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SAUROPOD DINOSAURS FROM THE EARLY CRETACEOUS OF MALAWI, AFRICA

Elizabeth M. Gomani

ABSTRACT

At least two titanosaurian sauropod taxa have been discovered in the Early Cretaceous Dinosaur Beds of northern Malawi, Africa. One of these, *Malawisaurus dixeyi*, is represented by cranial elements, 18 cervical vertebrae, 10 dorsal vertebrae, a sacrum, 51 caudal vertebrae, 24 chevrons, pectoral elements, pelvic elements, and dermal armor, all of which are described and illustrated. The cranial elements indicate that *Malawisaurus* had a short, high macronarian skull. *Karongasaurus gittelmani* gen. et sp. nov. is more derived than *Malawisaurus* but is represented only by a dentary and isolated teeth. Some indeterminate vertebrae may also belong to *Karongasaurus* or another taxon, but not to *Malawisaurus*. The shape of the teeth and jaw, and the restriction of teeth toward the anterior part of the jaw in *Karongasaurus* are different from *Malawisaurus* and suggest that *Karongasaurus* had a long, low skull. Thus, the sauropods from the Malawi Dinosaur Beds demonstrate extreme morphological variation in titanosaurian jaws, teeth, and probably skull shape. Variation in tooth and skull morphology, because of its relevance to feeding, was likely of significance in resource partitioning among titanosaurian sauropods in the Early Cretaceous ecosystem.

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KEY WORDS: Africa, Cretaceous, *Karongasaurus*, Malawi, *Malawisaurus*, Sauropod

PE Article Number: 8.1.27

Submission: 22 November 2004. Acceptance: 6 March 2005

INTRODUCTION

Titanosaurian dinosaurs were one of the most widely distributed groups of sauropods during the Cretaceous Period. At least two, perhaps three, taxa of sauropods have been discovered in Malawi including *Malawisaurus*, which is considered to belong to the Titanosauria (Bonaparte and Coria 1993; Wilson 2002; Wilson and Sereno 1998), and a new taxon. The goals of this study are to describe the material of sauropod dinosaurs from Malawi, which is mostly *Malawisaurus*, and to name the new sauropod taxon, which is repre-

Gomani, Elizabeth M., 2005. Sauropod Dinosaurs from the Early Cretaceous of Malawi, Africa, *Palaeontologia Electronica* Vol. 8, Issue 1; 27A:37p, 6.9MB;
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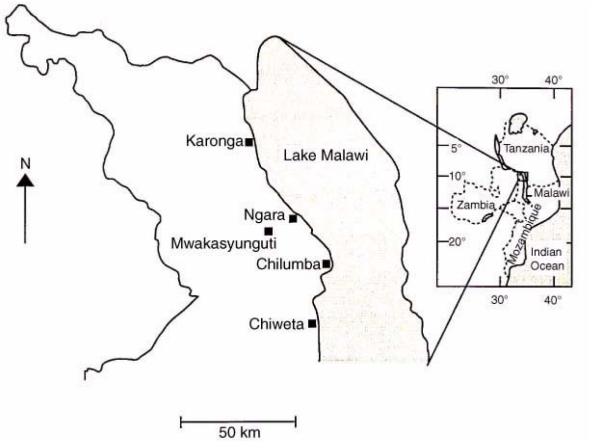

Figure 1. Location map of the Mwakasyunguti area, Karonga District, Malawi, Africa.

sented by a dentary, isolated teeth, and possibly vertebrae. *Malawisaurus* has not previously been fully described and illustrated although it has been incorporated into numerous phylogenetic analyses.

All the specimens described here were collected from the same area of the Dinosaur Beds (Dixey 1928; Jacobs et al. 1990, 1992) near Mwakasyunguti, Karonga District, northern Malawi (Figure 1). The Dinosaur Beds are considered to be of Early Cretaceous (?Aptian) age, based on biochronology (Colin and Jacobs 1990) and regional proximity to carbonatites (K-Ar dates of 123 + 3 to 111 + 13.1 Ma) to the north and south of the study area (Pentel'kov and Voronovsky 1979; Eby et al. 1995).

Materials and Methods

Fossils were collected in 1987, 1989, 1990, and 1992 field expeditions by the Malawi Dinosaur Project (MDP), a joint project between the Malawi Department of Antiquities and Southern Methodist University (SMU), Dallas, Texas, USA. The project opened up 17 quarries designated by the prefix CD followed by a sequential quarry number. More than half the specimens presented here were collected from CD-9 (Figures 2 and 3). The specimens collected by the MDP and utilized in this study are listed in Table 1. The specimens are catalogued as Mal followed by a number. Numbers following catalogue numbers indicate individual elements that were articulated or associated in the field. Specimens referred to *Malawisaurus* in the South African Museum and in the Natural History Museum, London, were also examined. Taxa that are well known, or have comparable elements to those from Malawi, or are known from other African regions, were used for comparison (Appendix 1). Anatomical and institutional abbreviations are listed in Appendix 2.

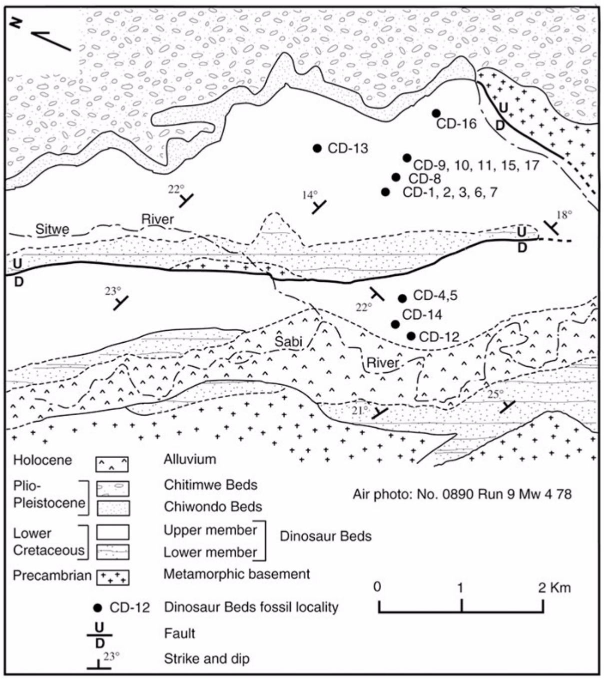

Figure 2. Geologic map of the Mwakasyunguti area showing location of fossil sites, modified from Jacobs et al. (1996) and Winkler et al. (2000).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen 1842
SAUROPODA Marsh 1878
TITANOSAURIA Bonaparte and Coria 1993
MALAWISAURUS Jacobs, Winkler, Downs, and Gomani 1993

Type Species. *Malawisaurus dixeyi* (Haughton 1928)

Malawisaurus dixeyi (Haughton 1928)
Figures 4-27, Tables 2-8

Emended Diagnosis

Malawisaurus is characterized by high-angled premaxillae; posteriorly broad, angled infratemporal fenestrae; short and divergent basipterygoid processes; dentary with 15 alveoli that extend two thirds the length of the element; thin splenial with a spenial foramen; broad but not spoon-shaped teeth with high-angled wear facets; undivided cervical neural spines and pleurocoels; cervical prezygapophyses extend beyond the anterior end of the centrum; presence of pre- and post-spinal laminae in distal cervicals; ribs in proximal and middle cervicals extend beyond the end of the succeeding centrum; elongate, eye-shaped pleuro-

Table 1. Specimens and specimen localities of sauropods from the Mwakasyunguti area, northern Malawi.

Taxon	Element	Specimen number	Locality
Malawisaurus	Basicranium	Mal-202-1	CD-9
Malawisaurus	Parietals	Mal-202-2, Mal-202-3	CD-9
Malawisaurus	Ectopterygoid	Mal-215	CD-9
Malawisaurus	Jugal	Mal-44	CD-9
Malawisaurus	Quadrate	Mal-203	CD-9
Malawisaurus	Premaxilla	Mal-6	CD-9
Malawisaurus	Maxillary fragment	Mal-106	CD-9
Malawisaurus	Dentary	Mal-174	CD-9
Malawisaurus	Splenial	Mal-284	CD-9
Malawisaurus	Isolated teeth	Mal-8, Mal-9, Mal-176, Mal-193-3, Mal-197-33, Mal-253, Mal-270, Mal-273, Mal-311	CD-9
		Mal-274	CD-10
Malawisaurus	Cervical vertebrae	Mal-180, Mal-187-1, Mal-193-1, Mal-243, Mal-244, Mal-245, Mal-246, Mal-278-1 to Mal-278-3, Mal-280-1 to Mal-280-6, Mal-291, Mal-301	CD-9
Malawisaurus	Isolated cervical ribs	Mal-64, Mal-146, Mal-147, Mal-149, Mal-162; Mal-187-2	CD-9
Malawisaurus	Dorsal vertebrae	Mal-181, Mal-182, Mal-236, Mal-237, Mal-238, Mal-239, Mal-240, Mal-241, Mal-242, Mal-283	CD-9
Malawisaurus	Dorsal ribs	Mal-282-1, Mal-282-2, Mal-285, Mal-292, Mal-293, Mal-294, Mal-295, Mal 296, Mal-297, Mal-298, Mal-299, Mal-308	CD-9
Malawisaurus	Sacrum	Mal-277-1	CD-10
Malawisaurus	Caudal vertebrae	Mal-233	CD-4
		Mal-2, Mal-185, Mal-191, Mal-197-1 to Mal-197-21, Mal-198, Mal-200, Mal-206, Mal-223, Mal-224, Mal-231, Mal-279-1 to Mal-279-2	CD-9
		Mal-186-1 to Mal-186-5, Mal-192-1 to Mal-192-4, Mal- 225-1 to Mal-225-4, Mal-226, Mal-228, Mal-229, Mal-232-1	CD-10
		Mal-227	CD-15
Malawisaurus	Chevrons	Mal-151	CD-4
		Mal-152-1, Mal-152-2, Mal-183-2, Mal-194, Mal-197-22 to Mal-197-31, Mal-219, Mal-234, Mal-287	CD-9
		Mal-195, Mal-220, Mal-277-2, Mal-277-3, Mal-288, Mal-310	CD-10
Malawisaurus	Sternal plates	Mal-188-1, Mal-188-2	CD-9
Malawisaurus	Coracoid	Mal-235	CD-9
Malawisaurus	Humeri	Mal-221, Mal-316, Mal-317	CD-9
		Mal-289	CD-10
Malawisaurus	Ulnae	Mal-218, Mal-309	CD-9
		Mal-190	CD-10
Malawisaurus	Radii	Mal-160	CD-11
		Mal-41	CD-12
Malawisaurus	Metacarpals	Mal-144, Mal-196, Mal-208-1, Mal-208-2, Mal-209, Mal-214	CD-9
Malawisaurus	Ischia	Mal-42, Mal-183-1	CD-9
		Mal-184	CD-10

coels on dorsal vertebrae; infradiapophyseal laminae of distal dorsals not forked; six sacral vertebrae; sacral neural spines fused into a dorsal plate that overhangs the neural arches; strongly procoelous proximal but platycoelous middle and distal caudals; proximal caudals with well-developed pre-spinal and post-spinal laminae; at least five V-shaped middle chevrons; and metacarpals with distal articular facets.

Table 1 (continued).

Taxon	Element	Specimen number	Locality
Malawisaurus	Proximal femur	Mal-20	CD-10
Malawisaurus	Fibula	Mal-189	CD-9
Malawisaurus	Tibia	Mal-207	CD-13
Malawisaurus	Metatarsal III?	Mal-145	CD-12
Malawisaurus	Metatarsal V	Mal-210	CD-9
Malawisaurus	Phalanges	Mal-211, Mal-212, Mal-213	CD-9
Malawisaurus	Dermal Armor	Mal-204	CD-9
Karongasaurus	Dentary	Mal-175	CD-9
Karongasaurus	Isolated teeth and tooth fragments	Mal-7, Mal-10, Mal-11, Mal-12, Mal-13, Mal-14, Mal-15, Mal-16, Mal-33, Mal-36, Mal-39, Mal-153, Mal-156, Mal-267, Mal-268, Mal-271, Mal-307, Mal-318,	CD-9
		Mal-319, Mal-324, Mal-269, Mal-272	CD-10
Titanosauridae gen et sp. indet.	Caudal vertebra	Mal-5	CD-4
Titanosauridae gen et sp. indet.	Caudal vertebra	Mal-1, Mal-3, Mal-222, Mal-230	CD-9

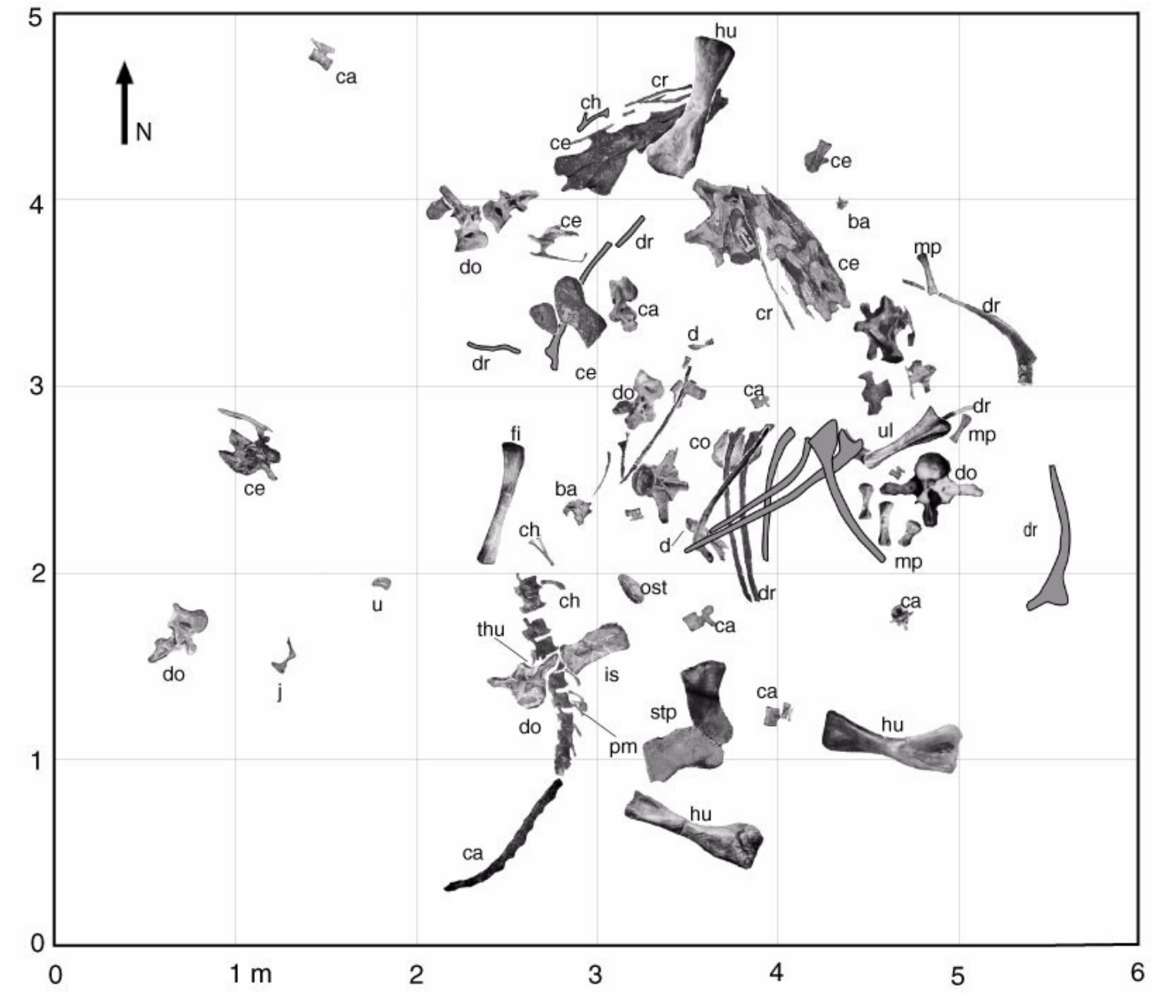

Figure 3. Quarry map of CD-9, Dinosaur Beds, Malawi. Elements illustrated are the larger specimens from the basal muddy sand (Winkler et al. 2000). Elements photographed in the field and laboratory. Grid is in meter squares. Abbreviations as in Appendix 2. Modified from Winkler et al. (2000).

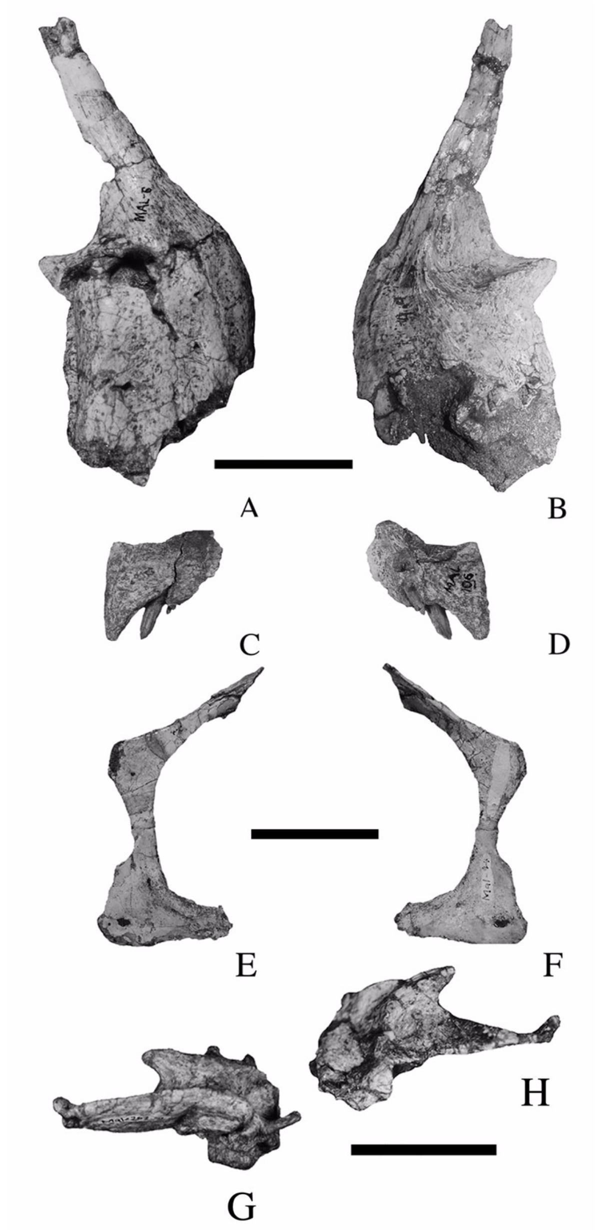

Figure 4. Premaxilla, fragmentary maxilla, jugal, and parietal of *Malawisaurus dixeyi.* A and B, right premaxilla (Mal-6); C and D, left maxillary fragment (Mal-106); E and F, right jugal (Mal-44); G and H, left parietal (Mal-202-2). A, C, and F, lateral view; B, D, and E, medial view; G, dorsal view; H, ventral view. A and B; C-F; and G and H, same scale. Scale bars = 40 mm.

Taxonomic Note

Malawisaurus dixeyi was initially named *Gigantosaurus dixeyi* by Haughton (1928) who considered the specimen to be closely related to Tanzanian specimens that were referred to *Gigantosaurus* (Fraas 1908). However, this generic name was preoccupied so the generic name for the Tanzanian specimens was changed to *Tornieria* (Sternfield 1911). Without justification, *G. dixeyi* was referred to as *Tornieria dixeyi*. The generic name *Tornieria* was later changed to *Janenschia* by Wild (1991). The specimens from Malawi that passed through these generic name changes or were collected subsequently are from the same area and same rock unit appear specifically identical, but are distinct from *Janenschia* from older beds in Tanzania. Therefore, Jacobs et al. (1993) erected a new generic name, *Malawisaurus,* to accommodate the Malawi taxon.

Geologic Age and Distribution

Early Cretaceous, Mwakasyunguti area, Karonga District, Malawi, Africa.

Description

Premaxilla. Except for the partial braincase that includes several bones, all cranial material was disarticulated. The right premaxilla (Mal-6; length = 45 mm; height = 65 mm; Figure 4A-B) with three unerupted teeth and four alveoli was briefly described by Jacobs et al. (1993, figure 1a). The body of the premaxilla is subrectangular in lateral view. The median symphysis is broad and oblique in medial view. The anterior margin of the premaxillary body rises nearly vertically from the dental margin in lateral view. The nasal process is narrow, anteroposteriorly flattened, dorsally oriented, and borders the large external naris anteriorly (Jacobs et al. 1993). The maxillary suture is tall and is immediately below the external naris. The premaxilla has a dorsal process and a dorsoventral groove ventral to the maxillary process that suggest the presence of a dorsoventral process of the maxilla.

