

## A NEW COELUROSAURIAN DINOSAUR FROM THE EARLY CRETACEOUS OF SOUTH AFRICA

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**ABSTRACT**—We report the well preserved skeleton of a small theropod dinosaur, *Nqwebasaurus thwazi*, gen. et sp. nov., from the Lower Cretaceous Kirkwood Formation of South Africa. *Nqwebasaurus* has an elongate three-digit manus with a partially opposable first digit, a long and slender pes with a highly reduced metatarsal IV, and preserves gastroliths (stomach stones) in its abdominal region. As a basal coelurosaurian, *Nqwebasaurus* pushes back the Gondwanan record of this derived group of tetanuran theropods approximately 50 million years. This confirms that coelurosaurians were present on the Gondwana supercontinent well before its main phase of fragmentation and supports the hypothesis that this clade could have achieved a global distribution early in their evolution. *Nqwebasaurus* is one of the most complete and best preserved Cretaceous theropods described thus far from Africa.

### INTRODUCTION

Despite a collecting history that extends back more than 150 years, little is known of Cretaceous dinosaurs from southern Africa (de Klerk et al., 1998). Whereas a relatively rich Cretaceous dinosaur fauna is known from northern Africa (Taquet, 1976; Sereno et al., 1994, 1996, 1998; Jacobs et al., 1996; Russell, 1996; Taquet and Russell, 1998), with few exceptions (e.g., Rich et al., 1983; Jacobs et al., 1993), the rest of the continent has remained poorly sampled (Jacobs et al., 1996). Though poorer in specimens, the dinosaur record of southern Africa is the oldest on that continent (de Klerk et al., 1992; Forster, 1999), extending back to 1845 when fragmentary remains of a sauropod and the stegosaur *Paranthodon africanus* were discovered by amateur scientists in rocks now known as the Kirkwood Formation (Atherstone, 1857; Galton and Coombs, 1981). This site, named Iguanodon Hoek by its discoverers, is one of many exposures of the Early Cretaceous Kirkwood Formation (Berriasian-Valanginian; McMillan, 1999) within the Algoa Basin in Eastern Cape Province, South Africa (see Ross et al., 1999, for a review of the geology of the Kirkwood Formation).

The Kirkwood Formation has continued to produce dinosaur remains, as well as those of other vertebrates, for over 150 years, although these remains have generally been rare, fragmentary, and difficult to identify beyond the ordinal level (Broom, 1904; Haughton, 1928; McLachlan and McMillan, 1976; Rich et al., 1983; Mateer, 1987; Forster et al., 1995; de Klerk et al., 1997, 1998). Dinosaur remains recovered from the Kirkwood Formation include at least two ornithischians: the stegosaur *Paranthodon africanus* (Galton and Coombs, 1981), represented by teeth and cranial fragments, and a new ornithomimid, represented by isolated elements and teeth (Rich et al., 1983) plus a nearly complete articulated specimen (de Klerk et al., 1997; to be described elsewhere). Saurischian dinosaur remains include at least two taxa of sauropods including *Algoasaurus bauri* (considered a nomen dubium by McIntosh, 1990) represented by teeth and fragmentary postcrania, and a possible diplodocid, represented by a caudal vertebra (de Klerk et al., 1997), and at least two taxa of small theropods, represented by isolated teeth, a proximal femur, and the articulated skeleton

described herein. Other vertebrate remains recovered from the Kirkwood Formation include sphenodontian, lepidosaur, turtle, crocodile, frog, and freshwater fish materials (Rich et al., 1983; Ross et al., 1999; de Klerk et al., 1998).

Recent joint Albany Museum-State University of New York at Stony Brook expeditions have recovered a significant amount of new dinosaur material from the Kirkwood Formation, including the first articulated remains. We describe here a small coelurosaurian theropod, represented by a nearly complete, articulated skeleton discovered by CFR and WJD in 1996. This specimen, the first well preserved and nearly complete taxon to be described from the Kirkwood Formation, provides important temporal and geographic range extensions for coelurosaurians in Gondwana.

Tetanuran theropods, which include coelurosaurians, the lineage leading to birds, were once hypothesized to have a nearly exclusively Laurasian distribution (e.g., Bonaparte, 1991a). However, numerous recent discoveries have demonstrated their occurrence in Gondwana, including Antarctica (Hammer and Hickerson, 1994), Argentina (Coria and Salgado, 1995; Novas and Puerta, 1997), and northern Africa (Rauhut and Werner, 1995; Sereno et al., 1996).

Despite these recent discoveries of basal tetanurans, more derived coelurosaurians remain extremely rare components of Gondwanan faunas. The handful of confirmed coelurosaurian taxa are restricted to the Late Cretaceous of northern Africa (Rauhut and Werner, 1995; Sereno et al., 1996) and Argentina (Novas and Puerta, 1997; Novas, 1998). Other possible Gondwanan coelurosaurians have been recently reported, including the fragmentary Australian taxon *Timimus hermani* referred to the Ornithomimidae (Rich and Vickers-Rich, 1994), and possible oviraptorosaur material from the ?Albian Santana Formation of Brazil (Frey and Martill, 1995) and the Aptian-Albian Otway Group of Australia (Currie et al., 1996). These taxa are younger than *Nqwebasaurus* and additional, better material is needed to confirm or refute their phylogenetic assignments. The presence of *Nqwebasaurus* in the Kirkwood Formation indicates that coelurosaurians were present in Gondwana at the beginning of the Cretaceous, and allows a more complete glimpse into early Cretaceous dinosaur life in southern Africa.

