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# Oldest camarasauromorph sauropod (Dinosauria) discovered in the Middle Jurassic (Bajocian) of the Khadir Island, Kachchh, western India

MARKUS MOSER, Stuttgart; UMESH B. MATHUR, Jaipur; FRANZ T. FÜRSICH, Würzburg; DHIRENDRA K. PANDEY, Jaipur & NEERA MATHUR, Jaipur

with 11 figures

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**Abstract:** Fragmentary isolated remains of large (up to 20 m or more) sauropods from the Middle Jurassic (Bajocian) Khadir Formation of Khadir Island (Kachchh, W India) are described and compared in detail. Three of the bone fragments (a metacarpal, a first pedal claw and a fibula) can be assigned with confidence to the Camarasauromorpha and represent the oldest known record of that derived dinosaur group. The new finds from western India further close a temporal and geographical gap in our knowledge of sauropods and contribute to understanding their early phylogeny.

**Keywords:** Camarasauromorpha • Sauropoda • Dinosauria • morphology • phylogeny • Middle Jurassic

**Kurzfassung:** Isolierte Überreste eines großen (bis zu 20 m oder mehr langen) Sauropoden werden aus der mitteljurassischen (Bajocium) Khadir Formation auf Khadir Island (Kachchh, W Indien) beschrieben und detailliert verglichen. Drei der Knochenfragmente (ein Metacarpale, eine erste Fußklaue und eine Fibula) können mit Sicherheit einem Vertreter der Camarasauromorpha zugeordnet werden und repräsentieren damit den ältesten Nachweis dieser abgeleiteten Dinosaurier-Gruppe. Die neuen Funde aus dem westlichen Indien schließen eine zeitliche und geographische Lücke in unserer Kenntnis der Sauropoden und tragen zum Verständnis ihrer frühen Phylogenie bei.

**Schlüsselwörter:** Camarasauromorpha • Sauropoda • Dinosauria • Morphologie • Phylogenie • Mitteljura

## Introduction

Terrestrial faunas from the Middle Jurassic – dominated by dinosaurs – are poorly known worldwide compared to other Mesozoic epochs. The only diverse fauna so far known is from the Lower Shaximiao Formation and equivalents of China (DONG 1980; MARTIN-ROLLAND 1999; PENG & SHU 1999). Other Middle Jurassic localities in Argentina, China, England, France, Portugal, Madagascar, Morocco, Kirghizia, Australia and possibly USA have yielded only few specimens and few species (cf. WEISHAMPEL et al. 2004; GILLETTE 1996; ALIFANOV & AVERIANOV 2003).

The Indian record of dinosaurs (about two dozen named species; for recent summaries see KUTTY & SENGUPTA 1990; LOYAL et al. 1996; CHATTERJEE & RUDRA 1996; SAHNI 2003; WEISHAMPEL et al. 2004) includes abundant fossil bones and eggs of sauropods and also rare remains of prosauropods, theropods and (questionable) ornithischians. The bulk of these finds have been recovered from the uppermost Cretaceous Lameta Group since the second half of the 19$^{th}$ century (HUENE & MATLEY 1933; JAIN & BANDYOPADHYAY 1997; MATHUR & PANT 1986; MATHUR & SRIVASTAVA 1987; MOHABEY 1998; PRASAD 1989; BHATT 2003; WILSON et al. 2003). Bones from equivalent beds extend the

Addresses of the authors: Markus Moser, Staatliches Museum für Naturkunde Stuttgart, Museum am Löwentor, Rosenstein 1, 70191 Stuttgart, Germany; e-mail <moser.smns@naturkundemuseum-bw.de>. – Umesh B. Mathur and Dhirendra K. Pandey, Department of Geology, University of Rajasthan, Jaipur 302004, India; e-mail <ubmathur@sancharnet.in>; <dhirendrap@satyam.net.in>. – Franz T. Fürsich, Institut für Paläontologie der Universität Würzburg, 97070 Würzburg, Germany; e-mail <franz.fuersich@mail.uni-wuerzburg.de>. – Neera Mathur, Department of Zoology, University of Rajasthan, Jaipur 302004, India.

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record of this fauna to Pakistan (MALKANI et al. 2001) and Meghalaya (MISHRA & SEN 2001).

The only reasonably complete non-Late Cretaceous finds represent at least six individuals of the basal sauropod *Barapasaurus tagorei* JAIN et al., 1975 from the Lower Jurassic Kota Formation (JAIN et al. 1975, 1979; BANDYOPADHYAY et al. 2002; GILLETTE 2003). The same beds also yielded some remains of another sauropod (*Kotasaurus yamanpalliensis* YADAGIRI, 1988, 2001; YADAGIRI et al. 1979) and a thyreophoran ornithischian (NATH et al. 2002). The age of the Kota dinosaurs is not well established and may be even (?) Middle Jurassic (PRASAD & MANHAS 2002; GILLETTE 2003). All dinosaur remains from India are incomplete and their affinities have been doubted – much of the material remains unnamed and even undescribed. Nevertheless, the presence of dinosaurs is documented throughout the Mesozoic beds of India except for the Lower Cretaceous, and only rather recently from the Middle Jurassic.

Marine Middle Jurassic (Bajocian to Oxfordian) sediments and their fauna are well known from India, especially from Kachchh. However, little attention has been paid to the fluvial sediments, despite of the realization by BISWAS (1971, 1980) that from Mainland Kachchh to Pachchham Island in the north there is a marine to non-marine facies transition. Such facies change also occurs in an eastward direction from Pachchham Island towards Khadir Island (BISWAS 1971, 1980). Therefore, there are good chances of encountering fluvio-deltaic sediments containing dinosaur fossils and other freshwater and terrestrial faunal elements in the Middle Jurassic sediments of the islands in the Rann of Kachchh. Since these outcrops are situated in a semi-arid climatic belt, with good outcrop conditions and moderate rates of erosion during monsoonal rains, the chances of discovering more dinosaur localities are excellent. Furthermore, the interfingering of fossiliferous fluvial and marine facies provides a basis for biostratigraphical dating of the terrestrial faunas.

The first discovery of Middle Jurassic dinosaurs in India was reported from the Jaisalmer District in Rajasthan (W India) by MATHUR et al. (1985, incorrectly recorded as Upper Jurassic by WEISHAMPEL et al. 2004). These remains were originally thought to belong to the Kuldhar Oolite Member of the Jaisalmer Formation of Callovian age (PANDEY & FÜRSICH 1994). However, most probably the sedimentary sequence at the fossil locality belongs to the continental Lathi Formation of Bajocian or pre-Bajocian age. The skeletal elements from Jaisalmer include a few large bones and a large number of "flat bones" (? scutes) and were identified as dinosaurian on the basis of bone histology, structure and sedimentary facies. The presence of (?) scutes may indicate that these remains belong to a basal thyreophoran dinosaur, but they could also belong to armored sauropods or crocodylomorphs. Indeed, MATHUR et al. (1985: 61) noted also the presence of a crocodilian vertebra, but the large size of some osteoderms (15 cm across and 2 cm thick) is suggestive of a dinosaurian origin.

A second occurrence of Middle Jurassic dinosaur bones was reported by GHEVARIYA & SRIKARNI (1992: figs. 15A, C, G) from Pachchham Island, Kachchh. These bones occur in conglomerate horizons interbedded with siltstone and sandstone with occasional coral beds. Besides large bones, they identified teeth, osteoderms and claws. From the basal beds they identified *Cladophlebis, Otozamites* and poorly preserved cones and petrified wood. No details of the locality or a description of the dinosaurian fossils were given.

More recently, the early Middle Jurassic (?Aalenian to Bajocian) Dingy Hill member of the Kaladongar Formation (Fig. 1) of Kunwar Bet (a small island, also spelled as Kuar Bet) in the Rann of Kachchh has yielded a number of dinosaur fossil bones. The material comprises more than 12 vertebrae, limb elements and many other bone pieces that were found in February 1999 by SATYNARAYANA et al. (1999). In January 2000 these workers collected 80 more pieces from the same area, which were deposited at the Border Security Forces Headquarter in the area (pers. comm. to UBM).

Another recently discovered Middle Jurassic dinosaur occurrence in India is reported by JANA & DAS (2002) from Jumara, Kachchh Mainland, in Middle Callovian beds of the Chari Formation (overlying the Patcham Formation). According to these authors, the collected fragmentary bone is identifiable as a proximal half of a sauropod tibia, based on size, general morphology and thin sections of the bone.

In 1999, on January 10$^{th}$, two of the present authors (FTF and DKP) came across a number of fossil bones while measuring sections through the Middle Jurassic rocks of Khadir Island in the Rann of Kachchh, just 55 km east of Kunwar Bet, the locality of SATYNARAYANA et al. (1999). Time did not permit a more extensive search of the area or exploratory excavations. Of the twenty to thirty pieces encountered only nine were transported back to the laboratory. Initially the dinosaurian nature of these bones was determined by us (UBM and NM) by means of histology. In this paper, the nine skeletal elements from the new locality are described and their systematic affinities, as well as their phylogenetic significance, are discussed.

**Repository**: All the material is housed in the collections of the Palaeontological Laboratory, Department of Geology, University of Rajasthan, Jaipur and registered as RUC1999I 200 to 208.

**Abbreviations**:

| | |
|---|---|
| BSP | Bayerische Staatssammlung für Paläontologie und Geologie, München |
| MB | Museum für Naturkunde, Berlin |
| RUC | Palaeontological Laboratory, Department of Geology, University of Rajasthan, Jaipur |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart |

## Geological Setting

The dinosaur bones were found between the small island Cheriya Bet and Khadir Island, one of the islands NE of Kachchh Mainland (Fig. 2). There, next to the salt flats of the Great Rann of Kachchh, the Hadibhadang Shale member crops out on low, receeding slopes. The bones occur in variegated to dark red argillaceous silt, some horizons of which are full of diagenetically formed gypsum and with occasional thin intercalations of fine- to medium-grained crossbedded sandstone (Fig. 3). The argillaceous silt overlies whitish, medium-grained sandstone with large-scale trough-crossbeds. At the northern edge of Khadir Island, this sequence is followed by a 9 m thick, friable, coarse-grained sandstone with large-scale trough-crossbedding that becomes well cemented towards the top and forms a small cliff. The depositional environment is clearly that of a floodplain with fluvial channels. This is indicated by the variegated and red colours, the lack of fossils apart from the bones and wood remains, and the sharp erosional base of the sandstones. One of the bones, which clearly had been strongly eroded previous to deposition, was used by a small oyster as an attachment surface, thus indicating at least a short euryhaline interval and redeposition. Ten metres above the cliff-forming sandstone marly silt with abundant gastropods and bivalves (*Bakevellia, Eomiodon, Protocardia, Tancredia* and nerineids) is the first clear evidence of fully marine conditions in the section.