Maxilla. The maxilla (Mal-106; 4C-D) is represented by a left anterior fragment with two replacement teeth present. The first tooth alveolus is 60 mm from the premaxilla-maxilla contact. The teeth are aligned nearly parallel to the anteroposterior axis of the preserved maxilla.

Jugal. A right jugal (Mal-44; Figure 4E-F) is a small, thin (width = 30 mm; height = 120 mm) bone, similar to that of *Camarasaurus lentus* (Madsen et al. 1995, figures 1e and 6c) in lateral view. The quadratojugal process is mediolaterally flattened while the postorbital process is mediodorsally curved to accommodate the jugal process of the postorbital. The posterodorsal curvature of the postorbital process suggests that the jugal extended along the posterodorsal margin of the postorbital. The infratemporal fenestra is obtuse-angled anteriorly as suggested by the shape of the posterior margin of the jugal.

Parietals. The parietals are small (left, Mal-202-2; length = 70 mm; Figure 4G-H; right, Mal-202-3; length = 67 mm). The supraoccipital and exoccipital articular surfaces are shallow depressions. The elements suggest that the supratemporal fenestrae are elongate mediolaterally. Both were found associated with the basicranium.

Quadrate. The right quadrate (Mal-203; 5A-D) is well preserved. The shaft is 160 mm high and nearly vertical. The head of the quadrate is rounded and is gradually inclined posteriorly. The posterior surface has a tall deep ovoid fossa (height = 70 mm; width = 50 mm; 45 mm into the pterygoid flange). The medial and lateral walls of the fossa are 5 mm thick. The fossa is at the dorsoventral midpoint of the shaft. The pterygoid process is centrally placed on the shaft, thin mediolaterally, and triangular in lateral view. The articular surface is suboval in ventral view.

Ectopterygoid. A left ectopterygoid (Mal-215; Figure 5E-F) is incomplete. It is lunate in lateral view. The medial surface has a well-developed groove for the palatine bone while the lateral surface has a well-developed contact surface for the maxilla.

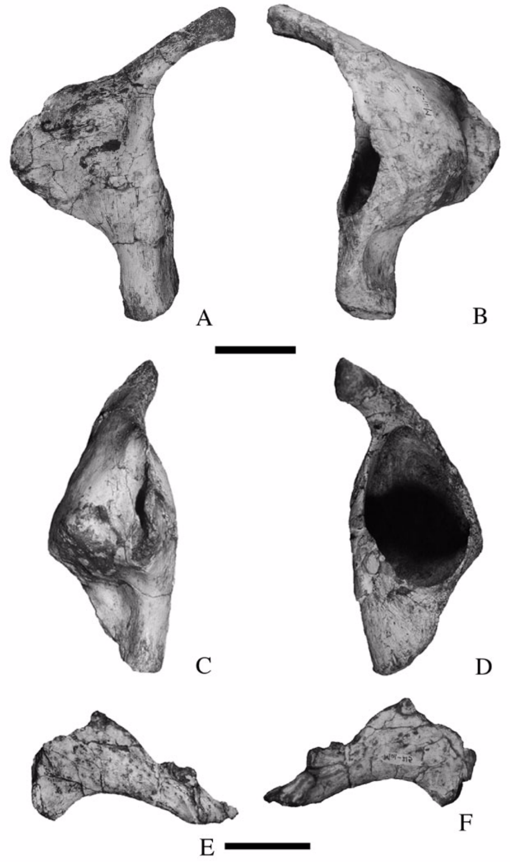

Figure 5. Quadrate and ectopterygoid of *Malawisaurus dixeyi.* A-D, right quadrate (Mal-203); E-F, left ectopterygoid (Mal-215). A and F, medial view; B and E, lateral view; C, anterior view; D, posterior view. A-D, and E-F, same scale. Scale bars = 40 mm.

Basicranium. The braincase (Mal-202-1; width at paraoccipitals = 140 mm; Figure 6) is represented by basioccipital, basisphenoid, exoccipital, laterosphenoid-orbitosphenoid complex, opisthotic, prootic, and supraoccipital. The bones are completely ossified, and their sutures are indistinct. The pituitary fossa is rounded and large. The canal for the optic nerve (II) is small, circular, and is directed anterolaterally. Posterior to the canal for the optic nerve, the rounded canal for the oculomotor nerve (III), and the trochlear canal for the trochlear nerve (IV) are found in sequence. The opening for the trigeminal nerve (V) is large and subcircular. A small notch on the laterosphenoid margin of the trigeminal canal probably carried the ophthalmic branch of the trigeminal nerve. Anterior and posterior grooves exit ventral to the canal for the trigeminal nerve. The anterior groove probably corresponds to the maxillary branch whereas the posterior groove corresponds to the mandibular branch of the nerve. Posterior to the canal for the trigeminal nerve is a small dorsoventrally elongate canal for the facial nerve (VII). In *Camarasaurus*, the trigeminal nerve and facial nerve openings are on the basisphenoid-laterosphenoid boundary (Madsen et al. 1995). Thus, these canals are assumed in *Malawisaurus* as delineating the basisphenoid-laterosphenoid boundary. The laterosphenoid is flat and projects laterally from the braincase wall. Ventral to the fenestra ovalis, in the middle ear region, is the metotic foramen (called the jugular foramen by Berman and McIntosh 1978) for cranial nerves IX to XI (glossopharyngeal, vagus, and spinal accessory nerves), and probably the jugular vein. The metotic foramen is mediolaterally narrow and elongate. The hypoglossal canal for cranial nerve XII is mediolaterally elongate. The foramen magnum is ovoid and higher (28 mm) than wide (20 mm). It is slightly larger than the occipital condyle. The occipital condyle is hemispherical but concave dorsally.

With the basicranium (Mal-202-1) oriented with the supraoccipital vertical, which is considered the normal orientation (Salgado and Calvo 1997), the occipital condyle projects and faces posteroventrally, the paroccipital processes project anteroventrally, and the basipterygoid processes project ventrally. The paroccipital processes are

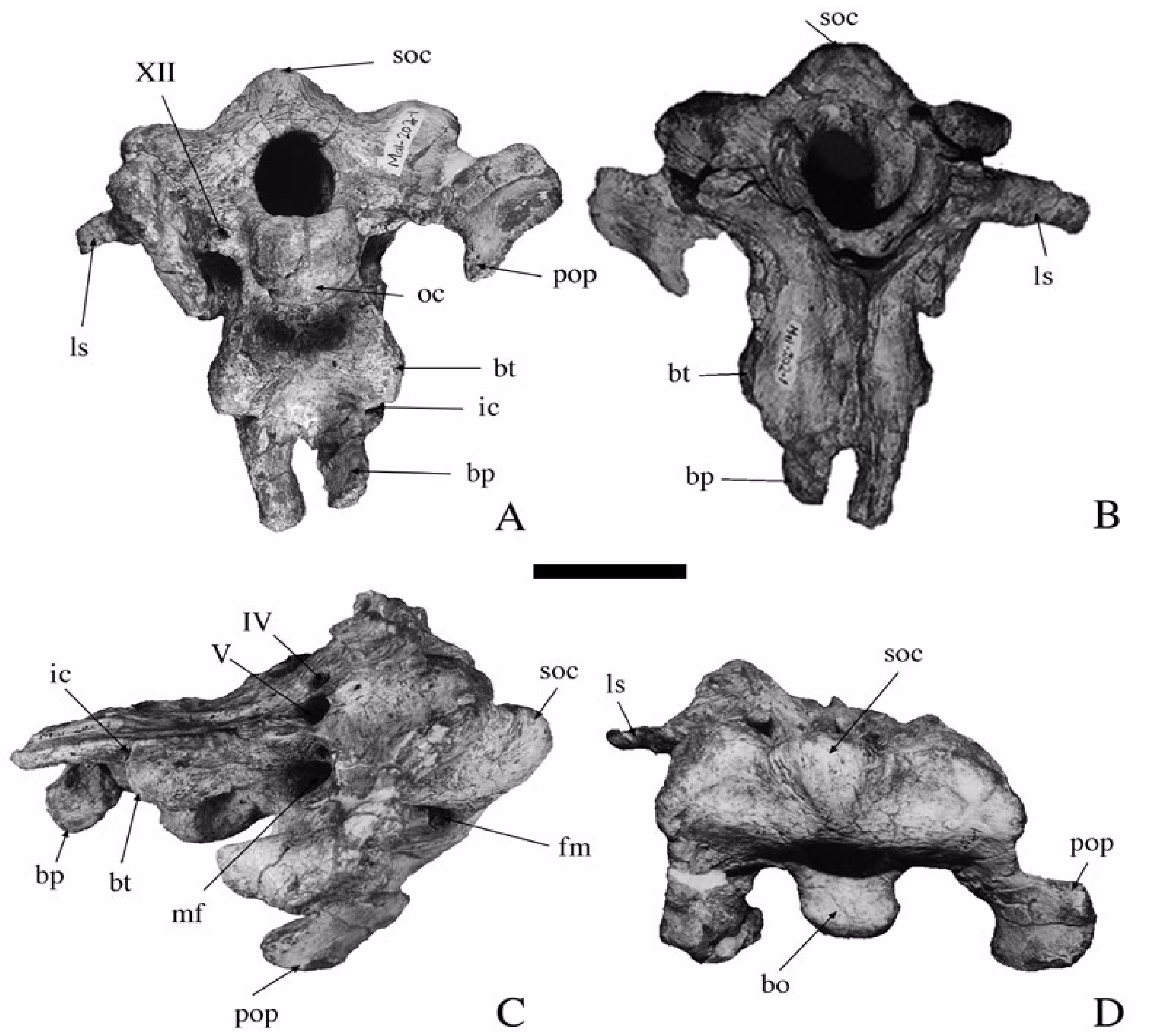

Figure 6. Basicranium (Mal-202-1) of *Malawisaurus dixeyi.* A, ventral view; B, dorsal view; C, lateral view; D, occipital view. Scale bar = 40 mm.

long, anteroposteriorly flattened wing-like structures that curve ventrally, typical of titanosaurians (Powell 1986; Chatterjee and Rudra 1996). Posterolaterally, the paroccipital process has a ventrally directed depression for the quadrate articulation. The basal tubera are large and separated by a wide shallow depression. Salgado and Calvo (1992) interpret the fusion of the basal tubera in *Amargasaurus* (MACN-15) as reflecting rigid attachment for vertebral muscles. By inference, the separation of the basal tubera would reflect a less extensive muscle attachment in Mal-202-1. The opening for the internal carotid artery is at the base of the basipterygoid process. The basipterygoid processes are short (25 mm long) and divergent. In sauropods, short basipterygoid processes are associated with vertical quadrates, whereas long basipterygoid processes are associated with highly anteriorly inclined quadrates (Chatterjee and Rudra 1996).

Dentary. The right dentary of *Malawisaurus* (Mal-174; Figure 7A-C) was briefly described by Jacobs et al. (1993, figure 1b, c). The preserved portion of the dentary is 252 mm long from the symphysis to the surangular notch. The dentary has a minimum of 15 tooth positions, including unerupted teeth in place. The tooth row is 159 mm long extending more than half the length of the dentary. The posteriormost tooth position is 23 mm anterior to the surangular notch. Replacement teeth are visible through three of the nutrient foramina. The rostral portion of the dentary appears linear due to crushing.

The dentary is slender and 50 mm deep. The surangular notch is triangular with its apex pointing

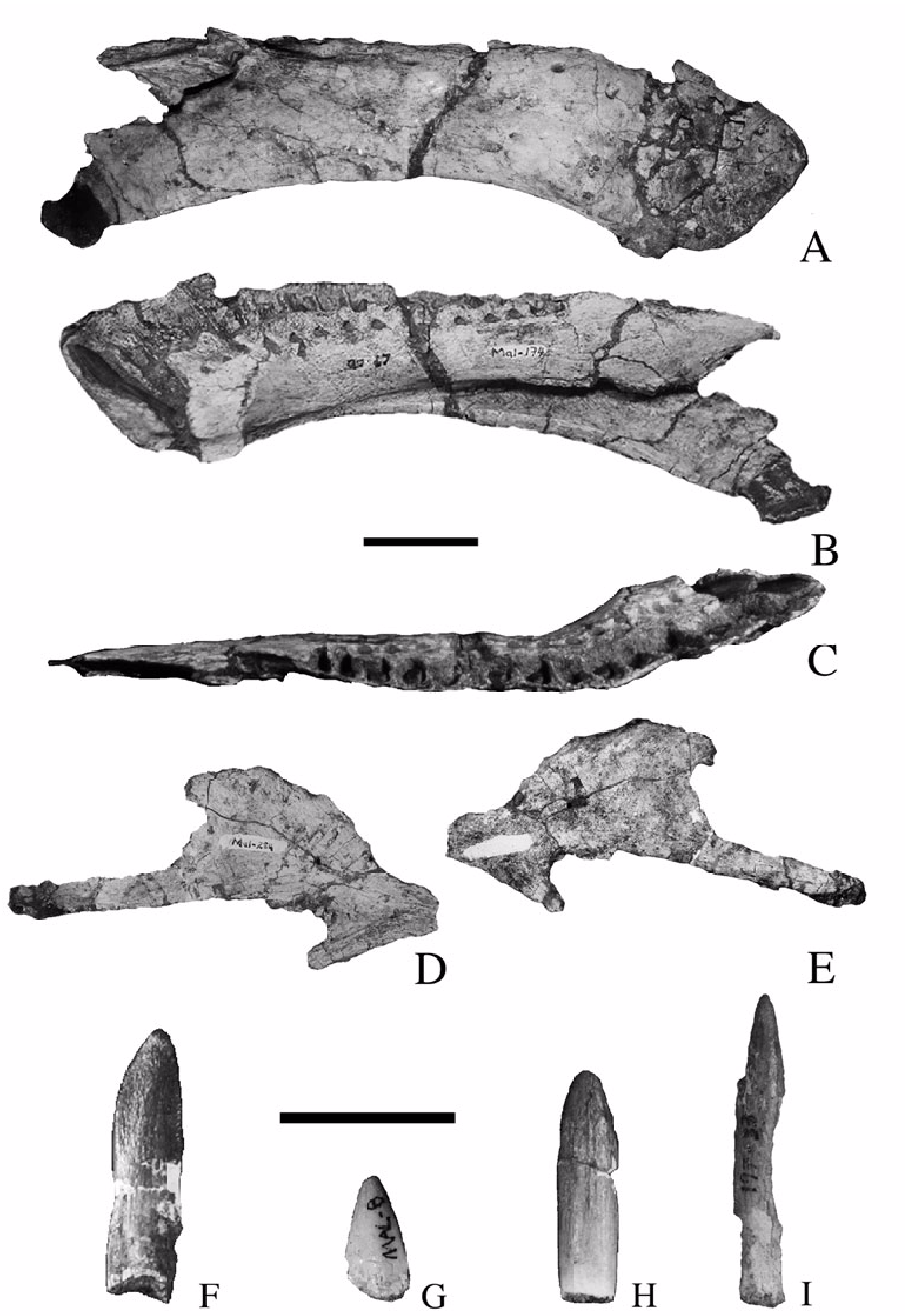

Figure 7. Mandible and teeth of *Malawisaurus dixeyi.* A-C, right dentary (Mal-174). The rostral portion of the dentary is crushed; D-E, splenial (Mal-284); F-I, teeth (F = Mal-176; G = Mal-8; H = Mal-193-2; I = Mal-197-33). A and D, lateral view; B and E, medial view; C, occlusal view; F and G, lingual view; H and I, labial view. A-E, and F-I, same scale. Scale bars = 40 mm in A-E and 20 mm in F-I.

anteriorly. The notch divides the dentary posteriorly into a dorsal ramus and a ventral ramus. The dorsal ramus is small, short, and triangular in lateral view whereas the ventral ramus is large, long, and quadrangular. The splenial groove on the medial surface is broadly open posteriorly, tapering forward to close approximately below the eighth tooth position (Jacobs et al. 1993).

Splenial. The element (Mal-284; Figure 7D-E) identified as splenial is thin (5 mm wide). A splenial foramen occurs on the anterior half of the element as in *Mamenchisaurus* (Russell and Zheng 1993). The posterior half of the element is separated into a long, slender ventral ramus and a short, broad dorsal ramus.

Teeth. Jacobs et al. (1993, figure 1d) described teeth of *Malawisaurus* briefly. Some teeth are present in the jaws (Mal-6, Mal-106, and Mal-174), and others are isolated (Figure 7F-I; mesiodistal width, range = 06 to 09 mm; average mesiodistal width = 7 mm; labiolingual widths, range = 4 to 5 mm; average labiolingual width = 5 mm). The roots of the teeth are nearly cylindrical and circular in cross section. The crowns are nearly cylindrical at the base and become lingually flattened towards the apex so that the crown is less convex lingually than labially. As the crowns become flattened, faint distal and mesial ridges emerge. The crowns are broadest close to the tip of the teeth. The surface is rugose. Anterior teeth in the premaxilla and the dentary are similar in size but broader than more posterior teeth in the maxilla and dentary. The maxillary teeth (Mal-106) curve anterolingually. Compared with the premaxillary teeth, the maxillary teeth of *Malawisaurus* are mesiodistally narrower and smaller. The maxillary teeth are more cylindrical than the premaxillary teeth and closely resemble teeth generally associated with titanosaurians (Sanz 1985; Powell 1986; Lucas and Hunt 1989; Scuitto and Martinez 1994; but see Kues et al. 1980).

Isolated teeth are assigned to *Malawisaurus,* because they have more convex labial surfaces than lingual surfaces, faint distal and mesial ridges, and crowns that are broader toward the apices of the crowns, and in all respects are similar to the teeth in the jaws of *Malawisaurus*. In having convex labial and flattened lingual surfaces, the teeth of *Malawisaurus* are like those of *Nemegtosaurus* (Nowinski 1971) and *Quaesitosaurus* (Kurzanov and Bannikov 1983). Anteroposterior decrease in tooth size and variability of curvature between anterior and posterior and between upper and lower teeth are features that are also present in *Camarasaurus* (Osborn and Mook 1921; Carey and Madsen 1972), *Nemegtosaurus* (Nowinski 1971) and *Quaesitosaurus* (Kurzanov and Bannikov 1983). In *Mamenchisaurus* (Russell and Zheng 1993), teeth diminish in size as crowns become more compressed.

Cervical Vertebrae. Presacral vertebrae are composed of highly pneumatized camellate bone (Wedel 2003). The centra are strongly opisthocoelous (sensu Romer 1956) with the anterior convexity centrally placed on the centrum. Eighteen cervical vertebrae (Figures 8-9, Table 2), including nine isolated vertebrae and two articulated sets (Mal-278, three vertebrae; Mal-280, six vertebrae), of at least two individuals, are attributed to Malawisaurus. The atlas-axis complex is not represented. Mal-180 (Jacobs et al. 1996, figure 5a), Mal-243, Mal-245, the Mal-278 set, the first four of the Mal-280 set, and Mal-301 are fairly well preserved while Mal-187-1, Mal-193-1, Mal-244, Mal-246, the last two of the Mal-280 set, and Mal-291 (= 89-78, Jacobs et al. 1993, figure 1e) are poorly preserved.

