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A DINOSAUR FAUNA FROM THE LATE CRETACEOUS (CENOMANIAN) OF NORTHERN SUDAN

by

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ABSTRACT

A dinosaur fauna from the Cenomanian of northern Sudan (Wadi Milk Formation) is described. It comprises at least nine, probably ten to eleven taxa: a dicraeosaurid, a titanosaurid and another undetermined sauropod (possibly a titanosaurid), two charcharodontosaurids, a dromaeosaurid, a probable hypsilophodontid and two iguanodontian ornithopods. It is one of the most diverse dinosaur faunas known from the Cretaceous of Africa. The environment was probably a semiarid savanna with some rivers, lined by dense vegetation, with abundant sauropods, less abundant theropods and rare ornithopods. Gigantic carcharodontosaurids were at the top of the food chain. At the present state of knowledge, the dinosaur fauna from the middle to late Cretaceous of Africa can be characterized by the presence of carcharodontosaurids, spinosaurids, titanosaurids, diplodocoids, and possibly iguanodontian ornithopods.

KEYWORDS: Africa, Cretaceous, Dinosauria, Palaeoecology, Palaeobiogeography

INTRODUCTION

Cretaceous dinosaur faunas from Africa have recently gained more attention (Jacobs *et al.* 1990, 1993, 1996; Sereno *et al.* 1994, 1996; Forster *et al.* 1995; Rauhut & Werner 1995), but they are still very poorly known (Russell 1995).

Articulated dinosaur remains have so far been found only in the ?Barremian and Aptian of Niger (Taquet 1976; Sereno *et al.* 1994), and the Cenomanian of Egypt (Stromer 1915, 1931, 1932, 1934, 1936) and Morocco (Lavocat 1954; Sereno *et al.* 1996). Therefore, isolated skeletal elements of dinosaurs from the Cretaceous of Africa can add important information for a more complete picture of African faunas.

In 1989, a new vertebrate locality was found in Cretaceous beds in Sudan (Buffetaut *et al.* 1990), the first to be discovered in the Cretaceous of this country. In the following years, several expeditions led by Dr. Christa Werner of the Free University of Berlin discovered a rich Cretaceous vertebrate fauna (Werner 1991, 1993, 1994a, b; Werner & Rage 1994; Rauhut & Werner 1995; Evans *et al.* 1996). Among the vertebrate remains are many isolated dinosaur bones and teeth, which are described and discussed in some detail below.

GEOLOGICAL AND PALAEONTOLOGICAL CONTEXT

Localities

Both vertebrate localities are found in northern Sudan, west of the Nile River (Figure 1). The first locality discovered is situated in the Wadi Abu Hashim, some 200 km north-west of Khartoum. Buffetaut *et al.* (1990) recognized two different sites at this positon; however, since the stratigraphic level and sedimentological setting are the same and vertebrate remains have now been found in a large area between these sites, the two localities are now regarded as one (c. Werner, pers. comm. 1994). Werner (pers. comm. 1995) gives the coordinates for this locality as 16°41.77' N; 31°8.7' E.

Figure 1. Position of the vertebrate localities in northern Sudan. 1: Wadi Milk Formation, Wadi Abu Hashim; 2: Shendi Formation.

More vertebrate remains have been found in the Shendi Formation, some 100 km northwest of the city of Shendi. According to Werner (pers. comm. 1996), at least seven different localities with fragmentary vertebrate remains are found in this Formation.

Geological setting

The fossils come from terrestrial sediments, which were deposited in several basins during the Cretaceous. Three different laterally interfingering formations can be distinguished: the Wadi Milk Formation, the Shendi Formation and the Omdurman Formation. The sediments consist mainly of silt- to sandstones, often showing tabular and trough cross-bedding. Some conglomerate layers and rare palaeosols are also present (Bussert 1993a,b).

Bussert (1993a) recognized two different depositional environments: 'braidplain deposits' and 'coastal plain deposits'. The first type is represented mainly by trough cross-bedded sandstones, which are interpreted as deposits of braided rivers, whereas the second type is characterized by finer-grained sediments, derived from meandering rivers, flood plains and lakes. Palaeosols are found in the coastal plain deposits. Palaeocurrent directions are mainly northward in the Wadi Milk Formation.

The Wadi Milk Formation consists mainly of braidplain deposits, which in the north interfinger with coastal plain deposits. The vertebrate locality in the Wadi Abu Hashim is located in the Wadi Milk Formation of the Humar Basin, a large tectonic depression being part of the Central African Fault Zone (Bussert *et al.* 1990). In the Wadi Abu Hashim area, lacustrine sediments form the base of the outcropping parts of the Wadi Milk Formation. Above these fine grained siltstones, sandstones, and coarse cross-bedded sandstones indicate a change in sedimentation from a lacustrine environment to braided rivers. The coarse sandstones are overlain by finer-grained floodplain deposits, and the section ends with more braided river-sediments (Buffetaut *et al.* 1990). The vertebrate remains come from the lacustrine sediments at the base of the outcrop.

Stratigraphy

Since no invertebrates or palynomorphs were found at the vertebrate localities (Werner 1994a), dating of the sediments is difficult. Palynomorphs from other parts of the Wadi Milk and Omdurman Formations indicate an Albian-Cenomanian (Schrank 1990; Schrank & Awad 1990) or Cenomanian - Late Cenomanian (Awad 1994) age. Macrofloral investigations result in an Aptian-Cenomanian age for other parts of the Humar Basin area (Lejal-Nicol 1987). Werner (1994a) dated the locality in the Wadi Abu Hashim as Cenomanian, based on the fish fauna.

In the Shendi Formation, no invertebrates or palynomorphs have been found, but since this unit represents a lateral equivalent of the Wadi Milk and Omdurman Formations, a similar age can be assumed.

Flora and fauna

Based on palynomorphs, the middle Cretaceous formations in northern Sudan can be referred to the microfloral province of Africa/South-America, indicating a palaeoposition close to the equator (Schrank 1990). The presence of fungi, gymnosperms, angiosperms, ferns, aquatic ferns and a high diversity of pteridophytes can be demonstrated on the basis of spores and pollen (Schrank 1990). The relatively high percentage of fern-spores compared to other localities of the same microfloral province, indicates a less arid environment than in other regions. Macrofloral remains are mainly represented by parts of conifers (Lejal-Nicol 1987). The only plant remains found at one of the vertebrate localities is an indeterminable leaf of an aquatic plant (Werner 1994a).

No invertebrate remains have been described from any of the formations so far.

Many of the vertebrates are still under study (e.g. the dipnoans by U. Gloy, the amphibians and reptiles by C. Werner). The following faunal lists are mainly based on Werner (1993, 1994a), modified after the results of the current research (Werner & Rage 1994; Evans *et al.* 1996) and this work.

Floral and faunal list of the Wadi Milk Formation at Wadi Abu Hashim

Plantae:
indeterminate aquatic plant

Vertebrata:
Chondrichthyes:
Elasmobranchii
Euselachii
Fam. Acrodontidae
cf. *Asteracanthus aegyptiacus*

Neoselachii
Rajiformes
Rajiformes indet.

Osteichthyes:
Actinopterygii
Polypteriformes
Fam. Polypteridae
Polypteridae indet.

Lepisosteiformes
Fam. Lepisosteidae
Lepisosteidae indet.

Osteoglossiformes
Fam. Osteoglossidae
Osteoglossidae indet.

Characiformes
Characiformes indet.

Sarcopterygii
Dipnoi
Fam. Protopteridae
Protopterus humei
Protopterus nov. sp.

Fam. Ceratodontidae
Neoceratodus tuberculatus

Amphibia:
Lissamphibia
Gymnophiona
Gymnophiona indet.
Caudata
Kababisha humarensis
Kababisha sudanensis

Anura
Anura indet.

Reptilia:
Chelonia
Pleurodira
Fam. Podocnemididae
3 taxa Podocnemididae indet.

Squamata
Lacertilia
Lacertilia indet.

Ophidia
Fam. Madtsoiidae
Gen. et sp. indet.

Fam. ?Aniliidae
Gen. et sp. indet.

Fam. ?Lapparentophiidae
Gen. et sp. indet.

Fam. ?Nigerophiidae
Gen. et sp. indet.

Fam. ?Russellophiidae
Gen. et sp. indet.
Ophidia Fam., Gen. et sp. indet.

Archosauria
Suchia
Crocodylomorpha
2 taxa Crocodylomorpha indet.

Fam. Dyrosauridae
Dyrosauridae gen. et sp. nov.

Dinosauria
Saurischia
Sauropodomorpha
Sauropoda
Fam. Dicraeosauridae
Dicraeosauridae gen. et sp. indet.

Fam. Titanosauridae
Titanosauridae gen. et sp. indet.
Sauropoda gen. et sp. indet. (Titanosaurid?)

Theropoda
Tetanurae
Superfam. Allosauroidea
Fam. Carcharodontosauridae
2 taxa Carcharodontosauridae gen. et sp. indet.

Coelurosauria
?Coelurosauria indet.

Fam. Dromaeosauridae
Subfam. Velociraptorinae
Velociraptorinae gen. et sp. indet.

Ornithischia
Ornithopoda
Fam. (?)Hypsilophodontidae
Hypsilophodontidae indet.

Fam. Iguanodontidae
Iguanodontidae gen. et sp. indet.

(?)Fam. Iguanodontidae
cf. *Ouranosaurus* sp.

Faunal list of the Shendi Formation

Vertebrata:
Osteichthyes:
Sarcopterygii
Dipnoi
Fam. Protopteridae
Protopterus humei
Protopterus nov. sp.

Amphibia:
Caudata
Caudata gen. et sp. nov.

Reptilia:
Chelonia
Pleurodira
2 taxa Pleurodira indet.

Archosauria
Suchia
Crocodylomorpha
3 taxa Crocodylomorpha indet.

Dinosauria
Saurischia
Theropoda
Theropoda indet.

DINOSAUR REMAINS FROM SUDAN

The dinosaur remains described here come mainly from the Wadi Milk Formation of Wadi Abu Hashim. Only a few isolated phalanges were found in the Shendi Formation; one of these is described and discussed separately below. The material is stored in the collections of the Institut für Paläontologie of the Free University, Berlin.

SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen 1842
Saurischia Seeley 1888
Sauropodomorpha Huene 1932
Sauropoda Marsh 1878

Sauropod remains are the most common dinosaur fossils in the Wadi Milk Formation. Mainly isolated vertebral centra and fragmentary limb elements have been found; other than teeth, cranial elements are missing. The systematic terms follow Upchurch (1998).

Family: Dicraeosauridae Huene 1927
Gen. et sp. indet.

Material: Three caudal vertebral centra (Vb-856, Vb-857, Vb-892), a proximal end of a left fibula (Vb-884), and the distal end of a right tibia (Vb-879).

Description: Vb-892 is an anterior caudal vertebra (Figure 2A). The centrum is procoelous and relatively short: without the posterior ball, its length is only 70 mm. The ventral side is almost plain, with well developed chevron facets at its posterior end. On the sides, a bony lamina runs from the mid-height of the anterior end to the attachment of the broken transverse process on the dorsal part of the middle of the centrum. The neural arch is broken. It was almost confluent with the anterior end, but slightly offset from the posterior end.

Both other caudal centra are from the middle portion of the tail (Figure 2B-D). The bones are heavily abraded. The vertebrae are amphi-platycoelous with a concave anterior and a plane posterior intervertebral facet. In the ventral half of the facets, a small bulge is found on both facets of Vb-857, but only on the posterior one in Vb-856. The sides of the centra are antero-posteriorly only slightly concave and dorso-ventrally considerably convex in Vb-857, while they are less convex dorso-ventrally but considerably concave antero-posteriorly in Vb-856.

The ventral surfaces of the centra are almost plain transversely. The chevron facets are relatively wide apart, with a shallow longitudinal groove between them. The ventral surface appears concave in lateral view, mainly because of the ventrally projecting chevron facets.

The broken attachments of the neural arches are slightly more than half the length of the centra (70 mm in Vb-857, 57 mm in Vb-856) and their anterior borders are almost confluent with the anterior intervertebral facets in Vb-857 and only a short distance offset from it in Vb-856. In Vb-857, a break on the lateral sides under the posterior end of the neural arch marks the former attachment of the transverse processes; in Vb-856, only a slight swelling is found in this position, indicating that this vertebra is from a more distal part of the tail than Vb-857.

