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# A REVIEW OF EUROPEAN TRIASSIC THEROPODS

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**ABSTRACT: The Upper Triassic theropod fossil record from Europe is reviewed in terms of validity of proposed taxa and the stratigraphical distribution of theropod remains. Only three species can presently be regarded as valid: *Liliensternus liliensterni* (HUENE), (?) *Liliensternus airelensis* CUNY & GALTON, and *Procompsognathus triassicus* FRAAS. (?) *L. airelensis* might represent a distinct genus, but more material is needed to confirm this. The genus *Syntarsus* RAATH, formerly known from southern Africa and North America is described from Europe for the first time. Theropods are first known from the fossil record in Europe in the Norian, and all determinable fossils represent members of the Coelophysoidea. Judged by the rarity of their fossil remains, theropods were obviously rather rare elements of the Upper Triassic terrestrial vertebrate fauna of Europe.**

**RÉSUMÉ: Le registre fossile des théropodes du Trias supérieur européen est révisé en terme à la fois de validité des taxons proposés et de répartition stratigraphiques des restes fossiles. Seule trois espèces peuvent être actuellement considérées comme valides: *Liliensternus liliensterni* (HUENE), (?) *Liliensternus airelensis* CUNY & GALTON et *Procompsognathus triassicus* FRAAS. (?) *L. airelensis* pourrait en fait appartenir à un nouveau genre, mais des restes plus complets seraient nécessaires pour confirmer cette hypothèse. Le genre *Syntarsus* RAATH, qui n'avait jusqu'à présent été décrit qu'en Afrique du Sud et en Amérique du Nord, l'est également pour la première fois en Europe. Les théropodes apparaissent en Europe à partir du Norien, et tous les fossiles identifiables appartiennent aux Coelophysoidea. Si l'on en croit la pauvreté de leurs restes fossiles, il semble évident que les théropodes représentaient des éléments relativement rares au sein des faunes de vertébrés terrestres du Trias supérieur d'Europe.**

## INTRODUCTION

In the light of new discoveries, especially in South America, the early history of theropod dinosaurs has been of great interest recent years (e.g. SERENO & NOVAS, 1992). Theropods are one of the most diverse dinosaur groups in the Late Jurassic and the Cretaceous, but little is still known about their origin, radiation and early diversification. Especially interesting in this respect is the first radiation of theropod dinosaurs, or dinosaurs in general, in the Upper Triassic (e.g. BONAPARTE, 1982; BENTON, 1984, 1993). Our knowledge of Upper Triassic theropods is mainly based on the American fossil record, although theropod remains are known from the Triassic all over the world (WEISHAMPEL, 1990).

The aim of the present paper is to review Triassic theropod records from Europe, in terms of the taxonomic validity of named species, and the stratigraphical distribution of theropod remains in the European Triassic, to determine the first appearance and taxonomic diversity of theropod dinosaurs in the Upper Triassic of Europe.

## THEROPODS FROM THE TRIASSIC OF EUROPE

In the following section, theropod taxa described from Europe are reviewed. See Figure 1 for the geographical occurrences, and Figure 2 for the stratigraphical distribution of theropodan remains.

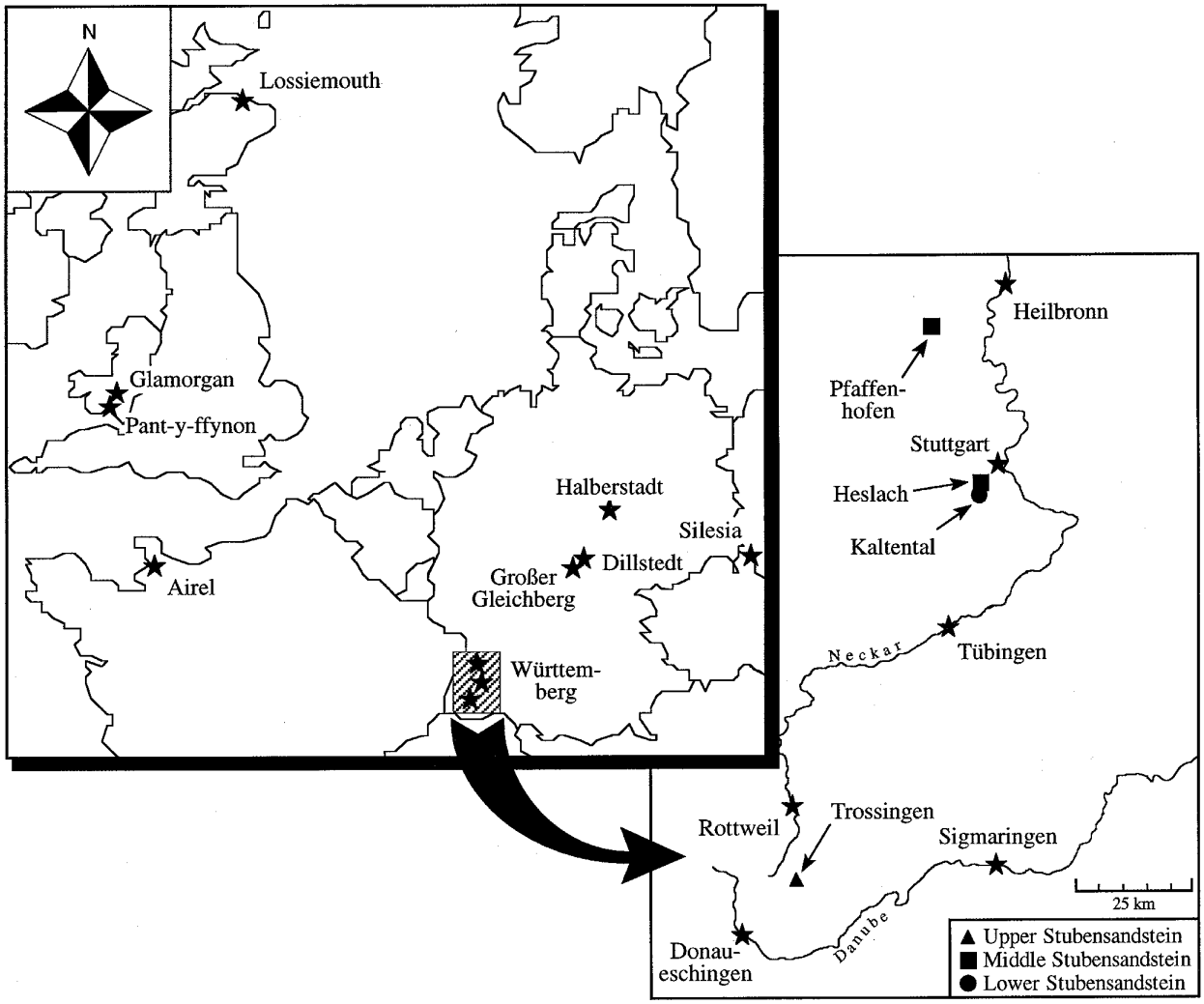


Fig. 1 - Map of the vertebrate localities mentioned in the text. The map of South Germany is based on BENTON (1994a).

