

The Taphonomy of Dinosaurs from the Upper Jurassic of Tendaguru (Tanzania) Based on Field Sketches of the German Tendaguru Expedition (1909–1913)¹

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With 23 figures and 2 tables

Abstract

Tendaguru is one of the most important dinosaur localities in Africa. The Tendaguru Beds have produced a diverse Late Jurassic (Kimmeridgian to Tithonian) dinosaur assemblage, including sauropods (*Brachiosaurus*, *Barosaurus*, *Dicraeosaurus*, *Janenschia*), theropods (e.g., *Elaphrosaurus*, *Ceratosaurus*, *Allosaurus*), and ornithischians (*Kentrosaurus*, *Dryosaurus*). Contrary to the well studied skeletal anatomy of the Tendaguru dinosaurs, the available taphonomic information is rather limited, and a generally accepted taphonomic model has not yet been established. Assessment of unpublished excavation sketches by the German Tendaguru expedition (1909–1913) document bone assemblages of sauropod and ornithischian dinosaurs from the Middle Saurian Bed, Upper Saurian Bed, and the Transitional Sands above the *Trigonia smeei* Bed, and shed some light on the taphonomy of the Tendaguru dinosaurs. Stages of disarticulation range from incomplete skeletons to solitary bones, and strongly argue for carcass decay and post-mortem transport prior to burial. The sauropod bone accumulations are dominated by adult individuals, and juveniles are rare or missing. The occurrence of bones in different superimposed dinosaur-bearing horizons indicates that skeletal remains were accumulated over a long time span during the Late Jurassic, and the majority of the bone accumulations are probably attritional. These accumulations are likely to have resulted from long-term bone input due to normal mortality events caused by starvation, seasonal drought, disease, old age and weakness. The depositional environment of the Middle and Upper Saurian Bed was mainly limnic to brackish in origin, while the palaeoenvironment of the Transitional Sands was marginal marine.

Key words: Dinosauria, taphonomy, Late Jurassic, Tendaguru, East Africa.

Zusammenfassung

Tendaguru zählt zu den bedeutendsten Dinosaurier-Lagerstätten Afrikas. Aus den Tendaguru-Schichten sind zahlreiche Skelettreste von Sauropoden (*Brachiosaurus*, *Barosaurus*, *Dicraeosaurus*, *Janenschia*), Theropoden (z.B. *Elaphrosaurus*, *Ceratosaurus*, *Allosaurus*) und Ornithischiern (*Kentrosaurus*, *Dryosaurus*) geborgen worden. Sie stammen aus der späten Jura-Zeit (Kimmeridge – Tithon). Während der Skelettbau der Tendagurusaurier gut untersucht ist, wirft die Taphonomie des Saurier-vorkommens von Tendaguru noch immer Fragen auf. Unklar ist bislang, wie die enormen Anreicherungen von Dinosaurierknochen in den Tendaguru-Schichten zustandekamen. Unveröffentlichte Grabungsskizzen der Deutschen Tendaguru Expedition (1909–1913) erweitern unsere Kenntnisse über die Taphonomie der Tendagurusaurier. In den ausgewerteten Grabungsskizzen sind Knochenansammlungen von Sauropoden und Ornithischiern aus dem Mittleren und Oberen Sauriermergel sowie aus den Übergangsschichten über der *Trigonia smeei*-Schicht dokumentiert. Die Lage und der Erhaltungszustand der Funde lassen auf erheblichen Zerfall der Kadaver und post-mortalen Transport von Skelettelementen vor der Einbettung schließen. Das Vorkommen von Saurierknochen in mehreren übereinanderliegenden Profilabschnitten der Tendaguru-Schichten zeigt, daß Skelettreste während der späten Jura-Zeit über einen längeren Zeitraum hinweg akkumuliert wurden. Die Ansammlungen von Skelettresten gehen wahrscheinlich auf „normale“ Sterbe-Ereignisse zurück, wie z. B. Verhungern, Verdursten, Krankheit, Altersschwäche und jahreszeitliche Dürre. Als Ablagerungsraum der Mittleren und Oberen Saurierschicht kommt ein küstennaher limnischer, zeitweise wohl auch brackischer Küstenstreifen in Betracht. Die knochenführenden Übergangsschichten unter- und oberhalb der Saurierschichten sind randlich marine Ablagerungen.

Schlüsselwörter Dinosaurier, Taphonomy, Oberjura, Tendaguru, Ostafrika.

1. Introduction

Tendaguru in southeastern Tanzania, East Africa, has yielded one of the most important Late Jurassic dinosaur assemblages. The first dinosaurs

were discovered by B. Sattler in 1907 (Hennig 1914a, Wild 1991), and E. Fraas was the first to excavate dinosaurs in the vicinity of Tendaguru Hill in September 1907 (Wild 1991). Shortly afterwards, Fraas (1908) described and figured some

¹ The paper is dedicated to Professor Dr. W. Janensch (1878–1969), leader of the German Tendaguru expedition (1909–1913), in appreciation of his outstanding contributions to the understanding of African dinosaurs.

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of these bones as “*Gigantosaurus*” *africanus* (= *Barosaurus africanus*) and “*Gigantosaurus*” *robustus* (= *Janenschia robusta*). Extensive collections of dinosaurs were made by the German Tendaguru expedition between 1909 and 1913 (Janensch & Hennig 1909; Hennig 1912a, b; Janensch 1914a, c), followed by field seasons of the British Tendaguru expedition between 1924 and 1931 (e.g., Migeod 1927, 1930, 1931; Parkinson 1930). The German and British expeditions yielded spectacular collections of dinosaurs and since that time Tendaguru has been known as one of the world’s most important Upper Jurassic dinosaur localities.

Whereas the British dinosaur collection remained undescribed (Russell et al. 1980), the German dinosaur material from Tendaguru has been well studied. Sauropods (e.g., *Brachiosaurus*, *Dicraeosaurus*), theropods (e.g., *Elaphrosaurus*, *Ceratosaurus*, *Allosaurus*), and ornithopods (*Kentrosaurus*, *Dryosaurus*) were identified and described in a series of monographs. Most of these works concentrated on the anatomical description of the Tendaguru dinosaurs (e.g., Hennig 1925; Janensch 1914b; 1929a, b; 1935, 1950a, 1955, 1961a, b). By contrast, the available taphonomical accounts are rather limited (e.g., Hennig 1912a, b; Janensch 1914a, c, 1929a, b) and detailed excavation plans have not been published so far.

The depositional environment and the origin of the bone accumulations recovered from the Tendaguru Beds are still under debate. Several taphonomic models have been suggested, among them the interpretation of Janensch (1914a, c), according to which the Tendaguru Saurian Beds are marginal-marine in origin. The attritional and catastrophic bone accumulations and remarkable pre-burial taphonomic biases have been taken into consideration in this model. Janensch (1914a, c) argued that dinosaurs had been trapped and killed in the mud or ‘mire-holes’ of lagoons that were temporarily exposed by ebbing tides (see also Hennig 1912a, b). This was followed by carcass flotation and decay in shallow water, prior to burial. Bone beds mainly consisting of disarticulated skeletal elements of *Dryosaurus* or *Kentrosaurus* were thought to result from sudden, catastrophic, mass-mortality events (e.g., Hennig 1912a, 1925; Janensch 1914a, c). Other workers argue that an estuarine environment existed in what is now the Tendaguru area (e.g., Abel 1927, Kitchin 1929, Parkinson 1930, Colbert 1984), and that dinosaur carcasses were washed in by rivers. They were transported

downstream and buried close to the mouth of rivers that flowed into the sea. Reck (1925), however, doubted catastrophic mass mortality and interpreted the depositional environment of the Saurian Beds as saline marshes. To date there is no taphonomic model that convincingly explains the enormous accumulations of dinosaur bones in the Tendaguru Beds.

The archive of the Institute of Palaeontology of the Museum of Natural History of the Humboldt University, Berlin, retains unpublished field sketches made by the German Tendaguru expedition (1909–1913). These field sketches are extremely important because primary field records of the expeditions are very scarce. The unpublished field records reveal details of the preservation characteristics of Tendaguru dinosaurs and enable some reassessment of the taphonomic interpretations suggested by previous workers. The main focus of this paper is to document and assess these unpublished Tendaguru field records.

Setting

2.1 Geological and palaeontological background

The Tendaguru Beds that have yielded the dinosaur assemblages crop out in southeastern Tanzania (Hennig 1914b, 1937; Janensch 1914a, c; Aitken 1956, 1961; Kent et al. 1971; Kapilima 1984; Zils et al. 1995a, b; Fig. 1). The sedimentary sequence was named after Tendaguru Hill (= steep hill; Dr. J. Kabudi, Daressalam, oral communication), which is located about 60 km northwest of the seaport of Lindi (Fraas 1908, Janensch 1914a, c). The following paragraph briefly summarises the original description by Janensch (1914c).

The Tendaguru Beds represent shoreline deposits that were laid down near an oscillating strandline during Late Jurassic and Early Cretaceous times (Janensch 1914a, c; Russell et al. 1980). There are three sedimentary cycles in the Tendaguru Beds (Hennig 1914b, Janensch 1914c). The series of sediments begins with sandy marls of the Lower Saurian Bed (Untere erste Saurierzone, Janensch 1914c; Unterer Sauriermergel, Janensch 1961a) which measure more than 20 m in thickness (Fig. 1). These strata pass gradually into the marine sandstones of the *Nerinea* Bed (Untere Sandsteinzone, Nerineenzone, Janensch 1914c; Untere Zwischenschichten, Janensch 1961a) which are overlain by greenish-

grey and reddish sandy marls of the Middle Saurian Bed (Mittlere zweite Saurierzone, Janensch 1914c; Mittlerer Sauriermergel, Janensch 1961a). Janensch (1914c) reports a thickness of about 25 m for the *Nerinea* Bed and some 15 m for the Middle Saurian Bed. The succeeding fine to coarse grained marine sandstones of the *Trigonia smeei* Bed (Mittlere Sandsteinzone mit *Trigonia smeei*, Janensch 1914c; Obere Zwischenschichten, Janensch 1961a), which measure about 20 m in thickness, separate the Middle Saurian Bed from the Upper Saurian Bed (Oberste dritte Saurierzone, Janensch 1914c; Oberer Sauriermergel, Janensch 1961a). The latter consists of greenish-grey and reddish sandy marls which reach some 40 m in thickness. The Upper Saurian Bed is overlain by sandy shallow marine sediments of the *Trigonia schwarzi* Bed (Obere Sandsteinzone mit *Trigonia schwarzi*, Janensch 1914c), the thickness of which was estimated at approximately 5 m.

Sandy or oolitic sediments at the boundaries between the Saurian Beds and the marine sandstone units (Zwischenschichten, *Nerinea* Bed, *Trigonia smeei* Bed) have been described as Transitional Beds (Übergangschichten), since marine invertebrates (e.g. belemnites) are associated with skeletal remains of dinosaurs (Hennig 1914b, Janensch 1914c). Transitional Beds containing marine invertebrates and dinosaurs have also been reported from the *Nerinea* Bed (Janensch 1961a). Sandy deposits below and above the *Trigonia smeei* Bed have been distinguished as the Lower and Upper Transitional Sands by Russell et al. (1980).

The age of the Tendaguru Beds has been controversial since the first dinosaurs were discovered in the vicinity of Tendaguru Hill (e.g., Janensch 1914c; Dietrich 1925, 1933; Kitchin 1929; Hennig 1937; Aitken 1956, 1961). The age of the Tendaguru Beds ranges from Late Jurassic to Early Cretaceous (e.g., Hennig 1914b; Janensch 1914c; Schuchert 1918, 1934; Dietrich 1933; Hennig 1937; Aitken 1956, 1961; Kapilima 1984), contrary to previous views that placed the sequence in the Cretaceous (e.g., Fraas 1908, Kitchin 1929), and there is general agreement that the *Trigonia schwarzi* Bed, above the Upper Saurian Bed, correlates well with the Early Cretaceous (e.g., Janensch 1914c, Lange 1914, Zwierzycki 1914, Dietrich 1933, Aitken 1961).

Hennig (1914b, 1937) believed that the Tendaguru Beds represent a nearly continuous sequence without major breaks. By contrast, Parkinson (1930) suggested a disconformity below

the *Trigonia schwarzi* Bed, a view that is strongly supported by palaeontological (Dietrich 1933, Spath 1927–1933, Aitken 1956, 1961) and geological evidence (Aitken 1956, 1961). The invertebrate fossil record indicates an Upper Valanginian (Oberes Valendis) to Aptian age (Dietrich 1933) or Hauterivian to Aptian age (Spath 1927–1933) for the *Trigonia schwarzi* Bed (Aitken 1956, 1961). The Jurassic-Cretaceous boundary is placed above the Upper Saurian Bed, which is thus regarded as entirely Late Jurassic in age (e.g., Dietrich 1933, Aitken 1956), and below the *Trigonia schwarzi* Bed, contrary to the opinion of previous workers who positioned this boundary either at the base (e.g., Hennig 1914b, Janensch 1914c), or within the Upper Saurian Bed (e.g., Hennig 1937). The stratigraphic work in the Tendaguru region is concisely summarized by Aitken (1961).

The present report is especially concerned with the Middle and Upper Saurian Beds and the Transitional Sands above the *Trigonia smeei* Bed. These units of the Tendaguru Beds are now generally considered to be Kimmeridgian to Tithonian in age (Aitken 1956, 1961; Russell et al. 1980; see also Schrank 1999, Schudack et al. 1999). Moreover, charophytes suggest a Kimmeridgian age for the Middle Saurian Bed (Schudack 1999).

The majority of dinosaur remains were recovered from the Middle and Upper Saurian Bed, occurring mainly as incomplete skeletons and solitary bones (Janensch 1914a, c; 1929a, 1961a). By contrast, the Lower Saurian Bed has only yielded a small number of isolated sauropod bones and theropod teeth (Janensch 1929a, 1961a).

The Middle and the Upper Saurian Bed show clear evidence of redeposition (Janensch 1961a: 179). This is consistent with the lithological characters of the matrix from the Middle Saurian Bed from Site Jg (WJ) which was searched for mammals (Heinrich 1998, 1999). The matrix occasionally contains assemblages of oncoids, mud clasts and lithoclasts consisting of reworked caliche nodules (Dr. M. Aberhan, Prof. Keupp, Dr. Schudack; oral communication). The latter were derived from palaeosoils that had developed in the Tendaguru palaeoenvironment, under a warm and seasonally dry (arid or semiarid) climate. In this connection it is interesting to note that the known invertebrate fossil record from the Middle and Upper Saurian Beds, which includes records of freshwater gastropods (e.g., Dietrich 1914, Hennig 1914c), evidence of *As-*

mussia (= *Estheria*) (Janensch 1933), and limnic to brackish ostracods (Schudak et al. 1999) is consistent with the sedimentological data.

Dinosaur bone assemblages, including concentrations of water worn limb bones of sauropods were also frequently found in the Transitional Sands above and below the *Trigonia smeei* Bed, and some of them show evidence of reworking (Janensch 1961a). Dinosaur remains have also been reported from the Transitional Sands above the *Nerinea* Bed (Janensch 1961a). The co-occurrence of dinosaur bones and marine to brackish invertebrates in these beds suggests a shallow marine to brackish depositional environment for the Transitional Sands (Janensch 1914c, 1961a).

The marine depositional environment of the *Nerinea* Bed, *Trigonia smeei* Bed, and *Trigonia schwarzi* Bed is indicated by the presence of marine invertebrates, including ammonites (e.g., Zwierziecky 1914, Dietrich 1933, Zeiss 1975), gastropods (e.g., Dietrich 1914, 1933; Hennig 1914c), lamellibranchs (e.g., Lange 1914, Dietrich 1933, Aitken 1961), and brachiopods (e.g., Lange 1914), but these all require further study. Moreover, with regard to the stratigraphic terminology, Aitken (1961) doubted that *Trigonia smeei* described from the Tendaguru Beds (e.g., Lange 1914, Dietrich 1933) was identical to *Trigonia smeei* from the type locality of Shapoor in Cutch (India), contrary to Cox (1952) who accepted their synonymy.

The field sketches of the German Tendaguru expedition cover sites in the Middle Saurian Bed, the Upper Saurian Bed, and the Transitional Sands between the *Trigonia smeei* Bed and the Upper Saurian Bed that yielded a diverse vertebrate fauna. As far as the land vertebrate assemblage of the Middle Saurian Bed is concerned, the dinosaurs are the most common element and include among others *Brachiosaurus brancai*, *Barosaurus africanus*, *Dicraeosaurus hansemanni*, *Kentrurosaurus aethiopicus*, *Dryosaurus lettow-vorbecki*, *Elaphrosaurus bambergi*, *Labrosaurus* (?) *stechowi*, *Ceratosaurus* (?) *roechlingi*, and *Allosaurus* (?) *tendagurensis* (Janensch 1914b, 1925b, 1929a, 1955, 1961a; Hennig 1925). Pterosaurs (Janensch 1914b, Reck 1931, Unwin & Heinrich 1999) and lizards (Broschinski 1999) and mammals (Heinrich 1998, 1999) also occur.

The land vertebrate fauna of the Upper Saurian Bed is also dominated by dinosaurs, namely by *Brachiosaurus brancai*, *Barosaurus africanus*, *Janenschia robusta*, *Dicraeosaurus sattleri*, *Kentrurosaurus aethiopicus*, *Elaphrosaurus bambergi*,

Labrosaurus (?) *stechowi* and *Ceratosaurus* (?) *roechlingi* (Janensch 1914b, 1929a, 1961, Hennig 1925). Pterosaurs (Reck 1931) and a mammal (Dietrich 1927, Heinrich 1991, 1999) were also reported.

The Transitional Sands below the Upper Saurian Bed and above the *Trigonia smeei* Bed yielded among others *Brachiosaurus brancai*, *Barosaurus africanus*, *Janenschia robusta*, *Dicraeosaurus sattleri*, and *Kentrurosaurus aethiopicus* (Janensch 1961a). Pterosaurs were also described (Reck 1931, Galton 1980).

2.2 Sites

Dinosaurs were first discovered at a few sites in the vicinity of Tendaguru Hill (Fraas 1908), and were subsequently collected from approximately one hundred sites during the field seasons of the German Tendaguru expedition between 1909 and 1913. Most of these sites are located close to Tendaguru Hill (see Janensch 1914a: 45; 1925a: 18), except for a small number of localities in the Mchuya and Makangaga area that are not considered here. The former is about 40 km, the latter approximately 80 km north of the Tendaguru region (Janensch 1914a, Fig. 1).

The German Tendaguru expedition was run by W. Janensch (1909–1911), assisted by E. Hennig (1909–1911), H. von Staff (1911), and H. Reck (1912–1913) who was supported by his wife Mrs. Ina Reck née von Grumbkow. The Tendaguru sites were worked intensively, and at important localities, the collecting period extended through three field seasons from 1909 to 1911, for example at Site S (Fig. 1) which yielded the type specimen of *Brachiosaurus brancai* (Janensch 1914a, c). In 1911, about 500 Africans were involved in the excavations. Together with their families about 900 people temporarily inhabited the region of Tendaguru Hill (Jaeger 1971).

The excavations met with outstanding success. African field crews supervised by the leaders of the German Tendaguru expedition and native foremen uncovered the bones, which were mapped, labelled, catalogued, packed, carried to the seaport of Lindi, and shipped to Germany (Janensch 1914a). Each site was indicated with lower case or capital letters, Roman numerals or other symbols (e.g., Nr.) combined with Arabic numerals (Janensch 1914a). Janensch (1914a, 1925a) published maps indicating the topographic and stratigraphic position of the principal sites of the Tendaguru area, most of which

are from the Upper and Middle Saurian Beds. Only a few sites are known from the Transitional Sands at the base and top of the Saurian Beds. A detailed account of the diggings at Tendaguru and the recovery of dinosaur bones is given by Janensch (1914a).

2.3 Excavation records

Documentation of the German Tendaguru expedition is largely incomplete. Records include a detailed field catalogue, containing lists of the dinosaur bones recovered with hand-written notes by Werner Janensch, Edwin Hennig, and Hans Reck. Sketchbooks of the German Tendaguru expedition with pencil and ink drawings by Werner Janensch, Edwin Hennig and Hans Reck, documenting single bones and skeletons, and watercolours of individual skeletal elements, possibly by Ina Reck, are also available. A few topographic quarry plans are also present in the sketchbook. The collection of records also contains Werner Janensch's photo album containing black and white photographs documenting the field seasons from 1909 to 1911. Most important are photographs of uncovered sauropod skeletons including *Dicraeosaurus hansemanni* (Site m) and *Brachiosaurus brancai* (Sites D, S, no). Three oil paintings completed by Ina Reck at Tendaguru Hill in 1912 were recently rediscovered in the Institute of Palaeontology of the Museum of Natural History of the Humboldt-University, Berlin. These paintings give some idea of the size of the quarries and field work at Tendaguru, possibly of Sites Jg (WJ) and St. This documentation, detailed above, forms the basis for this study.

