

The Early Permian tetrapod track assemblage of Nierstein, Standenbühl Beds, Rotliegend, Saar-Nahe Basin, SW-Germany

Das unterpermische Vorkommen von Tetrapodenfährten in den Standenbühl-Schichten bei Nierstein, Rotliegend, Saar-Nahe-Becken, SW-Deutschland

With 10 figures and 1 table

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Abstract: Discoveries of tetrapod tracks were made in the last two decades in the Standenbühl Beds of Upper Rotliegend age. The first study in the early 1980s presented a list of 18 ichnotaxa and related stratigraphic conclusions: The definition of an "Anhomoiichnium-Zone", is characterised by a track assemblage that argues apparently for a relatively late age of the included formations. The revision concerned the reinvestigation of the original and additional specimens in comparison with other occurrences. The result was a modified and reduced scale of the following taxa: cf. *Batrachichnus salamandroides*, *Limnopus zeilleri*, *Amphisauropus imminutus*, *Dromopus lacertoides*, cf. *Dimetropus* sp., and cf. *Ichniotherium* sp. This scale resembles the *Batrachichnus - Dromopus* assemblage of the Permian red beds, broadly distributed in the Rotliegend of Europe, and in the upper Wolfcampian of North America. In the present study the track material of the Standenbühl Beds is analysed ichnotaxonomically, together with detailed photographic documentation.

Zusammenfassung: In der Playa-Fazies der oberrotliegenden Standenbühl-Schichten wurden in den letzten Jahrzehnten Tetrapodenfährten entdeckt. Eine erste Bearbeitung zu Beginn der 1980er Jahre ergab eine Liste von 18 Ichnotaxa und darauf basierende stratigraphische Schlußfolgerungen: Die Definition einer „Anhomoiichnium-Zone“ nach einem Assemblage, welches angeblich ein relativ junges Alter der einbezogenen Horizonte belegen sollte. Die Revision des Originalmaterials und weitere Funde ergaben nun unter Einbeziehung vergleichbarer Vorkommen mit dem Nachweis von cf. *Batrachichnus salamandroides*, *Limnopus zeilleri*, *Amphisauropus imminutus*, *Dromopus lacertoides*, cf. *Dimetropus* sp., und cf. *Ichniotherium* sp. ein korrigiertes und zugleich reduziertes Formenspektrum. Dieses entspricht dem in der permischen Rotfazies in Europa und Nordamerika weit verbreiteten *Batrachichnus - Dromopus* Assemblage des Rotliegenden zeitgleich etwa dem oberen Wolfcamp. Im Vorliegenden ist das Fährtenmaterial der Standenbühl-Schichten anhand einer fotografischen Dokumentation ichnotaxonomisch analysiert.

1 Introduction and background

The sequence of the Saar-Nahe Basin is one of the representative successions of Permocarboniferous red beds in Central Europe. It has been subdivided lithostratigraphically into several groups and formations, reflecting the tectonic and sedimentological development as interpreted by the researchers. In the last four decades subdivisions by FALKE (1954, 1974), BOY & FICHTER (1982), and STAPF (1990) have been elaborated and introduced with some differences in the naming of the units. However, all studies agree upon the development of the upper part, the alluvial fan and playa sediments of the Nahe Gruppe, which consists of the Wadern, Kreuznach and Standenbühl Formations. The Nierstein Formation (sensu STAPF 1990) has been separated

from the Standenbühl Formation by a characteristic, locally separated development in the Niersteiner Horst area south of Mainz (Fig. 1). At the top of the Saar-Nahe sequence these playa sediments are several hundred meters thick and are understood as typical for the Upper Rotliegend (STAPF 1982). Due to their position, they are of principle value for correlations with the sequences in other basins and for understanding the Upper Rotliegend in general.

The discoveries of high frequencies of tetrapod tracks were made in the 1970s in nearly all other formations of the Saar-Nahe Basin as well in the Standenbühl Beds (FICHTER 1983, 1984), and led to stratigraphic usage. In relation to data from tracks recorded from other Rotliegend basins, BOY &

FICHTER (1988) established a zonation of the Rotliegend and the entire Permian by tetrapod tracks with the succession of "*Protritonichnites lacertoides*", "*Saurichnites intermedius*", "*Varanopus microdactylus*", "*Anhomoiichnium*", "*Harpagichnus*", and "*Rhynchosauroides* Zone". The "*Anhomoiichnium* Zone", in particular was referred to the Standenbühl Beds from Nierstein and was correlated by BOY & FICHTER (1988) to particular horizons of other Permian sequences which apparently contain comparable track occurrences. But these correlations are, in some respects, incompatible with many aspects evident from the integrated tetra-pod track assemblages. The incompatibilities, the character of the playa sediments which controls the track preservation, and the discovery of additional material in the outcrops at the vineyards of the Nierstein Horst, are the reasons for a reinvestigation of the track assemblage.

The present study incorporates several other investigations of Permian tetrapod tracks with the aim to analyse their possible contribution to the reconstruction of terrestrial fauna diversity (HAUBOLD et al. 1995a, b, HUNT et al. 1995, HAUBOLD 1996, 1998, MCKEEVER & HAUBOLD 1996, MORALES & HAUBOLD 1995). An important

contribution to the progress of the determination of Permian tetrapod tracks has been made before by GAND (1987), summarised in GAND & HAUBOLD (1988). In that study the Standenbühl track assemblage was not included nor has it been reinvestigated since. Also, the relatively late age of the formation within the Permian, as derived from the track content and correlation of "*Anhomoiichnium* Zone", was

questionable. The first step to a solution concerns the previous status of the ichnotaxon *Anhomoiichnium* itself. As has been demonstrated (HAUBOLD 1996), it was a combination of confusions and misinterpretations, which was not a concern of the late age of the Upper Rotliegend Standenbühl Beds within the Permian postulated by BOY & FICHTER (1988). The complex reinvestigation of tetrapod tracks point instead to a much older age. This is additionally confirmed now by the consequent application of numerical dating to