The position of the dinosaur bone horizon is more than 200 m below the top of the Patcham Formation, which corresponds to the top of the Bathonian. Moreover, the bone horizon lies approximately 150 m below a marker bed, the so-called Leptosphinctes Pebbly Rudstone (FÜRSICH et al. 2001) of the neighbouring Pachchham Island that contains the earliest ammonite from the Kachchh Basin, a Late Bajocian *Leptosphinctes*. This strongly favours an Early to Middle Bajocian age for the bones.

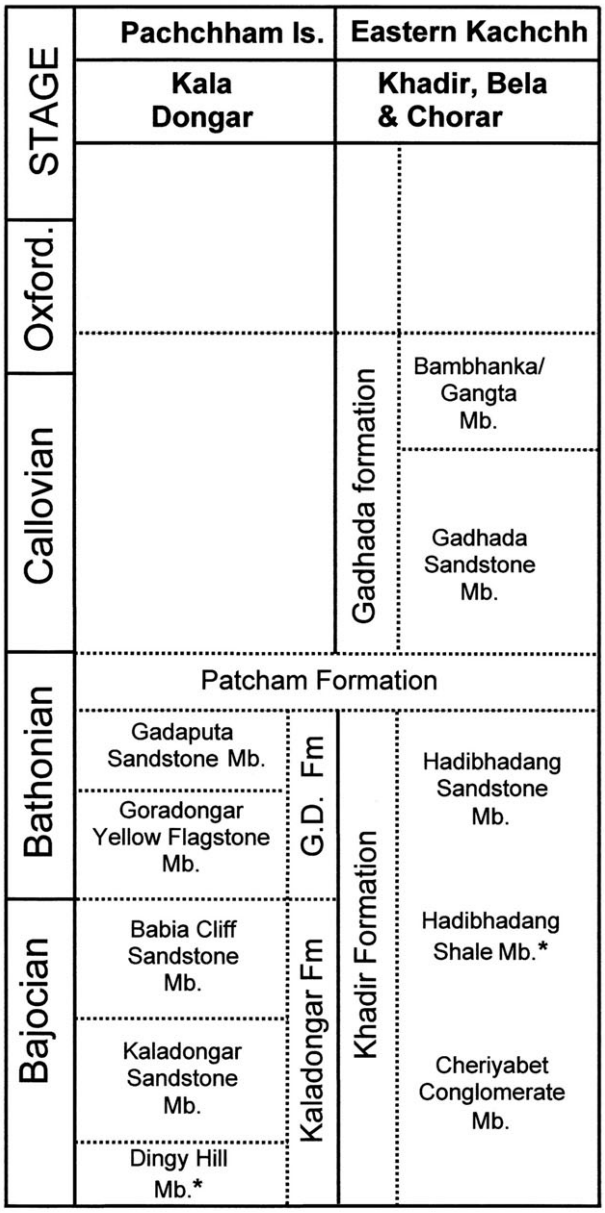



**Fig. 1.** Lithostratigraphic framework of Middle Jurassic rocks of Kachchh basin (W India), modified after BISWAS (1980).

## Systematic palaeontology

Dinosauria OWEN, 1842
(?) Sauropoda MARSH, 1878

**gen. et sp. indet.**

**Material**: Middle piece of a right rib (RUC1999I 201), fragment of a posterior caudal (RUC1999I 203), 2 proximal rib fragments (RUC1999I 204, 205), piece of spongiosa of a large long bone (RUC1999I 206), small fragment of the neural arch of a dorsal vertebra (RUC1999I 208). (Description below).
**Locality**: Southern margin of Cheriya Bet, 4 km N Gadhada, Khadir Island, in the Rann of Kachchh, about 95 km NNE of Bhuj (district headquarters of Kachchh) (Fig. 2). The bones were found weathered out from argillaceous silt and concentrated in a small gully, all within about 10 square metres.
**Horizon**: Hadibhadang Shale Member (Bajocian) of the Khadir Formation (Fig. 3). This member is roughly contemporaneous to the other Middle Jurassic dinosaur bearing beds of the Dingy Hill Member at Kunwar Bet (SATYANARAYANA et al. 1999) and probably the dinosaur beds of Jaisalmer (MATHUR et al. 1985) (Fig. 1).

Camarasauromorpha SALGADO, CORIA & CALVO, 1997
(= "Macronaria" WILSON & SERENO, 1998
= "Brachiosauria" UPCHURCH, 1998)

**gen. et sp. indet.**

**Comment**: Camarasauromorpha was proposed by SALGADO et al. (1997) explicitly as a node-based „clade including the most recent common ancestor of Camarasauridae and Titanosauriformes and all of its descend-

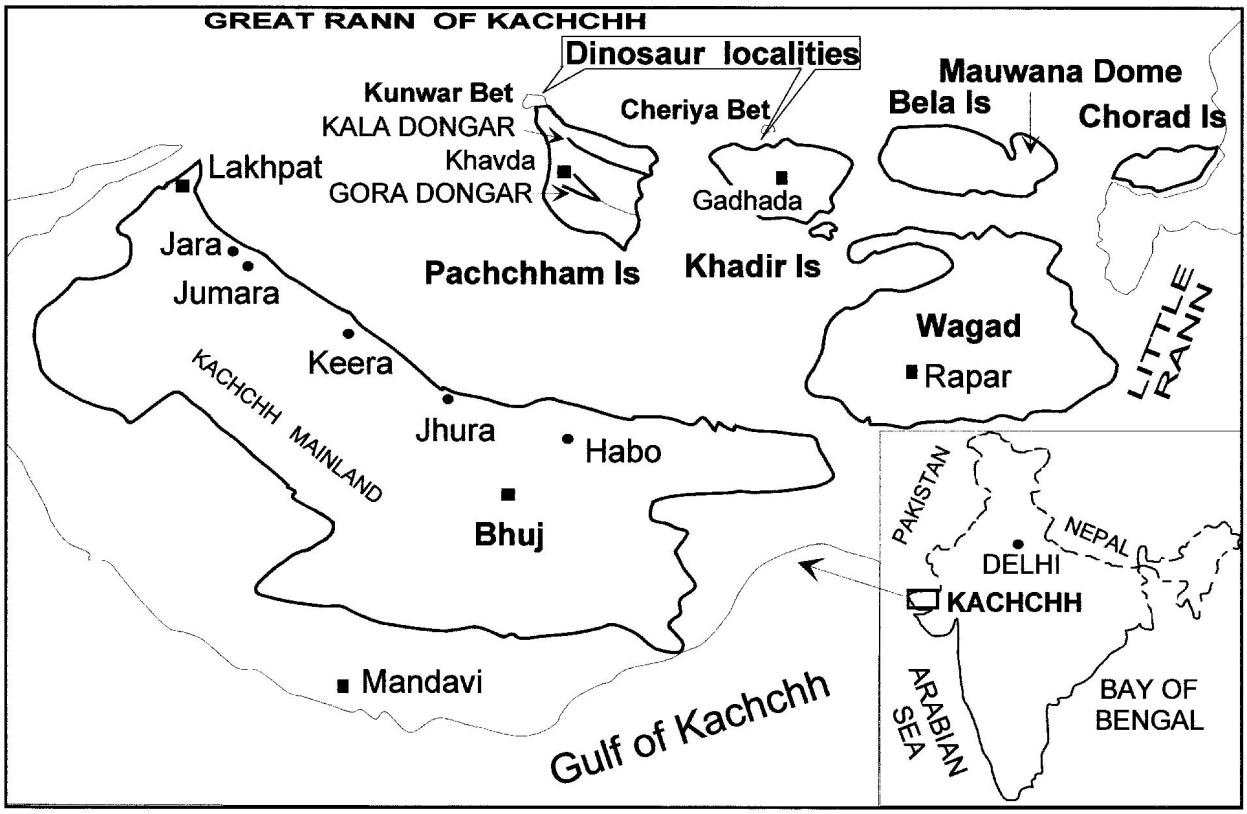



**Fig. 2.** Geographic map of Kachchh showing position of localities mentioned in the text.

ents" (contra UPCHURCH et al. 2004). "'Brachiosauria'" – in inverted commas – was proposed by UPCHURCH (1998) "as an informal name" for the same node. "Macronaria" was proposed by WILSON & SERENO (1998) as a "stem based clade", which is not a kind of valid taxon as no synapomorphies – unambiguously present in its basalmost member – could be cited in support. The characters listed by WILSON & SERENO (1998), WILSON (2002) or UPCHURCH et al. (2004) as synapomorphies thus characterize a taxon which is less inclusive than "Macronaria". Moreover, based on the actual content of taxa originally included, "Macronaria" has the same scope as Camarasauromorpha according to recent cladistic analysis of Sauropoda (WILSON 2002; UPCHURCH et al. 2004). The three neosauropod genera (*Atlasaurus*, *Bellusaurus* and *Jobaria*) closer to Camarasauromorpha than to Diplodocoidea now classified as the only non-camarasauromorph macronarians by UPCHURCH et al. (2004) were not considered by WILSON & SERENO (1998), and are neosauropods close to camarasauromorphs, which expresses the same phylogenetic placement.

**Material**: Distal end of a right metacarpal (RUC1999I 200), nearly complete right pedal claw (RUC1999I 202), proximal end of a left fibula (RUC1999I 207).
**Locality and horizon**: as above.

