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# ON SOME TRAILS FROM THE TRIASSIC BEDS OF EAST GREENLAND

BY

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WITH 27 FIGURES IN THE TEXT

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# CONTENTS

# PREFACE

The bulk of the material described in the present paper was collected by the author on the Danish Pearyland Expedition in the summer of 1947. A few specimens, however, were collected by earlier expeditions. Thus, one specimen was found in June, 1937, by Dr. HANS STAUBER, who was a member of Dr. LAUGE KOCH's geological expedition to East Greenland 1936—38, and two others were brought home by the author in the summer of 1946, when he was the leader of a small expedition to East Greenland sent out by the Committee of the Geological Survey of Greenland (G. G. U.).

I am greatly indebted to the leaders of the Danish Pearyland Expedition, EIGIL KNUTH and EBBE MUNCK, as well as to the Committee of G. G. U. for the opportunities afforded me for carrying out my researches in the Triassic deposits of East Greenland during the summers of 1946 and 1947, as well as for the permission to work out the material brought home.

I am further indebted to Dr. LAUGE KOCH and Dr. HANS STAUBER, who permitted me to describe, together with my own finds, the specimen collected by Dr. HANS STAUBER in 1937.

For good cooperation I wish to thank stud. mag. ESKE KOCH, stud. mag. ULRIK RØEN, and Mr. HENRY NIELSEN, who at various times assisted me during the field work.

A special thank I owe to the authorities of the British Museum of Natural History for the loan of a specimen of the Devonian trail *Paramphibius*.

Most of the photografic work was done by Mr. HALKIER, preparator in the Mineralogical and Geological Museum in Copenhagen, and the remainder by Mr. AHL, preparator in the Palaeozoological Department of the Swedish Riksmuseum. To both these gentlemen I want to express my best thanks. To Professor E. STENSIÖ, head of the Palaeontological Department of the Swedish Riksmuseum, I owe the deepest gratitude for his never failing readiness to assist in all such cases where the technical equipment available in Denmark is insufficiant.

The drawings have been made by Miss INGEBORG FREDERIKSEN, to whom I tender my most cordial thanks for her careful work.

Finally I wish to thank Dr. J. TROELSEN for looking through the English manuscript.

# MATERIAL AND LOCALITIES

In June, 1937, Dr. H. STAUBER during his investigations of the Triassic sediments exposed on the northeastern slopes of Rold Bjærge on the northwestern part of the Traill Ø collected a slab of sandstone showing some very interesting footprints.

In a preliminary report, STAUBER (1938) briefly mentions these footprints as those of a stegocephalian. A few years later I, after an investigation of the specimen, put forward the supposition (1940, p. 680) that the footprints discovered by STAUBER were made by a small bipedal reptile.

In his large monograph on the Triassic deposits of East Greenland, STAUBER still seems inclined to refer the footprints from Traill Ø to a stegocephalian (STAUBER 1942, pp. 61, 273), though adding (p. 61) in a footnote the word "Reptilfährte?." In the same paper (p. 167), STAUBER also reports a find of a "Stegocephalen?—Fährte" from the upper part of the Triassic beds in the Kap Biot area farther south, but the specimen could not be found in the collections brought home.

In the summer of 1946, I went to East Greenland to look for vertebrate fossils in the Triassic areas on Traill Ø and, especially, to make an attempt to secure more and, if possible, better preserved material of the presumed vertebrate footprints first discovered by STAUBER. However, difficult ice conditions forced me to spend the first part of the summer in the Triassic area at Kap Stosch, and here I took the opportunity to make a very careful search for fossil footprints on Dieners Bjærg as well as on the eastern part of Steensbys Bjærg. (The name Dieners Bjerg was given by LAUGE KOCH in 1929 to a rather small peak immediately east of Steensbys Bjærg and used in the same sense by several later investigators. On the map published by the Geodætic Institute, however, the name has been transferred to a somewhat higher peak situated southeast of LAUGE KOCH's Dieners Bjærg. Here the name is used in its original sense).

According to STAUBER (1942, pp. 61, 273), the trail from Traill Ø (in this paper numbered Fp. 1) originated from the upper part of the Triassic sequence and probably from beds corresponding to the *Myalina*

*kochi*-zone in the Kap Stosch area, and the reason for choosing to hunt for similar trails just on the slopes of Dieners Bjærg and Steensbys Bjærg was that here the upper part of the Triassic sequence is far better exposed than in the more westerly part of the Kap Stosch area.

My search, which lasted for about 10 days, was rewarded with the find of two slabs of sandstone with footprints, of much the same appearance as those brought home by STAUBER, a fairly satisfactory result considering that such footprints had never previously been observed in the Kap Stosch area in spite of the fact that several geologists and palaeontologists had worked here for longer or shorter periods.

Both slabs were found on the northern slope of Dieners Bjærg, one (Fp. 2) 155 m and the other (Fp. 3) 247 m above sea level. The *Proptychites*-beds here occur at an altitude of only about 40 m (LAUGE KOCH 1931, p. 51; E. NIELSEN 1935, p. 70) and the *Myalina kochi*-zone probably at an altitude of 275 m.

The next summer (1947), I again got an opportunity to visit the Kap Stosch area, and this time I chose as my field of work the northern slopes of Frebolds Bjærg between River 8 and River 10 (cf. E. NIELSEN 1935, pl. 1), where the upper part of the Triassic sequence is exposed on Falkeryg just east of the large fault through the valley of River 9 (Immacradal).

On the first day of my stay I set out to investigate the exposures on the upper part of Falkeryg, but already during the ascent through the lower part of the Triassic sequence I found a small slab of sandstone with a series of very distinct small tracks. (I follow K. E. CASTER (1938) in using the terms "trail" and "track" as proposed by A. W. PACKARD (1900), viz. the term trail is restricted to a series of footprints made by an individual and the term track restricted to the individual footprint (K. E. CASTER 1938, p. 5, footnote)). The specimen (Fp. 21) was lying loose on the surface, just above the bed of hardened sandstone (conglomerate IV) which lies below the marine *Proptychites*- beds (cf. E. NIELSEN 1935) and thus at a much deeper horizon than any of the previous finds. I was inclined to believe that the small slab had slid down from the upper part of Falkeryg, but in spite of careful search both in the *Anodontophora* (*breviform*) beds and in the accessible lower part of the *Anodontophora fassaensis* -beds I did not succeed in finding any footprint-bearing layers at all in the upper part of the Triassic sequence. I then made my descent somewhat east of Falkeryg and to my great astonishment I came, when passing the slopes just east of Rævekløft, across another small slab of sandstone showing undoubted footprints. This second specimen (Fp. 25) came from the almost unfossiliferous sandy beds between the ammonite-bearing middle and upper *Vishnuites*-zones, and thus at a still deeper horizon than the first one,

and I now began to realize that it might be worth while to look for the presumed vertebrate tracks even in the lower part of the Triassic series in this area.

Some days later when I was looking for fishes in the *Proptychites*-beds on Pyramiden just west of River 9, I found on the ripple-marked surface of a thin hardened layer of sandstone, which was still in situ, a very great number of small depressions, most of which on closer inspection I judged to be marks of the claws of small tetrapods, while a few seemed to be more complete footprints of similar forms.

This sandstone layer, from which I brought home a number of specimens (Fp. 26a, 26b, 27a, 27b, and 28—35), occurs about 1 m above the upper surface of conglomerate IV, and as one of the finds from the first day also was collected just above conglomerate IV, I now felt convinced that it would be worth while to concentrate the search on this horizon in the Triassic sequence.

The last day of my stay in the Kap Stosch area I, therefore, paid a visit to the eastern slope of Falkeryg and to the small ridges just east of Falkeryg, where I knew from my many years of work in the area that the beds just above the conglomerate IV were especially well exposed.

The result was most satisfactory. Well-preserved tracks, in most cases arranged as smaller or larger parts of beautiful trails, were extremely common on the surfaces of several more or less hardened bands of sandstone in the zone between conglomerate IV and the *Proptychites*-beds, and a quite considerable material was secured) specimens Fp. 4a, 4b, 5a, 5b, 6, 7a, 7b, 8a, 8b, 9—19, 20a, 20b, 20c, 22—24, and 36—41).

The following section was measured through the footprint-bearing beds on one of the small ridges on the eastern slope of Falkeryg:

| | |
|---|---|
| Above 406.7 m: | The *Proptychites rosenkrantzi*-zone with numerous marine fossils, mostly found in small concretions. A few hardened bands of sandstone with sparse trails. |
| 406.7—406.0: | Loose, coarse-grained, sandy beds with some not very much hardened bands of coarse-grained sandstone showing ripple-marks and a few trails. |
| 406.0—405.3: | Loose, clayey beds with some very hard bands of grey or brownish fine-grained sandstone. Ripple-marks and beautifully preserved trails extremely common. |
| 405.3—405.0: | Loose, coarse-grained, sandy beds with a number of thin bands of coarse-grained, grey sandstone. Ripple-marks common. No trails. |
| Below 405.0 m: | Conglomerate IV. The thickness in this place is about 45 m. |

In my stratigraphical description of the Kap Stosch area, I published a section from Falkeryg measured on the main ridge itself (E. NIELSEN, 1935, p. 59) and differing from the section, now measured, in showing clayey beds with small concretions with *Spirorbis*, *Claraia*, *Naticopsis*, and coproliths directly overlying conglomerate IV. At my reinvestigation of this section in 1947 I also found marine fossils just above conglomerate IV, but the section in this place is much obscured by debris, and the presence of marine fossils might quite possibly be due to downsliding of the overlying strata.

On Pyramiden, the stratigraphy of the footprint-bearing beds just above conglomerate IV agrees closely with that of the corresponding beds on Falkeryg, and thus on a stretch of at least 3 km we are able to trace the footprint beds lying just above conglomerate IV. Probably these beds have a much larger extension both east and west. On Stegocephalryg (E. NIELSEN 1935, p. 58), for instance, conglomerate IV is separated from the *Proptychites*-beds by a sequence of about 13 m of unfossiliferous sediments, and also on Stensiøs Plateau (op. cit. p. 60), beds dévoid of fossils are underlying the *Proptychites*-beds.

