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THE SECOND TITANOSAURIAN (DINOSAURIA: SAUROPODA) FROM THE MIDDLE CRETACEOUS GALULA FORMATION, SOUTHWESTERN TANZANIA, WITH REMARKS ON AFRICAN TITANOSAURIAN DIVERSITY

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ABSTRACT—The paleobiogeographic significance of continental Africa during the middle and Late Cretaceous is not well understood, in part due to incomplete sampling from large portions of the landmass during these intervals. Intensified field efforts in the Galula Formation exposed in southwestern Tanzania have revealed a diverse vertebrate fauna, including the novel titanosaurian *Shingopana songwensis*, gen. et sp. nov., described herein. Based on a left angular, cervical vertebrae, cervical and dorsal ribs, a left humerus, and a partial left pubis, *Shingopana* exhibits morphology indicating affinities with the Late Cretaceous aeolosaurine titanosaurs of South America. The bulbous expansion of the cervical vertebral neural spine is similar to the condition in *Bonitasaura salgadoi*, *Overosaurus paradasorum*, and *Trigonosaurus pricei*. The dorsal ribs of *Shingopana* also present proximal anterior and posterior flanges that previously were proposed to be unique to *Overosaurus*. Furthermore, *Shingopana* is diagnosed by a divided spinoprezygapophyseal lamina in the middle-to-posterior cervical vertebrae. Parsimony and both uncalibrated and tip-dated Bayesian phylogenetic approaches support *Shingopana* as the first African titanosaurian that is closely related to aeolosaurines. Comparisons with other African titanosaurs, such as the co-occurring *Rukwaitan biseptulus* and geographically proximate *Malawisaurus dixeyi*, suggest that southern African forms represent diverse taxa rather than forming a monophyletic group. Moreover, southern African forms exhibit stronger affinities with South American clades than with representative northern African form, suggesting that tectonically driven separation of the two landmasses may have influenced the development of progressively isolated southern African faunas throughout the Cretaceous.

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INTRODUCTION

The sparse Cretaceous African continental fossil record has limited the development and formal evaluation of hypotheses regarding the paleobiogeographic significance of the region (e.g., Krause et al., 2006; O'Connor et al., 2006; Ezcurra and Angolin, 2012). These limitations are largely due to the heterogeneous occurrence, exposure, and sampling of Cretaceous-aged rock units in Africa (Jacobs et al., 1996; Sampson et al., 1998; Forster, 1999; Sereno et al., 2004; Krause et al., 2006, 2007; O'Connor et al., 2006; Sereno and Brusatte, 2008; Upchurch, 2008; Mannion and Upchurch, 2011; Mannion and Barrett, 2013).

Historically, the northern African Cretaceous fossil record has been better sampled, serving as a predominant focus for African paleontology (e.g., Lavocat et al., 1954; Lapparent, 1960; Jacobs et al., 1988; Sereno et al., 1994, 1996, 1998, 1999, 2004; Rauhut and Werner, 1995, 1997; Smith et al., 2001; Rage and Cappetta, 2002; O'Leary et al., 2004; Smith and Lamanna, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Le Loeuff et al., 2010; Rodrigues and Keller, 2011; Fanti et al., 2013, 2015; Lamanna and Yoshikazu, 2014; Ibrahim et al., 2016). By comparison, the Cretaceous continental rock record and its associated fossils from southern Africa are far more limited, leaving much of the continent with limited input to large-scale analyses aimed at characterizing vertebrate distributions (Jacobs et al., 1996; Weishampel et al., 2004; O'Connor et al., 2006; Mannion and Barrett, 2013). To make matters more complicated, the majority of the current African Cretaceous fossil record is representative of the middle Cretaceous (Aptian–Cenomanian) compared with a more limited documentation of Late

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Cretaceous (post-Cenomanian) deposits (Jacobs et al., 1993, 1996; Weishampel et al., 2004; O'Connor et al., 2006; Sertich et al., 2006; Cavin et al., 2010; Mannion and Barrett, 2013; Lamanna and Yoshikazu, 2014). In contrast to the extensive Cretaceous continental fossil record of South America and the steadily expanding Cretaceous records of Madagascar, India, Asia, and Europe, the restrictive African continental fossil record features several sizable gaps within the heart of Gondwana (O'Connor et al., 2006).

Recent discoveries from the Rukwa Rift Basin of Tanzania offer an opportunity to begin to address these sampling gaps, and to test relationships among Cretaceous African faunas to explore whether new data from southern localities reflect cosmopolitan distributions or whether they suggest that southern Africa preserves a biogeographic sample that is distinct from faunas collected in northern Africa (and elsewhere). Titanosaurian sauropods are an ideal group for exploring this question, because they are present in both southern and northern Africa (e.g., Jacobs et al., 1993; Smith et al., 2001; Gomani, 2005; Gorscak et al., 2014). Titanosaurians are the only group of sauropod dinosaurs to persist until the end of the Mesozoic, outlasting other Cretaceous sauropod clades such as the brachiosaurids, euhelopodids, dicraeosaurids, and rebacchisaurids (Salgado and Bonaparte, 1991; Sereno et al., 1999; Barrett and Upchurch, 2005; Rauhut et al., 2005; Upchurch and Barrett, 2005; Wilson, 2006; Sereno et al., 2007; Whitlock, 2011; D'Emic, 2012; Mannion et al., 2013; McPhee et al., 2016). Titanosaurians, along with titanosauriforms more broadly, were the most successful clade of sauropod dinosaurs, exhibiting high taxonomic diversity and wide range of morphological variation (Salgado et al., 1997; Wilson, 2002, 2006; Powell, 2003; Upchurch et al., 2004; Barrett and Upchurch, 2005; Curry Rogers, 2005; Upchurch and Barrett, 2005; Salgado and Bonaparte, 2007; Novas, 2009; D'Emic, 2012; Mannion et al., 2013; Souza and Santucci, 2014). Additionally, titanosaurians are found on all major landmasses throughout the Cretaceous, a time of extensive geologic activity due to the continued fragmentation of Gondwana, and have the potential to aid in refining larger paleobiogeographic perspectives (Gheerbrant and Rage, 2006; Krause et al., 2006; Ali and Krause, 2011; Zaher et al., 2011; Cerda et al., 2012; Mannion and Barrett, 2013; Gorscak and O'Connor, 2016). Until recently, the African titanosaurian fossil record was limited in relation to the size and potential paleobiogeographic importance of this landmass (Jacobs et al., 1996; O'Connor et al., 2006; Mannion, 2009; Mannion and Barrett, 2013; Gorscak et al., 2014). This is in stark contrast to the titanosaurian fossil record of South America, boasting the majority of known titanosaurian species (e.g., Mannion and Otero, 2012; Wilson et al., 2016), including several proposed clades such as Aeolosaurini (Franco-Rosas et al., 2004; Santucci and de Campos-Arruda, 2011; however, see Martinelli et al., 2011), Rinconsauria (Calvo et al., 2007a), Lognkosauria (Calvo et al., 2007b, 2007c), and Saltasaurinae (Bonaparte and Powell, 1980).

Continuing efforts in the Galula Formation of southwestern Tanzania have improved our understanding of Cretaceous continental faunas of southern Africa (O'Connor et al., 2006, 2010; Roberts et al., 2010; Gorscak et al., 2014; Sertich and O'Connor, 2014). The current faunal composition of the Galula Formation includes representatives from several major continental (terrestrial and freshwater) clades, such as teleost fish, lungfish, turtles, crocodyliforms such as the notosuchian *Pakasuchus kapilimai* and the peirosaurid *Rukwasuchus yajabalijekundu*, and a possible gondwanatherian mammal (Krause et al., 2003; O'Connor et al., 2010; Gottfried et al., 2009; Sertich and O'Connor, 2014). Additionally, the most abundant fossil materials recovered from the Galula Formation are sauropod dinosaurs. Currently, the sauropods of the Galula Formation are represented by titanosaurians, including two undesigned caudal vertebral morphs

(O'Connor et al., 2006) and *Rukwaitan biseptus* (Gorscak et al., 2014). Both undesigned vertebral morphs exhibit affinities with lithostrotian titanosaurians (e.g., exhibiting procoelous middle caudal vertebrae; Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012), whereas *Rukwaitan* has been recovered as a non-lithostrotian titanosaurian (Gorscak et al., 2014), sister to *Malawisaurus dixeyi* (Bandeira et al., 2016), or as an early-branching member of the saltasaur lineage within Lithostrotia (Gorscak and O'Connor, 2016). Together with the titanosaurians recovered from the Aptian Dinosaur Beds of Malawi (*Malawisaurus* and *Karongasaurus gittelmani*; Jacobs et al., 1993; Gomani, 2005) and the Cenomanian Bahariya Formation of Egypt (*Paralititan stromeri* and *Aegyptosaurus baharijensis*; Stromer, 1932; Smith et al., 2001) and the close relative to Titanosauria *Angolatitan adamastor* of the Turonian Tadi Beds of Angola (Mateus et al., 2011; Mannion et al., 2013; D'Emic [2012] erroneously listed *Angolatitan* as a lithostrotian whereas it should be included in his *Chubutisaurus* and more derived titanosauriformes clade [M. D'Emic, pers. comm., 2016]), the titanosaurian fossil record of Africa is steadily increasing. Moreover, multiple fragmentary titanosaurian specimens have been reported from across Africa but remain too incomplete to adequately diagnose to lower taxonomic levels and/or await further description (Greigert et al., 1954; Lapparent, 1960; Broin et al., 1974; Kennedy et al., 1987; Bellion et al., 1990; Moody and Sutcliffe, 1990; Jacobs et al., 1996; Rauhut and Werner, 1997; Rauhut, 1999; Sereno et al., 1999; Wiechmann, 1999; O'Leary et al., 2004; Pereda Suberbiola et al., 2004; O'Connor et al., 2006; Sertich et al., 2006; Mannion and Barrett, 2013; Lamanna and Yoshikazu, 2014; Ibrahim et al., 2016).

Here we report on a second titanosaurian from the Namba Member of the Galula Formation exposed in southwestern Tanzania (Fig. 1). We describe this new species based on an angular and a set of associated and partially articulated postcranial elements from a single individual. This specimen is morphologically distinct from both *Rukwaitan* and *Malawisaurus*, adding to the taxonomic diversity of titanosaurian sauropods and permitting a closer examination of biogeographic patterns across the African continent.

Institutional Abbreviations—MAL, Malawi Department of Antiquities, Lilongwe, Malawi; RRB, Rukwa Rift Basin Project, Tanzanian Antiquities Unit, Dar es Salaam, Tanzania.

GEOLOGIC CONTEXT AND TAPHONOMY

The new materials were collected over the course of three field seasons (2002–2004) from the TZ-07 locality west of the city of Mbeya in southwestern Tanzania. At this locality, the amount of vegetation cover progressively obscures the amount of exposed rock up-section, including parts of the quarry. The exposed rock at TZ-07 is part of the younger Namba Member of the Galula Formation and is dominated by very-fine- to medium-grained sandstones with occasional overbank mudstone and siltstone lenses (Roberts et al., 2004, 2010) from which occasional well-preserved and associated fossils have been recovered (e.g., O'Connor et al., 2010; Gorscak et al., 2014). The quarry represents one such lens of mudstone, which preserves an assemblage of associated elements from a relatively small area exposed along the hillside. Unfortunately, the eastern edge of this fossil-bearing mudstone lens was already exposed prior to discovery so that its extent and size are not confidently known (Fig. 2). It is along this portion of the outcrop that the larger and more complete elements (e.g., humerus and dorsal ribs) were concentrated, and perhaps additional elements were lost to erosion. The closely associated and partially articulated elements almost certainly belong to a single individual, being found within a relatively small area (ca. 7.5 m²). Although this deposit contains well-preserved material (e.g., humerus, one of the cervical vertebrae),

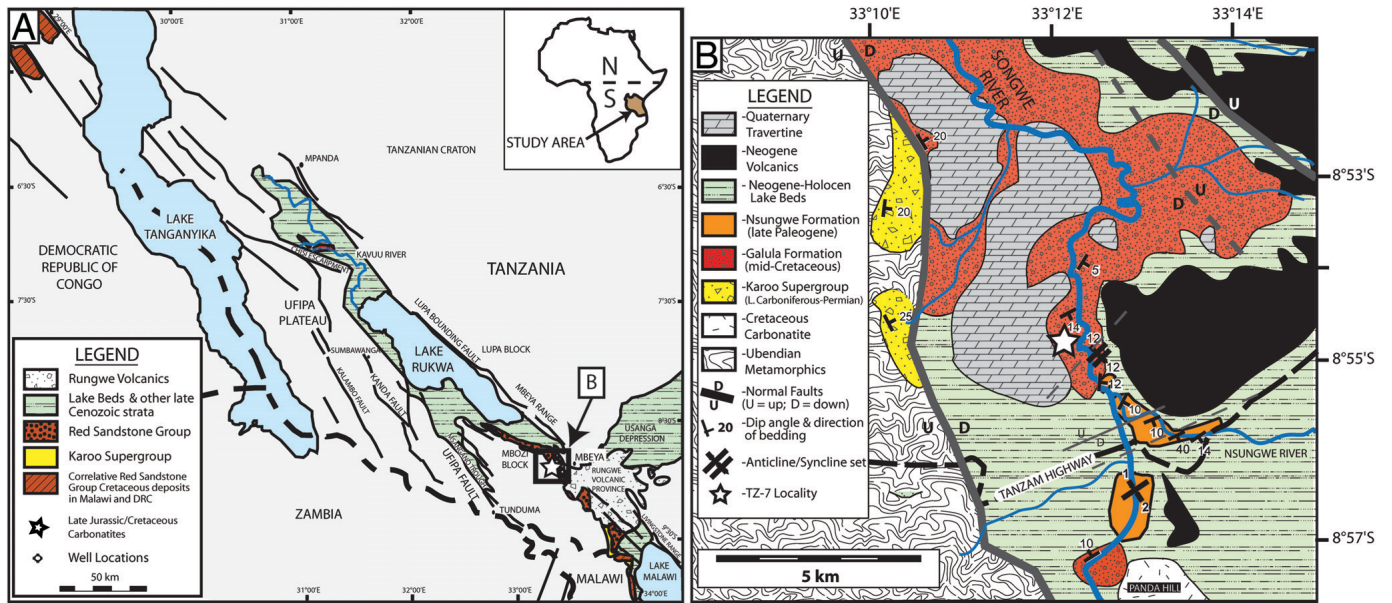


FIGURE 1. Expanded (A) and detailed (B) regional maps to illustrate exposures of the middle Cretaceous Galula Formation (spotted red) in southwestern Tanzania. The location of the type locality, RRBP TZ-07, of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100), is denoted by a white star in both A and B. The location of the Malawi Dinosaur Beds is noted in A and is shown to illustrate the proximity of the two units relative to one another.

much of the collected material is more fragmentary, with portions of the axial skeleton distributed away from the closely associated larger and more complete elements. The recovered materials are also peppered with traces of ancient borings, presumably from insects, that are infilled with matrix that is similar to the sediments in which the elements were encased.

Sedimentology

The TZ-07 locality is composed of nearly 150 m of vertical exposure, with the quarry located at the 70-m mark in the measured section (Roberts et al., 2004; O'Connor et al., 2006). The site represents a massive, sandy mudstone with abundant

bioturbation, including 2–6 cm diameter burrows, weak color banding, scattered small calcium carbonate nodules (<10 mm), and abundant bone chips. The horizon is a lenticular (<20 m wide) body of mudstone that reaches up to 55 cm thickness and is packaged between fine-grained, cross-laminated sandstones, above and below.