*Avipes dillstedtianus* HUENE, 1932

**Age:** Ladinian, Middle Triassic.

**Occurrence:** Grenzdolomit close to Dillstedt, Thüringen, Germany.

**Comments:** *A. dillstedtianus* was described by HUENE (1932) on the basis of the proximal ends of three articulated metatarsals from the lowermost Upper Triassic (Lettenkeuper) of Thuringia.

The proximal ends of the metatarsals are closely appressed and deeper than wide (see HUENE, 1932: taf. 1, f. 7). Distally, the shafts of the bones are separated from each other and appear to diverge.

As already mentioned by NORMAN (1990), the specimen probably represents a digitigrade animal, but the metatarsals do not show any characters that allow a referral to the Theropoda. Since there are a variety of digitigrade animals in the Upper Triassic, *A. dillstedtianus* can only be referred to as probable Archosauria gen. et sp. indet. (see also NORMAN, 1990).

*Dolichosuchus cristatus* HUENE, 1932

**Age:** Norian, Upper Triassic.

**Occurrence:** Lower or middle Stubensandstein, Stuttgart-Kaltental, Baden-Württemberg, Germany.

**Comments:** *Dolichosuchus cristatus* is based on an isolated tibia from the Stubensandstein of southern Germany (HUENE, 1932). The specimen (BMNH 38056) shows a large cnemial crest, and a lateral ridge for the attachment of the fibula; these characters indicate that it represents a theropod. However, the poor preservation of the element makes it generically and specifically indeterminate, so that *D. cristatus* must be treated as a *nomen dubium*. It should be noted, though, that, as already

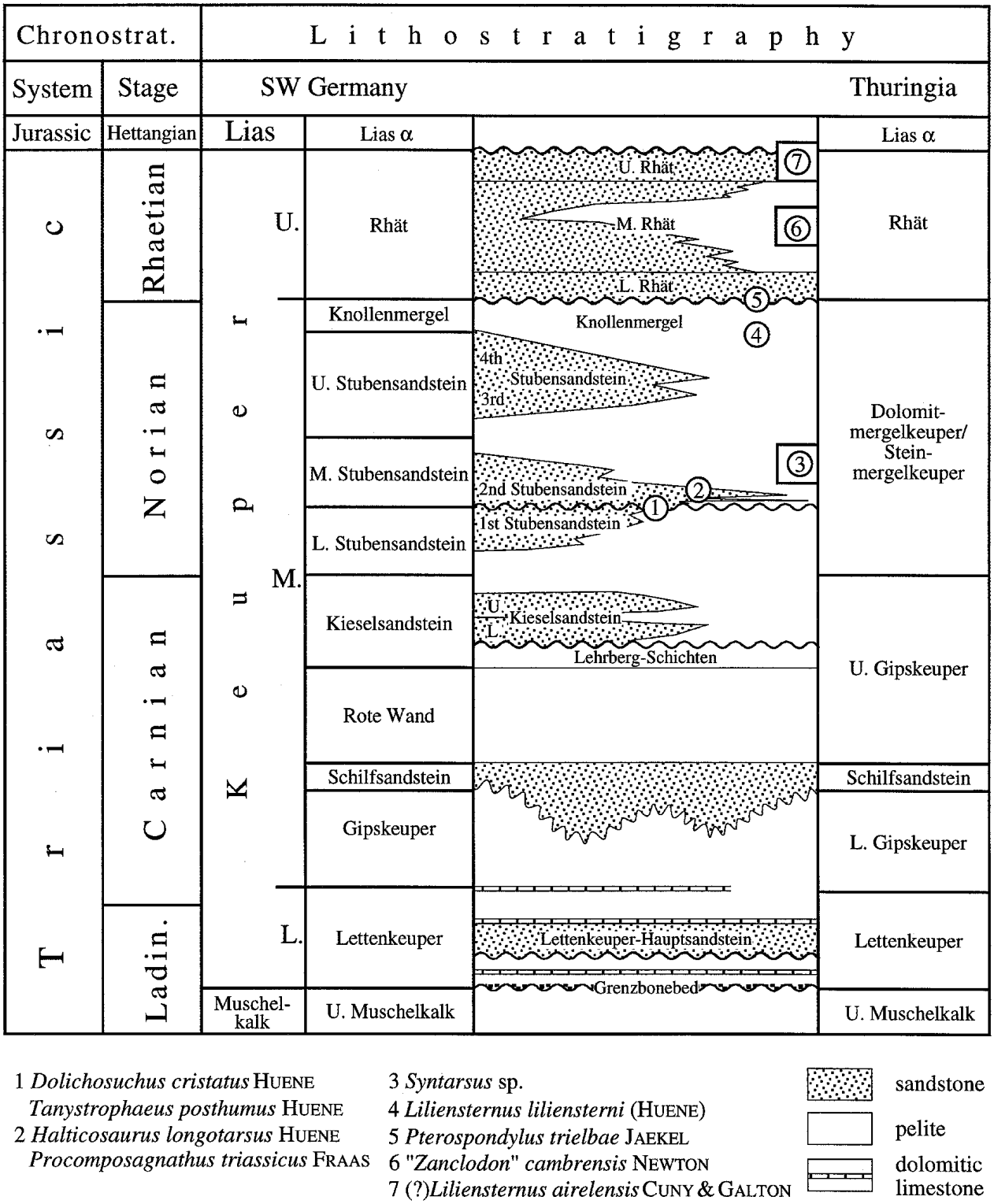


Fig. 2 - Synthesis of the lithostratigraphy of the German Keuper succession and its tentative correlation with the Triassic stages, modified from AIGNER & BACHMANN (1992). The approximate stratigraphic positions of the taxa are plotted in the diagrammatic lithostratigraphic section, taxa found outside of Germany are inserted in frames.

mentioned by HUENE (1934), the specimen shows great similarities to the tibiae of the slightly younger *Liliensternus liliensterni* (HUENE), and also of *Dilophosaurus wetherilli* (WELLES, 1984). This suggests that it probably represents a member of the Coelophysoidea ( = *Dilophosaurus* + Coelophysidae; HOLTZ, 1994).

