The trail of a large Silurian eurypterid

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The Upper Silurian red beds of Ringerike, Norway, have yielded a well preserved trail which probably belongs to the large eurypterid *Mixopterus kiaeri,* known from equivalent beds in the same area. Life-size models both of the eurypterid and of its trail have been prepared in order to study the functions of the appendages, particularly in relation to the animal's gait.

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In the following discussion the term track is limited to a single imprint of one appendage, while the term trail is used for a sequence of tracks formed by one individual (comp. Caster 1938). Arthropod trails occur occasionally in fine-grained, usually argillaceous sand- and siltstones. Only in a very few cases, however, has it been possible to determine the animal that made the impressions in the sediment. Trails which are supposed to have been formed by merostomes have occasionally been referred to as *"Merostomichnites"* (Fig. 2).

The trail described in the present paper was found by Hanken and Dr. J. Miller in 1971. It is unique in the sense that it may, with considerable certainty, be assigned to one particular eurypterid species, *Mixopterus kiaeri* Størmer.

In order to be able to study in detail the relations between the eurypterid and its trail as well as the general mode of life of the animal, a life-size model has been made (Pl. 2:7, Pl. 3:1–3). The rather complicated model was prepared by Hanken in collaboration with Dr. Størmer, and valuable technical assistance was rendered by Mr. A. Jensen.

The morphology of *Mixopterus kiaeri* is not known in detail. In assessing the structures and positions of the various appendages, it has therefore been useful to consider the corresponding structures in the genera *Lanarkopterus* and *Carcinosoma* which belong to the same superfamily Mixopteroidea.

The model is based on the holotype of *M. kiaeri* (H. 2044 of *Univ. Paleont. Museum,* Oslo, coll.). This specimen, however, is evidently somewhat larger than the one that made the trail. When making a reconstruction of the trail it therefore had to be slightly enlarged to fit the model. The reconstructed trail can be seen on Pl. 3:1. In the model we have chosen to illustrate the tail in the raised position not straight, and the anterior appendages (II-III) somewhat convergent.

The interpretation of the track structures, and their relation to a life-size model of *Mixopterus kiaeri* on its trail, has been discussed with several paleontologists. We wish in particular to express our thanks to Professor A. Heintz, Oslo, Cand. Real. B. Christiansen, Oslo, and Dr. J. Miller, Edinburgh, for valuable advice. Thanks are also due to Dr. W. Struve who kindly showed Dr. Størmer a trail described by Richter (1954) which shows certain features in common with the present one. We are also indebted to Mr. Aage Jensen, Paleontological Museum, Oslo, for valuable assistance in making the model, and to Mrs. Kari Ruud Öztürk and Mr. O. Brynildsrud, for making the drawings and photographs respectively. Dr. D. Worsley has kindly corrected the manuscript.

GEOLOGICAL SETTING

The Silurian of Ringerike, about 30 km NW of Oslo, is well exposed in the western flank of a broad syncline (Fig. 1). In his comprehensive and important paper *Das Obersilur im Kristianiagebiete* Kiær (1908) describes in detail the main Silurian section which he divided into stages 6–9, corresponding largely to the Llandoverian (6–7) and the Wenlockian (8–9). The marine sequence is succeeded by red beds, the Ringerike Sandstone Formation (assigned to stage 10) which Kiær assumed to be of Devonian age. However, with our present knowledge of the red bed faunas, the age of these continental deposits is more likely to be Ludlovian, with the basal

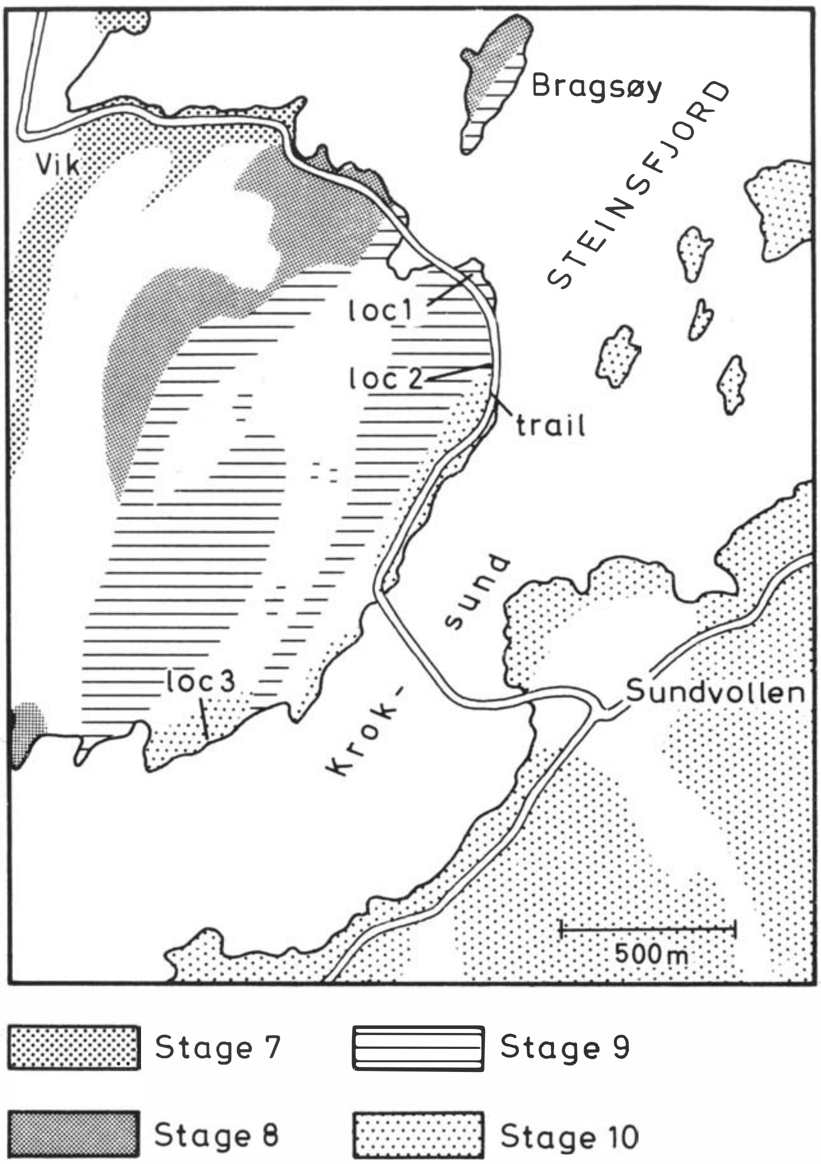

Fig. 1. Eurypterid localities at Kroksund, Ringerike showing the distribution of the Llandoverian (stage 7), Wenlockian (stage 8 and most of stage 9), Ludlovian (upper part of stage 9 and stage 10). Loc. 1 = Northern Nes, loc. 2 = Southern Nes, and loc. 3 = Rudstangen. The occurrence of the trail is marked just south of loc. 2 (modified after Kiær 1908 and Heintz 1969).

part being of late Wenlockian age. The uppermost marine beds (9g of Kiær), which are well exposed by the main road (E 68) along the shore of Kroksund, have a meager fauna of ostracodes, brachiopods, and bryozoans. Isolated bryozoans persist 1—2 m up into the overlying red beds.

Eurypterids have been found in the marine sequence, but they are most common in the continental deposits. Three different merostome faunas can be distinguished at three separate localities (Fig. 1).

LOCALITY 1. — At Northern Nes intermittent dark mudstones in shales and limestones of 9d contain the eurypterids *Baltoeurypterus tetragonophthalmus ("Eurypterus fischeri"), B.? latus,* and a small specimen of *Mixopterus* sp. (Størmer 1933, 1938), together with the alga *Chaetocladus capillatus* (Høeg & Kiær 1926).

