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GEOLOGY

LACERTOID FOOTPRINTS FROM THE EARLY MIDDLE TRIASSIC AT HAARMÜHLE, NEAR ALSTÄTTE, W. GERMANY

BY

H. K. H. HOLST, J. SMIT AND E. VEENSTRA [1]

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SUMMARY

A description is given of the tracks of a small quadrupedal lacertoid reptile from the early Middle Triassic at the Dutch-German border. The prints, found in the autumn of 1969, comprise footprints, scratchmarks, tailmarks, marks of the toescales and marks in connection with locomotion, and occur in laminated and rippled limestone, probably deposited on a tidal flat. A new species name is proposed to the footprints: *Rhynchosauroides haarmühlensis*.

INTRODUCTION

The locality where the footprints occur is at the Haarmühle, a well known outcrop 3 km W. of Alstätte, Westfalen, Germany.

Here early Middle Triassic limestones crop out in the bank of the river Aa. The early Middle Triassic limestone at this outcrop is developed in Wellenkalk facies, consisting of ripple-laminated light greenish-grey limestones. The ripples are covered with very thin marl laminae. Pelecypod shells of *Myophoria* and *Gervilleia* occur abundantly at some levels. Evidence of bioturbation has been found as well. The depositional environment was probably a tidal flat on which the animals searched for food at low tide.

The impressions of the feet were made when the thin marl laminae, covering the carbonate ripples, had already been deposited. The next high tide filled the impressions with carbonate sediment.

The photographic pictures in this article were made from these natural casts of the footprints.

The tracks have only been found in one single level, on which at least five individuals of about the same size 15–20 cm body-length without tail) have walked. They left footprints, taildrags (figs. 3 to 4), some imprints of toescales (fig. 5), scratchmarks (fig. 4) and some marks probably caused either by switching their tails or dragging their bellies over the bottom. (not visible on pictures.)

In general Triassic lacertoid footprints are known only from the early and late Triassic. Footprints from the early Middle Triassic have, as far

[1]) Geologisch Instituut, Nieuwe Prinsengracht 130, Amsterdam.