In sauropod cervical vertebrae, the interprezygapophyseal distance, development of laminae and fossae on the lateral surface of the neural arch, and the length of the diapophyses increase posteriorly (Osborn and Mook 1921; Gilmore 1936; Powell 1986; McIntosh et al. 1996a, b). In *Haplocanthosaurus* (Hatcher 1903), the penultimate cervical vertebra is wider than high and the last cervical vertebra is shorter than the preceding cervical vertebra. In *Camarasaurus* (Osborn and Mook 1921) and *Apatosaurus* (Gilmore 1936), the lengths of distal cervical vertebrae are less than the lengths of medial cervical vertebrae. Among titanosaurians, articulated cervical vertebrae are known in “Titanosauridae indet. DGM Series A” from Brazil, (12 cervical vertebrae, except the atlas, preserved in articulation with three proximal dorsal vertebrae; Powell 1986, 1987a) and in “Titanosauridae indet., DGM Series B” from Brazil (five cervical vertebrae articulated with 10 dorsal vertebrae; Powell 1986, 1987a). Thus, titanosaurians are considered to have 13 (Powell 1987a) cervical vertebrae. In “Titanosauridae indet. DGM Series A,” the neural spines are low and lean posteriorly in the second to sixth cervical vertebrae (Powell 1986). Based on comparison of the interprezygapophyseal distance, orientation of the neural spines, development of the posterior centrodiapophyseal and postzygodiapophyseal laminae and neural arch fossae, length of the diapophyses, and width/height ratio of centra with “DGM Series A and B,” *Apatosaurus* (Gilmore 1936), *Camarasaurus* (Osborn and Mook 1921; McIntosh et al. 1996a, b), and *Haplocanthosaurus*

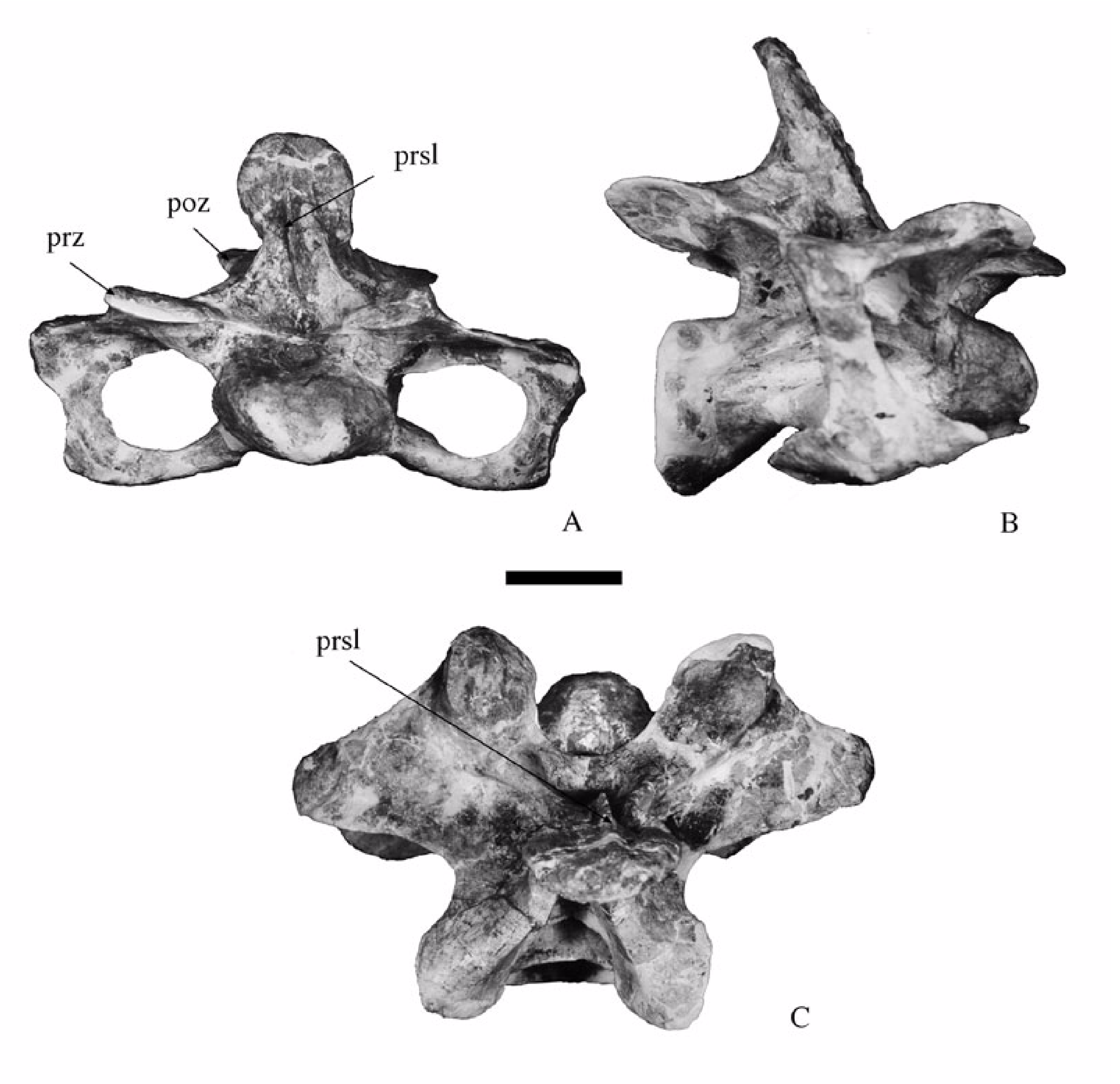

Figure 8. Posterior cervical vertebra of *Malawisaurus dixeyi* (Mal-245). A, anterior view; B, right lateral view; C, dorsal view. Sale bar = 0 mm.

(Hatcher 1903), the positions of *Malawisaurus* cervical vertebrae were estimated.

The anterior ball of each medial and distal cervical vertebra of *Malawisaurus* is medially depressed. The planes of the posterior cups are inclined anterodorsally and not perpendicular to the axes of the vertebrae, suggesting an anteriorly rising neck as in *Camarasaurus* (McIntosh et al. 1996a). The ventral surfaces of the centra are concave medial to the parapophyses but convex posteriorly. Undivided pleurocoels (*sensu* McIntosh 1990) are represented by small fossae directly ventral to the diapophyses as opposed to multiple large anteroposteriorly aligned fossae on the centra of other sauropods (*Amargasaurus* [MACN-15, Salgado and Bonaparte 1991]; *Apatosaurus* [Gilmore 1936]; *Brachiosaurus* [Janensch 1929a, 1950]; *Camarasaurus* [BYU 9047; Osborn and Mook 1921; McIntosh et al. 1996a]; *Dicraeosaurus* [Janensch 1929b]). The parapophyses are directed slightly ventrolaterally. Cranial and caudal peduncle fossae are small. Diapophyses project laterally and become progressively longer posteriorly.

The neural arches are low, long, and medially attached anteroposteriorly on the centra. The laminae on the lateral surfaces of the neural arches are rudimentary (*sensu* Wilson and Sereno 1998). There are only two laminae on the posterolateral surface of a neural arch, termed the posterior centrodiapophyseal and postzygodiapophyseal laminae by Wilson (1999). These laminae enclose the infrapostzygapophyseal fossa. The infrapostzyga-

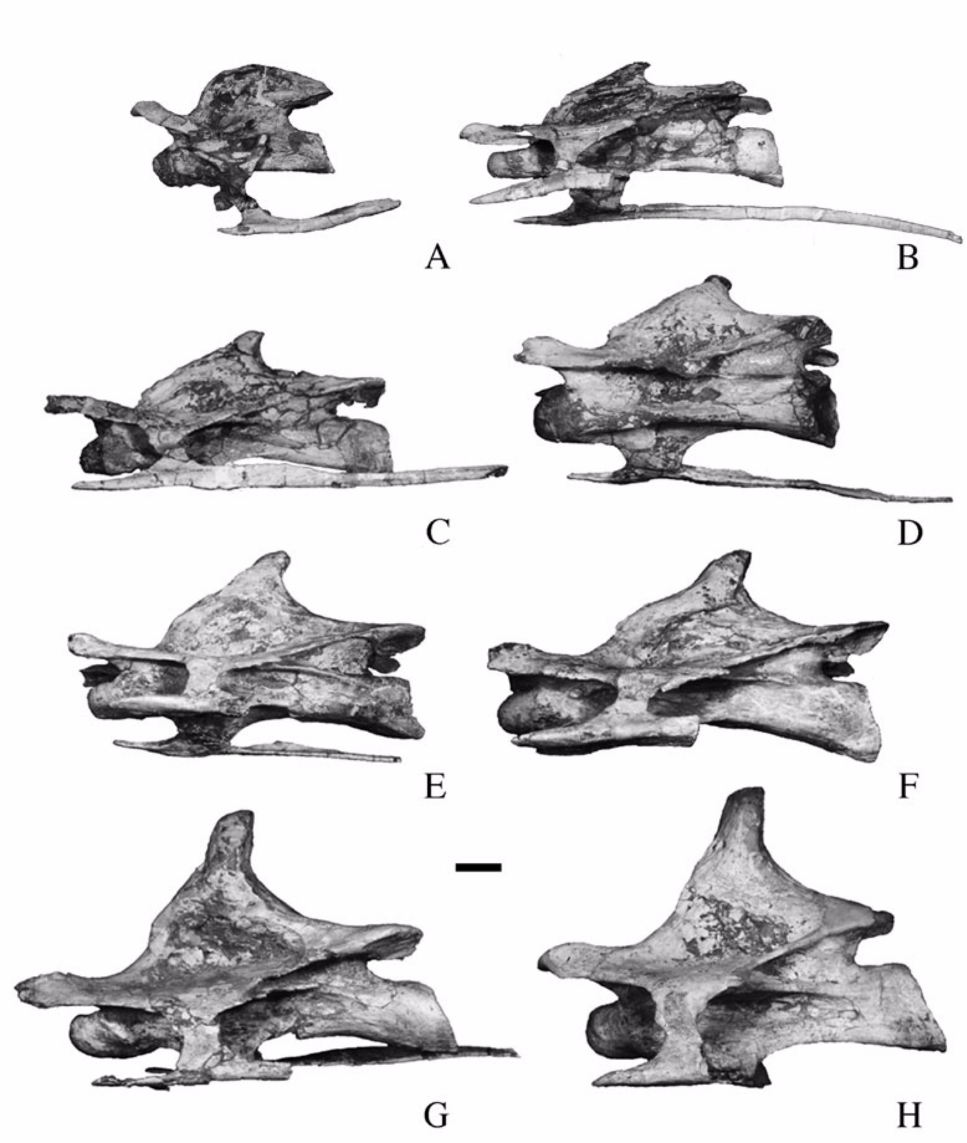

Figure 9. Cervical vertebrae of *Malawisaurus dixeyi,* anteroposterior progression. A = Mal-243; B = Mal-278-1; C = Mal-278-2; D = Mal-278-3; E = Mal-280-1; F Mal-280-2; G = Mal-280-3; H = Mal-280-4. A, B, C, F, G, and H, right lateral view, reversed; D and E, left lateral view. Distal ends of ribs have been removed. Scale bar = 50 mm.

pophyseal fossae enlarge and deepen posteriorly along the cervical column. The supradiapophyseal fossae (posterolateral to the spinoprezygapophyseal laminae and dorsal to the diapophyses) are shallow anteriorly but deepen and widen posteriorly along the cervical column.

The prezygapophyses are small and ellipsoidal in anteriorly cervical vertebrae, but are large and rounded in middle and posterior cervical vertebrae. They extend beyond the anterior end of the centrum in all cervical vertebrae. The prezygapophyses become more divergent posteriorly. Intraprezygapophyseal and intrapostzygapophseal laminae are present in the middle and posterior cervical vertebrae. The spinoprezygapophyseal laminae are sharp and thin in anterior cervical vertebrae but thicken posteriorly. Medial to each spinoprezygapophyseal lamina, at the base, is an ovoid depression in the anterior cervical vertebrae.

The neural spines are single in all cervical vertebrae. They are rounded and cant posteriorly in the anterior cervical vertebrae but become progressively more anteroposteriorly compressed and more vertical posteriorly. In anterior cervical vertebrae, the neural spines are medial to and are restricted towards the spinopostzygapophyseal laminae. In the posterior cervical vertebrae, the neural spines are supported by and rise directly

Table 2. Measurements (mm) of cervical vertebrae of *Malawisaurus dixeyi*, as preserved. Centrum and vertebral widths and heights were measured on the posterior end of the centra. Cervical positions are estimated anatomical positions. + = incomplete.

Cervical position	Specimen #	Centrum length	Centrum width	Centrum height	Vertebral width	Vertebral height
3	Mal-243	207	41	45	63+	182 +
4	Mal-180	250	61	46	157	187
5	Mal-278-1	320	65	60	153	182
6	Mal-278-2	340 +	76	70	190	162
7	Mal-278-3	363	80	75	147 +	255
8	Mal-280-1	389	110	60	273	180
9	Mal-280-2	415	120	85	295	200
10	Mal-280-3	420	140	90	285	296
11	Mal-280-4	415	125	144	252	310
12	Mal-245	295	175	125	505	3
13	Mal-246	250	165	85+	2+	85 +

from the spinoprezygapophyseal and the spinopostzygapophyseal laminae. Mal-245 has well-developed pre-spinal laminae. Short pre-spinal and long, deep post-spinal fossae occur medial to the spinozygapophyseal laminae in all cervical vertebrae.

Cervical Ribs. The cervical ribs (Figure 9) are coossified to the centra (Mal-243, Mal-180, Mal-245, Mal-278, Mal-280, and Mal-301) or are isolated fragments (Mal-64, Mal-146, Mal-147, Mal-149, Mal-162, and Mal-187-2). The ribs are nearly parallel to the long axes of the centra. The heads terminate at the anterior limits of their associated centra in proximal cervical vertebrae (Mal-180), but terminate posterior to the anterior ends of their associated centra in medial and distal cervical vertebrae. This is in contrast to "Titanosauridae indet. DGM Series A" where the heads of the ribs extend beyond the anterior ends of their associated centra (Powell 1986, 1987a). The ribs are thin and dorsoventally compressed, relatively broad transversely in their proximal halves, but thin and rounded rods in their distal halves. The shafts of the ribs in the proximal and medial cervical vertebrae extend up to 320 mm beyond the posterior ends of their associated centra, and even extend beyond the ends of the next succeeding centra. In the distal cervical vertebrae, the shafts of the ribs do not extend beyond the centra (Mal-245).

Dorsal Vertebrae. Ten isolated dorsal vertebrae (Figures 9-11, Table 3) are attributed to *Malawisaurus*. There are no hyposphene-hypantrum articular surfaces in any of the vertebrae. The posterior ends of the centra are flared. The neural arches are low and possess fossae that vary in size and shape on either side of each vertebra. Undivided and short neural spines are supported anteriorly by the spinodiapophyseal laminae, not by the spinoprezygapophyseal laminae as in Apatosaurus (Gilmore 1936), and posteriorly by the spinopostzygapophyseal laminae. All, except Mal-242 (where it cannot be observed), have well-developed pre-spinal and post-spinal laminae. The pre-spinal laminae are bifid at the base and are more prominent than the post-spinal laminae.

Among titanosaurians, the most complete articulated dorsal series known are in a specimen identified as "Titanosauridae indet. DGM Series B" from Brazil (10 dorsal vertebrae; Powell 1986, 1987a) and in *Opisthocoelicaudia* (10 or 11 dorsal vertebrae; Borsuk-Bialynicka 1977). The description and discussion of Powell (1986) imply that "DGM Series B," *Epachthosaurus* (MACN-CH 1317, cast), and *Neuquensaurus* (*Titanosaurus*) *australis* have 10 dorsal vertebrae, whereas the illustrations of *Neuquensaurus* (von Huene 1929, figure 10; Powell 1986, plate 56) suggest the presence of 11 dorsal vertebrae. Wilson and Sereno (1998, figure 47) indicate that although the number of dorsal vertebrae in titanosaurians varies between 10 and 12, 10 is the standard number. Thus, *Malawisaurus* is predicted to have 10 dorsal vertebrae.

In "DGM Series B," as well as other sauropods (Hatcher 1903; Osborn and Mook 1921; Powell 1986, 1987a; McIntosh and Williams 1988), the parapophyses move in position from being on the centrum in proximal dorsal vertebrae to being high on the neural arch in posterior dorsals. The transverse processes project laterally in the proximal dorsal vertebrae but dorsolaterally in the distal vertebrae. The interprezygapophyseal distance progressively decreases posteriorly along the dorsal series. Comparison with "DGM Series B" and other sauropods (Hatcher 1903; Riggs 1903; Osborn and Mook 1921; Gilmore 1936; Powell 1986, 1987a; McIntosh et al. 1996a; Jain and Bandyopadhyay 1997) using the positions of the parapophyses, the orientation of transverse processes, and the inter-

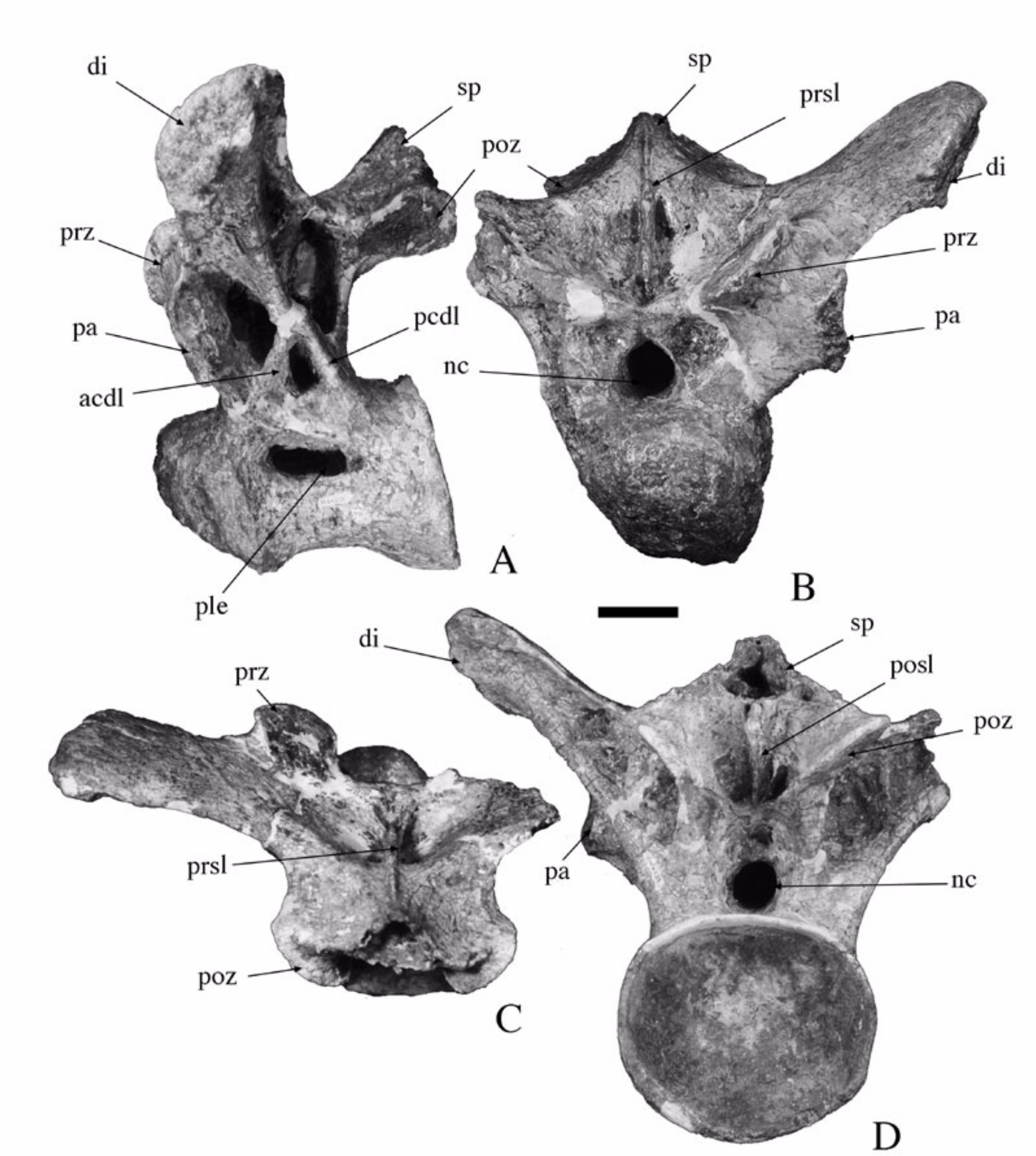

Figure 10. Anterior dorsal vertebra of *Malawisaurus dixeyi* (Mal-238). A, left lateral view; B, anterior view; C, dorsal view; D, posterior view. Scale bar =50 mm.

prezygapophyseal distances, indicates that Mal-181 (Jacobs et al. 1996, figure 5b, c), Mal-236, Mal-238, Mal-239, and Mal-283 occur in the proximal half of the dorsal series in positions one to five, while Mal-182 (Jacobs et al. 1996, figure 5d), Mal-237, Mal-240, Mal-241, and Mal-242 occur in the distal half of the dorsal series, in positions six to 10.

