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The postcranial Anatomy of Stegosaurian Dinosaur *Kentrosaurus* from the Upper Jurassic of Tanzania, East Africa

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with 2 Text-figures and 6 Plates

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The bones of the postcranial skeleton of *Kentrosaurus aethiopicus* HENNIG 1915 are illustrated with descriptions of the sacrum, ilium and dermal armor. The differences in the form of the bones of subadult and adult individuals are listed as growth differences, most of which probably occurred in all stegosaurs. The sacra have either four or five pairs of sacral ribs and the latter probably came from female individuals. The same sexual dimorphism of the sacrum is probably also present in *Dacentrurus armatus* and *Stegosaurus stenops*, the only other stegosaurian taxa represented by adequate sacral material. *Lexovisaurus* HOFFSTETTER 1957 from the Middle Jurassic of western Europe is a valid genus of stegosaur that is distinct from both *Kentrosaurus* and *Stegosaurus*.

Die postcranialen Skelettelemente von *Kentrosaurus aethiopicus* HENNIG 1915 werden abgebildet, Sacrum, Ilium und Dermalpanzer näher beschrieben. Unterschiedliche Knochenform bei halbwüchsigen und erwachsenen Individuen werden Wachstumsunterschieden zugeschrieben, deren Mehrzahl wohl bei allen Stegosauriern vorkommt. Die Sacra enthalten 4 oder - wohl bei weiblichen Tieren - 5 Rippenpaare. Dieser Sexualdimorphismus tritt wohl auch bei *Dacentrurus armatus* und *Stegosaurus stenops*, den einzigen Stegosauriern, von denen entsprechendes Material vorliegt, auf. *Lexovisaurus* HOFFSTETTER 1957 aus dem westeuropäischen Mitteljura ist ein valides Genus und von *Kentrosaurus* und *Stegosaurus* unterscheidbar.

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Introduction

HENNIG (1915) described representative material of the new stegosaur or plated dinosaur *Kentrosaurus aethiopicus* from the Tendaguru Beds (Upper Jurassic, Upper Kimmeridgian - Tithonian, AITKEN 1961) of Kindope, 3 km North-west of Tendaguru in what is now Tanzania, East Africa. HENNIG (1916a, July) provided additional details and, because *Kentrosaurus* was preoccupied by *Centrosaurus* LAMBE (1904), the new genus *Kentrurosaurus* was erected. NOPSCHA (1916, November) erected *Doryphorosaurus* to replace *Kentrosaurus* but HENNIG (1916b) pointed out that *Kentrurosaurus* HENNIG 1916a had priority. *Kentruro-*

saurus was the generic name used in the description of the complete skeleton and of a dentary by HENNIG (1925, 1936) and in the description of the mounted skeleton and of dorsal vertebrae by JANENSCH (1925, 1927). However, *Kentrosaurus* is a valid generic name because two generic names cannot be considered homonyms even if it is only one letter that is different (International Code of Zoological Nomenclature 1961 Article 56a). *Kentrosaurus* is used by ROMER (1966) and STEEL (1969) in recent reviews of stegosaurs. A review of the paleoecology of the dinosaurs of the Tendaguru is given by RUSSELL et al. (1980).

HENNIG (1915, 1925) listed extensive material of *Kentrosaurus* in the Humboldt Museum für Naturkunde in Berlin. However, most of this material is no longer available so it has either been mislaid or it was destroyed during World War II as was the case for much of the material of the Tendaguru ornithopod *Dryosaurus* (see JANENSCH 1955). No parts of the skull described by HENNIG (1915, 1925, 1936) are in the available material that includes most of the other syntypic specimens described by HENNIG (1915) plus six sacra, a suite of femora and two mounted skeletons, one of an adult (Pl. 1, Fig. 2; JANENSCH 1925) and the other of a subadult individual (Pl. 1, Fig. 1). The purpose of this paper is to provide a well illustrated supplement to the detailed description of *Kentrosaurus* given by HENNIG (1925). When references are made to figures in HENNIG (1925) I include an indication of the magnification (e. g. x 0.2) because this is not given and there are no scale lines shown. The names of institutions with cited specimens have been abbreviated as follows: BMNH, British Museum (Natural History), London; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; CUSM, Cambridge University, Sedg-

wick Museum, Cambridge, England; DNM, Dinosaur National Monument, Vernal, Utah, U.S.A.; HMN, Humboldt Museum für Naturkunde, East Berlin; MGSP, Museum of the Geological Survey of Portugal, Lisbon; MHNN, Musée d'Histoire Naturelle de Normandie at Friadel near Orbec, Normandy, France; MNHN, Muséum National d'Histoire Naturelle, Paris; UT, Universität in Tübingen, Institut und Museum für Geologie und Palaeontologie; USNM, United States National Museum, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

Systematics

Kentrosaurus HENNIG, 1915

Kentrosaurus HENNIG 1915:219-247

Kentrosaurus HENNIG 1916:175-182

Doryphorosaurus NOPS 1916:511-512

Type and only species: *Kentrosaurus aethiopicus* HENNIG.

Diagnosis: same as for only species, see below.

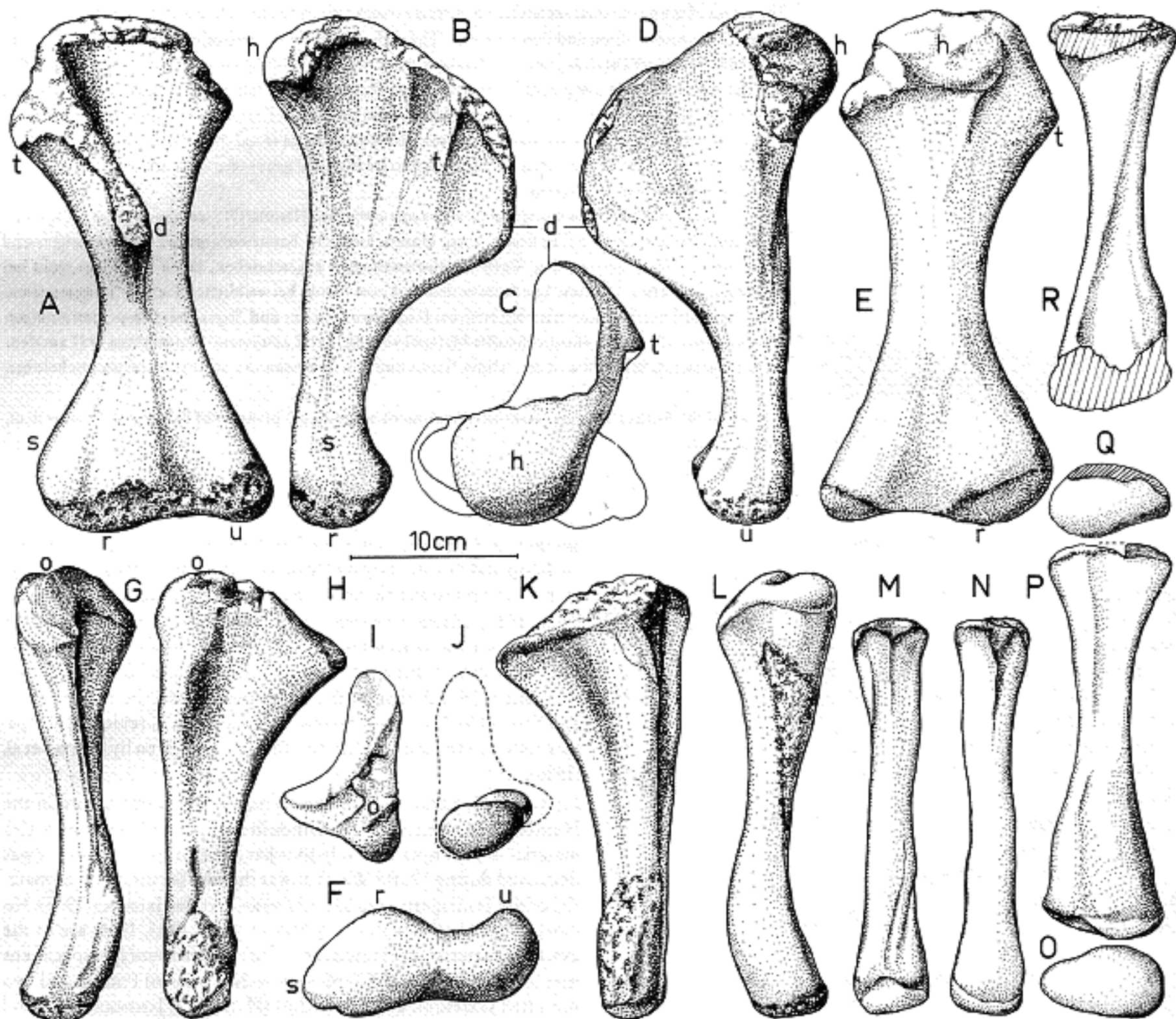
Distribution: Upper Jurassic of Tanzania, East Africa.

Kentrosaurus aethiopicus HENNIG, 1915

Text-figs. 1, 2, Pl. 1-6

Holotype: two associated middorsal vertebrae (HMN St694, 695) (designated for first time).

Syntypes: anterior caudal vertebra (HMN St856), left humerus (HMN St106), left ulna (HMN St461), right radius (HMN St77), right pubis (HMN St758), right ischium (HMN St335), left femur (HMN St463), left tibia (HMN St152), right fibula (HMN St297), eighth right flat spine (HMN St90), right parasacral spine HMN St345; the following syntypes figured by HENNIG (1915) could not be located and may have been destroyed in World War II - braincase (HMN St460), and terminal long spine (HMN St575).



Text-Fig. 1: *Kentrosaurus aethiopicus* from Upper Jurassic of Tanzania, East Africa, bones of fore limb X 0.25. The views are given for the pose as shown in the mounted skeletons (Pl. 1, Figs. 1, 2; Pl. 5, Figs. 13, 14) and the equivalent views for the fore limb of ornithomimid dinosaurs in which the humerus was held vertically are given in parenthesis. A-F, right humerus UT 1524/1 (was St129, see also Pl. 4, Figs. 1-3) in A - medial (or anterior) view; B - anterior (or lateral) view; C - proximal view; D - posterior (or medial) view; E - dorsal (or posterior) view; F - distal view; G-L - left

ulna UT 1524/2 (was St113) in G - medial (or dorsal) view; H - posterior (or medial) view; I - proximal view; J - distal view; K - anterior (or lateral) view; L - lateral (or ventral) view; M-R - left radius UT 1524/3 (was St515) in M - anterior (or lateral) view; N - posterior (or medial) view; O - distal view; P - posterior (medial) view (see also Pl. 6, Fig. 18); Q - proximal view; R - anterior (or lateral) view. Abbreviations: d = deltopectoral crest; h = head; o = olecranon process; r = radial condyle; s = supinator ridge; t = triceps ridge; u = ulnar condyle.

Type horizon and Locality: Middle Saurian Bed of the Tendaguru Beds (Upper Jurassic, Upper Kimmeridgian – Tithonian) of excavation St, Kindope, 3 km North-west of Tendaguru, Tanzania, East Africa.

Distribution: Middle and Upper Saurian Beds of Tendaguru Beds of Tendaguru region, Tanzania.

Diagnosis: Medium sized stegosaur with a total body length up to about 4.7 m. Neural canal of dorsal vertebrae large with tall side walls. Marked anticlivity of the neural spines of the caudal vertebrae of the posterior three quarters of the tail. Transverse processes extend as far as caudal vertebra 28 and those of anterior caudal vertebrae are rod-shaped with shallow bases. Hemal arches plough – share – shaped (L). Anterior angle between blade and the rest of the scapula is more than 90°. Ratio of lengths of humerus and femur 1.60–1.68. Anterior process of ilium widens anteriorly and is very deep, length of ilium equal to or longer than that of femur. Fourth trochanter present on larger femora. For metatarsal III the ratio of maximum height to maximum length is less than 1.5. The neck and anterior half of back carry six pairs of vertically standing plates, the sixth as a spine-plate with a remnant of the spine visible plus the diagonally inclined large base that projects vertically from the lateral surface of the plate. Rest of back carries three pairs of flat spines and tail carried five pairs of large spines. A large parasacral spine (borne above each ilium) has a lateral spine with a medially enlarged basal plate, the outline of which is sub-circular.

Description

Vertebral column

The cervical, dorsal and caudal vertebrae are well described by HENNIG (1925, Figs. 8–22, 26, Pl. 14, all about X 0.5) and most of the available vertebrae are inaccessible, being incorporated into the two mounted skeletons (Pl. 1, Figs. 1, 2). The exceptions are three vertebrae included in the syntype, a pair of middorsal vertebrae (Pl. 3, Figs. 11–16) designated as the holotype and an anterior caudal vertebrae (Pl. 3, Figs. 7–10).

Sacrum. The sacrum (HMN St439) illustrated by HENNIG (1925, Fig. 23, X 0.18) is now part of the mounted skeleton (JANENSCH 1925) but six of the other described sacra are still available (Pl. 2; Pl. 3, Figs. 1–6). The fusion of the transverse processes and the dorsal parts of the sacral ribs forms an almost completely solid dorsal sacral plate (Pl. 2, Fig. 2). The ribs also fuse laterally to form a solid sutural surface (Pl. 3, Fig. 1) against which the ilium fitted (Pl. 2, Figs. 2, 3, 5). HENNIG (1925) noted that the sacral plate had never been figured or mentioned for *Stegosaurus* and this is still the case but a complete sacrum that is exposed in dorsal view (DNM 0402) shows a sacral plate comparable to that of *Kentrosaurus*. A large sacral plate is also present in the stegosaurs *Lexovisaurus* (BMNH R1889), *Dacentrurus* (NORCSA 1911b; MGSP) and *Wuerhosaurus* (DONG 1973). Lateral views of sacra with different degrees of breakage (Pl. 3, Figs. 1, 2, 4, 5) supplement the ventral views (Pl. 2, Figs. 3, 8, 9; Pl. 3, Fig. 6) in providing information on the form of the sacral ribs.