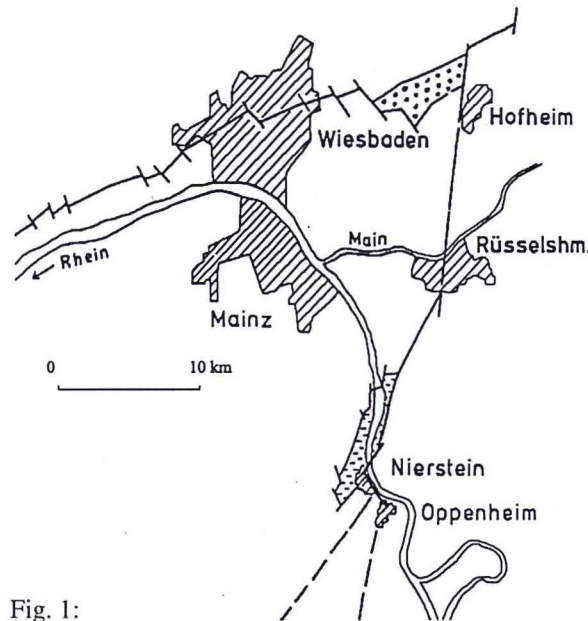


Fig. 1: Location of the Niersteiner Horst, a restricted elevation at the western flank of the Oberrhein-Graben (from STAPF 1982).

the correlation of the post-Variscian Saar-Nahe sequence, presented in a basin model, that is consistent in the aspects of stratigraphy, sedimentology, petrography, and tectonic development (SCHÄFER & KORSCH 1998).

2 Former studies

The first study of the tetrapod ichnofauna of the Standenbühl Beds was published by FICHTER (1983, 1984); 18 taxa have been described:

- Limnopus palatinus* FICHTER
- Saurichnites incurvatus* FRITSCH
- Saurichnites intermedius* FRITSCH
- Amphisauroides* sp.
- Anhomoiichnium diversum* (SCHMIDT)
- Anhomoiichnium orobicum* (DOZY)
- Chelichnus* ?*ambiguus* JARDINE
- Chelichnus* (*Barypodus*) ?*gravis* (SCHMIDT)
- Dimetropus leisnerianus* (GEINITZ)
- Foliipes abscisus* HEYLER & LESSERTISSEUR
- ?*Gilmoreichnus minimus* HAUBOLD
- Hyloidichnus arnhardti* HAUBOLD
- Ichniotherium cottae* (POHLIG)
- Jacobiichnus caudifer* (FRITSCH)
- Palmichnus renisus* SCHMIDT

- Phalangichnus alternans* SCHMIDT
- Varanopus microdactylus* (PABST)
- Protritonichnites lacertoides* (GEINITZ).

The *Limnopus* and *Saurichnites* species have been interpreted as amphibian and all others of reptilian in origin. The specimens are mainly housed in the following collections, Paläontologisches Institut of the Universität Mainz (PIM), Paläontologisches Museum, Sammlung Stapf Nierstein (SSN), and some are in the Naturhistorisches Museum Mainz (NHMM). The specimens contain tracks of variable sedimentologically controlled preservation. The red playa siltstone often displays undertracks of different layers. Trackways are rarely observed, due to the small size of most of the slabs collected in restricted outcrops.

Many of the names used by FICHTER (1983, 1984) and BOY & FICHTER (1988) in the determinations of the Nierstein tracks bear little or limited

morphological and taxonomical relation to the taxa primarily described from other formations. For example, *Chelichnus*, *Laoporus*, *Phalangichnus*, *Palmichnus* have been introduced from dune sandstone formations, the *Laoporus* ichnofacies (cf. LOCKLEY et al. 1994). These track types are nowhere related to tracks known from playa beds from Nierstein. In some cases the names used by FICHTER can be characterised as phantom taxa (sensu HAUBOLD 1996), like *Saurichnites* and *Anhomoiichnium*. These

determinations of FICHTER (1983, 1984) - related to some of most the fragmentarily preserved and extramorphological modified tracks - are partially understandable and may be due to the incomplete status of track studies and track taxonomy at that time. The preservation of ichnofossils in the Standenbühl Beds is influenced by the playa facies and the common phenomenon of undertracks does not completely display the anatomically controlled details within the track morphology.

3 Revision of the tetrapod ichnofauna from Nierstein

The following survey documents the re-evaluation of the original specimens described and sketched by FICHTER (1983, 1984). His determinations are given below in "quotation marks". Information from additional specimens, collected in the last decade by one of the authors (H. S.), is included here, see also Table 1. The most informative material, containing

some segments of trackways, is housed in the collection SSN, and is displayed in photographs below. The specimens of the collection PIM are, by comparison, less important, because of their fragmentary character: small pieces exhibit but few isolated tracks.

Tab. 1:

Tetrapod tracks of the Standenbühl Beds, Nierstein: 1) Comparison of the revised interpretation with the determinations of the described and sketched specimens by FICHTER (1993, 1984). 2) Inclusion of additional specimens of the Paläontologisches Museum Nierstein. Specimen numbers of collection SSN11.N XX (collection STAPF Nierstein) and collection PIM K XX (Paläontologisches Institut, Universität Mainz)

cf. <i>Batrachichnus salamandroides</i>	cf. <i>Amphisauropus imminutus</i>	<i>Dromopus lacertoides</i>	indeterminable
			<i>Amphisauroides</i> sp. K 275
		<i>Anhomoiichnium diversum</i> K 251, N 31	
			<i>Anhomoiichnium orobicum</i> K 227
	<i>Chelichnus ? ambiguus</i> N 9, 11		<i>Chelichnus/Laoporus ? ambiguus</i> K 245 - 247, 274
		<i>Chelichnus (Barypodus) ? gravis</i> N 31	
	<i>Dimetropus leisnerianus</i> N 22		
<i>Foliipes abscisus</i> N 27			
			<i>Hyloidichnus arnhardti</i> K 373
<i>Jacobiichnus caudifer</i> N 21			
<i>Limmopus palatinus</i> N 20			
			<i>Palmichnus renisus</i> K 220-224
	<i>Phalangichnus alternans</i> K 285		<i>Phalangichnus alternans</i> K 225, 226
	<i>Saurichnites incurvatus</i> K 227		
<i>Saurichnites intermedius</i> N 33	<i>Saurichnites intermedius</i> K 287 N 34		<i>Saurichnites intermedius</i> K 282
			<i>Varanopus microdactylus</i> K 268
Additional representative specimens of collection SSN 11			
N 19, 37	N 4, 14, 28, 30	N 2, 39, 44, 51-56	

cf. *Batrachichnus salamandroides* (GEINITZ), Fig. 2

A possible relation to *Batrachichnus* can be observed for specimens determined formerly by FICHTER under four different names:

