CAD assessment of the posture and range of motion of *Kentrosaurus aethiopicus* Hennig 1915

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Abstract A computer aided design analysis using high-resolution laser scans of the bones of the stegosaur *Kentrosaurus aethiopicus* Hennig 1915 from the Late Jurassic Tendaguru Formation indicates that in the habitual walking pose the forelimbs were probably held erect, and that strong humeral flexion and abduction mainly occurred in a defensive stance. Rapid gaits with unsupported phases could not be used. The neck allowed sufficient lateral flexion to guarantee good sight in all directions including posteriorly. The tail covered an arch of roughly 180° and had sufficient range to be used as a weapon. Possibly, the animal could accomplish tail blows against specific targets in sight. Also, a tripodal pose is suggested to have been possible, roughly doubling the maximum vertical feeding height of *Kentrosaurus*.

Abbreviations

MFN Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin. Collection numbers for reptiles MB.R.####, provisional collection numbers MB.I.####

IFGT Institut für Geowissenschaften der Eberhard-Karls-Universität Tübingen. Collection numbers GPIT ###

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FUB Freie Universität Berlin. Collection numbers of osteological collection IPFUB OS ##

ONP osteologically neutral position. Two vertebrae are in ONP if their zygapophyses fully overlap, and the centra faces are parallel (or, if the centra and haemapophyses are aligned for maximum contact area)

Introduction

The famous excavations of the Museum für Naturkunde Berlin (MFN) at and around Tendaguru hill in German East Africa (today Tanzania) between 1909 and 1912 yielded a rich Jurassic fauna of sauropods, most famously *Giraffatitan brancai* (Janensch 1914) (formerly considered to belong to *Brachiosaurus* Riggs 1903, see Taylor 2009), theropods, mammals and ornithopods, among them the stegosaur *Kentrosaurus aethiopicus* Hennig 1915. Of this latter species alone, the expedition brought home some 1,200 separate bones, representing roughly 50 individuals (Hennig 1925). Most elements were found isolated, and only a small number of fragmentary semi-articulated or at least closely associated partial skeletons could be retrieved (Hennig 1915, 1925). This is not surprising, considering that the Tendaguru Beds were deposited in lagoon-like shallow marine areas and on tidal flats (Aberhan et al. 2002), where most dinosaur carcasses decayed and were transported before burial (Heinrich 1999). Still, a partial adult individual of *Kentrosaurus aethiopicus* (the lectotype, MB.R.4800.1-37, see Mallison 2010a), consisting of a nearly complete sacrum, both ilia, several dorsal vertebrae, much of the tail and two limb elements, combined with the enormous number of other well-preserved

elements, allowed a composite skeleton to be mounted at the MFN in Berlin (Janensch 1925). This mount (termed "Berlin mount" or "MFN mount" here), with dragging tail tip, sprawling forelimbs and a strongly flexed trunk (Galton 1982, pl. 1, fig. 2; Janensch 1925, pl. XV) graced the museum until 2005 (except for a few years during and after World War II), when it was taken down for re-preparation of the bones during a museum renovation. At that time, high-resolution laser scans were made from all genuine bones. Afterwards, a new armature in a walking pose was created with the tail now held nearly horizontally off the ground, and a more lively and in the anterior trunk less flexed curvature of the trunk (Fig. 1) that better reflects today's understanding of biomechanics. However, the forelimbs are still strongly abducted and flexed. A second mount (GPIT 1542; here called "IFGT mount"), consisting of isolated bones, can be found in the IFGT, and was mounted in the nearly identical position as the Berlin mount under the direction of Friedrich von Huene (Maier 2003).

While Hennig gave highly detailed and well-illustrated descriptions of the osteology of *Kentrosaurus aethiopicus*

(Hennig 1915, 1916a, 1925), which were amended by Galton (1982) for postcranial material and cranial material rediscovered in a forgotten cabinet (Galton 1988), neither author attempted a detailed analysis of the range of motion of the animal, and some of Hennig's views on the palaeobiology of *Kentrosaurus* today appear antiquated. For example, he repeatedly stated that the tail was too stiff to be used as a weapon (Hennig 1916a, 1925), as did Janensch (1925). While Gilmore (1914) considered the tail spikes of the closely related North American genus *Stegosaurus* to function solely as a display, Bakker (1986) reiterated Lull's (1910) suggestion that *Stegosaurus* used its tail to club predators. Bakker (1986) noted that the large size of the deltoid crest of the humerus suggested a large *m. deltoideus*, which supposedly indicates the ability to rapidly and forcefully pivot around so that the tail faced the predator. The large *m. triceps* was interpreted as giving a "forward-lunge" capacity (Bakker 1986, p. 230). Today, there is compelling evidence in the form of a pathological *Allosaurus* vertebra that the (most likely stiffer than in *Kentrosaurus*) tail of *Stegosaurus* was employed for defensive purpose (Carpenter et al. 2005), as were the tails

Fig. 1 The new MFN mount of the lectotype of *Kentrosaurus aethiopicus* HENNIG 1915 (Tendaguru Formation, Tanzania), complemented by paralectotype material from the same locality and plaster replicas. This version was mounted in 2005. **a** Left lateral and slightly anterior view. Modified from http://commons.wikimedia.org/wiki/File:Fossil_Kentrosaurus_aethiopicus_in_Museum_f%C3%BCr_Naturkunde_Berlin_001.JPG, used under public domain license. **b** Right anterolateral view. Photo by C. Radke, used under permission from the MFN
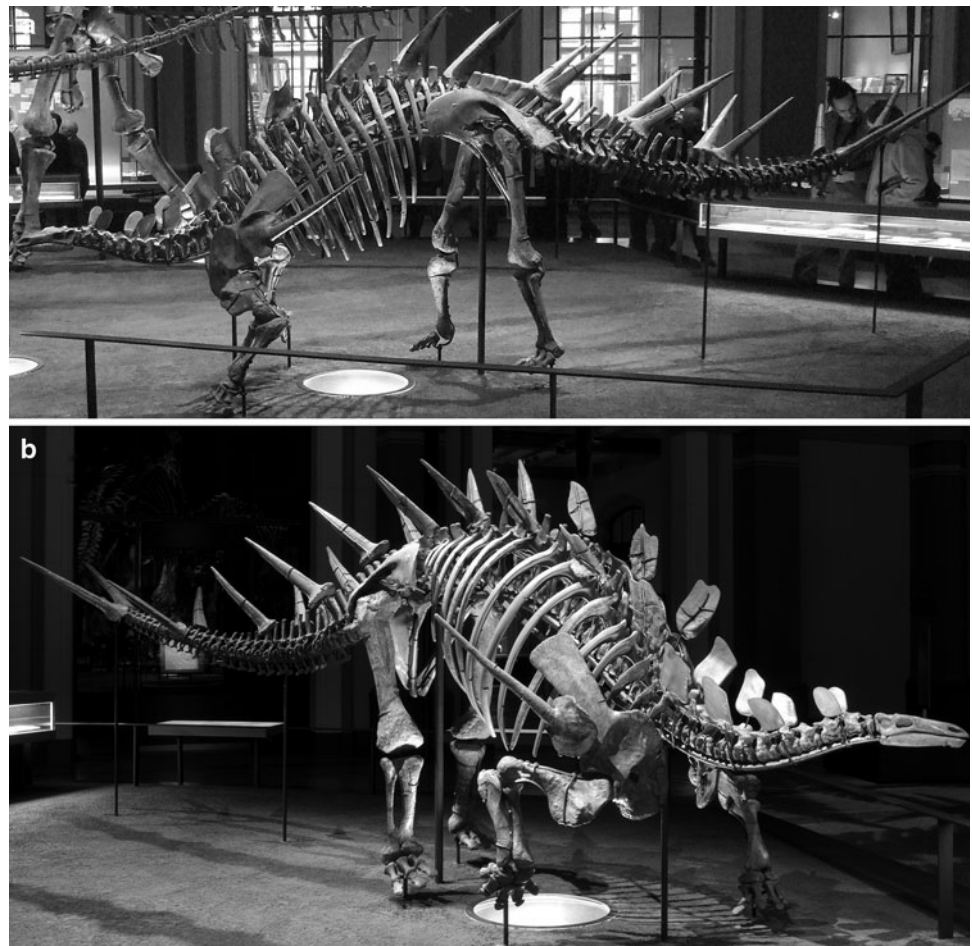
of ankylosaurs (Arbour 2009). Therefore, it is here assumed that *Kentrosaurus* also used its tail to defend against predator attacks.

Another controversial issue is the spread-eagled position of the forelimbs in both the MFN and IFGT mounts. Hennig (1925, p. 250) asserted that the curvature of the back indicated a 'strongly depressed' position of the anterior body, which results in a sprawling forelimb position. While strong humeral abduction was possible, it is questionable whether this forelimb position, which is unusual among quadrupedal dinosaurs, was habitually adopted during locomotion, as suggested by the MFN mount, which was erected in a 'walking pose' (Janensch 1925). Bakker (1986) figured stegosaurs standing, walking and even fighting with erect forelimbs, and flexing the tail strongly laterally, so that the tip points cranially.

Similarly controversial is the discussion on the ability of stegosaurs to rear into a bipedal or tripodal pose. Marsh (1880, 1881) initially described *Stegosaurus* as a bipedal animal, because of the low forelimb/hindlimb length ratio. Today's consensus is that stegosaurs were obligate quadrupeds (Marsh 1891, 1896; Gilmore 1914; Hennig 1915; Janensch 1925; Carpenter 1998; Galton and Upchurch 2004), and evidence from the ichnological records appears to bear this out (e.g., Lockley and Hunt 1998; Whyte and Romano 2001; Milàn and Chiappe 2009). The posterior position of the centre of mass has been repeatedly interpreted as indicating the ability to use a tripodal pose for feeding (Bakker 1986, 1978; Marsh 1891, 1896). "Tripodal pose" means standing on the hind limbs and using the tail as a "third leg" (Bakker 1986). However, Carpenter (1998) argues that at least *Stegosaurus* was unable to use a tripodal pose because of the rigidity imposed on the tail by the caudal osteoderms.

Large plates that could block tail motion are not known in *Kentrosaurus*, but both Hennig (1916b, 1925) and Janensch (1925) argued that the tail was stiff laterally. Janensch (1925), however, allowed that upward strikes had been possible to a limited degree. This mobility may have been sufficient for adopting a tripodal pose.

Here, the digital files of the MFN mount are used to study the motion range of the entire skeleton, in order to answer basic questions about the palaeobiology of *Kentrosaurus*. Range of motion studies suffer from a number of problems, and their results have to be interpreted cautiously, especially when the input data is limited to bone shapes (see below). Therefore, it makes no sense to attempt to determine to a fraction of a degree the motion possible in each single joint. Rather, for each body part, the probable influences of soft tissues and biomechanical considerations must be taken into account, and results compared to extant relatives or animals with similarly shaped bones. The range of motion of joints, determined on the basis of the bones

alone, without a detailed kinetic/dynamic analysis or musculature reconstruction, is only the first proxy for such an analysis of what motions the animal was capable of. Whether these motions were in fact performed regularly or exceptionally must remain unknown. However, when data from a range of motion study is combined with other evidence as described above, some motions can be confidently excluded as impossible or highly improbable, while others can be determined as easily possible. If the latter are of (apparently) obvious usefulness, it is prudent to assume that the animals probably performed them. For example, if a neck allows moving the head into a position from which a stegosaur can look backwards, it is reasonable to assume that the animal, when feeling threatened from behind, did move the head into a position that allowed a visual assessment of the threat. The focus of this work rests on determining the habitual postures for standing and locomotion, possible gaits, defence actions and feeding behaviour, as well as is possible based on skeletal motion limits. Other approaches may narrow down the range of results, but must always remain secondary to the limits imposed on motions by the sole preserved parts of the animal, the bones.

Material

When the old MFN mount of *Kentrosaurus* was disassembled in 2005/2006, high-resolution laser scans were created from most of the original bone material by D. Mackie of Research Casting International®, using a Konica Minolta Range 7 3D Laser Scanner. Of the remaining MFN material, nothing was scanned, nor the plaster replicas that complete the composite mount. Solely the plaster skull, based on an occiput and otherwise modelled on *Stegosaurus* (Janensch 1925), was scanned. Plaster replicas were mainly based on specimens of different sizes that did not fit the mount (Janensch 1925), and as much of this material is today either lost, mislaid or was destroyed during World War II, the replicas are the best remaining evidence, together with the figures in Hennig (1915, 1916b, 1925). Where possible, I used material of the MFN and IFGT mounts to re-assess the accuracy of these plaster replicas.