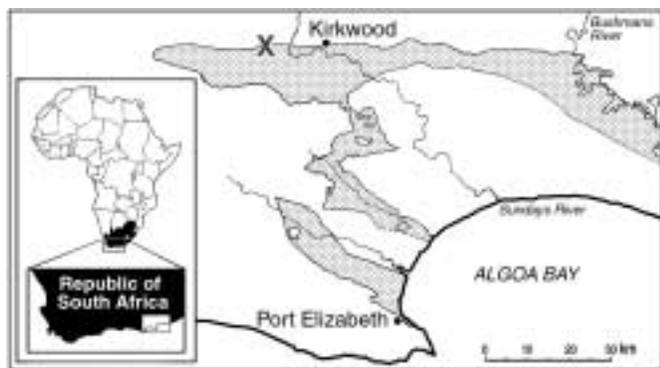


FIGURE 1. The X marks the locality where *Nqwebasaurus thwazi*, gen. et sp. nov., AM 6040, was discovered close to the town of Kirkwood, Eastern Cape Province, South Africa. Shaded areas define the surface and subsurface extent of the Kirkwood Formation, the middle unit of the Uitenhage Group, within the Algoa Basin.

#### SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

COELUROSAURIA von Huene, 1914

*NQWEBASAURUS THWAZI*, gen. et sp. nov.

(Figs. 2–4)

**Holotype**—Fragmentary skull and nearly complete articulated skeleton, AM 6040 (Albany Museum, Grahamstown, South Africa).

**Locality and Horizon**—17 km west of Kirkwood village (33°25'01"S; 25°15'83"E); unnamed uppermost member (coarse red-brown mudstone paleosol facies) of the Lower Cretaceous Kirkwood Formation (Berriasian–Valanginian), Uitenhage Group, Algoa Basin, Eastern Cape Province, South Africa (McMillan, 1999; Fig. 1).

**Etymology**—*Nqweba* (n-KWE-bah), Xhosa for the Kirkwood region; *sauros*, Greek for “lizard”; *thwazi* (TWAH-zee), Xhosa for “fast runner.”

**Diagnosis**—Basal coelurosaurian theropod possessing the following autapomorphies: ginglymus of metacarpal I very robust and asymmetrical, with hypertrophied articular surfaces and greatly enlarged lateral (ulnar) condyle; manual ungual phalanx of digit I elongate (length is four times proximal depth) and mediolaterally compressed; fibular shaft reduced distally to thin splint; metatarsal IV reduced in width to approximately half that of metatarsal III.

#### Description

The specimen is articulated, approximately 70% complete, and includes a fragmentary skull, seven postaxial cervical vertebrae, both pectoral girdles and forelimbs, partial femora, and both tibiae, fibulae, and pedes (Fig. 2, 3, 4C–E; measurements given in Table 1). The dorsal, sacral, and caudal vertebrae are largely absent, although some isolated centra and neural arches are present. Most of the pelvis has been eroded away, although the pubic shafts remain.

**Skull**—The disarticulated partial skull includes paired frontals, a parietal, palatine, parts of the braincase, and sclerotic ring. No teeth or jaw elements were recovered. The frontals are unfused and exposed in dorsal view. They are extremely elongate and transversely narrow, although neither is complete at its anterior or posterior end. The more complete right frontal measures 39 mm in length and 5 mm in width at mid-orbit, or nearly eight times as long as wide. The orbital margin is shal-

lowly embayed and extensive, showing that the frontal formed a large portion of the dorsal margin of a relatively large, round orbit, as in other coelurosaurians.

A number of small, thin plates, some overlapping one another, form a partial, distorted circle in the right orbital area, and represent part of the sclerotic ring. Other partial skull elements, scattered primarily anterior to the frontals, are fragmentary and poorly preserved. As such, no further morphologies can be described on these fragments at present.

**Axial Column**—Seven postaxial cervical vertebrae are exposed in right lateral and dorsal view. The first three are complete, but the subsequent vertebrae are progressively more fragmented and poorly preserved. The elongate cervical centra are dorsoventrally compressed, their width exceeding height on their anterior face. The articular faces appear to be nearly amphiplatyan, as in other coelurosaurians (Holtz, 2000). One small foramen opens beneath each transverse process, but whether this is pneumatic or vascular is unknown (O'Connor, 1999). The transverse processes are triangular in dorsal view, gently downcurved at their distal end, and restricted to the anterior half of the centra. The neural spines are extremely short. The elongate prezygapophyses arch downward, resulting in strongly flexed (dorsally convex) processes, as in other coelurosaurians (Gauthier, 1986; Holtz, 2000). The postzygapophyses are mediolaterally broad and joined on the midline for nearly their entire length. The first preserved cervical lacks epipophyses. The succeeding cervicals bear small epipophyses, located on the lateralmost edge of the postzygapophyses that increase in size down the column but never extend beyond the posterior margin of the postzygapophyses. No cervical ribs are preserved.

A few centra and neural arches from the disarticulated dorsal and caudal series are exposed in the specimen block. Their relative positions in the axial column cannot be determined, and no diagnostic morphologies are observed.

**Pectoral Girdle and Forelimb**—Both scapulae are preserved; the right scapula is exposed in lateral view, the left in medial view. The acromion process is strongly flared dorsally but narrow anteroposteriorly. The long and narrow scapular blade has a straight ventral margin that flares slightly ventrally only at the glenoid fossa. Distally, the scapular blade expands gradually along its dorsal margin to slightly over twice the width at the neck.

Both coracoids are preserved, lying together but separate from the scapulae, just in front of the right manus. The posteroventral process, as preserved, is nearly equal in length to the total glenoid diameter. However, the tips of the processes on both sides are eroded and its total length cannot be precisely determined. The posteroventral process is slightly recurved, tapered, and bears a well developed, scarred ridge that traverses its lateral face. The coracoid foramen is well separated from the articulation both medially and laterally. No sternal elements were recovered.

