



New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation in South Africa

Jonah N. Choiniere^{a,b,c,*}, Catherine A. Forster^d, William J. de Klerk^e

^a Department of Biological Sciences, The George Washington University, United States

^b Division of Paleontology, Richard Gilder Graduate School, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, United States

^c Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Johannesburg, WITS 2050, South Africa

^d Department of Biological Sciences, The George Washington University, 2023 G Street NW, Lisner Hall Room 340, Washington, DC 20052, United States

^e Department of Geology, Rhodes University, Department of Earth Science, Albany Museum, Somerset Street, Grahamstown 6139, South Africa

ARTICLE INFO

Article history:

Received 14 February 2012

Received in revised form 29 May 2012

Accepted 30 May 2012

Available online 15 June 2012

Keywords:

Coelurosauria

Ornithomimosauria

Phylogeny

Kirkwood Formation

Early Cretaceous

ABSTRACT

We performed additional preparation on the holotype skeleton of *Nqwebasaurus thwazi* and discovered new skeletal material. We describe this material, which includes a maxilla with small, conical, unserrated teeth and bones of the braincase, as well as parts of the holotype postcranial anatomy that were previously poorly documented. We incorporate this new anatomical information into a broadly sampled matrix designed to test theropod relationships. Our phylogenetic results hypothesize that *Nqwebasaurus* is the basalmost ornithomimosaur, and recover numerous characters supporting this relationship, including features of the maxilla, frontal, dentition, axial skeleton, forelimb and hindlimb. *Nqwebasaurus* is the first African ornithomimosaur and the first Gondwanan member of this group known from articulated skeletal material, supporting the hypothesis that coelurosaurian groups were cosmopolitan during their early evolutionary history. The presence of reduced dentition and a gastric mill in *Nqwebasaurus* strongly suggest that this taxon was herbivorous.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

The diverse dinosaur group Coelurosauria (Saurischia: Theropoda) (Gauthier, 1986) includes birds, charismatic carnivorous taxa like *Tyrannosaurus* and *Velociraptor*, and the feathered dinosaurs from China (Norell and Xu, 2005). New discoveries of the derived coelurosaurian clade Scansoriopterygidae (Coelurosauria: Avialae) from China imply that the major clades of coelurosaurs had differentiated by the Middle–Late Jurassic (Liu et al., 2006; Zhang et al., 2002, 2008), and recent discoveries of basal and stratigraphically old members of coelurosaurian groups like the Alvarezsauridae (Choiniere et al., 2010b), Troodontidae (Hu et al., 2009; Xu et al., 2010b), and Tyrannosauroidae (Averianov et al., 2010; Benson, 2008; Rauhut, 2003b; Rauhut et al., 2010; Xu et al., 2006) strongly support this hypothesis for the timing of the completion of major coelurosaurian diversification.

The fossil record of non-avian coelurosaurs is, however, biased towards the Late Cretaceous of Laurasia. Approximately 63% of coelurosaurian taxa are known from the Late Cretaceous, with

approximately 88% of these known from Laurasia (see Supplemental Information 1). Discoveries of non-avian coelurosaurs in Gondwana are far rarer (<10% of coelurosaur genera are from Gondwanan deposits) and are almost entirely limited to Late Cretaceous deposits (Forster, 1999). These Late Cretaceous Gondwanan coelurosaurs are from derived coelurosaurian groups like Dromaeosauridae (Makovicky et al., 2005; Novas and Pol, 2005; Novas et al., 2009; Novas and Puerta, 1997) and Alvarezsauridae (Bonaparte, 1991; Martinelli and Vera, 2007; Novas, 1996, 1997) and with the exception of an Early Cretaceous tyrannosaurid pubis from Australia (Benson et al., 2010a) and compsognathid material from Brazil (Naish et al., 2004), little is known about the anatomy or geographic distribution of stratigraphically older and phylogenetically more basal Gondwanan members of coelurosaurian groups such as Ornithomimosauria.

In 2000, de Klerk et al. described a new species of theropod, *Nqwebasaurus thwazi*, from the Early Cretaceous Kirkwood Formation of South Africa. Although they did not present a phylogenetic analysis of *Nqwebasaurus*, de Klerk et al. (2000) pointed out many characteristics of the skeleton that suggested it is a member of Coelurosauria, but its exact relationships remained unclear. Subsequent incorporation of *Nqwebasaurus* into phylogenetic analyses (e.g., Holtz et al., 2004; Makovicky and Turner, 2008) has suggested that it is indeed a coelurosaur, and possibly a member of the Compsognathidae. In addition to these phylogenetic analyses,

* Corresponding author at: Division of Paleontology, Richard Gilder Graduate School, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, United States. Tel.: +1 212 769 5868; fax: +1 212 769 5800.

E-mail addresses: jchoiniere@amnh.org, Jonah.choiniere@gmail.com (J.N. Choiniere), forster@gwu.edu (C.A. Forster), b.deklerk@ru.ac.za (W.J. de Klerk).

taxonomic assessments without analyses (e.g., Gishlick and Gauthier, 2007; Sereno, 2001) have suggested either basal coelurosaurian or ornithomimosaurian affinities for *Nqwebasaurus*. To date, *Nqwebasaurus* is the only known Early Cretaceous coelurosaur from Africa.

Additional preparation of the skull region of the *Nqwebasaurus* holotype (AM 6040) has revealed new osteological features relevant to its phylogenetic position. These features include a previously unknown maxilla and lacrimal and the more complete exposure and identification of the braincase and parietal bones. Surprisingly, the maxilla contains at least four small, unserrated, procumbent teeth, atypical for theropod dinosaurs. We report here on the newly-uncovered anatomy of this important Gondwanan coelurosaur taxon, describe additional skeletal elements not figured in the original description, and present the results of a broadly sampled phylogenetic analysis of the Coelurosauria that shows *Nqwebasaurus* is the earliest known member of the basal coelurosaurian clade Ornithomimosauria and the only member of this group known from Africa.

2. Material and methods

2.1. Abbreviations

Abbreviations for figures in captions; MPT: most parsimonious tree; AMNH, American Museum of Natural History, New York, USA; AM, Albany Museum, Grahamstown, South Africa; IGM, Mongolian Institute of Geology, Ulaanbaatar, Mongolia; LH, Universidad Autónoma de Madrid, Madrid, Spain; Fm, formation

2.2. Specimen preparation

Additional preparation of the specimen was performed using sharpened tungsten-carbide needles under high power magnification. The specimen was consolidated using a dilute solution of polyvinyl butyral resin (Butvar 76, Monsanto) in acetone.

2.3. Anatomical observations

Observations and measurements of *Nqwebasaurus* were made directly from the holotype (AM 6040) using standard techniques, including visual inspection with dissecting microscopes and magnifying lenses. Comparisons to other theropod taxa were made by direct inspection of catalogued specimens, or in some cases by reference to detailed anatomical observations published in peer-reviewed journals.

2.4. Phylogenetic analysis

The relationships of *Nqwebasaurus* were tested by incorporating it into a broadly-sampled phylogenetic data matrix designed to assess theropod relationships (Supplemental Information 2 and 3). This matrix was assembled in Mesquite v. 2.7 (Maddison and Maddison, 2009), and is composed of 568 morphological characters drawn from the literature and from personal observations for 97 theropod taxa. Characters in the matrix were mostly unordered, but were ordered where multi-state characters had 'absent' as one of their states or where character states were nested. The matrix was analyzed heuristically using the software package TNT v. 1.1 (Goloboff et al., 2003), under the parsimony criterion. Most-parsimonious trees were obtained using the following heuristic search parameters: hold 10,000 trees; 'Driven search' stabilizing consensus twice with a factor of 75 using Sectorial Search, Ratchet, Drift, and Tree Fusing with default settings; followed by an additional round of TBR swapping on MPTs. Bremer support

(Bremer, 1994) values for the resulting trees were calculated in TNT v1.1 using the following parameters: save suboptimal trees up to 10 steps longer than MPT, absolute supports, and saving 10,000 trees. Characters and synapomorphies were visualized on the MPTs using Mesquite v.2.7, TNT v1.1, and WinClada v. 1.00.18 (Nixon, 2002).

During the course of our anatomical research, we observed that *Nqwebasaurus* shares some derived traits shared with alvarezsaurids. We tested how many steps would be required to return a monophyletic Alvarezsauridae (*sensu* Choiniere et al., 2010) by running an analysis under identical protocol in TNT v1.1 where Alvarezsauridae + *Nqwebasaurus* were constrained to be monophyletic.

3. Systematic paleontology

Theropoda Marsh, 1881 (Marsh, 1881)
 Tetanurae Gauthier, 1986 (Gauthier, 1986)
 Coelurosauria von Huene, 1914 (Huene, 1914)
 Ornithomimosauria Barsbold, 1976 (Barsbold, 1976)
Nqwebasaurus thwazi de Klerk et al., 2000 (de Klerk et al., 2000)

3.1. Revised diagnosis

In addition to the autapomorphies listed by de Klerk et al. (2000), *Nqwebasaurus* is diagnosed by: unserrated maxillary teeth set into a groove rather than separate alveoli; straight rather than recurved maxillary tooth crowns; maxillary tooth crowns conical rather than mediolaterally compressed; ridge on the lateral margin of the dorsal surface of the distal end of metacarpal I extending proximally from lateral condyle.

3.2. Revised occurrence

The holotype of *Nqwebasaurus* (AM 6040) is from a small outcrop of mudstone paleosols of the Early Cretaceous (Berriasian–Valanginian; McMillan, 1999; Gomez et al., 2002) Kirkwood Formation (Fig. 1A) approximately 17 km west of Kirkwood Village (de Klerk et al., 2000). The Kirkwood Formation is one of three units that comprise the Uitenhage Group (Fig. 1B), a thick sequence of sedimentary fill within the Algoa Basin, the largest of several fault-controlled half-graben sedimentary basins that lie along the southern coast of Africa (Shone, 2006). The Uitenhage Group unconformably overlies rocks of the Paleozoic Cape Supergroup. The Kirkwood Formation consists of variegated mudstone paleosols and sandy fluvial channel fill, and overlies (in part) and interfingers with the conglomeratic alluvial facies of the Enon Fm. The Kirkwood Fm. also appears to be contemporaneous, in part, with the distal estuarine and marine facies of the Sunday's River Formation (Toerien and Hill, 1989). The Kirkwood "Lookout" locality, a cliff face on the southern bank of the Sundays River, 3 km south of the Kirkwood village, is now regarded as the stratotype of the formation (McLachlan and McMillan, 1976; Reddering, 2012; Rich et al., 1983: "Site 6").

4. Anatomical description

4.1. Skull

4.1.1. Maxilla

The left maxilla (Figs. 2 and 3) is nearly complete and is now well exposed in medial and ventral views, although the posterior tip of the jugal ramus is broken, and a portion of the ventral surface is obscured by a small piece of exogenous bone (possibly a portion

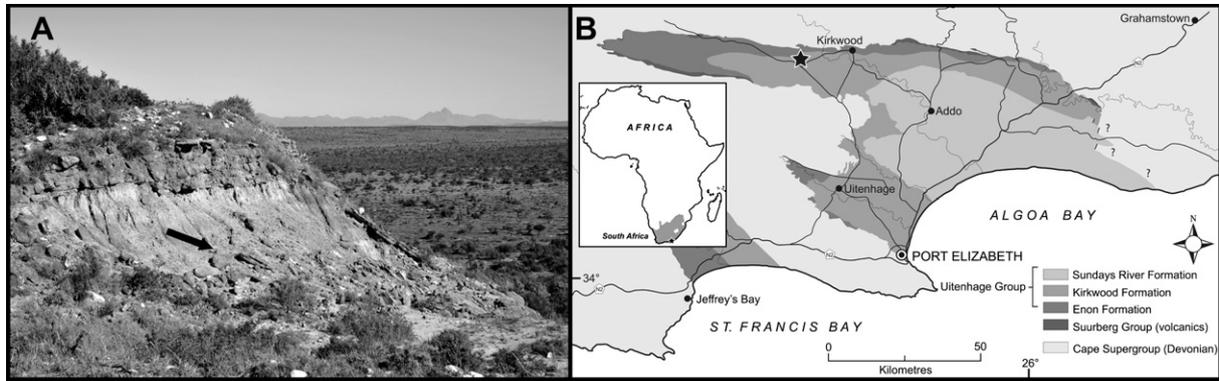


Fig. 1. Locality map and photograph of the site. (A) Photograph of locality of holotype of *Nqwebasaurus thwazi* (AM 6040); (B) geological map of Kirkwood area showing formations of the Uitenhage group, with fossil locality marked with a black star and towns marked with a black circle.

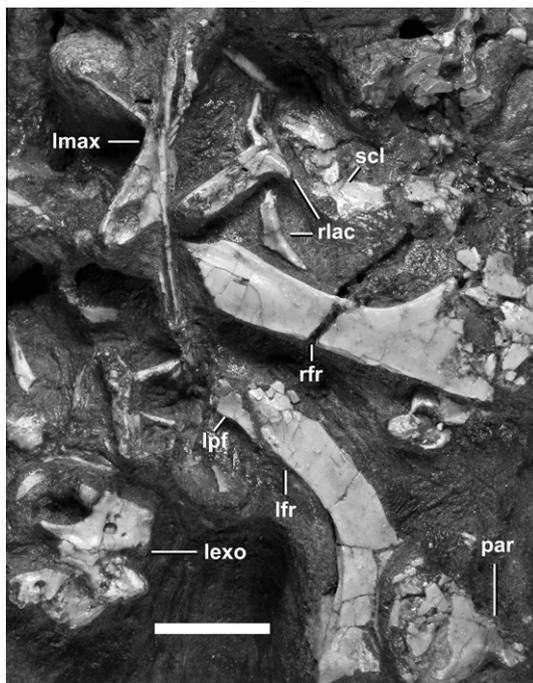


Fig. 2. Overview of skull bones of *Nqwebasaurus thwazi* (AM 6040). Abbreviations: lfr, left frontal; lexo, left exoccipital; lmax, left maxilla; lpf, left prefrontal; par, parietal; rfr, right frontal; rlac, right lacrimal; scl, sclerotic ring. Scale bar equals 2 cm.

of the dentary). Due to the fragile nature of the bone, and the complicated overlap in the skull elements, the maxilla cannot be further prepared at this time without damaging the specimen. Anterior to the nasal ramus, the anterior end of the maxilla is triangular in shape, being very long and shallowly angled posterodorsally. It comprises about one third of the overall length of the bone and is relatively longer but similar in overall shape to the parvicursorine alvarezsaurid *Shuvuuia* (IGM 100/0977; Chiappe et al., 1998), troodontids (e.g., *Byronosaurus* [Makovicky et al., 2003]), and ornithomimosaurids (e.g., *Pelecanimimus* [Perez, 2004; Perez-Moreno et al., 1994]). The nasal ramus is strongly inclined posterodorsally at approximately 28° from horizontal and its base is anteroposteriorly long. The nasal ramus grades smoothly into the anterior end of the maxilla, unlike the condition in some non-coelurosaurian tetanurans (Zhao and Currie, 1993) and in the basal tyrannosauroid *Guanlong* (IVPP V14531), where it is offset from the anterior end of the maxilla and rises abruptly, forming a step-like

junction. The morphology of the nasal ramus of the maxilla is similar to that seen in ornithomimosaurids (e.g. *Pelecanimimus* [LH 7777], *Harpymimus* [IGM 100/23]), in the alvarezsaurid *Shuvuuia* (Chiappe et al., 1998), and in the paravians *Mei* (Xu and Norell, 2004) and *Shanag* (Turner et al., 2007). The distal end of the nasal ramus is located well anterior to the level of the posterior end of the maxilla, as in *Pelecanimimus* (LH 7777) and *Shuvuuia* (IGM 100/0977; Chiappe et al., 1998), and unlike in most theropods where it terminates close to the level of the distal end of the ventral process. The dorsal edge of the nasal ramus bears a groove along its length. This groove is similarly well developed in ornithomimosaurids (e.g. *Pelecanimimus* [LH 7777], *Harpymimus* [IGM 100/23]), and in some dromaeosaurids (e.g., *Linheraptor* [Xu et al., 2010a]), where it marks the articulation with the long and robust nasal process of the premaxilla. In these taxa, the nasal process of the premaxilla extends posterior to the external naris to separate the maxilla from the nasal (Makovicky et al., 2004; Turner et al., 2007). We infer this condition to have been present in *Nqwebasaurus*, although it is possible that the maxillary process of the anterior end of the nasal could have been hypertrophied and left a similar groove.