Nevertheless, taphonomical analysis of the Tendaguru dinosaurs are greatly hampered by the loss of field records. There is, for instance, only a partial field book of the German Tendaguru expedition and this covers the time span before the expedition's arrival at Tendaguru Hill on April 16, 1909. Missing parts of the field book, quarry maps and excavation plans appear to have been destroyed by fire during World War II, possibly as a result of an air raid on November 12, 1943 that completely destroyed a collection room containing dinosaurs from Tendaguru. The type material of *Dryosaurus lettowvorbecki* has been missing since that time.

As mentioned previously, almost 100 dinosaur-bearing sites were discovered by the German Tendaguru expedition between 1909 and 1913. The available field sketches, however, cov-

er not more than 15 sites. Skeletal elements are roughly sketched in the quarry plans, partly in pencil, partly with ink. The bones are mostly labelled with arabic numerals combined occasionally with the symbols of the sites (e.g., C1, C2). Preliminary anatomical identifications of the bones are given in the field sketches and the Tendaguru field catalogue. Hand-written notes by W. Janensch indicate that some of these identifications were later reassessed. With a few exceptions, the length and width of the bones are not indicated in the field sketches.

Scale drawings of bone accumulations made with grids were probably lost during World War II, and arrows indicating compass directions are often lacking. Discrepancies between the specimen count given in the Tendaguru field catalogue and bones documented in the excavation sketches indicate that the quarry plans often represent only "snapshots" of the diggings, and do not completely reflect all details of the fossil vertebrate record encountered during the excavations. Moreover, the field sketches lack detailed data with respect to the contemporary fauna and sedimentology of the dinosaur-bearing beds exposed by the digging activities.

Despite these gaps, there is no doubt that the unpublished field records of the German Tendaguru expedition can contribute to a better understanding of the taphonomy of the Tendaguru dinosaurs. The field sketches record approximately the original position of skeletal elements and their position relative to one another. A broad spectrum of disarticulation stages can be recognized, and reveal interesting details of the taphonomic history of the Tendaguru dinosaurs that have not been documented so far. It is noteworthy that much of the skeletal material documented in the field sketches is housed today in the collections of the Palaeontological Institute of the Museum of Natural History, Humboldt University, Berlin. Therefore, some of the preserved field sketches could be "updated" and, for example, augmented with scales and ontogenetic data obtained from palaeohistological examinations of sauropod limb bones (Sander 1999, in press).

3. The field sketches

The majority of field sketches document dinosaur bone assemblages from the Upper Saurian Bed. Only a few quarry maps cover bone accumulations from the Middle Saurian Bed and the

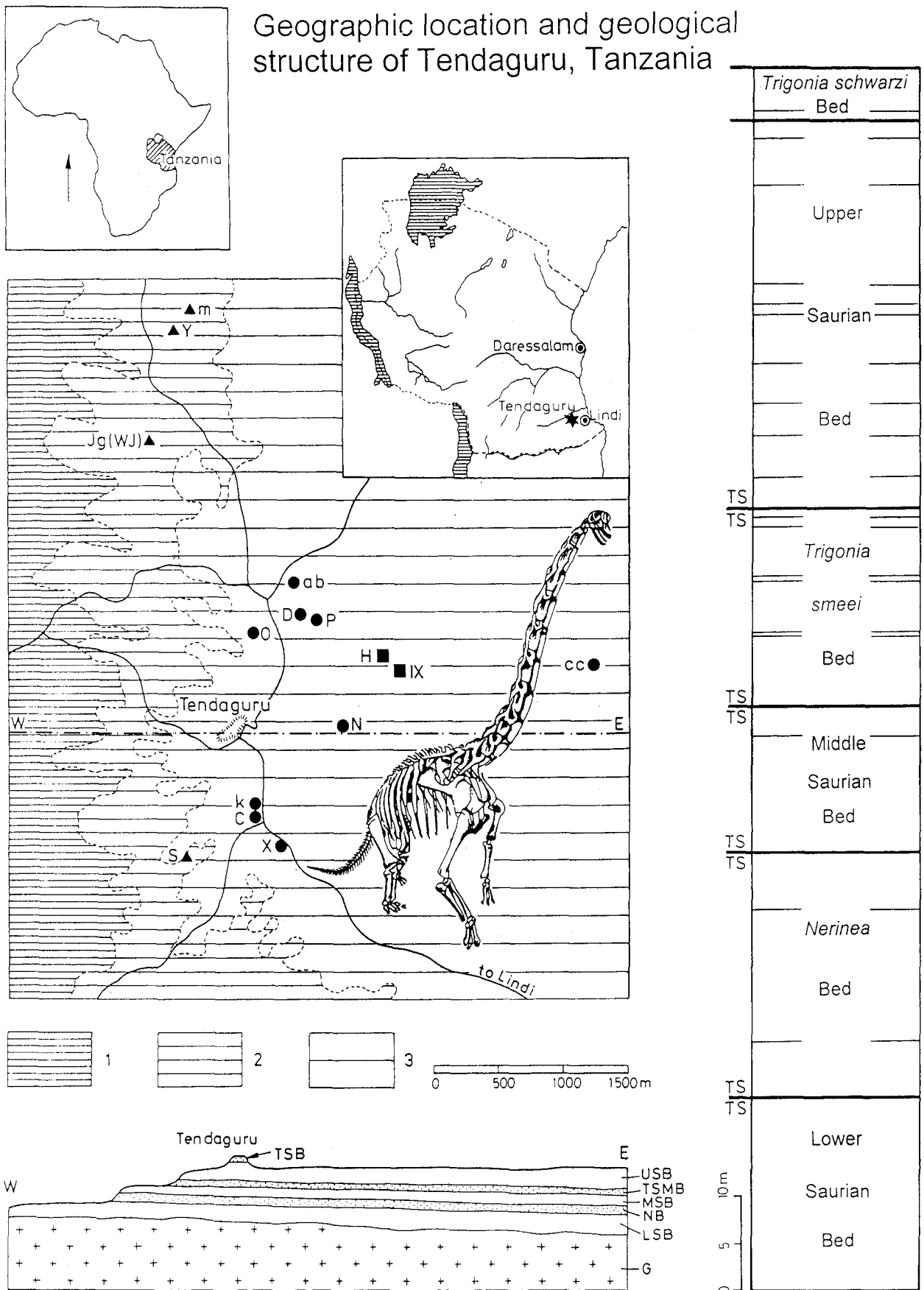


Fig. 1. Map of the Tendaguru area with geological sections and the location of the sites considered in the present account. Data from Hennig (1914b) and Janensch (1914c, 1925a). Note that the marine *Nerinea* Bed, the two *Trigonía* Beds, and the Transitional Sands were not mapped in the original site plan (Janensch 1925a: 18) and the Transitional Sands were not distinguished as separate stratigraphical units by Janensch (1914c). 1, Lower Saurian Bed; 2, Middle Saurian Bed; 3, Upper Saurian

Table 1

Stratigraphic distribution of selected dinosaur-bearing sites in the Tendaguru area.

Stratigraphy	Sites
Upper Saurian Bed	C, D, N, O, P, k, ab, cc, X
Transitional Sands between <i>Trigonia smeei</i> Bed and Upper Saurian Bed	H, IX
<i>Trigonia smeei</i> Bed	
Transitional Sands between <i>Trigonia smeei</i> Bed and Middle Saurian Bed	
Middle Saurian Bed	S, Y, Jg (= WJ), m
Transitional Sands between Middle Saurian Bed and <i>Nerinea</i> Bed	
<i>Nerinea</i> Bed	

Transitional Sands overlaying the *Trigonia smeei* Bed. No records are available from the Lower Saurian Bed, the Transitional Sands above and below the *Nerinea* Bed, and the Transitional Sands below the *Trigonia smeei* Bed. The topographic and stratigraphic position of the sites detailed in the present taphonomic account is indicated in Figure 1 and Table 1.

As in other vertebrates, the Tendaguru dinosaurs began their taphonomic history as carcasses with complete skeletons, followed by a broad spectrum of disarticulation stages and scattering of individual skeletal elements. Analysis of the field sketches and data given by Janensch (1929a) reveal that four main preservational categories occur in the Tendaguru Beds (Table 2): (1) skeletons, (2) partial skeletons, (3) bone accumulations dominated by disarticulated individual elements, and (4) solitary bones. These main preservational types can be further subdivided by using additional taphonomical criteria such as the degree of disarticulation and loss of bones (see Table 2).

The assignment of bone accumulations to disarticulation stages such as incomplete skeletons or partial skeletons is based on a simplified descriptive scheme that provides unambiguously defined taphonomic categories (Table. 2). According to this classification, partial skeletons only consist of one discrete skeletal unit (e.g., tail or hind limb), in contrast to skeletons that always comprise more than one of those units (e.g., tail and hind limb; fore limb, shoulder girdle and neck).

The skeletal elements are annotated with symbols used by the German Tendaguru field crew. With the exception of Fig. 11, triangles indicate specimens documented either by arabic numerals or by hand-written notes in the Tendaguru field catalogue and descriptions in the literature. The precise position and orientation of these bones is uncertain. The assessment of quantitative data and the azimuth orientation of bones must be treated with caution because of the incompleteness of the excavation records. Reference specimens that were used to calculate the scale for

Table 2

Disarticulation stages of a dinosaur skeleton (simplified). For explanation see text.

Disarticulation stages	Designation	Skeletal elements
A	Complete skeleton	articulated, no loss of bones
B	Complete skeleton	partly articulated, partly disarticulated; no loss of bones
C	Complete skeleton	disarticulated, no loss of bones
D	Incomplete skeleton	articulated, loss of bones
E	Incomplete skeleton	partly articulated, partly disarticulated; loss of bones
F	Incomplete skeleton	disarticulated, loss of bones
G	Complete partial skeleton	articulated, no loss of bones
H	Complete partial skeleton	partly articulated, partly disarticulated; no loss of bones
I	Complete partial skeleton	disarticulated, no loss of bones
K	Incomplete partial skeleton	articulated, loss of bones
L	Incomplete partial skeleton	partly articulated, partly disarticulated; loss of bones
M	Incomplete partial skeleton	disarticulated, loss of bones
N	Bone field	partly associated, partly disassociated
O	Bone field	disassociated
P	Solitary Bone	isolated

◀ Continued legende Fig. 1

Bed; **TSB**, *Trigonia schwarzi* Bed; **USB**, Upper Saurian Bed; **TSMB**, *Trigonia smeei* Bed; **MSB**, Middle Saurian Bed; **NB**, *Nerinea* Bed; **LSB**, Lower Saurian Bed; **G**, gneiss; **TS**, Transitional Sands.

▲ – Sites in the Middle Saurian Bed, ● – Sites in the Upper Saurian Bed, ■ – Sites in the Transitional Sands between the *Trigonia smeei* Bed and the base of the Upper Bed

several quarry plans are quoted in the captions of the textfigures.

The definition of taphonomic variables used in the description is as follows (Behrensmeyer 1991, Lyman 1996): MNI – minimum number of identified individuals; NISP – number of specimens documented in the field sketches; size of accumulation – area (m²) over which skeletal remains are recovered; density – number of specimens documented in the field sketches per m².

The following anatomical abbreviations are used in the quarry maps: as – astragalus, ca – caudal vertebra, c – rib, cc – cervical rib, cd – dorsal rib, co – coracoid, cr. – skull, cv – cervical vertebra, do – dorsal vertebra, fe – femur, fi – fibula, he – haemapophysis, hu – humerus, il – ilium, is – ischium, mc – metacarpal, mt – metatarsal, pb – pubis, pm – phalange (manus), pp – phalange (pes), ra – radius, sa – sacrum, sc – scapula, st – sternal plate, tb – tibia, ul – ulna, v – vertebra, ⊕ – specimen of known ontogenetic age. The right side is indicated by d and the left by s. Capital or lower case letters with arabic numerals are catalogue numbers of the German Tendaguru expedition.

Further abbreviations: GTE – German Tendaguru expedition, MNHB – Museum für Naturkunde der Humboldt-Universität zu Berlin, IPHB – Institut für Paläontologie am Museum für Naturkunde der Humboldt-Universität zu Berlin.

3.1 Sites in the Upper Saurian Bed

3.1.1 Tendaguru Site C

Location: Site C is situated approximately 0.7 km south of Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxon: *Barosaurus africanus*

Figure: 2

Reference: Janensch (1914a, 1929a, 1961a), GTE field catalogue: 3

Assemblage data

NISP: 37

MNI: 1

Number of taxa: 1

Designation: Single-individual, single-taxon assemblage.

Tendaguru, Site C Upper Saurian Bed *Barosaurus africanus*

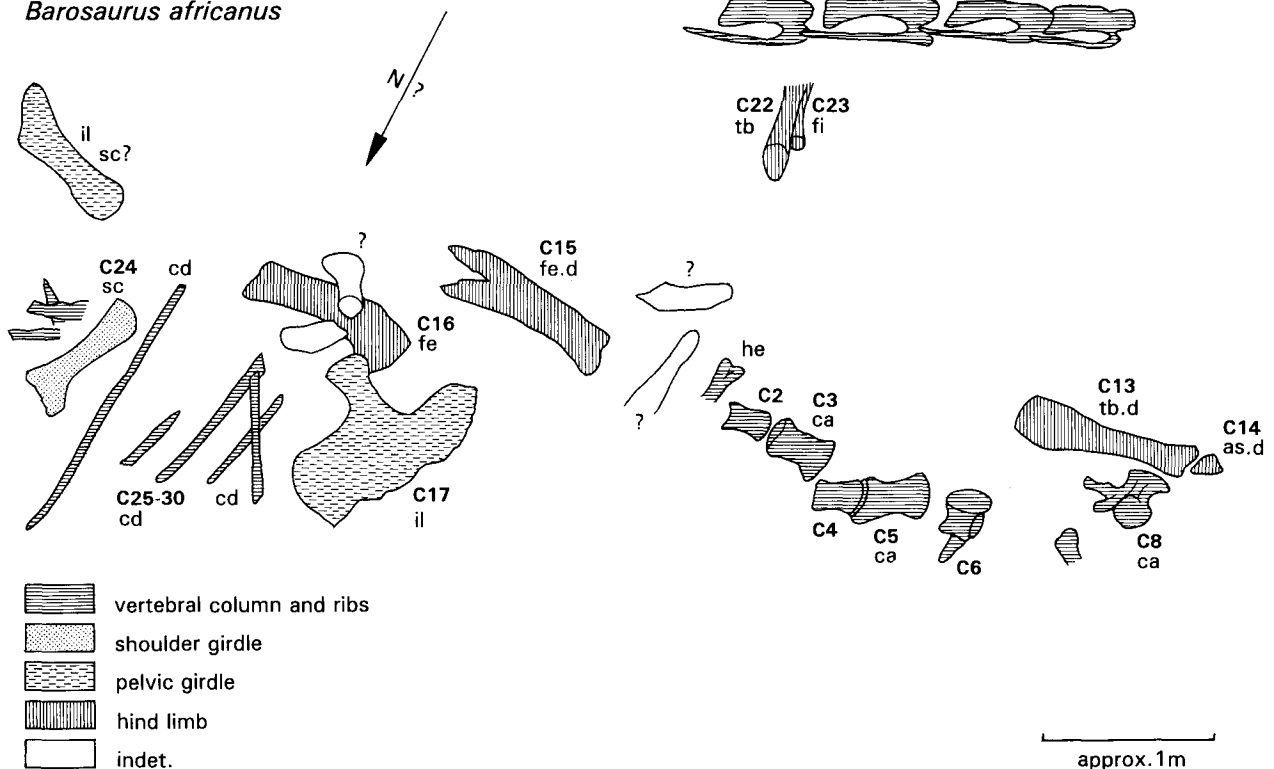


Fig. 2. Incomplete skeleton of *Barosaurus africanus* from Tendaguru Site C. A few bones are still articulated, but most are disarticulated. The length of the string of cervical vertebrae C18–21 (2.7 m) was used to calculate the scale for the quarry plan. Redrawn after a field sketch from W. Janensch

Quarry data

Size of accumulation: approximately 24.00 m²

Density: approximately 1.54

Modification data

Disarticulation stage: E

Measurements: The length of the caudal vertebrae was measured as 180 mm (C 2), 200 mm, (C3), and 200 mm (C5); that of the femur (C15) at 1320 mm (Janensch, GTE sketch book). The length of the left tibia (C13) was measured at 890 mm (Janensch 1961a).

Ontogenetic data: Unknown

Comments: The digging at Tendaguru Site C commenced in April 1909 (Janensch 1914a: 43). Cervical and caudal vertebrae, an ilium, a femur, tibia, fibula, and an astragalus assigned to an individual of *Barosaurus africanus* were recovered (Janensch 1929a: 5). Note the dominance of elements of the posterior body region. Most of the skeletal elements were disarticulated, but still closely associated (e.g., tibia and astragalus). The imperfect femur (C15), the tibia (C13), and the astragalus (C14) belong to one single hind limb

(Janensch, GTE field catalogue: 3). The associated tibia (C22) and fibula (C23) were found just below a string of articulated cervical vertebrae (C18–21) which measure 2.7 m in length. A string of articulated caudal vertebrae (C4 and 5) is also present. These articulated specimens suggest that some skeletal elements were still connected by soft tissue (ligaments or muscles) prior to burial. Several caudal vertebrae were disarticulated, but apparently still close to their proper anatomical order (Janensch, GTE field catalogue: 3), indicating minimal transport from the position in which the carcass finally came to rest. Extensive damage occurred to the ilium and one of the femora prior or subsequent to burial. Most of the long bones and the string of cervical vertebrae show a similar (? west to east) orientation.

3.1.2. Tendaguru Site D

Location: Site D is located about 1.0 km north-north-east of Tendaguru Hill.

Stratigraphy: Upper Saurian Bed



Fig. 3. Incomplete skeleton of *Brachiosaurus brancai* uncovered from the Upper Saurian Bed at Tendaguru Site D. Photograph: W. Janensch

Tendaguru, Site D
Upper Saurian Bed
Brachiosaurus brancai

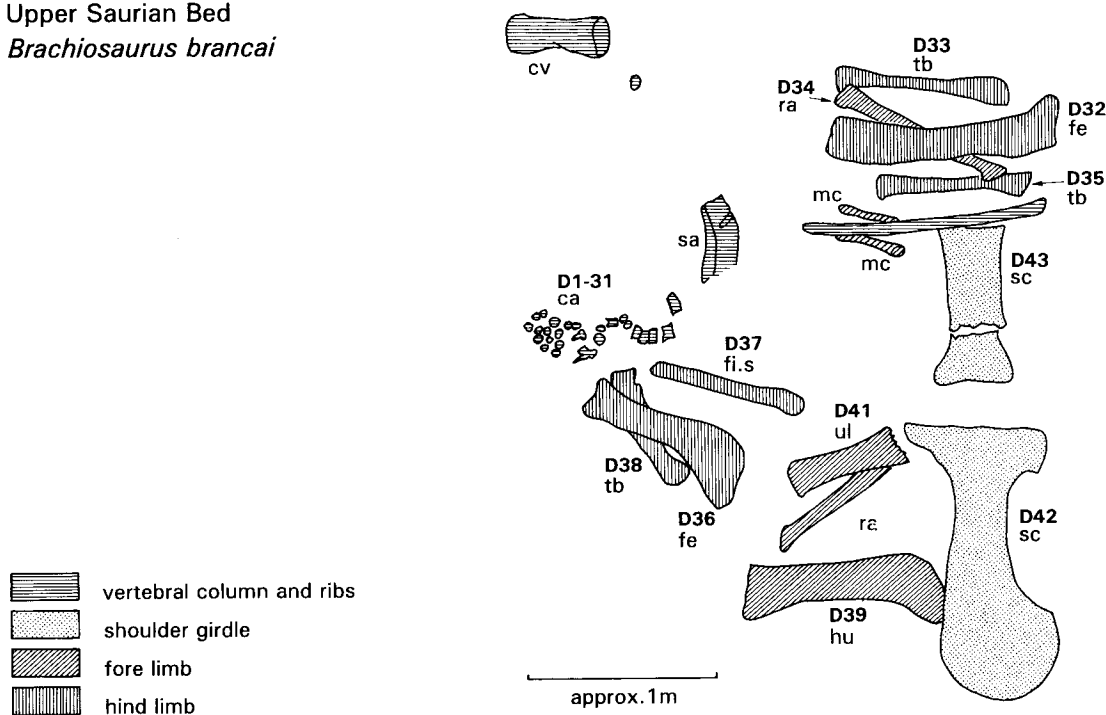


Fig. 4. Incomplete skeleton of *Brachiosaurus brancai* from Tendaguru Site D. The majority of the skeletal elements are disarticulated, but closely associated. Most caudal vertebrae were found in natural order. Some limb bones rest on top of one another. The measured length of the humerus D 39 (1600 mm) was used to calculate the scale for the quarry map. The orientation of the map is not known. Redrawn after a field sketch from W. Janensch

Taxon: *Brachiosaurus brancai*

Figures: 3, 4

Reference: Janensch (1914a, Fig. 16; 1929a; 1950a), GTE field catalogue: 4–5

Assemblage data

NISP: 50

MNI: 2

Number of taxa: 1

Designation: Multi-individual but single-taxon assemblage

Quarry data

Size of accumulation: approximately 22.00 m²

Density: approximately 2.27

Modification data

Disarticulation stage: F

Measurements: The length of the limb bones were measured as follows (Janensch 1961a: 230, tab. 18): humerus (D39): 1600 mm, femur (D36): 1550 mm, tibia (D?): 900 mm, and fibula (D?): 940 mm.