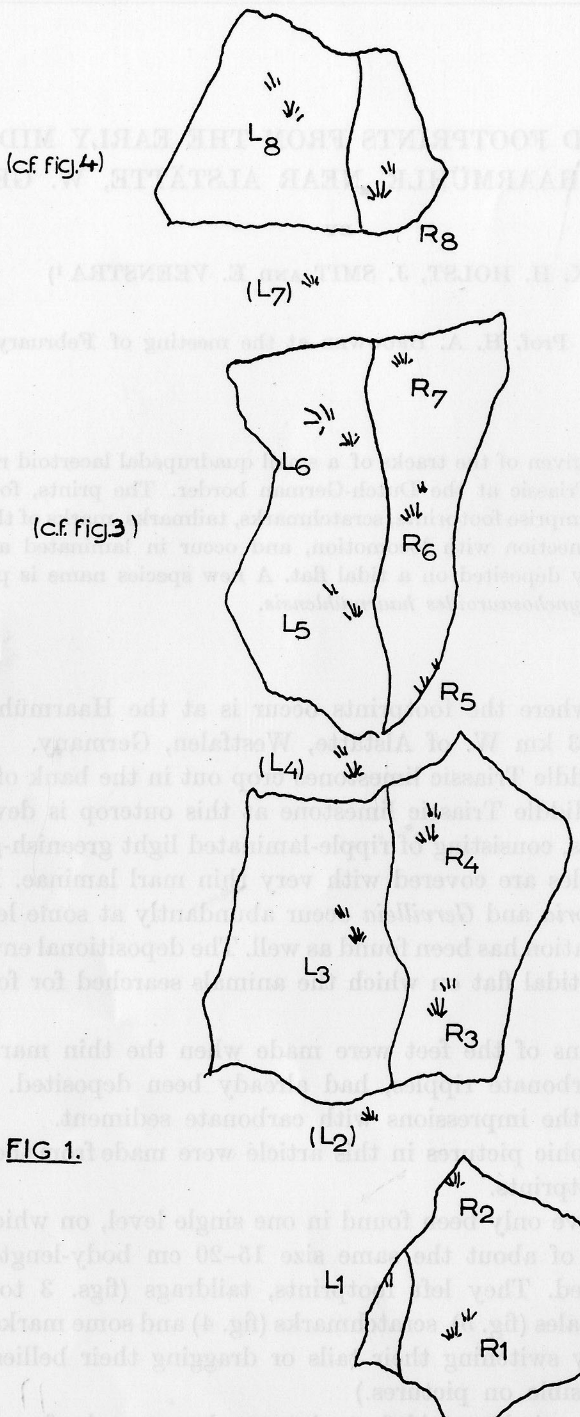

Fig. 1. Reconstruction of the track on four consecutive slabs of limestone. L2, L4 and L7 are missing on the slabs ($\times 1/8$).

as the authors could ascertain, never been described, with the exception of *Rhynchosauroides peabodyi* (FABER, 1958) found in the same Wellenkalk formation at Winterswijk, 21 km S.W. from the Haarmühle, in the Netherlands.

EXPERIMENTS

In order to obtain a better understanding of the Triassic tracks, we experimented with several lacertoid reptiles; an Iguana, two species of Cordilis (a spiny scaled lizard), a skink and a young crocodile, all with body-sizes from 8 to 20 cm (tail excluded).

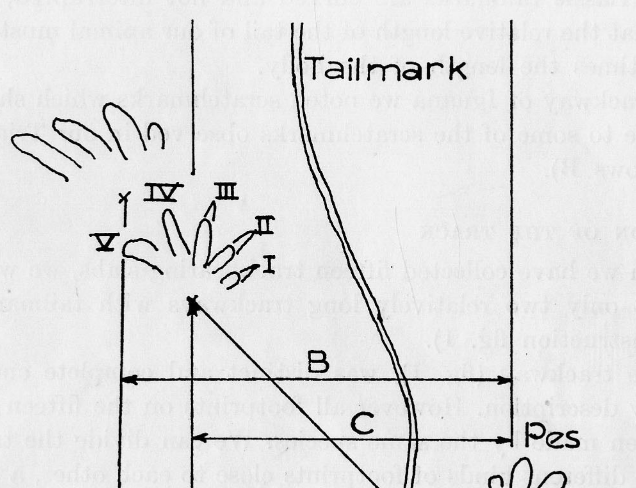

FIG. 2

Fig. 2. Dimensions of the footprints, ($\times \frac{1}{2}$). B=Interpes-distance; C=Intermanus-distance; A=Stride; α=Pace angulation.

We let these animals walk over a thick layer of fine humid sand and photographed and filmed their movements and resulting tracks. The results of the experiments strengthened our preliminary concepts about our Triassic animals, such as distinguishing pes and manus, showing the relations between scratchmarks and locomotion, and giving some suggestions about what relative length and what stiffness of the tail will give a sinusoid tailmark, as observed in our trackway. For example, a relatively long tail (i.e. 2 times the length of the body) leaves a straight groove, a short one (1 time the length of the body) leaves a curved, but interrupted one.

As our Triassic tailmarks are curved and not interrupted, it may be assumed that the relative length of the tail of our animal must have been about 1.5 times the length of the body.

In the trackway of Iguana we noted scratchmarks which show a great resemblance to some of the scratchmarks observed in our Triassic tracks (fig. 3, arrows B).

Description of the track

Although we have collected fifteen trackbearing slabs, we were able to reconstruct only two relatively long trackways with tailmarks (figs. 3 to 4, reconstruction fig. 1).