The medial surface of the nasal ramus is shallowly concave. The maxillary fenestra is tall, ovoid, and inclined posterodorsally so that the long axis is nearly parallel to the angle of the nasal ramus, whereas in many ornithomimosaurids including *Pelecanimimus* (LH 7777), *Garudimimus* (Kobayashi and Barsbold, 2005b), and *Shenzhousaurus* (Ji et al., 2003), the long axis of the maxillary fenestra is horizontally oriented. Unlike most other ornithomimosaurids, except for *Shenzhousaurus* (Ji et al., 2003) and *Harpymimus* (IGM 100/23), there is no evidence for a secondary maxillary fenestra located dorsal to first (this fenestra is called the “promaxillary fenestra” by Kobayashi and Barsbold [2005b]), but we wish to avoid confusing the promaxillary foramen with the promaxillary fenestra here). No evidence for a promaxillary foramen can be seen from the medial side of the maxilla, but it is unlikely this feature would be visible given that it generally extends anteriorly from the anterior rim of the antorbital fenestra. A small fossa is developed on the medial surface of the nasal ramus anterior to the ventral end of the maxillary fenestra. There is no indication of a foramen on the posterior edge of the maxillary pila, a common feature in ornithomimosaurids, alvarezsaurids and troodontids (Choiniere et al., 2010b), though sediment in this region may have obscured this feature.

The palatal shelf on the medial surface of the maxilla is anteroposteriorly long and extends medially to form a palate that would likely have been completely closed at least to the level of the posterior end of the nasal ramus of the maxilla. The palatal shelf extends to the premaxillary–maxillary contact, suggesting that it

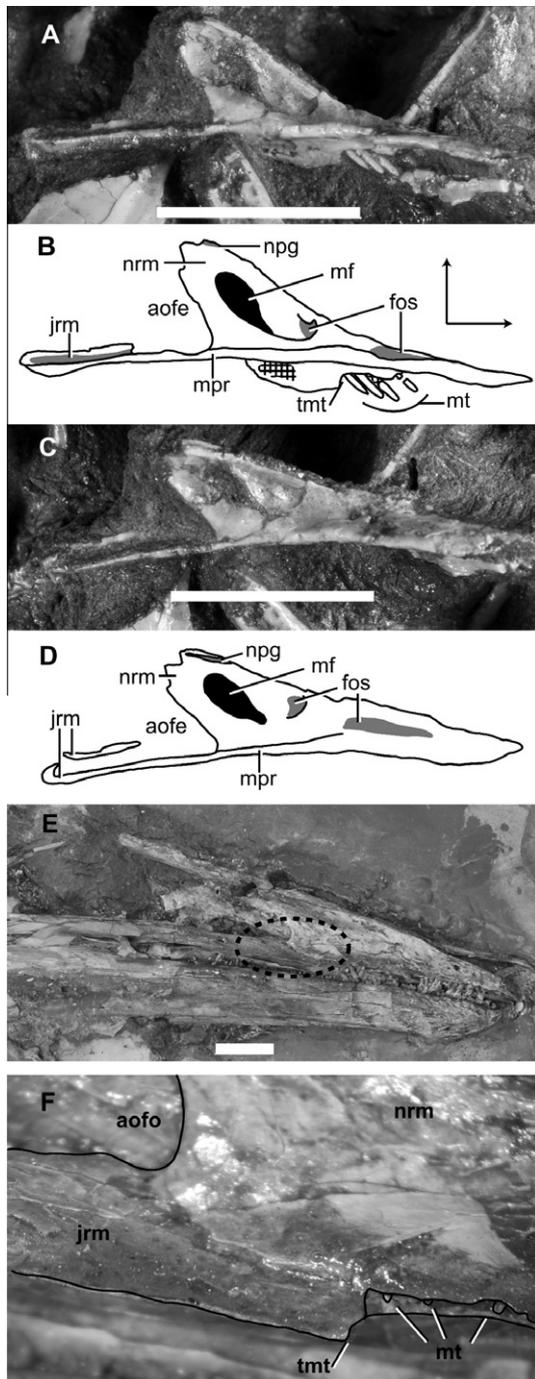


Fig. 3. Maxillae of *Nqwebasaurus thwazi* (AM 6040) and *Pelecanimimus polyodon* (LH 7777). (A–D) Left maxilla of *Nqwebasaurus* in: (A) medioventral view; (B) line drawing of medioventral view; (C) medial view; (D) line drawing of medial view; (E) lateral view of right maxilla of *Pelecanimimus*; (F) closeup of right maxilla of *Pelecanimimus* in lateral view with features outlined. Vertical arrow in (A–D) indicates dorsal direction, horizontal arrow indicates anterior direction. Dashed oval in (E) shows magnified area. Abbreviations: aofe, antorbital fenestra; afo, antorbital fossa; fos, fossa; jrm, jugal ramus of the maxilla; mf, maxillary fenestra; mpr, maxillary palatal ridge; mt, maxillary teeth; npg, nasal/premaxillary articular groove; nrm, nasal ramus of the maxilla; tmt, posterior terminus of maxillary tooth row. Scale bars equal 1 cm; (F) not to scale.

met the palatal shelf of the premaxilla. Along the medial surface of the maxillary palatal shelf, there is no evidence of a sutural contact with the vomer or adjacent maxilla. The palatal shelf grades into the maxillary body as it extends posteriorly and loses its contact with the contralateral shelf, but continues as a well-defined shelf

along the entire preserved portion of the jugal ramus. We therefore consider the development of the palatal shelf in *Nqwebasaurus* to be homologous to the extensive palatal shelves that are present in many coelurosaur, including tyrannosauroids, ornithomimosaur, dromaeosaurids, troodontids, alvarezsaurids and therizinosaurids. Such well-developed shelves are not present in most non-coelurosaurian tetanurans, the basal coelurosaur *Zuolong* (Choiniere et al., 2010a), or the basal tyrannosauroid *Kileskus* (Averianov et al., 2010). The morphology of the maxillary palate is poorly known in compsognathids, but in *Compsognathus* (Peyer, 2006), it appears to be poorly developed and the adjacent maxillae do not meet on the midline.

Posterior to the tooth row, which ends at the level of the nasal ramus of the maxilla, the ventrolateral rim of the maxilla is developed as a sharp ridge, as it is in all ornithomimosaur, including species with maxillary teeth (*Pelecanimimus* [LH 7777]) and species that have edentulous maxillae (e.g., *Gallimimus* [Osmólska et al., 1972]). In ornithomimosaur, the ridge-like posterior maxilla projects slightly laterally as well as ventrally, but this cannot be confirmed in *Nqwebasaurus*. A similar morphology of the posterior maxilla is also present in some basal avialans, like *Confuciusornis* (Chiappe et al., 1999), but the projection is impossible to determine because these taxa are only known from slab specimens. A ventrolateral maxillary ridge is not developed along the edentulous section of the posterior maxilla in the alvarezsaurid *Shuvuuia* (IGM 100/0977) or on the edentulous maxilla of the ceratosaurs *Limusaurus* (Xu et al., 2009). Thus, the morphology in *Nqwebasaurus* is uniquely shared with ornithomimosaur.

4.1.2. Maxillary teeth

Four small, procumbent teeth are observed in the maxilla (Fig. 3), but the majority of the anterior alveolar margin is obscured by matrix and bone fragments. The preserved teeth are the posteriormost four maxillary teeth, but based on the preserved length of the maxilla anterior to the exposed teeth there may have been as many as eighteen teeth in the maxilla. Procumbent posterior maxillary teeth are not known in any other theropod. The anterior (but not posterior) maxillary teeth of *Ornitholestes* (AMNH 619) and *Scipionyx* (Dal Sasso and Signore, 1998) are procumbent, as are the anterior dentary teeth of *Masiakasaurus* (Carrano et al., 2002; Sampson et al., 2001), *Proceratosaurus* (Rauhut and Milner, 2008), and *Haplocheirus* (Choiniere et al., 2010b). The preserved maxillary teeth of *Nqwebasaurus* are set in a trough-like alveolar groove and lack interdental septa. Because of the lack of interdental septa, it is possible that the teeth have shifted position during preservation and that in life position they were vertically oriented, as in most theropods. Despite the disarticulation of the bones of the skull, all of the teeth are oriented at exactly the same angle. This suggests that they have not been displaced from the maxilla. In comparison, in the ornithomimosaur *Pelecanimimus* (LH 7777), the posterior maxillary teeth are also set into an alveolar groove that lacks full septa, and despite the well-articulated skull, these teeth are splayed in several different directions. While the procumbent maxillary teeth may be a diagnostic feature of *Nqwebasaurus*, the possibility remains that this is an artifact of preservation.

The long maxillary tooth crowns of *Nqwebasaurus* are straight-sided with conical distal tips. They closely resemble the maxillary teeth of *Shuvuuia* (IGM 100/0977; Chiappe et al., 1998), and are unlike the labiolingually compressed crowns of most theropods. The roots of the teeth are cylindrical. The crowns are of uniform apico-basal length, and their mesiodistal width is approximately one-quarter of their apico-basal length. The posteriormost crown tapers apically to a sharp point, but the remaining crown tips are blunt. There are no serrations or carinae on any of the crowns, and the crowns are not labiolingually compressed. There are no constrictions between the roots and crowns, unlike the teeth of the basal

ornithomimosaur *Pelecanimimus* (LH 7777) and the maniraptorans *Mononykus* and *Archaeopteryx*, whose teeth have marked constrictions at the roots (Perle et al., 1994; Perle et al., 1993). The posterior terminus of the maxillary tooth row is located at the level of the anterior margin of the nasal ramus of the maxilla. This condition is only known within non-avian theropods in *Shuvuuia* (Chiappe et al., 1998) and *Pelecanimimus* (Perez-Moreno et al., 1994). Derived edentulous ornithomimosaur, such as *Gallimimus* and *Ornithomimus*, possess rhamphotheca on the anterior end of the tooth row (Barrett, 2005; Norell et al., 2001) that suggest feeding modes that are functionally reliant on the anterior tip of the snout, and this mode of feeding may also have been present for *Nqwebasaurus* given its tooth distribution.

4.1.3. Lacrimal

The right lacrimal (Figs. 2 and 4) is exposed in oblique medio-posterior view. It is broken into two pieces, one consisting of the ventral half of the jugal ramus and the other consisting of the posterodorsal process, the body, and the nasal ramus. As preserved, the lacrimal has been displaced laterally from the skull and rotated so that the lacrimal angle points laterally rather than dorsally.

The shaft of the jugal ramus is anteroposteriorly narrow except at the jugal contact where it is expanded posteriorly to approximately twice the midshaft width, and forms a long, sweeping contact with the jugal. In lateral view, the posterior margin of the jugal ramus is concave and marks the anterior border of the orbit. The posterodorsal process of the lacrimal is tall and posterodorsally-directed. Its body is mediolaterally inflated, tapers to a point distally, and is pierced at its midpoint by an anteroposteriorly directed foramen. A similar morphology is also seen on the lacrimal of the ornithomimid *Gallimimus* (IGM 100/1133; Osmólska et al., 1972). In theropods generally, the posterodorsal process does not have an inflated body, although in troodontids (e.g., *Byronosaurus* [IGM 100/984]) the body is wide but the lacrimal foramen is located laterally.

The nasal ramus is broken at the anterior end, and only the medial surface of the nasal ramus is visible. The nasal ramus is taller dorsoventrally than the jugal ramus is wide anteroposteriorly. The posterior half of its medial surface bears a shallow channel along its midline that extends posteriorly from a small, circular foramen in the middle of the shaft. The foramen is probably the lacrimal foramen, making the associated channel the nasolacrimal duct. The nasal ramus is broken at the anterior end. Little of the lacrimal body can be observed due to breakage and obscuring sediment.

4.1.4. Prefrontal

The left prefrontal (Figs. 2 and 6) lies anterolateral to the left frontal and confirms that the obliquely-oriented margin of the anterolateral frontal articulates with the prefrontal. A small depression on the dorsal surface of the frontal along this suture suggests that the prefrontal overlapped the frontal slightly, as it does in *Shuvuuia* (IGM 100/0977) and *Gallimimus* (IGM 100/1133; Osmólska et al., 1972) (IGM 100/1133). The prefrontal of *Nqwebasaurus* is relatively small compared to the hypertrophied prefrontals in all other ornithomimosaur (e.g., *Pelecanimimus* (LH 7777)).