### *Halticosaurus longotarsus* HUENE, 1907-8

**Age:** Norian, Upper Triassic.

**Occurrence:** Middle Stubensandstein, Weißer Steinbruch, Pfaffenhofen, Baden-Württemberg, Germany.

**Comments:** *Halticosaurus longotarsus*, the type species of the genus *Halticosaurus*, was described by HUENE (1907-8) on the basis of some fragments from the Stubensandstein of Pfaffenhofen (all bearing the collection number SMNS 12353). The material originally comprised a fragmentary dentary, parts of cervical, dorsal, sacral, and caudal vertebrae, fragments of a humerus, an ilium and two femora, and a complete metatarsal. Only one cervical vertebra (HUENE, 1907-8: taf. 97, f. 4), a dorsal vertebral centrum (op. cit.: taf. 97, f. 7), another fragmentary vertebral centrum (op. cit.: taf. 97, f. 6), the two femoral fragments (op. cit.: taf. 97, f. 1, 2) and the metatarsus (op. cit.: taf. 97, f. 9) could be located in the SMNS. All of the material is very badly preserved, and most of the fragments are not identifiable even as theropods. Furthermore, the original association of these specimens is very dubious. According to HUENE (1907-8), the remains were found "... together with *Sellosaurus Fraasi* and *Teratosaurus* (?) *minor* [both synonyms of *Sellosaurus gracilis*; note by the authors] ... in a marly layer intercalated in the Stubensandstein ..." (HUENE, 1907-8: 231; translated by O.R.), thus, it seems quite possible, that some of the material might represent a prosauropod. Indeed, the collection number also includes a skull of *Sellosaurus* HUENE (SMNS 12353a). The only remains that can be referred to the Theropoda with some certainty are the femoral fragments. One of them shows a spike-like lesser trochanter and a significantly downturned femoral head (Fig. 3), both characters also found in coelophysoids. Although *H. longotarsus* must be treated as a *nomen dubium*, the type series might therefore include remains of a coelophysoid theropod.

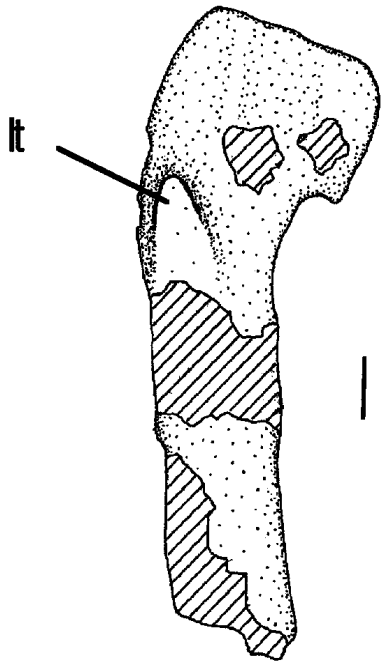


Fig. 3 - *Halticosaurus longotarsus* HUENE; SMNS 12353; proximal end of right femur, part of the type series; Stubensandstein, Pfaffenhofen, Germany; cranial view. Note the downturned femoral head and the spike-like lesser trochanter (lt). Scale bar indicates 1 cm.

HUENE (1921b) later referred some fragmentary remains from the Norian of Halberstadt to the same genus as cf. *Halticosaurus longotarsus*. This material (now in the HMN) is extremely fragmentary as well, and none of it can even be shown to be theropodan with any certainty.

### cf. *Halticosaurus orbitoangulatus* HUENE, 1932

**Age:** Norian, Upper Triassic.

**Occurrence:** Middle Stubensandstein, Weißer Steinbruch, Pfaffenhofen, Baden-Württemberg, Germany.

**Comments:** This taxon is based on a partial skull (SMNS 12353b) from the Pfaffenhofen quarry in the middle Stubensandstein of southern Germany. The skull is badly crushed, and the anterior end and most of the skull roof is missing. The specimen has been described in some detail by HUENE (1932), who referred this species to the family Podokesauridae within the Theropoda. However, the strongly anteriorly tapering antorbital fenestra closely resembles the condition seen in the sphenosuchian crocodile *Saltoposuchus* (see HUENE, 1921a; SERENO & WILD, 1992). Moreover, the teeth show an almost circular cross section at the base of the crown and longitudinal striations, but they lack well defined cutting edges and serrations. This is a condition often found in crocodylomorphs, but very rarely in theropods. Thus, since the specimen also lacks any clear theropod synapomorphies, *Halticosaurus orbitoangulatus* probably represents a sphenosuchian crocodile, rather than a theropod.

### *Liliensternus liliensterni* (HUENE, 1934)

**Age:** Norian, Upper Triassic.

**Occurrences:** Knollenmergel, Thüringen; ?Trossingen, Württemberg, Germany; ? Frick, Switzerland.

**Comments:** *Liliensternus liliensterni* is the best represented Triassic theropod from Europe. The taxon was originally described as *Halticosaurus liliensterni* by HUENE (1934), based on the associated, but disarticulated remains of two individuals from the Knollenmergel of Thüringen (HMN BM.R. 2175). Later, WELLES (1984) placed the species in the new genus *Liliensternus* and designated the larger individual as the lectotype. It must be noted, however, that the material may represent more than two individuals, and it seems almost impossible to separate the remains belonging to the larger and smaller individuals (W. D. Heinrich, pers. comm., 1996); therefore it is, at present, best to retain the whole material as the syntypes of the species.

The syntype of *Liliensternus* WELLES is one of the largest known Triassic theropods, with an estimated length of over 5 m (PAUL, 1988). Despite this large size, the individuals represented by the type material were probably juvenile to subadult, since the neurocentral sutures are still visible in the vertebrae, and only two fused sacrals are present (HUENE, 1934).

The anatomy of *Liliensternus* has briefly been described by HUENE (1934), WELLES (1984) and ROWE & GAUTHIER (1990). The taxon shows several derived characters shared with the Ceratosauria or more restricted ingroups of that clade, including a strong latero-ventral expansion of the dorsal rim of the acetabulum, a strongly downturned femoral head (HUENE, 1934; ROWE & GAUTHIER, 1990), and probably the presence of a subnarial gap (WELLES, 1984). By contrast with the illustration of the pelvis in ROWE & GAUTHIER (1990: f. 5.7), which only shows an obturator-notch in the pubis, a completely enclosed obturator foramen was present (HUENE, 1934: 159, taf. 15, f. 9b), opening dorso-medially as in *Syntarsus* (RAATH, 1969).

Within Ceratosauria, ROWE & GAUTHIER (1990) placed *Liliensternus* as a sister taxon to the clade comprising *Syntarsus* RAATH and *Coelophysis* COPE, basing this relationship on the presence of a well developed horizontal ridge on the maxilla. This view is followed here.

### *Liliensternus airelensis* CUNY & GALTON, 1993

**Age:** Rhaetian-Hettangian, Upper Triassic - Lower Jurassic.

**Occurrences:** Couches d'Airel, Normandie, France.

**Comments:** The holotype of this species comprises a fragmentary associated vertebral column and parts of the pelvis (Caen University, unnumbered). The material was originally described as *Halticosaurus* sp. by LARSONNEUR & LAPPARENT (1966). CUNY & GALTON (1993) referred it to the genus *Liliensternus* WELLES and made it the holotype of a new species.

Although the material is rather fragmentary, it can be said with some certainty that it does represent a distinct and diagnosable species. It must be noted, though, that its referral to the genus *Liliensternus* is questionable, since there are several major differences in the cervical vertebrae (e.g. the presence of two pairs of pleurocoels in *L. airelensis* versus only one pair in *L. liliensterni*; WELLES, 1984; CUNY & GALTON, 1993). However, the significance of these differences for distinguishing genera may only be decided if new, more complete material of L. airelensis is found. In all other characters, *L. airelensis* is very similar to *L. liliensterni*; therefore, it can be referred to the Coelophysoidea with some certainty.

