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The Early Permian tetrapod ichnofauna of Tambach, the changing concepts in ichnotaxonomy

Die unterpermische Tetrapodenfährten-Fauna von Tambach, die wechselnden Konzepte in der Ichnotaxonomie

With 8 figures und 1 table

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Abstract: Presently four ichnospecies are acceptable from the Tambach Formation of the Rotliegend at the Thüringer Wald area: *Ichniotherium cottae*, *Dimetropus leisnerianus*, "*Varanopus*" *microdactylus*, *Tambachichnium schmidti,* and one additional unnamed form which is discussed in comparison with specimens known from the Permian of the Estérel Basin in Southern France. Quantitatively dominating are the tracks of *I. cottae*, and *D. leisnerianus*. Of the other forms only few or unique specimens are recovered. The development of the systematic studies of the Tambach tracks is presented. The former descriptions contain about 28 names of possible generic affiliation and species range, but their meaning is sometimes multivariable. Tambach is one of the examples for the confusion in track ichnotaxonomy particularly in the Permian, though it concerns one famous, local and stratigraphic clear track-site only. The paper documents the taxonomic background of the names. The results demonstrate that one has to avoid interchanging of names that are characterised and named by different principles. Due to the fact that such interchanges are practised, any solution is rather difficult and attracks the opposition of the special researchers. The classification proposed by W. PABST (1908) for Permian tracks is oriented at every potentially possible morphological trait of the fossil tracks. Thus it is a classification of ichnological phenomena per se. The separated taxa are not related to biological categories and can not be evaluated as such. If this would nevertheless be done, this points to a non-realistic high diverse fauna. Another position is based on the biological oriented binomial principles. The taxa are characterised by anatomically controlled traits. This classification reflects the position of the trackmakers within the biological system. According to this principle the occurrence of Tambach points to an ichnofauna of low diversity. This corresponds to the interpretation of the trackmakers as diadectids, sphenacondontids, captorhinids, and araeoscelids. The summary of evidence is significant for an Early Permian age, and may be correlated to the Wolfcampian of North America.

Zusammenfassung: Gegenwärtig kann man vier Ichnospezies aus der Tambach Formation des Rotliegenden im Thüringer Wald anerkennen: *Ichniotherium cottae*, *Dimetropus leisnerianus*, „*Varanopus*" *microdactylus*, *Tambachichnium schmidti* und eine weitere, noch unbenannte Form, die vergleichend diskutiert wird mit Exemplaren aus dem Perm-Becken von Estérel in Südfrankreich. Quantitativ überwiegen Fährten von *I. cottae*, und *D. leisnerianus.* Von den anderen drei Formen liegen nur wenige Exemplare oder Unikate vor. Dargelegt wird die Entwicklung der Benennung der Tambacher Fährten. In den bisherigen Beschreibungen finden sich rund 28 Namen, die den Rang von Gattungen und Arten haben könnten, allerdings kann man ihre Bedeutung mitunter wahlweise multivariabel auslegen. Es handelt sich um ein umfangreiches Beispiel für die Konfusion in der Ichnotaxonomie speziell des Perms, obwohl es ein berühmtes, lokal und stratigraphisch klar fixiertes Vorkommen betrifft. Dokumentiert wird der taxonomische Hintergrund der Namen. Das Ergebnis zeigt, daß eine wechselseitige Vermengung der für die Fährtenformen eingeführten Namen vermieden werden sollte, die nach unterschiedlichen Prinzipien charakterisiert und benannt worden sind. Da aber bis heute solche Vermengungen praktiziert werden, ist eine Klärung eher schwierig, und trifft insbesondere unter den Forschern auf Widerstände. Auf der einen Seite steht die Klassifikation, wie sie W. PABST (1908) für die permischen Fährten vorgeschlagen hat. Diese orientiert sich an allen potentiell möglichen morphologischen Erscheinungen der Ichnofossilien. Damit ist es eine Klassifikation ichnologischer Phänomene an sich. Die danach separierten Taxa entsprechen nicht biologischen Kategorien und sind nicht als solche zu werten. Wenn dies dennoch versucht wird, resultieren Hinweise auf eine unrealistisch hoch diverse Fauna. Auf der anderen Seite steht eine biologisch orientierte binäre Benennung und Klassifikation. In dieser sind die Taxa nach anatomisch kontrollierten Merkmalen der Tetrapodenfährten charakterisiert. Damit wird die Position der Fährtenerzeuger im biologischen System reflektiert. Für das Vorkommen Tambach ergibt sich daraus eine relativ geringe Diversität der Ichnofauana. Ein solches Ergebnis korrespondiert mit der Interpretation der Erzeuger als Diadectiden, Sphenacodontiden, Captorhiniden und Araeosceliden. Insgesamt belegen diese Ergebnisse ein unterpermisches Alter, vergleichbar dem Wolfcamp in Nordamerika.

1 Introduction

The tetrapod tracks from the Tambach Sandstein present an amazing example for the changing conceptions in ichnotaxonomy. The first discovery of the tracks were made by H. F. SCHÄFER in 1887 (SCHEIBE 1890). The first short description was made by POHLIG (1892) followed by the extended studies of PABST (1895 - 1908). All of the material have been collected since from the locality Bromacker north of Tambach-Dietharz, Thuringia (Fig. 1). The Tambach Formation is positioned on the top of a Permocarboniferous sequence with a stratigraphic range from late Stephanian to Autunian/Saxonian. The lithostratigraphic subdivision into Gehren, Manebach, Goldlauter, Oberhof, Rotterode, and Tambach Formations has been elaborated in the last decades (i.e. HAUBOLD 1985, SCHNEIDER 1996). One can agree with PABST (1908: 347) that the study of Tambach tracks provide the background for many further descriptions of such material from the Rotliegend. Some later partial studies were published by LOTZE (1927), KORN (1933), and MÜLLER (1954). HAUBOLD (1971b, 1973a, b) considered the Tambach tracks as a part of more complex studies.

Following a critical analysis of the Tambach tracks, and their comparison with equivalent occurrences within the hitherto documentation's, only four ichnotaxa can be accepted. These can be well separated by means of their anatomical interpretation. However, the taxa remain somewhat problematical in different ways when treated by nomenclatoral principles.

- *Ichniotherium*, respectively *Saurichnites cottae* was introduced for the first time for material from the stratigraphically lower Goldlauter Formation of the Thuringian Forest Basin (POHLIG 1885), and the taxonomically identity with the material from the Tambach Formation has not finally been established.
- *Dimetropus leisnerianus* is related to a description GEINITZ (1863) introduced under the name *Saurichnites leisnerianus* to an insufficient specimen of the type serie, found in the Rotliegend of the Intra-Sudetic Basin.
- "*Varanopus*" *microdactylus* is generically undetermined, due to the formal unresolved meaning of the original version of *Varanopus* and in its relation to *Hyloidichnus*.
- Only *Tambachichnium schmidti* is out of question nomenclaturally. But this taxon is now, as before, restricted to one single specimen, a short trackway, only. Determinations of this species from other localities, e.g. from the Esterel Basin of southern France (GAND et al. 1995) do not resemble the type specimen from Tambach.

