

New dinosaurs link southern landmasses in the Mid-Cretaceous

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Abelisauroid predators have been recorded almost exclusively from South America, India and Madagascar, a distribution thought to document persistent land connections exclusive of Africa. Here, we report fossils from three stratigraphic levels in the Cretaceous of Niger that provide definitive evidence that abelisauroid dinosaurs and their immediate antecedents were also present on Africa. The fossils include an immediate abelisauroid antecedent of Early Cretaceous age (*ca.* 130–110 Myr ago), early members of the two abelisauroid subgroups (Noasauridae, Abelisauridae) of Mid-Cretaceous age (*ca.* 110 Myr ago) and a hornless abelisaurid skull of early Late Cretaceous age (*ca.* 95 Myr ago). Together, these fossils fill in the early history of the abelisauroid radiation and provide key evidence for continued faunal exchange among Gondwanan landmasses until the end of the Early Cretaceous (*ca.* 100 Myr ago).

Keywords: Cretaceous; biogeography; dinosaur; ceratosaur; abelisauroid

1. INTRODUCTION

Discovery of the horned predatory dinosaur *Carnotaurus sastrei* (Bonaparte 1985; Bonaparte *et al.* 1990) and close relatives (Bonaparte & Novas 1985; Bonaparte & Powell 1980) in rocks of Late Cretaceous (Maastrichtian) age in Argentina brought to light a new group of dinosaurs now recognized as abelisauroids. Similar-age fossils from India (Huene & Matley 1933; Wilson *et al.* 2003) and Madagascar (Sampson *et al.* 1998, 2001; Carrano *et al.* 2002) were linked to this group, which has figured prominently in what we term here the 'Africa-first' model for the break-up of Gondwana (Sampson *et al.* 1998; Hay *et al.* 1999). Unlike early palaeocoastline reconstructions that show several landmasses separated by intervening seaways early in the Cretaceous (Smith *et al.* 1994; Roeser *et al.* 1996), the 'Africa-first' model (Sampson *et al.* 1998; Hay *et al.* 1999) holds that Africa alone split away in the Early Cretaceous (*ca.* 140–120 Myr ago), with the remainder of Gondwana unified by two key land bridges until the Late Cretaceous (*ca.* 90–80 Myr ago) (figure 1, land bridges B, C). Abelisauroid dinosaurs provided the most convincing palaeontological support for these palaeocoastline maps. Despite multiple sites on Africa yielding large-bodied predators of Mid- and Upper Cretaceous age (Stromer 1915; Sereno *et al.* 1996, 1998), fossil evidence for abelisauroids has been limited to a single jaw fragment (Russell 1996), the assignment of which has been questioned (Sampson *et al.* 1998; Carrano *et al.* 2002). Below we provide clear evidence of the presence and diversification of abelisauroids on Africa during the Cretaceous.

2. NEOCOMIAN CERATOSAURIAN

Neocomian sediments preserving the remains of the sauropod *Jobaria* and theropod *Afrovenator* (Sereno *et al.*

1994) yielded an articulated trunk of a basal ceratosaurian: an immediate abelisauroid antecedent (figure 2). The first bones of this small-bodied theropod, consisting of disarticulated vertebrae and two partial limb bones, were discovered by A. F. de Lapparent in 1959 but incorrectly referred to the Late Jurassic genus *Elaphrosaurus* (Lapparent 1960, p. 31).

Theropoda (Marsh 1881)

Ceratosauria (Marsh 1884)

Spinostropheus gautieri gen. nov. comb. nov.

(a) *Holotype*

Disarticulated vertebrae, partial left humerus and partial right tibia, Musée National d'Histoire Naturelle, 1961–28, originally described as *Elaphrosaurus gautieri* (Lapparent 1960, p. 31, plates V, X and XI).

(b) *Referred specimen*

Articulated axial column preserving the third cervical to the anterior sacrals with complete cervical and more fragmentary dorsal ribs, Musée National du Niger (MNN) TIG6 (figure 2). Cervical and dorsal vertebrae overlap with the holotypic specimen.

(c) *Etymology*

Spinos, spine (Greek); *strophe*, vertebra (Greek). Named for the prominent epiphyseal processes on the cervical vertebrae and its moderate body size (estimated length 4 m). Lapparent (1960) named the type species *S. gautieri* after geologist F. Gautier, who discovered the type locality (In Tedreft).

