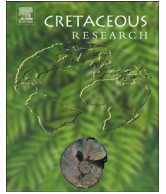


Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Review paper

Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia

Fernando E. Novas^{a,b,*}, Federico L. Agnolín^{a,c}, Martín D. Ezcurra^d, Juan Porfiri^e, Juan I. Canale^{b,f}^a Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina^b CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina^c Fundación de Historia Natural “Félix de Azara”, Universidad Maimónides, V. Virasoro 732, 1405 Buenos Aires, Argentina^d GeoBio-Center, Ludwig-Maximilian-University, Richard-Wager-Str. 10, 80333 Munich, Germany^e Centro Paleontológico Lago Barreales-Proyecto Dino, Universidad Nacional del Comahue, Avenida Megaraptor 1450, Lago Barreales, Neuquén CC.122, Argentina^f Museo Municipal Ernesto Bachmann, Dr. Natali S/N, Villa El Chocón 8311, Neuquén, Argentina

ARTICLE INFO

Article history:

Received 2 October 2011

Accepted in revised form 2 April 2013

Available online xxx

Keywords:

Cretaceous

Patagonia

Theropoda

Megaraptoridae

Paleobiogeography

Evolution

ABSTRACT

Patagonia has yielded the most comprehensive fossil record of Cretaceous theropods from Gondwana, consisting of 31 nominal species belonging to singleton taxa and six families: Abelisauridae, Noasauridae, Carcharodontosauridae, Megaraptoridae nov. fam., Alvarezsauridae, and Unenlagiidae. They provide anatomical information that allows improved interpretation of theropods discovered in other regions of Gondwana. Abelisauroids are the best represented theropods in Patagonia. They underwent an evolutionary radiation documented from the Early Cretaceous through to the latest Cretaceous, and are represented by the clades Abelisauridae and Noasauridae. Patagonian carcharodontosaurids are known from three taxa (*Tyrannotitan*, *Giganotosaurus* and *Mapusaurus*), as well as from isolated teeth, collected from Aptian to Cenomanian beds. These allosauroids constituted the top predators during the mid-Cretaceous, during which gigantic titanosaur sauropods were the largest herbivores. Megaraptorans have become better documented in recent years with the discovery of more complete remains. *Megaraptor*, *Aerosteon* and *Orkoraptor* have been described from Cretaceous beds from Argentina, and these taxa exhibit close relationships with the Aptian genera *Australovenator*, from Australia, and *Fukuiraptor*, from Japan. The Gondwanan megaraptorans are gathered into the new family Megaraptoridae, and the Asiatic *Fukuiraptor* is recovered as the immediate sister taxon of this clade. Although megaraptorans have been recently interpreted as members of Allosauroidea, we present evidence that they are deeply nested within Coelurosauria. Moreover, anatomical information supports Megaraptora as more closely related to the Asiamerican Tyrannosauridae than thought. Megaraptorans improve our knowledge about the scarcely documented basal radiation of Gondwanan coelurosaurs and tyrannosauroids as a whole. Information at hand indicates that South America was a cradle for the evolutionary radiation for different coelurosaurian lineages, including some basal forms (e.g., *Bicentenaria*, *Aniksosaurus*), megaraptorans, alvarezsaurids less derived than those of Laurasia, and unenlagiids, revealing that Gondwanan coelurosaurs played sharply differing ecological roles, and that they were taxonomically as diverse as in the northern continents. The unenlagiids represent an endemic South American clade that has been recently found to be more closely related to birds than to dromaeosaurid theropods. Analysis of the theropod fossil record from Gondwana shows the highest peak of origination index occurred during the Aptian–Albian and a less intense one in the Campanian time spans. Additionally, peaks of extinction index are recognized for the Cenomanian and Turonian–Coniacian time spans. In comparison, the Laurasian pattern differs from that of Gondwana in the presence of an older extinction event during the Aptian–Albian time-span and a high origination rate during the Cenomanian time-bin. Both Laurasian and Gondwanan theropod records show a peak of origination rates during the Campanian.

© 2013 Elsevier Ltd. All rights reserved.

* Corresponding author. Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Ángel Gallardo 470, 1405DJR Buenos Aires, Argentina.

E-mail address: fernovas@yahoo.com.ar (F.E. Novas).

1. Introduction

Cretaceous rocks from Patagonia in southern Argentina, have yielded the most comprehensive record of Cretaceous non-avian

theropods from the Southern Hemisphere. Currently 31 valid species have been named largely belonging to the following theropod clades: the ceratosaurians Abelisauridae and Noasauridae, the basal tetanurans Carcharodontosauridae and Megaraptora, and the highly derived coelurosaurians Alvarezsauridae and Unenlagiidae (see SI part 1). The fact that such disparate morphotypes are recorded in the Cretaceous of South America strongly indicates that an important evolutionary diversification of carnivorous dinosaurs occurred in the southern landmasses. However, the Patagonian record is still patchy if compared, for example, with some outstanding North American and Asian dinosaurian assemblages. Nevertheless, the Patagonian theropod record is by far the most relevant and informative among Gondwanan continents (i.e., Africa, Australia, Madagascar, India, and Antarctica). Some of the theropod species discovered in Patagonia are known on the basis of skulls and fairly complete skeletons (e.g. *Carnotaurus*, *Skorpiovenator*, *Giganotosaurus*, *Buitreraptor*), thus offering insights into the anatomy and phylogeny of abelisaurids, carcharodontosaurids, and maniraptorans. The remaining Cretaceous theropod species from Patagonia, although anatomically less well known, are informative enough to allow analysis of different aspects of theropod phylogeny, such as the basal coelurosaurian diversification. This rich and variegated fossil record of Patagonian theropods (Fig. 1) improves our understanding of the systematics and evolutionary history of the carnivorous dinosaurs of Gondwana as a whole.

The aims of the present paper are: 1) review the available Patagonian record of the Cretaceous non-avian theropods; 2) discuss the systematics of Gondwanan theropods in light of what we know from Patagonia; 3) evaluate the paleobiogeographic evolution of Gondwanan theropods with respect to their northern counterparts; and finally, 4) provide a picture of the macroevolutionary patterns observed in the evolutionary history of southern theropods.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; IGM, Mongolian Institute of Geology, Ulaan

Baatar, Mongolia; MACN-Pv; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MCF-PVPH, Museo Carmen Funes, Paleontología de Vertebrados, Plaza Huinca, Neuquén, Argentina; MCNA-PV, Museo de Ciencias Naturales y Antropológicas (J. C. Moyano) de Mendoza, Mendoza, Argentina; MDT-Pv, Museo Desiderio Torres, Sarmiento, Chubut, Argentina; MMCH-Pv, Museo Municipal “Ernesto Bachmann”, Villa El Chocón, Neuquén, Argentina; MPCA, Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio, Paleontología de Vertebrados, Trelew, Chubut, Argentina; MUCPv, Museo de la Universidad Nacional del Comahue, Neuquén, Neuquén, Argentina; NMV, Museum Victoria, Melbourne, Australia; PVL, Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán, Argentina; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA.

2. The fossil record of Patagonian theropods

The Mesozoic sedimentary basins that have yielded remains of Cretaceous theropods are the Neuquina Basin, at the NW corner of Patagonia, the San Jorge Basin, located on the Atlantic side of Central Patagonia, and the Austral Basin, extended on the southern extreme of Patagonia (Fig. 1). Stratigraphically, most discoveries come from continental units of ages ranging from Barremian to Maastrichtian (see SI part 1). This record is the richest in Gondwana, and currently constitutes a “Rossetta stone” facilitating understanding of the origin, evolution, and radiation of theropods from the southern hemisphere. Overall, the Patagonian record effectively provides a chronologically wider database for analysis of macroevolutionary patterns such as origination and extinction rates, and phylogenetic relationships, as well as constituting the most comprehensive tetrapod record from Gondwanan landmasses.

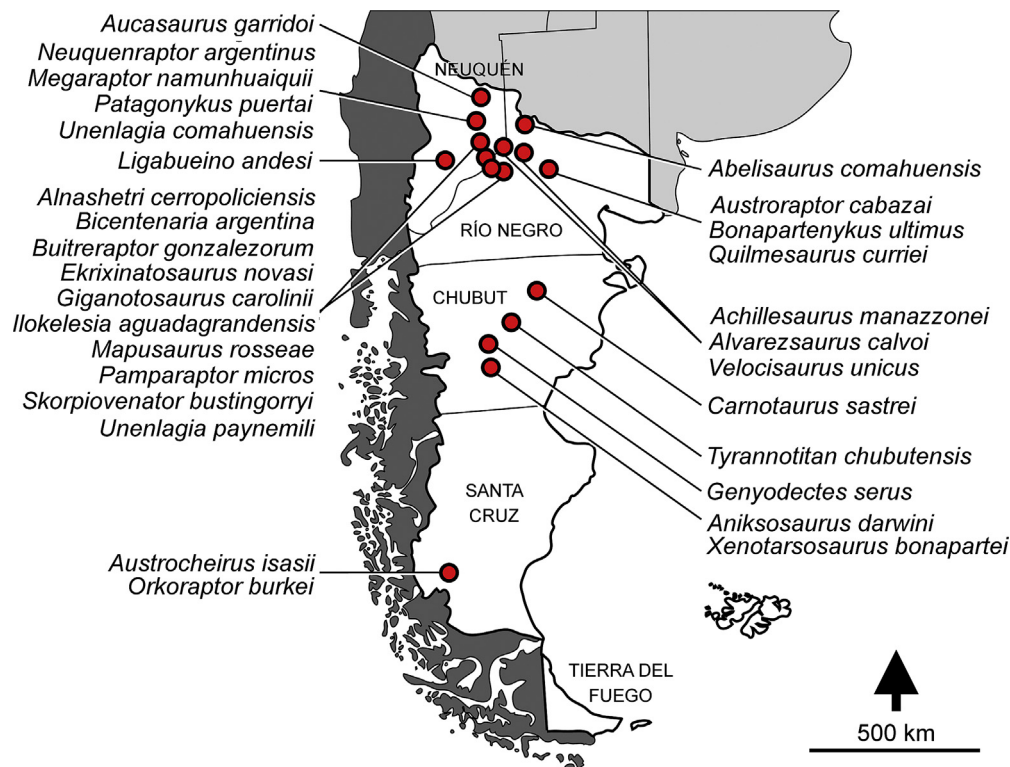


Fig. 1. Map of the Argentinean Patagonia showing the localities that have yielded currently known species of theropod dinosaurs. The direction of the arrow indicates north. Chile in dark gray and Argentina in light gray.

The Cretaceous beds of Patagonia have yielded at least five main theropod lineages, namely Abelisauroidae, Carcharodontosauridae, Megaraptora, Alvarezsauridae, and Unenlagiidae. Among these clades, the abelisauroids were the most abundant during the Late Cretaceous in Patagonia. Below we review each of these main theropod clades, devoting particular attention to their stratigraphic distribution and phylogenetic relationships.

2.1. Abelisauroidae

Abelisauroidae is a ceratosaurian group erected by Bonaparte (1991a) and defined phylogenetically as the least inclusive clade including the common ancestor of *Carnotaurus sastrei*, *Noasaurus leali*, and all descendants (Wilson et al., 2003). Abelisauroids underwent their main evolutionary radiation in Gondwana during the Cretaceous, but their fossil record indicates that Europe was also populated by these theropods. Abelisauroids attained considerable morphological disparity, taxonomic diversity, and numerical abundance in the southern continents, and their fossil remains have been recovered in Argentina, Brazil, Morocco, Niger, Libya, Madagascar, India, and France (Carrano and Sampson, 2008; Novas, 2009; Smith et al., 2010; Ösi and Buffetaut, 2011). These ceratosaurian theropods have not been recorded in the highly productive Late Cretaceous dinosaur beds from North America and Asia, thus supporting the hypothesis that abelisauroids were restricted to the southern landmasses and Europe.

Traditionally Abelisauroidae has been divided into two main branches: the Noasauridae, uniting small-sized and gracile abelisauroids (e.g., *Noasaurus leali*) (Bonaparte, 1991a), and the Abelisauridae, including medium to large, robust animals, such as the bizarre *Carnotaurus sastrei* (Fig. 2). The Noasauridae are known from Cretaceous beds in northern Argentina (Bonaparte and Powell, 1980), Madagascar (Sampson et al., 2001; Carrano et al., 2002, 2011), India (Novas et al., 2004; Carrano et al., 2011), and Niger (Serenó, 2010), with the Malagasy *Masiakasaurus knopfleri* (Carrano et al., 2002, 2011) being the most completely preserved noosaurid currently described. Up to now, noosaurids are only represented in Patagonia by the Barremian–early Aptian *Ligabueino andesi* (Fig. 3) and the Santonian *Velocisaurus unicus*. New material of the latter taxon reveals the presence of pedal unguals with proximally bifurcated collateral grooves and a deep, triangular depression on the ventral surface, both of which are features originally documented among abelisaurids (Novas and Bandyopadhyay, 2001). The new, and as yet undescribed, *Velocisaurus* specimen is also characterized by an elongated and gracile tibia, with its distal end bearing an almost flat anterior surface for articulation with the ascending astragal process, thus closely resembling the condition present among derived coelurosaurians (e.g., ornithomimids, tyrannosaurids; Welles and Long, 1974). The derived, coelurosaurian-like morphology of distal tibia and astragalus recorded among noosaurids contrasts with the more primitive, *Ceratosaurs*-like condition documented in abelisaurids, thereby revealing diversity in the anatomy, proportions and possibly function of abelisauroid hindlimbs.