### Description and comparison

Axial skeleton

small fragment of the basal part of the neural arch of a dorsal vertebra (RUC1999I 208) (Fig. 4.8)

**Description**: The fragment is approximately 80 mm high and represents the basal (or ascending) part of a neural arch of a dorsal vertebra above the contact to the corpus and below the processes. Several subparallel laminae are present, but the fragment is too much eroded to provide significant information for comparison and identification of them. The presence of subvertical, subparallel laminae reaching from the processes far down to the corpus vertebrae is restricted to anterior dorsal vertebrae in sauropods, whereas other vertebrae have oblique to horizontal laminae in lateral view (BONAPARTE 1999; WILSON 1999).

anterior half of a posterior caudal corpus (RUC1999I 203)(Fig. 4.5)

**Description**: The caudal corpus is fractured obliquely approximately in the middle, only the anterior half is preserved. The anterior facies articularis is transversally 63 mm wide and vertically 52.5 mm thick, the lower half is transversally broader, the rim is bulging. The maximum depth in the center of the concave facies articularis

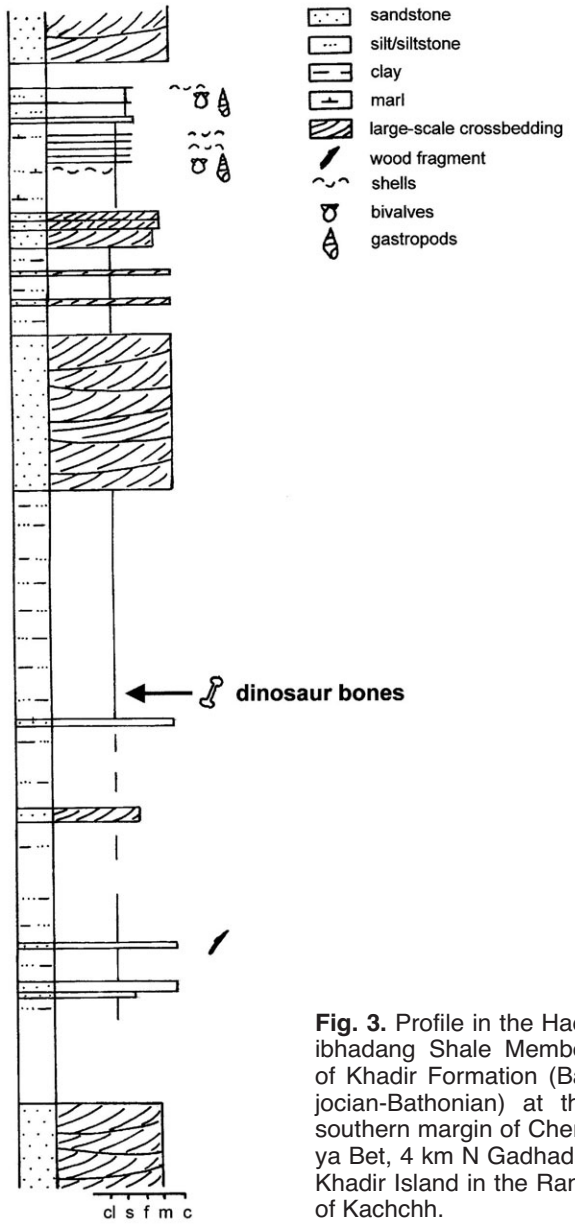



**Fig. 3.** Profile in the Hadibhadang Shale Member of Khadir Formation (Bajocian-Bathonian) at the southern margin of Cheriya Bet, 4 km N Gadhada, Khadir Island in the Rann of Kachchh.

is 5 mm. Remnants of the basis for the neural arch are visible and begin 18 mm behind the facies articularis.

**Comparison**: Shape and size fit well to posterior caudals of sauropods (e.g. *Diplodocus, Camarasaurus*). The fore-aft orientation is deduced from the remnants of the basis for the neural arch, which is situated nearer to the anterior facies articularis and well removed from the posterior facies articularis in sauropods.

ribs (RUC1999I 201, 204, 205)(Figs. 4.3, 4.4, 4.7, 5)

**Description**: The fragment of the middle region of a right dorsal rib (RUC 1999 I 201, Fig. 4.3) is 97 mm long. At the presumed proximal end it is craniodistally 53 mm thick and mediolaterally 35 mm wide, at the presumed distal end it is 51 mm thick and 33 mm wide. The rib piece shows no curvature in cranial or in medial view. In proximal view the lateral border is more bowed than the medial one. The compact bone wall is 5–7 mm thick, the inner structure spongiose. The outer surface is finely longitudinally striated. RUC1999I 204 and 205 are smaller fragments from the proximal region of dorsal ribs. RUC1999I 205 (Fig. 4.4) is from the right side and shows both the anterior and posterior bulging rim at the external margin. This, together with a rapid narrowing towards distal, indicates a very proximal position perhaps less than 10 cm from the articulating end. RUC1999I 204 (Fig. 4.7) is too small a fragment to determine left and right, but remnants of the anterior and posterior bulging rim are present and indicate the proximal position. A transverse section in microscopic view shows fibrolamellar bone with primary and scattered secondary osteons (Fig. 5).

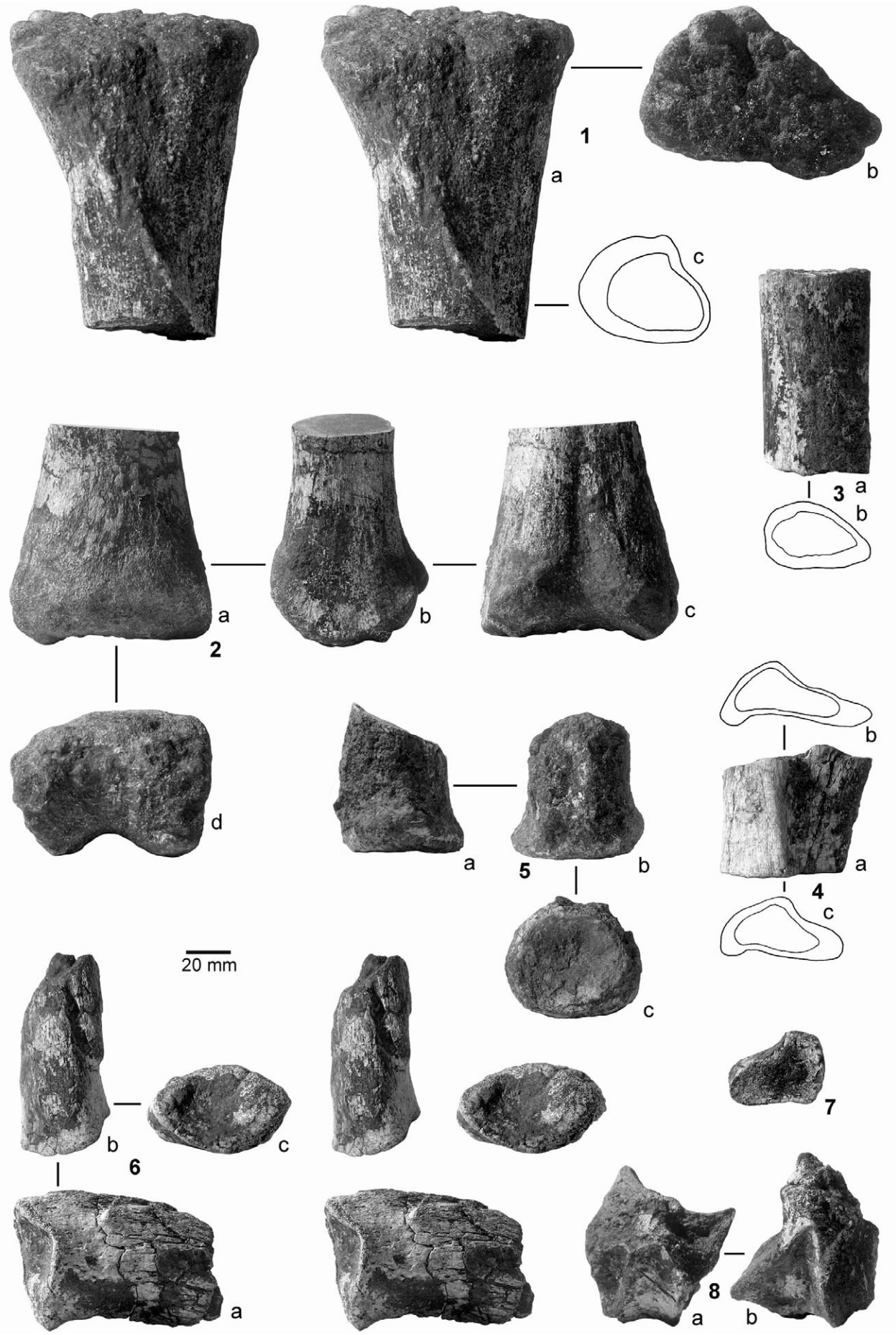
**Comparison**: The shape of the rib fragments RUC1999I 201, 204 and 205 is common to dinosaur ribs (e.g. *Kentrosaurus*, HENNIG 1925: Textbeilage 1), and size, form and inner structure (which is typical of dinosaur bones, CHINSAMY 1994: fig. 2) do not contradict an assignment to sauropods. The overall size and the lack of curvature in cranial or medial view in RUC1999I 201 favours a large animal.