The sacrum illustrated by HENNIG (1925, Fig. 23b) is similar to that of HMN St218 (Pl. 2, Fig. 9) in consisting of six fused centra. The first vertebra is a dorsosacral because it does not take any part in the formation of the sacral plate. The transverse process of the second vertebra forms the anterior margin of the sacral plate (see Pl. 2, Figs. 1–3, 6) so this modified dorsosacral is designated as the first sacral vertebra. Sacral vertebrae 2 to 5 bear four pairs of sacral ribs with vertebrae 2 to 4 as the true sacrum and vertebra 5 as a modified caudosacral, the neural spine of which is free and not fused to that of the fourth sacral vertebra (Pl. 2, Fig. 5, Pl. 3, Figs. 1, 2, 4, 5). The form of the sacrum of HMN St555 was similar to that of HMN St218 and the dorsally situated broken base of the transverse process of the first sacral vertebra is visible (Pl. 3, Fig. 5). However, in HMN St557 a slender sheet of bone forms a sacral rib that connects the first sacral vertebra to the anterior end of the sutural surface that was adjacent to the

acetabular part of the ilium (Pl. 2, Fig. 11). The broken base of this rib and of the transverse process is visible on the right side in HMN St557 and St773 (Pl. 3, Figs. 2, 4 cf. 5). In HMN St500 this rib is much stouter with anteroposteriorly expanded ends so that it is similar to the other sacral ribs (Pl. 2, Figs. 1, 3, 6). In HMN Ng20 this rib appears to be stouter than the adjacent sacral rib (Pl. 3, Fig. 6). Consequently the number of sacral ribs varies in *Kentrosaurus aethiopicus* with either four or five and the additional rib is carried by the first sacral vertebra. The sacral ribs supported by sacral vertebrae 2 to 5 are homologous so these are numbered 1 to 4 and the other sacral rib will be referred to as the additional (fifth) sacral rib (Pl. 2; Pl. 3, Figs. 1–5). The seven sacra are listed below in order of increasing size and for each the following data is given – specimen number, where illustrated, the number of sacral ribs and the combined ventral length in mm of the six fused centra:

1. HMN St773; Pl. 2, Figs. 7, 8, Pl. 3, Fig. 4;	5; ± 300
2. HMN St557; Pl. 2, Fig. 11, Pl. 3, Figs. 1–3;	5; 330
3. HMN St218; Pl. 2, Figs. 9, 10;	4; 345
4. HMN St439; HENNIG (1925, Figs. 23a, b)	4; 350
5. HMN Ng20; Pl. 3, Fig. 6	5; ± 350
6. HMN St555; Pl. 3, Fig. 5	4; 363
7. HMN St500; Pl. 2, Figs. 1–6	5; 445

From this list it is apparent that the number of sacral ribs is independent of size so it is not a growth difference but must be an individual difference and, as is discussed below (:144), individuals with five sacral ribs were probably females.

The expansion of the neural canal in the sacral region is described by HENNIG (1925) and it is partly exposed by breaks in a couple of the sacra. In HMN St218 (Pl. 2, Fig. 10) the maximum widths in mm of the neural canal from the dorsosacral to the fifth sacral vertebrae are 30, 40, 75, 50, ? and 30 respectively. The roof of the anterior part of the expanded neural canal is visible in HMN Ng20 (Pl. 3, Fig. 6). The maximum widths in mm are: ds 25, s1, 2 110, s3 40 and s5 30, the maximum heights are: s1, s2 100, s3 45 and s5 30.

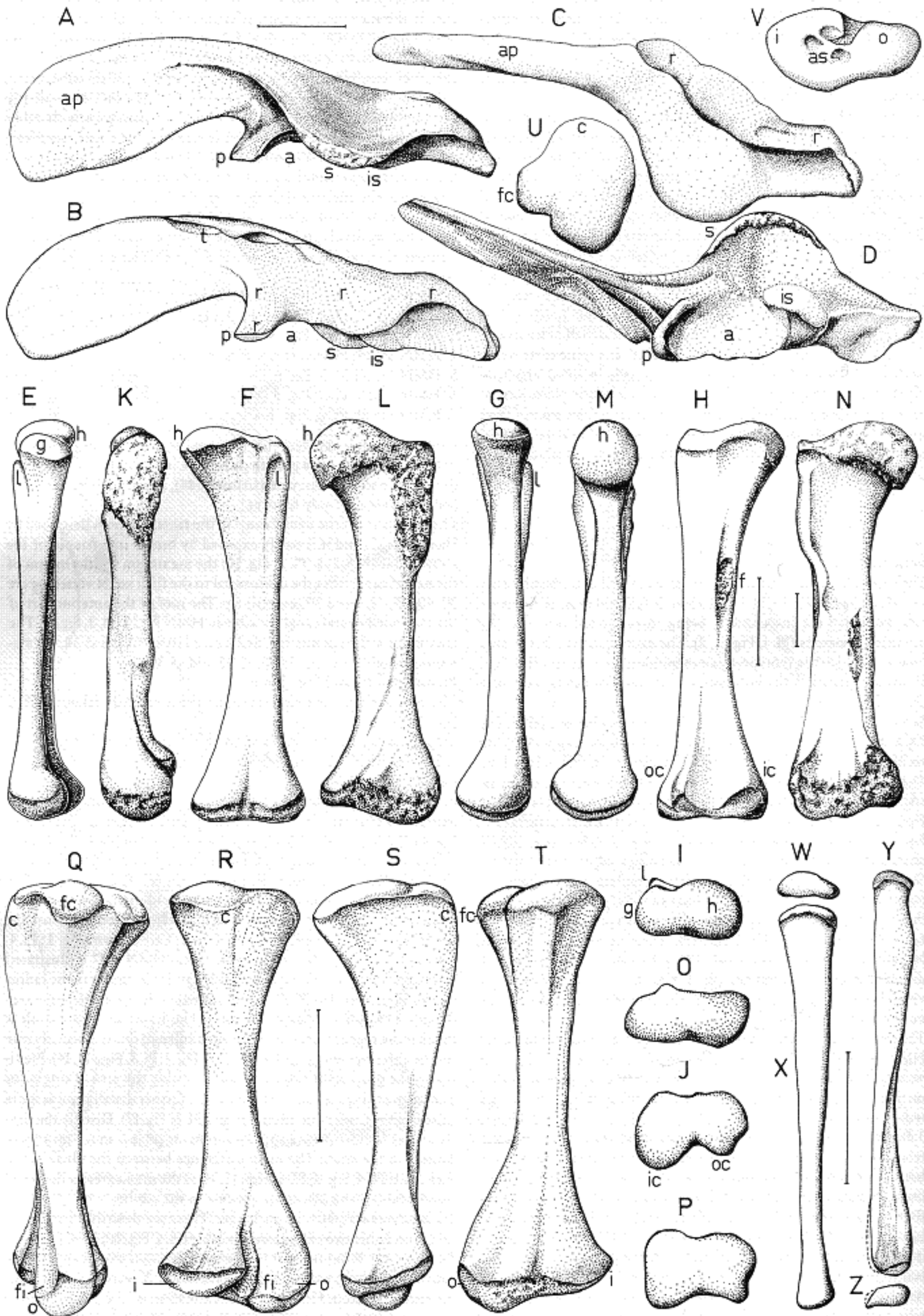
Pectoral Girdle and Fore Limb

The only available material is that on the mounted skeletons (Pl. 1, Figs. 1, 2).

Scapulocoracoid. This is described and illustrated by HENNIG (1915, 1925 – Fig. 39 X 0.22, Figs. 40, 41 X 0.32) and I show that of the right side (Pl. 6, Fig. 16).

Humerus, radius, ulna. The large syntypic left humerus (HMN St106) and ulna (HMN St461) are illustrated by HENNIG (1915, 1925 – Fig. 43 X 0.38, Fig. 45 X 0.32) and these are shown (Pl. 4, Fig. 6; Pl. 5, Fig. 14; Pl. 6, Fig. 17) along with those of the opposite side (Pl. 4, Fig. 5, Pl. 5, Fig. 13) plus appropriately sized radii (Pl. 4, Figs. 4, 5, 6; Pl. 5, Figs. 13, 14). For comparison, the humerus, radius and ulna of a subadult (lengths in mm of humerus and ulna 295 and 260 as against 350 for HMN St106 and 345 for HMN St461) are shown (Fig. 1; Pl. 4, Figs. 1–3; Pl. 6, Fig. 18). The syntypic radius HMN St77 is illustrated by HENNIG (1915, 1925 – Figs. 46 X 0.35) and it is similar to the radius shown (Text-figs. 1M–R, Pl. 6, Fig. 18) which is about the same size (length 233 mm as against 200 mm). The humerus of the adult is much more rugose than that of the subadult and this is especially true for the anterior view (Text-fig. 1B; Pl. 4, Fig. 3; Pl. 5, Figs. 13, 14). Proximally, the prominent ridge that was probably the area of origin for part of the triceps muscle extends much further distally and is more raised and rugose in the adult (see also Pl. 6, Fig. 17). Distally the condylar area is more rugose and the supinator ridge is much more prominent in the adult. The main difference between the ulnae (Text-figs. 1G–I; Pl. 4, Fig. 5; Pl. 6, Figs. 13, 14) is the much greater degree of ossification of the olecranon process in the adult.

Carpals, metacarpals and phalanges. These are described by HENNIG (1925) and only two carpals are available (Pl. 1, Fig. 20; Pl. 4, Figs. 4, 5; Pl. 5, Fig. 13). From the text in JANENSCH (1925), it would appear that metacarpals and phalanges from excavation X were utilized in the mounted skeleton. However, an examination of the photograph of the skeleton (JANENSCH 1925, Pl. 16) shows that these elements were



restored in plaster as is the case today. Consequently, no metacarpals or phalanges are available for study and we must rely on the description given by HENNIG (1925, only includes a proximal view of metacarpals I to V, the magnification of which cannot be determined) plus the plaster reconstructions on the mounted skeletons (Pl. 1, Fig. 20).

Pelvic Girdle

Ilium. The ilium of an adult (HMN St446) was briefly described by HENNIG (1925, Fig. 25 X 0.18) and it is shown along with a similar sized ilium (Pl. 5, Figs. 15, 16) plus that of a subadult (Text-figs. 2A-D; Pl. 4, Figs. 7-9). Parts of ilia that are still attached to the sacrum are also illustrated (Pl. 2, Figs. 1-6, 9). About half the length of the ilium consists of the laterally and slightly dorsally facing anterior process that is extremely deep (Text-fig. 2A) so that the more anterior part resembles the dorsal part of the scapula blade (Pl. 6, Fig. 16). The pubic peduncle is narrow in side view (Text-fig. 2A) and the ischiadic head is low but both are broad in ventral view (Text-fig. 1D; Pl. 4, Fig. 7) and form the anterior and posterior margins of the shallow iliac portion of the acetabulum. The central part of the acetabulum is not clearly defined laterally because it merges with the adjacent part of the ilium (Text-fig. 2D; Pl. 4, Fig. 7). The postacetabular part of the ilium is short (Text-figs. 2A, B, D). The dorsal part of the main body of the ilium forms a broad and mostly dorsally facing surface that medially abuts against the sacral plate formed by the fusion of the sacral ribs and the transverse processes of the sacral vertebrae (Text-figs. 2B, D; Pl. 2, Figs. 2, 4; Pl. 4, Fig. 9; HENNIG 1925, Fig. 23b). The sacral ribs fit against the surface medial to the acetabulum (Text-fig. 2B; Pl. 2, Figs. 1, 3, 5, 6, 9; Pl. 4, Fig. 9). The dorsal surface forms a supraacetabular flange that projects dorsolateral to the posterior two thirds of the acetabulum and extends posterior to the ischiadic head (Text-figs. 2A, C, D; Pl. 4, Figs. 7, 8). This flange overhung the proximolateral part of the femur (Pl. 5, Figs. 15, 16) and it was probably the area of origin of the *M. iliobtibialis* 2 whereas the *M. ilio-tibialis* 1 probably originated from the lateral surface of the anterior process.

Pubis. The syntypic left pubis (HMN St758) is figured in lateral and medial views by HENNIG (1915, 1925 - Fig. 29 X 0.275) and the anterior end is shown (Pl. 5, Fig. 15) along with a similar sized pubis (Pl. 5, Fig. 16).

Ischium. The syntypic right ischium (HMN St335) is shown in lateral and medial views (Pl. 5, Figs. 17, 18, see also HENNIG 1915, 1925, Fig. 32 X 0.34). The iliac head is massive, the distal part is bar-like, and most of the ventral part is thin.

Hind Limb

Femur. The syntypic left femur (HMN St463) is figured in posterior (HENNIG 1915), medial (HENNIG 1925, Fig. 33 X 0.25, plus end views ?

this femur Fig. 34 ? X 0.37) and lateral views (JANENSCH 1925) and it is shown plus the anterior view of a similar sized femur (Pl. 5, Fig. 15; Pl. 6, Figs. 1, 6) HENNIG (1925) gives the posterior outlines of nine different sized femur and discusses the age differences shown. Two small femora (UT 1524/5, length 460 mm, Text-figs. 2E-J; HMN St331, length 461 mm, Pl. 6, Figs. 7-9) and three large femora (HMN MTD length 635 mm, Pl. 1, Fig. 1, Pl. 6, Fig. 1; HMN bb1, length 778 mm, Text-figs. 2K-P, Pl. 6, Figs. 2-5; syntype HMN St463, length 635 mm, Pl. 6, Fig. 6) are illustrated to show the various differences. In small femora the lesser trochanter is a distinct finger-like process separate from the greater trochanter that is clearly delimited from the head (Text-figs. 2E, F, I; Pl. 6, Figs. 7, 8). In large femora this region is covered with bony growths so the three regions merge into one another (Text-figs. 2K, L, O; Pl. 6, Figs. 2, 4). However, large femora (Pl. 5, Figs. 15, 16; Pl. 6, Figs. 1, 6; HENNIG 1915, 1925) do not show the extreme expansion of the proximolateral part of the very large femur HMN bb1 (Pl. 6, Figs. 2-5). The ends of the small femora are smooth, not rough as in the large ones, and are less sharply delimited from the shaft that is proportionally more slender (Text-figs. 2E-H, K-N). The fourth trochanter is represented by a distinct ridge only in large femora (length above 530 mm; Pl. 6, Figs. 1, 6) and there are several ossified ligamentous masses that form longitudinal cords (not clearly shown, for details see HENNIG 1925) whereas the shaft of the small femora is smooth. Posterodistally the inner condyle is larger than the outer condyle (Text-figs. 2J, P) as in *Stegosaurus* (OSTROM & McINTOSH 1966:325, 327) and HENNIG (1925) is correct in deducing that the statement by GILMORE (1914:82) that the outer condyle is the larger was a slip of the pen. Tibia, fibula, astragalus and calcaneum. The syntypic left tibia (HMN St152, length 390 mm) and fibula (HMN St297, length 318 mm) figured by HENNIG (1915, 1925, Fig. 36 X 0.36, Fig. 38 X 0.36 specimen number given as HMN St597 but no such fibula is listed on p. 205 so probably should be St297) are those of subadult individuals and a slightly smaller tibia and fibula (lengths 333 mm, 305 mm) are illustrated (Text-figs. 2Q-Z; Pl. 6, Figs. 13-15). The proximal end of the tibia is massive (Figs. 2Q-U) and the transversely expanded distal end consists of an inner and outer malleolus that are separated anteriorly by a prominent edge and groove (Text-figs. 2Q, R, V; Pl. 6, Figs. 13, 15). The distal surface has a large indentation (Text-fig. 2V) that was presumably to receive the raised central part of the astragalus as is the case in *Stegosaurus* (GILMORE 1914). In adult individuals of *Kentrosaurus* the adjacent parts of the distal parts of the tibia and fibula are fused to each other and to the fused tarsals (astragalus, calcaneum) that form a rounded articular surface distally (Pl. 6, Figs. 10-12). The form of the distal parts of the tibia and fibula is modified by the deposition of bone in the spaces between them and, in addition, the medial surface of the proximal part of the fibula is larger (Pl. 6, Figs. 10, 11).