The richest record of the family Abelisauridae in the world consists of that of the Cretaceous beds of Patagonia. The presence of abelisaurid remains from the Puesto La Paloma Member of the Cerro Barcino Formation (Chubut Province, Argentina) indicates that the family was already present in southern South America since at least the Aptian–Albian (Rauhut et al., 2003). Younger records of Abelisauridae for Patagonia include the early Cenomanian *Ekrixinatosaurus novasi* (Fig. 4), the late Cenomanian–early Turonian *Ilokelesia aguadagrandensis* (Fig. 5) and *Skorpiovenator bustingorryi* (Fig. 6), the Cenomanian–Turonian *Xenotarsosaurus bonapartei*, the late Campanian *Abelisaurus comahuensis* (Fig. 7) and

Aucasaurus garridoi, and the Maastrichtian *Carnotaurus sastrei* and *Quilmesaurus curriei* (the latter taxon has been considered as a *nomen dubium* by Juárez Valieri et al., 2007).

Juárez Valieri et al. (2011) suggested that *Ekrixinatosaurus novasi* is probably the largest abelisaurid yet known, being even larger than *Carnotaurus sastrei*. This interpretation was based on the absolute skull size, which is larger in *Ekrixinatosaurus* (e.g., maxilla length: 44.8 cm; transverse width of skull roof at level of post-orbitals: 33 cm) than *Carnotaurus* (maxilla length: 28 cm; transverse width of skull roof at level of postorbitals: 26 cm). Nevertheless, comparisons of available hindlimb bones clearly show that the holotype of *Carnotaurus sastrei* is roughly 15% larger than *Ekrixinatosaurus novasi*. For example, the distal end of femur in *Carnotaurus* measures 18.6 cm in transverse width, versus 16.5 cm in *Ekrixinatosaurus*. Thus, it seems that *Carnotaurus* was larger in body size than *Ekrixinatosaurus*, but had a proportionately smaller skull.

Abelisauroids in general, but particularly abelisaurids, exhibit strongly reduced forelimbs and hands (Senter, 2009; Burch and Carrano, 2012). Indeed it has been proposed that abelisaurids, such as *Carnotaurus* and *Majungasaurus*, lacked grasping abilities, and that ungual manual phalanges were lacking on these taxa (Agnolín and Chiarelli, 2010). A recent analysis of the hand in *Carnotaurus* (Ruiz et al., 2011) reconstructed the hand of this abelisaurid as having an ungual phalanx on digit III. However, the fossil material on which these authors based their reconstruction remains unprepared, and most elements of the hand are still obscured by matrix, thus impeding reconstruction of the morphology of the hand of *Carnotaurus*. It must be noted that the element interpreted as an ungual by Ruiz et al. (2011) is here considered a bone of dubious identity. The element differs from theropod unguals in being stout and block-like, having a textured external surface, and in lacking any indication of a sharp edge or collateral vascular grooves. We thus follow Agnolín and Chiarelli (2010) in considering that there is no evidence for the presence of ungual manual phalanges in abelisaurid hands, a conclusion which is also supported by *Aucasaurus* (Coria et al., 2002) and *Majungasaurus* (Burch and Carrano, 2012).

Abelisaurids also exhibit stout hindlimbs, with a proportionally robust and short femur and tibia. A remarkable example of this condition is the Indian *Lametasaurus* (Matley, 1923; Novas et al., 2004), with a tibial length only three times the maximum anteroposterior diameter of its proximal end. In sharp contrast, the Patagonian *Carnotaurus sastrei* was originally interpreted (Bonaparte et al., 1990) as bearing elongate hindlimbs. However, Juárez Valieri et al. (2011) pointed out that the exceptionally slender proportions of the hindlimbs reconstructed for *Carnotaurus* may be artificial, an interpretation that we judge highly plausible (this is due to the fragmentary condition of both femora and tibiae in the holotype specimen of *Carnotaurus sastrei*). In other words, *Carnotaurus* may have had a shorter and stouter femur, in agreement with the remaining abelisaurids (e.g., *Ekrixinatosaurus*, *Rahiolisaurus*, *Majungasaurus*, *Aucasaurus*; Juárez Valieri et al., 2011; Novas et al., 2010).

The abelisauroid record of Argentina has served as a firm basis for taxonomical identification of isolated bones recorded in India (Novas and Bandyopadhyay, 1999, 2001; Novas et al., 2004; Méndez et al., 2010), Madagascar (Sampson et al., 2001), and Africa (Serenó et al., 2004; Novas et al., 2005; Smith et al., 2010). In this context, we provide the following observations regarding the African abelisaurid *Kryptops palaios*, recently described by Sereno and Brusatte (2008). The specimen was collected from levels of the Aptian–Albian Elrhaz Formation of Niger. *Kryptops* was founded on the association of postcranial bones (i.e., pelvic girdle and fused sacra, and some dorsal vertebrae) and an isolated maxilla

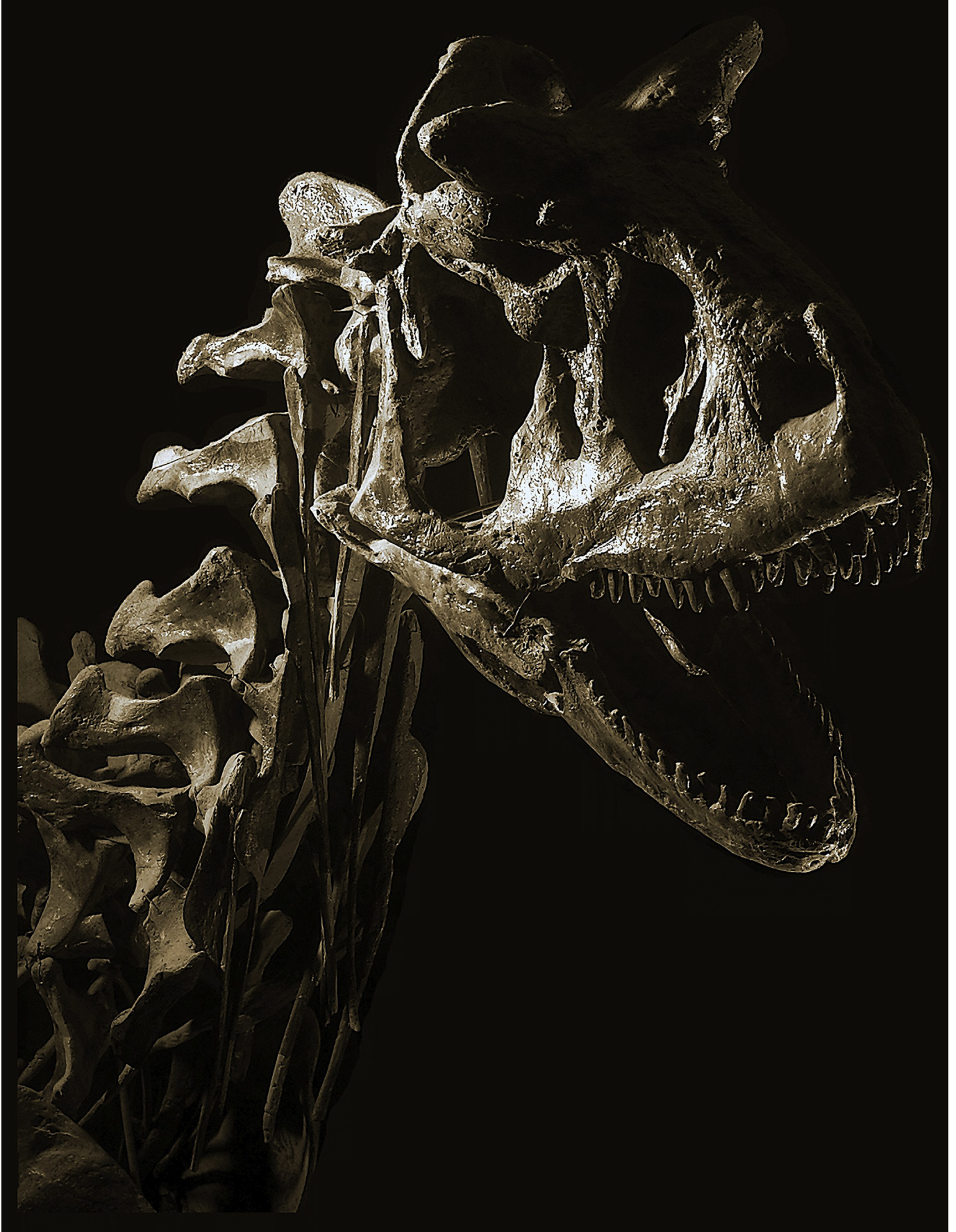


Fig. 2. Skull and neck of the aberrant abelisaurid *Carnotaurus sastrei* (MACN-Pv-CH 894, holotype). Note the well-developed frontal horns.

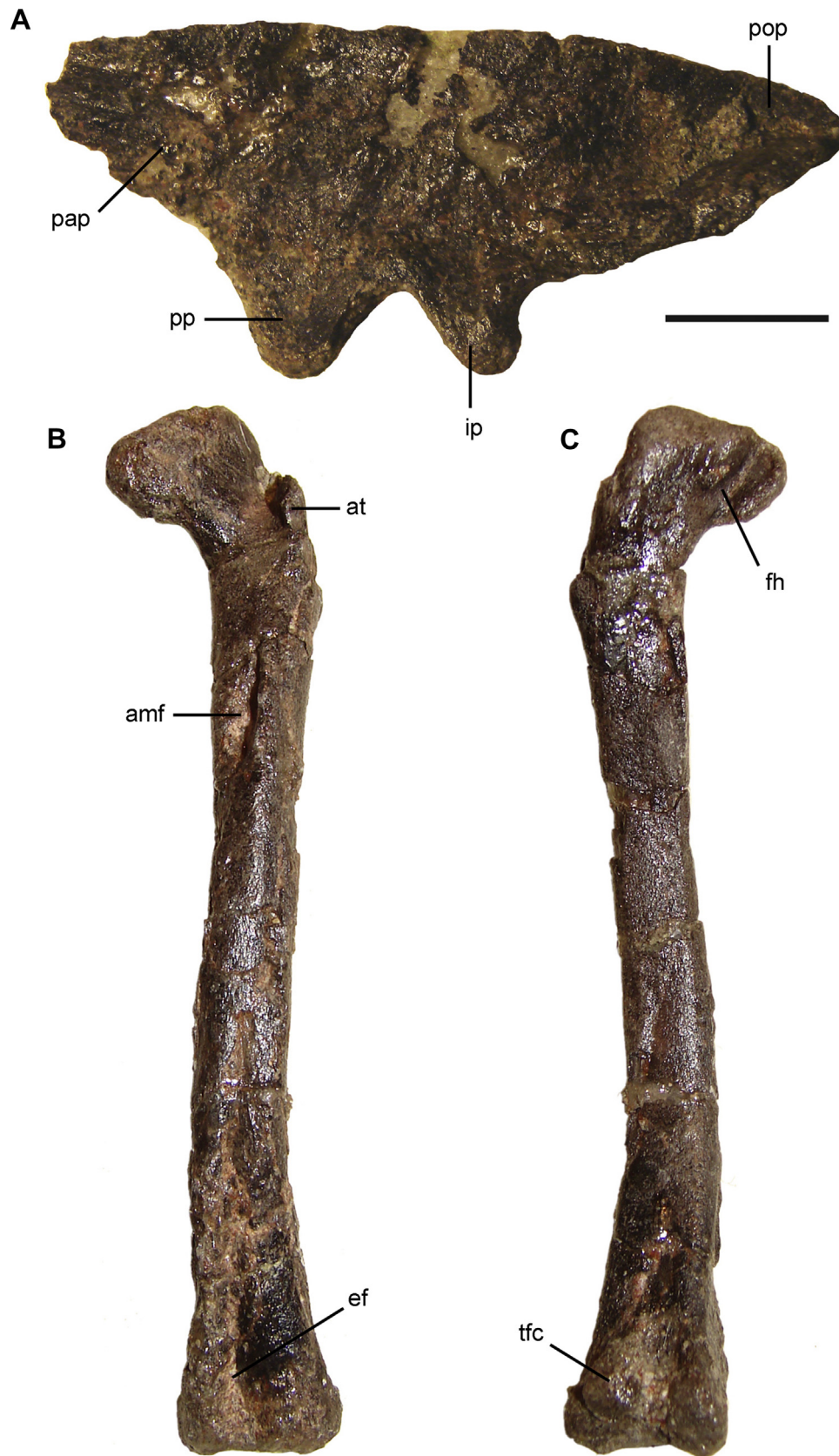


Fig. 3. Selected bones of *Ligabueino andesi* (MACN-Pv-N 42, holotype). (A) Right ilium in lateral view, left femur in (B) anterior and (C) posterior views. Abbreviations: amf, anteromedial fossa; at, anterior trochanter; ef, extensor fossa; fh, femoral head; ip, ischiadis peduncle; pap, preacetabular process; pop, postacetabular process; pp, pubic peduncle; tfc, tibiofibular crest. Scale bar equals 5 mm.