Vb-879 is a 200 mm long portion of the distal end of a right tibia (Figure 3A,B). The articular surface is 115 mm wide and 195 mm long. It is relatively narrow anteriorly and flares distally. A well developed latero-ventral indentation is present where the bone widens. The articular surface is slightly inclined proximally in a postero-anterior direction. Laterally, a facet for the articulation of the fibula is present on the posterior half of the bone.

The bone shows a triangular cross-section at the break, with the long side medial. At that point, it is 103 mm wide and 125 mm long.

Vb-884 represents a proximal end of a left fibula (Figure 3C, D). The articular surface is 210 mm long and 72 mm wide, and is widest in the middle. While it narrows only slightly posteriorly, it ends in a relatively sharp, slightly medially pointing tip anteriorly. Both these parts of the bone are inclined distally. The structure of the articular surface resembles that of Vb-848. The bone is broken 130 mm below the articular surface. Along its midline, a broad ridge runs from the broadest part of the surface to the break on the lateral side; the other parts of the bone are very narrow. At the break, the fibula is 154 mm long and 38 mm wide at its widest part.

Discussion: Procoelous anterior caudals, like Vb-892, are usually seen as a typical character of titanosaurids (Powell 1986; McIntosh 1990), but they also occur in diplodocoids and the euhelopodid *Mamenchisaurus* (Hatcher 1901; Janensch 1929; Gilmore 1936; Young 1954). A significant difference between the caudal vertebrae of titanosaurids and the specimen from Sudan

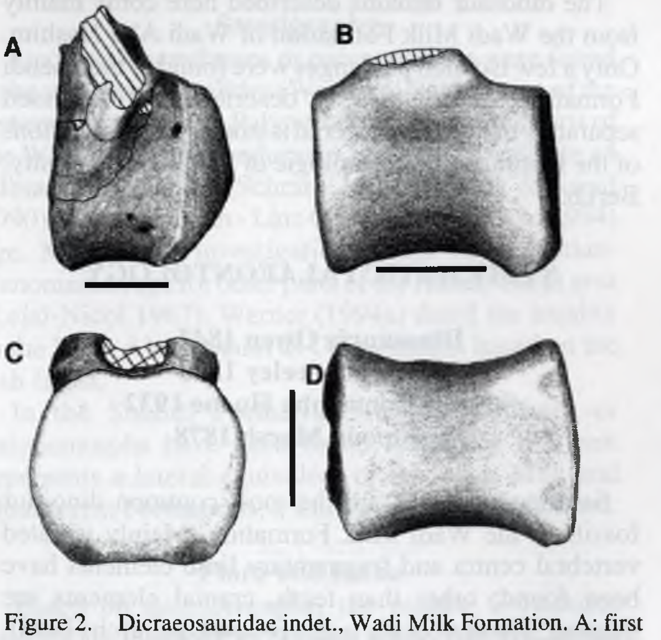

Figure 2. Dicraeosauridae indet., Wadi Milk Formation. A: first caudal vertebra; Vb-892; left lateral view. B-D: mid-caudal vertebra; Vb-856; B: left lateral view, C: posterior view, D: ventral view. Scale bars indicate 5 cm.

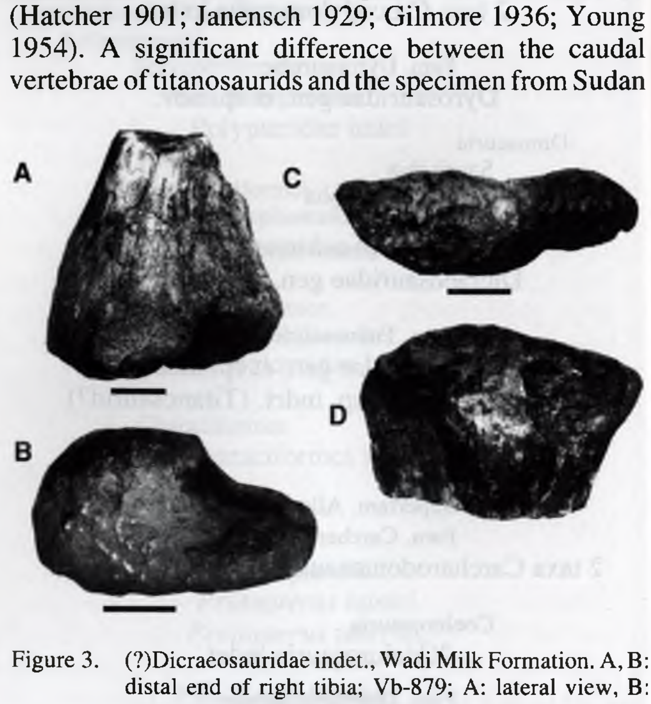

Figure 3. (?)Dicraeosauridae indet., Wadi Milk Formation. A, B: distal end of right tibia; Vb-879; A: lateral view, B: distal view. C, D: proximal end of left fibula; Vb-884; C: proximal view, D: lateral view. Scale bars indicate 5 cm.

is the bony lamina extending from the transverse process onto the centrum. In titanosaurids, this lamina is inclined posteriorly, rather than anteriorly, as it is in Vb-892 (Huene 1929; Powell 1986). Therefore, Vb-892 is referred to the Diplodocoidea.

Within diplodocoids, it differs from *Apatosaurus* in its more pronounced procoelous condition (Gilmore 1936), from *Diplodocus* in its lack of pleurocoels (Hatcher 1901), and there seem to be significant differences from the caudals of *Mamenchisaurus* in the development of the posterior intervertebral facet (Young 1954). On the other hand, the vertebra from Sudan is very similar to the second caudal of *Dicraeosaurus* (Janensch 1929: Taf. III, Figure 2) and is therefore referred to the Dicraeosauridae. The mid-caudals Vb-856 and Vb-857 also show strong resemblances to caudals of *Dicraeosaurus* in respect of their massive shape and widely separated and well developed chevron facets (Janensch 1929: Taf. III, Figure 18, pers. obs.), and for this reason they are assigned to the same taxon. In the tibia fragment, an antero-lateral projection of the fibular facet, such as found in most sauropods (e.g. Gilmore 1936: Figure 23D; Janensch 1961: Beilage K, Figure 3e; Ostrom & McIntosh 1966: Plate 75, Figure 1a), is absent. This projection is also absent from the distal tibiae of *Dicraeosaurus sattleri* and probably *Janenschia* (Janensch 1961). Since there are good arguments for the presence of a dicraeosaurine sauropod in Sudan, this limb fragment is tentatively also assigned to this taxon. The fibula Vb-884 is seemingly more slender than the fibulae of most sauropods (Huene 1929, Gilmore 1936, Janensch 1961, Ostrom & McIntosh 1966), but is similar to that of *Dicraeosaurus* (Janensch 1961).

Family: Titanosauridae Lydekker 1885
Gen. et sp. indet.

Teeth

Material: 53 teeth (Vb-721, Vb-900 to Vb-912).

Description: All the teeth are weakly spatulate to peg-like (Figure 4). The basal cross-section is round in most specimens, but the apical part of the crown is slightly flattened labio-lingually in several, but not all specimens. An unserrated cutting edge is developed mesially and distally. A few teeth show a slightly recurved crown (e.g. Vb-907); in this case, the mesial edge is restricted to the upper two thirds of the crown. The labial side is slightly more convex than the lingual one in all specimens. Enamel ornamentation is often found in the antapical part of the crown; it consists of several very small irregularly shaped ridges running parallel to the edges.

Many teeth show wear facets. While in some teeth the tip of the crown is simply worn away, several others show well defined triangular facets on the mesial or distal carina, sometimes inclined to the lingual, sometimes to the labial side. Janensch (1935-36)

Figure 4. Titanosauridae indet., Wadi Milk Formation. Teeth; A: Vb-721, lingual view, B: Vb-907, labial view, showing triangular apical wear facet, C: Vb-901, distal view, D: Vb-911, tooth of a juvenile individual, lingual view, E: Vb-907, tooth of a juvenile individual with partly preserved root and triangular wear facet, labial view. Scale bars indicate 1 cm.

described a similar phenomenon in the teeth of *Brachiosaurus brancai*, with the more lingually positioned facets found in the upper jaw and the more labially positioned ones in the lower jaw. If the same was true for the specimens from Sudan, 21 of the teeth showing wear facets represent teeth from the upper jaw and 14 from the lower jaw.

Discussion: Since the teeth of euhelopodids, "cetiosaurids", brachiosaurids and camarasaurids are much broader than the specimens from Sudan (Wiman 1929; Janensch 1935-36; Bonaparte 1986; McIntosh 1990), the latter must belong to a diplodocoid or titanosaurid, both groups which are characterized by relatively slender teeth (Marsh 1884; Huene 1929; Janensch 1935-36; Kues *et al.* 1980; Powell 1986; McIntosh 1990).

The teeth of diplodocoids are more slender than the elements from the Wadi Milk Formation (Marsh 1884, Janensch 1935-36), while the teeth of the titanosaurids *Laplatasaurus*, *Alamosaurus* and *Malawisaurus* are very similar to the specimens from Sudan (Powell 1979; Kues *et al.* 1980; Jacobs *et al.* 1993). Therefore, the teeth described above are referred to the Titanosauridae. The presence of two slightly different tooth types, one being more spatulate (similar to teeth of *Malawisaurus*; Jacobs *et al.* 1993), the other being very slender and showing an almost circular cross section (similar to teeth of Late Cretaceous titanosaurids; Powell 1979; Kues *et al.* 1980), may indicate the presence of different taxa.

Vertebrae

Material: One presacral (Vb-893) and fifteen caudal vertebrae (Vb-606, Vb-720, Vb-876, Vb-877, Vb-880, Vb-882, Vb-883, Vb-885, Vb-886, Vb-889, Vb-891, Vb-894, Vb-897, Vb-899, Vb-935).

Description: Vb-893 represents the anterior part of a presacral vertebral centrum (Figure 5). The lack of parapophyses on the centrum indicates that it is a posterior dorsal vertebra.

The anterior intervertebral facet is strongly convex, and the centrum is slightly higher than wide. The posterior intervertebral facet is broken away. Just below the former attachment of the neural arch, a pleurocoel

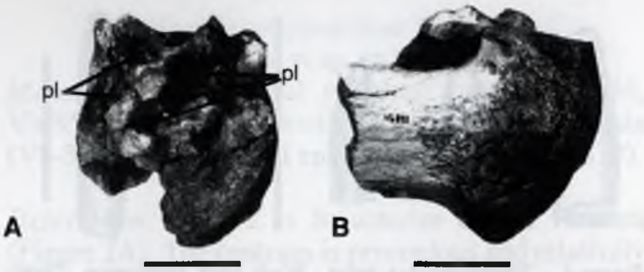

Figure 5. Titanosauridae indet., Wadi Milk Formation. Dorsal vertebrae; Vb-893; A: posterior view of the break, showing the arrangement of the pleurocoels (pl), B: right lateral view. Scale bars indicate 5 cm.

opening is found on both sides. The pleurocoels are longer than high and lead into large excavations in the interior of the centrum. The excavations are irregularly shaped and subdivided by thin laminae of bone. While the right pleurocoel leads into a large chamber extending in an obliquely ventral direction, the left excavation was much smaller and more dorsally placed. At the front end of the pleurocoels, a small, shallow groove in the shape of a recumbent letter 'L' is present on the sides of the vertebra. The neural arch is broken away, but its attachment most probably extended over the whole length of the centrum.

The vertebrae Vb-880 and Vb-883 represent biconvex first caudals.

The centra are wider than high, with a strongly convex posterior ball and a less convex anterior one. Well developed, but broken, transverse processes are present, mainly positioned on the anterior half of the centrum in Vb-880 (Figure 6), extending over the whole length in Vb-883. Below the processes, the centra are strongly convex dorso-ventrally. The ventral side is plain with a very slight depression in the middle in Vb-880, but slightly convex transversely in Vb-883. No chevron facets are present. Several large foramina are found on the lateral and ventral sides. A very large foramen, perhaps representing a vestigeal pleurocoel, is placed just below the attachment of the transverse process in Vb-883. The attachment of the well developed neural arch is situated mainly on the anterior half of the bone.