4.1.5. Quadrate

The ventral portion of the right quadrate is preserved among the loose pieces of bone recovered from the field jacket (Fig. 5). Both condyles are preserved, although the lateral edge of the lateral condyle has eroded away. The medial condyle is hemispherical and the lateral condyle is hemicylindrical, with the long axis oriented almost strictly mediolaterally. The articular surface of the medial condyle has a larger area than the lateral condyle. The morphology of the condyles differs from ornithomimosaur (e.g., *Gallimimus*

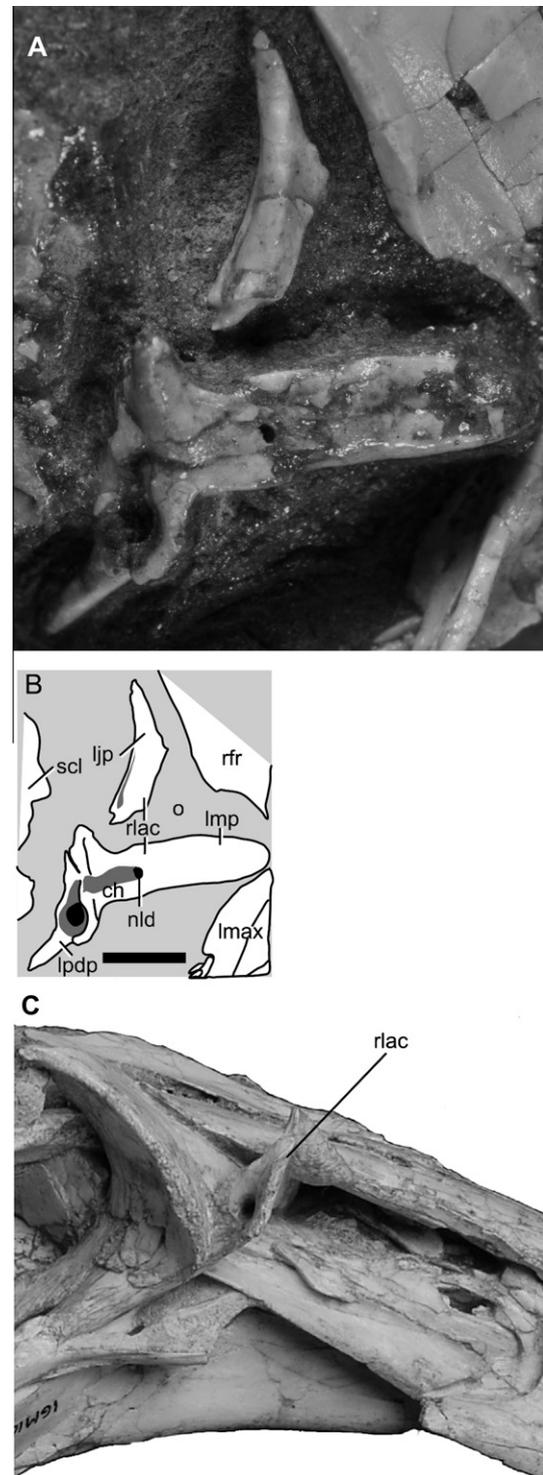


Fig. 4. Right lacrimal of *Nqwebasaurus thwazi* (AM 6040) in (A) medial view; (B) line drawing of medial view; and right lacrimal of *Gallimimus bullatus* (IGM 100/1133) in (C) lateral view. Abbreviations: ch, channel; ljp, left jugal process; lmax, left maxilla; imp, maxillary process of the lacrimal; lpdp, posterodorsal process of the lacrimal; nld, nasolacrimal duct; o, orbital region; rfr, right frontal; rjac, right lacrimal; scl, sclerotic ring. Scale bar equals 5 mm.

[IGM 100/1133]) and coelurosaurs generally (Choiniere et al., 2010a), where the quadrate condyles are subequal in size and are both angled anteromedially at approximately a 45° angle. The lateral condyle of *Nqwebasaurus* is similar, however, to that of *Shuvuuia* [IGM 100/1304; (IGM 100/1304; Chiappe et al., 1998)] in both its small size relative to the medial condyle and its

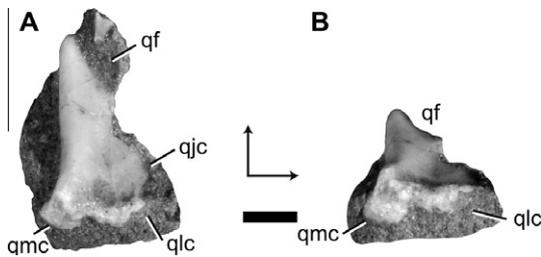


Fig. 5. Right quadrate of *Nqwebasaurus thwazi* (AM 6040). (A) Posterior view; (B) ventral view. Vertical arrow indicates dorsal direction, horizontal arrow indicates lateral direction for (A). Abbreviations: qf, quadrate foramen; qjc, quadratojugal contact; qlc, lateral condyle of the quadrate; qmc, medial condyle of the quadrate. Scale bar equals 5 mm.

mediolateral orientation. In dorsal view, a small portion of the proximal pterygoid ramus is preserved extending anteriorly from the medial edge of the body. The morphology of this flange is mostly obscured by matrix. A quadrate foramen is developed at mid-height of the preserved quadrate shaft. The position of the sutural scar for the quadratojugal on the lateral surface of the lateral quadrate condyle suggests that the quadrate foramen was bordered laterally by the quadratojugal. This cannot be confirmed because the quadratojugal is not preserved. In ornithomimosaur generally, the quadrate foramen is variably developed entirely within the quadrate shaft (e.g., *Garudimimus* [Kobayashi and Barsbold, 2005b]) or is poorly developed, often as only a deep fossa on the posterior surface of the shaft (e.g., *Gallimimus* [IGM 100/1133]).

4.1.6. Frontal

The frontals (Figs. 2 and 6) were briefly described by de Klerk et al., 2000 but are now more completely exposed. Both are mostly complete and oriented in approximately the same direction. They are separated by matrix along a straight, unfused midline suture. The posterior end of the right frontal has been broken into small pieces and the posterior end of the left frontal is overlain by a portion of the parietals, thus the exact path of the frontal–parietal suture is obscured.

The long, slender frontals are approximately eight times as long as they are wide (de Klerk et al., 2000), and they narrow considerably from posterior to anterior. The anterior ends of both frontals taper to form a sharply pointed anterior process whose apex is positioned just medial to the sagittal midline of the frontal. The anteromedial margin of the tapering anterior end would have articulated with the nasals (not preserved), which in turn would then have formed a posteriorly extending, wedge-shaped articulation between the anterior ends of the frontals. This nasal–frontal articulation would have extended posteriorly approximately 25% of the length of the frontals. This condition is relatively rare in theropods, but is present in a subadult specimen of *Gorgosaurus* (Holtz, 2004) and in *Shuvuuia* (Chiappe et al., 1998). The nasals may also extend between the medial edges of the anterior frontals in *Harpymimus* (IGM 100/23), but the distortion of the skull makes this difficult to confirm. In more derived ornithomimosaur (e.g., *Gallimimus* [Osmólska et al., 1972]), the nasals do not invade the medial contact between the anterior ends of the frontals.

The orbital margin is large and involves almost the entire curved lateral surface of the frontal. A flat, lenticular facet on the anterior end of the frontal orbital margin marks the posterolateral articulation with the prefrontal. The frontal orbital margin is indented by a shallow, concave groove that extends from the mid-point of the dorsal orbital rim to the postorbital process of the frontal. This groove was proposed as a tentative synapomorphy of *Nqwebasaurus* plus Compsognathidae (Makovicky and Turner, 2008), but it is also present in the ornithomimids *Pelecanimimus*

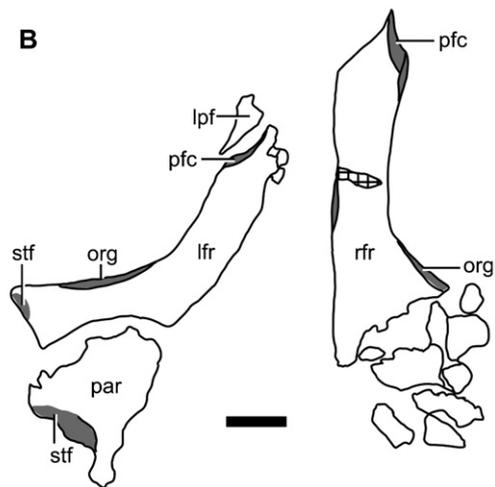
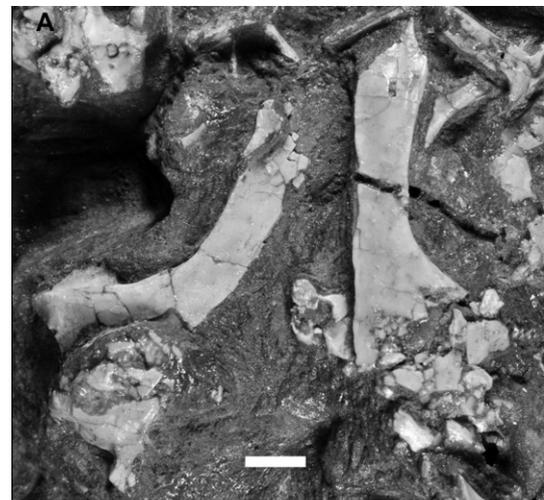


Fig. 6. Frontals, left parietal and left prefrontal of *Nqwebasaurus thwazi* (AM 6040). (A) Dorsal view; (B) line drawing of dorsal view. Hatched area indicates broken bone surface on right frontal. Abbreviations as in Fig. 3 and: org, groove on orbital rim of frontal; pfc, prefrontal contact; stf, supratemporal fossa. Scale bar equals 5 mm.

(LH 7777) and *Gallimimus* (IGM 100/1133; Osmólska et al., 1972; Pl. XXX, Fig. 1), in the alvarezsauroids *Shuvuuia* (IGM 100/1001) and *Haplocheirus* (IVPP V15988), and is probably more widespread among basal coelurosaurs.

The dorsal surface of the posterior end of the frontal is convex and the small postorbital process projects laterally and slightly ventrally as a tapering, triangular tab. A similarly pendant postorbital process is common in ornithomimosaur (e.g., *Pelecanimimus* (LH 7777)). A small, flattened scar on the posterolateral margin of the postorbital process marks the articulation with the postorbital. The dorsal surface of the posterior end of the frontal shows no evidence of emargination for the supratemporal fossa. This suggests that the supratemporal fenestra had little anterior extension onto the frontal, as in *Shuvuuia* (IGM 100/0977; IGM 100/1001; Chiappe et al., 1998) where the supratemporal fossa is small, but unlike ornithomimids (e.g., *Gallimimus* [Osmólska et al., 1972]) and tyrannosauroids (Holtz, 2004) where the supratemporal fenestra emarginates the entire posterior end of the frontal.

4.1.7. Parietal

The parietals were apparently fused (Figs. 2 and 6). The right margin and most of the dorsal surface of the parietal is broken. The posterolateral half of the left side of the parietal is intact,

including the proximal half of the squamosal process, and this portion has been rotated 90° counterclockwise from its original position. The preserved portion overlies the left frontal, and is separated from it vertically by approximately four millimeters of matrix. The left lateral side has a small depressed area that marks the medial extent of the supratemporal fenestra. Together with the small emargination of the frontal, this weak ridge shows that the supratemporal fenestra was subrectangular and relatively small, being less than half the anteroposterior length of the orbit.

The dorsal surface of the parietals would have formed a wide sheet of bone separating the supratemporal fenestrae. There is no evidence for either a sagittal or a transverse (“nuchal”) crest. Most theropods have some form of sagittal crest, and within Coelurosauria only in ornithomimosaur (e.g., *Gallimimus* [IGM 100/1133; Osmólska et al., 1972]), therizinosauroids (Clark et al., 1994), and alvarezsaurids (e.g., *Shuvuuia* [IGM 100/0977; Chiappe et al., 1998]) are the supratemporal fenestrae separated by such a wide, flat expanse of parietals. The posterior edge has a rugose, semicircular scar on its ventral aspect that likely represents the suture for the supraoccipital. The fracture pattern of the dorsal surface suggests that it may have been domed in life and then crushed during preservation. Although doming of the parietals is often considered a juvenile feature in theropods (Bever and Norell, 2009), it is present in adult or subadult specimens of *Shuvuuia* (IGM 100/1304) and *Gallimimus* (IGM 100/1133; Osmólska et al., 1972).

4.1.8. Exoccipital/opisthotic

The left exoccipital and opisthotic, including a portion of the paroccipital process (Figs. 2 and 7), are disarticulated from the skull. The paroccipital process is broken close to its base, and a small piece of bone adhering to the dorsal edge of the medial end of the process may be the missing piece of the distal end. The exoccipital contribution to the occipital condyle consists of a small, hemispherical knob. The medial surface of this knob is flat and smooth, indicating that the exoccipital and basioccipital were incompletely fused. This is not surprising given that the holotype of *Nqwebasaurus* is probably an immature individual (de Klerk et al., 2000) and that other theropod taxa, including the basal alvarezsaurid *Haplocheirus* (IVPP V15988), do not have complete fusion of these bones.

Four foramina are located lateral to the condylar portion of the exoccipital. Closest to the condyle are a pair of small nerve foramina. The close proximity of these openings to one another and to the occipital condyle indicates that they are probably openings for two branches of the hypoglossal nerve (CN XII). Their position is virtually identical to those of an indeterminate ornithomimid (IGM 100/987) (IGM 100/987; Makovicky and Norell, 1998) and the troodontid *Byronosaurus* (Makovicky et al., 2003). The largest of the four foramina is also the most dorsally located. This foramen

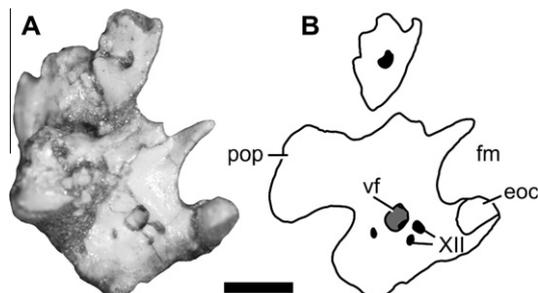


Fig. 7. Left exoccipital/opisthotic of *Nqwebasaurus thwazi* (AM 6040). (A) Posterior view; (B) line drawing of posterior view. Abbreviations: eoc, exoccipital portion of occipital condyle; fm, foramen magnum; pop, paroccipital process; vf, vagus foramen; XII, hypoglossal nerve. Scale bar equals 5 mm.

opens within a deep, subcircular fossa that creates a vestibular structure. This structure closely resembles the joint opening for the vagus and accessory nerves (CN X and XI) of *Falcarius* (Kirkland et al., 2005) and a large opening in the braincase of an indeterminate ornithomimid (IGM 100/987) identified as the opening for only CN X (Makovicky and Norell, 1998). The fourth foramen is the smallest opening in the exoccipital, and is located lateral to the exit of CN X and XI. In birds, the ostium canalis carotici has a similar position, although it is relatively larger (Baumel and Witmer, 1993), but a small opening for the glossopharyngeal nerve (IX) is also present close to this topological position. There is no depression of the posterior surface of the exoccipital in the region of the foramina that would indicate the presence of a subcondylar recess, unlike the well-developed subcondylar recesses of many coelurosaurs, including ornithomimosaur (Makovicky et al., 2004; Makovicky and Norell, 1998), basal therizinosauroids (Kirkland et al., 2005), and tyrannosauroids (e.g., *Guanlong* (IVPP V14531)). Subcondylar recesses are absent in many other coelurosaurs, however, including alvarezsaurids (e.g., *Haplocheirus* [Choiniere et al., 2010b]), the derived therizinosauroid *Erlikosaurus* (Clark et al., 1994), and troodontids (e.g., *Byronosaurus* [Makovicky and Norell, 2004; Makovicky et al., 2003]).