Taphonomy and Bone Modification

The recovered skeleton is almost completely disarticulated and roughly 10% complete. Elements are concentrated, and evidence of weak current alignment and sorting is present (Fig. 2). Moderate bone weathering is observed on many of the elements, as evidenced by an abundance of bone flaking and cracking, indicating bone weathering stages 1 and 2 of Behrensmeyer (1978). No unequivocal evidence of trample marks or carnivore tooth marks is present on the bones.

The concentration of vertebrate bone borings in the quarry is, however, unique throughout the Mesozoic continental fossil record of Africa, far exceeding any other documented fossil. The presence of borings is particularly abundant on certain elements, such as the cervical vertebrae, the humerus, the pubis, and several ribs, with almost all recovered bones in the quarry containing borings. The borings are infilled with lithified matrix (sandy mudstone) that is similar to the rock that encases the elements, rather than of the near-surface soil in the area. Over 150 discrete borings were recognized in total on 10 different bones from the quarry, and following careful measurement of the long and short axes of 136 of these traces (see Appendix S3, Supplemental Data), five discrete boring morphologies are identified following the descriptive bone boring classification schemes of Roberts et al. (2007), Britt et al. (2008), and particularly Pirrone et al. (2014). Bone borings from the quarry are divided into the following categories: (1) small, vertical tubes oriented perpendicular to the bone surface; (2) large, irregular tubes or possibly holes bored into the bone surface; (3) straight-meandering furrows that run along the bone surface; (4) wide, irregular channels that run along bone surfaces; and (5) rare pupation chambers excavated into the bone. The presence of bioglyphs associated with the borings is difficult to confidently determine; however, no

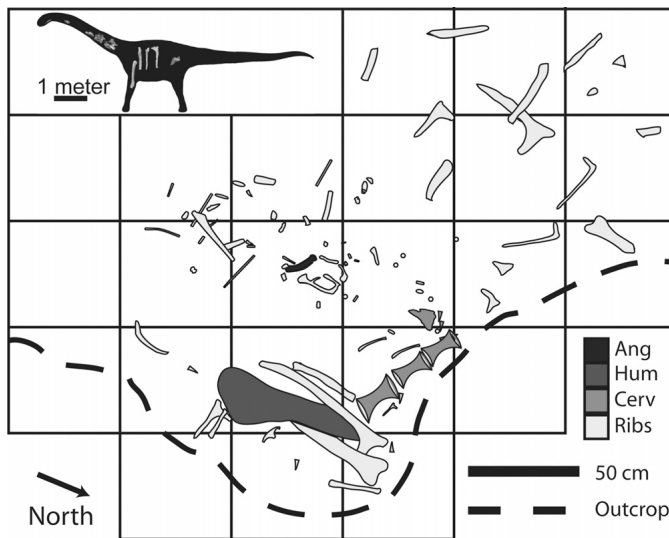


FIGURE 2. The quarry map from locality RRBP TZ-07 where *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100), was excavated, including a silhouette in the upper left corner illustrating the elements of the skeleton recovered and featured in the description. **Abbreviations:** ang, angular; cerv, cervical vertebrae; cm, centimeters; hum, humerus; ribs, cervical and dorsal ribs.

unequivocal examples are observed. Borings penetrate both cortical bone and spongy bone; most borings are non-branching, but branching furrows (group 3 borings) do exist; and many of the borings clearly follow cracks in the bones (dry bone fractures). Many of the borings are filled in with the rock matrix encasing the bone fragments.

Ichnotaxonomy

A wealth of recent work in the field of continental ichnology has focused on describing the range of possible bone boring morphologies observed in the fossil record (e.g., Thenius, 1998; Roberts et al., 2007; Pironne et al., 2014; Paes Neto et al., 2016; Parkinson, 2016; Xing et al., 2016). Many of the traces observed from the quarry represent general trace morphologies that have been observed and described from other fossil localities (e.g., holes, tubes/tunnels, channels, pits, furrows, striae, grooves). Because of this, bone boring groups 1–4 cannot be linked to specific named ichnotaxa. However, a single ichnotaxon is recognized in the quarry, represented by boring group 5 and assigned to the ichnogenus *Cubiculum* based on six borings from the distal end of dorsal rib A, from the shaft of dorsal rib B, and from the

humerus (Fig. 3; see Appendix 2S). Three ichnospecies of *Cubiculum* have been described, including *Cubiculum ornatus*, *Cubiculum inornatus*, and *Cubiculum levis*, and all are interpreted to be pupation chambers produced by insects, most likely those of carrion beetles (Roberts et al., 2007; Pironne et al., 2014; Xing et al., 2016). Based on the elongate shape of the borings (group 5), we can rule out *Cubiculum levis*, but because the matrix is covering the internal bone surfaces, it is difficult to determine whether the borings represent *Cubiculum ornatus* or *Cubiculum inornatus*. This diverse association of bone borings, including the ichnogenus *Cubiculum*, is consistent with the newly defined *Cubiculum* ichnofacies of Lucas (2016).

Interpretation

The sedimentologic, taphonomic, and ichnologic features associated with the quarry suggest a complex depositional and post-depositional history. The lenticular-shaped geometry of the sandy mudstone horizon hosting the quarry is typical of the few fine-grained deposits preserved in the Namba Member of the Galula Formation (Roberts et al., 2010). It is interpreted as a thin intrachannel fill deposit in which mudstone settled out in an

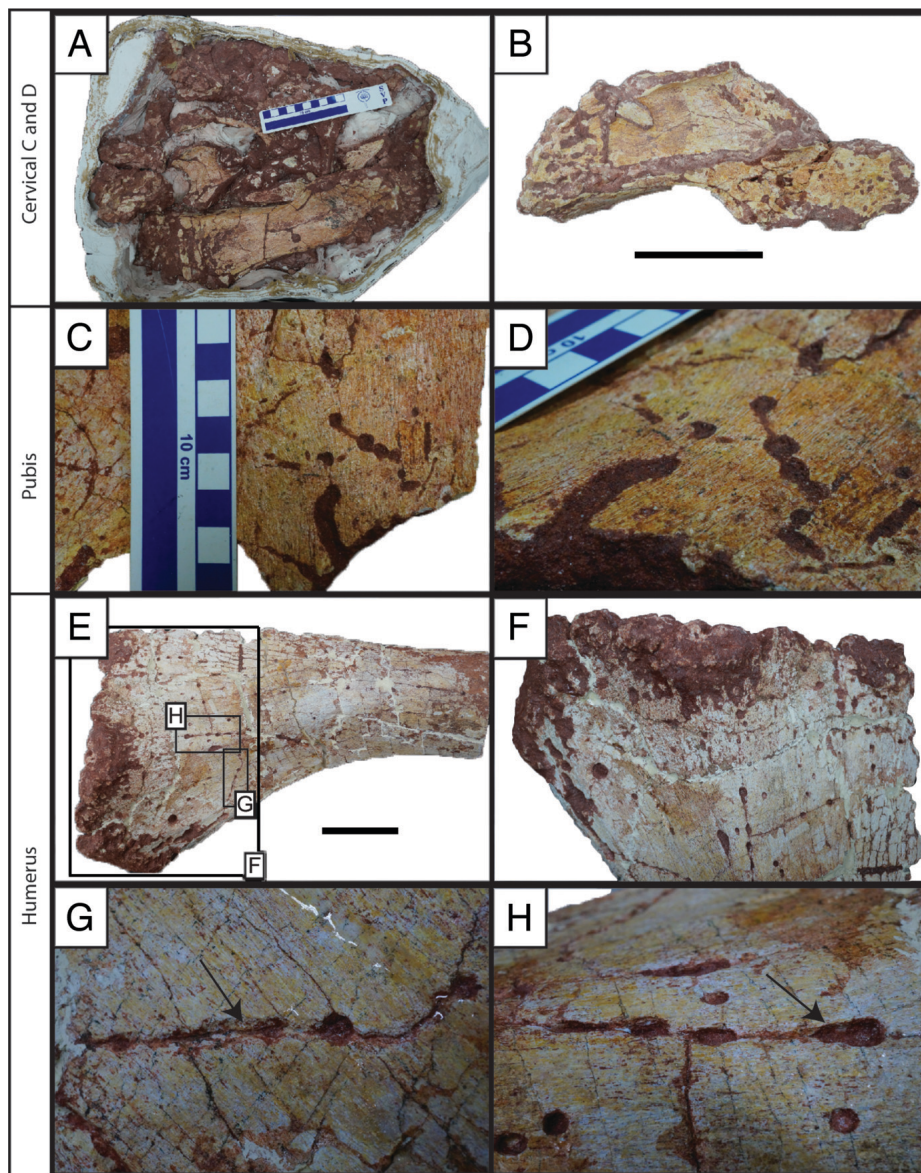


FIGURE 3. Examples of bone modifications in various elements from the *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100), skeleton. **A** and **B**, collection of intense bone borings present in the cervical vertebrae. **C** and **D**, examples of type 1–4 borings in the pubis. **E–H**, collection of bone borings in the humerus. **E** and **F** show overview perspective of intense bioturbation on humerus. **G**, close-up of type 3 borings. **H**, close-up view of type 1 and 2 borings (shown by black arrows). Scale bars equal 10 cm.

ephemeral segment of the channel on a large braidplain system (sensu Roberts et al., 2010), followed by intense bioturbation and weak soil forming processes (pedogenesis). This and other small intrachannel fill deposits are most likely associated with seasonal or cyclical changes in discharge along a large braidplain channel belt. The deposits likely formed as a segment of the channel was abandoned and filled with fine-grained sediments. The dinosaur carcass likely disarticulated on the surface around this small abandoned channel, where significant surface weathering of the bones took place prior to burial. After the carcass was buried, minor soil formation took place, as evidenced by the formation of weak soil horizons and development of small calcium carbonate nodules (in the Bk horizon) and pervasive bioturbation of the soil. The presence of bone-chip-filled borings and concentration of borings along dry bone fractures both suggest that insect modification of the bones took place after burial. The borings are highly random, and with the exception of six examples of the insect pupation boring *Cubiculum* (Fig. 4), all other borings appear to be produced as largely incidental excavations by soil-dwelling organisms. Although it is not possible to confidently speculate on the trace producer, the presence of pupation chambers is most commonly attributed to beetles. However, the range of boring sizes and diversity of borings, particularly those focused on weakness in the bone, such as dry bone fractures, suggests the work of colonial insects, such as termites or ants. Regardless of the tracemaker(s), the bone modifications and other taphonomic features clearly indicate considerable weathering of the carcass prior to burial, and that the bone modifications by insects were largely produced in the subsurface following burial. The presence of lithified sediments in the burrows and lack of modern soil or sediments filling the borings suggest that they were constructed shortly after burial, not by modern insects.

MATERIALS AND METHODS

Computed Tomography

Materials of *Shingopana songwensis* were scanned on a Philips Brilliance CT 64-channel scanner using the following protocol: 120 kV, 200 mA, and a slice thickness of 1.0 mm. Digital visualization of DICOM files was completed in Avizo 7.0.1 (Visualization Science Group [VGS], FEI, U.S.A.).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

SAUROPODA Marsh, 1878

TITANOSAURIA Bonaparte and Coria, 1993

LITHOSTROTIA Upchurch, Barrett, and Dodson, 2004

SHINGOPANA SONGWENSIS, gen. et sp. nov.

(Figs. 5–14)

Holotype—RRBP 02100, a partial skeleton of an individual including a left angular, partial anterior cervical vertebra, four partial middle-to-posterior cervical vertebrae, six partial cervical ribs, four partial dorsal ribs, a nearly complete left humerus, and a partial left pubis. Moreover, there are many incomplete and/or unidentifiable fragments pertaining to the axial skeleton such as cervical vertebral lamina and cervical and dorsal rib shafts and fragments.

Type Locality—*Shingopana songwensis* was recovered from locality TZ-07, approximately 8°56'S, 33°12'E, within the Rukwa Rift Basin, southwestern Tanzania (Fig. 1; specific locality coordinates on file at Ohio University and with the Tanzania Antiquities Unit). All recovered elements were in close association and partially articulated from a single quarry (Fig. 2). Additional fossils reported from this locality include the remains of teleost fish, two undesigned lithostrotian caudal vertebrae, non-avian theropod caudal vertebrae and teeth, notosuchian crocodyliforms (O'Connor et al., 2006, 2010), and a possible gondwanatherian mammal (Krause et al., 2003). The Namba Member is dominated by very-fine- to medium-grained sandstones with minor mudstone and siltstone lenses representing deposition within a broad fluvial braidplain system (Roberts et al., 2010).

Age and Distribution—Materials described herein were recovered from the upper portion of the Namba Member of the Galula Formation, Rukwa Rift Basin, southwestern Tanzania. Based on several lines of geologic and faunal evidence, the age of the Galula Formation has been estimated to the middle Cretaceous (Aptian–Cenomanian), with current age estimates at 100–110 Ma (Roberts et al., 2004, 2010, 2012; O'Connor et al., 2006, 2010).

Diagnosis—*Shingopana songwensis* is a titanosaurian sauropod diagnosed by the following autapomorphy: middle-to-posterior cervical vertebrae with divided spinoprezygapophyseal lamina (forming a spinoprezygapophyseal lamina fossa) near the base of an expanded neural spine. Several morphological characters support *Shingopana songwensis* within titanosauriforms (e.g., Wilson, 2002; D'Emic, 2012; Mannion et al., 2013): (1) camellate internal texturing of cervical vertebrae; (2) low infrazygapophyseal region of posterior cervical vertebra; (3) elongated cervical rib shaft extending past succeeding

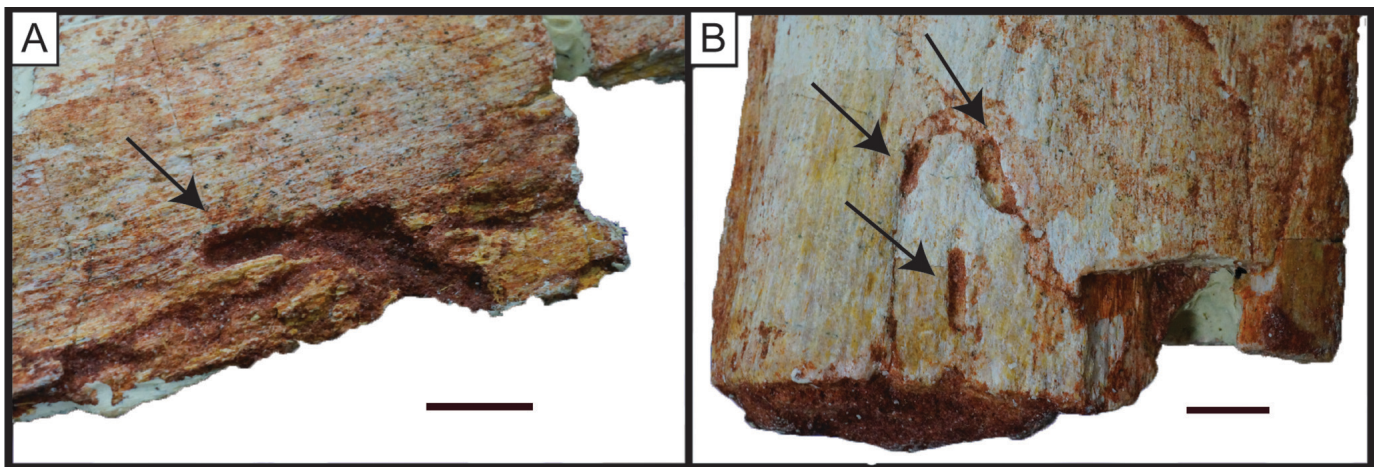


FIGURE 4. **A** and **B**, examples of bone boring group 5 (*Cubiculum inornatus*) in dorsal rib 2 (shown by black arrows). Scale bars equal 1 cm.