Vb-720, Vb-876, Vb-877, Vb-891, Vb-897, Vb-899 and Vb-935 represent strongly procoelous anterior caudals (Figure 7). The neural arches are restricted to the anterior half of the centra, but are unfortunately damaged or completely broken away in all specimens. The neural canal was relatively large and more or less circular in cross-section. Well developed, but broken, transverse processes are found in all elements on the anterior dorsal part of the sides. The ventral surfaces are almost plain, with well developed chevron facets. Several foramina are situated on the lateral and ventral surfaces of most elements. While the centra in Vb-876, Vb-877, Vb-891, and Vb-935 are higher than long, those of Vb-720, Vb-897 and Vb-899 are longer than high, indicating that the latter are from a more distal position in the tail.

Vb-882 and Vb-885 represent mid-caudals (Figure 8),

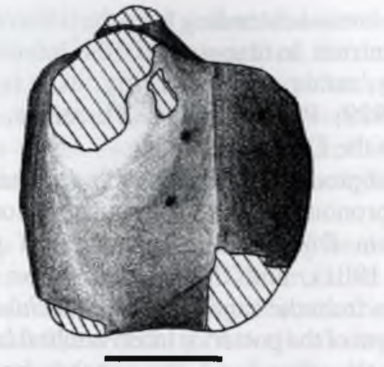

Figure 6. Titanosauridae indet., Wadi Milk Formation. Biconvex first caudal vertebra; Vb-880; left lateral view. Scale bar indicates 5 cm.

while all remaining centra are from the end of the tail (Figure 9). Vb-882 shows an almost rectangular cross-section, but Vb-885, which is obviously from a more distal position, appears to be more or less oval, its width being greater than its height. The centra expand strongly towards the intervertebral facets; this feature is especially striking at the posterior end in Vb-885. In Vb-882, the greatest expansion of the posterior ball lies in the upper half of the centrum. In both vertebrae, there is a small horizontal groove on the posterior ball. The chevron facets are relatively wide apart, more so at the anterior end than the posterior.

The broken attachments of the neural arches are located on the anterior half of the centra and are slightly more than half the centrum length. No transverse processes are present, but in Vb-882, a swelling on the lateral sides beneath the posterior part of the neural arch indicates the insertion of the process in more anterior caudals.

The posterior caudals Vb-606 and Vb-894 are the only other elements well enough preserved to warrant description (Figure 9).

Both vertebrae are relatively slender and show an almost circular cross-section in the middle. In Vb-606, the intervertebral facets are roughly hexagonal. The neural arch was obviously small and restricted to the anterior half of the centrum. As in Vb-885, several small foramina are situated close to the intervertebral facets and the posterior ball shows a shallow horizontal groove. The chevron facets are only weakly developed.

Vb-894 is rod-like, with only two small ridges instead of the neural arch. Although both intervertebral facets are damaged, the procoelous condition is clearly visible. As in the other vertebrae described above, a horizontal groove is present on the posterior face.

Discussion: The presacral vertebra Vb-893 shows irregularly shaped pleurocoels, a character found in titanosaurids (McIntosh 1990), and it is therefore referred to the Titanosauridae. Since biconvex first caudals are also a typical character of titanosaurids (Powell 1986; McIntosh 1990), it is very probable, that Vb-880 and Vb-883 belong to this family, too. The striking differences between these two elements may indicate the presence of more than one taxon.

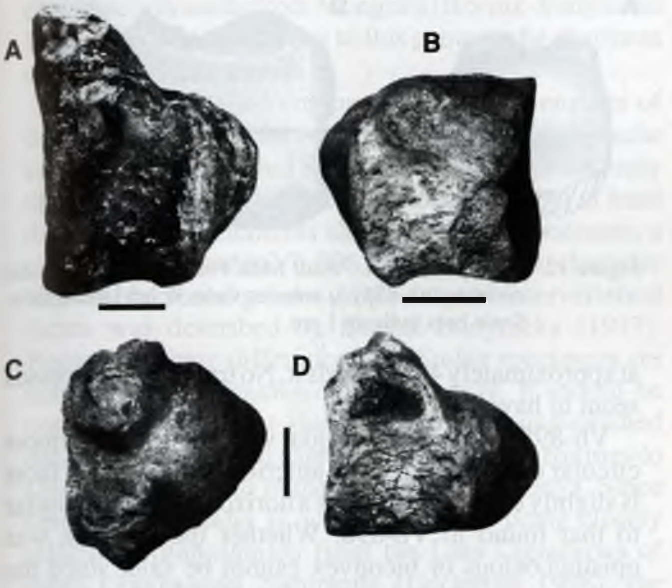

Figure 7. Titanosauridae indet., Wadi Milk Formation. A: anterior caudal vertebra; Vb-876; left lateral view. B: anterior caudal vertebra; Vb-897; right lateral view. C, D: anterior caudal vertebra; vb-899; C: dorsal view, D: left lateral view. Scale bars indicate 5 cm.

Although procoelous anterior caudals are also found in other sauropods (Janensch 1929; Gilmore 1936; Young 1954), the great expansion of the posterior ball in the Sudan vertebrae clearly indicates titanosaurid relationship (Powell 1986; McIntosh 1990). Since the caudal vertebrae are quite similar in different titanosaurids (e.g. Huene 1929; Powell 1986), the fossils from Sudan cannot be referred to a particular genus or species. It is possible that the titanosaurid *Aegyptosaurus*, originally described from the Cenomanian of Egypt (Stromer 1932), is also represented in the Wadi Milk Formation. It should be noted, however, that the taxon from Sudan obviously belongs to the crown group titanosaurids, judging by the procoelous posterior centra. Rod-like caudals like Vb-894 have been described for the genus *Saltasaurus* from the Late Cretaceous of South America (McIntosh 1990).

Because of the great similarity of the caudals of different titanosaurids, it is possible that the elements described above represent more than one species; several different taxa of titanosaurids are often found in one localitiy in the Late Cretaceous of South America, too (Powell 1986; Weishampel 1990).

Limb bones
Material: Distal end of a fibula (Vb-881).

Description: Vb-881 is the distal end of a ?right fibula (Figure 10). The preserved fragment is 210 mm long, its distal dimensions are 128 mm anterio-posteriorly and 107 mm medio-laterally. The cross-section of the bone at the break is semi-circular, with the lateral side rounded and the medial side straight. At this point, the antero-posterior length is 96 mm and the medio-lateral width 57 mm.

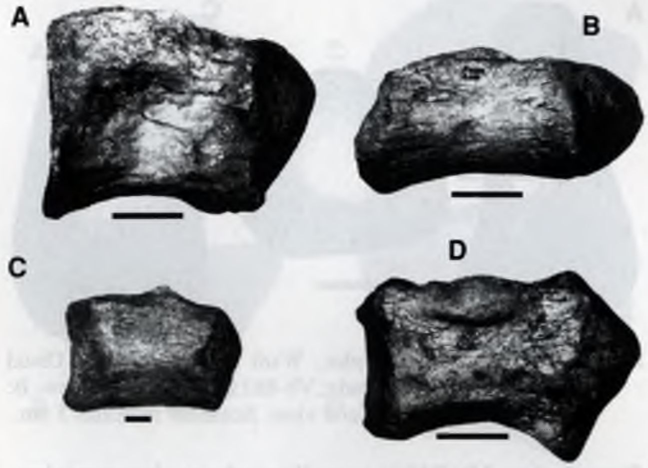

Figure 8. Titanosauridae indet., Wadi Milk Formation. A: mid-caudal vertebra; Vb-882; left lateral view. B, C: mid-caudal vertebra; Vb-885; B: left lateral view, C: dorsal view. D: posterior mid-caudal vertebra; Vb-889; left lateral view. Scale bars indicate 5 cm (A-C) and 1 cm (D).

The medial side is plain up to the distal articular surface, where a horizontal ridge is located. The articular surface is triangular and does not show any notable features, partly due to abrasion.

Discussion: This element is referred to the Titanosauridae because of the triangular shape of the distal articular surface. Such a shape is found in the fibulae of camarasaurids (Ostrom & McIntosh 1966) and titanosaurids, (Huene 1929, 1932). While the triangle is much lower in camarasaurids, the shape of the distal articular surface of a fibula of the South American titanosaurid, *Saltasaurus australis*, figured by Huene (1929: Lámina 16, Figure 5d), is strikingly similar to that of the specimen from Sudan.

Sauropoda indet.

Vertebrae

Material: Three vertebral centra (Vb-719, Vb-895, Vb-896).

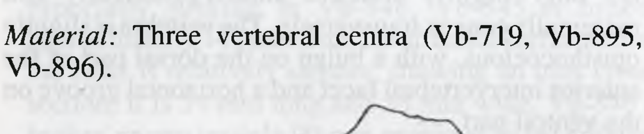

Figure 9. Titanosauridae indet., Wadi Milk Formation. A-C: posterior caudal vertebra; Vb-606; A: anterior view, B: left lateral view, C: posterior view. D: posterior caudal vertebra; Vb-894; left lateral view. Scale bars indicate 1 cm.

Figure 10. Titanosauridae indet., Wadi Milk Formation. Distal end of (?)right fibula; Vb-881; A: (?)anterior view, B: distal view, C: lateral view. Scale bar indicates 5 cm.

Description: Vb-719 is a small opisthocoelous vertebra, which is wider than high (Figure 11). The neural arch is missing; it has been separated from the centrum along its suture, indicating that the element derives from a juvenile individual. This is also supported by its small size, as well as by the cancellous appearance of the bone at the intervertebral facets and clearly visible bone fibres on the sides, both features that are typical for embryonic or very young dinosaurs (Britt & Naylor 1994). The lack of parapophyses implies that it is a dorsal vertebra.

Deep but simple pleurocoel excavations are found dorsally on the sides. These pleurocoels are simple pits which extend from the dorsal and lateral margins of the sides into the bone and reach their greatest depth just above the midline (in lateral view). The ventral side of the centrum is only slightly convex transversely, but strongly concave antero-posteriorly.

The suture of the neural arch extends over the whole length of the centrum. Its detailed structure cannot be described, because of erosion.

Vb-896 is a caudal vertebra with an almost rectangular cross-section (Figure 12). The lateral and ventral surfaces are only slightly concave antero-posteriorly and marginally convex transversely. The vertebra is slightly opisthocoelous, with a bulge on the dorsal part of the anterior intervertebral facet and a horizontal groove on the ventral part.

The neural arch has been detached along its suture, again indicating immaturity. The suture is slightly longer than the anterior half of the vertebra and shows four grooves separated by sharp ridges. While the anteriormost of these grooves stands at a right angle to the longitudinal axis of the bone, the last one is inclined

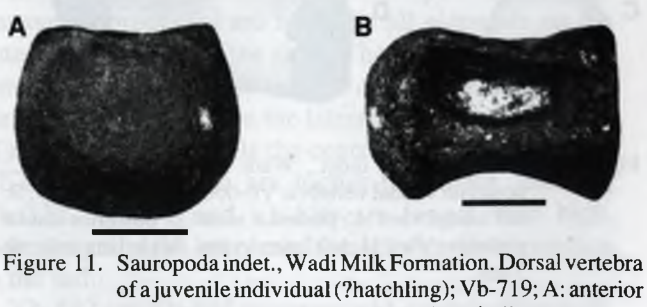

Figure 11. Sauropoda indet., Wadi Milk Formation. Dorsal vertebra of a juvenile individual (?hatchling); Vb-719; A: anterior view, B: left lateral view. Scale bars indicate 1 cm.

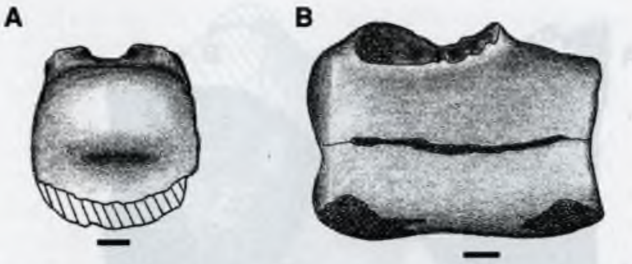

Figure 12. Sauropoda indet., Wadi Milk Formation. Mid-caudal vertebra; Vb-896; A: anterior view, B: left lateral view. Scale bars indicate 1 cm.

at approximately 45° towards it. No transverse processes seem to have been present.