As result, even 100 years after the first description, the tracks of one of the most famous and excellent recorded local ichnofaunas of the European Permian are relatively unclear in terms of nomenclature. This fact appears somewhat symbolic and symptomatic for the taxonomically knowledge of the Late Palaeozoic tetrapod tracks. There are two main reasons for this:

1) The principles of taxonomy and the related nomenclature are non-uniform;
2) The fossil tracks of the occurrences in many Permian basins and their formations have not yet been sufficiently compared, or the results of the comparisons are ambiguous and have been ignored. Both aspects together actually prevent an adequate understanding of track studies, and of the possible faunistic information.

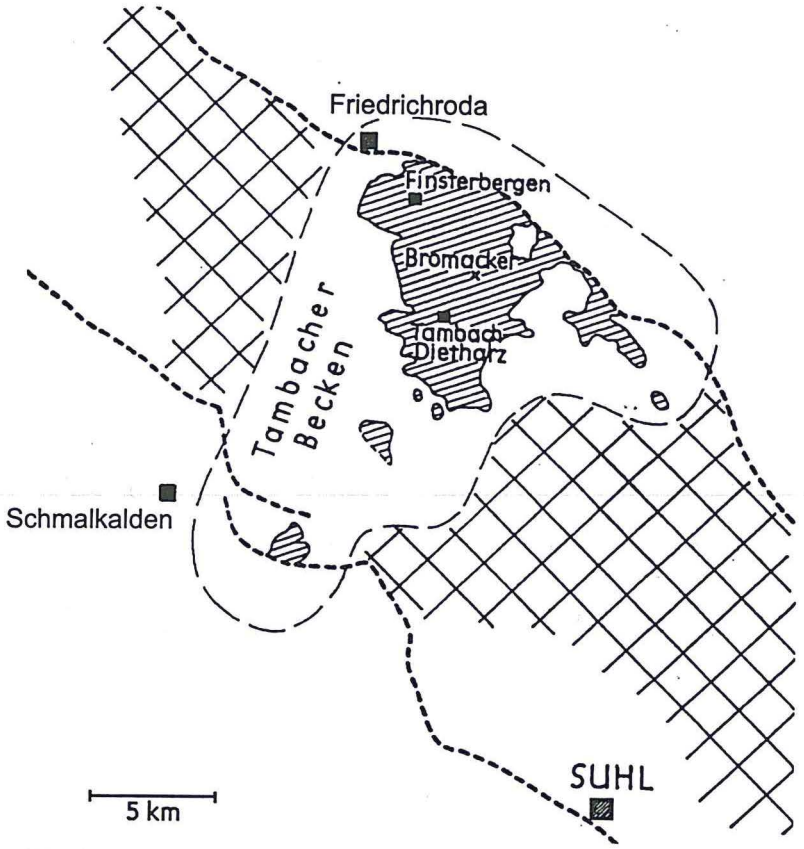

Fig. 1:
The Tambach Formation in the central Thuringian Forest, maximal outline of the primary depression, present distribution of the remaining sediments, and the location of the Bromacker. From HAUBOLD (1985).

2 The classification of tetrapod tracks after W. PABST (1908) and general problems for the ichnotaxonomy tetrapods

From the study of 66 specimens - track bearing slabs - from different occurrences of the Lower Permian of central Europe, PABST (1908) established the "Attempt to classify the Tetrapod traces of the Rotliegend" into eight "typical ichnospecies" (PABST 1908: 430):

Ichnium sphaerodactylum Klumpzehfährte
lump-digital track
Ichnium acrodactylum Spitzzehfährte
point-digital track
Ichnium pachydactylum Plumpzehfährte
clumsy-digital track
Ichnium gampsodactylum Krummzehfährte
crooked-digital track
Ichnium brachydactylum Kurzzehfährte
short-digital track
Ichnium rhopalodactylum Keulzehfährte
club-digital track
Ichnium anakolodactylum Gekürztzehfährte
shorten-digital track
Ichnium dolichodactylum Langzehfährte
long-digital track.

To these "Ichnospecies" PABST combined subspecies, which „originated probably from the same or closely related species of animals, that made the typical ichnospecies as well". Altogether PABST (1908: 450) classified the following "Ichnospecies, Subspecies, and Varieties":

1. Maingroup Brachydactylichnia
   Subgroup Sphaerodactylichnia
      Ichnium sphaerodactylum
   Subgroup Pachydactylichnia
      Ichnium pachydactylum
      Ichnium brachydactylum
      Ichnium rhopalodactylum
      Ichnium anakolodactylum
2. Maingroup Dolichodactylichnia
   Subgroup Acrodactylichnia
      Ichnium acrodactylum
   Subgroup Gampsodactylichnia
      Ichnium gampsodactylum
      Ichnium dolichodactylum.

This classification and the related nomenclature have never been accepted. However, there are some attempts for a partial establishment of PABSTs names. But, without a detailed analysis of the meaning of PABSTs system this, leads to an increasing confusion.

Nevertheless PABSTs system might be understandable from the view of his time: the low number of skeletal remains known from the European Permian. The reports of the discoveries in the Permian of North America were unknown to PABST (MARTENS 1994). Moreover, it was PABSTs intention to establish a perfect system into which every known fossil track would fit. From the very beginning, PABSTs system was in contradiction to studies which used the binomial nomenclature and which try to reflected principally the systematically and evolutionary position of the tetrapod ichnofaunas under study. Since its introduction, PABSTs system, due to its peculiarity, was like a barrier against the understanding and interpretation of Rotliegend tracks generally (HAUBOLD 1971b: 17). At least it was the reason for many nomenclatoral and taxonomically misunderstandings, as will be shown in the next sections.

2.1 The meaning of the ichnospecies after PABST

On the contrary to former and other researchers of his time (like GEINITZ 1861, and POHLIG 1892), it was PABSTs principle not to understand the tracks by the originating animals. Instead he intended to designate the tracks after the characters observed (PABST 1908: 342 pp.). His guideline was the recognition of the tracks by their own features. In consequence, he proposed a determination that ignores the relation to the trackmaker. The aim was a determination of tracks only. PABST mentioned the following characters as distinctive:

1) Size of imprints („Einzelfährten"),
2) morphology of the solepads and digits within the imprints („Einzelfährtenabdrücke"),
3) relative length of the digits compared to the sole,
4) size relation between length and width of the imprint („Einzelfährte"),
5) were the animals bipedal or quadrupedal (?), and
6) pattern of the gait, alternating or non alternating, after the position of the related manus-pes sets („Einzelfährtenpaare").

According to PABST, an ichnospecies corresponds in no way to the originating animal species (PABST 1908: 344). His reason was that the tracks of animals of the same species might look very different due to control by substrate, gait, and individual stage of each animal. In consequence, PABST argued that without primary knowledge of the trackmakers the related tracks must be ordered to systematically separated ichnospecies.

After these statements the ichnospecies („Fährtenart") is:

1) not equal with track-making animal species, because
2) tracks of the same ichnospecies might originate from different kinds of animals, and this also means that
3) the same kind of animal may produce different ichnospecies.

