

Post-cranial remains of ‘coelurosaurs’ (Dinosauria, Theropoda) from the Late Jurassic of Tanzania

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Abstract – Small theropod post-cranial material from Tendaguru, Tanzania, the only known Late Jurassic theropod locality in the Southern Hemisphere, is reviewed. Material originally described as ‘coelurosaurs’ includes at least one taxon of basal tetanuran and one taxon of small abelisauroid. Together with the abelisauroid *Elaphrosaurus* and the presence of a larger ceratosaur in Tendaguru, this material indicates that ceratosaurs were an important faunal element of Late Jurassic East African theropod faunas. One bone furthermore shares derived characters with the holotype of the poorly known Middle Jurassic Australian theropod *Ozraptor* and allows the identification of the latter as the oldest known abelisauroid, thus indicating an early divergence of ceratosaurids and abelisauroids within ceratosaurs. Abelisauroids might have originated in Gondwana and represent important faunal elements of Cretaceous Gondwanan theropod faunas in general.

Keywords: Jurassic, Gondwana, Theropoda, diversity, biogeography.

1. Introduction

Our knowledge of theropod dinosaur faunas from Gondwana has rapidly improved in the past twenty years. The description of numerous new taxa and identification of new groups have greatly changed our understanding of Cretaceous theropod evolution and biogeography (e.g. Bonaparte, 1985, 1991a, 1996; Sereno *et al.* 1994, 1996, 1998; Coria & Salgado, 1995; Novas, 1996, 1997; Sampson *et al.* 1998; Sampson, Carrano & Forster, 2001). Whereas Late Cretaceous Laurasian theropod faunas are dominated by coelurosaurs (tyrannosaurids, dromaeosaurids, ornithomimosaurids, oviraptorosaurs, therizinosaurids, etc.), Cretaceous theropod communities from the Southern Hemisphere are now known to consist of a mixture of a diverse assemblage of highly derived basal theropods (abelisaurids), several groups of basal tetanurans, and rare coelurosaurs (e.g. Rauhut, 1995, 1999; Bonaparte, 1996; Sereno *et al.* 1996, 1998; Novas, 1997). Unfortunately, however, the origin of the Cretaceous theropod faunas in the Southern Hemisphere is still poorly understood, mainly due to the poor Jurassic dinosaur record from Gondwana.

The German Tendaguru expeditions from 1909 to 1913 still represent the greatest effort to unravel the Late Jurassic history of dinosaurs in Africa and they yielded the most diverse dinosaur faunas from the Jurassic of the Southern Hemisphere (Maier, 2003).

Whereas the expeditions resulted in the discovery of thousands of specimens of sauropods, stegosaurs and ornithomimids, theropods are rather poorly represented (Janensch, 1914; Zils *et al.* 1995). Apart from the partial skeleton of *Elaphrosaurus* (Janensch, 1920, 1925, 1929), only isolated elements have been found, and theropod diversity and faunal composition in the Tendaguru beds is still poorly known, despite the fact that several taxa have been named on the basis of this material (Janensch, 1920, 1925).

Elaphrosaurus bambergi Janensch, 1920 was considered a coelurosaur by Janensch (1925) and later referred to the Ornithomimidae by Nopcsa (1928). This view was widely accepted until the early 1990s (e.g. Russell, 1972; Russell, Béland & McIntosh, 1980; Galton, 1982; Barsbold & Osmólska, 1990; Rich & Vickers-Rich, 1994), when the discoveries of abelisaurids in South America and more rigorous phylogenetic analyses led to the recognition of this taxon as a basal ceratosaurian and probably abelisaurian theropod (Holtz, 1994, 2000; Rauhut, 1998, 2003a). Janensch (1925) furthermore described three isolated small theropod tibiae from the Tendaguru beds without formal specific designation as ‘Coelurosaurier A’, ‘Coelurosaurier B’ and ‘Coelurosaurier C’. Janensch used the term ‘coelurosaur’ in the traditional sense to denominate small theropod dinosaurs, and the meagre small theropod material from Tendaguru is of great potential interest for understanding the origin, interrelationships and biogeography of small Gondwanan theropods in the Late Jurassic and Cretaceous.