The MFN mount consists of the lectotype (MB.R.4800.1-37) of *Kentrosaurus aethiopicus* and other genuine material, all of which are paralectotypes and shown in Mallison (2010a, fig. 1). Mallison (2010a) also lists all other material that was present in the MFN collection in fall 2009. The lectotype and most other original material stems from the 'Mittlere Saurierschichten' (Middle Saurian Beds), while manus and some plate/spike material reconstructed in plaster were based on 'Obere Saurierschichten' (Upper Saurian Beds) material (Janensch 1925). The pes was

reconstructed based on Middle Saurian Bed material of different size (Janensch 1925). Hennig (1925), Galton (1982) and Maidment et al. (2008) pointed to the low variability of elements present in both layers, and argued that this indicates the presence of probably only one species, so that the manus and pes material can be used.

Elements included in the composite mount at the IFGT (GPIT 1542) were figured in Galton (1982, pl. 1, fig. 1). GPIT 1542, much of which consists of plaster replicas, is still mounted in the original form today. Several elements of it were mechanically digitized with a Microscribe 3D digitizer by the author. See Mallison et al. (2009) for details on the technique and on the resulting file types.

All *Kentrosaurus* material in the MFN and IFGT was inspected firsthand, and the mounted material in both museums was compared to other specimens where possible, to determine it shows significant alteration of the external shape due to taphonomic processes. Restricting the research presented here to the MFN mount and comparison to the IFGT mount and a limited number of other elements may seem imprudent, given the extensive lists of material given by Hennig (1925). However, it must be taken into account that most of the material of *Kentrosaurus* was destroyed in World War II, that the IFGT mount could not be fully dismounted, and that Hennig and Janensch selected the best-preserved and thus most informative bones for both mounts (Maier 2003). There is probably more material of *Kentrosaurus* in the collection of the Natural History Museum London (Maier 2003), but nothing has been published on it to my knowledge.

Methods

File handling

The original high-resolution Polyworks©.ply files created by Research Casting International were transferred into binary polygon meshes (*.stl) in Geomagic Qualify 8.0© (Geomagic Inc.). The total size of 1.9 GB (~ 1.0 GB without osteoderms) cannot be handled easily with any CAD (computer aided design) software on a standard PC. Therefore, on each file a polygon decimation routine to 80% file size was performed repeatedly. The number of iterations depended on the original size of the scan and the complexity of the bone shape. To ensure that no important details were lost in the size reduction, large files and simple shapes were reduced more, while small scans or complex shapes were decimated less often. This created a second, much smaller data set (83 MB), from which a complete mount could be created. The "preserve edges" option was always used, so that sharp edges suffered as little as possible from "digital erosion" during the size reduction process. Nonetheless, in

most elements, the loss of data accuracy is significant and the final version is unsuitable for detailed range of motion analyses or osteological descriptions. Therefore, the full sized scans were used for all analyses, while the small files were only used as placeholders.

Throughout the analyses, neighbouring elements were given different colours, in order to ease the task of assessing the correct articulation. This results in a zebra-stripe overall appearance (Figs. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11)[1]. If mirror copies of elements were used, e.g., of some dorsal ribs, they were made semi-transparent.

Caveats

Articular cartilage

Studies like the one presented here deliver at best a cautious approximation of the desired results. While the osteological limits of motion are the first proxy for the motion capabilities of an extinct animal, many uncertainties exist regarding the limits of bone versus bone motion in the absence of clear bony stops. Archosaur fossils typically preserve very little of the cartilage caps on the articular ends of longbones (Wings et al. 2006; Schwarz et al. 2007). However, the shape and thickness of the articular cartilage is a factor significantly influencing the articulation of limb joints and their range of motion. Usually, the lack of cartilage preservation in fossil archosaurs leads to sometimes large gaps between structures that during life must have had closely corresponding sizes. In the case of *Kentrosaurus aethiopicus*, several bones, possibly stemming from several individuals, show unusual cartilage preservation, among them both ulnae of the Berlin mount (left ulna MB.R.4800.33 and right ulna MB.R.4807). Especially, the left ulna MB.R.4800.33 has a high and wide olecranon process, which on the outside shows a rugose texture unlike normal long bone shafts or articular ends, but generally similar to the texture described for preserved articular cartilage in a sauropod (Wings et al. 2006; Schwarz et al. 2007). Comparison with two other ulnae (IFGT St 113 and IFGT unnumbered, both today part of the IFGT mount numbered GPIT 1542) shows that some *Kentrosaurus* ulnae have a significantly different morphology, lacking a large proximal process (Fig. 3c, d). In lateral view, this shape is very similar to many other dinosaurs, even from such distant ones as, e.g., *Plateosaurus* (Mallison 2010c) and *Gallus* (own unpublished data). In contrast, the left ulna of the MFN mount (MB.R.4800.33) with its large olecranon is more reminiscent of a ceratopsid (Dodson et al. 2004) or mammalian ulna (Fig. 3c, d). The discrepancy in shape between these bones is best explained by hyperostosis in

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[1] Digital figure versions are available from the author

Fig. 2 Laser scan based digital files of dorsal vertebrae 1 through 11 of the MFN mount with left dorsal ribs 7 through 9 and right dorsal ribs 2, 3 and 6, in ONP. Transparent mirror copies of ribs are added where contralateral element are missing. **a** Dorsal view, including laser scan based files of the neck and the plaster skull model at maximum lateral flexion (cautious interpretation; see text for further explanation). **b** Anterior view (*scale bar* 0.5 m)
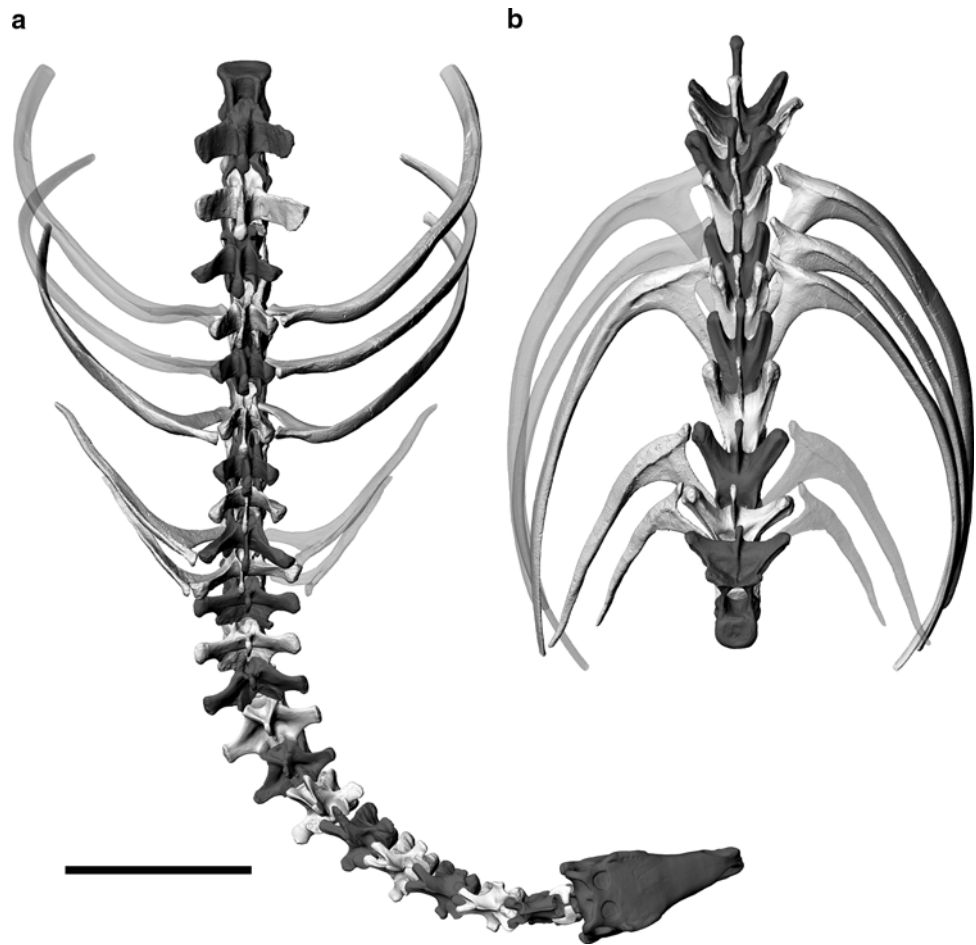
MB.R.4800.33, which has ossified the normally cartilaginous olecranon. Similar ossifications are present on other *Kentrosaurus* material, and will be discussed in detail elsewhere. The example of the ulnae highlights the difficulties that the lack of cartilage imposes on analyses of the range of motion. It may be legitimate to use the bony articular surface as a first approximation of the real joint shape (as suggested by, e.g., Bonnan and Senter 2007), because in extant adult archosaurs there is a general correlation between the shape of the articulation surface and the bone surface (Bonnan et al. 2009). However, the loss of $\sim 18\%$ of total bone length in the IFGT ulnae compared to left ulna MB.R.4800.33 and right ulna MB.R.4807 shows the scope of possible errors.

It is often claimed that the cartilage in dinosaur limb joints could not have been several centimetres thick, because articular cartilage is avascular, and supplied with nutrients by the synovial fluid through diffusion (e.g., M. Bonnan 2009, pers. comm.; D. Henderson 2010, pers. comm.). In fact, extant dinosaurs have proportionally much thicker cartilage caps than mammals, and their articular cartilage is pervaded by blood vessels (Graf et al. 1993). If one assumes a thin, mammal-like cartilage cap (Kummer

2005) on dinosaur long bones, many joints would not be functional, as exemplified by the knee of *Plateosaurus*, which would not allow smooth flexion and extension (Mallison 2010c). Rather, it would have a preferred articulation angle, caused by a flattening of the distal femur end, which would have acted as a weak locking mechanism (Mallison 2010c).

In addition to the left ulna of the MNF mount (MB.R.4800.33), the right ulna (MB.R.480) and especially the left humerus (MB.R.4804) appear also to preserve large amounts of cartilage on both proximal and distal articular ends, which leads to a significantly different morphology compared to other humeri. The analysis presented here only uses the left humerus MB.R.4804 in combination with the exceptionally preserved left ulna MB.R.4800.33, because this likely gives the most accurate results.

Soft tissues

Soft tissues can influence the motion range of joints, too (McGinnia 2004; Kummer 2005), but our understanding of stegosaurian musculature is limited, and detailed technical reconstructions, aside from being extremely time