Only one trackway (fig. 1), was distinct and complete enough for a satisfactory description. However all footprints on the fifteen slabs seem to have been made by the same species. We can divide the trackway in sets of two different kinds of footprints close to each other, a manus and a pes, so the animal must have been quadrupeded (fig. 7). The trackway represents eight left and right print-sets (fig. 1) of which 4 complete left manus and pes and 5 right manus and pes impressions.

One of the first problems to solve was, which imprint belonged to the pes and which to the manus (fig. 2). A comparison with Peabody (1948) and Baird (1964), as well as our experiments, made it possible to decide that the most forward print in each set is the pes and the other one the manus.

1) The pes has the widest interpace-distance;
2) the manus is turned inward, the pes outward (see fig. 3, L5 and L6 and fig. 7);
3) the digits of the pes are longer than the digits of the manus (see fig. 3, L6 and fig. 7);
4) Further scrutiny of the sets of prints shows that the forward print

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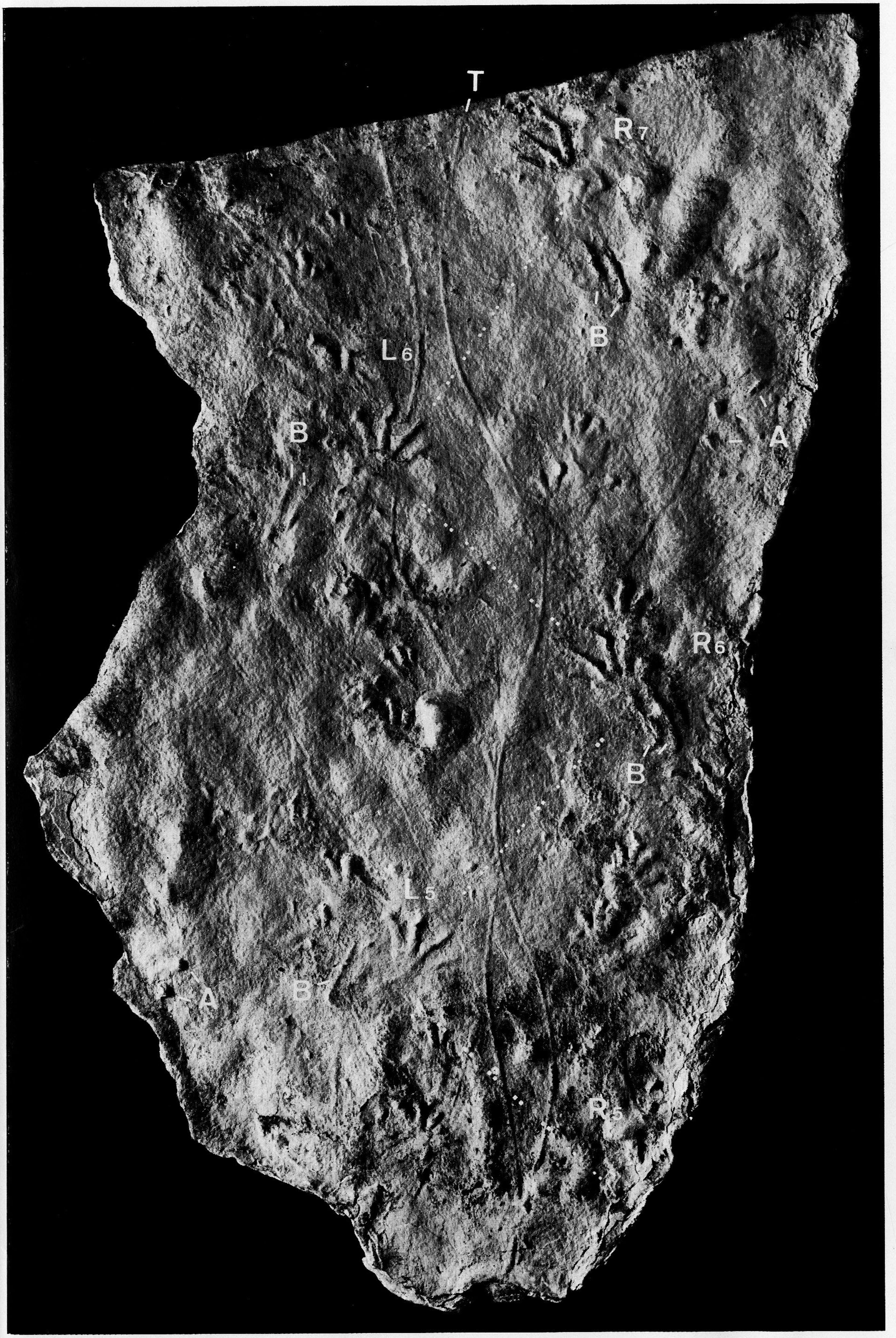
PLATE I