STAUBER (1942) subdivides, mainly on the basis of his stratigraphic studies in the more southern Triassic areas, the Triassic deposits of East Greenland in a lower marine (Marine Serie), a middle continental (Kontinentale Serie), and an upper marine-brackish (Bunte Serie) sequence. This tripartition is identical with that previously used by other investigators (KOCH 1930; SPATH 1931, 1936; E. NIELSEN 1935), STAUBER's three divisions corresponding in the northern area to the lower division with ammonites, the middle division with *Anodontophora* (*breviform*), and the upper division with *Anodontophora fassaensis*, respectively.

As is evident from the above, the trails here dealt with occur as well in the marine, as in the continental and the marine-brackish sequence. It might seem rather peculiar that trails of the same appearance are present both in marine and in continental deposits. However, as pointed out by STAUBER (1942) the so-called marine sequence was mainly deposited in very shallow water in an area almost completely cut off from the open sea, the faunas of which only occasionally invaded the shallow water area. The trails might, therefore, in the marine sequence have been made under much the same conditions as in the continental or in the marine-brackish sequence, viz. in, or on the beaches of, shallow lagoons with brackish or even fresh water. According to STAUBER the climate in the shallow water areas was arid and warm and in the neighbouring mountain areas tropical-subtropical with warm and humid conditions.

# DESCRIPTION OF THE MATERIAL

## General remarks.

The trails from the Triassic deposits of East Greenland are preserved either as prints on the upper surface or as casts on the lower surface of slabs of more or less fine-grained sandstone. For practical reasons, however, I refer in the following description to the specimens as if they were all preserved as prints.

The trails consist of two principally different kinds of footprints which in the following will be termed respectively digitate and simple tracks. Some of the trails in addition show a narrow median groove or furrow dealt with in the following descriptions as the tail track.

The digitate tracks occur in a right and a left longitudinal series and each track of one of the series opposes one of the tracks of the other series. The most complete digitate tracks show the impression of a quite strong rod or bar the posterior end of which in many cases is bifurcated and from the anterior end of which issue 3 or 4 more or less diverging rays of varying length. In less complete digitate tracks the impression of the bar is much shorter or even completely lacking and in the most extreme cases only the distal ends of the anterior rays have left their marks.

The simple tracks which in most trails are more numerous than the digitate ones are also arranged in regular patterns, which, however, as a rule are different not only in different specimens, but also on the two sides of the same trail. The tracks appear as rather short, straight or slightly curved furrows, which anteriorly taper to a point and which posteriorly in most cases end at a tiny elevation presumably consisting of material pushed backward when the track was made. The furrows are either single or fused together two and two forming V- or Y-shaped figures.

At a first glance, almost every one of the trails might seem to represent a type of its own, but there can be no doubt that the great variability of the material is due, at least to some extent, partly to the differing consistency of the surface on which the tracks were made, and

partly to the varying ways of motion of the individual animals who made the trails.

The grain size of the slabs of sandstone on which the trails are found varies from fairly coarse to extremely fine. In some cases the surface of the slabs shows ripple-marks, in other cases it is quite smooth, and in still other cases it shows irregular flow structures of varying appearance. Many of the trails were made under water, and we may assume that under such conditions the relatively coarse-grained sediments had a rather firm surface, while the most fine-grained sediments had a consistency much like that of soft mud. Other trails bear the appearance of having been made on fairly dry surfaces of rather loose, more or less coarse sand.

On some of the most fine-grained sandstones the individual impressions of the trails are extraordinarily narrow (fig. 23), a condition which probably must be explained by the tendency of very soft material to flow back into the impressions just after they were made.

The presence or absence of a bar impression in the digitate tracks or of a tail track; the varying divarication of the anterior ray prints in the digitate tracks; the varying arrangement of the simple tracks; as well as the varying length of the interval between successive digitate tracks of the same longitudinal series in relation to the width of the trail, might all be regarded as differences due to variations in the way of motion of individuals of the same species.

All this thus leaves us with only a few characters of more reliability for arranging the present material in systematic units, be it of specific or generic value. Of such characters, all of which refer to the digitate tracks, the following may be mentioned: The number of the rays, the relative length of the rays of the same track, and the shape of the individual rays.

By using these characters we are able to distinguish between four types of footprints that may be characterized in the following way:

1. Digitate track with four rays:
   a. Great difference in length between the longest and the shortest ray ..... Type A
   b. Only small difference in Length between the rays:
      I. Long and rather slender rays ..... Type B
      II. Short and more massive rays ..... Type C
2. Digitate track with three rays ..... Type D

Whether these four types represent four or a smaller or larger number of different species, and whether they represent one or more genera, I am unable to decide on the small material at hand.

In the following description I, therefore, prefer to avoid introducing systematic names as there is every probability that some of these names will turn out to be untenable when more knowledge is gained of the Triassic fauna of East Greenland.

To a fifth type (Type E) I refer some trails from the footprint beds just above conglomerate IV, exclusively because of their extremely small size. The exact details of the very small digitate tracks cannot be determined in any of the specimens, and I am, therefore, unable to decide whether these small trails possibly represent very young individuals of one of the species represented by the Types A—D.

A few further comments to the following descriptions of the trails are necessary.

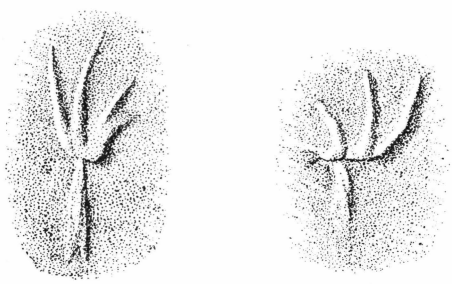
The 3 or 4 rays of the digitate tracks are numbered from the innermost to the outermost as respectively ray II to IV and ray I to IV.

The length of the digitate tracks is measured from the tip of the print of ray III to the posterior end of the bar impression.

The width of the trail is measured between the estimated anterior ends of the bar impressions of opposing digitate tracks.

## Type A.

Type characters: The digitate track with four slender, slightly curved rays (nos. I—IV). First ray very short, second ray somewhat longer, third ray considerably longer than



A B

Fig. 1. Type A. Casts of a right (A) and a left (B) digitate track. A, from trail Fp. 5a (fig. 2). B, from trail Fp. 4b (fig. 3). $^1/_1$.

the second, and fourth ray of about the same length as or slightly shorter than, the third.

To Type A I refer the specimens numbered Fp. 1, 2, 4a, 4b, 5a, 5b, 6, 7b, and 24. Specimens Fp. 1 comes from the lower part of the *Anodontophora fassaensis*-beds on Traill Ø, while all the others have been collected in the Kap Stosch area, viz., Fp. 2 in the *Anodontophora*

(*breviform*)-beds on Dieners Bjærg, and the others in the footprint-bed just above the conglomerate IV on the eastern slopes of Falkeryg.

The specimens numbered 4a, 4b, 5a, 5b, and 6 (figs. 1—5) are preserved as very distinct casts on the lower surfaces of three slabs of

Fig. 2. Type A. Trails Fp. 5a (right) and 5b (left). Preserved as casts. $^1/_2$.

Fig. 3. Type A. Trails Fp. 4a (right) and 4b (left). Preserved as casts. $^1/_2$.

fairly coarse sandstone. The three slabs were collected in the immediate neighbourhood of each other, and although they cannot be fitted together, it seems fairly certain that they all belong to the same band of sandstone and that their five trails were made by only two individuals, the specimens Fp. 4b, 5b, and 6 being parts of one and specimens Fp. 4a, and 5a parts of another trail.

Of the trail represented by specimens 4a and 5a (figs. 1A, 2, 3, 5) only parts of the right half are preserved. The length of the right digitate

track is 31 mm, of which the bar impression constitutes about 13 mm. The divarication between the first and the fourth ray is about 60°. The distance between successive digitate tracks is ca. 56 mm. In the interspace between successive digitate tracks we find two simple tracks, one of which, as shown in the figures, is placed a rather short distance

Fig. 4. Type A. Diagram of trail Fp. 5b (fig. 2). Restored parts ruled. $^1/_2$.

Fig. 5. Type A. Diagram of trail Fp. 4a (fig. 3). Restored parts ruled. $^1/_2$.

antero-medially to the posterior digitate track and the other a short distance laterally to the anterior digitate track. The longitudinal axes of these simple tracks are parallel to the axis of the trail.

The trail represented by the specimens Fp. 4b, 5 b, and 6 (figs. 1 B, 2—4) may be reconstructed in most details, as here the tracks of both the right and the left side are preserved.

The length of the digitate track is 23 mm, of which the bar impression constitutes about 11. The divarication between the first and the fourth ray is about 120°, thus far more than in the specimen described above. The width of the trail is about 75 mm and the distance between successive digitate tracks varies between 58 and 65 mm.

In the interspaces between successive digitate tracks we find four simple tracks on the left half of the trail and three on the right half, arranged as shown in the figures. Probably the hindmost and the inner-