LOCALITY 2. — A little further south by the main Kroksund-Vik road, another eurypterid locality was discovered in 1953 by Dr. R. Denison, Chicago. The following eurypterids have been preliminarily identified in dark grey shales: *Baltoeurypterus tetragonophthalmus, Nanahughmilleria* sp., *Pterygotus* sp., and fragments of large specimens of *Mixopterus* sp. (Størmer 1954). Ostracoderms occur in the more arenaceous beds; both these and the eurypterids are closely related to the K_1 —K_2 faunas of Estonia (Heintz 1969). The succeeding lower part of the red beds contains numerous animal trails in addition to mud cracks and ripple marks. Although these tracks are mostly diffuse and difficult to determine, the large well preserved trail described

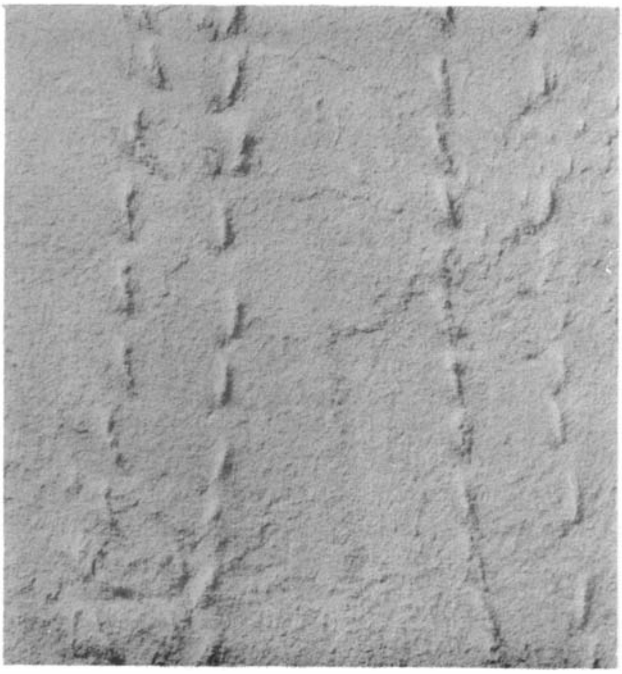

Fig. 2. Merostomichnites sp. trail. From Rudstangen. J. Kiær coll. x2.

below, was found by Hanken and Miller 10 m above the base of the red beds. Several diffuse trails at the same level might be of the same kind. Another large trail, not yet described, had previously been found a little farther up in the section.

LOCALITY 3. – This famous locality was discovered by Kiær (1911) at Rudstangen. The fossiliferous horizons belong to the lowermost part of the red beds, although the precise stratigraphic position is not certain. The fauna contains ostracoderms (Kiær 1924, Heintz 1939), crustaceans (Størmer 1935), and merostomes (Størmer 1934). The eurypterids are *Nanahughmilleria norvegica* (common), *Pterygotus holmi, Brachyopterella pentagonalis, Stylonurella ruedemanni, Stylonuroides dolichopteroides* and *Mixopterus kiaeri.* The xiphosurans are *Bunodes* sp. and *Kiaeria limuloides. Pterygotus, Mixopterus* and *Kiaeria* are the only large forms which occur in this fauna. Numerous trails of *Merostomichnites* type occur immediately below and above the fossiliferous beds at Rudstangen (Fig. 2).

Comparison with other faunas (Kjellesvig-Waering 1961) suggests that the lower eurypterid fauna (loc. 1) with *Baltoeurypterus* might have been largely marine while the uppermost one with *Nanahughmilleria* (loc. 3) belonged to a more brackish water environment. The middle fauna (loc. 2) which contains both species probably lived in a transitional environment. The large *Mixopterus* specimens probably belonging to *M. kiaeri* occur in the two upper faunas.

The Rudstangen fauna was primarily regarded as Downtonian (Størmer 1934). The occurrence of eurypterids identical with, or at least closely related to *Nanahughmilleria norvegica,* in the presumed Lower Downtonian beds of Stonehaven, Scotland, was one of the main reasons for this age determination. The Lower Downtonian age of the Stonehaven beds is based on its vertebrate fauna (Westoll 1951: 6,26 and Cocks et. al. 1971:118). The occurrence of *Baltoeurypterus* together with *Nanahughmilleria* and ostracoderms similar to those in K_1 (Kaarema formation) of Estonia (Størmer 1938 and Heintz 1969:24–25) indicate, however, that the eurypterid faunas belong to the Ludlovian and possibly appeared already in the Wenlockian. Recent studies by Basset & Rickards (1971) and Bockelie (1973:321) suggest that the whole of stage 9 is of Wenlockian age. The probable occurrence of *Nanahughmilleria norvegica* in the Stonehaven beds may suggest that also these deposits may be older than the Downtonian, possibly Lower Ludlovian as the Rudstangen fossils.

DESCRIPTION OF THE TRAIL

The trail occurs in a red, argillaceous siltstone. The preserved part of the trail (Pls. 1,2:1-4, Figs. 3–4) is 520 mm long and the width varies from 160 mm – 170 mm. The trail has three pairs of tracks on either side of a broad median groove. For the sake of identification the paired impressions are designated A, B, C, and numbered from 1 to 12. The A, B, C tracks on the left side have odd numbers and the C, B, A tracks on the right side have even numbers. Each number refers to one transverse band or axis, e.g. C_8, B_8, and A_8.

The median groove is called the m-track. Other tracks which may not belong to the main trail are named the X-, Y-, O_1-, O_2-, O_3- and n-tracks.

THE A-TRACKS. – (Pl. 1,2:1,2, Figs. 3, 4). These tracks are the largest and most significant. They form the straight lateral border of the trail. A_6 and A_8 are the best preserved impressions (Pl. 2:2, Fig. 4). The tracks are hook-shaped with a convex, longitudinally directed steep lateral wall. Posteriorly the wall changes its direction from longitudinal to transverse and even slightly anteromedian. The outer wall of the main furrow becomes steeper posteriorly so that its transverse part is vertical. The inner wall of the longitudinal part of the track is rather steep near its bottom but flattens out upwards.

These A-tracks are characterised by distinct *mounds* or elevations behind the median portions of the transverse parts of the main furrows (Pl. 2:2, Fig. 4). Each mound forms a median continuation of a transverse flat ridge or inflated surface behind the transverse furrow. The inflated surface has a steep anterior and a very moderate posterior slope.

In addition to the main furrow and mound, well preserved A-tracks and their surroundings show numerous *accessory grooves and ridges* (these structures are well demonstrated in A_6, A_8, and A_{10} (Pl. 2:2, Fig. 4). Concentric grooves and ridges occur around the posterior side of the mound, and are evidently wrinkles formed by the compaction of the mounds. In A_8 the concentric wrinkles are crossed by three radial grooves. Since these radial grooves distinctly cross the concentric ridges the former must be younger. Posteriorly the three grooves diverge slightly and fade out. Similar grooves, but more faint and close set, are present or indicated in A_6 and A_{10}. However in these cases there are two set of grooves, one more lateral than the other. In addition

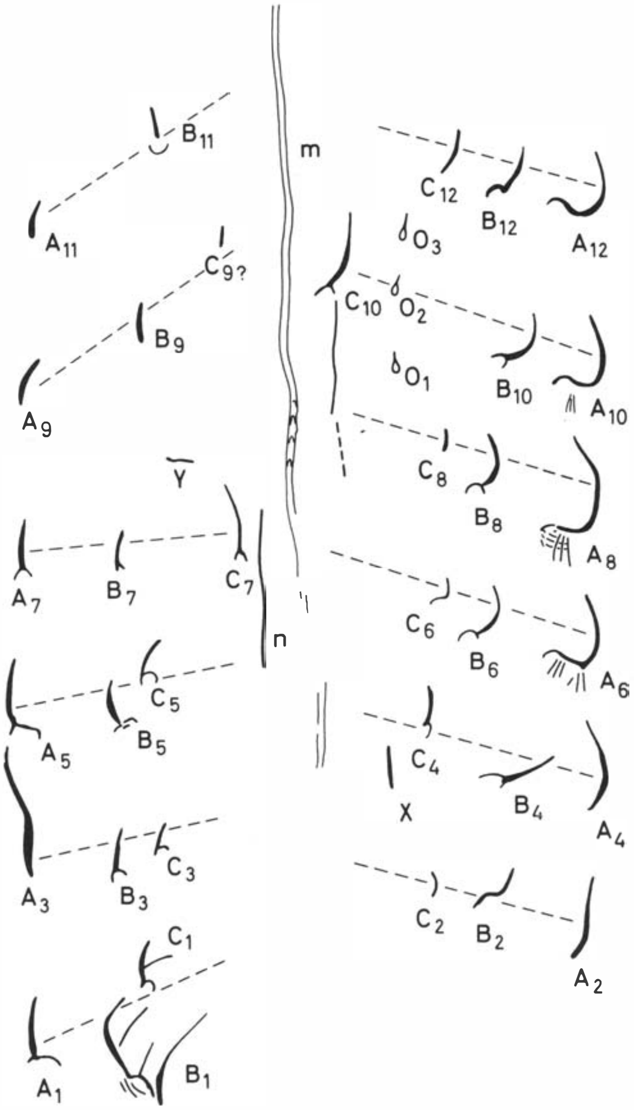

Fig. 3. Trail with designations. Stippled lines indicate bands of three tracks. x0,5.