Fig. 3. Sets R5, R6, R7, L5 and L6 with connected tailmark (T) Clawtip impressions (arrows A), scratchmarks (arrows B). ($\times 1/2$)


T
R7
B
L6
B
A
R6
B
L5
A
B
R5

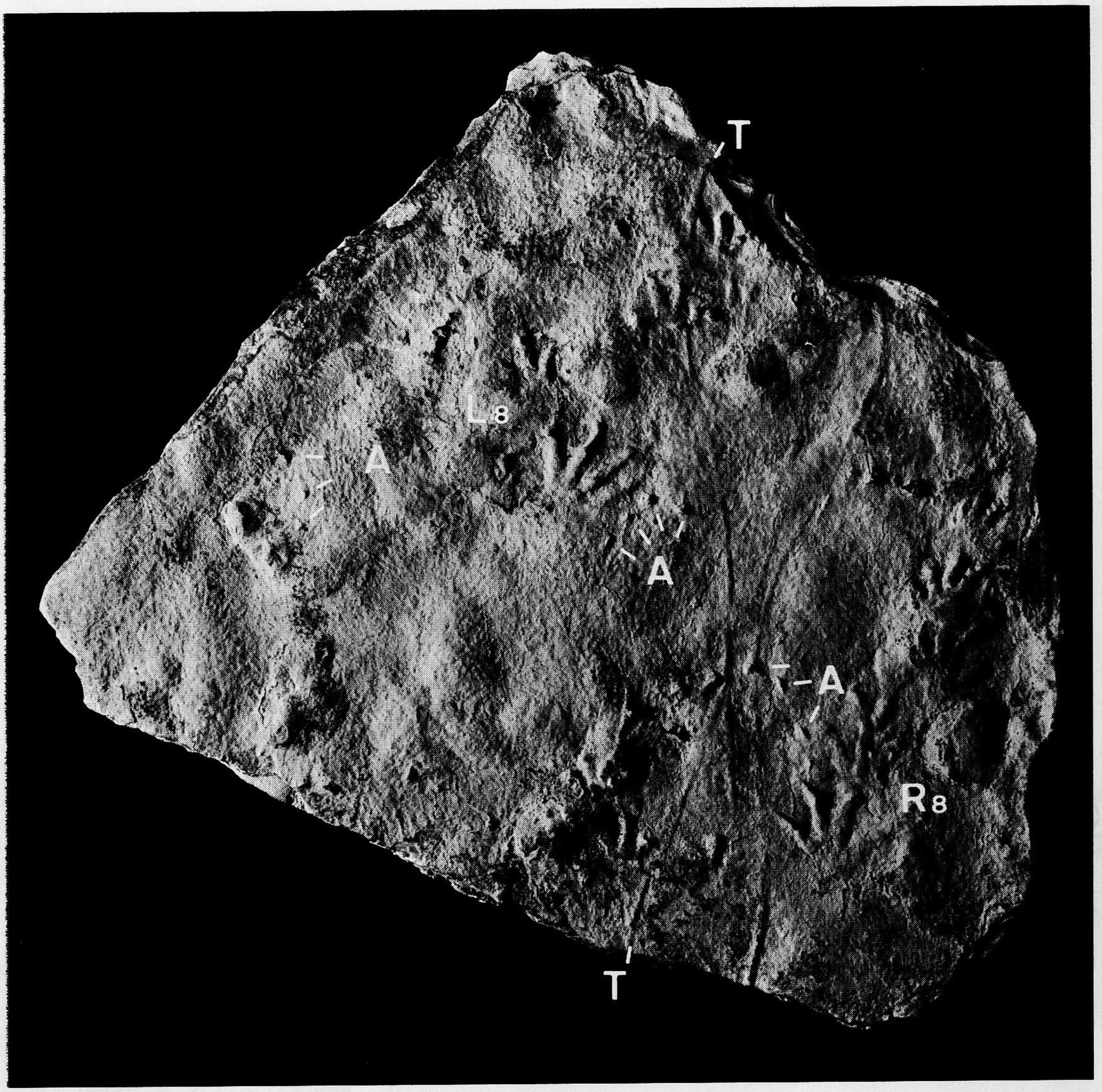


Fig. 4

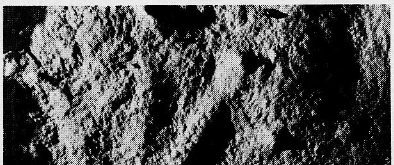


Fig. 5

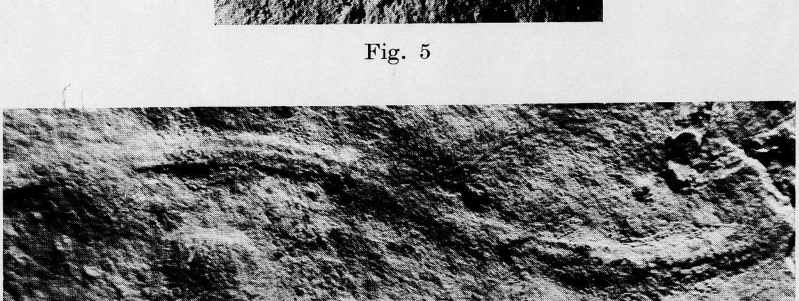


Fig. 6

is noticeably less distinct than the other one. PEABODY (1948) and BAIRD (1964) also mentioned that in lacertoid tracks the manus is more complete than the pes. BAIRD (1964) mentions that sometimes the pes is overlooked, if it is only represented by a curved row of four little pits made by the clawtips of the pes. We observed several examples of these rows of pits (figs. 3 to 4, arrows A).

Considering these observations we assume that in its locomotion our Triassic animal evidently placed the pes in its next step just in front of the manus impression of its previous step. The *Rhynchosauroides* described by BAIRD (1964) and other lacertoid reptiles described in literature, as well as the recent reptiles in our experiments, placed the pes next to the manus or slightly behind it.

At the tips of the toes of the manus in our fossil tracks we often find small scratches, obviously made by the claws of digits I, II and III (fig. 3, R7). Noteworthy are the scratches in the rear of sets R6, R7, L5 and L6 (fig. 3, arrows B). We assume they were made by digits II and III of the pes, as in our experiments similar scratches were made by the same digits in the track of Iguana.

Connected with the footprints are beautifully curved tailmarks. Especially the ones shown in figs. 3 and 4 form an uninterrupted sinusoid track, with a "wave-length" of 18–19 cm (which is the stride of our animal), and with an amplitude of ca. 1.5 cm. In other slabs we frequently found short interrupted tailmarks, probably due to uplifts of the tail or brusque movements.

One tailmark shows three longitudinal ridges which may be caused by rows of scales like those we find on the tail of recent Iguana (fig. 6).

DISCUSSION AND CONCLUSION

Considering the following facts and probabilities:

1) the animal has scales (fig. 5);
2) lived near a marine environment;
3) lived in a warm, probably dry climate (evaporites have been found in the underlying Buntsandstein).

We may exclude the possibility that the animal was an amphibian, so the tracks could only have been made by reptiles.