Pes. HENNIG (1925, Figs. 50-52 X 1) described the only articulated pes (HMN Ki 112) and it is shown in dorsal and ventral views together with end and side views of the metatarsals (Pl. 5, Figs. 1-7). Another metatarsal III (Pl. 5, Figs. 8-12) differs in a few respects from that of HMN Ki 112 (Pl. 5, Figs. 1, 2, 4, 7). In both there is a prominent ventral rugosity on the proximal part (Pl. 5, Figs. 2, 12). However, in proximal view the outline of the proximal end of UT 1524/8 is approximately that of an isosceles triangle whereas the proximal end of HMN Ki 112 is proportionally deeper (Pl. 5, Figs. 4, 8-10). Distally the medial condyle is proportionally much larger (Pl. 5, Figs. 7, 10).

Dermal Armor.

The dermal spines are described in detail by HENNIG (1925) on the basis of a large number of different specimens but unfortunately very few figures are given. Most of the available spines are on the reconstructed skeleton (Pl. 1, Fig. 2) that is described by JANENSCH (1925) who discusses his deductions concerning the placement of the spines, the positions of which are certain only for the terminal pair. JANENSCH (1925) divides the plates and spines of *Kentrosaurus* into four groups. The first nine pairs of plates and spines are grouped together with a

Text-Fig. 2: *Kentrosaurus aethiopicus* from Upper Jurassic of Tanzania, East Africa, bones of pelvis and hind limb. A-D, left ilium UT 1524/4 (was St133) X 1/6 (see also Pl. 4, Figs. 7-9) in: A - lateral view; B - medial view (in reverse so right); C - dorsal view; D - ventral view; E-P - left femur UT 1524/5 X 1/6 (E-J) and right femur (see also Pl. 6, Figs. 2-5; in reverse so left) HMN bb1 X approx. 0.1 (K-P) in E, K - lateral view; F, L - anterior view; G, M - medial view; H, N - posterior view; I, O - proximal end; J, P - distal end; Q-V - left tibia UT 1524/5 (was St94) X 1/4 (see Pl. 6, Figs. 13-15) in Q - lateral view; R - anterior view; S - medial view; T - posterior view; U - proximal end; V - distal end; W-Z - right fibula UT 1524/6 (was St130) X 1/4 in W - proximal view; X - lateral view; Y - posterior view; Z - distal view. Abbreviations: a = acetabulum; ap = anterior process; as = surface for astragalus process; c = cnemial crest; f = area of fourth trochanter; fc = fibular condyle; fi = surface for fibula; h = head; i = inner malleolus; ic = inner condyle; is = ischiadic head; l = lesser trochanter; m = medial condyle; o = outer malleolus; oc = outer condyle; p = pubic peduncle; r = surface for sacral ribs; s = supraacetabular flange; t = surface for transverse process of first sacral vertebra. Scale lines represent 10 cm.

long, straight and steeply placed (two edged) flat spine at the posterior end of the row and a high, rhomboidal plate at the other end. JANENSCH (1925:266) notes that this transition (Pl. 1, Fig. 2) occurs cranially in the following manner: The spines become shorter and more horizontally inclined, a posterior border and then a thinner anterior one show up more distinctly, the character of the spine changes by increased flattening into a thin perpendicular plate, the height of which increases and the length of which decreases. The second group consists of spine pairs ten to twelve, the stocky spines (Plumpstacheln) of HENNIG (1925). These spines are two edged, somewhat rhomboidal in cross section, stocky and steeply inclined with a large, oval shaped base. The third group consists of spine pairs thirteen and fourteen, the long spines (Langstacheln) of HENNIG (1925), and these slender spines were held more horizontally than the stocky spines as shown by the smaller angle that the base makes with the longitudinal axis of the spine. The last group, the round spine (Rundstacheln) of HENNIG (1925, parasacral spine of HOFFSTETTER, 1957) consists of one pair of spines, the enormously expanded basal plates of which were probably embedded more laterally in the skin immediately above the flat area formed by the posterior part of the ilium and the sacrum (Pl. 5, Figs. 15, 16).

The first four pairs of plates are plaster (Pl. 1, Fig. 2) with plates one to three freely restored whereas the fourth is based on a very thin plate (JANENSCH 1925) that is no longer available. However, HENNIG (1925:240) described this thin plate (HMN VIII 20), the outline of which was roughly rhomboid with a vertical height of 150 mm (190 mm measured diagonally). HENNIG (1925) noted that, apart from the lack of an expanded base and the much smaller height, this plate resembled the dorsal and tail root spines of *Stegosaurus* (GILMORE 1914, Pls. 23, 24). The shape was similar and the upper half carried a similar series of parallel longitudinal wrinklins that extended into the apex. Most of the fifth right plate (HMN Ng28) is real (Pl. 1, Figs. 3, 4) and it is figured by HENNIG (1925, Fig. 56, lateral view X 0.4) who noted its similarity to the neck plate from the shoulder region of *Stegosaurus* (GILMORE 1914). The width of HMN Ng28 is 126 mm and most of the plate is thin except the rounded basal region that has a maximum thickness of 45 mm that favors the medial side (Pl. 1, Figs. 3, 4). HENNIG (1925, Fig. 56) originally restored this plate with a gently rounded apex and there is no evidence for the two tips shown (Pl. 1, Fig. 3).

The sixth left spine plate (HMN St546, Pl. 5, Figs. 19–21) is perfectly preserved and it is figured by HENNIG (1925, Fig. 55, lateral view X 0.42). The medial surface is flat (Pl. 5, Fig. 19) but laterally there is a perpendicular and diagonally inclined large flange (Pl. 5, Figs. 20, 21) that in life was probably imbedded just below the skin. This plate is a much modified spine because this flange is the base of a spine that is still visible and the tip of which forms the posterior apex of the plate (Pl. 5, Fig. 21). The length and width of this plate are 243 mm and 115 mm and the maximum thickness measured perpendicular to the medial surface is 90 mm.

Both sides of the seventh right flat spine (HMN St285, Pl. 1, Figs. 5, 6) are gently convex and the width proximally is 75 mm with a maximum thickness of 35 mm. The eighth right flat spine (Pl. 1, Figs. 7, 8) is complete with a length of 360 mm and it is more spine-like than the seventh with a larger basal area, the width and thickness of which are 110 mm and 75 mm respectively. The anterior part of the spine is more spike-like whereas most of the posterior part is more plate-like (Pl. 1, Fig. 7). The syntypic spine HMN St90 (Pl. 4, Figs. 10–13, HENNIG 1915) is another eighth left flat spine but the medial and lateral surfaces are more uniformly curved (Pl. 4, Figs. 10, 13). The expanded base (Pl. 4, Figs. 11) is transversely concave (Pl. 1, Fig. 8; Pl. 4, Figs. 10, 12) whereas in the seventh it is convex (Pl. 1, Fig. 6). The base of the ninth left flat spine (Pl. 1, Fig. 9) has a width of 88 mm, a thickness of 60 mm, and ventrally the surface is convex.

The tenth left stocky spine has a massive base with thick edges that are notched by numerous grooves (Pl. 1, Figs. 12, 14) and a transversely concave ventral surface (Pl. 1, Fig. 13). The anterior edge becomes

more lateral in position passing distally (Pl. 1, Fig. 13). These spines are similar to those of *Stegosaurus sulcatus* (USNM 4937) illustrated by GILMORE (1914, Fig. 65) who did not confuse right and left in his figure, a possibility that was suggested by HENNIG (1925). The eleventh left stocky spine has a slightly less massive base (Pl. 1, Fig. 15) and the twelfth is incomplete (Pl. 1, Fig. 16).

The proportionally small subcircular base (Pl. 1, Fig. 18) of the thirteenth right long spine is sharp-edged and set at a smaller angle to the long axis of the spine (Pl. 1, Fig. 17) than it is in the stocky spines (Pl. 1, Figs. 14–16). The fourteenth or terminal pair of long spines are incomplete distally and the proportionally elongate base (Pl. 4, Fig. 24) makes an even smaller angle with the longitudinal axis of the spine (Pl. 1, Fig. 19). An almost perfect terminal pair of long spines (HMN St684) preserved with the last five caudal vertebrae (Pl. 4, Figs. 20–23) shows that these spines projected well beyond the posterior end of the vertebral column (Pl. 4, Fig. 20). The syntypic terminal long spine (HMN St575) described by HENNIG (1915, 1925, Fig. 54. ? right in dorsal view X 0.22) could not be located.

The syntypic right parasacral spine (HMN St345) is figured in dorsal view by HENNIG (1915, 1925, Fig. 57 X 0.25, round spine or Rundstachel) and is shown (Pl. 4, Figs. 14–17) along with another example (Pl. 4, Figs. 18, 19). The spine is twisted along its length and dorsally it merges gently with the adjacent surface of the large basal plate (Pl. 4, Figs. 14–16, 19; HENNIG 1925, Fig. 57 X 0.3). The ventral surface of the basal plate is rugose and the proximal margin of the spine is clearly defined (Pl. 4, Figs. 17, 18). The large spine was probably lateral in position and posteriorly directed with the basal plate positioned above the posterior part of the ilium and the adjacent part of the sacral plate (Pl. 4, Figs. 15, 16).

Discussion

Sexual Dimorphism.

As noted above (:141), the number of sacral ribs is either four or five in *Kentrosaurus* (Pl. 2, Figs. 9, 3) and this could be regarded as a specific difference. However, six of the seven sacra available came from the same excavation (St) and HENNIG (1925) and JANENSCH (1925), on the basis of their study of the enormous amount of *Kentrosaurus* collected from the Tendaguru, concluded that it was all referable to one species, *K. aethiopicus* HENNIG 1915. The number of sacral vertebrae apparently does not vary in living species of reptiles and birds (GALTON 1974). However, in man about 90 per cent of the population have a normal sacral count of five vertebrae but about 5 percent have either some degree of fusion between the last lumbar vertebra and the sacrum (so count is six) or the first sacral vertebra is partially or completely separate from the sacrum (so count is four) (HOLLINSHEAD 1967). The sacral count is either five or six in the North American species of the ornithomimid dinosaur *Camptosaurus* (see GILMORE 1909). However, the holotypes of four of the species (*C. dispar*, *medius*, *nanus*, *browni*) all came from Quarry 13 near Como, Wyoming and all of the Morrison material of *Camptosaurus* is probably referable to one species, *C. dispar* (see GALTON & POWELL, 1980). The sacral count is also either five or six in the ornithomimid dinosaur *Hypsilophodon foxii*, all the material of which came from a 1 m thick bed of the Wealden (Lower Cretaceous) exposed for about 3 km on the cliffs on the southwest coast of the Isle of Wight, England (GALTON 1974). The sacral difference in *Hypsilophodon foxii* cannot be correlated with any valid specific differences and, because of the approximately equal distribution of the two types (three with five ribs, five with six ribs), it was concluded that this was a sexual variation rather than an individual variation comparable to that in man (GALTON 1974). The sacral variation in *Kentrosaurus aethiopicus* is also considered to be a sexual difference because of the distribution (for excavation St three of each type) and the lack of evidence for more than one species of *Kentrosaurus* from excavation St (HENNIG 1925, JANENSCH 1925).

To date only two other genera of stegosaurs are represented by more than one sacrum, *Stegosaurus* from the Morrison Formation (Upper

Jurassic) of western North America and *Dacentrurus* from the Kimmeridgian (Upper Jurassic) of England, France and Portugal. Only two of the species of *Stegosaurus* described to date have sacra and GILMORE (1914, Figs. 22, 23) shows four sacral ribs in *S. unguatus* and five in *S. stenops* and, on the basis of the available material (see also OSTROM & MCINTOSH 1966), these appear to represent separate species. However, OSTROM & MCINTOSH (1966: 281) illustrate another sacrum of *S. stenops* with four sacral ribs and, if this referral is correct as appears to be the case, then the sacral count is either four or five in this species.

Five sacra of *Dacentrurus* have been discovered to date from the Upper Jurassic of Europe. Four of these have five sacral ribs and include the holotypes of *Omosaurus armatus* OWEN 1875 (type species of *Dacentrurus* LUCAS 1902) from England and *Dacentrurus* (= *Omosaurus*) *lennieri* (NOPCSA, 1911b) from France plus two sacra referred to *D. lennieri* (LAPPARENT & ZBYSEWSKI 1957, Pl. 34, Fig. 146 plus unfigured MGSP specimen to be described) from Portugal. The range of variation shown by these sacra is comparable to that shown by the sacra of *Kentrosaurus aethiopicus* with five sacral ribs (Pl. 2, Figs. 3, 8, 11; Pl. 3, Fig. 6) and, as will be discussed elsewhere, I regard *Omosaurus lennieri* NOPCSA 1911b as a junior synonym of *Omosaurus armatus* OWEN 1875. One sacrum with four sacral ribs from Portugal is referred to *Dacentrurus armatus* (ZBYSEWSKI 1946, LAPPARENT & ZBYSEWSKI 1957, Pl. 34, Fig. 147) and the form of this sacrum is very similar to that of HMN St218 (Pl. 2, Fig. 9). Examination of the Portuguese sacrum (MGSP) confirms that there were only four sacral ribs. The transverse process of the first sacral vertebra forms the anterior margin of the sacral plate but it does not support a sacral rib. In addition, the fourth sacral rib extends to the posterior part of the ischiadic head of the ilium so there is no room for another sacral rib (see ZBYSEWSKI 1946, Pl. 5, Fig. 8). Consequently, the number of sacral ribs is either four or five in *Dacentrurus armatus*. The sample of three specimens from Portugal with the ratio for four and five ribbed sacra at 1:2 is statistically insignificant but it is suggestive of sexual dimorphism. If a sexual dimorphism is involved then individuals of *Dacentrurus armatus*, *Kentrosaurus aethiopicus* and *Stegosaurus stenops* with five sacral ribs are probably females whereas those with four sacral ribs are probably males.