SSN11.N20 "*Limnopos palatinus*" (1984, Abb.1)

SSN11.N33 "*Saurichnites intermedius*" (1984, Abb. 6)

SSN11.N21 "*Jacobiichnus caudifer*" (1984, Abb. 18)

SSN11.N27 "*Foliiipes abscisus*" (1984, Abb. 26)

Fig. 2A.

Additional specimens of the same incomplete and problematic status are SSN11.N19 (Fig. 2B) and SSN11.N37. In summary, no specimens are known

from the Standenbühl Beds that would be determinable, without restrictions, as *Batrachichnus salamandroides*. For the common understanding it has to be noted that the former nomenclatorial versions "*Saurichnites*" *salamandroides* and "*Anthichnium*" *salamandroides* should be replaced by *Batrachichnus salamandroides* in respect at least to the generic identity of the respective tracks known from Permian Red Beds of North America and Europe (HAUBOLD et al. 1995a: 137; HAUBOLD 1996: 37).

***Limnopos zeilleri* (DELAGE)**

The ichnospecies *L. zeilleri* can be established using the specimens PIM K213, K214 (personal comm. of G. GAND), and cf. *Limnopos* sp. from the Rehbacher

Steig in the collection BEILING 1 II (now NHMM). The taxon is understood here in the sense as reinvestigated by GAND (1985, 1987).

***Amphisauropus imminutus* HAUBOLD, Fig. 3**

The record of this ichnotaxon from the Standenbühl Beds is related to specimen SSN11.N6 (Fig. 3) which shows well-preserved imprints and the trackway pattern. The existence and information given from this specimen is the background for the evaluation of some rather fragmentary and extramorphological preserved

tracks, which have been available for the former description as listed below. At the present state of knowledge, all these tracks are obvious extramorphological variations of *A. imminutus*, significant of Rotliegend playa sediments

cf. *Amphisauropus imminutus*, Fig. 4 - 5

The following specimens with former determinations of FICHTER can be mentioned here:

PIM K277 "*Saurichnites incurvatus*" (1984, Abb.2)

PIM K287 "*Saurichnites intermedius*" (1984, Abb. 3)

SSN11.N34 "*Saurichnites intermedius*" (1984, Abb. 5)

Fig. 4A

SSN11.N11 "*Chelichnus ?ambiguus*" (1984, Abb. 10)

Fig. 4B

SSN11.N22 "*Dimetropus leisnerianus*" (1984, Abb. 15)

PIM K285 "*Phalangichnus alternans*" (1984, Abb. 20)

Also determinable probably as *A. imminutus* are SSN11.N4 (Fig. 5A), N14 (Fig. 4C), N28 (Fig. 5B).

Amphisauropus is known as one of the significant Early Permian track types, and can be separated from

Batrachichnus and *Limnopos* in having manus imprints with five digits, when the tracks are adequately recorded anatomically (SSN11.N6). Another character is given by the trackway pattern, the manus imprints are inward and those of the pes imprints are oriented outward relative to the direction of progress. Furthermore the imprints of *Amphisauropus* are broader than those of *Batrachichnus*. However, in the case of incomplete, extramorphologically, influenced records, the determination remains open in the scale from *Batrachichnus*, *Limnopos* to *Amphisauropus* (see HAUBOLD 1996: 50).

Indeterminable specimens, Fig. 6

Related to cf. *Batrachichnus salamandroides* or to *Amphisauropus imminutus* are

PIM K247 "cf. *Laoporus ambiguus*" (FICHTER 1983, Abb. 23c)

PIM K220-224 "*Palmichnus renisus*" (1983, Abb. 16-18)

PIM K 245, K246 "cf. *Chelichnus* sp." (1983, Abb. 23)

PIM K225-226 "*Phalangichnus alternans*" (1983, Abb. 20a, b)

PIM K268 "*Varanopus microdactylus*" (1984, Abb. 21)

SSN11.N9 "*Chelichnus ?ambiguus*" (1984, Fig. 13)

Fig. 6A

PIM K282 "*Saurichnites intermedius*" (1984, Abb. 4)

PIM K275 "*Amphisauroides* sp." (1984, Abb. 7)

PIM K273 "*Hyloidichnus arnhardi*" (1984, Abb. 17)

PIM K274 "*Chelichnus ?ambiguus*" (1984, Abb.12)

PIM K227 "*Anhomoichnium orobicum*" (1984, Abb. 26a).

A determination of this material, depending on the fragmentary status, remains indeterminate. In addition, a record on a larger surface exhibited on a NHMM-specimen (Fig. 6B) allows no decision between *Batrachichnus* and *Amphisauropus*. Following the evidence known from trackways on some surfaces from the same horizons, the above listed, mostly isolated tracks, can be assigned to *Batrachichnus*, *Limnopos*, and *Amphisauropus*, according to the potential scale of variable, and extramorphological, preservation as discussed before.