### *Procompsognathus triassicus* FRAAS, 1913

**Age:** Norian, Upper Triassic.

**Occurrence:** Middle Stubensandstein, Weißer Steinbruch, Pfaffenhofen, Baden-Württemberg, Germany.

**Comments:** *Procompsognathus triassicus* was named by Fraas on the basis of "... the major part of an extremely delicate dinosaur skeleton, including the skull, the middle part of the body with the legs and the anterior part of the tail" (FRAAS, 1913: 1099; translated by O.R.). HUENE (1921a) later referred another partial skull and a left manus (both bearing the collection number SMNS 12352) from the same locality to this species and gave a detailed description of the type material (SMNS 12591). In his review of *P. triassicus*, OSTROM (1981) noted that the partial skull and manus cannot belong to this species, but he otherwise accepted the association of the skull and postcranium SMNS 12591. He furthermore concluded that *P. triassicus* represents a primitive theropod within its own family, the Procompsognathidae.

SERENO & WILD (1992) reviewed the type material again, and argued that the skull and the postcranial skeleton represent different animals. According to this paper, the skull SMNS 12591 belongs to the crocodylomorph *Saltoposuchus connectens* HUENE, which is known from the same locality, while the postcranial material represents an early theropod. Just one year later, CHATTERJEE (1993) in a short abstract, argued against the crocodylomorph nature of the skull and referred it to the Theropoda again.

The question whether the skull and postcranial skeleton were found in association originally and belong to the same individual, is very difficult to answer. While HUENE (1921a: 360) and BERCKHEMER (1938: 194) had no doubts about the association of the skull and postcranial skeleton, Fraas already noted that the holotype specimen "... is the major part of a ... dinosaur skeleton in three pieces, ..." (FRAAS, 1914: 129; translation by O.R.). Since these specimens were purchased from the local quarry manager, together with several other vertebrate fossils (SERENO & WILD, 1992), no data on their original association in the quarry exists, and they might well be from different parts of the quarry (R. Wild, pers. comm., 1996). The skull has been reprepared, and a detailed description, currently being carried out by S. Chatterjee (pers. comm., 1996), will certainly reveal new information on its anatomy and systematic position. Pending this new information, this review will only focus on the postcranial material.

Sereno & Wild (1992) listed six theropod synapomorphies in the postcranium of *Procompsognathus* FRAAS, so that there can be little doubt as to the theropod nature of this specimen. Its systematic position within Theropoda, however, is much more difficult to establish. OSTROM (1981) and SERENO & WILD (1992) noted that the pubis was similar to *Coelophysis* and especially *Segisaurus* CAMP in showing a "... slightly bowed, rectangular pubic apron ..." (OSTROM, 1981: 193) and in being "... anteroposteriorly compressed ..." and lacking a pubic boot (SERENO & WILD, 1992: 437). However, all of these features are also present in prosauropods (e.g. HUENE, 1926) and do therefore probably represent the plesiomorphic character state for theropods. Thus, the development of the pubis only implies that *P. triassicus* is a primitive theropod.

SERENO & WILD also note the presence of a "... sigmoid trochanteric shelf ... identical to that in ceratosaurs such as *Syntarsus* and *Coelophysis*." (SERENO & WILD, 1992: 437). Although NOVAS (1996) noted that the presence of a trochanteric shelf is a synapomorphy of the Dinosauriformes, rather than a ceratosaurian one, the exact shape of this structure in *P. triassicus* might be taken as an indication of a ceratosaurian relationship for this taxon. A further argument for placing *Procompsognathus* in the Ceratosauria, and maybe even in the Coelophysoidea, might be the presence of elongate dorsal vertebrae and more or less triangular dorsal transverse processes. For the present, however, more material is needed to confirm the systematic position of this species within Theropoda.

Although it is difficult to give a formal diagnosis for *P. triassicus*, it is provisionally regarded as a valid taxon here. Possible characters to distinguish it from other Triassic theropods include an elongate hindlimb (ratios tibia/femur: c. 1.2; Mt III/femur: c. 0.74).

### *Pterospondylus trielbae* JAEKEL, 1913

**Age:** ? Norian, Upper Triassic.

**Occurrence:** Knollenmergel, Baerecke quarry, Halberstadt, Sachsen-Anhalt, Germany.

**Comments:** The species is based on an isolated dorsal vertebra, found within a shell of the Triassic turtle *Proganochelys* BAUR (JAEKEL 1913). The centrum is low and elongate (Fig. 4), resembling the condition seen in *Procompsognathus*. On this basis, HUENE (1921b, 1932) referred this species to the Procompsognathidae and noted that it might be congeneric with *Procompsognathus*. However, the transverse processes are both triangular and strongly backturned, a condition also seen in *Syntarsus* (RAATH, 1969), and noted as a synapomorphy of the Ceratosauria by ROWE & GAUTHIER (1990). Unfortunately, not much can be said about the transverse processes in the anterior dorsal vertebrae of *Procompsognathus*, except that they also seem to be more or less triangular (see above).

The transverse processes in *Dilophosaurus* WELLES and *Liliensternus* are less strongly backturned and not as significantly triangular, as is the

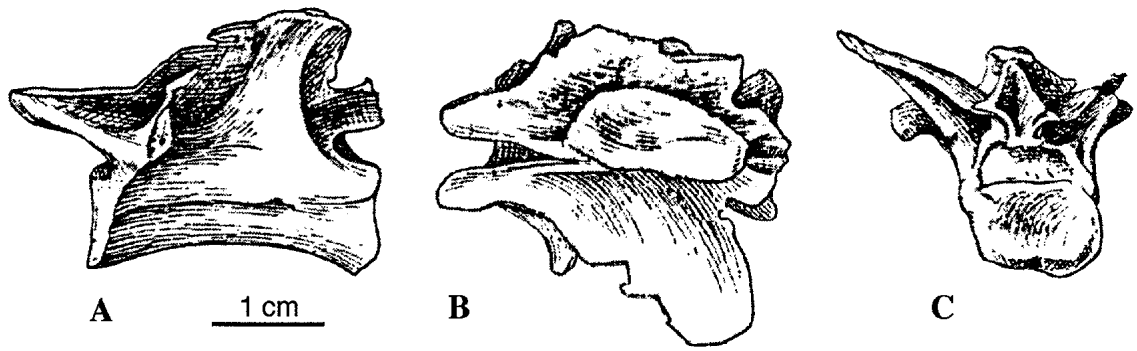


Fig. 4 - *Pterospondylus trielbae* JAEKEL; isolated dorsal vertebra, holotype; Knollenmergel, Halberstadt, Germany. **A** - Left lateral view. **B** - Dorsal view. **C** - Posterior view. Modified from HUENE (1921b). Scale bar indicates 1 cm.

case in *Syntarsus* or *P. trielbae*, indicating that this character may rather represent a synapomorphy of a more restricted ingroup of the Ceratosauria. Thus, the vertebra from Halberstadt probably represents a member of the Coelophysidae. *P. trielbae* cannot be formally diagnosed and must be treated as a *nomen dubium*.

