterized by four anterior radiating blade imprints and a posteriorly directed bar impression. These tracks are practically identical with the impressions made by the whorled pushing apparatus on the sixth pair of appendages of *Limulus* and are best described as "pusher prints" (Caster, 1938). The pusher prints have been recorded on one trail only where they are more deeply and sharply impressed than other tracks, and seem to have been made by the principal organs of locomotion during walking. Imprints of other feet form irregular pits elongated in the direction of movement. They show no apparent order.

Two sets of pusher prints appear to be present on this trail and, in places, two sets of median grooves(Pl. 3, fig. 1 at b). This and the very irregular pattern of parts of the trail might have been formed by two animals attached to each other, as can be seen frequently today during the mating season of *Limulus polyphemus* on Atlantic beaches and intertidal flats of North America. The male climbs on the back of the female and holds firmly to her abdominal margins while she drags him along.

A very characteristic part of the trail is the above-mentioned median groove or furrow which more commonly is feather-like in appearance as though made by a rigid tail that was moved to both sides while the animal was moving forward. At one place the nature of the imprints suggests that the tail might have been lashed furiously (Pl. 2, fig. 5 at a). These impressions lie at the crossing of two nearly equally wide trails. Before meeting, the trails are lightly impressed, whereas after meeting the combined trails are deeply impressed (Pl. 2, fig. 5, 6; Pl. 3, fig. 1). It is suggested that the male limulid spotted the female at this place and attached himself to her, thus putting additional weight on her. Thus a much more deeply impressed trail was made leading away from the meeting place. In the lightly impressed trail, believed to have been made by the female before the meeting, the tail imprints form a straight line as if the tail had not been as strongly moved in crawling as later when the female carried the male.

A deep angular groove (Pl. 2, fig. 5 at b) at the meeting point of the two trails was probably made by the edge of the cephalothorax while the male was struggling to attach himself to the female. Furious striking of the tail aided the animal in this. The many impressions and furrows made by the tail along these double trails suggest that the telson was rigid and ensiform.

The outside border of another trail is a continuous longitudinal groove (Pl. 2, fig. 2). These grooves resemble those made by *Limulus* when using the outer edges of his cephalothorax like sleigh runners.

In one long continuous trail these lateral grooves are more or less discontinuous (Pl. 3, fig. 3 at a). They have been imprinted by the side margins of the cephalothorax when the animal settled down between forward movements.

The same trail consists partly of a series of transverse impressions similar to a "printer's brace" (Caster, 1938, p. 8). These structures end on both sides in longitudinal grooves (Pl. 3, fig. 3c). The shape of these imprints is similar to that of the inner edge of the underside of the cephalothorax of Limulus, which is the posterior end of the expanded hypostomal plate.

## SWIM TRAILS

Caster (1938, p. 9) has stated that simple tracks of *Paramphibius* are more abundant than pusher impressions. This is also true for the Tonganoxie material. Most simple tracks are Y-shaped markings and chelicerous markings (Pl. 3, fig. 5; Pl. 4, fig. 3 at a) which are made with closed claws, the Y-shaped markings being made by claws that opened and closed while making the imprint. The rarity of pusher imprints indicates that crawling was not the type of locomotion most commonly used by the Tonganoxie animals. The limulids seem preferably to have swum close to the bottom, as can be observed in the mating season of *Limulus polyphemus* in the channel systems of East Coast estuaries today. Thus, most of the trails were made by limulids swimming close to the bottom and dragging the telson behind, and sometimes also the appendages.

