Extramorphologic Variation in Chirotherian Footprints and their ichnotaxonomic Indications. Examples from the Middle through Upper Triassic (Anisian – Carnian) of Northern Bavaria, Germany

HENDRIK KLEIN & HARTMUT HAUBOLD

Abstract
Numerous chirotherian tracks, especially imprints on surfaces of the marginal siliciclastic facies of the Lower Muschelkalk (middle Anisian) and the Benker Sandstein (Ladinian) of N-Bavaria, Germany, permit differentiation into the ichnogenera Synaptichnium and Brachychirotherium based on details of their imprint morphology. However, the characteristic specimens are differentiated also by their low relief versus high relief preservation. Furthermore, intermediate morphs between the morphotypes can be demonstrated on the surfaces, making the objective determination more difficult. This gave rise to the application of landmark methods, making the single methodic steps descriptively and visually traceable. Each studied specimen is successively documented by a photo, outline sketch and the selected landmarks. The anatomically significant points in the footprints (landmarks) have been connected as polygons and then compared by superimposition. Based on the similarity of the polygon shape it seems obvious that differences in imprint morphology are due to substrate controlled variation. Therefore, separate ichnotaxa cannot be demonstrated for the imprint forms on the examined surfaces. A further study pertains to the holotype of Chirotherium wondrai and a pes imprint on the same surface from the Ansbacher Sandstein (Carnian). The second imprint shows considerable differences from the type. Measured angles of the cross-axis differ by 13 degrees due to modified preservation. From the results of this study, some principal questions concerning the ichnotaxonomy of some Middle Triassic chirotherians can be derived. Besides Synaptichnium, this refers to the evidence for Brachychirotherium in this time interval, which seems to be doubtful. By landmark analysis data, Brachychirotherium, as represented by the genotype B. hassfurtense, seems to be a characteristic chirotherian restricted to the Upper Triassic. Synaptichnium has not been fully recognized so far with respect to its extramorphologic variation on the track surfaces of the older part of the Triassic.

Introduction, Material, Methods

As opposed to body fossils, the shape of which is mainly determined anatomically, the morphology of trace fossils can vary to a significant degree. Controlling factors of this variability are mainly the behavior of the track makes and its interaction with the (heterogeneous) substrate. For tetrapod tracks this means that the anatomical facts of the manus and pes complex represented in the imprint shape may be overprinted in many different ways and thus may be preserved extramorphologically altered. Resulting differences from the real manus and pes morphology may lead to diverging and even false conclusions, which will articulate themselves at first in ichnotaxonomy. Depending on this now are assessments of biological diversity and composition of ichnofaunas. In this context misjudgments of the chirotheres of the Triassic are to be claimed. Mainly, this concerns the overestimation of characters that are not anatomically controlled, and that in some cases relate only to the diagnosis of isolated individual imprints. This results in a plethora of ichnotaxa that cannot be confirmed, leading to a questionable systematic hierarchy and making an interpretation of the forms more difficult or even lead them ad absurdum. For that matter, there are seminal studies on chirotheres and trend-setting studies for the systematics and interpretation (Peabody 1948, Baird 1957, Haubold 1967, 1971a, b, Demathieu 1970). After a pause in research of roughly 3 decades current works on the differentiation of this core type of tetrapod track now tie into these (Karl & Haubold 1998, 2000, Haubold & Klein 2002 as well as Klein & Haubold 2003).

The present study is intended to demonstrate to what degree deviations from the optimal imprint shape are possible on selected finds from trackway horizons of the Middle to Upper Triassic, and to what extent this is connected to taxonomic consequences.