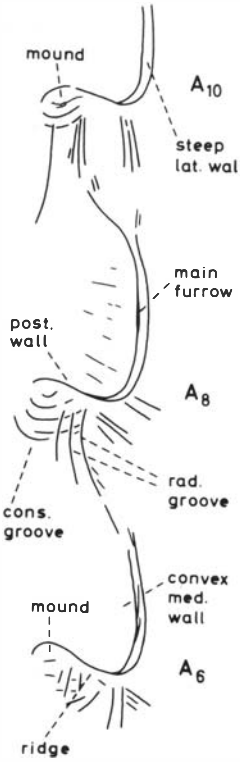

Fig. 4. Details of A-tracks on the right side of the trail. x1.2.

occur more diagonal grooves directed towards the bend of the main furrow. Very faint parallel grooves are suggested on the smooth area inside the main furrow of A_8.

In some cases, e.g. in A_4, A_6, and A_8 the main furrow continues almost to the furrow in front. From being longitudinal the furrow attains an anteromedian direction towards the mound in front.

THE B-TRACKS (Pls. 1,2:1). – The imprints are with a few exceptions smaller than the A-tracks. The B-tracks have a sigmoid shape, the transverse continuation of the main furrow is practically missing. The generally convex longitudinal furrow abuts posteriorly to a mound similar to that of the A-track but without a lateral flat ridge. The mound is demonstrated in B_1, B_3 –B_6 and B_8 –B_{10}. In B_1 concentric grooves and ridges are also indicated on the mound (Pl. 2:1, Fig. 3).

Unlike the corresponding furrow in the A-track the B-track furrows are almost symmetrical in cross section, this is well seen in B_1, B_3 and B_5. B_2 and B_4 differ from the rest of the B-tracks in that the direction of the curved furrow is nearly transverse, indicating a twisting of the distal portion of the appendage.

B_1 (Pl. 2:1) is bigger than the other B-tracks, its length equalling that of the A-tracks. Unique for this B-track is the presence of four slightly curved grooves running posterolaterally to the track which they reach at about a right angle. The concave side of the grooves faces posteromedially. The posterior groove abuts the mound and extends for a short distance. The other grooves meet the furrow in the middle and at both ends.

THE C-TRACKS. – These tracks (Pl. 1, Fig. 3) are smaller than the others, C_1 and C_3 to C_5 are fairly well preserved. Particularly C_5 shows the convex to sigmoidal furrow with the mound at the posterior end. It has an anteromedian position in relation to B_5. As in the B-tracks the furrow has equally sloping sides. The position and direction of the C-tracks varies to some extent. In C_7 and C_{10} which have an unusual median position the main furrow is prolonged into a faint groove. In the first case the groove extends forward from the furrow, in the second case it leads into the furrow from behind. In C_{10} only the posterior half of this groove seems to be real, the anterior part resembles other "lines" which occur several places, and evidently represent borders between slightly different levels of the rock. The mound of C_{10} is cut off. C_1 is placed in front of the corresponding B-track (Pl. 2:1), and this track also has a concave groove leading into the main furrow.

Although the A, B, C-tracks are arranged in transverse bands slightly converging forwards, a considerable variation of this pattern exists (Fig. 3). The A_1, B_1, C_1 tracks form a triangle rather than a line. In this case, however, the walking legs were kept in an oblique position so that the lateral spines touched the ground. Smaller deviations are found in A_5, B_5, C_5. Differences are also seen in the position of the B- and C-tracks in relation to the median line. C_7 and C_{10} have a marked median position; the longitudinal furrow forming a continuation of these tracks probably results from a vertical position of the legs so that the tip of the appendage was apt to touch the ground even when it normally should be lifted up. The direction of the main furrow of all the tracks is usually longitudinal, but more transverse furrows are seen in B_2, B_4, and B_{10}. The bands of the A-, B-, C-tracks (stippled lines in Fig. 3) alternate on opposite sides. If C_9 and B_{11} belong to A_9 and A_{11} bands respectively, the direction of these bands deviate from the other bands. Since the direction of the m-tracks is fairly constant the change in direction of the bands can hardly indicate a turn of the trail.

THE X- AND Y-TRACKS (Pl. 1, Fig. 3). – These additional tracks situated near C_4 and C_7 do not seem to have any direct relation to the other tracks. The X-track is straight with a longitudinal direction while the other is straight and transverse. Both lack the mound behind.

THE O_1 – O_3 - TRACKS (fig. 3). – These small tracks occurring between C_8 and C_{12} evidently belong to one side of a trail of a small arthropod walking along the same trail. The longitudinal furrows have a distinct mound at one end.

THE m-TRACK (Pl. 1,2:3,4). – The median groove forming this track occurs mainly in the anterior half of the trail. The distance from the groove to the lateral margins of the trail varies from 80–88 mm to the right border and 74–84 mm to the left border. A slight undulation is expressed in the course of the groove. In plan the suggested saddles and lobes succeed each other with a wave-length which largely equals the distance between the transverse ABC bands. The groove or furrow has a fairly constant width of 2 mm. The sides of the shallow groove are relatively steep while the bottom is slightly concave. Of interest are indications of parabolic impressions along the bottom of the groove (Pl. 2:3,4).

THE n-TRACK (Pl. 1, Fig. 3). – This faint longitudinal groove possibly belongs to the track, in which case it might have been formed by a lateral spine of a walking leg.

PRELIMINARY INTERPRETATION OF STRUCTURES

Before we try to identify the arthropod that made the trail it is necessary to interpret the structures which made it. Judging from the good preservation of some parts of the trail it is obvious that each type of track was made by a specific appendage. This implies that the three pairs of tracks were made by three pairs of appendages, presumably legs.

The A-tracks have a deep longitudinal furrow with a steep lateral wall and a median wall that flattens out in the upper part. This indicates that the distal portion of the appendage which made this imprint was broad and flat. The hook-shaped track, of which the transverse portion is a wall abutting a flat area rather than a distal wall of a furrow, probably indicates that the flat appendage had a rounded distal outline. These features show that *the appendage was broad and flattened and had a rounded distal outline, and that these features fit well a paddle-like appendage, which could have been a swimming leg.*

The B- and C-tracks resemble the A-track but are not hook-shaped, and the inner wall of the furrow does not flatten out to the same degree. This indicates that the appendage making the tracks was pointed, perhaps a broad, somewhat flat spine. Imprints of lateral spines occur in one band (B_1, C_1). The structures show that the *appendages which made the B- and C-tracks could have been walking legs with one distal and at least one pair of lateral spines.*

The median m-track might have been formed by a tail-spine of the metasoma, but since the track is relatively broad and shallow, it is unlikely to have been produced by a pointed tail or spine. The track must have been made by a blunt fairly long appendage which occasionally reached the ground. Its median position and shape would seem to indicate an appendage or structure protruding from the underside of the animal, which could be a genital appendage.

WHAT KIND OF ANIMAL MADE THE TRAIL?

When we try to identify the animal which made this trail the following conditions have to be fulfilled: (1) Only three pairs of legs took part in the gait of the arthropod, the last pair being of the swimming leg type, the others of the spiniferous walking leg type. (2) A long genital appendage was present.

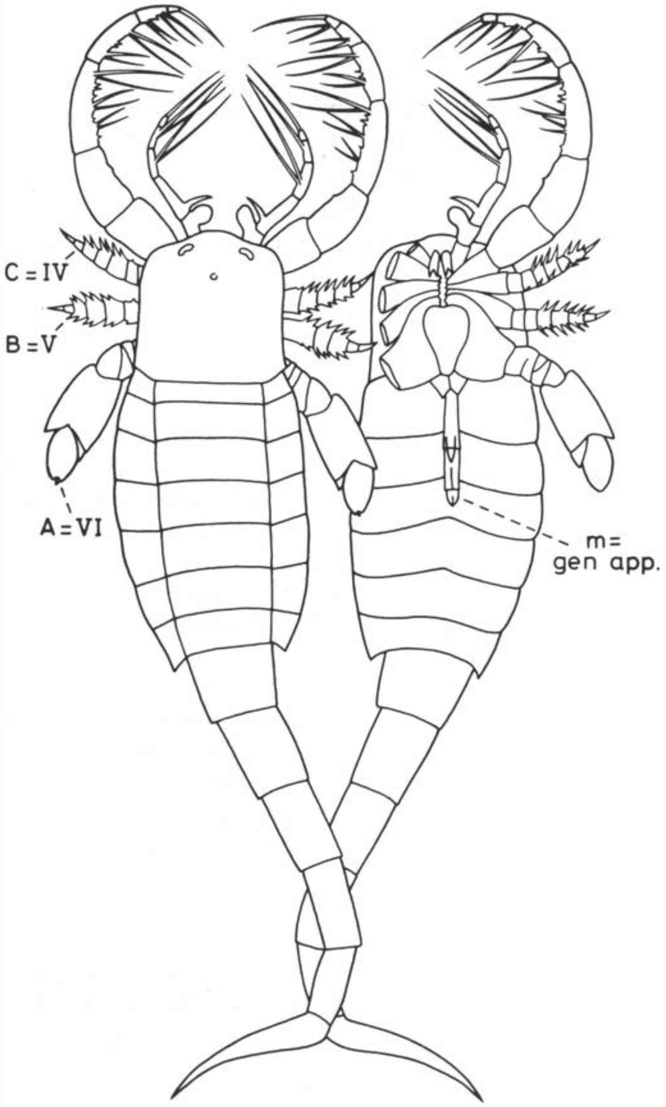

***Fig.** 5. Mixopterus kiaeri* **Størmer. Reconstruction of dorsal and ventral surface. A, B, C, m refer to track. About x0.2.**

