Acta Palaeontologica Polonica
Vol. 28, No. 1—2 pp. 123—132 Warszawa, 1983
Second Symposium on Mesozoic Terrestial Ecosystems, Jadwisin 1981

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ARCHOSAUR EVIDENCE IN THE BUNTSANDSTEIN (LOWER TRIASSIC)

HAUBOLD, H.: Archosaur evidence in the Buntsandstein (Lower Triassic). Acta Palaeont. Polonica, 28, 1—2, 123—132, 1983.

The vertebrate ichnofauna of the German Bunter, primarily horizons of the Hardegsen and Solling Formations, contains archosaur footprints of the genera *Brachychirotherium*, *Chirotherium*, *Isochirotherium*, *Rotodactylus*, and *Synaptichnium*. Footprint morphology, trackway pattern and stratigraphic occurrence show that only *Synaptichnium* and *Brachychirotherium* correspond with advanced proterosuchians and pseudosuchians. *Chirotherium* and *Isochirotherium* are above the pseudosuchian level. *Rotodactylus* somewhat resembles *Lagosuchus*. In the Lower Triassic existed at least five lines of fully terrestrially adapted archosaurs. From trackway evidence, the archosaurs of the Lower Triassic show a more complex radiation of terrestial locomotion types than would be expected from the presently known fossil bone record. The footprint fauna of the Buntsandstein may contain thecodonts as well as transitional (non pseudosuchian) forms which may foreshadow later crocodiles, ornithischians, and saurischians.

Key words: footprints, thecodonts, dinosaurs, Middle Buntsandstein, Triassic.

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INTRODUCTION

The first discovery of *Chirotherium* footprints was made about 150 years ago at the German locality of Bunter near Hildburghausen (southern part of the German Democratic Republic), published by Sickler (1834, 1836) and Kaup (1835). Following many problematical interpretations and much discussions during the last century, in 1914 Watson and in 1917 Walther suggested that the *Chirotherium* prints were made by animals like primitive dinosaurs. Soergel (1925) followed this suggestion in his widely known reconstruction. More recently clearer taxonomical differentiation of the footprints has been made by Peabody (1948), Demathieu (1970), and Haubold (1971 *a*, *b*), showing a broad scale of morphology of the trackmakers. At present time we have a substantial distribution of different types, especially in horizons of the German Bunter, the French Triassic, and the North American Moenkopi Formation of Lower and Middle Triassic (Demathieu and Haubold 1972, 1974).

Archosaurs are known from osteological data in the Lower Triassic, but the relationships of all these forms to evolutionary lines of higher Triassic age are questionable. The proterosuchians are aquatically specialised forms and thus cannot be fully accepted either as forerunners of later archosaurs, nor as makers of all of the known footprint types. The same applies to the few Lower Triassic pseudosuchians (*Euparkeria*, *Ctenosauriscus*, and others). Typical rauisuchids, which are, for example following Krebs (1966) accepted as makers of the footprints of the chirotherians, are not known before the higher Anisian. Because of this, interpretation of Lower Triassic footprints introduces more general questions of the early archosaur radiation. The author does not intend here to give an additional theory of archosaur origin. It is intended only to demonstrate the significance of footprints in understanding the range and abundance of early archosaur lines over the presently known level of osteological datas.

FAUNA AND STRATIGRAPHIC AGE OF THE BUNTSANDSTEIN

The Lower Triassic horizons of Buntsandstein, primarily the Hardegsen and Solling formations ("Formation" corresponds to the German "Folge") contain archosaur footprints of the ichno-genera *Brachychirotherium*, *Chirotherium*, *Isochirotherium*, *Rotodactylus*, and *Synaptichnium*, most of them with several different species. The taxonomic range of every genus must be compared with osteological families or higher categories and the differences between the genera involved suggest an adaptive range justifying an order or an even larger category, as will be shown below by examining available characters. The trackways of archosaurs are the generally dominat elements of all footprint-bearing strata and occur together in various species associations. Faunules of the Hardegsen Formation contains *Synaptichnium* and *Isochirotherium*; this and all other genera occur in the Solling Formation mostly in association with footprints of lepidosaurs (*Rhynchosauroides*) and of therapsids (*Dicynodontipus*). For the Solling time footprint evidence indicate a large radiation of terrestrial forms. In particular, the sandstone and siltstone layers of the Thuringian Chirotherian Sandstone contain the first recorded species of *Chirotherium*, *Brachychirotherium*, and *Rotodactylus* (fig. 1).