All the dorsal vertebrae possess small, anteroposteriorly elongate, eye-shaped (*sensu* Calvo and Salgado 1995) pleurocoels that are restricted to the dorsal half of the centrum. The pleurocoels face laterally in dorsal vertebrae one to three and dorsolaterally in the other dorsal vertebrae. In Mal-239 and Mal-283, the parapophyses are subrounded and situated on the centrum. Their ventral limit is 20 mm below the ventral limit of the pleurocoels. Mal-283 is interpreted as the first dorsal of *Malawisaurus,* because its parapophyses are immediately anterior to the pleurocoels, and the diapophyses face ventrolaterally as in the first dorsal vertebra of other sauropods (Hatcher 1903; Osborn and Mook 1921; Powell 1986, 1987a; McIntosh and Williams 1988). The centrum is shorter and the zygapophyses are smaller than in the posterior cervical vertebrae but are similar to the first dorsal vertebra of “Titanosauridae indet.

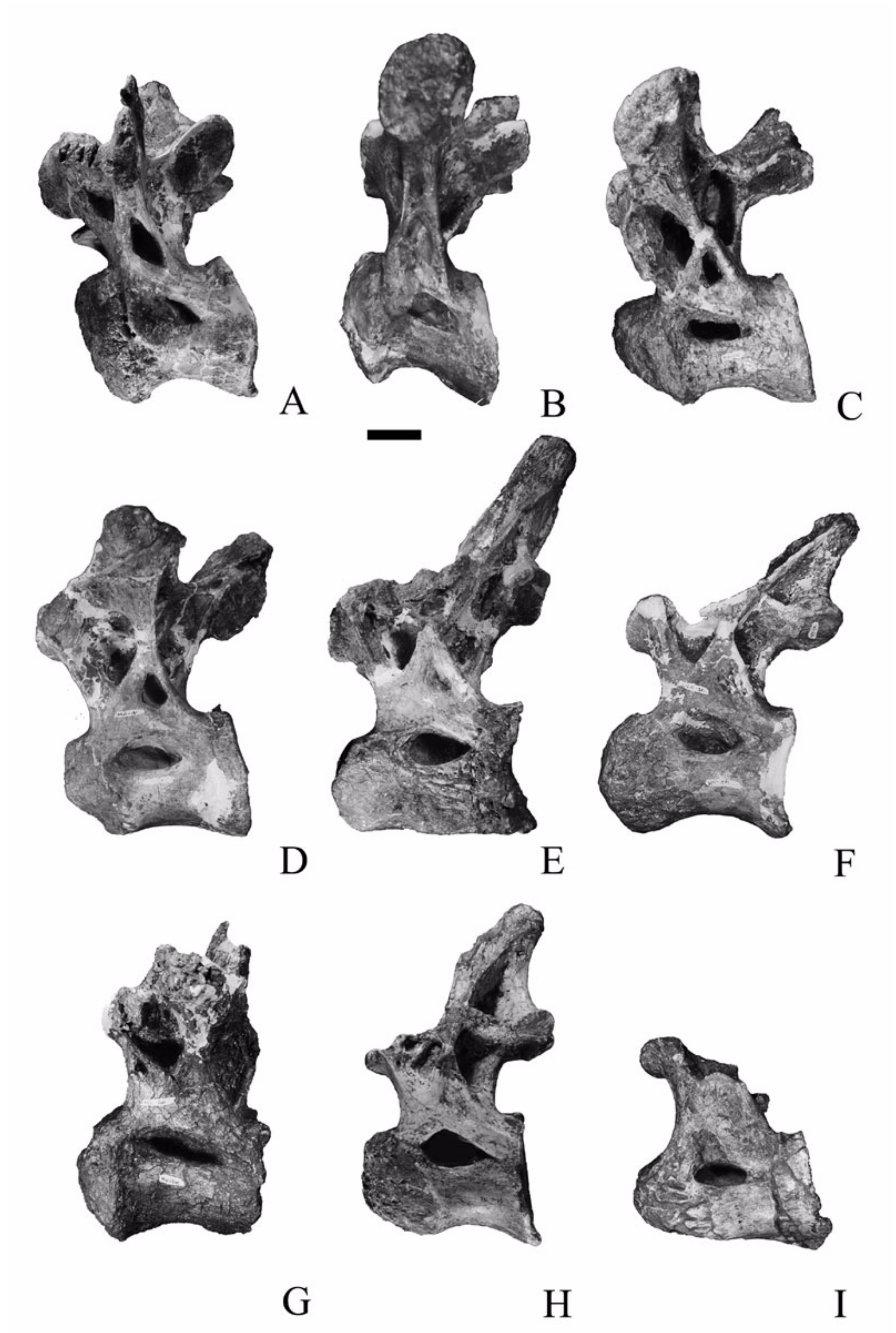

Figure 11. Dorsal vertebra of *Malawisaurus dixeyi,* anteroposterior progression. A = Mal-239; B = Mal-236; C = Mal-238; D = Mal-181; E = Mal-237; F = Mal-241; G = Mal-240; H = Mal- 182; I = Mal-242. A-E and G-I, left lateral view; F, right lateral view, reversed. Scale bar = 50 mm.

DGM Series A and B" and of *Neuquensaurus* (Powell 1986, 1987a).

Parapophyses are anterior to the pleurocoels in Mal-239. Although the parapophyses are on the centrum in the second dorsal vertebrae of "Titanosauridae indet. DGM Series A" from Brazil, the centrum is much shorter than in the first dorsal vertebra (Powell 1986). The centrum of Mal-239 is much shorter than that of Mal-283 (Table 3) and might be the second dorsal vertebra of *Malawisaurus*. In Mal-236, the parapophyses are crescentic and extend from the centrum to the lower portion of the neural arch. In "DGM Series B," the parapophyses on the third dorsal vertebra are on the neural arch and the centrum is wider than high. The centrum of Mal-236 is similarly wider than high. Mal-

Table 3. Measurements (mm) of dorsal vertebrae of *Malawisaurus dixeyi*, as preserved. Dorsal position is the interpreted approximate anatomical position in the dorsal series. Centrum and vertebral widths and heights were measured on the posterior end of the centra. Vert. width = total preserved vertebral width; Vert. height = total preserved vertebral height; Preszyg. dist. = interprezygapophyseal distance; + = incomplete; † = data unavailable; - = element not preserved.

Dorsal position	Specimen #	Centrum length	Centrum height	Centrum height	Vertical width	Vertical height	Prezygopophysis distance
1	Mal-283	200	170	80	540	380	†
2	Mal-239	1.3	159	110	435+	308+	79
3	Mal-236	121	168	115	458	290+	70
4	Mal-238	201	118	104	320+	27.7+	74
5	Mal-181	165	104	93	265+	292+	52
6	Mal-237	182	131	120	252+	355	23
7	Mal-241	185	97	110	164+	3.5+	22
8	Mal-240	182	128	110	282	276+	20
9	Mal.-182	172	111	107	146+	332+	17
10	Mal-242	155	101	103	110	180	-

236 is also similar to third dorsal vertebrae of *Apatosaurus* (Riggs 1903, Gilmore 1936) and *Camarasaurus* (Osborn and Mook 1921) in that half of its parapophysis arises from the centrum. Thus, Mal-236 might be the third dorsal vertebra of *Malawisaurus*.

In all other dorsal vertebrae, the parapophyses are high on the neural arch. In Mal-238, the parapophyses are crescentic, and their dorsal limits are slightly lower than the dorsal limits of the prezygapophyses. In Mal-181 (Jacobs et al. 1996), the parapophyses are at the same level as the prezygapophyses. Parapophyses on the neural arch, but below or at the same level as the prezygapophyses, occur in dorsal vertebrae three to five of "DGM Series B." In Mal-237 and Mal-240, the parapophyses are subtriangular with medial depressions. The dorsal limits of the parapophyses are 40 mm higher than the prezygapophyses. In Mal-241, Mal-182, and Mal-242 the neural arches are not complete, and the parapophyses and diapophyses are not preserved. However, the decrease in interprezygapophyseal distance suggests a posterior progression from Mal-181, Mal-237, Mal-241, Mal-240, and Mal-182 in that order. Mal-242 is considered the most posterior and may be the last dorsal vertebra of *Malawisauru,s* because its centrum is the least excavated among the dorsal vertebrae, similar to the last dorsal vertebrae of *Camarasaurus lewisi* (BYU 9047; McIntosh et al. 1996a) and of *Brachiosaurus* (Riggs 1904). Thus, based on parapophyseal position, interprezygophyseal distance, and size of lateral fossae on the centrum, the anatomical position of *Malawisaurus* dorsal vertebrae were approximated.

The prezygapophyses are at approximately the same level as the postzygapophyses in Mal-283 and in Mal-239, and are lower than the postzygapophyses in dorsal vertebrae posterior to the second, Mal-239. Neural arches are attached to the anterior half of centra in Mal-283, Mal-239, Mal-236, Mal-238, and Mal-181, interpreted anatomical positions one to five, and are centrally attached to centra in Mal-237, Mal-241, Mal-240, Mal-182, and Mal-242, interpreted anatomical positions six to 10. In dorsal vertebrae one to three (Mal-283, Mal-239, and Mal-236), the posterior limits of the neurocentral junction are anterior to the posterior limits of the pleurocoels. The neural arch attachments extend the entire lengths of the pleurocoels in dorsal vertebrae four to nine (Mal-238, Mal-181, Mal-237, Mal-241, Mal-240, and Mal-182), and extend beyond the posterior limits of the pleurocoels in dorsal 10 (Mal-242).

The centrodiapophyseal laminae are dorsally broad and ventrally forked into wide anterior and posterior centrodiapophyseal laminae in all the dorsal vertebrae except in Mal-242. The fossae between the anterior and posterior centrodiapophyseal laminae are deep in Mal-283, Mal-239, Mal-236, Mal-238, and Mal-181, dorsal vertebrae one to five, shallow in Mal-237, Mal-241, Mal-240, and Mal-182, dorsal vertebrae six to nine, and have completely disappeared in Mal-242, dorsal 10, so that the centrodiapophyseal laminae in Mal-242 are massive and not forked. The posterior centrodiapophyseal laminae and the centropostzgapophyseal laminae are separate in Mal-283, Mal-239, and Mal-236, dorsal vertebrae one to three, but merge in all dorsal vertebrae posterior to Mal-236.

The transverse processes are directed laterally in Mal-238, Mal-239, and Mal-236, and are slightly dorsolaterally inclined in Mal-283, Mal-181, Mal-237, and in Mal-240. Diapophyses are ellipsoidal, longer dorsoventrally than anteroposteriorly in Mal-283, Mal-239, Mal-236, and Mal-238, but longer anteroposteriorly than dorsoventrally in Mal-

181, Mal-237, and Mal-240. The diapophyses face ventrolaterally in Mal-283, Mal-239, Mal-236, and Mal-238, and laterally in Mal-181, Mal-237, and Mal-240.

The neural spine is paddle shaped in anterior view in each of the anterior dorsals and taper dorsally in the posterior dorsals. The neural spine lacks lateral pendant processes. It is inclined posteriorly in any anterior dorsal vertebrae and becomes vertical posteriorly. Narrow longitudinal fossae occur lateral to the pre-spinal laminae in Mal-181, Mal-237, and Mal-182, and lateral to the post-spinal laminae in Mal-238. In other dorsal vertebrae, the presence of longitudinal fossae on the neural spines cannot be determined because the spines are incomplete.

Dorsal Ribs. Twelve dorsal ribs (Figure 12A-B, Table 4) are attributed to *Malawisaurus*. Comparison with *Apatosaurus* (Riggs 1903), *Camarasaurus* (BYU 9047; Osborn and Mook 1921; McIntosh et al., 1996a; McIntosh et al. 1996b), *Brachiosaurus* (Janensch 1950), and *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) suggests that Mal-295, Mal-296, Mal-297, Mal-298, and Mal-308 occur in the proximal half of the series, from the first to the fifth position, whereas the remainder occur in the distal half of the series, posterior to the fifth rib. The posterior surfaces of Mal-282-1 and Mal-282-2, around positions seven and eight, have quadrangular pneumatic cavities 30 mm from the capitulum-tuberculum split (Gomani et al. 1999, figures 1d, e) indicating that pneumatization extends beyond the anterior one third of the dorsal series mentioned for the Mendoza titanosaurian by Wilson and Sereno (1998, p. 52, character 97). The shafts are flattened in all the ribs.

Sacrum. The sacrum (Figure 13 A-B; anteroposterior length = 574 mm; half width across sacral two = 310 mm; narrowest half width across sacral three = 266 mm; half width across sacral six = 395 mm) consists of six vertebrae that are completely fused.

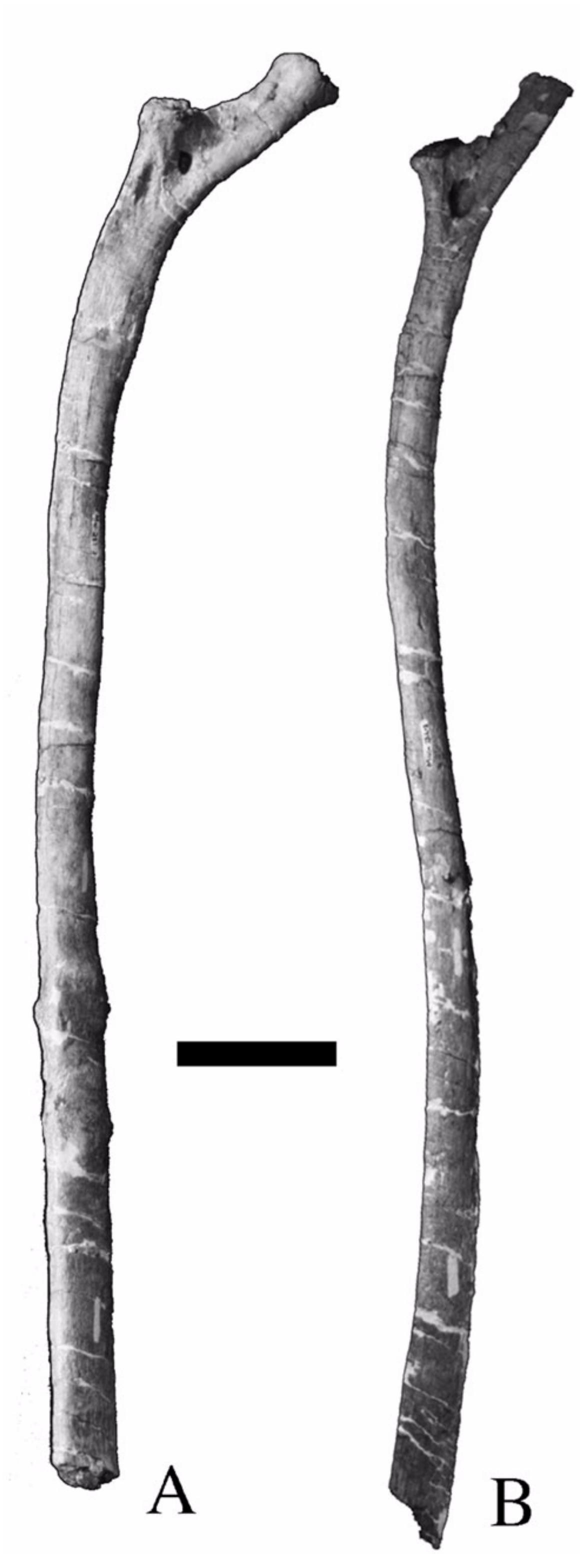

Figure 12. Dorsal ribs of *Malawisaurus dixeyi.* A and B, dorsal ribs, A = Mal-282-2; B = Mal-282-1; posterior view. Scale bar = 100 mm.

Table 4. Measurements (mm) of dorsal ribs of *Malawisaurus dixeyi*, as preserved. The anatomical positions are interpreted. + = incomplete

Anatomical position	Specimen #	Length	Width across head and tubercle
1	Mal-298	760+	155
2	Mal-297	640+	220
3	Mal-296	760+	210
4	Mal-295	800+	170
5	Mal-294	870+	160+
5?	Mal-299	905+	100
8	Mal-293	400+	95+
9	Mal-285	850+	90+
10	Mal-292	730+	80+

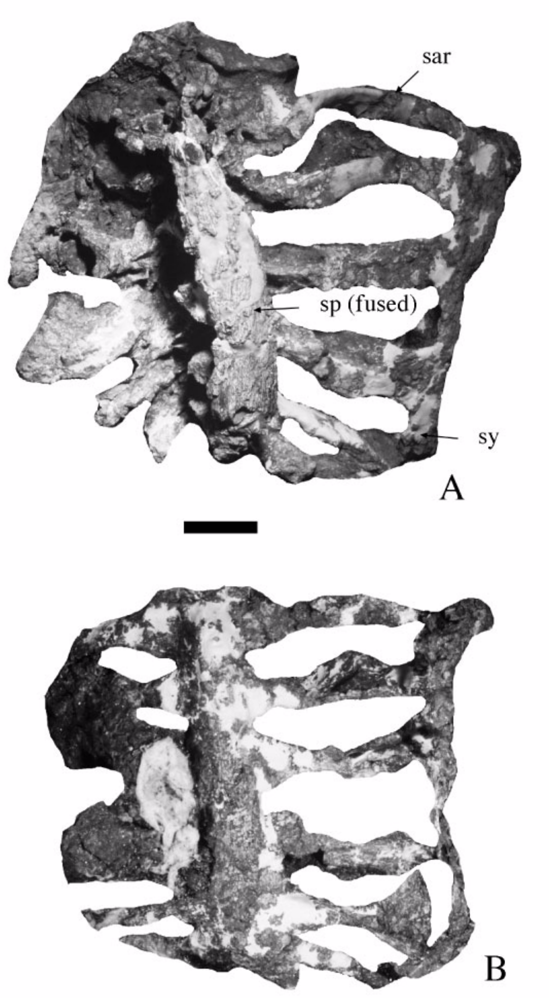

Figure 13. Sacrum of *Malawisaurus dixeyi* (Mal-277-1). A, dorsal view; B, ventral view. Scale bar = 100 mm.

The posterior end of sacral six is not completely preserved. The prezygapophyses and postzygapophyses are fused. Neural spines are entirely coossified and form a plate that overhangs the neural arches as in Titanosauridae indet. n. sp. C from Brazil (Campos and Kellner 1999) and in *Epachthosaurus* (Powell 1986). The dorsal surface is roughened with longitudinal grooves. The lateral walls of the neural spines are thin and strengthened by well-developed laminae as in *Opisthocoelicaudia* (Borsuk-Bialynicka 1977). Except for the ribs of the dorsosacral, all the ribs are medially thin, and the laminae are fused to the parapophyses and diapophyses as in Titanosauridae indet. n. sp. B from Brazil and other sauropods. The sacral ribs of the dorsosacral are higher on the neural arch while the ribs of the other sacral vertebrae rise from the ventral surfaces of the associated sacral vertebrae. The ribs of sacral vertebrae two to five have subcircular fenestrae proximally as in *Saltasaurus* (PVL 4017; Powell 1986). Sacral rib two has an expanded distal ventral plate that overhangs part of sacral rib three. Ribs two and three lean posteriorly, ribs four and five lean anteriorly in ventral view, and ribs one and six are vertical. The ventral openings that separate rib three from ribs two and four are large relative to other openings. Unlike in the Brazilian sacra (Campos and Kellner 1999), the distal ends of all sacral ribs in Mal-277-1 are completely coalesced to form the sacricostal yoke as in *Opisthocoelicaudia* (Borsuk-Bialynicka 1977).

Caudal Vertebrae. Fifty-one caudal vertebrae (Figures 14-16, Table 5) of at least three individuals of *Malawisaurus* have been described by Jacobs et al. (1993, figure 2b, c; Gomani 1999b, figure 1). The centra are strongly procoelous (*sensu* Romer 1956) in the most anterior caudal vertebrae (Mal-191, Mal-225-1, Mal-232-1, Mal-279-1, and Mal-279-2), becoming slightly procoelous to platycoelous (*sensu* Romer 1956) in more the posterior of the anterior caudal vertebrae (Mal-225-2, Mal-225-3, Mal-225-4, Mal-227, and Mal-228), and platycoelous in the medial and distal caudal vertebrae (sets of Mal-197, Mal-196, and Mal-192, and isolated vertebrae [Mal-2, Mal-198, Mal-206, Mal-223, Mal-224, Mal-226, Mal-229, Mal-231, Mal-232-1, and Mal-233]). In the procoelous tail vertebrae, the posterior ball is restricted to the dorsal half of the centrum. For a complete description and additional measurements of *Malawisaurus* caudal vertebrae see Gomani (1999b, table 2).