Appendicular skeleton

distal portion of a right metacarpal (RUC1999I 200)(Figs. 4.2, 6, 7)

**Description**: The distal fragment of the metacarpal (RUC1999I 200) is 95 mm mediolaterally wide and was originally 108 mm long, before at the broken proximal end a slice was cut for histological investigations. In distal view the craniocaudal thickness, measured at the

**Fig. 4.** (?) Sauropoda, gen. et sp. indet. (3–5, 7, 8), and Camarasauromorpha, gen. et sp. indet. (1, 2, 6), from the Hadibhadang Shale Member of the Khadir Formation (Bajocian-Bathonian) from Cheriya Bet, Khadir Island in the Rann of Kachchh (India). All figures to same scale (20 mm). Outline figures: inner line indicates transition from compact to spongiose bone structure. – **1**: Proximal end of left fibula (RUC 1999 I 207), **a**. stereopair of medial view, **b**. proximal view, **c**. sketch of transverse section in distal view. – **2**: Distal end of right Metacarpale II (RUC 1999 I 200) in **a**. cranial, **b**. medial, **c**. caudal and **d**. distal view. – **3**: Middle piece of right rib (RUC 1999 I 201), **a**. in craniolateral (external) view, **b**. sketch of transverse section in distal view. – **4**: Proximal piece of a right rib (RUC 1999 I 205), **a**. in cranial view, **b, c**. sketches of transverse sections in distal view. – **5**: Anterior half of a posterior caudal centrum (RUC 1999 I 203) in **a**. left lateral, **b**. dorsal, **c**. proximal view. – **6**: First right pedal claw (RUC 1999 I 202). Stereopairs of **a**. lateral, **b**. volar, **c**. proximal views. – **7**: Proximal piece of rib (RUC 1999 I 204) in proximal or distal view. – **8**: Basal fragment of neural arch of anterior dorsal vertebra (RUC 1999 I 208), **a**. oblique-ventral (?), **b**. lateral (?) view.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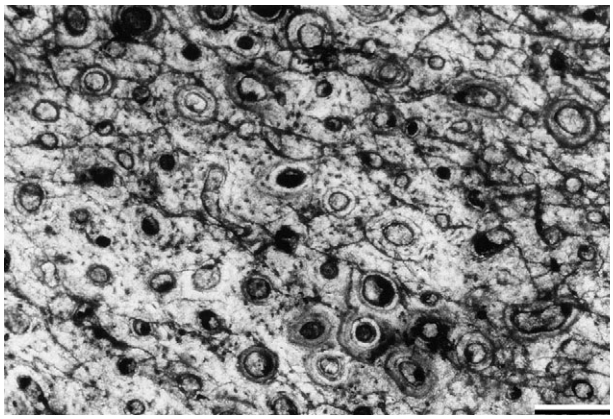


**Fig. 5.** Thin section of a rib (RUC 1999 I 204) in microscopic view showing fibrolamellar bone with primary and scattered secondary osteons. – Scale bar 200 $\mu$m.

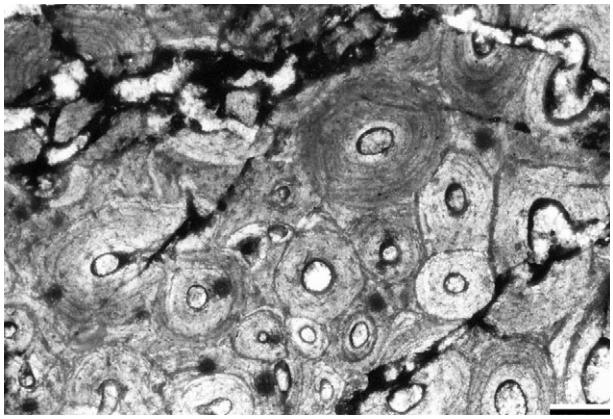


**Fig. 7.** Thin section of a metacarpal (RUC 1999 I 200) in microscopic view. At least three generations of secondary osteons can be observed, leaving nearly no primary lamellar bone. Multiple cracking with black coatings occur in predominantly radial and concentric orientation. – Scale bar 200 $\mu$m.

condylus medialis, is about 70 % of the mediolateral width. The condylus medialis is slightly larger than the condylus lateralis. The fossa intercondylaris is a shallow depression on the ventral side, diminishing distoproximally, and barely visible near the broken proximal end of the metacarpal fragment. The condylus lateralis is incomplete at the laterodistal edge, probably due to post-depositional erosion. Volar (or anterior) the metacarpal is slightly convex. The polished section of RUC1999I 200 (Fig. 6) shows a small distinct rim (or cortex) of compact bone passing with about 1–3 mm transition into the cancellous spongiosa. The compacta is anteromedial 8 mm thick and posterolateral 1 mm. There is no trace of an open medullary cavity. In thin-section (Fig. 7) the cortex is made up of dense Haversian system or plexiform bone: no lines of arrested growth are visible. At least three generations of secondary osteons can be observed, the primary lamellar bone is almost totally consumed. Multiple cracking in predominantly radial and concentric orientation occurs and even osteons are commonly cracked. The cracks and also the vascular canals show black coating – presumably caused by pyrite – while open space is filled with clear sparite and / or brown ferrous hydroxides.

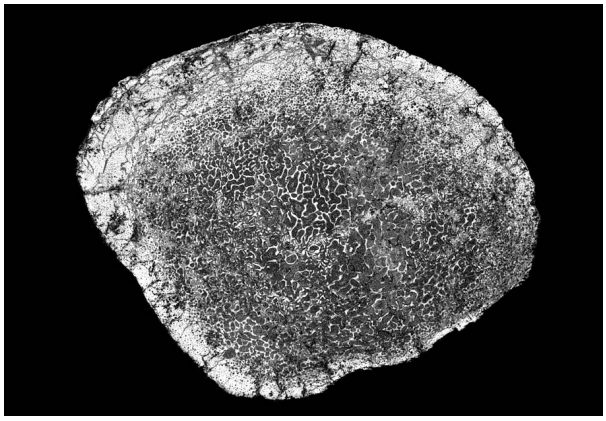


**Fig. 6.** Polished transverse section of a metacarpal (RUC 1999 I 200) showing a small distinct rim of compact bone passing with rapid transition into the cancellous spongiosa. – Scale 1 : 1

**Measurements** of RUC1999I 200 (in mm):

| | |
|---|---|
| proximodistal length (after slice was cut) | 100 |
| mediolateral width across condyles | 94 |
| mediolateral width of shaft at the proximal broken end | 61 |
| dorsoventral thickness of shaft at the proximal broken end | 49 |
| dorsoventral thickness of condylus medialis | 68 |
| dorsoventral thickness of condylus lateralis | 61 |
| dorsoventral thickness at the fossa intercondylaris | 58 |
| maximum depth of the fossa intercondylaris | 11 |

**Comparison**: At first sight a deceptive similarity is seen to distal ends of femora, especially to some stegosaur femora that lack a fossa intercondylaris cranialis and a fossa ectocondylaris, have a shallow fossa intercondylaris caudalis, and a small or in some sections even no open medullary cavity. However, it differs from femora in having a clearly convex dorsal (anterior) surface. The large size already points to a sauropod origin of the metapodium.

Metacarpals and metatarsals of sauropods differ in their proportions: Metatarsals are always short and stocky, thus have articular ends rapidly thinning towards the shaft. Metacarpals are usually elongated, slender bones with articular ends gently thinning towards the shaft, but rarely short and stocky metacarpals occur (e. g. in *Apatosaurus*; MCINTOSH 1990). The elongated RUC1999I 200 therefore undoubtedly represents a metacarpal bone.

Towards a topological identification, in distal view the ends of the metacarpals are characteristically shaped, but variation of morphology among different species and individuals is common. Also, the shapes in different metacarpal positions are similar, so identifica-

tion is difficult. RUC1999I 200 resembles the metacarpal II of *Camarasaurus* (Fig. 8B) and even more closely the metacarpal II of *Janenschia* (Figs. 8C, D). Other metacarpals of *Camarasaurus, Janenschia* and *Apatosaurus* can be probably excluded due to their distinct distal view (Figs. 8a–c).

Considering taxonomical identification, in dorsal/ventral view the metacarpals of *Diplodocus* differ markedly in being much more slenderly built and shorter (about only two times longer than wide), which is also the primitive condition in prosauropods and basal sauropods such as the "cetiosaurid" *Shunosaurus* (ZHANG 1988). In *Brachiosaurus* the metacarpals are greatly elongated (about four times longer than wide) and articular ends are gently thinning towards the shaft, thus resembling RUC1999I 200, which in outline shape most closely matches again to a metacarpal II of *Brachiosaurus* (HEINRICH, pers. comm. 2003). RUC1999I 200 is incomplete and the length/width ratio cannot be determined by measurement, but the very gentle, continuous thinning towards the mid-shaft cut, with no sign of being close to a turning point where re-thickening towards the proximal end begins, indicates a length/width ratio higher than 3/1. Elongated metacarpals are reported also in *Atlasaurus* from the Bathonian/Callovian of Morocco (MONBARON et al. 1999). Because of sharing this synapomorphy of the Camarasauromorpha (SALGADO et al. 1997), already *Atlasaurus* has been identified as one of the oldest representatives of this group (MONBARON et al. 1999). In absolute size, RUC1999I 200 reaches about 80 % of the metacarpal width of *Brachiosaurus* and equals the size of *Janenschia* and *Camarasaurus*, thus indicating a large sized camarasauromorph.