The Lower Triassic age (Scythian) of the formations mentioned are unqestionable. Only Krebs (1966, 1976) argues, in connection with his very strict interpretation of chirotherians as rauisuchids, for Anisian age. The motive for Krebs' modification seems to lie in the gap between the

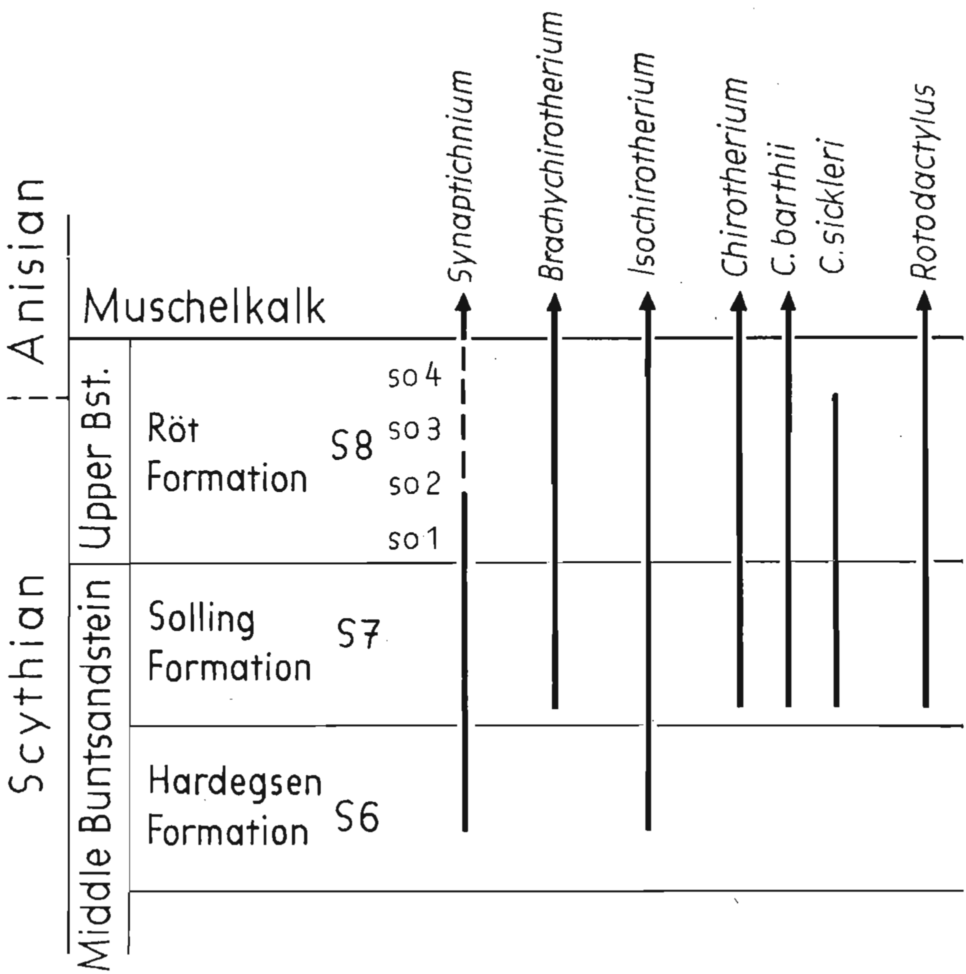

Fig. 1. Distribution of the archosaur footprint genera in the German Bunter. Stratigraphic classification cf. Richter-Bernburg (1974). All genera, and very common species *Chirotherium barthii*, occur up to the Anisian/Ladinian boundary.