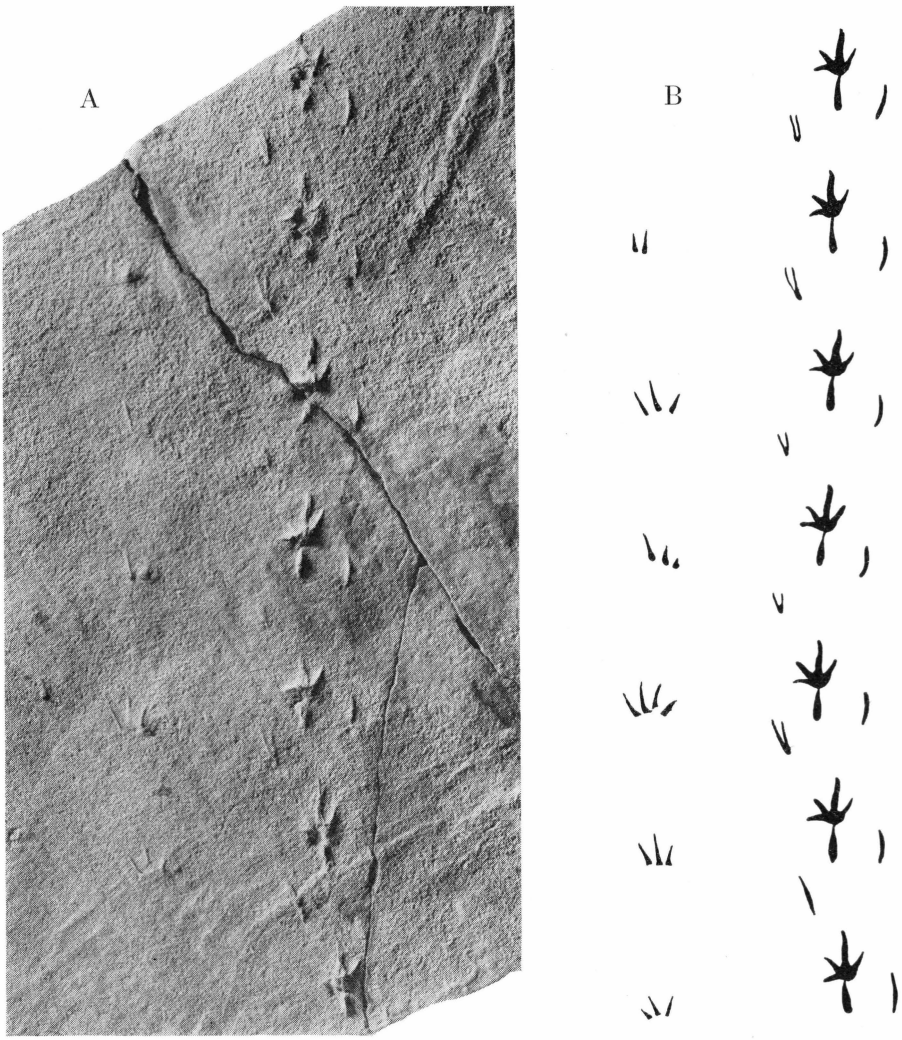



Fig. 6. Type A. A, trail Fp. 7 b. Preserved as a cast. $^2/_3$. B, slightly restored diagram of the same trail. $^2/_3$.

most simple track on the left side are analogous to the hindmost and the innermost on the right side, while the third simple track on the right side is analogous either to the lateral or to the foremost simple track on the left side.

The other specimens referred to Type A are not quite as satisfactorily preserved as those already described.

Fig. 7. Type A. Diagram of trail Fp. 24. Restored parts ruled. $^1/_2$.

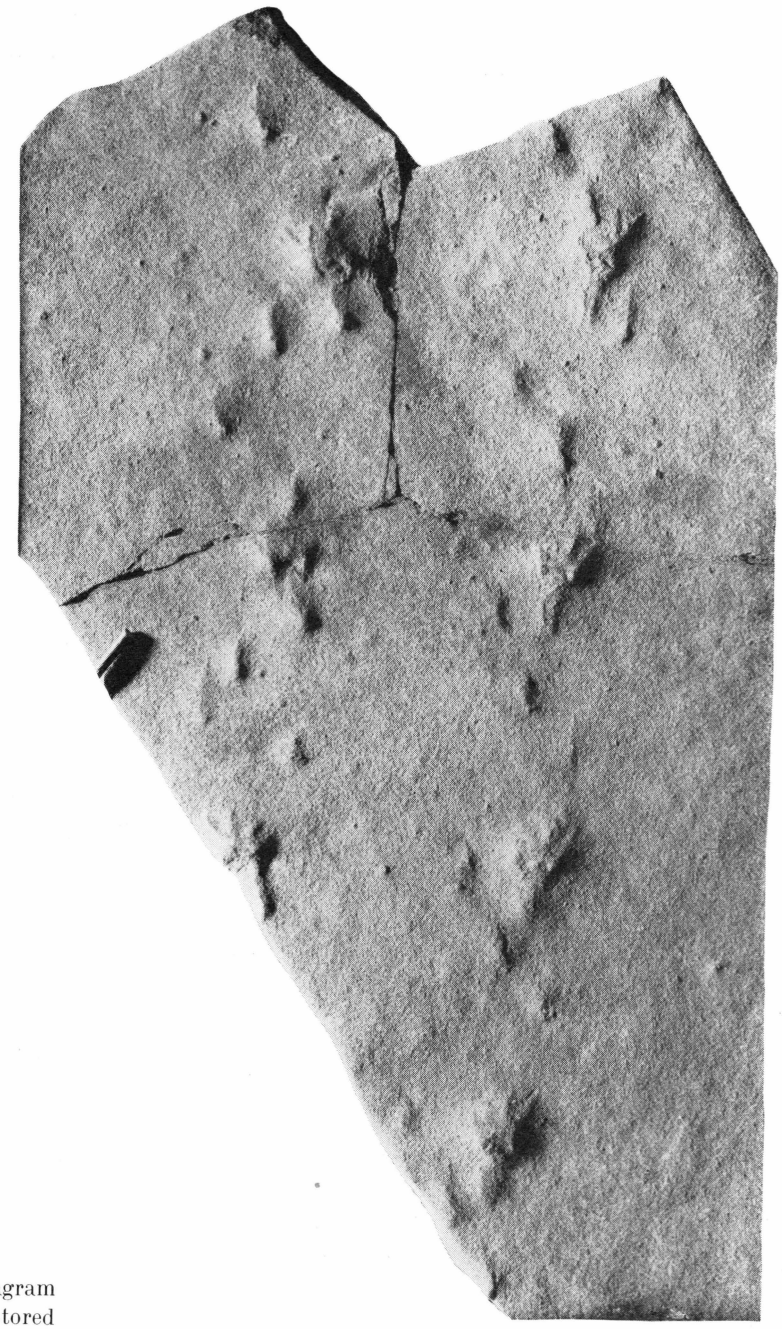


Fig. 8. Type A. Trail Fp. 1. Preserved as a cast. $^1/_2$.

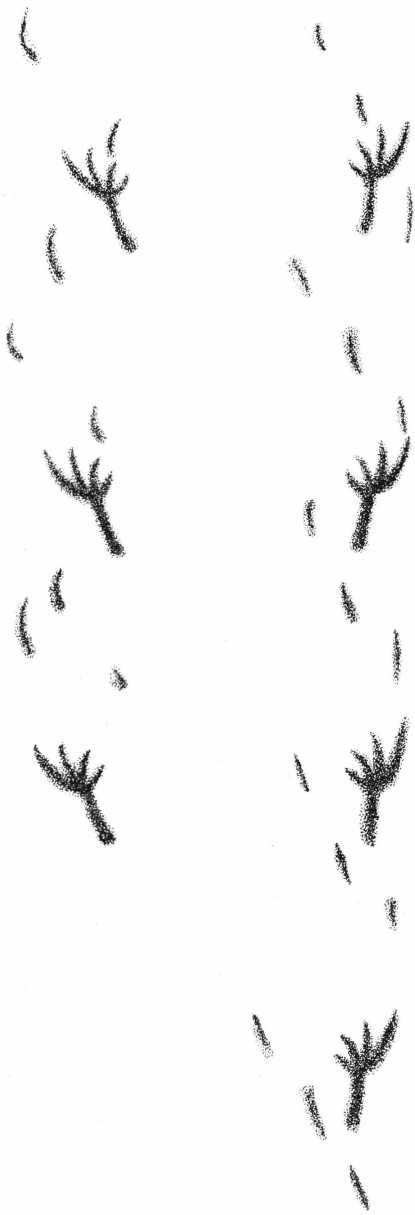


Fig. 9. Type A. Diagram of trail Fp. 1 (fig. 8). Most of the digitate tracks partly restored. $^1/_2$.

Fig. 10. Type A. Diagram of trail Fp. 2. Restored parts ruled. $^1/_2$.

Specimen Fp. 7b (fig. 6) is a rather long trail preserved as a cast on the lower surface of a slab of extremely fine-grained sandstone. The left half of this trail shows a continuous series of tolerably distinct digitate tracks and a regular pattern of simple tracks while the right half is almost obliterated, showing only faint remnants of six digitate tracks.

Judging from the best preserved part of the trackway, the digitate tracks agree in shape with those already described, although they are considerable smaller.

The length of the digitate track is about 15 mm, of which about 6 mm is occupied by the bar impression. The width of the trail is ab. 35 mm, and the distance between successive digitate tracks varies from 29 to 32 mm.

Between each two successive digitate tracks we observe two simple tracks situated antero-medially and antero-laterally, respectively, to the digitate track immediately behind. The antero-medial tracks are V-shaped.

Specimen Fp. 24 (fig. 7) shows a continuous series of three right digitate tracks accompanied by a number of simple tracks and is preserved as a cast on the lower surface of a slab of rather coarse-grained sandstone.

The only complete digitate track shows a first ray which is relatively longer than normal in Type A, but this might possibly be explained by the not very satisfactory state of preservation of the specimen. In other respects the track agrees quite well with those already described.

The length of the digitate track is 24 mm, 12 of which are taken up by the bar impression. The distance between two successive digitate tracks varies from 85 to 90 mm. In the interspace between two successive digitate tracks we find four simple tracks arranged as shown in the figures.

Specimen Fp. 1 (STAUBER'S specimen) is a trail preserved as a rather poor cast on the lower surface of a slab of coarse-grained sandstone (figs. 8, 9).

The trail consists of three right and four left digitate tracks besides a large number of simple tracks, which are arranged on each side of the trail in a regular pattern.

The digitate tracks are so poorly preserved that their details are very difficult to make out. There can be no doubt, however, that they are referable to Type A. The length of the tracks are about 28 mm. The width of the trail varies from 70 to 75 mm, and the distance between successive digitate tracks are 72, 78, and 83 mm, respectively, the hindmost interval being the shortest and the foremost one the longest.

On the left side of the trail, which is the better preserved one, the simple tracks are arranged three and three together in oblique rows

directed anteriorly and somewhat medially. As shown in the diagram (fig. 9), the interspaces between the successive rows of simple tracks decrease in size in an anterior direction, while, as just mentioned, the interspaces between successive digitate tracks increase in size forward. Accordingly, while the hindmost digitate track is separated by a rather great interspace from the row of simple tracks next in front, the corresponding interspaces grow gradually smaller towards the anterior end of the trail, and the foremost digitate track is in fact situated in the foremost oblique row itself between the middle and the posterior simple tracks.

On the right side of the trail a somewhat similar arrangement of the simple tracks in oblique rows may be observed. Here, however, the digitate tracks are situated between the anterior and the middle simple tracks of the oblique rows.