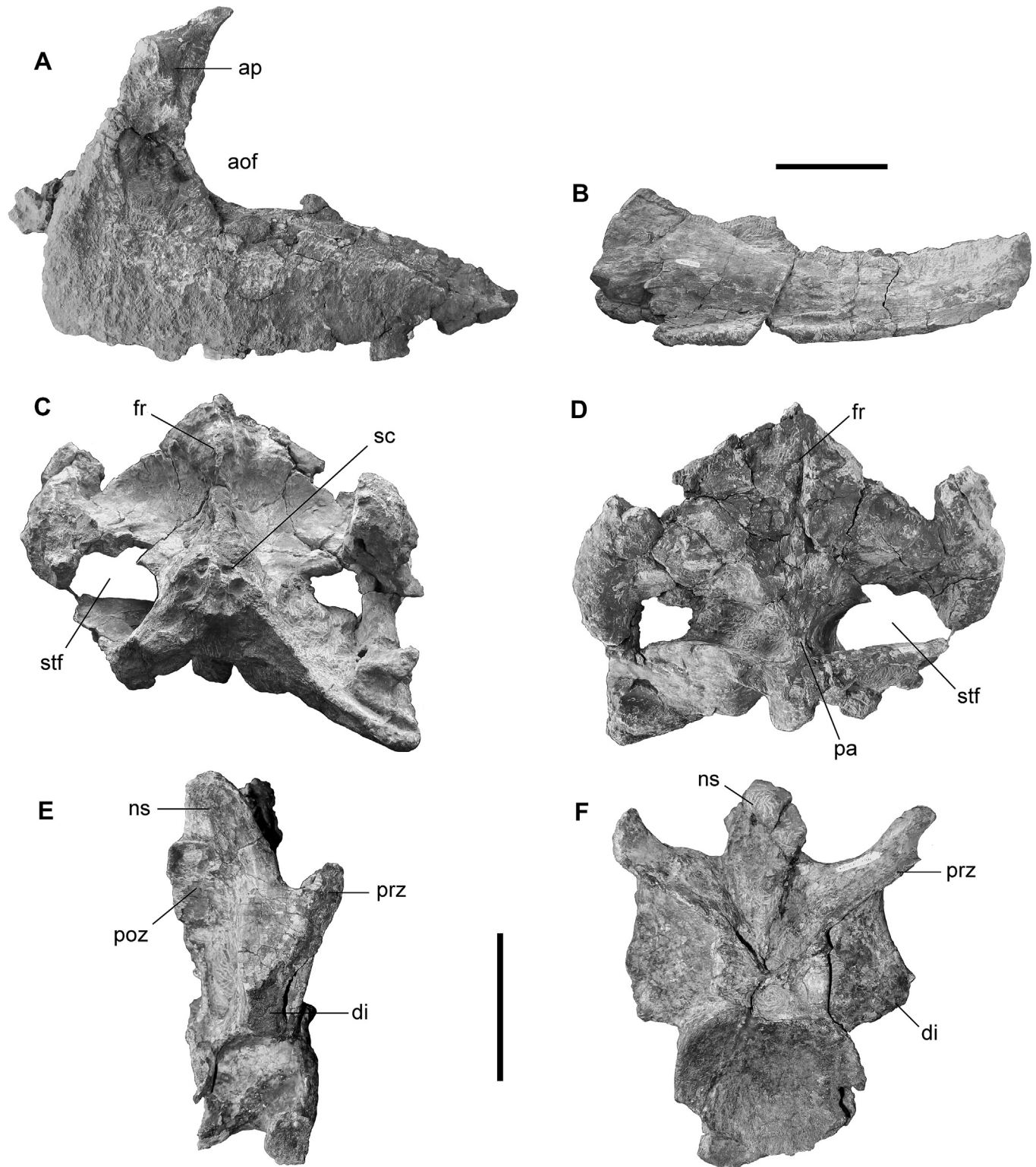


Fig. 4. Selected bones of *Ekrixinatosaurus novasi* (MUPv-294, holotype). (A) Left maxilla in lateral view, (B) right dentary in lateral view, skull roof in (C) dorsal and (D) ventral views, and posterior cervical vertebra in (E) right lateral and (F) anterior views. Abbreviations: aof, antorbital fenestra; ap, ascending process; di, diapophysis; fr, frontal; ns, neural spine; pa, parietal; poz, postzygapophysis; prz, prezygapophysis; sc, sagittal crest; stf, supratemporal fenestra. Scale bar equals 20 cm in (A–D) and 10 cm in (E–F).

collected 15 m away from the postcranial elements. Previous authors assumed that all these elements pertained to a single individual, and based on the shape of the maxilla, they referred *Kryptops* to the Abelisauridae. Although the maxilla exhibits apomorphic features supporting its assignment to this family (e.g.,

extensive external neurovascular texturing, reduction of the antorbital fossa, and subvertical ascending process), the postcranial bones exhibit a morphology inconsistent with those of Abelisauridae, Abelisauroidae, or even Ceratosauria. As noted by [Sereno and Brusatte \(2008\)](#), the vertebrae and pelvic girdle assigned to

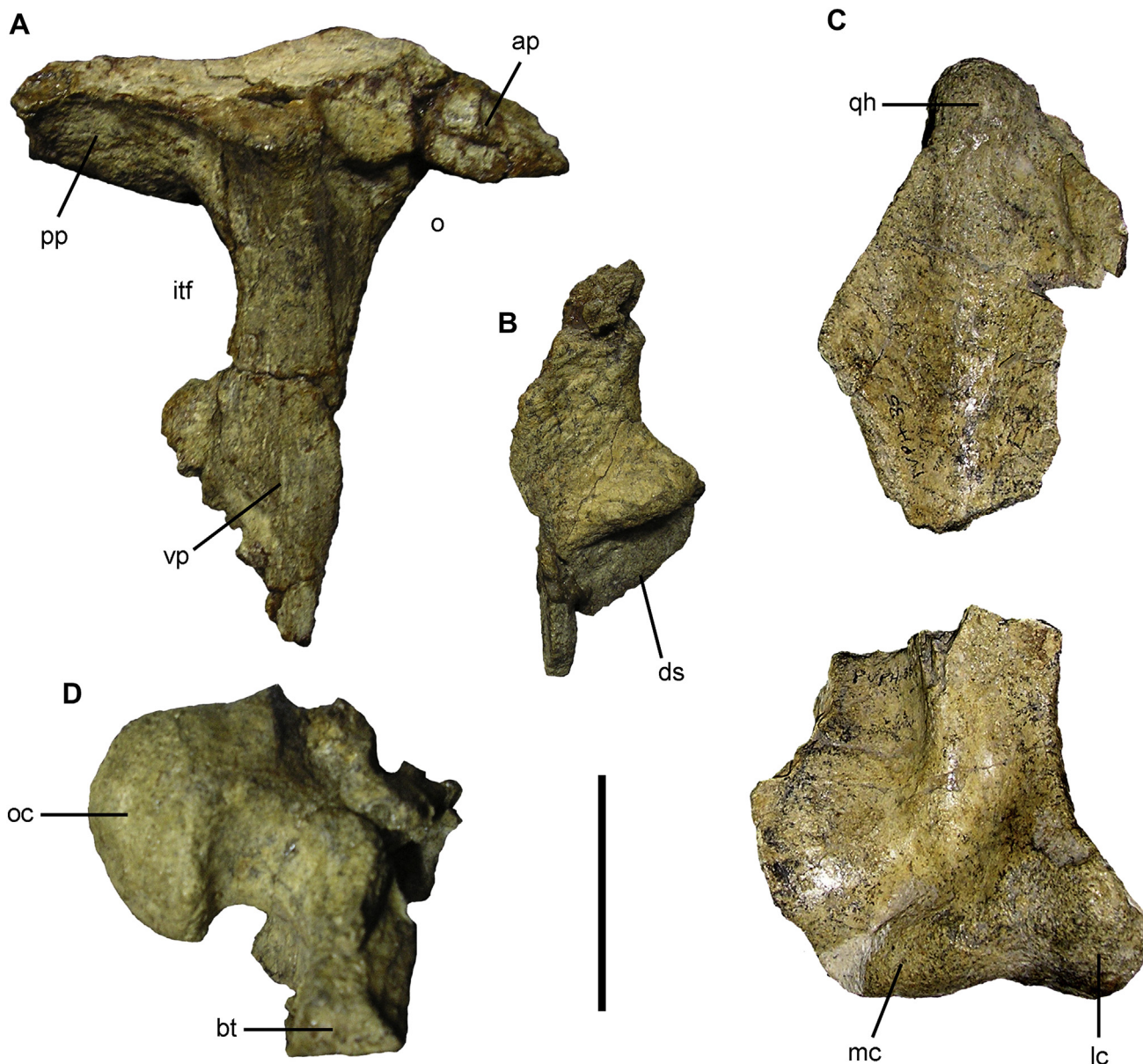


Fig. 5. Selected skull bones of *Ilokelesia aguadagrandensis* (MCF-PVPH-35, holotype). (A) Right postorbital in lateral view, (B) distal end of left postorbital in lateral view, (C) right quadrate in posterior view and (D) basisoccipital in right lateral view. Abbreviations: ap, anterior process; bt, basal tubera; ds, distal step; itf, infratemporal fenestra; lc, lateral condyle; mc, medial condyle; o, orbit; oc, occipital condyle; pp, posterior process; qh, quadrate head; vp, ventral process. Scale bar equals 5 cm.

Kryptops exhibit major differences from these elements in abelisaurids. Furthermore, the postcranial bones assigned to *Kryptops* exhibit allosauroid features, such as dorsal vertebrae with strongly developed interspinous ligament scars in the neural spines, and a pubis with an anteriorly concave shaft and strongly enlarged pubic boot. Moreover, the presence of high posterior dorsal and sacral neural spines and highly pneumatized sacral vertebrae support their referral to Carcharodontosauridae rather than to Abelisauridae. Accordingly, the hypodigm of *Kryptops* should be restricted to the holotype maxilla that possesses abelisaurid affinities, while the postcranium shows allosauroid features. It must be noted that similar observations and conclusions on the systematic position of *Kryptops* has been recently reached by Carrano et al. (2012).

The most recent phylogenetic analyses conducted in order to assess abelisauroid relationships are those of Carrano and Sampson

(2008), Canale et al. (2009) and Pol and Rauhut (2012). These analyses found a monophyletic Noosauridae (Carrano and Sampson, 2008; Canale et al., 2009). The Indian *Laevisuchus*, the European *Genusaurus*, and the Patagonian *Velocisaurus* were included by Carrano and Sampson (2008) within Noosauridae, and *Ligabueino* and the Jurassic African *Elaphrosaurus* were included by Canale et al. (2009) within this family group. Pol and Rauhut (2012) considered Noosauridae to be composed of *Noosaurus*, *Velocisaurus*, *Masiakasaurus* and *Laevisuchus*, whereas *Elaphrosaurus* was included together with *Limusaurus* and *Spinostropheus* within an informal clade of “elaphrosaurs”. It should also be noted that *Elaphrosaurus* was found by Carrano and Sampson (2008) to be outside Abelisauroidae, thus yielding a polyphyletic Noosauridae sensu Canale et al. (2009). The monophyly of Noosauridae was supported by the following synapomorphies by Carrano and Sampson (2008): maxilla with a short and rectangular palatal

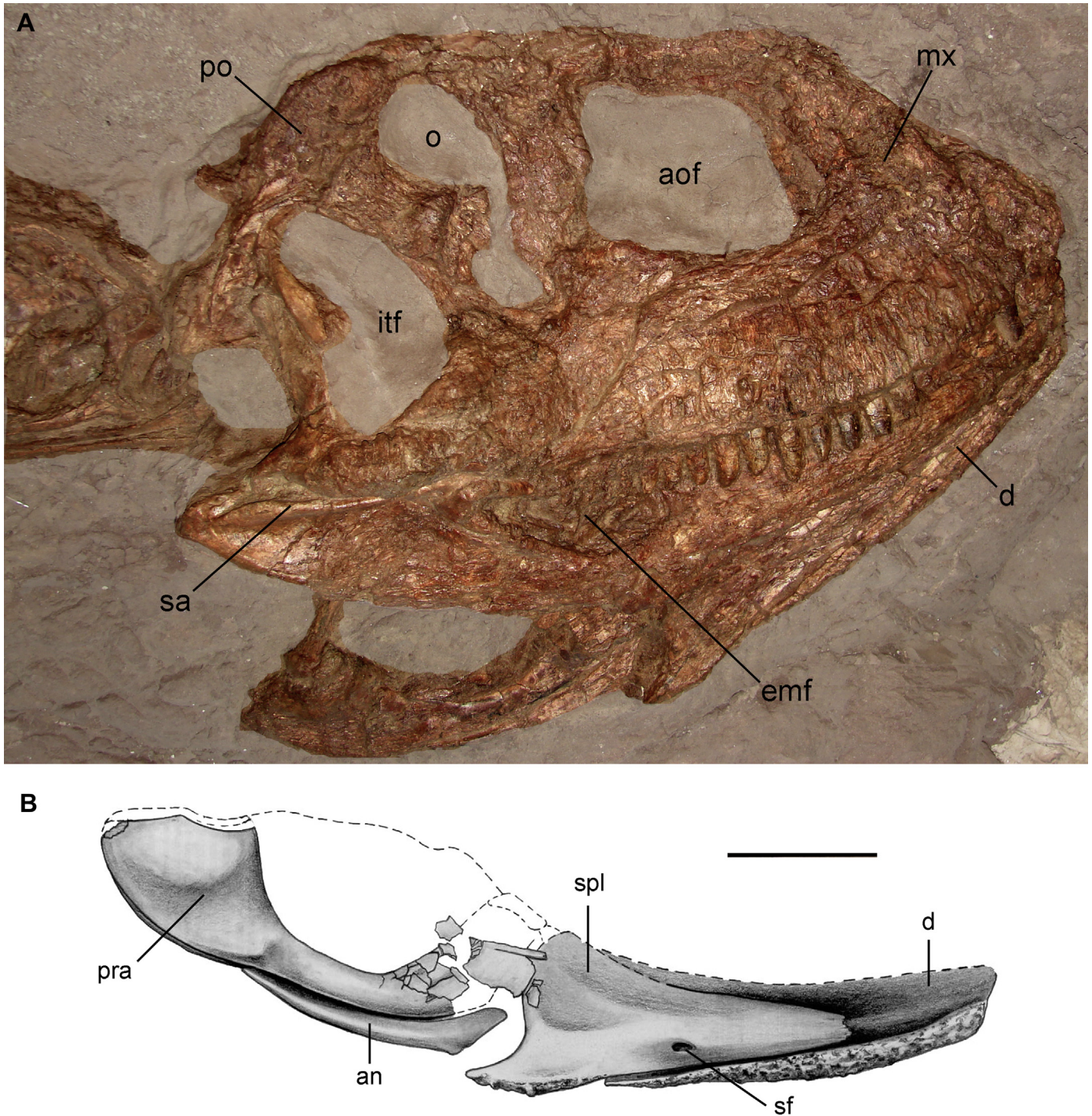


Fig. 6. Skull bones of *Skorpiovenator bustingorryi* (MMCH-Pv 48, holotype). (A) Skull in right lateral view and (B) left mandible in medial view. Abbreviations: an, angular; aof, antorbital fenestra; d, dentary; emf, external mandibular fenestra; itf, infratemporal fenestra; mx, maxilla; o, orbit; po, postorbital; pra, prearticular; sa, surangular; sf, splenial foramen; spl, splenial. Scale bar equals 10 cm.