(d) *Localities and horizon*

The holotypic and referred specimens were discovered in the Niger Republic, the former at In Tedreft and the latter at Fako, *ca.* 250 km northwest and 100 km southwest of Agadez, respectively; Tiourarén Formation (*ca.*

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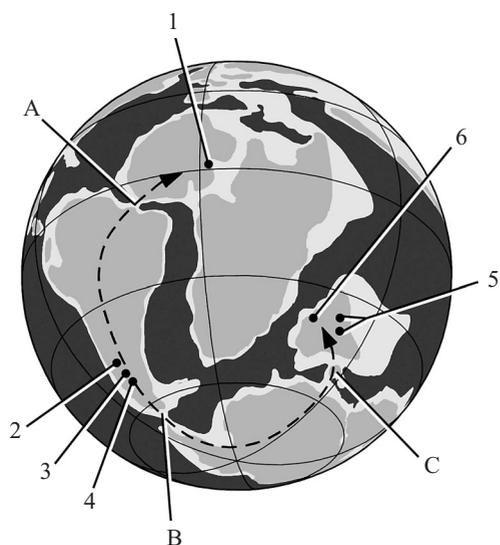


Figure 1. Early Late Cretaceous (Early Cenomanian, *ca.* 97 Myr ago) palaeogeographic map (Scotese 2001) showing all known Late Cretaceous abelisaurid localities (numbers) and key land bridges (letters). The arrow shows the southern high-latitude dispersal route of the 'Africa-first' and 'pan-Gondwana' models of Cretaceous biogeography. The 'Africa-first' model argues that land bridge A was broken in the Early Cretaceous, 30–50 Myr earlier than land bridges B and C; the 'pan-Gondwana' model argues for final separation at land bridge A at the end of the Early Cretaceous. Land bridges: A, Walvis Ridge, Rio Grande Rise; B, Palmer Land Block, South Georgia Island Terrane; C, Kerguelan Plateau, Gunnerus Ridge. Abelisaurid localities: 1, *Rugops primus*; 2, *Aucasaurus garridoi*; 3, *Abelisaurus comahuensis* and *Ilokelesia aguadagrandensis*; 4, *Carnotaurus sastrei*; 5, *Rajasaurus narmadensis*; 6, *Majungatholus atopus*.

135 Myr ago, Neocomian) in association with the sauropod *Jobaria* and basal tetanuran *Afrovenator* (Sereno *et al.* 1994).

(e) **Diagnosis**

Spinostropheus gautieri is a basal ceratosaurian characterized by mid-cervical vertebrae with strongly canted anterior articular face on centrum (30° angle to posterior centrum face), partitioned anterior pleurocoels, dorsoventrally flattened epipophyseal processes and broad subrectangular neural spines (figure 2*b,c*).

(f) **Description**

Spinostropheus is intermediate in age and phylogenetic position between the Late Jurassic ceratosaurian *Elaphrosaurus* (Janensch 1925) and Late Cretaceous abelisauroids (figure 4). As in abelisauroids, the cervical vertebrae of *Spinostropheus* have paired pleurocoels (figure 2*a,b*), mid-dorsal vertebrae have prominent parapophyses (figure 2*c*), and cervical ribs have broadened bifurcate spines that interlock with adjacent cervical ribs (figure 2*d*). A prominent ridge on the cervical neural arches is a key synapomorphy linking *Spinostropheus* with abelisauroids, which further develop this ridge as a lamina (figure 2*b*, eprl; figure 4, node 2).

3. APTIAN–ALBIAN ABELISAUROIDS

Mid-Cretaceous rocks (Aptian–Albian, *ca.* 110 Myr ago) in Gadoufaoua, Niger, have yielded partial skeletons of a noasaurid and abelisaurid. The noasaurid consists of a small (1 m) articulated skeleton showing many abelisauroid and noasaurid synapomorphies, including pneumatized presacral and sacral neural arches, proportionately long presacral centra, and others (Carrano *et al.* 2002). The abelisaurid preserves a maxilla and pelvic girdle, the former of which bears the distinctive abelisaurid pit-and-groove texturing of the skull bones. These fossils push back the basal divergence among abelisauroids deep into the Early Cretaceous (figure 4, nodes 3, 5), as had been foreshadowed by discovery of an abelisaurid jaw in the earliest Late Cretaceous (Cenomanian) of Argentina (Lamanna *et al.* 2002).