The drag marks shown in Plate 3, figure 4 are very similar to a trail from the Lower Devonian Hunsrückschiefer of Germany, described by Richter (1941, p. 250, fig. 15a,b). This trail is about 6 mm. wide, whereas the Tonganoxie trail is 10 mm. wide. Both trails consist of a long series of marks spreading V-shaped from a central line like hairs of a feather. Commonly the small imprints are slightly concave to the outside (Pl. 3, fig. 4 at a). They are arranged more or less symmetrically on both sides of the middle groove. To the side of this telson imprint, about 40 to 50 mm. from the middle groove, are small V- or U-shaped imprints that may have been made by the legs (Pl. 3, fig. 5). The pointed part of the V or U coincides with the direction of the pointed Vs in the telson imprints and the long axes of these tracks are parallel to the main groove. On the other side of the same telson imprint are two smaller and more weakly imprinted feather-like structures, which are parallel to the main groove of the trail (Pl. 3, fig. 4 at b, c). The one closer to the telson groove (Pl. 3, Fig. 4 at b) begins as irregular grooves and abruptly changes to a feather-like structure. The outer feather-like structure (Pl. 3, figure 4 at c) shows only imprints on the inner side of its continuous furrow. The current marks on this slab indicate that the animal moved against the current.

McKee (1954, p. 73, pl. 11, fig. A) has described and illustrated a trail from the Triassic Moenkopi Formation of Arizona which is very similar to the one described here. The Triassic trail shows a "foxtail-like" (McKee) middle part and at least two lines on either side of it. McKee interpreted it as a series of swim marks of a small crustacean in very shallow water.

Richter (1941, p. 252) has described a trail from the Lower Devonian Hunsrückschiefer made by an animal which had some kind of median, probably long, appendage. On both sides of the median groove made by this appendage are small, widely separated grooves, which show that the animal may have walked rather than crawled, with body lifted high, and only touched the sediment with the end of the appendages. The Tonganoxie material includes both Moenkopi and Hunsrück types. The animal may have been partly swimming and partly walking, or perhaps just balancing the body with the feet while swimming. The *Limulus* trails which Caster (1938) described were made by young animals that did not walk on long legs. Richter stated that at least at times of reproduction adult limulids walk on long legs. Two other Tonganoxie trails are preserved just as telson imprints without any other types of tracks (Pl. 3, fig. 2, 6). One trail trends in a nearly straight line across the slab (Pl. 3, fig. 2). Here the feather pattern is developed without any interruptions. A second trail of this type made by a larger animal (Pl. 3, fig. 6) also runs fairly straight, but the feather pattern is not very well developed. Locally, this structure is interrupted by a straight groove which is interpreted as an area where the telson was not moved laterally while the animal was moving forward. The telson was used possibly as balancing organ when swimming close to the bottom. Juvenile Recent limulids are much better swimmers than adults. Therefore, when an adult moves along dragging its telson behind, the resulting drag marks may be expected to be more irregular than those made by a young limulid, and perhaps similar to the one here illustrated.

A curved feather-like trail is shown in Plate 4, figure 1. After a turn of about 90 degrees an additional feather mark, and later a number of scratches are present. It looks as though the swimming limulid lost its balance in the curve because of current impact and stabilized its swimming position with the maxilliped, and later also with the endognaths.

One long continuous trail seemingly was made by an animal dragging telson, maxillipeds, and some endognaths while swimming very close to the bottom (Pl. 4, fig. 2). The telson marks are the most continuous element; the other tracks are intermittent.

Plate 4, figure 3 shows a trail made by an animal sliding close to the bottom. In this example the chief locomotive action was probably by the gill books aided slightly by feet. Straight drag marks of the telson are seen in places. The endognath imprints are drawn out into long lines and the outermost ones are Y-shaped. Pusher imprints are indistinct; perhaps the pushers did not take part in the locomotive action.

One quite different type of trail might also have been made by a limulid. It runs across a slab at an angle of 90 degrees to current marks (Pl. 4, fig. 4). The trail consists of about ten series of four to six paired chelate imprints. Because no pusher marks are present, it seems that the animal swam a very short distance, settled down, then rose, swam, and settled down again, without attempting to walk.

## INTERPRETATION

The range in width of trails, as well as in width and length of the telson impressions, indicate that limulids of varying sizes lived on the

Tonganoxie flats. Large trails may have been imprinted by adults and small trails by their offspring. There is some indication that the younger animals were able to swim better than the older ones, which glided rather than swam over the bottom, by a method of locomotion that is best described as part walking, part paddling.