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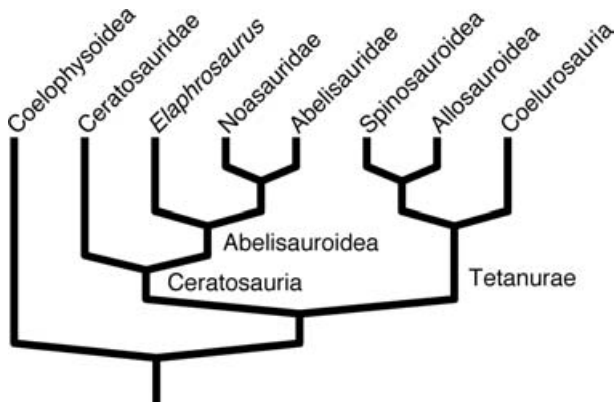


Figure 1. Generalized cladogram demonstrating the relationships of the taxa mentioned in the text. Based on Rauhut (2003a) and Wilson *et al.* (2003).

The purpose of the present paper is to re-evaluate the small theropod material from Tendaguru in the light of current understanding of theropod systematics.

2. Materials and methods

Only the post-cranial elements will be taken into account here; the more abundant tooth material from Tendaguru will be reviewed in a separate work (Rauhut & Heinrich, unpub. data). Apart from the partial skeleton of *Elaphrosaurus*, only a few skeletal elements of small theropod dinosaurs are present in the material from Tendaguru. Among this material, the tibiae originally described by Janensch (1925) are the most informative elements; the rest of the material consists of a poorly preserved distal end of a left ischium, two fragmentary fibulae, and several rib fragments. Most of the material is derived from the Middle Saurian Bed and is thus of probable late Kimmeridgian age (Aberhan *et al.* 2002), but a few elements, most notably the tibia MB.R.1751 and the distal end of an ischium, MB.R.1756, are from the Upper Saurian Beds and thus of latest Tithonian to Berriasian age (Aberhan *et al.* 2002). Comments on other small theropod material from the Southern Hemisphere are based on personal observations and published accounts. The phylogenetic position of the theropod remains is evaluated on the basis of published analyses of theropod interrelationships (Fig. 1; e.g. Sereno, 1999; Holtz, 2000; Rauhut, 2003a) and comparisons with other taxa of known phylogenetic position. (MB: Museum für Naturkunde, Humboldt-Universität zu Berlin, Germany.)

3. 'Coelurosaur' material from Tendaguru

In the following, the three small theropod tibiae from Tendaguru will be evaluated, because this is the material on which Janensch (1925) based his 'Coelurosaurier A,

Table 1. Measurements (in mm) of the small theropod tibiae from the Late Jurassic of Tendaguru

	Length	Proximal width	Proximal depth	Distal width	Distal depth
MB.R.1763 (‘Coelurosaurier A’)	163	17	30	25	11
MB.R.1750 (‘Coelurosaurier B’)	209*	–	–	29	12
MB.R.1751 (‘Coelurosaurier C’)	255	25	46	35	15

Width refers to transverse width, depth refers to anteroposterior width.

* Length as preserved.

B, and C’. Only very brief comments on the other small theropod material will be added.

3.a. ‘Coelurosaurier A’

3.a.1. Description

This taxon is represented by an isolated right tibia (MB.R.1763; Figs 2, 3) from the stegosaur locality ‘St’ (Janensch, 1925). The element is 161 mm long and slender (for detailed measurements see Table 1). The shaft is slightly flexed, so that the lateral side is convex and the medial side concave. The cnemial crest is only moderately expanded, considerably higher proximodistally than long anteroposteriorly, and anteriorly and slightly proximally directed. It arises out of the anteromedial side of the tibial shaft, where it continues distally as a well-developed ridge for the proximal two-thirds of the bone. Proximally, the cnemial crest turns slightly laterally. The impression of this turn is pronounced by the presence of an oblique ridge on the lateral side of the anterior end of the cnemial crest. The medial condyle of the proximal articular end forms a crest medially that is continuous with the cnemial crest. The articular facet extends from this crest laterally onto the flat proximal surface of the fibular condyle. The fibular condyle consists of a larger, subspherical posterior condyle and a smaller, triangular anterior part and is offset from the cnemial crest anteriorly by a broad, U-shaped incision (Fig. 3a). It is considerably shorter than the medial condyle of the proximal end posteriorly, and is separated from the latter by a small, V-shaped gap. The medial condyle has a small, triangular, posteriorly pointing process. A small fibular crest was obviously present on the anterolateral side of the proximal shaft, but is largely eroded away. It was proximally placed, ending only 40 mm below the proximal end, short (*c.* 21 mm), and slightly posteroproximally inclined. The crest is offset from the proximal end, but connected with the anterior end of the fibular condyle by a low, rounded edge. Distally from the fibular crest, a narrow, slightly concave facet runs over the anterolateral surface of the shaft distally and narrows towards its distal end. The shaft is triangular in outline in its central part, with a flat