African noasaurids and abelisaurids of similar (Cenomanian) age, it now is apparent, were also present in Morocco. *Deltadromeus agilis*, originally described as a basal coelurosaurian from Morocco (Sereno *et al.* 1996), is reinterpreted here as a basal noasaurid (figure 4, node 3). *Deltadromeus* and the smaller Malagasy genus *Masiakasaurus* (Sampson *et al.* 2001; Carrano *et al.* 2002) are the only nonavian dinosaurs with strongly reduced distal condyles on the fourth metatarsal of the pes. An abelisaurid maxilla, in addition, has come to light recently from the same rocks in Morocco. Its rugose external texture and subrectangular alveoli lend credence to the initial record of abelisaurids on Africa (Russell 1996) from the same horizon.

4. CENOMANIAN ABELISAUROID SKULL

An early Late Cretaceous skull (figure 3) provides unequivocal evidence of the presence of basal abelisaurids on Africa and is remarkably similar to more fragmentary remains found recently on South America (Lamanna *et al.* 2002).

Theropoda (Marsh 1881)

Ceratosauria (Marsh 1884)

Abelisauroida (Bonaparte 1991)

Abelisauridae (Bonaparte & Novas 1985)

Rugops primus gen. et sp. nov.

(a) **Holotype**

Partial cranium lacking the posterolateral portions of the skull roof and palate (MNN IGU1).

(b) **Etymology**

Ruga, wrinkle (Latin); *opsi*, face (Greek); *primus*, first (Latin). Named for its significance as one of the earliest abelisaurids with textured external skull surfaces.

(c) **Locality and horizon**

Near In Abangharit, Niger Republic; Echkar Formation (*ca.* 95 Myr ago, Cenomanian) in association with rebbachisaurid and titanosaurian sauropods, spinosaurid and carcharodontosaurid theropods, and baurusuchid and arripesuchid crocodylomorphs.