Growth Differences

From the description given above and by HENNIG (1925), the following are some of the differences between the bones of a subadult individual and those of an adult (Pl. 1, Figs. 1, 2; femoral lengths 465 mm and 635 mm). In addition, HENNIG (1925) gives some details about the sacrum of a juvenile individual (HMN Ig872).

1. Centrum and neural arch (and transverse process for caudals) of vertebrae of subadults are unfused and fused in adults (Pl. 3, Figs. 7-16).
2. Lack of fusion of different parts of the sacrum in younger individuals:
 - a. Centrum of dorsosacral vertebra is free in juveniles but fused to the centrum of the first sacral vertebra in subadults and adults (Pl. 2, Figs. 5, 9, 11; Pl. 3, Figs. 1, 2, 5).
 - b. The transverse processes and sacral ribs are unfused in juveniles and fused together to form a solid sacral plate with a continuous lateral surface for the ilium in subadults and adults (Pl. 2, Fig. 2; Pl. 3, Fig. 1).
 - c. Sacral plate and ilium are unfused in subadults (Pl. 2, Fig. 2; Pl. 3, Figs. 1, 4) and fused together in adults (Pl. 2, Figs. 1-6, 9; Pl. 3, Fig. 4).
3. The articular and nonarticular surfaces of the bones of the appendicular skeleton are relatively smooth in subadults (Pl. 4, Figs. 1-3, Pl. 6, Figs. 7-9) whereas in adults the ends are much more rugose and the rest of the surface is more strongly striated (Pl. 5, Figs. 13, 14; Pl. 6, Figs. 1-6, 17).
4. The angle that the anterior edge of the blade makes with the rest of the scapula (Pl. 6, Fig. 16) becomes smaller with increasing size.
5. The scapula and coracoid are separate in subadults and fused together in adults.

6. The coracoid foramen is enclosed by the coracoid in adults and open in subadults.
7. The triceps ridge and the supinator ridge of the humerus of an adult (Pl. 5, Figs. 13, 14; Pl. 6, Fig. 17) are much more raised and rugose than those of a subadult (Text-figs. 1A-F; Pl. 4, Figs. 1-3).
8. The olecranon process of the ulna is small in subadults (Text-figs. 1H, K) and large in adults (Pl. 5, Figs. 13, 14).
9. The posterior ramus ("postpubic" rod) of the pubis is less twisted dorsolaterally along its length in subadults than it is in adults (see HENNIG 1915, Fig. 10, 1925).
10. The obturator foramen of the pubis is enclosed by the pubis in some adults and is open in all subadults.
11. The femora of adults (Text-figs. 2K-P; Pl. 6, Figs. 1-6) and subadults (Text-figs. 2E-J; Pl. 6, Figs. 7-9) show the following differences:
 - a. Head is much more spherical and more clearly defined from the shaft in adults than in subadults (Pl. 6, Figs. 1-3, 8, 9).
 - b. Lesser trochanter is a slender finger-like process in subadults and fused to the greater trochanter in adults (Pl. 6, Figs. 1, 2, 4, 6-8).
 - c. Proximally the lateral surface is smooth in subadults whereas that of adults is covered with bony growths (Pl. 6, Figs. 4, 6, 7; in a very large femur the shape of the bone is altered because the growth region projects anteriorly, posteriorly and laterally, Pl. 6, Figs. 2, 4, 5).
 - d. The shaft is more slender relative to the ends in subadults than it is in adults.
 - e. Longitudinal ossified ligamentous cords are present on the shaft of adults but not in subadults.
 - f. There is practically no trace of a fourth trochanter in femora with a length of less than 530 mm. (Pl. 6, Figs. 8, 9) but above this length a raised area is present and the whole of the shaft thickens in the region of the fourth trochanter (Pl. 6, Figs. 1, 6).
12. The tibia, fibula, astragalus and calcaneum are separate bones in subadults but are fused together in adults with bone developing to a varying extent in the intervening spaces (Text-figs. 2Q-Z; Pl. 6, Figs. 10-15).
13. Proximally the part of the fibula adjacent to the tibia develops a flange-like area (Pl. 6, Figs. 10, 11) that is not present in subadults.

Specimens representing subadult stegosaurs are rare and are also known for *Dacentrurus* (femoral length about 557 mm, MGSP, holotype of supposed sauropod *Astrodon pusillus* LAPPARENT & ZBYSEWSKI 1957, see GALTON in press a), from the Upper Jurassic of Portugal; a tibia of *Lexovisaurus* (BMNH R2854, length 320 mm) from the Middle Jurassic of England, and *Stegosaurus* (YPM 4634, femoral length 520 mm; a few other isolated bones, CM, USNM; DNM juvenile, femoral length 298 mm; GALTON in press b) from the Upper Jurassic of the western interior of the U.S.A. Most of the age differences listed above are probably true for all stegosaurs because differences 1, 2b, c, 3, 5-10, 11a-c, e and 12-14 also occur in *Stegosaurus* and differences 1, 2c, 11a-c, e, f and 12 in *Dacentrurus*. These lists of shared age differences would undoubtedly be much increased with the discovery of additional material (especially for *Dacentrurus*) because most of the gaps reflect the absence of subadult examples of the bones concerned.

Status of *Lexovisaurus* HOFFSTETTER

HULKE (1887) described the very incomplete skeleton of a stegosaur (BMNH R1989, includes sacrum, ilia, femur) from the Lower Oxford Clay (Middle Callovian, Middle Jurassic, horizon incorrectly given as Kimmeridge Clay in original description) near Peterborough, England as *Omosaurus durobrivensis*, the type species of the genus *Lexovisaurus* HOFFSTETTER 1957. NOPCSA (1911a) described another more complete skeleton of a slightly smaller individual (BMNH R3167, femoral length 905 mm as against 979 mm) from the same locality as the holotype of *Stegosaurus priscus*, a taxon which HOFFSTETTER (1957) makes a junior synonym of *Omosaurus durobrivensis* HULKE 1887.

HOFFSTETTER (1957) also referred to *Lexovisaurus durobrivensis* (HULKE) a partial skeleton (MHNN, casts in MNHN) from the Middle Callovian near Argences, Normandy, France and this specimen is illustrated by GALTON et al. (1980). A description of all the material of *Lexovisaurus* is in preparation and this genus is clearly separated from *Stegosaurus* (for figures see GILMORE 1914, OSTROM & MCINTOSH 1966) by the following differences.

1. The swollen tops of the neural spines of the caudal vertebrae of *Lexovisaurus* are weakly developed (see GALTON et al. 1980), being comparable to those of *Dacentrurus* (OWEN 1875) and are not massive as in *Stegosaurus* in which most of the tail carried large plates dorsally.
2. A fourth trochanter is present on the femur of *Lexovisaurus* (BMNH R1989, GALTON & BOINE 1980; MHNN, GALTON et al. 1980) and absent in *Stegosaurus*.
3. *Lexovisaurus* carried at least on large, tall (+510 mm) and thin plate (CUSM J. 46874, HUENE, 1901, GALTON 1980), the height of which was over twice the width (230 mm) whereas in *Stegosaurus* the height and width of the large plates are about equal.
4. One dermal spine of *Lexovisaurus* (CUSM J.48679) is two edged with a moderately expanded base so it is similar in form to the thirteenth long spine of *Kentrosaurus* (Pl. 1, Figs. 17, 18). In spines of *Stegosaurus* (USNM, YPM) the proximal end is obliquely angled with practically no thickening of the base. The only exception are a pair of massive spines of *Stegosaurus sulcatus* (USNM 4937, GILMORE 1914) that have a base that is even larger than that of the largest stocky spine of *Kentrosaurus* (Pl. 1, Figs. 12-14).
5. A parasacral spine is present in *Lexovisaurus* (BMNH R3167, NOPCSA 1911a; Figs. 9a-c; MHNN, GALTON 1980, GALTON et al. 1980) but, despite abundant material (CM, DNM, USNM, YPM) it is completely unknown in *Stegosaurus* and was probably not present.

HOFFSTETTER (1957) noted that *Lexovisaurus* resembled *Kentrosaurus* in several respects (1, 2, 4, 5 above, ratio of lengths of femur to humerus 1.70 *Lexovisaurus*, 1.60-1.68 *Kentrosaurus*, 1.8-2.3 *Stegosaurus*). However, an examination of the available material shows that *Lexovisaurus* is a valid genus that differs from *Kentrosaurus* in the following respects:

1. The neural canal of the dorsal vertebrae of *Lexovisaurus* (BMNH R3167; MHNN, GALTON et al. 1980) is small and most of the neural arch below the zygapophyses is solid bone as in *Stegosaurus*. In *Kentrosaurus* the neural canal is very tall, reaching almost to the prezygapophyses (Pl. 3, Figs. 15, 16) and only a small part is subdivided dorsally by a thin transverse septum (Pl. 3, Figs. 11, 12, 15, 16).
2. In *Lexovisaurus* the transverse processes of the anterior caudal vertebrae are deep and two pronged, with a small dorsolateral ramus and a large ventrolateral ramus (GALTON et al. 1980) as in *Stegosaurus*. In *Kentrosaurus* the anterior transverse processes are shallow, more rod-like, single and more laterally directed (Pl. 3, Figs. 7, 8).

3. The transverse processes extend posteriorly only as far as caudal vertebra 11 in *Lexovisaurus* (GALTON et al. 1980) whereas in *Kentrosaurus* (Pl. 1, Fig. 2) they extend as far as caudal 27.
4. In *Lexovisaurus* the neural spines of most of the caudal vertebrae are posterodorsally inclined (BMNH, MHNN, GALTON et al. 1980) whereas in *Kentrosaurus* the neural spines posterior to the ninth caudal are more vertically inclined or actually vertical and from caudal nineteen the neural spines are anterodorsally inclined (Pl. 1, Fig. 2).
5. The anterior process of the ilium of *Lexovisaurus* (BMNH R1989) is uniformly slim in lateral view whereas that of *Kentrosaurus* is deep and expands passing anteriorly (Pl. 5, Figs. 15, 16).
6. The hemal arches or chevrons of *Lexovisaurus* are of the normal ornithischian pattern with a single longitudinal axis (NOPCSA 1911a, GALTON et al. 1980) whereas those of *Kentrosaurus* are L shaped (Pl. 1, Fig. 2).
7. There is no evidence in *Kentrosaurus* for any large (+510 mm X 230 mm), thin plates with only a moderately expanded base as occur in *Lexovisaurus* (HUENE 1901, NOPCSA 1911a, GALTON 1980, GALTON et al. 1980).

Thus *Lexovisaurus* shows resemblances and differences to both *Kentrosaurus* and *Stegosaurus*. The common ancestor for all three genera was probably a Lower Jurassic form resembling *Lexovisaurus* but with the following differences:

1. Large neural canal in dorsal vertebrae (so similar to *Kentrosaurus*).
2. A proportionally shorter femur.
3. No large dermal plates.
4. Possibly no parasacral plate (if present then subsequently lost in *Stegosaurus*).

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Literature

- AITKEN, W. G. (1961): Geology and palaeontology of the Jurassic and Cretaceous of southern Tanganyika. - Bull. Geol. Surv. Tanganyika, 31: 1-144, 14 Taf., 14 Tab.
- DONG, Zhi-ming (1973): Dinosaurs from Wuerho. Reports of Palaeontological Expedition to Sinkiang (II). - Mem. Inst. Vert. Paleont. Palcoanth. Acad. Sinica, 11: 45-52, 4 Abb., 7 Taf., Peking.
- GALTON, Peter M. (1974): The ornithischian dinosaur *Hypsilophodon foxii* from the Wealdon of the Isle of Wight. - Bull. Brit. Mus. (Natur. Hist.), (Geol.) 25: 1-152c, 64 Abb., 2 Taf., London.
- (1980): Armored dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of England. - Géobios, 5: 825-837, 1 Abb., 1 Taf., Lyon.
- (in press a): A juvenile stegosaurian dinosaur from the Upper Jurassic of Portugal, the holotype of the small sauropod *Astrodon pusillus*. - N. Jb. Geol. Paläont. Abh., Stuttgart.
- (in press b): Juveniles of the stegosaurian dinosaur *Stegosaurus* from the Upper Jurassic of North America. - J. Vertebrate Paleont., Norman.
- GALTON, Peter M. & BOINE, G. (1980): A stegosaurian dinosaur femur from the Upper Jurassic of Cap de la Hevé, Normandie. - Bull. Soc. géol. Normandie et Amis de Muséum du Havre, 67 (4): 31-38, 1 Taf., Le Havre.