The last specimen referred to Type A, specimen Fp. 2 (fig. 10), is preserved on a slab of fairly coarse sandstone from the *A.* (*breviform*)-beds on Dieners Bjærg.

The slab shows two successive right digitate tracks and anterior to each of these tracks three simple tracks, the two largest of which are situated at about equal distances from the digitate track next behind and that next in front, while the third one is situated quite near the posterior end of the digitate track in front.

Both digitate tracks are incomplete, and therefore their exact length is difficult to measure. However, it was probably slightly smaller than the length of the digitate track in specimen Fp. 1. The distance between the two successive digitate tracks is ab. 115 mm.

In none of the specimens referred to Type A, a tail track has been observed.

## Type B.

Type characters: The digitate track with four slender, straight or very slightly curved rays (nos. I—IV). The first and fourth ray of about the same length and not very much shorter than the second and the third ray.

To this type I refer the specimens Fp. 12, 14, 20b, 21, 22, and 33, three of them—Fp. 14, 20b, and 22—, however, only with doubt. All the specimens come from the footprint-bearing beds just above conglomerate IV on Falkeryg except specimen Fp. 33, which was collected in the corresponding beds on Pyramiden.

The most complete specimens referred to Type B is Fp. 21, 22, and 11—13), a short trail on a slab of rather fine-grained sandstone. The trail shows three right and two left digitate tracks, and, as shown in fig. 13, these five tracks belong to four different pairs. The left half of

the trail is rather badly damaged and shows no simple tracks, but on the right half a simple very distinct single track is situated just medially to each digitate one.

Of the five digitate tracks, only two right ones are complete, and curiously enough these two (fig. 11), differ to a fairly large extent. In one of the tracks, the first ray is separated throughout its length from the second one, while the other track the proximal parts of the first and second rays seem to have become fused. Moreover, there is a fairly considerable difference between the tracks with respect to the appearance of the proximal parts of the rays, one of the tracks showing some curious

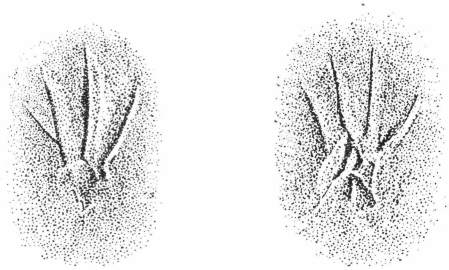



Fig. 11. Type B. Two right digitate tracks from trail Fp. 21 (fig. 12). $^3/_2$.

impressions which look like impressions of small pads, while no such structures are found in other specimens. At least the latter of these differences, however, might be explained by assuming that the track shown in fig. 11 B is to some extent filled out by some fine-grained matrix the surface of which shows impressions which have nothing to do with the print itself.

Apart perhaps from its extreme distal part, the bar impression is lacking, a difference from Type A which, as already mentioned (p. 11), not necessarily has any specific value.

The length of the digitate track is about 12 mm, and the divarication between the first and the fourth ray about 60°.

The width of the trail is ab. 50 mm, but the distance between successive digitate tracks is only about 22 mm.

As shown in the figures, the simple tracks are long, straight furrows extending parallel to the axis of the trail. The medial wall of the furrow is much steeper than the lateral one. The elevations usually found at the posterior end of the simple tracks are lacking.

Specimen Fp. 12 shows a small part of the right half of a trail on a slab of very fine-grained sandstone.

Two successive right digitate tracks are preserved, and the foremost of these is almost complete. The length of this track is about 11 mm,

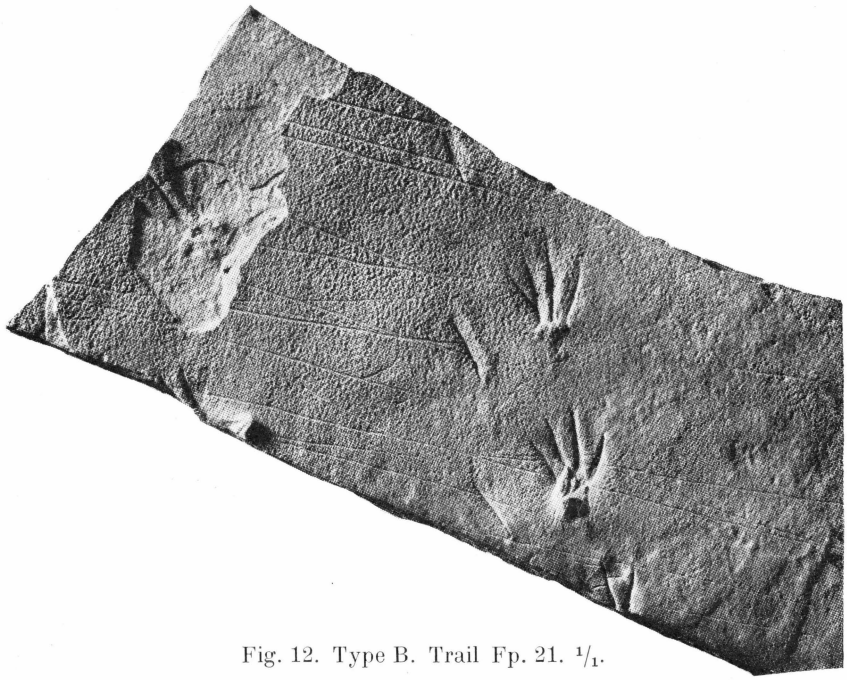


Fig. 12. Type B. Trail Fp. 21. $^1/_1$.

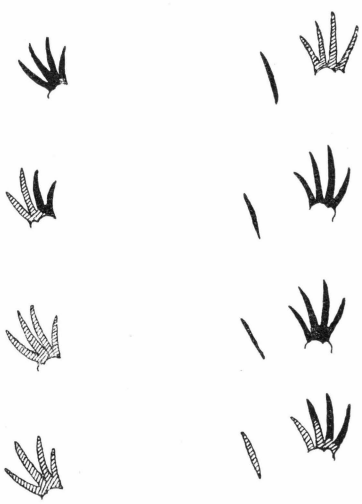


Fig. 13. Type B. Diagram of trail Fp. 21 (fig. 12). Restored parts ruled. $^3/_4$.

and the distance between the two tracks ab. 23 mm. Medially of the most complete digitate track we find a very distinct simple track extending in a longitudinal direction and ending posteriorly in a small elevation. Some other simple tracks on the same surface evidently do not belong to the trail here under discussion.

Specimen Fp. 33 is a isolated, probably right digitate track on a slab of fine-grained sandstone. The track is surrounded by several simple tracks, but probably the simple tracks and the digitate tracks do not belong to the same trail.

Specimen Fp. 20b, which only with doubt is referred to Type B, shows a continuous series of four right digitate tracks, preserved as casts on the lower surface of a slab of fine-grained sandsstone.

Of the foremost and the hindmost track only a small part is preserved, and the second track from behind is also rather badly damaged. Thus only a single track is satisfactorily preserved, and this track differs from those already referred to Type B in possessing a long and well marked bar division. The length of the track is 20 mm, of which the bar impression constitutes 9 mm. The distance between successive tracks is about 46 mm.

Just medially to each of the two best preserved digitate tracks a distinct simple track may be seen. It is developed as a long and narrow furrow extending in a mainly longitudinal direction and being slightly curved with the concavity directed medially. Posteriorly this simple track terminates in a small elevation.

Each of the two other specimens referred with doubt to Type B (Fp. 14 and 22) consists of a single digitate track on a small slab of fine-grained sandstone. In both tracks, the first ray is somewhat shorter than in the specimens just described, but otherwise they represent the normal characters of Type A.

### Type C.

Type characters: The digitate track with four acuminate rays (nos. I—IV), the basal parts of which are relatively broad, and all of which are of about the same length.

To this type I refer specimens Fp. 17—19, all of which come from the footprint-bearing beds just above conglomerate IV on Falkeryg. To the same type probably also belong specimens Fp. 26a, 27a, 28—32, 34, and 35a, which have been collected in the corresponding beds on Pyramiden.

Specimen Fp. 17 shows two successive left digitate tracks on a slab of rather fine-grained sandstone. Of the two tracks the hindmost one (figs. 14, 15A) is very beautifully preserved, while of the foremost one only a small part remains. The length of the more complete track is about 20 mm, of which the bar division constitutes 12 mm.

The first ray is directed almost straight inward, and the divarication between the first and the fourth ray is about 105°. The width of the trail cannot be measured. The distance between the two tracks measures ab. 65 mm. No single tracks have been observed.

Specimen Fp. 18 shows a single digitate track, the size of which probably was about the same as in the preceeding specimen. Both the ray prints and the bar impression in specimen Fp. 18 are narrower

Fig. 14. Type C. Digitate track (left). Specimen Fp. 17 (fig. 15A). $^3/_2$.

than in specimen Fp. 17, a difference which, as already explained (p. 11), is probably due to the different consistency of the fine-grained material on the surface of which the prints were made.

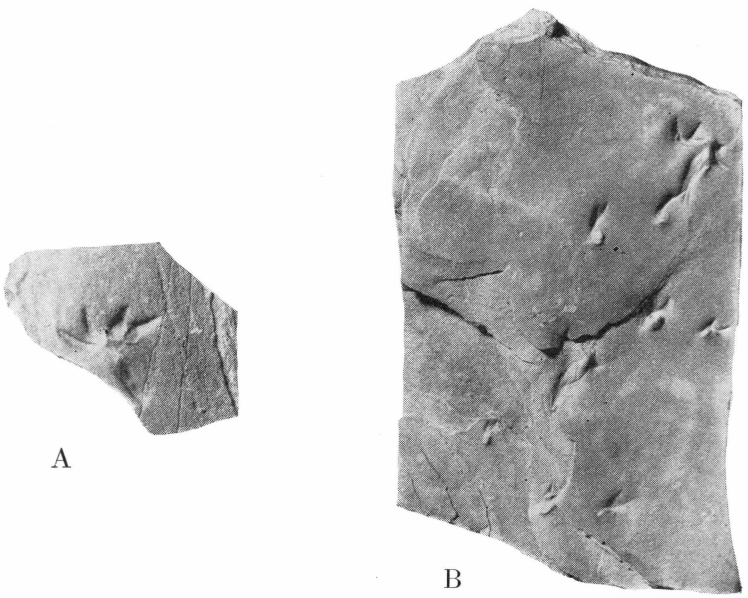



Fig. 15. Type C. A, a single left digitate track. Specimen Fp. 17 (fig. 14) $^3/_4$. B, trail Fp. 19. $^3/_4$.