Material
The studies material stems from collections of the author since 2000 in northern Bavaria, SE of...
Bayreuth, from the level of the Lower Muschelkalk and its lateral sandy equivalents (Middle Triassic, Anisian), as well as the Benker Sandstone (Middle Triassic, Keuper, Upper Ladinian). From the latter horizon also come specimens and unpublished photographs from the estate of W. WEISS, who published some works on tracks from the Benker Sandstone (WEISS 1976, 1981). Furthermore, the holotype of Chirotherium wandrei HELLER and another form from the type surface from the Ansbach Sandstone (Upper Triassic, Middle Keuper, Carnian) of Altseligensbach (Middle Frankonia) were included. Paleogeographically this tractsite is on the western rim of the Vindelician highland that formed the eastern border of the Germanic Basin. For the paleogeography and stratigraphic position of the track horizons see Figs. 1 and 2.

The material listed below is catalogued using the following abbreviations:

UEN – University Erlangen-Nürnberg, Institute for Paleontology.
UMOB-SZ – Urweltmuseum Oberfranken, Bayreuth, Collection Zapf.
WW – unpublished photographs by W. Weiss, current location of specimens unknown.

More recent specimens from the border facies of the Muschelkalk and the Benker Sandstone not yet introduced to the collections are consecutively numbered with the following shorts:

BKS – Benker Sandstone
UMBD – Lower Muschelkalk border facies

Methods

The comparative description of the imprints is amended with a landmark analysis, a morphometric technique. For this the available pedal imprints of chirotheres are first captured via homologous fixed points, so-called landmarks. In the next step the landmarks of each footprint are connected to form a polygon, and this polygon so to speak represents a morphometric abstraction of the respective imprint shape. The resulting polygons are then superimposed at the correct scale, so that shape changes show up geometrically. The resulting presentations are so to speak free of the sometimes little significant verbally descriptive and interpretatively colored explanations.

Further explanations on the first application on chirotheres can be found in KARL & HAUBOLD (1998, 200) as well as in KLEIN & HAUBOLD (2003). The following fixed points were defined as landmarks and form the basis for the polygons (cf. Fig. 3A1): the base of the claw of toes I-IV, the proximal rim of toe III (including the metatarsal-phalangeal pad), the respective midpoint of toes I and IV (without the claws) at their lateral rims (method following KARL & HAUBOLD 1998), and the proximal and distal borders of the basal pad of toe V, here called V1 and V2. V2 is located at the height of a kink [break, indentation] that marks the base of the narrow ?phalanx of toe V.

In order to illustrate the method and thus the results comprehensively Figs. 4, 4, 5 and 7 show of each specimen investigated

1. a photograph,
2. the outline drawing and
3. the deduced polygon next to each other.

An overview of all specimens is given in Fig. 8, and only in Fig. 9 is the real analysis of the landmarks and polygons is presented on the abstracted level.

Starting with the general level of knowledge on chirotheres first the taxonomic assignment of the investigated forms is described. In the next step the material is described as well as the documentation of the forms via polygons. This, then, forms the basis for the comparative discussion and taxonomic conclusions. The selection of finds from the Middle Triassic was intentional, because the knowledge of forms of this age is to date comparatively incomplete. However, they are intermediate between the classic chirotheres of the lower Triassic and those of the Upper Triassic. Forms of both sections are sometimes listed using the same genus names, but this does not do the morphological differences justice. But exactly there differences are to be seen in the context of the progressive development of the locomotory apparatus of archosaurs. The common tracks are a central source of information on the locomotory diversification of archosaurs. This source can only be tapped convincingly if the morphological analysis of imprints as well as the taxonomy of the tracks – the ichnotaxonomy – are based on transparent principles.

In this sense the analytical study of morphology and variability especially of the Middle Triassic forms can help to overcome previous errors and to open up key information so far unused, with which the potential of the character-riek chirothere for the understanding of the evolution of Triassic reptiles can be better revealed then previously.

At this point the authors would like to express their heartfelt thanks to Prof. Bernd SCHRÖDER, Bonn. His knowledge of the Triassic of northern Bavaria and his hints were decisive for the discovery of tracks in the Muschelkalk-boundary facies. H. ZAPF, Ottmannsreuth, is thanked for providing photographs from the estate of W. WEISS.
Fig. 1: Paleogeography of Central Europe in the Middle Triassic (after Geyer 2000) and localities A, B and C of the studied tracks, for stratigraphy cf. Fig. 2.