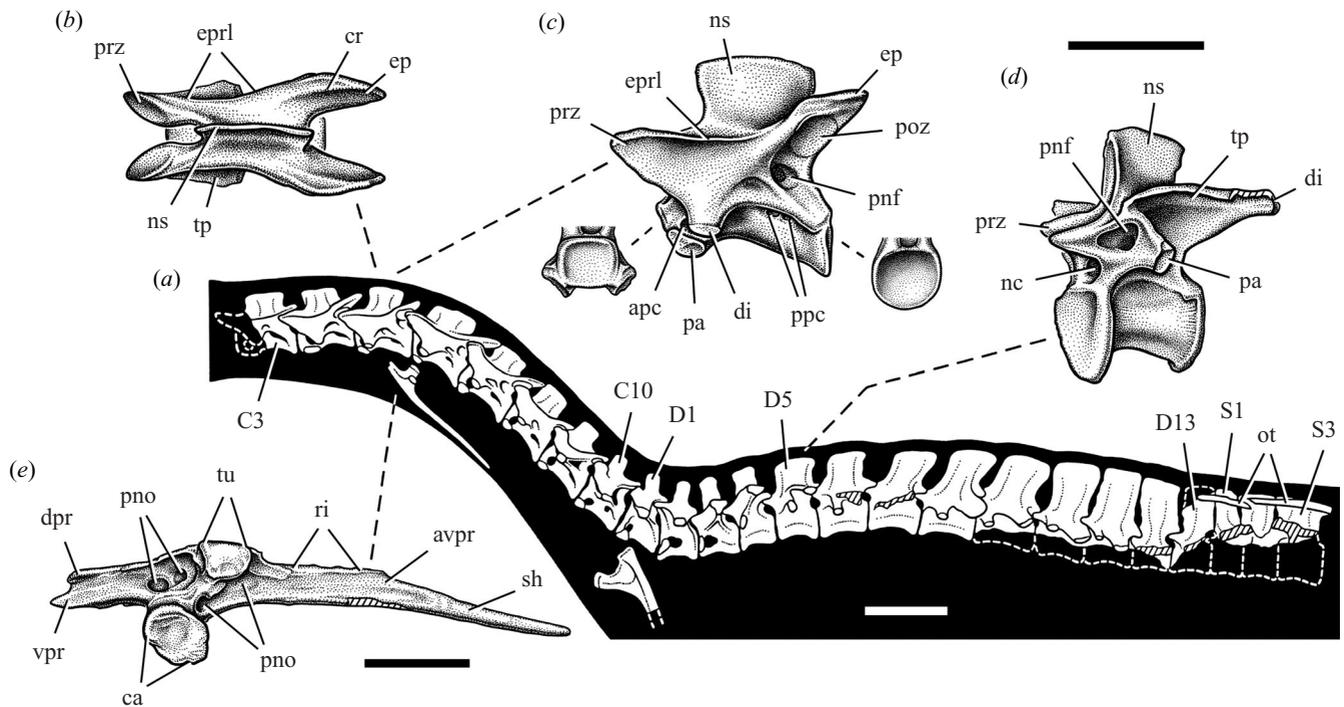


Figure 2. *Spinosropheus gautieri*, basal ceratosaurian (MNN TIG6). (a) Silhouette reconstruction in left lateral view based on an articulated presacral column. (b) Fifth cervical vertebra in dorsal view. (c) Fifth cervical vertebra in lateral view with anterior and posterior views of the articular faces of the centrum. (d) Fifth dorsal vertebra in anterolateral view. (e) Mid-cervical rib (reversed from left) in dorsomedial view. Cross-hatching indicates broken bone. Scale bars: (a) 10 cm; (b)–(d) 5 cm; (e) 2 cm. Abbreviations: 1–15, vertebral number; apc, anterior pleurocoel; avpr, articular surface for succeeding ventral process; C, cervical; ca, capitulum; cr, crest; D, dorsal; di, diapophysis; dpr, dorsal process; ep, epiphysis; eprl, epiphysseal-prezygapophysseal lamina; nc, neural canal; ns, neural spine; ot, ossified tendon; pa, parapophysis; ppc, posterior pleurocoel; pnf, pneumatic fossa; pno, pneumatic opening; poz, postzygapophysis; prz, prezygapophysis; ri, ridge; S, sacral; sh, shaft; tp, transverse process; tu, tuberculum; vpr, ventral process.

(d) *Diagnosis*

Abelisaurid characterized by small fenestra in the skull roof between the prefrontal, frontal, post-orbital and lacrimal, and a row of seven small invaginated depressions on the dorsal surface of each nasal.

(e) *Description*

The skull exhibits many abelisaurid hallmarks, including its textured external surface, U-shaped dental arcade, broad maxillary-jugal contact, socket on the maxilla for the anteroventral process of the nasal, and subrectangular alveoli (figure 3). *Rugops* lacks several derived features of latest Cretaceous abelisaurids, including the thickened skull roof, cranial horn(s) and robust orbital brows (figure 4, nodes 6, 7). The orbital brow is present but poorly formed in *Rugops* (figure 3b); a fenestra is maintained between the brow (lacrimal plus post-orbital) and the original orbital margin, and a partly co-ossified prefrontal can still be distinguished. The incipient brow in *Rugops* suggests that the fully formed lacrimal-post-orbital brow in later abelisaurids evolved independently from that in other theropods groups.

A row of seven pits is present on the dorsal aspect of the snout near the external margin of each nasal; their function remains uncertain (figure 3b). They do not appear to be connected to each other within the nasal or to pneumatic spaces in the antorbital region. In dorsal view, grooves for vascular supply pass into each of the pits

(figure 3a), which may have served as an anchor for sensory structures or soft tissues involved in display.

The remarkable similarity between *Rugops* and a maxilla described recently from similar-age rocks in Patagonia (Lamanna *et al.* 2002) suggests that they are closely related (figure 3d). The pattern of external ornamentation, often diagnostic among abelisaurids, is nearly identical; both show the predominance of grooves over pits and an unusual series of curved grooves under the antorbital fenestra (figure 3d). Internal details of both maxillae also closely correspond, such as the relatively elevated position of the dental lamina and the fine striae marking its surface.