The forelimb is 43% the length of the hind limb, somewhat shorter in proportion than in other coelurosaurians (Holtz, 2000). The robust humerus is slightly sinuous in lateral view with laterally expanded, anteroposteriorly compressed distal condyles. The strong deltopectoral crest is nearly twice the width of the shaft and is sharply set off at its distal end. The crest extends distally approximately one-third the length of the humerus. The ulna and radius are straight and approximately equal in width at their midshafts. Their proximal ends are poorly preserved on both sides. The forearm is shorter than the upper arm, the radius being 76% of the length of the humerus. Distally, the ulna has a flat facet where it meets the radius, and both elements contribute equally to the antibrachial-carpal joint.

The carpus and manus are well preserved on both sides, exposed in dorsal view on the right and palmar view on the left

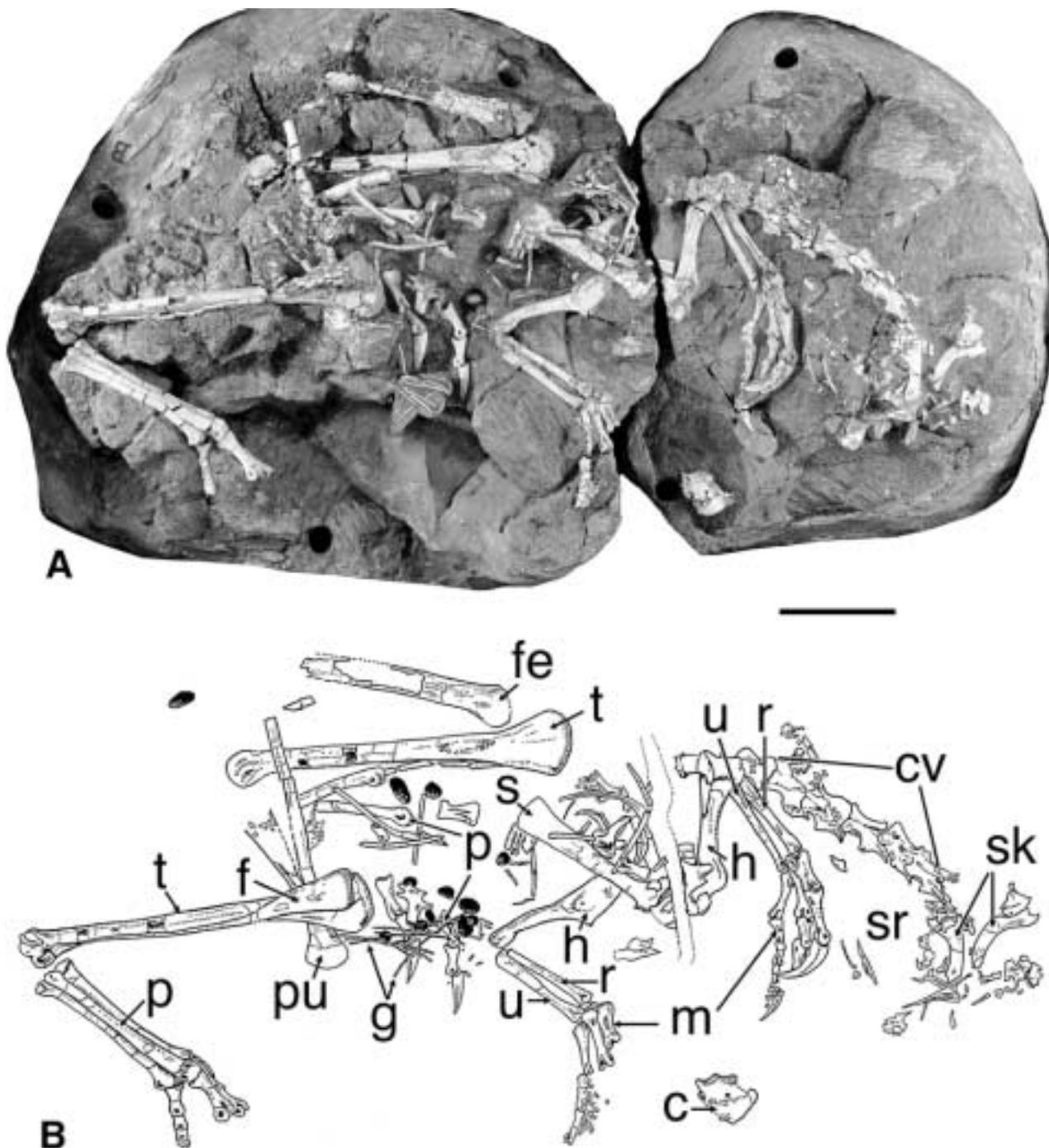


FIGURE 2. Right lateral view of the skeleton of *Nqwebasaurus thwazi*, gen. et sp. nov. The specimen is lying on its left side and facing to the right. **A**, as preserved in two blocks of matrix. Most of the gastralia were removed in a small block to facilitate preparation of the underlying left digits; this block of gastralia can be seen just below those digits. The gastralia are shown in their original position in **B**, a line drawing of the skeleton with elements labeled. The dark, ovate objects scattered throughout the abdominal region are gastroliths. **Abbreviations:** **c**, coracoid; **cv**, cervical vertebrae; **f**, fibula; **fe**, femur; **g**, gastralia; **h**, humerus; **m**, manus; **p**, pes; **pu**, pubis; **r**, radius; **s**, scapula; **sk**, skull parts; **sr**, sclerotic ring; **t**, tibia; **u**, ulna. Scale bar equals 5 cm.