Fig. 2: Archosaur track horizons in the Triassic of N-Bavaria and S-Thuringia. Arrows and A, B and C mark position of the tracks taken into account. Stratigraphic sequence after BEUTLER (1998), HAGDORN et al. (1998) and LEPPER & ROELING (1998), see also Haubold & Klein (1998: Fig. 2).
2 Taxonomy, systematics and classification

A starting point is the differentiation of the chirotheres following HAUBOLD (1971b) into four ichnogenera:

Chirotherium
Isochirotherium
Brachychirotherium
Synaptichnium.

The verification of diagnostic characters of two of these taxa justifies the classification of the material from the Middle Triassic as cf. Brachychirotherium and cf. Synaptichnium. The forms of the Upper Triassic (Middle Keuper, Ansbach Sandstone) are for the moment classified as hitherto as Chirotherium wondrai HELLER and cf. Chirotherium wondrai HELLER, respectively. Overall, this ichnospecies seems somewhat problematic; a clarification must be reserved for future studies. For a better understanding the diagnoses for the taxa will be recapitulated in the following (after HAUBOLD 1971a, b, KARL & HAUBOLD 1998, 200).

Brachychirotherium

Pes / manus posture plantigrade to semi-digitigrade. Foot imprint rounded to oval with broad sole. Pedal toe group I-IV almost as wide as long. Angle between I and IV > 40°. Toes generally moderately spread, short and plump with strong, rounded pads and narrow claws. Toes III and II longest, toe IV always preserved. Pedal toe V with a phalangeal segment that is not or only moderately separated from the metatarsal-phalangeal pad. The former directed slanting forward, never recurved. The pentadactyle manus is smaller, manual toe group I-IV usually broader than long, otherwise like foot. Trackway of type species B. hassfurtense unknown.

Synaptichnium

Lacertoid chirotheres, relatively small, ca. up to 100 mm pes length. Length of pedal toes increasing from I through IV. Toe V latero-proximal to the anterior toe group. Sizes of manus / pes areas as 1 : 1.8 to 3.7, on average 1 : 2.5. Relatively wide gauge, pace angulation rarely over 160°, on average only up to 140°.

Chirotherium wondrai

Pes length 180 mm (type), per broad, plantigrade, extended heel, narrow phalangeal part of toe V in lateral position, toe II longer than IV and nearly as long as III, toe group I-IV as long as wide, transverse axis 78°, manus squat with short toes. Trackway unknown.

3 Description of material

The investigated chirotheres are limited to form that must be placed close to the ichnogenera Synaptichnium and Brachychirotherium based on their morphology and characters. In the following they are described from the sections of the Middle Triassic as cf. Synaptichnium and cf. Brachychirotherium. Additionally, a form from the Upper Triassic is included that was introduced as Chirotherium wondrai by HELLER in 1952. Of this the holotypy and an additional imprint from the type surface were studied.

3.1 Siliciclastic border facies of the Lower Muschelkalk (Middle Triassic, Anisian)

cf. Synaptichnium

The material consists of numerous slabs with isolated footprints (foot length up to 10 cm) and associated manus (UMBD 1 – 5 and 7; Fig. 3A – C, 4D, 8a – e, g), as well as several trackways consisting of 3 to 5 consecutive pes/manus sets. Seeveral specimens show skin imprints. The foot is, if optimally preserved, long, slender, pentadactyle and semiplantigrade, with toe length increasing from I – IV. The phalangeal and metatarsal-phalangeal pads are sturdy and round to long-oval, toe V is located proximo-laterally of toe group I-IV and often is distally slender (?phalangeal part), but equipped with a sturdy basal pad and often proximally extended to form a long "heel". The claws of I through IV are longitudinal, shapr-tipees and often directed outwards. The relatively large manus print, at least 1/3 of the pes print area, is rounded in its circumference and plantigrade to semiplantigrade. The toe imprints show well developed pads and small pointed claws on I through IV. Toe II is longest, V is located proximo-laterally being I-IV and can be missing from the print. In the trackway the feet are more strongly rotated outwards than the hands.
**cf. Brachychirotherium**