### *Saltopus elginensis* HUENE, 1910

**Age:** Upper Carnian, Upper Triassic.

**Occurrence:** Lossiemouth Sandstone Formation, Grampian, Scotland.

**Comments:** This taxon is based on a partial postcranial skeleton of a small, long-limbed tetrapod from the Late Carnian of Elgin, Scotland (HUENE, 1910; BENTON & WALKER, 1985). The specimen (BMNH R 3915) comprises the major parts of a dorsal, sacral and caudal vertebral column, fragments of the forelimb and the hindlimbs. Skull remains are not present (*contra* NORMAN, 1990). The material is extremely poorly preserved. The bones are either indicated as imprints (counterslab) or at least superficially remineralized as goethite (see BENTON & WALKER, 1985); original bone material is preserved only occasionally (pers. obs.). Not much can therefore be said about the anatomy of the animal in detail.

The skeleton, as preserved on the main slab, lies on its belly, as judged by the impressions of the neural spines in the counterslab and the orientation of the hindlimbs. From both, the specimen on the main slab and the impressions on the counterslab, the number of sacral vertebrae is probably two, rather than four, as argued by HUENE (1910), or three, as noted by NORMAN (1990). In contrast with the illustrations by HUENE (1910: taf. 1), the ilium is rather short, especially its preacetabular part. Again, the impressions of this bone in the counterslab show the shortness of the ilium much better than the remineralized bone remains on the main slab. The limbs are very long and slender, the lower elements being especially elongated (ratio tibia/femur: c. 1.4). The femur is slightly curved. In the lower limbs, the tibia and fibula seem to be of subequal width, and the metatarsals are long and slender. As judged by the impressions of the toes of the left hindlimb in the main slab, the number of digits used for locomotion was probably three, but there is an impression of a further, significantly shorter digit medial to these.

In conclusion, the material represents a small, cursorial bipedal animal with elongated hindlimbs. However, the shortness of the ilium, the low number of sacral vertebrae and the subequal width of the lower limb bones make it seem rather unlikely that it represents a theropod. A short ilium and only two sacrals are found in *Herrerasaurus* REIG (NOVAS, 1993), but the sacral ribs of this species are much more massive than seems to be the case in the type specimen of *Saltopus* HUENE. Characters like elongated hindlimbs, bipedality, mainly three digits used in locomotion, and cursorial habits are also present in primitive dinosauriformes like *Marasuchus* SERENO & ARCUCCI, 1994. Therefore, *S. elginensis* can only be treated as a probable dinosauriform *nomen dubium*.

### ? *Syntarsus* sp.

**Age:** ? Norian, Upper Triassic.

**Occurrence:** Pant-y-ffynnon fissure filling, South Glamorgan, Wales.

**Comments:** A few theropod remains were found in the Late Triassic fissure fillings of southern Wales and south-east England. The most significant of these is an articulated left pelvic girdle (Fig. 5A), including parts of the sacrum, the posteriormost dorsal vertebrae and an associated left femur (Fig. 5B-C), lacking the distal end (BMNH PV RU P 77/1 and RU P 76/1) from the locality Pant-y-ffynnon in southern Wales (WARRENER, 1983).

The dorsal vertebrae are long and rather low, with low, but long neural spines. The sacral vertebrae are fused, with the sutures between single vertebrae being only visible as slight swellings. The pubis and ischium are fused to the ilium, but not to each other. The completely preserved ilium of the specimen is only 52 mm long. It is dolichoiliacic, the preacetabular part being significantly shorter than the postacetabular one, and shows a well developed brevis shelf and a strong lateral expansion of the dorsal rim of the acetabulum. The distal end of the pubis is missing. The preserved part shows a slightly bowed shaft, a small, dorso-medially opening obturator foramen and a much larger pubic foramen underneath it. In anterior view, the fused pubes form a rather broad apron. The ischium also lacks its distal end. The obturator process is not offset from the pubic peduncle and distally there is a small notch between the process and the ischial shaft. The femur shows a downturned femoral head and a well developed trochanteric shelf. The fourth trochanter is represented by a long, low, proximally placed flange.

In all of their characters, the specimens are extremely similar to the coelophysid *Syntarsus* (RAATH, 1969; ROWE & GAUTHIER, 1990); thus, they are tentatively referred to this genus, despite their significantly older age (see also WARRENER, 1983). A very similar theropod appears also to be present in the Upper Triassic (Norian) of the Ghost Ranch quarry of North America (PAUL, 1993). However, there is some confusion about the theropod specimens from this locality, and the theropod described as *Coelophysis* by COLBERT (1989) is clearly distinct

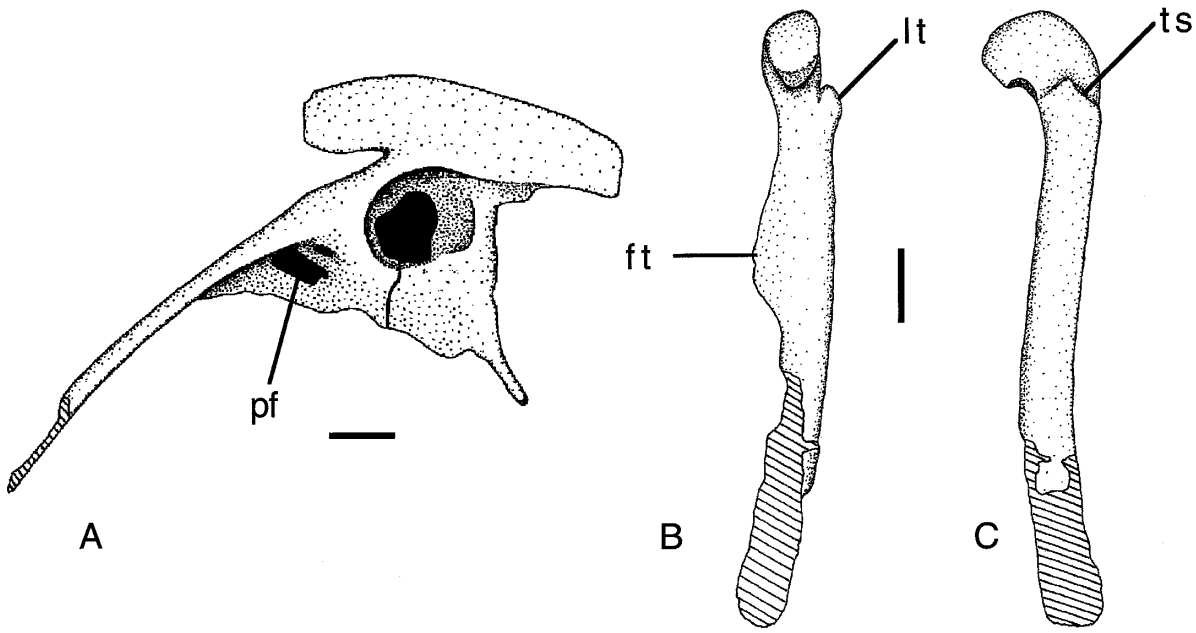


Fig. 5 - ?*Syntarsus* sp.; fissure fillings, Pant-y-ffynnon, Wales. **A** - BMNH PV RU P 77/1; left side of the pelvis; lateral view; pf - pubic foramen. **B** - BMNH RU P 76/1; left femur; medial view; ft - fourth trochanter, lt - lesser trochanter. **C** - BMNH RU P 76/1; left femur; cranial view; ts - trochanteric shelf. Scale bars indicate 1 cm.