Fig. 3 a–b Laser scan based digital files of dorsal vertebrae 1 through 11 of the MFN mount with left dorsal ribs 7 through 9 and right dorsal ribs 2, 3 and 6 in left lateral view. Transparent mirror copies of ribs are added where contralateral elements are missing. *Light grey* and *dark grey* areas: most dorsal and most ventral scapula positions in shallow orientation. *Light grey* area with black rim: steepest and most posterior possible scapula position. For further explanations see text. Sacrum is assumed horizontal, different angles of the dorsal 11 with the horizontal in **a** and in **b** result from extension of the posterior dorsals (not shown). *Scale bar* 0.5 m, dorsals in ONP (**a**), dorsals extended by ∼2° per intervertebral joint (**b**). **c–d** Laser scan based digital file of the left ulna (MB.R.4800.33) of the MFN mount (on the *left* in **c**, on *top* in **d**) and mechanical digitizing based files of left ulna (IFGT field number St 133, in the *middle* in **c** and **d**) and right ulna (IFGT unnumbered, on the *right* in **c**, on the *bottom* in **d**). Both IFGT ulnae are part of the IFGT mount (GPIT 1542). *Scale bar* 0.25 m, anterior (**c**) and lateral (**d**) views. *Arrows* point at proximal process in MB.R.4800.33
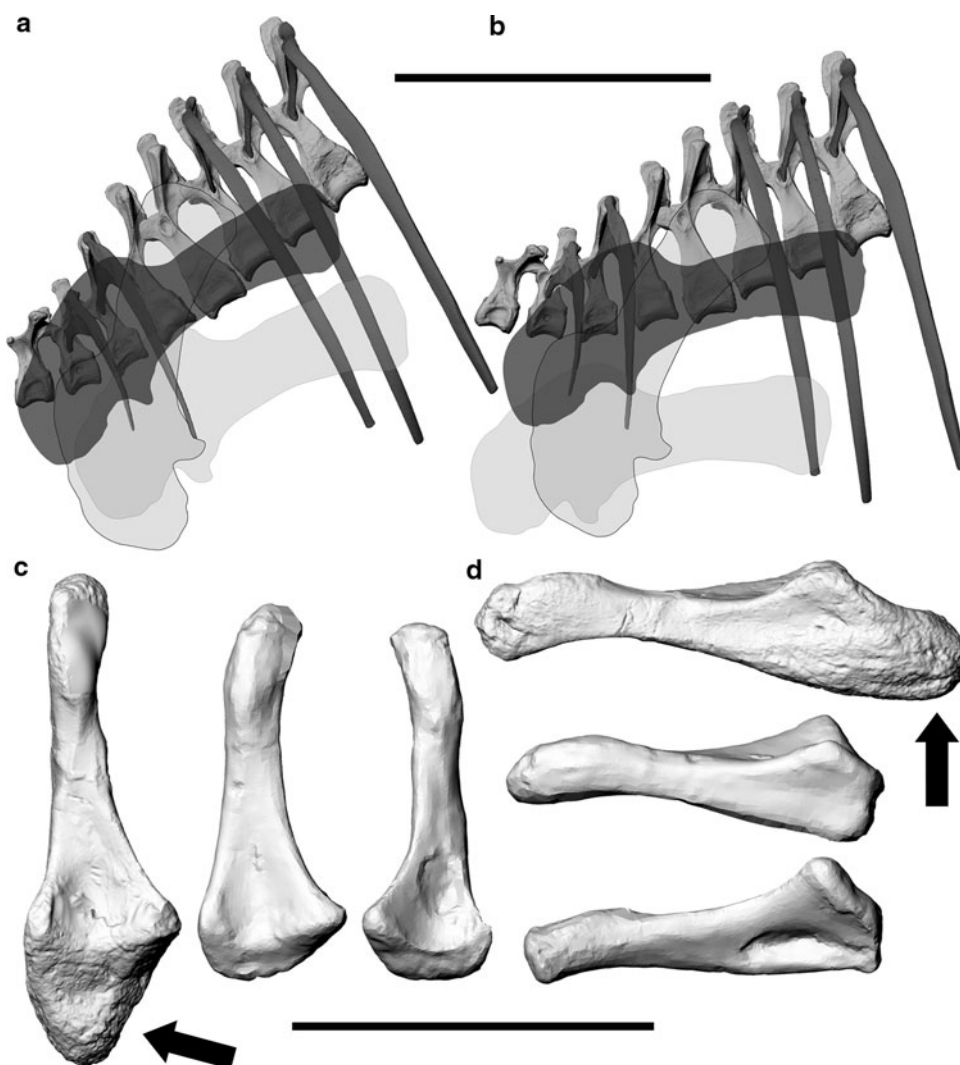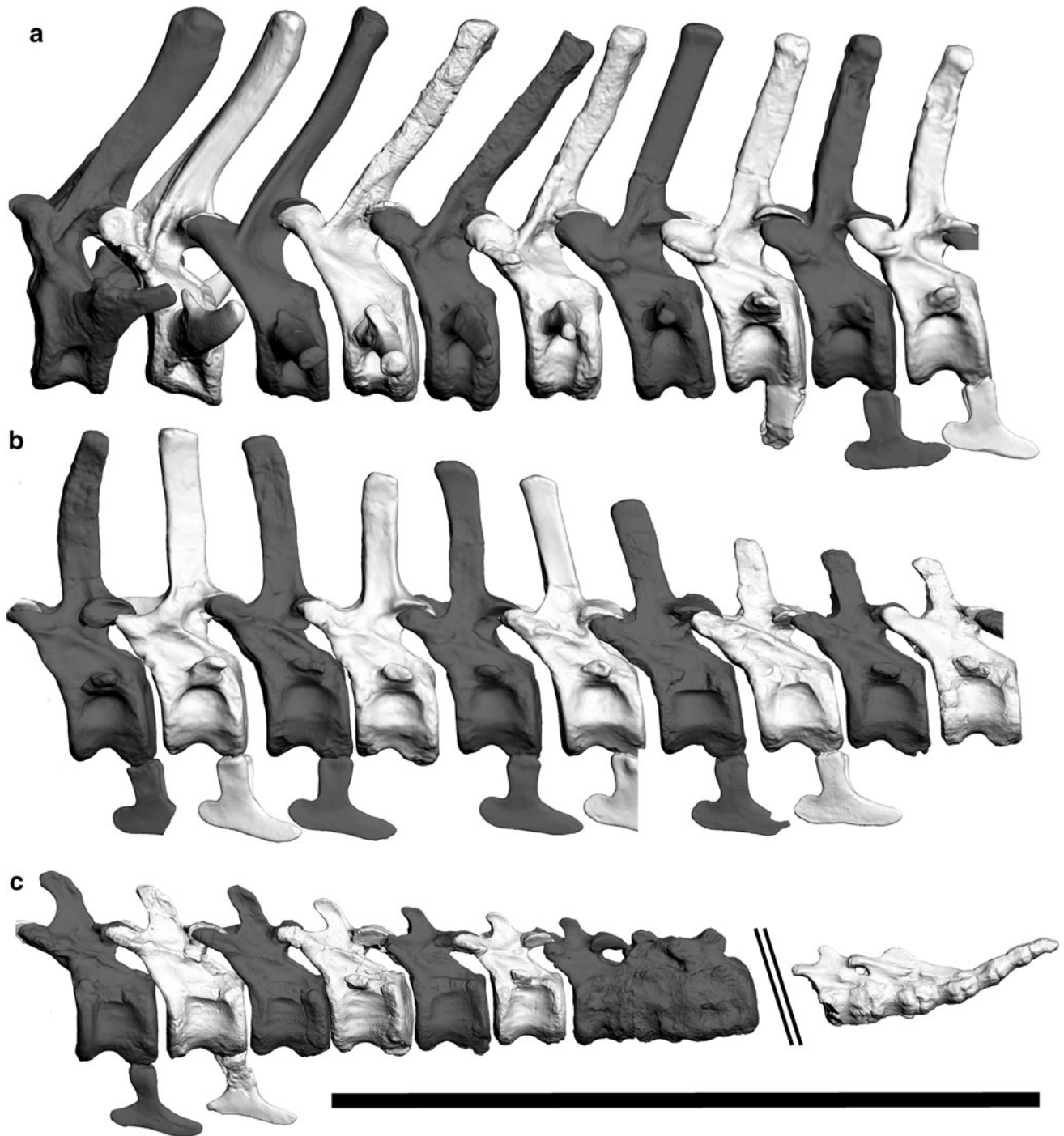
Fig. 4 Laser scan based digital files of the plaster replica of the skull, all cervical and dorsals and the sacrum of the MFN mount, in left lateral view in ONP (*scale bar* 0.5 m)
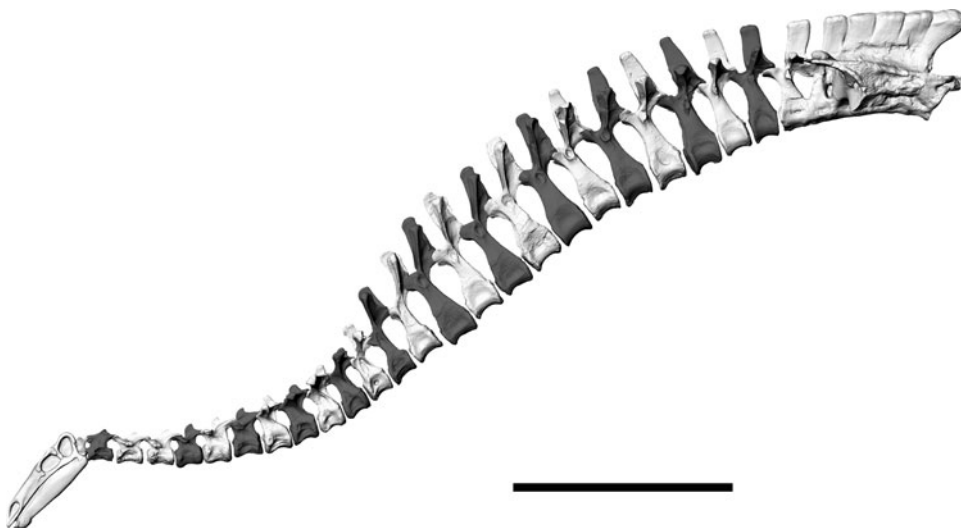
consuming, involve large uncertainties on muscle paths, types and volumes. Additionally, range of motion analyses suffer from further uncertainties if the bones do not stem from one individual, but from several animals of different size and ontogenetic age. For example, in the neck of the IFGT *Kentrosaurus* mount no two neighbouring vertebrae

Fig. 5 Laser scan based digital files of the tail of the MFN mount in left lateral view and in ONP (*scale bar* 0.25 m). **a** Caudals 1 through 10. **b** Caudals 11 through 20. **c** Caudals 21 through 29 and coossified six distal caudals. Note that the MFN mount lacks the first caudal, which in other specimens is incorporated into the sacrum as a caudosacral (Hennig 1925)

stem from the same individual. In the dorsal series of the MFN mount only three vertebrae stem from the lectotype (Mallison 2010a), and in the neck only one neighbouring pair is from one individual (Janensch 1925).

Other factors

Other factors influence the accuracy and usefulness of a bone-based range of motion study as well. For example,
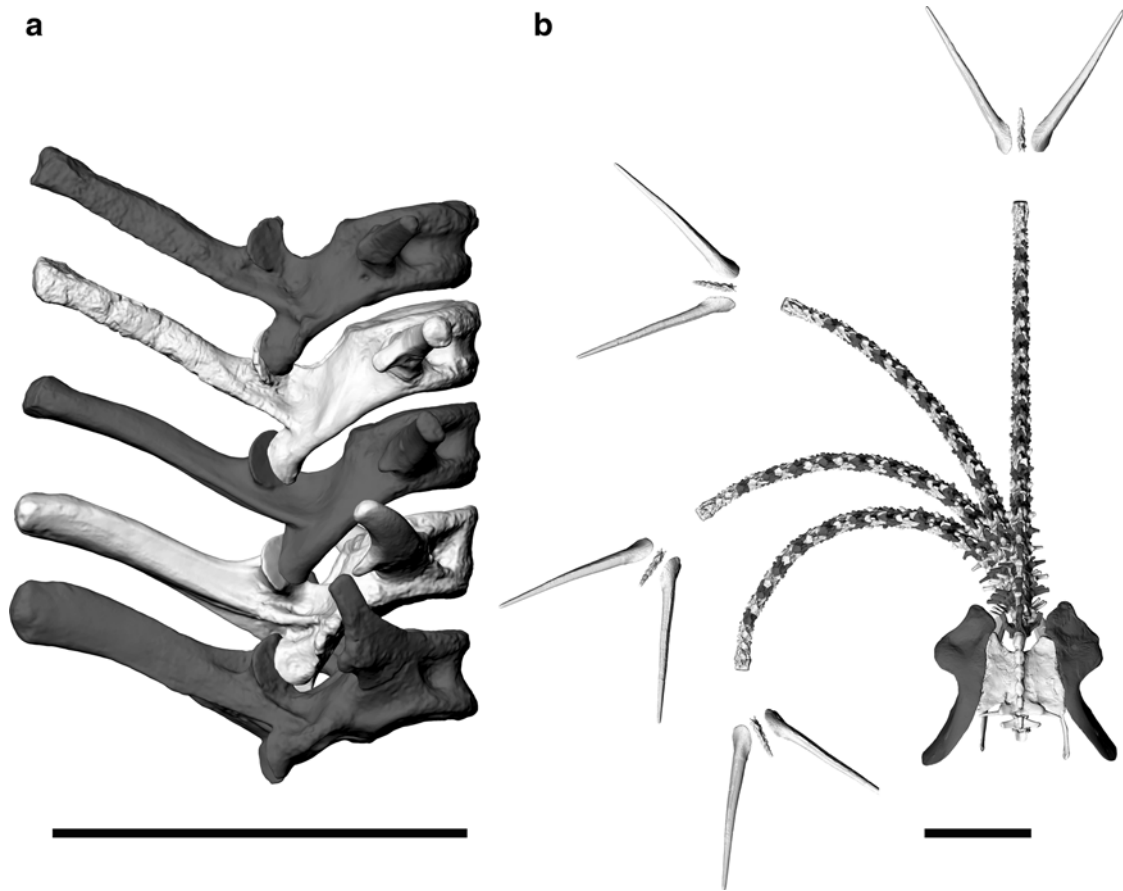
Fig. 6 a Caudals 1 through 5 in lateral view arranged so that centra faces are as parallel as possible. Note that the MFN mount lacks the first caudal, which in other specimens is incorporated into the sacrum as a caudosacral (Hennig 1925). See text for further explanation. **b** Dorsal view of the sacrum, ilia, tail and distal tail spikes of the MFN mount in dorsal view, with tail copies flexed by 2°, 5° and 6°, respectively. *Scale bars* 0.25 m (**a**) and 0.5 m (**b**)

taphonomic damage to the articulation surfaces of bones may prevent an exact determination of alignment and motion range. The biggest unknown, however, is the uncertainty whether a possible motion was actually performed by an extinct animal. All healthy humans can learn to walk on their hands only, but we never do so in regular life. Also, behaviour is always dependant on the environment, which itself is usually insufficiently known for extinct taxa. For example, tripodal feeding requires that sufficiently tall edible plants were available in the habitat of *Kentrosaurus*. What kind of vegetation exactly was available to *Kentrosaurus* is difficult to say, because the flora of the Tendaguru Formation and the hinterland is not well known. How much of a potential feeding range was thus actually used by the animal depends on factors such as the plant cover present in the natural habitat and fodder preferences, and speculations on this topic are beyond the scope of this paper. Similarly, defence behaviour depends not only on the motion range of the tail, but also on what predators were present, and whether they attempted to attack *Kentrosaurus*. In the absence of solid proof (e.g.,

like the smashed and healing *Allosaurus* tail vertebra presented by Carpenter et al. 2005), any conclusion presented here must remain conjecture.