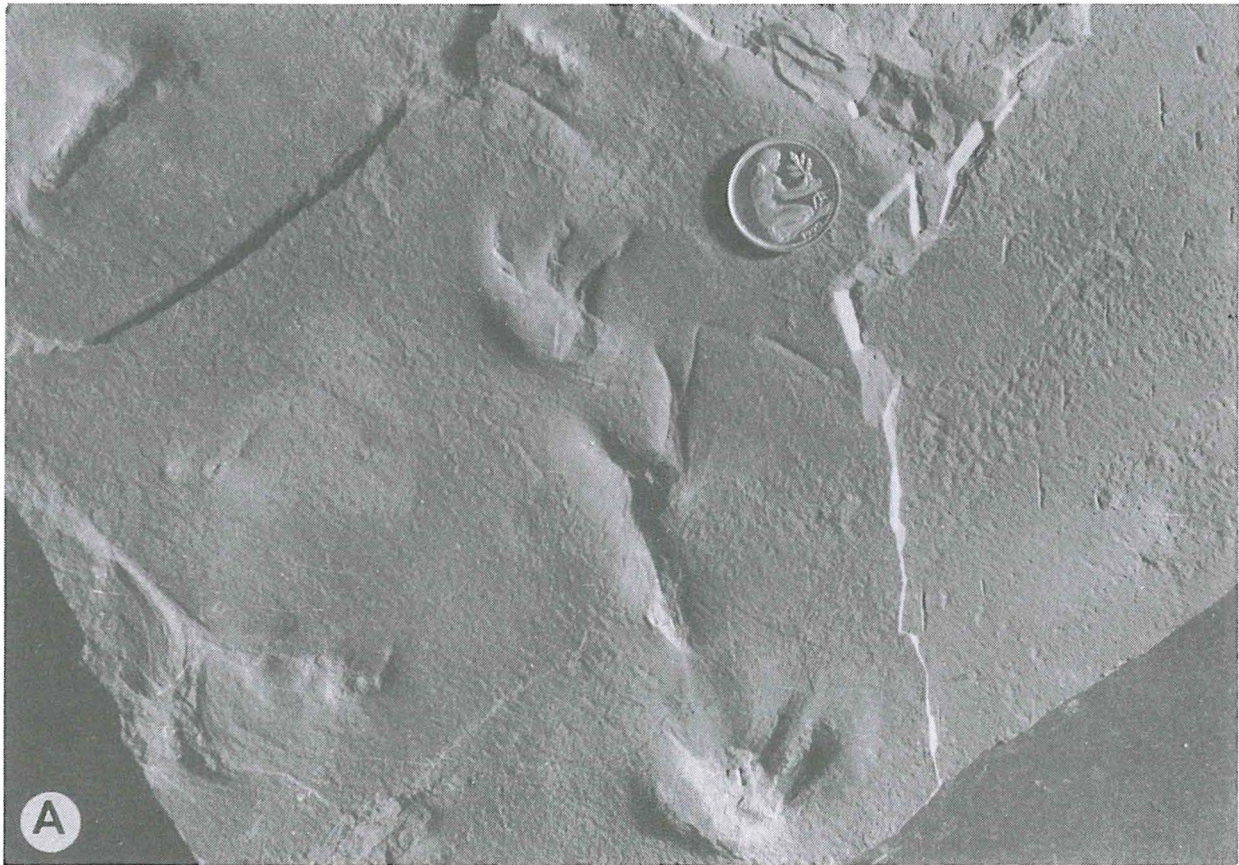


Fig. 2: cf. *Batrachichnus salamandroides*.

A - The specimen SSN11.N27 was formerly determined as "*Foliipes abscisus*".

B - surface with some trackway segments SSN11.N19. Scale, diameter of the coin 2 cm.



Fig. 3: *Amphisauropus imminutus*, SSN11.N6. Surface with relatively complete record, manus imprints directed inward, those of the pes parallel the direction of movement. Impressions of digit tips I-IV are prominent. Scale in cm.