first occurence of *Chirotherium* and that of the first rauisuchians and most of other pseudosuchians. Krebs' arguments for Anisian age of Buntsandstein also include the existence of *Macrocnemus* and *Tanystropheus* — typical Anisian elements — in the Buntsandstein. But *Macrocnemus* and *Tanystropheus* occur, according to Ortlam (1967) and Wild (1980), at the Uppermost Röt Formation (*so 4*, comp. fig. 1) at the fifth Violet horizon (VH 5). These strata are indeed correlated with the lowermost Anisian but are much younger than the Hardegsen and Solling horizons (cf. Richter-Bernburg 1974). It must be concluded, then that the footprints of these horizons are clearly older than most typical pseudosuchian occurrences and are also older than the important transitional thecodont *Lagosuchus*, discribed by Bonaparte (1975).

MAIN CHARACTERS OF EARLY ARCHOSAURIAN FOOTPRINTS

The adaptive trend of most of the terrestrial archosaurs since the Triassic was orientated to the complex development of erect gait and bipedalism, in connection with a digitigrade and tridactyl pes. This originated from types having a quadruped sprawling gait and lacertoid pes with five functional digits. It can be shown that in the Lower Triassic archosaur footprints exhibit tendencies towards bipedalism, more erect gait, tridactylism, and a mesotarsal foot joint.

Four points are significant in impressions and trackways of their range of development of these features:

1. Reduction of the manus as function of bipedalism;
2. Stride length in relation to width of trackway and pace angulation (small trackway pattern) as a function of semierect to erect gait;
3. Reduction of pes digits I and V as a function of tridactylism;
4. The cross axis of the pes (ankle between digit III and metatarsal joint of front digits I — IV), and the outward orientation of the pes axis (digit III) to the direction of movement. An oblique cross axis requires a crurotarsal joint for pes movement; this condition was supplied by an oblique pes orientation. A more rectangular cross axis may demand a mesotarsal joint.

The gradual acquisition of these characters in the archosaur locomotion types of chirotherians and *Rotodactylus* are the proof of broader interpretation, as was suggested by Demathieu and Haubold (1978 and 1982).

INTERPRETATION OF THE BUNTSANDSTEIN FOOTPRINTS

Synaptichnium Nopcsa, 1923
(fig. 2*a*—*d*)

Known species: *S. hildburghausensis* (Rühle v. Lilienstern, 1939), *S. primum* Demathieu et Haubold, 1982, *S.* cf. *pseudosuchoides* Nopcsa, 1923, *Synaptichnium* sp. Demathieu et Haubold, 1982.

Synaptichnium has relatively large manus impressions and as well as pes are of lacertoid habit. Digits show no reduction in the direction of tridactylism, and pes digit IV is longer or has the same length as III. Pace angulation was maximally 160°, and on average only 140°; trackway width is relatively high, and its ratio to stride length is about 2. In the broad, short-striding trackways, the distance of manus-pes in a set is high and shows a low semierect gait. The cross axis measures 50°—65°. In these characters the known species of *Synaptichnium* have affinities to proterosuchians (*S. primum*), to primitive pseudosuchians as *Euparkeria* (*S. pseudosuchoides*), and also to rauisuchids (*Synaptichnium* sp.). The known foot bones of Middle Triassic rauisuchids allow reconstruction, which reveals resemblances more to advanced *Synaptichnium* than to *Chirotherium*.

Brachychirotherium Beurlen, 1952
(fig. 2*e*—*g*)

Known species: *B. harrasense* (Haubold, 1967), *B. praeparvum* (Haubold, 1967), *B. kuhni* Demathieu et Haubold, 1982.