Swimming legs constituting the last prosomal limbs (VI) occur in eurypterids, and have as an exception been described in a xiphosuran (Størmer 1972). However, a long median appendage is unknown in members of the latter group, which also have more than three pairs of walking legs taking part in the gait (Caster 1938). It is therefore very probable that *the trail was made by a large eurypterid.*

As mentioned above (p. 257) the large eurypterids present in the same beds are *Pterygotus holmi* and *Mixopterus kiaeri*. *Pterygotus* with its slender spineless walking legs and short genital appendage could not have produced the present track. *Mixopterus* on the other hand corresponds very well with the form we are looking for. This eurypterid (Fig. 5, Størmer 1934, Fig. 13, 14) is of the right size, the two first pairs of legs (II, III) are highly specialized and are not used for walking. The two succeeding pairs (IV–V) are typical spiniferous walking legs, and the last legs (VI) form a pair of characteristic swimming legs. *Mixopterus* also has a long ventro-medially placed genital appendage of Type A (regarded by Størmer & Kjellesvig-Waering, 1969, as belonging to a male). The terminal joint is not preserved in Norwegian specimens but since the related *Lanarkopterus* (Ritchie 1968) has a blunt termination this might also have been the case in *Mixopterus*. Even if a bifurcate termination should be found in fossil specimens of *Mixopterus* the two spines might have been held close together when the animal was alive.

The great morphological correspondence, as well as the common occurrence, makes it very probable that the present trail was made by the eurypterid Mixopterus kiaeri Størmer.

MODE OF FORMATION AND PREDIAGENETIC PRESERVATION OF TRAIL

In a study of Upper Carboniferous limulid tracks in North Cornwall, Goldring & Seilacher (1971:434), assume that "Optimal conditions for the preservation of the tracks occurred when silt and clay sediment was deposited from low velocity currents, sufficient to maintain adequate oxygenation of the bottom waters but insufficient to extensively scour the substrate". Limulid trails are regarded as being formed in an offshore environment preferably a brackish or freshwater lagoon.

The *Mixopterus*-trail is preserved in a red argillaceous silt which presumably was deposited in a well oxygenated environment. Desiccation polygons in the beds immediately above and below those containing the trail suggest shallow water and emergence. The trail therefore was probably formed in the intertidal zone (if the environment was marine or estuarine) or the trail may have been formed on or near the shore of a lake. In the present trail the mounds formed by the push of the paddles have concentric wrinkles on their surface. Such compaction wrinkles could hardly have been formed and preserved in a soft mud. The wrinkles show that the thin layer of mud on the top of the silt was very cohesive and preserved the tracks in full relief.

A dragging of the genital appendage along the bottom is hardly present in aquatic invertebrates, and this indicates that the body was weighed upon, and that additional weight could have been due to the specimen of *Mixopterus kiaeri* being either partly emerged or above the water when it made the trail. In these cases the tail was probably held in a raised position to keep the balance as mentioned below.

Some of the individual tracks, particularly the A-tracks, are deep and well preserved. A_6, A_8, and A_{10} on the right side are hook-shaped while A_9 and A_{11} on the left side are only slightly convex and lack the transverse portion forming the rear wall. The reason for this is probably that the latter are *undertracks* (Goldring & Seilacher 1971). Other undertracks may be seen in B_9 and B_{11}, and the B- and C-tracks on the right side of the trail where the sediment has obviously been removed.

THE MOVEMENT OF THE THREE PAIRS OF LEGS IN *MIXOPTERUS*

The mound or terminal elevation of the end of each track-furrow is the result of a push and compaction of the silt by one of the legs. Usually the mounds are formed at the rear end of the tracks (Fig. 6D), but, in certain cases they may also be formed in front (Fig. 6B). The latter case may occur either when the leg is thrust forward into the sediment, or when the leg is withdrawn from the track furrow as demonstrated by Goldring & Seilacher in *Limulus* (1971:426).

When we began the studies of the trail we were inclined to believe that the mounds were formed in front of the tracks. The main reason for this assumption is the presence of three radial furrows crossing the concentric wrinkles on the mound A_8 (Pl. 2:2, Fig. 4). The furrows were thought to have been made by the three-pointed tip of the swimming leg dragged over the mound. However, this explanation would imply very complicated and improbable movements of the swimming leg, and the radial furrows which occur at one track only might be explained merely as tension grooves or wrinkles formed on the skin of a moist surface (comp. accessory grooves and ridges in A_6 and A_{10} in Fig. 4).

However, further studies of the trail and movements of the swimming leg indicate that the

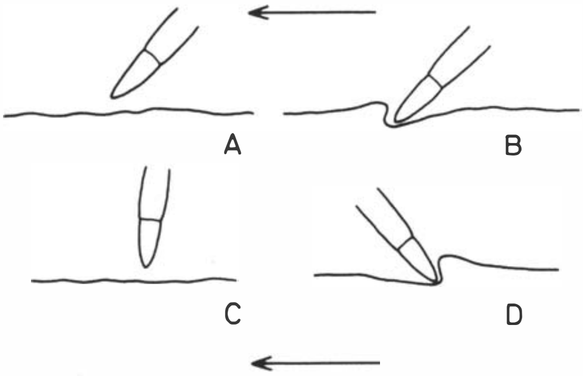

Fig. 6. The direction of movement in relation to the mound formed in front or behind the track.

mounds or terminal elevations were formed at the rear end of the track. This conforms with Caster's (1938) studies of Paleozoic and Recent Xiphosura. Similar mounds are indicated in the Lower Cambrian *Diplichnites* and the Upper Devonian *Kouphichnium* (Häntzchel 1962, Figs. 121:1, 124:2). The same is the case with the Lower Devonian *Palmichnium* discussed below (Figs. 11B, 12B).

The presumed movements of the swimming leg are demonstrated in Fig. 7. In the first phase (1) the swimming leg touched the ground in a nearly transverse position with the proximal portion of the leg practically horizontal, while the distal portion comprising the paddle was inclined to face laterally. The distal portion of the paddle made the deep lateral furrow, and it was in this position that the forward push started. The push continued into the next phase (2) in which the appendage, due to the forward movement of the body, became more outstretched and the paddle less inclined. The paddle produced a push backwards and formed the posterior wall and the mound and ridge behind. A transverse furrow would not be formed by the moderately inclined paddle. In the third phase (3) the appendage is fully extended. The previous inclination evidently took place at the "knee" formed by the tibia (this specialized joint is well demonstrated in *Carcinosoma,* Clarke & Ruedemann 1912, Figs. 57, 58). In the last phase (4) the posterolaterally extended leg is lifted slightly from the ground and carried forward to attain the original nearly transverse position in the first phase. In Fig. 7 the distances and corresponding time intervals between the succeeding phases are assumed to be equal, but we do not know the actual length of the time intervals. The duration of the protraction and retraction (time off and on the ground) is unknown. The forward continuations of some of the A-tracks (A_4, A_6, A_8) might indicate that the swimming legs were not lifted much above the ground,