Ontogenetic data: Unknown

Comments: The excavations at Site D commenced on June 21, 1909 (Janensch, GTE field

catalogue: 4). The dig yielded a skeleton consisting of a series of 29 caudal vertebrae, a poorly preserved sacrum, pelvic bones (ilium, pubis), dorsal ribs, two anterior limbs without feet, two scapulae, femora, tibiae, and fibulae (Janensch 1914a, 1929a: 7; 1950a; GTE field catalogue: 4–5). Only some of these are documented in the field sketch. The dimensions of the limb bones indicate a medium-sized individual of *Brachiosaurus brancai* (Janensch 1961a: 230, tab. 18). The series of caudal vertebrae resting next to the badly preserved sacrum was found almost in natural articulation (Janensch 1950a). The association of the remaining disarticulated elements is evident. The scapula (D42) was apparently found lying upon the head of humerus D39, and several other limb bones were found one on top of the other (e.g., tibia D38 and femur D36; radius D34 and femur D32). Plate-like elements such as the shoulder blades seem to be oriented in a nearly horizontal plane, and the scapula D43 and ulna D41 are broken. Most of the elongated limb bones are oriented nearly parallel, and the two scapulae are positioned transverse to the prevailing compass direction of the heavy limb bones.

Most bones documented appear to derive from a single individual preserved as an incom-

plete skeleton. Originally, the leg bones D34 and D35 were tentatively identified as fibula (?) and radius (?) respectively (Janensch, GTE sketch book). Later, Janensch (GTE field catalogue: 4, hand-written note) identified these bones as fibula and tibia. If properly identified, the existence of three tibiae indicates the presence of at least two individuals of *Brachiosaurus brancai*. Unfortunately, a reassessment of the limb bones from Site D is not possible, since the location of the collection is not known.

3.1.3 Tendaguru Site N

Location: Site N is located about 0.9 km east of Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxon: *Brachiosaurus brancai*

Figure: 5

Reference: Janensch (1914a: 44), GTE field catalogue: 19

Assemblage data

NISP: 21

MNI: 1

Number of taxa: 1

Designation: Single-individual, single-taxon assemblage

Quarry data

Size of accumulation: Unknown

Density: Unknown

Modification data

Disarticulation stage: F

Measurements: No measurements are available.

Ontogenetic data: Unknown

Comments: The excavation at Site N commenced in September 1909 (Janensch, GTE field catalogue: 9). The dig produced a disarticulated incomplete skeleton, with a scapula, complete and fragmentary humerus, radius, and ribs. At a little distance to these bones there were two ischia, a dorsal vertebra, a caudal vertebra, ribs, and a large fragmentary bone (N9) tentatively identified as a fragmentary scapula (Janensch, GTE field catalogue: 19). The bone accumulation at Site N is dominated by elements of the anterior appendicular skeleton. In total, 21 skeletal elements assigned to *Brachiosaurus brancai* were collected from site N (Janensch, GTE field catalogue: 19). The bones are attributable to one individual of *Brachiosaurus brancai*. Except for a few skeletal elements, most of the long bones are oriented nearly parallel, possibly reflecting wave action or current action. Some of them such as the humerus and ischia are broken.

Tendaguru, Site N

Upper Saurian Bed

Brachiosaurus brancai

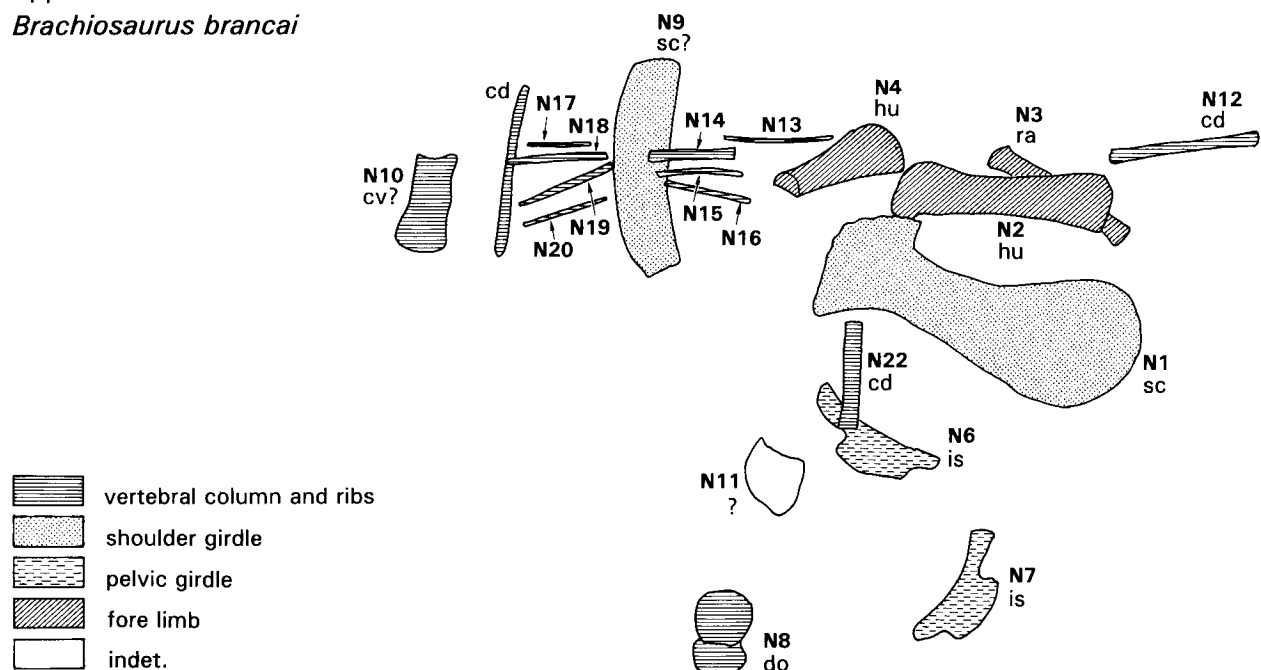


Fig. 5. Incomplete skeleton of *Brachiosaurus brancai* from Tendaguru Site N. All skeletal elements are completely disarticulated. Scale and orientation of the map are not known. Redrawn after a field sketch from W. Janensch

3.1.4 Tendaguru Site O

Location: Site O is located about 0.8 km north of Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxon: *Dicraeosaurus sattleri*

Figure: 6 (colour figure on p. 36)

Reference: Janensch (1914a, 1929a, 1961a), GTE field catalogue: 20

Assemblage data

NISP: 17

MNI: 1

Number of taxa: 1

Designation: Single-individual, single-taxon assemblage

Quarry data

Size of accumulation: approximately 7.00 m²

Density: approximately 2.43

Modification data

Disarticulation stage: F

Measurements: The length of the right limb bones were measured as follows (Janensch 1961 a): humerus (O3): 610 mm, ulna: 410 mm, femur (O2): 980 mm, tibia (O4): 580 mm, fibula (O5): 620 mm.

Ontogenetic data: Janensch (1929a: 10) believed that the skeletal elements originated from a subadult individual of *Dicraeosaurus sattleri*, however, histological examinations of a right femur (O2) and a right humerus (O3) suggest that both limb bones belong to an adult individual of this species (Sander 1999, in press).

Comments: Digging by the German Tendaguru expedition's crew at Site O commenced at the beginning of October 1909 (Janensch, GTE field catalogue: 47). Janensch (1914a: 44; 1929a: 10) reported a scapula, pelvic bones, centra of caudal vertebrae, and an imprecisely determined number of fore and hind limb elements, all assigned to *Dicraeosaurus sattleri*. All bones are disarticulated, but closely associated. There are two groups of long bones oriented with their long axes in two perpendicular directions. The bone accumulation at Site O is dominated by

Tendaguru, Site O
Upper Saurian Bed
Dicraeosaurus sattleri

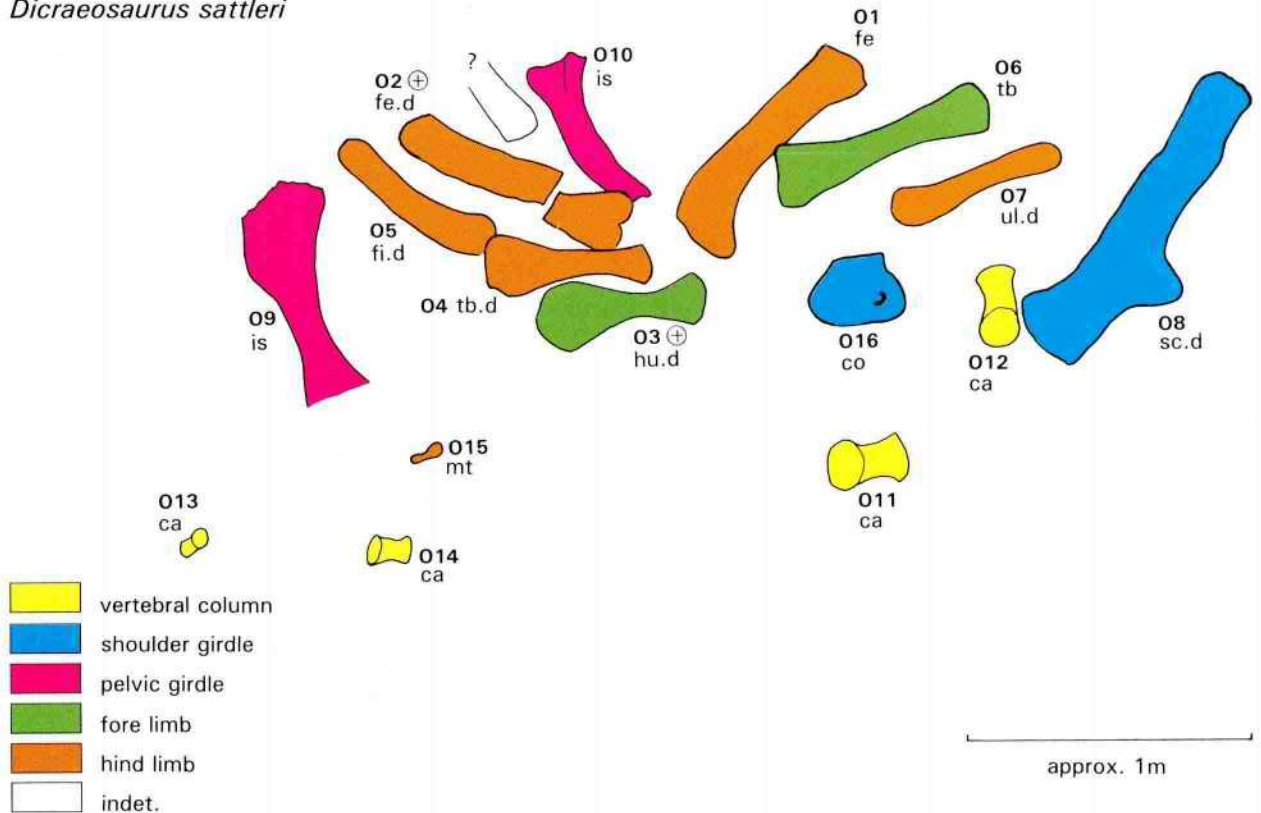


Fig. 6. Incomplete skeleton of *Dicraeosaurus sattleri* from Tendaguru Site O. The specimen is completely disarticulated. Note the dominance of large limb bones. The measured length of the humerus O3 (610 mm) was used to calculate the scale for the quarry map. The orientation of the map is not known. Redrawn after a field sketch from W. Janensch

heavy limb bones (humerus, ulna, femora, tibiae, fibula). This may indicate that most smaller bones had been almost completely removed from the carcass by currents prior to burial.

3.1.5 Tendaguru Site P

Location: Site P is located at Nterego, approximately 1.2 km north-north-east of Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxon: *Janenschia robusta*

Figure: 7 (colour figure on p. 37)

Reference: Janensch (1914a, 1922, 1929a, 1961a), Bonaparte et al. (in press), GTE field catalogue: 21–22

Assemblage data

NISP: 65

MNI: 2

Number of taxa: 1

Designation: Multi-individual but single-taxon assemblage

Quarry data

Size of accumulation: approximately 24.00 m²

Density: approximately 2.74

Modification data

Disarticulation stage: H (find I), K (find III, IV) and L (find II)

Measurements: The length of the left limb bones were measured as follows: humerus (P8): 890 mm, radius (P11): 620 mm, ulna (P12): 670 mm, tibia (P5): 850 mm, astragalus (P6): 210 mm.

Ontogenetic data: Unknown

Comments: Digging at Site P commenced in October 1909 (Janensch, GTE field catalogue:

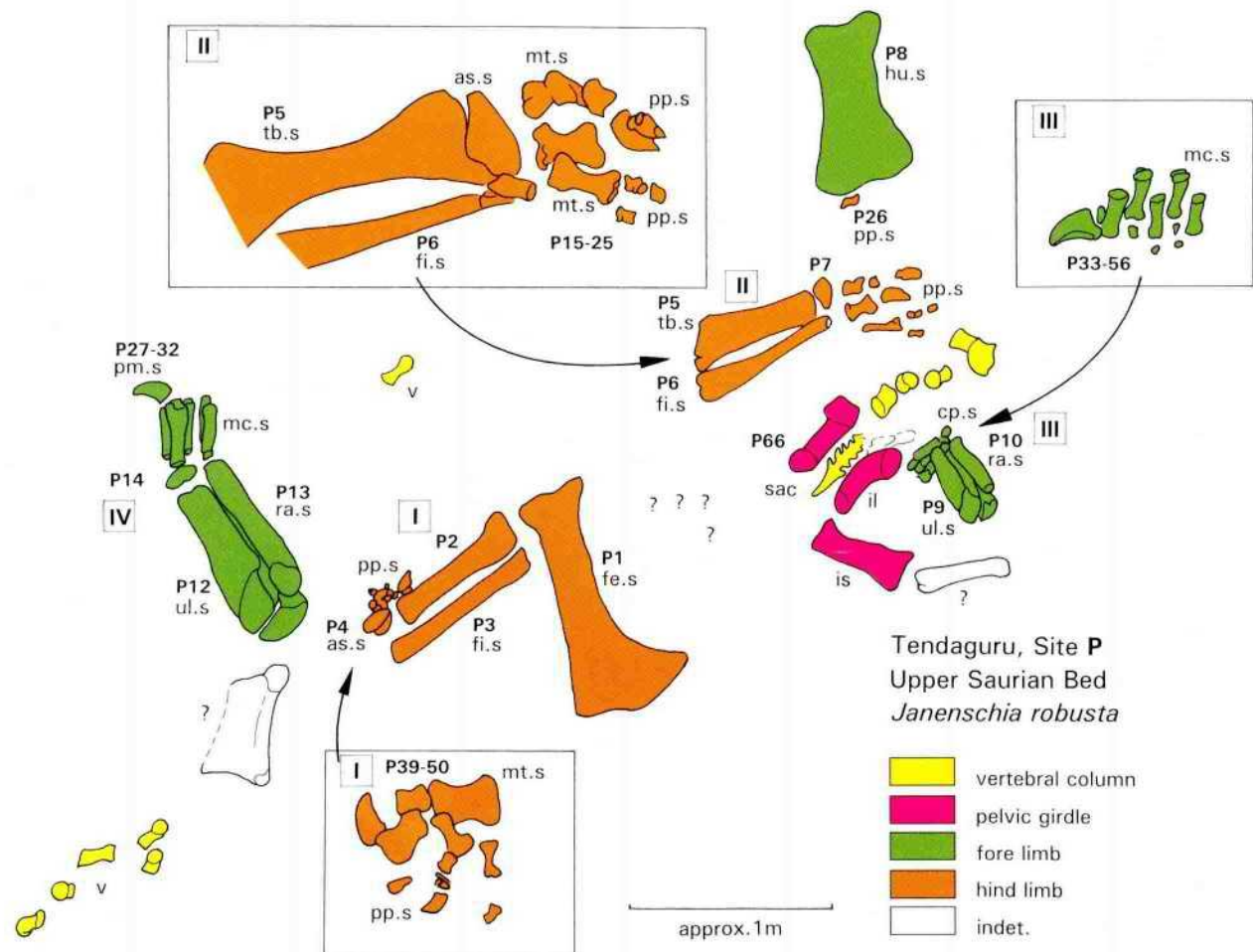


Fig. 7. Partial skeletons of *Janenschia robusta* from Tendaguru Site P. The bone assemblage consists mainly of two articulated left fore limbs and two articulated left hind limbs. Pelvic elements rest next to the sacrum, and some vertebrae are scattered over the quarry floor. The measured length of the humerus P8 (890 mm) was used to calculate the scale for the quarry map. The orientation of the map is not known. Redrawn after a field sketch from W. Janensch

21–22) Four partial skeletons of *Janenschia robusta* were uncovered, along with additional scattered postcranial bones (GTE field catalogue; Janensch 1922, 1929a; Bonaparte et al., in press). According to Janensch's unpublished excavation sketches and hand-written notes (GTE field catalogue: 21), partial skeleton I consists of a reasonably complete left hind limb, with femur, tibia, fibula, and the foot, including astragalus, metacarpals, and phalanges. The foot bones were still close to their natural anatomical position, while femur, tibia and fibula were slightly disarticulated. Close to this bone accumulation lay partial skeleton IV, represented by an incomplete left fore limb, with radius, ulna, carpal, metacarpals, and phalanges. Nearly all these bones were found in their proper anatomical order. Partial skeleton II consists of an incomplete hind limb, including tibia, fibula, and slightly disarticulated and scattered foot bones (astragalus, metatarsals, phalanges). Partial skeleton III includes the radius, ulna, and the manus of an incomplete left fore limb. In addition to the four partial skeletons, dinosaur bones found at site P include, among others, a left humerus, a sacrum, and several disarticulated vertebrae scattered over the quarry floor. Janensch (unpublished sketchbook) also noted ribs in his excavation map but no location data are given. The association of these bones with the four partial skeletons remains far from clear. The long axes of the two anterior lower legs (partial skeletons III, IV), the femur of partial skeleton I, and the single humerus were similarly oriented. The two posterior lower legs (finds I, II) are deposited with their long axes perpendicular to the preferred orientation of partial skeletons III and IV.

The low degree of disarticulation, especially of the feet, suggests that soft tissue must have remained attached to the limb bones when they were deposited. The taphonomic evidence also suggests that the partial skeletons were buried close to the point where the original corpses came to rest. In addition, several limb bones show signs of strong weathering due to processes subsequent to burial (Janensch 1914a: 44; 1961a).

Taphonomic and anatomical analyses show that the four partial skeletons belong to a single species, and represent two individuals of *Janenschia robusta* (Janensch 1922, 1929a: 7; GTE field catalogue: 21–22). Tendaguru Site P is the only known site, so far, that has provided specific information on the fore and hind limbs of *Janenschia robusta*.

3.1.6 Tendaguru Site k

Location: Site k is situated about 0.7 km south of Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxon: *Barosaurus africanus*

Figure: 8 (colour figure on p. 39)

Reference: Janensch (1914a, 1929a, 1961a), GTE field catalogue

Assemblage data

NISP: 50

MNI: 1

Number of taxa: 1

Designation: Single-individual, single-taxon assemblage

Quarry data

Size of accumulation: approximately 19.00 m²

Density: approximately 2.62

Modification data

Disarticulation stage: E

Measurements: The length of skeletal elements is as follows (Janensch 1961a): left scapula (k34): 1340 mm, right humerus (k37): 970 mm, left ulna (k38): 740 mm, left ischium (k44): 880 mm, left tibia (k41): 860 mm.