*Limulus* today does not live permanently on intertidal or river flats, but migrates there in early summer only to spawn. The young limulids may stay for a while in the intertidal pools of the large mud flats and then swim to the sea below low-tide level where their actual habitat is. I have seen many young specimens of *Limulus polyphemus* in the small pools of the Barnstaple Harbor flats on Cape Cod. The animals are easily detected at the end of their crisscrossing trails at the bottom of the pools. On the east coast of the United States *Limulus polyphemus* spawns in brackish or marine waters. *Carcinoscorpius rotundicauda*, distributed from the Philippines to the Bay of Bengal, goes into brackish water and, close to Calcutta, has been found 150 km. inland in practically fresh water (Buchsbaum & Milne, 1960). Ancient limulid remains, therefore, do not provide evidence as to salinity of the depositional environment. However, they suggest brackish waters.

Many xiphosuran trails have been described. *Paramphibius* trails (Caster, 1938) are very similar to the Tonganoxie trails, although the Tonganoxie limulids must have had pushers with three or four blades, not five as in *Paramphibius*. The limulids here described also used their telson much more extensively than *Paramphibius*.

Modern limulid trails are more similar to the Tonganoxie trails, than are the Upper Devonian *Paramphibius* trails.

A Lower Devonian trail described by Richter (1941, p. 249, fig. 15a,b) is very similar to some Tonganoxie specimens. Abel (1935) was the first to recognize limulid trails in the fossil record, reporting them in the Upper Jurassic of Solnhofen. Here specimens of *Mesolimulus* have been found at the end of trails showing that the animals died in their tracks.[1] The environment of the Solnhofen lime mud flats was hostile to life and the tracks of limulids show the animals' death struggles.

Dunbar (1923) described a *Paleolimulus* from the Lower Permian insect beds of Elmo, Kansas. He compared this specimen with similar forms which lived during Late Devonian and Permian times. Paleolimulus is very similar to modern *Limulus* and it is expected that both animals would form similar trails in similar environments. The maker of the Tonganoxie trails could, therefore, well have been a species of *Paleolimulus*.

## CONCLUSION

Two types of trails can be recognized on the bedding planes of siltstone layers in the Tonganoxie Sandstone Member. Land plants are present in abundance and good preservation. These beds were deposited rapidly in a coal swamp environment which seems to have formed under freshwater conditions, as indicated by the rich flora present. The plants found in the silt beds up to 1 m. above the coal were imbedded more or less in place, because *Sphenophyllum* stalks and well-preserved tree trunks are found in upright position.

The two types of trails have been interpreted respectively as of limulid and isopod origin. Isopods and limulids today are by no means restricted to the sea. The Indo-Pacific species *Trachypleus* and *Carcinoscorpius* seem to have a greater tolerance for wide environmental changes than does the North American *Limulus*. The trails seem to indicate that the Pennsylvanian limulids came to the Tonganoxie flats in the mating season. If comparison with modern limulids is at all acceptable, this indicates that the animals had left their usual shallow sublittoral environment and came to the shore, or into an estuary, or a river. Absence of marine fossils and evidence offered by the sediment (Lins, 1958) seem to indicate deposition in a river valley close to its mouth, possibly with brackish-water influence reaching some distance upstream. In the higher parts of the Tonganoxie Sandstone animals indicating a brackish to marine environment are found. This suggests transgression of the sea, which climaxed in deposition of the Westphalia Limestone. Rapid sedimentation, or an environment hostile to bot-

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[1] The workers of the Eichstätt-Solnhofen limestone quarries know the trails of *Mesolimulus* well and whenever they find one they try to uncover them up to their end, because in most cases the fossil *Mesolimulus* is found there. Specimens of *Mesolimulus* and imprints of their death struggle are sold for a price to geologists and tourists.

tom life, seems to explain the absence of burrows throughout most of the Tonganoxie.

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