The rhynchosauroid tracks from the late Triassic, described by BAIRD

PLATE II

Fig. 4. Sets R8 and L8 with connected tailmark. Clawtip impressions see arrows A (Tailmark=T) (× 1/2).

Fig. 5. Toescales of the manus. At the end of the digits clawtipmarks (× 1/2).

Fig. 6. Tailmark divided in three ridges (× 1/1).

(1964), show a great general resemblance to our fossil tracks, but differ in detail. Similarities are:

1) *Rhynchosauroides palmatus* (Lull 1942) (Baird, 1964 p. 121 fig. 2c) has comparable dimensions;

2) digit IV of the manus and digit II of the pes of *R. palmatus* points in the direction of movement, as is the case in our tracks;

3) the pes of *R. palmatus* is less clearly impressed, as in our tracks;

4) interpace-distance and stride have the same ratio as in our tracks and both tracks have the same pace-angulation.

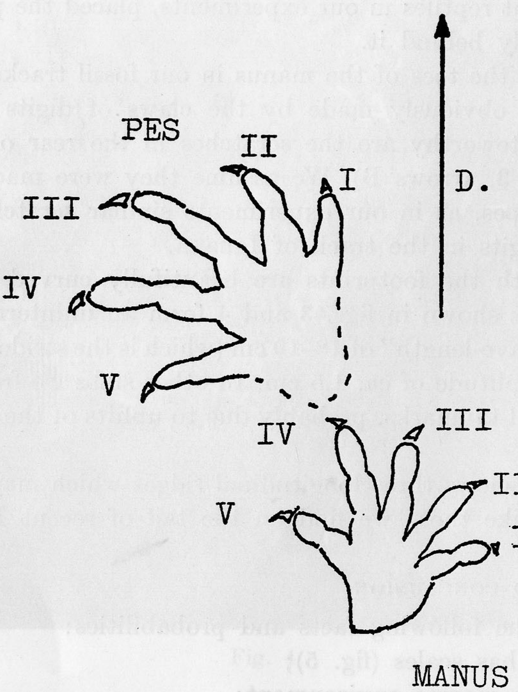


Fig. 7. Reconstruction of left pes and manus impression of Rhynchosauroides haarmühlensis. Arrow points in the direction of movement (× 1/1).

In some aspects however, *R. palmatus* differs from our specimen:

1) in the manus-form and the slightly more pronounced curvature of the digits. *R. palmatus* has digit V perpendicular to digit IV, in our species, however, the angle between digit V and IV is ± 40° (fig. 11);

2) *R. palmatus* places its pes next to its manus, our animal places its pes in front of the manus.

Because of the resemblances between our tracks and *Rhynchosauroides palmatus* (Lull, 1942) as described by Baird (1964), we assume that our footprints belong to the ichnogenus *Rhynchosauroides*. However the differences show that they do not belong to the same species.

Faber (1958) has found in Winterswijk, Netherlands, the only footprints known by the authors from the Wellenkalk. So the first thing we did, was to compare our footprints with these from Winterswijk, named *Chirotherium peabodyi* Faber 1958. Baird (1964) reinvestigated these same footprints from Winterswijk and reinterpreted this track to be quadrupedal and belonging to the ichnogenus *Rhynchosauroides*.