(Fig. 4C, D). The carpus consists of two adjacent carpals, both preserved somewhat out of articulation on the left and right sides. The medial (radial side) carpal is slightly larger than the lateral (ulnar side) carpal, and is proximodistally compressed. It has a concave proximal end that presumably capped the distal radius. The distal surface is convex, presumably fitting into the transversely concave surface on the proximal end of metacarpal

(MC) I. The lateral carpal is nearly cuboidal and, on the right manus, appears to contact the lateral side of the distal radius and the medial half of MC II.

The two carpals are not fused to each other and, as preserved, are not closely appressed to either the metacarpals or antebrachium. Although the convex distal surface of the medial carpal may be interpreted as an incipient trochlea, there appears to be

TABLE 1. Measurements (mm) of elements of *Nqwebasaurus thwazi*, AM 6040. Because histological features suggest that this specimen is a sub-adult, these measurements may not reflect adult proportions. \* = estimated measurement.

| Element      | Left   | Right |
|--------------|--------|-------|
| scapula      |        | 64.7  |
| humerus      |        | 58.5* |
| ulna         |        | 44.5* |
| radius       |        | 44.2  |
| metacarpal 1 | 16.7   | 17.1  |
| metacarpal 2 | 26.5   |       |
| metacarpal 3 | 20.0   |       |
| femur        | 118.0* |       |
| tibia        |        | 140.7 |
| metatarsal 1 |        | 9.5*  |
| metatarsal 2 |        | 65.8  |
| metatarsal 3 |        | 72.7  |
| metatarsal 4 |        | 67.3  |

no strong development of either a semilunate carpal or a fused semilunate carpal block with a well developed distal trochlea (sensu Gauthier, 1986), as reported in many other coelurosaurians. However, the two carpals of *Nqwebasaurus* appear to be situated in positions homologous to those forming the semilunate carpal block in other tetanurans. We therefore tentatively identify them as distal carpals 1 and 2 (Chure, 1999). Due to its subadult status, it is not known how carpal morphology, ossification, and fusion would have progressed ontogenetically.

The elongate manus (168% the length of the forearm) bears only three digits, a derived character within Tetanurae (Fig. 4C, D; Holtz, 2000; Sereno, 1999). The manus has a phalangeal formula of 2-3-4-x-x, and exhibits some unique modifications, particularly of digit I. The first metacarpal is relatively robust, short, and asymmetrical, as in other tetanurans. However, the distal condyles are highly derived, exhibiting great disparity in size, shape, and orientation. The condyle on the lateral (ulnar) side is greatly enlarged in a palmodorsal direction to more than twice the depth of the medial (radial) condyle. In dorsal view, the lateral condyle is only slightly longer than the medial condyle, but extends more proximally along the shaft. As viewed distally, the intercondylar ginglymus is angled approximately 45 degrees towards MC II (Fig. 4C inset). Although the func-

tional morphology of this specialized metacarpo-phalangeal joint requires further study, certain actions can be posited on the basis of articular surface morphology. Flexion at this joint must have directed the digit off the axial line of rotation. The left manus shows that the flexed digit I had the potential to partially oppose digits II and III. Additionally, hyper-development of both the distal flexor and extensor surfaces on MC I indicate the potential for large excursions at this joint.

Metacarpal II is twice the length of MC I but more gracile at its midshaft (58% the width of MC I at midshaft). Metacarpal III is 71% the width of MC II at midshaft, although its distal end is only half that of either MC I or MC II. Metacarpal III is intermediate in length between MC I and MC II. Despite differences in length and midshaft width, all three contribute nearly equally to the carpo-metacarpal joint. Proximally, MC II is flattened where it closely contacts MC I. Near the distal end of this tight articulation, MC I possesses a small flange of bone that slightly overlaps the shaft of MC II (Fig. 4C). The close apposition of MC I and II, coupled with this small flange, indicate a tight connection between proximal ends of these two metacarpals. Additionally, these two metacarpals lie in parallel on both mani. The proximomedial surface of MC III is also flattened to meet MC II, although both mani show MC III to be slightly divergent from MC II.

All three metacarpals bear extremely deep excavations between well-developed trochleae on their flexor aspect. Deep excavations occur between distal trochleae on the flexor aspect of all phalanges, which also have enlarged heels. These morphologies indicate that extreme flexion, perhaps as much as 90 degrees, was possible at the metacarpo-phalangeal and interphalangeal joint of all digits.

The ungual phalanx of digit I is laterally compressed and four times as long as deep. The unguals of digits II and III are also laterally compressed and elongate, although not to the degree seen in digit I, and they are also shallower dorsoventrally. All unguals are gently curved and possess low, elongate flexor tubercles. The vascular groove is centered along the lateral face of the manual unguals, as in other coelurosaurians (Holtz, 2000).