Figure 2. Isolated right tibia of a basal tetanuran theropod from the Late Jurassic of Tendaguru, Tanzania (MB.R.1763; 'Coelurosaurier A' of Janensch, 1925). (a) Anterior view (stereopair). (b) Medial view (stereopair). (c) Posterior view (stereopair). (d) Lateral view (stereopair). Scale bar is 50 mm.



Figure 3. Isolated right tibia of a basal tetanuran theropod from the Late Jurassic of Tendaguru, Tanzania (MB.R.1763; 'Coelurosaurier A' of Janensch, 1925). (a) Proximal view. (b) Distal view. Scale bar is 10 mm.

posterior surface that is offset from the slightly convex anterolateral side by a pronounced edge, but curves more smoothly into the convex medial side. Distally, the shaft becomes anteroposteriorly flattened. The distal articular end is triangular in outline, with a higher medial part and a long, slightly posteriorly flexed lateral part (Fig. 3b). The lateral malleolus extends slightly further distally than the medial and is gently convex transversely distally. The medial malleolus is flattened distally. On the anterior side, an almost vertical step subdivides the proximal part of the distal expansion into two subequal sides and sharply flexes medially distally. This step represents the proximomedial bracing for the ascending process of the astragalus and thus indicates that this process was restricted to the lateral half of the astragalus. On the anterior side of the lateral malleolus,

a flat, slightly anterolaterally directed area indicates the connection with the distal end of the fibula.

3.a.2. Phylogenetic position

This tibia differs considerably from those of basal theropods, such as coelophysids (Raath, 1969; Rowe, 1989) and *Dilophosaurus* (Welles, 1984) in that the fibular condyle is offset from the cnemial crest by an U-shaped incision and reduced posteriorly, and the distal end is broadly triangular in outline, all synapomorphies that it shares with more derived theropods. It lacks the ceratosaurian synapomorphy of a hypertrophied cnemial crest (e.g. Janensch, 1925; Bonaparte, Novas & Coria, 1990; Carrano, Sampson & Forster, 2002) and shares the tetanuran synapomorphy of a fibular crest that is clearly offset from the proximal end of the bone (Rauhut, 2003a). This indicates that this element represents a member of the Tetanurae. The step on the anterior side of the distal end might be another tetanuran synapomorphy, since it is absent in basal theropods and small ceratosaurs, such as *Elaphrosaurus* (Janensch, 1925) and *Masiakasaurus* (Carrano, Sampson & Forster, 2002). However, this step probably represents the reduced anterolateral part of the distal tibia of more basal theropods, and the situation in basal ceratosaurs and abelisauroids is unclear due to fusion of the tibia with the proximal tarsals in these animals.

Within tetanurans, MB.R.1763 most probably represents a basal form, as indicated by the short and very proximally placed fibular crest, which is furthermore connected to the proximal end by a low, rounded ridge. This ridge might represent a remainder of the low crest that connects the fibular crest with the proximal end in basal theropods. An important difference from coelurosaurs is indicated by the step on the anterior side of the distal tibia. In all coelurosaurs, with the possible exception of the most basal forms (Rauhut & Xu, in press), the ascending process of the astragalus arises out of the entire breadth of the bone and covers the entire anterior surface of the distal tibia. The step in the tibia of 'Coelurosaurier A' indicates that it was restricted to the lateral half of the astragalus body, as in non-coelurosaurian theropods. Thus, MB.R.1763 represents a basal tetanuran, but most probably not a coelurosaur (*sensu* Gauthier, 1986), unless it was one of the most basal representatives of this clade.