There are several isolated footprints (length up to 10 cm), usually associated with those of the hands (UMBD 6, 9 and 10, Fig. 4B, C, D, 8f, I, j). The foot imprint is pentadactyle and plantigrade to semiplantigrade, the toe group I-IV is roughly as wide as long, with short, pumil (rounded) toes, broad and stout, in parts badly defined pads and small claws. The toe group I - IV shows the length relation I < II < III = IV or I < II < IV < III. Toe V is proximolaterally behind I – V and on its distal end is partly strongly recurved (?phalangeal part). The stout basal pad of toe V is often secondarily lengthened to a “heel”. The manus print is tetradactyle to pentadactyle and rounded, with short, plump toes and broadly defined pads and small claws. Toe II is the longest. So far, no trackways have been found.

### 3.2 Benker Sandstone (Middle Triassic, Upper Ladinian)

**cf. Synaptichnium**

A figure in Weiβ (1981: p. 444, Fig. 5) with the caption Synaptichnium sp. And two unpublished photographs by this author (WW1 and 2, Fig. 5A, C) show footprints with associated manus prints from the lower part of the Benker Sandstone from Katzeneichen near Bayreuth. Weiβ (1981) also lists Synaptichnium pseudosuchoides and Synaptichnium hildburghausense from the Benker Sandstone. The forms on the photographs show important diagnostic characters of Synaptichnium (see above) and thus are here classified as cf. Synaptichnium. All imprints are shallow, i.e., they are preserved as shallow positive relief. The 7 to 10 cm long footprints are slender and plantigrade to semiplantigrade, the toes are slender with rounded to long-oval phalangeal and metatarsal-phalangeal pads and strong, pointed claws. The length of the claws increases from I through IVth toe. Pedal toe V is located posterolateral to toe group I-IV and shows a narrow ?phalangeal part as well as a stout basal pad partly lengthened to a “heel”. The relatively large tridactyle to pentadactyle manus prints (they are at least 1/3 f the pes print area) are located antero-medially of the foot and are compared to the latter more inwards rotated. They are plantigrade to semiplantigrade and compared to the pes prints overall more rounded. The toes show stout pads and small, pointed claws, manual toes II is the longest.

**cf. Brachchirotherium**

Several isolated footprints are available with length between 6 and 28 cm., as well as surfaces with numerous pes and manus prints, furthermore a 9-part trackway (UMOB-SZ2, BKS 1; Fig. 5B, 8k and m). The footprints show the diagnostic characteristics of Brachchirotherium, such as a broad area of the sole, short plump (rounded) toes with broad pads and narrow claws, as well as a massive basal pad on toe V, on which a ?phalangeal part is not or only slightly distinguished. The latter can, however, in some cases be curved back. Proximally, the basal pad is often extended into a “heel”. Pedal toes II and III are the longest, toe IV is shorter, on smaller and more slender imprints sometimes as long as III. The manus prints are pentadactyle, their outline rounded-quadratic, with short, plump (=relatively short and rounded) toes and small claws. Toe II is the longest. The trackway shows strong outward rotation of the feet axes and a relatively wide gauge with a pace angulation of ca. 140°.