**Pelvic Girdle and Hind Limb**—Most of the pelvis had eroded away by the time the specimen was discovered; only the pubic shafts remain partially preserved. The pubic shaft is oval

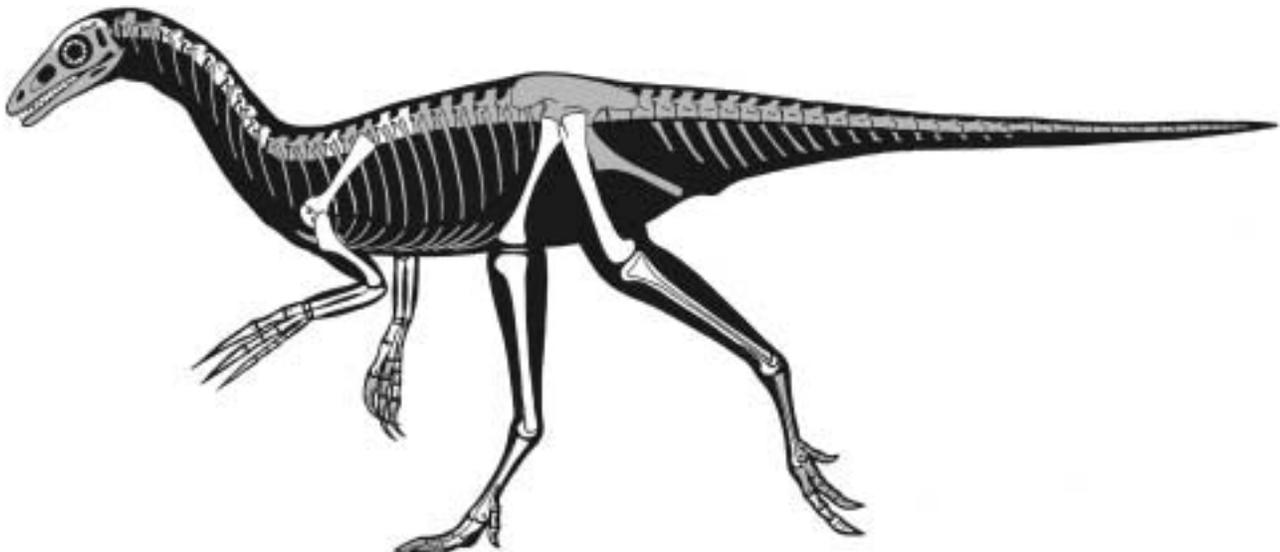


FIGURE 3. Reconstruction of the skeleton of *Nqwebasaurus thwazi* gen. et sp. nov. Preserved elements are shown in white, missing elements are shaded gray.