Chevrons. Among titanosaurians, only *Alamosaurus* (25 chevrons; Gilmore 1946) and *Opisthocoelicaudia* (at least 19 chevrons; Borsuk-Bialynicka 1977) have complete series of chevrons preserved. Based on comparison with *Alamosaurus*, 24 recovered chevrons of three different morphologies are considered to belong to *Malawisaurus* (Figures 17-18, Table 6). The chevrons belong to at least two individuals. Mal-192-22, Mal-197-24, Mal-197-25, Mal-197-26, Mal-197-27, Mal-197-28, and Mal-197-29 were found in natural articulation, and Mal-194, Mal-197-23, Mal-197-30, and Mal-197-31 were found in close association with an articulated tail of 21 vertebrae (Mal-197-1 to Mal-197-21; Gomani 1999a, b) of *Malawisaurus*. Mal-195, Mal-277-2, Mal-277-3, and Mal-310 were associated with the sacrum (Mal-277-1), Mal-255, and the Mal-186 articulated caudal sets. *Malawisaurus* is interpreted as having at least 25 chevrons based on comparison with *Alamosaurus* (Gilmore 1946). The anteroposterior length of chevrons decreases to the fifth chevron in *Alamosaurus* (Gilmore 1946),

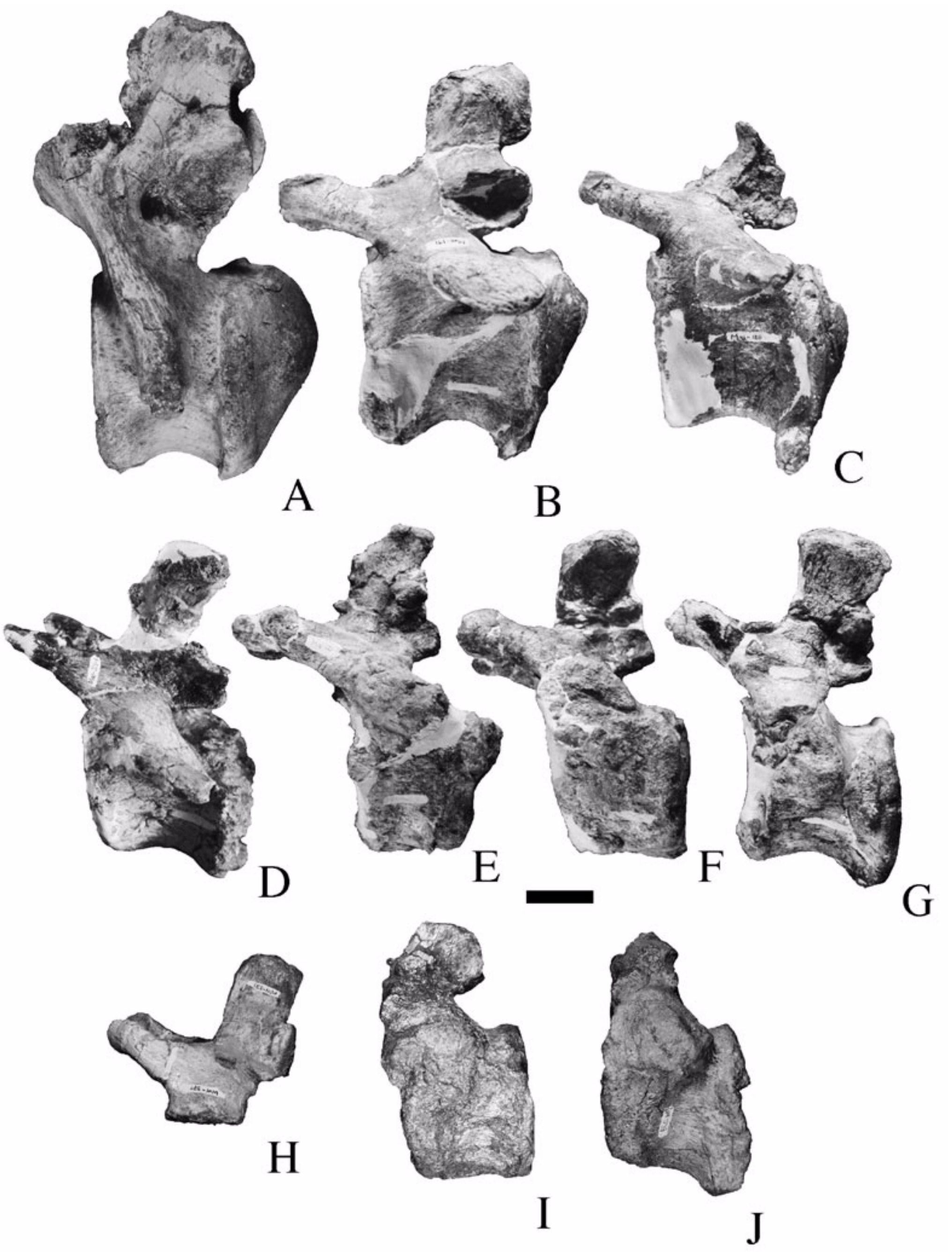

Figure 14. Anterior caudal vertebrae of *Malawisaurus dixeyi.* A = Mal-200; B = Mal-191; C = Mal-185; D-G = articulated set, Mal-225-1 to Mal-225-4; H = Mal-231; I = Mal-228; J = Mal-227. A, H, and J, right lateral view; B, C, D, G, and I, left lateral view. Scale bar = 40 mm.

to the sixth or seventh chevron in *Brachiosaurus* (Janensch 1950, figures 109-136), and to the seventh chevron in *Opisthocoelicaudia* (Borsuk-Bialynicka 1977). In these taxa and in *Camarasaurus* (BYU 9047; McIntosh et al. 1996a) the length of the haemal canal relative to the length of the spine increases posteriorly. In *Alamosaurus*, a V-shaped chevron first appears between caudal vertebrae 16 and 17 and is referred to as chevron 16 (Gilmore 1946). Thus, in one articulated caudal series (Mal-197) of *Malawisaurus* (Gomani 1999a, b), the first V-shaped chevron (Mal-197-26) is interpreted as the sixteenth chevron. Hence, based on comparison with these taxa and this interpreted position of Mal-197-26, the morphology, proximodistal length, and the length of the haemal canal relative to the length of the spine, the anatomical positions of isolated chevrons of *Malawisaurus* were estimated.

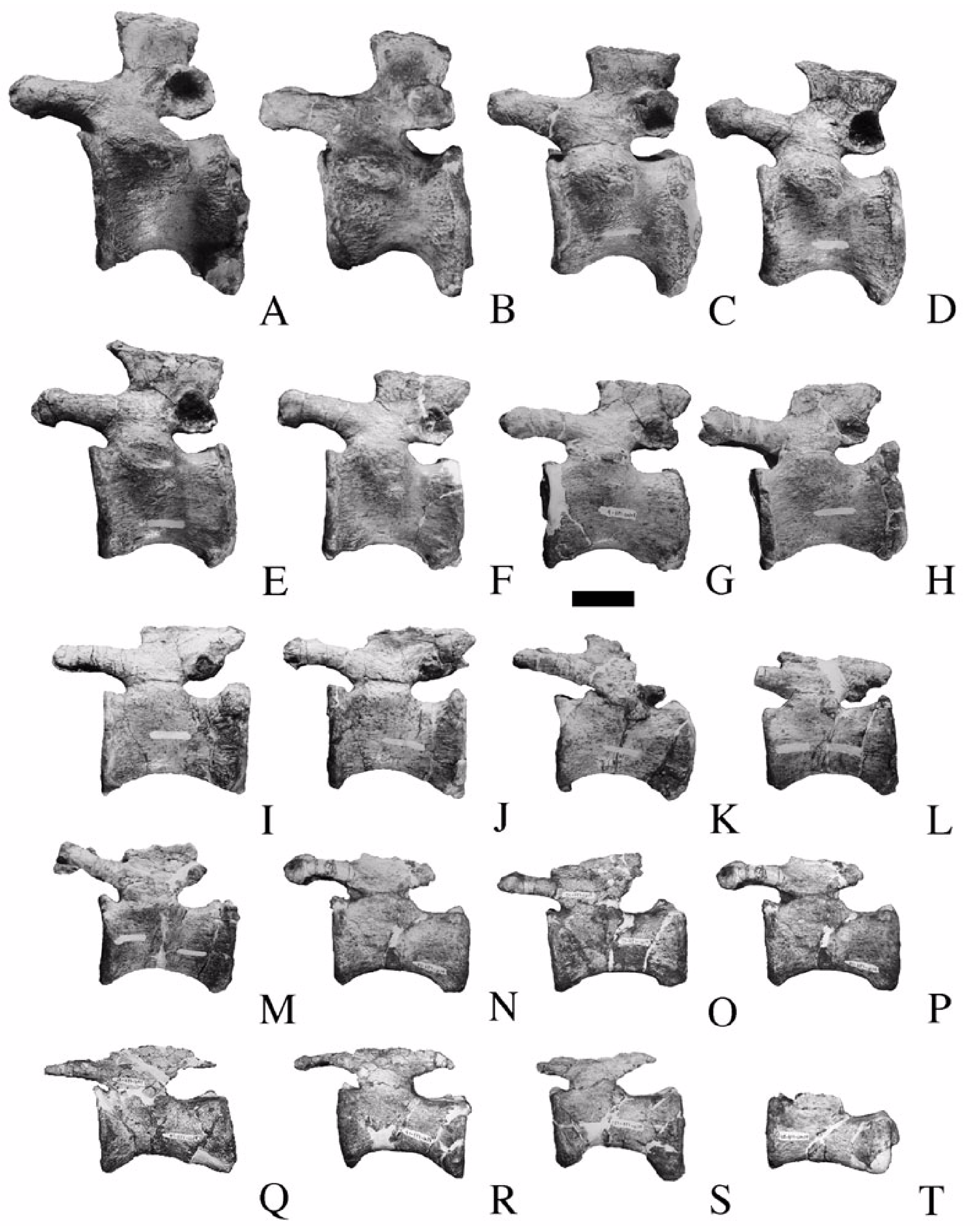

Figure 15. An articulated set of middle to posterior caudal vertebrae of *Malawisaurus dixeyi* (Mal-197-1 to Mal-197-20). Right lateral view, reversed. Scale bar = 40 mm.

All chevrons lack a bridge of bone so that the haemal canal is open, unlike the completely enclosed haemal canals or forked chevrons in diplodocids and dicraeosaurids (Osborn 1899; Hatcher 1901; Gillette 1991).

The first morph (Y-shaped; Figures 17A-F and 18A-E) has two arms that unite below the haemal canal to form a spine. All Y-shaped chevrons except Mal-195 have laterally compressed spines and arms with subequal steep anteroventrally sloping and gentle anteriorly facing articular facets. In Mal-195 the spine is dorsoventrally flattened. The heads on the arms curve medially and have a single articular facet that faces dorsomedially so that

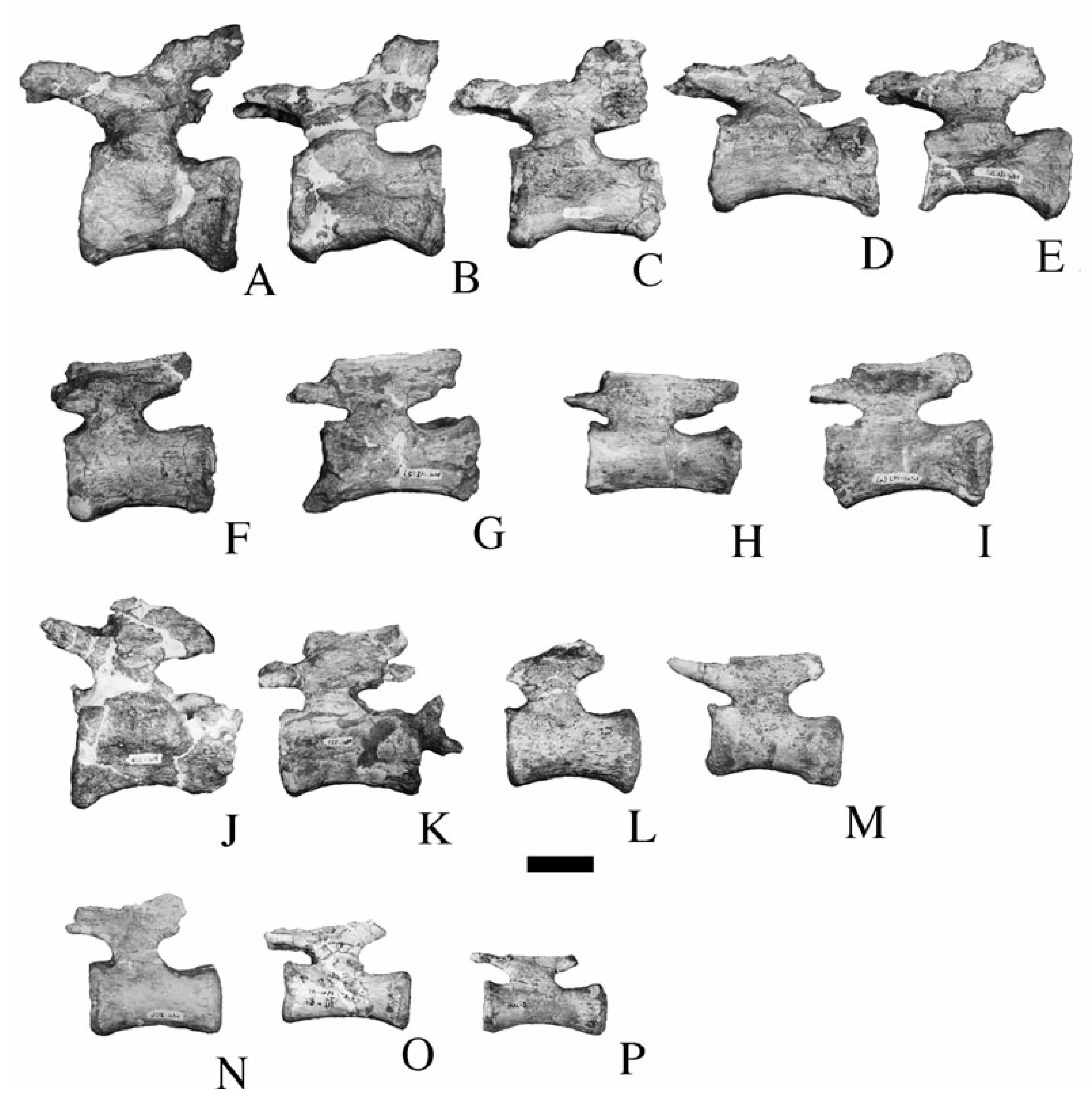

Figure 16. Middle and posterior caudal vertebrae of *Malawisaurus dixeyi.* A-E = articulated set of middle caudal vertebrae (Mal-186-1 to Mal-186-5); F-I = articulated set of posterior caudal vertebrae (Mal-192-1 to Mal-192-4); J-M, isolated posterior caudal vertebrae. J = Mal-223; K = Mal-224; L = Mal-198; M = Mal-2, anteroposterior progression. A-L, right lateral view, reversed; M, left lateral view. Scale bar = 40 mm.

when articulated with vertebrae, it would make an acute angle with the vertebrae column. The spine has a low, broad median ridge on the posterior surface that divides into two smaller ridges posteroventrally. The arms are thicker medially than laterally as opposed to being thicker posteriorly than anteriorly in other Y-shaped chevrons. The spine is slightly depressed on the anterior surface. Based on these features, Mal-195 is interpreted as the first chevron. This matches the less developed chevron articular facet on caudal vertebra Mal-200 as compared to more posterior vertebrae. In *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), the spines of the first four chevrons are dorsoventrally flattened as in Mal-195. A first chevron that is slightly different from the posterior chevrons also occurs in *Brachiosaurus* (Janensch 1950, figure 109) and *Mamenchisaurus hochuanensis* (Yang and Zhao 1972).

The second morph (V-shaped; Figures 17G-J and 18F-H) has two arms but lacks the spine. The arms have small articular facets that face anterodorsally as opposed to the anteriorly facing articular facets of the Y-shaped chevrons. The third

Table 5. Measurements (mm) of caudal vertebrae of *Malawisaurus dixeyi*, as preserved. Caudal position corresponds to approximate anatomical position. Centrum width measured at the anterior end of the centrum; centrum height measured from ventral end of the centrum to the ventral margin of the neural canal anteriorly; + = incomplete; - = not preserved.

Caudal position	Specimen #	Centrum length	Centrum width	Centrum height	Total height of vertebra
2	Mal-200	125	140	120	258
4	Mal-191	124	120	104	209
5	Mal-185	125	110	138	20 +
6	Mal-225-2	84	106	99	202
7	Mal-225-4	89	75+	97	20
8	Mal-231	-	-	-	111+
10	Mal-197-1	99	95	90	198
11	Mal-197-2	97	91	86	178
12	Mal-197-3	95	87	85	170
13	Mal-197-4	94	80	81	158
14	Mal-197-5	96	73	75	1.9
15	Mal-197-6	99	71	76	137
16	Mal-197-7	99	71	75	133
17	Mal-197-8	99	68	73	123
18	Mal-197-9	103	60	70	50
19	Mal-197-10	101	62	70	48
20	Mal-197-11	93	62	70	42
21	Mal-197-12	94	56	61	103
22	Mal-197-13	95	59	64	103
23	Mal-197-14	91	58	61	87+
24	Mal-197-15	91	5.9	5.9	10.4
25	Mal-197-16	92	60	59	95
26	Mal-197-17	87	52	56	90
27	Mal-197-18	90	52	51	99
28	Mal-197-19	85	55	51	78
29	Mal-197-20	90	51	41	59+
30	Mal-197-21	34+	46+	40+	40+
31	Mal-206	76	44	42	80
32	Mal-198	75	37	34	68
33	Mal-2	70	37	30	55

morph (rod shaped; Figures 17K-L) has two separate arms. The arms are laterally compressed and have anterodorsal facing articular facets in Mal-152-2 and Mal-197-31. Mal-197-23 is elongate and cylindrical.

Alamosaurus has 15 Y-shaped chevrons in positions 1 to 15, three V-shaped chevrons in positions 16 to 18, and seven rod-shaped chevrons in positions 19 to 25. The articulated series of *Malawisaurus* (Mal-197) has five V-shaped chevrons, the last (Mal-197-30) of which is larger than Mal-152-1. This suggests that Mal-152-1 occurs distal to Mal-197-30 or belongs to a smaller individual. Although the actual position of Mal-152-1 relative to Mal-197-30 cannot be determined definitely, Mal-152-1 is considered to be distal to Mal-197-30. It is clear that *Malawisaurus* has at least five V-shaped chevrons, more than the three in *Alamosaurus* (Gilmore 1946).

Sternal Plate. Left (Mal-188-1; Figure 19A, B; length = 490 mm; width = 300 mm; depth range = 5 mm to 50 mm) and right (Mal-188-2) sternal plates were found articulated (Jacobs et al. 1993, figure 1f). They are semilunar, typical of titanosaurians (Salgado et al. 1997), and their medial articular surfaces are irregularly ridged. The distal end of the sternal plate is indented probably for the attachment of the cartilaginous sternal ribs as in *Alamosaurus* (Gilmore 1946).

Coracoid. The left coracoid (Mal-235; Figure 19C) is slightly damaged. Typical of titanosaurians, the bone is roughly quadrangular (301 mm by 230 mm) and thickens towards the glenoid fossa. The glenoid fossa is rugose. The lateral surface is convex, and the medial surface is concave as in *Apatosaurus* (Gilmore 1936), *Camarasaurus* (Osborn and Mook 1921), and in *Isisaurus colberti* (Jain and Bandyopadhyay 1997). The coracoid foramen is elliptical and restricted to the dorsal portion of the element penetrating diagonally from the lateral surface through the bone.