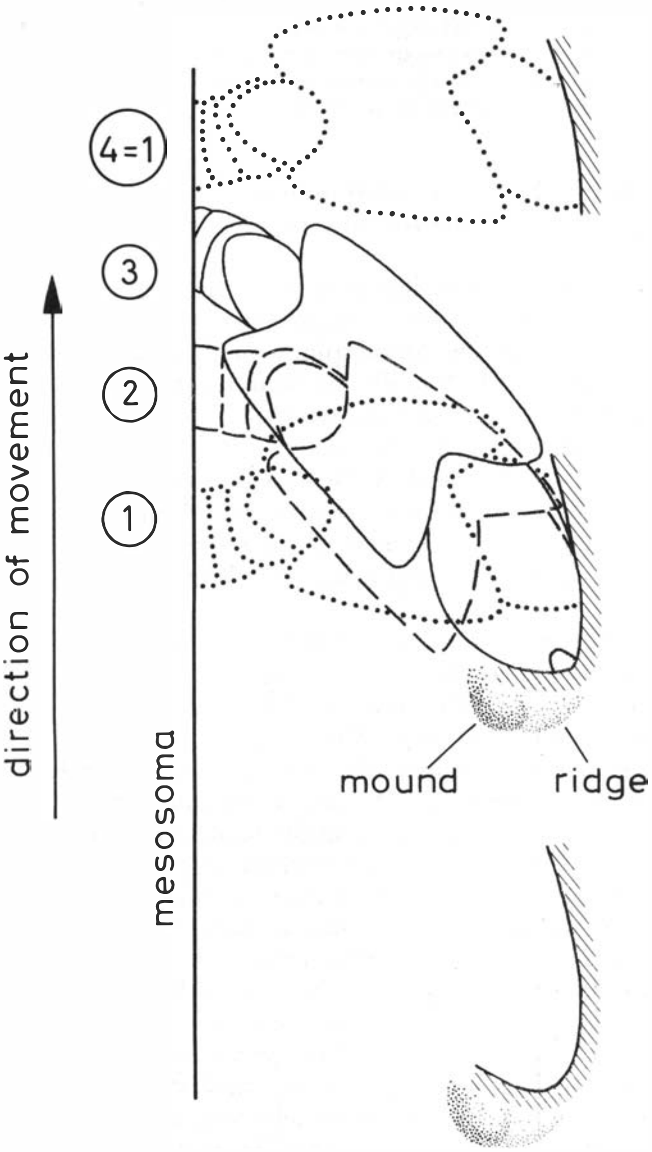

Fig. 7. Four phases in the movement of the swimming leg (VI). The second phase is shaded in order to distinguish this leg from that of the first and third phase.

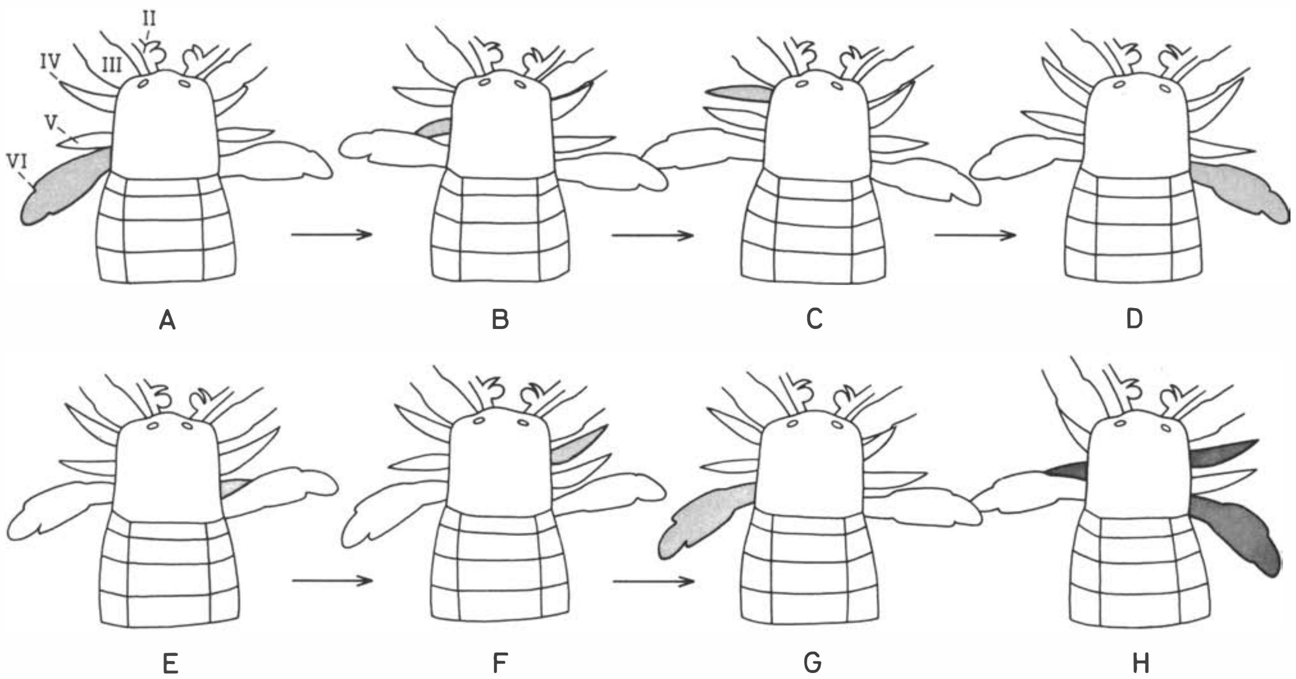

Fig. 8A-G. Probable slow gait of *Mixopterus kiaeri* when making the present trail. The seven phases illustrate one cycle of movements of the left swimming leg. The foot leaving the ground within one phase is shaded, those not shaded rest on the ground. The lifting of the swimming leg (VI) is succeeded by the next leg in front (V), and then the first walking leg (IV) is lifted. The limbs are drawn in an outstretched position. Particularly the two walking legs had a more vertical position during the gait. Fig. 8H suggests a more rapid gait when the animal was fully emerged. In this case, like in most insects, three legs (shaded) rested on the ground at the same time (two on one side and one on the other alternatively). In other cases the swimming legs might have been kept as flappers above the ground, and only two pairs of legs were engaged in the walking.

and that the time of protraction was correspondingly short. This interpretation of the structures presents a simple and apparently reasonable explanation for the features displayed in the fossil trail.

The two walking legs (IV and V) made the B- and C-tracks. The first leg seems to be slightly bigger than the second. Both had normally a more vertical position than the swimming leg. In a few cases the legs had a more outstretched position so that the lateral spines touched the ground and produced the impression demonstrated in B_1 and C_1 (Pl. 2:1, Fig. 3). With regard to the walking legs the strongest weight must have been placed on the second walking leg which therefore should have made the deepest and biggest impression, i.e. the B-track.

The median furrow or m-track, which we interpret as caused by the dragging along the ground of the genital appendage, indicates an undulation with a wave-length corresponding to the distances between succeeding A-tracks. The undulation of the median track evidently has something to do with the gait of the animal, and may suggest a slight swinging of the body during locomotion.

In order to interpret the movements of the three pairs of legs in *Mixopterus* it might be useful to consider the mode of movement in the Hexapoda which have the same number of walking legs. As pointed out by Hughes (1952), Chapman (1969), Manton (1972) and others, a hexapod always has at least 3 legs on the ground at the same time. These legs are arranged as a tripod around the point of gravity of the insect. Each leg alternates with the contralateral leg of the same body segment (except in swimming and jumping). The pattern of gait and the number of legs touching the ground simultaneously depend, however, on the relative duration both of protraction (the time when the legs are above the ground), and of retraction (the time when the legs are placed on the ground). When the ratio is 1:1 the gait pattern is the simple one where one leg on one side and two legs on the other are in protraction and retraction alternatively. Changes in this pattern occur when the speed changes. At a slow gait five legs might touch the ground at the same time. From what it said above there are reasons to believe that the speed was low when the trail was made. The pattern of the slow gait of an insect demonstrated by Champman (1969, Fig. 79) has been used in preparing an illustration of the probable gait of *Mixopterus kiaeri* when it made its trail (Fig. 8A–G). This pattern of gait was hardly typical of this eurypterid walking on the sea bottom. At normal speed the pattern might have been the simple one, two to one on either side, as mentioned above for most insects (Fig. 8H). It is probable, however, that in certain cases the swimming legs were held as balancing or swimming flappers above the ground, and did not make any tracks in the sediment.