Reconstruction of the digital skeleton

General remarks

The digital skeleton of *Kentrosaurus* was created in McNeel Associates Rhinoceros 4.0 NURBS Modeling for Window©, following the protocol described in Mallison (2010b) for *Plateosaurus*. This protocol for articulation of individual elements was used because it minimizes the influence of preconceived notions, since only those skeletal elements directly articulating are visible during their placement. Therefore, apparent or real overall curvatures of the vertebral column as reconstructed so far do not influence the articulation of a newly added vertebra to its neighbour. Simply stated, the digital skeleton is built by adding bones one by one. For each element added only those other elements are set visible that directly articulate

Fig. 7 Laser scan based digital files of the left forelimb (and left scapula in **a–d**) of the MFN mount. Scapula position corresponds roughly to that of Fig. 8. *Scale bar* 0.25 m, anterior view (**a**, **d**), lateral view (**b**). **c** View perpendicular to main axis of glenoid (anterolateral view). **e** Medial view. **f** Posterior view
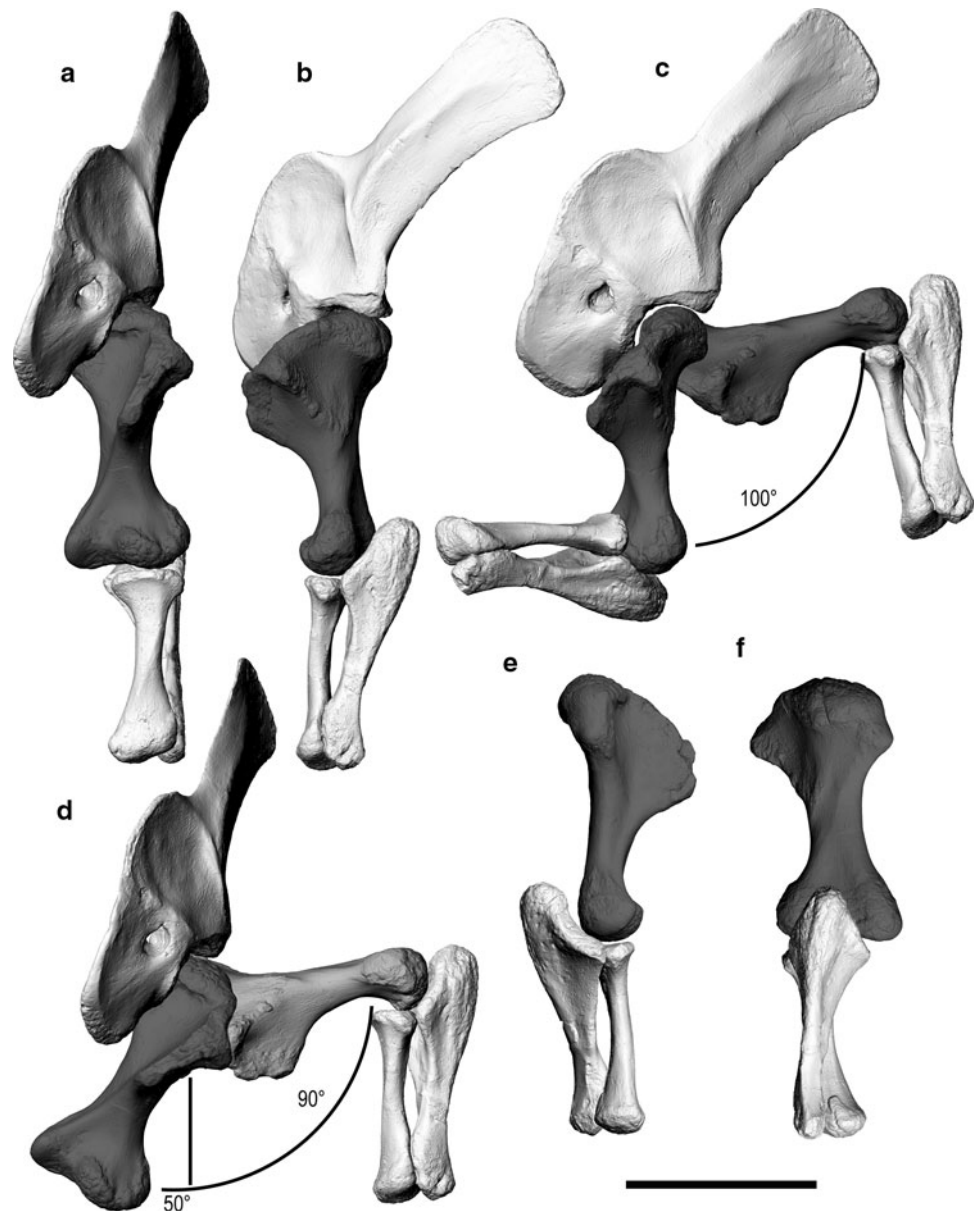
with it, while the rest of the skeleton is hidden. Articulation is assessed in three parallel views along the longitudinal, transverse and vertical axis of the animal, as well as a freely rotatable perspective view. Problematic areas are created at least twice, starting from opposite ends. For example, the neck can be started with the axis and built caudally, or built cranially starting with the first dorsal. Only if these two versions agree, the result is accepted. Otherwise, all work must be repeated to identify the potential sources of errors. Space was left for missing elements between the digital models of the original material.

Two versions of the digital skeleton were created, one using the full sized laser scan files, and one using the drastically reduced files. The former model could only be

created in sections, rendered views of which were combined to create full resolution figures. Analyses were conducted using only these full resolution files, while the smaller model served solely for the creation of illustrations and as placeholders for the high-resolution bone files in files with many bones. To ease the task of assessing the 3D articulation of neighbouring elements a zebra-stripe colour scheme was adopted, with elements alternately coloured light and dark grey.

Vertebral column

To achieve osteological neutral posture (ONP) the centra were placed with parallel faces, and the zygapophyses with maximal overlap of the apparent articulation area. Where
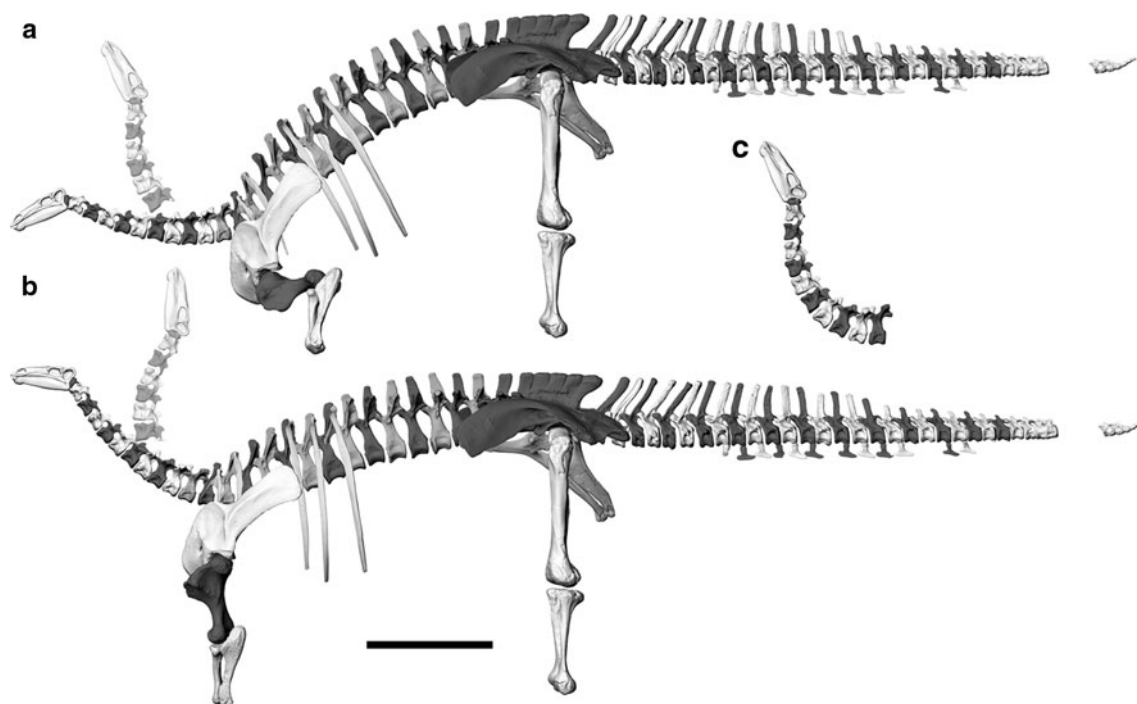
Fig. 8 Laser scan based digital files of the complete MFN mount including the scan of the plaster replicas of the skull but without the osteoderms. Transparent skulls show position at full neck extension (*scale bar* 0.5 m). **a** In ONP. **b** In suggested habitual pose for locomotion. **c** Neck at maximal extension

this was not possible (e.g., large parts of the tail), zyga-pophysal overlap was deemed more important than parallel centra faces, assuming that non-parallel sided intervertebral discs were present. The thickness of the intervertebral discs, however, was not estimated or assumed in any way. The space between the digital vertebra files results solely from the articulation process as described.

It appears questionable whether ONP corresponds in any way to a habitual posture (Taylor et al. 2009), as most extant animals seem to hold at least their necks in positions that do not agree with the criteria of ONP, or even within the motion range limits used by Stevens and Parrish (1999, 2005a, b), during resting and most other activities (Christian and Dzemski 2007; Taylor et al. 2009). Still, ONP was used because it represents, in the absence of osteological stops, roughly a middle position in the range of motion (Taylor et al. 2009).

Pectoral and pelvic girdles

The pelvis is easy to reconstruct, because of its massive construction, which leads to large contact areas between the sacrum and the ilia. In mature individuals, full fusion was described by Hennig (1925). The right pubis (MB.R.4810) and the sacrum and ilia may belong to the same individual. However, the left pubis (MB.R.4809) and

left ischium (MB.R.4811) stem from different individuals, because they are of slightly different size, but still articulate well with the other bones of the pelvis.

The shape of the pectoral girdle as well as its position on the ribcage cannot be determined with certainty. There are only six ribs from the relevant area of the ribcage that have a size roughly fitting the dorsal vertebrae, two right ribs apparently fitting dorsals 2 and 3, a pair fitting dorsal 6, and two left ribs fitting dorsals 7 and 8 (Janensch 1925). Thus, the possible shape of the ribcage is poorly constrained. Figure 2 shows the anterior dorsals with these ribs, as well as mirror versions of those where no contralateral part is available, in dorsal and anterior views. This is the best possible, but still speculative, representation of the ribcage. Ribs with higher resistance to compaction exists where the m. serratus attaches the scapula to the ribcage in extant animals (Fujiwara et al. 2009), but the very low number of preserved ribs with the uncertainty of their assignment to specific vertebrae means that variation in rib shape is barely helpful for determining the position of the scapula.