process, anteroventral border of antorbital fenestra demarcated by a raised ridge, less than 12 maxillary teeth, paradental plates obscured in medial view, cervical neural spines positioned at the level of the anterior half of the centrum, anterior cervical vertebrae with long and thin epiphyses, dorsal vertebral centrum length more than twice centrum height, mid-sacral centra not constricted transversely, femur with a medial epicondyle represented by a long flange, metatarsal II with a reduced width relative to the widths of

metatarsals III and IV, and metatarsal IV with a distal end taller than broad. In the same way, the monophyly of Noasauridae is supported by the following synapomorphies recognized in the analysis by Canale et al. (2009): cervical vertebrae postzygapophyses swept back and posteriorly surpassing the posterior end of vertebral centrum, cervical neural arches low and elongated, and ilium with an acute preacetabular process that is subequal in length to the postacetabular process. It should be noted that none of the

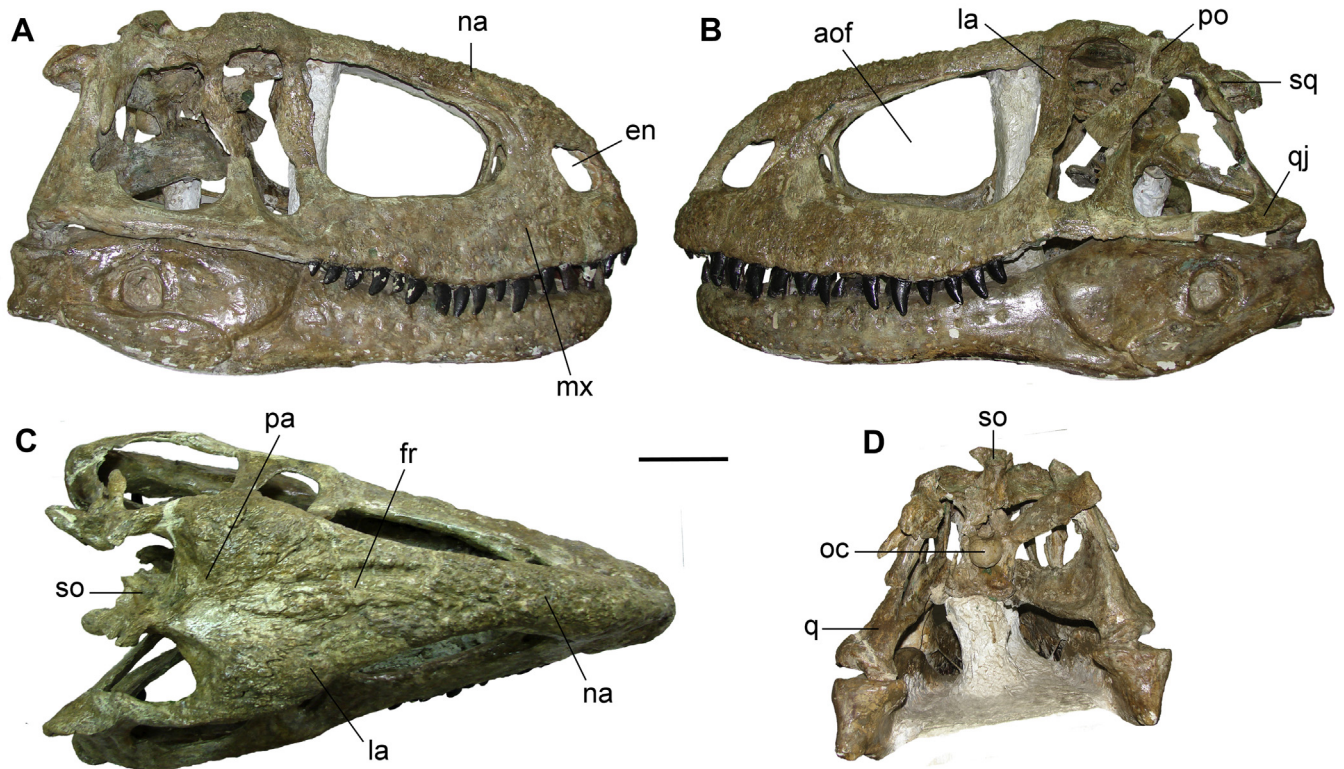


Fig. 7. Skull of *Abelisaurus comahuensis* (MPCA-11098, holotype) in (A) left lateral, (B) right lateral, (C) dorsal and (D) posterior views. Abbreviations: aof, antorbital fenestra; en, external naris; fr, frontal; la, lacrimal; mx, maxilla; na, nasal; oc, occipital condyle; pa, parietal; po, postorbital; q, quadrate; qj, quadratejugal; so, supraoccipital; sq, squamosal. Scale bar equals 20 cm.

noasaurid synapomorphies found by Carrano and Sampson (2008) and Canale et al. (2009) are present simultaneously in both analyses. Later, Pol and Rauhut (2012), obtained the following noasaurid synapomorphies: cervical neural spines positioned at the level of the anterior half of the centrum, mid-cervical vertebrae with postzygapophyses overhanging the centrum posteriorly, elongate dorsal vertebral centrum, and reduced shaft and proximal end of metatarsal II. It is worth noting that the above mentioned phylogenetic analyses on noasaurid relationships differ from each other regarding the genera that are considered members of the family. Consequently, the monophyly, taxonomic composition, and list of synapomorphic features of the Noasauridae are still under debate. A phylogenetic analysis including a comprehensive list of characters and increased taxonomic sample is needed in order to shed light on the phylogenetic relationships of this group of small-sized abelisauroids.

Regarding Abelisauridae, Carrano and Sampson (2008) and Canale et al. (2009) found a consistent taxonomic content for the group, with *Rugops* as its most basal representative. However, Pol and Rauhut (2012) found the recently described Jurassic *Eoabelisaurus mefi* as the most basal member of Abelisauridae (see below). Carrano and Sampson (2008) listed the following unambiguous synapomorphies of Abelisauridae: maxilla and nasal with a sculptured external surface, prefrontals partly or completely fused in adults, contact between the postorbital and lacrimal that excludes the frontal from the orbital rim, lacrimal fossa covered by a dermal ossification, and paracanthals vertically striated or with a ridged surface (Fig. 8). However, Canale et al. (2009) recovered the following synapomorphies of Abelisauridae: external surface of the cranial roof bones with large tubercles on nasals and small-sized tubercles among the remaining cranial roof bones, including postorbital and lacrimal; tooth apex centrally positioned, with

mesial margin strongly convex and distal margin straight or slightly curved; premaxillary and maxillary interdental plates bearing vertical ridges; premaxilla with a reduced palatal process; antorbital fenestra with a ventral margin located at the same level as the ventral margin of the antorbital fossa; antorbital fossa anteroposteriorly reduced; and maxilla with a large lateral articulation surface for the nasal (Fig. 8). Both phylogenetic analyses agree in the recognition of dermal cranial bones (e.g., premaxilla, maxilla, nasal) with a sculptured lateral surface and paracanthals with a ridged medial surface as synapomorphies of Abelisauridae.

Phylogenetic hypotheses about the relationships within Abelisauridae differ substantially between the hypotheses presented by Carrano and Sampson (2008) and Canale et al. (2009). Carrano and Sampson (2008) depicted *Ekrixinatosaurus* as the sister taxon of a node that encompasses a South American clade made up of *Ilokelesia* and *Carnotaurus*, and an Indo-Malagasy group including *Majungasaurus*, *Indosaurus* and *Rajasaurus*. Following this phylogenetic arrangement, Carrano and Sampson (2008) stated that “the simplest explanation for this pattern is that the Indo-Malagasy forms dispersed from South America into these two regions, although this could have occurred prior to tectonic separation (direct terrestrial dispersal) or after (vicariance)”. Based on this evidence, Carrano and Sampson (2008) do not favor an early severing of Africa from the remaining southern landmasses (i.e., the “Africa-first” hypothesis; Sampson et al., 1998), nor a late connection between Africa and other Gondwanan continents into the Late Cretaceous (Wilson et al., 2003; Sereno et al., 2004).

Alternatively, the analysis conducted by Canale et al. (2009) recovered a South American abelisauroid clade, Brachyrostra, composed of *Carnotaurus*, *Aucasaurus*, *Ilokelesia*, *Ekrixinatosaurus* and *Skorpiovenator*. Brachyrostrans are characterized by strongly ornamented and shortened skulls with a progressive trend to

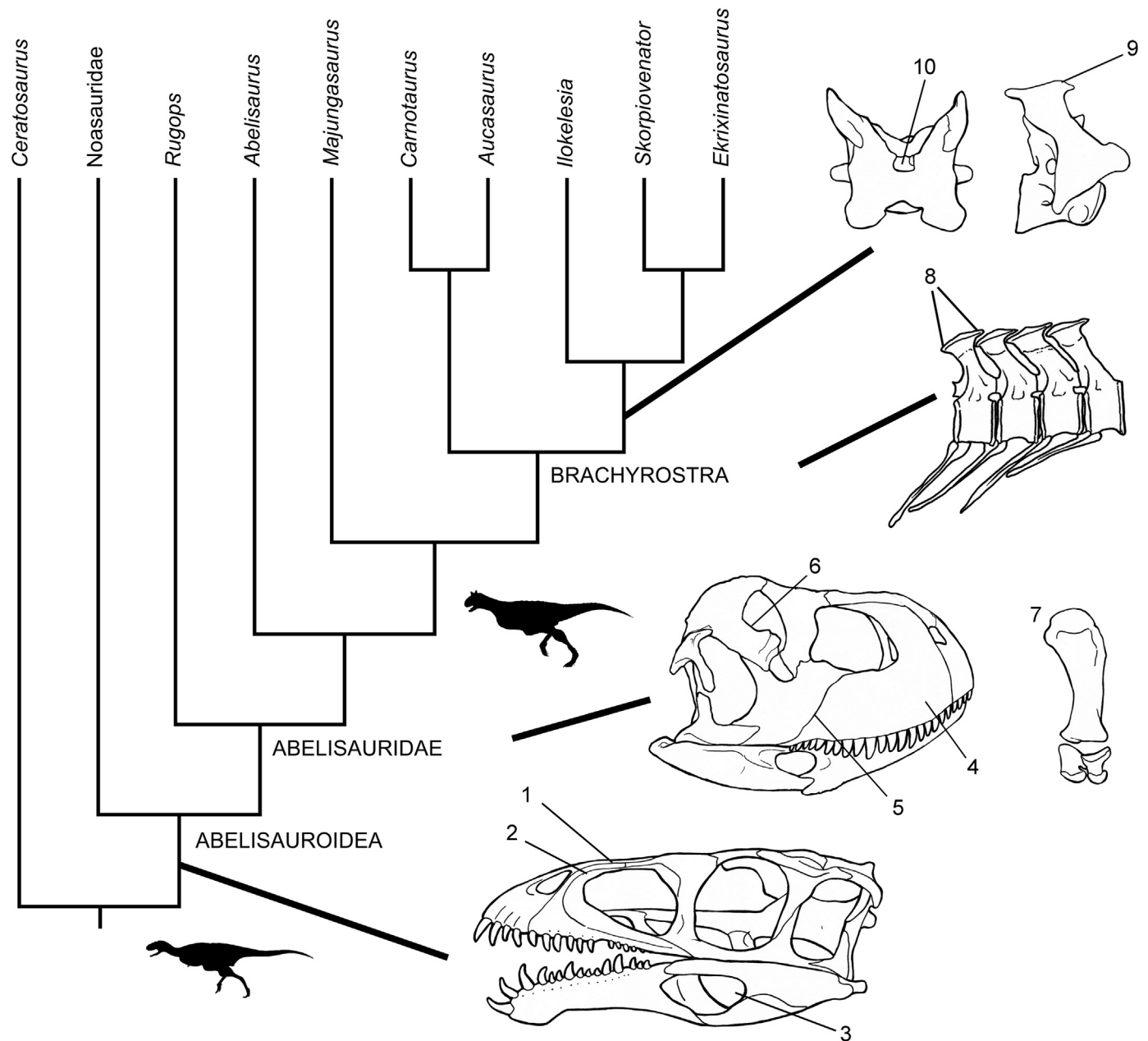


Fig. 8. Time calibrated phylogenetic tree showing the relationships of the main Abelisauroid clades. Node 1 (Abelisauroidea): 1 – reduced ascending process of maxilla, 2 – reduced antorbital fossa, 3 – expanded mandibular fenestra. Node 2 (Abelisauridae): 4 – anteroposteriorly shortened and dorsoventrally tall maxilla, 5 – oblique jugal–maxilla contact, 6 – anteriorly inclined distal end of postorbital, 7 – reduced forelimbs, lacking ungual phalanges. Node 3 (Brachyrostra): 8 – caudal transverse processes anteroposteriorly expanded. Node 4 (Carnotaurini): 9 – cervical epiphyses with anterior process, 10 – very reduced cervical neural spines.

enclosure of the orbit (Fig. 8). The Patagonian *Abelisaurus* and the Malagasy *Majungasaurus* are interpreted as successively closer sister taxa of Brachyrostra. One of the most interesting conclusions reached by Canale et al. (2009) is the basal position of *Majungasaurus* with respect to Brachyrostra, being distantly related to *Carnotaurus*. The latter phylogenetic arrangement contrasts with previous hypotheses in which both taxa appeared to be more closely related to each other than to other abelisaurids (Sampson et al., 1998; Sereno, 1999; Wilson et al., 2003; Sereno et al., 2004). In congruence with the vast majority of previous analyses, *Rugops* and *Abelisaurus* were recovered as successive sister groups of the remaining abelisaurids (i.e., Carnotaurinae; Sampson et al., 1998; Sereno, 1999; Carrano et al., 2002; Coria et al., 2002; Wilson et al., 2003; Sereno et al., 2004).