5. TIMING OF AFRICAN ISOLATION

The new African abelisauroid material raises serious questions about the strongest faunal evidence (abelisauroid dinosaurs) supporting the 'Africa-first' model for the fragmentation of Gondwana (Sampson *et al.* 1998). The model shows a circum-African seaway in the Early Cretaceous (*ca.* 140–120 Myr ago) that isolated the continent from other Gondwanan landmasses, which later separated in the Late Cretaceous (*ca.* 80 Myr ago). The new fossils, however, show that Africa was already home to both noasaurids and abelisaurids before the close of the Early Cretaceous (figure 4). The early Late Cretaceous abelisaurid *Rugops* and its close South American

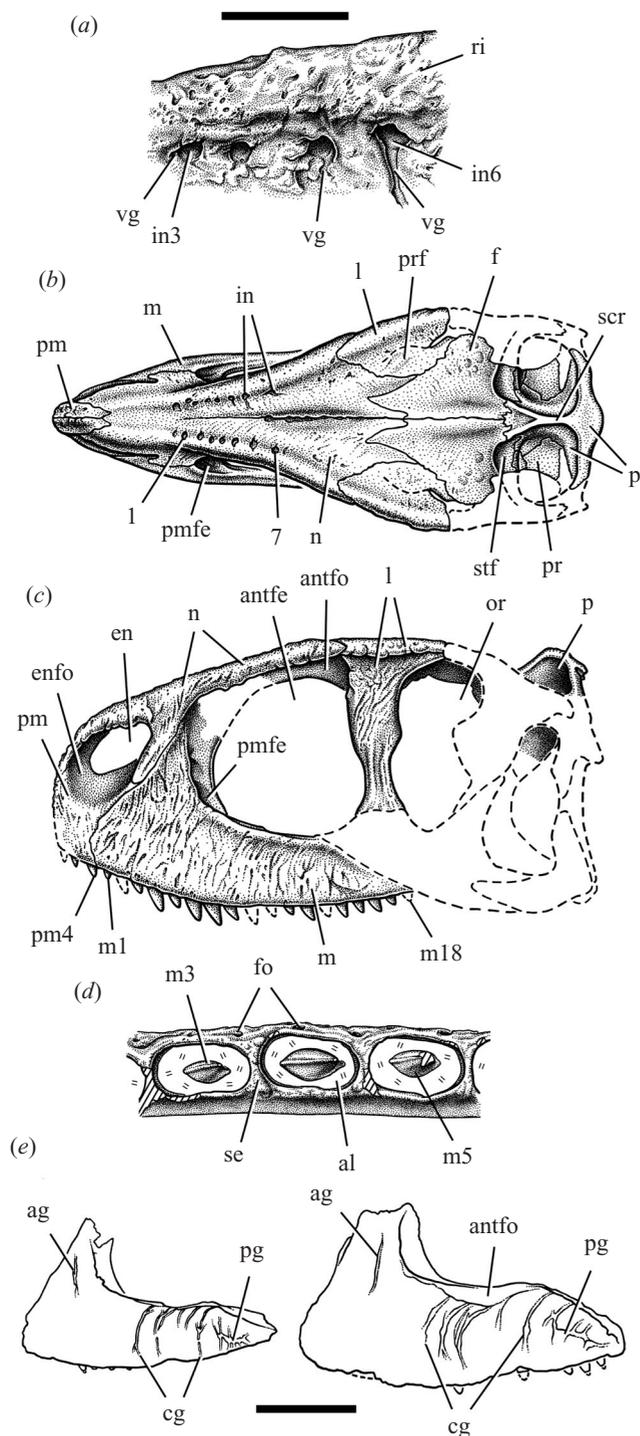


Figure 3. Cranium of the abelisaurid *Rugops primus* (MNN IGU1). (a) Invaginations 3–6 of right nasal in dorsal view. (b) Cranium in dorsal view. (c) Cranium in lateral view (skull lengths for (b) and (c) 31.5 cm). (d) Third to fifth alveoli of the left maxilla in ventral view. (e) Comparison of the left maxillae of (left) *Rugops primus* and (right) a contemporary Patagonian abelisaurid (Lamanna *et al.* 2002) showing similar pattern of grooves. Scale bars: (a) and (d) 2 cm; (e) 10 cm. Abbreviations: 1–18, tooth positions or number of nasal invagination; ag, anterior groove; al, alveolus; antfe, antorbital fenestra; antfo, antorbital fossa; cg, curved grooves; en, external naris; enfo, external narial fossa; f, frontal; fo, foramen; in, invagination; l, lacrimal; m, maxilla; n, nasal; or, orbit; p, parietal; pg, posterior groove; pm, premaxilla; pmfe, promaxillary fenestra; pr, prootic; prf, prefrontal; ri, ridge; scr, sagittal crest; se, septum; stf, supratemporal fossa; vg, vascular groove.

relative, furthermore, indicate that trans-Atlantic interchange may have been operative as late as 95 Myr ago, confirming similar evidence of fossil crocodylians that link these continents (Buffetaut & Taquet 1977, 1979; Sereno *et al.* 2003).