3.b. 'Coelurosaurier B' and 'C'

Janensch (1925, pp. 52–3) described a partial tibia, also from the stegosaur locality 'St' in the Middle Saurian beds as 'Coelurosaurier B' (MB.R.1750; Figs 4e–h, 5c, d) and a complete, slightly larger element from the Upper Saurian beds of the locality 'H' as 'Coelurosaurier C' (MB.R.1751; Figs 4a–d, 5a, b). Janensch (1925, p. 53) noted several slight differences, most notably that there is a sharp ridge extending proximally from the lateral malleolus on the lateral side in MB.R.1750. Other differences noted by Janensch, such as the more distally expanded lateral malleolus in MB.R.1750, and the slightly narrower facet for the ascending process of the astragalus and broader lateral facet for the contact with the fibula in MB.R.1751, might be due to differences in preservation or individual variation. Apart from these differences, MB.R.1750 was obviously not much shorter than MB.R.1751, but is considerably more slender. Whether these slight differences represent individual, sexual or taxonomic differences cannot be determined on the basis of the material available, but the two tibiae certainly represent closely related taxa and can thus be treated together here.

3.b.1. Description

The complete tibia MB.R.1751 ('Coelurosaurier C') is 257 mm long, whereas MB.R.1750 ('Coelurosaurier B') measures 209 mm as preserved, with an estimated 35–45 mm missing (for further measurements see Table 1). The shaft of MB.R.1751 is slightly flexed, so that it is convex laterally and concave medially, whereas the shaft of MB.R.1750 seems to be straight. The cnemial crest of MB.R.1751 ('Coelurosaurier C') is more strongly developed than in MB.R.1763 ('Coelurosaurier A'), but seemingly less so than in

most ceratosaurs and basal tetanurans, although its exact extent cannot be determined due to erosion at the anterior end. The cnemial crest seems to be mainly anteriorly and very slightly laterally, and not or only very slightly proximally, directed. As in MB.R.1763 ('Coelurosaurier A'), there is a small, oblique ridge on the lateral side of the anterior expansion, but the cnemial crest is less clearly offset from the fibular condyle. The latter is damaged laterally, but seems to have been rectangular in outline and was offset from the medial condyle posteriorly by a wide, U-shaped intercondylar groove (Fig. 5a). The articular surface extends further proximally towards the medial margin of the proximal end, as in MB.R.1763 ('Coelurosaurier A'). Posteriorly, the medial condyle is rounded and lacks the small triangular process seen in MB.R.1763. A well-developed fibular crest was present, but is damaged in both specimens. It was proximally placed and connected to the anterior end of the fibular condyle by a low but sharply defined crest. In contrast to MB.R.1763 ('Coelurosaurier A'), there is no distally extended ridge below the cnemial crest on the anteromedial side in MB.R.1750 and 1751. The anterior side is flattened, resulting in the shaft being wider transversely than deep anteroposteriorly over most of its length. The posterolateral and posteromedial sides smoothly blend into each other, so that the shaft cross-section is semi-oval. At the lateral margin of the anterior side, a narrow flat to slightly concave area extends over most of the length of the shaft below the crista fibularis and indicates the attachment of the fibular shaft. The distal end is strongly flattened anteroposteriorly and expanded transversely, more to the lateral than to the medial side. The distal articular surface is broadly triangular in outline (Figs 5b, c). The anterior side of the distal end is flattened, with a broad, rectangular, vertical ridge that is confluent with the medial margin of the bone forming the medial border of the anterior facet for the ascending process of the astragalus. In the better preserved distal end of MB.R.1750 ('Coelurosaurier B'), a slightly depressed facet for the ascending process of the astragalus is present on the anterior surface (Fig. 5d). This facet is trapezoidal in outline, higher than wide and extends slightly further proximally on the lateral than on the medial side. The facet is subdivided by a low, rounded, vertical medial ridge. A very similar facet seems to have been present in MB.R.1751 ('Coelurosaurier C'), but has been largely obliterated by erosion. Lateral from the facet, the anterior side flexes slightly laterally for the flat surface that indicates the distal contact with the fibula. The lateral malleolus extends further distally than the medial and is distally convex. On the distal surface of the medial malleolus, a broad, well-developed groove extends from the mid-section of the distal articular surface posteromedially. This groove is present in both specimens, but better developed in MB.R.1750 ('Coelurosaurier B'). As noted above, a



Figure 4. Isolated tibiae of small abelisauroids from the Late Jurassic of Tendaguru, Tanzania (top row: MB.R.1751; 'Coelurosaurier C' of Janensch, 1925; bottom row: MB.R.1750; 'Coelurosaurier B' of Janensch, 1925). (a) Anterior view (stereopair). (b) Lateral view (stereopair). (c) Posterior view (stereopair). (d) Medial view (stereopair). (e) Anterior view (stereopair). (f) Lateral view (stereopair). (g) Posterior view (stereopair). (h) Medial view (stereopair). Scale bars are 50 mm.