MODE OF LIFE OF *MIXOPTERUS*

In the water the eurypterid was able to swim, and to walk on the bottom. It was hardly a good swimmer and kept near the bottom. It is not likely that it swam on its back like the Xiphosura or the more stream-lined eurypterids (Størmer 1934:62). During swimming the prosomal legs (IV–V) were probably directed backwards, producing smaller lateral strokes (Fig. 9A) while the

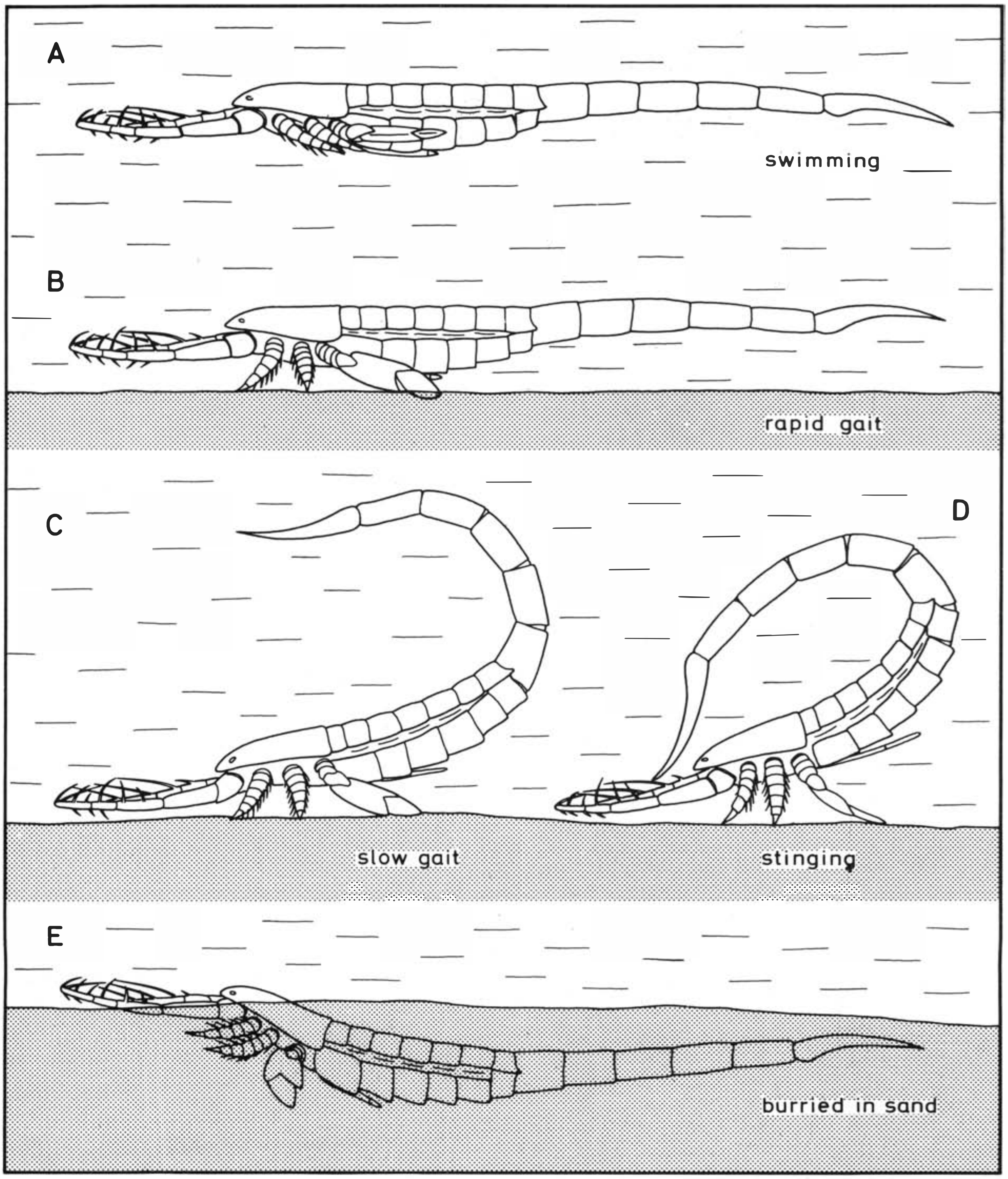

Fig. 9. Body-positions of *Mixopterus*, lateral view. A. During swimming the opisthosoma was probably extended, and the prosomal appendages directed mainly backwards and sidewards. The postlaterally directed paddle was moved slightly up and down. B. The body was probably also extended when the eurypterid walked rather fast on the bottom. C. The raised opisthosoma would give a better balance, especially if the body was partly or completely out of the water. D. The stinging of the prey was probably accomplished as in recent scorpions. E. In looking for prey, *Mixopterus kiaeri* might have been buried in the sand, except for the "cage" formed by the anterior appendages (II, III), and the anterior portion of the prosoma.

swimming legs were used as flaps moving in a vertical plane. A forward propulsion by rapid strokes of the ventral plates (Størmer 1934:62) might have been possible but was hardly characteristic of this form.

When walking on the bottom the common insect method was probably frequently used (Fig. 9B). The long outstretched abdomen would be largely counterbalanced by the two heavy specialized frontal appendages (II, III) which were kept above the bottom. *Mixopterus kiaeri* was evidently able to raise its tail (Fig. 9C, Pl. 2:7 and Pl. 3:1–3). The outspread appendages provided a good foothold and stable base for the body. While walking on land, the raised tail

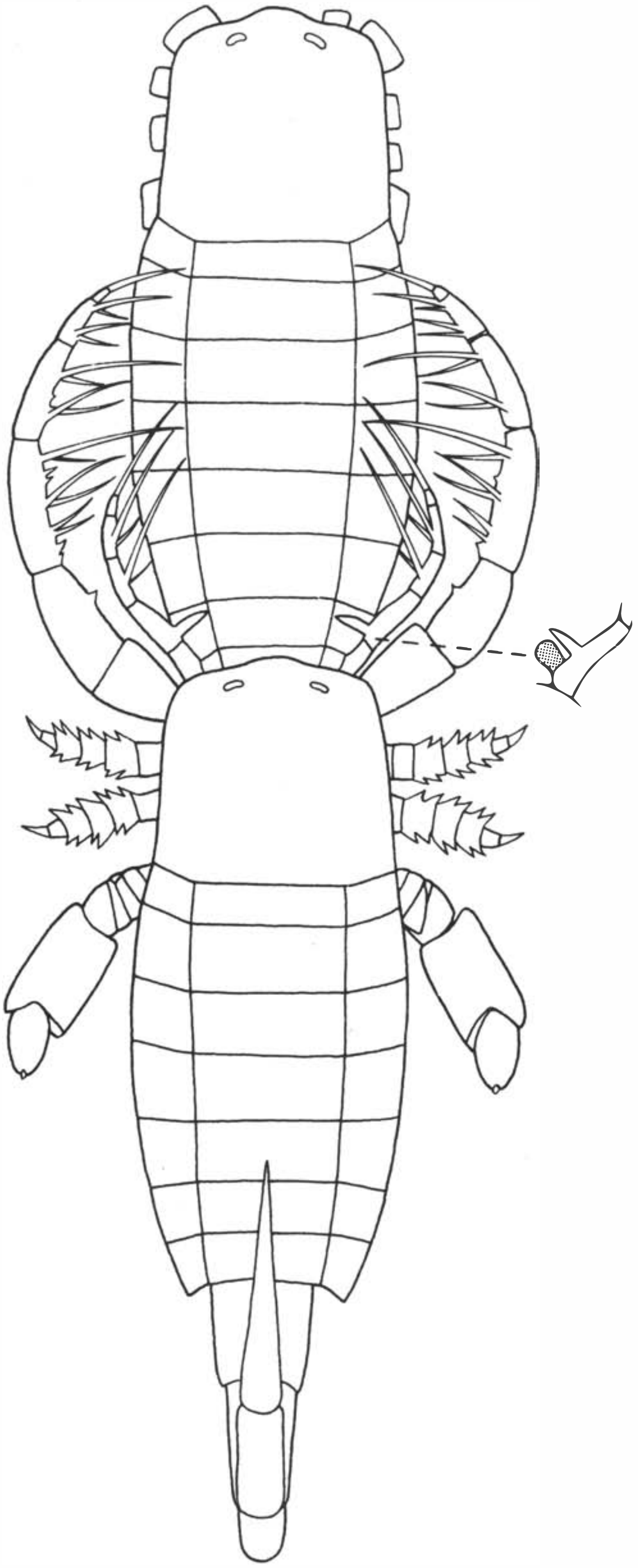

Fig. 10. Possible position of female and male of *Mixopterus kiaeri* during mating. A part of the clasping organ is shown to the right. Also in this fig. the legs are drawn in an outstretched position.

would facilitate the balance of the body. In the water when the weight of the body was small, this was less important. An overhead thrust and push of the tail would enable the telson spine to sting prey held between the front legs (Fig. 9D). Whether the spine was poisonous or not is not known. In waiting for prey it seems reasonable to assume that *Mixopterus* buried itself in the silt or sand; the swimming legs in particular were well-fitted for digging. Only the frontal legs and frontal portion of the prosoma with the eyes were kept above the sediment (Fig. 9E). When a prey approached the outstretched frontal appendages could be clasped together forming a catching organ or cage. The stiff and flat spines (except the pretarsus) of two pairs of appendages (II, III) where not movable.

The structure of the present trail suggests that *Mixopterus* was able to walk on land. Because of the weight of this large arthropod, the locomotion above the water must have been difficult. With moist gills well concealed above the ventral plates, the respiration would present no problems.