Ontogenetic data: Unknown

Comments: Skeleton k was found close to the remains of *Barosaurus africanus* from Sites A and B (Janensch 1914a, 1929a). The collecting site was discovered in 1910 (Janensch 1914a). In specimen k, all the main body regions (e.g., skull, axial skeleton, appendicular skeleton) are represented. Janensch (1929a: 6) reported a braincase, maxilla, cervical and dorsal vertebrae, anterior caudal vertebrae, ribs, scapula, coracoid, humerus, ulna, ischium, femur, tibia, and fibula, all assigned to *Barosaurus africanus*. There are two clusters of skeletal elements, one of which comprises mostly bones of the anterior body region (e.g., braincase, cervical vertebrae, scapula, coracoid, humerus), whereas the other contains bones from the posterior body region (e.g., ischium, femur, tibia, fibula, caudal vertebrae). Only a few skeletal elements are articulated: two strings of dorsal vertebrae (k12 and k13, k14 and k15) and two articulated caudal vertebrae (k 20, k21) have been found (Janensch GTE field catalogue: 48). The remaining skeletal elements were disarticulated but still closely associated. Most of the cervical vertebrae and caudal vertebrae were

apparently found in their natural anatomical order (Janensch, GTE field catalogue: 48), and haemapophyses were associated with the centra of the caudal vertebrae.

The excavation plan (Fig. 8) shows that the limb bones, ischia, scapula, and most of dorsal ribs are embedded with their long axes trending approximately northwest to southeast. The heads of all the dorsal ribs are directed southwards. The fibula is water-worn (Janensch, GTE field catalogue: 49).

The arrangement of the skeletal elements appears to have been modified by water currents. However, the presence of articulated and disarticulated vertebrae found in almost natural anatomical order, the orientation of the dorsal ribs, and the presence of a braincase indicate that the carcass was embedded and decayed close to the place where it came to rest.

3.1.7 Tendaguru Site ab

Location: Site ab is located approximately 1.2 km northnortheast of Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxa: *Barosaurus africanus*, *Dicraeosaurus satterli*, *Brachiosaurus brancai*?, Sauropoda indet.

Figure: 9 (colour figure on p. 40)

Reference: Janensch (1961a), GTE field catalogue: 40–41

Assemblage data

NISP: 37

MNI: 5

Number of taxa: (4)

Designation: Multi-individual, multi-taxon assemblage

Quarry data

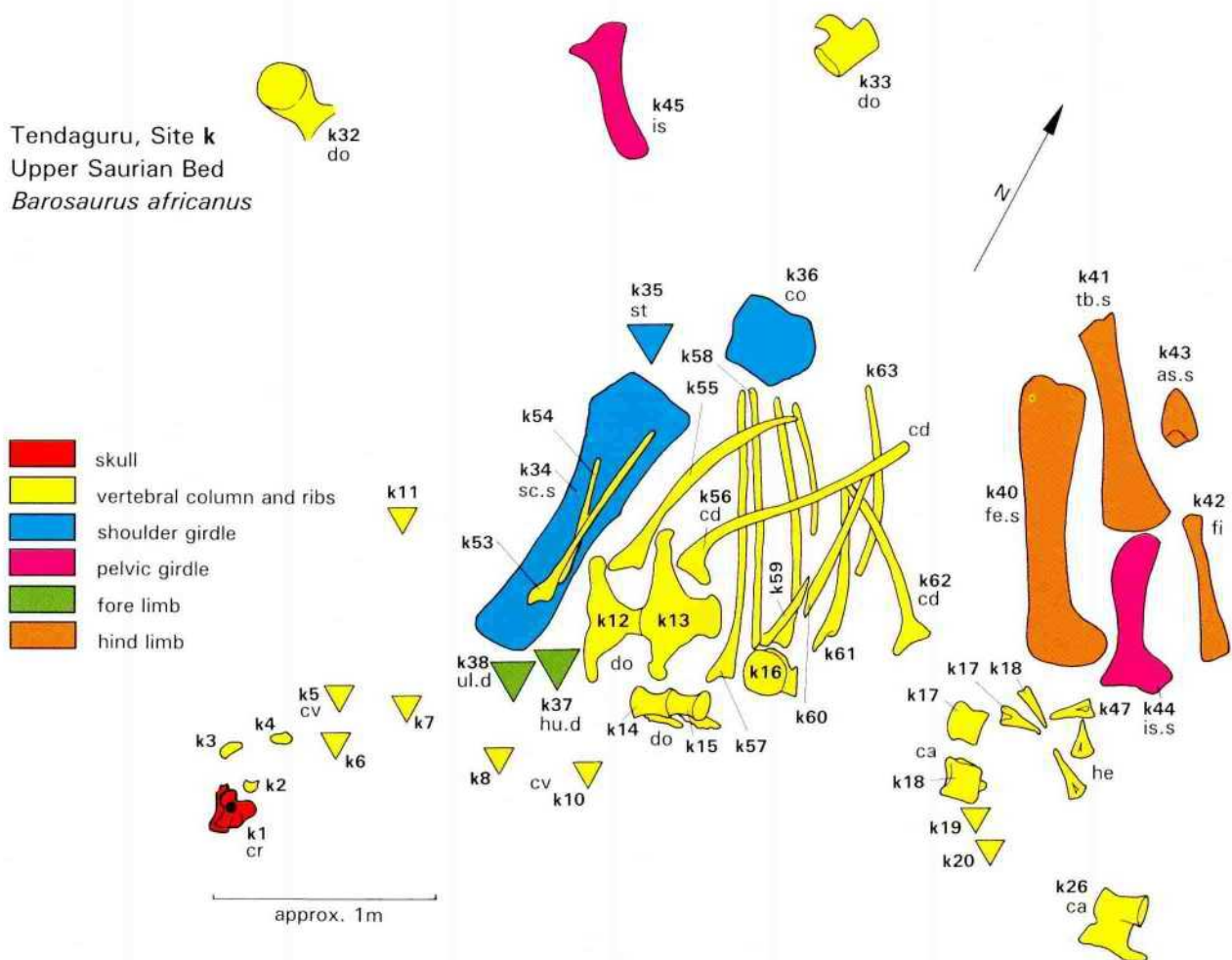


Fig. 8. Incomplete skeleton of *Barosaurus africanus* from Tendaguru Site k, in an advanced stage of disarticulation, with braincase and cervical vertebrae resting next to the anterior appendicular and trunk elements. The caudal vertebrae are close to the pelvic and hind limb elements. Most skeletal elements are disarticulated, but still closely associated. The measured length of the scapula k34 (1340 mm) was used to calculate the scale for the quarry map. Redrawn after a field sketch from W. Janensch

Size of accumulation: approximately 10.00 m²

Density: approximately 3.61

Modification data

Disarticulation stage: O

Measurements: *Dicraeosaurus sattleri*, length of three left humeri: 620 mm (ab1), 620 mm (ab2), 580 mm (ab10); *Barosaurus africanus*, length of a left tibia (ab4): 650 mm.

Ontogenetic data: Histological data obtained from two left humeri (ab2, ab10) indicate that these limb bones are from two adult individuals of *Dicraeosaurus sattleri* (Sander 1999, in press).

Comments: There are no excavation data given by Janensch (1914a, 1929a, 1961a), except for the GTE field catalogue. The dig commenced at the beginning of October, 1909. Remains of at least five individual sauropods were recovered from the Upper Saurian Bed at Site ab. All bones are disarticulated and scattered, appar-

ently randomly, across the excavation floor. Several bones are imperfect and show distinct signs of breakage. Scattering and mixing of skeletal elements from different taxa and individuals suggests that there was much transport of bones prior to burial. Some of the heavy limb bones are oriented northwest to southeast, others are embedded with long axes trending approximately west to east. The presence of three left humeri (ab1, ab2, ab10) reveals that the diplodocid *Dicraeosaurus sattleri* is represented by at least three individuals. Two tibiae (ab4, ab5) belong, apparently, to one individual of *Barosaurus africanus* (Janensch, GTE field catalogue: 40), and two large femora are tentatively assigned to *Brachiosaurus brancai* (Janensch, GTE field catalogue: 40). A huge uncatalogued limb bone that was not collected (Janensch, field sketch, handwritten note) was tentatively identified as a humerus of *Brachiosaurus brancai*.

Tendaguru, Site ab
Upper Saurian Bed

- Barosaurus africanus*
- Brachiosaurus brancai*?
- Dicraeosaurus sattleri*
- Sauropoda indet.

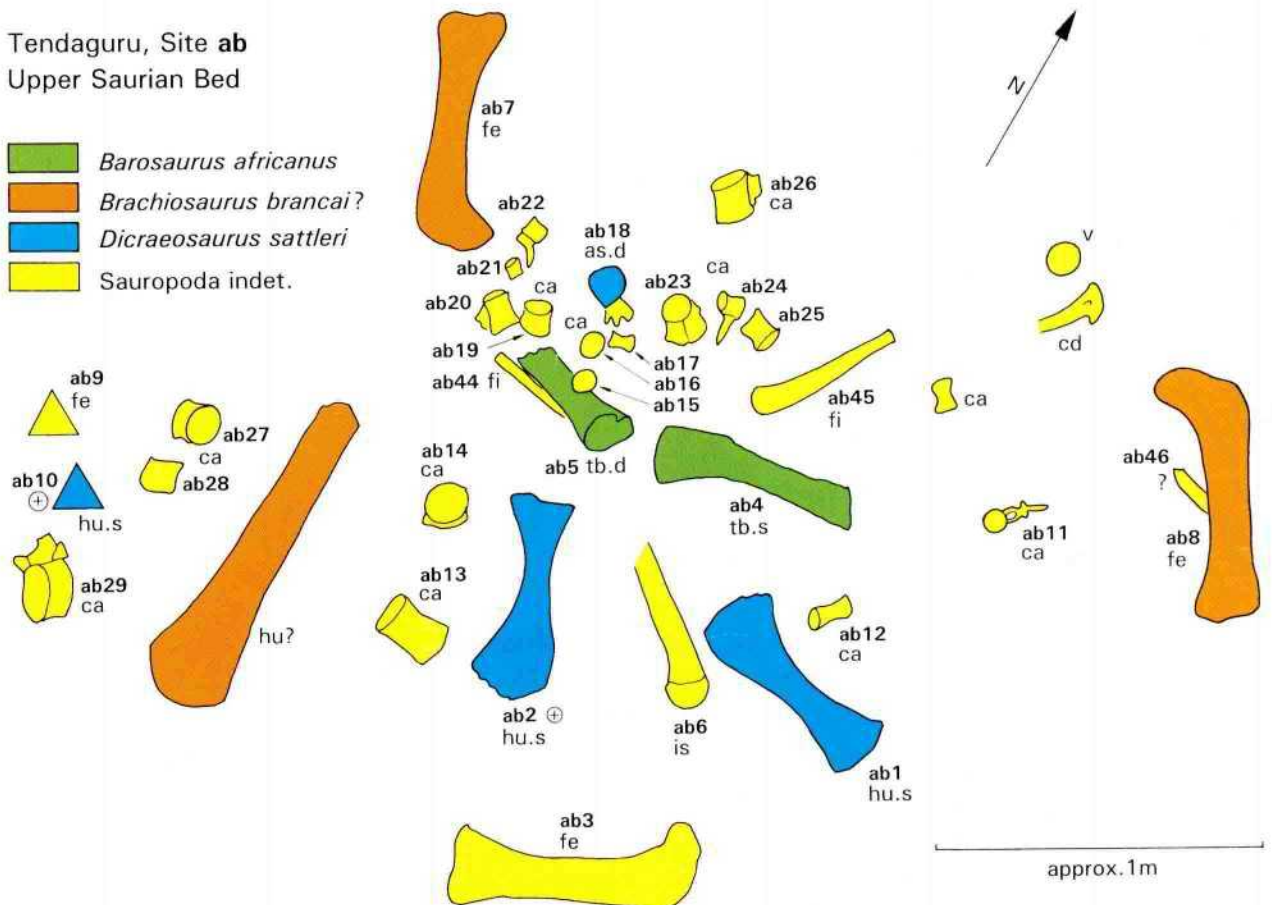


Fig. 9. Bone field from Tendaguru Site ab. The accumulation consists mainly of disarticulated sauropod limb bones and vertebrae. Scattering is evident. Note the presence of three left humeri of *Dicraeosaurus sattleri*, one of which, humerus ab1 (620 mm), was used to calculate the scale for the quarry map. Redrawn after a field sketch from W. Janensch

3.1.8 Tendaguru Site cc

Location: Site cc is situated approximately 2.9 km eastnortheast from Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxon: *Brachiosaurus brancai*

Figure: 10 (colour figure on p. 41)

Reference: GTE-field catalogue: 142

Assemblage data

NISP: 15

MNI: 1

Number of taxa: 1

Designation: Single-individual, single-taxon assemblage

Quarry data

Size of accumulation: approximately 24.00 m²

Density: approximately 1.6

Modification data

Measurements: Length of a right humerus (cc2): 1080 mm.

Disarticulation stage: F

Ontogenetic data: According to Sander (1999, in press), humerus cc2 belongs to an adult individual of *Brachiosaurus brancai*.

Comments: Taphonomic data for Site cc are poor. Remains found here include cervical vertebrae, a dorsal vertebra, several dorsal ribs, a scapula, a humerus, and bone fragments (Janensch, GTE field catalogue: 142). All elements are disarticulated, but still associated. A preferred orientation of the bones is not discernable.

The documented skeletal elements are mainly from the anterior body region (neck, anterior appendicular skeleton) of a carcass that underwent maceration and decay prior to burial.

3.1.9 Tendaguru Site X

Location: Site X is located about 1.0 km south-south-east from Tendaguru Hill.

Stratigraphy: Upper Saurian Bed

Taxon: *Kentrosaurus aethiopicus*, Sauropoda indet.

Figure: 11

Reference: Hennig (1925), GTE field catalogue: 113–114

Assemblage data

NISP: 115

MNI: (7)

Number of taxa: (2)

Tendaguru, Site cc
Upper Saurian Bed
Brachiosaurus brancai

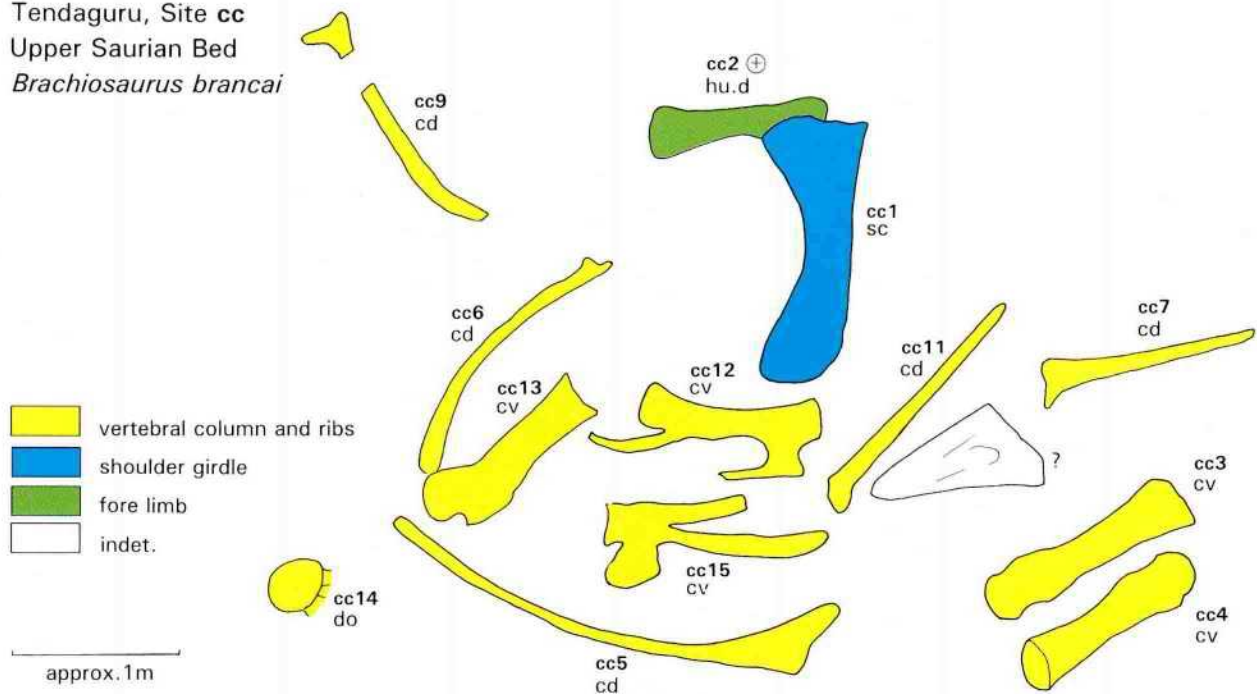


Fig. 10. Incomplete skeleton of *Brachiosaurus brancai* from Site cc in an advanced state of disarticulation. All bones are disarticulated. The measured length of the humerus cc2 (1080 mm) was used to calculate the scale for the quarry map. The orientation of the map is not known. Redrawn after a field sketch from W. Janensch

Designation: Multi-individual, multi-taxon assemblage
Quarry data
Size of accumulation: approximately 30.00 m²
Density: approximately 3.83
Modification data
Measurements: See Hennig (1925)
Disarticulation stage: N (O?)
Ontogenetic data: Unknown
Comments: Digging at Site X commenced in August, 1909 (Janensch, GTE field catalogue:

113). The quarry map (Fig. 11) is based on a field plan preserved in the GTE sketch book and a detailed list of skeletal elements assigned to *Kentrosaurus* (Hennig 1925: 228–229). Bones of *Kentrosaurus aethiopicus* are the most common skeletal elements of dinosaurs recovered from the Upper Saurian Bed at Site X, constituting more than 95% of the total dinosaur finds. The documented bone cluster is dominated by isolated hand and foot bones which formed a pavement on the quarry floor. Scattering and mixing of the skeletal elements is evident. Judging from the data by Hennig (1925: 228–229), the skeletal remains belong to at least 6 individuals

Tendaguru, Site X
Upper Saurian Bed

Site plan and disposition of bones in the central part of the excavation

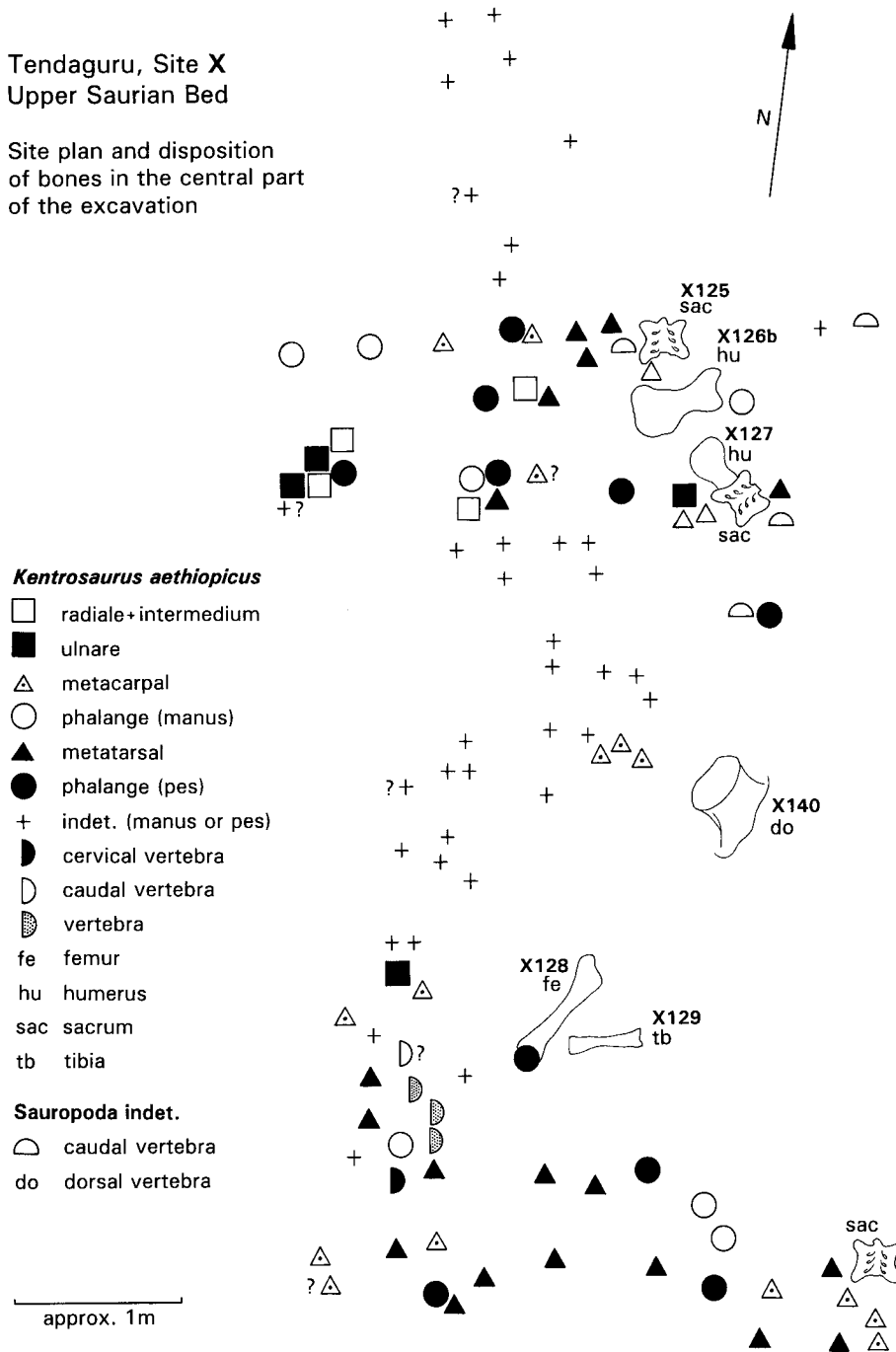


Fig. 11. Bone field in the central part of Tendaguru Site X. The accumulation is dominated by manus and pes elements of *Kentrosaurus aethiopicus*. Scattering is evident. Because of space limitation the catalogue numbers could only be shown for some bones. Redrawn after a field sketch from W. Janensch or E. Hennig

of *Kentrosaurus aethiopicus*. Moreover, isolated sauropod vertebrae are also present.