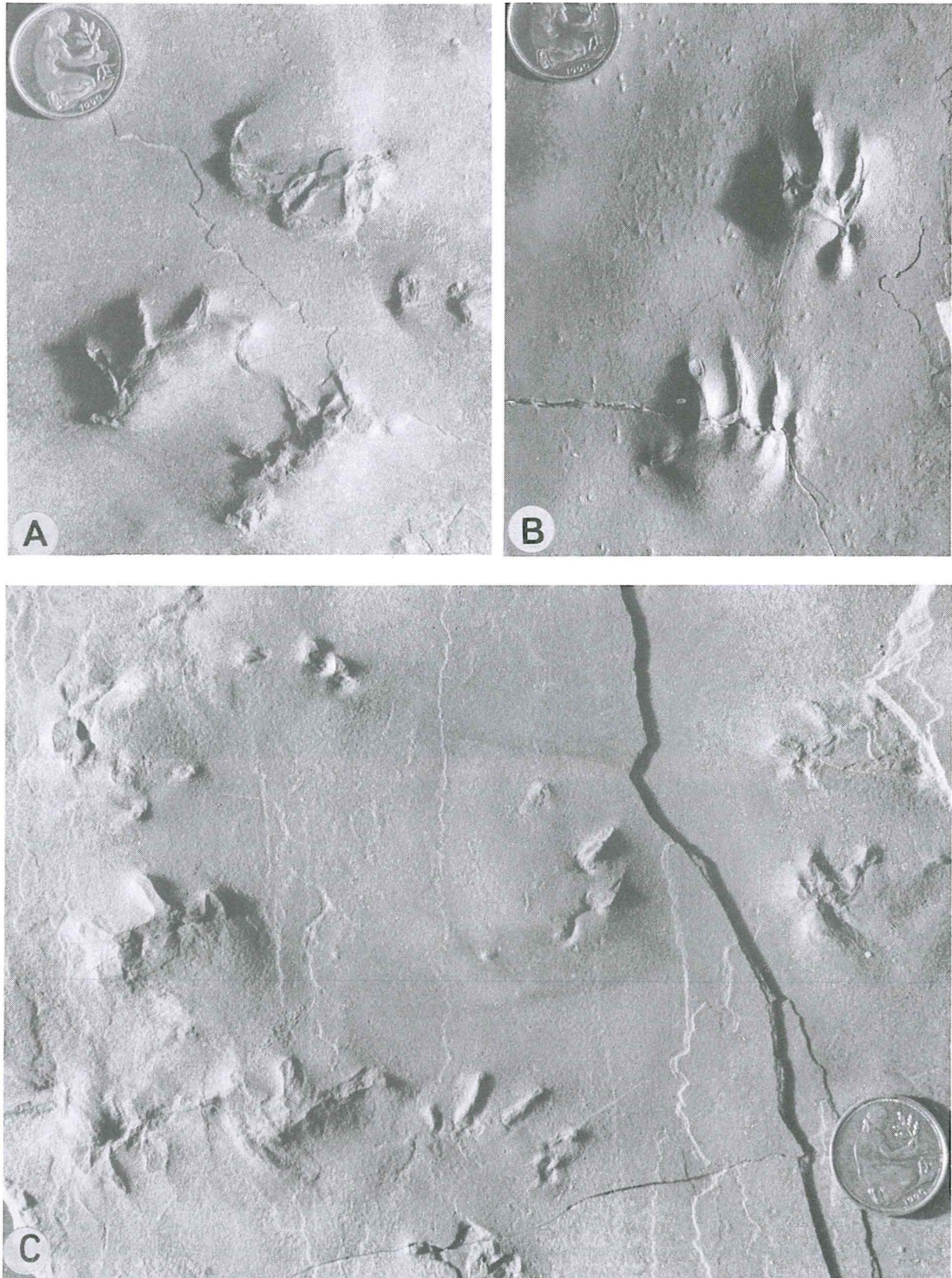


Fig. 4: Tracks of variable preservation, partially undertracks, the prominent digit tips are extramorphological elongated in some imprints, all are determinable as cf. *Amphisauropus imminutus*.

A - SSN11.N34 (formerly "*Saurichnites incurvatus*").

B - SSN11.N11 (formerly "*Chelichnus ?ambiguus*").

C - SSN11.N14. Scale - diameter of the coin 2 cm.

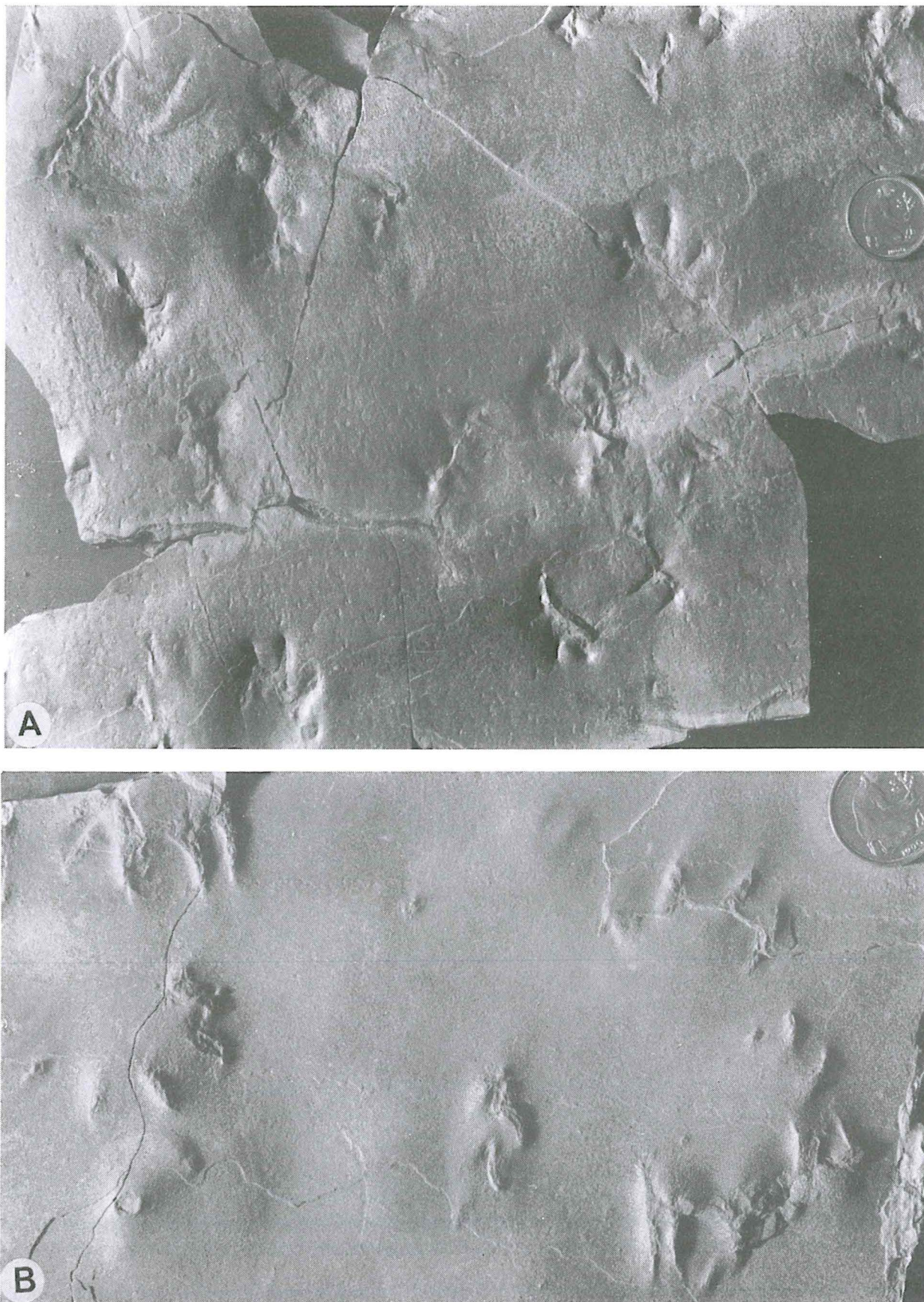


Fig. 5: cf. *Amphisauropus imminutus*, tracks of variable preservation (some tracks could be identified as cf. *Batrachichnus salamandroides*, compare with Fig. 2B).