Furthermore PABST wrote literally "the term ichnospecies combines tracks of very close to nearly perfect correspondence, because complete correspondence of two trackways is impossible" (German original „der Begriff Fährtenart vereinigt

Fährten von größter bis fast zu völliger Übereinstimmung werdender Ähnlichkeit, da vollkommene Übereinstimmung zweier Fährten undenkbar ist"). Consequently there may be useful characters for the differentiation, which are usually of no specific value, like size and occurrence. "Tracks of the same ichnospecies from different sites show only limited agreement" (Original: „Zwischen Fährten verschiedener Fundorte derselben Fährtenart ist nur bedingte Übereinstimmung vorhanden"). Thus the tracks give no evidence for the exact correlation of the sites. In consequence „fossil tracks are no index fossils". And due to the limited similarity of tracks from different sites, PABST always adds the name of the locality to the name of the ichnospecies. This concept of the ichnospecies as related to the characters of the tracks per se is, according to PABST, the preferable background for the description, instead of the relation between fossil tracks and their potential trackmakers. The latter exists in the imagination of the researcher only (Original:„als wenn man die fossilen Fährten mit jenen nur in der Phantasie ihrer Bearbeiter vorhandenen Fährtentieren in Zusammenhang zu bringen sucht"). *Anmerkung: Das ist eine Erkenntnis, der auch PABST zustimmt, daß also die Erzeuger doch nicht nur in der Phantasie der Bearbeiter der fossilen Fährten existieren. Auch wenn PABST es mit dem Hinweis auf die Phantasie vermutlich nicht so wörtlich gemeint haben mag, hier liegt der Ansatz zur Bewertung seiner Klassifikation. Sie ist bewußt und prinzipiell separiert von irgendeiner paläobiologischen Anwendung.*

Concerning the nature of the trackmakers of the Rotliegend, PABST (1908: 346) mentioned: they were eotetrapods, and obviously tracks of salamandroid and lacertoid animals. This is in agreement with the names *Saurichnites salamandroides* and *Saurichnites lacertoides* as introduced long before by GEINITZ (1861). This position was the reason for PABST neither to use nor to continue or elaborate, in the sense of the binomial nomenclature the unquestionably valid names *Saurichnites salamandroides* and *Saurichnites lacertoides*.

2.2 Evaluation of PABSTs classification and some consequences

An analysis of PABSTs methodology might be useful presently because of the repetitive appearance of comparable tendencies in ichnotaxonomy, and their resulting confusions. These confusions are due first of all to the multilateral set of characters of tracks, consisting of a combination of extramorphologically and anatomically controlled features. These features might be evaluated differently by specialists. There is still a tendency to describe and determine the tracks per se, and to include facial and other extramorphological traits into the diagnoses of the ichnotaxa and their related interpretation.

Using the principles of PABSTs classification, variable imprints of tracks and variable patterns of tracks on the course of the same trackway justify one to name different species, subspecies, and varieties. In other words, particular segments and single tracks of a trackway may get different names, although they belong to the same trackway of an individual. In consequence, each ichnological bias can be classified and named. However, such principles can hardly be the basis of palaeobiological and faunistic studies.

Recall the particular situation of tetrapod tracks which are almost like body fossils: they are not parts of animals, but rather casts of parts which are nearly identical with the manus and pes of the trackmakers. Possible deformations might be eliminated as far as possible by comparisons. The aim is the recognition of the most optimal anatomically controlled form of the tracks as a basis of the characterisation of an ichnotaxon. It is only at this level that it makes sense to classify the tracks and name them binomial. Under such conditions, the only possibility to adapt any names from PABST to the binary nomenclature are names of the subgroups like Ichnium acrodactylum, which could be changed into *"Dimetropus acrodactylus"*. (But see below and Tab. 1, which binomial combinations were already proposed by PABST). I am of the contrary opinion, because no one "ichnospecies" of PABSTs finalistic and perfectionistic system seems to be formally useful:

1) *Ichnium sphaerodactylum*, *I. acrodactylum*, and *I. gampsodactylum* are subjective synonyms of former descriptions.
2) *Ichnium pachydactylum*, *I. brachydactylum*, *I. rhopalodactylum*, *I. anakolodactylum*, *I. dolichodactylum* and *I. acrodactylum* are, on the one hand subjectiv synonyms, and on the other they are principally ambiguous in the version of PABST. The described features are not related to certain anatomical traits, but mainly to any possible extramorphological variations.

The tracks of many animals can display the patterns like lump-, point-, clumsy-, crooked-, short-, long-, shorten-, and club-digital („klump-. spitz-, plump-, krumm-, kurz-, lang-, gekürzt- and keulzehig"). Moreover, tracks of the same animal can be preserved as club-digital = lump-digital = clumsy-digital („keulzehig = klumpzehig = plumpzehig"), depending on the substrate and on the individual gait. One example is the *Batrachichnus* tracks from the Abo Formation, Robledo Mountains, in New Mexico (HAUBOLD et al. 1995). This fact also tells us that the variability of small tracks can become extremely high under certain conditions. In this ichnotaxon the extramorphological variability reaches the possible maximum at pes lengths below 30 mm (HAUBOLD 1996). The preservation of large tracks is relatively more stable and less variable, as can be demonstrated from Rotliegend track beds for *Ichnium sphaerodactylum*, *I. acrodactylum* and *I. gampsodactylum*, the

equivalents of *Ichniotherium*, *Dimetropus* and *Dromopus*.

PABSTs system is very restricted and can not be developed further more, due to its missing relation to the system of tetrapods. But the latter is one of the accepted basic principles in the studies of tracks (SEILACHER 1964: 300, HAUBOLD 1971: 4 and 1996: 25, and BROMLEY 1996: 176). This principle mainly refers to osteological, faunistic and biostratigraphic analyses, the potential results of track studies. One should be careful not to lose this principle, nor to be unaware of its ramifications, as has occasionally happened. In many cases, today and in the past, fossil tetrapod track-taxa have been diagnosed by their maximum similarity under addition of statistical methods. This kind of diagnoses, and the mixture of different principles in diagnosing ichnotaxa of Permian tetrapods, is the main background for apparently arbitrary and incompatible determinations and interpretations. So the results of many publications appear to be polarised. On the one hand, there are results presenting highly diverse ichnofaunas (ELLENBERGER 1983, 1984, FICHTER 1983, 1984, MCKEEVER 1994, GAND et al. 1995, SCHULT 1995). On the other side the same ichnofaunas are less diverse (GAND 1987, GAND & HAUBOLD 1988) and, after recent analyses, the diversity is reduced to only a few central ichnotaxa (HAUBOLD et al. 1995, HAUBOLD 1996, MCKEEVER & HAUBOLD 1996) and reflects a cosmopolitan character of Early Permian tetrapod ichnofaunas (HUNT & LUCAS 1998).

From the time of PABST through until today, due to divergent principles of nomenclature and ichnotaxonomy, neither the ichnotaxa nor the ichnofaunas are comparable in some cases. The controlling factors of track and trackway preservation - anatomy of the foot skeletons, gait, and substrate influences - are evaluated very differently. Two main questions usually remain undecided:

1) Which kind of preservation is optimal to a certain facies, which preservation records the anatomical structures in the best manner?
2) Would only few optimally preserved tracks be more important than statistical averages of many tracks along the trackway or from a larger surface?

Tab. 1:
Synonymy of the tetrapod ichnotaxa from the Tambach Sandstone in the three main periods. Names related to the binomial nomenclature are in *italics*.