- GALTON, Peter M., BRUN, Roger & RIOULT, Michael (1980): Skeleton of the stegosaurian dinosaur *Lexovisaurus* from the Middle Callovian (Middle Jurassic) of Argences (Calvados), Normandy. *Bull. Soc. géol. Normandie et Amis du Muséum du Havre*, 67 (4): 39–60, 5 Abb., 1 Taf., Le Havre.
- GALTON, Peter & M. POWELL, H. Philip (1980): The ornithischian dinosaur *Camptosaurus prestwichii* from the Upper Jurassic of England. – *Palaeontology* 23: 411–443, 13 Abb., 2 Taf., 3 Anlag., London.
- GILMORE, Charles W. (1909): Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and descriptions of two new species. – *Proc. U. S. Nat. Mus.*, 36: 197–332, 18 Abb., 15 Taf., Washington.
- (1914): Osteology of the armored Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. – *Bull. U. S. Nat. Mus.*, 89: 1–143, 73 Abb., 37 Taf., Washington.
- HENNIG, Edwin (1915): *Kentrosaurus aethiopicus*, der Stegosauridae des Tendaguru. – *Sitz. – Ber. Ges. naturforsch. Fr. Berlin* 1915: 219–247, 14 Abb., Berlin.
- (1916a): Zweite Mitteilung über den Stegosauriden vom Tendaguru. – *Sitz.-Ber. Ges. naturforsch. Fr. Berlin*, 1916: 175–182, 1 Taf., Berlin.
- (1916b): *Kentrurosaurus*, non *Doryphorosaurus*. – *Centralbl. Min. Geol. Pal.*, 1916: 578, Stuttgart.
- (1925): *Kentrurosaurus aethiopicus*, die Stegosaurier-Funde von Tendaguru, Deutsch-Ostafrika. – *Palaeontographica Suppl.* 7 (1,1): 101–254, 57 Abb., 4 Taf., Stuttgart.
- (1936): Ein Dentale von *Kentrurosaurus aethiopicus* HENNIG. – *Palaeontographica Suppl.* 7 (1,2): 309–312, 2 Abb., Stuttgart.
- HOLLINSHEAD, W. Henry (1967): *Textbook of Anatomy*. Second Edition. – 994 S., 998 Abb., New York (Harper & Row).
- HUENE, Friedrich von (1901): Notizen aus dem Woodwardien-Museum in Cambridge. – *Centralbl. Min. Geol. Pal.*, 1901: 715–719, 3 Abb., Stuttgart.
- JANENSCH, William (1925): Ein aufgestelltes Skelett des Stegosauriers *Kentrurosaurus aethiopicus* E. HENNIG aus den Tendaguru-Schichten Deutsch-Ostafrikas. – *Palaeontographica Suppl.*, 7 (1,1) 257–276, 2 Taf., Stuttgart.
- (1927): Die Rumpfwirbel von *Kentrurosaurus*. – *Sitz. – Ber. Ges. naturforsch. Fr. Berlin*, 1925: 7–8, Stuttgart.
- (1955): Der Ornithopode *Dysalotosaurus* der Tendaguruschichten. – *Palaeontographica Suppl.* 7 (1,3): 105–176, 40 Abb., 6 Taf., Stuttgart.
- LAMBE, Lawrence M. (1904): On the squamosa-parietal crest of the horned dinosaurs *Centrosaurus apertus* and *Monoclonius canadensis* from the Cretaceous of Alberta. – *Trans. Roy. Soc. Canada (2)* 10: 3–12, 1 Abb., 2 Taf., Ottawa.
- LAPPARENT, Albert, F. DE & ZYBSZEWSKI, Georges (1957): Les dinosauriens du Portugal. – *Mém. Servs. géol. Port.*, (N. S.) 2: 1–63, 12 Abb., 36 Taf., Lisboa.
- LUCAS, Frederick A. (1902): The generic name *Omosaurus*. – *Science (N. S.)* 16: 435, New York.
- NOPCSA, Franz (1911a): Notes on British dinosaurs Part IV. *Stegosaurus priscus* sp. nov. – *Geol. Mag.* (5) 8: 109–115, 145–153, 9 Abb., London.
- (1911b): *Omosaurus lennieri*, un nouveau dinosaurien du cap de la Hevé. – *Bull. Soc. géol. Normandie*, 30: 23–42, 7 Taf., Le Havre.
- (1916): *Doryphorosaurus* nov. nom. für *Kentrosaurus* HENNIG. – *Centralbl. Min. Geol. Pal.*, 1916: 511–512, Stuttgart.
- OSTROM, John H. & MCINTOSH, John S. (1966): MARSH'S dinosaurs. The collections from Como Bluff. – 388 S., 13 Abb., 150 Taf., New Haven (Yale University Press).
- OWEN, Richard (1875): *Monograph of the fossil Reptilia of the Mesozoic formations (Parts II) (Genera Bothriospondylus, Cetiosaurus, Omosaurus)*. – *Palaeontogr. Soc. Monogr.*, 29: 15–94, 16 Abb., 19 Taf., London.
- ROMER, Alfred S. (1966): *Vertebrate paleontology*. Third edition. – 468 S., 443 Abb., 3 Taf., Chicago (University of Chicago Press).
- RUSSELL, Dale, BÉLAND, Pierre & MCINTOSH, John S. (1980): Paleocology of the dinosaurs of Tendaguru (Tanzania). – *Mem. Soc. géol. Fr. (N. S.)* 139: 169–175, 2 Abb., Paris.
- STEEL, Rodney (1969): Ornithischia. – *Handbuch der Paläoherpetologie* 15: 1–84, 2 Abb., Stuttgart (Gustav Fischer).
- ZYBSZEWSKI, Georges (1946): Les ossements d'*Omosaurus* découverts près de Baleal (Peniche). – *Comun. Serv. géol. Port.*, 27: 3–12, 10 Taf., Lisboa.

Kentrosaurus oder *Kentrurosaurus*

Eine Bemerkung zur Nomenklatur

Im vorstehenden Aufsatz entscheidet sich GALTON unter Berufung auf die Regelfassung der IRZN von 1961 zugunsten von "*Kentrosaurus* HENNIG, 1915".

Das eigentliche Nomenklaturproblem hat er dabei nicht eingehender erörtert, nämlich die Frage, ob der gewählte Name überhaupt verfügbar ist.

Als HENNIG 1915 den Gattungsnamen *Kentrosaurus* einführte, stieß dieser auf *Centrosaurus* LAMBE, 1904. Zoologische Nomenklaturregeln gab es schon vor 1961, und seit 1905 sind sie allgemein verbindlich. Nach der 1915 gültigen Regelfassung reichte der Unterschied zwischen K und C nicht aus, um einen Namen verfügbar zu machen. *Kentrosaurus* HENNIG, 1915 war daher homonym mit *Centrosaurus* LAMBE, 1904 und mußte verworfen werden. HENNIG hat also im Einklang mit den damals geltenden Regeln und damit völlig zu Recht das Homonym verworfen und durch *Kentrurosaurus* HENNIG,

1916 ersetzt. Er ist damit der Substitution durch *Doryphorosaurus* NOPCSA, 1916 zuvorgekommen.

Da *Kentrosaurus* HENNIG, 1915 niemals verfügbar geworden ist, ist *Kentrurosaurus* HENNIG, 1916 der älteste verfügbare Name des fraglichen Sauriers.

"Die Verwerfung eines homonymen Gattungsnamens ist immer endgültig". [R. RICHTER (1948) Einführung in die Zoologische Nomenklatur, Frankfurt a. M.: S. 188]. Es sollte dabei bleiben.

Es braucht hier nicht im einzelnen diskutiert zu werden, ob der Name *Kentrosaurus* etwa durch Gebrauch mit ausreichender Indikation zwischen 1961 und 1970 verfügbar geworden ist. Selbst wenn das der Fall wäre, so wäre nur ein primäres jüngeres Synonym entstanden.

Plate 1

Kentrosaurus aethiopicus from the Upper Jurassic of Tanzania, East Africa.

Fig. 1; Mounted skeleton of subadult individual, in lateral view, UT 1524/MTD, femoral length 465 mm., total restored body length of about 425 cm (but note that restored with about ten more caudal vertebrae than HMN MTD) approx. X 1/26 (for views of individual bones see Text.-figs. 1, 2A-J, Q-Z and Pl. 4, Figs. 1-3, 7-9, 18, 19; Pl. 6, Figs. 13-15, 18).

Fig. 2: Mounted skeleton of adult individual in lateral (and slightly posterior) view, HMN MTD (for details see JANENSCH 1925), femoral length 635 mm, total restored body length of about 475 cm, approx. X 1/25 (for views of individual bones see Pl. 1, Figs. 3-19; Pl. 4, Figs. 4-6; Pl. 5, Figs. 13-16, 19-22; Pl. 6, Figs. 1, 6, 10-12, 16, 17).

Figs. 3, 4: fifth right dermal plate, HMN Ng28, X 1/4 in: 3 - medial view; 4 - anterior view.

Figs. 5, 6: seventh right flat plate, HMN St285, X 1/6 in: 5 - lateral view; 6 - anterior view.

Figs. 7, 8: eighth left flat spine, HMN MTD, X 1/6 in: 7 - lateral view; 8 - anterior view.

Fig. 9: ninth left flat spine, HMN MTD, X 1/5 in lateral view.

Figs. 10-11: parasacral spine, HMN MTD, X 1/6 in: 10 - lateral view; 11 - lateral view.

Figs. 12-14: tenth left stocky spine, HMN MTD, X 1/6 (12) or X 1/8, in: 12 - lateral view; 13 - anterior view; 14 - medial view.

Fig. 15: eleventh left stocky spine, HMN MTD X 1/8, in medial view.

Fig. 16: twelfth right stocky spine, HMN MTD, X 1/8 in lateral view.

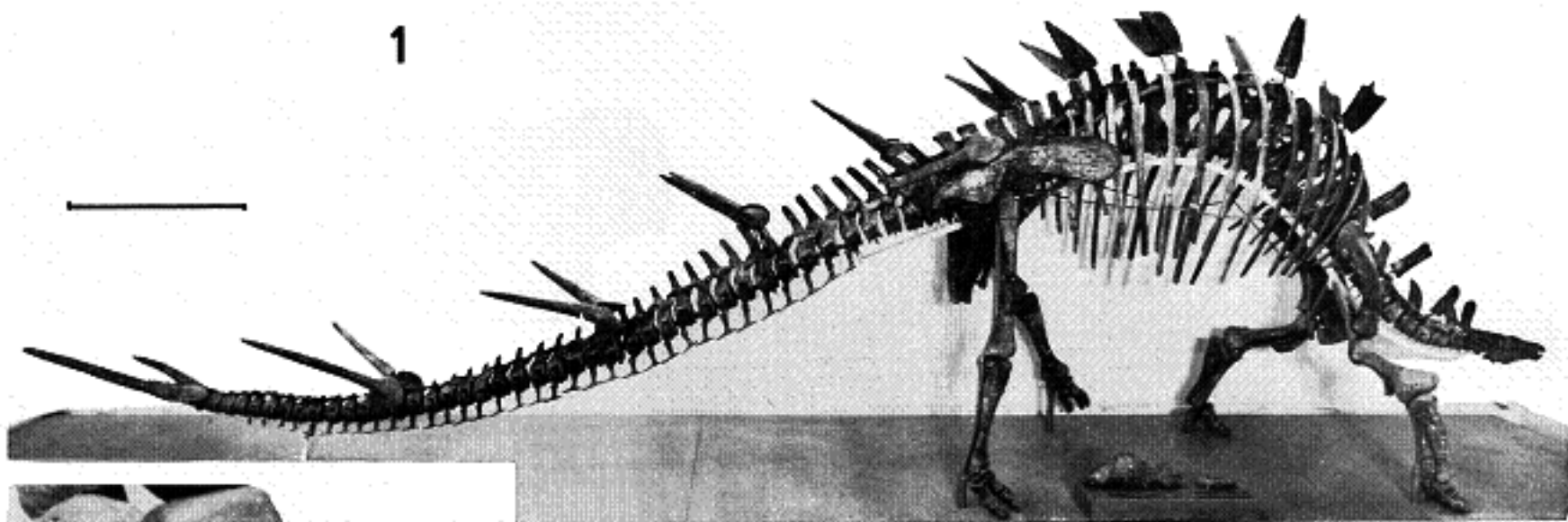
Fig. 17, 18: thirteenth right long spine, HMN MTD in 17 - lateral view X 1/6; 18 - anterior view, X approx. 1/6.

Fig. 19: fourteenth or terminal long spines HMN MTD in dorsal view X 1/10 (see also Pl. 4, Fig. 24).

Fig. 20: restoration of right manus, HMN MTD X 1/4 in anterior view.

Scale lines represent 50 cm. (1, 2) or 10 cm.

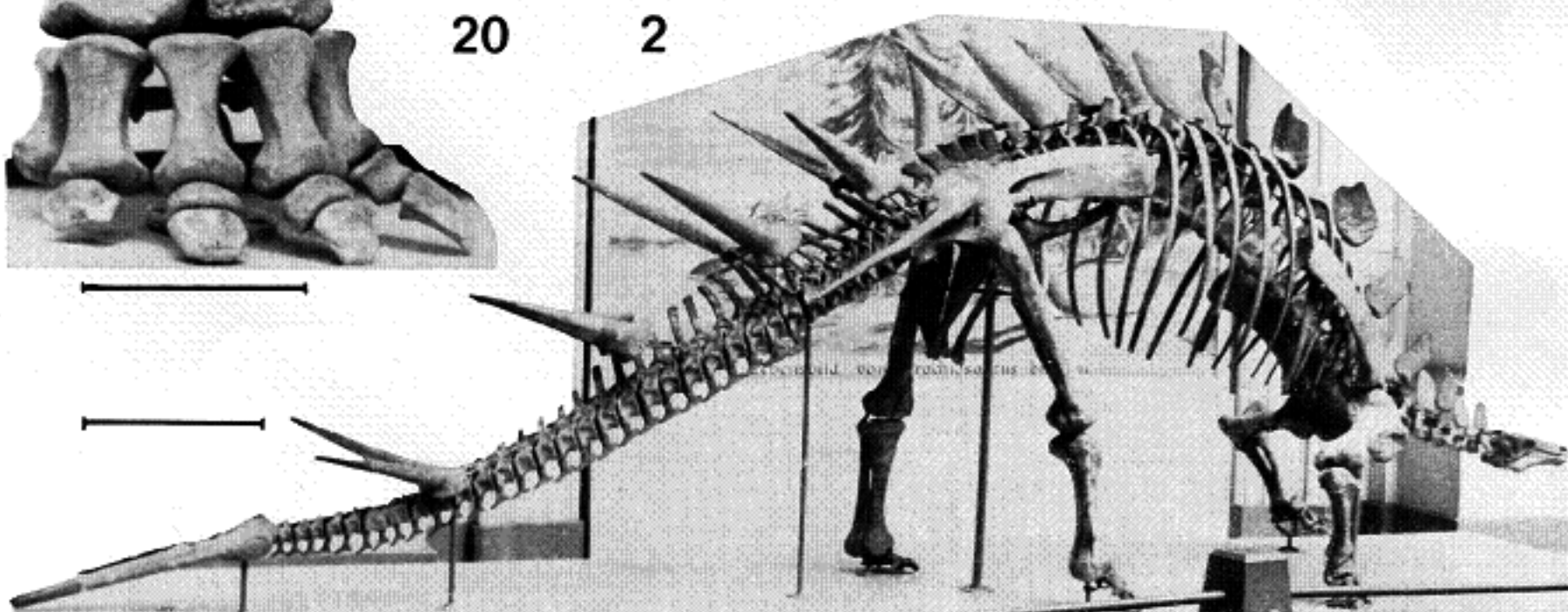
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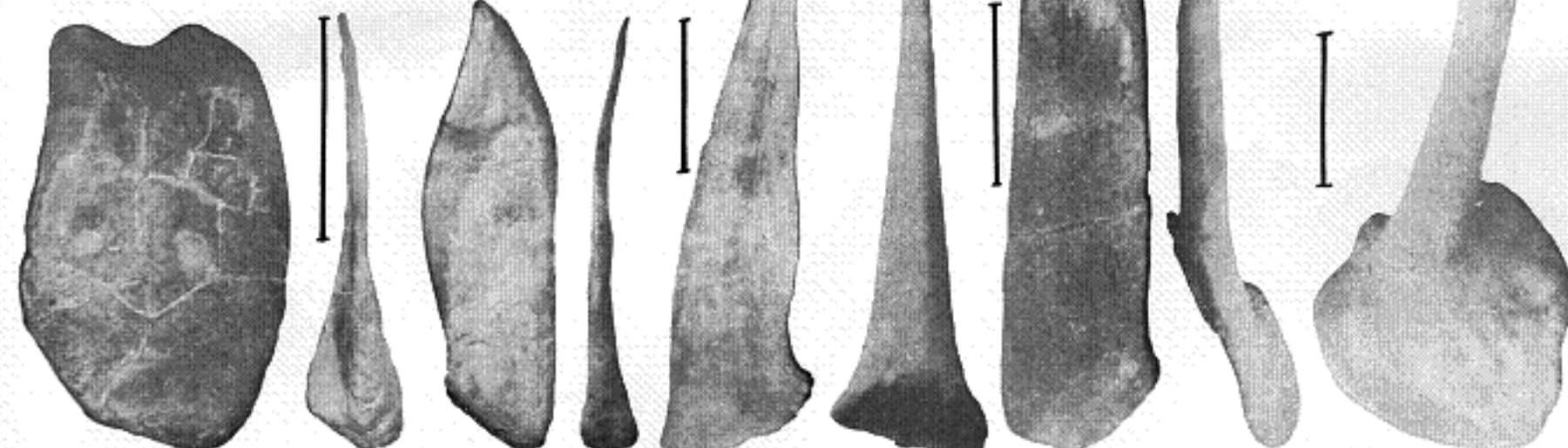
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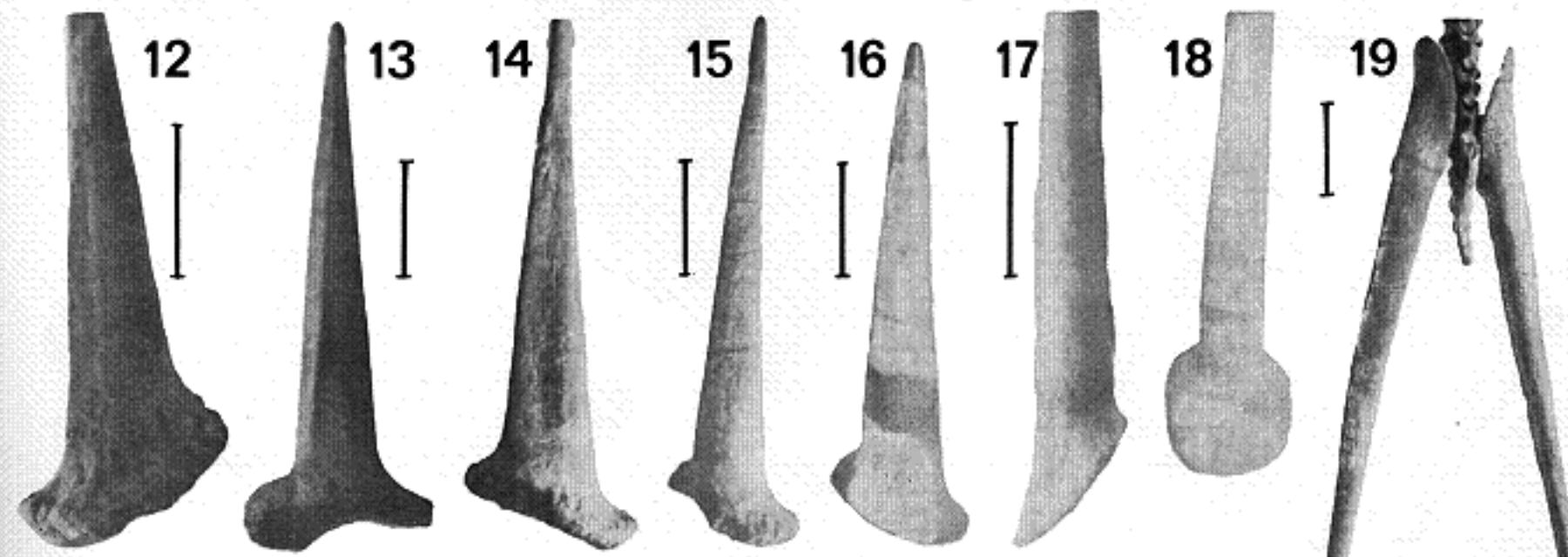