The paroccipital process is short and laterally projecting. The ventral rim of the paroccipital process is level with mid-height of the occipital condyle, as in most theropods (Rauhut, 2003a). As in most non-avian theropods, the exoccipital forms three supporting lamina for the paroccipital process: a ventral lamina that grades smoothly into the ventral margin of the process; a medial lamina that forms a cylindrical ridge extending along the posterior surface of the process along its midline; and a dorsal lamina that grades smoothly into the dorsal margin. Preservation of *Nqwebasaurus* does not allow complete removal of the exoccipital/opisthotic from the matrix surrounding the fossil, thus the anterior and lateral surfaces cannot be seen.

4.1.9. Parasphenoid

The parasphenoid is preserved lying lateral to the right sclerotic ring and oriented so that its long axis is perpendicular to the long axis of the right frontal (Fig. 8). The overall length of the preserved portion of the parasphenoid is slightly more than half the length of the frontal – even accounting for the missing portions the length likely was not much greater than this. The dorsal surface of the cultriform process has been eroded, and the proximoventral portion of the parasphenoid where it contacts the basisphenoid is broken. The base of the cultriform process is inflated and hollow, but the degree of inflation is considerably less than that seen in derived ornithomimosaur and troodontids, where it forms a parasphenoid bulla (Makovicky et al., 2004; Makovicky and Norell, 2004). The cultriform process tapers rapidly from the inflated proximal portion, extending anteriorly as a hollow conical feature. The process is much longer than in most ornithomimosaur (e.g., *Garudimimus* [Kobayashi and Barsbold, 2005b]), but is comparable in length to that of other coelurosaurs (e.g., *Haplocheirus* [IVPP V15988]) and to the basal ornithomimosaur *Pelecanimimus* (LH 7777). Only the posterodorsal portion of the proximal contact with the basisphenoid can be seen – matrix and broken bone bits obscure the rest. The proximal surface is divided into two shallowly concave areas by a low, dorsoventrally oriented bony ridge along the midline of the skull.

4.2. Axial skeleton

4.2.1. Cervical vertebrae

The lateral surfaces of cervical vertebrae 3–7 (Fig. 9) have been further exposed since the original description (de Klerk et al., 2000). This new exposure confirms the presence of a presumably

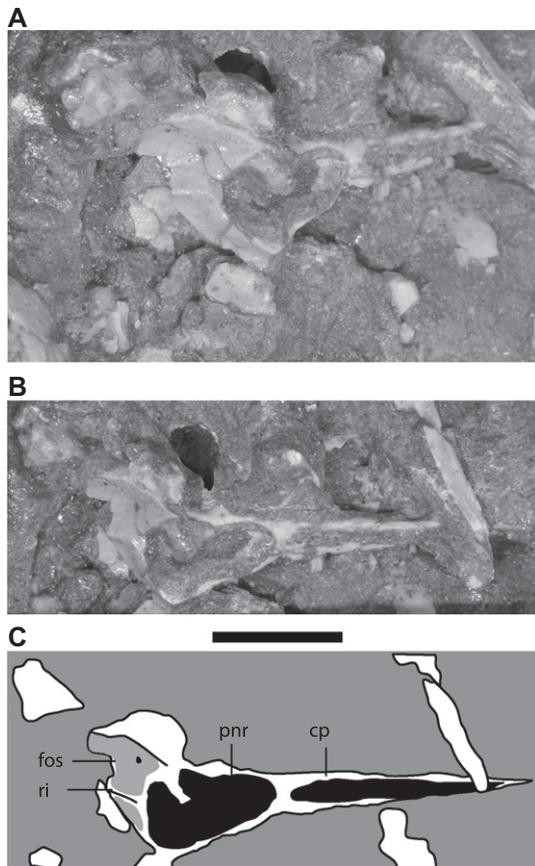


Fig. 8. Parasphenoid of *Nqwebasaurus thwazi* (AM 6040) in: (A) oblique postero-dorsal view; (B) dorsal view; (C) line drawing of (B). Abbreviations: cp, cultiform process; fos, fossa; pnr, pneumatic recess; ri, ridge. Scale bar equals 5 mm.

pneumatic foramen located between the parapophysis and the transverse process of the sixth cervical vertebra. This condition also seems likely for the fourth, fifth and seventh cervical vertebrae, although matrix infill continues to obscure this feature. On the lateral surfaces of cervical centra 4–7, a weakly developed lamina runs between the posterior edge of the parapophysis and the ventral edge of the posterior end of the centrum. This lamina turns abruptly ventrally after leaving the parapophysis, meeting the ventrolateral margin of the centrum at the level of the posterior edge of the neural spine. A second lamina, more dorsally located, parallels this ventral one. This more dorsal lamina begins at the posteroventral edge of the transverse process and is best developed in cervical vertebrae 4–7. Laminae are not present on the lateral surface of cervical centrum 3. Similar laminae have been observed in *Falcarius*, *Avimimus* and *Lophostropheus* (Kirkland et al., 2005; Zanno, 2010), and in a small Morrison Formation theropod (Makovicky, 1997).

de Klerk et al. (2000) noted that the left and right postzygapophyses were connected by a horizontal sheet of bone, or an “intra-zygapophyseal lamina” (Wilson, 1999). This sheet is excavated dorsally by an interspinous ligament pit that creates a triangular trough, with its narrow end at the posterior margin of the neural spine and its widest end at the posterior margin of the postzygapophyses. A similar bony web connecting the postzygapophyses is present in the cervical vertebrae of alvarezsauroids (Choiniere et al., 2010b), *Guanlong* (IVPP V14531; limited to the anterior cervical vertebrae), *Falcarius* (UMNH VP14700), *Avimimus* (IGM, uncatalogued specimen), *Gallimimus* anterior cervicals (Osmólska et al., 1972), and possibly in *Pelecanimimus* (LH 7777), although preservation of this feature is poor in the latter taxon. A dorsoventrally thin, laterally projecting sheet of bone connects the bases of the postzygapophyseal facets to the posterior surface of the transverse processes, forming a shelf that overhangs the lateral surface of the neural arches.

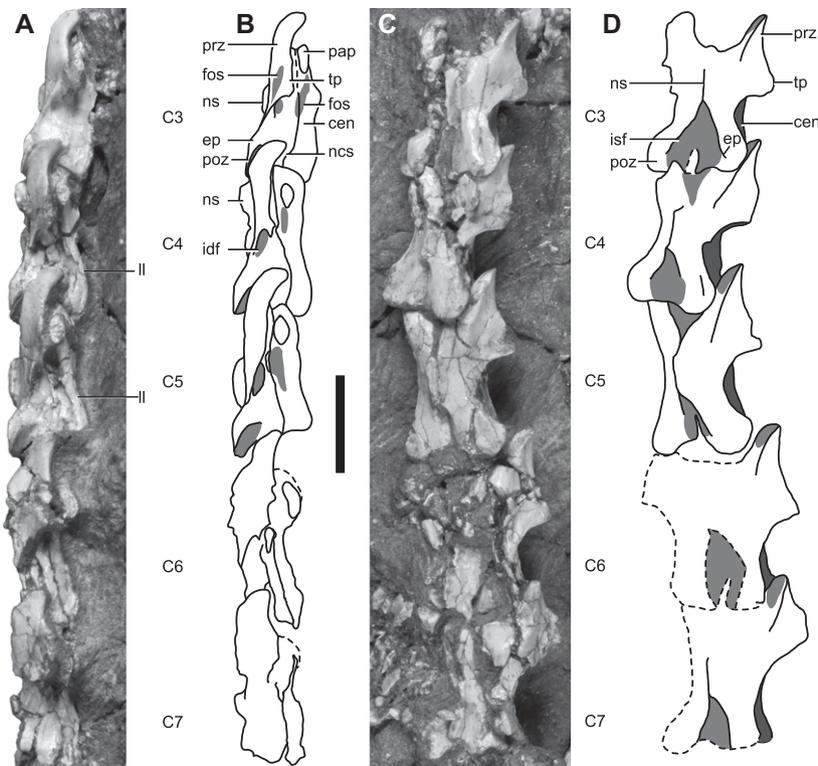


Fig. 9. Cervical vertebrae of *Nqwebasaurus thwazi* (AM 6040). (A) Right lateral view; (B) line drawing of right lateral view; (C) dorsal view; (D) line drawing of dorsal view. Abbreviations: C3–C7; cervical vertebrae three through seven; cen, centrum; ep, epipophysis; fos, fossa; idf, infradiapophyseal fossa; ll, lateral laminae; ncs, neurocentral suture; ns, neural spine; pap, parapophysis; prz, prezygapophysis; poz, postzygapophysis; tp, transverse process. Scale bar equals 1 cm.

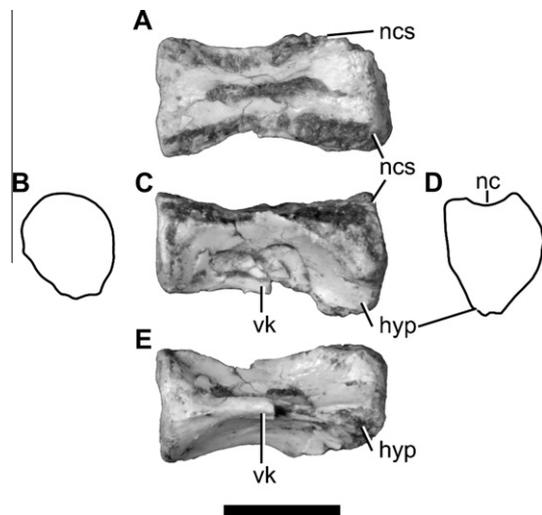


Fig. 10. Dorsal vertebra of *Nqwebasaurus thwazi* (AM 6040). (A) Dorsal view; (B) line drawing of posterior view; (C) right lateral view; (D) line drawing of anterior view; (E) ventral view. Abbreviations as in Fig. 10 and: hyp, hypapophysis; nc, neural canal; vk, ventral keel. Scale bar equals 5 mm.

4.2.2. Anterior dorsal

The centrum of an anterior dorsal vertebra (Fig. 10) was discovered in the loose fragments from the original block. The centrum bears a strong ventral keel and a well-developed hypapophysis on the anterior end. The almost completely abraded parapophyses are located dorsally on the centrum. There are no foramina on the lateral surface of the centrum, and no lateral laminae as in the cervical vertebrae, although the lateral surface of the centrum is deeply concave. The centrum is shallowly amphicoelous. Excluding the ventral expansion of the hypapophysis, both the anterior and posterior articular facets are subcircular.

The neural arch of a more posterior dorsal is preserved and can only be seen in ventral view. The transverse processes are medio-laterally short and anteroposteriorly about one quarter of the length of the neural arch. The parapophysis is located slightly below the level of the diapophysis and is flush with the lateral surface of the neural arch. The transverse process is supported by a single lamina that is located on the posterior portion of its ventral surface. The recess on the anterior portion of this lamina is very shallow; the posterior recess is deeper and is not subdivided by accessory laminae.

4.3. Appendicular skeleton

4.3.1. Coracoid

The pectoral girdle was well described by de Klerk et al. (2000), but inspection of the coracoid (Fig. 11) resulted in two observations that are relevant to the phylogenetic position of *Nqwebasaurus*. First, the shapes of the preserved portions of the coracoids strongly suggest that the overall morphology was dorsoventrally low. This shape is uncommon in theropods. Basal theropods and non-coelurosaurian tetanurans generally have subcircular coracoids, and derived coelurosaurian theropods (e.g., maniraptorans) tend to have dorsoventrally tall coracoids. Only ornithomimosaurs (Makovicky et al., 2004) and alvarezsauroids (e.g., Haplocheirus [Choiniere et al., 2010b]) share this coracoid shape. Although the posteroventral process is long and the posterior end of the coracoid is low in *Falcarius* (Zanno, 2006), in that therizinosauroid taxon the anterior end of the coracoid is much taller.

Second, the coracoid tubercle of *Nqwebasaurus* is developed as an anteroposteriorly long, ridge-like structure, as it is in the

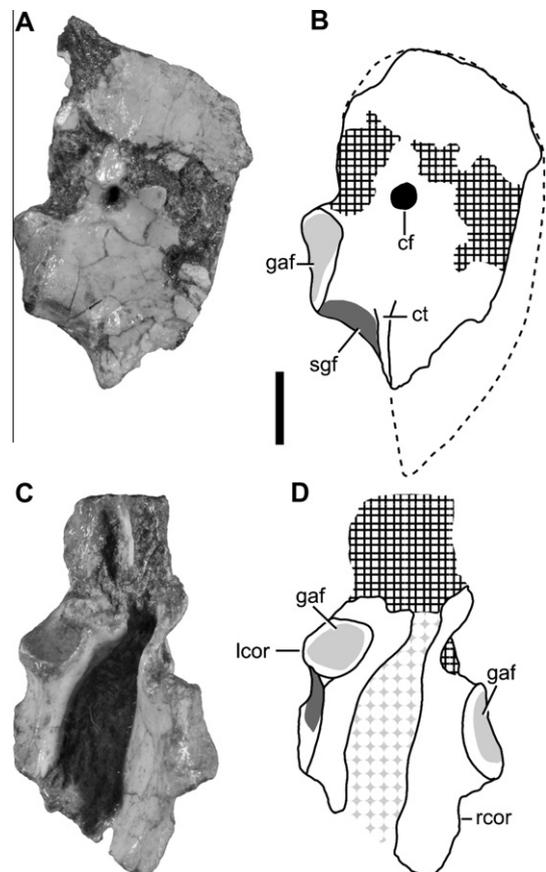


Fig. 11. Coracoids of *Nqwebasaurus thwazi* (AM 6040). (A) Right coracoid, right lateral view; (B) line drawing of right coracoid right lateral view; (C) coracoids, proximal view; (D) line drawing of coracoids, proximal view. Hatched area shows damaged bone surface. Abbreviations: cf, coracoid foramen; ct, coracoid tubercle; gaf, articular facet of the glenoid; lcor, left coracoid; rcor, right coracoid; sgf, subglenoid fossa. Scale bar equals 5 mm.

alvarezsauroids *Patagonykus* (Novas, 1997) and *Bonapartenykus* (Agnolin et al., 2012), and in some ornithomimosaurs (e.g., *Archaeornithomimus* [Makovicky et al., 2004]). No other coelurosaurians have a ridge-like coracoid tubercle, although this morphology is common among non-coelurosaurian tetanurans (e.g., *Allosaurus* [Benson, 2009]), where it is generally less prominent. There is a fossa present between the ventral lip of the glenoid and the coracoid tubercle in *Nqwebasaurus*, however this fossa is not as deep or as well-developed as in derived ornithomimosaurs.