Humerus. Four humeri (left, Mal-221, Figures 20A-D; right, Mal-289, Figure 20E; right, Mal-316; and left, Mal-317; Table 7) of possibly three individuals (different sizes and quarries) are well preserved and complete. The proximal end is slightly more expanded than the distal end. The head is rugose and placed more medially than laterally and

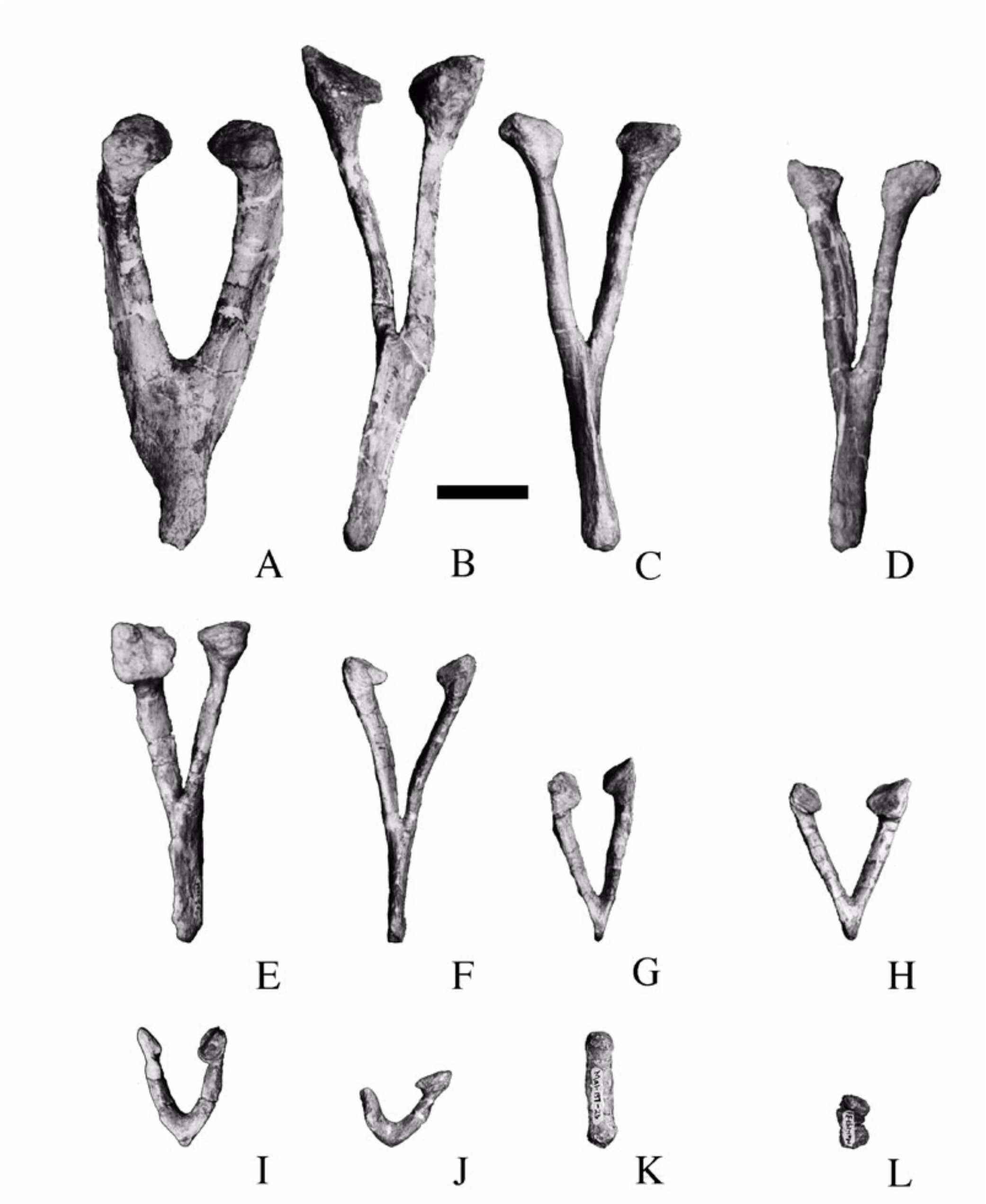

Figure 17. Chevrons of *Malawisaurus dixeyi,* posterior view, anteroposterior progression. A = Mal-195; B = Mal-277-3; C = Mal-219; D = Mal-197-22; E = Mal-220; F = Mal-197-24; G = Mal-197-27; H = Mal-197-28; I = Mal-197-30; J = Mal-152-1; K = Mal-197-23; L = Mal-197-31. Scale bar = 40 mm.

directed posteriorly as in *Alamosaurus* (Gilmore 1946), *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), and *Saltasaurus* (Powell 1986). The anterior surface is hollowed out and has a strongly marked facet proximally, below which is a well-marked depression for muscular attachment. The deltopectoral crest overhangs the center of the shaft on the proximal anterolateral margin. The shaft is straight and rounded. The ulna and radial condyles are strongly pronounced. The ulnar condyle is more prominent than the radial condyle.

Ulna. Three ulnae (Mal-190, Mal-218, Figure 21A-C, left; Mal-309; Table 7) of at least two different individuals are present. Mal-218 is well preserved, but Mal-190 and Mal-309 are less well preserved. The olecranon process is strongly developed and protrudes above the articular surface. The articular surface is concave medially, convex laterally. The shaft is triangular in section and has a deep radial

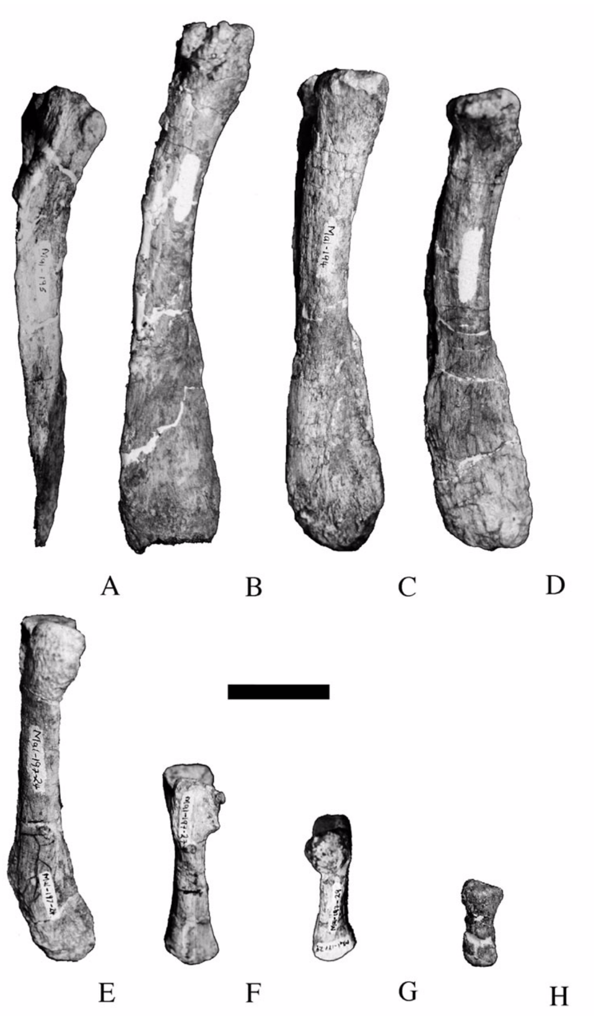

Figure 18. Chevrons of *Malawisaurus dixeyi,* lateral view, anteroposterior progression. A = Mal-195; B = Mal-219; C = Mal-194; D = Mal-197-22; E = Mal-197-24; F = Mal-197-27; G = Mal-197-29; H = Mal-152-1. Scale bar = 40 mm.

fossa proximally, and is quadrangular distally. A strong posterior tuberosity for muscle attachment emerges about 240 mm down and extends to the distal end. The distal end has a medially concave reniform outline.

Radius. A complete right radius (Mal-41; Figure 21D-G, Table 7) was found with a distal fragment (Mal-160) of a right humerus. The proximal and distal ends are about equally expanded and rugose. The proximal end is slightly concave and semicircular, whereas the distal end is slightly convex and ovoid. A longitudinal groove occurs on the posterior surface.

Manus. Four complete, associated metacarpals, and two fragmentary metacarpals are preserved. Based on comparison with *Alamosaurus* (Gilmore 1946), *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), and *Neuquensaurus* (von Huene 1929; Powell 1986) the associated metacarpals pertain to Mc I to IV. The proximal end of right metacarpal I (Mal-196; Figure 22A-D, Table 7) is roughly triangular and rugose. The shaft is rounded proximally and becomes mediolaterally compressed distally. The lateral surface has a triangular roughened surface proximally to articulate with metacarpal II. A ridge occurs midshaft on the lateral surface. The distal end is rectangular.

Metacarpal II (Mal-208-2, right, Mal-214, left distal fragment; Figure 22E-H, Table 7) has an oval proximal end. The proximal surface is rugose and generally convex. The shaft is transversely compressed and somewhat constricted medially. The medial surface of the shaft has a well-developed ridge proximally and a depression distally. The distal surface is subrectangular, convex, and rugose.

Metacarpal III (Mal-209 right, Figure 22I-J, Table 7) has a triangular proximal end with a posterior acute angle. In lateral view, about one third of the proximal portion is paddle shaped while the distal portion is more rounded. The lateral surface is flat and rugose, broad proximally and narrow distally. The distal end is rectangular and is widest anteromedio-posterolaterally. Mal-209 is shorter and more slender than metacarpal II.

Metacarpal IV (Mal-208-1, right, Mal-144, left proximal fragment; Figure 22K-N, Table 7) has a strongly twisted shaft. The proximal end is expanded and subrectangular. The proximal surface is slightly convex. The shaft is medially constricted and slightly twisted. About 20 mm from the distal end is a well-defined broad triangular tuberosity on the anterior surface. This is similar to *Alamosaurus*. The distal end is expanded mediolaterally, and the articular surface is convex.

In *Alamosaurus*, the lengths of the metacarpals decrease laterally (Gilmore 1946). The manus is reported but not illustrated in *Saltasaurus* and *Aeolosaurus* (Powell 1986). In *Opisthocoelicaudia*, metacarpal I is the longest, whereas metacarpals II and III are approximately the same length. In *Camarasaurus* (McIntosh et al. 1996a, b) and in *Apatosaurus* (Gilmore 1936, p. 226, top table) the third metacarpal is the longest and the two lateral metacarpals are the shortest. In *Malawisaurus*, the length of metacarpals decreases laterally.

There is no direct evidence of phalanges although the distal ends of metacarpals have articular surfaces that suggest the presence of phalanges. Titanosaurians are said to have no manual phalanges. If manual phalanges were present in *Malawisaurus*, this would suggest that basal titanosaurians had manual phalanges that were lost in more derived species.

Table 6. Measurements (mm) of chevrons of *Malawisaurus dixeyi*, as preserved. Chevron position corresponds to the interpreted anatomical position. - = chevron lacks spine; other symbols as in previous tables.

Chevron position	Specimen #	Chevron length	Arm length	Arm width	Spine width	Spine height	Morph
1	Mal-195	200	111	12	20	9	Y-shape
2	Mal-277-3	202	80	11	15	39	
3	Mal-288	210	120	†	†	†	
4	Mal-287	215	125	†	†	†	
5	Mal-183-2	221	95	10	11	26	
6	Mal-219	206	113	11	1.5	37	
7	Mal-194	204	100	12	1.7	35	
8	Mal-277-2	201	108	10	12	39	
9	Mal-197-22	19.2	102	10	15	36	
13	Mal-220	135	79	8	7	26	
14	Mal-197-24	130	85	7	7	24	
15	Mal-197-25	110	75	7	9	30	
16	Mal-197-26	94	70	8	-	-	V-shaped
17	Mal-197-27	85	70	8	-	-	
18	Mal-197-28	72	50	6	-	-	
19	Mal-197-29	60	40	6	-	-	
20	Mal-197-30	55	40	6	-	-	V-shaped
21	Mal-152-1	40	32	7	-	-	
22	Mal-197-23	51	51	7	-	-	Rod shaped
24	Mal-152-2	21+	21+	5	-	-	
25	Mal-197-31	23	23	3	-	-	

Ischium. Three ischia (left, Mal-42, length = 400 mm; width = 125 mm at the widest point, and = 90 mm at the narrowest point, Figure 23A, [Jacobs et al. 1993, figure 1g]; Mal-184; right, Mal-183-1, length = 382 mm; width = 114 mm at the widest point and = 100 mm at the narrowest point, Figure 23B) have dorsoventrally broad pubic articular facets. Opposite the pubic peduncle is a small, well-defined tubercle on the lateral surface for muscle attachment. The posterior blade is plate-like and short (Jacobs et al. 1993). The angle between the posterior surface of the ischium and the ischium-ischium articular surface is steep as in *Alamosaurus* (Gilmore 1946) and *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), suggesting that the cross section of the ischium shaft is nearly coplanar.

Femur. The femur (Figure 24, Table 8) is represented by a right proximal fragment (Mal-201; length of the preserved portion = 0.745 m). The anterior and posterior surfaces of the proximal end are damaged. The proximal portion is medially deflected and has a lateral bulge. The shaft of the femur is flattened anteroposteriorly and widened transversely so that it has an elliptical cross section with the long axis oriented mediolaterally. The humerus/femoral ratio is 0.72 in *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), 0.74 in *Titanosaurus* (McIntosh 1990), 0.78 in *Aegyptosaurus* (McIntosh 1990), and 0.80 in *Rapetosaurus* (Curry Rogers and Forster 2001) with an average of 0.76. The larger humerus of *Malawisaurus* (Mal-221) is 0.722 m. Thus, the estimated length of Mal-201 is 0.950 m.

Tibia. The surface of the right tibia (Mal-207; Figure 25, Table 8) is weathered. The tibia has a prominent and anteriorly projecting cnemial crest. The shaft is slightly twisted and medially constricted. A lateral groove occurs at the distal end of the shaft. The distal posteroventral process is broad transversely.

Fibula. The proximal end of the right fibula (Mal-189; Figure 25E-H, Table 8) is expanded anteroposteriorly. The proximal surface is crescent shaped. The proximal tibial scar on the medial surface is triangular and well marked. The shaft is flattened medially and convex laterally. About 230 mm downshaft on the lateral surface is an elongate lateral trochanter for muscle attachment (flexors of digits; Borsuk-Bialynicka 1977) beyond which the bone becomes more cylindrical. The distal end is triangular in cross section.

Pes. Metatarsal III? (Mal-145) is represented by a small fragment. The articular surface is subrectangular in outline and is concave as in the proximal surface of metatarsal III of *Opisthocoelicaudia* that articulates with the astragalus. Based on these observations, Mal-145 is interpreted as the proximal fragment of metatarsal III of *Malawisaurus*.

Metatarsal V (right; Mal-210; Figure 26A-B, Table 8) is flattened mediolaterally. The proximal end is semicircular, convex, and expanded. The shaft is laterally compressed. The medial surface is more concave proximally than distally. The distal end is convex and ellipsoidal.

A proximal right pedal phalanx, probably of digit I (Mal-213; Figure 26C-D), is conical proxi-

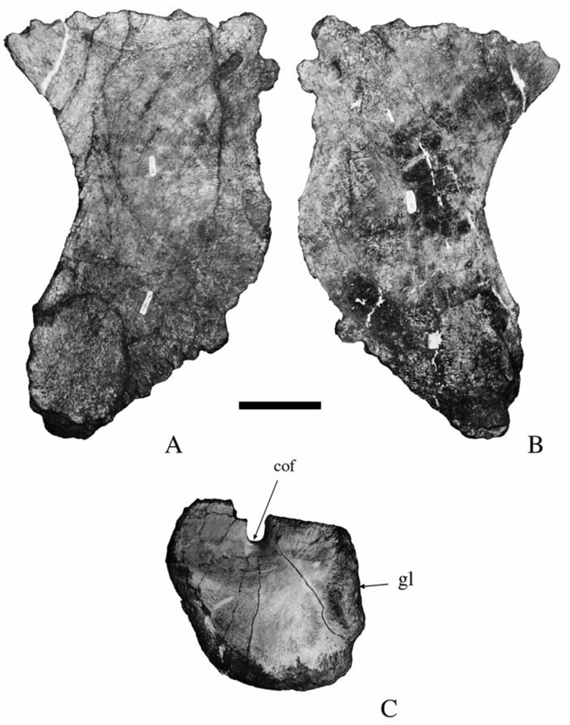

Figure 19. Pectoral girdle of *Malawisaurus dixeyi.* A and B, left sternal plate (Mal-188-1); C, left coracoid (Mal-235). A, dorsal view; B, ventral view; C, lateral view. Scale bar = 100 mm.

mally with the apex of the cone being placed laterally. The ventral surface is shallowly depressed medially.

The left ungual (Mal-211; Figure 26E-G, Table 8) probably of digit I, is compressed laterally. The proximal surface is concave while the distal end is pointed. Longitudinal grooves occur on the interpreted lateral surface as in *Apatosaurus* (Gilmore 1936) and in *Camarasaurus* (BYU 9047; McIntosh et al. 1996). Although shallow grooves occur, the medial surface is relatively smooth compared to the lateral surface. The ventral surface has a proximal medial tuberosity. In lateral view, it arcs ventrally to the point.

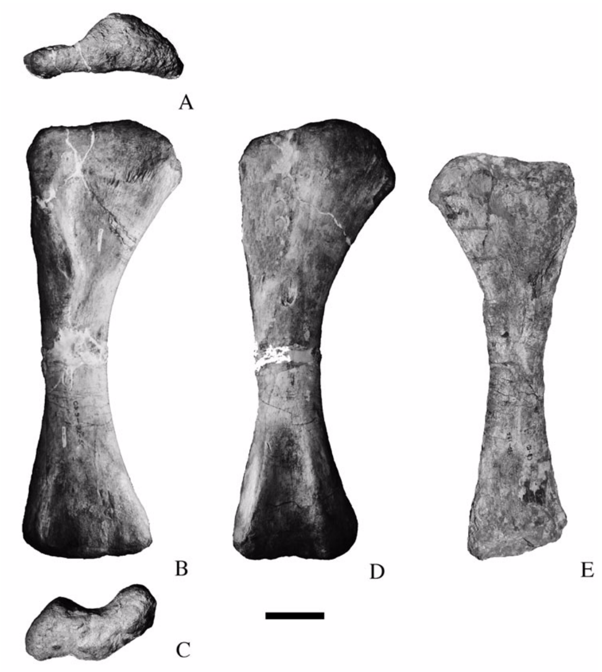

Figure 20. Humeri of *Malawisaurus dixeyi.* A-D, left (Mal-221), right (Mal-289). A, proximal view; B and E, anterior view; C, distal view; D, posterior view. Scale bar = 100 mm.

Another left ungual (Mal-212; Figure 26H-J) is smaller than Mal-211. In *Apatosaurus*, the shapes of the ungual phalanges are similar in the first, second, and third digits. The sizes decrease laterally. Thus, Mal-212 is likely a more lateral phalanx than Mal-211, probably from the second digit.

Armor. Previously it was reported that *Malawisaurus* lacked direct evidence of dermal armour, but calcite pseudomorphs shaped like dermal scutes were found associated with the bones in the same quarry (Jacobs et al. 1993, figure 2e). A large dermal scute was more recently discovered (Mal-204; Figure 27). It is 190 mm long and 95 mm wide. The morphology of this dermal armour is similar to the large dermal scutes associated with *Saltasaurus*

Table 7. Measurements (mm) of forelimb elements of *Malawisaurus dixeyi*. Widths were measured mediolaterally. Msht = midshaft; Mc = metacarpal.

Element (specimen #)	Length	Proximal width	Midshaft width	Distal width	Length/msht width
Humerus (Mal-221)	722	259	1.0	212	66
Humerus (Mal-289)	650	259	105	200	62
Humerus (Mal-316)	730	265	110	190	66
Humerus (Mal-317)	720	260	100	215	72
Ulna (Mal-190)	411	146	78	78	53
Ulna (Mal-218)	515	183	70	88	74
Radius (Mal-41)	41	101	42	75	105
Mc I (Mal-196)	255	57	28	38	91
Mc II (Mal-208-2)	235	46	23	37	102
Mc III (Mal-209)	200	30	29	43	69
Mc IV (Mal-208-1)	153	48	31	71	49

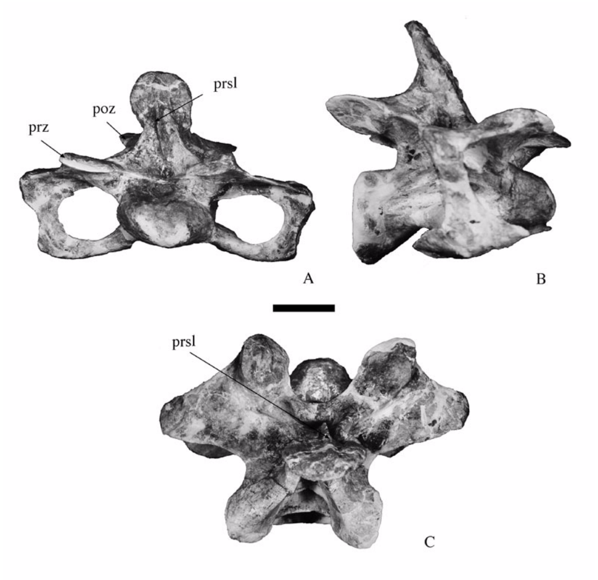

Figure 21. Ulna and radius of *Malawisaurus dixeyi*. A-C, left ulna (Mal-218); D-G, right radius (Mal-41). A and D, proximal view; B, lateral view; C and F, distal view; E, anterior view; G, lateral view. Scale bar = 100 mm.