The dorsoventral placement of the scapulae is somewhat limited by the shape of the ribcage, but since this shape is itself insufficiently known, a wide range of possible placements remains possible. If the rib distribution in *Kentrosaurus*, as proposed by Hennig (1925) and Janensch (1925), is accepted, the anterior dorsal ribs show straight
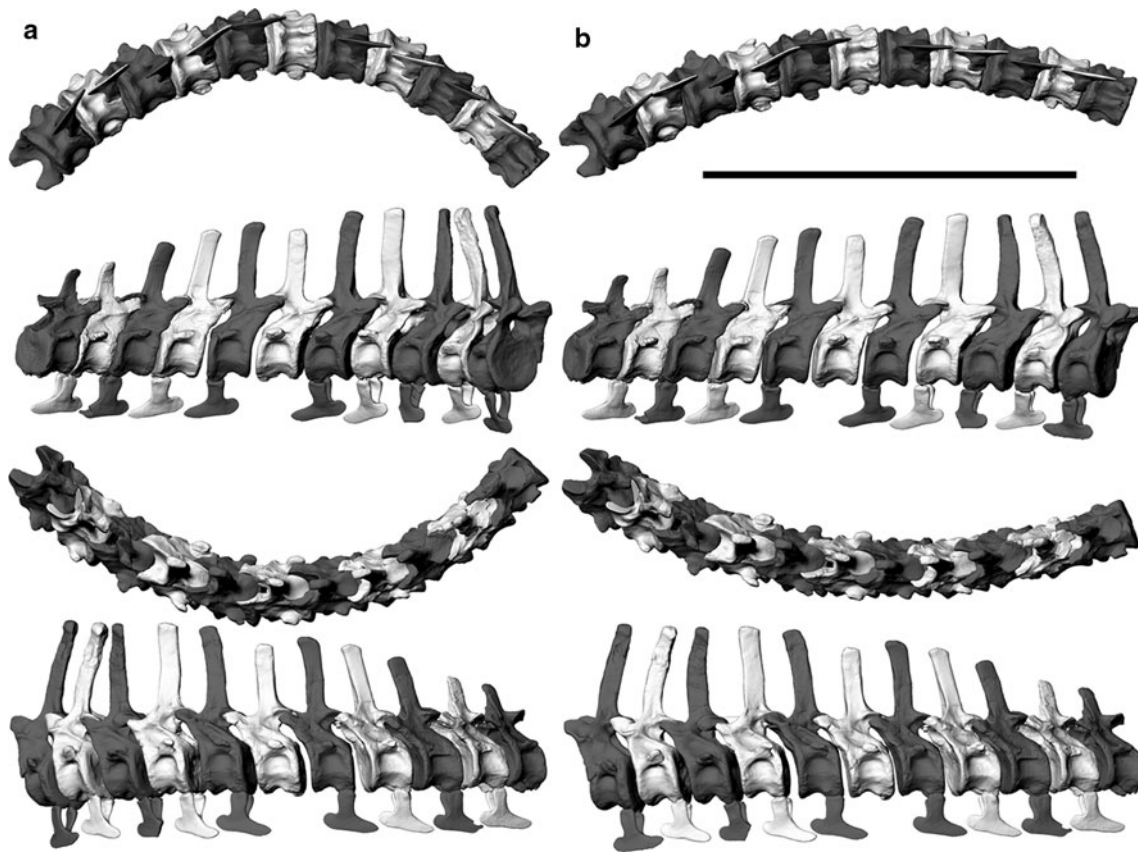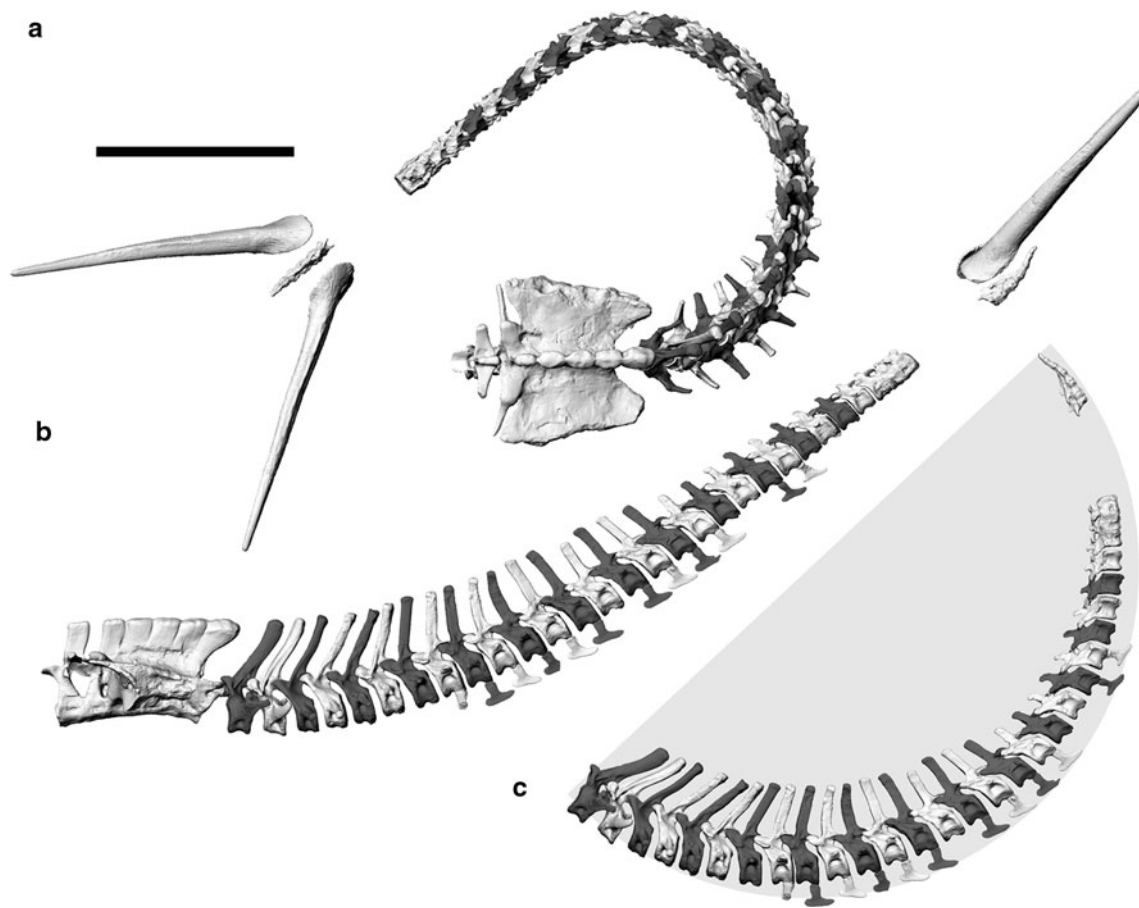
Fig. 9 a–b Laser scan based digital files of caudals 9 through 19 (not counting the missing caudosacral) of the MFN mount in (from *top* to *bottom*) ventral, right lateral, dorsal and left lateral views, at 5° (**a**) and at 10° lateral flexion per intervertebral joint (**b**) (*scale bar* 0.5 m)

shafts, while further posteriorly on the trunk, ribs have curved shafts with a high-oval cross section (Fig. 2). Possibly, the straight-shafted ribs represent the area of the trunk that received large forces from the shoulder musculature. This would indicate that the scapula had an anterior position. However, ribs from dorsals 4 and 5 are not reliably known, so that the area of straight-shafted ribs cannot be determined exactly.

The anterior edge of the coracoids is roughened and pitted, indicating either a medial contact between them, or articulation with the sternals. The MFN mount does not have any plaster replicas of sternal plates, and no finds of sternals were mentioned by Hennig (1915, 1916b, 1925) and Janensch (1925). No unequivocal sternal plates are known from stegosaurs, and only Gilmore (1914) tentatively identified sternal plates comprising of a pair of small triangular elements in *Stegosaurus*. Therefore, it is assumed that the gap between the coracoids was relatively small.

The angle between the horizontal and the scapular blade dictates how the angle the humerus can cover in the glenoid is orientated versus the vertical, influencing possible stride length and weight distribution between limb pairs. Again, without a well-preserved ribcage the correct position is

hard to estimate. However, a steep position, with the blade of the scapula at roughly a 55° angle from the horizontal, allows a placement with only minimal or without overlap with the curved dorsal ribs 6 and 7, independent of the angle between the dorsal series and the horizontal. In Fig. 3a, b one steep and two shallow positions are suggested that cover most of the possible range for the scapula. These positions are shown for ONP of the dorsals in Fig. 3 a, and for a slightly extended dorsal column (see below) in Fig. 3b. Of these positions, the dorsal and shallow one result in the distal tip of the scapular blade fully overlapping dorsal ribs seven, while the ventral and shallow position overlaps dorsal rib six and has practically no overlap area between the anterior ribs and the scapulocoracoid. Both positions are possible, but appear unlikely, so that an intermediate dorsoventral placement is probable. The steep position in Fig. 3a, b illustrates the most posterior position possible. The anterior edge of the coracoids may well have rested under the base of the neck, as is the case in birds. Overall, the angle between the half-angle of glenoid motion range and the vertical varies between 20° and 65° for the ONP position, and 0° and 45° for the extended position.

Fig. 10 Laser scan based digital files of the tail and tail tip osteoderms of the MFN mount (*scale bar* 0.5 m). **a** In dorsal view with the anterior half of the tail at 10° lateral flexion per intervertebral joint, and the distal half in ONP. **b** With the sacrum in left lateral view at 2.5° extension per intervertebral joint. **c** In left lateral view at 5° extension per intervertebral joint. *Light grey* area marks a semi-circle covering the entire tail length, as described as the position in the field by Hennig (1913, 1925), and as suggested to represent the opisthotonic posture. Length of gap at the tail end between caudal 29 and distal caudals according to Janensch (1925)

For the analyses, a steep, anterior orientation was chosen. This position is roughly similar to that in a wide range of dinosaurs, e.g., prosauropods *Plateosaurus* (Mallison 2010b, c) and *Seiitad ruessi* (Sertich and Loewen 2010), most sauropods (Remes 2008), and ceratopsians (*Triceratops*; Fujiwara 2009). Depending on the position of the dorsal series, this step scapula placement means that the angle between scapula blade and dorsal series varies between 10° and 40°. Smaller and larger angles are biomechanically not useful, because the pectoral musculature cannot act effectively, and the corresponding positions can therefore be excluded.

Limbs

In contrast to the vertebral column, there is no position for limb elements that is inherently preferable as "neutral" compared to others. While it is tempting to use the half-angle of the possible motion range in any given articulation, the requirements for the use of limbs for a wide range of possible motion sequences, such as locomotion, mating, descend into resting poses and standing up from them, as well as recovery into an upright pose after falls, means that the habitual standing and midstance postures do not necessarily correspond to any specific angle of the possible motion range. A good example is the human knee, which during normal walking is used at angles that do not even include the half-angle, and stays at significantly lower flexion angles even during the support phase in rapid walking. Here, data in addition to the shape of the articulation surfaces were used, such as limb bone shaft curvature. For example, a circular femur shaft cross section may indicate a permanently flexed limb posture (e.g., in *Plateosaurus*, Mallison 2010b; *Tyrannosaurus*, Gatesy et al. 2009). Conversely, a femur shaft that is antero-posteriorly flattened indicates compressive forces as the main load. This is the case in graviportal animals such as elephants, which are, however, much heavier than *Kentrosaurus*, and
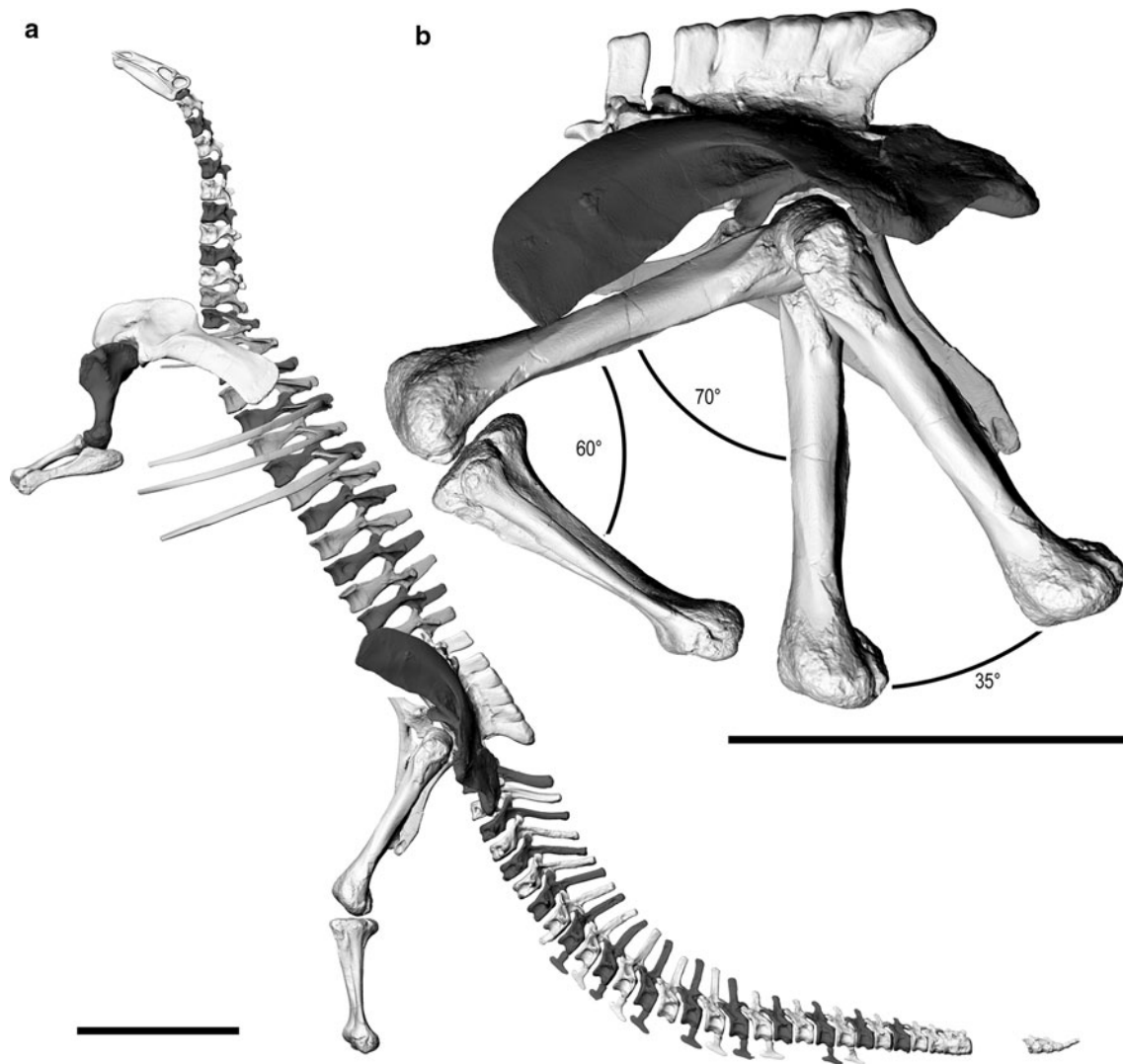
Fig. 11 Laser scan based digital files of the MFN mount (*scale bars* 0.5 m). **a** Complete mount without osteoderms in rearing pose, with scan of the plaster replica of the skull. **b** Sacrum, left ilium, left pubis, mirrored right ischium and left hindlimb in left lateral view, with copies of the femur at maximum protraction (*left*) and retraction (*right*)