Vb-895 is a posterior caudal vertebra with an almost circular cross-section. The anterior intervertebral facet is slightly convex and shows a horizontal groove similar to that found in Vb-896. Whether the vertebra was opisthocoelous or biconvex cannot be said, since the posterior part is missing. Instead of a neural arch, there are two small ridges dorsally. Although the bone is heavily damaged, it can be said with some certainty that it was probably not much longer than twice its height.

Discussion: The deep pleurocoels characterize the centrum Vb-719 as a saurischian vertebra. In large theropods like *Allosaurus*, the shape of the pleurocoels in the opisthocoelous anterior dorsal vertebrae is different, and these vertebrae show strongly developed parapophyses on the centrum (Madsen 1976). Pleurocoels similar to those in Vb-719 are found in some small theropods, but their dorsal vertebrae are usually not opisthocoelous (e.g. *Deinonychus*; Ostrom 1969). Therefore, the specimen from the Wadi Milk Formation is referred to the Sauropoda.

The element from Sudan differs from juvenile *Apatosaurus* and *Camarasaurus* dorsal vertebrae in showing deep pleurocoels (Carpenter & McIntosh 1994). Although cervical vertebrae of a juvenile *Camarasaurus* are similar to Vb-719 in respect of shape and development of pleurocoels, an important difference is the presence of parapophyses on the vertebral centrum in the former (Carpenter & McIntosh 1994). A dorsal centrum of a juvenile *Phuwiangosaurus* is quite similar in lateral view, but differs in the presence of a faint ventral keel (Martin 1994). A probably juvenile dorsal vertebra of the titanosaurid *Laplatasaurus* is very similar to Vb-719 in its general shape, and perhaps also in the development of the pleurocoels (Huene 1929: Lámina 22, Figure 18).

Since only few juvenile sauropod remains have been found so far, the systematic position of the Sudan specimen must remain unresolved for the present. However, the chances are that it belongs to one of the taxa described above, possibly to a titanosaurid.

The caudal vertebrae Vb-895 and Vb-896 probably belong to the same taxon, judging by the similar morphology of the anterior intervertebral facet. The anteriorly placed neural arch in Vb-896 indicates sauropod relationships for these specimens.

So far, within sauropods, opisthocoelous caudals have been described only in the Late Cretaceous taxon

Opisthocoelicaudia from Mongolia (Borsuk-Bialynicka 1977). A further similarity to this genus is the shortness of the posterior caudals.

However, detailed comparison reveals a number of differences between the vertebrae of *Opisthocoelicaudia* and the specimens from Sudan. In the Asian genus, only the first fifteen caudals are opisthocoelous, but at least the first sixteen elements show transverse processes, a character not found in Vb-896. Furthermore, no character like the horizontal groove on the anterior intervertebral facets was described by Borsuk-Bialynicka (1977). Because of these differences, the Sudan specimens are not referred to *Opisthocoelicaudia* here. It should be noted, however, that Harris & Russell (unpublished data) also recognized sauropod bones with affinities to *Opisthocoelicaudia* in the Cretaceous of Kenya. Since *Opisthocoelicaudia* is now regarded as being closely related to titanosaurids from the Late Cretaceous of other Gondwanan continents (Upchurch 1998), the presence of a closely related taxon from Africa would not be too surprising.

Limb bones

Material: Five limb bone fragments (Vb-845 to Vb-848, Vb-878).

Description and discussion: Vb-848 and Vb-878 are parts of the stylopod. They are referred to the Sauropoda because of their relatively large size and the poorly developed articular surfaces.

Vb-848 (Figure 13A,B) shows a slightly concave, oval proximal articular surface with a transverse width of 104 mm and an antero-posterior length of 135 mm. The surface consists of many small grooves and bumps, as seen in many sauropods. The bone narrows towards the break, which is 100 mm from the articular surface. While the posterior end of the surface is confluent with the shaft of the bone, the anterior end overhangs it, forming a ridge. The cross-section at the break is almost circular, with a width of 62 mm and a length of 64 mm.

This bone probably represents the proximal end of a radius (cf. e.g. Huene 1929: Lámina 11, Figure 4; Ostrom & McIntosh 1966: Plate 50). Because of its poor preservation, nothing further can be said about its identity.

Vb-878 (Figure 13C,D) shows a roughly oval proximal articular surface, which is 115 mm wide and 190 mm long. The bone is heavily eroded. It narrows towards the break, which is approximately 180 mm from the articular surface. At the break, the element is 45 mm wide and 120 mm long antero-posteriorly, with a sharp anterior and a rounded posterior margin.

The fragment from Sudan probably represents the proximal part of a right fibula. It shows similarities with the fibulae of *Saltasaurus australis* and *Apatosaurus louisae* (Huene 1929; Gilmore 1936), but because of its incompleteness and poor preservation, no further conclusions can be drawn.

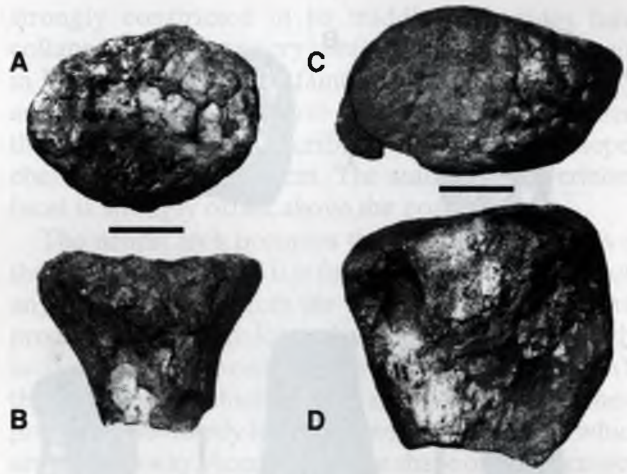

Figure 13. Sauropoda indet., Wadi Milk Formation. A, B: proximal end of a radius; Vb-848; A: proximal view, B: lateral view. C, D: proximal end of a right fibula; Vb-878; C: proximal view, D: lateral view. Scale bars indicate 5 cm.

Vb-847 is the proximal end of a metacarpal (Figure 14A, B). The shape of the articular surface is triangular, with an anterior width of 75 mm, a posterior width of 27 mm and a length of 102 mm. The anterior margin slightly overhangs the shaft of the bone. The bone is broken some 115 mm beyond the articular surface; at this point, it is oval in cross-section with a length of 50 mm and a width of 39 mm.

The element shows great similarities to metacarpal III of *Apatosaurus* and to metacarpal IV of *Janenschia* (Gilmore 1936; Janensch 1961), and therefore most probably represents a 3rd or 4th metacarpal of a sauropod. It cannot be referred to a particular taxon.

Vb-845 and Vb-846 are distal ends of metapodial elements (Figure 14C-H). The articular surfaces are roughly trapeziform, showing the typical small grooves and bumps. The articular surface is relatively narrow in the middle, but expands proximo-distally at the sides, more so medially than laterally. This expansion is especially striking in Vb-846. Vb-845 is broken approximately 140 mm from the articular surface. Here, the bone is relatively slender, showing an oval cross-section. It is 59 mm long and 55 mm wide. Vb-846 is broken approximately 90 mm proximal to the articular surface and is semi-circular in cross-section with a length of 49 mm and a width of 61 mm.

Vb-846 is very similar to the distal ends of metatarsals III or IV of a number of sauropods (Janensch 1961; Ostrom & McIntosh 1966) and therefore probably represents such an element. In Vb-846, the shape of the articular surface indicates that it is a metatarsal, while the relatively slender shaft rather implies identification as a metacarpal (see Janensch 1961; Ostrom & McIntosh 1966). None of the elements can be assigned to a particular genus or species of sauropod.

Theropoda Marsh 1881

Theropod remains are the second most common dinosaur fossils in the Wadi Milk Formation. Some vertebral centra and isolated limb bone fragments have

Figure 14. Sauropoda indet., Wadi Milk Formation. A, B: proximal end of a 3rd or 4th metacarpal; Vb-847; A: medial or lateral view, B: proximal view. C-E: distal end of a ?metatarsal; Vb-845; C: ?lateral view, D: anterior view, E: distal view. F-G: distal end of a metatarsal; Vb-846; F: ?lateral view, G: anterior view, H: distal view. Scale bars indicate 5 cm.

been found; teeth are rare in the collections from Sudan. In the following account, the systematic terms follow Sereno *et al.* (1996).

Tetanurae Gauthier 1986
Superfamily: Allosauroidea Currie et Zhao 1993
Family: Carcharodontosauridae Stromer 1931

Gen. et sp. indet.

Material: Three vertebrae (Vb-607, Vb-717, Vb-870).

Description: All these bones are caudal vertebrae, Vb-607 and Vb-717 being from the proximal portion of the tail, while Vb-870 represents a posterior mid-caudal (Figure 15). The vertebral centra are relatively well preserved in these elements, but the neural arches are broken, leaving just the rim of the neural canal in Vb-607 and Vb-717. All vertebra are amphicoelous, with the posterior intervertebral facet being less concave than the anterior one. The shape of the facets is oval to almost circular and the anterior facets are clearly offset above the posterior ones.

The bones are strongly waisted in the middle. In Vb-607 (Figure 15A,B), there are large grooves on either side, which deepen towards the posterior end to a small pneumatic foramen. The sides of this element have collapsed, showing almost identical collapse structures on both sides, suggesting that large pneumatic cavities were present within the bone. Very similarly shaped, though shallower, grooves are also found on the sides of Vb-717 (Figure 15C, D), but no foramina are present and the sides are not collapsed. In Vb-870, only very shallow depressions are found on the sides.

The ventral sides of all the vertebrae are keeled, with a very shallow longitudinal groove in the middle of the keel. Well developed chevron facets are found on both ends.

The preserved part of the neural arch in Vb-607 and Vb-717 is slightly wider than the middle of the centrum at its base, but it narrows dorsally. The neural arches are fused to the centra without any visible suture. Above the lateral grooves, a horizontal ridge, which bends dorsally in its posterior part, is present on the neural arch. No transverse processes are present on the preserved parts of the arches. The neural canal is oval and relatively large. The arches extend over almost the total length of the centra.

Discussion: Vb-606 has been figured by Buffetaut *et al.* (1990) as "large amphicoelous dorsal vertebra ... of a carnivorous dinosaur". However, the presence of chevron facets clearly indicates that it is a caudal vertebra.

Figure 15. Carcharodontosauridae indet., Wadi Milk Formation. A, B: anterior caudal vertebra; Vb-607; A: anterior view, B: left lateral view. C, D: anterior caudal vertebra; Vb-717; C: left lateral view, D: posterior view. E, F: mid-caudal vertebra; Vb-870; E: left lateral view, F: ventral view. Scale bars indicate 5 cm.

Within well known theropods, the vertebrae from Sudan show greatest similarities to the caudal vertebrae of *Torvosaurus* and allosaurids (Gilmore 1920; Madsen 1976; Britt 1991). As in the elements from the Wadi Milk Formation, the caudals of *Allosaurus* show a ventral keel with a shallow longitudinal groove, a strong constriction at mid-centrum compared with the diameter of the intervertebral facets, an anterior facet which is slightly offset above the posterior one, and a very similar development of the chevron facets (Gilmore 1920; Madsen 1976). The main differences between the vertebrae from Sudan and those of *Allosaurus* is the presence of pleurocoels in the anterior caudal Vb-607.

Within non-coelurosaurian tetanurans, pleurocoelous anterior caudals are found only in carcharodontosaurids (Rauhut 1995; Sereno *et al.* 1996); therefore, the specimens from Sudan are referred to the Carcharodontosauridae. One caudal vertebra referred to *Bahariasaurus* by Stromer (1934: Tafel II, Figure 25) shows great similarity to the elements from the Wadi Milk Formation: the pleurocoels are placed within a lateral groove, which is very similar to that found in Vb-607 and Vb-717, the anterior intervertebral facet is offset above the posterior one, pleurocoels are restricted to the anterior caudals, and a shallow longitudinal groove on the ventral keel is present. However, the type of *Bahariasaurus* may not be diagnostic, and at least some of the elements referred to this genus by Stromer (1934) probably represent a distinct coelurosaurian theropod (Sereno *et al.* 1996; Sereno pers. comm. 1996). According to the pleurocoelous condition of the vertebra figured by Stromer (1934: Tafel II, Figure 25), at least this and the associated specimens (No. 1912 VIII 62; see Stromer 1934: p. 28) represent a carcharodontosaurid, maybe *Carcharodontosaurus*.