Anterior of the digitate track we observe four small simple tracks arranged in two groups, each of which contains two short antero-medially pointing furrows separated by a fairly large elevation.

A third group of simple tracks, also containing two short furrows separated by an elevated area, may be seen some distance postero-laterally to the digitate track.

Specimen Fp. 19 (fig. 15B) shows two successive left digitate tracks on a slab of very fine-grained sandstone. Although they are rather poorly preserved, there can be no doubt that the tracks belong to the same general type as those of specimens Fp. 17 and 18. The length of the most complete track is about 13 mm, and the distance between the two tracks is 44 mm. Together with the digitate tracks we may observe a number of simple tracks arranged in pairs. In the interspace between the two digitate tracks two such pairs of simple tracks are present, one situated antero-laterally to the other. The simple tracks are all V-shaped, and the divarication between the two branches of the V is the same within the same pair of simple tracks but of another size in the postero-medial than it is in the antero-lateral pair.

Specimens Fp. 26a (fig. 17A), 27a, 28—32, 34, 34, and 39, which probably is referable to Type C, are preserved on the upper surfaces of a number of slabs of fairly coarse-grained sandstone and differ from the specimen described above in consisting of small triangular impressions grouped four and four together and associated with simple tracks some of which are V-shaped.

From the arrangement of the triangular impressions there can be no doubt that they represent tips of rays of digitate tracks of much the same shape as those already referred to Type C. That the basal parts of the rays as well as the bar division left no impressions on the surface is either due to the already hardened condition of the surface at the time when the tracks were made; or to a difference in the way of motion of the animals who made the tracks in the two localities.

In many specimens from Pyramiden a great number of digitate and simple tracks are present on the same surface. However, their mutual arrangement seems quite haphazard, and in no case is it possible to decide which prints belong to the same trackway.

## Type D.

Type characters: The digitate track with only three rays (nos. II—IV), the middle and largest of which is directed forward, while the two others are directed medially or antero-medially and laterally or antero-laterally, respectively.

To this group I refer specimens Fp. 26b and 27b from the foot-print-bearing beds just above conglomerate IV on Pyramiden; specimen Fp. 23 from the corresponding beds on Falkeryg; and specimen Fp. 25

from a slab of sandstone collected on the surface of the middle *Vishnuites*-beds just east of Rævekløft.

Three of the four specimens show only a single digitate track, while the fourth one (Fp. 25) shows two successive digitate tracks. specimens Fp. 23 and 25 show moreover, a few simple tracks. As none of the specimens shows tracks from both sides of a trail nor a tail track, it is not possible to decide whether the digitate tracks found are left or right ones, and, accordingly, it is also impossible to decide which one of the rays is the outer ray, and which one the inner one.

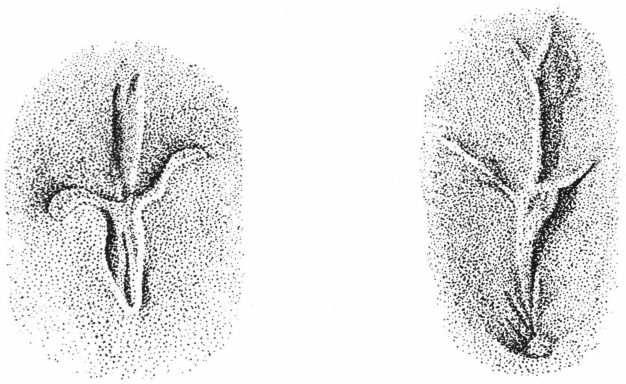



Fig. 16. Type D. A, digitate track. Specimen Fp. 26b (fig. 17A). $^3/_2$. B, digitate track. Specimen Fp. 23 (fig. 17B). Preserved as a cast. $^3/_2$.

In all four specimens, the digitate tracks show a long bar impression, which forms a backward continuation of the print of the forwardly directed middle (third) ray. In specimens Fp. 26b, 27b, and 23, the middle ray bifurcates in its most distal part, a fact which will be commented upon in a later chapter (p. 38).

Specimen Fp. 23 (figs. 16B, 17B) is preserved as a cast on the lower surface of a slab of rather coarse-grained sandstone. The length of the digitate track is about 30 mm, of which the bar impression constitutes 15 mm. The divarication of the outer and the inner ray is about 110°. A short distance anterior of the middle ray we find three small simple tracks arranged, as shown in fig. 17B, in an oblique row. The posterior one of these tracks is a single furrow, while the two others consist of two small oblong impressions separated by a rather large elevation.

The two three-rayed digitate tracks from Pyramiden (Fp. 26b and 27b)differ from the specimen from Falkeryg, partly in their smaller size (length of the most complete one (figs. 16A, 17A) about 20 mm), and partly in the strong backward curvature of their outer and inner

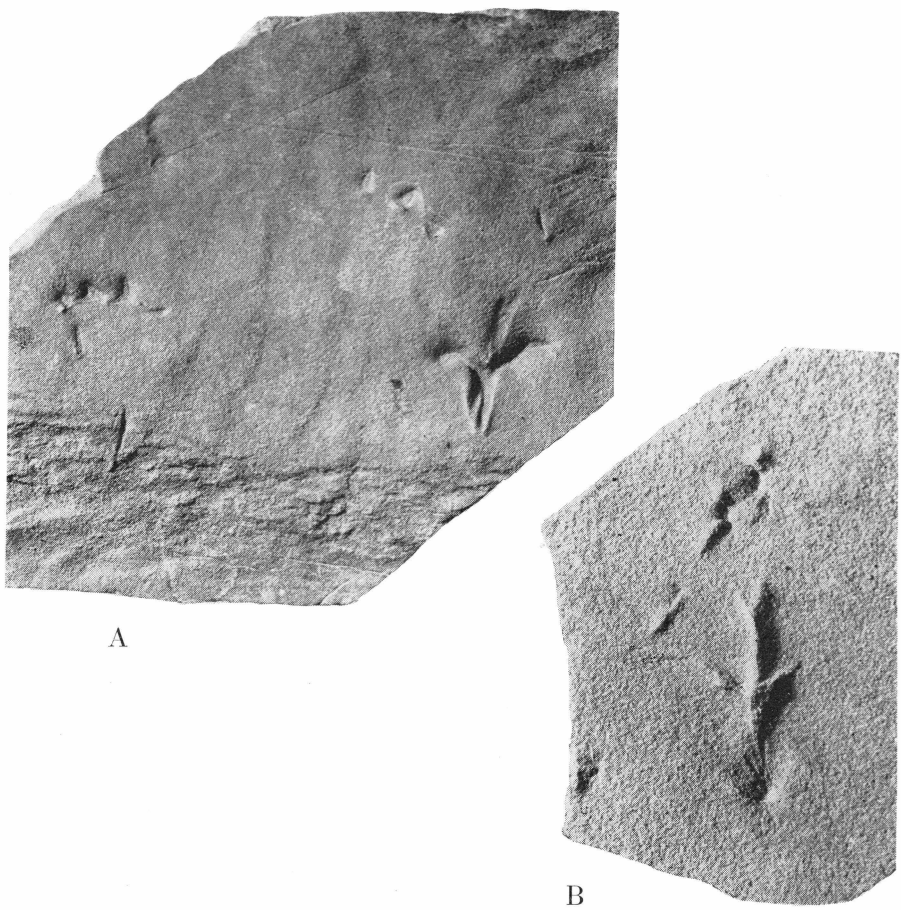



Fig. 17. Type D. A, digitate track (at right). Specimen Fp. 26b (fig. 16A). On the same slab are, furthermore, ray prints of two digitate tracks which are probably referable to Type C and which are listed as Fp. 26a. $^1/_1$. B, trail Fp. 23 (fig. 16B). Preserved as a cast. $^1/_1$.

ray. No simple tracks are associated with any of these two digitate tracks.

Specimen Fp. 25 (fig. 18), which, as already mentioned, shows two successive digitate tracks associated with a number of simple tracks, is preserved as a cast on the lower surface of a slab of fine-grained sandstone.

The outlines of the two digitate tracks, of which only the foremost one is complete, are rather poorly defined, a fact that is probably due to the very soft material in which the prints were made.

As far as can be ascertained, the complete track agrees in shape very well with the two three-rayed digitate tracks from Pyramiden

but measures in length no less than 42 mm. The distance between the two tracks is between 90 and 100 mm.

The arrangement of the presumed simple tracks of which four are found in the interspace between the two digitate tracks, is shown in fig. 18.

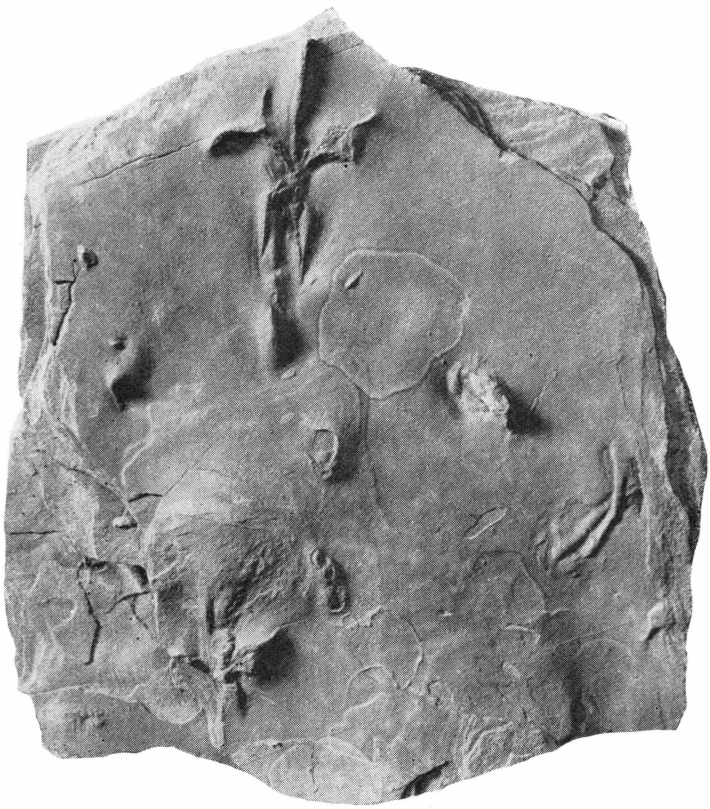


Fig. 18. Type D. Trail Fp. 25. Preserved as a cast. $^3/_4$.