PABST 1895 - 1897	PABST 1900/1905/1908	NOPCSA 1923 - HAUBOLD 1984
	***Ichniotherium cottae* (Pohlig, 1885)**	
Ichnium sphaerodactylum = *Sphaerodactylichnium cottae*	Ichnium sphaerodactylum, tambacense I. sphaerod. tamb., ssp. Minor	*Acibates sphaeorodactylum* *Korynichnium sphaerodactylum* *Korynichnium celer* *Korynichnium minor*
	Dimetropus leisnerianus (Geinitz, 1863)	
Ichnium acrodactylum = *Ichniotherium schaeferi* = *Acrdactylichnium schaeferi*	Ichnium acrodactylum, tambacense I. acrod. tamb., ssp. alternans, I. acrod. tamb., ssp. curvata, I. acrod. tamb., ssp. Dispar	*Herpetichnus acrodactylus* *Herpetichnus alternans* *Chirotherium pabsti* *?Herpetichnus pabsti* *Chirotherium rubrum* = *? Herpetichnus rubrum*
	„Varanopus" microdactylus (PABST, 1897)	
Ichnium microdactylum	Ichnium dolichodactylum, tambacense Ichnium brachydactylum, tambacense	*Procolophonichnium ? microdactylum* *Varanopus microdactylus* *Hardakichnium microdactylum* *Chelichnus brachydactylus* *Palmichnus tambachensis*
	Tambachichnium schmidti Müller, 1954	
		Tambachichnium schmidti

3 Further development of the systematic and ichnotaxonomy of Tambach tracks

Before an attempt to generalise this knowledge, the development of nomenclature and ichnotaxonomy from the example of the Tambach track-fauna should be demonstrated using the following steps. For control and reconstruction the original specimens are mentioned by which the names have been introduced. Abbreviations in front of the **specimen numbers** concern the collections: **GN** - Museum der Natur Gotha, **HF** - Institut für Geologische Wissenschaften und Geiseltalmuseum der Martin-Luther Universität Halle, und **PMJ** - Phyletisches Museum Jena.

Whereas PABST (1896, 1897), under the influence of binomial principles, named three ichnospecies only - *Ichnium cottae*, *I. acrodactylum*, and *I. microdactylum* - a few years later he changed to a modified system of naming. All these names are **not written in *italics***, to demonstrate there different, respectively non-binomial status. As shown before, his finalistic classification (PABST 1908) separated from the trackbearing surfaces of the Tambach Sandstone eight „Fährtenarten" and „Unterarten" (important figured specimens):

a) Ichnium sphaerodactylum, tambacense (GN 1840, 1851, 1852)
Ichnium sphaerodactylum tambacense, subsp. minor (GN 1918)
b) Ichnium brachydactylum, tambacense (GN 1841, 1843
c) Ichnium acrodactylum, tambacense (GN 1762, 1825, 1828, 1983)
Ichnium acrodactylum tambacense, subsp. alternans (GN 1823)
Ichnium acrodactylum tambacense, subsp. dispar (GN 1762)
Ichnium acrodactylum tambacense, subsp. curvata (GN 1827)
d) Ichnium dolichodactylum, tambacense (GN 1785)
(= *Ichnium microdactylum* and Ichnium sphaerodactylum minus, tambacense).
A generalised interpretation concerns an origin of "salamandroid" and "lacertoid eotetrapods".

In succeeding compilations from NOPCSA (1923) to KUHN (1963), the incompatibility of PABSTs classification with the principles of binomial nomenclature became obvious. With the intention to compare and adapt the Tambach track fauna with other described and named occurrences of Permian red beds, this ichnofauna appeared highly diverse, consisting ten ichnospecies. However, all of them must be, necessarily, of less understandable status:
Acibates/Korynichnium sphaerodactylum
Korynichnium celer
Korynichnium minor
?Herpetichnus/Chirotherium pabsti
?Herpetichnus/Chirotherium rubrum
Herpetichnus acrodactylus
Herpetichnus alternans
?Chelichnus brachydactylus
Procolophonichnium microdactylum
Tambachichnium schmidti.

In later studies by HAUBOLD (1971a, b, 1973a, b), that are related for the first time after PABST to a reinvestigation and study of the original specimens, five ichnospecies have been separated (figured originals):
Ichniotherium cottae (GN 1351, 1515)
Dimetropus leisnerianus (GN 1823, 1827, 1828)
Varanopus microdactylus (GN 1785=„1875", PMJ P 1322)
Palmichnus tambachensis (GN 1842)
Tambachichnium schmidti (PMJ P 1321).

In this period the interpretation concerned an origin by pelycosaurs, procolophonomorphs and lepidosaurs. In the light of application of the principles of binomial nomenclature and comparative studies to other track sites, there are currently only four track taxa acceptable from the Tambach Sandstein, because *Palmichnus tambachensis* is an extramorphological variation of *Varanopus microdactylus*:
Ichniotherium cottae (POHLIG, 1885)
Dimetropus leisnerianus (GEINITZ, 1863)
"Varanopus" microdactylus (PABST 1897)
Tambachichnium schmidti MÜLLER, 1954.

4 Present state of knowledge

Today, the interpretation is more precise due to the discovery of skeletal remains in strata of the Tambach Formation near to the track-bearing surfaces (BERMAN & MARTENS 1993, BERMAN et al. 1998, BOY & MARTENS 1991, SHUMIDA et al. 1996). However, an absolute agreement of track and skeletal evidence should be postulated with caution, though presumed sometimes. The potential and osteologically recorded trackmakers are partially related to diadectids, pelycosaurs, captorhinomorphs and diapsids. Additional precision is given by the correlation to the fauna of the upper Wolfcampian (SHUMIDA et al. 1996) confirming, in the case of *Ichnotherium*, the formerly discussed origination by *Diadectes* (NOPCSA 1923), although caseids and edaphosaurids have been discussed too. ROMER & BYRNE (1931: 36) had already argued in their study of the *Diadectes* pes against a correlation with *Ichniotherium*. *Dimetropus* resembles the sphenacodontids. The interpretations of *"Varanopus"* as protorothyridid, and of

Tambachichnium as araeoscelid, are in agreement with both skeletons and the correlation with the upper Wolfcampian, and solves former contradictions. The former interpretation of these tracks as originated by procolophonids and lepidosaurs respectively diapsids (MÜLLER 1954, HAUBOLD 1973) was proposed due to a presumed much younger age of the Tambach Sandstone within the Rotliegend and Permian, i.e. Upper Rotliegend and Saxonian.

The development in the determination of the tracks from the Tambach Sandstein, in an abbreviated overview, is as follows (see also Tab. 1):

Ichniotherium cottae (POHLIG, 1885), Fig. 2 - 4

This track type was first recognised and introduced by POHLIG (1885), based on specimens from the Goldlauter Formation, Rotliegend, Gottlob quarry in Friedrichroda (Fig. 2), under the name *Saurichnites cottae*. A type specimen from this locality has never been designated. All principal studies of this track type concern the material from Tambach, where at least 70% of all observed tracks belong to.