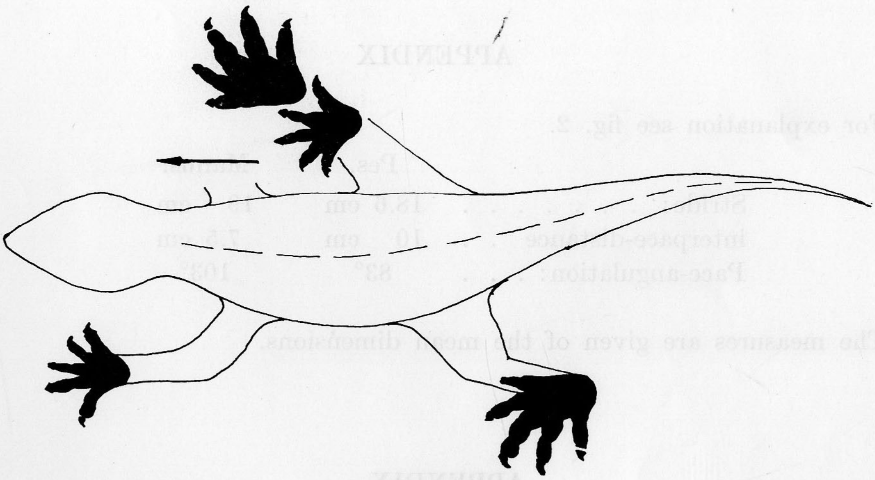


Fig. 8. Reconstruction of a triassic lacertoid reptile, which could possibly have made the footprints from the Haarmühle (after Baird 1957).

This *R. peabodyi* (Faber, 1958) again shows too many differences compared with our tracks, to place it in the same ichnospecies:

1) some dimensions of *R. peabodyi* (i.e. stride, pace-angulation and inter-manus-distance) differ from the ones in our track (Faber, 1958 and our appendix);

2) the ratios of the digit-lengths of *R. peabodyi* and our species differ quite a bit;

Digits of manus:	I	II	III	IV	V
R. peabodyi:	1	1.2	1.8	2.7	?
our species:	1	1.4	2	2.4	?

3) digit V of the manus of *R. peabodyi* is almost perpendicular to digit IV. In our species we find digit V in a more forward position and at an angle of about 40° with digit IV (fig. 7). On the strength of these arguments we state that our tracks do not belong to the ichnospecies *R. peabodyi*, and as we did not find in the available literature any descriptions of similar footprints, we propose the name *Rhynchosauroides haarmühlensis* for the footprints in the early Middle Triassic at the Haarmühle [1]).

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[1]) For reconstruction see fig. 8.

ACKNOWLEDGEMENTS

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APPENDIX

For explanation see fig. 2.

	Pes.	Manus.
Stride:	18.6 cm	19 cm
interpace-distance . .	10 cm	7.5 cm
Pace-angulation: . . .	83°	103°

The measures are given of the mean dimensions.

APPENDIX

Lengths in mm. For explanation see figs. 1 and 2.
Impression of the manus: the lengths are given of the free digits.

DIGITS	I	II	III	IV	V
Set R1:	8	9.5	14	17	10.5
R2:	9	10	14	17	10
R3:	7	10	12.5	15.5	—
R4:	6.5	9.2	12.5	16.5	11
R5:	—	—	—	—	—
R6:	6	9.4	13	17.5	10
R7:	6.5	9.5	14	16.5	9.2
R8:	6.5	10	13.5	15.5	11
L1:	9	15	—	—	—
L2:	—	—	—	—	—
L3:	6.5	9.2	12.5	16.5	9.5
L4:	—	—	—	—	—
L5:	6	9.2	12	16	11.5
L6:	7	9.5	13	16.5	8.5
L7:	—	—	—	—	—
L8:	7	10	13	16	—

Impressions of the pes: the lengths are given of the free toes.
Only the pes of set L6 is complete.

DIGITS	I	II	III	IV	V
Set R1:	5	14	13 ?	—	—
R2:	—	—	—	—	—
R3:	8	11.5	—	—	—
R4:	7	11.5	—	—	—
R5:	—	—	—	—	—
R6:	8.5	12.3	14 ?	—	—
R7:	—	—	—	—	—
R8:	?	?	—	—	—
L1:	—	—	—	—	—
L2:	—	—	—	—	—
L3:	8	12.5	15.5 ?	—	—
L4:	—	—	—	—	—
L5:	9.5	12.5	—	—	—
L6:	8.5	14	17.5	19.5	13
L7:	—	—	—	—	—
L8:	10	13.5	—	—	—

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