4.3.2. Manus

The manus was well-described by de Klerk et al. (2000), but several features warrant additional description here (Fig. 12). The lateral condyle of the distal end of metacarpal (MC) I is hypertrophied relative to the medial condyle, a diagnostic feature of *Nqwebasaurus* listed by de Klerk et al. (2000). A pronounced, mediolaterally narrow and dorsoventral tall ridge extends proximally from the lateral condyle for about one third of the length of the metacarpal, deflecting slightly medially as it extends proximally. This ridge is separated by a small notch from a more proximal ridge, also extending along the lateral margin of the dorsal surface of MC I. The proximal ridge forms an articular surface with the closely appressed base of MC II. Although the proximal ridge is a common feature in the first metacarpals of theropods, the distal ridge is autapomorphic for *Nqwebasaurus*. Metacarpal III has a pronounced ridge along the medial margin of its dorsal surface that forms a large facet for articulation for medial

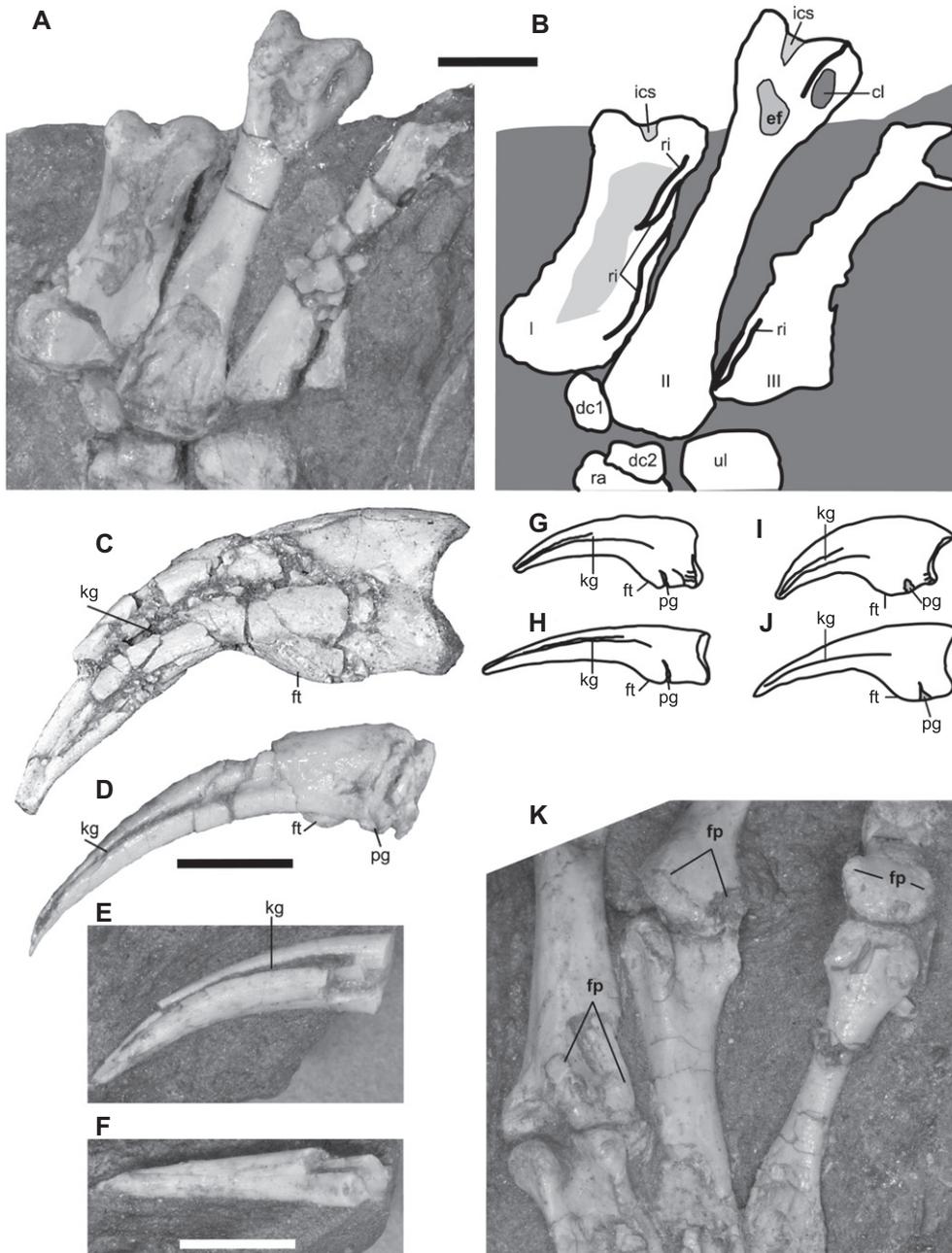


Fig. 12. Manus of *Nqwebasaurus thwazi* (AM 6040), *Pelecanimimus polyodon* (LH 7777) and *Harpymimus* (IGM 100/29). (A) Right metacarpus of *Nqwebasaurus* in dorsal (extensor) view; (B) line drawing of (A); (C) left ungual I-2 (reversed) of *Nqwebasaurus* in lateral view; (D) left ungual III-4 of *Nqwebasaurus* in lateral view; (E and F) distal end of left manual ungual II-3 of *Nqwebasaurus* in: (E) lateral view, (F) ventral view. (G) Line drawing of manual ungual I-2 of *Pelecanimimus* in lateral view. (H) Line drawing of manual ungual III-4 of *Pelecanimimus* in lateral view. (I) Line drawing of manual ungual I-2 of *Harpymimus* in lateral view. (J) Line drawing of manual ungual III-4 of *Harpymimus* in lateral view. (K) Left metacarpus and proximal phalanges of *Nqwebasaurus* in ventral view. Abbreviations: cl, collateral ligament pit; dc1–2, distal carpals one and two; ef, extensor fossa; ft, flexor tubercle; fp, flexor process; I–III, metacarpals one through three; ics, intercondylar sulcus; kg, keratin groove; pg, proximal groove; ra, radius; ri, ridge; ul, ulna. Scale bars equal: (A, B, and K) 5 cm; (C–F) 5 mm. Line drawings not to scale.

articulation with the base of MC II, although these two metacarpals are displaced slightly.

The unguis of the manus are heterogeneous in their shape. The first manual ungual (I-2) is recurved, as is typical for theropods, although its radius of curvature is not as tight as in some coelurosaurs, such as dromaeosaurids, oviraptorosaurs, and troodontids. Manual ungual I-2 bears a well-developed, but dorsoventrally low, flexor tubercle that is slightly separated from the proximal articular surface. This morphology stands in stark contrast to the two lateral unguis II-3 and III-4. These unguis are subequal in

length to I-2, lack flexor tubercles entirely and are much less recurved than I-2 (having a greater radius of curvature). A similar discrepancy in ungual morphology is rare in theropods, but is known in some ornithomimosaur, particularly in *Struthiomimus* and *Ornithomimus* (Nicholls and Russell, 1985; Osborn, 1916), although these taxa bear small flexor tubercles on II-3 and III-4. In the basal ornithomimosaur *Pelecanimimus* (LH 7777) and *Shenzhousaurus* (Ji et al., 2003), these unguis are similar in their radius of curvature to those of *Nqwebasaurus*, but the flexor tubercles are well-developed.

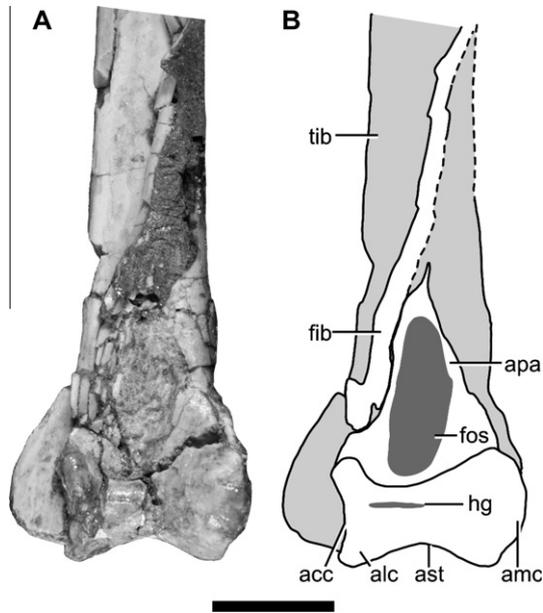


Fig. 13. Right distal tibia, fibula and astragalus of *Nqwebasaurus thwazi* (AM 6040). (A) Anterior view; (B) line drawing of anterior view. Abbreviations: apa, ascending process of the astragalus; acc, calcaneal facet of the astragalus; alc, lateral condyle of the astragalus; amc, medial condyle of the astragalus; ast, distal tarsal contact of the astragalus; fib, fibula; fos, fossa; hg, horizontal groove. Scale bar equals 1 cm.

4.3.3. Astragalus

The astragalus was briefly described by de Klerk et al. (2000), but it was not independently figured and additional preparation has revealed new details (Fig. 13). Preparation now shows that the astragalar condyles have a weak horizontal groove across the lateral half of anterior surface. This groove is present and extends across the entire anterior surface of the condyles in many non-coelurosaurian theropods (e.g., *Sinraptor* [Currie and Zhao, 1993]). In coelurosaurs it is only present in the basal tyrannosauroids *Guanlong* (IVPP V14531) and *Dilong* (Xu et al., 2004), the basal coelurosaurs *Tanycolagreus* (Carpenter et al., 2005) and *Coelurus* (YPM 9163), and the maniraptorans *Xinjiangovenator* (Rauhut, 2005) and *Alvarezsaurus* (Bonaparte, 1991). In the latter taxon, similar to the condition in *Nqwebasaurus*, the groove is only developed on the lateral side, although the holotype material of *Alvarezsaurus* is heavily abraded. The ascending process is very tall, as in coelurosaurs generally, and the anterior surface is embayed by a tall, ovoid fossa that extends onto the dorsal margin of the lateral condyle. Only alvarezsauroids among theropods exhibit this condition (Chiappe et al., 2002), although the condition in the basal alvarezsauroid *Haplocheirus* is unknown (Choiniere et al., 2010b) and it may be a derived feature within that group. In addition to the fossa, the ascending process is separated by a transverse groove from the astragalar condyles, as in all coelurosaurs (Rauhut, 2003a).

4.3.4. Pes

The phalanges of pedal digit IV (Fig. 14) were only partially figured by de Klerk et al. (2000). Successive phalanges of that digit become progressively proximodistally shorter, and pedal phalanx IV-3 is proximodistally shorter than it is dorsoventrally tall. Similarly short phalanges on pedal digit IV have a sporadic distribution in theropods, being present in abelisauroids (e.g., *Masiakasaurus* [Carrano et al., 2002]), oviraptorosaurs (e.g., *Avimimus* [IGM, uncat-alogued specimen]), *Mononykus* (Perle et al., 1994), and ornithomimosaurs (Makovicky et al., 2004). The large alvarezsauroid *Kol* (Turner et al., 2009) also has short pedal phalanges on digit IV, but the extensor processes in that taxon are much longer than in

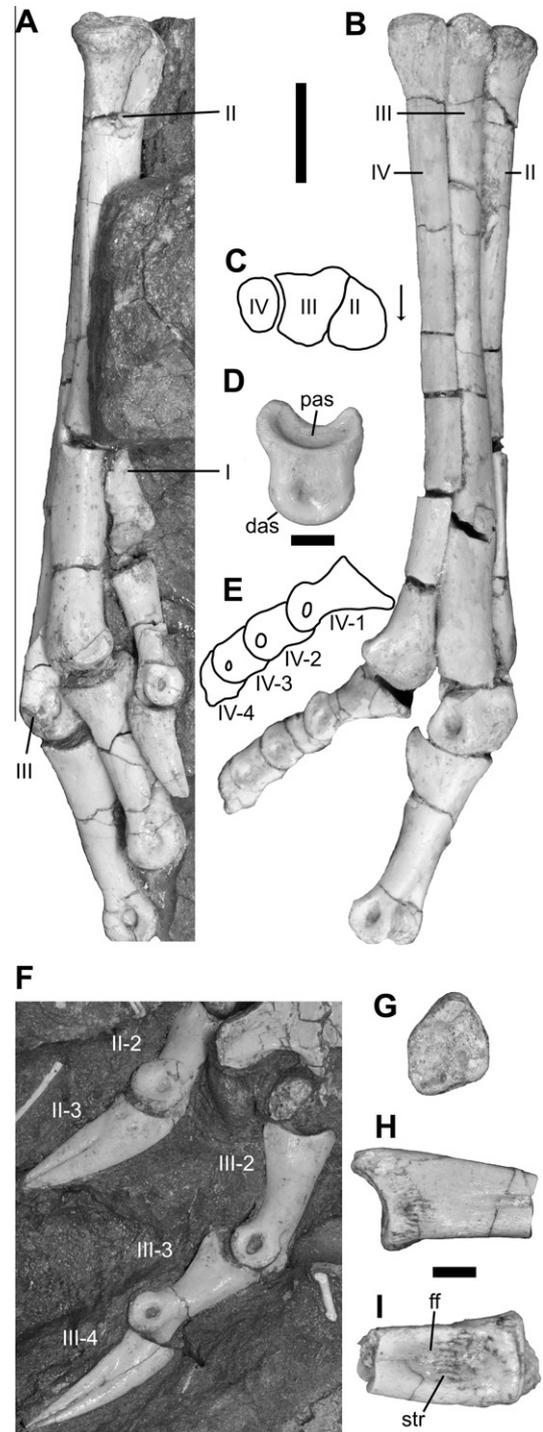


Fig. 14. Right metatarsus and pedal elements *Nqwebasaurus thwazi* (AM 6040). (A) Right metatarsus medial view; (B) right metatarsus and pes, anterolateral view; (C) line drawing of proximal right metatarsals; (D) isolated pedal phalanx of digit IV lateral view; (E) line drawing of right phalanges of digit IV, lateral view; (F) left pedal phalanges. (G–I) Left pedal ungual IV-5 in: (G) proximal view; (H) lateral view; (I) ventral view. Abbreviations: ff, flexor fossa; I–IV, metatarsals one through four; II-2–III-4, pedal phalanges; str, striations. Scale bar equals: (A, B, E and F) 1 cm; (C and G–I) 4 mm.

Nqwebasaurus and the corresponding extensor fossae are much deeper and mediolaterally narrower.

Pedal ungual IV-5 has been fully prepared from the block, and it is now possible to fully view the ventral surface, which was accurately described as flat in lateral view by de Klerk et al. (2000).