POHLIG 1892, p. 60: *Ichniotherium cottae* (first introduction of the generic name in relation to the specimen from Tambach GN 1351, together with a photo made by PABST)

PABST 1895, p. 573, 575: *Sphaerodactylichnium cottae* = *Ichnium sphaerodactylum* (= *Ichniotherium cottae*)

PABST 1896, p. 808, figures of specimens GN1351, 1352, 1367, 1393, 1748*: Ichnium sphaerodactylum* „Klumpzehfährte" - lump-digital track

PABST 1908, p. 347 ff., 430, 442: Sphaerodactylichnia from Tambach; Ichnium sphaerodactylum, tambacense GN 1351 and many others, and I. sphaerodactylum, tambacense, subspecies minor, GN 1819

NOPCSA 1923, p. 135: *Acibates sphaerodactylum*

LOTZE 1927, p. 174: *Korynichnium sphaerodactylum*, subsp. *minor*

KORN 1933, p. 169: *Korynichnium celer*

KUHN 1963, p. 32: *Korynichnium sphaerodactylum, K. minor, K. celer*

HAUBOLD 1971 a, p. 36; 1971b, p. 34; 1973 a, p. 23; 1973 b, p. 251: *Ichniotherium cottae*, with designation of the (lecto)type GN 1351

HAUBOLD 1984, p. 87, Abb. 57:2: *Ichniotherium cottae*

HAUBOLD 1996, Abb. 2: *Ichniotherium cottae* (example of "Compound Specimen").

Ichniotherium cottae is one of the most significant tetrapod track type of Permocarboniferous age. Its osteological interpretation, formerly argued to edaphosaurs and caseids (HAUBOLD 1971, 1973, 1984), can be now much more precisely related to *Diadectes* (personal discussion with D. BERMAN and S. SHUMIDA 1998). The recent discoveries of *Diadectes* from Tambach is evidence of a consolidation of manus and pes that corresponds with the sole pads of *Ichniotherium*. Now, as before, it may be remarkable that this track type has been found common in formations of the Thuringian Rotliegend, in the Tambach, and in the earlier Oberhof and Goldlauter Beds. All other reports are less clear.

Fig. 2: *Ichniotherium cottae* (HF 57), Goldlauter Formation, Gottlob quarry in Friedrichroda. In the horizons of this older Formation the preservation is less complete compared to those of the Tambach Sandstein.

Fig. 3: *Ichniotherium cottae* (exhibit of GN), Tambach Sandstein, segment of a trackway in representative preservation.

Fig. 4: *Ichniotherium cottae* (HF 51), Tambach Sandstein, deep plantigrade tracks of a trackway-segment, and imprints preserved in low relief as digit tips only.

Dimetropus leisnerianus (GEINITZ, 1863), Fig. 5

PABST 1895, p. 575: *Ichniotherium schaeferi* = *Acrodactylichnium schaeferi* = *Ichnium acrodactylum*
PABST 1897, p. 701, fig. of specimen GN 1760, 1762: *Ichnium acrodactylum* „Spitzzehfährte" - point-digital track
PABST 1900: Ichnium acrodactylum, subsp. alternans, dispar, and curvata
PABST 1905, 1908, p.367 ff., 433, 443: Ichnium acrodactylum, tambacense; Ichnium acrodactylum tambacense, subsp. alternans, dispar, and curvata; Acrodactylichnia von Tambach (GN 1762 and many others)
NOPCSA 1923, p. 139, 140, 144: *Herpetichnium acrodactylum* = *Saurichnites leisnerianus*; *Chirotherium pabsti* = *Ichnium acrodactylum; Chirotherium rubrum* = I. acrodactylum, tambacense, subsp. dispar
KUHN 1963, p. 27, 28, 31: *?Herpetichnus pabsti, ?H. rubrum, H. acrodactylus, H. alternans*
HAUBOLD 1971 a, p. 34; 1971 b, p. 32; 1973 a, p. 20; 1973 b, p. 251; 1984, p. 100, Abb. 66; 1996, p. 53, Abb. 14, Abb. 15: *Dimetropus leisnerianus* GN 1762, 1765, 1820, 1823, 1827, 1828, 1833, 1985, 1986.

Less than 30 % of the observed tracks from the Tambach Formation belong to *D. leisnerianus*. The history in the understanding of this in second dominating track type is confused like those in *Ichniotherium cottae*. NOPCSA (1923) first suggested the specific agreement of *Saurichnites leisnerianus* to the significant Acrodactylichnia from Tambach, and HAUBOLD (1971) argued for the relation to *Dimetropus*. PABST (1908) saw no correlation to any other occurrences. Instead he classified *S. leisnerianus* from the type locality under the Pachydactylichnia as Ichnium pachydactylum because of the clumsy-digital track preservation. He did not realise this kind of preservation along some trackways of Ichnium acrodactylum from Tambach, although the large slabs GN 1823 and GN 1828 display the pachydactylum style.

Dimetropus leisnerianus is not well established primarily from the type specimen („Originalhandstück" of GEINITZ 1863, figured by PABST 1908: Kap. 23, Fig. 1), but the other material from Albendorf show one of the significant *Dimetropus* or Acrodactylum preservation, respectively. After all, *D. leisnerianus* should become stabilised by name (HAUBOLD 1996: 53). The pachydactylum outlook in *D. leisnerianus* and I. acrodactylum is referable to the dominating impression of both the distal metacarpal and metatarsal phalangeal pads, together with isolated digit tips in front of them. Such variation reflects the osteology of the spenacodontid autopods.

In other tracks, also classified by PABST under I. pachydactylum, the digits are indeed of clumsy, rounded outline. Such tracks differ from the *Dimetropus*/I. pachydactylum variation, and have been classified under *Amphisauropus* (HAUBOLD 1971, 1996). The *Amphisauropus*/I. pachydactylum variation, respectively track type is not at all known from Tambach. This is one more example of the incompatibility of PABSTs system of names with the binomial principles. Different from the situation in *I. cottae*, where the presumed originator *Diadectes* is known from immediately overlying horizons, the spenacodontid originators of the likely common *Dimetropus* are not yet recorded by bones in the Tambach Formation.

"Varanopus" microdactylus (PABST, 1896), Fig. 6

PABST 1897, p. 706, fig. of specimen: GN 1785: *Ichnium microdactylum* „Kleinzehfährte" - small-digital track
PABST 1900, 1905: Ichnium dolichodactylum, tambacense GN 1785; Ichnium brachydactylum GN 1841
PABST 1908, p. 365, 384, 438, 440: Ichnium brachydactylum, tambacense, GN 1841, 1843; Ichnium dolichodactylum, tambacense, GN 1785
MÜLLER 1954:, p. 190: *"Procolophonichnium" ? microdactylum* JP 1
KUHN 1963, p. 15: *?Chelichnus brachydactylus*
HAUBOLD 1971 a, p. 30-31; 1971 b, p. 27-28; 1973 a, p. 13; 1973 b, p. 251; 1984, p. 101, Abb. 67: 1, 3, 4: *Varanopus microdactylus* type GN 1785, and paratype PMJ P 1322 (=JP 1); *Palmichnus tambachensis*, GN 1841, 1842, 1843
MÜLLER 1984, p. 107: *Hardakichnium microdactylum* JP 1.

Besides the former two ichnospecies dominating the Tambach track surfaces, *"Varanopus" microdactylus* is known by five specimens, three represent longer trackways. Opposite to the nomenclatoral situation in *I. cottae* and *D. leisnerianus*, *I. microdactylus*, as first introduced by PABST, is an acceptable ichnospecies name because it was named earlier (PABST 1897), before he developed his separate classification. In this classification PABST himself did not use *microdactylus*, instead it was transferred to the Dolichodactylichnia - Gampsodactylichnia, and named I. dolichodactylum (= long- digital track: PABST 1900, 1908). An extramorphological variation he classified under I. brachydactylum (= short-digital track). Before the frequent record and knowledge of such tracks in some Permian formations, I separated them under *Palmichnus tambachensis* (HAUBOLD 1971, 1984). The interpretation of *"V." microdactylus* is now with

respect to the earlier age of the Tambach Formation within the Permian (Shumida et al. 1996), at best understandable as made by captorhinomorphs, like the protorothyridid *Thuringothyris* from Tambach.