from the Welsh specimens. In all the comparable characters (shape of the dorsal vertebral centra, width of pubes in anterior view, development of trochanteric shelf), the specimens are furthermore very similar to *Procompsognathus*, and new discoveries might prove that they are referable to this genus.

### *Tanystrophaeus posthumus* HUENE, 1907-8

**Age:** Norian, Upper Triassic.

**Occurrences:** ? Middle Stubensandstein, Stuttgart-Heslach, Baden-Württemberg, Germany.

**Comments:** *T. posthumus* is based on a single caudal vertebra (SMNS 4385) collected by S.F.J. von Kapff in the sixties of the 19th century (A.H., unpubl. data). The specimen has first been described and figured by MEYER (1865: 114, pl. 27, fig. 4-6), but he did not assign it to a particular taxon. HUENE (1907-8) first realized the theropod nature of the vertebra and made it the type of a new species. The specimen is now kept in the collections of the Staatliches Museum für Naturkunde Stuttgart, where it is labelled as "*Nicrosaurus* sp.".

The vertebra represents a relatively stout posterior caudal with strongly elongated prezygapophyses (Fig. 6). No transverse processes are present, and the neural spine is very low.

This element is readily identified as a theropod caudal vertebra, because of the presence of elongated prezygapophyses. It shows a rather broad ventral groove, similar to that found in the caudal vertebrae of *Liliensternus*. However, the specimen is generically and specifically indeterminable, so that *T. posthumus* must be regarded as a *nomen dubium*.

### *Velocipes guerichi* HUENE, 1932

**Age:** Norian, Upper Triassic.

**Occurrence:** Lissauer Breccia, Gorny Slask, Poland.

**Comments:** The holotype of *V. guerichi* is a proximal end of a long bone. HUENE (1932) described it as the upper half of a left theropod fibula, but the specimen is extremely poorly preserved and even its identification as a fibula may be doubted. Therefore, *V. guerichi* can only be regarded as a *nomen dubium* (see also NORMAN, 1990).

### "*Zanclodon*" *cambrensis* NEWTON, 1899

**Age:** Rhaetian, Upper Triassic.

**Occurrence:** Rhaetic beds, Mid-Glamorgan, Wales.

**Comments:** This species is based on a natural mould in a sandstone slab from the Uppermost Triassic of southern Wales. It was first described by NEWTON (1899) as *Zanclodon cambrensis* and later referred to the genus *Megalosaurus* BUCKLAND. MOLNAR, KURZANOV & DONG (1990) noted that this

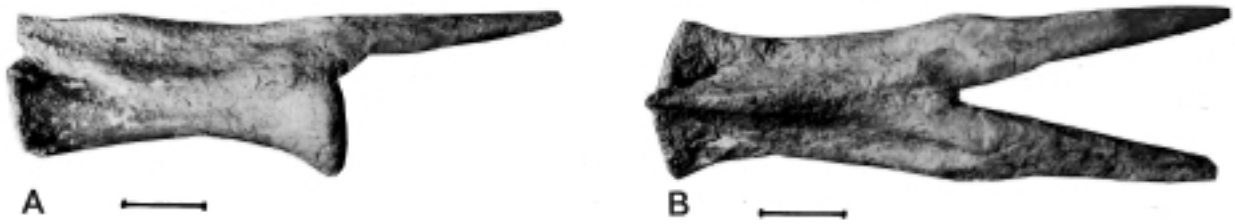


Fig. 6 - *Tanystrophaeus posthumus* HUENE; SMNS 4385; isolated caudal vertebra, holotype; Stubensandstein, Stuttgart-Heslach, Germany. **A** - Right lateral view. **B** - Dorsal view. Scale bars indicate 1 cm.

dentary agrees with *Megalosaurus* in six of the nine characters, listed by MADSEN (1976) to distinguish between *Allosaurus* and *Megalosaurus*; the other three cannot be determined. Three of the characters were regarded as shared derived features: the angular rostral margin, separate interdental plates and exposed replacement teeth (MOLNAR, KURZANOV & DONG, 1990). However, an angular rostral margin is also found in *Liliensternus liliensterni* (HUENE, 1934), *Syntarsus kayentakate* ROWE, 1989, and even the prosauropod *Sellosaurus gracilis* HUENE (GPIT PV 18318a; pers. obs.). The interdental plates are separate in *Plateosaurus engelhardti* MEYER (HMN MB.R. 1937; pers. obs.), *Dilophosaurus wetherilli* (WELLES) (WELLES, 1984), *Sinraptor dongi* CURRIE & ZHAO, 1993, and *Compsognathus longipes* WAGNER (OSTROM, 1978), amongst many others. The third character was described "... replacement teeth exposed at base between interdental plates ..." by MADSEN (1976: 10). This character is clearly correlated with the separate interdental plates. Thus, all of these characters probably represent the plesiomorphic conditions within theropods and cannot therefore be used to link "*Z.*" *cambrensis* with *Megalosaurus*. Although all determinable characters of the specimen agree quite well with *Liliensternus liliensterni* or *Dilophosaurus wetherilli* (e.g. the presence of very low and broad interdental plates), its systematic position must remain unsolved.

"*Z.*" *cambrensis* does not show any derived characters that would allow a formal diagnosis of the species. It might represent a distinct taxon, but at present it can only be regarded as a *nomen dubium*.

## DISCUSSION

### STRATIGRAPHY OF THE GERMAN KEUPER AND DISTRIBUTION OF THEROPOD REMAINS

A synthesis of the Mid-European Keuper succession is compiled in Figure 2, largely based on the deposits in South Germany. The lithologic description below follows GEYER & GWINNER (1991) and AIGNER & BACHMANN (1992), and we refer to these publications for further readings.