It should be noted that the brachyrostran *Ilokelesia aguadagrandensis* (Fig. 5) was formerly described by Coria and Salgado (2000) as the basalmost abelisaurid. Nevertheless, recent analyses have posited *Ilokelesia* nested within derived abelisaurids. Coria and Salgado (2000) described the left postorbital of *Ilokelesia* as having a relatively acute and unexpanded end of the jugal process, lacking a distal fan-shaped expansion, although this condition appears to be due to the poor preservation of the bone. In fact, the distal end of the right postorbital is preserved in the holotype of *Ilokelesia aguadagrandensis*, allowing recognition of the typical abelisaurid morphology as possessing a subrectangular distal end with a well-developed distal fan-shaped expansion (Fig. 5A).

The recovery of an abelisaurid clade restricted to South America (i.e., Brachyrostra) suggests a new model for abelisaurid diversi-

fication. It suggests that at least from the Cenomanian to the Maastriichtian, most South American abelisaurids may have been isolated from other Gondwanan relatives. This is in concordance with some paleogeographical reconstructions of the sequence of isolation of the Gondwanan landmasses (Krause et al., 2007), but does not necessarily apply to the diversification of the remaining Cretaceous terrestrial tetrapods from South America (see below).

The phylogenetic arrangement proposed by Canale et al. (2009) affects previous hypotheses regarding primary homology of the origin of horns among abelisaurids. The presence of horn-like structures in the skull roof was thought to represent an apomorphy of Carnotaurinae (= *Rajasaurus* + (*Majungasaurus* + *Carnotaurus*)) (Sereno et al., 2004). However, the latter interpretation is not supported by Canale et al. (2009) because they are optimized as independent neomorphisms, in which the horn-like prominences present in abelisaurid taxa differ in position as well as in bone composition (i.e., a single frontal eminence in *Majungasaurus*, a pair of frontal horns in *Carnotaurus*, and dorsally inflated postorbitals in *Skorpiovenator* and *Ekrixinatosaurus*).

The morphological diversity of abelisauroids has been recently increased with the description of the basal form *Austrocheirus isisii* (Ezcurra et al., 2010). The holotype specimen of this taxon comes from the late Turonian–early Coniacian Pari Aike Formation of Santa Cruz Province (Fig. 9), representing the southernmost abelisauroid record. *Austrocheirus* represents the earliest known large abelisauroid bearing non-atrophied hands. The evidence provided by this taxon suggests that the strong forelimb reduction recorded in derived abelisaurids is not directly correlated with their increased body size, but rather that such shortening of forelimb bones seems to be an evolutionary event exclusive to Abelisauridae within Ceratosauria (Ezcurra et al., 2010). *Austrocheirus* was found within a polytomy at the base of Abelisauroida with *Noasaurus*, *Ligabueino*, *Masiakasaurus*, *Elaphrosaurus*, and Abelisauridae (Ezcurra et al., 2010). Thus, *Austrocheirus* indicates the presence of medium-sized (roughly 8 m, based on comparisons with *Ceratosaurus*; Madsen and Welles, 2000) basal abelisauroids at least until the Coniacian. Rauhut (2012) has recently considered *Austrocheirus* as an indeterminate theropod, casting doubts about its abelisauroid affiliation, based on alternative identifications of metacarpal III and manual phalanx described by Ezcurra et al. (2010). However, the element originally identified as metacarpal III exhibits lateroventrally deflected distal condyles which are separated by a wide and deep median notch, and shaft proportionally short proximodistally, a set of traits supportive of the identification made by Ezcurra et al. (2010). Besides, the available isolated non-ungual phalanx exhibits distal condyles strongly asymmetrical in ventral view, and with the lateral condyle much more proximally extended than the medial one, constituting features supportive of its original identification as a manual element. In sum, we keep original interpretation of *Austrocheirus* as a member of Abelisauroida, pending further information.

The oldest records of abelisauroid theropods include *Berberosaurus liassicus* from the Early Jurassic of Africa (Allain et al., 2007), *Eoabelisaurus mefi* from Middle Jurassic beds of Central Patagonia (Pol and Rauhut, 2012), *Elaphrosaurus bambergi* from the Late Jurassic (Tithonian) of Tanzania (Janensch, 1920), and *Limusaurus inextricabilis* from the Late Jurassic of China (Xu et al., 2009). We agree with Rauhut (2012) in considering the recent report of a basal abelisauroid from the Middle Jurassic of England as problematic and its systematic position should be regarded as an indeterminate averostran (contra Ezcurra and Agnolín, 2012a). The discoveries of *Berberosaurus* and *Eoabelisaurus* have been interpreted in support that the origin of Abelisauroida must be traced back to the Early Jurassic. However, recent reanalyses of *Berberosaurus* (Carrano and Sampson, 2008; Ezcurra et al., 2010) indicate that this taxon may be

better considered as a basal non-abelisauroid ceratosaurian. Regarding *Eoabelisaurus*, Pol and Rauhut (2012) found this taxon as a Middle Jurassic member of Abelisauridae, thus weakening the interpretation that the paleobiogeographical diversification of the group was in concert with the continental fragmentation of Gondwana during the Cretaceous (Sereno et al., 2004; Carrano and Sampson, 2008; Canale et al., 2009). Pol and Rauhut (2012) recognized several synapomorphies supporting *Eoabelisaurus* as a member of Abelisauridae, including: 1) laterally covered lacrimal antorbital fossa, 2) broad cervical prespinal fossae, 3) anteroposteriorly short anterior caudal neural spines, 4) absence of a ventral groove in the anterior caudals, 5) presence of rudimentary centrodiaepophyseal laminae in the anterior mid-caudals, 6) reduced distal ginglymus in the manual phalanges, and 7) presence of a flexor depression in the pedal unguals. However, some of these characters deserve comments regarding their respective distributions among Ceratosauria: character 1 is also observed in *Ceratosaurus nasicornis* (USNM 4735); character 2 is also present in *Noasaurus leali* (PVL 4061); character 3 is also present in *Ceratosaurus nasicornis* (e.g., USNM 4735, fourth caudal vertebra; Madsen and Welles, 2000: plate 17e); character 5 was recently reported for the noasaurid *Masiakasaurus* (Carrano et al., 2011) and its condition is unknown in *Laeviusuchus*, *Noasaurus* and *Velocisaurus*; and finally, character 6 is also present in the “elaphrosaur” *Limusaurus* (Xu et al., 2009), but it is absent in *Ceratosaurus* (Gilmore, 1920: 105, 106) and *Masiakasaurus* (Carrano et al., 2011: fig. 20). Accordingly, characters 1, 2, 3, and 5 do not represent unambiguous apomorphies of Abelisauridae, but probable apomorphies of Abelisauroida or Ceratosauria. In sum, we consider that the phylogenetic relationships of *Eoabelisaurus* deserve further testing in future quantitative analyses.

2.2. Carcharodontosauridae

The Carcharodontosauridae includes all the allosauroid theropods that are more closely related to *Carcharodontosaurus* than to *Allosaurus* or *Sinraptor* (Holtz et al., 2004). Although members of this theropod family were first recorded in Cenomanian beds of Africa (i.e., *Carcharodontosaurus saharicus*), the most complete fossil record currently known of this group comes from Patagonia. The most complete and informative carcharodontosaurids are *Giganotosaurus carolinii* (Candeleros Formation; Coria and Salgado, 1995) (Fig. 10), represented by an almost complete skeleton that includes a partial skull, and *Mapusaurus roseae* (Huincul Formation; Coria and Currie, 2006), represented by several specimens corresponding to different ontogenetic stages (Coria and Currie, 2006). To this list must be added *Tyrannotitan chubutensis* from the Aptian Cerro Castaño Member of the Cerro Barco Formation, which adds valuable information about the early history of the group (Novas et al., 2005) (Fig. 11).

The Cretaceous Carcharodontosauridae constitutes the youngest clade of Allosauroida. The latter group also includes the Late Jurassic *Allosaurus* from North America (Madsen, 1976), and the Sinraptoridae from Asia and Europe (Currie and Zhao, 1993; Benson, 2010) (Fig. 12). Derived carcharodontosaurids evolved large skulls, reaching lengths in *Giganotosaurus* of 190 cm from premaxilla to quadrate (Calvo and Coria, 2000), thus surpassing the length of the largest skull of *Tyrannosaurus rex* (140 cm long; Larson, 1991). This group of medium to gigantic theropods possess widely fenestrated skulls, in some cases with heavily sculptured facial bones, especially in derived forms (Fig. 12). The fusion of cranial bones (frontal to its counterpart, prefrontal to lacrimal) is also a common trait. In carcharodontosaurids the postorbital is in contact with the lacrimal above the orbit (excluding the frontal from the orbital rim) and has an anteriorly projected suborbital



Fig. 9. Outcrops of the Mata Amarilla Formation (Upper Cretaceous) at the shore of Viedma Lake, the fossil site where the holotype of *Austrocheirus isasii* was collected.

flange. Some authors (Holtz and Rey, 2007) have hypothesized that larger forms as *Mapusaurus* and *Carcharodontosaurus* hunt and fed upon the huge coeval titanosaurian sauropods such as *Argentinosaurus* (Bonaparte and Coria, 1993) and *Paralititan* (Smith et al., 2001).

It was previously thought that the Carcharodontosauridae was a group of Gondwanan distribution (Currie and Carpenter, 2000; Novas et al., 2005; Coria and Currie, 2006), but now it is relatively well established that this clade attained a global distribution by the Early Cretaceous, as evidenced by the Patagonian *Tyrannotitan*, the European *Concavenator* from the Barremian of Spain (Ortega et al., 2010), *Eocarcharia* from Aptian beds of Niger (Sereno and Brusatte, 2008), and *Kelmaysaurus* from the Early Cretaceous of China (Brusatte et al., 2012). Moreover, recent findings appear to indicate that carcharodontosaurids were already present by the Late Jurassic, as suggested by the discovery of the genus *Veterupristisaurus* in the Tithonian Tendaguru Formation of Tanzania (Rauhut, 2011). Moreover, *Shaochilong* from Turonian beds of China (Brusatte et al., 2009), indicates the survival of carcharodontosaurids in the post-Cenomanian of Asia. The subfamily Carcharodontosaurinae is restricted to the African–South American realm (i.e., *Carcharodontosaurus*, *Mapusaurus*, *Giganotosaurus*) (Brusatte and Sereno, 2008) (Fig. 12). Carcharodontosaurines constituted some of the dominant large predatory dinosaurs from

the Aptian to Cenomanian, sharing the role of top predators with the similarly large spinosaurids.

Carcharodontosaurid phylogeny has been the focus of much research, and in the last 15 years more than 15 cladistic studies have been presented focusing on Allosauroidae and Carcharodontosauridae (i.e., Sereno et al., 1996; Harris, 1998; Forster, 1999; Currie and Carpenter, 2000; Holtz, 2000; Coria and Currie, 2002a; Rauhut, 2003; Holtz et al., 2004; Novas et al., 2005; Coria and Currie, 2006; Smith et al., 2007, 2008; Brusatte and Sereno, 2008; Sereno and Brusatte, 2008; Brusatte et al., 2009; Benson, 2010; Benson et al., 2010a; Ortega et al., 2010; Eddy and Clarke, 2011). This makes Allosauroidae one of the most debated archosaurian clades in terms of its internal phylogenetic relationships. Although allosauroid phylogeny has been debated, a consensus is now emerging, and three recent datasets (i.e., Brusatte and Sereno, 2008; Benson et al., 2010a; Eddy and Clarke, 2011) recovered the same basic topology with Sinraptoridae, *Allosaurus* and *Neovenator* as successively closer sister taxa of Carcharodontosauridae. Another point of agreement is the recognition of a group of derived gigantic Cenomanian allosauroids including *Carcharodontosaurus*, *Giganotosaurus* and *Mapusaurus*. Several authors proposed *Tyrannotitan* as a basal carcharodontosaurid, being sister to the clade formed by *Giganotosaurus* and *Carcharodontosaurus* (Novas et al., 2005; Smith et al., 2007; Sereno and Brusatte, 2008; Benson et al., 2010a). On the other