Polished cross-sections and thin-sections are of some usefullness in identifiying bone fragments as dinosaurian by the presence of several generations of secondary osteons not present in other large terrestrial Mesozoic vertebrates (MATHUR & PANT 1988), and initially this helped to identify this bone as possibly dinosaurian. The inner structure of RUC1999I 200 (Figs. 6–7) is identical to that of known sauropod bones, which has been described in detail e. g. for the Middle Jurassic (Bathonian) brachiosaurid *Lapparentosaurus* from Madagascar (DE RICQLÈS 1983; RIMBLOT-BALY et al. 1995). The pyrite coating and occurrence of ferrous hydroxides in thin-sections of long bones of *Diplodocus* and Pleistocene mammals with principally similar bone structure has been explained by PFRETZSCHNER (2000, 2001) as

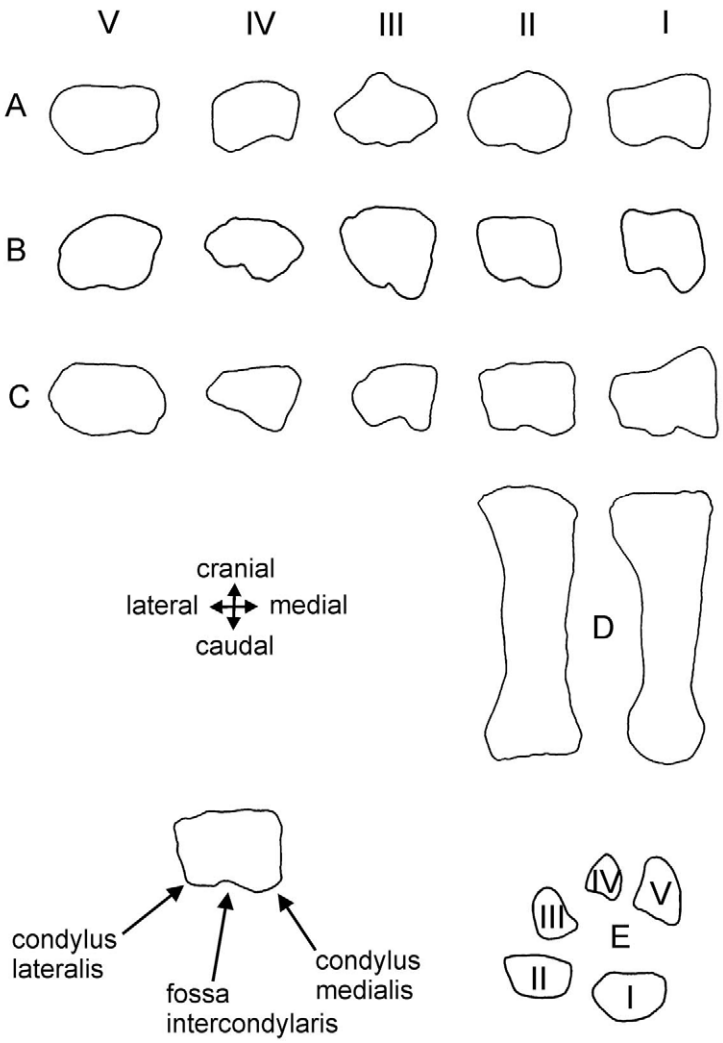



**Fig. 8.** Comparison of right metacarpals of different sauropods (not to scale). – **A–C**: Proximal view. A. *Apatosaurus louisae* HOLLAND (after GILMORE 1936: fig. 16D, reversed). B. *Camarasaurus* sp. (YPM 4633, after OSTROM & MCINTOSH 1966: pls. 55–59, fig. 5, reversed). C. *Janenschia robusta* (FRAAS) (after JANENSCH 1961, Beilage D, figs. 1–5c). – **D**: Mc II in dorsal or volar view (left) and lateral view (right) of *Janenschia robusta* (FRAAS) (after JANENSCH 1961, Beilage D, figs. 2a, b). – **E**: Mid sections of right metacarpals of *Janenschia robusta* (FRAAS) (after JANENSCH 1961, Beilage C, fig. 2d).

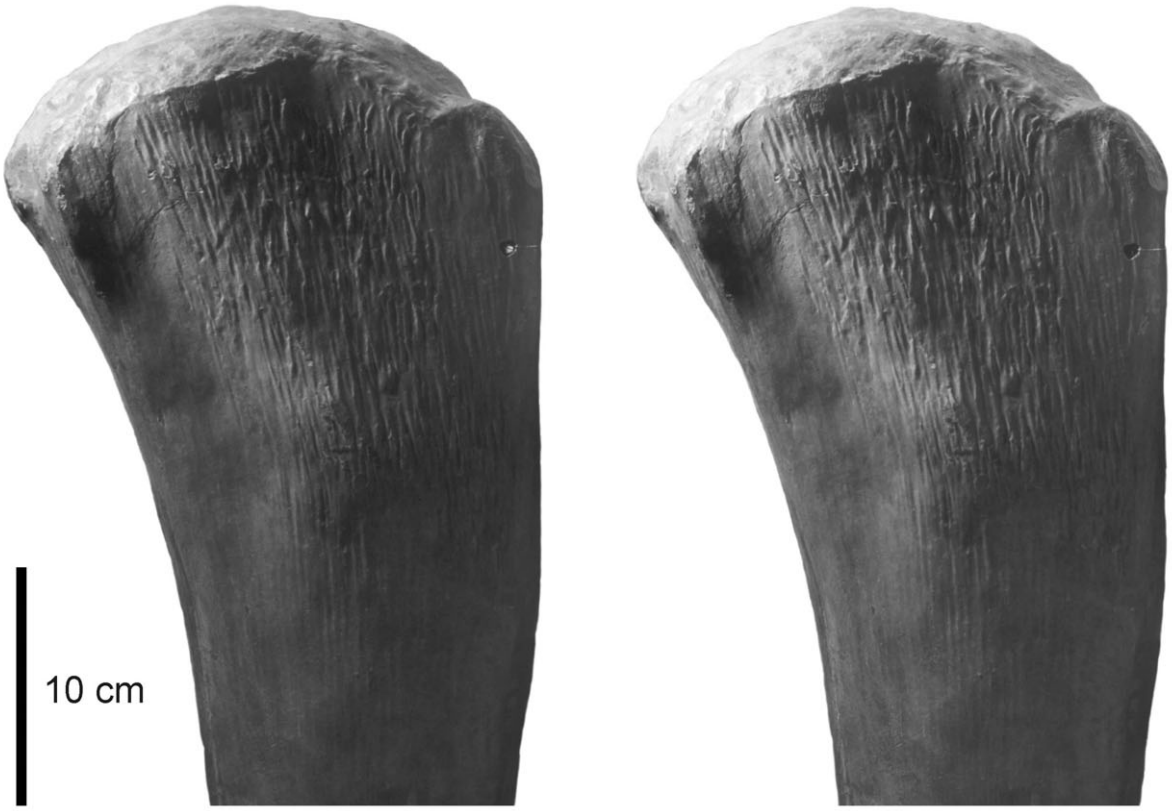



**Fig. 9.** Stereopair of proximal end of left fibula of *Diplodocus carnegii* HATCHER in medial view showing the concave facies articularis tibialis with a longitudinally striated area ligamentosa completed ventrally by an inconspicuous linea diagonalis fibulae which is developed as a shallow diagonal ridge or bending (BSP, uncatalogued cast).

mineralization due to earliest microbial activity (decay) and early diagenesis; the same processes are assumed to be represented here.

spongiosa of a large long bone (RUC1999I 206)[not figured]

**Description**: A piece of bone, measuring about 100 × 65 × 40 mm, consists entirely of spongiosa. The meshwork is homogeneous and shows no approximation to the denser rim of the compact bone wall. There is also no indication of a central open medullary cavity. Derivation from a large long bone (like femur, tibia or humerus) is to be assumed. An incomplete (due to erosion) valve of an oyster (Ostreidae indet.) is attached to the eroded surface of the bone.

**Comparison**: The medullary cavity in long bones is usually open in smaller and up to moderately large dinosaurs; in very large, graviportal forms the cavity tends to close (e.g. in stegosaurs) or is closed completely without a remnant of less dense meshwork, as seen in sauropods (cf. RIMBLOT-BALY et al. 1995: fig. 4).

proximal end of a left fibula (RUC1999I 207) (Figs. 4.1, 10G)

**Description**: The caput fibularis is nearly flat and triangular in proximal view with the long medial edge being roughly straight caudally and curving convexly towards the craniolateral edge. The craniolateral edge is straight, the short caudolateral edge is convex in proximal view. The lateral corner is situated about 30 mm above (proximally) the two equal high cranial and caudal corners. The facies articularis femoris is rugose with some rugosities extending radially as notches to the edges. The facies medialis of the corpus fibulae contains a triangular facies articularis tibialis which is nearly completely occupied by the longitudinally striated area ligamentosa. The linea diagonalis fibulae is developed as a prominent, slightly rugose ridge, with an angle of about 30° against the long axis of the shaft.

A muscle scar, probably the impressio musculi iliofibularis, is developed as a shallow, smooth and subcircular depression on the facies laterocaudalis next to the margo caudalis and about 50 mm below the caudal corner of the caput fibularis.

The broken shaft of the corpus fibulae reveals a regular ovoid cross-section which is only disturbed by the ridge of the linea diagonalis fibulae (Fig. 4.1c). Except for the craniomedial side where it is thin (3 mm),

the compacta builds a thick (9 mm) rim passing inconspicuously into the spongiosa. There is no open medullary cavity.

**Measurements** (in mm):

| | |
|---|---|
| proximodistal length | 146 |
| craniocaudal extension of caput fibulae | 110 |
| lateromedial extension of caput fibulae | 78 |
| craniocaudal width at broken end of corpus fibulae | 64 |
| lateromedial width at broken end of corpus fibulae | 57 |

**Comparison of sauropodomorph fibulae**: The fibula of sauropodomorphs is seldom analyzed, described or figured in detail. However, the fibula contains a number of peculiar muscle scars, articular surfaces and a general morphology that make it an interesting object for phylogenetic and functional morphology studies. The information on sauropodomorph fibulae presented here concerns only the proximal part of the fibula, which is the part preserved in the left fibula RUC1999I 207.

The large size of the piece and absence of an open medullary cavity are suggestive, although not conclusive, of a sauropod origin (CHRISTIANSEN 1998). Moreover, as a general character only Sauropoda possess the prominent facies articularis tibialis (formerly at least partly interpreted as a muscle scar, e.g. by MCINTOSH 1990) in the following way: The concave facies articularis tibialis is a (sub)triangular region on the facies medialis which contains two distinguishable morphological features: the area ligamentosa (or fovea ligamentosa, DONG et al. 1983; actually the ligamentous area is an elevation within the proximomedial concavity) for attachment with the tibia, and the linea diagonalis fibulae running obliquely from the proximocaudal corner downwards the medial surface to the mediocranial edge at the trochanter anterior, thus bordering the facies articularis tibialis. A distinct linea diagonalis fibulae extending towards the cranial shaft side is absent in theropods and prosauropods. In stegosaurs a linea diagonalis fibulae is present, but well removed from the caput fibulae and less steep (cf. GILMORE 1914: pl. 25).

There are two features of RUC 1999 I 207 of phylogenetic and diagnostic interest: The prominent linea diagonalis fibulae and the triangular proximal outline. In order to evaluate the character conditions in various sauropodomorphs, a description regarding these characters is added for several sauropodomorph representatives in the section below.