### 3.3 Ansbach Sandstone (Upper Triassic, Carnian)

**Chirotherium wondrai Heller**

Heller described this form in 1952 together with other trackway and imprints from the Ansbach Sandstone, a part of the Stuttgart Formation of the Middle Keuper. The holotype (UEN F84; Fig. 7A1 top, 7A2 A3, 8p) shows a plantigrade footprint with a broad sole area (length 18 cm) and moderately inclined transverse axis (ca. 78°). Pedal toes II and III seem nearly equally long; however, this length ratio has been secondarily caused. This is evident because of sliding track on the edges of the toes as well as deeply imprinted and protracted claw furrows. The part of the toes preserved with rounded and broad pads looks rather short and plump in contrast. For the toe a length relationship is found of I < II < IV < III. Toe V has a stout basal pad, which is lengthened posteriorly to a “heel”. The distal end (terminal phalanx) of V is slender, separated from the basal pad, and more or less bent back. The manus print is pentadactyle and semiplantigrade to semidigitigrade. Compared to the foot the hand seems rounded, it has short, stubby toes and small claws on I – IV. Manual toes V is very slender and located posterolateral of toe group I – IV. A second chirotheroid footprint of
the same size below (posterior) the holotype (UEN F84; Fig. 7A, bottom, 7A, 8q) shows an extremely tilted transverse axis at 65°. Toe V is extended into a long “heel” at its proximal end, the distal end (terminal phalanx) is strongly reflexed. A vague hint at a manus print is located in front of pedal toes III and IV.

### 4 Comparison of forms, discussion and conclusions

The initial starting point for the study of chirotherians from the group of forms of *Synaptichnium* and *Brachychirotherium* was the ample material from the sandy border facies of the Lower Muschelkalk (Middle Triassic, Anisian) SE of Bayreuth in northern Bavaria. Here, surfaces with trackway assemblages were documented in the course of systematic excavations by the authors (cf. HAUBOLD & KLEIN 2002), as they were previously only known from horizons in the Middle Triassic of France and Italy (DEMATHIEU 1970, DEMATHIEU & GAND 1973, GAND 1975, 1977, COUREL & DEMATHIEU 1976, AVANZINI 1999, 2000, AVANZINI & NERI 1998).

During the attempt of a classification of the track forms investigated it became evident, surprisingly, that the imprints initially recognizable as *Synaptichnium* and *Brachychirotherium* were not always clearly demarcated against each other. On one hand the diagnostic characters of the respective taxa can be found on the respective imprints, on the other hand there are transitions visible on the morphology of imprints of one and the same surface. Consequently, the forms shown in Fig. 3A-C and 4A as well as 8a-e and g (UMBD 1 – 5 and 7) obviously represent the same morphotype, and this must be classified, based on the characters present (see above) as cf. *Synaptichnium*. The comparison of the polygons determined for UMBD 1, 2, 4 and 5 (Fig. 3A, B, C, 8a, b, d and e) also results in a remarkable correspondence, by the projection showing the alignment of the forms along a common basis (Fig. 9a). The slight differences in the position of individual toes likely stay within the limits of normal variability. However, the polygon of UMBD 1 reflects a somewhat more pronounced difference in the position of toe II. The reason for this is explained, however, by sliding in the substrate and is not anatomically caused. In the polygons the axis V1-V2 marks the orientation of toe V and allows assessing it relative to the toe group I-V. Here, e.g., the difference in rotation is expressed that is rooted in the function of the fifth toe. It had for the foot posture of chirotheres merely a supporting and stabilizing function.

On the footprints as shown in Fig. 4B, C, D and 8f, i and j (UMBD 6, 9 and 10) a second morphotype can be recognized. The short, plump toes with broad pads as well as the proportions of the toes, IV < III, conform to the expression of *Brachychirotherium*. Congruent with this is the classification as cf. *Brachychirotherium* as used so far. Comparable forms were already described and classified from the Lower and Middle Triassic (HAUBOLD 1967, 1971a, b, DEMATHIEU 1970, DEMATHIEU & GAND 1973, DEMATHIEU & LEITZ 1982, GAND, 1975, 1977). The genotype *Brachychirotherium hassfurtense* (UEN F 22, Fig. 8r), however, is from the Upper Triassic (Carnian) and has proven to be slightly differently proportioned. The genus assignment of this form is therefore in need of a critical discussion.