(?)Carcharodontosauridae indet.

Vertebra

Material: One caudal vertebra (Vb-871).

Description: This vertebra is the most complete specimen from the Wadi Milk Formation (Figure 16). It shows a part of the neural spine and the transverse processes. The vertebra is amphicoelous, relatively long and strongly constricted in its middle. The sides have collapsed, showing a very similar structure to that found in Vb-607. Only a very faint keel is present ventrally, and the longitudinal groove is slightly more prominent than in the elements described above. Well developed chevron facets are present. The anterior intervertebral facet is strongly offset above the posterior one.

The neural arch occupies the anterior four-fifths of the vertebral centrum. It is fused to the centrum without any visible suture. From the well developed transverse processes, which are located on the posterior half of the arch just above the centrum, a ridge runs to processes at the front end which point antero-dorsally. These processes obviously led to the prezygapophyses, which are broken away. According to the shape of the processes, the prezygapophyses were elongated. Above the transverse processes, the bone is strongly bent medially towards the neural spine. The neural spine extends over the complete length of the neural arch and is 68 mm high in its middle, both ends being extensively damaged. The neural canal is relatively large.

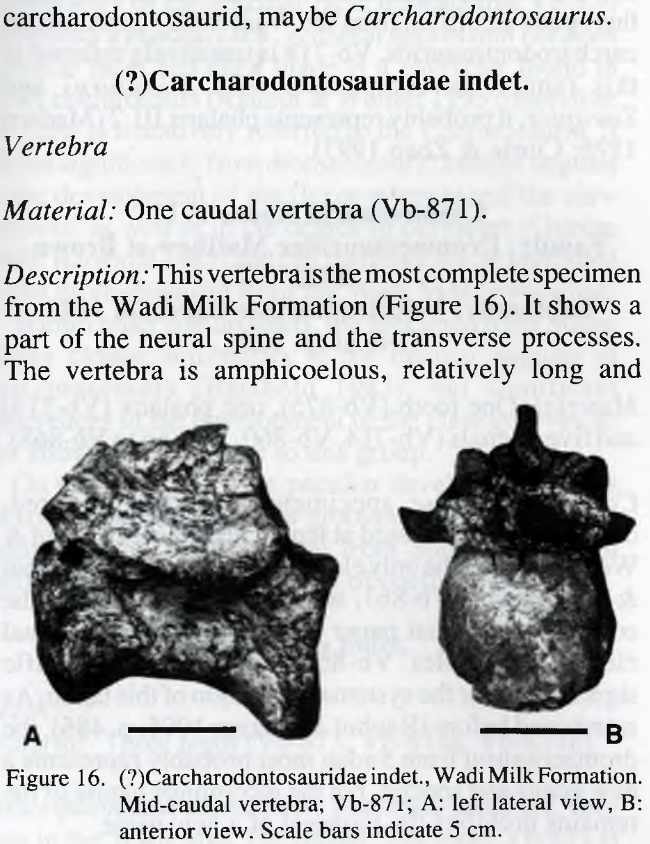

Figure 16. (?)Carcharodontosauridae indet., Wadi Milk Formation. Mid-caudal vertebra; Vb-871; A: left lateral view, B: anterior view. Scale bars indicate 5 cm.

Discussion: This vertebra probably represents a mid-caudal between the 16th and 19th caudal, judging from comparison with *Allosaurus* (Madsen 1976).

Again, great similarities to the caudals of *Torvosaurus* and *Allosaurus* are noted (Gilmore 1920; Madsen 1976; Britt 1991). Differences are the more pronounced offset of the facets and the obvious presence of internal cavities in Vb-871.

Internal cavities and strongly offset facets are found in *Carcharodontosaurus* and a caudal vertebra originally referred to *Bahariasaurus* (Stromer 1931, 1934; see above). Since the shape of the internal cavities also seems to have been very similar to those in Vb-607, Vb-871 can be referred to the Carcharodontosauridae. The differences in the development of the ventral keel and the longitudinal groove, as well as the presence of internal cavities in a posterior mid-caudal indicate that Vb-871 represents a different taxon from the elements described above.

Limb bones

Material: Proximal end of a metatarsal (Vb-849) and a phalanx (Vb-718).

Description: Vb-849 represents the proximal part of a right metatarsal III with a fused distal tarsal III (Figure 17). The proximal end of Vb-849 is 140 mm long antero-posteriorly and 95 mm wide medio-laterally. The bone narrows towards the break, at which it shows an oval cross-section with a length of 85 mm and a width of approximately 51 mm.

The proximal articular surface forms a wide overhanging rim anteriorly, it narrows towards its middle and abruptly widens again posteriorly. The posterior end is offset medially and inclined at an angle of approximately 25° medio-posteriorly against the anterior one.

Figure 17. (?)Carcharodontosauridae indet., Wadi Milk Formation. Proximal end of right metatarsal III with attached distal tarsal III; Vb-849; A: proximal view, B: medial view. Scale bar indicates 5 cm.

The medial wall of the bone is more or less straight in its anterior part, but strongly concave posteriorly. The lateral side is more or less straight, with an almost rectangular bulge on its proximo-posterior part. Under the overhanging rim of the articular surface, the anterior side becomes convex transversly. A muscle scar is located directly above the break on this side.

The distal tarsal is heavily abraded, but seems to have been of approximately the same shape as the distal tarsal III of *Allosaurus* (Madsen 1976: Figure 25B,C).

Vb-718 is a well preserved stout pedal phalanx (Figure 18). Its broad proximal articular facet is strongly

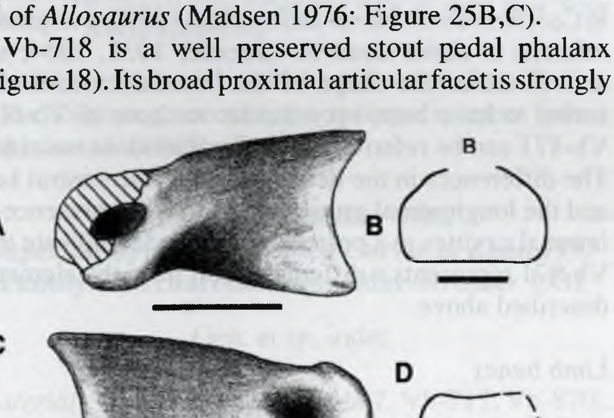

Figure 18. (?)Carcharodontosauridae indet., Wadi Milk Formation. Pedal phalanx; Vb-718; A: left lateral view, B: proximal outline, C: right lateral view, D: distal outline, E: dorsal view, F: ventral view. Scale bars indicate 5 cm.

concave dorso-ventrally, but almost plain transversely. No median ridge is present. The distal articular facet forms a wide ginglymoidal arch which extends further proximally on its ventral side than dorsally. The dorso-ventrally well rounded facet is only slightly concave transversely. The collateral ligament fossae are very deep in the middle of the arch, shallow significantly in a dorso-proximal direction and end above the ventral proximal extension of the articular facet. On the dorsal side, a triangular groove is found proximal to the articular facet. The ventral side is almost plain. A wide area in front of the proximal articular facet is covered with small ridges and grooves, indicating the insertion of the flexor tendon. A similar structure is found to a lesser extent on the dorsal side in front of the proximal facet.

Discussion: Specimen Vb-849 from the Wadi Milk Formation is very similar to the third metatarsals of *Torvosaurus, Sinraptor* and *Allosaurus* (Madsen 1976; Britt 1991; Currie & Zhao 1993). The closest similarity is found in *Sinraptor* (Currie & Zhao 1993: Figure 26B). Since *Sinraptor* and carcharodontosaurids both belong to the superfamily Allosauroidea, and carcharodontosaurids are probably the only large theropods present in the Wadi Milk Formation, Vb-849 is tentatively referred to this family.

The general morphology of phalanx Vb-718 is similar to that of many large theropods and ornithopods (Madsen 1976; Norman 1986; Currie & Zhao 1993). Significant differences to ornithopods are found in the development of the collateral ligament fossae (Taquet 1976; Norman 1986), so the element is referred to the Theropoda.

Within theropods, the pedal phalanges are very similar in widely differing taxa. However, since the only large theropods identified from the Wadi Milk Formation are carcharodontosaurids, Vb-718 is tentatively referred to this family. In comparison with *Allosaurus* and *Sinraptor*, it probably represents phalanx III-2 (Madsen 1976; Currie & Zhao 1993).

Coelurosauria Huene 1914
Family: Dromaeosauridae Matthew et Brown 1922
Subfamily: Velociraptorinae Barsbold 1983
Gen. et sp. indet.

Material: One tooth (Vb-875), one phalanx (Vb-713) and five unguals (Vb-714, Vb-860, Vb-866 to Vb-868).

Comments: These specimens have been figured, described and discussed at length elsewhere (Rauhut & Werner 1995). The only element not described in Rauhut & Werner was Vb-867, which was discovered in the collection after that paper was submitted. The ungual closely resembles Vb-868 and is of no specific significance for the systematic position of this taxon. As mentioned before (Rauhut & Werner 1995: p. 486), the dromaeosaurid from Sudan most probably represents a new genus and species, but the incomplete nature of the remains prohibits the proposal of a new name.

?Coelurosauria indet.

Material: A proximal part of an ungual (Vb-839).

Description: Vb-839 represents the distal portion of a manual ungual (Figure 19). The articular facet is more or less triangular in outline, with its greatest width ventrally. It is strongly concave in lateral view and does not show any medial ridge. The flexor tubercle is very strongly developed. Distal to the articular facet, the bone narrows significantly. On the dorsal margin, a small depression is situated between the articular facet and the claw blade. The claw grooves begin at the articular facet at about half the height of the specimen and run at a steep angle dorsally. They meet on the dorsal margin just 21 mm away from the proximal end. On the ventral side, a longitudinal groove is present, beginning in front of the flexor tubercle. It cannot be stated with certainty whether this groove represents an erosional feature or an original character of the claw. The width of the claw remains constant over its entire preserved length. The claw was obviously not very strongly curved.

Figure 19. ?Coelurosauria indet., Wadi Milk Formation. Manual ungual; Vb-839; A: left lateral view, B: proximal outline, C: ventral outline. Scale bars indicate 1 cm.

Discussion: The very striking flexor tubercle and the morphology of the articular facet indicate that Vb-839 represents a manual claw. A dorsal depression between articular facet and claw blade is a character found in many coelurosaurs (Rauhut & Werner 1995); therefore the claw is tentatively referred to the Coelurosauria. It differs significantly from dromaeosaurid manual unguals in the development of the flexor tubercle and the claw grooves, as well as in the degree of curvature (Ostrom 1969; Barsbold 1983) and can therefore not be attributed to the dromaeosaurid from the Wadi Milk Formation.

Within other coelurosaurs, the specimen from Sudan shows closest similarities to the manual unguals of oviraptorosaurs (Barsbold 1983), but significant differences in the development of the claw grooves do not allow an assignment to this group.

On the other hand, the peculiar development of the flexor tubercle and the claw grooves might represent an autapomorphy of the ungual from Sudan and might therefore indicate a new taxon of coelurosaurs.

Theropoda indet.

Teeth

Material: Three teeth (Vb-873, Vb-874a, Vb-874b).

Description and discussion: Theropod teeth are very rare in the Wadi Milk Formation. The tooth Vb-873 is the most complete specimen in the collection. The crown is 20 mm high and c. 9 mm long. It is strongly compressed laterally, but only slightly recurved. Both carinae show serrations. The denticle count is 3.5 denticles per mm on the mesial carina and 3 per mm on the distal one. The denticles are rounded or slightly inclined apically in the upper parts of the crown. Downward pointing grooves are found between the bases of the denticles. The antapical part of the mesial carina is damaged. The tooth enamel is smooth.

Downward pointing grooves at the bases of the denticles are found in *Allosaurus*, tyrannosaurids and *Carcharodontosaurus* (Stromer 1931; Currie *et al.* 1990; Rauhut & Kriwet 1994). Since the teeth of *Carcharodontosaurus* are also relatively straight (Stromer 1931), Vb-873 might represent a small or juvenile carcharodontosaurid.