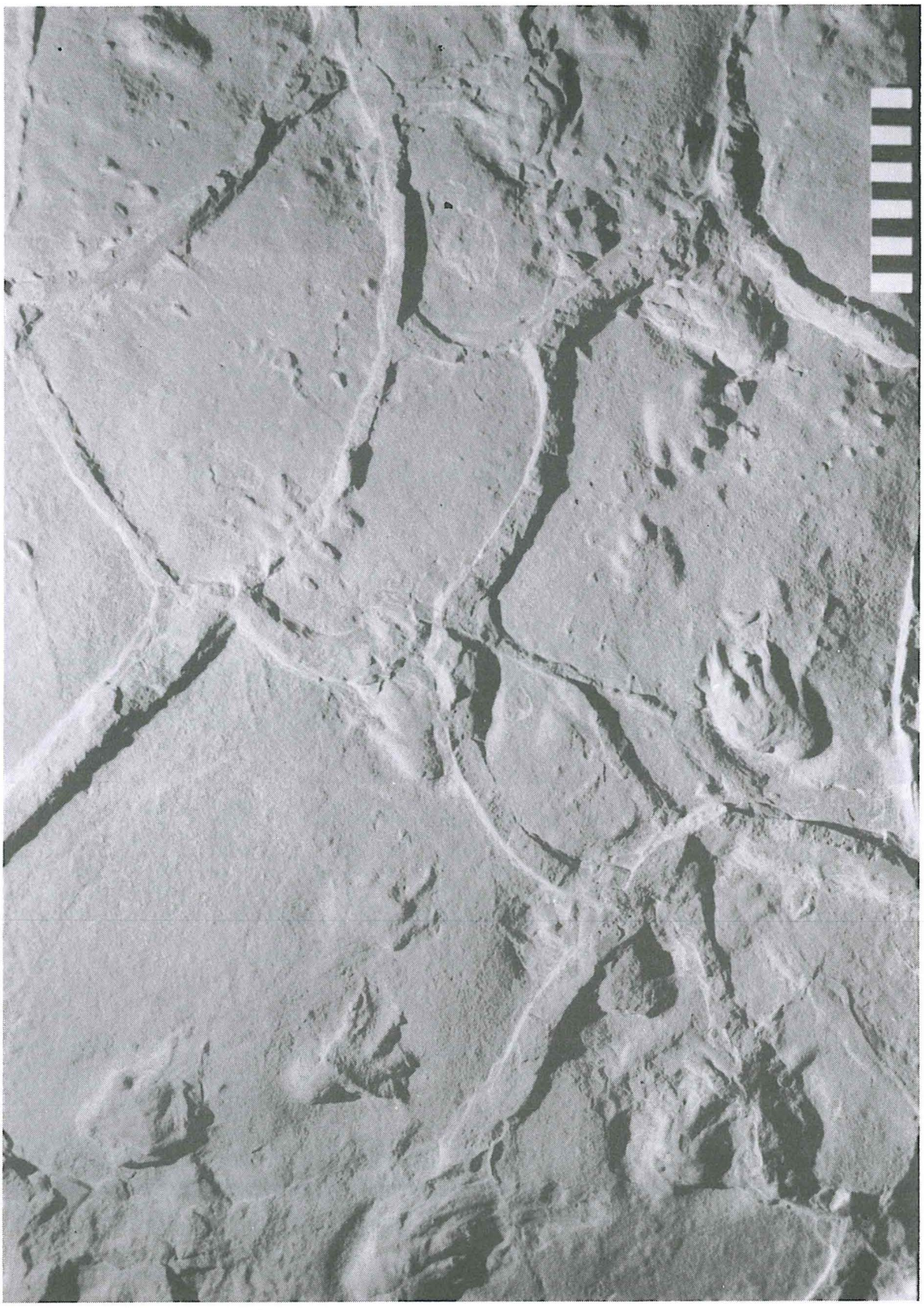

Fig. 5: *Dimetropus leisnerianus* (GN 1828), Tambach Sandstein, the surface shows variable deep casts of imprints, belonging to different trackways. Scale in cm.

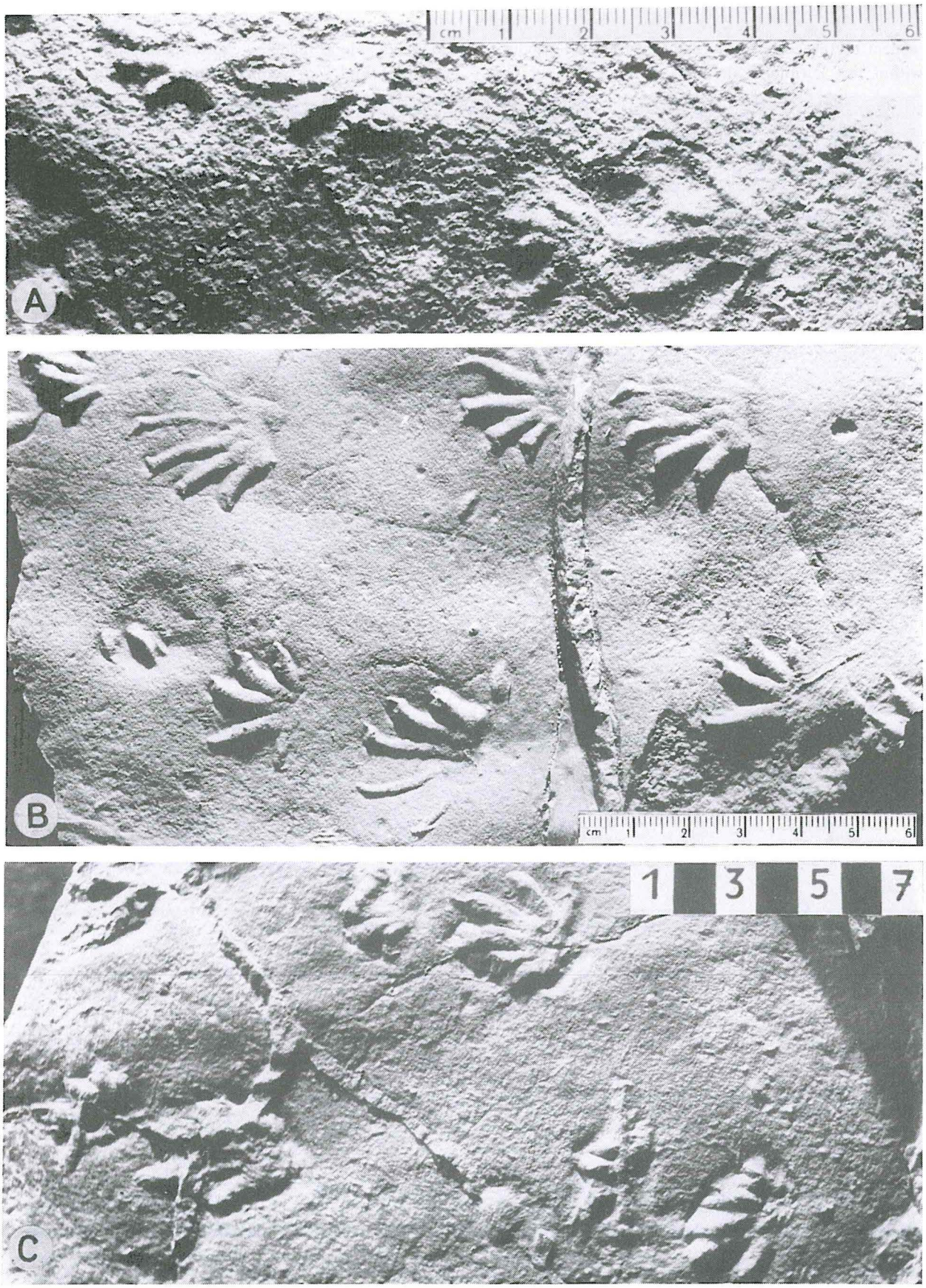

Fig. 6: "*Varanopus*" *microdactylus*, Tambach Sandstein, segments of three trackwaysin different kind of preservation.