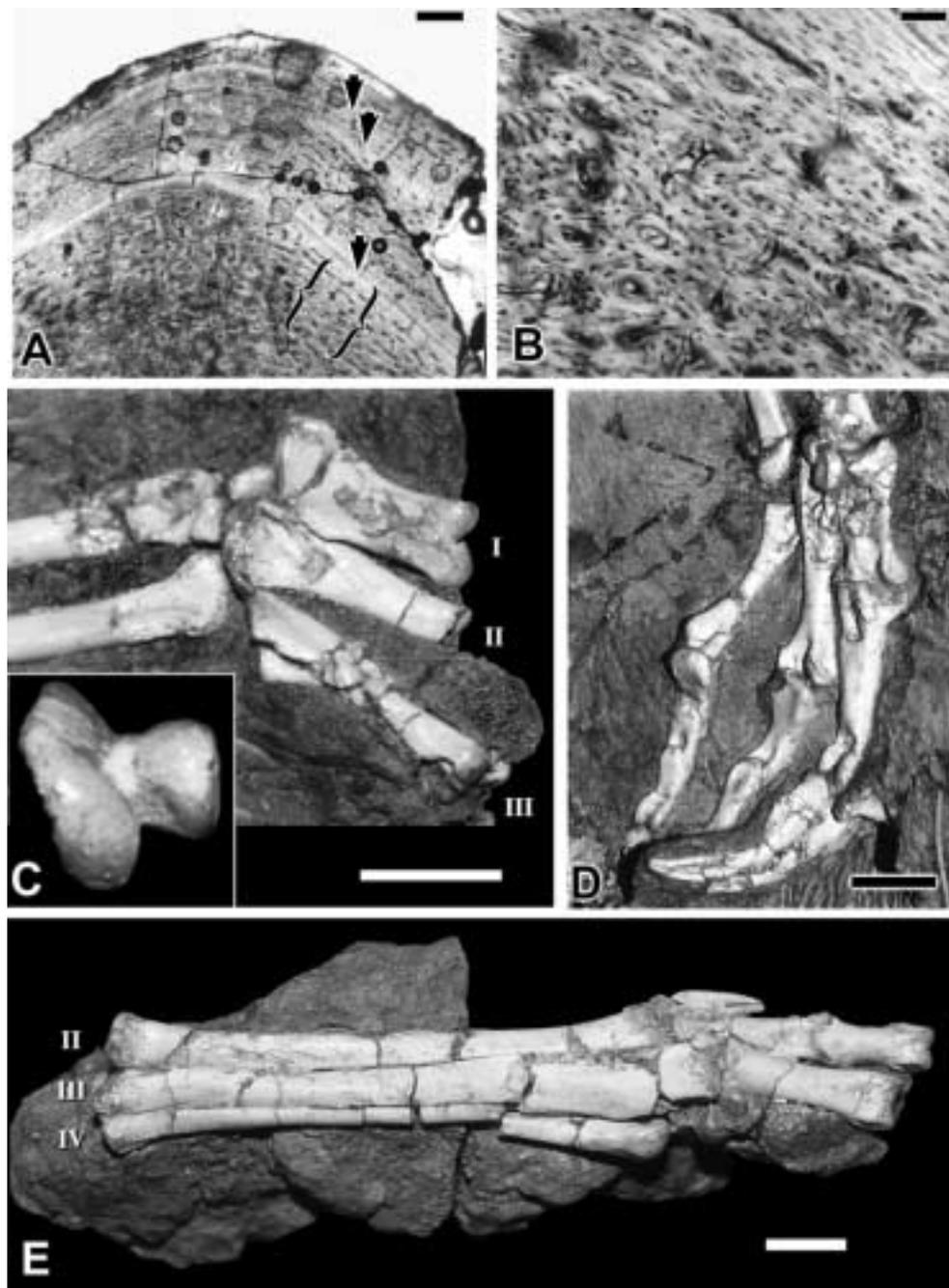


FIGURE 4. *Nqwebasaurus thwazi*, gen. et sp. nov.: **A**, transverse thin-section of the midshaft of the left femur at low magnification. The compacta is distinctly stratified into three cycles of growth. Arrowheads indicate these three annuli and rest lines. Scale bar equals 220 microns; **B**, higher magnification of bracketed area in **A** showing the primary nature of the compacta. Scale bar equals 46 microns; **C**, right carpus and manus in dorsal view. Note the small flange on the first metacarpal that overlaps metacarpal II. Inset photo is an enlarged, distal view of metacarpal I showing the greatly enlarged lateral condyle and angled intertrochlear groove; **D**, left carpus and manus in ventral view showing the long, blade-like first ungual. The two carpals are preserved slightly out of articulation; **E**, right pes in dorsal view showing the greatly reduced fourth metatarsal. Scale bars for C–E equal 1 cm.

in cross-section for most of its length, the diameter being slightly greater anteroposteriorly. Although fragmentary, the pubes appear to have a long, thin pubic apron. Much of the actual apron is damaged or missing but is represented by the broken base of the apron flange centered along the inner surface of the pubic shafts. Fragmentary pieces of the apron float in the matrix between the shafts. Distally, the pubes expand equally anteriorly and posteriorly into a small, mediolaterally narrow, pubic

foot. The pubic foot has a very indistinct outline; it may have been finished in cartilage in life and thus not fully preserved in this subadult specimen (see histology section below).

Both femora are fragmentary. The proximal end of the right femur shows that the head extends above the level of the greater trochanter, that it is slightly anteroposteriorly compressed, and that it is directed dorsomedially from the shaft. Laterally, the expanded greater trochanter is anteroposteriorly broad, proxi-

mally placed, and separated from the femoral head by a distinct neck. Although the lesser (anterior) trochanter is broken away, it is clear that there is no trochanteric shelf and that this trochanter was quite proximal in position. There does not appear to be an accessory trochanter. A portion of the left femoral shaft is preserved, showing a slight anteroposterior curvature. The fourth trochanter is not preserved. The fragment of distal right femur not only lacks an anterior intercondylar groove, but is slightly convex across this extensor surface.

The tibia (approximately 120% the length of the femur) has a straight and gracile shaft that is slightly anteroposteriorly compressed. A large cnemial crest arises from the medial side of the shaft and hooks laterally at its distal end. In lateral view, the proximal articular surface is slightly convex, curving gently anteroventrally across the dorsal surface of the cnemial crest. The cnemial crest is blunt and grades smoothly into the tibial shaft. The fibular condyle, when viewed from above, is relatively small and divided equally into distinct anterior and posterior portions. Distally, the tibia abruptly expands transversely to 2.25 times the width at midshaft, the lateral malleolus being only slightly larger than the medial malleolus.

Both fibulae are preserved in articulation with the tibiae. In proximal view, the fibular head is mediolaterally compressed and semilunar in shape. Removal of the left tibia reveals an extensive spoon-shaped fossa on the medial surface of the proximal fibula, as seen in other coelurosaurians (Holtz, 2000; Sereno, 1999). The fibular shaft is apomorphically reduced to only 20% the diameter of the tibia. The distal fibula is not exposed on the left side, while the right fibula is fractured near its distal end and its contact with the calcaneum is missing.

The right tarsus is well preserved. The astragalus bears a broad, anteroposteriorly compressed, tall ascending process, as in other coelurosaurians. The proximal end of the ascending process is damaged by postmortem mineral growth, and its complete length is indeterminable. However, the preserved portion demonstrates that the astragalus length is at least 17% that of the tibia. A shallow fossa indents the base of the ascending process. There is no horizontal groove crossing the anterior face of the astragalus condyles, a feature also absent in most coelurosaurians (Holtz, 2000; Sereno, 1999). The astragalus bears a low, robust ridge where it contacts the calcaneum in a straight butt joint. The astragalus is not fused to the crus and, where preserved, retains a clear sutural contact with the tibia. The small, blocky calcaneum (20% the width of the astragalus) is broken proximally; thus no trace of a fibular facet is preserved. It is neither fused to the astragalus nor to the tibia. A small, free distal tarsal—proximodistally compressed and rectangular in outline—tightly caps MT III.

Combining left and right sides, all elements of the long and slender pes are present. The metatarsals (MT) are tightly appressed along their entire lengths but are not fused to one another. Metatarsal II makes the largest contribution to the ankle joint, followed successively by MT III and IV. The greatly reduced MT I is nearly straight and limited to the distal end of MT II. When viewed proximally, MT III is weakly hourglass-shaped, while MT II is triangular and MT IV nearly oval.

Metatarsals II and IV are subequal in length, and exceeded in length slightly by MT III (Fig. 4E). Despite the excellent preservation and articulation of the right foot, no MT V is preserved. However, a weak ridge on the flattened proximolateral surface of MT IV indicates that MT V was probably present. The shaft of MT III is pinched plantarly, as in other tetanurans, and assumes a trapezoidal cross-section at midshaft. Metatarsals II and III are robust and approximately subequal in width, but the shaft of MT IV is highly reduced in diameter (42% the width of MT III at midshaft; Fig. 4E). The shaft of MT IV is also somewhat dorsoplantally reduced in depth. A reduced MT IV also occurs in the Argentine theropod *Velocisaurus unicus*,

which also has a greatly reduced MT II (Late Cretaceous, Rio Colorado Fm.; Bonaparte, 1991b). Distally, the metatarsals of *Nqwebasaurus* are only slightly expanded mediolaterally and do not diverge.