(PVL 4017-112), whereas the pseudomorphs are similar to the small dermal scutes of *Saltasaurus* (PVL 6017-118) and small dermal scutes of the titanosaurian from Madagascar (FMNH PR 2021; Dodson et al. 1998).

KARONGASAURUS, gen. nov.

Type Species. *Karongasaurus gittelmani* sp.nov.

Holotype. Mal-175; a dentary with conical replacement teeth; paleontological collection of the Malawi Department of Antiquities.

Etymology. Referring to Karonga District in northern Malawi where the fossil was collected.

Diagnosis

Dentary strongly curved towards symphysis; the rostral end of the dentary is not perpendicular to the long axis of the dentary; dorsal margin of the buccal surface flares outward anteriorly; tooth row restricted to the anterior portion of the jaw; pencil-like teeth with wear facets oblique to the labiolingual axis.

Karongasaurus gittelmani sp. nov.

Figure 28

Type and only species. *K. gittelmani* sp. nov.

Holotype. A left mandible, Mal-175.

Referred Specimens. Isolated teeth (Table 1; Mal-7, Mal-10, Mal-11, Mal-12, Mal-13, Mal-14, Mal-15, Mal-16, Mal-33, Mal-36, Mal-39, Mal-153, Mal-156, Mal-267, Mal-268, Mal-269, Mal-271, Mal-272, Mal-307).

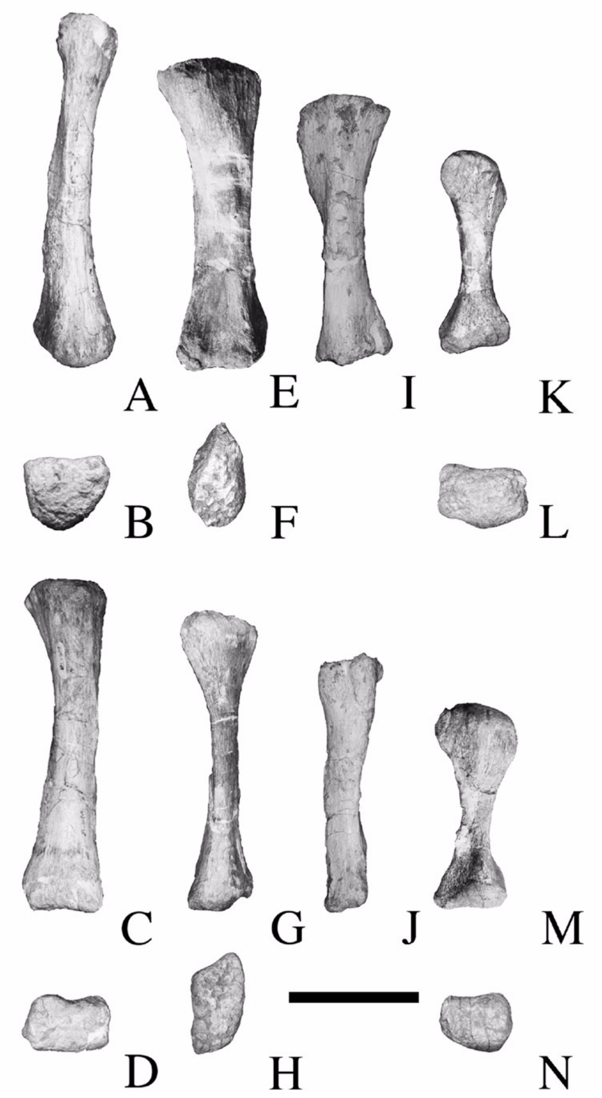

Figure 22. Right metacarpals of *Malawisaurus dixeyi*. A-D, metacarpal I (Mal-196); E-H, metacarpal II (Mal-208-2); I and J, metacarpal III (Mal-209); K-N, metacarpal IV (Mal-208-1). A and I, lateral view; B, F, and L, proximal view; C, G, J, and M, anterior view; D, H, and N, distal view; E, medial view; K, posterior view. Scale bar = 100 mm.

Diagnosis. As for genus.

Geologic Age and Distribution. Early Cretaceous, Mwakasyunguti area, Karonga District, Malawi, Africa.

Etymology. In honor of Steve Gittelman, friend of science, for his work as president of the Dinosaur Society.

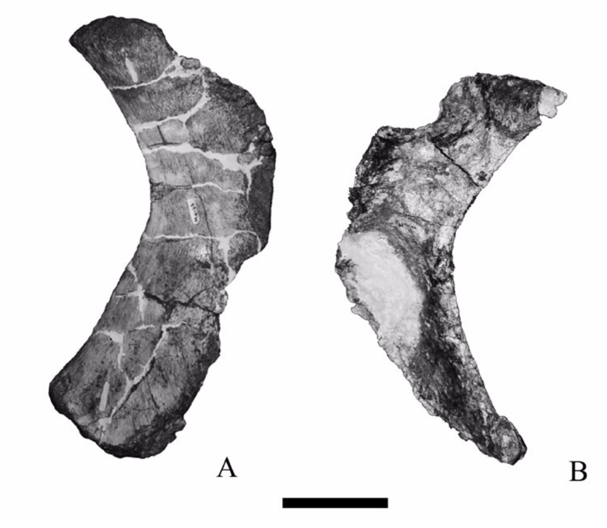

Figure 23. Ischia of *Malawisaurus dixeyi.* A and B, ischia; A = Mal-42, left; B = Mal-183-1, right; ventral surface of the posterior process of Mal-183-1 is damaged. Scale bar = 100 mm.

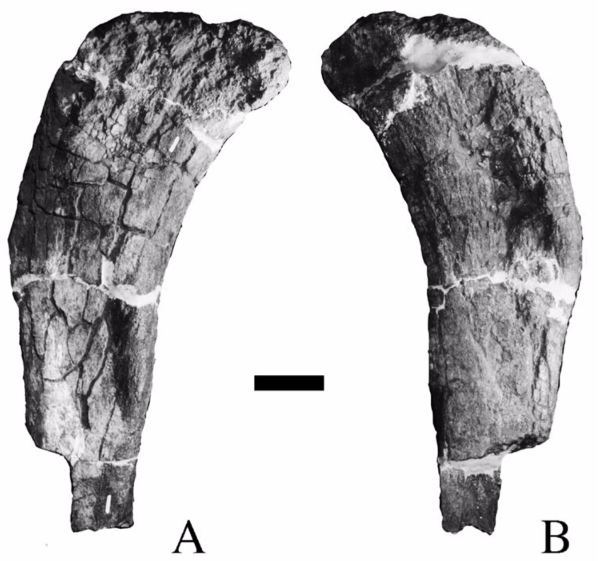

Figure 24. Proximal right femur of *Malawisaurus dixeyi* (Mal-201). A, posterior view; B, anterior view. Scale bar = 100 mm.

Description

Dentary. The left dentary (Mal-175; Figure 28A–B) is shallow and has 12 tooth positions, even though the symphyseal region is incomplete. The mandible is 138 mm long from the symphysis to the surangular notch and has an 80 mm tooth row. Three unerupted pencil-like teeth are in place. The most posterior tooth position is 62 mm anterior to the surangular notch, almost one third of the distance seen in the mandible of *Malawisaurus* (Figure 28B; Jacobs et al. 1993). The dorsal margin of the dentary posterior to the tooth row forms a sharp ridge. Anteriorly the dentary is strongly curved towards the symphysis and the dorsal margin of the buccal surface flares outward. The anterior limit of the splenial groove lies below the fourth tooth position from the rear.

Teeth. Slender conical isolated teeth (Figure 28C-E; anteroposterior width range = 30 to 50 mm; average anteroposterior width = 0.4; labiolingual width range = 30 to 40 mm; average labiolingual width = 35 mm) similar to those in the dentary of *Karongasaurus* are therefore attributed to *Karongasaurus*. These are more cylindrical than those of *Malawisaurus*. The crowns have faint anterior and posterior ridges and are more acute cones toward the apex than in *Malawisaurus*. Wear facets are high angled on the lingual (Mal-153, Mal-272), anterior, and posterior surfaces (Mal-13, Mal-156).

Discussion

The short tooth row and presence of conical teeth in *Karongasaurus* set it apart from *Brachiosaurus*, *Camarasaurus*, *Euhelopus*, *Malawisaurus, Mamenchisaurus, Omeisaurus*, and *Shunosaurus*, all of which have long tooth rows and broad teeth. *Karongasaurus* shares these characters with *Antarctosaurus wichmannianus* (von Huene 1929, Powell 1986), dicraeosaurids (Janensch 1935), diplodocids (McIntosh and Berman 1975; Berman and McIntosh 1978), *Nemegtosaurus* (Nowinski 1971), *Quaesitosaurus* (Kurzanov and Bannikov 1983), and *Rapetosaurus* (Curry Rogers and Forster 2001). Unlike dicraeosaurids and diplodocids, where the wear facets on teeth are nearly horizontal, the wear facets on *Karongasaurus* teeth are

Table 8. Measurements (mm) of hindlimb elements of *Malawisaurus dixeyi*, as preserved. Widths were measured mediolaterally. Msht = midshaft; + = incomplete; † = data unavailable.

Element (specimen #)	Length	Proximal width	Midshaft width	Distal width	Length/midshaft width
Femur (Mal-201)	745+	280	†	†	†
Tibia (Mal-207)	540	141	42	103	129
Fibula (Mal-189)	590	120	52	87	114
Metatarsal V (Mal-210)	118	49	37	75	32
Pedal claw (Mal-211)	104	64	41	19	21

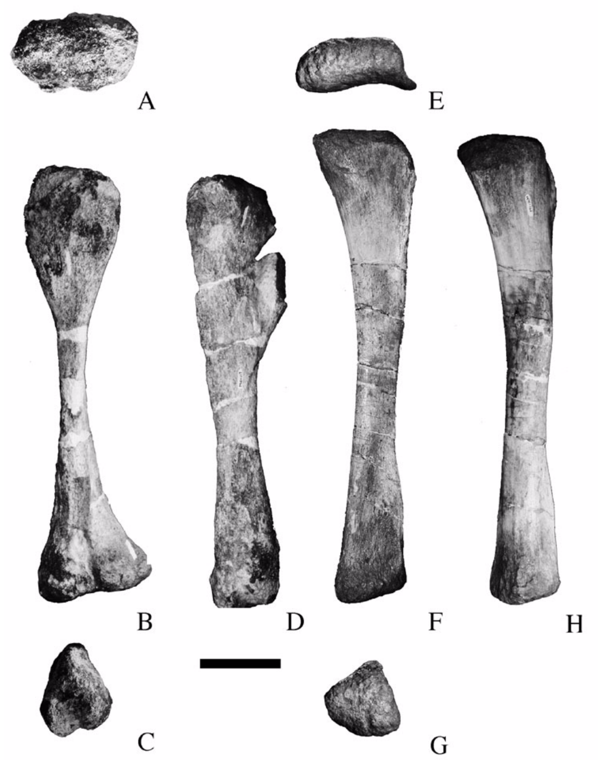

Figure 25. Tibia and right fibula of *Malawisaurus dixeyi*. A-D, right tibia (Mal-207); E-H, right fibula (Mal-189). A and E, proximal view; B, posterior view; C and G, distal view; D, anteromedial view; F, medial view; H, lateral view. The shaft of Mal-207 is exfoliated. Scale bar = 100 mm.

steep angled as in *Antarctosaurus wichmannianus*, *Nemegtosaurus*, and *Quaesitosaurus* (Calvo 1994). These taxa have been considered to be either diplodocids or titanosaurians (von Huene 1929; Powell 1986; McIntosh 1990; Jacobs et al. 1993; Chatterjee and Rudra 1996; Salgado and Calvo 1997; Sereno et al. 1999; Upchurch 1999). However, *Nemegtosaurus*, and *Quaesitosaurus* are considered titanosaurians in the recent analysis of Curry Rogers and Forster (2001, see also Wilson 2002).

The dentary of *Karongasaurus* is distinct because the rostral mandibular curvature toward the symphysis is less strong than in *Nemegtosaurus*, *Quaesitosaurus*, *Antarctosaurus wichmannianus,* and diplodocids, in which the mandible is U-shaped in dorsal view. The dentary of *Karongasaurus* flares outward anteriorly from the inflection point, a feature not observed in other sauropods. The dentary of *Rapetosaurus* is not known, and therefore cannot be used for comparison.

Postcranial elements found in the Dinosaur Beds lack certain characters (e.g., forked chevrons, deeply cleft neural spines of distal cervical and proximal dorsal vertebrae) that would, if present, suggest diplodocoid affinity (*sensu* Wilson and Sereno 1998). Therefore, by default stemming from the presence of *Malawisaurus*, a known titanosaurian, but no other higher level taxon demonstrably present, until more data are found to suggest otherwise, *Karongasaurus* is considered titanosaurian. If correct, this implies that the possession of slender teeth, the anteromedial mandibular curvature, and the anterior restriction of teeth were characters acquired independently from their presence in diplodocoids.

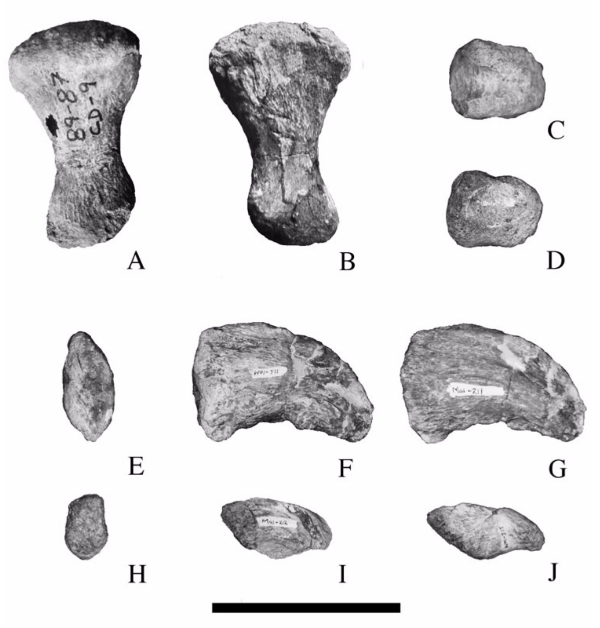

Figure 26. Pedal elements of *Malawisaurus dixeyi*. A and B, right metatarsal V (Mal-210); C and D, proximal phalanx (Mal-213); E-G, left ungual (Mal-211), probably of digit I; H-J, left ungual (Mal-212), probably of digit II. A, G, and J, lateral view; B, F, and I, medial view; C, dorsal view; D, ventral view; E and H, proximal view. Scale bar = 100 mm.

TITANOSAURIDAE, gen. et sp. indet.

Geologic Age and Distribution. Early Cretaceous, Mwakasyunguti area, Karonga District, Malawi, Africa.

Description

One small sauropod caudal vertebra (Mal-5; Figure 29; undesignated morph 1 of Gomani 1999a, figure 2c) cannot be assigned to a named taxon with confidence. The centrum of Mal-5 (posterior fragment) is procoelous (*sensu* Romer 1956). A posterior ball is centrally positioned on the centrum. The ventral surface of the centrum is flat. The chevron articular facets are poorly developed posteroventral protuberances on the centrum. The

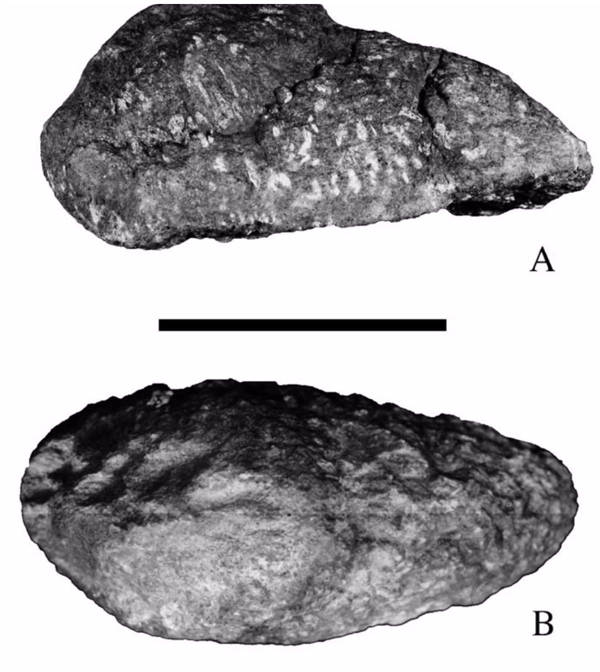

Figure 27. Dermal armor (scute) of *Malawisaurus dixeyi* (Mal-204). A, lateral view B, dorsal view. Scale bar = 100 mm.

neural arch is not preserved. The width and height of the centrum, measured from the posterior end, are 38 mm and 53 mm, respectively.

The size and the placement of the posterior ball on the centrum of Mal-5, in comparison with strongly procoelous caudal vertebrae of other titanosaurians (SAM 8992; Janensch 1929a; Gilmore 1946; Powell 1986; MUCPv 204; Salgado 1996; Salgado and Calvo 1993; Jain and Bandyopadhyay 1997; Kellner and de Azevedo 1999), suggest that Mal-5 is a middle or a posterior caudal vertebra (Gomani 1999a, b).

Among sauropods, strongly procoelous caudal vertebrae are known in *Mamenchisaurus* (Young 1958; Yang and Zhao 1972) and in Titanosauria. However, the middle and posterior, but not the posteriormost caudals of *Mamenchisaurus* are platycoelous. The most posterior caudals of *Mamenchisaurus* are biconvex. Thus, it is more likely that Mal-5 pertains to Titanosauridae, a family of titanosaurians more derived than *Malawisaurus*. Because it cannot be assigned to *Malawisaurus*, it is possible, but not demonstrated, that it may pertain to *Karongasaurus*.

TITANOSAURIA, gen. et sp. indet.

Geologic Age and Distribution. Early Cretaceous, Mwakasyunguti area, Karonga District, Malawi, Africa.

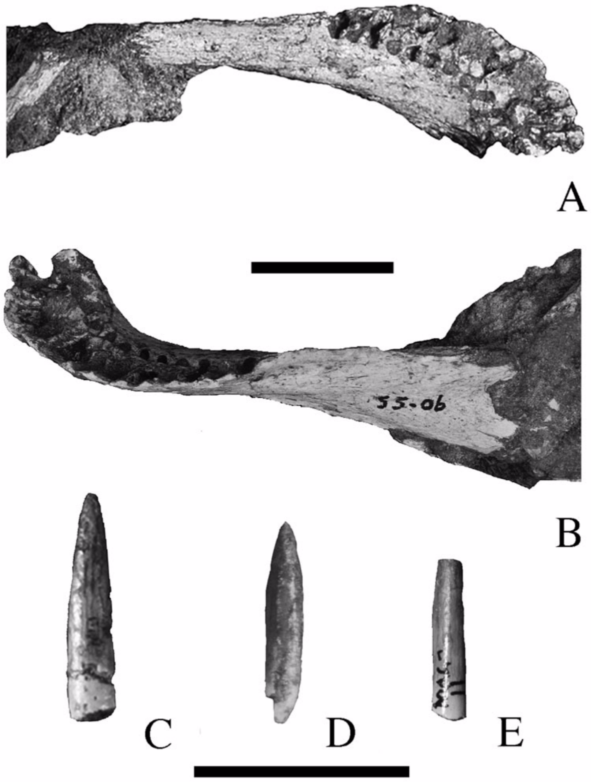

Figure 28. *Karongasaurus gittelmani* gen. et sp. nov. A and B, left dentary (Mal-175); C-E, teeth. C = Mal-36; D = Mal-7; E = Mal-11. A, medial view; B, occlusal view; A-B and B-E, same scale. Scale bars = 40 mm in A and B, 20 mm in C-E.

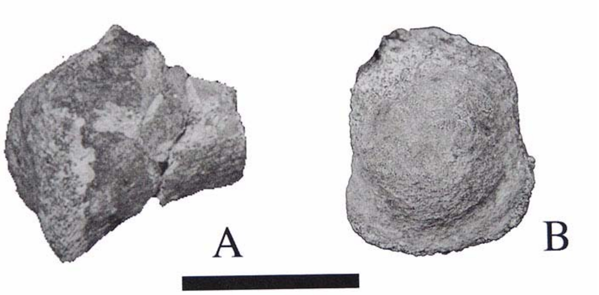

Figure 29. Middle or posterior caudal vertebra of Titanosauridae gen. et sp. indet. (Mal-5). A, lateral view; B, posterior view. Scale bar = 40 mm.