The dominance of scattered and mixed hand and foot bones confirms the impression that there was substantial transport and sorting of bones prior to burial. However, the origin of the mass accumulation of kentrosaurian bones is difficult to explain owing to the lack of precise data. It is possible that carcasses of mired and drowned kentrosaurs floated or were washed away, whereas the hands and feet remained in the mud, which was subsequently reworked by currents or waves to form a pavement of bones. This interpretation would agree well with the taphonomic model proposed by Janensch (1914c). However, it is also possible that the hand and foot bones found at Site X were winnowed away from the decaying carcasses of *Kentrosaurus aethiopicus* and thus resulted from current sorting. Whatever happened, the place of burial is apparently not the place of death.

3.2 Sites in the Transitional Sands above the *Trigonia smeei* Bed

3.2.1 Tendaguru Site H

Location: Site H is located 1.3 km northeast of Tendaguru Hill

Stratigraphy: Transitional Sands between the *Trigonia smeei* Bed and the base of the Upper Saurian Bed

Taxa: *Barosaurus africanus*,

Figure: 12 (colour figure on p. 43)

Reference: Janensch (1929a), GTE field catalogue: 11

Assemblage data

NISP: 24

MNI: 1

Number of taxa: 1

Designation: Multi-individual but single-taxon assemblage

Quarry data

Size of accumulation: approximately 14.00 m²

Tendaguru, Site H

Transitional Sands between
Trigonia smeei-Bed
and Upper Saurian Bed

Barosaurus africanus

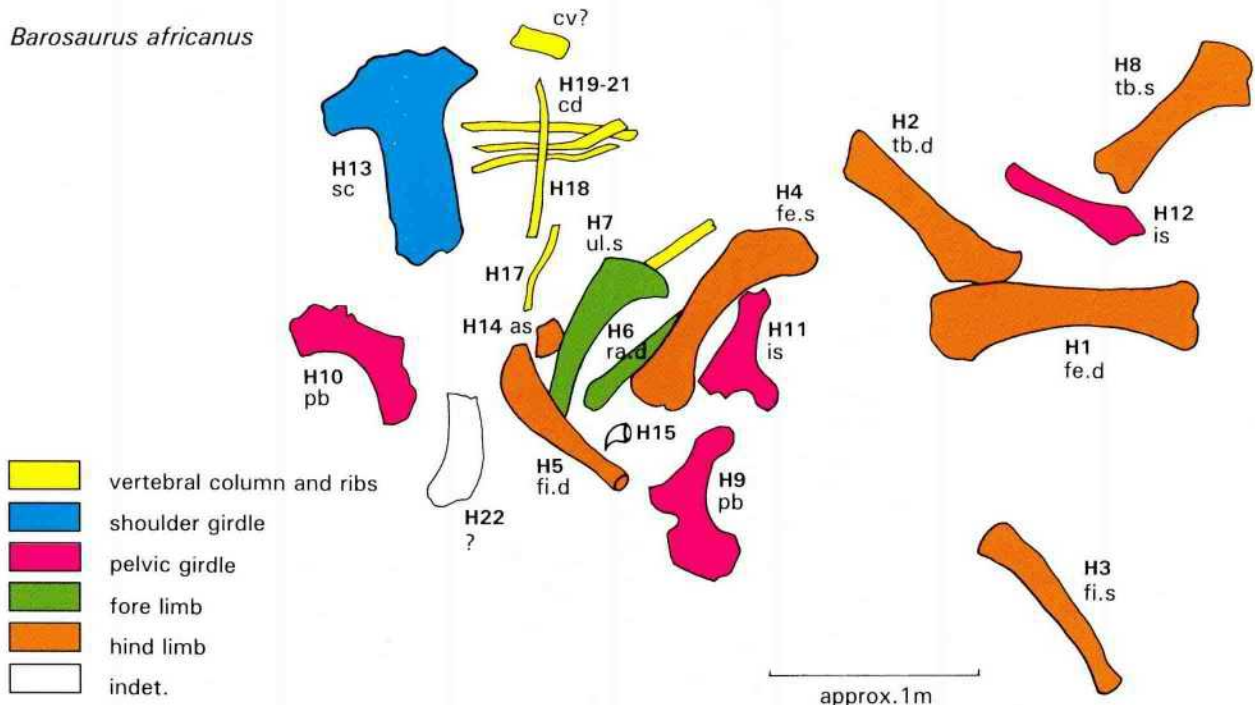


Fig. 12. Incomplete skeleton of *Barosaurus africanus* from Tendaguru Site H. The accumulation is dominated by limb bones and pelvic elements. Some limb bones rest on top of one another. The orientation of the map is not known. Redrawn after a field sketch from W. Janensch

Density: approximately 1.71

Modification data

Disarticulation stage: F

Measurements: Right radius (H6): 700 mm; left ulna (H7): 750 mm; right femur (H1): 1200 mm; left femur (H4): 1290 m; right tibia (H2): 880 mm; left fibula

(H3): 920 mm; right fibula (H5): 960 mm.

Ontogenetic data: Unknown.

Comments: The dig at Site H commenced in August, 1909 (GTE field catalogue: 11), and produced disarticulated and scattered bones of *Barosaurus africanus*, including ribs, scapula, ulna, radius, ischium, pubis, femur, tibia, and fibula (Janensch 1929a: 6). Some of these bones,

such as the right femur (H1) and the right tibia (H2), are still associated, but much of the material recovered is imperfect (e.g. scapula H13, pubes H10). The dominance of heavy long bones and the remarkable scarcity of small skeletal elements suggests that there was much post-mortem transportation of bones from the carcasses prior to burial. Because of the size differences between the two femora found (H1: 1200 mm; H4: 1290 mm), it is concluded that the bone accumulation from Site H contains skeletal remains of at least two individuals of *Brachiosaurus brancai*.

In addition to these skeletal remains, Site H has yielded non-sauropod bones not documented in the field sketch, among them a coelurosaurian tibia and a metatarsal of *Kentrosaurus aethiopicus*.

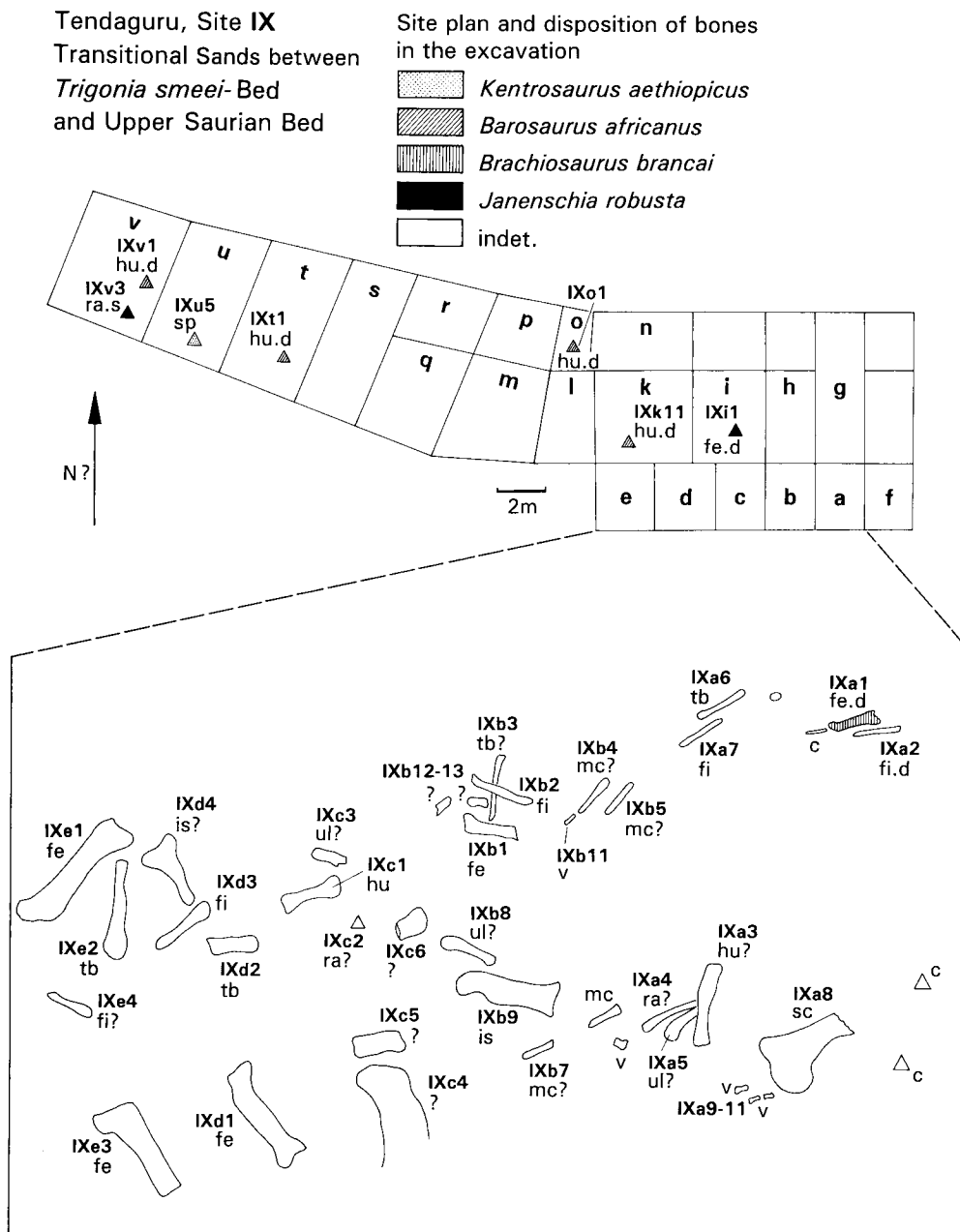


Fig. 13. Bone field from Tendaguru Site IX. The accumulation consists mainly of disarticulated limb bones from sauropods scattered over the quarry floor. Redrawn after a field sketch from W. Janensch

cus (GTE field catalogue: 11). Their precise provenance is uncertain. Other discoveries from Site H include marine invertebrates (e.g., belemnites) indicating a marginal marine palaeoenvironment for the dinosaur-bearing Transitional Sands above the *Trigonia smeei* Bed, as formerly suggested by Janensch (1914c).

3.2.2 Tendaguru Site IX

Location: Site IX is situated about 1.4 km northeast of Tendaguru Hill.

Stratigraphy: Transitional Sands between the *Trigonia smeei* Bed and the base of the Upper Saurian Bed

Taxa: *Barosaurus africanus*, *Brachiosaurus brancai*, *Janenschia robusta*, *Kentrosaurus aethiopicus*

Figure: 13

Reference: Janensch (1914c), GTE field catalogue: 108–112.

Assemblage data

NISP: Unknown

MNI: Unknown

Number of taxa: (4)

Designation: Multi-individual, multi-taxon assemblage

Quarry data

Size of accumulation: The precise size of the excavation floor is not known. The exposed quarry floors a–f measure, in total, roughly 13.0 m by 2.5 m (s. Fig. 13)

Density: Unknown

Modification data

Disarticulation stage: O (N?)

Measurements: *Brachiosaurus brancai*, length of a right femur (IXa1), 1180 mm; length of left femur (IX1): 880 mm; *Barosaurus africanus*, length of left humerus (IX94): 640 mm; length of right humeri: 660 mm (IXk11), 730 mm (IXv1), 380 mm (IXx9).

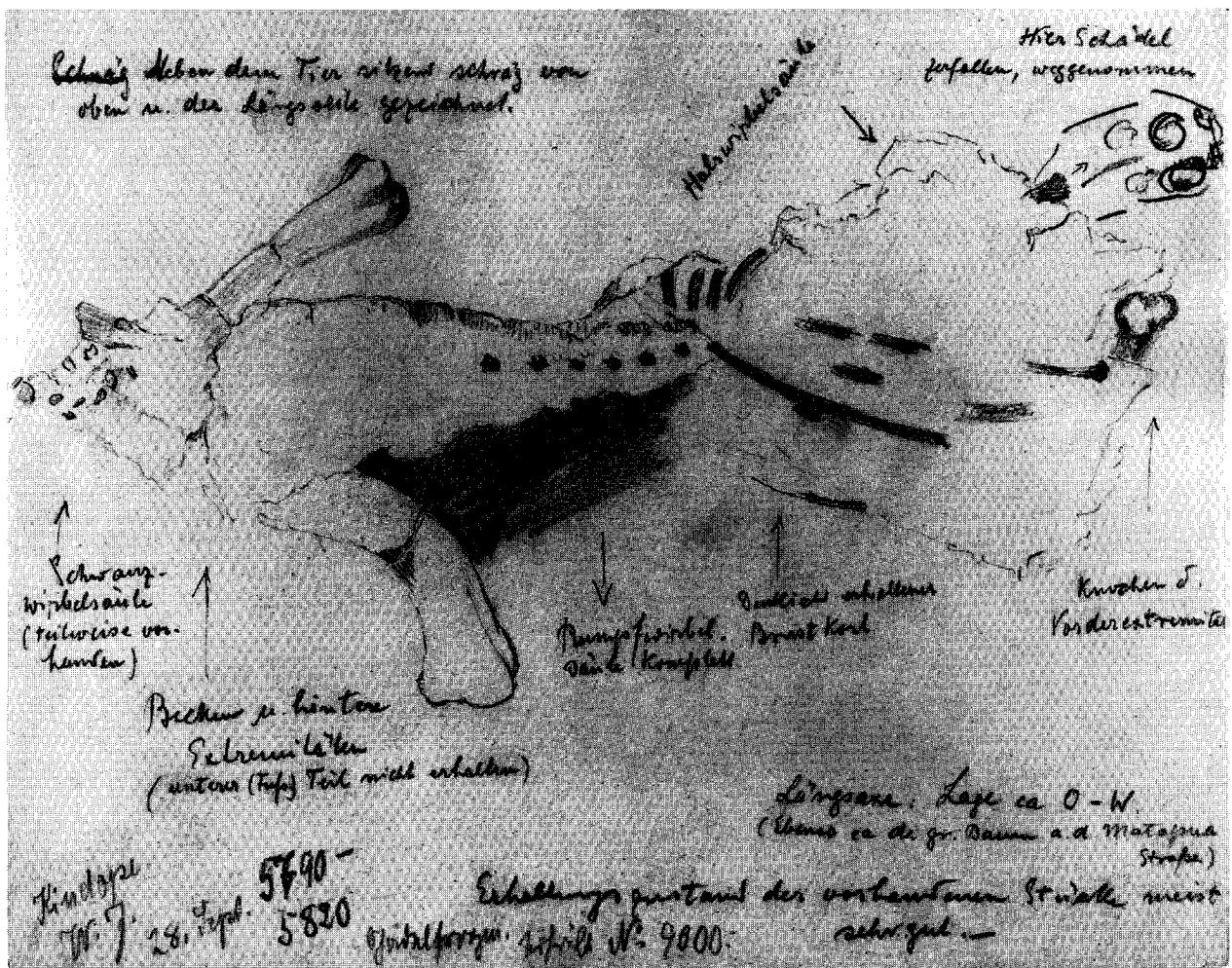


Fig. 14. Incomplete skeleton of *Dryosaurus lettow-vorbecki* from Tendaguru Site Jg (WJ). Original field sketch from I. Reck or H. Reck

Ontogenetic data: According to Sander (1999, in press), humerus IX94 is from a juvenile individual of *Barosaurus africanus*, while femur IX1 is from an adult individual of *Brachiosaurus brancai*.

Comments: Excavations at Site IX commenced on August 17, 1909. About 150 individual bones of dinosaurs were collected from Site IX which was located between the *Trigonia smeei*-Bed and the Upper Saurian Bed (GTE field catalogue: 108), although only some of these were mapped (Fig. 13). Partial skeletons were not found, and the majority of bones were disarticulated and scattered over the excavation area, though some of them may have still been associated. Janensch (1914c: 44) reported that most of the bones were embedded horizontally and concentrated in a distinct bone-bearing layer. He also noted the dominance of bones from the appendicular skeleton (Janensch 1914c: 44). A closer study of the 130 identified bones from Site IX reveals that 85 (= 65,4%) are leg elements, including humeri, radii, ulnae, femora, tibiae, and fibulae (GTE field catalogue: 108–112). Other elements (e.g., vertebrae, pha-

langes, ribs) are under-represented or completely missing (e.g., skull elements, lower jaws).

Some bones are well preserved, others in poor condition. The epiphyses of several limb bones are considerably worn due to rolling and abrasion by the embedding sands (Janensch 1914a, c), and there is no doubt that the skeletal remains were current modified. Moreover, the scattering and the state of preservation of the skeletal elements suggest a long period of time during which the bones were transported by waves and/or currents from the carcasses to the place of permanent burial.

Only a few catalogued limb bones have been identified taxonomically. Most of them apparently belong to sauropod dinosaurs. A minimum of four individuals of *Barosaurus africanus* are indicated by four right humeri. Skeletal remains of *Brachiosaurus brancai*, *Janenschia robusta*, and *Kentrurosaurus aethiopicus* are apparently less common than those of *Barosaurus africanus*, but precise specimen counts are not available. Belemnites have frequently been found at Site IX (GTE field catalogue: 108).

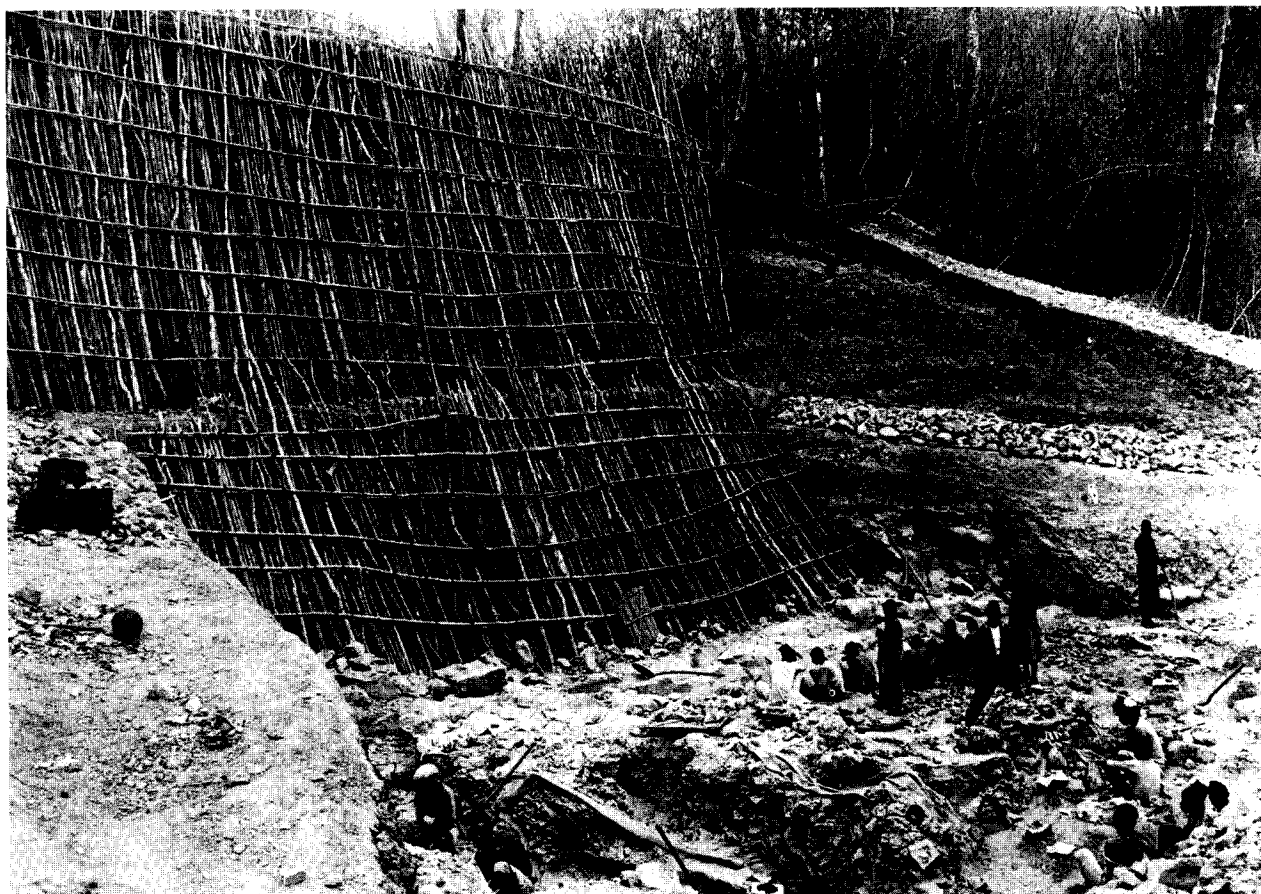


Fig. 15. Tendaguru Site S, the type locality of *Brachiosaurus brancai*. Photograph: W. Janensch

3.3 Sites in the Middle Saurian Bed

3.3.1 Tendaguru Site Jg (= WJ)

Location: Tendaguru Site Jg (= WJ) is located approximately 2.3 km north-north-west of Tendaguru Hill.