Plate 2

Kentrosaurus aethiopicus from the Upper Jurassic of Tanzania, East Africa.

Figs. 1-6: sacrum with left ilium HMN St500 X 1/8 in: 1 - anterior view; 2 - dorsal view; 3 - ventral view; 4 - posterior view; 5 - left lateral view; 6 - left anterolateral view.

Figs. 7-8: sacrum HMN St773 X 1/6 in: 7 - posterior view; 8 - ventral view (see also Pl. 3, Fig. 4).

Figs. 9-10: sacrum HMN St218 X 1/6: 9 - ventral view with partial ilia; 10 - dorsal view to show bases of sacral ribs and neural canal.

Fig. 11: sacrum HMN St557 X 1/6 in ventral view (see also Pl. 3, Figs. 1-3).

Abbreviations: a = acetabulum; d = dorsosacral vertebra; i = ilium; il = surface for ilium; n = neural canal; ns = neural spine; p = sacral plate; r = additional sacral rib (fifth, borne by first sacral vertebra); rl - 4 = sacral ribs 1 to 4 (borne by sacral vertebra 2 to 5); sl - 5 = sacral vertebra 1 to 5; t = transverse process of first sacral vertebra; tp = transverse process. Scale lines represent 10 cm.

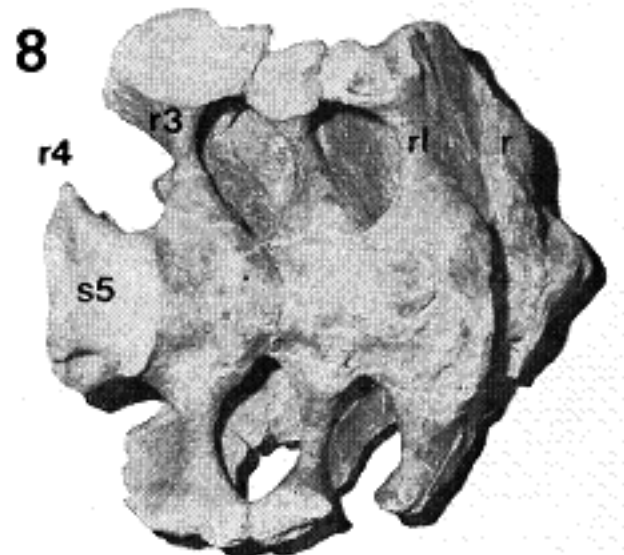
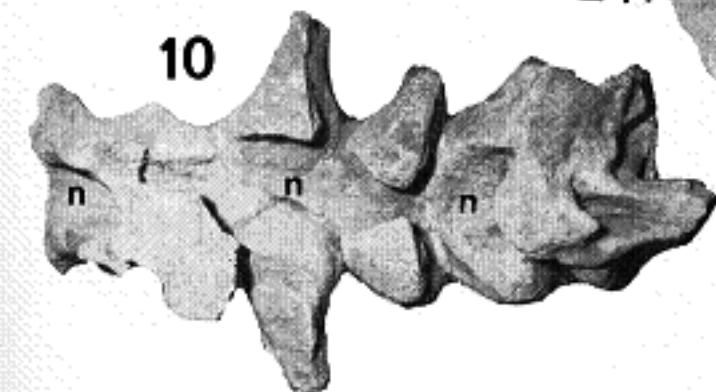
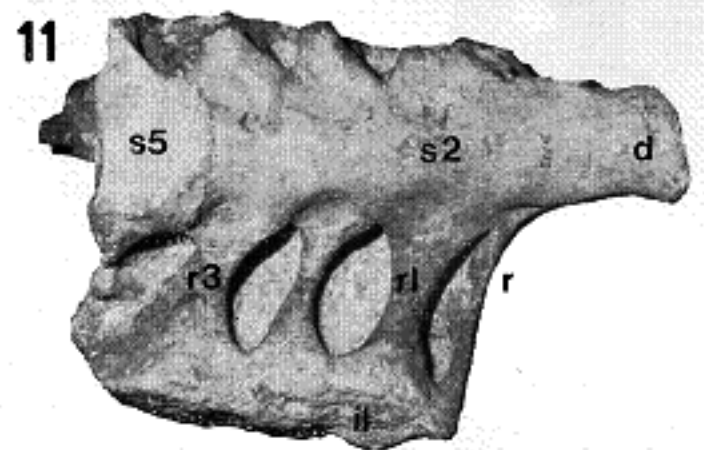
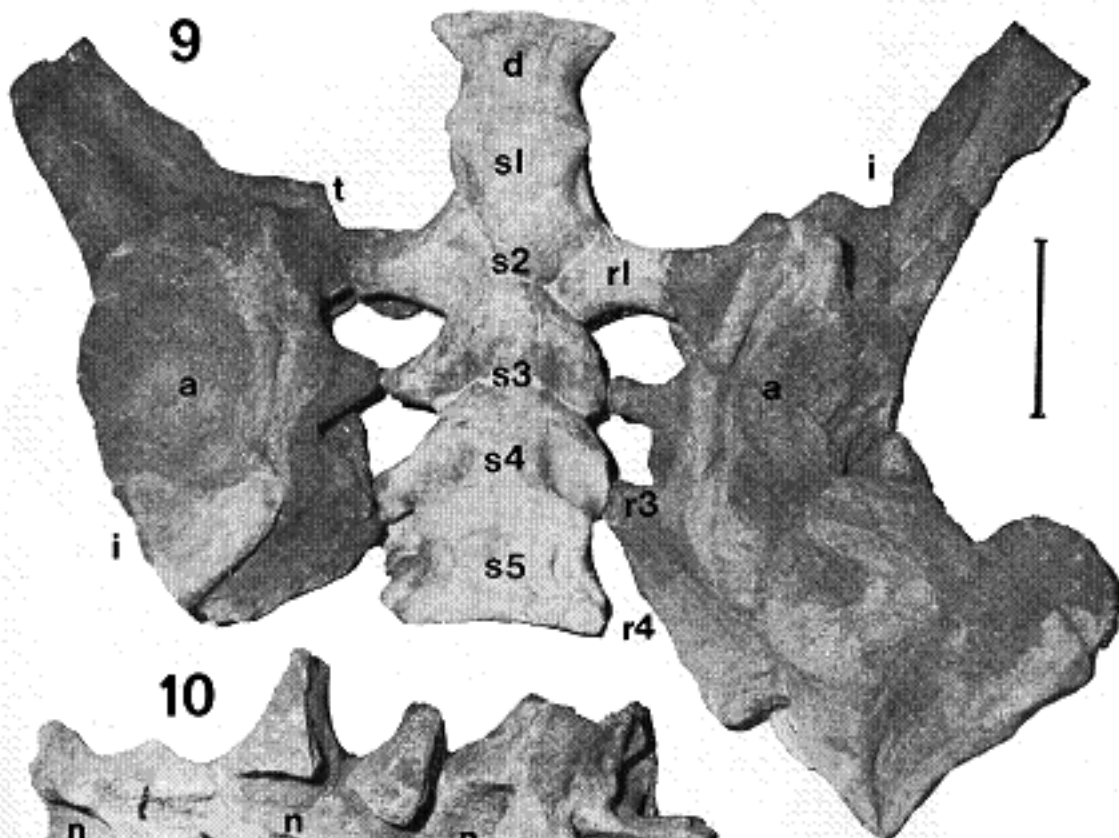
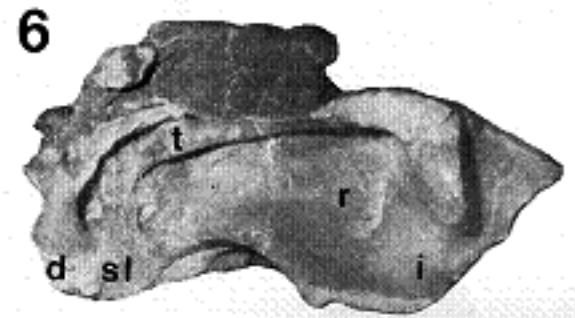
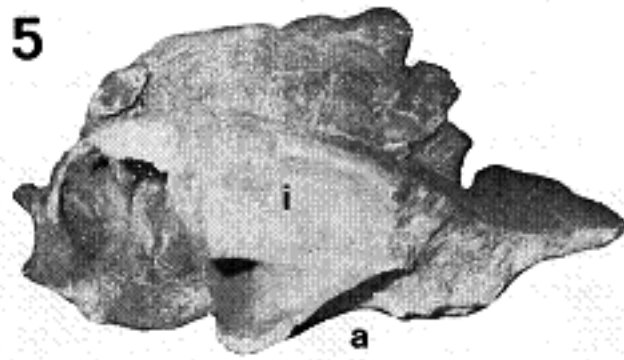
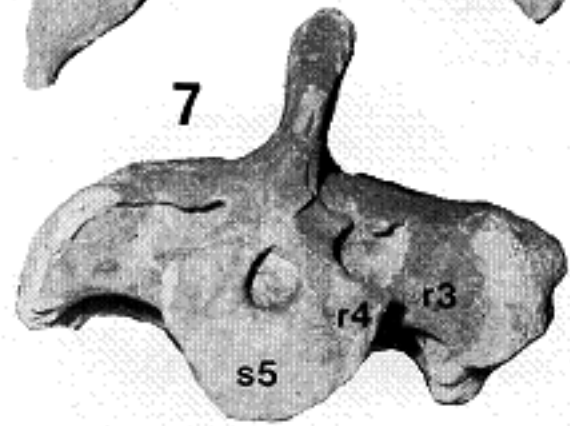
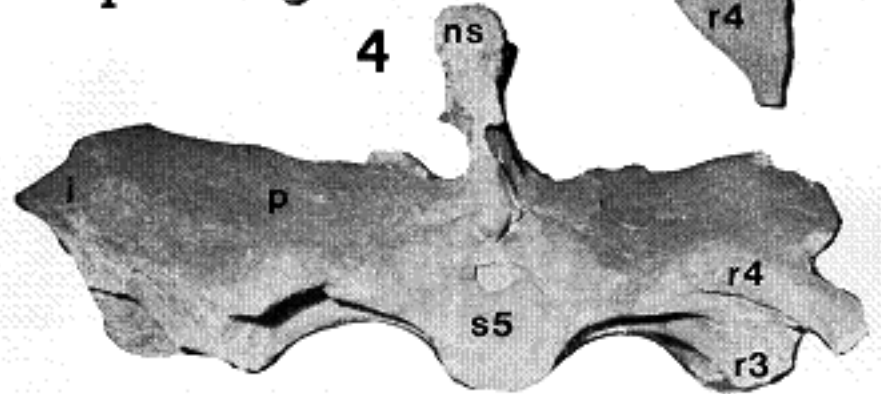
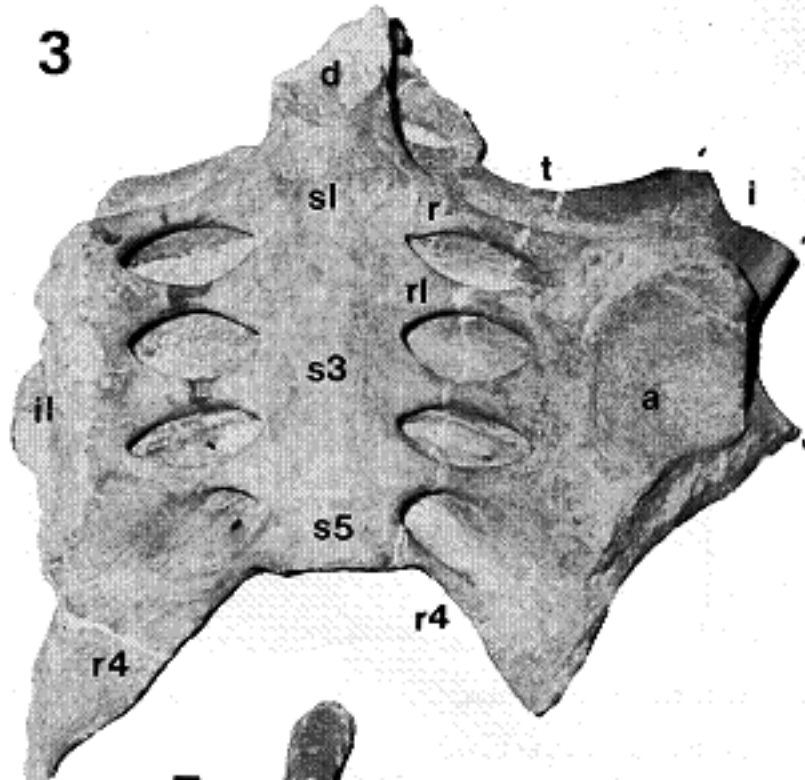
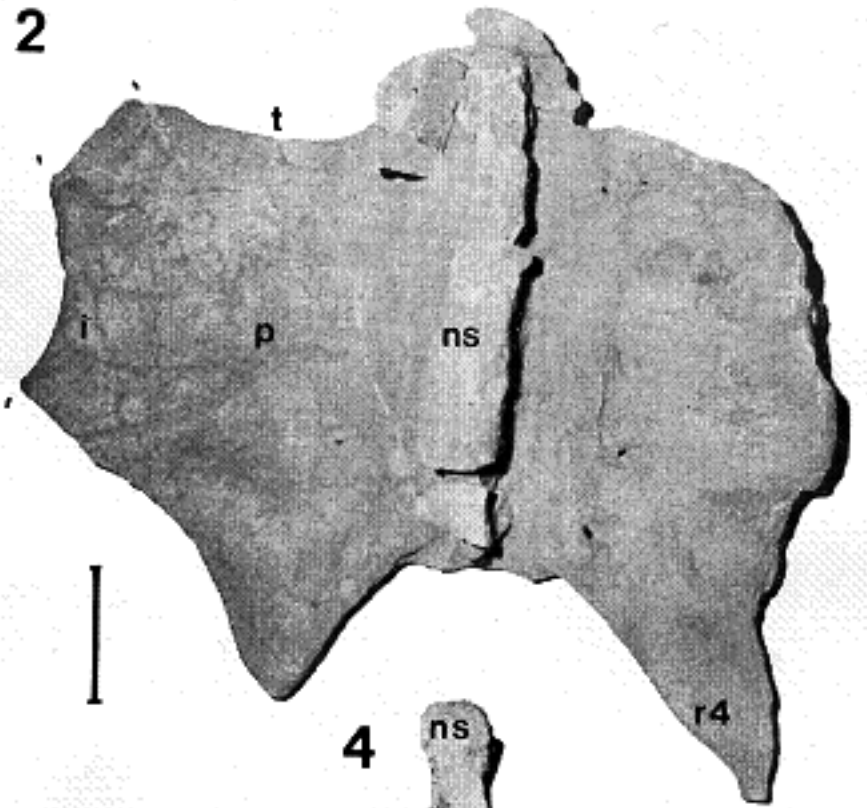
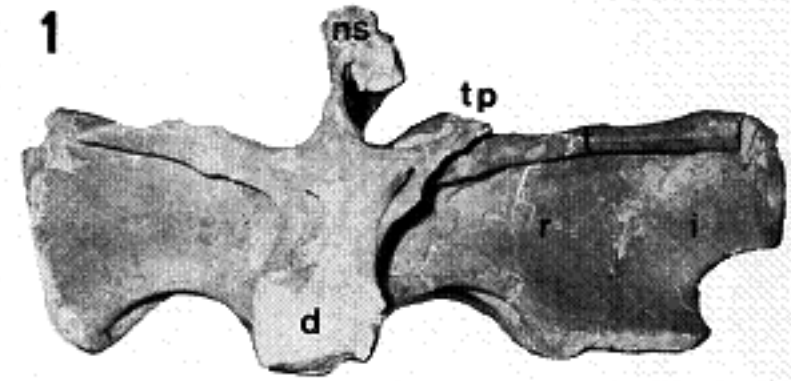