Figure 5. Isolated tibiae of small abelisauroids from the Late Jurassic of Tendaguru, Tanzania. (a, b) MB.R.1751 ('Coelurosaurier C' of Janensch, 1925). (a) Proximal view. (b) Distal view. (c, d) MB.R.1750 ('Coelurosaurier B' of Janensch, 1925). (c) Distal view (stereopair, slightly exaggerated to better illustrate morphology). (d) Anterior view of the distal end, illustrating facet for the ascending process of the astragalus (stereopair; exaggerated to better illustrate morphology). Scale bars are 10 mm.

sharply defined ridge extends from the lateral malleolus proximally and disappears some 11 mm proximal of the facet for the ascending process of the astragalus.

3.b.2. Phylogenetic position

These two tibiae differ from those of basal theropods, such as coelophysids and *Dilophosaurus*, in that the distal end is anteroposteriorly compressed and triangular in outline. However, they differ from tetanurans in that the cnemial crest is less clearly offset from the fibular condyle and the fibular crest is connected to the proximal end. Within non-tetanuran theropods, an anteroposteriorly flattened distal end of the tibia with a flat anterior surface is only found in small ceratosaurs more derived than *Ceratopsaurus*, such as *Velocisaurus* (Bonaparte, 1991b) and *Masiakasaurus* (Carrano, Sampson & Forster, 2002). In more basal theropods, and theropod outgroups, the distal end of the tibia is round to oval in cross-section and the lateral end of the anterior side is incised for the ascending process of the astragalus. The situation in most abelisauroids is unclear, since no distal tibiae are known for *Abelisaurus*, *Carnotaurus* or *Majungatholus*, and the tibia is fused with the proximal tarsals in *Xenotarsosaurus* (Martínez *et al.* 1986). However, the anterior distal side of the tibia seems to have a pronounced oblique step in the abelisauroid *Pycnonemosaurus* (Kellner & Campos, 2002), whereas in *Rajasaurus*, the anterior side of the distal tibia seems to be flat and has a depressed facet for the ascending process of the astragalus (Wilson *et al.* 2003), similar to that seen in MB.R.1750 ('Coelurosaurier B'). Thus, the flat anterior side of the distal tibia might be a synapomorphy of all abelisauroids, or of a possibly monophyletic clade of mainly small

abelisaurs, the noasaurids (Coria & Salgado, 2000; Carrano, Sampson & Forster, 2002; Wilson *et al.* 2003), that is convergently present in *Rajasaurus*. The material from Tendaguru shares another apomorphic feature with abelisaurs, including at least some noasaurids. This is the broad medial vertical ridge on the anterior side of the distal end, which seems to be present in *Velocisaurus* (Bonaparte, 1991b), *Masiakasaurus* (Carrano, Sampson & Forster, 2002), and the medium-sized, probable abelisauroid *Quilmesaurus* (Coria, 2001). Such a ridge is absent in all other theropods, with the possible exception of *Chilantaisaurus* and spinosaurids (Rauhut, 2003a). The presence of both of these characters, in combination with the lack of tetanuran synapomorphies, in the two elements from Tendaguru indicates that they represent small abelisauroids (*sensu* Rauhut, 2003a).

3.c. Other small theropod material from Tendaguru

The other small theropod material from Tendaguru is very fragmentary and rather uninformative. The distal end of a left ischium MB.R.1756 from the Upper Saurian Beds shows that the distal ischium was expanded to form a moderate ischial 'boot' (Fig. 5). Within coelurosaurs, ischial boots are known only in a few ornithomimosaurids (Barsbold & Osmólska, 1990), but very similar moderately expanded boots are present in all abelisaurs for which pelvic material is known (Janensch, 1925; Bonaparte, Novas & Coria, 1990; Coria, Chiappe & Dingus, 2002). This specimen comes from the same locality as the tibia MB.R.1751 and fits well in size and preservation with the latter and might thus represent the same taxon.