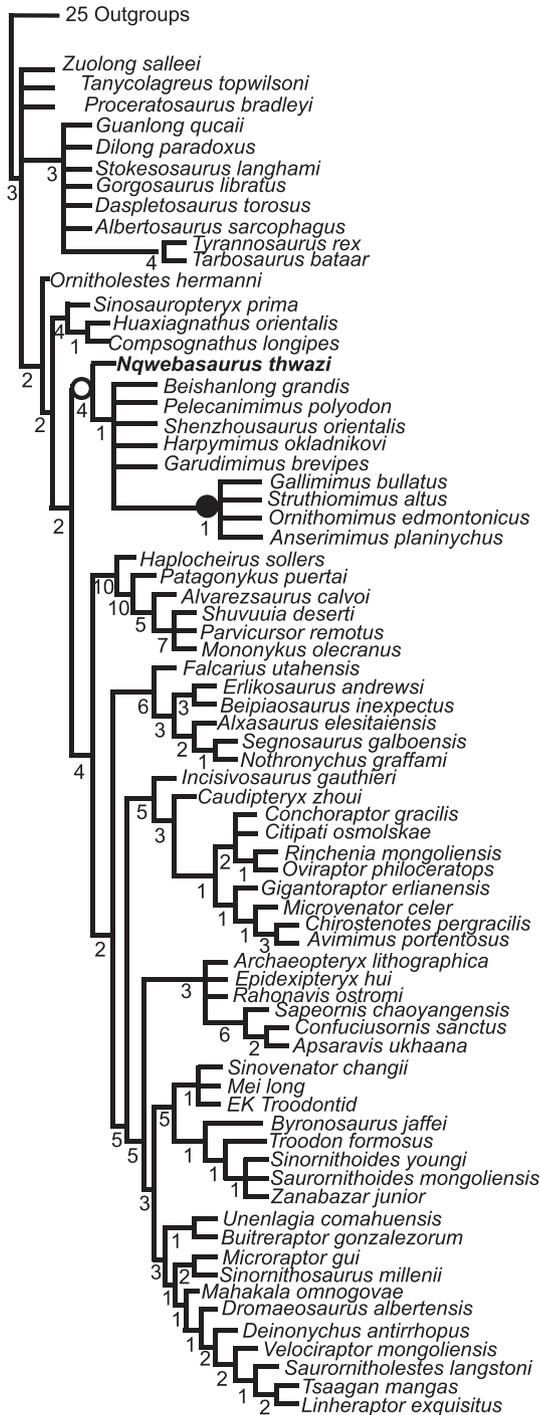


Fig. 15. Phylogenetic relationships of *Nqwebasaurus thwazi*. Strict consensus of 176 MPTs from analysis described in 2.3. L equals 2985, CI equals 0.223, RI equals 0.606; open circle denotes the node Ornithomimosauria, closed circle denotes Ornithomimididae. Numbers below nodes are Bremer Supports.

The proximal end of the ventral surface of IV-5 bears a deep fossa for the attachment of flexor tendons. Marked, axially-oriented striations within this fossa suggest a strong attachment of these tendons. This flexor fossa is also present on pedal ungual II-3. In general, theropod pedal unguals either bear no flexor tubercle and a convex or flat ventral surface, or a weakly developed flexor tubercle. A deep flexor fossa is only known in ornithomimosaur (Makovicky et al., 2004; Makovicky et al., 2009; Shapiro et al., 2003) and in the abelisauroid *Majungasaurus* (Carrano, 2007),

although in that taxon and in some ornithomimosaur this fossa contains a weakly developed flexor tubercle (Longrich, 2008).

5. Results

5.1. Phylogenetic results

The heuristic search described in 2.4 resulted in 176 most parsimonious trees of length 2985, ensemble consistency index 0.223, and ensemble retention index 0.606 (Figs. 15 and 16). Relationships within Theropoda were generally in agreement with recently published analyses of non-tetanuran theropodan relationships, non-coelurosaurian tetanuran relationships, and coelurosaurian relationships.

Nqwebasaurus is recovered as the basalmost member of the Ornithomimosauria (Figs. 15 and 16). Numerous synapomorphies support the monophyly of this clade, although none are exclusive features of Ornithomimosauria. These synapomorphies and their distributions outside of Ornithomimosauria are: maxillary process of premaxilla extending posteriorly to separate maxilla from external nares (also present in dromaeosaurids [Norell and Makovicky, 2004], *Archaeopteryx* [Mayr et al., 2005], *Ornitholestes* [AMNH 619], and many non-coelurosaurian tetanurans); maxillary fenestra situated at anterior border of antorbital fossa (also present in various non-coelurosaurian tetanurans [Benson, 2009; Rauhut, 2003a], *Byronosaurus jaffei* [Makovicky et al., 2003], *Tsaagan mangas* [Norell et al., 2006] and *Linheraptor exquisitus* [Xu et al., 2010a]); lateral margin of maxilla developed as a sharp, lateroventrally extending shelf adjacent to tooth row (also present in *Erlikosaurus andrewsi* [Clark et al., 1994] and *Confuciusornis sanctus* [Chiappe et al., 1999]); orbital margin of frontal with lateral groove for reception of postorbital (also present in *Dilong paradoxus* [Xu et al., 2004], and *Compsognathus longipes* [Makovicky and Turner, 2008]); posterior end of maxillary tooth row terminates anterior to the level of the nasal ramus of maxilla (also present in *Shuvuuia deserti* [Chiappe et al., 1998]); loss of serrations on maxillary teeth (also present in parvicursorine alvarezsaurids [Chiappe et al., 2002], *Avialae* [Perle et al., 1993], *Mei long* [Xu and Norell, 2004], *Byronosaurus jaffei* [Makovicky et al., 2003], and *Buitreraptor gonzalezorum* [Makovicky et al., 2005]); maxillary teeth set in open groove (also present in *Shuvuuia deserti* [IGM 100/977], known in the dentary but not maxillary teeth of some troodontids [Currie, 1987; Makovicky and Norell, 2004]); maxillary tooth roots cylindrical (also known in *Baryonyx walkeri* [Charig and Milner, 1986, 1997], *Suchomimus tenerensis* [Serenó et al., 1998], parvicursorine alvarezsaurids [Perle et al., 1993], Therizinosauroida [Clark et al., 2004], and *Archaeopteryx lithographica* [Martin, 1984]); anterior cervicals with poorly developed epiphyses (also known in *Limusaurus inextricabilis* [Xu et al., 2009], *Masiakasaurus knopfleri* [Carrano et al., 2002], and *Alvarezsaurus calvoi* [Bonaparte, 1991], and parvicursorine alvarezsaurids); coracoid tubercle elongated and ridge-like (also known in some non-coelurosaurian tetanurans [Benson et al., 2010b]); paired flexor processes on ventral surface of proximal ends of proximalmost manual phalanges [Serenó, 2001] (also known in *Tanycolagreus topwilsoni* [Carpenter et al., 2005] and *Alvarezsauridae sensu Choiniere et al., 2010b*; flexor tubercles on manual unguals small (also known in some non-coelurosaurian tetanurans, such as *Compsognathus longipes* [Gishlick and Gauthier, 2007], *Alvarezsauridae sensu Choiniere et al., 2010b*), and *Epidexipteryx hui* [Zhang et al., 2008]); pedal phalanges of digit IV antero-posteriorly short with proximal and distal articular surfaces extremely close to each other (also known in Ceratosauria [Carrano and Sampson, 2008], *Tyrannosaurus rex* [Brochu, 2003], *Tarbosaurus bataar* [Maleev, 1974], *Avimimus portentosus* [Vickers-Rich et al., 2002], *Alvarezsaurus calvoi* [Bonaparte, 1991], *Mononykus olecranus*

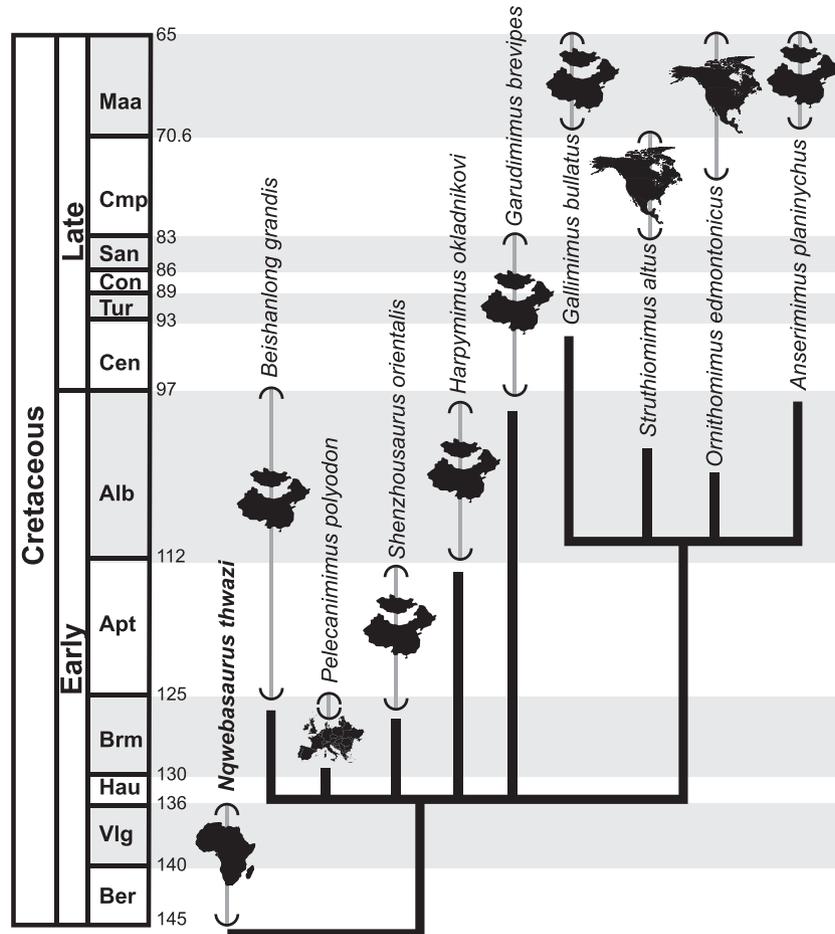


Fig. 16. Temporally-calibrated phylogeny of the Ornithomimosauria, showing continental distribution of terminal taxa and listing unambiguous synapomorphies at nodes. Country and continent silhouettes not to scale, China and Mongolia separated slightly for clarity, eastern Europe omitted. Numbers to right of Ages are dates in millions of years from present and are from Gradstein et al. (2004). Abbreviations: Alb, Albanian; Apt, Aptian; Brm, Barremian; Ber, Berriasian; Cen, Cenomanian; Cmp, Campanian; Con, Coniacian; Hau, Hauterivian; Maa, Maastrichtian; San, Santonian; Tur, Turonian; Vlg, Valanginian.

[Perle et al., 1994], and some therizinosauroids [Clark et al., 2004]); ventral surfaces of pedal unguals flat in lateral view (also known in parvicursorine alvarezsaurids and *Avimimus portentosus* [Vickers-Rich et al., 2002]); single flexor fossae on ventral surface of proximal ends of pedal unguals (also known in *Majungasaurus crenatissimus* [Carrano, 2007]).

Ornithomimosauria inclusive of *Nqwebasaurus* is well-supported in this analysis, with a Bremer support of four. Ornithomimosauria is recovered here as a basal clade within Coelurosauria, and the sister taxon to Maniraptora. Relationships within Ornithomimosauria are poorly resolved, although the derived group Ornithomimidae is recovered as monophyletic and is composed of Late Cretaceous North American and Asian ornithomimosaurians including *Struthiomimus*, *Gallimimus*, *Ornithomimus edmontonicus*, and *Anserimimus*. Although non-ornithomimosaurid ornithomimosaur relationships vary in the most-parsimonious trees, in no trees is the taxon *Pelecanimimus* recovered in a basal position. Instead, it is alternately placed as the sister-taxon to Ornithomimidae or as the sister taxon to *Shenzhousaurus* which are then sister to Ornithomimidae.

Constraining Alvarezsauridae *sensu* Choiniere et al., 2010 to be monophyletic inclusive of *Nqwebasaurus* yielded 84 trees of length 2989, ensemble consistency of .223, and ensemble retention index of .606. Thus, trees recovered under this constraint are four steps longer than MPTs recovered under no constraints. Topologies recovered under these constraints vary only slightly from those produced without constraints, and in all constrained trees,

Nqwebasaurus is recovered as a basal alvarezsaurid, which is in turn the basalmost taxon within Maniraptora.

6. Discussion

Members of derived coelurosaurian groups are relatively well-known in the Late Cretaceous of South America (Bonaparte, 1991; Makovicky et al., 2005; Martinelli and Vera, 2007; Novas, 1996; Novas and Pol, 2005; Novas and Puerta, 1997) and Madagascar (Forster et al., 1996; Forster et al., 1998), and show phylogenetic signals consistent with Gondwanan endemism (Makovicky et al., 2005). Our phylogenetic results show that the Early Cretaceous coelurosaur fauna of Gondwana includes members of the basal coelurosaur groups Ornithomimosauria, Compsognathidae (Naish et al., 2004) and Tyrannosauridae (Benson et al., 2010a), and isolated bones suggest that these basal coelurosaurian lineages persist at least until the late Early Cretaceous in Australia, although the presence of ornithomimosaurians on that continent is still awaiting verification (Benson et al., 2010a; Benson et al., 2012; Rich and Vickers-Rich, 1994). These data support the hypothesis that coelurosaurian lineages were biogeographically widespread before Pangaea breakup (Makovicky et al., 2005), and that end-Jurassic vicariance produced endemic coelurosaurian lineages unique to Gondwana and Laurasia. In context of this hypothesis, the recognition of *Nqwebasaurus* as a basal ornithomimosaur predicts that new Gondwanan ornithomimosaur discoveries should show

phylogenetic affinity to *Nqwebasaurus* and that Early Cretaceous Gondwanan members of other coelurosaurian lineages will show affinities with Late Cretaceous Gondwanan forms. Testing these predictions awaits the collection of new fossil coelurosaur material from the Early Cretaceous of Gondwana.

It is surprising that the late Barremian (Buscalioni et al., 2008) taxon *Pelecanimimus* is not recovered as the basalmost member of the Ornithomimosauria, given that most previous phylogenetic research on ornithomimosaur relationships hypothesizes this position (Bronowicz, 2011; Ji et al., 2003; Kobayashi and Barsbold, 2004, 2005a; Makovicky et al., 2004; Makovicky et al., 2009; Perez-Moreno et al., 1994). It is also surprising that in the MPTs, *Beishanlong* is sometimes recovered as the basalmost ornithomimosaur except for *Nqwebasaurus*. The characters supporting a derived position for *Pelecanimimus* in our analysis are primarily on the forelimb (depending on its exact position in each fundamental tree), and include the straight humerus (it is sigmoidal in *Nqwebasaurus* and *Beishanlong*), the presence of a syndesmosis between the distal radius and ulna (absent in *Nqwebasaurus* and *Beishanlong*), subequal length of the manual metacarpals (unknown in *Beishanlong*), and the relatively weak curvature of all the manual unguals (the first manual ungual is strongly recurved in *Beishanlong* and *Nqwebasaurus*). Although the skull of *Beishanlong* is unknown, if tooth loss follows a progressive evolutionary trajectory in Ornithomimosauria, then our phylogenetic results predict that *Beishanlong* had dentary and maxillary teeth that were likely simplified relative to the primitive coelurosaurian condition.