Stratigraphy: Middle Saurian Bed

Taxon: *Dryosaurus lettow-vorbecki*

Figure: 14

Reference: GTE sketchbook

Assemblage data

NISP: Unknown

MNI: 1

Number of taxa: 1

Designation: Single-individual, single-taxon assemblage

Quarry data

Size of accumulation: Unknown

Density: Unknown

Modification data

Measurements: Not available

Disarticulation stage: ? (complete or incomplete skeleton)

Ontogenetic data: Unknown

Comments: Excavations at Site Jg (WJ) commenced in 1910 and continued through the years 1911 and 1912 (Branca 1914; Janensch 1914c; GTE field catalogue: 73). Quarry Jg (WJ) is one of the richest dinosaur-bearing sites in the surroundings of Tendaguru Hill. It produced thousands of bones of the small ornithomimid dinosaur *Dryosaurus lettow-vorbecki* (Janensch 1950c, 1955, 1961b). Judging from matrix kept in the Berlin Tendaguru collection, isolated vertebrae and limb bones of *Dryosaurus lettow-vorbecki* are the most common elements found in the Middle Saurian Bed at Site Jg (WJ). Skull fragments and teeth are fairly rare. Site Jg (WJ) has not only produced isolated bones but also partial and fairly complete skeletons (Fig. 14). Strings of vertebrae with closely associated chevrons also occur. The dryosaurs from Site Jg (WJ) are thought to have died close to the places where they were buried (Janensch 1914a, c).

Tendaguru, Site S
Middle Saurian Bed
Brachiosaurus brancai

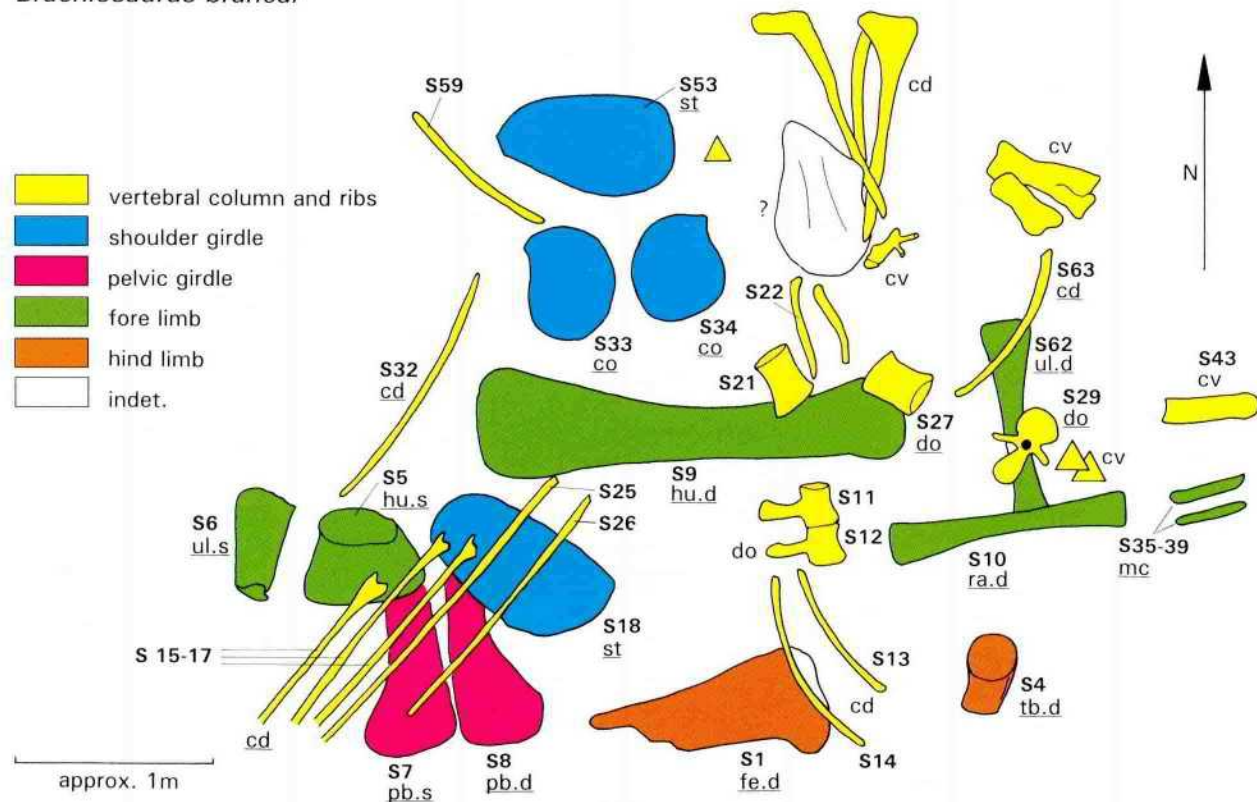


Fig. 16. Incomplete skeletons of *Brachiosaurus brancai* from Tendaguru Site S. Anatomical identifications of skeleton SII are underlined. Elements of skeleton SI could not be identified with certainty. The measured length of the humerus S9 (213.0 cm) was used to calculate the scale for the quarry map. Redrawn after a field sketch from W. Janensch

A drawing of an in-situ skeleton of *Dryosaurus lettow-vorbecki*, preserved in the GTE sketchbook shows, a fairly complete skeleton recovered in 1912 (Fig. 14). An articulated skull seems to be present, and most of the vertebral column appears to be preserved in natural articulation, as do the dorsal ribs. The caudal vertebral column is partly preserved. From the fore limbs, nothing but the proximal section of a right humerus or ulna was documented. The left femur is spread slightly away from the trunk, and the proximal sections of both femora are apparently closely associated with the pelvic region. The lower legs were either not found or not documented in the field sketch. Unfortunately, the location of the documented skeleton of *Dryosaurus lettow-vorbecki* is not known.

3.3.2 Tendaguru Site S

Location: Site S is located approximately 1.0 km southsouthwest of Tendaguru Hill

Stratigraphy: Middle Saurian Bed

Taxon: *Brachiosaurus brancai*

Figures: 15, 16 (colour figure on p. 47) and 18

Reference: Janensch (1914a, c; 1929a, 1950a, b; 1961a), GTE field catalogue: 25–28

Assemblage data

NISP: Not precisely known

MNI: 2

Number of taxa: 1

Designation: Multi-individual, single-taxon assemblage

Quarry data

Size of accumulation: ?

Density: ?

Modification data

Disarticulation stage: E (skeleton SII), L (skeleton SI)

Measurements: Skeleton SII, length of selected elements of the appendicular skeleton

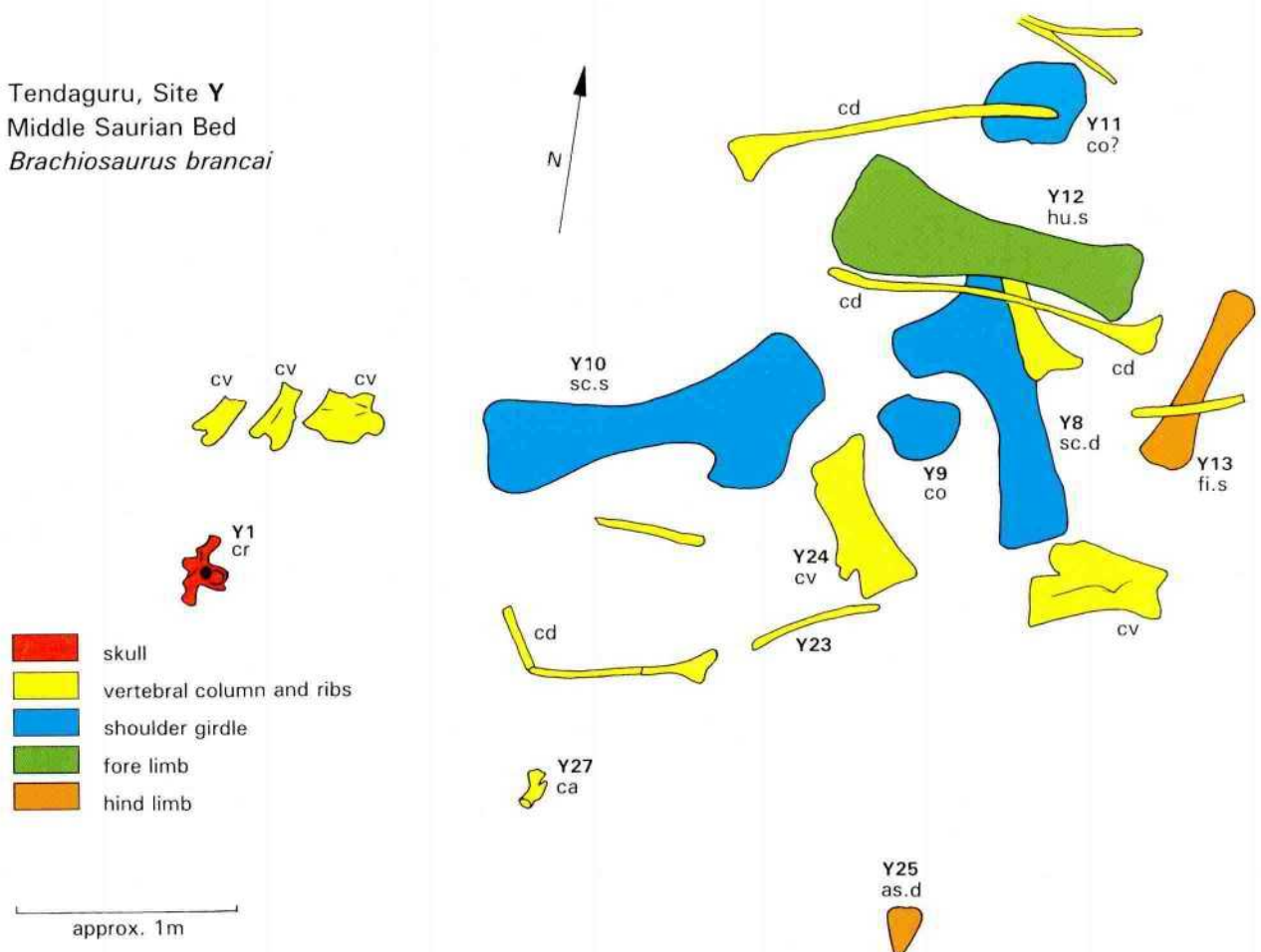


Fig. 17. *Brachiosaurus brancai* from Tendaguru Site Y. The incomplete skeleton consists of disarticulated elements from the anterior part of the body. The measured length of the scapula Y8 (154.0 cm) was used to calculate the scale for the quarry map. Redrawn after a field sketch from W. Janensch

(Janensch 1961a): left sternal plate: 1100 mm; right coracoid: ca. 840 mm; right humerus: 2130 mm; right radius: 1240 mm; right Ulna: 1300 mm; mc I dext.: 595 mm; mc II dext.: 635 mm; mc III dext.: 595 mm; mc IV dext.: 570 mm; mc V dext.: 490 mm; right femur: ca. 1960 mm, right fibula: 1190 mm.

Ontogenetic data: Judging from solitary limb bones that are at least one tenth larger than those of skeleton SII, it could be concluded that the SII specimen was not yet fully grown (Janensch 1938).

Comments: The dig commenced on October 11, 1909 and Tendaguru Site S was worked by the German Tendaguru until 1911 (Janensch 1914a). Site S is the type locality for *Brachiosaurus brancai* and remains of two individuals were found. Skeleton SI, the type specimen of

Brachiosaurus brancai, is a partial skeleton, comprising the skull, six cervical vertebrae and (?) dorsals (Janensch 1929a: 8). Specimen SII which is larger than SI, is an incomplete skeleton of *Brachiosaurus brancai* (Janensch 1914a, c; 1929a; 1950a, b; 1961a), including skull bones, a nearly complete presacral vertebral column (11 cervical and 11 dorsal vertebrae), cervical and dorsal ribs, most of the anterior appendicular skeleton (left scapula, coracoids, sternals, right anterior limb, left humerus, ulna, and radius), parts of the pelvic girdle (e.g. both pubes bones), and incompletely preserved hind limbs (e.g., imperfect right femur, right tibia and fibula, and foot bones). The sacrum and the caudal series were already missing when the specimen was discovered, most likely due to erosion (Janensch 1914c).

Janensch (1914a, c) reported that the humerus and a tibia of the SII individual were found in

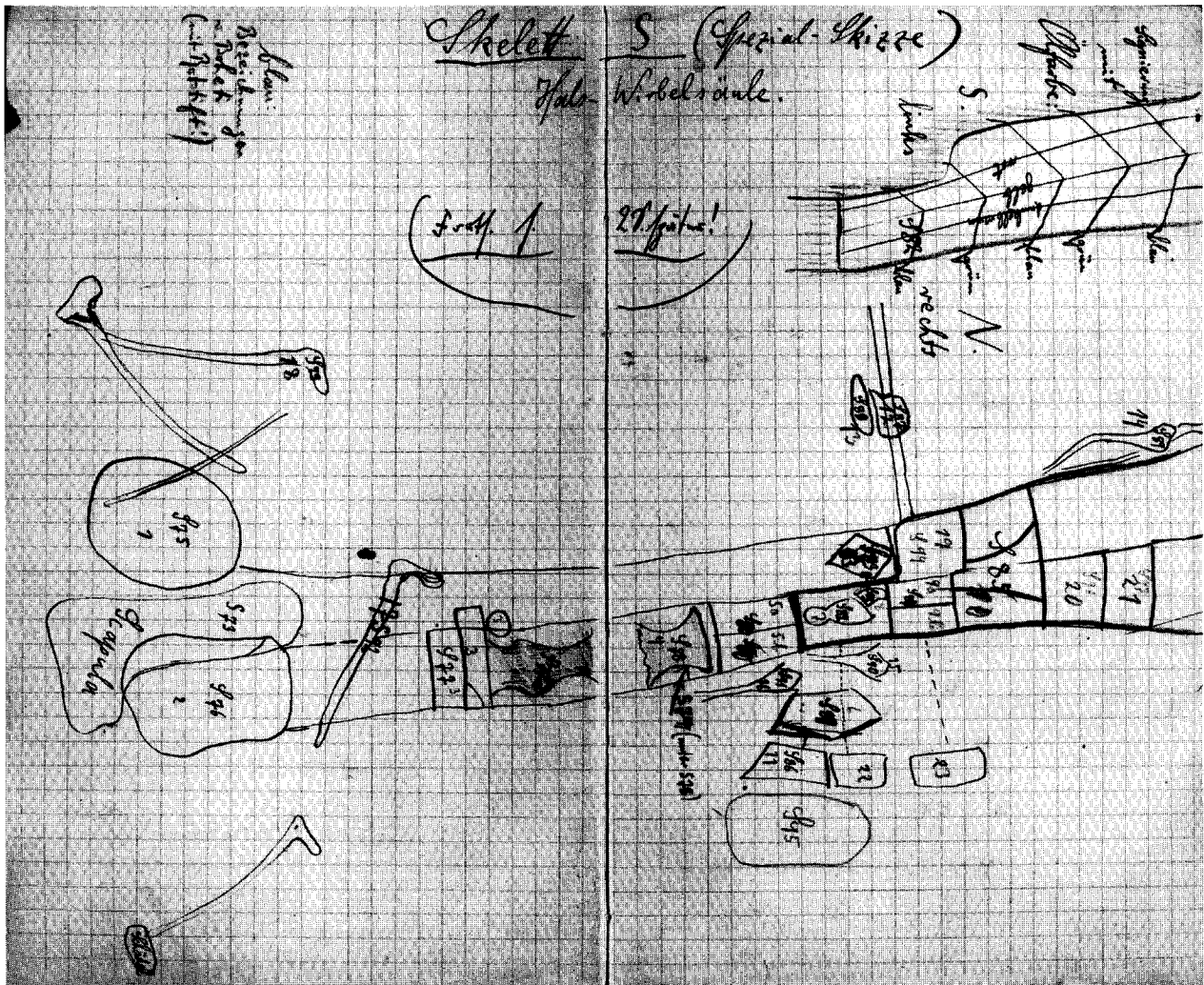


Fig. 18. *Brachiosaurus brancai* from Tendaguru Site S. The articulated series of vertebrae from skeleton SII includes anterior dorsals and cervical vertebrae. Original field sketch from W. Janensch. The skeletal elements in the figure are tentatively identified as follows: S73 – left scapula; S76 – dorsal vertebra 2; S77 – dorsal vertebra 1; S78 – cervical vertebra 13; S82–S87 (? S80, ? S88) – cervical vertebra 12; S89–S91 – cervical ribs; S92–S93 – dorsal ribs; S96–S97 (? 94) – cervical vertebra 11

an upright position, suggesting that the animal mired in soft mud. The proximal section of this humerus shows distinct traces of abrasion, indicating that the skeleton was affected by moving water prior to burial (Janensch 1914c). The bones of the right fore limb were found in natural order, but not articulated, and several bones (e.g., coracoids, right humerus, radius ulna) were embedded in a horizontal position (Fig. 16). The distal part of the left anterior limb was absent upon discovery, possibly due to post-depositional erosion (Janensch 1914a, c).

Sections of the reasonably complete presacral vertebral column of specimen SII are roughly documented in two separate field sketches, partly in pencil, partly in ink. One of these two field sketches is reproduced in the present account (Fig. 18). According to Janensch (1950a: 33), the anterior section of the vertebral column, including presacral vertebrae 3 to 15, were found in natural order. The three anteriormost presacral vertebrae (3–5) are well preserved and do not show signs of abrasion, while the remaining presacral vertebrae (6–15) are articulated and display close, bone-to-bone contact, except for presacral vertebra 8 which was slightly dislocated. The dorsal parts of presacral vertebrae 9 to 15 are missing, possibly due to attrition by the fine sands in which the remains were embedded (Janensch 1950a). The string of presacral vertebrae (3 to 15) was recovered from a massive limy sandstone bed, unlike presacral vertebrae 17 to 24 which were found together with other bones from skeleton SII in marls below the limy sandstone bed (Janensch 1950a: 33). The majority of these posterior presacral vertebrae were disarticulated, except for vertebrae 23 and 24 which were found in bone to bone contact (Janensch 1950a: 33).

The sediments exposed at the place of burial show that low-energy dinosaur-bearing marls passed into higher-energy sandy deposits. The shape of most bones recovered from Site S has not been substantially changed by taphonomic or diagenetic processes. The taphonomic evidence obtained from skeleton SII suggests carcass maceration and decay of a mired individual of *Brachiosaurus brancai* prior to burial (Janensch 1914c).

3.3.3 Tendaguru Site Y

Location: Site Y is located about 3.1 km north of Tendaguru Hill.

Stratigraphy: Middle Saurian Bed

Taxon: *Brachiosaurus brancai*

Figure: 17 (colour figure on p. 48)

Reference: Janensch (1929a), GTE field catalogue: 37

Assemblage data

NISP: 23

MNI: 1

Number of taxa: 1 (2)

Designation: Single-individual, single-taxon assemblage

Quarry data

Size of accumulation: approximately 21.00 m²

Density: approximately 1.1

Modification data

Measurements: length of a left scapula: 1540 cm; length of a right astragalus: 160 mm (Janensch 1961a).

Disarticulation stage: F

Ontogenetic data: The remains of *Brachiosaurus brancai* recovered from Site Y are from a medium-sized individual (Janensch 1950a: 33).