The Lower Keuper or Lettenkeuper starts with the Grenz-bonebed, which is unconformably overlying the marine Muschelkalk. The Lower Keuper is mainly a succession of variegated shales intercalated with thin dolomitic beds, probably laid down in a brackish-water environment. Several fluvial sandstone beds occur regionally in different stratigraphic positions within the succession. A gradual shift towards a marine depositional environment results in the Gipskeuper deposits (stacked dolomite-gypsum sequences, topped by deposits of a playa-like environment). The Schilfsandstein is again probably a fluvial rather than a deltaic sandstone as presumed previously, which has yielded a variety of temnospondyl amphibians (BENTON, 1994a). Coloured mudstones deposited in an arid desert-like environment make up the Rote Wand and Kieselsandstein. The latter unit includes a series of dolomitic beds, the Lehrbergschichten, and, interdigitating with the shales, a fluvial sandstone (Kieselsandstein).

Similarly, the following Stubensandstein can be subdivided into fluvially dominated deposits (Sandsteinkeuper) protruding from the margins into the German Basin towards the north and northwest, where they interdigitate with variegated playa pelites and lacustrine dolomites (Steinmergelkeuper) in the depositional centre of the German Basin. The marginal deposits comprise four heterochronous large-scaled alluvial fans termed first to fourth Stubensandstein. Note that the next following unit, the Knollenmergel, in parts evidently represent a heterochronous facies deposited in a playa environment: in southern Württemberg, the lower beds of the Knollenmergel replace the third and fourth Stubensandstein laid down contemporaneously in central and eastern Württemberg (BRENNER & VILLINGER, 1981). In northern and eastern Germany, the Knollenmergel is topped by thick fluvial sandstones ("Hauptsandstein") grading into flood-

plain deposits, which both are by convenience referred to the Lower Rhaetian. These again are overlain unconformably by marine sandstones and shales, which can be safely dated as Rhaetian by a fauna including the bivalve *Rhaetavicula contorta* (PORTLOCK). In South Germany, the Rhaetian is represented by much condensed and patchy deltaic deposits ("Rhät-sandstone" and "Rhät-shales") following the marine Rhaetic transgression.

About half of the taxa treated here are derived from the South German Stubensandstein, and for this reason it is necessary to review the stratigraphic position of this unit in more detail. The specimens from Pfaffenhofen (*Procompsognathus triassicus*, the theropod *nomen dubium Halticosaurus longotarsus*, and the archosaurian "*Halticosaurus*" *orbitoangulatus*) can be safely placed into the middle Stubensandstein (STOLL, 1929; BRENNER, 1978). Much more difficult to establish is the lithostratigraphic position of *Tanystrophaeus posthumus* (HESLACH) and *Dolichosuchus cristatus* (KALTENTAL), since there are numerous abandoned Stubensandstein quarries around Stuttgart and the exact provenance of the specimens was never recorded. The Heslach quarry, also the source of a number of important phytosaur remains and the rauisuchian *Teratosaurus* MEYER (KAPFF, 1859; MEYER, 1861; GALTON, 1985b), corresponds probably to the site "Heslacher Wand", which is most likely middle Stubensandstein (BRENNER, 1978). The quarry near Kaltental which produced the famous association of 22 specimens of the stagonolepidid *Aetosaurus* FRAAS was placed in the lower Stubensandstein (WILD, 1989), but it is by no means sure whether *Dolichosuchus* comes from the same site. Additionally, all the lithostratigraphic referrals are debated, and the only safe conclusion is that both specimens must have been derived from lower or middle Stubensandstein.

Two alternative hypotheses have been advocated to calibrate the lithostratigraphic units of the German Keuper Succession (discussed in BENTON, 1994a, 1994b). Both unanimously agree that the Stubensandstein must be considered Norian in age, but conflicting palynologic, magnetostratigraphic and palaeoclimatic evidence has led to different assessments of the time span of this unit within the stage. In the first interpretation, the Stubensandstein comprises almost the whole Norian, except for the Knollenmergel, which is commonly referred to the uppermost part of the Norian. According to the alternative view, the Stubensandstein is restricted to the upper part of the Norian only. Currently, there is not sufficient data available to correlate one of the subunits of the Stubensandstein with the alpine Triassic strata convincingly and to clinch this question. WILD (1989) assigned a Middle Norian age to the lower Stubensandstein because of the co-occurrence of *Aetosaurus* therein and in the datable Calcare di Zorzino in North Italy. This would point towards a Middle to Late Norian Age for the whole Stubensandstein. However, as outlined before, the referral of *Aetosaurus* to the lower Stubensandstein is debatable, and it could well occur in the middle Stubensandstein (e.g. BRENNER, 1973). Furthermore, LUCAS & HUNT (1993) proposed the Revueltian biochron (Lower Norian) for the Southwestern United States, characterised, among other vertebrates, by the aetosaur *Paratypothorax* LONG & BALLEW (see also HUNT & LUCAS, 1992). *Paratypothorax* occurs in the lower Stubensandstein (WILD, 1991), but also in the middle (A.H., unpubl. data), arguing for an Early Norian age of both subunits. However, the utility of vertebrate biochrons for dating strata on widely separate continents has yet to be tested. We consider the Stubensandstein spanning most of the Norian as the more likely interpretation at the moment. Both hypotheses may be tested when dates are established for specimens referable to the phytosaur *Mystriosuchus* FRAAS from the marine Dachsteinkalk of the Austrian Alps (reported preliminarily by BUFFETAUT, 1994). In the German Basin, *Mystriosuchus* is entirely restricted to the middle Stubensandstein.

*Liliensternus liliensterni* comes from the Knollenmergel of Thuringia and can therefore be dated as Late Norian with some certainty (see above). This conclusion is furthermore substantiated by the fact that the remains of *L. liliensterni* were found in association with remains of *Plateosaurus engelhardti* (HUENE, 1934), which is well known from the Late Norian of southern Germany and Switzerland (SANDER, 1992).

*Syntarsus* sp. comes from Pant-y-ffynnon quarry, one of the numerous fissure fillings in Carboniferous limestone strata of Wales and Southwest England. These fillings have a complex depositional history and dating is difficult (see FRASER, 1994), being mainly achieved by their contents of vertebrates. Pant-y-ffynnon has yielded, among other taxa, the crocodylomorph *Terrestrisuchus* CRUSH (which has been suggested as a synonym of the middle Stubensandstein *Saltoposuchus*) and the gliding diapsid *Kuehneosaurus* ROBINSON. Vertebrates seem to exclude a post-Triassic age, but the locality can be considered Late Triassic at best, ranging anywhere from Late Carnian to Rhaetian (BENTON & SPENCER, 1995).