Horned abelisaurids (figure 4, node 7) are known only from latest Cretaceous (Campanian–Maastrichtian) rocks on South America, India and Madagascar and thus may still be used to support a temporally restricted version of the ‘Africa-first’ model, with exchange involving horned abelisaurids occurring from *ca.* 90–80 Myr ago among Gondwanan landmasses exclusive of Africa. Recent discovery of the hornless abelisaurid *Aucasaurus* in South America (Coria *et al.* 2002), however, casts doubt on this scenario, as *Aucasaurus* is at least 80 Myr old (Dingus *et al.* 2000) and is regarded as the closest known relative of the younger horned *Carnotaurus* from the same continent. Post-Cenomanian dinosaurs on Africa, in addition, are so poorly known (Carrano *et al.* 2002) that the existence of horned abelisaurids on Africa cannot be determined.

Other faunal evidence (notosuchian crocodylomorphs (Buckley *et al.* 2000) and gondwanatherian mammals (Sampson *et al.* 1998)) no longer supports the ‘Africa-first’ model. African crocodylomorphs of mid-Cretaceous age (Aptian–Albian) are most closely related to taxa of comparable age on South America (Buffetaut & Taquet 1977, 1979; Sereno *et al.* 2003), and the absence of gondwanatheres reflects only the non-existent record of mammals on Africa during most of the Cretaceous.

Geological evidence also contradicts the ‘Africa-first’ model (Hay *et al.* 1999) and early palaeocoastline maps (Smith *et al.* 1994), which show Africa either first or last, respectively, to pull away from other landmasses. Both palaeogeographical scenarios may have misinterpreted intercontinental connections. Well-constrained geological evidence (Reyment & Dingle 1987; Pittman *et al.* 1993; Maisey 2000) pinpoints the final separation of South America and Africa in the latest Albian (*ca.* 100 Myr ago), significantly later than proposed by the ‘Africa-first’ model (*ca.* 140–120 Myr ago). Conversely, geological (Barker & Burrell 1977; Munschy *et al.* 1992; Storey *et al.* 1992) and palaeontological (Maisey 1993) evidence for intermittent land bridges among Gondwanan landmasses argues against early separation (*ca.* 140–120 Myr ago) of South America and Africa as ‘West Gondwana’ from eastern landmasses (Antarctica, India, Madagascar) (Goldblatt 1993; Smith *et al.* 1994).

6. THE PAN-GONDWANA HYPOTHESIS

Here, we propose an alternative ‘pan-Gondwana’ model (Sereno *et al.* 1996; Scotese 2001) in which three narrow, probably intermittent, passages connected major Gondwanan landmasses during the Early Cretaceous (figure 1, land bridges A–C). These were severed during a relatively brief interval at the beginning of the Late Cretaceous (*ca.* 100–90 Myr ago, from the latest Albian/earliest Cenomanian to the Coniacian). The presence of a trans-Atlantic passage (land bridge A) until the end of the Early Cretaceous distinguishes the ‘pan-Gondwana’ model from the ‘Africa-first’ model and more closely matches the most recent palaeocoastline maps (Scotese 2001). A permanent equatorial seaway of significant depth between South