The method of mating of *Mixopterus* might have been somewhat similar to that of the horseshoe crabs. The presumed clasping organ on appendage II consists of a flat round lobe with a scimitar-shaped flat spine behind and resembles the clasping organ in *Limulus* (Størmer & Kjellesvig-Waering 1969). The organ in the eurypterid male could attach itself to the lateral corners of the last prosomal segment (Fig. 10). At the same time the pleurae of the anterior portion of the mesosoma might have been held between the spines of the frontal appendages. The long genital appendage of the male might have been directed, on one side of the tail of the female, to the point where the eggs were placed by the female (Størmer 1973:145).

RELATED TRAILS

In trying to find related structures we have to look for trails which have three tracks arranged along a more or less transverse axis on either side of the median line.

A Permian trail described as *Paleohelcura* by Gilmore (Häntzschel 1962: Fig. 128, 4a, b) shows three tracks along alternating, anterolateral directed axes on either side of a median furrow probably made by a pointed telson.

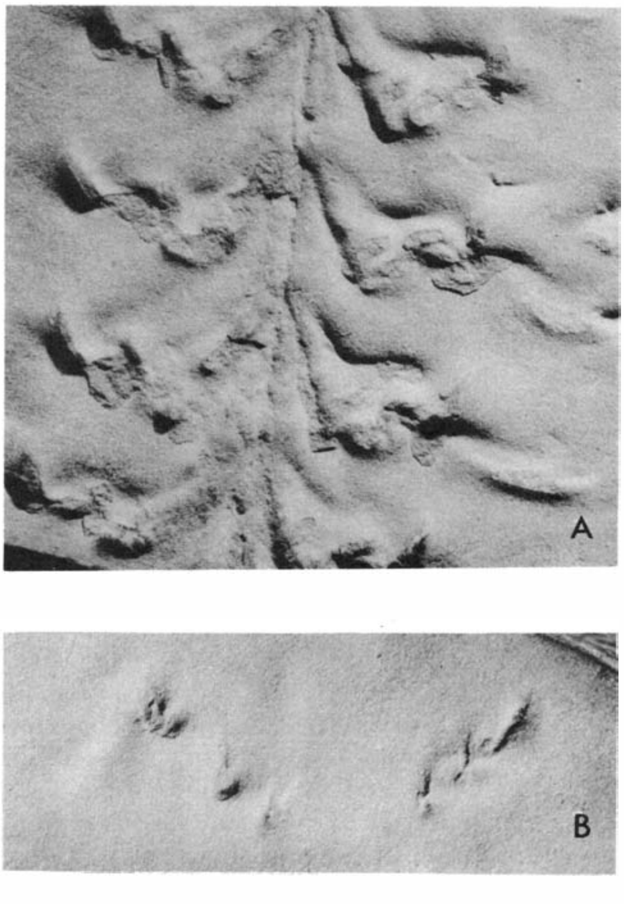

Fig. 11. Palmichnium palmatum Richter, a trail from the Lower Devonian of Germany. Above detail of trail with median impressions of coxae. Below tracks where the coxae did not touch the ground. The inner "C-tracks" on the right side shows a small mound at the end of the furrow.

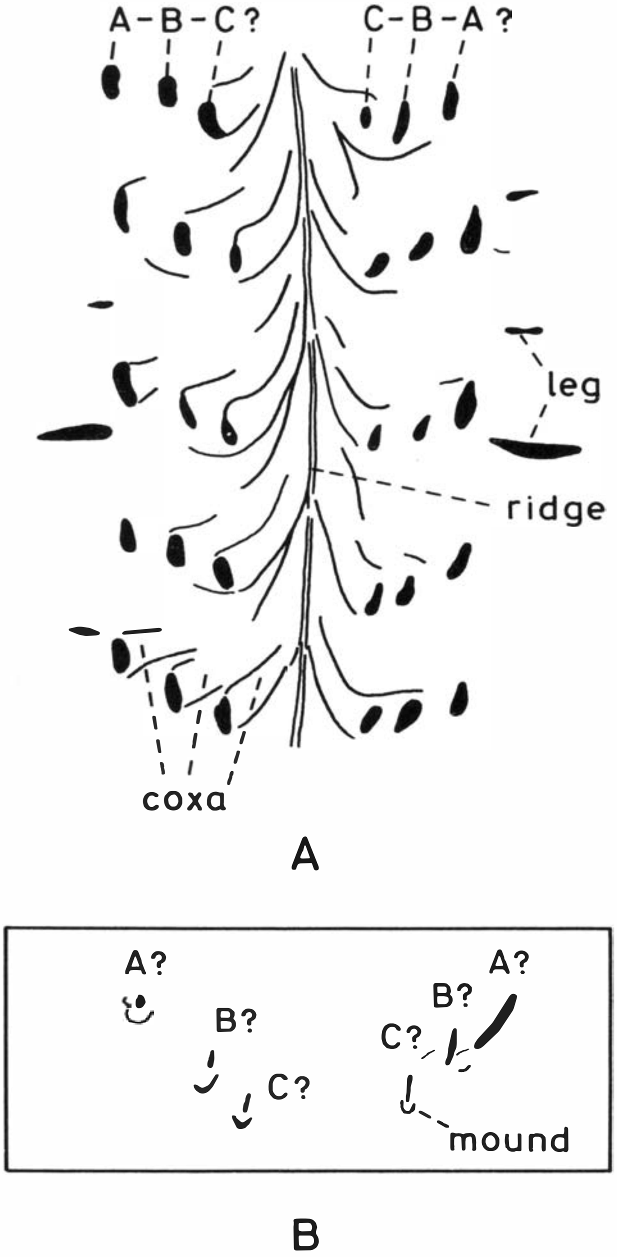

Fig. 12. **The same trail. Above a partly diagrammatic drawing of the trail. Below a drawing of the other tracks in Fig. 11.**

More details are demonstrated in a well preserved Lower Devonian trail from the Rhein area, Germany, described by Richter (1954). The palmbranch-like trail was said to have been about 10 m long when collected, and the distance between the "A"-tracks is 11 cm against 16 cm in our trail. The trail (Figs. 11, 12) which was named *Palmichnium palmatum,* was interpreted as the trail of an eurypterid. Instead of a median furrow the trail has a median ridge which is interpreted as representing the mud pressed up between opposing limbs.

During a visit to the Forschungsinstitut Senckenberg, Frankfurt am Main, Størmer had the opportunity to study the type specimen, and Dr. Struve very kindly made some new photographs of the trail. In addition to the main trail illustrated by Richter, there are a few single groups of tracks which lack the median lobes close to the median line (Figs. 11B, 12B). The axis of the three tracks on either side have anterolateral directions forming an angle of about 45° to the median line. In the main trail this angle varies, and may approach 90°, i.e. a transverse direction of the axis. It is interesting to notice that the pits or short furrows (Figs. 11B and 12B) have a little mound at one end just as in limulids and in *Mixopterus.* This indicates that the direction of movement of the trail was the opposite of that suggested in Richter's illustrations. The forward divergence of the track axis differs from that in *Mixopterus,* but such a difference may be found in one and the same animal, e.g. in the Thysanura (Manton 1972, Figs. 8G, H).

The three tracks on the more or less transverse axis may probably be interpreted as ABC-CBA tracks. The club-shaped median structures probably represent the imprints of the coxae. In eurypterids these wedge-shaped joints are usually transversely directed except for the two posterior coxae which have a more posterolateral orientation. The median portion of the coxal imprints have a certain resemblence to the triangular median lobes in the coxae of scorpions. However, in Lower Devonian time the lobes were not developed to such a degree (Størmer 1970). A transverse furrow lateral to the A-track (leg, Fig. 12A) may represent the lateral margin of a proximal joint of a bent anterior appendage such as the large appendage (III) in *Mixopterus.*

The difference between the simple and the more complicated tracks (Figs. 11A, B, 12A), is evidently due to the weight of the animal when it made the tracks. In the latter case the heavy body was pressed down so that also the coxae left imprints in the mud. When the main trail was made the tide may have gone out so that the arthropod had to drag itself on a wet subaerial surface. When the simple tracks were made, however, the water may still have been present. But how could the arthropod drag itself along on the surface and at the same time leave good impressions of the individual coxae? The evident reason for this is the animal lifted itself on the three pairs of legs, which were able to lift the body off the ground. In the next moment, however, the body fell down making imprints of the coxae in the mud before it again was lifted by the legs. The lack of alternation of the axis or bands of tracks on either side supports the assumption of a simultaneous lifting action of the six legs. The strong median prolongation of the coxal tracks might be due to a certain forward drag of the anterior portion of the coxae during the formation of their tracks.

A close identification of the arthropod that made this trail is hardly possible, it might have been an eurypterid, although not necessarily a member of the Mixopteroidea.