Plate 3

Kentrosaurus aethiopicus from the Upper Jurassic of Tanzania, East Africa.

Figs. 1-3: sacrum HMN St557 X 1/6 in: 1 - left lateral view; 2 - right lateral view; 3 - posterior view (see also Pl. 2, Fig. 11).

Fig. 4: sacrum HMN St773 X 1/6 in right lateral view (see also Pl. 2, Fig. 8).

Fig. 5: sacrum HMN St555 in right lateral view, X 1/6.

Fig. 6: sacrum HMN Ng20 in ventral view, X 1/6.

Figs. 7-10: anterior caudal vertebra, syntype HMN St856 X 1/5 in: 7 - anterior view; 8 - left lateral view; 9 - posterior view; 10 - ventral view.

Figs. 11-16: two associated middorsal vertebrae, holotypes HMN St694 (12, 13, 16) and St695 (11, 14, 15) X 1/5 in: 11, 12 - posterior view; 13, 14 - right lateral view; 15, 16 - anterior view.

For abbreviations see Plate 2. Scale lines represent 10 cm.

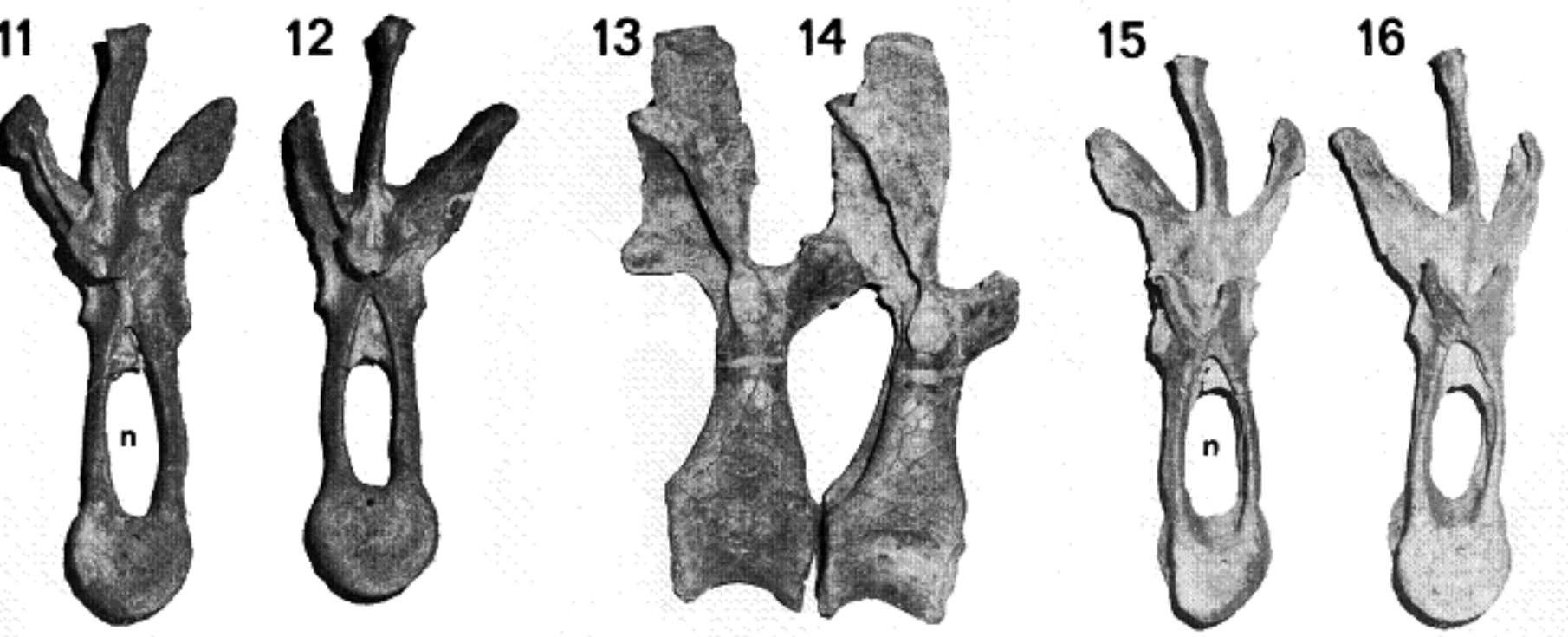
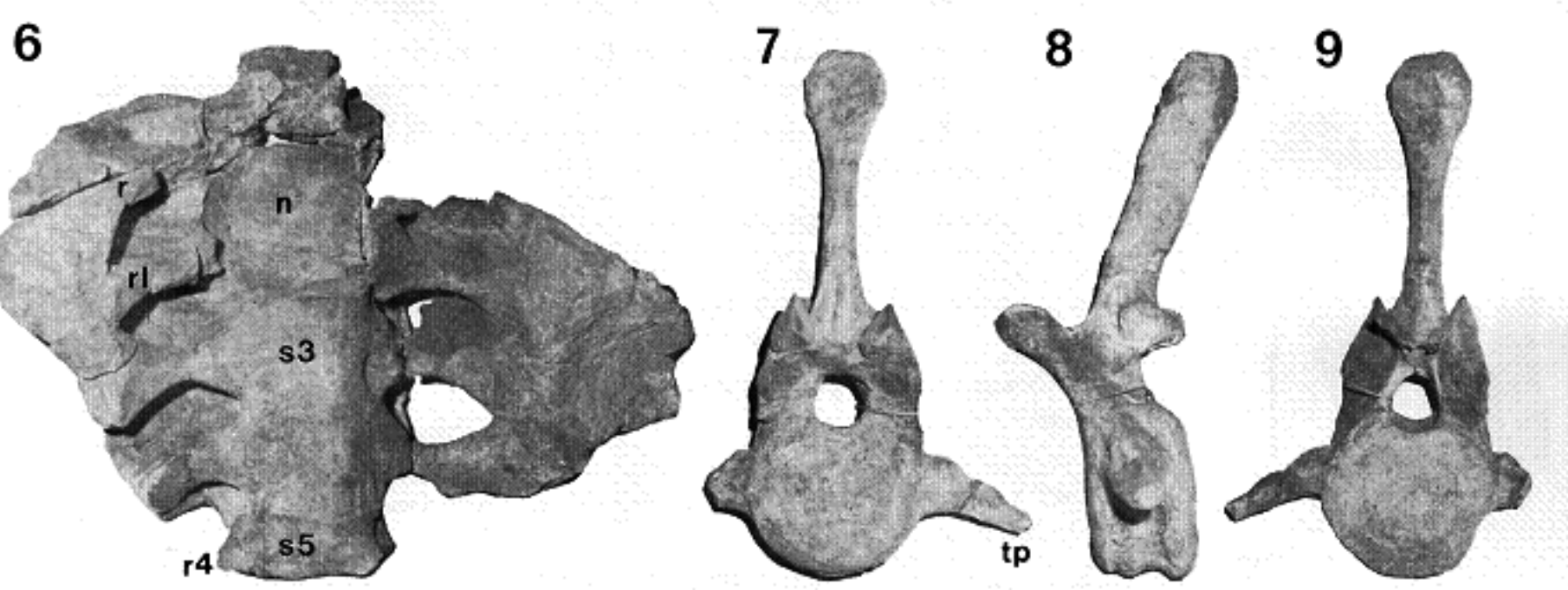
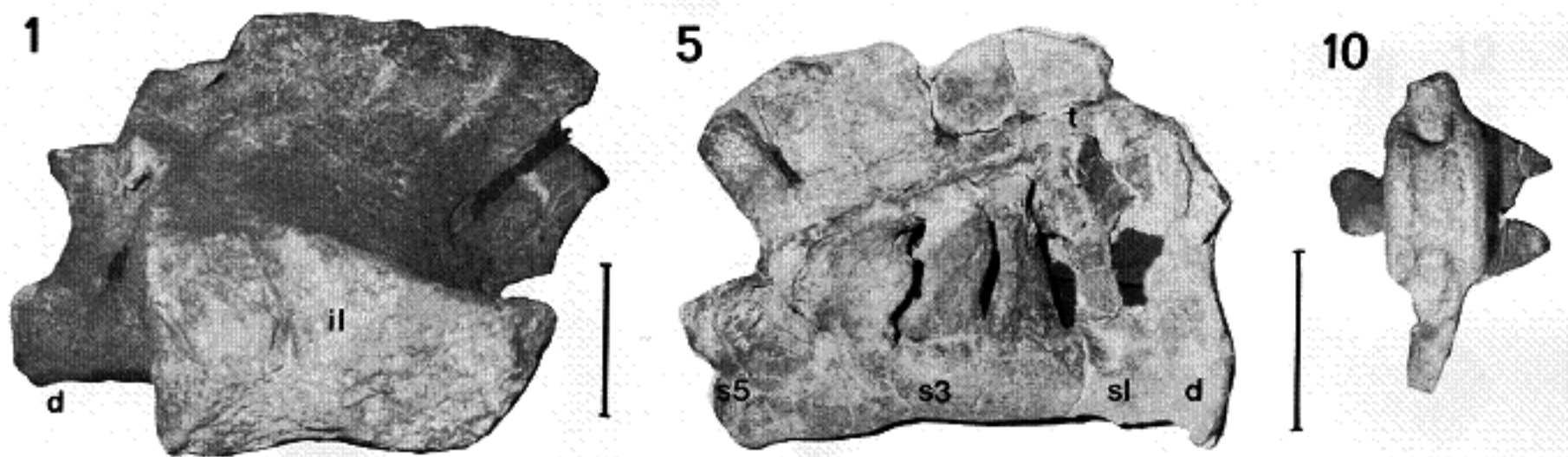
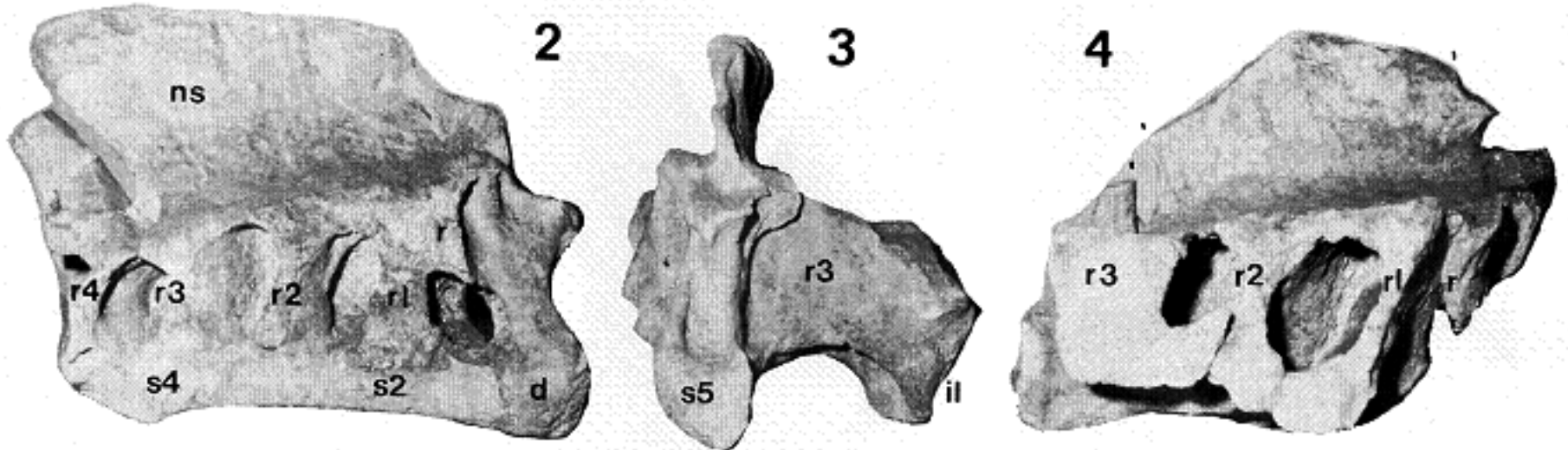


Plate 4

Kentrosaurus aethiopicus from the Upper Jurassic of Tanzania, East Africa.