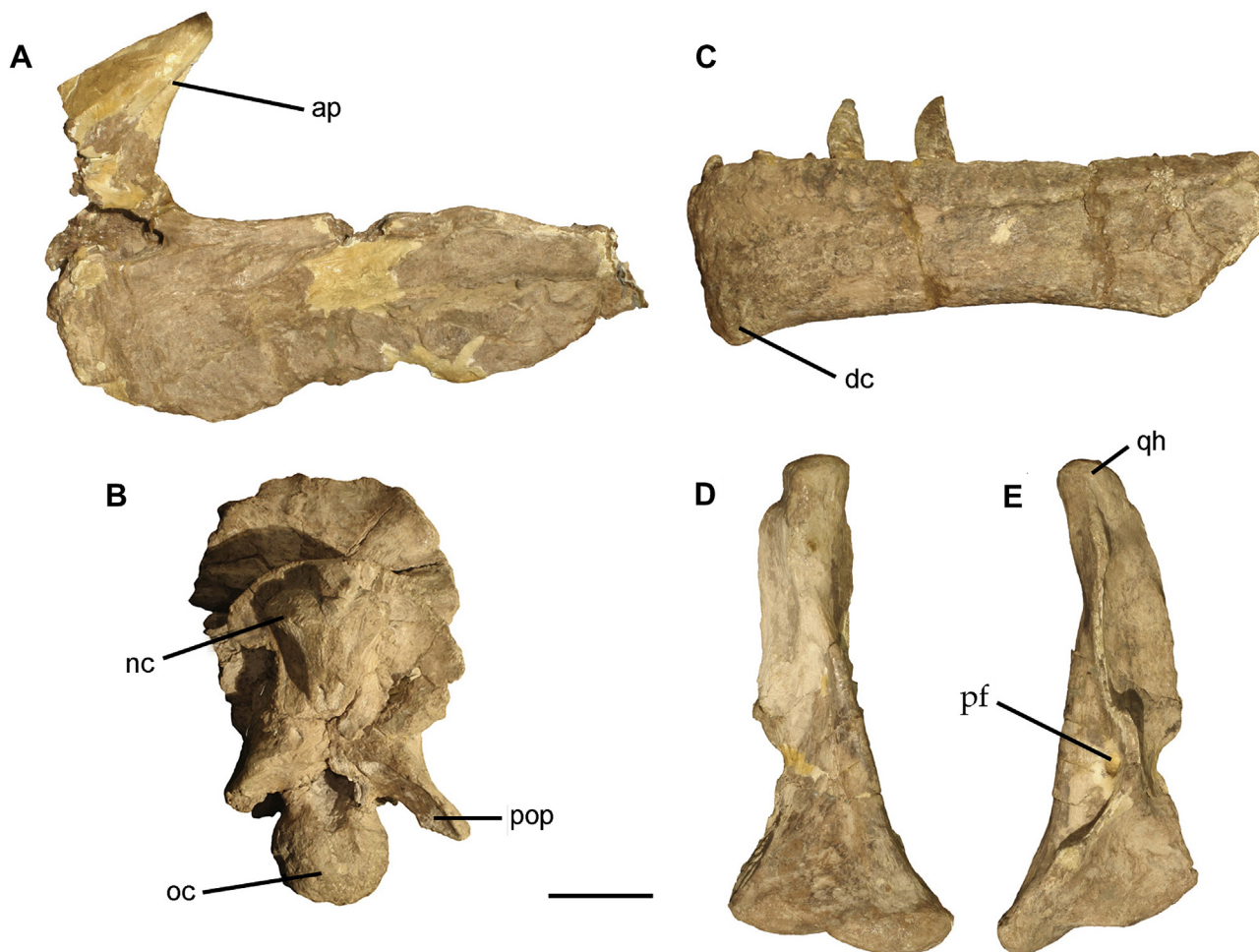


Fig. 10. Selected skull elements of *Giganotosaurus carolinii* (MMCH-Pv 1, holotype). (A) Left maxilla in lateral view, (B) braincase in dorsal view, (C) anterior end of left dentary in lateral view and right quadrate in (D) posterior and (E) medial views. Abbreviations: ap, ascending process; dc, dentary chin; nc, neural crest; oc, occipital condyle; pf, pneumatic foramen; pop, paraoccipital process; qh, quadrate head. Scale bar equals 10 cm.

hand, Coria and Currie (2006) suggested that *Tyrannotitan* may be a more derived carcharodontosaurid, closely related to the South American *Giganotosaurus* and *Mapusaurus*. In agreement with the latter proposal, the cladistic analysis here conducted (see SI) places *Tyrannotitan* inside Giganotosaurini (i.e., a clade of derived carcharodontosaurines also including *Giganotosaurus* and *Mapusaurus*). These three Patagonian taxa share a postorbital process of the jugal with an anteroposteriorly wide base, absence of pleurocoels on caudal vertebrae, a femur with a reduced fourth trochanter, a poorly defined cruciate ridge on the distal femur, and a shallow extensor groove on the distal femur (Coria and Currie, 2006; Brusatte and Sereno, 2008). Following these analyses, the South American giganotosaurinins and the African *Carcharodontosaurus* form the Gondwanan subfamily Carcharodontosaurinae. The Laurasian carcharodontosaurids *Shaochilong* and *Acrocanthosaurus* are successively sister taxa to Carcharodontosaurinae. *Eocarcharia*, *Concavenator* and *Neovenator* are here positioned in an unresolved polytomy at the base of Carcharodontosauridae.

Anatomical information afforded by Patagonian carcharodontosaurids allows testing of previous interpretations regarding the taxonomic diversity of African theropods. An example is the identification of some isolated and unusual neck vertebrae belonging to a large and bulky dinosaur, originally described as “*Spinosauros B*” by Stromer (1934). These vertebrae from the Cenomanian of northern Africa were considered by Russell (1996) as

being sufficiently different from other theropods to justify the erection of a new taxon, *Sigilmassasaurus brevicollis*. These cervicals are distinguished by their broad, low, and strongly opisthocoelous centra, a reniform caudal articular surface, a prominent keel on their ventral surface, and the presence of a single pleurocoel behind the parapophyses. The internal bone organization is of the camerate type, the neural spines are weakly developed, and the epiphyses are absent. Sereno et al. (1996) and Brusatte and Sereno (2008) interpreted these cervicals as belonging to *Carcharodontosaurus saharicus*, proposing *Sigilmassasaurus brevicollis* as a subjective junior synonym of *Carcharodontosaurus saharicus*. However, none of the *Sigilmassasaurus*-like cervicals were found in association with cranial material of *Carcharodontosaurus* (Paul Sereno, pers. comm. to FEN). Moreover, as noted by Novas et al. (2005a), these cervicals differ markedly from those of the better-known Patagonian carcharodontosaurids (i.e., *Giganotosaurus*, *Tyrannotitan*, and *Mapusaurus*), which bear dorsoventrally deep centra, a weakly developed ventral keel (if present), strongly developed epiphyses, a sharp prezygoepiphysal ridge, and double pleurocoels. Also, in *Giganotosaurus* and *Tyrannotitan* at least, the internal bone tissue is of camellate type. Overall, the *Sigilmassasaurus*-like cervical vertebrae do not correspond to *Carcharodontosaurus*, nor to Carcharodontosauridae. Preliminary results presented by Evers et al. (2012) provided conclusive evidence for the spinosaurid affinities of *Sigilmassasaurus*.

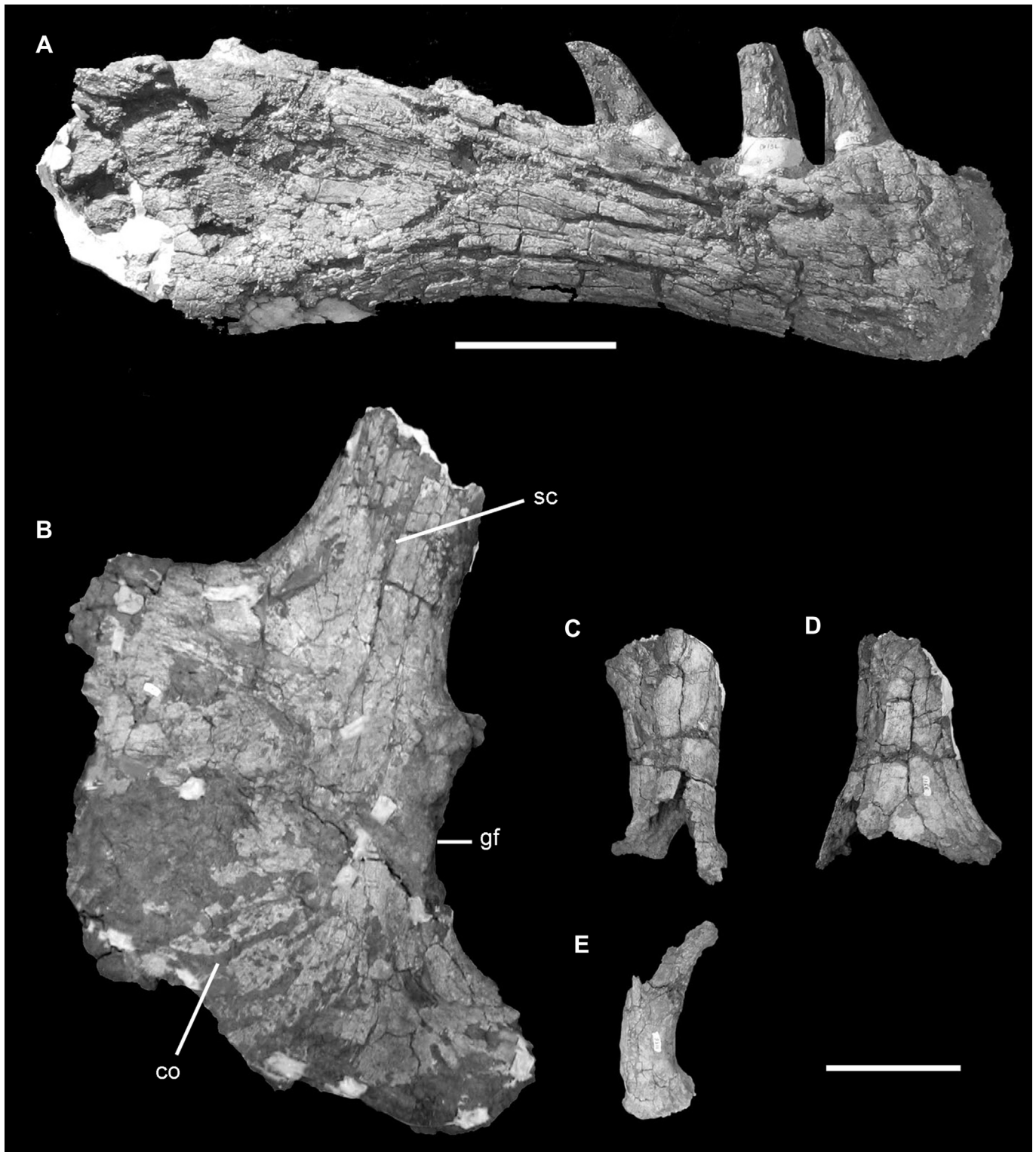


Fig. 11. Selected bones of *Tyrannotitan chubutensis* (Museo Provincial Egidio Feruglio, Chubut province, MPEF-PV 1157). (A) Right dentary in lateral view, (B) left scapulocoracoid in lateral view, left humerus in (C) anterior and (D) lateral views and (E) distal end of left radius in lateral view. Abbreviations: co, coracoid; gf, glenoid fossa; sc, scapula. Scale bar equals 20 cm.

2.3. Coelurosauria

Coelurosauria is a diverse clade of tetanuran theropods that are phylogenetically defined as the most inclusive clade containing *Passer domesticus* but not *Allosaurus fragilis*, *Sinraptor dongi* and

Carcharodontosaurus saharicus (Holtz, 1994; Sereno, 2005). To date, the fossil record of Laurasian coelurosaurs provides the most complete and informative resource for understanding the clade's anatomy and evolution. However, documentation of coelurosaurian theropods from the southern continents has increased considerably