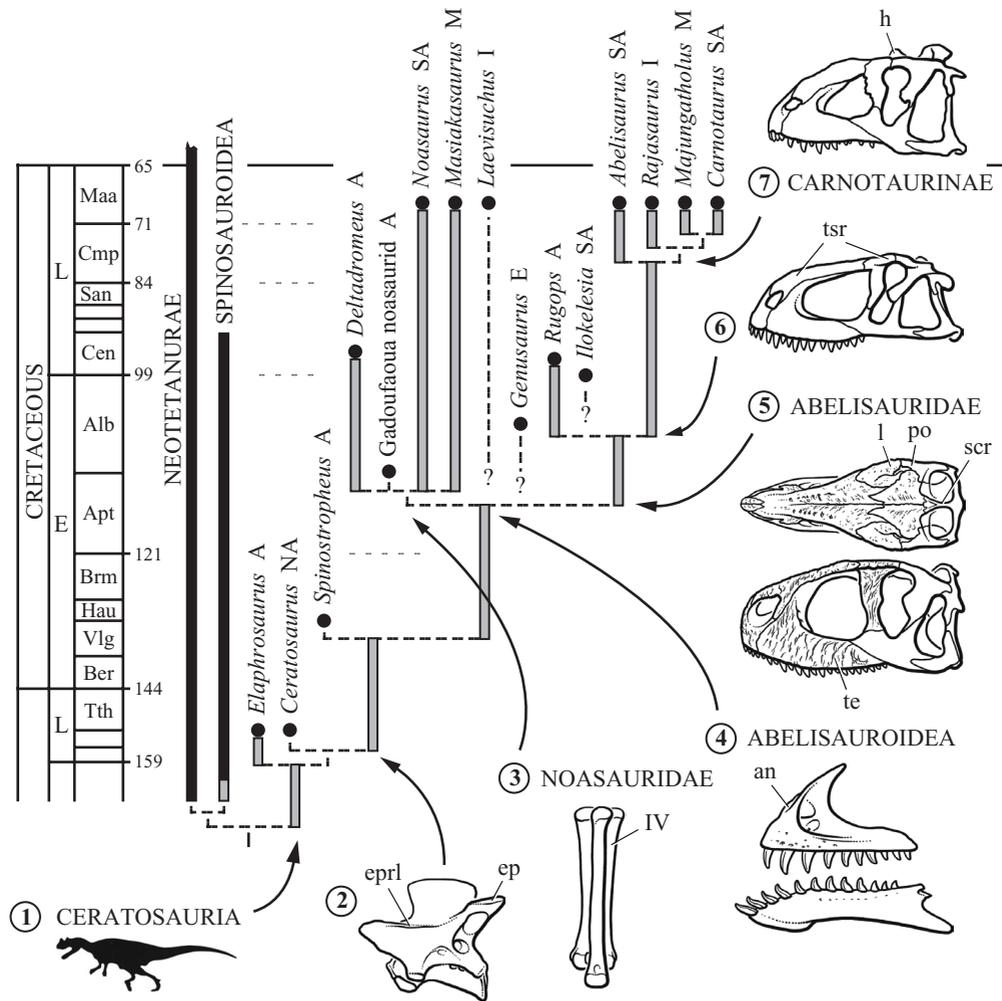


Figure 4. Phylogenetic, temporal and palaeobiogeographic relationships among ceratosaurian theropods (169 characters, 205 steps; retention index = 0.93; see electronic Appendix A for discussion of phylogenetic nomenclature and phylogenetic analysis). The stratigraphic range of *Carnotaurus* is extended into the Campanian based on the age of the closely related South American abelisaurid *Aucasaurus* (Coria *et al.* 2002). Skeletal modifications include: node 1, a suite of cranial and postcranial characters that arose during the undocumented Early and Middle Jurassic history of the clade; node 2, prominent epipophyseal-prezygapophyseal lamina; node 3, metatarsal IV distal end reduced; node 4, anterolateral articulation for nasal process, intramandibular socket; node 5, groove-and-pit ornamentation, basic abelisaurid skull design; node 6, thickened skull roof; node 7, frontonasal horn. Abbreviations: A, Africa; E, Europe; I, India; M, Madagascar; NA, North America; SA, South America; an, articular surface for nasal; ep, epiphysis; epri, epipophyseal-prezygapophyseal lamina; h, horn; l, lacrimal; po, postorbital; scr, sagittal crest; te, textured external skull surface; tsr, thickened skull roof; IV, fourth metatarsal.

America and Africa was in place no earlier than the end of the Albainian or dawn of the Late Cretaceous. The absence of a hierarchical biogeographic pattern among fossils or recent organisms from Gondwanan landmasses (Maisey 1993) is consistent with a narrow time interval for their permanent separation.

We thank members of the 1997 and 2000 expeditions for discovery of the material; C. Abraczinskas for drawing from specimens and executing final drafts of reconstructions; E. Dong, A. Gray and T. Keillor for fossil preparation and casting; and J. Hopson and F. Lando for reviewing an earlier draft of the paper. For permission to conduct fieldwork, we are indebted to the Niger Republic and to B. Gado (Institut de Recherche en Science Humaine) and I. Kouada (Ministère de L'Enseignement Supérieur de la Recherche et de la Technologie). We thank M. Carrano, C. Forster and S. Sampson for access to fossils in their care. This research was funded by The David and Lucile Packard Foundation, National Geographic Society, Comer Science and Education Foundation, and Nathan Myhrvold.

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