A - SSN11.N4.

B - SSN11.N28. Scale - diameter of the coin 2 cm.

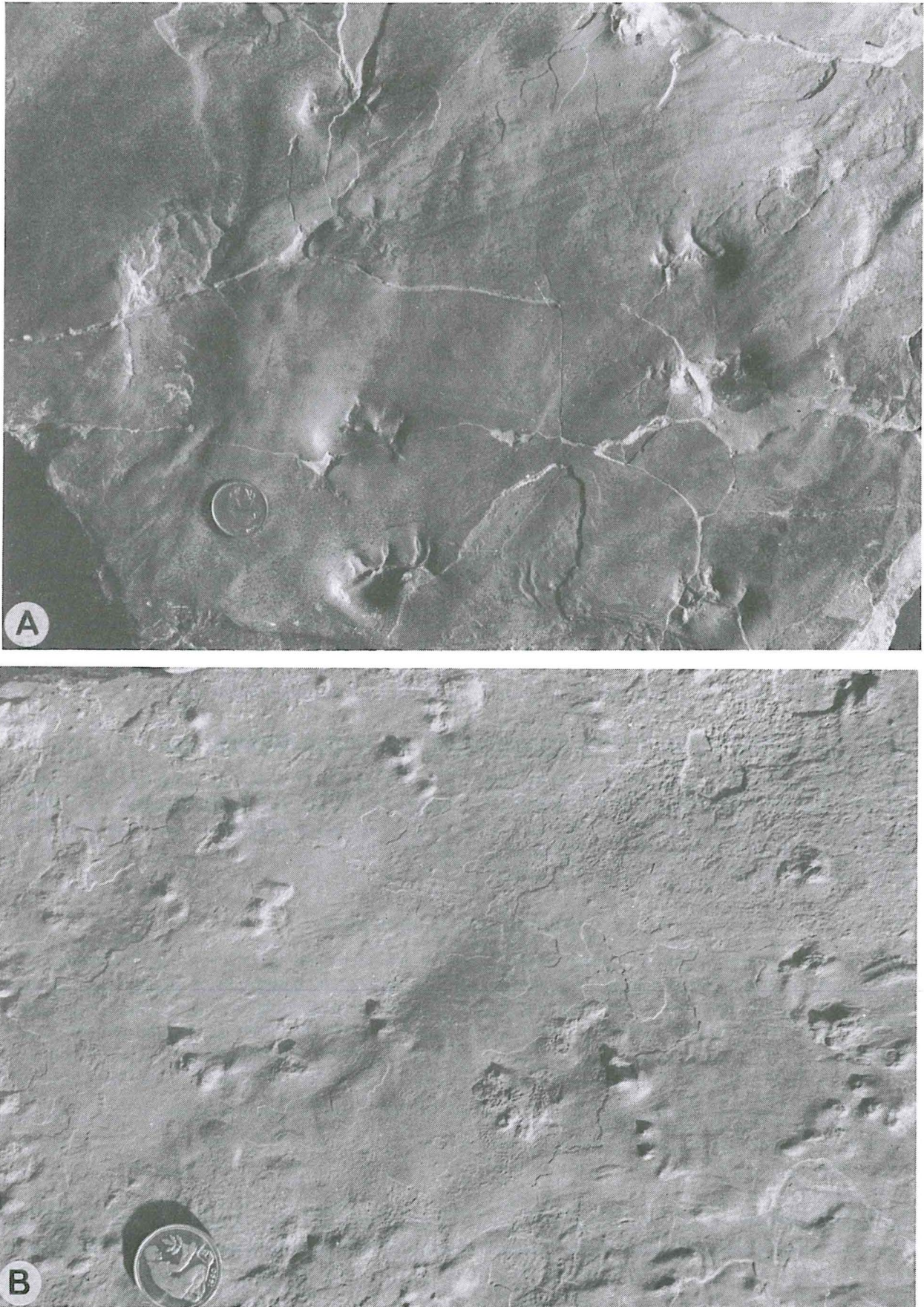


Fig. 6: Problematical specimens, which may be related to cf. *Batrachichnus salamandroides* or to cf. *Amphisauropus imminutus*.

A - SSN11.N9, tracks as undertracks in siltstone.

B - NHMM, prominent digit tips, preserved in a sand - siltstone intercalation. Scale - diameter of the coin 2 cm.

***Dromopus lacertoides* (GEINITZ), Fig. 7, 8 and 9A**

Dromopus is recorded by the specimens SSN11.N2 (already figured in HAUBOLD 1996: Abb. 22A), SSN11.N39 (Fig. 9A), N44 (Fig. 7A), N51 (HAUBOLD 1996: Abb. 22B), N52-56 (Fig. 7B, C, Fig. 8) in complete pentadactyl tracks of *D. lacertoides*. Other specimens show a transition to a reduced number of digits, like the didactylous variation of the ichnospecies *D. didactylus*. Also, the significant pattern of the digit in *D. didactylus*, known from Permian horizons in France (GAND 1987; figured in HAUBOLD 1996: Abb. 21A-C), cannot be identified within the Nierstein material. Some fragmentary specimens that should be discussed under *Dromopus* are mentioned by FICHTER under the following names:

PIM K251 "cf. *Anhomoiichnium diversum*" (1983: Abb. 28)

SSN11.N31 "*Anhomoiichnium diversum*" and "*Chelichnus (Barypodus) ? gravis*" (1984: Abb. 8, and 14).

It mainly seems to be the determination of the last specimen which led to creation of the "*Anhomoiichnium* Zone" by BOY & FICHTER (1988). But all characteristics, as far as recognisable, point to *Dromopus*. Additional specimens of *D. lacertoides* are PIM K83, K206, K228, and K232-242 (personal comm. G. GAND).