A - type specimen (GN 1785). **B** - paratype (JPM P1322). **C** - original (GN 1841) of three different names, "Ichnium brachydactylum, tambachense" (PABST 1908), "*?Chelichnus brachydactylus*" (KUHN 1963), and *"Palmichnus tambachensis*" (HAUBOLD 1971a, b).

Tambachichnium schmidti MÜLLER, 1954, Fig. 7A

MÜLLER 1954, p. 195, type JP 2, Procolophonomorpha
HAUBOLD 1971 a, p. 45; 1971 b, p. 31; 1973 a, p. 28; 1973 b, p. 251; 1984, p 101, Abb. 67:2, PMJ P 1321 (=JP 2); Lepidosauria
MÜLLER 1984, Abb. 7 u. 8 JP 2.

T. schmidti is stable in nomenclature due to its late introduction and rarity, only one specimen, the type, a trackway-segment with three manus pes sets has so far been found. Although the record is very restricted, the lacertoid track morphology and the trackway pattern are significant: long stride, high pace angulation, and manus imprints are overstepped by the pes. The interpretation is concerned to a diapsid, probably an advanced araeoscelid. The manus and pes structure may be more digitigrade than in *Dromopus* as well as the locomotory abilities. A small relative of the possible originator has been uncovered from Tambach in 1997 (National Geogr., **192**: 5, 1997).

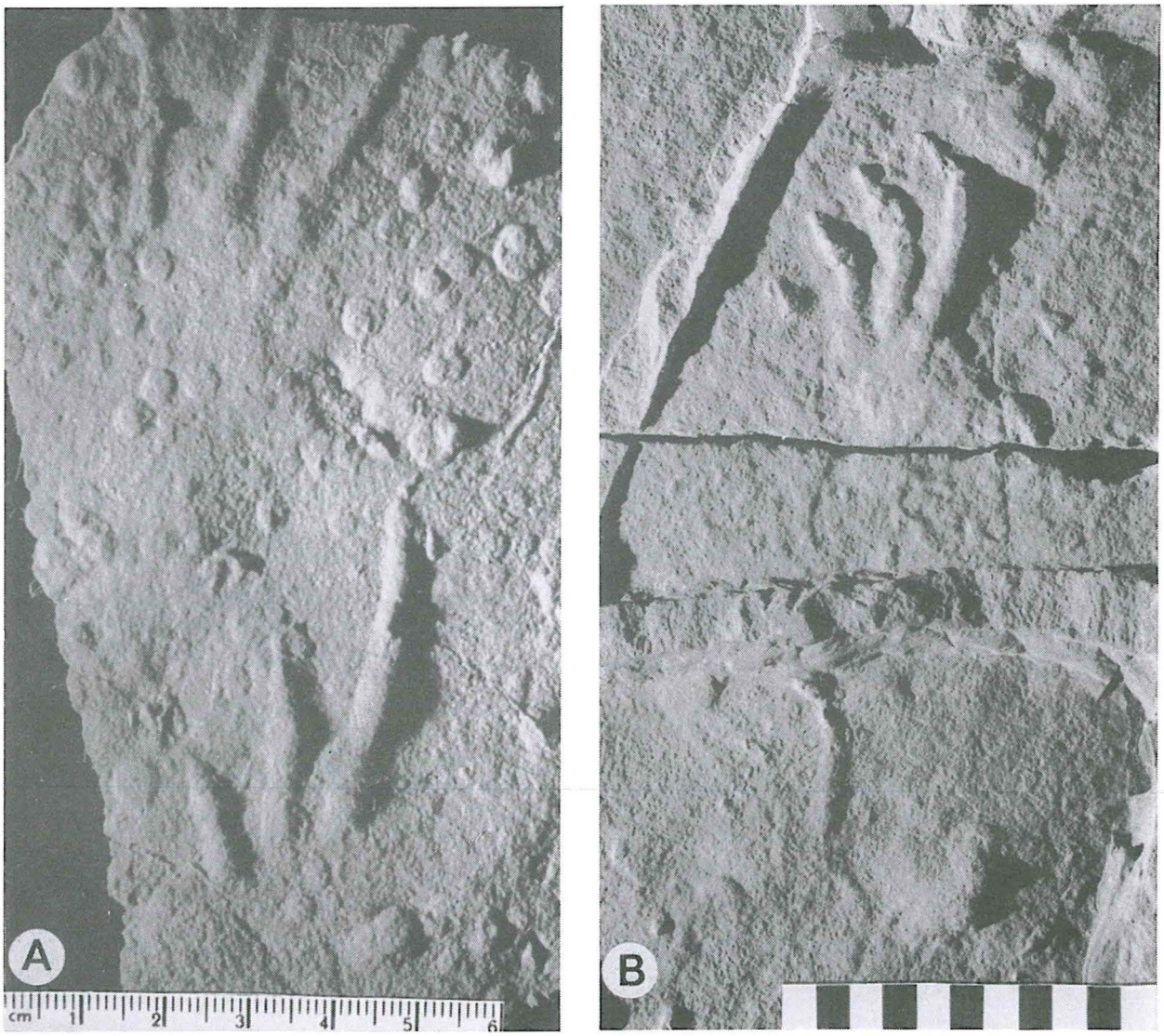

Fig. 7: The two unique track-types of the Tambach Sandstein.
A - *Tambachichnium schmidti*, the most complete manus-pes set of the type specimen (JPM P1321), the length of digits increases from II to IV; the tip of digit V is only recorded from the manus track.
B - unnamed type of track, only one cast in the center of the large slab (GN 1828) is rather complete recorded along a trackway-segment.

A new, unnamed tracktype, Fig. 7B and 8

A potential fifth ichnospecies may represent an incomplete preserved trackway-segment on slab GN 1828, on which one track is rather complete recorded (Fig. 7B), a cast (?) of a pes-imprint with a length of 9,0 cm. The position of additional tracks recorded by casts of low relief allow the measurement of the stride length of 60 to 65 cm, and of the pace angulation with 120°. The track figured here has been compared in GAND et al. (1995; GAND personal comm.) with trackway no. 12 from the site Saint-Sébastien, St. Raphael, Mitan Formation of the Estérel Basin. Erroneously GAND et al. (1995: 122) used the name *"Tambachnium schmidti"*, that of the other unique track type from Tambach (compare Fig. 7A). The similarity of the track of GN 1828 from Tambach to those of trackway no. 12 *"Tambachnium schmidti"* from Saint-Sébastien (Fig. 8A), and as well as to trackway no. 2 *"Pseudosynaptichnium esterelense"* (Fig. 8B) seems convincing and remarkable. However, neither the nomenclatorial nor the stratigraphic aspects should be discussed here, both are obviously rather complex and complicated.