in dinosaur taxa with tail clubs such as anklyosaurs and glyptodonts (Gillette and Ray 1981; Vickaryous et al. 2004). The flattened shaft indicates that bending moments in anteroposterior direction were comparatively low, meaning that large excursion angles of the femur did not coincide with high accelerations, e.g., during rapid locomotion (Hildebrand and Goslow 2003).

The femur of *Kentrosaurus* does not show shaft curvature, and is anteroposteriorly flattened (Figs. 1, 8, 11b). Therefore, the limb was mainly exposed to compressive and lateral bending stresses, indicating a subvertical position when standing, and low limb excursion angles during locomotion. It was therefore placed vertically for the ONP model, assuming a standing posture. The influence of articular cartilage on the articulation of limb elements is described further below.

Osteoderms

Hennig (1925) and Janensch (1925) present a good case for the positioning of the various types of osteoderms they describe across the trunk and tail of *Kentrosaurus*, especially with regards to the apparent bilateral symmetry. However, due to the lack of well-articulated specimens it is unclear whether the spikes and plates were distributed at relatively regular intervals along the anteroposterior axis, or whether there were gaps between the different types. For example, it is possible that the tip of the tail possessed one pair of spikes (as indicated by an articulated find; Hennig 1925) or two pairs as in other stegosaurs (Galton and Upchurch 2004). Hennig (1925) mentions regularly spaced pairs of spikes found along an articulated tail, so that the position at least of the tail spikes in the old and new MFN

mounts (Fig. 1) is reasonable (see discussion in Janensch 1925). Since it appears unlikely that osteoderms were mobile, only the most distal tail spike pair is of interest, because it experiences the greatest lateral displacement during motion. All other osteoderms are ignored in the present work. Those present as real bone on the MFN mount are listed and shown in Mallison 2010a (tab. 1, fig. 1).

Range of motion analyses

Motion range limits were determined three-dimensionally by articulating the joint "straight" (e.g., tibia and fibula forming a straight line with the femur), and if such a position was not possible or reasonable (e.g., in the elbow), the bones were angled in increments, until articulation was achieved. Then, the joint was flexed by rotation of a copy of the more distal element around the estimated axis of rotation perpendicular to the plane of view (i.e., flexion and extension of the joint were tested in lateral and medial views, abduction and adduction were assessed in anterior and medial views, and inversion and eversion were created in the dorsal and ventral views). The resulting articulations were assessed in all three axial and in one freely rotatable perpendicular view. Extreme positions were determined by a trial and error process, in which the amount of, e.g., flexion was gradually increased, until the resulting joint articulation became impossible. If adjustments such as sliding of one bone versus the other were needed (i.e., if the axis of rotation was slightly misjudged, or if the articulation surfaces did not allow a simple rotation), these were made and again controlled in all views. Large adjustments were rarely needed. However, in such cases intermediate positions were also tested for their feasibility.

These analyses were conducted using partial assemblages of the high-resolution files (e.g., the entire neck, the anterior first six dorsals), following the rules and methods detailed in Mallison (2010c). The possible motion range in each articulation was tested by displacing one element against the other, and the resulting articulation was controlled and adjusted in three axial and one freely rotatable perspective view. Again, only directly connected elements were included in each case, so that the influence of pre-conceiving notions and implied motion ranges based on previously assessed skeleton parts was minimized.

The amount of overlap that remains between the zygapophyses during maximum flexion is hotly debated in the literature (e.g., Stevens and Parrish 1999, 2005a, b; Christian and Dzemski 2007; Taylor et al. 2009). In light of the research of Christian and Dzemski (2007) and Taylor et al. (2009) it seems plausible that zygapophysal articulations especially in the neck can move so that overlap of significantly less than 50% occurs. Stevens and Parrish

(2005a, p. 191) mentioned that lateral flexion of giraffe necks leads to barely any overlap. In the zygapophyses, the two articulation surfaces may separate to create a gap between them (i.e., gape), as they do in humans when they bend down to touch their toes with their fingers. Here, a cautious approach was adopted, that allowed overlap of less than 50% and gaping only if the overall posture indicated that gravitational or other expected forces would, under any imaginable circumstances, lead to re-articulation when flexion was reduced, and where otherwise no or only very limited motion would be possible. An example of this is lateral flexion of the neck, where overlap of 50% or more of the zygapophyses would lead to contact of the lateral rims of the central faces in some vertebrae. Reduced or even no overlap on the outer side of flexion (i.e., on the right side when flexing to the left, and vice versa) does not result in a risk of disarticulation, because the axial soft tissues would contain the vertebrae, and lead to re-articulation when the lateral flexion angle is reduced. Similarly, a safe return to neutral posture from maximal ventral flexion of the neck requires only minimal overlap of the zygapophyses as long as there is no torsion or lateral flexion movement, so that only 10% overlap were required here.

Results

Standing posture (in ONP)

Vertebral column

The presacral vertebral column exhibits two areas of marked curvature in ONP (Fig. 4), a ventral bend in the posterior and mid dorsals caused by ventral keystoning of the dorsals, and a dorsal curve in the cervicals and the first two dorsals, caused by dorsal keystoning. In the cervical and dorsals, the pre- and postzygapophyses are often not of corresponding size. In the dorsals, ONP can in some cases not be achieved at all, because the wedge-shape of the centra of some vertebrae is so strongly developed that the dorsal neighbouring centra would have to touch in order to create full overlap of the zygapophyses. These problems are probably caused by the composite nature of the cervical and dorsal series.

If the neural canal of the sacrals is (arbitrarily) positioned horizontally, the upward turn at the base and throughout the neck is sufficient to bring the atlas–axis complex into the horizontal, cancelling the effect of the ventral curvature in the trunk (Fig. 4). If the neck/skull articulation is placed flexed, as it habitually is in most extant animals (Taylor et al. 2009), the tip of the snout is nearly 0.9 m lower than the acetabulum. A more likely position of the neck, extended at the base and straight in the

middle part (Taylor et al. 2009), brings the skull into a position slightly above the base of the neck.

The apparent neutral position of the tail (Figs. 5, 6) in the vertical plane in relation to the sacrum is difficult to determine in the digital skeleton, due to the lack of a caudosacral vertebra in the mount, and due to the sacrum being dorsoventrally compressed. It is unclear if and how deformation has altered the orientation of the zygapophyses and the centrum face in the last sacral. However, examination of the other sacra in the MFN and IFGT collections indicated a straight emergence of the tail base from the sacrum. The tail in itself articulates perfectly straight if the zygapophyses are brought into 100% overlap position.

The long axes of the centra of the first five caudals are not parallel to the neural canal. The first three caudals show ventrally directed keystoning and thus appear to suggest a downward curve of the tail. In Fig. 5, the neural canals were lined up straight, and the zygapophyses were placed fully overlapping, and as a result the centra are not articulating in ONP with each other. ONP-articulating the centra leads to an unrealistic zigzag of the neural canal and misalignment of the zygapophyses in various directions (Fig. 6a). Therefore, the keystoning is probably the result of taphonomic deformations.

Limbs

Due to the sub-vertical femur position, the lower hind limb must also be placed sub-vertically, as in extant graviportal elephants. Both hind limbs were positioned vertical in anterior view (i.e., the foot is below the acetabulum, not the body midline), because the ONP posture corresponds to a standing pose. The resulting standing track width is 0.55 m for fully erect hind limbs.

The forelimb can also be placed vertically, with the humerus as well as radius and ulna in a sub-vertical position, even if the steepest plausible scapula position is used (Fig. 7a, b, e, f). The track width of the forelimbs in the sprawling pose is roughly 1 m, nearly doubling that of the hind limbs. A fully upright forelimb position results in a track width of slightly less than 0.4 m. Slight abduction of the humeri allows track widths of up to 0.6 m, without compromising the essentially erect nature of the forelimb.

Entire skeleton

Overall, the combination of unequal limb lengths and anteriorly downwards curving dorsal series seems to suggest a posture in which the neural canal of the sacrals and the tail are sub-horizontal or slightly posteriorly inclined, as shown in Fig. 4. The exact angle depends mainly on the position of the pectoral girdle on the ribcage, and how the height of the tarsus, carpus and manus are reconstructed.

If all body parts that were treated separately above are combined into a full digital skeletal mount, it becomes apparent that a sub-horizontal position of the sacrum and ONP of the vertebral column combined forces an extreme sprawl in the forelimbs (Fig. 8a). The extreme ventral curvature of the dorsal series places the elbow and shoulder joints at or slightly above the same level as the tibia midshaft. A posture with erect forelimbs, combined with a modest extension of the dorsal series of 2° per intervertebral joint, requires a rotation of the sacrum of only 5° (Fig. 8b). In this position the tail tip stays well clear of the ground, if the tail is kept in ONP. In Fig. 8b it is shown with the first five articulations extended by 1° each, to create a horizontal position.

Which of the two (or any intermediate) positions is correct cannot be determined, and a detailed discussion of the importance of ONP in the trunk for reconstructing the habitual posture of an extinct animal is beyond the scope of this work.

Range of motion

Neck

The range of motion of the neck is difficult to determine, because the vertebrae were found as isolated bones, and do not belong to one individual. Many intervertebral articulations are thus between elements of slightly different size and ontogenetic age, which creates problems such as broader prezygapophyses than postzygapophyses, so that the limit on lateral flexion cannot accurately be determined. A cautious limit on lateral flexion, requiring significant zygapophysal overlap of at least 50% where this is possible, allows roughly a 110° curve over the entire length of the neck (Fig. 2a). The anterior part of the neck is extremely mobile laterally, with almost horizontal zygapophyses, while the base and especially the middle section are stiffer, the latter a common characteristic of extant animals (Taylor et al. 2009). Maximum lateral flexion as cautiously reconstructed here displaces the orbitae 0.4 m laterally of the body midline (Fig. 2a). A more generous interpretation of motion limits allows the animal to touch the sides of the anterior body with the snout, a motion well possible for practically any extant mammal with a long neck.

Trunk

As mentioned above, the keystoning in some dorsals is so strongly developed that ONP cannot be achieved. Flexion sufficient to bring the neighbouring faces of the centra into parallel position often leads to overlap of the distal ends of the ribs, as already noted by Janensch (1925). Extension limits are difficult to determine, and depend on the

reconstructed thickness of the intervertebral discs. Probably, lateral motions, flexion, and extension were limited by soft tissues, as in humans (Kummer 2005). It seems plausible that the dorsal vertebral column could at least be extended to a fully straight position.