Nqwebasaurus has many anatomical similarities with members of the Alvarezsauridae, a basal maniraptoran lineage whose phylogenetic relationships have been an area of active debate (Chiappe et al., 1997; Chiappe, 1996; Chiappe et al., 1998; Novas and Pol, 2002; Perle et al., 1993; Sereno, 2001; Zhou, 1995). These include features of the skull and dentition such as reduction of the posterior tooth row and simplified teeth, features of the axial column such as bony laminae connecting the postzygapophyses of the anterior cervical vertebrae, features of the forelimb including a ridge-like coracoid tubercle and a medial tab on the base of metacarpal one, and features of the hindlimb including a deep fossa on the anterior base of the ascending astragalar process and antero-posteriorly short phalanges on pedal digit four. Nevertheless, our phylogenetic analysis strongly supports a position for *Nqwebasaurus* within Ornithomimosauria. It is likely that as taxon sampling increases in the coelurosaur tree at the bases of Ornithomimosauria and Alvarezsauridae, respectively, new relationships may be found that indicate some of these features are plesiomorphies at stem nodes connecting these taxa or that these characters together with as-yet undiscovered synapomorphies may support a sister taxon relationship between these groups.

The tooth crowns of *Nqwebasaurus* are similar to those of derived parvicursorine alvarezsaurids (Chiappe et al., 1998; Perle et al., 1994; Perle et al., 1993), and may suggest that these taxa shared a common feeding strategy. Ornithomimosaurians are characterized by a progressive loss of dentition over evolutionary time (Kobayashi and Barsbold, 2005a; Makovicky et al., 2004; Makovicky et al., 2009). The only other ornithomimosaur to bear maxillary teeth is the late Barremian *Pelecanimimus* from Spain (Perez-Moreno et al., 1994). The maxillary tooth crowns of *Pelecanimimus* differ from those of *Nqwebasaurus* in bearing a pronounced constriction between the crown and root and in bearing anterior and posterior carinae (although these do not bear serrations). It is possible that the modified dentition of *Pelecanimimus* represents a divergence in feeding strategy from other basal ornithomimosaurians, although filter feeding is unlikely based on energetic and anatomical grounds (Barrett, 2005). Tooth loss is known in four coelurosaurian groups, and in each case the presence of simplified, conical, incisiform teeth presages evolutionary

loss of dentition in that area (Zanno and Makovicky, 2011). The complete loss of dentition posterior to the nasal ramus of the maxilla in both *Pelecanimimus* and *Nqwebasaurus* and the presence of simple incisiform posterior teeth in the maxilla of the latter taxon is consistent with data from the ornithomimosaur dentary that suggests that loss of dentition in ornithomimosaurians proceeded from posterior to anterior (Zanno and Makovicky, 2011). The conditions in *Nqwebasaurus* and also *Pelecanimimus* may be a transitional stage where there is decreased reliance on the posterior end of the mouth for feeding, but anterior teeth have yet to be lost. Although the procumbency of the maxillary dentition in *Nqwebasaurus* may be due to diagenetic factors, it is interesting that in other theropod taxa with shifts in tooth morphology, procumbency (albeit of the premaxillary and/or dentary teeth) is a common occurrence (Zanno and Makovicky, 2011).

Gastroliths were previously reported in the abdominal region of *Nqwebasaurus* (de Klerk et al., 2000), and although uncommon in theropods generally, they are known in living and extinct birds (Zanno and Makovicky, 2011), some oviraptorosaurs (Ji et al., 1998), the edentulous ceratosaur *Limusaurus* (Xu et al., 2009) and in several ornithomimosaurians (Ji et al., 2003; Kobayashi et al., 1999). The size and distribution of the gastroliths in *Nqwebasaurus* is consistent with the presence of a gastric mill, and the estimated mass of the gastroliths compared to the estimated mass of *Nqwebasaurus* falls on the regression line of modern birds and extinct non-avian theropods reported in a recent study (Wings and Sander, 2007) (see Supplemental Information 4 for calculations). Recent assessment of herbivorous characteristics in ornithomimosaurians (Barrett, 2005) and in coelurosaurians generally (Zanno and Makovicky, 2011) indicates that the presence of a gastric mill allows confident inference of herbivory in extinct non-avian dinosaurs. Thus, we infer that *Nqwebasaurus* had a gastric mill, was herbivorous, and that herbivory in Ornithomimosauria had already evolved by the earliest Early Cretaceous. Together with tooth reduction, which is another correlate of herbivory (Zanno and Makovicky, 2011), these data indicate that dietary specialization in this clade was likely an early component of its divergence.

Previous hypotheses of ornithomimosaurian relationships have shown near-perfect stratigraphic consistency. Our phylogenetic results, where *Pelecanimimus* occupies a relatively more derived position and with *Beishanlong* as a relatively basal taxon, fit stratigraphic distribution of the group more poorly, although the presence of *Nqwebasaurus* in the earliest Cretaceous does improve the fit of the coelurosaur fossil record to stratigraphy overall.

7. Conclusion

New preparation on the holotype of *Nqwebasaurus* has allowed us to identify the maxilla, exoccipital-opisthotic, and revealed new features of other parts of the skeleton. This information, together with a new phylogenetic analysis for coelurosaurian relationships, posits *Nqwebasaurus* as the basalmost, and stratigraphically earliest ornithomimosaur. *Nqwebasaurus* is the first ornithomimosaurian taxon known from Africa and the first Gondwanan ornithomimosaur known from more than fragmentary material. The presence of reduced dentition and a gastric mill confirm that herbivory evolved very early during ornithomimosaurian evolution. Its stratigraphic age and basal position within Coelurosauria make *Nqwebasaurus* an important taxon for understanding early coelurosaurian evolution and highlight the need for more coelurosaurian fossils from Gondwana.

Acknowledgments

Research was supported by the George Washington University, the Jurassic Foundation, and the Albany Museum, Grahamstown.

The authors wish to thank: R. Prevec for assistance with figures; A. Buscalloni, K. Tsogtbataar, T. Chinzorig, M. Norell, D. Varrichio, J. Horner, and M. Carrano for specimen access; R. Benson and P. Makovicky for their thoughtful reviews; A. Turner, and J. Conrad for useful discussions; Richard, Kitty, the owners of Asante Sana, V. de Klerk, and Maisey for material support during this research.

J.N.C. is currently supported by a Kalbfleisch Fellowship and Gerstner Scholarship made available through the Richard Gilder Graduate School at the American Museum of Natural History.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jafrearsci.2012.05.005>.

References

- Agnolin, F.L., Powell, J.E., Novas, F.E., Kundrat, M., 2012. New alvarezsaurid (Dinosauria, Theropoda) from uppermost Cretaceous of north-western Patagonia with associated eggs. *Cretaceous Research* 35, 33–56.
- Averianov, A.O., Krasnolutskii, S.A., Ivantsov, S.V., 2010. A new basal coelurosaur (Dinosauria: Theropoda) from the Middle Jurassic of Siberia. *Proceedings of the Zoological Institute RAS* 314, 42–57.
- Barrett, P.M., 2005. The diet of ostrich dinosaurs (Theropoda: Ornithomimosauria). *Palaeontology* 48, 347–358.
- Barsbold, R., 1976. K evolyutsii i sistematike pozdnemezozoykskikh khishchnykh dinozavrov (The evolution and systematics of late Mesozoic carnivorous dinosaurs) (Russian). The Joint Soviet-Mongolian Paleontological Expedition, *Transactions* 3, 68–75.
- Baumel, J.J., Witmer, L.M., 1993. *Osteologia*. In: Baumel, J.J. (Ed.), *Handbook of Avian Anatomy: Nomina Anatomica Avium*, Second ed. Publications of the Nuttall Ornithological Club No. 23, Cambridge, pp. 45–132.
- Benson, R.B.J., 2008. New information on *Stokesosaurus*, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. *Journal of Vertebrate Paleontology* 28, 732–750.
- Benson, R.B.J., 2009. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society* 158, 882–935.
- Benson, R.B.J., Barrett, P.M., Rich, T.H., Vickers-Rich, P., 2010a. A southern tyrant reptile. *Science* 327, 1613.
- Benson, R.B.J., Carrano, M.T., Brusatte, S.L., 2010b. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97, 71–78.
- Benson, R.B.J., Rich, T.H., Vickers-Rich, P., Hall, M., 2012. Theropod fauna from Southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. *PLoS ONE* 7, e7122.
- Bever, G.S., Norell, M.A., 2009. The perinate skull of *Byronosaurus* (Troodontidae) with observations on the cranial ontogeny of paravian theropods. *American Museum Novitates* 3657, 1–51.
- Bonaparte, J.F., 1991. Los vertebrados fosiles de la Formacion Rio Colorado de Neuquen y cercanias, Cretacico Superior, Argentina. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” Paleontologia* 4, 17–123.
- Bremer, K., 1994. Branch support and tree stability. *Cladistics* 10, 295–304.
- Brochu, C.A., 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology* 22, 1–137.
- Bronowicz, R., 2011. New material of a derived ornithomimosaur from the Upper Cretaceous Nemegt Formation of Mongolia. *Acta Palaeontologica Polonica* 56, 477–488.
- Buscalloni, D.A., Fregenal-Martínez, M.A., Bravo, A., Poyato-Ariza, F.J., Sanchíz, B., Báez, A.M., Cambra-Moo, O., Martín-Closas, C., Evans, S., Marugán-Lobón, J., 2008. The vertebrate assemblage of Buenache de la Sierra (Upper Barremian of Serranía de Cuenca Spain) with insights into its taphonomy and palaeoecology. *Cretaceous Research* 29, 687–710.
- Carpenter, K., Miles, C., Cloward, K., 2005. New small theropod from the Upper Jurassic Morrison Formation of Wyoming. In: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington and Indianapolis, pp. 23–48.
- Carrano, M.T., 2007. The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 27, 163–179.
- Carrano, M.T., Sampson, S.D., 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Paleontology* 6, 183–236.
- Carrano, M.T., Sampson, S.D., Forster, C.A., 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 22, 510–534.
- Charig, A.J., Milner, A.C., 1986. *Baronyx*, a remarkable new theropod dinosaur. *Nature* 324, 359–361.
- Charig, A.J., Milner, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London* 53, 11–70.
- Chiappe, L.M., 1996. Phylogenetic position of *Mononykus* from the Upper Cretaceous of the Gobi Desert. *Memoirs of the Queensland Museum* 39, 557–582.
- Chiappe, L., Norell, M., Clark, J., 1997. *Mononykus* and birds: methods and evidence. *The Auk* 114, 300–302.
- Chiappe, L.M., Norell, M., Clark, J.M., 1998. The skull of a relative of the stem-group bird *Mononykus*. *Nature* 392, 275–278.
- Chiappe, L.M., Qiang, J., Norell, M.A., 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. *Bulletin of the American Museum of Natural History* 242, 1–89.
- Chiappe, L.M., Norell, M.A., Clark, J.M., 2002. The Cretaceous, short-armed Alvarezsauridae: *Mononykus* and its kin. In: Chiappe, L.M., Witmer, L.M. (Eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, Los Angeles, London, pp. 87–120.
- Choiniere, J.N., Clark, J.M., Forster, C.A., Xing, X., 2010a. A basal coelurosaur (Dinosauria: Theropoda) from the Late Jurassic (Oxfordian) of the Shishugou Formation in Wucuiwan, People's Republic of China. *Journal of Vertebrate Paleontology* 30, 1773–1796.
- Choiniere, J.N., Xu, X., Clark, J.M., Forster, C.A., Guo, Y., Han, F., 2010b. A basal alvarezsaurid theropod from the early Late Jurassic of Xinjiang, China. *Science* 327, 571–574.
- Clark, J.M., Altangerel, P., Norell, M.A., 1994. The skull of *Erikosaurus andrewsi*, a Late Cretaceous “Segnosaur” (Theropoda: Therizinosauridae) from Mongolia. *American Museum Novitates* 3115, 1–39.
- Clark, J.M., Maryanska, T., Barsbold, R., 2004. Therizinosauridae. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, second ed. Berkeley, pp. 151–164.
- Currie, P.J., 1987. Bird-like characteristics of the jaws and teeth of troodontid theropods. *Journal of Vertebrate Paleontology* 7, 72–81.
- Currie, P.J., Zhao, X.-J., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30, 2037–2081.
- Dal Sasso, C., Signore, M., 1998. Exceptional soft-tissue preservation in a theropod dinosaur from Italy. *Nature* 392, 383–387.
- de Klerk, W.J., Forster, C.A., Sampson, S.D., Chinsamy, A., Ross, C.F., 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. *Journal of Vertebrate Paleontology* 20, 324–332.
- Forster, C.A., 1999. Gondwanan dinosaur evolution and biogeographic analysis. *Journal of African Earth Sciences* 28, 169–185.
- Forster, C.A., Chiappe, L.M., Krause, D.W., Sampson, S.D., 1996. The first Cretaceous bird from Madagascar. *Nature* 382, 532–534.
- Forster, C.A., Sampson, S.D., Chiappe, L.M., Krause, D.W., 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279, 1915–1918.
- Gauthier, J., 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8, 1–55.
- Gishlick, A.D., Gauthier, J.A., 2007. On the manual morphology of *Compsognathus longipes* and its bearing on the diagnosis of Compsognathidae. *Zoological Journal of the Linnean Society* 149, 569–581.
- Goloboff, P.A., Farris, S., Nixon, K.C., 2003. T.N.T.: Tree Analysis Using New Technology, 1.1 ed. the authors. Tucuman, Argentina.
- Gradstein, F.M., Ogg, J.G., Smith, A.G., 2004. *A Geologic Time Scale 2004*. University Press, Cambridge, UK, p. 589.
- Gomez, B., Bamford, M., Martínez-Delclòs, X., 2002. Lower cretaceous plant cuticles and amber (Kirkwood Formation, South Africa). *Comptes Rendus Palevol* 1, 83–87.
- Holtz Jr., T.R., 2004. Tyrannosauroida. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, Berkeley, pp. 111–136.
- Holtz Jr., T.R., Molnar, R.E., Currie, P.J., 2004. Basal Tetanurae. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, Berkeley, Los Angeles, London, pp. 71–110.
- Hu, D., Hou, L., Zhang, L., Xu, X., 2009. A pre-Archaeopteryx troodontid theropod from China with long feathers on the metatarsus. *Nature* 461, 640–643.
- Huene, F.v., 1914. Beitrage zur geschichte der Archosauria (Contribution to the history of the archosaurs). *Geologie und Palaentologie Abhandlungen* 13, 1–56.
- Ji, Q., Currie, P.J., Norell, M.A., Ji, S.a., 1998. Two feathered dinosaurs from northeastern China. *Nature* 393, 753–761.
- Ji, Q., Norell, M.A., Makovicky, P.J., Gao, K.-Q., Ji, S.a., Yuan, C., 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. *American Museum Novitates* 3420, 1–19.
- Kirkland, J.I., Zanno, L.E., Sampson, S.D., Clark, J.M., DeBlieux, D.D., 2005. A primitive therizinosaurid dinosaur from the Early Cretaceous of Utah. *Nature* 435, 84–87.
- Kobayashi, Y., Barsbold, R., 2004. Phylogeny of Ornithomimosauria and its paleobiogeographic implications. In: 19th International Congress of Zoology, Beijing, China, pp. 50–52.
- Kobayashi, Y., Barsbold, R., 2005a. Anatomy of *Harpymimus okladnikovi* Barsbold and Perle 1984 (Dinosauria: Theropoda) of Mongolia. In: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington and Indianapolis, pp. 97–126.
- Kobayashi, Y., Barsbold, R., 2005b. Reexamination of a primitive ornithomimosaur, *Garudimimus brevipes* Barsbold, 1981 (Dinosauria: Theropoda), from the Late Cretaceous of Mongolia. *Canadian Journal of Earth Sciences* 42, 1501–1521.
- Kobayashi, Y., Lu, J.-C., Dong, Z.-M., Barsbold, R., Azuma, Y., Tomida, Y., 1999. Herbivorous diet in an ornithomimid dinosaur. *Nature* 402, 480–481.