Size of the manus was somewhat more reduced relative to that of the pes. The trackway pattern is characterised by normal pace angulation of 150°—160°. Reduction of digits is not very significant. The cross axis very oblique at 50°—60°, and the

Fig. 2. Manus-pes impressions of *Synaptichnium*, *Brachychirotherium*, and *Chirotherium*: a—*S. primum*, b—*S.* cf. *pseudosuchoides*, c—*Synaptichnium* sp., d—*S. hildburghausensis* (*Synaptichnium* shows lacertoid habit of proterosuchians and pseudosuchians); e—*B. harrasense*, f—*B. kuhni*, g—*B. praeparvum* (the pes of all brachychirotherians shows a very oblique cross axis of typical pseudosuchians with crurotarsal pes joint); h—*C. sickleri*, i—*C. barthii* (in *Chirotherium* the dominance of pes digit group II — IV points toward tridactylism). Scale 2,5 cm. IV — pes digit four.

outward direction of pes digit III is more than 25°. Pace angulation and pes axis are indices of an agile quadrupedal, semierect gait, and also of a crurotarsal pes joint; this points towards typical pseudosuchians, perhaps like the Upper Triassic aetosaurids.

Chirotherium Kaup, 1835
(fig. 2*h*—*i*)

Known species: *Chirotherium barthii* Kaup, 1835, *C. sickleri* Kaup, 1835.

Manus was three or more times smaller than pes. Additional reduction of the manus is suggested by light impressions and the occasional absence of manus tracks; this points to partial bipedalism. That quadrupedal gait was nearly erect is suggested by the small trackway pattern, involving normal pace angulation of 160°—170°. Tridactylism of the pes is present in the closed digit group II—IV, of which III is the longest. Digit I was somewhat separated from the group of II—IV. The cross axis measured 80°—90° and the pes axis (digit III) was orientated 5°—20° outwards from the direction of movement. Until now *Chirotherium* has been compared with rauisuchids. But the nearly rectangular cross axis and tridactylism do not correspond to pseudosuchians, pointing instead, together with trackway pattern, to a more advanced thecodont of dinosaurian-like habit.

Isochirotherium Haubold, 1971
(fig. 3)

Known species: *I. soergeli* (Haubold, 1967), *I. herculis* (Egerton, 1839), *I. hessebergense* (Haubold, 1971), *I. jenense* (Haubold, 1971), *I. archaeum* Demathieu et Haubold, 1982.

Plane of manus less than 20% from that of pes, most manus impressions are smaller because incomplete. The earliest species — *I. archaeum* — shows permanent bipedalism. Only this species has a broader trackway with 100° pace angulation and cross axis only of 70°. The normal trackway pattern resembles that of *Chirotherium* in its pace angulation of 160°—170°, and the cross axis is 75°—90°. The dominant pes digits are III and II. IV is reduced and may be somewhat separated from the group of I—III. So the tendency of tridactylism seems concentrated, unusually, in the first three digits. Pes digit V is reduced and heel-like, and impressions of phalangeal pads may be missing. These characters are not usually those of pseudosuchians, and *Isochirotherium* seems to represent a group of thecodonts with partial affinities to dinosaurs or crocodiles.

Rotodactylus Peabody, 1948
(fig. 4)

In the Solling Formation occurs only the species *R. matthesi* Haubold, 1967 very abundant in footprint faunules. It was quite different from the chirotherians in impressions of autopods as well as in trackways. *Rotodactylus* may be characterised as a progressive lacertoid type. Trackway pattern shows relatively broad trackways, pes angulation up to 160°, and very long stride from which results overstep of manus by pes (fig. 4) impressions. Stride and trackway pattern show an extremly variable speed, something quite rare in reptilian trackways generally.