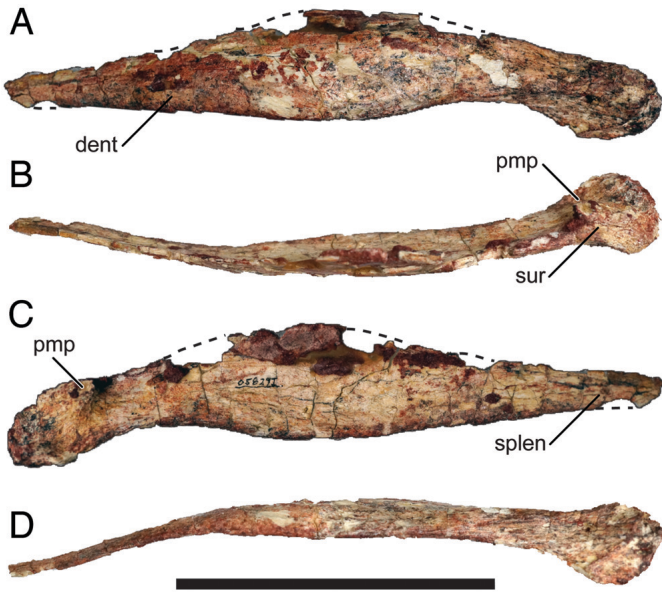


FIGURE 5. Left angular of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). **A**, lateral, **B**, dorsal, **C**, medial, and **D**, ventral views. **Abbreviations:** dent, dentary articular facet; pmp, posteromedial projection; splen, splenial facet; sur, surangular facet. Scale bar equals 10 cm.

vertebra; (4) proximal region of dorsal ribs with pneumatic foramina; (5) squared proximolateral corner of humerus; and (6) undivided radial condyle of humerus. Characters that support lithostrotian affinities include (1) undivided and shallow lateral fossa of the cervical centrum; (2) absence of a ventral midline keel on the cervical centra; (3) elongated (i.e., not subcircular) cervical parapophysis; and (4) mediolateral narrowing of neural canal of the cervical vertebrae (Wilson, 2002; D’Emic, 2012; Mannion et al., 2013). The bulbous expansion of the cervical vertebral neural spine suggests affinities with the Late Cretaceous South American titanosaurians *Bonitasaura salgadoi* (Gallina and Apesteguía, 2015), *Overosaurus paradasorum* (Coria et al., 2013), and *Trigonosaurus pricei* (Campos et al., 2005), and anterior dorsal ribs with anterior and posterior proximal flanges suggest affinities with *Overosaurus*.

Etymology—*Shingopana*, ‘shingo’ is the Kiswahili word for neck and ‘pana’ is the Kiswahili word for wide, in reference to the bulbous expansion of the neural spine exhibited by the well-preserved cervical vertebra A. The Latinized specific epithet, *songwensis*, refers to the Songwe area and geologic sub-basin of southwestern Tanzania from which the type specimen was recovered.

DESCRIPTION

Angular

A nearly complete left angular was recovered from the quarry and represents the lone cranial element preserved of *Shingopana* (Fig. 5). Overall, the element is elongate, laminar, and slightly sigmoidal. Generally, the medial surface is concave and the lateral surface is convex. The dorsal margin of the angular is broadly convex, whereas the ventral margin is concave along the posterior third of the element and tapers anteriorly. The lateral surface exhibits a weakly defined groove to accommodate the dentary, and the medial surface hosts a faint fossa to accommodate the splenial. The posterior end of the element exhibits a dorsomedial projection for a medial articulation with both the

prearticular and articular and a faint lateral slot for articulation with the surangular dorsolaterally. This projection keys with the surangular as in *Tapuiasaurus macedoi* from the middle Cretaceous of Brazil and *Rapetosaurus krausei* from the Maastrichtian of Madagascar but differs from that in *Nemegtosaurus mongoliensis* from the Maastrichtian of Mongolia (Wilson et al., 2016). The posterior end of the angular is thickened relative to the rest of the element and rounded transversely. The posterior end is deflected slightly ventrally, similarly to that in *Tapuiasaurus* (Wilson et al., 2016) but unlike the angulars of *Sarmientosaurus musacchioi* (Martínez et al., 2016) and *Rinconosaurus caudamirus* (Calvo and González Riga, 2003:pl. 1b) from the early Late Cretaceous of South America.

Cervical Vertebra

The holotype of *Shingopana* preserves an anterior cervical centrum in addition to several partial cervical vertebrae from the middle-to-posterior region of the cervical series. However, most of the cervical vertebrae were recovered as broken clusters containing fragments of the centrum and neural arch. Fragments of neural arch laminae exist but are too limited in preservation for any meaningful and confident description and comparison. Overall, the partially preserved material of the cervical vertebral column (i.e., the vertebrae and cervical ribs) exhibit the distinctive camellate internal structure common in somphospondyliian titanosauriforms (Wilson, 2002; D’Emic, 2012; Mannion et al., 2013). This internal morphology is apparent along the many fractures and eroded surfaces (Figs. 6–9).

The anterior cervical vertebra is represented by a partial centrum that preserves most of the ventral and right lateral surfaces (Fig. 6). The ventral surface is mostly intact except along the anterior and right margins. The ventral surface is slightly concave near the base of the parapophysis and is relatively smooth. The centrum is transversely narrowest at mid-length and is relatively tall; however, the extents of the cotyle and the condyle are unknown due to the element’s incompleteness. The lateral surface exhibits no pleurocoel but is mildly concave between the bases of the parapophysis and diapophysis. The partial posterior centrodiapophyseal lamina is the only preserved lamina. Fortunately, *Shingopana*

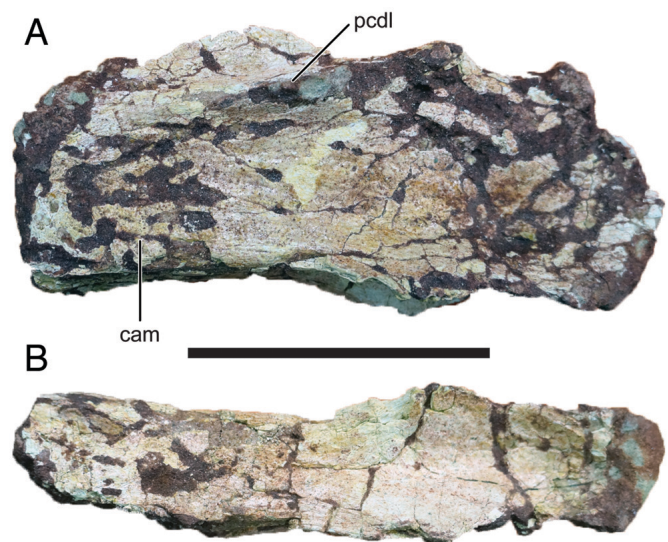


FIGURE 6. Anterior cervical vertebra of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). **A**, right lateral and **B**, ventral views. Anterior towards the right. **Abbreviations:** cam, camellate texturing; pcdl, posterior centrodiapophyseal lamina. Scale bar equals 10 cm.

TABLE 1. Selected measurements (in mm) of *Shingopana songwensis*, gen. et sp. nov., RRBP 02100.

Element	CL	ACH	ACW	PCH	PCW
ACV	190*	—	—	61	33
CVA	353	90	129	101	96
CVB	290*	—	—	100	90
CVC	275*	—	—	94	63
CVD	265*	—	73*	50*	85
	TL	PW	MW	DW	MidCircum
Angular	199	—	36	—	—
Humerus	815	320	130	263	330
	TL	PrAPL	MidAPL	DisAPL	W
DR 1	524*	72	45	—	20
DR 1, distal shaft	359*	—	—	75	21
DR 2	713*	65	—	75	17
DR 3	638*	113*	25	—	18
DR 4	506*	169*	62	—	22

Dashes indicate where measurements could not be taken due to damage, absence, or inaccessibility. Asterisks indicate estimated measurement due to distortion, uncertainty, and/or incompleteness. **Abbreviations:** **ACH**, anterior centrum height; **ACV**, anterior cervical vertebra; **ACW**, anterior centrum width; **CL**, centrum length; **CVA–D**, cervical vertebrae A–D; **DisAPL**, distal anteroposterior length; **DR 1–4**, dorsal ribs 1–4; **DW**, width at distal-most part of element; **MidAPL**, midshaft anteroposterior length; **MidCircum**, midshaft circumference; **PCH**, posterior centrum height; **PCW**, posterior centrum width; **PrAPL**, proximal anteroposterior length; **TL**, total length.

preserves a mostly intact cervical vertebra (herein referred to as cervical vertebrae A; Table 1; Fig. 7) that consists of the centrum and most of the neural arch. Much of the right parapophysis, left diapophysis, and left lateral and dorsal portions of the neural arch (including the left pre- and postzygapophysis) are not preserved. The left cervical rib is preserved minus

the distal shaft and remains attached to the left parapophysis. Three other cervical vertebrae are informative but variably preserved: cervical vertebrae B, a partial cervical vertebra with both centrum and neural arch that best preserves morphology on the right side (Fig. 7); cervical vertebrae C, a partial cervical vertebral centrum and partial cervical rib

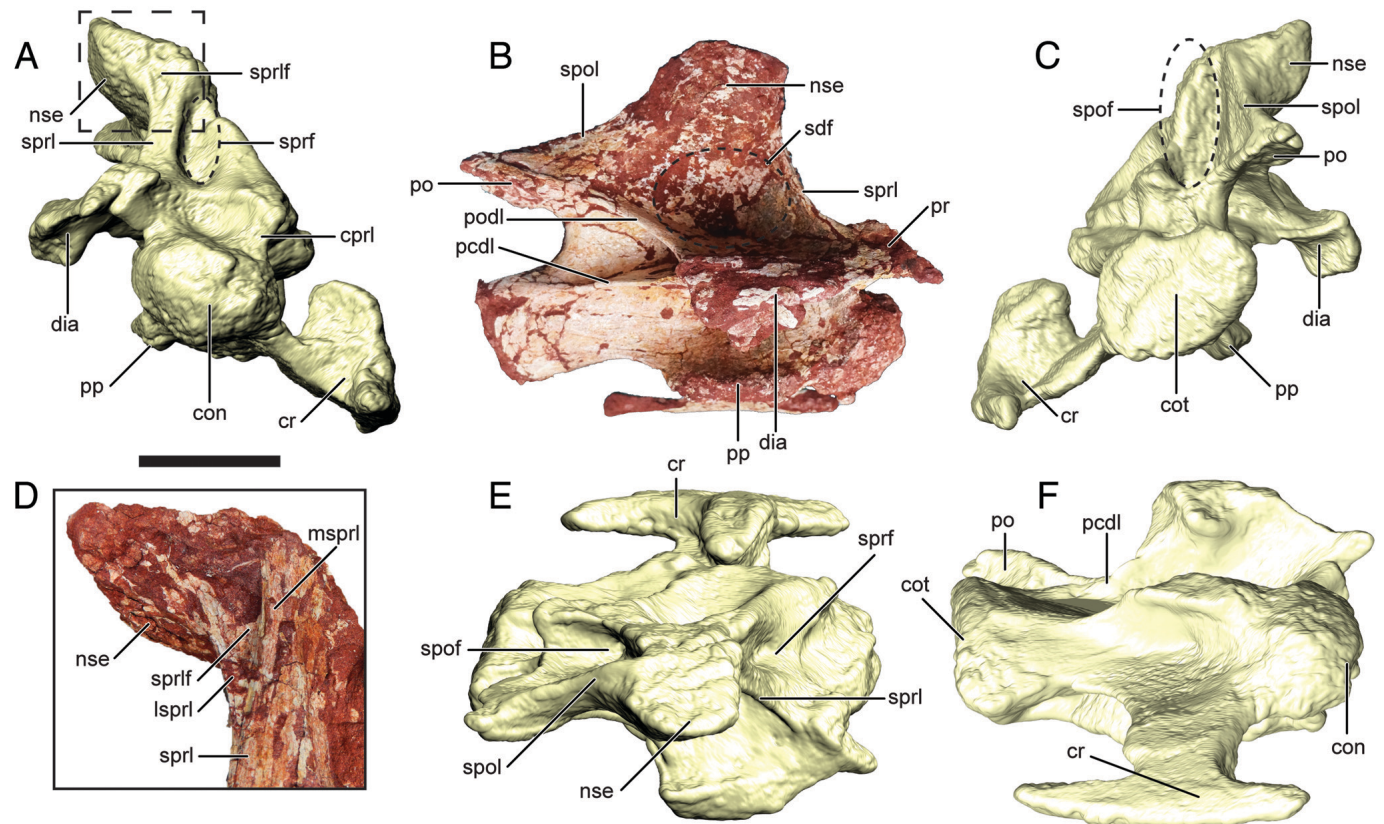


FIGURE 7. CT-rendered images (A, C, E, F) and photographs (B, D) of cervical vertebra A of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). A, anterior, B, right lateral, and C, posterior views; D, close anterior view of dotted box in A; E, dorsal and F, ventral views. Anterior towards the right in B, E, and F. **Abbreviations:** **con**, condyle; **cot**, cotyle; **cr**, cervical rib; **crpl**, centroprezygapophyseal lamina; **dia**, diapophysis; **lsprl**, lateral branch of the spinoprezygapophyseal lamina; **msprl**, medial branch of the spinoprezygapophyseal lamina; **nse**, neural spine bulbous expansion; **pcdl**, posterior centrodiaepophyseal lamina; **po**, postzygapophysis; **podl**, postzygadiapophyseal lamina; **pp**, parapophysis; **pr**, prezygapophysis; **sdf**, spinodiapophyseal fossa; **spof**, spinopostzygapophyseal fossa; **spol**, spinopostzygapophyseal lamina; **sprlf**, spinoprezygapophyseal lamina fossa; **sprl**, spinoprezygapophyseal lamina; **sprlf**, spinoprezygapophyseal lamina fossa. Scale bar equals 10 cm.