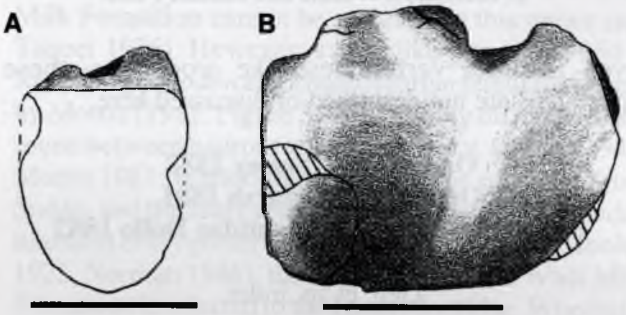

Figure 20. Theropoda indet., Wadi Milk Formation. Two fused sacral vertebrae; Vb-852; A: posterior view, B: right lateral view. Scale bars indicate 5 cm.

Vb-874a and Vb-874b are only apical parts of tooth crowns. The denticles are slightly inclined apically and at least Vb-874b seems to have been strongly recurved. The systematic position of these fragments is unsure. Some other tooth fragments are present, but they are too fragmentary for description.

Vertebrae

Material: Two fused sacral vertebrae (Vb-852).

Description: This specimen is badly damaged (Figure 20). The posterior intervertebral facet of the posterior vertebra is plain, the anterior centrum is broken at its front end. The ventral side is sharply keeled and straight in lateral view. No grooves or pleurocoels are present on the sides. The two centra are firmly fused, the suture forming a horizontal swelling on the sides. The neural arches are not preserved.

Discussion: The specimen shows strong similarities to the fused sacrals of a juvenile tyrannosaurid in the Museum of the Rockies, Bozeman (MOR 533E), and for that reason is referred to the Theropoda.

Indeterminate limb elements

Several isolated phalanges with theropod affinities were found in the Wadi Milk Formation. However, since similar elements are found in other dinosaurs and

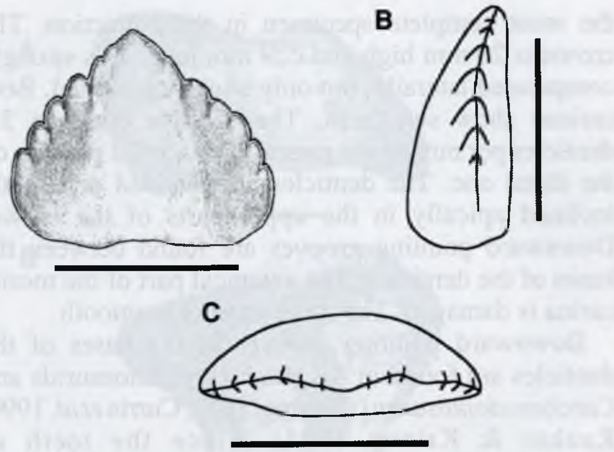

Figure 21. ?Hypsilophodontidae indet., Wadi Milk Formation. Tooth; Vb-936; A: lingual view, B: mesial view, C: occlusal view. Scale bars indicate 1 mm.

even in other vertebrates, like crocodiles, these specimens are not described or discussed here.

Ornithischia Seeley 1888
Ornithopoda Marsh 1881
Family: (?)Hypsilophodontidae Dollo 1882

Gen. et sp. indet.

Material: One tooth (Vb-936).

Description: Vb-936 is a leaf-shaped tooth crown with large marginal denticles (Figure 21). The specimen is very small, with a basal length of 1,43 mm, a basal width of 0,53 mm and a crown height of 1,17 mm. The crown is strongly compressed labio-lingually.

Four large denticles are present mesial to the well developed apical one; on the distal carina, the count is five. On both sides of the apex, two additional smaller denticles are present. Both carinae are slightly bent to the lingual side, making the labial side more convex than the lingual one. A constriction between crown and root is obviously present, but no basal cingulum can be recognized.

Discussion: The leaf-shaped crown and large denticles characterize the specimen from Sudan as an ornithischian tooth. Within ornithischians, very similar teeth are found in the most primitive members of this group ('fabrosaurids', e.g. *Lesothosaurus*) and hypsilophodontids (Galton 1983; Sereno 1991). Since no 'fabrosaurids' have been described from the Cretaceous to date, Vb-936 is tentatively referred to the Hypsilophodontidae. The lack of longitudinal ridges confluent with the marginal denticles, a character seen as a synapomorphy of hypsilophodontids by Weishampel & Heinrich (1992), might be due to the presumably early juvenile ontogenetic stage of the specimen, as has been suggested by Galton (1983).

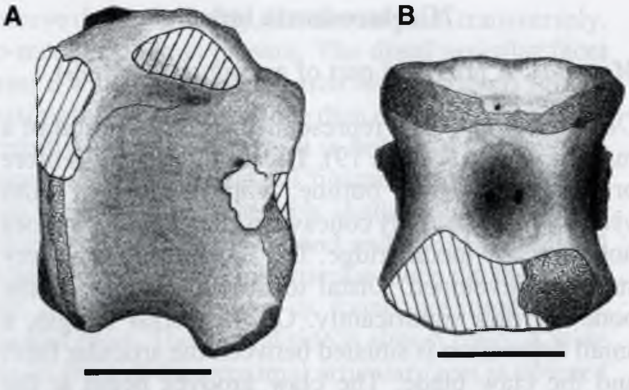

Figure 22. cf. *Oranosaurus* sp., Wadi Milk Formation. Anterior caudal vertebra; Vb-723; A: left lateral view, B: ventral view. Scale bars indicate 5 cm.

Iguanodontia Dollo 1882
Family: ?Iguanodontidae Gervais 1852
cf. *Ouranosaurus* sp. Taquet 1976

Material: Two caudal vertebrae (Vb-723, Vb-853).

Description: Both vertebrae are amphicoelous, with only shallow concavities on the intervertebral facets. While Vb-723 (Figure 22, 23A-C) is a vertebra from the anterior mid-caudal region, Vb-853 (Figure 23D) comes from the posterior portion of the tail.

In Vb-723, the intervertebral facets are subrectangular rather than round. The sides are almost plain dorso-ventrally and only weakly concave antero-posteriorly. On the ventral side, there is a deep longitudinal groove between two well developed lateral ridges. Within the groove are two small parallel pits. The well developed chevron facets are especially striking at the posterior end.

The rim of the neural canal and the attachment of the transverse processes are the only remaining parts of the neural arch preserved. The neural arch occupies almost the entire length of the centrum. The transverse processes were directed laterally and slightly posteriorly.

In Vb-853, the cross-section of the centrum is almost hexagonal, due to a weak ridge dividing the sides into two planes, the upper being slightly inclined dorsally, the lower one ventrally. Except for this feature, the sides are almost plain. The ventral side is also plain, showing only very weak indications of the lateral ridges. A single small pit is located in the middle. The neural arch, which originally occupied the entire length of the centrum, is broken away.

Discussion: The subrectangular shape of the vertebrae indicates that they are ornithischian elements. Within ornithischians, the greatest similarities are found in the caudal vertebrae of advanced ornithopods (Ankylopollexia in Sereno 1986; see e.g. Nopcsa 1925; Casamiquela 1964; Taquet 1976; Norman 1986). Caudal vertebrae of *Iguanodon* usually show a plain or slightly convex ventral surface (Hooley 1925; Norman 1986), although Owen (1851) figured a vertebra of this genus with a ventral groove. This groove, however, is shallower than in Vb-723 and no small pits are present.

A ventral groove like that found in Vb-723 is present in *Ouranosaurus* and hadrosaurids (pers. obs.; see e.g. Nopcsa 1925; Taquet 1976). Since *Ouranosaurus* is found in the Cretaceous of Africa and the elements from Sudan are almost identical to caudal vertebrae of this taxon (pers. obs.; see Taquet 1976), the specimens are tentatively referred to this genus.

Whether *Ouranosaurus* is a representative of the family Iguanodontidae is disputed: while it is placed in this family by Norman (1990) and Norman & Weishampel (1990), Sereno (1986) considers it to be the sister group of hadrosaurids.

Iguanodontidae indet. (?*Iguanodon* sp.)

Material: Distal end of a femur (Vb-850).

Description: Vb-850 represents a heavily damaged distal end of a left femur (Figure 24). Only the posterior part of the medial condyle is well preserved, the anterior side is abraded and the lateral condyle broken. The transverse width of the articular surface is approximately 135 mm. The medial condyle is significantly wider than the lateral one. The postero-proximal extension of the articular surface exceeds the medial height of the condyle, giving the appearance of a cleft between the femoral shaft and the posterior part of the condyle. The distal part of the condyle is only slightly convex over most of its length, but is strongly bent proximally in its posterior part. A ridge runs down from the posterior part of the medial side of the femoral shaft to the bend and widens just above the articular surface.

The extensor groove was obviously relatively deep, as far as this can be judged from the heavily abraded anterior surface.

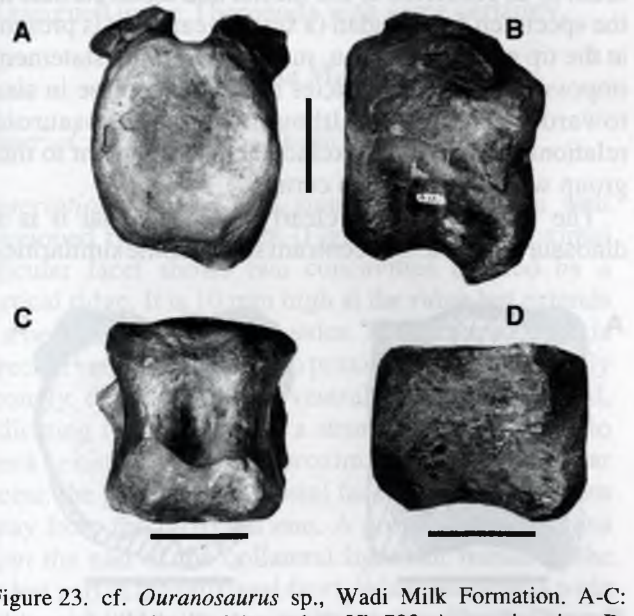

Figure 23. cf. *Ouranosaurus* sp., Wadi Milk Formation. A-C: anterior caudal vertebra; Vb-723; A: anterior view, B: left lateral view, C: ventral view. D: mid-caudal vertebra; Vb-853; left lateral view. Scale bars indicate 5 cm.

Discussion: VB-850 shows significant differences from theropod femora in the presence of a cleft between the shaft of the bone and the posterior extension of the medial condyle (e.g. Gilmore 1920; Osmólska *et al.* 1972; Madsen 1976; Ostrom 1976; Currie & Zhao 1993). Although a cleft like this is found in the femur of *Camarasaurus* (Ostrom & McIntosh 1966), significant differences in the general shape, and the shape of the distal outline between Vb-850 and sauropod femora, do not allow an assignment of the former element to the Sauropoda (Huene 1929; Janensch 1961; Ostrom & McIntosh 1966).

Within ornithischians, the femur fragment from Sudan differs from most taxa in the character of the cleft between femoral shaft and posterior extension of the articular surface. For example, this character is not found in *Ouranosaurus*, so the fragment from the Wadi Milk Formation cannot be assigned to this genus (see Taquet 1976). However, a cleft like that in Vb-850 is found in *Iguanodon* and a hadrosaurian femur illustrated by Morris (1981: Figure 3). Since many differences are found between hadrosaurian femora (e.g. Colbert 1948; Morris 1981; Wellnhofer 1994) and the specimen from Sudan, and the latter resembles the femur of *Iguanodon* in almost every preserved detail (see Dollo 1883, Hooley 1925, Norman 1986), the fragment from the Wadi Milk Formation is referred to the Iguanodontidae. Whether it represents the genus *Iguanodon* cannot be said; the presence of the closely related taxon *Lurdusaurus* in the Aptian of Niger (Tacquet & Russell 1999) raises the possibility that the latter taxon is also present in Sudan.

Ornithopoda indet.

Material: One caudal vertebra (Vb-854).