Dromopus, with the traditionally acceptable

ichnospecies *D. agilis* and *D. lacertoides* (HAUBOLD et al. 1995a: 145, HAUBOLD 1996: 55), is another major tetrapod track element of Late Carboniferous and Early Permian red beds. Contrary to the characteristic pattern, there are some possible questionable or wrong determinations due to incomplete preservation and related subjectivistic interpretations. One of the extreme examples can be exhibited with specimen SSN11.N31: In the sketch of the track morphology the fracture of the rock piece is enclosed to establish the determination "*Chelichnus (Barypodus)*" of FICHTER (1984: 222, Abb. 14). Likewise, the relation of other tracks present on the same small surface to *Anhomoiichnium diversum* as determined by FICHTER (1984: 218, Abb. 8) is unacceptable, while the outline sketches given by this author resemble the characteristics of *Dromopus*. For comparison, one is referred to an already published photograph of the specimen SSN11.N31 (HAUBOLD 1996: Abb. 11B). The status of *Anhomoiichnium*, originally introduced by DOZY (1935) for a trackway on a small slab from the Collio Formation, has already been documented and revised after the type specimen in the Natural History Museum of Leiden (HAUBOLD 1996: 38, Abb. 11A). As a result, *Anhomoiichnium* is not an acceptable valid ichnotaxon, instead it is a possible variation of *Batrachichnus*.

Dimetropus*, Fig. 9B, *Ichniotherium*, Fig. 10, and ?*Hyloidichnus

Fragmentary specimens, mostly isolated tracks, may represent some other ichnotaxa, cf. *Dimetropus* sp., cf. *D. nicolasi* GAND & HAUBOLD, and may be identified after some specimens from Nierstein, Rehbacher Steig, in the collection BEILING 26 and 27 II (now NHMM,

Fig. 9B). cf. *Ichniotherium* sp. is present in specimen SSN11.N82 (Fig. 10). ? *Hyloidichnus* sp. May, perhaps, be added to the list after specimen PIM K211.

Revised list of ichnotaxa

From the reinvestigation of the specimens, a reduced list of no more than seven ichnotaxa resulted. Only three taxa are clearly identifiable, the other four taxa can be documented only from a few isolated and less clear tracks:

cf. *Batrachichnus salamandroides* (GEINITZ)

Limnopus zeilleri (DELAGE)

Amphisauropus imminutus HAUBOLD

Dromopus lacertoides (GEINITZ)

cf. *Dimetropus* sp.

cf. *Ichniotherium* sp.

? *Hyloidichnus* sp.

The determinations presented here are comparatively different from the first results of FICHTER. This is due to some nomenclatorial and taxonomical principles derived from detailed analyses of comparable material from many Early Permian occurrences (see HAUBOLD 1996). Necessarily, these studies have been prior to the revision presented here.

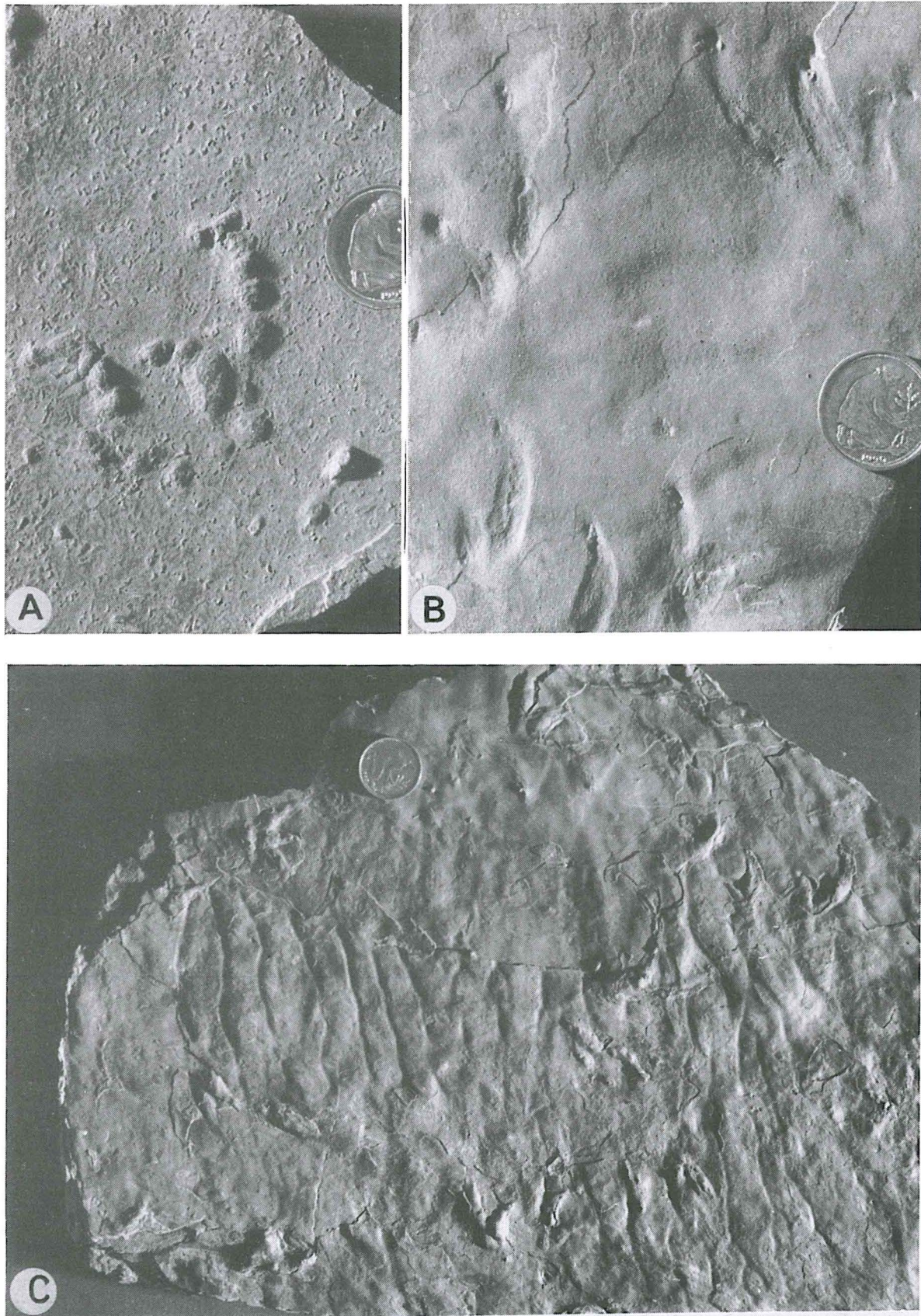


Fig. 7: *Dromopus lacertoides*, tracks of variable preservation.