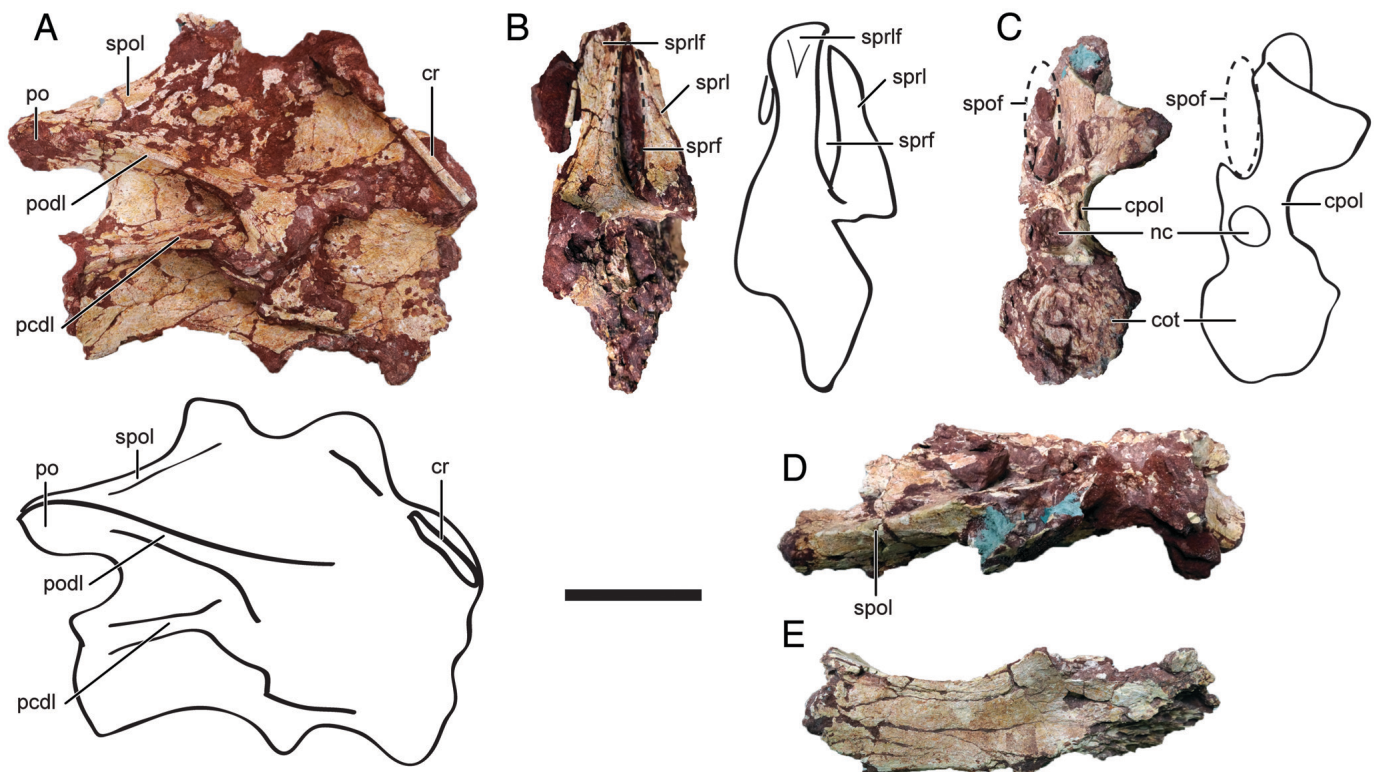


FIGURE 8. Photographs (A–E) and interpretative outlines (A–C) of cervical vertebra B of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). A, right lateral, B, anterior, C, posterior, D, dorsal, and E, ventral views. Anterior towards the right in A, D, and E. **Abbreviations:** cot, cotyle; cpol, centropostzygapophyseal lamina; cr, cervical rib; nc, neural canal; pap, parapophysis; pcdl, posterior centrodiapophyseal lamina; po, postzygapophysis; podl, postzygodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; sprlf, spinoprezygapophyseal lamina fossa. Scale bar equals 10 cm.

(Fig. 8); and cervical vertebrae D, a partial cervical vertebral centrum.

The following description of the cervical vertebrae is based primarily on cervical vertebrae A unless explicitly stated otherwise. The opisthocelous centrum is elongate. The rim of the cotyle appears to be equally developed: the ventral lip does not extend further posteriorly than the dorsal lip, as in the posterior cervical vertebrae recovered for *Rukwatitan* (Gorscak et al., 2014), although this may reflect serial position differences in the cervical region. The centrum does not appear much wider than tall, although it is difficult to ascertain the exact morphology because of the distortion. The lateral margin of the centrum is invaded by a shallow fossa that does not pierce the surface to invade the internal bone structure. The fossa is deepest anteriorly at the level of the diapophysis and parapophysis. A weakly developed oblique ridge is visible within the lateral fossa on the centrum that demarcates anterodorsal and posteroventral subregions, but not to the extent and complexity of diplodocids (Wilson, 2002). The surfaces within the ansa costotransversaria (sensu Wedel and Sanders, 2002) exhibit minimal excavations related to pneumatic influences; however, extensive excavation is present within the capitulotubercular region of the cervical ribs (see below). The ventral surface of the centrum is moderately deep between the parapophyses. The cervical vertebrae of *Shingopana* lack the ventral keel, carotid process, and shallow fossa on the ventral surface of the centrum that characterize *Rukwatitan* (Gorscak et al., 2014). The ventral surface is smooth, as in cervical vertebrae referred to *Malawisaurus* (MAL-180, MAL-187-1, MAL-193-1, MAL-243–246, MAL-278-1–3, MAL-280-1–6; MAL-291, and MAL-301; Gomani, 2005; E.G., pers. observ., 2014, 2015). The parapophysis projects

ventrolaterally compared with the ventrally projecting parapophysis of euhelopodids (D’Emic, 2012). The parapophysis is dorsoventrally compressed and not subcircular like in most non-lithostrotian titanosauriforms (D’Emic, 2012). The centroprezygapophyseal lamina is short, stout, and undivided, as is the centropostzygapophyseal lamina. The posterior centrodiapophyseal lamina is well developed and blends into the centrum prior to contacting the rim of the cotyle posteriorly. There is no evidence for the anterior centrodiapophyseal lamina, a feature that is reported yet variably developed in the posterior cervical vertebrae of the titanosaurians *Bonitasaura* (Apesteguía, 2004; Gallina and Apesteguía, 2015), *Ligabuesaurus leanzai* (Bonaparte et al., 2006), *Mendozasaurus neguyelap* (González Riga, 2005), *Overosaurus* (Coria et al., 2013), *Rukwatitan* (Gorscak et al., 2014), and *Uberabatitan ribeiroi* (Salgado and Carvalho, 2008). The pre- and postzygodiapophyseal laminae are well developed.

The distance between the prezygapophyses, although incompletely preserved, appears to be similar to the width of the centrum. The interprezygapophyseal lamina is only weakly developed. The posterior portion of the prezygapophyseal articular facet is mostly oriented dorsally with a slight medial inclination. The prezygapophysis extends slightly further anteriorly than does the condyle of the centrum and likely would have extended even further if it were complete, similar to the condition in certain titanosaurians such as *Trigonosaurus* (Campos et al., 2005), *Rapetosaurus* (Curry Rogers, 2009), and in some posterior cervical vertebrae attributed to *Malawisaurus* (Gomani, 2005; E.G., pers. observ., 2014, 2015). The postzygapophysis is similar to the prezygapophysis: weakly developed interpostzygapophyseal lamina, the distance between

postzygapophyses is as wide as the centrum, and the articular facet is angled ventrally with a slight lateral deflection to match the prezygapophyseal orientation. Additionally, the postzygapophysis is situated directly dorsal to the posterior margin of the centrum and does not extend posteriorly beyond the edge of the cotyle as in *Saltasaurus loricatus* (Zurriaguz and Powell, 2015) and *Isisaurus colberti* (Jain and Bandyopadhyay, 1977). The robust, pillar-like spinoprezygapophyseal lamina is nearly vertical (Fig. 7A). Dorsally, the spinoprezygapophyseal lamina is divided into medial and lateral laminae: the medial lamina courses onto the neural spine, whereas the lateral lamina courses laterally along the bulbous neural spine expansion (Fig. 7A, D). A distinct spinoprezygapophyseal lamina fossa is expressed between the medial and lateral laminae (Fig. 7D). However, in cervical vertebra B (Fig. 8B), the dorsal portion of the spinoprezygapophyseal lamina is occupied by a shallow fossa and not fully divided into two laminae (although we note that this observation remains tentative due to the state of preservation of the neural spine). A similar condition is exhibited in the posterior cervical vertebra (13?) of *Bonitasaura*; however, the spinoprezygapophyseal lamina is divided into fully distinct medial and lateral laminae (Gallina and Apesteguía, 2015). In the context of comparable cervical vertebra of *Malawisaurus*, *Overosaurus*, *Rapetosaurus*, *Trigonosaurus*, and *Uberabatitan* (Campos et al., 2005; Gomani, 2005; Salgado and Carvalho, 2008; Curry Rogers, 2009; Coria et al., 2013), a proposed autapomorphy for *Shingopana* is the spinoprezygapophyseal lamina fossa within middle-to-posterior cervical vertebrae (Fig. 7D). Both spinoprezygapophyseal and spinopostzygapophyseal fossae are deep and do not appear to exhibit prespinal and postspinal laminae, respectively. This is similar to cervical vertebrae attributed to *Malawisaurus* (e.g., this taxon occasionally exhibits the prespinal but not the postspinal lamina: E.G., pers. observ., 2014, 2015), *Uberabatitan*, and *Trigonosaurus*, but unlike the situation in some titanosaurians (e.g., *Alamosaurus sanjuanensis*) and select titanosauriforms more broadly (Salgado et al., 1997; D’Emic, 2012; Mannion et al., 2013). The spinodiapophyseal fossa (bounded by the neural spine, diapophysis, and spinopre- and spinopostzygapophyseal lamina) is relatively deep and undivided (Fig. 7B). There is no evidence for a spinodiapophyseal lamina or an epipophyseal-prezygapophyseal lamina in *Shingopana*, whereas the latter lamina may have been present in *Rukwatitan* (Gorscak

et al., 2014). Similar to the condition in the middle-to-posterior cervical vertebrae of *Bonitasaura*, *Overosaurus*, and *Trigonosaurus*, *Shingopana* exhibits a prominent bulbous lateral expansion of the neural spine (Campos et al., 2005:figs. 3–8; Coria et al., 2013:fig. 2b). The neural spine expansion is prominent anteriorly and merges posteriorly with the spinopostzygapophyseal lamina (Fig. 7B). The anterior margin of the bulbous expansion is near vertical as it merges with the spinoprezygapophyseal lamina. The bulbous expansion is rugose along the ventrolateral surface, and the erosional surfaces expose internal camellate texturing (Fig. 7D). Unfortunately, due to the state of preservation, the height and morphology of the dorsal half of the neural spine cannot be ascertained.

The other cervical vertebrae of *Shingopana* are variably preserved. Of these, cervical vertebra B is represented by most of the right half of the element except for the parapophysis, the condyle, the prezygapophysis, and the dorsal margin of the neural spine (Fig. 8). Moreover, the diapophysis and its associated laminae are ventrally crushed/displaced against the centrum. The morphology of this vertebra is generally similar to the that of cervical vertebrae A described above. Evidence for the neural spine expansion is only partially evident, although the state of preservation precludes any conclusive statements.

A third specimen, cervical vertebra C (Fig. 9), is represented by a partial centrum quite similar in morphology to the preceding two vertebrae, although extremely fragmentary. Finally, cervical vertebra D is represented by a partial centrum that is only mildly concave along the ventral surface and lacking any signs of a keel, fossa, or carotid process. The remaining cervical vertebral fragments are mostly laminar remains, internal bone structure, or unidentifiable parts. Several middle cervical vertebral centra are elongated (e.g., cervical vertebra D), reaching a length-to-posterior height ratio near 4.0, exceeding the 3.0 threshold characteristic of titanosauriforms (D’Emic, 2012). However, the cervical vertebrae are not as elongate as middle cervical vertebrae of some titanosauriforms such as the euhelopodid *Erketu ellisoni* (5.5; Ksepka and Norell, 2006) or the representative titanosaurians *Malawisaurus* (4.7; Gomani, 2005), *Muyelensaurus pecheni* (>4.0; Calvo et al., 2007a), *Pitekunsaurus macayai* (5.8; Filippi and Garrido, 2008), and *Rukwatitan* (4.9; Gorscak et al., 2014).

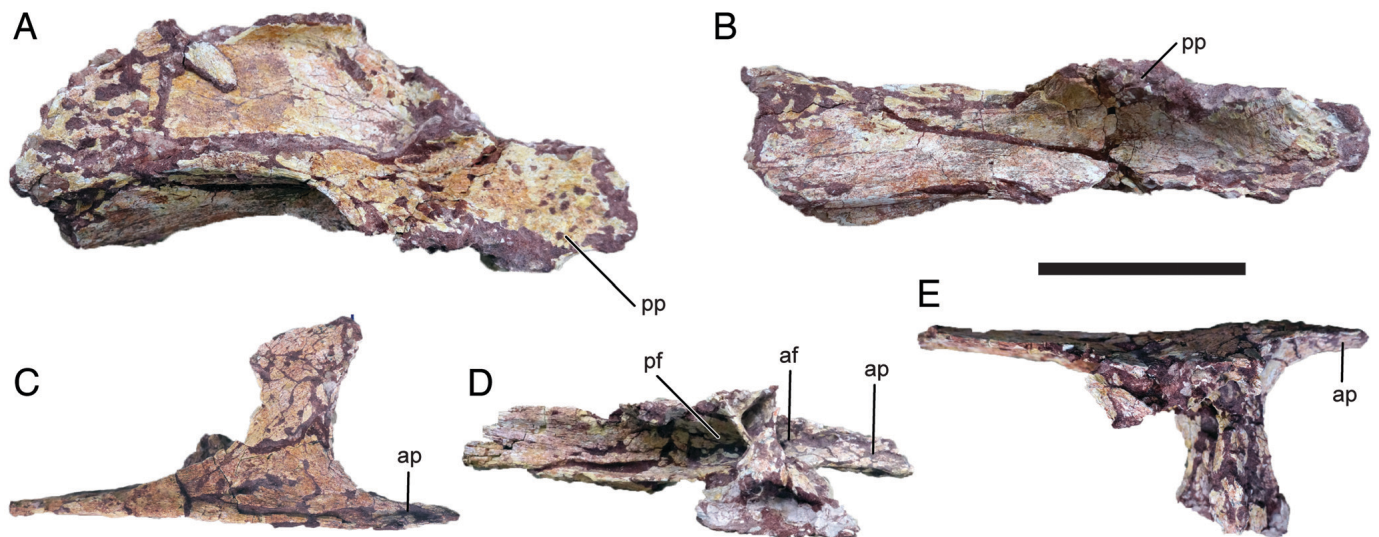


FIGURE 9. Photographs of partial cervical vertebra C (A–B) and accompanying cervical rib (C–E) of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). A, right lateral, B, ventral, C, ventral, D, medial, and E, dorsal views. Anterior towards the right in A–E. **Abbreviations:** af, anterior fossa; ap, anterior projection; pf, posterior fossa; pp, parapophysis. Scale bar equals 10 cm.