Description: Vb-854 is an amphicoelous distal caudal centrum (Figure 25). The shape of the intervertebral facets is oval to subrectangular. While the lateral sides are strongly convex dorso-ventrally, the ventral surface is almost plain. Chevron facets are only present at the posterior end and they are widely spaced. The neural arch, which originally occupied the anterior three fourths

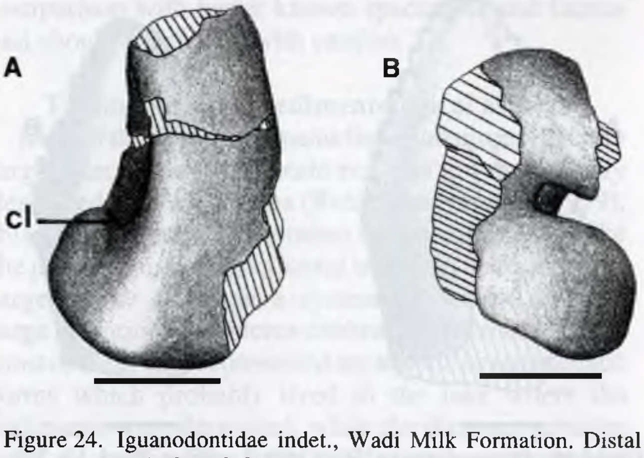

Figure 24. Iguanodontidae indet., Wadi Milk Formation. Distal end of a left femur; Vb-850; A: medial view, note the cleft (cl) between shaft and posterior extension of the condyle B: distal view. Scale bars indicate 5 cm.

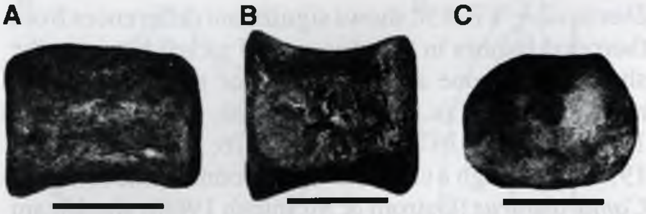

Figure 25. Ornithopoda indet., Wadi Milk Formation. Posterior mid-caudal vertebra; Vb-854; A: left lateral view, B: dorsal view, C: anterior view. Scale bars indicate 5 cm.

of the centrum, has been separated from it along its suture. Nothing can be said about the structure of this suture because of abrasion.

Discussion: The specimen closely resembles distal caudal vertebrae of *Prosaurolophus* (pers. obs.), and it is therefore referred to the Ornithopoda. Since similar vertebrae are found in *Iguanodon bernissartensis*, the element described above may belong to the same taxon as the femur fragment Vb-850.

Dinosauria indet.

Material: One tooth (Vb-722), a vertebra (Vb-855) and a distal end of a femur (Vb-851).

Description: Vb-722 is a leaf-shaped tooth crown with a strong constriction at its base (Figure 26). It is 3,6 mm high and 2,5 mm wide at its widest. It is almost circular in cross-section at its base. Apically the tooth is flattened labio-lingually and slightly bent to the lingual side. Thirteen large denticles are present on the mesial and at least twelve on the distal carina, the lower part of which is slightly damaged. The denticles are inclined apically and are largest in the middle of the carina. There, denticle spacing is 2,5 denticles per mm. Both carinae are slightly bent to the lingual side. On the lingual side are two shallow parallel grooves with a length of approximately 1,5 mm.

Vb-855 represents an amphicoelous caudal vertebra (Figure 27). The intervertebral facets are almost circular and the sides are strongly concave antero-posteriorly, but only moderately convex dorso-ventrally. The ventral surface shows two well developed chevron facets at the posterior end with a shallow groove between them. The neural arch, which originally occupied the anterior three fourths of the centrum, has been separated from it along its suture. Two well developed but broken transverse processes are present on the anterior part of the attachment of the neural arch.

Vb-851 is the poorly preserved distal end of a right femur (Figure 28). The articular surface is approximately 120 mm wide. The medial condyle is wider than the lateral. The articular surface is steeply inclined proximally in its anterior part. The extensor groove is shallow. The cross-section of the bone is subrectangular at the break.

Discussion: Werner (1994a) illustrated the tooth (Vb-722) and referred it to the Ornithopoda.

Large marginal denticles are found in ornithischians, primitive sauropodomorphs and therizinosauroids (e.g. Galton 1983, 1990a, b; Coombs & Maryanska 1990; Russell & Dong 1993). However, the teeth of ornithischians differ significantly in the shape of the crown (Galton 1983, 1990b; Sues & Galton 1987; Coombs & Maryanska 1990), making an ornithischian relationship for Vb-722 seem unlikely. Although the teeth of some prosauropods show a similar shape in combination with large marginal denticles, the fact that no prosauropods are known from sediments younger than the Early Jurassic (Galton 1990a) does not allow an assignment of the Sudan specimen to this group. In the therizinosauroid *Alxasaurus*, a similar tooth shape in combination with large marginal denticles is also found (Russell & Dong 1993). However, the denticles of Vb-722 seem significantly different from those on the teeth of *Alxasaurus*, which do not become significantly smaller towards the apex and even cover the tip in the Mongolian taxon (Russell & Dong 1993), while they seem to be restricted to the mesial and distal carinae in the specimen from Sudan (a small wear facet is present at the tip of this specimen, making a definite statement impossible, but the denticles strongly decrease in size towards the apex). Although a therizinosauroid relationship cannot be excluded, an assignment to this group would be far from certain.

The size of Vb-855 clearly indicates that it is a dinosaur vertebra. The centrum shows some similarities

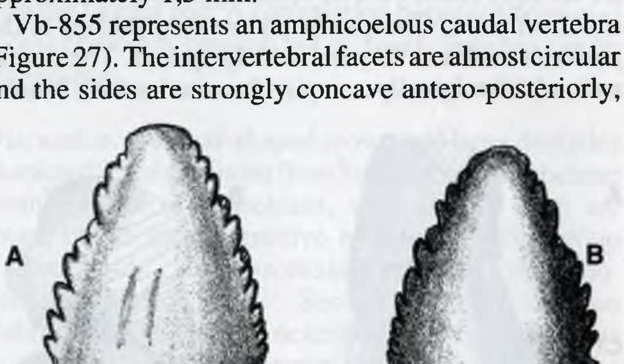

Figure 26. Dinosauria indet., Wadi Milk Formation. Tooth; Vb-722; A: lingual view, slightly rotated mesially, B: labial view. Scale bars indicate 1 mm.

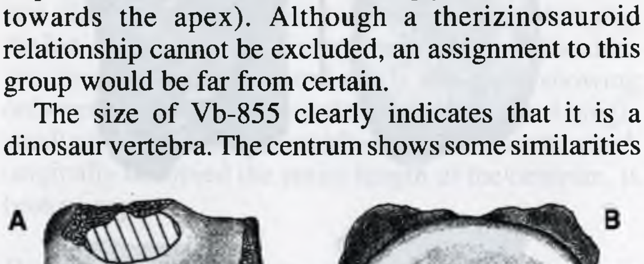

Figure 27. Dinosauria indet. (?Sauropoda), Wadi Milk Formation. Mid-caudal vertebra; Vb-855; A: left lateral view, B: anterior view. Scale bars indicate 5 cm.

Figure 28. Dinosauria indet., Wadi Milk Formation. Distal end of right femur; Vb-851; A: medial view, B: distal view. Scale bars indicate 5 cm.

to caudal vertebrae of brachiosaurids in respect of its general shape (Janensch 1950), therefore it might represent a further taxon of sauropod. However, since there are differences in the attachment of the transverse processes, no assignment of the element is proposed here.

The femur fragment Vb-851 resembles theropod femora in its general shape, but no femur with a similar steep angulation of the articular surface has been observed by the author; therefore, the specimen is assigned for the time being to Dinosauria indet.

Dinosaur remains from the Shendi Formation

Only few of the bones found in the Shendi Formation may be referable to dinosaurs. They are exclusively isolated phalanges. These elements show a proximal articular facet with a medial vertical ridge and a well developed ginglymoidal distal articular facet. Since similar elements are also found in other groups of vertebrates, these specimens are not described or discussed in detail here. Only one of the phalanges can be assigned to the Theropoda with some certainty.

(?)Theropoda Marsh 1881

Material: One phalanx (Vb-861).

Description: Vb-861 is a stout phalanx with a well developed flexor tubercle (Figure 29). The proximal articular facet shows two concavities divided by a vertical ridge. It is 10 mm high at the ridge but extends to a height of 15 mm at the sides. The flexor tubercle is directed ventrally rather than proximally. It is extremely strongly developed. The ventral part is roughened, indicating the insertion of a strong flexor tendon. No 'neck' exists between the proximal and distal articular facets: the ginglymoidal distal facet begins only 5 mm away from the proximal one. A prominent ridge runs from the end of the collateral ligament fossae to the widest part of the proximal facet. While the bone is wide below this ridge, it narrows dorsally. The collateral ligament fossae are L-shaped and situated ventral to the midline rather than dorsal. The distal articular facet is

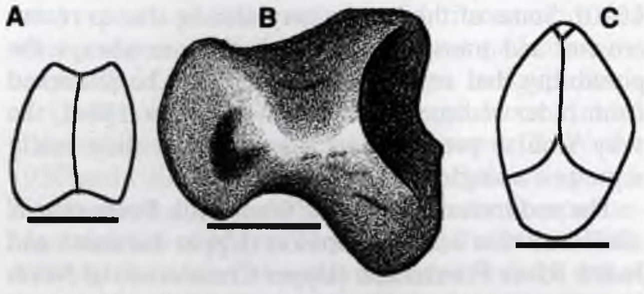

Figure 29. (?)Theropoda indet., Shendi Formation. Pedal phalanx; Vb-861; left lateral view, with distal (left) and proximal (right) outlines. Scale bars indicate 1 cm.

deeply grooved. In front of the facet, a shallow triangular groove is present on the dorsal side. Two small foramina are located within this groove.

Discussion: The strongly developed flexor tubercle indicates that the phalanx described above did not touch the ground during walking. It seems to be well adapted for rapid and/or strong flexion of the digit. Although it cannot be excluded that it represents a manual phalanx of a theropod, its morphology is more consistent with pedal phalanges.

Pedal phalanges showing a strongly developed flexor tubercle in combination with a stout shape are found in troodontids (Osmólska 1987; Osmólska & Barsbold 1990). However, since there are significant differences in the direction of the tubercle and the development of the collateral ligament fossae, the specimen from Sudan is not referred to the Troodontidae here.

In summary, Vb-861 can only be seen as an element of an undetermined small theropod with possible troodontid affinities. It should be noted that a very similar but less well preserved element is also present in the material from the Wadi Milk Formation (Vb-859, not figured).

TAPHONOMY AND PALAEOECOLOGY

The reconstruction of the palaeoecology of the Sudan dinosaurs is difficult, because of the poor preservation of the specimens and the limited data on taphonomy. Therefore, the ideas presented here are mainly based on comparison with better known specimens and faunas and should be viewed with caution.

Taphonomic and sedimentological aspects

Most of the dinosaur remains from Sudan are relatively large. Since small vertebrate remains are more easily destroyed than larger ones (Behrensmeyer *et al.* 1979), this does not necessarily mean that small animals like the probable hypsilophodontid were less abundant than larger ones. Although a systematic search revealed large quantities of microvertebrates (Werner 1994a), most of the groups represented are aquatic or semiaquatic forms which probably lived in the lake where the sediments were deposited, while the dinosaur remains were washed in. The latter conclusion is supported by the signs of abrasion on almost all of the bones, indicating subaerial exposure over some time (Behrensmeyer

1990). Some of the breaks may also be due to recent erosion and transport. Although there is always the possibility that some of the bones may be reworked from older sediments (see Behrensmeyer 1984), the very similar preservation suggests that they really represent a single fauna.

The sedimentology of the Wadi Milk Formation is similar to that of the Morrison (Upper Jurassic) and Judith River Formations (Upper Cretaceous) of North America (Dodson 1971; Dodson *et al.* 1980; Bussert 1993a,b). In all cases, the sediments are dominated by fluvio-lacustrine deposits, showing rapid lateral changes. The climate was warm and there were seasonal changes in the water supply. Since the dinosaur faunas of the Morrison and Judith River Formations are among the best known in the world, and given the similarities in the sedimentology, the taphonomic and palaeoecological data from the North American Formations may be used for comparison with the Wadi Milk Formation.