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EXPLANATIONS OF THE PLATES

Plate 1

The trail. From Silurian siltsone, 10 m above the transition from green to red sediments in the roadside (E 68) profile, Kroksund-Vik, Ringerike. A drawing of the trail is shown in Fig. 3. x3/4. Specimen belonging to the collections of the Paleontological Museum, University of Oslo (PMO 93913).

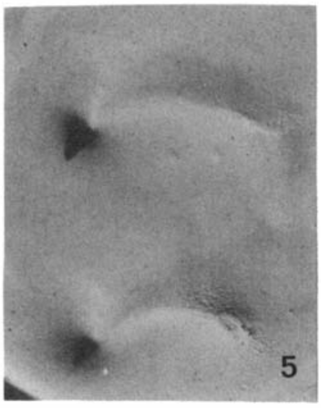
Plate 2

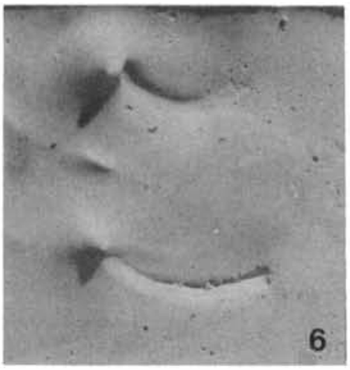
Fig. 1. Details of tracks B_1 and C_1. x1,5. *Fig. 2.* Details of tracks A_8 and A_{10}. Compare Fig. 4. x1.5. *Fig. 3.* The median groove or m-track. x1.7. *Fig. 4.* Detail of the m-track. Rounded areas at the bottom of the groove. x2. *Figs. 5-6.* Artificial tracks in plaster. The tracks were made by a blunt and flat stick pushed from right to left. A distinct mound is formed at the distal point of the furrow. *Fig. 7.* A model of *Mixopterus kiaeri* in anterodorsal view. The trail below is not well demonstrated.

Plate 3

Figs. 1-3. A model of *Mixopterus kiaeri.* x1/3. *Fig. 1.* Dorsal view of the model. The tracks formed by the appendages are indicated. *Fig. 2.* Ventral view showing the chelicerae, coxae, metastoma and the genital appendage. *Fig. 3.* Lateral view.

Plate 1





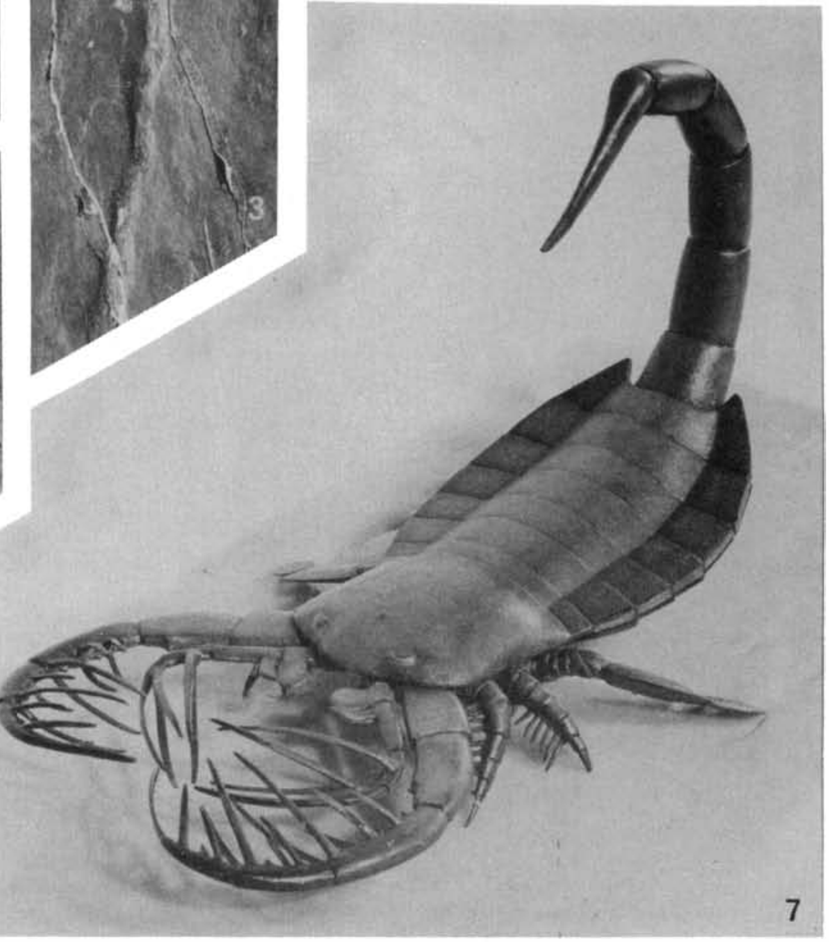


Plate 2

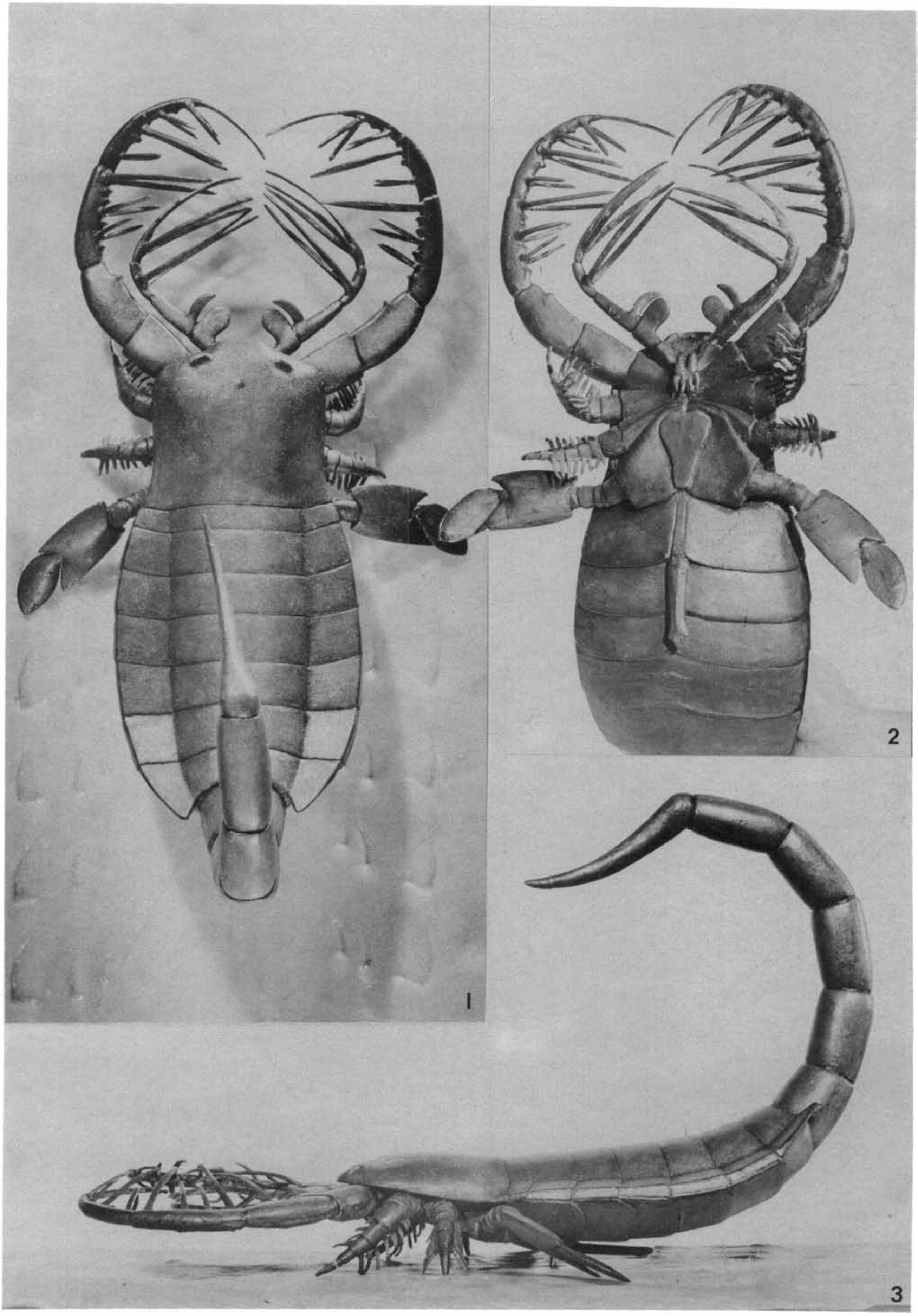


Plate 3