Comparison of the polygons or UMBD 6 and 9 in Fig. 9b firstly shows continuity within the morphotype similar to *Brachychirotherium* for the surfaces of the Muschelkalk border facies of northern Bavaria. The reason for the obviously varying rotation of the axis of the fifth toe has been explained above. Fig. 8h shows a further form (UMBD 8), the characteristics of which on one hand hint at *Synaptichnium*, e.g., the slender toes, the lateroproximal position of toe V, as well as a relatively large hand. On the other hand the toe proportions of IV < III as well as the length-width ratio of 1:1 of the anterior toe group I-IV are typical for *Brachybotherium*. The comparison of polygons in Fig. 9b and c hints at a larger similarity of UMBD 8 to UMBD 6 and 9 (cf. *Brachybotherium*). This is, however, caused by a greater counterclockwise (to the left) rotation of these forms, whereas UMBD 2 (cf. *Synaptichnium*) is rotated clockwise, and has a length ratio of toes III < IV. Because of the position of the landmarks the counterclockwise displacement correlates in part with the width as well as the overall size of the imprint (Klein & Haubold 2003). This becomes evident in the superimposition of the polygons and can thus be used as a basis of classification, but with a certain restraint. If one ignores the differing rotations, according to the landmark analysis only the length ratio of toes III and IV remains as a significant character for the differentiation of these morphotypes. This is at first true for the investigated surfaces of the Muschelkalk border facies. However, characters diagnostic for Brachybotherium such as “broad pads” and
“narrow claws” are not captured in the landmark analysis. But it becomes evident that these characters also can be connected differently with each other in the imprints. Comparing the forms in Fig. 3B, 4B and 8b, f and h (UMBD 2, 6 and 8) shows UMBD 8, as mentioned, having characteristics of both *Brachychirotherium* and *Synaptichnium*. The imprint on Fig. 8c (UMBD 3) also shows characters of both ichnogenera: Foot stout and broad, toe V with only an oval basal pad as in *Brachychirotherium*. Toes and claws and toe III = IV correspond to Synaptichnium. Such a combination of characters can also be found on specimens UMBD 7, 9 and 10, and depicted in Fig. 4A, C and D and 8g, i and j, respectively. The indications for a taxonomic separation are furthermore interfered with by another, extramorphological phenomenon: the forms similar to *Synaptichnium* are usually imprinted very shallow, while those close to *Brachychirotherium* are deeply imprinted. This relationship that can generally be seen on the surfaces is, in the end, taxonomically decisive.

In summary it is to be noted that there are continuous transitions between the apparently distinct morphotypes. These indicate variants of shape that are controlled by the substrate. This is confirmed by the free combination of characters on tracks along uniform surfaces as well as in the indications from the landmark analysis. Thus, for the forms from the siliciclastic border facies of the Lower Muschelkalk a differentiation into two separate taxa cannot be justified.