The age of *Pterospondylus trielbae* is usually given as Rhaetian (e.g. HUENE, 1932; NORMAN, 1990). The section in the Baerecke quarry, as summarized by SANDER (1992), consisted of two successions: a lower claystone layer, which is considered to represent the equivalent of the Knol-

TABLE I
Summary of the age, occurence, and taxonomic status of theropod taxa from the Triassic of Europe.

| NAME | AGE | OCCURENCE | TAXONOMIC STATUS |
|---|---|---|---|
| *Avipes dillstedtianus* HUENE, 1932 | Ladinian | Lettenkeuper, Thuringia, Germany | ? Archosauria, *nomen dubium* |
| *Dolichosuchus cristatus* HUENE, 1932 | Norian | Stubensandstein, Baden-Württemberg, Germany | Theropoda, *nomen dubium* |
| *Halticosaurus longotarsus* (HUENE, 1907-8) | Norian | Stubensandstein, Baden Württemberg, Germany | Theropoda, *nomen dubium* (at least *partim*) |
| *"Halticosaurus" orbitoangulatus* HUENE, 1932 | Norian | Stubensandstein, Baden-Württemberg, Germany | ? Crocodylomorpha, *nomen dubium* |
| ? *Liliensternus airelensis* CUNY & GALTON 1993 | Rhaetian-Hettangian | Airel quarry, Normandy, France | Theropoda, valid species |
| *Liliensternus liliensterni* (HUENE, 1934) | Norian | Knollenmergel, Thuringia, Germany | Theropoda, valid species |
| *Procompsognathus triassicus* FRAAS, 1913 | Norian | Stubensandstein, Baden Württemberg, Germany | Theropoda, provisionally regarded as valid species |
| *Pterospondylus trielbae* JAEKEL, 1913 | ? Norian | Knollenmergel, Thuringia, Germany | Theropoda, *nomen dubium* |
| *Saltopus elginensis* HUENE, 1910 | Carnian | Lossimouth Sandstone Formation, Scotland | Dinosauriformes, *nomen dubium* |
| *Tanystrophaeus posthumus* HUENE, 1907-8 | Norian | Stubensandstein, Baden-Württemberg, Germany | Theropoda, *nomen dubium* |
| *Velocipes guerichi* HUENE, 1932 | Norian | Lissauer Breccia, Gorny Slask, Poland | Vertebrata, *nomen dubium* |
| *"Zanclodon" cambrensis* NEWTON, 1899 | Rhaetian | Rhaetic sandstone, Wales | Theropoda, *nomen dubium* |

lenmergel, overlain by sand- and siltstones of probably Rhaetian age. According to JAEKEL (1913), at least a part of the turtle remains were derived from the lower part of the section of the Baerecke quarry. Since the holotype of *P. trielbae* was found within a turtle carapace, it might therefore be of Late Norian age, rather than Rhaetian.

"*Zanclodon*" *cambrensis* comes from a sandstone bed in southern Wales. The slab was derived from a stack of building material, and its exact stratigraphic position (above or below the *Rhaetavicula contorta* beds) is uncertain (NEWTON, 1899). However, the sandstone unit, where the specimen came from is considered to be Rhaetian (WARRINGTON *et al*., 1980).

The stratigraphic position of ?*Liliensternus airelensis* has been discussed in some detail by CUNY & GALTON (1993). The specimen might be either late Rhaetian or early Hettangian in age.

## THE TRIASSIC THEROPOD FAUNA OF EUROPE

Only three theropod species from the Upper Triassic of Europe can presently be regarded as being valid (see also TABLE I): *Liliensternus liliensterni*, ?Liliensternus airelensis and *Procompsognathus triassicus*. Furthermore, a species of *Syntarsus* was most probably present in the Upper Triassic of Europe as well. Both *L. liliensterni* and *P. triassicus* come from the Norian of southern Germany, the specimen of *Syntarsus* derives from probably Norian fissure fillings in Wales, while ? *L. airelensis* was found in sediments spanning the Triassic-Jurassic boundary in northern France, and might even be of lowermost Jurassic age.

Apart from the remains discussed above, only a few other fragments can be assigned to the Theropoda with any certainty. GALTON (1985a) noted a probable theropod femur fragment from the Stubensandstein of Pfaffenhofen, BUFFETAUT & WOUTERS (1986) described some probable theropod teeth

from the Norian of France, and SANDER (1992) referred several teeth from the Knollenmergel of Frick (Switzerland) and Trossingen (southern Germany) to cf. *Liliensternus*. However, since teeth of theropod dinosaurs do not differ significantly from the serrated teeth of other Triassic archosaurs, the identification of isolated serrated teeth from Triassic beds as theropod is always doubtful. For the same reason, taxa based on isolated teeth (e.g. "*Megalosaurus*" *cloacinus* QUENSTEDT, "*Megalosaurus*" *obtusus* HENRY, "*Plateosaurus*" *ornatus* HUENE; see HUENE, 1907-8, 1932; GALTON, 1985b) are not included in this review.

In addition to the skeletal remains, supposed theropod footprints have been described from different localities (e. g. HADERER, 1990). However, there are many sources of error in identifying prints (KING & BENTON, 1996), and, apart from theropods, other animals including protodinosaurs or early ornithischians might have produced tridactyl prints, hence footprint evidence is not taken into consideration here.

Thus, the earliest certain records of theropod dinosaurs in Europe come from the upper parts of the Lower Norian. Since there are vertebrate localities in the pre-Norian Upper Triassic in Europe, and especially in Germany, the Upper Triassic is well represented by terrestrial sediments (see above), the appearance of theropod dinosaurs at that time is interpreted here as representing the first radiation of theropods in Europe.

Furthermore, all identifiable theropod remains appear to belong to the Coelophysoidea, within the Ceratosauria. The presence of the genus *Syntarsus* in particular is interesting; this taxon is well known from the lowermost Jurassic of southern Africa and North America (ROWE & GAUTHIER, 1990), and might have been present in the Norian of North America as well (PAUL, 1993). Since the oldest theropods are known from the Carnian of South America (SERENO & NOVAS, 1992), and coelophysoids first appear in the fossil record in the early Norian (ROWE & GAUTHIER, 1990), there would appear to have been a rapid radiation of ceratosaurian theropods in the late Carnian / early Norian. These conclusions are in general accordance with ideas proposed by BENTON (1984, 1993a), that dinosaur radiation was rapid in the Upper Triassic, possibly following an extinction event.

An interesting aspect of the Upper Triassic theropod fossil record, not only of Europe, but in general, is the complete absence of theropods other than herrerasaurids and ceratosaurs. Given the sister-group relationship of ceratosaurs and tetanurans (GAUTHIER, 1986; HOLTZ, 1994), the latter group must have been present in the Late Triassic. The lack of tetanuran fossils from the Triassic either reflects geographic isolation of this group during that time, or their rareness in Upper Triassic vertebrate faunas.

In this context, another aspect is worth mentioning: there are many fossil vertebrate localities, and dinosaurs are quite abundant in the European Upper Triassic (see e.g. WEISHAMPEL, 1990), but theropod remains are rather rare. Although this may partly be due to the taphonomy of the localities (SANDER, 1992), it might reflect genuine rarity of theropods in the Upper Triassic vertebrate fauna of Europe.

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## ABBREVIATIONS

BMNH - Natural History Museum, London, UK; GPIT - Institut und Museum für Geologie und Paläontologie Tübingen, Germany; HMN - Museum für Naturkunde, Humboldt Universität, Berlin, Germany; SMNS - Staatliches Museum für Naturkunde Stuttgart, Germany.

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