Digit III is the longest, followed by II, IV and I, respectively. The relatively short digit IV terminates at the end of the second pedal phalanx of digit III. The short ungual phalanges of digits II–IV are subtriangular in cross section, and have a nearly flat ventral surface.

**Gastralia**—Tiny, rod-like bones, here interpreted as gastral-ia, occur in the abdominal region just anterior to the distal pubes (Fig. 2). These elements occur mostly as a series of parallel rods ranging in midshaft diameter from 0.5 mm to 1 mm. Some of the complete segments (maximum length 30 mm) taper to sharp points at their ends. Numerous smaller broken fragments of gastral-ia occur in random orientation throughout the matrix in the abdominal region.

**Gastroliths**—At least 12 small, round to ellipsoidal stones are preserved scattered throughout the abdominal region of *Nqwebasaurus* (Fig. 2). The maximum diameter of these stones ranges from 5.2 to 14.5 mm, with an average of 8.0 mm. The stones are of diverse lithologies, although fine-grained quartzites predominate. The quartzite pebbles are smooth and polished whereas pebbles of the softer rock types appear etched. Small, polished or etched stones are not found in the sediment surrounding the specimen, nor are they commonly found anywhere in the mudstone facies of the Kirkwood Formation. We interpret these stones as gastroliths, presumably used in the mechanical breakdown of ingested food. Well documented cases of gastroliths occur in other dinosaurs (e.g., *Psittacosaurus*) and extant archosaurs (crocodilians and birds), but are extremely rare in theropods. Reported cases of gastroliths in theropods include *Baryonyx* (Charig and Milner, 1986) and *Caudipteryx* (Ji et al., 1998).

**Bone Histology**—The specimen is small, representing an animal that would have stood approximately 30 cm high at the hips. Although neurocentral sutures in the cervical series appear fused, neural arches and centra are disarticulated on the preserved dorsal and caudal vertebrae, suggesting this specimen had not yet reached maturity. To better assess the ontogenetic age of the specimen, transverse histological thin sections were cut from the midshaft of the femur and tibia and examined under a polarizing microscope (Chinsamy and Raath, 1992; Fig. 4A–B).

At least three growth lines, consisting of zones, annuli, and rest lines, are present in the compact bone of each element (Chinsamy, 1997). Zones between consecutive annuli consist of richly vascularized fibrolamellar bone tissue (Fig. 4A). All tissues are primary, and no resorption cavities or secondary osteons are evident (Fig. 4B). The medullary cavity margin of the femur appears resorptive, indicating that medullary expansion is still underway. Similarly, the tibia exhibits an uneven peripheral margin that appears to be a zone of active bone deposition.

The cycles present suggest that AM 6040 has undergone some period of growth and is not a young juvenile. However, the absence of inner circumferential lamellae and any secondary reconstruction (such as erosion cavities or secondary osteons), and the presence of resorptive medullary margins and uneven peripheral margins, indicate AM 6040 is a subadult or late juvenile, and not a mature adult. Even allowing for considerable additional growth, the adult was likely a relatively small animal.

#### PHYLOGENY AND BIOGEOGRAPHIC IMPORTANCE

*Nqwebasaurus* exhibits many characters that nest it phylogenetically within Tetanurae, including an elongate three-fingered manus, reduction of the trochanteric shelf, a tall and

broad astragalar ascending process, a reduced distal fibula, metatarsal III wedge-shaped at midshaft, and a highly reduced and distally positioned metatarsal I (Gauthier, 1986; Holtz, 1994, 2000; Sereno et al., 1996; Sereno, 1999). Within Tetanurae, *Nqwebasaurus* possesses a number of characters that support its inclusion within Coelurosauria, the clade that includes, among other taxa, Avialae (e.g., *Archaeopteryx*, modern birds) and Maniraptora (e.g., oviraptorids, dromaeosaurids, troodontids).

Although a cladistic analysis of Coelurosauria is beyond the scope of this paper, a number of hypotheses concerning its phylogenetic relationships have been recently published (Gauthier, 1986; Holtz, 1994, 2000; Sereno et al., 1996; Sereno, 1999). In his recent phylogenetic analysis of Dinosauria, Sereno (1999) lists 13 characters distributed at the Coelurosauria node. Only one of these characters is preserved in *Nqwebasaurus* (the others are primarily cranial or pelvic): the presence of a large fossa occupying most of the proximomedial aspect of the fibula. This character state is present in *Nqwebasaurus*.

Holtz (2000), in his extensive reanalysis of theropod relationships, optimizes character state transformation in both accelerated and delayed modes. To minimize assumptions, we consider only the character state distributions using delayed transformations here. Holtz (2000) lists 12 Coelurosauria characters, five of which can be scored in *Nqwebasaurus*. These characters are: (1) round orbit; (2) cervical centra amphiplatyan; (3) greater trochanter of femur cleft from femoral head; (4) fibula proximal end 75% or more the proximal width of the tibia; and (5) femoral head set off at more than 90 degrees from shaft (head directed dorsally).

The first character, round orbit, may be present in *Nqwebasaurus*, although only the frontal contribution to the orbit is preserved. Nevertheless, the size and shape of the frontal orbital margin, coupled with the extensive portion of the orbit formed by the frontal, is consistent with the morphology of other coelurosaurians. However, since the ventral portion of the orbit is not preserved, the presence of this character cannot be confirmed in *Nqwebasaurus*. The remaining four character states are present in *Nqwebasaurus*.