Basal Sauropodomorpha. The most basal sauropodomorph known so far is *Saturnalia tupiniquim* LANGER et al., 1999 from the Late Triassic of Brazil. The fibula is described in detail by LANGER (2003: 21, figs. 5E–G), who notes the craniocaudal expansion of the caput fibulae, the presence of a rugose trochanter anterior for the insertion of the m. iliofibularis and the presence of another muscle scar in the mediocranial corner. In the caudal portion of the medial facies, the facies articularis tibialis contains as a short diagonal ridge, fitting underneath the condylus fibularis of the tibia. This structure is also shared by *Herrerasaurus* (NOVAS 1994: fig. 8F) and therefore represents probably the plesiomorphic condition for dinosaurs. Similar "ridges" are found in prosauropods (see below) and have been interpreted as muscle scars (e.g. HUENE 1926), possibly for the m. popliteus (cf. HUTCHINSON 2002). However, it is not entirely clear if the roughened area does not indicate a simple ligamentous connection to the tibia, and the term area ligamentosa is used here. The m. popliteus – it is supposed here – may have inserted on the linea diagonalis fibulae.

*Plateosaurus engelhardti* MEYER, 1837 (Fig. 10A, SMNS 13200, 12951 from Trossingen, MB skeleton 42 from Halberstadt, BSP 1962 I 153 from Ellingen, cf. MOSER 2003: pl. 37 fig. 2, and BSP 1965 X 92 from Lauf, cf. MOSER 2003: pl. 27 fig. 5; also see HUENE 1926): The proximal surface is roughly crescent-shaped or trapezoidal, sometimes subrectangular, but usually with a maximum mediolateral extension in the cranial half of the craniocaudal length. The (latero-)cranial edge is slightly higher than the caudal edge. The facies articularis tibialis is – as usual – part of the medial surface of the craniocaudal expanded proximal shaft and in overall shape strongly concave to rather flat (as opposed to the convex cranial, lateral and caudal shaft surfaces). The area ligamentosa is developed as a roughened, noticeable swelling situated about in the middle of the proximal concavity, but always closer to the cranial side of the shaft. Furthermore, the area ligamentosa is well removed from the facies articularis femoris and distally runs out where the expanded proximal end of the fibula converges into the slender part of the shaft (corpus fibulae). A narrow, shallow trough may separate the area ligamentosa from the cranial border of the proximal concavity, and a wider one always separates it from the caudal border. A linea diagonalis fibularis is not discernible. The caudomedial shaft side is in the most proximal part ridge-like and in medial view is separated by a rounded step from the rest of shaft.

*Ruehleia bedheimensis* GALTON (2001, 2002) was recently proposed as a new prosauropod and is based on the material unearthed by HUGO RÜHLE VON LILIENSTERN in the 1930ies at Römhild in Thuringia (Germany). The material was briefly described by HUENE in RÜHLE VON LILIENSTERN et al. (1952) and GALTON (2001, 2002), with more details to be published elsewhere (GALTON, pers. comm.). Despite its earlier assignment by HUENE to *Plateosaurus, Ruehleia* clearly differs from this classical prosauropod (pers. obs.). Several characters not mentioned by GALTON (2001, 2002) – including the presence of four sacrals S1, S2, and a CS1 in addition to a true dorsosacral (DS1); dorsals with laterally expanded large parapophyses and strong, truncated transversal processes, the latter character similar to the condition in *Massospondylus* – remove *Ruehleia* from the Plateosauria and place it closer to the Sauropoda. Fibular characters (Fig. 10B, MB RvL 1): In overall

morphology the fibula is much like that of *Plateosaurus*, in proximal view the outline is subrectangular. However, the area ligamentosa is a much more prominent ridge-like elevation in the anterior third of the medial surface. There is no linea diagonalis fibulae present.

Early Sauropoda. The fibulae of the alleged Triassic sauropods *Isanosaurus attavipachi* BUFFETAUT et al. (2002) and *Antetronitrus ingenipes* YATES & KITCHING (2003) are either unknown or remain undescribed, respectively.

*Vulcanodon karibaensis* RAATH, 1972 (Fig. 10C; description based on COOPER 1984: 218, fig. 7C, 24). In proximal view the fibula is crescentic, which is much due to the inturned crista anteromedialis as in prosauropods. Well removed from the proximal end of the fibula, the crista anteromedialis bears a deep trochanter anterior (not present in prosauropods). The facies articularis tibialis is described by COOPER (1984) as being "marked by a large, distinctly striated, subtrigonal area". Despite this clear statement and the corresponding figure showing the character (COOPER 1984: fig. 7C), WILSON & SERENO (1998) cited the area ligamentosa ("broad triangular scar for tibia") only as a synapomorphy (no. 62) in support of an "unnamed clade *Barapasaurus* + *Omeisaurus* + Neosauropoda". However, they noted that the condition is unknown in the fibula of the next sister taxon *Shunosaurus* and "may be present" in the basal sauropod *Vulcanodon* and finally (followed by WILSON 2002, character no. 207), they coded this character as absent in *Vulcanodon*. However, the area ligamentosa with a striated surface is visible and bordered distally by a faintly developed linea diagonalis fibulae which extends diminishing towards the anterior shaft border at about 45°: thus the character is unambiguously present.

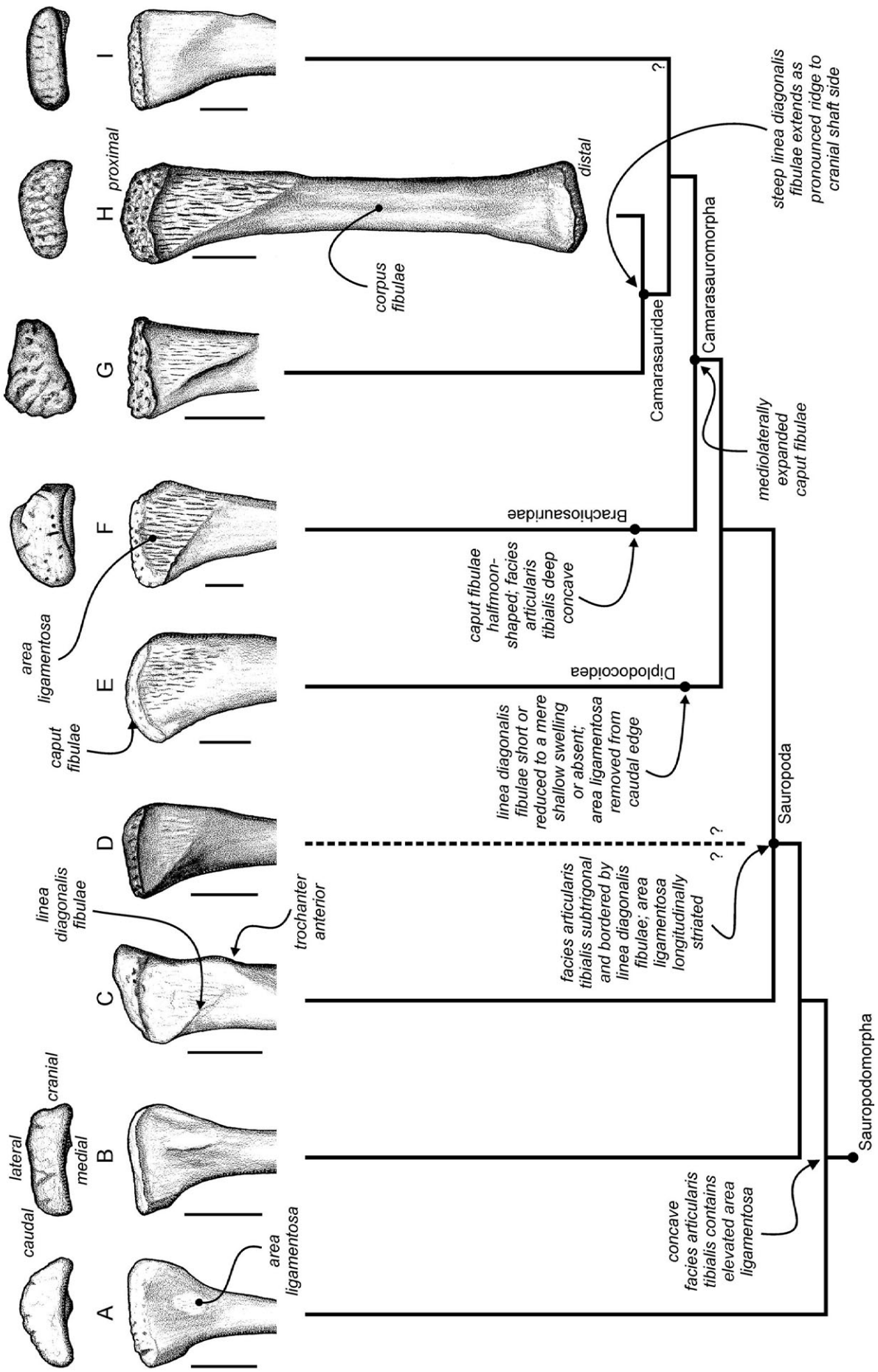
*Tazoudasaurus naimi* ALLAIN et al. (2004) is a newly found basal sauropod from the Early Jurassic of Morocco. The preliminary description by ALLAIN et al. (2004) notes a triangular proximal outline, and a broad and flat medial surface. An autapomorphic feature is seen in a 20 cm long lateral crest, which is very prominent (ALLAIN, pers. comm. to MM 2004). The material is still covered by some sediment and awaits final preparation and a full description.

*Kotasaurus yamanpalliensis* YADAGIRI, 1988 (Fig. 10D): The short description of the *Kotasaurus* fibula by YADAGIRI (1988: 117, 2001: 249, figs. 5I, J, the scale is 5 cm, figs. 8 N, O) is essentially equal to that for the *Vulcanodon* fibula. The linea diagonalis fibulae borders the area ligamentosa probably much the same way as in *Vulcanodon*; the kink in the linea seen in YADAGIRI's fig. 5J is not visible in his fig. 8O and may be erroneous. However, the figures indicate a less prominent trochanter anterior than in *Vulcanodon*.