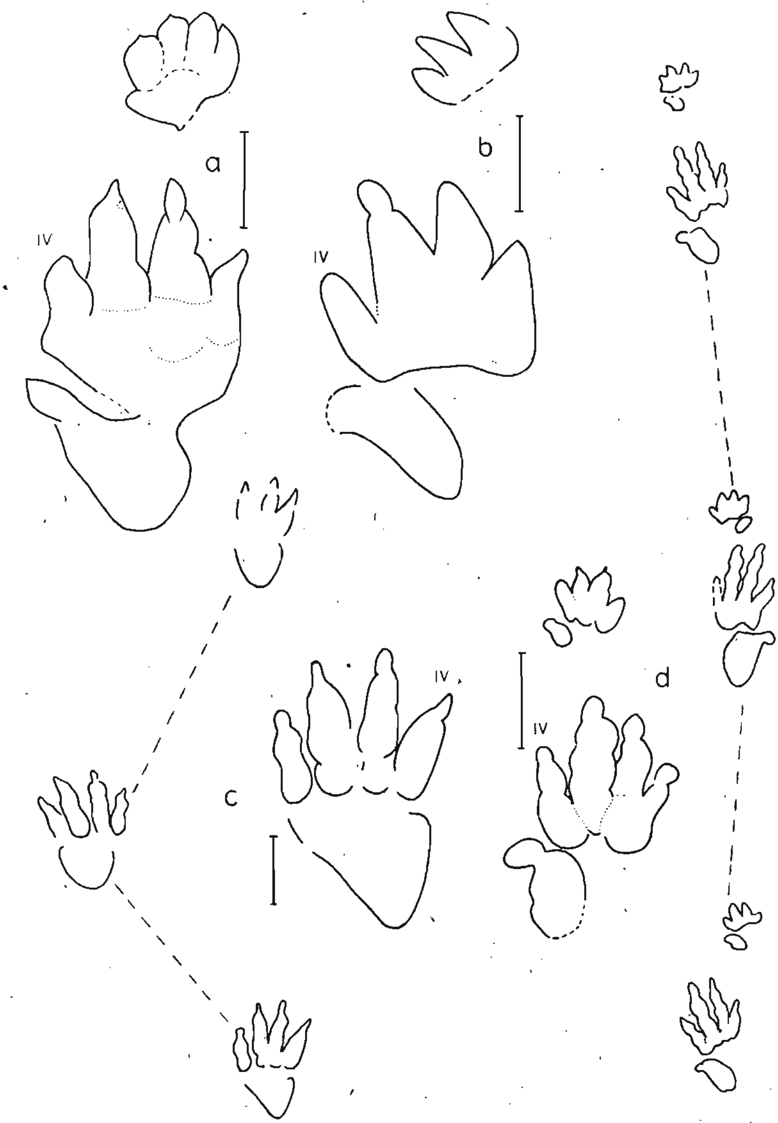

Fig. 3. Manus-pes impressions and trackways of *Isochirotherium*: a—*I. hessbergense*, b—*I. jenense*, c—*I. archaeum* (with relative broad trackway and pes), d—*I. soergeli* (shows the very small trackway pattern, with about 170° pace singulation of a erect quadrupedal gait). Scale 5 cm.

The digit group II—IV is subparallel and closed-together. Digits I and V are only impressed as points, V in the characteristic heel-like backward position. The only reasonable interpretation seems to be that these animals belonged to an early specialised thecodontian group. The pes joint was probably mesotarsal because of the very digitigrad impressions and the closed digit group II—IV, but possibly it showed the transitional lacertoid and rabbit-like habit, as in *Lagosuchus*, the most similar genus of Middle Triassic age.