Figure 6. Distal end of a left ischium of an abelisauroid theropod from the Late Jurassic of Tendaguru, Tanzania; MB.R.1756. Lateral view (stereopair). Scale bar is 50 mm.

4. Discussion

4.a. Juveniles or small taxa?

To evaluate the significance of the small theropod remains from Tendaguru, it must first be determined if the material represents truly small taxa or juveniles of larger species. Janensch (1920, 1925) described several taxa of large theropod, all based on very fragmentary material. Although the material is not diagnostic, and these species have to be considered *nomina dubia* (Rauhut, unpub. data), it can be noted that the large theropod fauna from Tendaguru includes at least one species of ceratosaur (Rowe & Gauthier, 1990; Madsen & Welles, 2000; Carrano, Sampson & Forster, 2002) and two or more taxa of basal tetanuran (Janensch, 1925; Molnar, Kurzanov & Dong, 1990; pers. obs.). Furthermore, *Elaphrosaurus bambergi* represents a species of medium-sized abelisauroid (Janensch, 1920, 1925; Holtz, 1994, 2000; Rauhut, 1998, 2003a).

The basal tetanuran tibia MB.R.1763 ('Coelurosaurier A') differs significantly from the type tibia of '*Allosaurus tendagurensis*' (Janensch, 1925) and a slightly smaller and more slender tibia of large basal tetanurans (Janensch, 1925, pl. 6, Fig. 6) in the much less developed cnemial crest, the different shape of the fibular condyle and the cross-section of the proximal half of the shaft. The finished appearance of the articular ends furthermore indicates that this element is at least not derived from a hatchling or young juvenile and, given its small size, represents a rather small taxon. Thus, this specimen clearly indicates the presence of another, smaller taxon of basal tetanuran.

Likewise, MB.R.1751 ('Coelurosaurier C') differs from the tibiae of a large ceratosaur (MB.37 and MB.69; Janensch, 1925, pl. 6, Fig. 5) in the size and shape of the cnemial crest and the more anteroposteriorly com-

Table 2. Overview of different theropod taxa represented by comparable postcranial material from the Late Jurassic of Tendaguru

Specimen number	Material	Identification in Janensch (1925)	Identification here
MB.R.1763	Tibia	Coelurosaurier A	Basal tetanuran
MB.R.1750	Tibia	Coelurosaurier B	Abelisauroid
MB.R.1751	Tibia	Coelurosaurier C	Abelisauroid*
MB.Tibia 67	Tibia	<i>Allosaurus(?) tendagurensis</i>	Basal tetanuran
MB.TL 42	Tibia	Theropoda	Basal tetanuran
MB.69 & 37	Tibiae	? <i>Ceratosaurus roechlingi</i>	Basal ceratosaur
MB.dd	Partial skeleton	<i>Elaphrosaurus bambergi</i>	Valid species; basal abelisauroid

* Possibly the same taxon as MB.R.1750.

pressed distal end. The tibia of *Elaphrosaurus* differs significantly in the entire morphology of the proximal end (Janensch, 1925; Galton, 1982; Chure, 2001). The distal end of MB.R.1750 ('Coelurosaurier B') differs from the large ceratosaurian tibiae in the stronger anteroposterior compression and from both the large ceratosaur and *Elaphrosaurus* in the presence of a depressed, subdivided facet for the ascending process of the astragalus. Thus, these two elements also indicate the presence of at least one further taxon of ceratosaur in the theropod fauna of Tendaguru, apart from *Elaphrosaurus* and the large taxon represented by MB.37 and 69. It should be noted again that these elements come from different levels and are not contemporaneous, and thus they add only one additional taxon to their respective faunas, regardless of whether MB.R.1750 and 1751 represent the same, or two different taxa.

The question of whether these elements represent juvenile or adult theropods is more difficult to answer, partially due to the rather poor preservation of the more complete element MB.R.1751 ('Coelurosaurier C'). However, the distal end of MB.R.1750 ('Coelurosaurier B') shows well-finished bone surfaces and fine details of the articular end, indicating that again it is not a very young individual and thus probably represents a rather small taxon. The fact that neither MB.R.1750 nor MB.R.1751 has the proximal tarsals fused to the tibia, as is the case in other abelisaurs (Martínez *et al.* 1986; Carrano, Sampson & Forster, 2002), might indicate, however, that these elements represent subadult rather than fully adult individuals.