## Type E.

Type character: Extraordinarily small trails.

To Type E I refer specimens Fp. 8a, 8b, and 9, which were collected in the footprint-bearing beds just above conglomerate IV on Falkeryg, and which are preserved on two slabs of ripple-marked fine-grained sandstone.

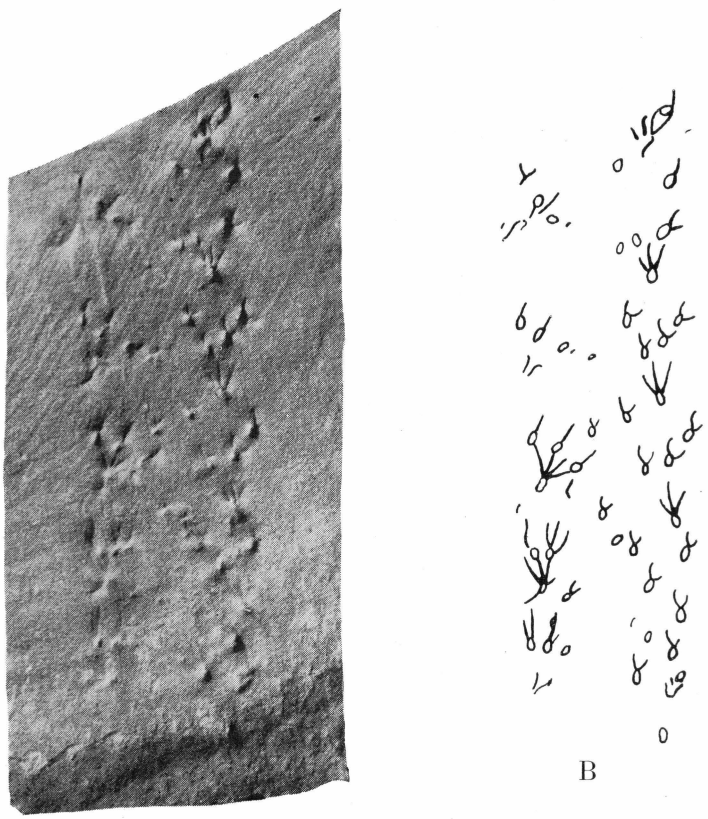
On some stretches the details of these diminutive trails (figs. 19, 20) ar fairly distinct, and here we are able to distinguish a number of small digitate tracks associated with numerous small, often V-shaped simple tracks that form a regular pattern on each side of the trail. The digitate tracks are arranged in two longitudinal series, and each track in one

series opposes, or nearly opposes, one of the tracks in the other series. Most of the digitate tracks show three rays (nos. II—IV). In a few tracks, however, a faint impression of a fourth ray (no. I) seems to be

Fig. 19. Type E. Tracks Fp. 8a (below) and 8b (above). $^3/_4$.

present. The third ray is only slightly longer than the second or fourth ones, and the divarication between the second and the fourth ray is less than 90°. The length of the digitate tracks is between 2 and 3 mm. The width of the trail is ab. 9—11 mm, and the distance between successive digitate tracks varies from 4 to 10 mm.

At the posterior end of the digitate tracks and the simple tracks, we find a small distinct elevation as indicated in fig. 20 B. A continuous tail track may be seen in specimen Fp. 8b as an almost straight furrow, and shorter sections of a tail track are present in both of the other specimens.



A B

Fig. 20. Type E. A, trail Fp. 8b (fig. 19). $^3/_2$. B, diagram of the same trail. The small unshaded areas surrounded by an unbroken line represent the elevations behind digitate and simple tracks. $^3/_2$.

## Specimens not referred to any of the previous types.

In addition to the specimens already described, the present material includes several others which I at the present time prefer not to refer to type. These specimens are Fp. 7a, 10, 11, 13, 15, 16, 20a, 36—39, 40, and 41 from the footprint-bearing beds just above conglomerate IV on Falkeryg, and specimen Fp. 3 from the *Anodontophora* (*breviform*)-beds on Dieners Bjerg.

Some of these specimens are, however, sufficiently interesting to deserve a short description.

Specimen Fp. 13, which is preserved as a cast on the lower side of a slab of fairly coarse-grained sandstone, shows two successive left digitate tracks and, anterior to each digitate track, two small simple tracks, one of which is situated some distance antero-medially of the other.

Fig. 21. Trail Fp. 16. Preserved as a cast. $^3/_4$.

Each digitate track shows four slender rays of about the same length and, in addition, a well-marked but rather short bar division. My reason for hesitating in referring the specimen to Type B is that the first and second ray have apparently become fused to a rather considerable extent, and a similar fusion has apparently taken place between the third and the fourth ray.

Specimen Fp. 16 (fig. 21) is preserved as a cast on the lower surface of a slab of very fine-graind sandstone.

The specimen shows a series of five successive left digitate tracks associated with numerous simple tracks that are arranged three or four

together in antero-medially directed rows. On the right side of the trail digitate tracks are apparently completely lacking and on that part of the surface of the slab where we should expect to find them, we find instead an irregular pattern of deep and straight, short furrows, either single or combined to peculiar triradiate structures. Probably these

Fig. 22. Specimen Fp. 36. $^2/_3$.

furrows represent the right half of the trail, the left half of which is preserved on the same slab, but they bear an amazing similarity to certain fossil trails made by insects (cf. ABEL 1935, figs. 226, 227).

Specimens Fp. 20a, 36, 37, and 38 are of interest on account of the deviating shape of their tracks. In specimen Fp. 36 (fig. 22) the rays of the digitate tracks are abnormally long and in the other specimens Fp. 20a (fig. 23), 37 (fig. 24), and 38 the simple tracks are extraordinarily long and often very strongly bent. The appearance of these tracks strongly suggests that they were made by swimming animals the limbs

Fig. 23. Specimen Fp. 20a. $^2/_3$.

of whom during their movements made the long grooves in a very soft bottom.

Specimen Fp. 7a (fig. 25), which is preserved on a slab of very fine-grained sandstone, is a fairly long trail showing no less than 16 digitate tracks in addition to numerous simple tracks and a long, almost straight tail track.

The exact outlines of the digitate tracks, which as shown in the diagram fig. 25 B, represent 9 successive pairs, cannot be determined, and it is also uncertain whether the number of rays is three or four. The shape of the digitate tracks as shown in the diagram must therefore be regarded as only sketchy.

The length of the digitate track is ab. 10 mm, the width of the

Fig. 24. Specimen Fp. 37. $^3/_4$.

trail is ab. 40 mm, while the distance between successive digitate tracks varies from 26 to 30 mm.

The simple tracks, some of which are V-shaped as shown in the diagram, are arranged in a regular pattern on each side of the trail, and as usual the pattern on the right side differ fairly strongly from that of the left.

As indicated on the diagram, the simple tracks usually terminate at one end close to a small elevation, and, moreover, a regular pattern of elevations no combined with simple tracks also belongs to the trail.

It is sincerely to be hoped that more and better preserved material of this complicated trail will be obtained during the future work in the Kap Stosch area.

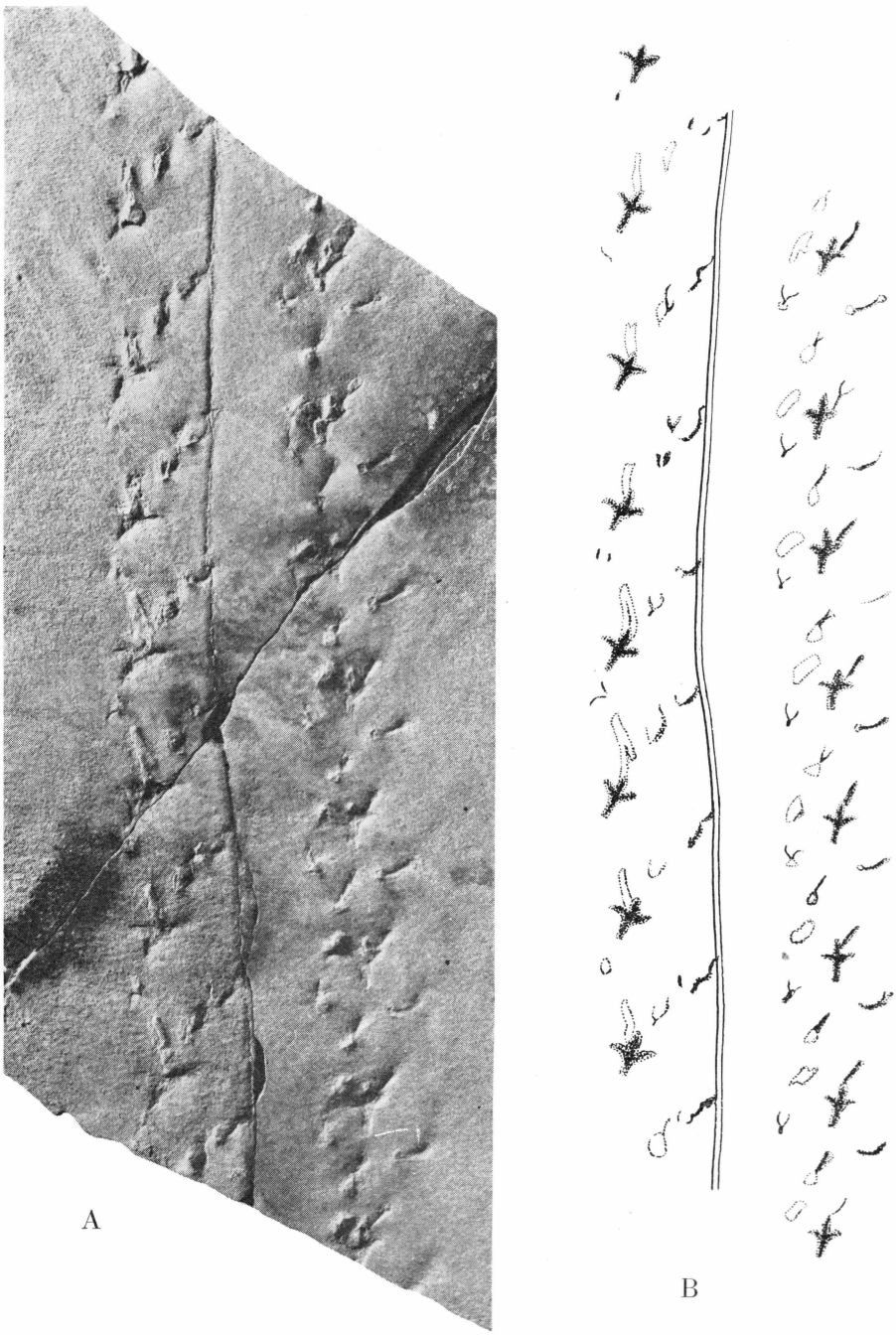



Fig. 25. A, trail Fp. 7a. $^2/_3$. B, diagram of the same trail. Unshaded areas surrounded by a dotted line indicate elevations. Most of the digitate tracks somewhat restored. $^2/_3$.