Description

There are five isolated caudal vertebrae (Figure 30, Table 9; undesignated morph 2 of Gomani 1999a, figure 3) of different morphology from that ascribed to *Malawisaurus* and to Titanosauridae indet. (Mal-1 [Jacobs et al. 1993]; Mal-3, Mal-222, and Mal-230 [Gomani 1999a]). The middle (Mal-230) and posterior (Mal-1, Mal-3, Mal-222) caudal vertebrae of Titanosauria indet. have quadrangular

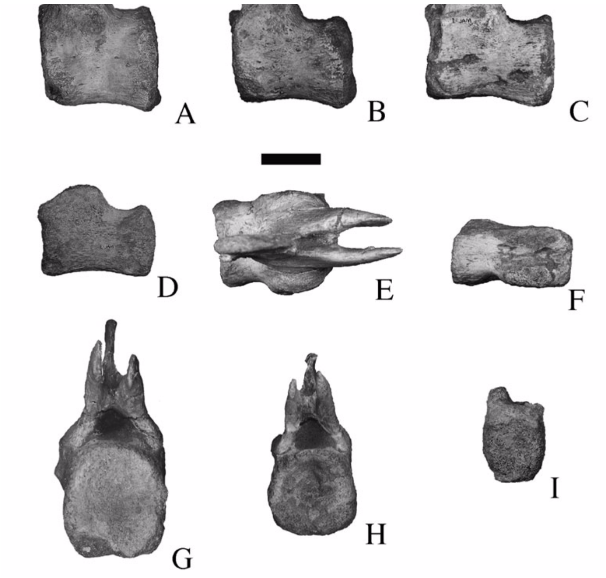

Figure 30. Caudal vertebrae of Titanosauria indet. A and G middle caudal (Mal-230); B, C, D, E, F, H, and I, posterior caudals; B and E = Mal-222; C and H = Mal-1; D, F, and I = Mal-3. A, B, C, and D; right lateral view, reversed; E, and F, dorsal view; G-I, anterior view. Scale bar = 40 mm.

centra that have nearly flat ventral surfaces, flat lateral surfaces, and poorly developed chevron articular facets. This contrasts with *Malawisaurus* in which the rounded centra have broad, shallow grooves on the ventral surface, slightly concave lateral surfaces, concave ventral surfaces in lateral view, and prominent chevron articular facets. It is not clear whether these vertebrae belong to a different taxon or represent biological or taphonomic variability in *Malawisaurus*. If they are determined to be taxonomically distinct, which appears likely, there are at least three taxa of sauropods present in the Dinosaur Beds, and it is unclear which of the indeterminate vertebrae, if any, pertain to *Karongasaurus*, although some lines of evidence lead to reasoned speculation (see below).

DISCUSSION AND CONCLUSIONS

Dentaries and teeth demonstrate the presence of at least two sauropods in Malawi, *Malawisaurus* and *Karongasaurus*. Based on differences in the morphology of the caudal vertebrae that have been generally recognized as significant, titanosaurian caudal vertebrae from Malawi also represent at least two taxa including *Malawisaurus* and Titanosauridae indet. *Malawisaurus* has platycoelous medial caudal vertebrae, whereas a procoelous middle or posterior caudal vertebra is distinct from *Malawisaurus* and referred to Titanosauridae indet. A third taxon may be represented by vertebra referred to Titanosauria indet.

Phylogenetic analyses that include *Aeolosaurus*, *Alamosaurus*, *Andesaurus*, *Antarctosaurus*, *Argentinosaurus*, *Epachthosaurus*, *Malawisaurus*, *Nemegtosaurus*, *Neuquensaurus*, *Opisthocoelicaudia*, *Quaesitosaurus*, *Rapetosaurus*, *Saltasaurus*, and *Titanosaurus* (Upchurch 1995, 1998, 1999; Salgado et al. 1997; Curry Rogers and Forster 2001; see also Wilson 2002) indicate that *Andesaurus* and *Malawisaurus* are basal titanosaurians. In fact, *Malawisaurus* is the most complete Early Cretaceous titanosaurian known. It is represented by cranial elements, 18 cervical, 10 dorsal, six sacral, and 51 caudal vertebrae, 24 chevrons, pectoral elements, pelvic elements, and dermal armor. Phylogenetic analyses also indicate that taxa with cylindrical teeth and strongly procoelous posterior caudal vertebrae (or opisthocoelous in the case of *Opisthocoelicaudia*) are more derived than those with broad teeth and platycoelous middle and distal caudal vertebrae.

Skull Shape and Morphological Diversity in Malawi Sauropods. Cranial material attributed to titanosaurians includes one or two partial braincases of *Titanosaurus indicus* from the Late Cretaceous of India (Berman and Jain 1982; Chatterjee and Rudra 1996), a maxilla from India (von Huene and Matley 1933), a partial braincase and partial skull roof of *Saltasaurus* (PVL 4017-161) from the Late Cretaceous of Patagonia (Powell 1986, 2003), a premaxilla of Titanosauridae indet. from the Late Cretaceous of Patagonia (Scuitto and Martinez 1994), a premaxilla (PVL 3670-12) that Powell (1979) identified as *Laplatasaurus* but later referred to as Titanosauridae indet. (Powell 1986, 2003), a fragmentary braincase from the Late Cretaceous of France (Le Loeuff et al. 1989), the

Table 9. Measurements (mm) of caudal vertebrae of Titanosauria indet. as preserved. Caudal position corresponds to approximate anatomical position. + = incomplete.

Caudal position	Specimen #	Centrum length	Centrum width	Centrum height	Total height of vertebra
Middle	Mal-230	85	65	78	170
Posterior	Mal-222	81	64	65	133
	Mal-1	86	57	64	138
	Mal-3	82	44	54	70

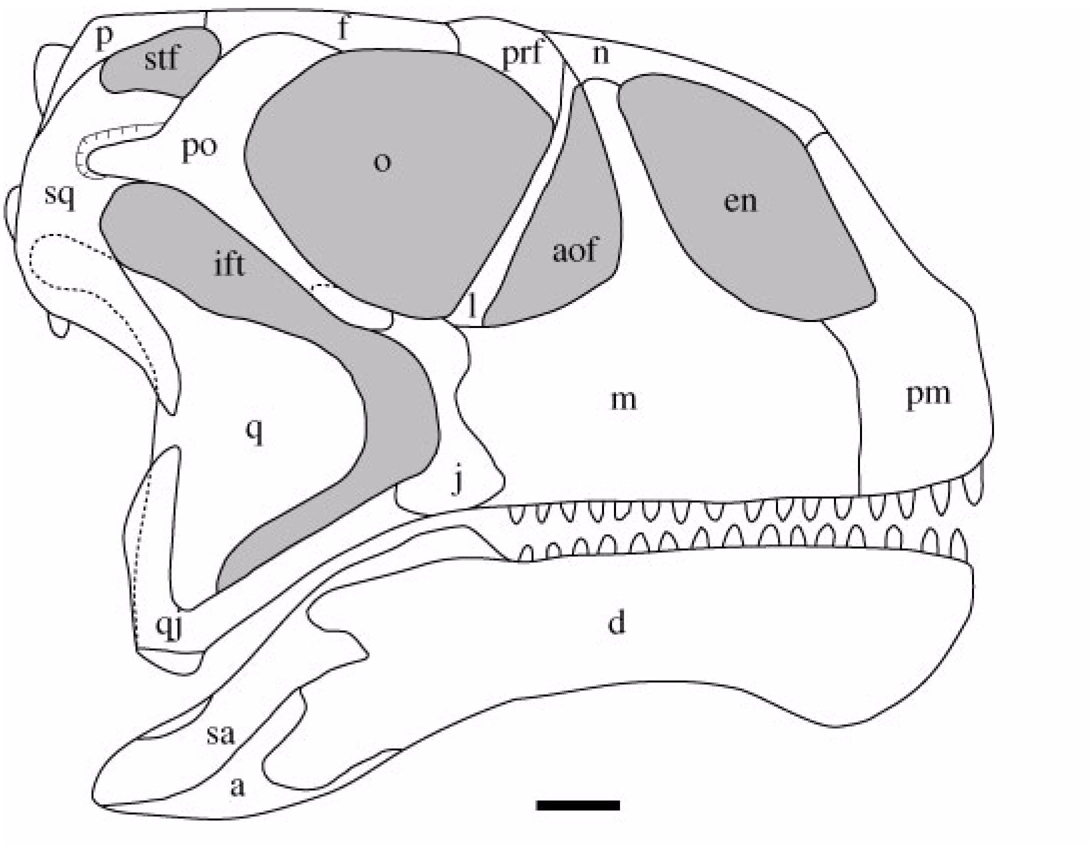

Figure 31. Reconstruction of the skull of *Malawisaurus dixeyi*.

braincase, quadrate, quadratojugal, squamosal, and the lower jaws of *Antarctosaurus wichmannianus* (MACN 6904) from the Late Cretaceous of Patagonia (von Huene 1929; Powell 1986, 2003), two partial braincases of *Antarctosaurus septentrionalis* from the Late Cretaceous of India (von Huene and Matley 1933; Chatterjee and Rudra 1996), a nearly complete disarticulated cranium of *Rapetosaurus* from the Late Cretaceous of Madagascar (Curry Rogers and Forster 2001, 2004), and the specimens of *Malawisaurus* from the Early Cretaceous of Malawi.

There are two basic morphs of sauropod skulls: one high and short, the other low and elongate (Wilson 2002). The high, short morph is referred to as a macronarian skull, whereas the low, elongate morph is generally referred to as a diplodocoid skull (Coombs 1975; McIntosh and Berman 1975; Berman and McIntosh 1978; Salgado and Calvo 1997; Wilson 2002). The macronarian skull is present in *Brachiosaurus*, *Camarasaurus*, *Datousaurus*, *Euhelopus*, *Mamenchisaurus*, *Omeisaurus*, *Shunosaurus*, and most prosauropods, whereas the diplodocoid skull is present in *Apatosaurus*, *Diplodocus*, and dicraeosaurids (Salgado and Calvo 1997; see also Tidwell and Carpenter, 2003).

Comparison of cranial features of *Malawisaurus* with macronarian and diplodocoid skulls suggests that *Malawisaurus* had a high, short macronarian skull (Figure 31). The anterior section of the suture between premaxilla and maxilla appears to have been nearly vertical as suggested by the highly angled articular surface for the maxilla on the premaxilla. The high premaxilla also suggests that *Malawisaurus* had a high, short, and blunt snout, and separate nares positioned rostrally and facing laterally. The tooth row extends more than half the length of the dentary. The mandibular symphysis is oblique to the long axis of the mandible. The occipital condyle projected posteroventrally and the basipterygoid processes projected ventrally. The quadrate axis was nearly vertical, the pterygoid process of the quadrate was approximately perpendicular to the long axis of the pterygoid, the pterygoid process was directed anteriorly as in *Brachiosaurus* (Janensch 1935) and *Camarasaurus* (Osborn and Mook 1921), and the mandibular articulation was placed posteriorly beneath the level of the occipital condyle. Thus, this study demonstrates that at least some titanosaurians, including *Malawisaurus*, had high and short crania, as compared to others such as *Rapetosaurus*, which had low and elongate crania (Curry Rogers and Forster 2001, 2004).

In addition, the titanosaurians *Nemegtosaurus* (Nowinski 1971), and *Quaesitosaurus* (Kurzanov and Bannikov 1983; Curry Rogers and Forster 2001) had slender teeth restricted to the anterior portion of the mandible, and also had low and elongate crania. If that association of characters is general within titanosaurians, by implication *Karongasaurus* would also have had a low and elongate cranium. Further, phylogenetic analyses indicate that titanosaurians with slender teeth and which have strongly procoelous middle and posterior caudal vertebrae are derived relative to basal titanosaurians (Upchurch 1995; Salgado et al. 1997; Curry Rogers and Forster 2001). Thus, both *Karongasaurus* and Titanosauridae indet. from the Dinosaur Beds are derived relative to *Malawisaurus*. If those characters are linked, the vertebra assigned to Titanosauridae indet. may belong to *Karongasaurus*.

In any case, *Malawisaurus* and *Karongasaurus* are two distinct titanosaurian taxa that coexisted in the Early Cretaceous of Malawi and exhibited quite different morphological features, certainly in their lower jaws and teeth, and probably also in their skull shapes. Cylindrical teeth, an anteriorly restricted tooth row, and a long, low skull shape evolved as a complex at least twice, once within diplodocoids and once within titanosaurians. This character complex is functionally and adaptively important for feeding. Its multiple origins, and its variance from the macronarian skull pattern, implies that *Malawisaurus* and *Karongasaurus* were ecologically distinct. If so, differences seen in the lower jaw, teeth, and probably the skull of these herbivores were significant in the ecological partitioning of their Early Cretaceous environment. Although the macronarian and diplodocoid skull morphs are well known to occur together, for example in the Jurassic of Africa, in the Early Cretaceous of Malawi approximately equally divergent skull morphs are exhibited at a lower systematic level among titanosaurians alone.

ACKNOWLEDGMENTS

This work is part of the Malawi Dinosaur Project, a cooperative project between colleagues from Malawi and the United States. L.L. Jacobs and D.A. Winkler of Southern Methodist University have been instrumental in the field, laboratory, and in completion of this study. I thank Z. Kaufulu of Chancellor College, University of Malawi, and Y. Juwayeyi, the Director of Antiquities at the time this study was done. Malawian colleagues (especially W. Michala, J. Chilachila, S. Mithi, H. Simfukwe, E.S.Tambala, A.Topeka, J. Chimzimu, and D. Banda of the Malawi Department of Antiquities), the staff of Museums of Malawi in Blantyre, and the villagers around Mwakasyunguti and Ngara have been helpful in the field and laboratory. I also thank K. Newman, A. Winkler, L. MacLatchy, L. Taylor, J. Congleton, A. Mohamed, V. Yarborough, D. Vineyard, Y-N Lee, Y. Kobayashi, J. Head, J. Harris, my family, my friends, and all those who have contributed to this study in one way or other. P. Curry, P. Rose, J.A. Wilson, and M. Bonnan reviewed the manuscript at one stage or another.

The following people allowed access to collections in their charge: J. Bonaparte, F. Novas, and G. Rougier (Museo Argentino de Ciencias Naturales, Buenos Aires); J. Powell (Museo de Ciencias Naturales, Tuçuman); A. Fiorillo (Dallas Museum of Natural History); A. Milner (The Natural History Museum, London); J. Clack (University Museum of Zoology, Cambridge); the late H. Jaeger and W.-D. Heinrich (Museum für Naturkunde, Berlin); and G. King (South African Museum). Thanks also for access to specimens at the Field Museum of Natural History, Chicago, Illinois; Brigham Young University, Earth Science Museum, Provo, Utah; National Museum of Science, Tokyo, Japan, special exhibit on dinosaurs of Gondwana; Instituto Miguel Lillo de la Universidad de Tuçuman, Tuçuman, Argentina; Museo Paleontológico “Egidio Feruglio” Trelew, Argentina; Museo Argentino de Ciencias Naturale “Bernadino Rivadavia” Buenos Aires, Argentina; the temporary Dinoworld exhibit at the Dallas Museum of Natural History; and the Shuler Museum of Paleontology at Southern Methodist University.

This project was supported by the National Geographic Society, the Dinosaur Society, American Airlines, the Institute for the Study of Earth and Man at Southern Methodist University, The Saurus Institute, Caltex Oil (Malawi) Limited, the Malawi Department of Antiquities, the Dallas Paleontological Society, the Graduate Student Assembly of Southern Methodist University, and Johnson and Johnson Orthopaedics.

W. Downs was an important member of the Malawi Dinosaur Project. His efforts in Malawi are greatly appreciated, as are those of F. Morocco and J. Khomu, all three of whom worked together at Mwakasyunguti and have since seen their final fieldwork.

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Appendix 1. Sauropod taxa used for comparison.

Taxon	**Source**
Titanosaurians	
Aeolosaurus	Powell 1986, 1987a; Salgado and Coria 1993
Alamosaurus	Gilmore 1946; Lucas and Hunt 1989
Andesaurus	MUCPv 132; Calvo and Bonaparte 1991
Argentinosaurus	PVPH-1, cast; Bonaparte and Coria 1993
Epachthosaurus	MACN-CH 1317, cast; Powell 1986
Gondwanatitan	Kellner and Azevedo 1999
Isisaurus	Wilson and Upchurch 2002
Janenschia	SAM 8992; Janensch 1922, 1929a; Wild 1991
Macrurosaurus	Seeley 1876
Neuquensaurus	von Huene 1929; Powell 1986
Opisthocoelicaudia	Borsuk-Bialynicka 1977
Pellegrinisaurus	MPCA 1500; Powell 1986; Salgado 1996
Rapetosaurus	Curry Rogers and Forster 2001
Saltasaurus	PVL 4017; Bonaparte and Powell 1980; Powell 1986, 1992
Titanosaurus	von Huene 1929; von Huene and Matley 1933; Berman and Jain 1982; Powell 1986; Jain and Bandyopadyay 1997
cf. *Titanosaurus* sp. “DGM Series A, B, and C” from Brazil	Powell 1986, 1987a, b
Titanosauridae indet. n. sp. A, B, and C from Brazil	Campos and Kellner 1999
Unnamed titanosaurian from Argentina	MACNv 204, cast; Salgado and Calvo 1993
Other sauropods	
Amargasaurus	MACN-N 15, cast; Salgado and Calvo 1992
Antarctosaurus	MACN 6906, 6904; von Huene 1929; Powell 1986
Apatosaurus	CM 11162, cast; Riggs 1903; Gilmore 1936
Brachiosaurus	Riggs 1904; Janensch 1929a, 1935, 1950
Camarasaurus	BYU 9047; CM 11338, cast; McIntosh et al. 1996a, b
Dicraeosaurus	Janensch 1929a, b, 1935
Diplodocus	CM 3452, cast; Osborn 1899; Hatcher 1901; Holland 1906, 1924; McIntosh and Berman 1975
Haplocanthosaurus	Hatcher 1903, McIntosh and Williams 1988
Mamenchisaurus	Young 1958; Yang and Zhao 1972; Russell and Zheng 1993

Appendix 2. Abbreviations used in the text and on figures.

Anatomical. a, angular; acdl, anterior centrodiapophyseal lamina; aof, antorbital fenestra; ba, basicranium; bo, basioccipital; bp, basipterygoid process; bt, basaltubera; ca, caudal vertebra; ce, cervical vertebra; ch, chevron; co, coracoid; cof, coracoid foramen; cr, cervical rib; d, dentary; di, diapophysis; do, dorsal vertebra; dr, dorsal rib; en, external naris; f, frontal; fi, fibula; fm, foramen magnum; gl, glenoid; hu, humerus; ic, canal for the internal carotid artery; ift, infratemporal fenestra; is, ischium; j, jugal; l, lacrimal; ls laterosphenoid; m, maxilla; mf, metotic foramen; mp, metapodial; n, nasal; nc, neural canal; o, orbit; oc, occipital condyle; ost, osteoderm; p, parietal; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina; ple, pleurocoel; pm, premaxilla; po, postorbital; pop, paraoccipital process; posl, post-spinal lamina; poz, postzygapophysis; pra, preantorbital opening; prf, prefrontal; prsl, pre-spinal lamina; prz, prezygapophysis; q, quadrate; qj, quadratojugal; Roman numerals, canals for cranial nerve IV, V, XII; sa, surangular; sar, sacral rib; snf, subnarial foramen; soc, supraoccipital; sp, neural spine; sq, squamosal; stf, supratemporal fenestra; stp, sternal plate, sy, sacricostal yoke; thu, theropod ungula; u, ungula; ul, ulna.

Institutional. BYU, Brigham Young University, Provo, Utah, USA; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; DGM, Museo de la División de Geología y Mineralogía de la Dirección Nacional de Producción Mineral, Rio de Janeiro, Brazil; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MACN-CH, Museo Argentino de Ciencias Naturales, “Bernadino Rivadavia” Buenos Aires, Colección Chubut, Argentina; MACN- N, Museo Argentino de Ciencias Naturales, “Bernadino Rivadavia” Buenos Aires, Neuquen, Argentina; Mal, Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi; MPCA, Museo Provincial “Carlos Ameghino” de Cipolletti, Rio Negro, Argentina; MUCPv, Museo de la Universidad Nacional del Comahue, Paleovertebrados, Comahue, Argentina; PVL, Instituto Miguel Lillo de la Universidad de Tuçuman, Tuçuman, Argentina; PVPH, Paleontología de Vertebrados, Museo “Carmen Funes”, Plaza, Huincul, Provincial del Neuquén, Argentina; SAM, South African Museum, Cape Town, South Africa; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.