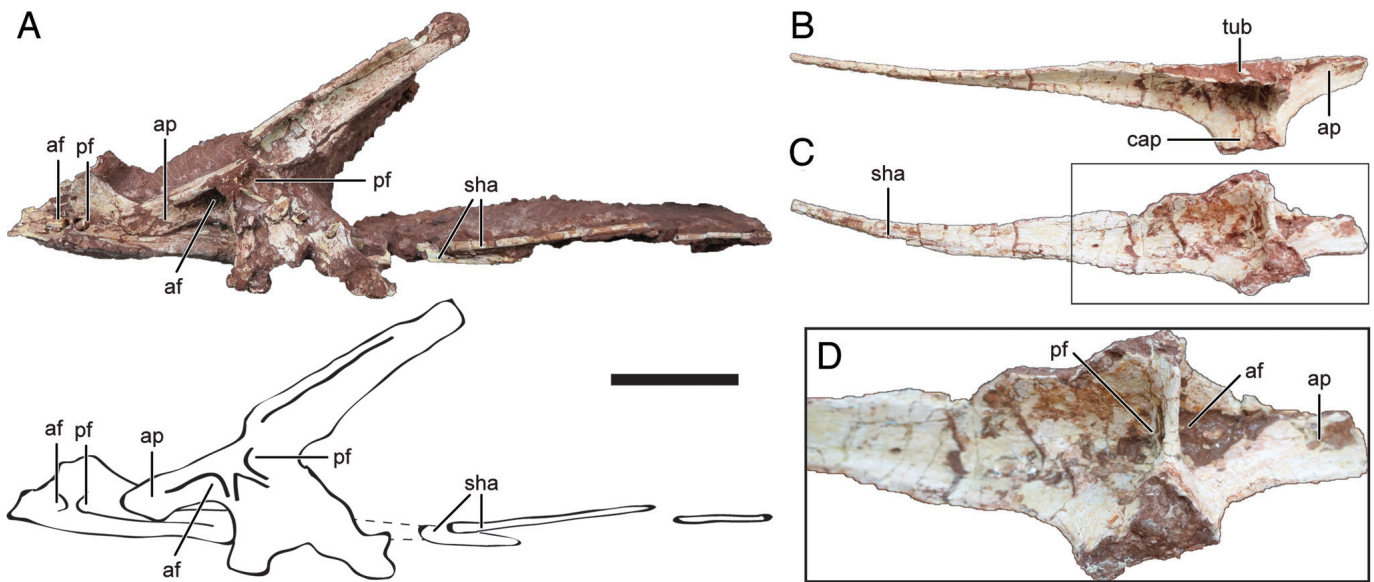


FIGURE 10. Photographs (A–D) and interpretive outline (A) of select cervical ribs of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). Two partial cervical ribs, one left and one right, recovered in close association (A), and another partial left cervical rib (B–D). A, dorsal view with interpretive outline; B, dorsal view; C, medial view; D, close medial view of inset from C. **Abbreviations:** af, anterior fossa; ap, anterior process; cap, capitulum; pf, posterior fossa; sha, rib shaft; tub, tuberculum. Scale bar equals 10 cm.

Several cervical ribs of *Shingopana* are either partially preserved with their respective vertebra, preserved as isolated elements, or recovered as fragments (Figs. 9, 10). The erosional and broken surfaces expose the camellate internal structure. Extensive anterior and posterior fossae are present in the capitulotubercular region, with thin laminae separating these two fossae (Fig. 10A, D). Overall, the ventral and lateral margins are relatively thin sheets of bone and not as thick as the cervical ribs of *Rukwatitan*. The proximal portion of the cervical rib transitions from laminar-like along the lateral and ventral margins to subcircular in cross-section along the shaft posteriorly. The cervical ribs are typical of most titanosauriforms in that the rib shaft—or its continuation as a co-ossified tendon (Cerda, 2009; Klein et al., 2012)—extends posteriorly to at least the length of the succeeding cervical vertebra. The anterior projection of the cervical rib extends to approximately the anterior margin of the condyle on the cervical vertebra A. However, incomplete preservation of the anterior-most end of the cervical rib precludes an exact determination of its anterior termination. It is the same situation for the other cervical ribs recovered as part of *Shingopana*. The anterior projection of the cervical rib of *Shingopana* differs from the condition in *Rukwatitan*, where the anterior projection is short and roughly extends to the junction of the condyle and the centrum body (Gorscak et al., 2014:fig. 4e, f). The elongated extension of the anterior projection of *Shingopana* is similar to the condition seen in other titanosauriforms that preserve the cervical rib with the cervical vertebra such as the euhelopodids *Erketu* (Ksepka and Norell, 2006) and *Phuwiangosaurus sirindhornae* (Suteethorn et al., 2009) and the titanosaurians *Malawisaurus* (Gomani, 2005), *Muyelensaurus* (Calvo et al., 2007a), and *Trigonosaurus* (Campos et al., 2005).

Dorsal Ribs

Four partial right disarticulated dorsal ribs were recovered that preserve portions of the proximal region (i.e., capitulum, tuberculum, and capitulotubercular web) as well as significant portions of the shaft (Fig. 11). Although the distal ends are not preserved in many of the recovered specimens, one of the three well-preserved

ribs includes a nearly complete distal end (Fig. 11A–D). Additional dorsal rib fragments were recovered but are too fragmentary to be informative. The four most complete dorsal ribs are here designated DR1–4. DR1 preserves the proximal portions of the capitulum, tuberculum, and capitulotubercular web; DR2 preserves most of the shaft but no remnants of the capitulum or tuberculum; DR3 preserves the capitulotubercular web but not the capitulum or tuberculum; and DR4 is the best-preserved dorsal rib, preserving most of the capitulum, tuberculum, and capitulotubercular web. Camellate internal texturing is visible from the proximal region of dorsal ribs, where broken margins and erosional surfaces are present. However, it is difficult to assess the extent of the camellate internal structure throughout the shaft because this texture is not visible within the cross-sections distally. The extent of the capitulotubercular webbing is minimal because this region is less sculpted (i.e., pneumatic fossae and ridges are barely present). This differs from the dorsal ribs of *Rukwatitan* in which capitulotubercular webbing is extensive and exhibits well-defined ridges and fossae (Gorscak et al., 2014). In *Malawisaurus*, the dorsal ribs exhibit distinct pneumatic foramina that pierce the shaft (MAL-282-1, 2; Gomani, 2005:fig. 12a, b), differing from the otherwise minimal capitulotubercular sculpturing in *Shingopana*. The differences among these titanosaurians are likely due, in part, to several confounding factors, including serial variation, ontogenetic effects, and/or interspecific variation. The capitulum of DR4 is ridge-like, extends perpendicular to the long axis of the rib shaft, and courses distally along the proximal third of the preserved shaft. By contrast, the tuberculum in DR1 is plank-like and aligned with the shaft. At the level of the capitulum of DR4, the posterior margin of the shaft expands as a gentle curve. The shafts of the dorsal ribs are plank-like (i.e., transversely expanded), as is the case in most titanosauriforms (Wilson, 2002; D’Emic, 2012; Mannion et al., 2013). The anterior and posterior margins of the proximal shafts of DR1, 3, and 4 taper and are flange-like, similar to the morphology described and figured for anterior dorsal ribs in *Overosaurus*. These anterior and posterior flanges were proposed as an autapomorphy for *Overosaurus* (Coria et al., 2013). The presence of this trait in *Shingopana* is interesting given the estimated age and location of this specimen (middle Cretaceous

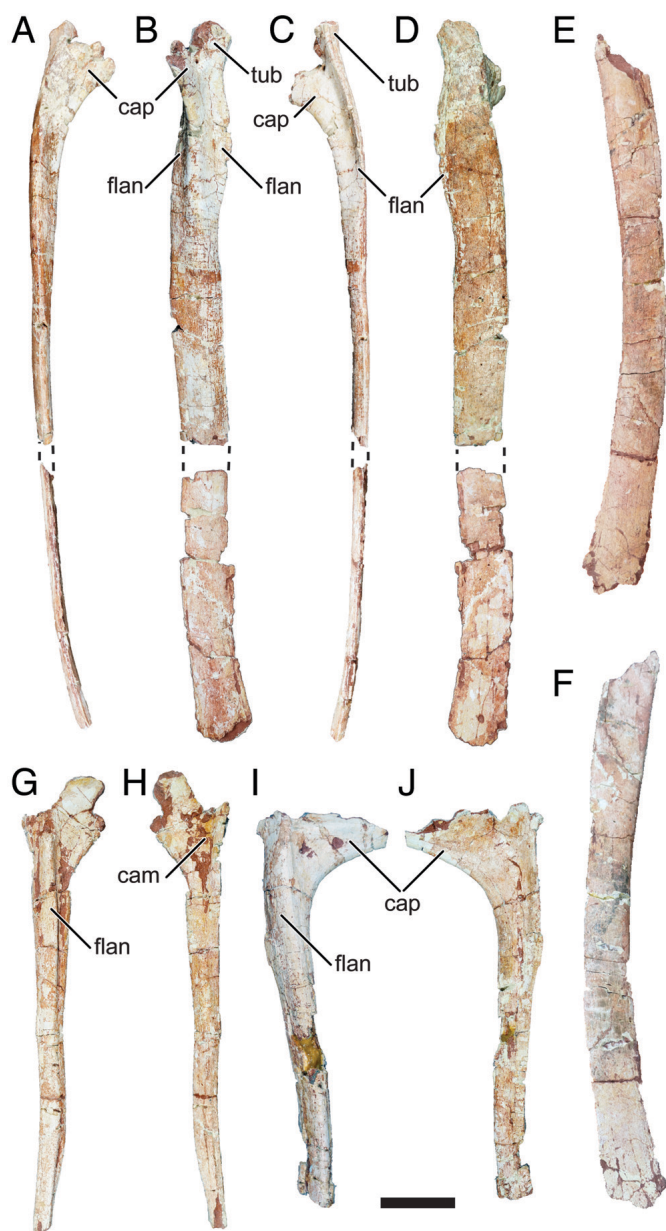


FIGURE 11. Right dorsal ribs (DR) of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). **A–D**, DR1; **E–F**, DR2; **G–H**, DR3; **I–J**, DR4. **A**, **G**, and **I**, anterior; **B** and **F**, medial; **C**, **H**, and **J**, posterior; and **D** and **E** lateral views. **Abbreviations:** **cam**, camellate texturing; **cap**, capitulum; **flan**, anterior or posterior flanges; **tub**, tuberculum. Scale bar equals 10 cm.

Galula Formation of Tanzania), because *Overosaurus* derives from the Campanian Anacleto Formation of Argentina (Coria et al., 2013). The distal end of DR1 is more mediolaterally compressed than the more proximal portions of the rib shaft, and the distal margin is gently convex.

Humerus

The right humerus of *Shingopana* is well preserved except for minimal erosion along the proximal and proximolateral margins, the deltopectoral crest, and the distal condyles (Fig. 12). The proximal margin of the humerus is relatively level and forms a perpendicular angle with the lateral margin, forming the squared

corner typically seen throughout titanosauriforms and in most titanosaurs (Wilson, 2002; Upchurch et al., 2004; D’Emic, 2012; Mannion et al., 2013). The proximal-most portion of the humeral head is eroded, but the remaining portion is positioned within the medial half of the shaft and is roughly triangular in shape (Fig. 12C). The humeral head does not significantly protrude posteriorly and is not well developed. The deltopectoral crest is not preserved but appears to have persisted to about mid-shaft and does not appear to exhibit significant transverse expansion, a derived state seen in some titanosaurs (Wilson, 2002; Upchurch et al., 2004; D’Emic, 2012; Mannion et al., 2013). The extent of the erosion includes the lateral margin; hence, no decisive statement can be made about the presence or absence of a posterolateral bulge, a proposed saltasaurid characteristic (D’Emic, 2012). Notably, this feature is also present in *Malawisaurus*, suggesting that it may be more widespread than previously considered (MAL-221; E.G., pers. observ., 2014, 2015). The wide coracobrachialis fossa is shallow, and the tubercle for the attachment of the coracobrachialis muscle is a weakly developed shelf. The medial margin of the humerus angles slightly anteriorly. The proximomedial corner is slightly rounded and is more angular at the contact with the medial margin of the humerus. The medial margin is moderately concave, and the lateral margin of the humerus is only weakly concave along the length of the humerus. The proximal and distal transverse widths are significantly wider than the midshaft, with the proximal width exceeding the distal width by a factor of 1.4. The humerus of *Shingopana* is different from that of *Bonitasaura* in that the proximomedial humerus is more developed and the distal humerus is less transversely expanded compared with the midshaft; however, the *Shingopana* and *Bonitasaura* humeri are too incomplete in their own regard for further comparisons (Gallina and Apesteguía, 2015). The humerus is markedly flat along the anteroposterior axis and exhibits an elliptical cross-section at midshaft, unlike the subquadrangular cross-section of *Rukwatitan* (Gorscak et al., 2014). The posterior humeral surface exhibits a faint longitudinal ridge from the humeral head to about midshaft, similar to, but not as developed as that in *Diamantinasaurus matildae* (Poropat et al., 2015). The posterior supracondylar fossa is shallow and bounded by subtle but distinct ridges (Fig. 12B). The distal condyles are weakly developed and restricted to the distal margin of the humerus. The radial condyle is moderately eroded, whereas the ulnar condyle is only partially eroded. The eroded radial condyle precludes any definitive statement concerning the potential anterior notch seen in most non-titanosaurs; however, based on what is preserved, there is no evidence for a distinctive notch (D’Emic, 2012; Mannion et al., 2013).

The humerus of *Shingopana* differs significantly from that of the other Galula Formation titanosaurian, *Rukwatitan* (Gorscak et al., 2014), in several features: (1) the coracobrachialis fossa of *Rukwatitan* is much deeper, due to the well-developed deltopectoral crest and strong, anteromedially deflected medial margin of the humerus; (2) a more pronounced coracobrachialis tubercle in *Rukwatitan*; (3) the distal end is more transversely expanded in *Shingopana* than in *Rukwatitan*; (4) the midshaft cross-section of *Rukwatitan* is subquadrangular whereas that of *Shingopana* is strongly elliptical; (5) *Rukwatitan* exhibits well-developed posterior features such as a humeral head, a posterior protuberance along the posterior ridge, and well-developed supracondylar fossa; and (6) the distal radial condyle is incipiently expanded anteriorly in *Rukwatitan*. The morphological differences between the *Shingopana* and *Rukwatitan* humeri alone present a strong case for two titanosaurs within the Namba Member of the Galula Formation. Interestingly, the *Shingopana* humerus compares more favorably with that of *Malawisaurus* of the geographically proximate Aptian Dinosaur Beds of Malawi. A humerus (MAL-221) referred to *Malawisaurus* expresses similar characteristics