- Liu, Y., Liu, Y., Ji, S.A., Yang, Z., 2006. U–Pb zircon age of the Daohugou Biota at Ningcheng of Inner Mongolia and comments on related issues. *Chinese Science Bulletin* 51, 2634–2644.
- Longrich, N.R., 2008. A new, large ornithomimid from the Cretaceous Dinosaur Park Formation of Alberta, Canada: implications for the study of dissociated dinosaur remains. *Palaeontology* 51, 983–997.
- Maddison, W.P., Maddison, D.R., 2009. Mesquite: A Modular System for Evolutionary Analysis, 2.71 ed.
- Makovicky, P.J., 1997. A new small theropod from the Morrison Formation of Como Bluff, Wyoming. *Journal of Vertebrate Paleontology* 17, 755–757.
- Makovicky, P.J., Norell, M.A., 1998. A partial ornithomimid braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia). *American Museum Novitates* 3247, 1–16.
- Makovicky, P.J., Norell, M.A., 2004. Troodontidae. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, Berkeley, Los Angeles, London, pp. 184–195.
- Makovicky, P.J., Turner, A.H., 2008. Phylogenetic insights on Gondwanan coelurosaurs. In: Calvo, J.O., Valieri, R.J., Porfiri, J.D. (Eds.), III Congreso Latinoamericano de Paleontología de Vertebrados Neuquen. Universidad Nacional del Comahue, Neuquen, Patagonia, Argentina, p. 149.
- Makovicky, P.J., Norell, M.A., Clark, J.M., Rowe, T., 2003. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). *American Museum Novitates* 3402, 1–32.
- Makovicky, P.J., Kobayashi, Y., Currie, P.J., 2004. Ornithomimosauria. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, 2 ed. University of California Press, Berkeley, Los Angeles, London, pp. 137–150.
- Makovicky, P.J., Apesteguía, S., Agnolín, F.L., 2005. The earliest dromaeosaurid theropod from South America. *Nature* 437, 1007–1011.
- Makovicky, P.J., Li, D., Gao, K.-Q., Lewin, M., Erickson, G.M., Norell, M.A., 2009. A giant ornithomimosaur from the Early Cretaceous of China. *Proceedings of the Royal Society of London, Series B* 277, 191–198.
- Maleev, E.A., 1974. Giant carnososaurs of the family Tyrannosauridae. Results of the Soviet-Mongolian Paleontological Expedition 1, 132–191.
- Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. *American Journal of Science* 3, 417–423.
- Martin, L.D., 1984. The relationship of *Archaeopteryx* to other birds. In: Hecht, M.K., Ostrom, J.H., Viohl, G., Wellnhofer, P. (Eds.), *The Beginnings of Birds*, Proceedings of the International *Archaeopteryx* Conference. Eichstatt, Germany, pp. 177–183.
- Martinelli, A.G., Vera, E.I., 2007. *Achillesaurus manazzonei*, a new alvarezsaurid theropod (Dinosauria) from the Late Cretaceous Bajo de la Carpa Formation, Rio Negro Province, Argentina. *Zootaxa* 1582, 1–17.
- Mayr, G., Pol, B., Peters, D.S., 2005. A well-preserved *Archaeopteryx* specimen with theropod features. *Science* 310, 1483–1486.
- McLachlan, I.R., McMillan, I.K., 1976. Review and stratigraphic significance of southern cape Mesozoic palaeontology. *Transactions of the Geological Society of South Africa* 79, 197–212.
- McMillan, I.K., 1999. The Foraminifera of the Late Valanginian to Hauterivian (Early Cretaceous) Sundays River Formation of the Algoa Basin, Eastern Cape Province, South Africa. *Annals of the South African Museum* 106, 1–120.
- Naish, D., Martill, D.M., Frey, E., 2004. Ecology, systematics and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil. *Historical Biology* 16, 57–70.
- Nicholls, E.L., Russell, A.P., 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). *Palaeontology* 28, 643–677.
- Nixon, K.C., 2002. WinClada, 1.00.08 ed.
- Norell, M.A., Makovicky, P.J., 2004. Dromaeosauridae. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, Berkeley, Los Angeles, London, pp. 196–209.
- Norell, M.A., Xu, X., 2005. Feathered Dinosaurs. *Annual Review of Earth and Planetary Sciences* 33, 277–299.
- Norell, M.A., Makovicky, P.J., Currie, P.J., 2001. The beaks of ostrich dinosaurs. *Nature* 412, 873–874.
- Norell, M.A., Clark, J.M., Turner, A.H., Makovicky, P.J., Barsbold, R., Rowe, T., 2006. A new dromaeosaurid theropod from Ukhaa Tolgod (Omnogov, Mongolia). *American Museum Novitates* 3545, 1–51.
- Novas, F.E., 1996. Alvarezsauridae, Cretaceous basal birds from Patagonia and Mongolia. *Memoirs of the Queensland Museum* 39, 675–702.
- Novas, F.E., 1997. Anatomy of *Patagonykus puertai* (Theropoda, Avialae, Alvarezsauridae), from the Late Cretaceous. *Journal of Vertebrate Paleontology* 17, 137–166.
- Novas, F.E., Pol, D., 2002. Alvarezsaurid relationships reconsidered. In: Chiappe, L.M., Witmer, L. (Eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, pp. 121–128.
- Novas, F.E., Pol, D., 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. *Nature* 433, 858–861.
- Novas, F.E., Puerta, P.F., 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* 387, 390–392.
- Novas, F.E., Pol, D., Canale, J.L., Porfiri, J.D., Calvo, J.O., 2009. A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proceedings of the Royal Society of London, Series B* 276, 1101–1107.
- Osborn, H.F., 1916. Skeletal adaptations of *Struthiomimus*, *Ornitholestes*, *Tyrannosaurus*. *Bulletin of the American Museum of Natural History* 35, 733–771.
- Osmólska, H., Roniewicz, E., Barsbold, R., 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica* 27, 103–123.
- Perez, B.P., 2004. *Pelecanimimus polyodon*: anatomia, sistemática y paleobiología de un Ornithomimosauria (Dinosauria: Theropoda) de Las Hoyas (Cretácico Inferior; Cuenca, España), Facultad de Ciencias, Departamento de Biología. Universidad de Paleontología. Universidad Autónoma de Madrid, Madrid, p. 147.
- Perez-Moreno, B.P., Sanz, J.L., Buscalloni, A.D., Moratalia, J.J., Ortega, F., Rasskin-Gutman, D., 1994. A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* 370, 363–367.
- Perle, A., Norell, M.A., Chiappe, L.M., Clark, J.M., 1993. Flightless bird from the Late Cretaceous of Mongolia. *Nature* 362, 623–626.
- Perle, A., Chiappe, L.M., Barsbold, R., Clark, J.M., Norell, M., 1994. Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. *American Museum Novitates* 3105, 1–29.
- Peyer, K., 2006. A reconsideration of *Compsognathus* from the Upper Tithonian of Canjuers, southeastern France. *Journal of Vertebrate Paleontology* 26, 879–896.
- Rauhut, O.W.M., 2003a. The Interrelationships and Evolution of Basal Theropod Dinosaurs. The Palaeontological Association.
- Rauhut, O.W.M., 2003b. A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology* 46, 903–910.
- Rauhut, O.W.M., 2005. Post-cranial remains of 'coelurosaurs' (Dinosauria, Theropoda) from the Late Jurassic of Tanzania. *Geological Magazine* 142, 97–107.
- Rauhut, O.W.M., Milner, A., 2008. Cranial anatomy and systematic position of the Middle Jurassic theropod dinosaur *Proceratosaurus* from England. *Journal of Vertebrate Paleontology* 28, 130A.
- Rauhut, O.W.M., Milner, A.C., Moore-Fay, S., 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society* 158, 155–195.
- Reddering, J.S.V., 2012. Kirkwood Formation (Uitenhage Group), Including the Swartkops and Colchester Members, Catalogue of South African Lithostratigraphic Units. Council for Geosciences, SA Committee for Stratigraphy, Pretoria.
- Rich, T.H., Vickers-Rich, P., 1994. Neoceratopsians and ornithomimosaurids: dinosaurs of Gondwanan origin? Research and Exploration 10, 129–131.
- Rich, T.H., Molnar, R.E., Vickers-Rich, P., 1983. Fossil vertebrates from the Late Jurassic or Early Cretaceous Kirkwood Formation, Algoa Basin, Southern Africa. *Transactions of the Geological Society of South Africa* 86, 281–291.
- Sampson, S.D., Carrano, M.T., Forster, C.A., 2001. A bizarre new predatory dinosaur from Madagascar. *Nature* 409, 504–506.
- Sereno, P., 2001. Alvarezsaurids: birds or ornithomimosaurids? In: Gauthier, J., Gall, L.F. (Eds.), *New Perspectives on the Origin and Early Evolution of Birds*. Peabody Museum of Natural History, New Haven, pp. 69–98.
- Sereno, P.C., Beck, A.L., Duthiel, D.B., Gado, B., Larsson, H.C.E., Lyon, G.H., Marcot, J.D., Rauhut, O.W.M., Sadleir, R.W., Sidor, C.A., Varrichio, D.J., Wilson, G.P., Wilson, J.A., 1998. A long-snouted predatory dinosaur from Africa and the evolution of the spinosaurids. *Science* 282, 1298–1302.
- Shapiro, M.D., You, H.-L., Shubin, N.H., Luo, Z., Downs, J.P., 2003. A large ornithomimid pes from the Lower Cretaceous of the Mazongshan area, northern Gansu province, People's Republic of China. *Journal of Vertebrate Paleontology* 23, 695–698.
- Shone, R.W., 2006. Onshore post-Karoo Mesozoic deposits. In: Johnson, M.R., Anhaeusser, C.R., Thomas, R.J. (Eds.), *The Geology of South Africa*, Geological Society of South Africa and Council for Geosciences, Johannesburg and Pretoria, pp. 541–571.
- Toerien, D.K., Hill, R.S., 1989. The Geology of the Port Elizabeth Area, Geological Sheet, 3324 ed. Geological Survey, Pretoria, p. Port Elizabeth scale 1:250000.
- Turner, A.H., Hwang, S.H., Norell, M., 2007. A small derived theropod from Öösh, Early Cretaceous, Baykhangor Mongolia. *American Museum Novitates* 3557, 1–27.
- Turner, A.H., Nesbitt, S.J., Norell, M.A., 2009. A large alvarezsaurid from the Cretaceous of Mongolia. *American Museum Novitates* 3648, 1–14.
- Vickers-Rich, P., Chiappe, L.M., Kurzanov, S., 2002. The enigmatic birdlike dinosaur *Avimimus portentosus*: comments and a pictorial atlas. In: Chiappe, L.M., Witmer, L.M. (Eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley, pp. 65–86.
- Wilson, J.A., 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* 19, 639–653.
- Wings, O., Sander, P.M., 2007. No gastic mill in sauropod dinosaurs: new evidence from analysis of gastolith mass and function in ostriches. *Proceedings of the Royal Society of London, Series B* 274, 635–640.
- Xu, X., Norell, M.A., 2004. A new troodontid dinosaur from China with avian-like sleeping posture. *Nature* 431, 838–841.
- Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q., Jia, C., 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature* 431, 680–684.
- Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jie, C., Zhao, Q., 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature* 439, 715–718.
- Xu, X., Clark, J.M., Mo, J., Choiniere, J., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C.-k., Han, F.-l., Guo, Y., 2009. A Jurassic ceratopsian from China helps clarify avian digital homologies. *Nature* 459, 940–944.

- Xu, X., Choiniere, J.N., Pittman, M., Tan, Q., Xiao, D., Li, Z., Tan, L., Clark, J.M., Norell, M.A., Hone, D.W.E., Sullivan, C., 2010. A new dromaeosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China. *Zootaxa* 2403, 1–9.
- Xu, X., Ma, Q., Hu, D., 2010. Pre-*Archaeopteryx* coelurosaurian dinosaurs and their implications for understanding avian origins. *Chinese Science Bulletin* 55, 3971–3977.
- Zanno, L.E., 2006. The pectoral girdle and forelimb of the primitive therizinosauroid *Falcarius utahensis* (Theropoda, Maniraptora): analyzing evolutionary trends within Therizinosauroidea. *Journal of Vertebrate Paleontology* 26, 636–650.
- Zanno, L.E., 2010. Osteology of *Falcarius utahensis* (Dinosauria: Theropoda): characterizing the anatomy of basal therizinosauroids. *Zoological Journal of the Linnean Society* 158, 196–230.
- Zanno, L.E., Makovicky, P.J., 2011. Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. *Proceedings of the National Academy of Sciences* 108, 232–237.
- Zhang, F., Zhou, Z., Xu, X., Wang, X., 2002. A juvenile coelurosaurian theropod from China indicates arboreal habits. *Naturwissenschaften* 89, 394–398.
- Zhang, F., Zhou, Z., Xu, X., Wang, X., Sullivan, C., 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* 455, 1105–1108.
- Zhao, X.-J., Currie, P.J., 1993. A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30, 2027–2036.
- Zhou, Z., 1995. Is *Mononykus* a bird? *The Auk* 112, 958–963.