Fibulae of a limited number of other sauropodomorphs from the Lower and Middle Jurassic are preserved, but few have been described, and neither descriptions nor figures provide enough details of the fibular morphology for a reasonable comparison. The Middle Jurassic *Shunosaurus* (DONG et al. 1983: 24, fig. 12; ZHANG et al. 1984: pl. 2 fig. 8) and Upper Jurassic *Mamenchisaurus* (YOUNG & ZHAO 1972: 16, pl. 7 fig. 2a, b) both possess a crescent-shaped caput fibulae. In the late Middle Jurassic *Omeisaurus* (DONG et al. 1983: pl. 13 fig. 7) as well as *Mamenchisaurus* (YOUNG & ZHAO 1972: pl. 7 fig. 2b) the linea diagonalis fibulae is a rather inconspicuous diagonal rise bordering the longitudinally striated area ligamentosa, which is concave proximal to the linea diagonalis. In *Cetiosaurus,* UPCHURCH & MARTIN (2003: 229) note the presence of the triangular facies articularis tibialis and the trochanter anterior. In the Callovian *Ferganasaurus* the presence of the facies articularis tibialis is mentioned, but the accompanying figure shows a rather smooth surface (ALIFANOV & AVERIANOV 2003: fig. 15A), which may support the assumed closer affinities with the Diplodocoidea (see below). For the vast majority of Early and Middle Jurassic sauropods and many of the later forms no details of the fibular morphology are available (*Abrosaurus*, *Amygdalodon*, *Barapasaurus*, *Bothriospondylus*, *Datousaurus*, *Gongxianosaurus*, *Jobaria*, *Klamelisaurus*, *Lapparentosaurus*, *Nigersaurus*, *Ohmdenosaurus*, *Omeisaurus*, *Patagosaurus*, *Rhoetosaurus*, *Tehuelchesaurus*, *Volkheimeria*, *Zizhongosaurus;* for references see UPCHURCH et al. 2004).

Diplodocoidea. In *Diplodocus carnegii* HATCHER, 1901 (Figs. 9, 10E; BSP unnumbered cast) the mediolaterally flattened fibula is crescent-shaped in proximal outline, the subtrigonal facies articularis tibialis is concave. The area ligamentosa is developed as a central elevation – thus reminding somewhat of prosauropods – beginning mid-proximally and extending downwards to the anterior border. The fine longitudinal striations therefore only cover less than about half of the medial surface. The linea diagonalis fibulae is nearly absent ex-

**Fig. 10.** Medial views of left fibulae of different sauropodomorphs. – **A**: *Plateosaurus engelhardti* MEYER (SMNS 13200, 12951). – **B**: *Ruehleia bedheimensis* GALTON (MB Bedheim 1). – **C**: *Vulcanodon karibaensis* RAATH (after COOPER 1984: fig. 7C). – **D**: *Kotasaurus yamanpalliensis* YADAGIRI (right fibula reversed, after YADAGIRI 2001: fig. 5J, with corrections from fig. 8O, and YADAGIRI 1988). – **E**: *Diplodocus carnegii* HATCHER (BSP, unnumbered cast). – **F**: *Brachiosaurus brancai* JANENSCH (right fibula reversed, after JANENSCH 1961: Beilage K, figs. 2b, d). – **G**: Camarasauromorpha gen. et sp. indet. (RUC 1999 I 207). – **H**: *Camarasaurus grandis* MARSH (after OSTROM & MCINTOSH, pl. 77, figs. 2, 5). – **I**: *Janenschia robusta* (FRAAS) (right fibula reversed, SMNS 12144). – Scale: 10 cm. – The fibular character distribution is arbitrarily fitted onto a phylogenetic tree by UPCHURCH (1998), with *Ruehleia* inserted after unpublished data (pers. obs.) and such nodes indicated, that are possibly supported by fibular characters (the phylogenetic position of *Kotasaurus* is presently unknown). The scheme can be easily transferred to the slightly differing phylogenies of WILSON (2002) and UPCHURCH et al. (2004).


caudal
lateral
cranial
medial
A
B
C
D
E
F
G
H
I
proximal
distal
area ligamentosa
linea diagonalis fibulae
trochanter anterior
caput fibulae
area ligamentosa
corpus fibulae
concave facies articularis tibialis contains elevated area ligamentosa
facies articularis tibialis subtrigonal and bordered by linea diagonalis fibulae; area ligamentosa longitudinally striated
linea diagonalis fibulae short or reduced to a mere shallow swelling or absent; area ligamentosa removed from caudal edge
caput fibulae halfmoon-shaped; facies articularis tibialis deep concave
mediolaterally expanded caput fibulae
steep linea diagonalis fibulae extends as pronounced ridge to cranial shaft side
Sauropodomorpha
Sauropoda
Diplodocoidea
Brachiosauridae
Camarasauridae
Camarasauromorpha
?
?
?

cept for an inconspicuous, smooth swelling marking the border of the facies articularis tibialis. In *Apatosaurus* (GILMORE 1936: fig. 24; PETERSON & GILMORE 1902: 496; SMNS 10375) the caput fibulae is subrectangular in proximal outline and slender. The area ligamentosa is finely striated, the linea diagonalis fibulae is only developed in the caudal half of the facies medialis fibulae. In *Tornieria africana* (FRAAS, 1908) (pers. obs., SMNS 12142, MB R 2612, 2616) the fibula is similar to that of *Apatosaurus*: in proximal view the fibulae are slender subrectangular or slightly crescent-shaped, the area ligamentosa is not elevated and usually weakly – if at all – striated. The linea diagonalis fibulae is seen as a faintly discernible slender ridge only in its caudal part. In *Rebbachisaurus* (CALVO & SALGADO 1995), *Suuwassea* (HARRIS & DODSON 2004: 205), *Haplocanthosaurus* (MCINTOSH & WILLIAMS 1988: 21) and *Dicraeosaurus* (JANENSCH 1961: 212, Beil. L fig. 2; HEINRICH, pers. comm. 2003) the fibula corresponds to the mentioned bauplans, according to the brief descriptions given.

Camarasauromorpha. In the Middle Jurassic putative camarasauromorph *Bellusaurus* DONG (1990: 54, fig. 12, pl. 3 fig. 6) the area ligamentosa is well striated and the linea diagonalis fibulae is discernible. The angle between the long axis of the shaft and linea diagonalis fibulae is about 45˚.

*Brachiosaurus brancai* JANENSCH, 1914 (Fig. 10F, MB R 2588; others: MB R 2688, 2609, 2690; cf. JANENSCH 1961: Beilage K, fig. 2). The fibula of *Brachiosaurus* is thick-halfmoon shaped in proximal view, with the facies articularis tibialis being deeply concave and well delimited from the convex shaft surface by a linea diagonalis fibulae which is ridgelike in the proximocaudal part and transforms into a rounded swelling in the distocranial part. The angle between linea and vertical axis of the corpus fibulae is approximately 45˚. The area ligamentosa with its fine to well-marked striations extends througout the facies articularis tibialis.

*Camarasaurus grandis* (MARSH, 1877): The proximal end of the *Camarasaurus* fibula is thick-crescentic or sometimes nearly subtriangular in outline (Fig. 10H; OSTROM & MCINTOSH 1966: pl. 77 fig. 5; but cf. compressed fibular head of *Camarasaurus supremus* in OSBORN & MOOK 1921: fig. 111). The very rough striated area ligamentosa extends over the whole facies articularis tibialis and is bordered by a very pronounced, strong, knobby, ridge-like linea diagonalis fibulae, which is steeply inclined with about 30˚ to the vertical axis and extending down from the proximocaudal corner towards the cranial shaft surface untill about one-third of the fibular length. RUC1999I 207 (Fig. 10G) resembles closely the morphology of the *Camarasaurus* fibula (Fig. 10H), except that the maximum mediolateral extension of the proximal outline is well within the caudal half. This difference could be caused by heterochronous growth of the caput fibulae, which would lead to a caudal expansion of the caput only at a later adult stage; however, MARTIN (1994) found in growth stages of the titanosaur *Phuwiangosaurus* – and WILHITE & CURTICE (1998) confirmed this for *Camarasaurus* – that the growth in limb bones of sauropods was isometric.

Titanosauria. *Janenschia robusta* (FRAAS, 1908) (SMNS 12144, Fig. 10I; cf. FRAAS 1908: pl. 11 figs. 3, 4): The proximal end is rather slender, with a rounded subrectangular outline; the facies articularis tibialis is flat and bordered by only a slight swelling which marks the linea diagonalis fibulae. An area ligamentosa is barely discernible. The angle between the long axis of the shaft and linea diagonalis fibulae is about 45˚. The trochanter anterior is a well developed depression. The Upper Jurassic *Janenschia* was included in the Titanosauridae e.g. by MCINTOSH (1990) and WILD (1991), but BONAPARTE et al. (2000) redescribed *Janenschia* as a camarasaurid. The earlier conclusion is now again supported by the lack of a strong developed, steep linea diagonalis fibulae known only in the camarasaurid *Camarasaurus* and RUC1999I 207.

The fibula of the Lower Cretaceous titanosaur *Phuwiangosaurus* (MARTIN et al. 1999: fig. 40) shows a rounded subrectangular proximal outline and a concave facies articularis tibialis, which appears to be rather smooth and not bordered by a distinct linea diagonalis. Thus *Phuwiangosaurus* appears to be similar to *Janenschia*.

In the Upper Cretaceous titanosaur *Opisthocoelicaudia* (BORSUK-BIALYNICKA 1977: fig. 16A, pl. 11 fig. 5, pl. 13 fig. 3, pl. 14 figs. 2b, c; Upper Cretaceous of Mongolia) the caput fibularis is crescentic, the facies articularis tibialis is concave and in its cranioproximal corner there are two deep foveae ligamentosae. The linea diagonalis fibulae is barely seen and just a slight elevation. The impressio musculi iliofibularis (which may contain a impressio musculi flexoris digitorum longi) on the facies lateralis is described as an oval, rough concave surface; from the figure (BORSUK-BIALYNICKA 1977, fig. 16A3) it is obvious, that this muscle scar is larger and more elongated in *Opisthocoelicaudia* than in RUC1999I 207.