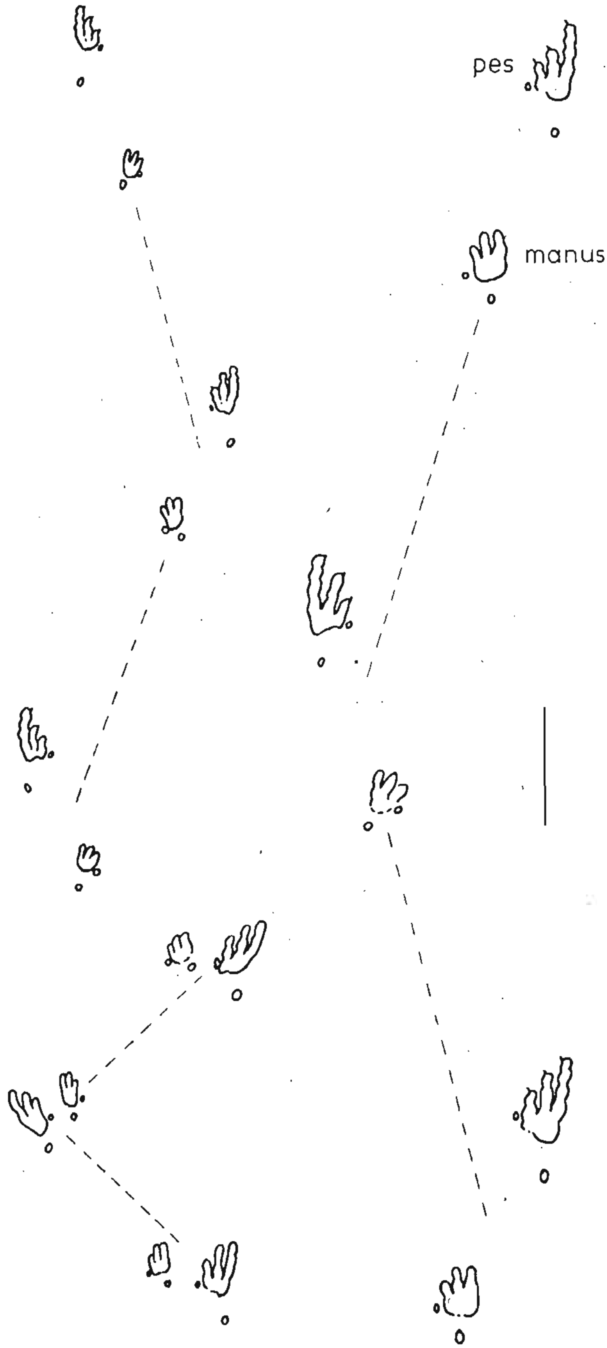

Fig. 4. Trackways with different stride in dependence of the variable speed of *Rotodactylus matthesi* — a very agile pseudosuchian. Scale 5 cm.

ARCHOSAUR FOOTPRINTS FROM MIDDLE TRIASSIC

A well represented continuation of Buntsandstein footprints in Middle Triassic deposits is found at the eastern border of the French Massif Central at the Anisian/Ladinian boundary. The faunules were summarized and described by Courel and Demathieu (1976), Demathieu (1977), and Gand (1978, 1979). All genera of archosaur footprints known from the Buntsandstein are also present in these beds: *Synaptichnium* (2 species), *Brachychirotherium* (4), *Chirotherium* (2), *Isochirotherium* (6), and *Rotodactylus* (3); but there are not the same species with exception of *Chirotherium barthii*. Additional archosaur footprints are the chirotherian like *Sphingopus*, the crocodiloid *Dahutherium*, and the tridactyls *Coelurosaurichnus* and *Anchisauripus*. They show fully developed tridactylism and bipedal erect gait, and may be interpreted as true theropods. The association of these footprints with representatives of typical chirotherians shows that chirotherians may not be direct forerunners of tridactyls, at least not these of that time.

However, in the Middle Triassic, footprint faunules continue the picture of archosaur associations at a broad thecodont-dinosaurian level. The problem of the missing bone equivalents (comp. Demathieu and Haubold 1974, 1978) also occurs in the Middle Triassic. The majority of pseudosuchians as well as of dinosaurs are not known from osteological data before the Upper Triassic. From Upper Triassic beds we know only *Brachychirotherium* and a few *Chirotherium* (in the form of the two atypical species *C. lulli* and *C. wondrai*). The restriction of typical *Chirotherium*, *Isochirotherium*, *Synaptichnium*, and *Rotodactylus* to the Lower and Middle Triassic solves the problem of the interpretation of these footprints; it suggests the thecodont and pseudosuchian origin of *Synaptichnium* and *Brachychirotherium*, and the more transitional (thecodont-dinosaurian) origin of *Chirotherium*, *Isochirotherium*, and *Rotodactylus*.

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