Kentrosaurus lacks special osteological stops blocking lateral flexion in the dorsals, such as the sauropod hyposphene–hypantrum complex (Apesteguia 2005), so that lateral mobility was probably blocked by soft tissues and the ribs. However, since the latter can overlap in many extant animals with non-rigid trunks, the exact motion range cannot be determined. Here, a conservative motion of maximally 45° along the entire trunk is assumed to be possible. The vertebrae alone would allow nearly 120°.

Tail

The zygapophysal articulation surfaces in the tail are medially inclined, with digitally measured angles varying between 40° and 56° in the anterior caudals. Further posteriorly, the angle decreases slightly, to an average of 42°. However, many zygapophyses are either obviously deformed or damaged, so that it is not possible to determine whether there is a distinct point where the angle changes, or whether there is a gradual reduction. Angles around 45° are also seen in crocodiles (in *Crocodylus porosus* IPFUB OS 13, however, the zygapophyses of the first few caudals are less steeply angled), as well as Komodo dragons (*Varanus komodensis*, C. Mehling and J. Conrad, 2009, pers. comm.). Within Dinosauria, the angles vary both between taxa and even individuals of the same taxon (e.g., *Plateosaurus*, Mallison 2010c; Huene 1926; Galton 1986, 1990).

The maximum angle for lateral flexion in *Kentrosaurus*, determined by digitally articulating the bones, with such steeply inclined zygapophyses likely is around 5°–15° per intervertebral joint, comparable to that in crocodiles (excluding the base of the tail, which has differently oriented zygapophyses in crocodiles) and Komodo dragons. Notably, the supposedly stiff tails of dromaeosaurids with their long bundles of ossified tendons apparently had similar mobility as that assumed here for the less limited tail of *Kentrosaurus*. Norell and Makovicky (1999, fig. 21) figure an S-curved, articulated tail of *Velociraptor mongoliensis* in dorsal view. Tracing the path of the tail axis of the *Velociraptor* specimen in Rhinoceros 4.0® allows measuring the angle across the first bend as 98° for the first ten caudals, which translates to nearly 10° per intervertebral joint. Apparently, it requires extremely elongate zygapophyses and chevrons running down the entire length of the tail as in *Deinonychus antirrhopus* OSTROM 1969 to stiffen a tail (Ostrom 1969). Even a complex latticework pattern of ossified tendons as seen in hadrosaurs and other ornithischians at best had a minor influence on lateral mobility (Organ 2006). For *Kentrosaurus*, mobility in vivo can thus be assumed to be similar to the extant taxa. In them, in vivo lateral motion is stopped by soft tissues, and thus smaller than articulation of the bones alone indicates. Crocodiles and *Varanus komodoensis* are capable of a greater than 180° curve over the length of the entire tail (pers. obs.), which corresponds to angles of slightly less than 11° per joint. Figure 6b shows the tail of *Kentrosaurus* in dorsal view, with copies flexed 2.5°, 5° and 6°. Figure 9a, b shows a detail from the medial tail [caudals 9 through 19, not counting the (missing) caudosacral], where the best-preserved sequence of caudals can be found, at 5° and 10° flexion. The distance between the body midline and the tip of the tail is 150.8 cm for 5° flexion. Ten degree flexion of only the anterior two-thirds of the tail already leads to the tips of the final spikes overlapping the trunk (Fig. 10a). A 180° curve of the entire tail is possible with a flexion value of less than 6° per joint. Note that in this example the first (missing) caudal is assumed to be immobile, because its transverse processes appear to have touched the ilia in life, and it has co-ossified with the sacrum as a caudosacral in other sacra of *Kentrosaurus* (Hennig 1925). Flexion between it and the sacrum would increase the angles given above. Swinging from side to side, the tail can therefore cover a sufficient arc to act as a defensive measure.

Ankylosaurs had laterally much stiffer tails than *Kentrosaurus*, able to move through an overall angle of only 90° (Arbour 2009), and ankylosaurs show large variations in the angles of the zygapophyses between different tail segments (Christiansen 1996). In *Stegosaurus*, the plates on the tail may have parted it into a set of stiff rods (Carpenter et al. 2005), greatly reducing the overall mobility. In contrast, the flexed *Kentrosaurus* tail forms a smooth, continuous curve in dorsal view, and its motion covered a much greater area.

In the vertical plane, tail motion is strictly limited. The anticlinality of the neural spines limits extension to probably about 5° per intercaudal joint for the entire tail, barely leaving room for the interspinal soft tissues. In this context it is important to note that Hennig (1913, 1925) described the position of two well-preserved articulated tails in the field as "roughly semicircular". If this position corresponds to opisthotonic posture, which is highly likely for a well-articulated and continuously curving specimen, this position would indicate the maximum in vivo extension (Faux and Padian 2007). A semicircular position can be achieved by extension of 5° per intervertebrate joint (Fig. 10c). However, even the much lower value of 2.5° extension per joint along the anterior half of the tail lifts the tail spikes by ~1 m (Fig. 10b; the exact value depends on the orientation of the sacrum). Tail flexion is similarly

limited, with the haeampophyses blocking motion at $\sim 4°$ per joint. This motion range is sufficient to allow the tail tip to touch the ground if the sacrum is held roughly horizontally. Torsion appears possible to a minimal degree, by compression of the cartilage in the zygapophysal articulations. The exact amount possible depends on the elastic properties of the soft tissues, and cannot be determined.

Forelimb

Pectoral girdle

For the range of motion assessment it is assumed that there is no scapular mobility, i.e., the glenoid remains in a fixed position relative to the trunk. This is an arbitrary decision, and the lack of clavicles as well as ossified sternals in *Kentrosaurus* may be related to scapular motion. However, if motion was possible, it is impossible to determine its amount and direction, making any discussion moot.

The placement of the pectoral girdle on the ribcage is here chosen as described above, which results in a 45° angle between the transverse axis of the glenoid and the body's sagittal plane in dorsal view, i.e. protraction of the humerus results in an anteromedial motion of its distal end. A somewhat different position may also be possible, with the angle varying by $\pm 10°$. The angle of the scapular blade in lateral view can also be varied, which has implications for the limb motion range, but its curvature allows only a narrow range of position variations (Fig. 3a, b).

Shoulder

The humerus has a motion range that is unusually large for a non-avian dinosaur, but it must be kept in mind that previous studies (Carpenter and Smith 2001; Gishlick 2001; Carpenter 2002; Senter and Parrish 2005; Senter and Robins 2005; Senter 2006a, b) are mostly limited to theropods. Especially noteworthy are the high degree of abduction possible (Fig. 7d), and the difference between the abduction angles possible in protracted and retracted position, $\sim 45°$ and $\sim 90°$, respectively. The angle between the fully extended and flexed positions is $\sim 100°$ (Fig. 7c). The steep scapula position assumed here means that protraction to the vertical is barely possible. Retraction allows elevating the elbow to slightly above the level of the glenoid, both in parasagittal and abducted positions (Fig. 7c, d). Adduction is possible to $\sim 50°$ (Fig. 7d). Using the scapula position suggested here the manus can easily cross the body midline. However, in any pose with a far dorsally placed scapula strong adduction would likely lead to collision with the ribcage.

Elbow

The radius is anteriorly positioned in relation to the ulna at the proximal end, similar to the condition in advanced sauropods (Bonnan 2003; Upchurch et al. 2004) and *Triceratops* (Fujiwara 2009). However, the ulna does not form a V-shape in proximal view, but rather an L, so that the radius is not as tightly constrained as in sauropods (Bonnan 2003; Upchurch et al. 2004). Radius and ulna together form a well-defined and deep trough for articulation with the humerus, allowing extension to almost straight (10°) and flexion to at least 120° (Fig. 7).

The radius' proximally anterior, not lateral, position results in permanent pronation of the manus, as in sauropods and ceratopsians (Bonnan 2003; Fujiwara 2009). However, the medial axis of the hand probably was not directed fully forward, but angled between 20° and 30° laterally. Supination by radius rotation appears to have been impossible, because of the high-oval shape of the proximal radius end, which blocks longitudinal rotation. Only minimal sliding motion appears to have been possible at the distal end of the zeugopodium.

Wrist and digits

An assessment of the motion range in the wrist and manus is difficult, due to the lack of good material. Based on the figures in Hennig (1925) and Janensch (1925) and the few remaining elements still in the MFN collection, the manus appears to have shown the typical compact constitution of all stegosaurs, with a very short metacarpus and broad, short digits. Because of this similarity to *Stegosaurus* (Hennig 1925), the analysis of manus articulation and posture of *Stegosaurus* by Senter (2010) is probably the best guide for interpretation. As pointed out by Senter (2010), the figures of the lost or destroyed metacarpals in Hennig (1925) indicate a semi-circular arrangement of the metacarpus. A single preserved metacarpal in the MFN collection (MFN unnumbered) is highly similar to the figures in Hennig (1925), confirming their accuracy. Such a manus configuration requires significant wrist flexion during the swing phase of the limb.

Hindlimb

Hip

Protraction of the femur appears to have been possible to roughly 70° from vertical (Fig. 11b), an angle that certainly was not exploited during locomotion, but rather relates to resting positions. Retraction to the level of the ischia, the likely limit, requires 34° from vertical if the sacrum is held horizontal (Fig. 11b). Adduction by 10° is sufficient to

bring the foot under the body midline, and is easily possible. Adduction by 4° barely allows the protraction of the swing limb without abduction to avoid a collision with the supporting limb, resulting in a minimal track width of roughly 0.4 m. Larger adduction angles require the swing limb to be abducted during protraction. Abduction is limited by the ilia, but possible to 20° with the femur vertical to protracted, so that the distal ends of the femur cleared the body when the animal lied down. Inversion and eversion cannot be judged.

Knee

The knee can be fully straightened (Fig. 8), and flexed strongly to at least 60° (Fig. 11b). It appears to be a simple hinge joint, in which slight sliding and inversion/eversion motions may have played a minor role.

Ankle

The sole lower limb and foot preserved in near-articulation (MB.R.2951.1-11, Hennig 1925, fig. 49) show that the distal carpals were either absent or reduced to flat discs. The astragalus and calcaneum co-ossified with the tibia and fibula in adult individuals (Hennig 1915, 1925). The metatarsus was likely held steeply, and the ankle was probably a simple hinge joint. While the exact arrangement and habitual posture of the metatarsus in the ankle, and thus the limits of extension and flexion, are unclear, the distal surface of the astragalus allows for at least 90° of motion, with the half-angle pointing slightly anteriorly of ventral. However, the complete lack of distal tarsals makes a detailed analysis of ankle function and motion range speculative.

Discussion

Posture and locomotion

The range of motion of the forelimb includes the classical, sprawling position seen in the old MFN and current IFGT mounts as well as an upright, parasagittal position as suggested for other stegosaurs by, e.g., Bakker (1986). Therefore, the positions used in life can only be determined through indirect evidence.

The humeri of *Kentrosaurus* bear superficial resemblance to those of some Paleozoic amphibians and some large reptiles with sprawling gaits, such as *Bradysaurus baini* Seeley 1892 (MB.I.026.21). Also, it is highly similar to those of dinosaurs classically reconstructed with sprawling forelimbs (ankylosaurs and ceratopsians). This is seen by some as an indication that *Kentrosaurus*

permanently used a sprawling forelimb posture (e.g., D. Henderson 2009, pers. comm.). However, there are significant morphological differences to animals with a sprawling gait, who are usually unable to bring the forelimb into a fully parasagittal position. For example, in *Bradysaurus* the glenoid is curved, facing mainly laterally and partly ventrally. In contrast, the glenoid in *Kentrosaurus* is a simple trough, opening ventrally and only minimally laterally, and allows adduction of the humerus well across the body midline (Fig. 7d). A laterally directed glenoid (as in birds) cannot be created when articulating the pectoral girdle of *Kentrosaurus*, because the anterior dorsal ribs have nearly straight shafts (Fig. 2b), so that even a massive dorsal displacement of the scapulae still results in a glenoid directed mainly ventrally, and only minimally laterally. The likely angle between the rib shafts and the vertical is only 20°, and the glenoid surface is angled roughly 10° outwards compared to the medial surface of the scapulacoracoid. The main compressive force in the glenoid therefore acted at most at a 30° angle to the vertical.