A - SSN11.N52. B - SSN11.N4. C - SNN11.N56.

Whereas A and B may be undertracks or are due to preservation in a relatively consistent substrate, B exhibits the phalangeal pads of the prominent digits, perhaps due to a wetter substrate. Scale - diameter of the coin 2 cm.



Fig. 8: *Dromopus lacertoides*, the surface exhibits first of all the imprints of the distal parts of the digits, SSN11.N55. Scale - diameter of the coin 2 cm.



Fig. 9: A - *Dromopus lacertoides*, SSN11.N39, record of relatively complete digits II to V in addition to those of distal digit tips. B - cf. *Dimetropus* sp., isolated track, (?undertrack) NHMM. Scale - diameter of the coin 2 cm.



Fig. 10: The prominent, large digit tips may be indicative of cf. *Ichniotherium* sp., SSN11.N82. About 35% of original size.

4 Consequences of ichnostratigraphy and ichnotaxonomy

The track assemblage of the Standenbühl Beds from Nierstein is an example for the need to re-evaluate and reorganise taxonomy and nomenclature of Permian tetrapod tracks. The first study displayed a seemingly highly diverse ichnocoenosis. As documented here, the reinvestigation of the specimens proved that this previous extended list is a composite mixture of names, recorded from many occurrences of various ichnofacies from the Permian. Recent research on the mechanisms controlling the preservational variations of tetrapod tracks show that the ichnofacies of red beds and eolianites are taxonomically incompatible, and the recorded tracks have to be determined and classified after different taxonomical preferences (HAUBOLD et al. 1995 b, HAUBOLD 1996, LOCKLEY et al. 1995, MCKEEVER & HAUBOLD 1996).

A mixture of elements known from both ichnofacies are the ichnotaxa as determined by FICHTER. In addition to the red bed taxa *Limnopus*, *Saurichnites*, *Dimetropus*, *Gilmoreichnus*, and *Hyloidichnus*, are the listed taxa like *Chelichnus*, *Barypodus*, *Palmichnus*, and *Phalangichnus*, which are exclusively representative for tracks of the dune facies of the mainly eolian Late Permian Cornberg Sandstein. This composition is the central argument of BOY & FICHTER (1988) for a relatively high stratigraphic position of the "Anhomoiichnium Zone", and the tracks called *Chelichnus*, *Barypodus*, *Palmichnus*, and *Phalangichnus* are interpreted as new immigrants. The age of the Standenbühl Beds, as derived from the „Anhomoiichnium Zone“, seems not to be adequate and acceptable after reinvestigation of the track assemblage. Moreover, the track zonation of these authors is questioned principally from both the status of *Anhomoiichnium* and from the composition of Nierstein Upper Rotliegend track assemblage.

In fact, the Standenbühl track assemblage represents a restricted spectrum of about four determinable ichnotaxa only: cf. *Batrachichnus salamandroides*, *Limnopus zeilleri*, *Amphisauropus imminutus*, and *Dromopus lacertoides*. This assemblage is related to the Lowermost Permian ichnofaunas, which are known and widely distributed in Europe with the ichnogenera *Batrachichnus*, *Limnopus*, *Amphisauropus*, *Ichniotherium*, *Dromopus*, *Dimetropus*, *Gilmoreichnus*, and some others. This becomes more evident by inclusion of knowledge from

other parts of Pangaea, especially from North America. Following the overview given by HUNT & LUCAS (1998), the cosmopolitan red bed tetrapod ichnofauna of broad distribution in the Early Permian consists the following principal elements: *Batrachichnus*, *Limnopus*, *Dromopus*, *Gilmoreichnus*, and *Dimetropus*. Due to the incompleteness and restricted sample size, not all of these ichnogenera are confirmed from Nierstein, although a correlation within the Permian can be established. The evidence of the *Batrachichnus* - *Dromopus* assemblage of Rotliegend age is, by current knowledge, presumably comparable to assemblages of upper Wolfcampian age.

The stratigraphic evidence of the ichnotaxa from the Standenbühl Beds of Nierstein, as presented by FICHTER (1983, 1984) and by BOY & FICHTER (1988), cannot be verified. The determinations and the related interpretations seem to represent a case of using tetrapod ichnotaxa to justify the traditional stratigraphic model, which provides for a relatively late age for formations near the top of sequences in the Permian Saar-Nahe Basin. In particular the age of the so-called Upper Rotliegend is one of the classic enigmas in Central European stratigraphy. The majority of the Intra-Variscan Rotliegend deposits in the Saar-Nahe and Saale depressions were stratigraphically positioned within the Variscan sequence based on their highest formations, such as the Standenbühl Beds (see KRÖMMELBEIN 1991: Map 11, and GEBHARDT et al. 1991: Fig. 8). During the last decade the estimated age of these deposits shifted increasingly downward to a correlation with the upper Wolfcampian to lower Leonardian and Sakmarian to Artinskian respectively (SCHNEIDER et al. 1995a and b: Fig. 2, Table 2). The tetrapod tracks in their modified interpretation of upper Wolfcampian age provide evidence for a much more restricted time interval of the typical Rotliegend sequences. Their uppermost occurrences correspond with the absolute numerical dating of about 285 Ma as demonstrated by SCHÄFER & KORSCH (1998) for the Saar-Nahe Basin.

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