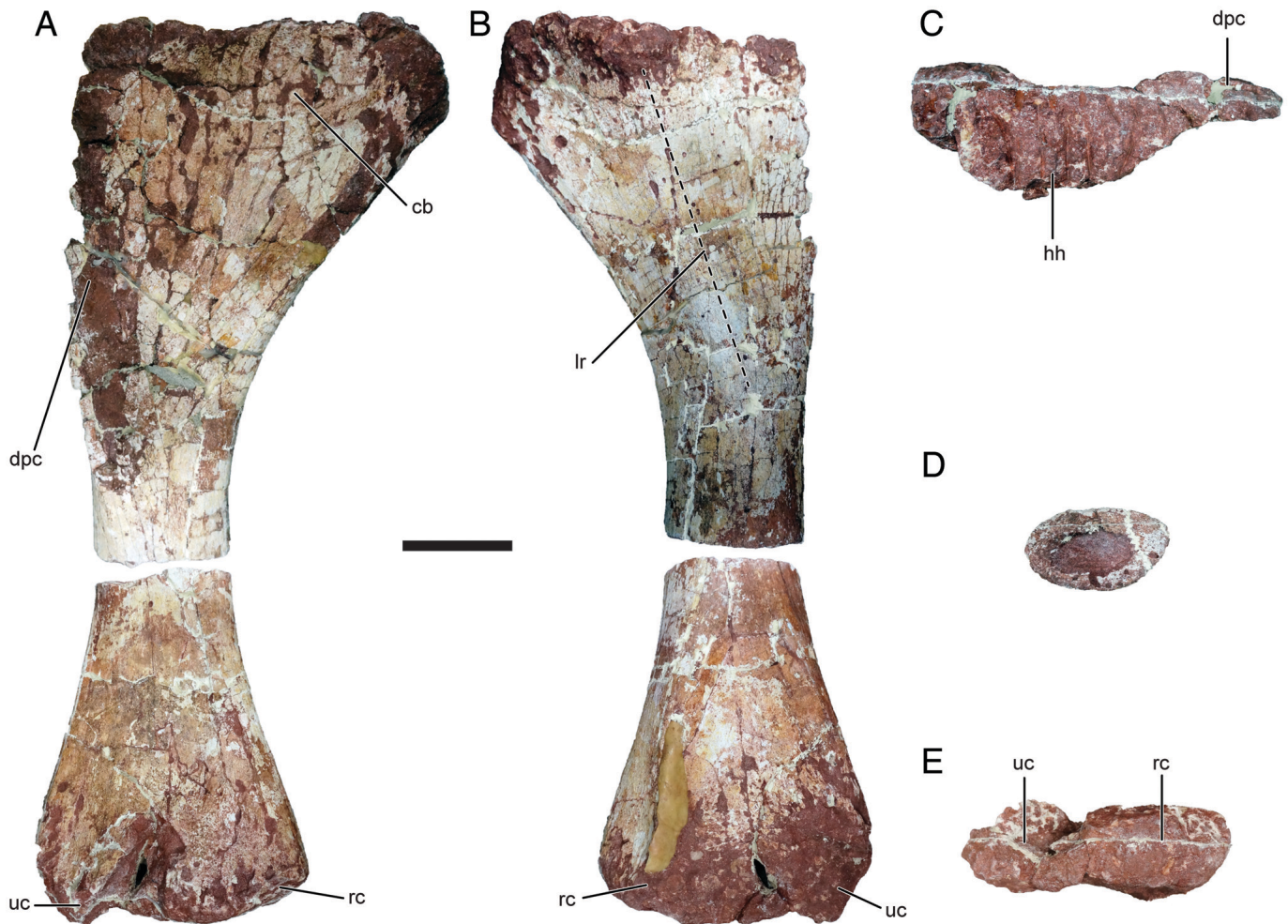


FIGURE 12. Right humerus of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). **A**, anterior, **B**, posterior, **C**, proximal, **D**, cross-sectional, and **E**, distal views. Anterior towards top in **C–E**. **Abbreviations:** **cb**, coracobrachialis scar; **dpc**, deltopectoral crest; **hh**, humeral head; **lr**, longitudinal ridge; **rc**, radial condyle; **uc**, ulnar condyle. Scale bar equals 10 cm.

to that of *Shingopana* (Gomani, 2005:fig. 20a–d; E.G., pers. observ., 2014): (1) shallow coracobrachialis fossa; (2) similar degrees of concavity along the medial and lateral margins; (3) shallow supracondylar fossa; and (4) similar proportions. Additional comparisons with *Angolatitan* (Mateus et al., 2011) from the Late Turonian Tadi Beds of Angola also support a distinct morphotype: (1) *Shingopana* lacks the proximomedial projection described in *Angolatitan*; (2) the proximal margin is weakly sigmoidal, whereas the humeral head is more elevated in *Angolatitan*; (3) the deltopectoral crest persists to midshaft in *Shingopana* rather than to about a third of the humeral length in *Angolatitan*; (4) the lateral margin of the humerus in *Angolatitan* is virtually straight and not concave; and (5) the distal condyles of *Angolatitan* are moderately expanded anteriorly. Finally, comparisons with the humerus of *Paralititan* from the Cenomanian Bahariya Formation of Egypt (Smith et al., 2001) are also distinctive: *Paralititan* exhibits (1) a similar elevation of the humeral head as in *Angolatitan* (Lamanna and Yoshikazu, 2014); (2) strongly developed humeral head, anteromedial and anterolateral margins, and posterior longitudinal ridge; and (3) well-developed supracondylar fossa.

Several derived humeral characters exhibited by select titanosaurs appear notably absent in *Shingopana*, although the condyles do

not preserve enough detail to make fully unequivocal interpretations. In any case, *Shingopana* appears to lack (1) distally divided radial and ulnar condyles (e.g., *Alamosaurus* and the Saltasaurini; Wilson, 2002; D’Emic, 2012); (2) anteriorly and posteriorly expanded distal condyles (Wilson, 2002; Mannion et al., 2013); and (3) a deep supracondylar fossa that characterizes Titanosauria/somphospondylians, an equivocal clade from the Mannion et al. (2013) LCDM analysis; however, a squared proximolateral corner is also a synapomorphy of this clade and is present in *Shingopana*. The humeral character states present in *Shingopana* suggest affinities with non-saltosaurid somphospondylians; however, the humerus of *Shingopana* also bears resemblances to the humerus of the lithostrotian *Malawisaurus*.

Pubis

A partial left pubis preserves most of the ischial peduncle and part of the margins surrounding the obturator foramen (Fig. 13). The ischial peduncle is a transversely narrow sheet of bone and is slightly convex medially for articulation with the ischium. The obturator foramen is elliptical based on the preserved posterior and ventral margins; however, the orientation of the long axis with respect to the pubic blade of the obturator foramen

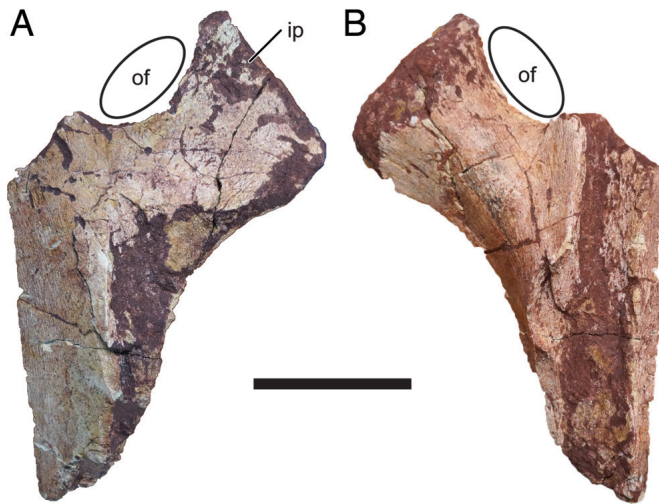


FIGURE 13. Partial left pubis of *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100). **A**, external and **B**, internal views. **Abbreviations:** ip, ischial peduncle; of, obturator foramen. Scale bar equals 10 cm.

cannot be determined for comparisons with other titanosaurians (Mannion and Calvo, 2011). The pubic blade is not preserved.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic affinities of *Shingopana* were assessed using the data matrix of Gorscak and O'Connor (2016). This data set is one of the larger titanosaurian matrices and includes 45 operational taxonomic units, the majority of which are titanosaurians, and 492 morphological characters, with 262 variable characters for the parsimony analysis and an additional 230 autapomorphic characters for the Bayesian analyses in order to capture the morphological evolution along terminal branches to better inform the model likelihood, topology structure, and date estimates (Lewis, 2001; Lee and Palci, 2015; Gorscak and O'Connor, 2016). The inclusion of the *Shingopana* data increases this data set to 46 taxa and 493 morphological characters (including the additional autapomorphy for *Shingopana*). Because both *Overosaurus* and *Shingopana* exhibit the laminar anterior and posterior flanges of the anterior dorsal ribs, this character has been removed from the autapomorphy list for *Overosaurus* and placed within the variable characters list (see Appendix 3S). For the following phylogenetic analyses, all characters were treated as unordered and independent. We conducted three sets of analyses: a parsimony analysis, an uncalibrated Bayesian analysis, and time-calibrated Bayesian analysis using tip-dating methods.

Parsimony Analysis

Parsimony analysis was conducted in PAUP 4.0b10 (Swofford, 2003) using stepwise, random addition and tree-bisection-reconnection options with 10,000 replications within the heuristic search setting. The heuristic search obtained 22,320 most parsimonious trees, each with a tree length of 743 steps (Fig. 14A). The majority-rule consensus tree is nearly identical to the parsimony tree reported in Gorscak and O'Connor (2016). *Shingopana* is placed within the aeolosaur lineage of the tree (titanosaurians more closely related to *Aeolosaurus* than to *Saltasaurus*; using this informal definition avoids the instability of Aeolosaurini addressed by Martinelli et al., 2011). *Shingopana* is recovered as the sister taxon of the clade composed of Late Cretaceous South American titanosaurians (*Panamericansaurus schroederi*, *Gondwanatitan faustoi*, *Overosaurus*, *Aeolosaurus maximus*, and *Trigonosaurus*) and the Early Cretaceous (Albian)

European titanosaurian *Normanniasaurus genceyi* (Fig. 14A). Other African titanosaurians in this analysis retained similar phylogenetic positions as in the results of Gorscak and O'Connor (2016): *Angolatitan* within Andesaurioidea; *Rukwatitan* as a non-lithostrotian titanosaurian; *Malawisaurus* within a clade of titanosaurians that preserve nearly complete crania along the aeolosaur lineage of Lithostrotia (e.g., *Nemegtosaurus*, *Rapetosaurus*, *Tapuiasaurus*); and *Paralititan* within the saltasaur lineage of Lithostrotia (titanosaurians more closely related to *Saltasaurus* than to *Aeolosaurus*).

Bayesian Analysis

Bayesian analyses were conducted in MrBayes 3.2.5 (Ronquist et al., 2012b). Models implemented either equal or variable (drawn from a gamma distribution) rates of character evolution under the Mk likelihood model of morphological evolution (Lewis, 2001). The analysis persisted for 20 million generations with sampling occurring every 1000 generations and utilized one hot and one cold chain sampling tree space. Afterwards, the first 25% of the samples were discarded to eliminate the initial climbing phase, and the remainder of the samples were used to construct the all-compatible consensus tree. The log-likelihood score for the equal-rates model is -3881.60 and the variable-rates model is -3860.63 . Using the Bayes factor (BF; Kass and Raftery, 1995), there is strong support for the variable-rates model over the equal-rates model (BF = 41.94). In the resultant topology of the variable-rates model (Fig. 14B), *Shingopana* is recovered within the aeolosaur lineage of the topology as the sister taxon to *Normanniasaurus* (Albian of France; Le Loeuff et al., 2013) and the aeolosaurines (e.g., *Aeolosaurus maximus*, *Gondwanatitan*, *Panamericansaurus*; Franco-Rosas et al., 2004; Santucci and de Arruda-Campos, 2011; however, see Martinelli et al., 2011). It should be noted that posterior probabilities are low in this region of the topology (0.18 for the node from which *Shingopana* branches), and this is likely due to the amount of missing data and lack of overlapping elements among taxa in the data set. Topologically, the Bayesian analysis and the parsimony analysis are in agreement with the general placement of *Shingopana* as an aeolosaur-lineage member bearing a close relationship to *Rapetosaurus*, *Normanniasaurus*, and aeolosaurine titanosaurians. Other African titanosaurians were recovered in similar positions as in Gorscak and O'Connor (2016): *Angolatitan* as a non-titanosaurian titanosauriform; *Malawisaurus* as the sister to the rest of Lithostrotia (*Rukwatitan* as a member of the saltasaur lineage of Lithostrotia (in contrast to the parsimony result reported herein and in Gorscak and O'Connor, 2016); and *Paralititan* within a clade composed of *Epachthosaurus sciuttoi*, *Saltasaurus loricatus*, and *Neuquensaurus australis*, all within Saltasauridae.

Tip-Dated Bayesian Analysis

Tip-dating phylogenetic methods (e.g., Ronquist et al., 2012a; Wood et al., 2013; Lee et al., 2014) were used to co-estimate phylogenetic relationships and divergence date estimates following the protocol in Gorscak and O'Connor (2016). These analyses utilized BEAST 2.1.3 for the phylogenetic analysis (Bouckaert et al., 2014) and the R package BEASTMaster to construct the XML file (Matzke, 2015a, 2015b). The birth-death skyline serial sampling tree model was assumed, which is able to vary birth (speciation) and death (extinction) rates through time and performed the analysis with a log-normal relaxed clock model (Stadler et al., 2013). The analysis, similar to the uncalibrated Bayesian analysis, tested for both equal and variable (drawn from a gamma distribution) rates of character change, ran for 20 million generations with sampling occurring every 1000 generations followed by a burn-in of 25%. A uniform sampling prior was placed over each stratigraphic range of the respective taxon to account for uncertainty in the tip dates and aid in estimating branch lengths and nodal heights (see Appendix 4S). The variable rate model is strongly preferred over the equal-rates model (log-likelihood scores of -3802.33 and

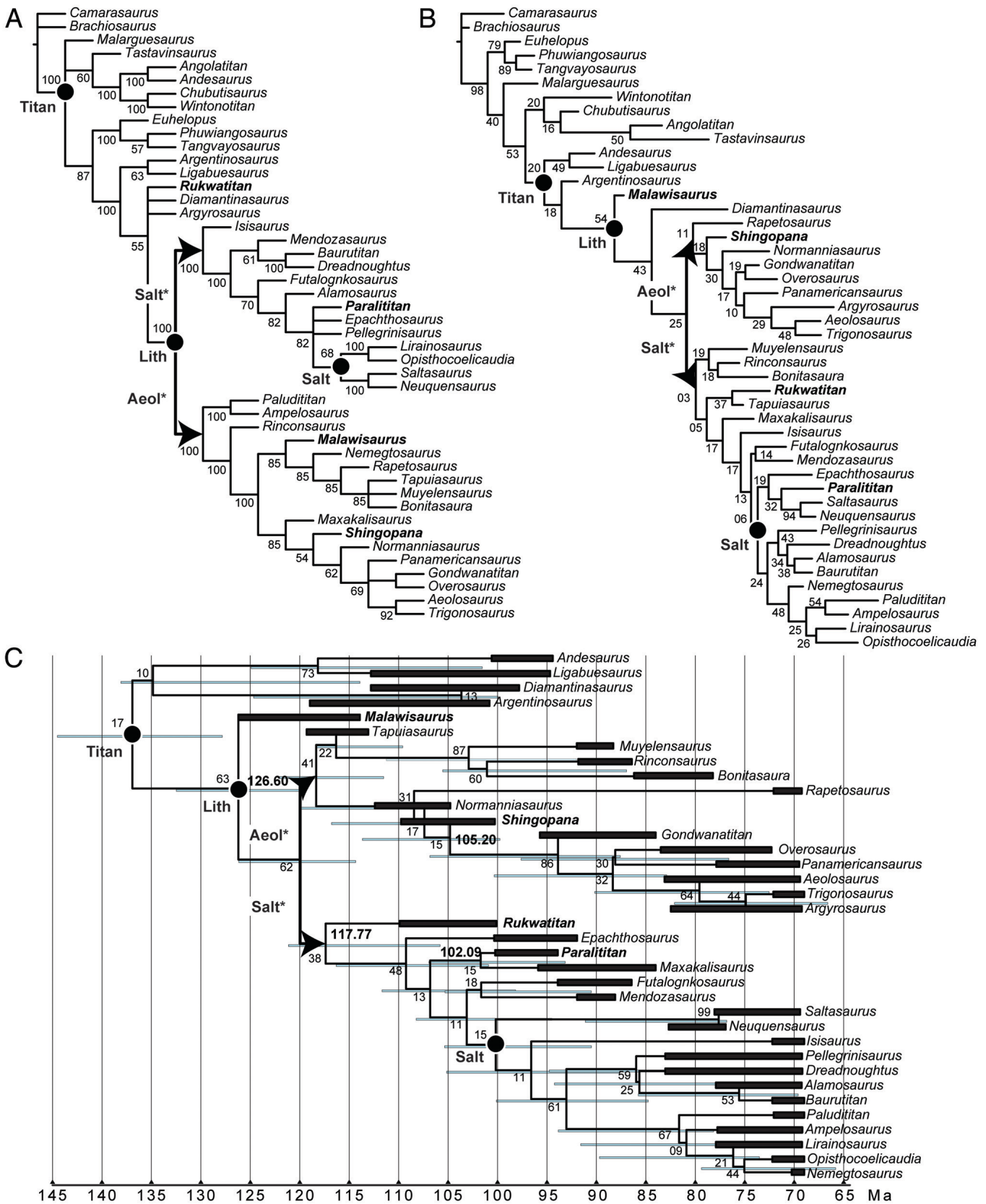


FIGURE 14. Results of the parsimony, uncalibrated Bayesian, and time-calibrated Bayesian phylogenetic analyses. **A**, majority-rule consensus tree of the parsimony analysis with frequency of clades next to respective nodes. **B**, uncalibrated Bayesian topology with posterior probabilities next to respective nodes. **C**, tip-dated Bayesian topology of titanosaurs with posterior probabilities at each node and select estimated nodal ages in bold. **Abbreviations:** **Aeol***, aeolosaur lineage, titanosaurs more closely related to *Aeolosaurus* than to *Saltasaurus* as indicated by the arrowed branch; **Lith**, Lithostrotia; **Salt**, Saltasauridae; **Salt***, saltasaur lineage, titanosaurs more closely related to *Saltasaurus* than *Aeolosaurus* as indicated by the arrowed branch; **Titan**, Titanosauria. Timeline in **C** is in million years ago (Ma).