Differences between the Morrison and Judith River Formations are found in the taphonomy of the dinosaurs: while single articulated or disarticulated skeletons are often found in the Judith River Formation (Dodson 1971), dinosaur localities in the Morrison Formation are characterized by a multispecific assemblage of disarticulated bones (Dodson *et al.* 1980). In comparison, the dinosaur locality from the Wadi Milk Formation is clearly of the Morrison type. Similarities to Morrison dinosaur faunas are also found in the combination of taxa (at higher taxonomic levels): sauropods are most abundant, followed by theropods, and ornithopods are rare. While the relative rarity of theropods might reflect lower population densities compared with the sauropods, the ornithopods possibly lived in a more distal environment (see Dodson *et al.* 1980). Differences between the Morrison and Wadi Milk Formations are found in the higher abundance of aquatic and semiaquatic vertebrates in the latter (Dodson *et al.* 1980; Werner 1994a). This implies a more steady water supply in the Sudanese formation, as is also indicated by palynological and sedimentological data (Schrank 1990; Bussert 1993b). Another difference is the presence of articulated skeletons in the Morrison Formation, as in Dinosaur National Monument, Utah, USA, although this may be more apparent than real and may be due to the different states of research carried out in the wo formations.

In summary, the similarities between the Morrison and Wadi Milk Formations indicate similar, rather uniform landscapes with abundant sauropods, less abundant theropods and rare ornithopods.

Biological aspects

Titanosaurids and dicraeosaurids posess a relatively short neck in comparison with most other sauropods (McIntosh 1990). While feeding in high tree crowns, as suggested by Bakker (1978), seems quite plausible for the giraffe-like brachiosaurids, the shorter neck of titanosaurids may imply that these animals preferred plants growing at moderate heights.

According to Bakker (1978), large iguanodonts probably fed on low growing vegetation. If this was also the case in the iguanodonts from Sudan, they might have lived sympatrically with the sauropods. However, as mentioned above, their rarity implies a more distant habitat.

Hypsilophodontids probably fed on different plants than the larger herbivores. A diet of fruits and seeds might have been suitable for them, and therefore they might well have lived sympatrically with the sauropods, or the iguanodonts, or both.

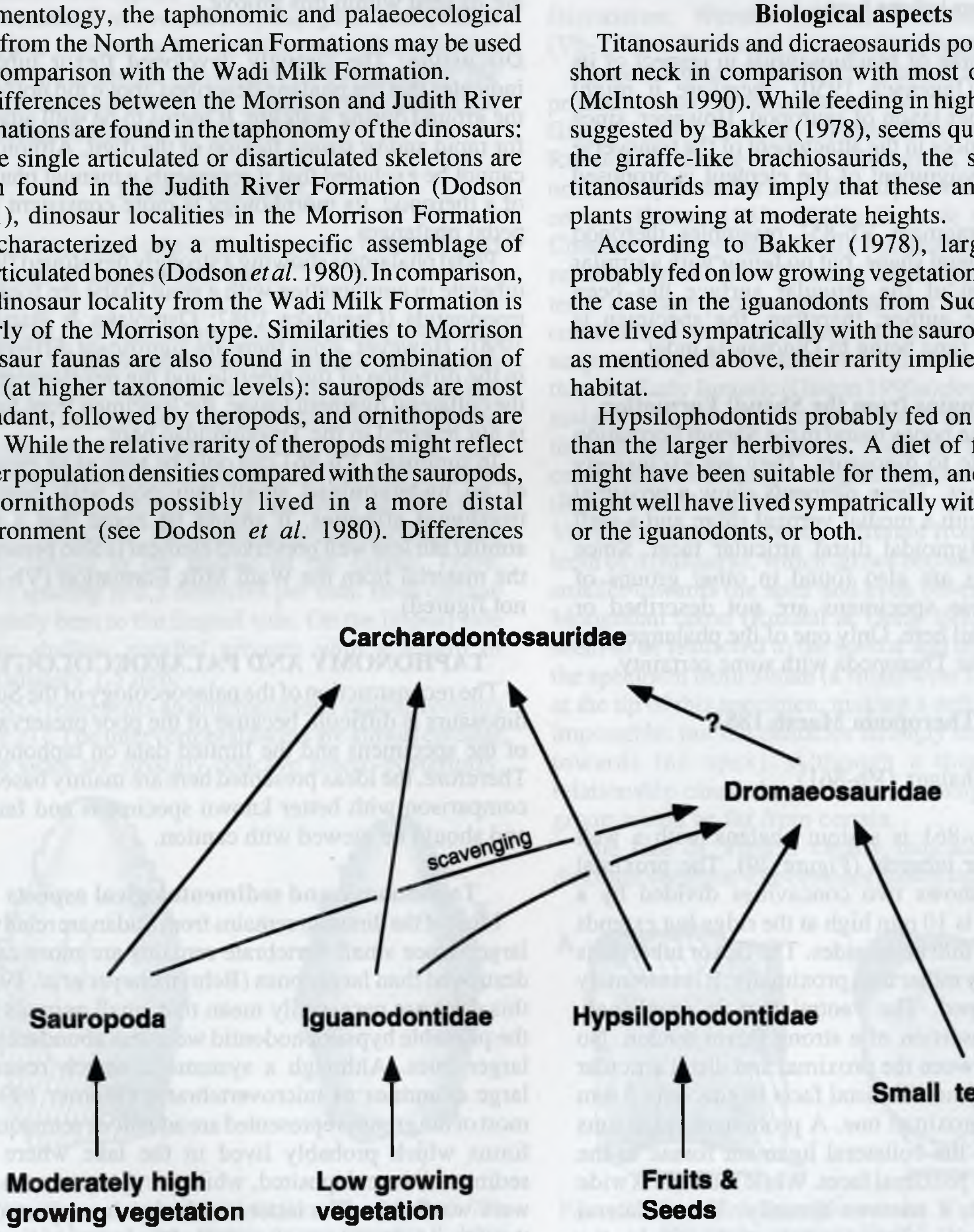

Figure 30. Hypothetical food-chain for the dinosaurs from Sudan. Arrows indicate the direction of energy flow.

Ostrom (1969, 1970) made a strong argument for pack-hunting in the velociraptorine dromaeosaurid *Deinonychus*. If this behaviour also occured in the dromaeosaurid from the Wadi Milk Formation, this taxon might not only have fed on small tetrapods, like the amphibians or lizards, or the hypsilophodontids, but also on the iguanodonts. The sauropods, however, seem to be too large to be killed even by a pack of the rather small dromaeosaurids, although scavenging might well have occurred.

The very large carcharodontosaurids were probably able to bring down any prey. Even if the iguanodonts and sauropods lived in different habitats, the presumed high activity of theropods (Molnar & Farlow 1990) would have allowed them to feed on both.

A hypothetical food chain for the Sudanese dinosaurs is presented in figure 30.

CRETACEOUS DINOSAUR FAUNAS FROM AFRICA

Little is known about African dinosaurs from the early stages of the Early Cretaceous. In the earliest Cretaceous of the Kirkwood Formation in South Africa, remains of stegosaurs, dryosaurids, camarasaurids, brachiosaurids and teeth of titanosaurids and undetermined theropods are found (Rich *et al.* 1983; Forster *et al.* 1995; Forster pers. comm. 1995). In the ?Barremian of Niger, the tetanuran theropod *Afrovenator* and a sauropod with camarasaurid affinities are present (Sereno *et al.* 1994; Sereno & Wilson pers. comm. 1995). The probably latest occurrence of stegosaurids in Africa is in the Early Cretaceous (?Aptian; Mateer *et al.* 1992) of Malawi (Jacobs *et al.* 1990). In the same locality, the primitive titanosaurid *Malawisaurus* and undetermined theropod teeth were found (Jacobs *et al.* 1990, 1993, 1996).

Several dinosaur localities are known from the Aptian and Albian (see Weishampel 1990). Remains of carcharodontosaurids, small theropods ('*Elaphrosaurus*' *iguidiensis*), the diplodocoid sauropod *Rebbachisaurus*, and iguanodontids are quite abundant, and spinosaurids, brachiosaurids, titanosaurids, dryosaurids, and nodosaurids have also been reported (Lavocat 1954; Lapparent 1960; Bassoulet & Iliou 1967; Taquet 1976, 1984; Schlüter & Schwarzhans 1978; Galton & Taquet 1982; Bouaziz *et al.* 1988; Jacobs *et al.* 1988; Buffetaut 1989; Weishampel 1990; Russell 1996; Sereno *et al.*, 1998; Tacquet & Russell 1999).

Dinosaurs from the early Late Cretaceous of Africa include carcharodontosaurids, spinosaurids, coelurosaurs, including dromaeosaurids, other small theropods (cf. *Elaphrosaurus*; Stromer 1934), titanosaurids, dicraeosaurids, a possible hypsilophodontid, and iguanodontids (Stromer 1915, 1931, 1932, 1934, 1936; Werner 1994a; Rauhut & Werner 1995; Sereno *et al.* 1996; this article). Only very few localities are known from the higher parts of the Late Cretaceous. In the early Senonian of Niger, remains of carcharodontosaurids and titanosaurids were found (Broin *et al.* 1974), and Harris & Russell (unpublished data) report a probable spinosaurid, titanosaurids and other undetermined theropods and sauropods from the unspecified Late Cretaceous of Kenya. In Egypt, strata of Campanian to Maastrichtian age have yielded undetermined theropod remains (Stromer & Weiler 1930) and a titanosaurid sauropod (Wiechmann in prep.). Titanosaurids might have been present in the Campanian-Maastrichtian of Niger (Taquet 1976; Buffetaut 1988). Although western Africa was separated from the rest of the continent by shallow epicontinental seaways several times during the Late Cretaceous, there was probably not much endemism, since land bridges between those two landmasses often existed (Reyment & Dingle 1987). Whether the dinosaur fauna from the Campanian of Madagascar can be regarded as a Late Cretaceous African dinosaur fauna is doubted, since this island might have been isolated during Late Cretaceous times (Besse & Courtillot 1988). Therefore the finds from Madagascar are not taken into consideration here.

In summary, dinosaur faunas from the middle to Late Cretaceous of Africa are probably characterized by the presence of carcharodontosaurids, spinosaurids, titanosaurids, diplodocoids (dicraeosaurs) and possibly iguanodontian ornithopods. Most of these groups probably represent the biological inheritance from Jurassic times.

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APPENDIX

Measurements of the dinosaur specimens from Sudan. Vertebral measurements refer to the vertebral centra. All measurements are given in mm.

Dicraeosauridae gen. et sp. indet.:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-856	106	89	90+	96
Vb-857	128	110	113+	113+
Vb-892	101	126	146	114

Titanosauridae gen. et sp. indet.:
Teeth:

No.	Crown height	Basal length	Basal width
Vb-721	29	9.5	9
Vb-900	23	7	6.9
Vb-901	17.5	5.1	4.9
Vb-901	10	3.4	3
Vb-903	15.7	5.3	4.6
Vb-907	15.5	7.3	5.7
Vb-910	17.8	7.1	6.1
Vb-911	6.7	2.1	1.9

Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-606	92	44	49	46
Vb-720	249	174	210+	192
Vb-876	172	176	150++	146+
Vb-880	149	133	161	154
Vb-882	176	139	125+	106
Vb-883	135	108+	133+	151
Vb-885	188	84	112+	131
Vb-886	62+	24+	33+	29+
Vb-889	77+	50	47+	41
Vb-891	139	135+	148+	141
Vb-893	-	109+	96	-
Vb-894	67	27	22	21
Vb-897	118	113	113+	106
Vb-899	162	121	135	127

Sauropoda indet:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-719	31	21	24	25+
Vb-895	-	33	34+	-
Vb-896	87	58	55	55

Carcharodontosauridae:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-607	137	148	131	127
Vb-717	136	129	c. 120	110
Vb-870	130	105	90	87
Vb-871	136	79	76	83

Phalanx:

No.	Length	Proximal height	Proximal width	Distal height	Distal width
Vb-718	105	60	94	42	78

cf. *Ouranosaurus* sp.:
Vertebrae:

No.	Length	Height	Anterior width	Posterior width
Vb-723	96	112	94	90
Vb-853	99	78+	69	70

Ornithopoda indet.:
Vertebra:

No.	Length	Height	Anterior width	Posterior width
Vb-854	88	67	86	83

Dinosauria indet.:
Vertebra:

No.	Length	Height	Anterior width	Posterior width
Vb-855	72	88	87	85