Based on this situation the investigation was expanded to specimens from other levels and surfaces of the Middle and Upper Triassic with the question if there are similar constellations present. First, similar forms on surfaces of the so-called Benker Sandstone (Middle Triassic, Upper Ladinian) were studied. There are two morphotypes (Fig. 5A, B, C and Fig. 8k, l, m and n, respectively) previously classified as cf. *Synaptichnium* and cf. *Brachychirotherium*. The former shown in Fig. 5B and Fig. 8k and m show the diagnostic characters of *Brachychirotherium* (see above). In contrast, tracks similar to *Synaptichnium* can be recognized in Fig. 5A and C, and 8n and o (WW1 and 2), whereby the characteristic toe proportions III < IV are only visible on WW 2 (Fig. 5C, 8n). In the other cases the toe proportions usually are III = IV or III > IV. As in the specimens from the Lower Muschelkalk the ratio of toe length proves to be relatively variable. Fig. 5B and 8k and m (UMOB-SZ 2, BKS 1 (1) show cf. Brachychirotherium with relatively short pedal toe IV compared to III. On the same surface (Fig. 6) there is also a somewhat more slender form as a shallow relief (BKS 1(2); Fig. 8l), which is intermediate between the form in [Fig.] 8m the morphotype classified as cf. *Synaptichnium*. In the landmark analysis (Fig. 9d), respectively in the polygon superimposition, a good correspondence results for the smaller imprint shapes, with divergences reflecting the position or length of IV, which however, as explained above, also vary within each morphotype. Even the large track /UMOB-SZ 2) has, in principle, the same polygon shape. Again, the shallow relief of cf. Synaptichnium must be emphasized compared to the deep relief of cf. *Brachychirotherium*. A difference that was already recorded in the Muschelkalk border facies. In summary, there is no sufficient reason for two taxa in the Benker Sandstone as well. The landmark analysis proves the existence of two shape variants, so that there are very likely morphological transitions that can be explained by different substrate conditions: Damp substrate – shallow imprints – “cf. *Synaptichnium*”, Damp substrate – deep impressions – “cf. *Brachychirotherium*.

*Chirotherium wondrai*: A further subject of the investigation is the (holo-)type of *C. wondrai* HELLER from the Ansbach Sandstone (Upper Triassic, Carnian) and additional forms from the same surface. Besides the type specimen there is a nearly equally sized footprint, which is recognizable as *Chirotherium*, but shows significant differences to the pattern on *C. wondrai* (UEN F 84, Fig. 7A1 bottom, 7A4, 8q). In particular, the transverse axis is comparatively inclined at 65°, on the holotype-print (UEN F84, Fig. 7A1 top, 7A2 – A4, 8p) this angle is 78°. The proportions of the toes also show differences. An application of the landmark analysis was not possible, because of the insufficient preservation of the second imprint. A polygon was only created of the type. Knowing the circumstances of discovery and that both forms on being on one surface belong together one can assume that it is a variability in shape of *C. wondrai* caused by preservation. If these imprints had been found separate on different surfaces and different localities one had, because of the differing characters, probably described these as separate taxa. This underscores the importance of connected surfaces for the appraisal and classification of tracks. The deeply imprinted type itself shows well-developed marks connected to the backwards gliding and immersion into the substrate at the sides of the claws and toe pads.

The imprints of the claws are overall artificially lengthened by the slipping of the foot and do not correspond to the original anatomical conditions. The toes, or toe pads, respectively, appear therefore strongly shortened in their length.
This signals caution in the assessment also of other forms and gives hints for the generation of short-toed forms, as they are for example present in many brachychirotheres. The polygon of *C. wondrai* must therefore be assessed with caution. The superimposition of *C. wondrai* and the forms from the Benker Sandstone (Fig. 9d) shows a stronger counterclockwise (to the left) rotation compared to the small imprint forms (relation to size see above) and a slight shift to the left compared to the large forms, but also similarities in the overall shape. A close relationship of *C. wondrai* to the forms of, e.g., the Benker Sandstone and from the sandy Muschelkalk border facies is possible, based on the landmark results.

A taxonomic relevance of these results is indicated, but will not be pursued further here for *C. wondrai*. The investigation of the tracks from the border facies of the Muschelkalk as well as the Benker Sandstone and the Ansbach Sandstone show to what degree the footprints of chirotheres can vary and be altered extramorphologically. Once again this indicates that previously distinguished taxa must be regarded critically in this respect. These insights must be taken into account accordingly for the introduction of new ichnotaxa. For *Synaptichnium* and *Brachychirotherium* new questions arise after the observations described at least for the chirotheres of the Middle Triassic regarding the differentiation of ichnospecies so far listed under these genera.