# DISCUSSION

As mentioned above (p. 6) Dr. H. STAUBER who collected the first specimen of the trails dealt with in this paper assumed it to be the trail of a stegocephalian. STAUBER does not state his reasons for this assumption. Very probably, however, it was at least to a certain degree based on the fact that the only tetrapods so far known from the Triassic deposits of East Greenland were stegocephalians.

The present author's later assumption that STAUBER's specimen as well as the two specimens found in 1946 (E. NIELSEN 1940, p. 680; 1947, p. 240) were trails, not of stegocephalians but of small bipedally leaping reptiles, was based mainly on the general agreement between these trails and some previously known presumed tetrapod trails, viz. *Kouphichnium lithographicum* OPPEL from the Upper Jurassic Lithographic Stone of Bavaria and *Micrichnus scotti* ABEL from the Upper Triassic in the neighbourhood of Princeton, N. Y.

*Kouphichnium lithographicum* was described as early as 1862 by A. OPPEL. Later the same form has been discussed by several other authors, and especially O. ABEL (1926, 1935) has made it the subject of a very careful analysis. In their interpretations of *Kouphichnium* the different authors prior to 1926 have arrived at very different results, which may briefly be summarized as follows: OPPEL (1862) and J. WALTER (1904) considered the tracks to be those of *Archaeopteryx;* FIGUIER (1863), FRAAS (1866), and WINKLER (1886), those of pterosaurians; ABEL (1911, 1912) and F. NOPCSA (1923), those of small coeluroid dinosaurians.

Later on, after his investigations in 1926 of *Kouphichnium* and of *Micrichnus scotti* (discovered by himself during a visit to the U.S.A.), ABEL, being more cautious than in his earlier papers, leaves the question open as to whether we are dealing with the tracks of birds, mammals, or reptiles, and in 1935 he ends (p. 123—124) his discussion of *Micrichnus* as follows:

"Die einzige Form, die sich, wenn auch nur in sehr entfernte Beziehungen zu *Micrichnus scotti* bringen liesse, wäre *Scleromochlus taylori*

aus der Trias von Lossiemouth bei Elgin in Schottland. Ebenso wäre etwa an *Saltopus* oder *Hallopus* zu denken."

In the next chapter of the same work he writes (pp. 140—141) regarding the systematic position of *Micrichnus* and *Kouphichnium:*

"Die Zeit aus der uns die Fährtentype *Micrichnus* erhalten geblieben ist, würde ja mit jener Zeit zusammenfallen, in der aus anderen Gründen die Existens des Vogelstammes bereits angenommen werden darf. Aber einstweilen bieten uns die Fährten des unbekanntesn Tieres, das den Fährtentypus *Micrichnus* hinterliess, ebensowenig einem sicheren Anhaltspunkt zur Beantwortung dieser Frage wie die Fährtentype *Kouphichnium* aus dem oberen Jura Deutschlands, aus derselben Zeit, aus der uns die Reste von *Archaeopteryx* vorliegen. Ebensogut wäre es ja auch denkbar, dass die beiden Fährten von Vertretern eines Wirbeltierstammes hinterlassen wurden, von dem wir bis heute noch nichts weiter als nur die Fährten kennen. Die Tiere müssen ja sehr klein gewesen sein, etwa von der Grösse einer Wüstenspringmaus und gerade aus der Tithonstufe Bayerns haben wir bis jetzt noch kein einziges Säugetier kennengelernt obwohl diese ja schon seit sehr langer Zeit existiert haben. Ob wir uns mit der Annahme zufrieden geben sollen, das *Micrichnus* und *Kouphichnium* Fährten kleiner springender Dinosaurier gewesen sind, oder ob wir einstweilen lieber auf den Versuch verzichten sollen eine Beziehung zur irgendwelchen uns bekannten Wirbeltiergruppen herzustellen, ist schwer zu entscheiden. Ich neige eher der Meinung zu, dass wir bei der Denkung vorzeitlicher Lebensspuren so vorsichtig als nur möglich zu Werke gehen mussen, um nicht die Versuche ihrer Erklärung in Misskredit zu bringen. Darum erscheint es mir richtiger, die Frage nach der systematischer Stellung der Erzeuger der beiden Fährtentypen *Kouphichnium* und *Micrichnus* einstweilen unbeantwortet zu lassen."

In the same connection ABEL (pp. 91, 123, 141) calls attention to the fact that tracks of small bipedally leaping land vertebrates are also known from Upper Carboniferous deposits, viz. *Crucipes parvus* BUTTS from Kansas City, Missouri (E. BUTTS, 1891, p. 19; O. ABEL, 1935, pp. 88—90, fig. 68) and *Ornithoides* (?) *heringi* GEINITZ from Ölsnitz, Sachsen (H. SCHMIDT, 1927, p. 521, fig. 4; 1928, p. 178; O. ABEL, 1935, pp. 90—91, figs. 70—71) and suggests (p. 91) that *Ornithoides* (?) *heringi* may be "eine Vorstufe" to *Micrichnus* and *Kouphichnium.*

For the sake of completeness we must here also mention two papers by O. JAEKEL and M. WILFARTH, respectively, dealing with tracks of the *Kouphichnium* type from the Lithographic Stone. JABKEL's paper was published in 1929 and thus later than ABEL's work on *Kouphichnium*, the results of which JAEKEL, however, completely ignores. The main object of the investigations by JAEKEL is a gelatine cast of one of the specimens of

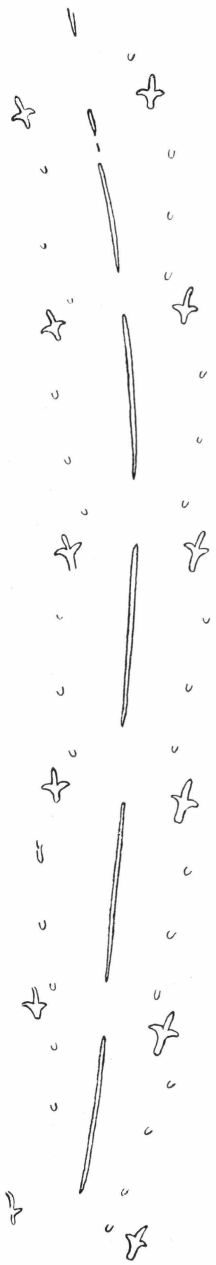


Fig. 26. *Kouphichnium lithographicum* Oppel. After Abel (1926).

*Kouphichnium* already described by Abel, and on the basis of this cast Jaekel postulates the existence of a proavian creature, *Protornis bavarica*, assumed to be less specialised in a bird-like direction than the contemporary *Archaeopteryx*. Wilfarth (1937) interprets the trails as those of the small dinosaurian *Ornitholestes*.

The trails of *Kouphichnium* and *Micrichnus* consist of two kinds of footprints interpreted by Abel as prints of the hind feet and of the fore feet, respectively. In many cases moreover a tail track is present.

The prints of the hind feet are fairly large and show, in addition to three or four toe prints, at least in *Kouphichnium* a shorter or longer metatarsal impression. They are arranged in two longitudinal series in such a way that each print in one of the series opposes one of the prints in the other series.

The prints on the fore feet in *Micrichnus* appear as small grooves or furrows described by Abel (1926, p. 46) as "kleine, scharfrandige, sehr schmale und lange Abdrücke." In *Kouphichnium* the prints of the fore feet are small impressions the details of which are very difficult to make out. According to Abel (1926, p. 47; 1935, p. 133) the small impressions in a few cases show three quite distinct small fingers, but his figure of a specimen in which the prints of these small fingers should be especially distinct (Abel, 1926, fig. 25; 1935, fig. 108) is by no way convincing. As far as I can see from this excellent photograph the small impressions are in some cases V-shaped and in others single straight furrows. The arrangement of the small prints is only known in detail in *Kouphichnium*, where the prints form a regular pattern on each half of the trail. The pattern differs from specimen to specimen and in some cases even from side to side in the same trail. Fig. 26 shows a trail with three small impressions arranged in an oblique row between each two successive

prints of the hind foot. In other cases only one or two impressions are present in each interspace between successive prints of the hind foot.

As will be understood from this short description the intricate pattern of the tracks of *Kouphichnium* is principally the same as that of the tracks of some of the trails from Greenland, and as moreover the digitate tracks of the Greenlandic Type D closely agree in shape with the prints of the hind feet of *Kouphichnium*, there can be no doubt that the trails from Greenland were made by animals closely related to *Kouphichnium*. (The similarity between the prints of the hind feet of *Kouphichnium* and the digitate tracks of Type D even goes as far as to the bifurcation of the third toe (ray), a feature which in the case of *Kouphichnium* has caused a great deal of discussion (ABEL 1926, pp. 49—52; 1927, p. 516; 1935, pp. 133—134; JAEKEL 1929, pp. 234—235)).

According to ABEL *Kouphichnium* moved by leaping on its hind legs, while the hands touched the ground trice between each leap, or in the words of ABEL (1926, p. 48) "..... dass zwischen je zwei Sprüngen des Tieres die Hände gleichzeitig auf den Boden gesetzt worden sind, dann gehoben wurden und, etwas mehr gespreizt, weiter vorne niedergesetzt wurden, worauf ein drittes Mal das Vorsetzen der noch stärker gespreitzen Arme erfolgte: dann erst geschah der Sprung."