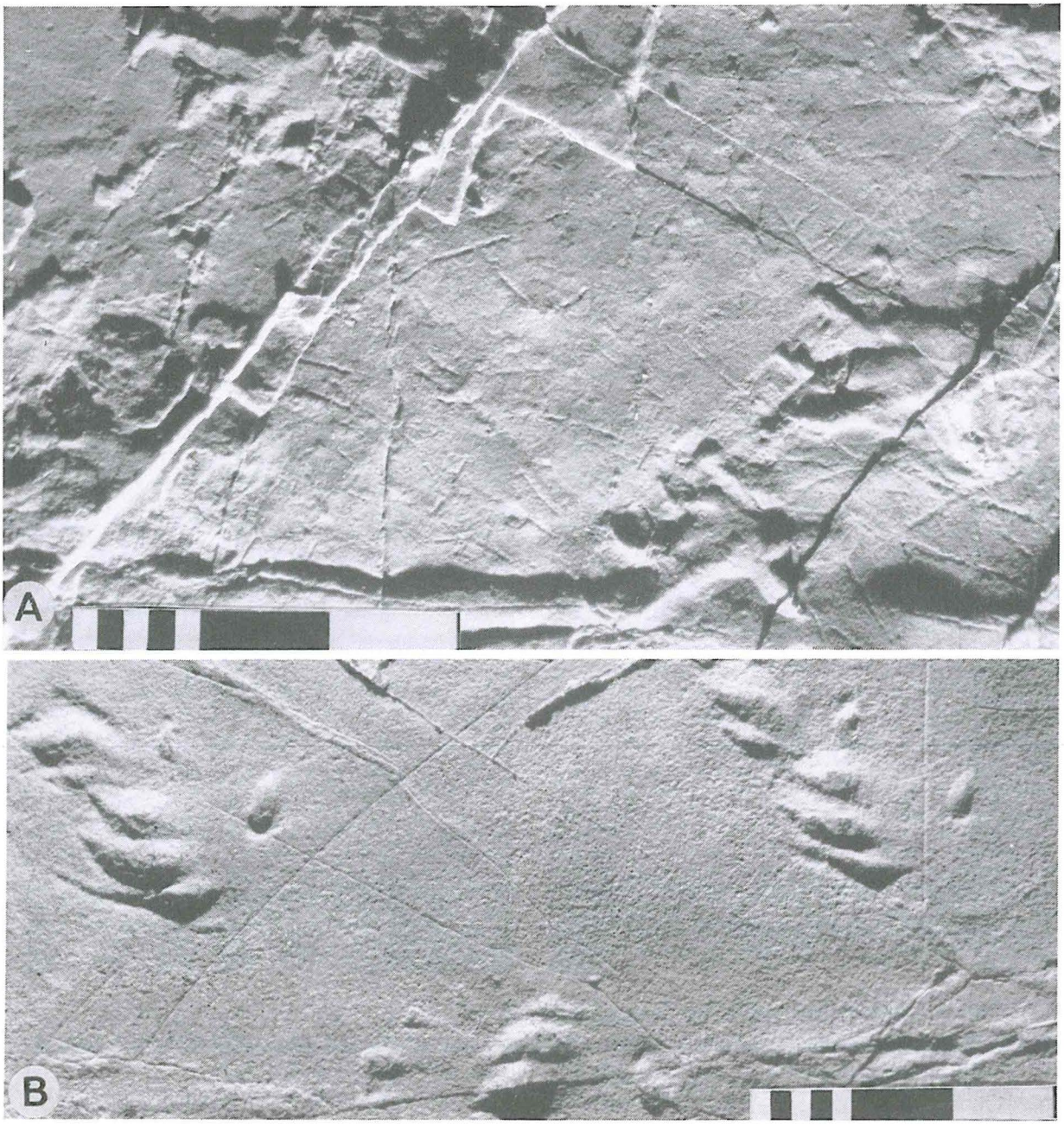

Fig. 8: Trackway-segments nos. 12 and 3 from Mitan Formation, Estérel Basin, Saint-Sébastian, St. Raphael (Provence), which are comparable to track on Fig. 7B from Tambach.
A - *"Tambachichnium schmidti"* as determined by GAND et al. (1995). **B** - *Pseudosynaptichnium esterelense* GAND et al. (1995). Photographs made from casts in the collection of the Université de Dijon.

5 Reasons for divergent evaluations of Permian ichnofaunas

From the analysis of PABSTs classification in the two previous sections some parallels became clear to ichnotaxonimical procedures in other occurrences of Permian age. In most cases the comparable phenomena are usually ignored, presumably due to a positivistic point of view of some researchers; i.e. the non-critical assumption that a discovered ichnofauna is new and unique, although there are most probably more or less variations in preservation already recorded elsewhere.

PABST (1908) correctly pointed to a limited agreement of tracks from different occurrences, and he rejected stratigraphical comparisons. This is in contrast to some later researchers of Permian tetrapod ichnofaunas, who, like PABST classified by resemblance only.

A stratigraphical evaluation is justified only when the morphological traits of the ichnotaxa are closely related to anatomically representative impressions.

The inconsequent handling of the above discussed problems are the background and reason for an inflationistic and partly chaotic nomenclature of Permian and Late Palaeozoic ichnotaxa. Due to these facts, the derived ichnostratigraphical correlations and zones are problematic.

The scenario is:

Case 1: Identical or anatomically similar species of animals will produce very different tracks in substrates from the same site which provide different consistencies. Tracks of identical animals in different sites where substrate and facies differ, independent of geological age, will even be much different.

The simple positivistic presumption that the tracks of a discovered site with a certain kind of preservation are - principally - osteologically controlled necessarily leads to a free determination and naming of taxa, and may allow any stratigraphic correlation. Due to these conditions, tracksites of the same age in reality, may be interpreted as different in age.

Case 2: Variations caused by substrate and facies of any age may correspond. According to the principle of similarity, they will be determined as the same anatomically related ichnotaxon, and, evidently, must be of the same geological age.

The reality is upside down. Case 1 represents facially different tracks from the same kind of animals; case 2 represents tracks from different animals looking similar due to facies influences. Examples are discussed under "Compound-Specimens" and "Phantom-Taxa" by HAUBOLD (1996: 35 pp.).

The classification and system of PABST are obviously consequent and conclusive in themselves, representing a model that might have been adequate to the knowledge of 1900. The actual state of knowledge, however, points to the need of an antomically related track classification.

The fact that Permian ichnogenera are correlated to osteologically defined families to orders is well established now. This is an additional reason for a relatively low number of ichnotaxa (HAUBOLD 1996: 29 and 32), and the resulting low diversity of Permian track faunas. One evidence for this is the demonstrated correspondence of the ichnotaxa from Abo tracksites with the skeletal remains from the late Wolfcampian in New Mexico (HAUBOLD et al. 1995 a), and the comparable fundamentally revised correlation of the Tambach Formation by the terrestrial tetrapod taxa from the locality Bromacker, heretofore known from the Permocarboniferous of North America, with an earliest Permian, Wolfcampian age (SHUMIDA et al. 1996).

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