Comments: The excavations at Site Y commenced in 1910 (GTE field catalogue: 37). The bone accumulation from Site Y represents an incomplete skeleton, dominated by bones from the anterior body half. From the posterior skeleton only a fibula was found. Site Y has yielded a monospecific bone accumulation assigned to *Brachiosaurus brancai*. All bones documented are disarticulated. Janensch (1929a: 8) noted a braincase, eight cervicals, ribs, scapula, coracoid, humerus, and a dorsal vertebra. The skeleton is apparently current-modified, with a scapula resting next to a humerus and dorsal ribs. The cervical vertebrae are approximately in anatomical order (Janensch 1929a: 8), and the braincase lies close to them. The majority of the long bones were embedded with their long axes oriented west to east (e.g., right scapula, left humerus, dorsal ribs). Only a few elongated bones (e.g., left scapula, left fibula) are approximately oriented north to south. Some bones were embedded on top of one another (e.g., right scapula, left humerus). The taxonomic allocation of a small elongate caudal vertebra that was found south of the left scapula is far from clear.

3.3.4 Tendaguru Site m

Location: This site was situated close to Kindope, about 3.2 km north of Tendaguru Hill.

Stratigraphy: Middle Saurian Bed

Taxon: *Dicraeosaurus hansemanni*

Figure: 19

Reference: Janensch (1914a; 1929a, b, 1936, 1961a), GTE field catalogue

Assemblage data

NISP: Unknown

MNI: 1

Number of taxa: One-individual assemblage

Designation: Single individual assemblage, single-taxon assemblage

Quarry data

Size of accumulation: Unknown

Density: Unknown

Modification data

Measurements: The length of the preserved pelvic elements and limb bones is as follows (Janensch 1961a): right ilium: 840 mm; right pubis: 795 mm; right ischium: 750 mm; right fe-

mur (m5): 1220 mm; left tibia (m1): 760 mm; left fibula (m3): 800 mm, left astragalus: 165 mm

Disarticulation stage: E

Ontogenetic data: Unknown

Comments: One of the most important discoveries of the 1910 field season was the type specimen of *Dicraeosaurus hansemanni*, recovered from the Middle Saurian Bed at Site m near Kindope (Janensch 1914a). Unfortunately, a quarry plan is not available. The more important taphonomic data published by Janensch (1929a, b) are briefly summarized below.

The skeleton is incomplete, but remarkably well preserved. Much was found in natural articulation. The skull, proatlas, and axis have not been not recorded. A series of vertebrae ranging from cervical 2 to caudal 19 lay in natural order. Only the anterior end of the tail was recovered; the posterior tail section beyond caudal 19 was lost prior to discovery. The preserved part of the tail is slightly recurved (Janensch 1929b: 41). Ilium, pubis, parts of the ischium, and the femur of the right body side were discovered in situ. The left femur was found close to the sacrum. The sternal plates, coracoids, scapulae, and ante-



Fig. 19. Type specimen of *Dicraeosaurus hansemanni* from Tendaguru Site m. Photograph: W. Janensch

rior limbs have not been recorded. Except for the femora, the hind limbs are represented by the articulated left lower leg (tibia, fibula, and astragalus), found just above the posterior section of the neck. Feet are not recorded. The well-preserved right dorsal ribs are still articulated with the dorsals. The left dorsal ribs are incompletely preserved and scattered, but close to the skeleton. Some vertebrae suffered considerable damage: nearly all the left diapophyses are missing in the section ranging from dorsal 13 to caudal 1, and of the posterior dorsals, the left parapophyses, the left neurapophyses and the centra are water worn. Three caudals were found at some distance from the skeleton. Their association with the preserved caudal series of skeleton m is uncertain.

According to Janensch (1929b: 41), the carcass floated quite a long distance in quiet water before it came to rest on its right side. Afterwards, the anterior section of the neck was flexed ventrally, rotated and became separated from the posterior cervicals. Subsequently, this section came to rest in an oblique position adjacent to the carcass prior to burial. Afterwards, exposed parts of the skeleton, including the left dorsal and sacral diapophyses, the left rib cage, the left pelvic girdle, and perhaps the left hind limb were abraded, truncated and dispersed close to the skeleton. The skull, most of the appendicular skeleton (e.g., sternal plates, anterior limbs, right lower leg, both feet, and ? left hind limb) and the posterior section of the tail were probably lost during post-mortem transport from the place of death to the site of burial.

4. Discussion: taphonomic patterns in Tendaguru dinosaurs

4.1 Occurrence of bones

Most field sketches preserved in the archives of the IPHB document bone accumulations for the sauropod dinosaurs *Brachiosaurus*, *Barosaurus*, *Dicraeosaurus*, and *Janenschia*. Quarry plans documenting bone assemblages for ornithischians (*Dryosaurus*, *Kentrosaurus*) are rare. Nothing can be said about the original position of skeletal remains of theropods (e.g., *Elaphrosaurus*) due to the lack of field sketches for these taxa.

The documented skeletal remains recovered from quarries in the vicinity of Tendaguru Hill represent a broad spectrum of disarticulation and

disassociation. They belong to a sequence of disarticulation stages recognized in the Tendaguru Beds (Tab. 2), including (1) incomplete skeletons with bones partially articulated (e.g., *Dicraeosaurus hansemanni*, Site m; *Brachiosaurus brancai*, Site S), (2) complete or incomplete partial skeletons (e.g. *Janenschia robusta*, Site P), (3) assemblages of predominantly disarticulated skeletal elements concentrated in bone fields (e.g. *Barosaurus africanus*, Site C; *Kentrosaurus aethiopicus*, Site X), and (4) solitary bones. Virtually complete dinosaur skeletons have not been found in the Tendaguru Beds so far (Henig 1912b). Partial skeletons show a similar broad spectrum of disarticulation stages as incomplete skeletons (Table 2), but both may reflect different taphonomic histories. A partial skeleton, for example, may not only result from gradual "in-situ" carcass decay at the site of death or final deposition but also from early post-mortem truncation and pre-burial transport of carcass parts from the site of death or from the original location of carcass deposition.

Mono- and multispecific assemblages of dinosaurian skeletal elements have been recognized. Monospecific assemblages, for instance, are documented for *Barosaurus africanus* (e.g., Site C), *Brachiosaurus brancai* (e.g., Site S), *Dicraeosaurus hansemanni* (Site m), and *Dryosaurus lettow-vorbecki* (Site Jg = WJ). These assemblages are usually represented by incomplete or partial skeletons, and they are mainly known from the Middle Saurian Bed (e.g., Sites m and S) and the Upper Saurian Bed (Sites C, D, N). Multispecific assemblages have been documented, for instance, from Site ab (*Barosaurus africanus*, *Brachiosaurus brancai*, *Dicraeosaurus sattleri*), and Sites IX and X (*Barosaurus africanus*, *Brachiosaurus brancai*, *Janenschia robusta*, *Kentrosaurus aethiopicus*). Multispecific assemblages are typical of the Transitional Sands above the *Trigonia smeei* Bed (Site IX), but have also been documented in the Upper Saurian Bed (e.g., Sites ab, X).

Calculations of the MIN's reveals that single-individual assemblages (e.g., *Barosaurus africanus*, Sites C; *Brachiosaurus brancai*, Sites D, M; *Dicraeosaurus sattleri*, Site O) and multi-individual assemblages (e.g., *Brachiosaurus brancai*, Site S; *Janenschia robusta*, Site P) both occur. The Middle and Upper Saurian Beds have yielded both single-individual assemblages (e.g., *Dicraeosaurus hansemanni*, Middle Saurian Bed, Site m; *Barosaurus africanus*, Upper Saurian Bed, Site k) and multi-individual assemblages

(*Brachiosaurus brancai*, Middle Saurian Bed, Site S; *Janenschia robusta*, Upper Saurian Bed, Site P). The documented bone assemblages from the Transitional Sands above the *Trigonia smeei* Bed are multi-individual in nature (e.g. *Barosaurus africanus*, Site H; *Barosaurus africanus*, *Brachiosaurus brancai*, *Janenschia robusta*, *Kentrosaurus aethiopicus*, Site IX). Single-individual assemblages are more frequently documented than multi-individual assemblages.

The documented multi-individual assemblages consisting of incomplete or partial skeletons of sauropods are always monospecific. Examples include the skeletons SI and SII of *Brachiosaurus brancai* from the Middle Saurian Bed Site S, and the partial skeletons I–IV of *Janenschia robusta* from Upper Saurian Bed Site P. In addition, Janensch (1929a: 9) reported two individuals of *Dicraeosaurus hansemanni* from the Middle Saurian Bed at Site dd.

The Middle Saurian Bed has yielded the best preserved skeletons from Tendaguru, some of which, notably those of *Brachiosaurus brancai* (Site S) and *Dicraeosaurus hansemanni* (Site m), are on display in the Museum of Natural History of Humboldt University, Berlin. An unpublished field sketch of Site Jg (WJ) indicates that reasonably complete skeletons of ornithischians (*Dryosaurus lettow-vorbecki*) were also found. Moreover, the Middle Saurian Bed has produced enormous concentrations of disarticulated skeletal remains of smaller ornithischians such as *Kentrosaurus aethiopicus* from Sites St, He and X (Janensch 1914c, Hennig 1915, 1916, 1925) and *Dryosaurus lettow-vorbecki* from Site Jg (Janensch 1914c, 1955, 1961b; Galton 1981).

Reported recoveries of theropod dinosaurs include several disarticulated and scattered skeletal elements from Tendaguru Site dd that are apparently derived from a single skeleton of *Elaphrosaurus bambergi* (Janensch 1925b: 7; Galton 1982). Included in this collection, but undocumented in field sketches, are 17 presacral vertebrae, 18 caudal vertebrae, a chevron bone, two imperfect ribs, both scapulae and coracoidea, right humerus, two metacarpals, sacrum, left pubis, two ilia and ischia, left femur, tibia, fibula, astragalus, and two phalanges (Janensch 1925b: 7, 1929c: 280). In addition, several localities of the Middle Saurian Bed, such as the collecting sites St and H (Janensch 1920, 1925b), produced isolated limb bones and teeth.

Samples from the Middle Saurian Bed housed in the Berlin Tendaguru collection confirm the impression that skeletal remains of *Dryosaurus*

lettow-vorbecki are extraordinarily abundant at Site Jg (WJ). Here, the matrix is dominated by vertebrae and limb bones, some partly articulated, and some partly disarticulated. Isolated bones are also very common. By contrast, skull bones and teeth are very rare, as are small hand and foot bones. It should be mentioned that bones from *Dryosaurus lettow-vorbecki* (Site Jg) and sauropod caudal vertebrae (Site dd) encrusted with calcite have repeatedly been found. These calcite rinds, measuring 2 mm to 5 mm in thickness, are infillings of post burial shrinking cracks. Janensch (1925b: 7) also reported calcareous rinds that covered bones of *Elaphrosaurus bambergi* recovered from Tendaguru Site dd.

Skull material from sauropods is extremely rare, although the Middle Saurian Bed at Site t has yielded a disarticulated complete skull of *Brachiosaurus brancai* with 56 teeth in its jaws, and Tendaguru site dd, for instance, produced braincases of *Dicraeosaurus hansemanni* and *Barosaurus africanus* (Janensch 1935).

Janensch (1914c) reported water worn bones of *Brachiosaurus brancai* (skeleton SII) from Site S as well from *Dicraeosaurus hansemanni* from Site m. The material from the Middle Saurian Bed is evidently current modified. Most skeletal elements were apparently carried away from carcasses, skeletons or partial skeletons, possibly by currents or wave action.

Bone accumulations from the Transitional Sands above the *Trigonia smeei* Bed are dominated by disarticulated sauropod dinosaur limb bones. Much of the material is in poor condition, confirming Janensch's (1914a, c) interpretation that there was much destruction, transportation, and sorting of bones. Abraded epiphyses are thought to be evidence of water action (Janensch 1914a, c; 1961a). Most of the bones rest horizontally next to one another, possibly due to wave action or wave-induced currents (Janensch 1914a, c). There is no doubt, that this material underwent sorting through a broad spectrum of post-mortem processes prior to burial.

Russell et al. (1980: 172) reported the dominance of *Barosaurus africanus* in the Transitionals Sands above and below the *Trigonia smeei* Bed and noted "a significantly higher number of elements from the left side" of the barosaur body. From Site Ki, Transitional Sands below the *Trigonia smeei* Bed, Hennig (1925: 247) mentioned a complete but somewhat disarticulated left lower leg of *Kentrosaurus aethiopicus*, including the tibia, fibula, and bones of the pes.

Most quarry maps from the Upper Saurian Bed primarily document disarticulated skeletal materials from sauropods (e.g., *Brachiosaurus brancai*, Sites D, N, cc; *Dicraeosaurus sattleri*, Site O). Incomplete skeletons (e.g., *Barosaurus africanus*, Site k) and partial skeletons (e.g., *Janenschia robusta*, Site P) also occur, with both partly articulated, and partly disarticulated bones. As mentioned above, most of the bone accumulations appear to represent single-individual assemblages, although, multi-individual assemblages have also been recognized. Janensch (1922, 1961a) reported an articulated manus skeleton of *Janenschia robusta* from Site Nr. 5 and *Brachiosaurus brancai* from Site R, as well as two articulated pes skeletons of *Barosaurus africanus* from Sites XIII and 28, suggesting that sauropod dinosaurs became mired in soft mud (Janensch 1914c: 249). Fore- and hind-limb skeletons (e.g. *Janenschia robusta* from Site P) and strings of vertebrae (e.g. *Barosaurus africanus* from Site C) and accumulations of disarticulated bones (e.g. *Barosaurus africanus*, *Dicraeosaurus sattleri*, and ? *Brachiosaurus brancai* from Site ab) show that the carcasses underwent considerable pre-burial decay, as formerly suggested by Janensch (1914c, 1961a) and Hennig (1925).

The Upper Saurian Bed produced mass accumulations of skeletal elements of the ornithischian *Kentrosaurus aethiopicus* (Hennig 1925). A bone field uncovered at Site X, for instance, consists mainly of isolated and jumbled elements from the manus and pes (Janensch 1914c, Hennig 1925) reflecting a secondary concentration of dinosaurian material (Fig. 10). Hennig (1915: 244; 1925: 247) reported an incomplete skeleton of *Kentrosaurus aethiopicus* from Site bb which is close to the top of the Upper Saurian Bed. The skeleton includes a left scapula and coracoid, imperfect left pubis, fragmentary ischium, both femora, a caudal vertebra, and fragments of ribs and vertebrae (Hennig 1925: 247). Field sketches are not available, the stage of disarticulation is unknown.

Isolated bones and teeth indicate the presence of theropod dinosaurs in the Upper Saurian Bed, among them *Ceratosaurus*, *Allosaurus* and *Elaphrosaurus* (Janensch 1925b, 1929c). Bones are very rare, and teeth are more frequently preserved. According to Janensch (1925b: 61), a left quadratum, left fibula, and three imperfect caudal vertebrae recovered from Site Mw are assignable to one individual of *Ceratosaurus* (?) *roechlingi*.

4.2 Bone representation

The great majority of sauropod bone accumulations either documented in the field sketches or listed by Janensch (1929a, GTE field catalogue) are incomplete skeletons or partial skeletons. The field sketches examined in this account and data given by Janensch (1929a) show that some skeletal elements are more frequently recorded than others. Skull remains for instance, are extremely rare, whereas appendicular skeletal elements usually dominate the bone assemblages examined. This raises the question, to what extent certain skeletal elements better survived the taphonomical filters than others. This question is difficult to answer, however, because no first-hand data are available. According to the records of sites, not all bones found have been documented in field sketches. In addition, poorly preserved bones were not collected at some sites (Janensch, GTE field catalogue). In order to minimize the affects caused by collector preferences, individual bone representation diagrams were replaced in the present account by a body-part representation diagram. This diagram (Fig. 20) reflects only “summarily” the presence of body parts recognized in skeletons, but does not consider the abundance of individual skeletal elements within the distinguished body parts.

The analysis of incomplete skeletons and partial skeletons of Tendaguru sauropods from about 30 sites, partly documented in the field sketches, partly listed by Janensch (1929a) led to the following conclusions (Fig. 20): (1) As expected, the paired elements of the appendicular skeleton dominate the fossil record of Tendaguru sauropods. (2) In Tendaguru diplodocids (*Barosaurus africanus*, *Dicraeosaurus hansemanni* and *Dicraeosaurus sattleri*) that have longer hind limbs than fore limbs, the rear limbs and pelvic elements are dominant. (3) In Tendaguru brachiosaurids (*Brachiosaurus*) that have longer fore limbs than hind limbs, the anterior appendicular skeleton with its huge fore limbs and shoulder girdle dominate the fossil record.

Body-part representation is strongly influenced by the degree of carcass decay that was reached before burial. Therefore, the taphonomic pattern found is not only an “overprinting” of distinctive skeletal traits of the sauropod skeletons. It also suggests a considerable amount of pre-burial sorting of dinosaur bones in the Tendaguru Beds. The presence of tiny and very delicate pterosaurian and mammalian remains in the Middle and Upper Saurian Bed at Tenda-

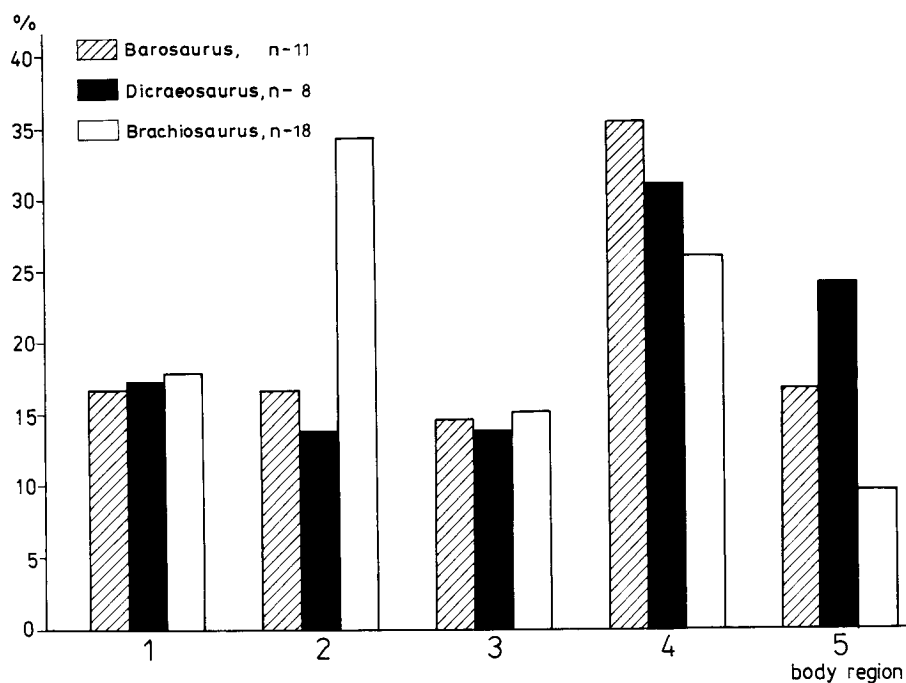


Fig. 20. Frequency distribution of main body regions in sauropod skeletons from Tendaguru. For explanation see text. 1 – skull and neck, 2 – shoulder girdle and fore limbs, 3 – sacral and dorsal vertebrae, dorsal ribs, 4 – pelvic elements and posterior limbs, 5 – tail

guru (Reck 1931, Galton 1980, Unwin & Heinrich 1999, Dietrich 1927, Heinrich 1998, 1999) indicates, however, that this taphonomic pattern cannot be due to post-burial destruction of smaller sauropod skeletal elements.

4.3 Burial position

The burial position of carcasses of dinosaurs is difficult to assess because of the relatively small number of reasonably complete skeletons recovered from the Tendaguru Beds. Moreover, the skeletons documented in the field sketches display different burial positions.

The specimen of the dryosaurid *Dryosaurus lettow-vorbecki* recovered from the Middle Saurian Bed at Site Jg (WJ) was buried on its belly, with the left femur spread away from the trunk, and a cervical vertebral column that was not straight or only slightly recurved (Fig. 13). The skull and neck were apparently still articulated.

Russell et al. (1980: 172) mentioned that Tendaguru barosaurs “preferred to die laying on their left side”. The upright position of both left humerus and left tibia of skeleton SII of the brachiosaurid *Brachiosaurus brancai* (Fig. 16) suggests that the animal became mired in soft mud and died laying on its belly. In-situ decomposition of soft tissues is indicated by the series of articulated cervical vertebrae as well as by parallel oriented dorsal ribs resting closely on each other (Fig. 16). Except for the cervical vertebrae, the majority of skeletal elements are concen-

trated close to these two limb bones, indicating that dispersal of bones was minimal. The place of death must therefore have been the place of final deposition.