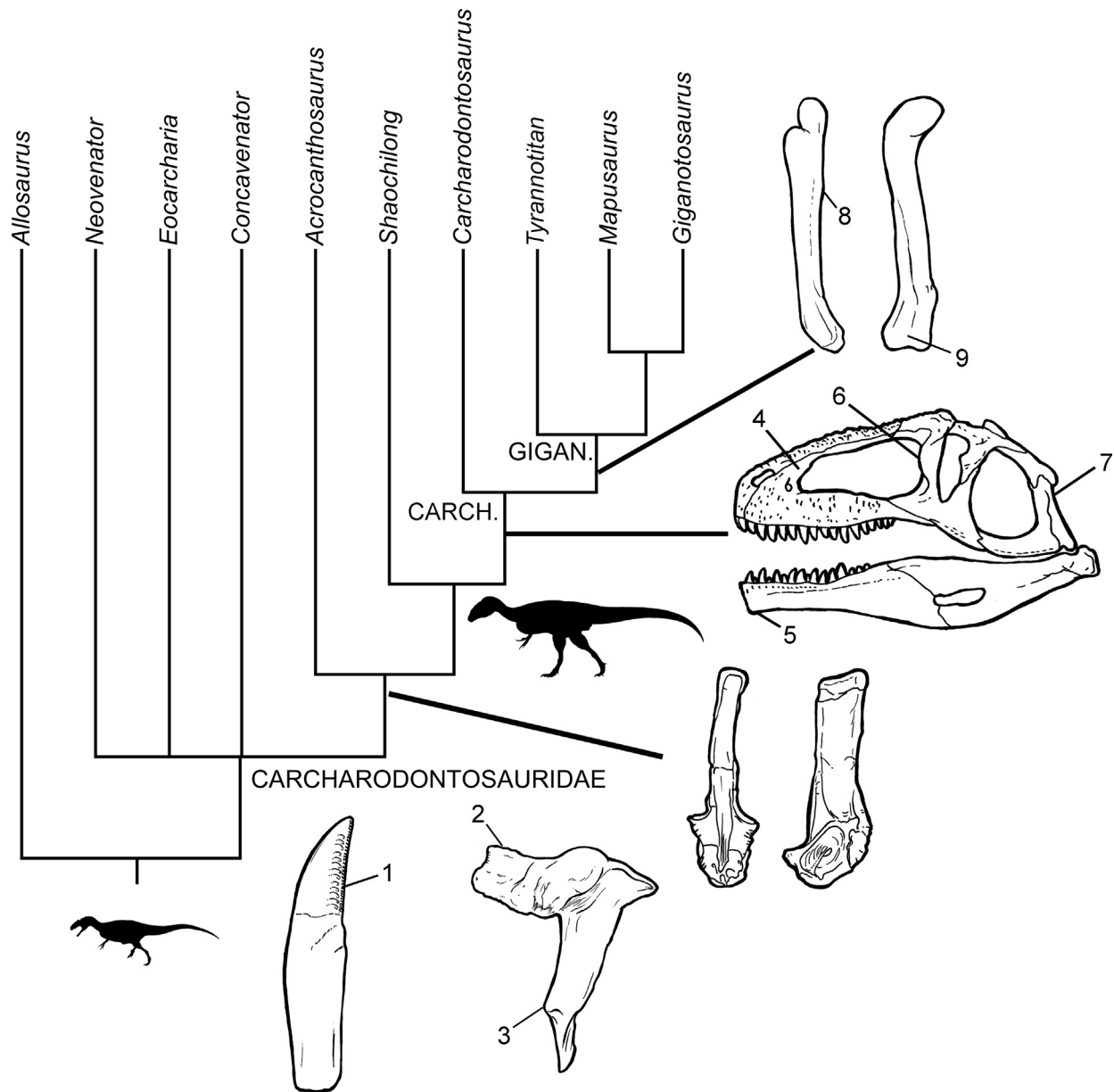


Fig. 12. Time calibrated strict consensus tree showing the relationships of the main carcharodontosaurid clades. Node 1 (Carcharodontosauridae): 1-blade-like teeth with marginal enamel wrinkles, 2-postorbital with postorbital boss and 3-orbital process. Node 2 (*Acrocanthosaurus* + Carcharodontosaurinae): tall dorsal neural spines which are “H” shaped in section. Node 3 (Carcharodontosaurinae): 4-reduced ascending process and antorbital fossa on the maxilla, 5-subrectangular chin, 6-anterior process on lacrimal, 7-anterodorsally inclined occiput. Node 4 (Giganotosaurini): 8-femur with reduced fourth trochanter and 9-shallow anterior distal extensor groove. Abbreviations: CARCH., Carcharodontosaurinae; GIGAN., Giganotosaurini.

since 1990, yielding valuable evidence regarding their diversification in Gondwana (e.g., Kellner, 1999; Novas, 1997a, 2009; Novas and Puerta, 1997; de Klerk et al., 2000; Martill et al., 2000; Makovicky et al., 2005; Novas et al., 2009, 2012; Agnolín et al., 2012; Choiniere et al., 2012). Remains of at least 13 non-avian coelurosaur nominal species have been recovered from different Cretaceous beds in South America, Africa, Madagascar, and Australia. In particular, Cretaceous beds from Patagonia greatly enlarged our understanding of the evolutionary history of Coelurosauria as a whole. The list of coelurosaurs from this region of South America includes the basal *Aniksosaurus darwini* (Bajo Barreal Formation, Cenomanian; Martínez and Novas, 2006) and *Bicentenario argentina* (Candeleros Formation, Cenomanian; Novas et al., 2012), the alvarezsaurids *Alvarezsaurus calvoi* (Bajo de la Carpa

Formation, Santonian; Bonaparte, 1991b), *Patagonykus puertai* (Portezuelo Formation, late Turonian–early Coniacian; Novas, 1996, 1997a), *Achillesaurus manazzonei* (Bajo de la Carpa Formation, Santonian; Martinelli and Vera, 2007), *Bonapartenykus ultimus* (Allen Formation, Maastrichtian; Agnolín et al., 2012), and *Alnashetri cerropoliciensis* (Candeleros Formation, Cenomanian; Makovicky et al., 2012), and the unenlagiids *Unenlagia comahuensis* (Portezuelo Formation, late Turonian–early Coniacian; Novas and Puerta, 1997), *Unenlagia paynemili* (Portezuelo Formation, late Turonian–early Coniacian; Calvo et al., 2004a), *Buitreraptor gonzalezorum* (Candeleros Formation, Cenomanian; Makovicky et al., 2005), *Neuquenraptor argentinus* (Portezuelo Formation, late Turonian–early Coniacian; Novas and Pol, 2005), *Pamparaptor micros* (Portezuelo Formation, late Turonian–early Coniacian; Porfiri et al.,

2011, but see below for an alternative interpretation) and *Austroaptor cabazai* (Allen Formation, Maastrichtian; Novas et al., 2009). In addition, it is here proposed that megaraptoran theropods are not allosauroids closely related to carcharodontosaurids, but basal members of Coelurosauria (see below).

2.3.1. Basal Coelurosauria

Bicentenaria argentina is a very basal coelurosaur known from more than a hundred bones belonging to different individuals (Novas et al., 2012). Its basal position within Coelurosauria is suggested by retention of double neural spines on the proximal caudal vertebrae, the distal end of femur showing a mediolateral crest, and by a transversely narrow ascending process of the astragalus. *Bicentenaria argentina* was placed as a very basal coelurosaur, nested between the archaic allosauroids and the lineage leading to the avian radiation (Novas et al., 2012). Its basal position and the absence of closely related taxa imply an extensive ghost lineage for the *Bicentenaria* lineage of about 70 million years. *Bicentenaria* was a medium sized theropod approximately 3 m long with elongate and gracile hindlimb bones, and an overall morphology reminiscent to that of some basal coelurosaurs such as *Tanycolagreus*, *Coelurus*, *Ornitholestes*, *Aniksosaurus* and *Santanaraptor*. The body size of these basal coelurosaurs is considerably less than those of non-coelurosaurian averostrans, such as ceratosaurians, spinosaurids, and allosauroids. Quantitative analyses indicate two main episodes of drastic size reduction in the evolutionary history of Coelurosauria (Novas et al., 2012): the first episode occurred at the base of the clade, as represented by *Bicentenaria*, *Zuolong*, *Tanycolagreus*, *Coelurus* and *Aniksosaurus*; and a second major size reduction took place at the base of Paraves (Turner et al., 2007a). The reductions in body size documented among coelurosaurs would have allowed adult individuals to exploit ecological niches not occupied by larger basal theropod clades. This hypothesis would explain the marked evolutionary radiation of Coelurosauria during the Middle and Late Jurassic.

Another basal coelurosaur recorded in the Cretaceous of Patagonia is *Aniksosaurus darwini* (Martínez and Novas, 2006) (Fig. 13). Some plesiomorphic features present in *Aniksosaurus* closely resemble the basal tetanuran *Allosaurus*, including the stout proportions of the fore- and hindlimb bones. *Aniksosaurus* was included for the first time in a numerical phylogenetic analysis by Choiniere et al. (2010a) who recovered this taxon as a basal compsognathid based on the presence of a fibular crest that extends from the proximal articular surface in the tibia. However, in *Aniksosaurus* the proximal margin of the fibular crest is clearly below the proximal articular surface of the tibia (MDT-PV 1/50), as it is the plesiomorphic state for tetanurans (Rauhut, 2003). Moreover, *Aniksosaurus* exhibits some plesiomorphic features absent in the remaining compsognathids and maniraptorans, such as a distal end of the tibia with a notch for the reception of the ascending astragalar process (Fig. 13D). Accordingly, the compsognathid affinities of *Aniksosaurus* are here regarded with caution. In contrast, the phylogenetic analysis performed by Novas et al. (2012) indicate that *Aniksosaurus* may represent a basal maniraptoriform coelurosaur.

In addition to *Bicentenaria* and *Aniksosaurus*, four more basal representatives of Coelurosauria have been recovered in other regions of Gondwana: the African *Nqwebasaurus*, from the Lower Cretaceous Kirkwood Formation, the Australian *Timimus*, from the Aptian–Albian Eumeralla Formation (Benson et al., 2012), and *Mirischia* and *Santanaraptor*, both from the Aptian Santana Formation of northeastern Brazil. This evidence demonstrates that a disparity of coelurosaurian clades, different from those recorded in Laurasia, radiated in Gondwana during the course of the Cretaceous (Novas, 2009).

2.3.2. Megaraptora

The first evidence for the presence of an enigmatic lineage of large-clawed theropods was provided by Novas (1998) with the description of *Megaraptor namunhuaiquii* from the late Turonian–early Coniacian Portezuelo Formation of NW Patagonia. The holotype of *Megaraptor* is composed of a fragmentary postcranium, including ulna, manual phalanx I-1, metatarsal III and the manual ungual of digit I (originally interpreted as the pedal ungual of digit II; Calvo et al., 2004b). This genus was formerly considered (Novas, 1998) as a probable member of Coelurosauria based on the gracile proportions of both phalanx I-1 and metatarsal III. However, general morphology of *Megaraptor* remained unknown until recently, when more complete specimens came to light (Calvo et al., 2004b). This new source of information allowed Calvo et al. (2004b) to recognize some basal tetanuran characters in *Megaraptor*: scapular blade craniocaudally wide with respect to its proximodistal length, proximal third fan-shaped, presence of fourth metacarpal and pubis with a notably expanded proximal end. These authors also indicated that *Megaraptor* represented a new lineage clearly distinct from other basal tetanurans, such as spinosaurids and carcharodontosaurids. The first quantitative phylogenetic analysis to evaluate the relationships of *Megaraptor* was conducted by Smith et al. (2007), who recovered this taxon as a derived member of Carcharodontosauridae, based on vertebral features previously identified by Calvo et al. (2004b). Brusatte and Sereno (2008) also supported allosauroid affinities for *Megaraptor*. However, a revised version of the dataset of Smith et al. (2007) recovered *Megaraptor* within Spinosauridae (Smith et al., 2008), a hypothesis supported by the presence of a suite of forelimb features.

Sereno et al. (2008) described the unusual and highly pneumatized theropod *Aerosteon riocoloradensis* from the Santonian Cañadón Amarillo Formation of western Argentina (Fig. 14), suggesting allosauroid affinities for this taxon. Novas (2009) advanced the possibility that *Aerosteon* and *Megaraptor* were closely related basal tetanurans sharing a similar morphology in the postorbital, cervical and caudal vertebrae, scapula and pubis. Subsequently, Benson et al. (2010a) conducted a comprehensive study on basal tetanuran phylogeny, including *Megaraptor* and *Aerosteon*. These authors recovered a monophyletic group formed by *Megaraptor*, *Aerosteon* and a suite of taxa previously considered either as basal coelurosaurs (i.e., *Orkoraptor burkei*, *Chilantaisaurus tashuikouensis*; Novas et al., 2008; Benson et al., 2010a) or basal allosauroids (i.e. *Fukuiraptor kitadanensis*, *Neovenator salerii*, *Australovenator wintonensis*; Hutt et al., 1996; Azuma and Currie, 2000; Hocknull et al., 2009). This new clade, named Neovenatoridae by Benson et al. (2010a), was found by these authors as deeply nested within Allosauroidea. Additionally, the neovenatorids were recovered as the sister-taxon of Carcharodontosauridae, both forming the new clade Carcharodontosauria (Benson et al., 2010a). Within Neovenatoridae, the European *Neovenator* and the Asiatic *Chilantaisaurus* were depicted as successive sister taxa to the new group Megaraptora, a clade conformed by *Megaraptor*, *Orkoraptor*, *Aerosteon*, *Australovenator*, and *Fukuiraptor*. Two megaraptoran clades were recognized by Benson et al. (2010a), one including the Asiatic *Fukuiraptor* and the Australian *Australovenator* and the other composed of the South American *Megaraptor* and *Aerosteon*, whereas the Patagonian *Orkoraptor* was recovered as a wildcard taxon occupying different positions within Megaraptora (Benson et al., 2010a). In this phylogenetic context, megaraptorans were envisaged as “coelurosaur parallels” in Cretaceous ecosystems, allowing them to coexist with large-bodied abelisaurids and carcharodontosaurids (Benson et al., 2010a).