For a summary of theropod taxa from Tendaguru represented by post-cranial remains, see Table 2.

4.b. Theropod faunal composition

With the identification of at least one of small basal tetanuran taxon and one or more small abelisauroid taxa, the theropod fauna of Tendaguru seems to have a rather different taxonomic composition from that of the Late

Jurassic of North America and Europe. In the fauna of the Morrison Formation, small theropods are mainly represented by coelurosaurs, such as *Coelurus* and *Ornitholestes* (Marsh, 1879; Osborn, 1903; Ostrom, 1980), tyrannosauroids (Madsen, 1974; Foster & Chure, 2000), and maniraptorans (Jensen & Padian, 1989; Chure, 1994, 1995). Likewise, Late Jurassic small theropod faunas from Europe include the basal coelurosaur *Compsognathus* (Wagner, 1861; Bidar, Demay & Thomel, 1972; Zinke, 1998), tyrannosaurs (Zinke, 1998; Rauhut, 2000, 2003b), and a variety of maniraptorans (Zinke, 1998; Rauhut, 2000). The only ceratosaurs identified from the Late Jurassic of the Northern Hemisphere so far are the medium-sized basal taxon *Ceratosaurus* (Marsh, 1884; Madsen & Welles, 2000; Antunes & Mateus, 2003) and a close relative of the medium-sized basal abelisauroid *Elaphrosaurus* (Galton, 1982; Chure, 2001). However, these taxa, especially the abelisauroid, seem to be very rare elements of the fauna.

The revision of small theropod skeletal elements from the Late Jurassic of Tendaguru does not reveal any evidence for the presence of coelurosaurs (*sensu* Gauthier, 1986) in the Late Jurassic of East Africa. With the presence of *Elaphrosaurus*, a probable close relative of *Ceratosaurus* (Rowe & Gauthier, 1990; Madsen & Welles, 2000), and at least one other, small ceratosaur, the medium-sized to small theropod fauna from the Late Jurassic of East Africa seems to be more dominated by ceratosaurs than by coelurosaurs. This is in general accordance with the abundance of ceratosaurs of all sizes in Cretaceous theropod faunas of the Southern Hemisphere and may indicate that these faunal associations might already have been established by the end of Jurassic time. However, more fossil evidence from the Late Jurassic of Gondwana is needed to test this hypothesis.

4.c. Evolutionary and biogeographic aspects of the Tendaguru theropods

Apart from their addition to the theropod fauna of the Late Jurassic of East Africa, the abelisauroid remains from Tendaguru are also of significance for our understanding of small abelisauroid origin and evolution. The small tibia MB.R.1750 ('Coelurosaurier B') shares the derived character of a depressed, subdivided facet for the ascending process of the astragalus with the holotype of the Middle Jurassic Australian theropod *Ozraptor* (Fig. 7; Long & Molnar, 1998). This allows identification of the otherwise very poorly preserved holotype of *Ozraptor* as the oldest known representative of the Abelisauroidea. The presence of this clade already in the Bajocian of Australia not only indicates an early divergence of ceratosaurs from the lineage leading towards tetanurans, which is in general accordance with predictions on the basis of phylogenetic analyses (e.g. Sereno, 1999; Holtz,

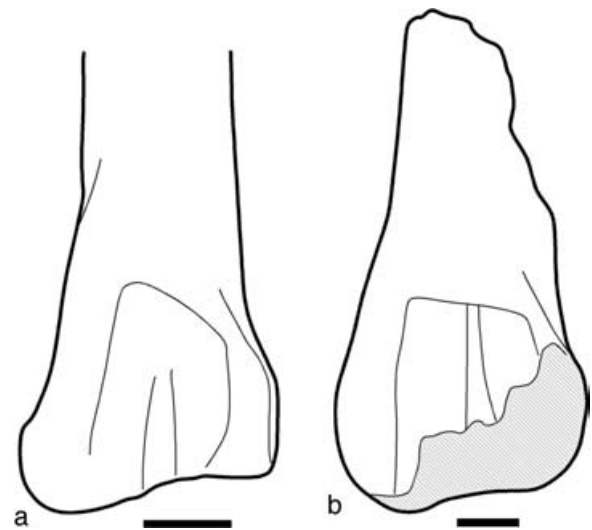


Figure 7. Comparison of the anterior side of the distal end of MB.R.1750 (a) and the type specimen of the Middle Jurassic Australian theropod *Ozraptor* (b). Not to scale; left tibia of *Ozraptor* reversed for comparison. Scale bars are 10 mm.