–3888.458, respectively, with a Bayes factor of 172.26). The resultant topology (Fig. 14C) recovers *Shingopana* along the aeolosaur lineage as the sister to the Late Cretaceous South American portion of this clade (e.g., *Aeolosaurus maximus*, *Argyrosaurus superbus*, *Gondwanatitan*, *Overosaurus*, *Panamericansaurus*, *Trigonosaurus*), where its placement is consistent with both the uncalibrated Bayesian analysis and the parsimony analysis despite relatively low posterior probabilities (18% in the uncalibrated and 15% in the tip-dated Bayesian analyses). *Shingopana* is estimated to have diverged from the rest of the aeolosaurian clade around 105 million years ago (Ma; 95% highest posterior density [HPD]: 121.34–97.32 Ma), which is in line with current geophysical models that postulate the final separation between South America and Africa around 100 Ma (Torsvik et al., 2009; Seton et al., 2012). Finally, the placement of *Shingopana* within the aeolosaur lineage suggests that this clade was more widespread than previously known (Gorscak and O'Connor, 2016), including members present in South America (e.g., *Tapuiasaurus*, Rinconsauria), Europe (*Normanniasaurus*), Madagascar (*Rapetosaurus*), and now continental Africa (*Shingopana*).

One noticeable difference between the two methodological approaches is that the titanosaurian clade with significant cranial material from the parsimony analysis (e.g., *Bonitasaura*, *Nemegtosaurus*, *Tapuiasaurus*, and *Rapetosaurus*) is recovered as polyphyletic in the Bayesian analyses. This result of the former is likely due to the virtue of preserving cranial elements, whereas the majority of titanosaurians are known from the postcrania (Zaher et al., 2011; Wilson et al., 2016). A strength of the Bayesian approach is that many different phylogenetic hypotheses are sampled and are integrated into a consensus tree that embeds phylogenetic uncertainty. The analysis samples fully resolved topologies that include branch lengths, divergence dates, and relationships and then evaluates the fit to the phenotypic data, stratigraphic data, and evolutionary models simultaneously (Lee and Palci, 2015; O'Reilly et al., 2016). For example, in the tip-dated Bayesian topology (Fig. 14C), the strict reading of the topology suggests that the

Late Cretaceous Mongolian titanosaurians *Nemegtosaurus* and *Opisthocoelicaudia* were sister taxa, or potentially the same genus, within the Eurasian clade of titanosaurians (Paul, 1996; Wilson, 2005; Currie and Fanti, 2017). This may seem like an odd result given that *Nemegtosaurus* is known from a skull and *Opisthocoelicaudia* from postcrania. However, the temporal information taken from stratigraphic data, the tree and morphological evolution models (Lewis, 2001; Stadler et al., 2013), at least some cranial characters with other taxa (e.g., basioccipital depression between foramen magnum and basal tubera in *Lirainosaurus* and longitudinal groove of supraoccipital in *Ampelosaurus*), and autapomorphic characters used to inform terminal branch lengths are all pieces of evidence used to jointly estimate the potential placements of *Nemegtosaurus* from the sample of topologies despite missing data (e.g., see discussion on missing data in Ronquist et al., 2012a; Lee et al., 2014; Wright and Hillis, 2014; and Guillerme and Cooper, 2016). At the very least, the posterior probabilities are there as a gauge of the inherent uncertainty of the estimated topology where model-based approaches tend to be more accurate at the cost of precision when compared with parsimony (O'Reilly et al., 2016). In other words, the Eurasian clade composed of *Ampelosaurus*, *Lirainosaurus*, *Opisthocoelicaudia*, *Nemegtosaurus*, and *Paludititan* may be reasonably accurate with a relatively well-supported posterior probability of 67%, but the internal relationships are less precise with lower posterior probabilities (e.g., 9%, 21%, and 44%) due to the fundamentally different approach of estimating topologies in model-based analyses than parsimony. Just as the fossil record is incomplete, so too should the analyses accommodate and reflect this uncertainty.

DISCUSSION

Comparative Morphology of *Shingopana*

Shingopana is distinct from the other Namba Member titanosaurian, *Rukwatitan*, in lacking several of the reported autapomorphic and apomorphic characters of the cervical vertebrae

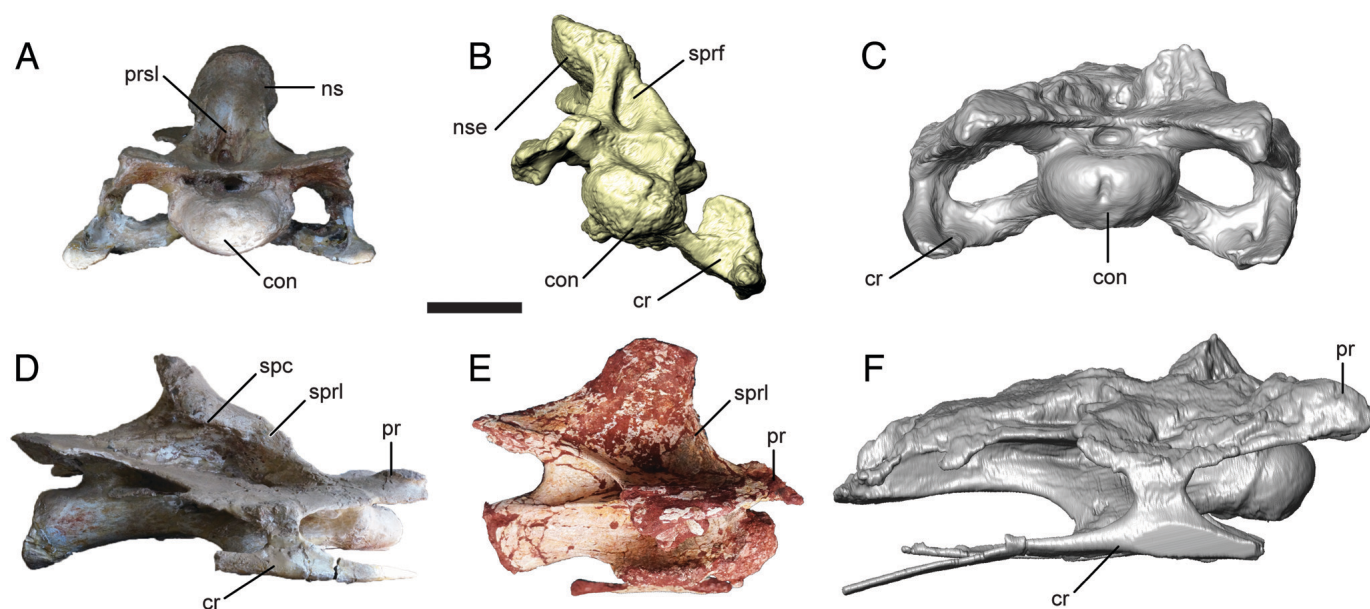


FIGURE 15. Comparisons of cervical vertebrae of *Malawisaurus dixeyi*, *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100), and *Rukwatitan biseulptus*. **A** and **D**, MAL-280-2 of *M. dixeyi*; **A**, anterior and **D**, right lateral views. **B** and **E**, cervical vertebra A of *S. songwensis*, gen. et sp. nov. (RRBP 02100); **B**, anterior and **E**, right lateral views. **C** and **F**, penultimate cervical vertebra of *R. biseulptus* (Gorscak et al., 2014); **C**, anterior and **F**, right lateral views. **Abbreviations:** con, condyle; cr, cervical rib; ns, neural spine; nse, neural spine bulbous expansion; pr, prezygapophysis; prsl, prespinal lamina; spc, spinoprezygapophyseal and spinopostzygapophyseal laminae confluence; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina. Scale bar equals 10 cm.

and humeri. Importantly, the cervical vertebrae of *Shingopana* differ from those of both *Malawisaurus* and *Rukwatitan* in several aspects (Fig. 15). The neural spines of the cervical vertebrae of *Malawisaurus* (Fig. 15A, D) are anteroposteriorly short and do not have the bulbous expansions exhibited by *Shingopana* (Gomani, 2005; E.G., pers. observ., 2014, 2015); however, some cervical vertebrae of *Malawisaurus* exhibit a slight expansion that connects the spinoprezygapophyseal and spinopostzygapophyseal laminae with a tall neural spine dorsally, but not to the extent of expansion seen in *Shingopana*.

The *Shingopana* humerus shares more features with *Malawisaurus* than it does with *Rukwatitan*, *Angolatitan*, and *Paralitian* (Fig. 16). Comparisons are not possible with the other Malawi Dinosaur Beds titanosaurian, *Karongasaurus*, because this taxon is currently known from only a dentary and several referred teeth (Gomani, 2005). In Lamanna and Yoshikazu (2014), two features were suggested to link *Angolatitan* and *Paralitian*: an acute projection at the proximomedial humeral margin and an elevated humeral head. Notably, these humeral features now appear more widespread within titanosauriforms (e.g., González Riga and David, 2014), and that relationship was not recovered in the present analysis. The humerus of *Rukwatitan* also differs from humeri of *Angolatitan* and *Paralitian* (Gorscak et al., 2014). *Rukwatitan* and *Paralitian* appear to share a pronounced medial margin, although in the latter it extends further distally along the humerus. Taken together, if humeri are any indication of dinosaurian diversity, then the morphological variation in African titanosaurians appear to be a mix of a generalized somphospondyliian morph (*Shingopana*, *Malawisaurus*) and morphs with various derived features (*Rukwatitan*, *Paralitian*, *Angolatitan*) that would imply biomechanical, postural, and locomotor variation. Body sizes of African titanosaurians seem to exhibit substantial variation as well: using maximum humeral length as a

proxy for body size (e.g., Campione and Evans, 2012), *Malawisaurus* and *Shingopana* are much smaller (ca. 730 and 790 mm, respectively; MAL-316; Gomani, 2005) than *Rukwatitan* (1020 mm; RRBP 03151; Gorscak et al., 2014), *Angolatitan* (1100 mm; Mateus et al., 2011), and what was reported for *Aegyptosaurus* (1000 mm; Stromer, 1932), whereas *Paralitian* overshadows them all (1690 mm; Smith et al., 2001). Of course, without additional materials that span the range of ontogenetic stages, histology samples to better estimate maturity, or associated materials to further support presence of a skeletally mature individual, this assessment remains coarse. Overall, based on available materials, *Shingopana* appears to be more closely related to taxa (i.e., aeolosaurines) not previously reported from Africa. At the very least, *Shingopana* expands the morphological and taxonomic variation of titanosaurians during their early evolutionary history on the African continent.

As discussed above, of the limited titanosaurian cervical vertebrae known, there appears to be a wide range of variation in neural spine morphology (González Riga, 2005; Gallina, 2011). The neural spine expansion appears distinct from the lateral expansion described in some mid-posterior cervical vertebrae in *Alamosaurus* (Lehman and Coulson, 2002; Tykoski and Fiorillo, 2017), *Futalognkosaurus dukei* (Calvo et al., 2007b, 2007c), and *Mendozasaurus* (González Riga, 2005), in which the spine is more laminar (potentially as an exaggerated spinodiapophyseal lamina), vertically oriented, and distinct from the spinopre- and spinopostzygapophyseal laminae. Furthermore, the posterior cervical vertebrae of *Overosaurus* and *Trigonosaurus*, the two titanosaurians with reported bulbous neural spine expansions, do not exhibit any evidence for the lamina expansions that are present in *Futalognkosaurus*, suggesting that the two states may represent two different morphologies (Campos et al., 2005; Coria et al.,

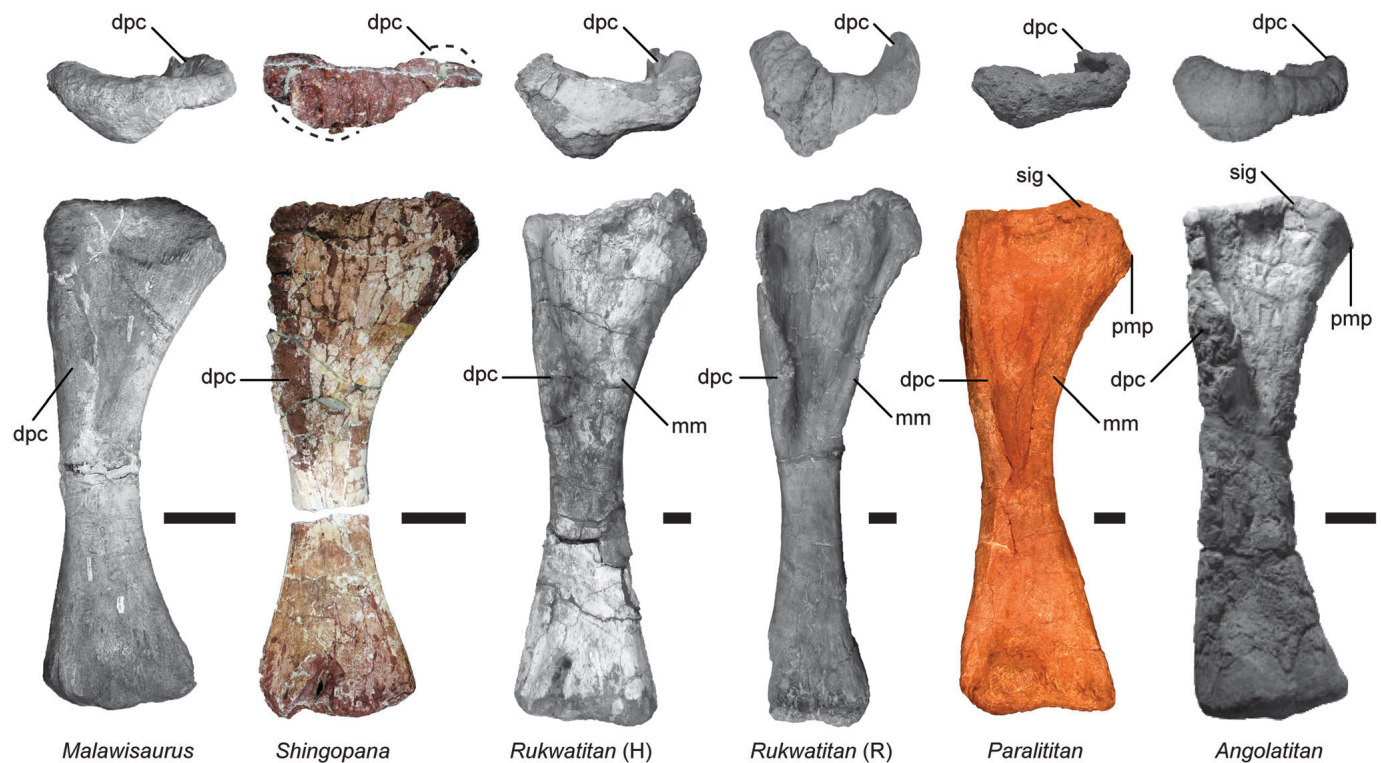


FIGURE 16. Comparisons of humeri of *Malawisaurus dixeyi* (MAL-221; Gomani, 2005); *Shingopana songwensis*, gen. et sp. nov. (RRBP 02100); *Rukwatitan bisepultus* holotype (Gorscak et al., 2014); *R. bisepultus* referred specimen (RRBP 03151; Gorscak et al., 2014); *Paralitian stromeri* (Smith et al., 2001); and *Angolatitan adamastor* (Mateus et al., 2011). **Abbreviations:** dpc, deltopectoral crest; mm, medial margin; pmp, proximomedial process; sig, sigmoidal margin of elevated humeral head. Scale bars equal 10 cm.