4.4 Individual size and age class distributions

The following account of the size distribution of Tendaguru sauropods (*Brachiosaurus brancai*, *Barosaurus africanus*) is based upon the humeri and femora, and that of the ornithischians (*Dryosaurus lettow-vorbecki*) upon the femora, because these bones are better represented in the collection than other limb bones of these taxa. Metric data were taken from Janensch (1961a and unpublished) and from Sander (1999, in press), augmented by my own measurements.

The number of the measured specimens is rather small, making quantitative assessments difficult. Therefore, sauropod specimens from different dinosaur-bearing horizons were put together to form time-averaged populations, as explained in the diagrams (Figs 21 and 22). Both humeri and femora of *Brachiosaurus brancai* were assigned to 30.0 cm intervals, those of *Barosaurus africanus* to 14.0 cm intervals. Life-age data of sauropod individuals are based on histological examinations by Sander (1999, in press).

A data set published by Janensch (1961b) as well as my own measurements can be used to establish a femur-size distribution-diagram for

Dryosaurus lettow-vorbecki. The femora of *Dryosaurus lettow-vorbecki* are assigned to 5.0 cm intervals. The diagram (Fig. 23) is based on a collection of femora recovered from the Middle Saurian Bed at Tendaguru Site Jg (WJ) Unfortu-

nately, histological data that could calibrate the size classes with ontogenetic data are not available. Paleohistological studies on femora of *Dryosaurus lettow-vorbecki* from Tendaguru indicate rapid and uninterrupted growth (Chinsamy 1995).

Fig. 21 shows the humerus- and femur-size distribution of *Brachiosaurus brancai*. The histograms reveals that the populations are dominated by humeri and femora ranging in length from 144 to 174 cm. Based on life history studies by Sander (1999, in press), humeri and femora of these dimensions are probably assignable to

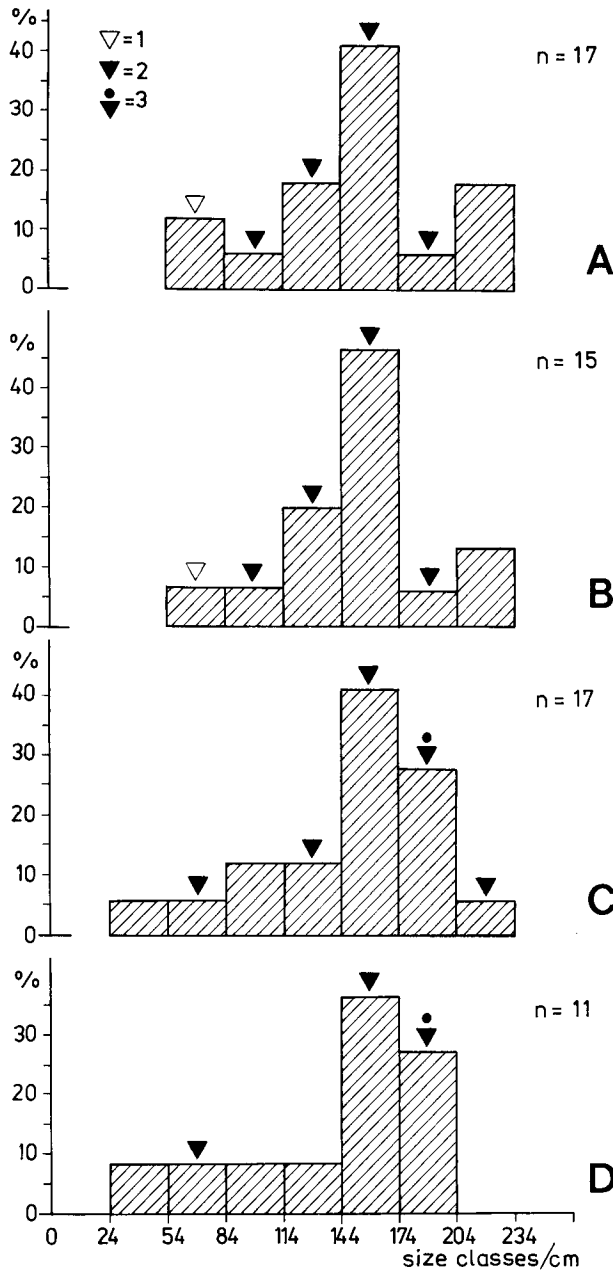


Fig. 21. Size-class distribution of humeri and femora of *Brachiosaurus brancai* from Tendaguru. Data grouped together as follows: **A** – subset of humeri from the Middle Saurian Bed (n=3), Upper Saurian Bed (n=12), and Transitional Sands overlaying the *Trigonia smeei* Bed (n=2), **B** – subset of humeri from the Middle Saurian Bed (n=3) and Upper Saurian Bed (n=12), **C** – subset of femora from the Middle Saurian Bed (n=11), Upper Saurian Bed (n=3) and Transitional Sands (n=3), **D** – subset of femora from the Middle Saurian Bed (n=11). **1** – juvenile individuals; **2** – adult individuals; **3** – old adult individuals. The age determination is based upon life history studies by Sander (1999, in press). Metric data from Janensch (1961a), Sander (1999, in press) and own measurements

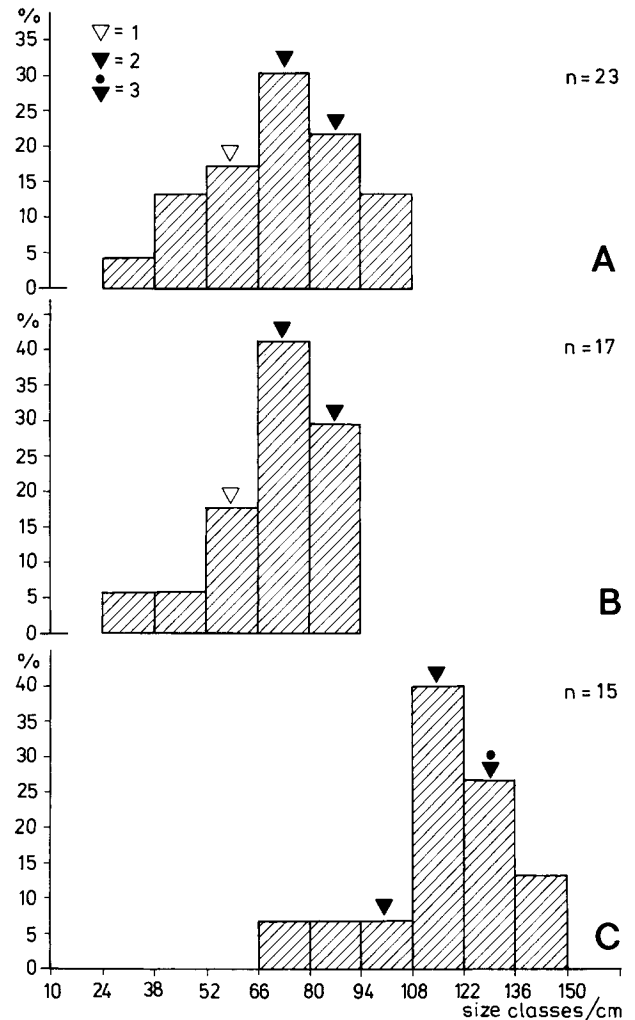


Fig. 22. Size-class distribution of humeri and femora of *Barosaurus africanus* from Tendaguru. Data grouped together as follows: **A** – subset of humeri from the Upper Saurian Bed (n=5), and Transitional Sands overlaying the *Trigonia smeei* Bed (n=18), **B** – humeri from the Transitional Sands overlaying the *Trigonia smeei* Bed (n=17), **C** – subset of femora from the Upper Saurian Bed (n=7), and Transitional Sands overlaying the *Trigonia smeei* Bed (n=8). **1** – juvenile individuals; **2** – adult individuals; **3** – old adult individuals. The age determination is based on life history studies by Sander (1999, in press). Data from Janensch (1961a), Sander (1999, in press) and my own measurements

adult individuals. Adult individuals have also been found in the adjacent humerus size classes (114–143 cm, 174–203 cm), suggesting that about 60% of the measured specimens of *Brachiosaurus brancai* may belong to adult individuals. Old adult individuals are most likely represented in the highest humeri-size class (204–233 cm).

Humeri of juvenile individuals of *Brachiosaurus brancai* are distinctly underrepresented, and neonates have not been found so far (Figs. 21A, 21B). The “first” appearance of old adult individuals in femur-size class 174–203 cm and the “last” appearance of adults in femur-size class 204–233 cm (Figs. 21C, 21D) indicates that the age groups overlap to significant degree, and include individuals of different size. A similar interval of overlap is to be expected between juvenile and adult specimens.

Consideration of the size frequency histograms for the humerus and femur of *Barosaurus africanus* reveals that adult individuals apparently prevail (Fig. 22), as in *Brachiosaurus brancai*. Diagram 22A, which approaches a unimodal size-class distribution is difficult to assess, since

the sample is based on time-averaged bone assemblages.

In this connection, it is worth mentioning that histological data obtained from three humeri of *Dicraeosaurus sattleri* from the Upper Saurian Bed (Sites ab and O) also suggest that adult individuals predominate in the bone assemblages (Sander 1999, in press), as is the case for *Brachiosaurus brancai* and *Barosaurus africanus*. A femur of *Janenschia robusta* collected from the Upper Saurian Bed at Tendaguru Site 22 is attributable to an old adult individual (Sander 1999, in press).

Dryosaurus lettow-vorbecki (Fig. 23) displays a bimodal femur-size-distribution, with two peaks, one at the beginning and one close to end of the plot, suggesting either that juvenile and adult individuals prevail or that sexual dimorphism occurs. Sexual dimorphism cannot be excluded with certainty, but it seems more likely that the bimodality is the result of individual size variation. If this is correct, the pattern of size-distribution may allow conclusions to be drawn regarding on the origin of the mass accumulations of *Dryosaurus lettow-vorbecki*, discussed below.

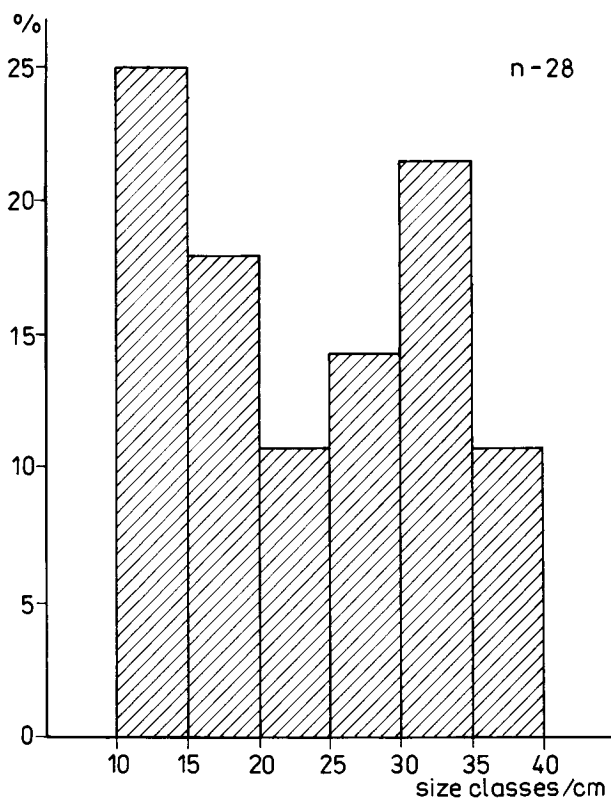


Fig. 23. Size-class distribution for the femur of *Dryosaurus lettow-vorbecki* from the Middle Saurian Bed at Tendaguru Site Jg (WJ). Metric data from Janensch (1961b: 164) and measurements obtained from recently recovered femora. Total number of femora: 28

4.5 Attritional or mass mortality?

The origin of the extraordinary concentrations of dinosaur bones in the Tendaguru Beds has been the of subject of speculations ever since the first discovery of dinosaurs in the Tendaguru area. The interpretation has to consider attributes of the recovered bone assemblages, paleoecological aspects, and peculiarities of the depositional environment that influenced the involved taphonomical processes.

According to Janensch (1914a, c; 1961a), the dinosaur-bearing deposits were possibly laid down in a lagoonal environment separated from the sea by reefs. The sedimentation was thought to have been affected by tides, episodic storms (hurricanes), wind waves, earthquakes, and changes in the regional climate (Janensch 1914c). The invertebrate fossil record suggests a brackish to limnic depositional environment for the Middle and Upper Saurian Bed (Dietrich 1914; Henig 1914b, c; Schudack 1999; Schudack et al. 1999), and records of *Asmussia* (= *Estheria*) from the Upper Saurian Bed may indicate periods of drought (Janensch 1933, Russell et al. 1980).

As mentioned above, Janensch (1914c) suggested that the dinosaur bone assemblages from

Tendaguru resulted mainly from abrupt catastrophic killing events. Unfortunately, the precise relationships of the quarried dinosaur bones to the enclosing sediments are far from clear, due to the loss of many records. In addition, the precise stratigraphic position of the dinosaur-bearing sites within the Lower, Middle, and Upper Saurian Bed is unknown. This is especially regrettable, since the depositional environment of the Tendaguru Beds underwent remarkable changes during the Late Jurassic and Early Cretaceous. The dinosaur-bearing sites in the Transitional Sands that connect the Saurian Beds with the shallow marine sandstone beds are undoubtedly marginal marine in origin because marine invertebrates are associated with the dinosaurs. A humerus of *Brachiosaurus brancai* covered by oysters is reported, for instance, from Site Aa which is in the Transitional Sands above the Middle Saurian Bed (Janensch, GTE field catalogue: 140). As previously mentioned, the state of preservation of bones recovered from the Transitional Sands suggests transport and redeposition of bones prior to burial. Therefore, these enormous concentrations of disarticulated dinosaur bones probably represent time-averaged bone accumulations rather than a short-term mass mortality event.

As mentioned above, most of the documented skeletal accumulations from the Middle and Upper Saurian Beds are single-individual and monospecific. Multi-individual assemblages are rare, and death assemblages of *Brachiosaurus brancai*, *Dicraeosaurus sattleri*, and *Barosaurus africanus* are apparently dominated by limb bones of adult individuals. This taphonomic pattern does not necessarily support the catastrophic mass mortality model, since killing agents that produced mass mortality should have affected all individual age classes of the sauropod populations.

However, this conclusion should be made with caution because actualistic studies on large extant land mammals reveal that patterns of bone accumulations may result from patterning in behaviour (Haynes 1993). Younger African elephants, for instance, sometimes die "much nearer the inner areas" of die-off sites "than older individuals" due to aggressive interactions at excavated wells during severe drought (Haynes 1993:131). As in extant African elephant populations (Haynes 1990, 1993), seasonal drought could have resulted in social fissioning and ephemeral aggregations of adult and old adult Tendaguru sauropods at shrinking water sources and feeding sites.

In addition, articulated sauropod limb bones buried in an upright position (Janensch 1914c) indicate that the body weight of the animals could have been an important selective taphonomic filter for the dinosaurs from Tendaguru. So, for instance, the body weight of the juvenile Tendaguru sauropods may have been below the threshold for becoming stuck in the mud, unlike the adult animals that passed more frequently the "point of no return" due to their heavier body weight.

A similar taphonomic model has been suggested for the Late Triassic (Norian) prosauropods *Plateosaurus* (Sander 1992) and *Sellosaurus* (Hungerbühler 1998). Sander (1992: 256) argues that the absence of juvenile individuals of *Plateosaurus engelhardti* in several European Knollenmergel sites is due to the "lower foot pressure" of juvenile animals that were thus "below the threshold for becoming mired" in shallow depressions.

Hennig (1925) believed that spatially limited mass accumulations of disarticulated bones of *Kentrosaurus aethiopicus* from the Middle Saurian Bed (Site St) and the Upper Saurian Bed (e.g., Sites He and X), containing individuals of various size and age, resulted from a sudden mass death event (see also Weigelt 1927). Rich concentrations of disarticulated skeletal remains of *Dryosaurus lettow-vorbecki* recovered from the Middle Saurian Bed at Site Jg (WJ) were also thought to represent an instance of sudden mass mortality (Janensch 1914c). Most limb bones (e.g., femur, tibia, fibula) were found parallel to one another, with their long axis oriented northwest to southeast, indicating that these bones were accumulated under the influence of wave action (breakers) or wave-induced currents (Janensch 1914c: 256). Janensch (1914c) supposed that herds of small ornithischians that had entered lagoons during periods of drought were killed by the returning flood and became embedded close to the place of death. If this scenario is correct, *Dryosaurus lettow-vorbecki* left rapidly formed mass assemblages of bones in the Tendaguru Beds that resulted from an external catastrophic killing event. Accumulations of sauropod bones in the Middle and Upper Saurian Beds are also thought to have been caused by similar killing events, since the huge sauropod dinosaurs were also considered to be gregarious land animals (Janensch 1914c).

By contrast, Reck (1925) who quarried Tendaguru Site Jg (WJ) in 1912 doubted the cata-

strophic mass mortality. He argued (Reck 1925: 9–10): “So sehr auch das herdenartige Auftreten einzelner Arten, und besonders die Herdenzusammensetzung aus Tieren jeder Größe und jeden Alters für sie zu sprechen scheint, so stehen doch auch ihr unüberwindliche Hindernisse entgegen, wenn man dem Sprachgebrauch entsprechend unter Katastrophe nur ein seltenes, verheerendes Naturereignis versteht Aber zwei Hauptmomente führen zur Ablehnung solcher Theorie: die großzügig gleichmäßigen, außer durch die Transgressionen nicht unterbrochenen, feinklastischen Sedimentationsverhältnisse und die regellose Verteilung der Funde in der Vertikalen innerhalb der Mergelmassen. Dadurch wird die Supposition jeder Katastrophe unhaltbar, wenn man nicht jeweils einen ganzen Mergelhorizont als Niederschlag und Zeugnis einer Katastrophe ansprechen will. Dagegen aber spricht alles Als generelles Entstehungsprinzip der Lagerstätte kommt die Katastrophe nicht in Betracht”. Reck (1925), on the basis of his studies of the Tendaguru region, concluded that the dinosaur bones were irregularly dispersed within the Tendaguru saurian beds, and that the origin of the bone accumulation could not be explained by catastrophic mass mortality. This distribution pattern suggests that the bone accumulations resulted from recurring “normal” death events of dinosaur individuals over a long period of time rather than from a catastrophic, short-term mass mortality event.

In addition to this argument, further support for an attritional origin is found in the femur-size distribution pattern of *Dryosaurus lettow-vorbecki* which represents an age profile, dominated by juvenile and adult individuals (Fig. 23). This pattern (Fig. 23) shows a striking similarity to the so-called U-shaped or attritional mortality type of profile that is due to a long-term input of bones resulting from “normal”, ecologically related deaths in different-aged population members (Lyman 1996). This pattern differs remarkably from the unimodal L-shaped, catastrophic or mass mortality pattern in which younger age classes dominate and older age classes become successively underrepresented (Lyman 1996). At the present stage of investigation, I do not draw the conclusion, that the mortality profile in *Dryosaurus lettow-vorbecki* is attritional in origin, since possible influence of the sexual dimorphism is far from clear and the interpretation of U-shaped mortality profiles is mainly based on experience with extant and fossil mam-

mals. Nevertheless, it is worth noting, that the interpretation as an attritional mortality profile also agrees more closely with the data obtained from the Tendaguru sauropods (Figs. 21, 22) as well as with the distribution pattern of bones within the Tendaguru dinosaur beds.

The invertebrate fossil record and seasonality indicated by reworked caliche nodules might indicate playa lake-like water bodies close to an oscillating shoreline, and subject to either seasonal or long-term droughts. Cross-bedded sandstone beds within the Middle and Upper Saurian Beds, in turn, might be explained by seasonally rainy intervals that resulted in water flows, temporary lakes, and ponds. These ephemeral water bodies might have been refuges and die-off sites for Tendaguru dinosaurs during seasonal drought. Most likely, the palaeoenvironment in the Tendaguru region was much more diverse than generally thought so far.

In the absence of direct taphonomic studies and substantial parts of the documentation of the original expedition, it is beyond the scope of the present account to establish a detailed taphonomic model for the Tendaguru dinosaur accumulation. However, the existence of a number of superimposed dinosaur-bearing horizons (Saurian Beds, Transitional Sands) shows that dinosaur bones were accumulated over a long time span during the Late Jurassic. The fossil record also reveals that extraordinarily suitable conditions for the preservation of dinosaurian bones occurred repeatedly. The year-to-year input of bones resulting from short-term intervals of mortality due to drought might have been considerable and “simulates” sudden catastrophic mass mortality events. If so, the Tendaguru fossil record may reflect attritional mortality rather than sudden catastrophic mass mortality.

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