1994; Rauhut, 2003a), but also an early divergence of ceratosaurs and abelisauroids within ceratosaurs. Indeed, if future analyses confirm the presence of a monophyletic clade of small abelisauroids that forms the sister group to abelisauroids (Coria & Salgado, 2000; Carrano, Sampson & Forster, 2002; Wilson *et al.* 2003), and the material from Tendaguru can be shown to belong to this clade, a Jurassic origin of abelisauroids must be postulated. This is in general accordance with recent evidence that suggests a pre-Late Cretaceous radiation of abelisauroids (Lamanna, Martínez & Smith, 2002; Rauhut *et al.* 2003), in contrast to a diversification of this clade after the separation of Africa and South America, as originally hypothesized by Sampson *et al.* (1998).

So far, ceratosaurs are only known from the Late Jurassic of North America (Marsh, 1884; Madsen & Welles, 2000), Europe (Antunes & Mateus, 2003) and East Africa (Janensch, 1925; Rowe & Gauthier, 1990; Madsen & Welles, 2000), and the Early Cretaceous of Patagonia (Rauhut, 2004), whereas abelisauroids are well documented from the Late Jurassic of Africa (Holtz, 1994; Rauhut, 1998, 2003a; this work) and the Cretaceous of South America (e.g. Bonaparte, 1991a,b, 1996; Coria & Salgado, 2000; Coria, 2001; Coria, Chiappe & Dingus, 2002; Kellner & Campos, 2002), India (Molnar, 1990; Chatterjee & Rudra, 1996; Wilson *et al.* 2003), Madagascar (Sampson *et al.* 1998; Sampson, Carrano & Forster, 2001), and Europe (Buffetaut, Mechin & Mechin-Salessy, 1988; Accarie *et al.* 1995). The abelisauroid record from the Cretaceous of Africa is still rather poor, although some fragmentary material has been reported recently (Russell, 1996), and fragmentary material described by Stromer (1934) as cf. *Elaphrosaurus bambergi* and some remains

described by Stromer & Weiler (1930) might also pertain to this clade (Carrano, Sampson & Forster, 2002). Furthermore, Wilson *et al.* (2003) consider the putative coelurosaur *Deltadromeus* (Serenó *et al.* 1996) to be an abelisauroid, and recently described material from the Lower Cretaceous and lowermost Upper Cretaceous of Niger (Serenó, Wilson & Conrad, 2004) greatly contributes to our knowledge of African abelisaurs. Cretaceous theropods from Australia are still poorly known, and only the genus *Rapator*, known from a single metacarpal (Huene, 1932), has been suggested to represent an abelisauroid (Molnar, 1992). However, the small Early Cretaceous Australian theropod *Kakuru* has a flattened anterior side of the distal end of the tibia with a medial vertical ridge (Molnar & Pledge, 1980), both characters that might be synapomorphies of small abelisauroids (see above). Thus, abelisauroids seem to have been present in the Cretaceous of Australia as well.

Thus, abelisauroids had a long evolutionary history that reaches back to at least the early Middle Jurassic period. However, the early history of this group is still poorly known, mainly due to the poor late Early and Middle Jurassic dinosaur fossil record (see, e.g. Weishampel, 1990). Furthermore, current evidence suggests that the origin of abelisauroids might be found in Gondwana, for which the theropod fossil record is poorer still than for the Northern Hemisphere (Rauhut, 2003a). By Late Jurassic times, ceratosaurs, including abelisauroids, had diversified and represented an important faunal element of Gondwanan theropod faunas. By that time, the evolutionary pathways of the non-avian theropod faunas from the Northern and Southern hemispheres had probably already separated, with coelurosaurs of all sizes becoming the dominant theropods in the north, whereas large and small abelisauroids seem to have been important faunal elements in the Cretaceous theropod faunas of all southern continents. As noted by Buffetaut (1989) and Le Loeuff (1991), the European Cretaceous theropod fauna seems to have been a mixture of more typical Gondwanan and Laurasian elements.

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