Ceratopsians did not have sprawling forelimbs (Fujiwara et al. 2009). The sprawling ankylosaur reconstructions simply follow the same argument as the sprawling stegosaur reconstructions. It is implicitly assumed that the largest forces, which cause the shape of the bone, are present in locomotion. However, like stegosaurs (Carpenter et al. 2005), ankylosaurs show tail adaptations that indicate the use of the tail as a weapon at least in adults (e.g., Arbour 2009), so that the largest forces may have acted during defence behaviour, not locomotion. If said behaviour occurred in a sprawled pose, it is to be expected that the humerus is superficially similar to those of animals in which locomotion in a sprawling pose creates the largest stresses. It should also be noted that the prosauropod *Plateosaurus* has a similarly shaped glenoid (Huene 1926; Mallison 2010b, c), as incidentally do all sauropods (Remes 2008), basal Ornitopoda (Norman et al. 2004) and hadrosaurs (Horner et al. 2004), and that some of these also have humeri with expanded proximal and ends (albeit to a lesser degree than stegosaurs, which themselves have humeri with less expanded ends than typical sprawlers). Still, the proponents of a sprawling posture for ceratopsians and stegosaurs do not suggest a sprawling pose for prosauropods, sauropods or hadrosaurs.

Aside from the fact that the anatomy of the glenoid does not indicate a sprawling posture for *Kentrosaurus*, there is further evidence for an erect posture. The abducted, flexed forelimb position of, e.g., the IFGT and MFN mounts results in a limb length ratio of around 0.3 (i.e., the effective hind limb length is more than three times that of the forelimb). Note that due to the lack of manus and pes elements limb length is here measured in lateral view as the

distance of the geometric centre of the glenoid/acetabulum from the distal end of the ulna/tibia. For a quadruped, a ratio of 0.3 is unrealistically low, and similarly low rations are not seen in other quadrupedal dinosaurs, suggesting extremely limited locomotory capabilities for a sprawling *Kentrosaurus*. In fact, the limb length ratio is even lower than that of *Plateosaurus*, an animal that could not practically walk quadrupedally even if it had been capable of manus pronation (Mallison 2010b, d).

There is no apparent advantage in a sprawling position for use in locomotion, nor is the posture seen in the direct ancestors of stegosaurs. It creates high torque requirements in the shoulder and elbow, and is in extant animals not seen in endurance locomotion, for which the erect hind limb posture is suited. Additionally, protraction of the limb is limited (Fig. 7b, c), further decreasing stride length. Abduction of the humerus at moderate to large extension angles requires strong inversion, so that the dorsal side of the humerus faces dorsally, as in reptiles with sprawling gaits. For full flexion, however, inversion is not possible, so that the zeugopodium cannot point ventrally. Even using strong undulation of the anterior body only much shorter strides can be achieved than in the hind limb. Therefore, locomotion in a sprawling pose is severely limited.

In contrast, an erect forelimb pose results in a more favourable effective limb length ratio of 0.57. This ratio is similar to that of some probably quadrupedal prosauropods (*Riojasaurus*, Bonaparte 1971) and sauropods such as *Diplodocus* (McIntosh 1990; Upchurch et al. 2004), and thus well within the normal range for quadrupedal locomotion in dinosaurs. A (near-) parasagittal forelimb posture is ancestral, and requires lower limb torques then a sprawling pose. It also creates a larger vertical distance between the base of the neck and the ground, which increases the maximum possible feeding height in a quadrupedal pose and allows better circumferential visibility. The slight lateral inclination of the glenoid may indicate that the posture was not fully erect (90°), but that the humerus was outwardly canted by a small angle (up to 30°). However, the direction of largest force in the glenoid, which defined the articulation surface direction, needs not necessarily stem from locomotion, so that the outward angle may relate to other behaviour, such as defence.

The erect forelimb posture is also conformal to the ichnofossil evidence. Trackways attributed to stegosaurs with manus and pes tracks are rare. Both *Stegopodus czerkasi* LOCKLEY AND HUNT 1998 and *Deltapodus brodricki* WHYTE AND ROMANO 1994, the latter originally thought to be a sauropod track (Whyte and Romano 1994) but later recognized as a stegosaurian track (Whyte and Romano 2001), show a slightly wider manus than the pes trackway width. This is also true for an American specimen assigned to *Deltapodus* by Milàn and Chiappe (2009). Taking into account that the hindlimb, supporting most of the weight, was probably slightly adducted at midstance during locomotion, the track width ratio between fore- and hind limbs determined here for erect limbs is at or slightly above 1:1, as seen in fossil trackways. A sprawling forelimb pose would create a track in which the manus would be placed far further form the track midline than in any ichnofossil ascribed to a stegosaur.

The ratio of femur to tibia length of *Kentrosaurus* is unusual compared to the majority of large terrestrial animals. Typically for stegosaurs and other armoured and slow-moving animals such as ankylosaurs and gylptodonts (Gillette and Ray 1981; Vickaryous et al. 2004), the femur is much longer than the tibia, and even longer than tibia and metatarsus combined. In the case of the MFN mount, the femora are roughly 1.5 times as long as the tibia (Figs. 1, 8, 11), although it must be kept in mind that on both sides femur and tibia do not stem from the same individual. Even if the real ratio was slightly lower, in combination with the short metatarsus known from an articulated lower hind limb (MB.R.2951.1-11) limb protraction in rapid gaits is severely hindered. However, in a trot or even gallop, the femur would have to be protracted to extreme angles at the end of the swing phase in order to allow the forward-swinging heel to clear the ground just before the initial contact of the foot with the ground. Low limits of femur protraction and retraction during locomotion indicate that *Kentrosaurus* was not capable of using rapid (running) gaits, and thus incapable of outrunning fast predators.

Agonistic and antagonistic behaviour

The morphology of the forelimb, with the massive humerus, the large olecranon process of the ulna, and the ability to abduct the limb to more than horizontal suggests that an activity was regularly performed that caused large lateral forces on the anterior body. Because there are good indications that the tails of many extant archosaurs are used in defence, as there is fossil evidence that the tail of probably *Stegosaurus* was used for clubbing predators (Carpenter et al. 2005), it is likely that *Kentrosaurus* also defended itself by swinging its tail, attempting to strike approaching predators, and so created large lateral forces on the anterior body. The tail itself clearly had sufficient mobility to be used as a weapon. The dorsoventral mobility of the tail, combined with the variability of the hip orientation would have allowed *Kentrosaurus* to strike targets between the ground and up to heights of 3 m with ease. Therefore, even the torso or heads of very large theropods were in danger of injury. A sprawling position of the forelimbs appears to offer advantages for such a mode of defence. It broadens the support base significantly,

increasing stability. Also, it allows lateral motions of the anterior body induced by transfer of rotational inertia from tail swings to be countered by elbow extension instead of humeral abduction. While the latter action was performed by powerful muscles in *Kentrosaurus*, the elbow extension was additionally aided by the exceptionally large moment arm caused by the high and massive olecranon process (Fig. 3c, d). For desired lateral motions, e.g., pivoting the entire animal rapidly, a broader base and inclusion of the elbow-extending musculature (mainly m. triceps brachii) is also advantageous, in combination with the lower position of the anterior body, which leads to a reduced moment arm between the centre of mass and the forefeet's contact point with the ground. A potentially important disadvantage of a sprawling posture is the lower point of view, because it creates large dead areas, as the skull cannot be brought into a sufficiently high position to give clear sight over the body.

Blindly waving the tail may have been a good strategy to reduce a predator's chances for a successful attack, but aimed strikes with a tail require the ability to "check six" (look backwards), or some other method for tracking a target. The lateral mobility of the neck of *Kentrosaurus* was at least sufficient to allow such active defence measures, as the skull could be positioned with the orbitae significantly laterally displaced from the body midline and an eye pointing backward (Fig. 2a). However, this means that the entire other side is blocked from view by the animal's body, creating a high risk of being blindsided in a coordinated attack by several predators. Keeping a circling predator continuously in sight when using a sprawling forelimb pose also required *Kentrosaurus* to perform rapid neck motions during which the animal lost sight of the attacker.

Alternatively, full extension of the neck (Fig. 8c) in a sprawling pose allows good sight on both sides of the body, but leaves a large blind area posteriorly, if the forelimbs are placed sprawling (Fig. 8a). Combined with an erect forelimb posture, full extension of the neck lifts the orbitae above the level of the back and tail (Fig. 8b). This allows unobstructed sight posteriorly without lateral bending of the body, so that the neck does not have to be moved. In the close relative *Stegosaurus*, a dense pattern of ossicles has been found covering the throat (Marsh 1881; Carpenter 1998), which indicates that this areas required special protection. An extended neck pose combined with erect forelimbs, while allowing 360° circumferential view, potentially exposed the throat to attacks, from a direction (frontal) that was furthest from the protection by the tail tip. Given the fact that the throat was barely exposed when the neck was held level, the special throat armour may indicate that strong neck extension was a regularly employed strategy during antagonistic behaviour.

Tail swinging may also have played a role in intraspecific fighting, although this most likely took the form of mock combat, or involved only slow tail swings, due to the high risk of serious injury of full power tail spike hit (Carpenter et al. 2005). Certainly, waving the tail was an impressive display.

A further discussion of defence behaviour requires a detailed kinetic/dynamic analysis, and is thus beyond the scope of this study.

Feeding height

In a quadrupedal stance, *Kentrosaurus* could easily feed at ground level (even with erect forelimbs), and up to a height of ~ 1.7 m (Fig. 8a, b). A bipedal pose is easily possible given the motion limits of the skeleton. It requires that the centre of mass is located directly above the support point, i.e., the hind feet. *Kentrosaurus* had a long and muscular tail, short forelimbs, a relatively short neck and a proportionally small anterior body. Thus, the centre of mass probably rested much closer to the hindlimbs than the forelimbs. Henderson (1999) calculated a very posterior center of mass position for *Stegosaurus*, using 3-D mathematical slicing, interestingly on the basis of a drawing in Paul (1987) that shows fully erect forelimbs. Due to the long femora, even modest protraction angles of $\sim 35°$–$40°$ produce a 0.30–0.35 m offset between the acetabulum and the pes, which is easily sufficient to bring the entire body weight over the pedes. How steeply the body could be rotated upwards depends on the possible extension of the tail. Assuming that inter-caudal articulations could at most extend 5° the high number of elements still allows a sufficient curvature for the tail to rest on or be fully lifted off the ground at hip rotation angles of $\sim 60°$ (Fig. 11a). Indeed it seems questionable whether stegosaur tails provided support as a 'third leg' as suggested, e.g., by Bakker 1986). If the body is rotated by less than 45°, only the distal end of the tail can touch the ground.

Rearing as suggested in Fig. 11a, with a slightly extended trunk, increases the maximum potential feeding height from approximately 1 m (sprawling forelimb and ONP posture) to 3.3 m. Compared to a quadrupedal pose with full extension of the neck and erect forelimbs rearing results roughly in a doubling of the maximum potential feeding height. This is a significant shift, because entirely different plant types may have been available as fodder, mainly young trees and high bushes, compared to herbaceous and low, shrubby plants.

In this context it is interesting to note that most stegosaurs have very similar body proportions to *Kentrosaurus* (Galton and Upchurch 2004), while only *Miragaia longicollum* from the Late Jurassic has significantly longer forelimbs and an extremely long neck (Mateus et al. 2009).

Both factors shift the centre of mass forward, decreasing rearing ability, but increasing feeding height without rearing. Probably, if stegosaurs used a tripodal pose for feeding, *Miragaia* did so less frequently than other stegosaurs.

Conclusions

In summary, digital articulation and manipulation of the digital scans of the best available material of *Kentrosaurus aethiopicus* shows that, from an osteological point of view,

– Both a sprawling and an erect forelimb posture were possible for standing, locomotion and defence.
– Limb proportions and the anteroposterior motion ranges of femur and humerus made gaits with unsupported phases impossible.
– The tail had sufficient lateral and dorsoventral mobility to be used as a clubbing device.
– A sprawling forelimb posture was advantageous for tolerating the large laterally directed forces that tail swinging may have placed on the anterior body, because it created a wider and thus more stable base, and allowed the use of the strong elbow-extending musculature in addition to the pectoral musculature.
– The neck had sufficient lateral flexibility to allow the animal to look backwards, and sufficient dorsal mobility to allow elevation of the skull above the level of the back.
– The trackway width for a sprawling forelimb posture does not agree with the ichnological record, and is roughly double that of the hind limbs.
– An erect forelimb posture leads to an only slightly wider trackway than in the posterior extremities, conformal with trackways assigned to stegosaurs.
– Hip and tail had sufficient mobility to allow the adoption of a tripodal pose.

Based on these results, it can be inferred that *Kentrosaurus* likely used an erect forelimb posture for locomotion, but a sprawled pose for defensive behaviour. The latter may have included extreme neck extension or lateral flexion to gain sight of enemies, and tail strikes at targets may thus have been aimed. *Kentrosaurus* may have used a tripodal pose for feeding at roughly double the height possible in a quadrupedal position. Future biomechanical studies of *Kentrosaurus* are needed to gain detailed insight into the kinematics and dynamics of both locomotion and defence behaviour.

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