2013). Additionally, *Saltasaurus* is described with rugosities in a similar region of the neural spine of the cervical vertebrae (Powell, 1992; Campos et al., 2005). The neural spines of *Maxakalisaurus topai* are described as “blunt and transversely thickened” (Kellner et al., 2006:7). Therefore, it is not unreasonable to consider that several distinct morphologies, all of which reposition the attachment of certain epaxial musculature away from the midline, occurred in the middle-to-posterior cervical region of the vertebral column within titanosauriforms, including titanosaurians (González Riga, 2005; Gallina, 2011; Taylor and Wedel, 2013). These encompass (1) the bulbous lateral expansion exhibited by middle-to-posterior cervical vertebra of *Shingopana*, cervical vertebra 9 of *Trigonosaurus* (Campos et al., 2005), posterior cervical vertebra of *Overosaurus* (Coria et al., 2013:fig. 2), and the recovered posterior cervical 13? of *Bonitasaura* (Gallina, 2011:fig. 3); (2) a laminar lateral expansion of the neural spine in posterior cervical vertebrae of *Futalognkosaurus* (Calvo et al., 2007c:figs. 11, 12), some cervical vertebrae attributed to *Malawisaurus* (MAL-291; Jacobs et al., 1993; E. G., pers. observ., 2014, 2015), middle cervical vertebra of *Mendozasaurus* (González Riga, 2005:figs. 2, 3), cervical 9 of *Puertasaurus reuili* (Novas et al., 2005:fig. 1a–d), multiple cervical vertebrae of *Alamosaurus* (Lehman and Coulson, 2002: fig. 2; Tykoski and Fiorillo, 2017), and middle-to-posterior vertebrae of *Quetecsaurus rusconii* (González Riga and David, 2014:fig. 6); (3) the lateral tuberosities present on cervical vertebrae of *Saltasaurus* (Powell, 1992:figs. 6–8) and *Maxakalisaurus* (Kellner et al., 2006); (4) a lateral expansion of the spinoprezygapophyseal lamina in *Ligabuesaurus* (Bonaparte et al., 2006:fig. 3); and (5) highly reduced neural spines with pronounced epiphyses seen in euhelopodids and several non-euhelopodid titanosauriforms (D’Emic, 2012). Additionally, the middle-to-posterior cervical vertebrae of *Malawisaurus* exhibit a moderate lateral expansion of the neural spine at the confluence of the spinoprezygapophyseal and spinopostzygapophyseal laminae (MAL-245, MAL-278 series, MAL-280 series; Gomani, 2005; E.G., pers. observ., 2014, 2015). The neural spine morphology of *Malawisaurus* is anteroposteriorly compressed and expanded transversely, resembling a paddle shape that sits at the confluence of the spinoprezygapophyseal and spinopostzygapophyseal laminae (D’Emic, 2012). The weakly expanded confluence of the spinoprezygapophyseal and spinopostzygapophyseal laminae within the cervical vertebrae of *Malawisaurus* may be homologous with the bulbous expansion (E.G., pers. observ., 2014), but this hypothesis remains to be tested because the cervical vertebrae that display the bulbous neural spine in *Shingopana*, *Overosaurus*, and *Trigonosaurus* do not preserve the dorsal end of the neural spine for in-depth comparisons. The mostly complete cervical vertebral series of *Rapetosaurus* and the few cervical vertebrae of *Isisaurus* do not exhibit such developed neural spine modifications (Jain and Bandyopadhyay, 1997; Curry Rogers, 2009). Furthermore, these derived morphological features may be functionally equivalent to bifurcated neural spines as exhibited by euhelopodids, non-titanosauriforms such as diplodocids, and the macronarian *Camarasaurus*, and they are likely to have been present in the titanosaurian *Opisthocoelicaudia skarzynskii* based on the presence of bifurcated anterior and middle dorsal vertebrae (Borsuk-Bialynicka, 1977). However, considering the limited information on titanosaurian cervical vertebral series in general, the extent of neural spine variation, and the homologies within the cervical vertebral series in different taxa, is far from completely understood. Prior to discovery of *Shingopana*, the temporal range for bulbous expansions of the cervical vertebral neural spine had been restricted to the Late Cretaceous: the Maastrichtian *Trigonosaurus* (Campos et al., 2005) and the Campanian *Overosaurus* (Coria et al., 2013). *Shingopana* shows that this morphology was present during the

middle Cretaceous and also present in Africa (110–100 Ma; Roberts et al., 2010).

Other non-saltosaurid titanosaurians with cervical vertebral material include *Aeolosaurus maximus* (Santucci and Arruda-Campos, 2011), *Bonitasaura* (Apesteguía, 2004; Gallina and Apesteguía, 2015), *Gondwanatitan* (Kellner and Azevedo, 1999), *Muyelensaurus* (Calvo et al., 2007a), *Pitekunsaurus* (Filippi and Garrido, 2008), and *Rinconsaurus* (Calvo and González Riga, 2003). Although highly fragmentary (partial cervical vertebral centra with no neural arch) and unknown in position within the axial column, the reported cervical vertebral centrum of *Gondwanatitan* differs from that of *Shingopana* by exhibiting paired fossae and a strong keel on the ventral surface. Features of *Shingopana* that are reported for *Rinconsaurus* include an oblique ridge within the lateral fossa of the cervical centrum and potentially what is described as a “distally expanded” neural spine (Calvo and González Riga, 2003:337). The figured fragmentary posterior cervical vertebra of *Rinconsaurus* (Calvo and González Riga, 2003:pl. 1f) is broadly similar to cervical vertebrae A of *Shingopana*, except that the diapophysis and corresponding laminae appear to be more dorsally placed on the neural arch, although this may be due to positional and/or interspecific variation. Additionally, the incomplete humerus of *Rinconsaurus* does not appear to substantially differ from the humerus of *Shingopana*, although the figure and description are limited (Calvo and González Riga, 2003:pl. 3c). The middle cervical vertebra of *Muyelensaurus* does not appear nor is described to have a bulbous neural spine and the centropostzygapophyseal lamina is positioned much closer to the margin of the cotyle (Calvo et al., 2007a:fig. 5); however, the humerus of *Muyelensaurus* differs substantially from that of *Shingopana* by being markedly more slender (Calvo et al., 2003:fig. 12b). The cervical vertebrae of *Shingopana* does not differ considerably from the described posterior cervical vertebrae of *Pitekunsaurus*, with the exception of the proposed autapomorphic fossae on the spinopostzygapophyseal lamina of the latter and the bulbous expansion of the neural spine in the former. The description of the neural spine morphology in *Pitekunsaurus* is similar to that described for *Maxakalisaurus* and *Saltasaurus*, with the presence of neural spine tuberosities (Filippi and Garrido, 2008). As for *Aeolosaurus maximus*, the reported cervical vertebrae are highly fragmentary but the posterior centrodiapophyseal lamina courses posterovertrally across the lateral margin of the centrum (Santucci and de Arruda-Campos, 2011), differing considerably from the axially aligned posterior centrodiapophyseal lamina in *Shingopana* (Fig. 7B). Currently, the distribution of these cervical vertebral features is poorly known, and whether they represent autapomorphies, homoplasies, or synapomorphies remains ambiguous. Until better-preserved and associated materials are recovered, the functional significance and phylogenetic distribution of the various cervical vertebral neural spine morphs within titanosaurians remain unclear.

Phylogenetic Position of *Shingopana*

Shingopana represents the second titanosaurian from the middle Cretaceous Galula Formation of Tanzania. Based on multiple (and different) phylogenetic approaches used herein, *Shingopana* represents a close relative to the aeolosaurine titanosaurians. Although originally defined as the most inclusive clade containing *Gondwanatitan faustoi* and *Aeolosaurus rionegrinus*, but not *Saltasaurus loricatus* and *Opisthocoelicaudia skarzynskii* (Franco-Rosas et al., 2004), we opt for the informal and more succinct aeolosaur-lineage definition to avoid previously proposed concerns on the membership of Aeolosaurini (Martinielli et al., 2011). Furthermore, the results of our phylogenetic analyses are consistent with previous analyses concerning

aeolosaurian titanosaurians (e.g., Calvo et al., 2007a, 2007b, 2007c; Santucci and de Arruda-Campos, 2011; Coria et al., 2013).

The presence of aeolosaur-lineage titanosaurians in Africa supports that the group may have been more widespread than previously considered (Gorscak and O'Connor, 2016). Aeolosaur-lineage members include the Aptian European titanosaurian *Normanniasaurus*, the Late Cretaceous Malagasy *Rapetosaurus*, and now the middle Cretaceous African *Shingopana*. Collectively, these taxa indicate a suite of members that diverged during the Aptian–Albian from their otherwise Late Cretaceous South American sister clade. In particular, the presence of a bulbous neural spine of the mid-posterior cervical vertebra is a key character linking *Shingopana* with *Bonitasaura* and aeolosaurines *Overosaurus* and *Trigonosaurus* (Coria et al., 2013; Campos et al., 2005).

Taken together, African titanosauriformes in the current dataset (*Angolatitan*, *Malawisaurus*, *Paralititan*, *Rukwatitan*, and *Shingopana*) hint at a more phylogenetically diverse middle Cretaceous fossil record, given the limited number of established African taxa when compared with more numerous forms recovered from South America. Based on the current analysis, both *Rukwatitan* and *Paralititan* represent middle Cretaceous (Aptian–Cenomanian) members of the saltasaur lineage within lithostrotian titanosaurians. By contrast, *Shingopana* represents a middle Cretaceous member of the aeolosaur lineage within lithostrotian titanosaurians, and *Malawisaurus* represents an early-branching lithostrotian titanosaurian from the Aptian. Finally, *Angolatitan* represents a non-titanosaurian titanosauriform (Mateus et al., 2011; LSDM analysis: Mannion et al., 2013; Gorscak and O'Connor, 2016; M. D'Emic, pers. comm., 2016; contra LCDM analysis: Mannion et al., 2013). This glimpse into the diversity of titanosaurians across Africa and South America in the middle Cretaceous (Aptian–Cenomanian) interval is perhaps not surprising, given that the two continents were connected until roughly 100 Ma (Torsvik et al., 2009; Seton et al., 2012).

Biogeographic Implications


Emerging data from the Rukwa Rift Basin in Tanzania offers a regional biogeographic framework for future tests of cosmopolitanism versus north-south provinciality on the African continent. In discussing these faunal patterns, we recognize that a continent-level treatment likely grossly oversimplifies biogeographic provinciality and habitat connectivity throughout Africa during the Cretaceous and that a north-south division of the continent may be a better perspective (Fig. 1A). The post-Cenomanian fossil record of Africa is sparser still; hence, examining the existence and persistence of regional provinciality awaits the recovery of more complete and diagnostic materials. Currently, *Karongasaurus*, *Malawisaurus*, *Rukwatitan*, and *Shingopana* represent the composition of middle Cretaceous southern African titanosaurians, whereas *Paralititan* and, historically, *Aegyptosaurus* represent the northern African titanosaurians along with several fragmentary forms (e.g., Rauhut, 1999; Sereno et al., 1999; O'Leary et al., 2004; Mannion and Barrett, 2013; Lamanna and Yoshikazu, 2014; Ibrahim et al., 2016). The regional biotic similarity hypothesis of O'Connor et al. (2006) posits that the geographically proximate and potentially contemporaneous faunas of the Dinosaur Beds of Malawi and the Galula Formation of Tanzania would be expected to exhibit overlapping or closely related taxa more so than with other regions (e.g., northern Africa). Currently, both comparative morphology and phylogenetic methods herein support *Shingopana*, *Malawisaurus*, and *Rukwatitan* as distantly related forms (i.e., not forming an endemic monophyletic group). The relationship of *Karongasaurus* with these titanosaurians remains ambiguous due to lack of comparable elements, although its dentary and referred teeth


are distinct from those of *Malawisaurus* (Gomani, 2005). The material and phylogenetic analyses of the Rukwa Rift Basin and Dinosaur Beds titanosaurians have yet to provide diagnostic materials or evidence for a monophyletic group that would be present between the two faunas (contra Bandeira et al., 2016). Moreover, the members within southern African faunas do not overlap and/or are not closely related to northern African faunas. The current evidence supports a southern African fauna that may have been partially influenced by the northward rifting of South America and Africa that facilitated the development of a progressively isolated fauna (Gorscak and O'Connor, 2016). According to the results of our tip-dated Bayesian analysis, the pattern of divergence dates between subequatorial African and South American titanosaurian lineages appear to have been continuous, spanning roughly 20 million years, mirroring the separation of these two continents: *Malawisaurus* around 126.60 Ma (95% HPD: 141.43–114.47 Ma); *Rukwatitan* around 117.77 Ma (95% HPD: 129.77–102.75 Ma); *Shingopana* around 105.20 Ma (95% HPD: 121.34–97.32 Ma). Compared with the supra-equatorial African *Paralititan*, this lineage is estimated to have diverged around 102.09 Ma (95% HPD: 117.10–92.02 Ma). This pattern is similar to that of the small-bodied crocodyliforms from both the Dinosaur Beds of Malawi and the Galula Formation of Tanzania. The recently described *Rukwasuchus yajabalijekundu* was recovered as a close relative to northern African peirosaurids, but *Pakasuchus kapilimai* and *Malawisuchus mwakasyungutiensis* were recovered as serially paraphyletic taxa to South American ziphosuchid notosuchians (Sertich and O'Connor, 2014). However, the current paleobiogeographic assessment for titanosaurian sauropod dinosaurs requires the recovery of more African faunas, to help test these and other hypotheses regarding Cretaceous Gondwanan paleobiogeography.

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