*Nqwebasaurus* also exhibits the derived state for a number of characters that are distributed elsewhere amongst basal coelurosaurians: (1) articular surface of cervical vertebrae broader than deep with kidney-shaped articular surfaces; (2) midcervical centra length about twice the diameter of the anterior articular face; (3) loss of the transverse groove across the anterior face of the astragalus (also listed by Sereno [1999] within Coelurosauria); (4) flexed cervical prezygapophyses; (5) radius/humerus length ratio greater than 76% (it is exactly 76% in *Nqwebasaurus*); (6) manual ungual region palmar to ungual groove subequal in width to region dorsal to ungual groove; (7) manual ungual cross-section blade-like and more than three times as deep as wide; and (8) metacarpal III clearly shorter than metacarpal II (Holtz, 2000).

Despite the lack of a complete phylogenetic analysis, we feel that *Nqwebasaurus* can be confidently placed within Coelurosauria based on the derived characters listed above. As such, the presence of any coelurosaurian in southern Africa at the onset of the Cretaceous requires a reexamination of the historical biogeography of this large and important clade. Two explanations for the distribution of coelurosaurians in Gondwana have been advanced. First, because nearly all known member taxa occur in Upper Jurassic and Cretaceous strata in the northern hemisphere, a Laurasian origination and diversification for this clade has been hypothesized (Bonaparte, 1996). Rarely occurring Gondwanan coelurosaurians thus have been viewed as immigrants from this primarily northern radiation (e.g., Rauhut and Werner, 1995). Second, the recent discovery of Late Cretaceous coelurosaurians in Morocco and Argentina, coupled

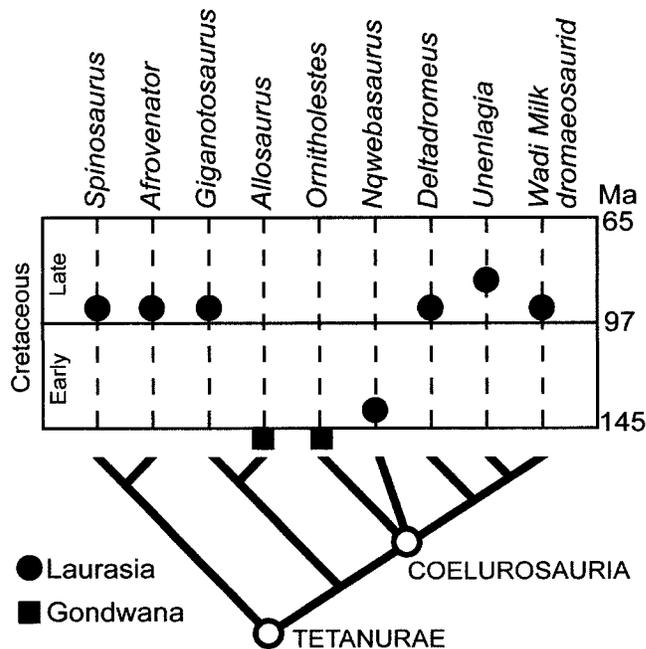


FIGURE 5. Summary of the phylogenetic, temporal, and biogeographic relationships among selected coelurosaurian and basal tetanuran taxa. Although the exact phylogenetic position of *Nqwebasaurus* among coelurosaurians is not known, it appears to be a basal member of this clade and thus is placed in this position here. The phylogeny depicted is based on that of Sereno et al., (1996). Known Gondwanan coelurosaurians depicted are *Nqwebasaurus*, *Deltadromeus* (Cenomanian, Morocco), *Unenlagia* (Coniacian, Argentina), and dromaeosaurid material from the Wadi Milk Formation (Cenomanian, Sudan).

with a minimally Late Jurassic origin of this clade, has prompted the suggestion that coelurosaurians were globally distributed by the Late Jurassic (Sereno et al., 1996). However, this hypothesis has not been supported by fossil evidence as neither Late Jurassic nor earliest Cretaceous coelurosaurians have been confirmed from Gondwana.

*Nqwebasaurus* is the oldest Gondwanan coelurosaurian, predating known North African taxa by approximately 50 million years (Fig. 5). Because all major southern landmasses still retained subaerial connections in the earliest Cretaceous (e.g., Scotese, 1991), the presence of *Nqwebasaurus* at the southern tip of Africa confirms that coelurosaurians could have been widely dispersed throughout Gondwana prior to continental isolation. This hypothesis of an early cosmopolitanism for coelurosaurians is also consistent with the recent report of a therizinosaur (a derived coelurosaurian) from Lower Jurassic strata in China (Zhao and Xu, 1998), which, if true, suggests that coelurosaurian origins predate even the breakup of Pangaea.

*Nqwebasaurus* can be used to support Late Jurassic coelurosaurian cosmopolitanism, but cannot verify this hypothesis in lieu of additional evidence. Whether the Gondwanan coelurosaurian legacy reflects a separate southern radiation of this clade, periodic immigration, extensive and continuous interchange with Laurasia, or some combination of these factors, can only be tested through finer resolution of coelurosaurian phylogeny and additional occurrences. Although older coelurosaurians may be known from Laurasia, the paucity of Jurassic dinosaurs from Africa and elsewhere in Gondwana cautions against a priori assumptions of a Laurasian origination and diversification for Coelurosauria.

The Cretaceous biogeographic history of African dinosaurs has rested nearly exclusively on better sampled, younger taxa

from northern Africa. Poor sampling of Cretaceous dinosaur faunas in southern and central Africa has confounded the testability of biogeographic hypotheses, as data from this large geographic area are either greatly restricted or absent. Hopefully, as the African fossil record continues to grow, we will be able to address not only inter-continental biogeographic questions, but intra-continental ones as well.

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