A more complex situation and question arises from the comparison with chirotheres in the context of the Lower through Upper Triassic. According to the polygons the forms from the Muschelkalk border facies show only limited conformity to the standard forms of *Synaptichnium* and *Brachychirotherium*. These are *Synaptichnium diabloense* from the Moenkopi Formation of Arizona and the genotype of *Brachychirotherium, B. hassfurtense* from the Coburg Sandstone of the Hassberge Formation (Fig. 9e). This means that there are by all means indications of distinctive differences, the taxonomic relevance of which, however, still has to be quantified in the context of substrate caused variability. Especially evident here is the rotation and proportions of the polygon of *B. hassfurtense*, which differs from other chirotheres. It is left to future studies to clear up in how far the forms so far listed as *Brachychirotherium* from, e.g., the Middle Triassic, justify this classification at all. As further consequence other chirotheres also need to be studied regarding the aspect of variability. The anatomically controlled imprint morphology versus the extramorphologically controlled needs to be analyzed, and to be reconsidered (ichno-)taxonomically, and potentially to be replaced.
Fig. 3
Pes and manus imprints of cf. *Synaptichnium* from the siliciclastic border facies of the Lower Muschelkalk (Anisium) SE of Bayreuth with photographs, outline drawings as well as the position of fixed points and the resulting polygon on the pes prints.
Scales all 5 cm.

Translated by H. Mallison heinrich.mallison@gmail.com 26.08.2011
Note that page numbers are not identical to original manuscript!
Fig. 4
Imprints from the shape spectrum of cf. *Syanaptichnium* through cf. *Brachychotherium* from the level of the Muschelkalk border facies SE of Bayreuth. For B and C landmarks and polygons are fixed. A shows skin scale structure. The differences in substrate condition control overall shape, toe proportions and width of toe prints via imprint depth.

Scales all 5 cm.
Fig. 5
Form from the Benker Sandstone (Middle Triassic, Upper Ladinium) SE bayreuth with position of landmarks and polygons for the pes prints A and B. A₁-A₃ and C₁-C₂: *cf.* *Synaptichnium* = slender toes are preserved because of shallow relief. B₁-B₃; *cf.* *Brachychothereium* = because of higher relief the toes are broad and point laterally oriented sliding and abrading marks.

A₁-A₃: WW 1  B₁-B₃: UMOB-SZ2  C₁-C₂: WW 2
Unpublished photographs by W. Weiss. Scales in the drawings all 5 cm.
Fig. 6: Track surface from the level of the Benker Sandstone with pes and manus imprints that depending on preservation would have to be classified as cf. *Brachychirotherium* through cf. *Synaptichnium* (BKS 1). Outline drawings and polygons of this surface are shown in Fig. 8l and m.

Fig. 7: Pes and manus prints of *Chirotherium wondrai* HELLER from the Ansbach Sandstone (Upper Triassic, Carnian) of Altseligenbach, middle Frankonia (UEN F 84). A1 top, A2-A3: Holotype with position of landmarks and the polygon. A1 bottom: additional imprints with inclined transverse axis. The different modes of preservation that simulate separate taxa become apparent. On the left in the picture a tridactyle, grallatorid form ("Atreipus"). Scale in the drawings 5 cm.
Fig. 8: Overview of the studied forms of chirotheres from the Middle through Upper Triassic of N Bavaria with the respective polygons.

a-j: Lower Muschelkalk border facies (UMBD 1-10).

k-o: Benker Sandstone (k – UMBO-SZ2, l – BKS 1 (2), m – BKS 1 (1), n – WW 2, o – WW 1).

p and q: Ansbach Sandstone (UEN F84, C. wondrai holotype and additional imprint).

r: Brachychirotherium hassfurtense (UEN F22, lectotypical from KARL & HAUBOLD 1998).

s: Synaptichnium diabloense holotype (from PEABODY 1948) from the Moenkopi Group (Lower Triassic, Olenikum) of N America.

Scales all 5 cm.
Fig. 9:
Comparison of polygons by superimposition along a common baseline, in dependence on method of KARL & HAUBOLD (1998).
a-d to scale, e adjusted in size.