No living animal as far as I know moves in this most extraordinary way, however, if as generally assumed *Kouphichnium* was of vertebrate origin, the explanation given by ABEL seemed the only one possible. Accordingly I attempted to adopt the same explanation also for the trails from East Greenland, but in some of the Greenlandic specimens the pattern of the simple tracks was so intricate that it seemed absolutely impossible that they could have been made by successive prints of a single pair of small hands. For such specimens I was therefore forced to the assumption that each hand at the same time had made at least two prints, and as these two prints were situated rather far from each other, the hands at least must have been of the same size as the feet. If this assumption was correct at least some of the animals who made the trails from Greenland were rather different from *Kouphichnium* although moving in principally the same way. This peculiar fact first arose my doubt as to the correctnes of ABEL's interpretation of *Kouphichnium*, and this doubt grew stronger when by a happy coincidence I came across a small paper dealing with certain trails from the Buntsandstein near Nagold (O. LINCK 1943). Some of the trails treated in that paper in many respects showed a close resemblance to the trails from Greenland, but to my great astonishment they were referred not to vertebrates but to limulids. LINCK referred to a paper dealing with certain Devonian trails from U.S.A. (CASTER 1938). These Devonian trails were first described in 1935 under the name of *Paramphibius* by Dr. BRADFORD

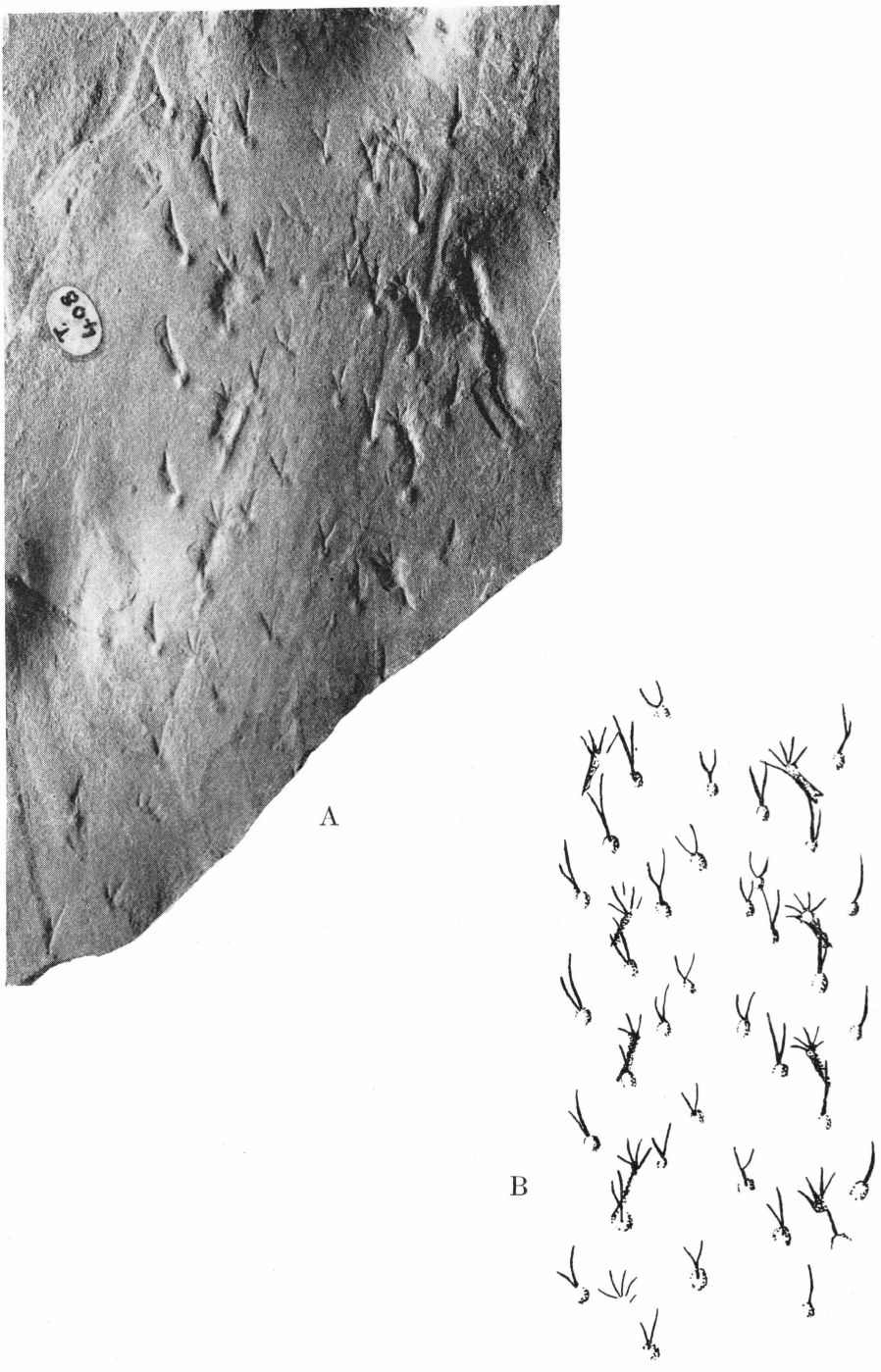



Fig. 27. *Paramphibius didactylus* WILLARD. A, trail of specimen T. 408 from the British Museum of Natural History. B, diagram of part of the same trail Nat. size.

WILLARD, who considered that the animal who made the trails occupied a systematic position between crossopterygians and the most primitive stegocephalians. CASTER, however, points out the great similarity between *Paramphibius* and the trails of immature specimens of the recent *Limulus polyphemus* and draws the conclusion that *Paramphibius* was a merostome, probably closely related to the Devonian xiphosuran *Protolimulus*.

CASTER's descriptions and his excellent figures both of *Paramphibius* and of the trails of *Limulus polyphemus* left to me no doubt that the trails from Greenland were of limulid instead of vertebrate origin, and for this view I found a further support by studying myself two specimens of *Paramphibius* from the collections of the British Museum of Natural History, one of which is shown in fig. 27.

According to CASTER *Paramphibius* shows two kinds of footprints, which he described as respectively pusher-prints and simple tracks. The arrangement and shape of these two kinds of footprints are much the same as that of respectively the digitate and the simple tracks in the Greenland trails, which tracks as already mentioned are comparable to the prints of respectively the feet and the hands in *Kouphichnium*. *Limulus* has 6 pairs of cephalothoracic or prosomal appendages serving as organs both of locomotion and manducation. All of them are chelate, but the hindmost pair differs from the others in having one segment more and in that the distal end of their fifth segment (propodos) bears a whorl of four (sometimes five? (CASTER 1938, p. 12)) leaf-like movable blades (CASTER) or spines (STÖRMER 1944). The sixth segment of the hindmost appendages (dactylus) does not as in the other prosomal appendages take part in the formation of the chela, which is here formed by the seventh segment (unguis) and a movable spine. The tracks made by the five foremost pairs of prosomal appendages (simple tracks) are straight or V-shaped furrows, while the tracks of the sixth pair of prosomal appendages (pusher-prints) resemble in an astonishing degree the tracks of certain tetrapods. The "toes" of the pusher-prints are the impressions of the blades on the distal part of the propodos and the "metatarsus" the impression of the distal end of the propodos (the sole), the dactylus (the heel), and in some cases also of the unguis and the spine of the distal end of the dactylus.

This resemblance of the pusher-prints to the footprints of vertebrates has caused many misinterpretations or in CASTER's word (1938, p. 20): "it seems to be almost inevitable that arthropod trails, and especially those of Limuloids should first be interpreted as of vertebrate origin. "In two later papers (1941, 1944) CASTER has treated some previously much discussed "vertebrate" trails in accordance with his interpretation of *Paramphibius* and among these also the trails of both

*Kouphichnium* and *Micrichnus*. In these papers I found the final support for the view that the trails from Greenland were of limulid, not of vertebrate origin.

That limulids lived in the Eotriassic shallow water areas of East Greenland, is in so far surprising as no remnants of limulids have ever been collected from the well investigated and highly fossiliferous Eotriassic deposits. Judging from the observations of CASTER on the methods of locomotion of *Limulus* the trails from Greenland were made partly by animals swimming near the bottom or possibly half-walking and half swimming, and partly by animals walking on the beaches. *Limulus* apparently only seeks the shallow water during the mating season (CASTER 1938, p. 17), and similar habits for the Greenland limulids may perhaps be the explanation of the lack of any fossil remnants. The different types of digitate tracks (pusher-prints) in the trails from Greenland make it probable that more than one species are represented in the Eotriassic fauna, however, only little is known of the variability of the pushers in *Limulus*, and until a much more comprehensive material has been collected, it serves no purpose to discuss the systematic value of the distinguishing characters of the different types described in this paper.

# SUMMARY

In 1937 Dr. H. STAUBER discovered what he considered the trail of a stegocephalian in Triassic deposits on Traill Ø. The same trail was later interpreted by the present author as that of a small bipedal reptile.

In the course of investigations carried out in the coastal mountains east of Kap Stosch during the summers of 1946 and 1947, it was found that trails similar to the specimen from Traill Ø were of fairly common occurrence in the Triassic beds of this area and especially in the beds just below the *Proptychites rosenkrantzi*-zone.

On the basis of the best preserved specimens brought home the author distinguishes between 5 different types of trails. In the mutual arrangement of the footprints the best known of these types, and very probably also the less complete trails, agree fairly closely with certain trails previously described from other parts of the world, viz. *Kouphichnium lithographicum* OPPEL and *Micrichnus scotti* ABEL. *Kouphichnium* and *Micrichnus* were previonsly believed to be the trails of small bipedally leaping tetrapods, probably reptiles. The trails from Greenland also closely resemble some Devonian trails, *Paramphibius*,from U.S.A. As demonstrated by CASTER (1938, 1941, 1944) *Paramphibius*, *Kouphichnium*, and *Micrichnus* must be the trails of merostomes related to the recent *Limulus*. There can therefore be no doubt that the trails from Greenland are of limulid, not of vertebrate origin.

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