Figs. 1-3: right humerus UT 1524/1 (was St129) X 1/6 (see also Figs. 1A-F) in: 1 - medial view; 2 - posterior view; 3 - anterior views.

Figs. 4-5: right radius, ulna and proximal carpals HMN MTD in: 4 - medial view; 5 - posteromedial view, X 1.3 & 1.4.

Fig. 6: Left distal end of humerus, radius and ulna HMN MTD (ulna syntype St 461, radius from excavation r, JANENSCH 1925) X 1.2 in anterior view.

Figs. 7-9: Left ilium UT 1524/4 (was St133) X approx. 0.1 (see also Figs. 2A-D) in: 7 - ventral view; 8 - lateral view; 9 - medial view.

Figs. 10-13: Left flat spine, syntype HMN St90 X 0.15 in: 10 - lateral view; 11 - anterior view; 12 - proximal view; 13 - medial view.

Figs. 14-17: right parasacral spine, syntype HMN St345 X 0.15 in: 14 - medial view; 15 - dorsal view; 16 - lateral view; 17 - ventral view.

Figs. 18-19: right parasacral spine, UT 1524/7 X 0.15 in: 18 - ventral view; 19 - dorsal view.

Figs. 20-23: last five caudal vertebrae and terminal pair of long dermal spines, HMN X 0.15 in: 20 - ventral view; 21 - right lateral view; 22 - dorsal view; 23 - left lateral view.

Fig. 24: terminal caudal spine HMN MTD in right lateral view, X 0.1 (see also Pl. 1, Fig. 19).

For labels of structures see Text-figures 1 and 2. Scale lines represent 10 cm.

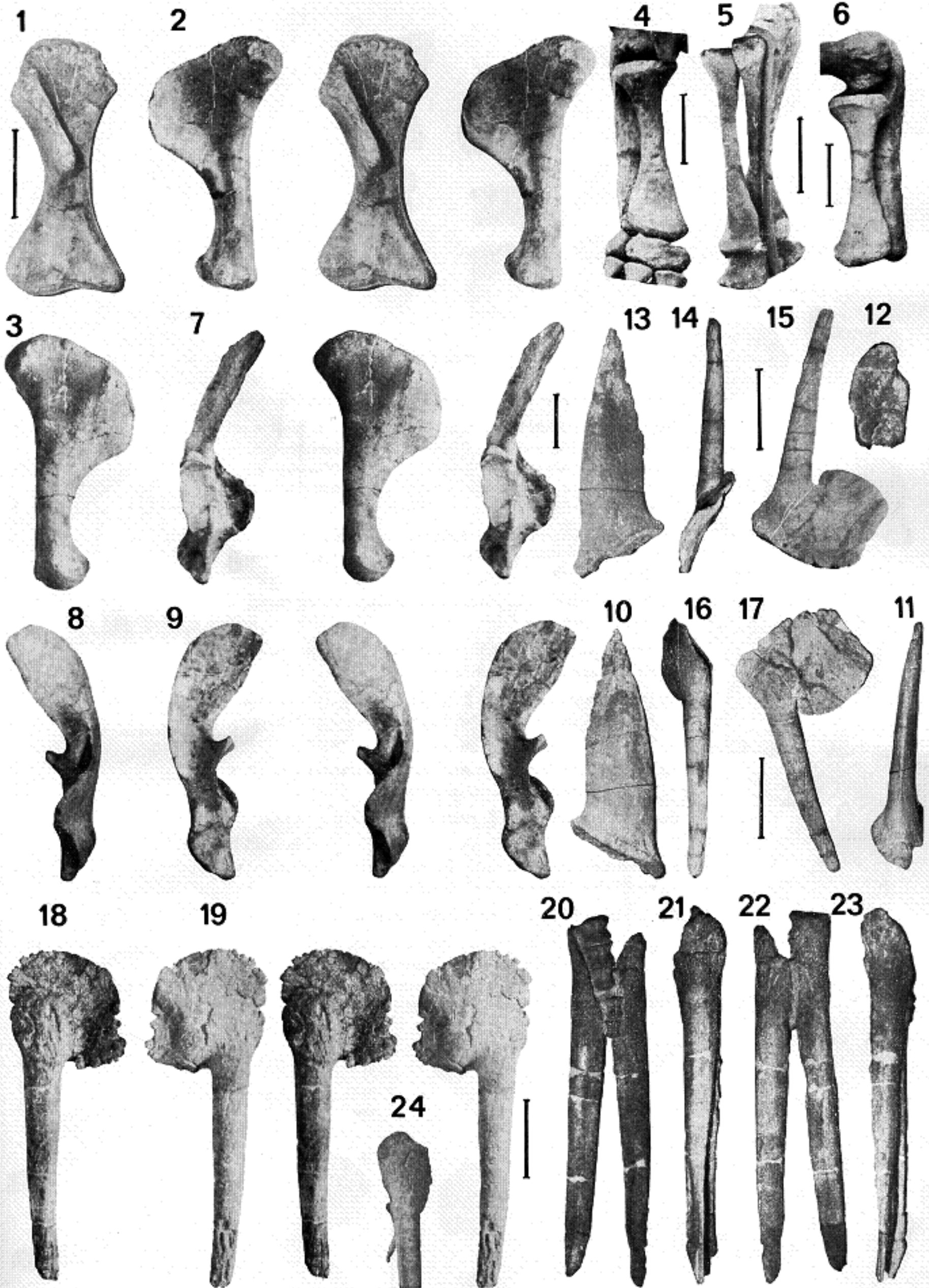


Plate 5

Kentrosaurus aethiopicus from the Upper Jurassic of Tanzania, East Africa.

Figs. 1-7: right pes HMN K:112 X 0.25: 1-2 - complete pes in dorsal (1) and ventral views (2); 3 - metatarsal II in medial and proximal views; 4 - metatarsal III in proximal and lateral views; 5 - metatarsal IV in proximal and medial views; 6 - metatarsal II in distal view; 7 - metatarsal III in distal view.

Figs. 8-12: right metacarpal III UT 1524/8 (was WJ8536) X 0.3 in: 8 - medial view; 9 - lateral view; 10 - distal view; 11 - anterior view; 12 - posterior view.

Fig. 13: right humerus, radius, ulna and proximal carpals, HMN MTD in anterior view, X approx. 1/7.

Fig. 14: syntypic left humerus (HMN St106) and ulna (HMN St461) plus radius (from excavation r, JANENSCH 1925) in anterior view, X approx. 1/7.

Fig. 15: left lateral view of pelvic girdle and proximal end of femur HMN MTD (ilium St446, pubis syntype St758, femur syntype St463) X approx. 0.1.

Fig. 16: right lateral view of pelvic girdle and proximal end of femur HMN MTD (ilium St439, pubis St462) X approx. 0.1.

Figs. 17-18: right ischium, syntype HMN St335 X 0.15 in 17 - lateral view; 18 - medial view.

Figs. 19-21: Left sixth dermal spine plate HMN MTD (St546) X 0.24 in: 19 - medial view; 20 - anterior view; 21 - lateral view.

Fig. 22: Left tenth dermal spine HMN MTD in anterior view, X 1/6.

Abbreviations: a - anterior process of pubis; c - carpals; f - proximal end of femur; h - humerus; i - ilium; il - surface for ilium; m - metacarpals; p - phalanges; r - radius; s - parasacral spine; u - ungual phalanx; ul - ulna; 2, 4 - digits 2 and 4. Scale lines represent 4 cm (1-12) or 10 cm.

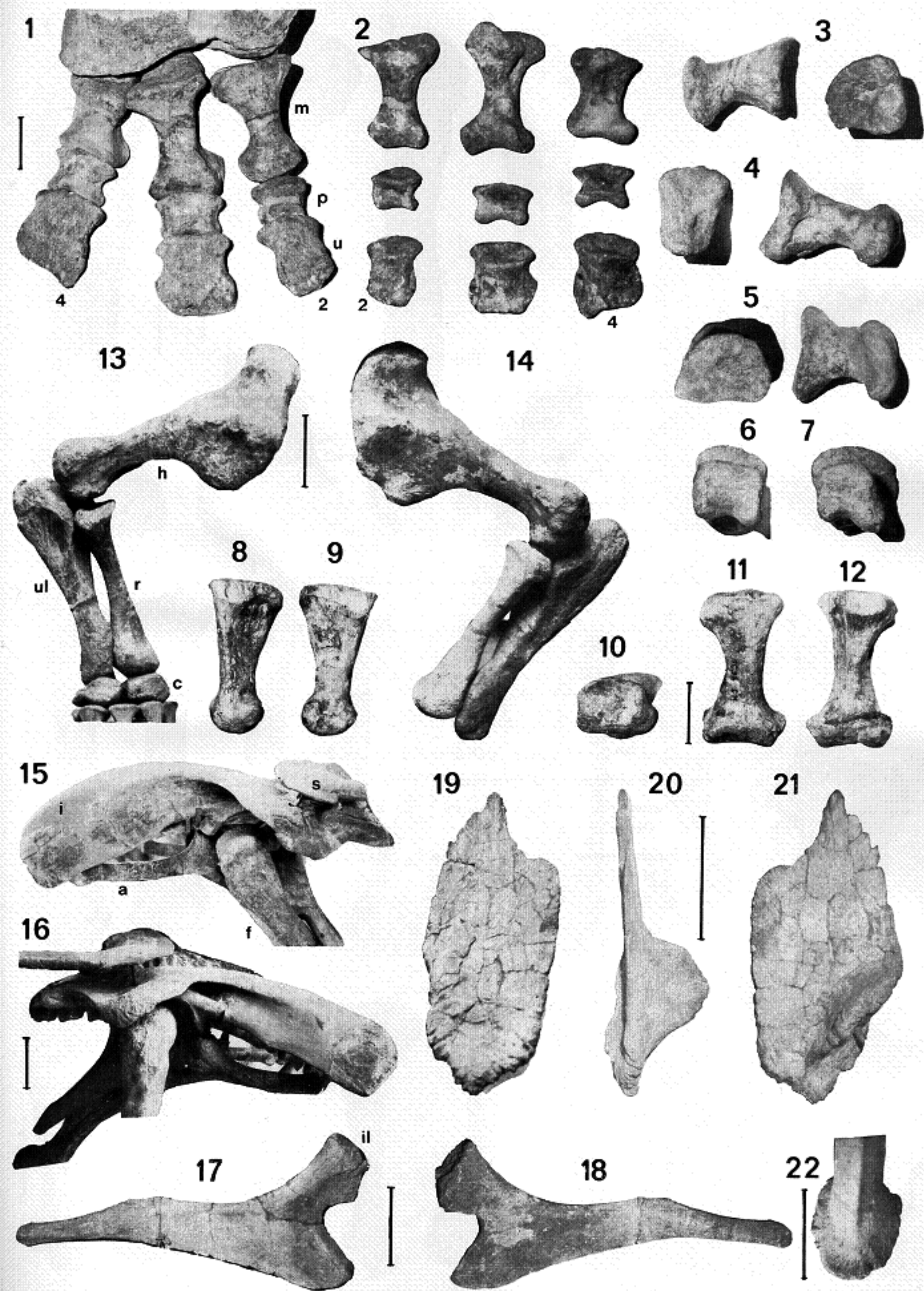


Plate 6

Kentrosaurus aethiopicus from the Upper Jurassic of Tanzania, East Africa.

Fig. 1: right femur, HMN MTD in anterior view, X 0.16

Figs. 2-5: right femur, HMN bbl X 1/8 in: 2 - anterior view; 3 - medial view; 4 - lateral view; 5 - posterior view.

Fig. 6: left femur HMN St 463 in postero lateral view, X 0.16.

Figs. 7-9: right femur, HMN St 331 X 1/6 in: 7 - lateral view; 8 - anterior view; 9 - medial view.

Fig. 10: right tibia, fibula, astragalus and calcaneum HMN MTD in anterior view, X 0.15.

Figs. 11-12: left tibia, fibula, astragalus and calcaneum HMN MTD X 0.15 in: 11 - anterior view; 12 - lateral view.

Figs. 13-15: left tibia UT 1524/5 X 0.16 (see also Figs. 2Q-V) in 13 - lateral view; 14 - posterior view; 15 - anterior view.

Fig. 16: right scapulocoracoid HMN MTD in lateral view, X 0.1.

Fig. 17: left humerus, syntype HMN St106 in dorsal view, X 0.15.

Fig. 18: Left radius UT 1524/3 in posterior view (shown upside down) X 1/5.

Abbreviations: c = coracoid; f = fourth trochanter; fi = fibula; s = scapula; t = tibia.

For structures in figures 1-15 and 17 see Text-figs. 1 and 2. Scale lines represent 10 cm.