A juvenile specimen of the Upper Cretaceous titanosaurid *Alamosaurus* was described by LEHMAN & COULSON (2002: 164, fig. 10) with the proximal end of the fibula being triangular, like RUC1999I 207. Thus, it is possible that the triangular outline is a juvenile character, diminished later through allometric growth. The very knobby caput fibulae of RUC1999I 207 and its overall small size – compared to the large metacarpal RUC1999I 200 – is also suggestive of a juvenile. However, RUC1999I 207 is already broader mediolaterally than the fullgrown *Apatosaurus* fibula described above.

Conclusions derived from sauropodomorph fibulae: Contrary to WILSON & SERENO (1998) and WILSON (2002), a distinctly bordered, roughly trigonal facies articularis tibialis with a longitudinally striated area ligamentosa is a synapomorphy of Sauropoda, as has been recognized by MCINTOSH (1990) and others before. A steep and very pronounced linea diagonalis fibulae in

form of a diagonal knobby ridge as in RUC1999I 207 is only shared with *Camarasaurus* (Figs. 10G, H). Thus, it is concluded that RUC 1999 I 207 represents an early camarasaurid and that the pronounced linea diagonalis fibulae is possibly a synapomorphy of this family. A synapomorphy of the Camarasauromorpha may be a mediolaterally expanded caput fibulae – possibly with a subtriangular outline – which is present in at least some representatives (*Alamosaurus* juvenile, *Brachiosaurus*, *Camarasaurus*, and the juvenile RUC1999I 207). A more pronounced linea diagonalis fibulae and mediolaterally expanded caput fibulae may be biomechanically linked to a "wide-gauge" gait (cf. WILSON & CARRANO 1999).

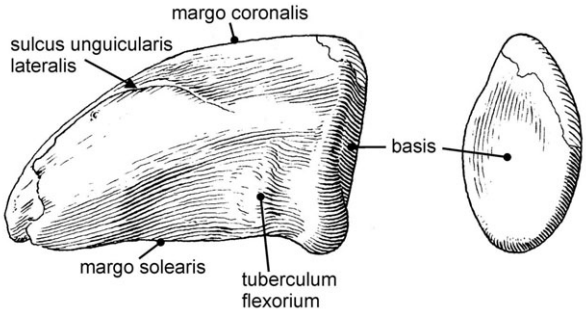



**Fig. 11.** Pedal claw (ungual) of *Brachiosaurus brancai* JANENSCH (from JANENSCH 1961, Beilage O, figs. 3a–b) with anatomical captions inserted.

### greater portion of the (?) first right pedal claw (RUC1999I 202)(Fig. 4.6)

**Description**: The right claw lacking the tip (RUC1999I 202) is 90 mm long and the dorsoventral long axis of the basis is 64 mm wide. The bone has practically no compact bone wall except for a thin coat and all the surface is extensively perforated and reveals bundles of occasionally ramifying and fusing longitudinal tubes of less than 1 mm in diameter. The basis is incomplete at the lateroventral edge. The facies articularis encompasses the whole basis, which is asymmetrically ellipsoid with both ends moderately pointed; it is concave along the dorsoventral long axis and also along the mediolateral short axis. A 1 mm wide shallow notch runs from the lateroventral border towards the center of the basis, which is otherwise rather smooth. The short axis is about 25° inclined in dorsal view against the proximodistal axis of the claw. The claw is moderately curved. Immediately before the basis the corpus ungularis is shallowly constricted. The margo solearis is situated a bit laterally of the long axis of the basis. From 30 mm distal of the basis towards the broken distal tip the margo solearis is developed as a knobby ridge. The margo coronalis is more rounded mediolaterally but the dorsal proximodistal curvature is much the same as at the margo solearis, indicating a total length of the claw of perhaps up to 150 mm. Arising from the facies lateralis next to the margo coronalis about 30–35 mm distal from the basis, a 5 mm wide and 3 mm deep sulcus unguicularis lateralis is running proximodistally towards the margo coronalis ultimately replacing it. In dorsal view the sulcus unguicularis is exactly perpendicular to the short axis of the basis. The facies lateralis is slightly concave while the facies medialis is convex in equal degree. On the facies medialis next to the margo coronalis and just before (proximal) the onset of the above described sulcus on the facies lateralis, a circular, flat, and knobby tuberculum extensorium of about 20 mm diameter is situated. On the opposite side on the facies lateralis next to the margo solearis and at the same distance from the basis a second insertion mark, the tuberculum flexorium, with the same form and size is found. The distal end is broken irregularly and obviously eroded prior to deposition.

**Comparison**: The near absence of compact bone wall is typical of osteoderms and distal phalanges. In prosauropod and theropod dinosaurs typically a well developed sulcus unguicularis (or sulcus neurovascularis) runs along or below most of the curved midline of the symmetrical claw on both the lateral and medial sides. The basis is divided by a vertically (dorsoventral) oriented crista cotylaris. In sauropods a tendency to reduction of claws, beginning with outer claws, is seen (e. g. in *Shunosaurus*, ZHANG 1988: figs. 49, 55), the remaining claws being stout, rather blunt and clearly asymmetrical. The basis is undivided. These claws do not always have sulci unguicularis, which are rather shallow and irregularily developed, often only on the facies lateralis. Examples of sulci unguicularis unequally developed are seen in *Janenschia* (FRAAS 1908: pl. 11 figs. 1, 5, pl. 12 fig. 3), *Barosaurus* (JANENSCH 1961: Beilage Q), *Mamenchisaurus* (YOUNG & ZHAO 1972: fig. 12) and *Omeisaurus* (DONG et al. 1983: pl. 12 fig. 6). Both a sulcus unguicularis lateralis and a shorter and deeper situated sulcus unguicularis medialis are reported in *Klamelisaurus* (ZHAO 1993: 134). Sulci are absent or very poorly developed in *Camarasaurus* (OSTROM & MCINTOSH 1966: pl. 63, 88).

A well developed deep sulcus unguicularis lateralis, which runs high from the lateral side towards the dorsal midline, has been described only in pedal claws of *Brachiosaurus*, a left II 3 and a left I 2 (Fig. 11; JANENSCH 1961: 221–222; Beilage O, fig. 3, fig. 5; labelled erroneously as right phalanx in figure caption). Also a tuberculum flexorium matching that of RUC1999I 202 in position and development is seen in these claws. It is concluded that RUC1999I 202 is the (?) first claw of the right foot of a brachiosaur-like sauropod attaining about 75 % the size of the same bone in *Brachiosaurus*.

## Discussion

Sauropods are the most frequently found faunal elements of the otherwise scant terrestrial vertebrate local-

ities of the Middle Jurassic. Also a small number of Early Jurassic sauropods have been described. The rich Jurassic localities of China (Sichuan, Xinjiang and Xizang) have added considerably to our knowledge of sauropod diversity (MARTIN-ROLLAND 1999; GILLETTE 2003), but most findings have not yet been described in detail. The new finds from western India help to close a temporal and geographical gap in our knowledge of sauropods and contribute to their phylogeny.

The nine bones from the Bajocian of the Khadir Island are all assignable to sauropods or dinosaurs at least. Moreover, three of them can be compared to certain sauropod genera more closely. The fibula indicates close relationship with *Camarasaurus*, the metacarpal bears resemblence to *Janenschia, Camarasaurus* and *Brachiosaurus*; and the claw is most similar to claws of *Brachiosaurus*. In recent phylogenetic analyses of sauropods, Camarasauridae, Brachiosauridae and Titanosauria have been grouped together in the Camarasauromorpha SALGADO, CORIA & CALVO, 1997 (see also WILSON & SERENO 1998; UPCHURCH 1998; WILSON 2002; UPCHURCH et al. 2004). The earliest representatives of this group so far known are from the Bathonian of Madagascar (*Lapparentosaurus*; RIMBLOT-BALY et al. 1995) and the Late(?) Middle Jurassic from China (*Abrosaurus* and *Datousaurus*; OUYANG 1989; ZHANG & CHEN 1996) and Morocco (*Atlasaurus*; MONBARON et al. 1999). However, the ages of the terrestrial sequences in China are not well constrained (DONG 1992; LUCAS 1996a, b, 2001; ZHANG & LI 1997; MARTIN-ROLLAND 1999), and should be regarded as preliminary. A camarasaurid from the "Middle or Upper Jurassic" of Argentina was announced (RICH et al. 1997) but later described as a new cetiosaurid *Tehuelchesaurus* of Callovian (?) age (RICH et al. 1999). Most recently GARCÍA et al. (2003) alluded to *Tehuelchesaurus* as a basal titanosauriform sauropod though reasons for this assignment were not provided.

It is not possible to say whether all or some of the here described nine bones belong to one single taxon – at least the possibility cannot be ruled out –, but we can say that the bones clearly belong to differently sized individuals. Either these bones together or at least three of them each evidently represent one of the oldest camarasauromorph dinosaurs known so far. Late Middle Jurassic Camarasauromorpha have been previously recognized from ?Argentina, Morocco, Madagascar and China. To this record, DAY et al. (2002) added a trackway evidence for a possible titanosaur from the Middle Bathonian of England. Therefore, no camarasauromorph has been documented so far in pre-Bathonian sediments. The sauropod remains presented here push back the minimum age of the origin of camarasauromorph sauropods about 10 million years to the earliest Middle Jurassic. However, this conclusion must be treated with some caution, as most pre-Late Jurassic sauropods lack comparable material or sufficient descriptions and our material can only be excluded definitively from Diplodocoidea (*Diplodocus*, *Apatosaurus*, *Dicraeosaurus, Barosaurus* and allies) but not from all the "eosauropods" (sensu BONAPARTE 1987 or "Cetiosauridae" sensu MCINTOSH 1990). However, this is the first sauropod described with a probable body size reaching about 20 m or more (as deduced from the large metacarpal) known from early Middle Jurassic times. The remains of camarasauromorphs from the Bajocian of India described here fill in the palaeobiogeographical gap of this group in Gondwana.

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