However, we believe that the allosauroid affinities of megaraptorans are based on several features whose distribution among Tetanurae is problematic; for example, some of the purported



Fig. 13. Selected skeletal remains of *Anikosaurus darwini* (MDT-Pv 1/49). Left ilium in (A) lateral and (B) ventral views, (C) right femur in posterior view, (D) left foot in anterior view and (E) distal end of right tibia in anterior view and. Abbreviations: I–IV, first to fourth pedal digit; ac, acatubulum; bf, brevis fossa; cf, coppedicus fossa; fap, facet for the reception of the ascending process of teh astragalus; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; ip, ischial peduncle; pap, preacetabular process; pf, popliteal fossa; pop, postacetabular process; pp, pubic peduncle; tc, tibial condyle; tfc, tibiofibular crest. Scale bar equals 5 cm.

allosauroid, carcharodontosaurian, and/or neovenatorid traits show a wider distribution among Tetanurae (e.g., acromial process subrectangular, single meckelian foramen in dentary, presence of ulnar olecranon process, camellate internal vertebral structure,

strongly constricted posterior dorsal vertebrae; see *SI parts 2 and 3*), and others are present not only among carcharodontosaurids, but also in tyrannosauroids (e.g., femoral head proximomedially inclined, pubic boot enlarged, neural spines of posterior dorsals

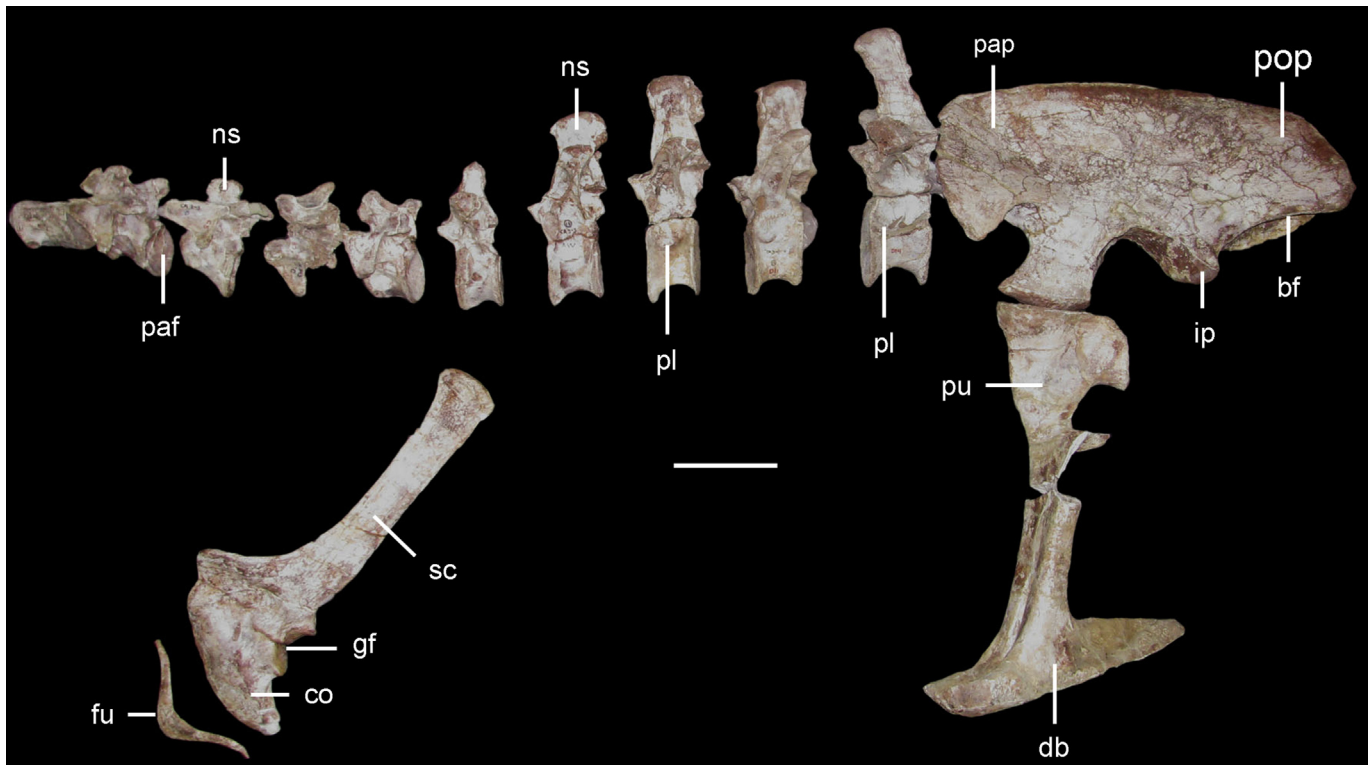


Fig. 14. Selected postranial bones of *Aerosteon riocoloradensis* (MCNA-PV 3137, holotype) left lateral view, except for the furcula in anterior view. Abbreviations: bf, brevis fossa; co, coracoid; db, distal boot; fu, furcula; gf, glenoid fossa; ip, ischiadic peduncle; ns, neural spine; paf, posterior articular facet; pap, preacetabular process; pl, pleurocoel; pop, postacetabular process; pu, pubis; sc, scapula. Scale bar equals 20 cm.

anteriorly inclined, pneumatic quadrate, see *SI parts 2 and 3*). Also, features listed as shared by Megaraptora and *Neovenator* (Benson et al., 2010a) are present in tyrannosaurids (e.g., *Tyrannosaurus*) or among other tetanurans (e.g., middle-posterior dorsal vertebrae with small, flange-like lateral extensions of postzygapophyseal facets, iliac cuppedicus fossa bounded dorsomedially by a prominent shelf, femoral lateral condyle projected further distally than the medial condyle, anterolateral process of tibial lateral condyle curves ventrally as a pointed process). In this regard, several of the synapomorphies recognized in support of the clade Carcharodontosauria (Benson et al., 2010a) are questionable, and deserve further testing within the context of a phylogenetic dataset also including tyrannosauroids and other basal coelurosaurids.

In order to test the phylogenetic relationships of neovenatorids among tetanurans, we constructed a new data matrix including relevant characters from the Benson et al. (2010a) and Brusatte et al. (2010a) datasets, that are informative for allosauroids and tyrannosauroids, respectively (see *SI parts 2 and 3*). It is worth mentioning that the analysis conducted by Benson et al. (2010a) only included three basal representatives of Coelurosauria (e.g., the compsognathid *Compsognathus* and the basal tyrannosauroids *Tanycolagreus* and *Guanlong*), thus numerous potential synapomorphies with more derived coelurosaurids (especially Tyrannosauridae) remained unsampled. The resulting most parsimonious trees here recovered depict *Megaraptor* and its lineage as members of Coelurosauria. The European *Neovenator* is nested within Allosauroidae among the most basal members of Carcharodontosauridae, together with *Eocarcharia* and *Concavenator*. It should be noted that this position of *Neovenator* is consistent with that obtained by Benson et al. (2010a), although the clade Neovenatoridae is monotypic under the current topology. The purported basal megaraptoran *Chilantaisaurus* is found here as a non-megaraptoran

tetanuran of problematic affinities. Benson et al. (2010a) defined Megaraptora as the most inclusive clade comprising *Megaraptor namunhuaiquii* but not *Chilantaisaurus tashiukouensis*, *Neovenator salerii*, *Carcharodontosaurus saharicus* or *Allosaurus fragilis*. Accordingly, following the recovered topology of our phylogenetic analysis, the taxonomic content of Megaraptora is the same as that of Coelurosauria. However, the taxa placed within Megaraptora by Benson et al. (2010a) remain as a monophyletic clade here. Thus, we propose the following modified diagnosis for Megaraptora to maintain its original taxonomic content: stem-based clade including all theropods more closely related to *Megaraptor namunhuaiquii* than to *Chilantaisaurus tashiukouensis*, *Neovenator salerii*, *Carcharodontosaurus saharicus*, *Allosaurus fragilis*, *Baryonyx walkeri*, *Tyrannosaurus rex*, and *Passer domesticus*. In addition, we consider that the morphology observed in the Gondwanan megaraptorans differs from that of the Asiatic *Fukuiraptor* (see *SI parts 2 and 3*). Accordingly, we erected the new clade Megaraptoridae nov. to include the southern megaraptorans, being defined as a stem-based clade including all theropods closer to *Megaraptor namunhuaiquii* than to *Fukuiraptor kitadaniensis*, *Chilantaisaurus tashiukouensis*, *Neovenator salerii*, *Carcharodontosaurus saharicus*, *Allosaurus fragilis*, *Baryonyx walkeri*, *Tyrannosaurus rex*, and *Passer domesticus*.

Several synapomorphies support the position of Megaraptora within Coelurosauria, which emerge from the phylogenetic analysis here performed (Fig. 15; see a detailed explanation of each feature in *SI part 2*): 1) maxillary and dentary teeth with reduced or absent mesial denticles (this condition is present in *Fukuiraptor*, *Australovenator*, and *Orkoraptor*, and has also been reported in compsognathids, basal tyrannosauroids and basal oviraptorosaurians; Rauhut, 2003; Novas et al., 2008); 2) iliac cuppedicus fossa dorsomedially bounded by a prominent shelf (a very deep cuppedicus fossa that is bounded by a prominent shelf of bone is documented

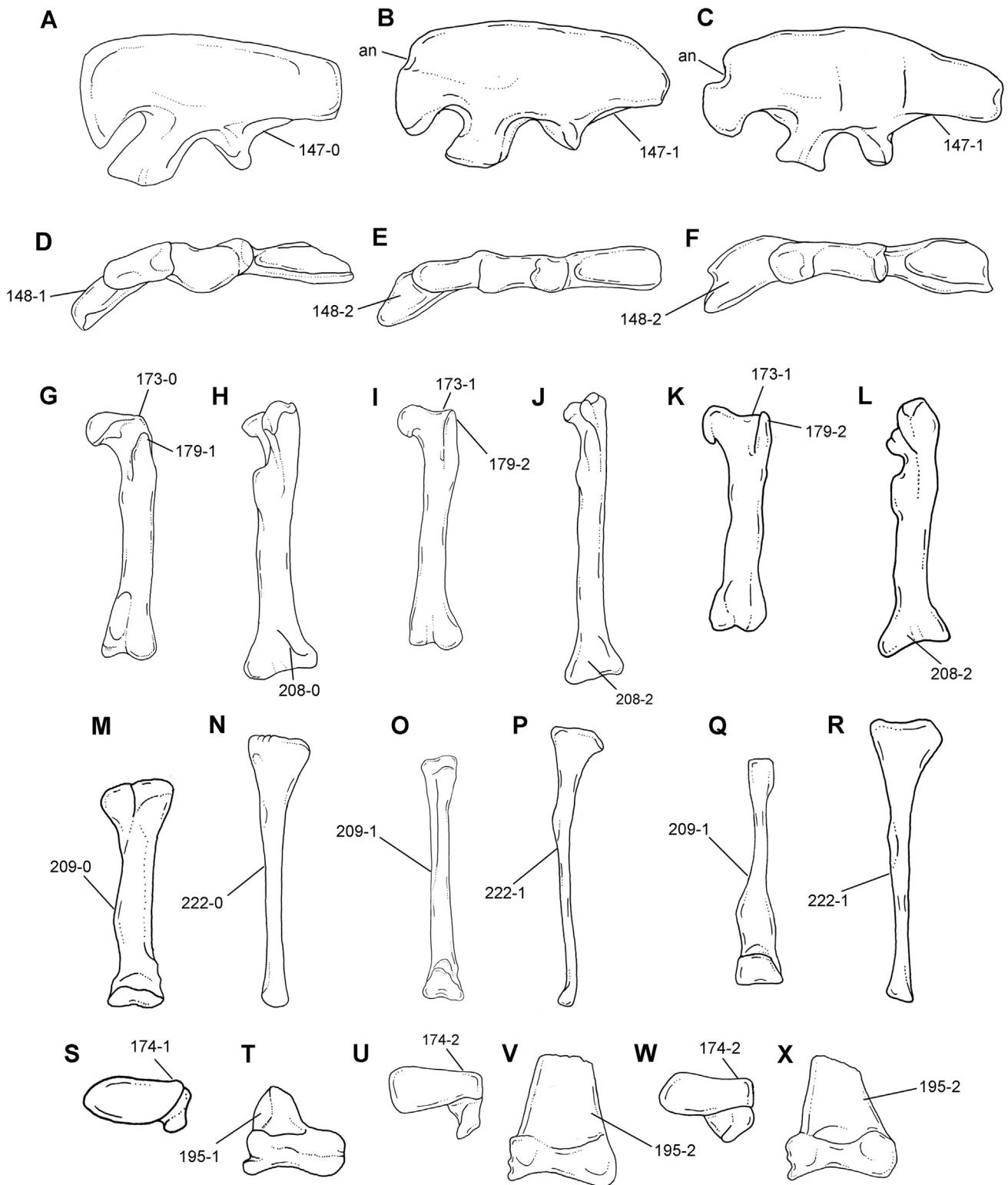


Fig. 15. Comparison of selected bones of a basal tetanuran (*Allosaurus*), megaraptorans (*Aerosteon*, *Australovenator*) and Tyrannosauridae (*Tyrannosaurus*). (A–H) *Allosaurus*, (I, J) *Aerosteon*, (K–P) *Australovenator* and (Q–X) *Tyrannosaurus*. (A, I, Q) Iliac in left lateral view, (B, J, R) ilia in ventral view, (C, K, S) left femur in anterior view, (D, L, T) left tibia in anterior view, (E, M, U) left metatarsal III in anterior view, (F, N, V) left fibula in lateral view, (G, O, W) left femoral head in proximal view, and (H, P, X) right astragali in anterior view. Numbers indicate characters and codings considered in the text and in SI parts 2 and 3. Not to scale. (A–H) redrawn from Madsen (1976), (I, J) drawn from photographs of the authors, (K–P) redrawn from Hocknull et al. (2009), and (Q–X) redrawn from Osborn (1917) and Brochu (2003).

in *Chilantaisaurus* and most coelurosaurids, including tyrannosaurids, ornithomimids, *Caudipteryx*, *Khaan* specimen IGM 100/1002, dromaeosaurids and basal birds, as well *Aerosteon*; this feature was also convergently acquired by *Neovenator*; Novas, 1996; Rauhut,

2003; Benson and Xu, 2008; Brusatte et al., 2009); 3) iliac brevis fossa almost hidden in lateral view by the brevis shelf (in *Torvosaurus*, *Allosaurus*, *Neovenator*, and *Giganotosaurus*, the brevis fossa is widely exposed in lateral view; on the contrary, in *Stokesosaurus*,

Tyrannosauridae indet. AMNH 5468; *Tarbosaurus*; *Alioramus*; *Tyrannosaurus rex*, *Khaan*, IGM 100/1002, *Deinonychus*, *Archaeopteryx*, *Unenlagia*, *Rahonavis*, and the megaraptoran *Aerosteon*, the brevis shelf projects more ventrally and it meets the caudal surface of the ischiac pedicle of ilium; Rauhut, 2003; Novas, 2004; Sereno et al., 2008); 4) femoral greater trochanter prominent and proximally projected (in *Allosaurus*, *Neovenator* and *Mapusaurus* the greater trochanter is continuous with the femoral head and is more distally located than the proximal margin of the femoral head whereas the greater trochanter in coelurosaurs is offset from the femoral head by an anteroposterior groove on its proximal end, a condition reported in several deinonychosaurians, oviraptorids, therizinosaurids, tyrannosaurids and birds; Madsen, 1976; Holtz, 1994, 2000; Rauhut, 2003; Coria and Currie, 2006; Brusatte et al., 2009); 5) femoral head square in proximal view, with lateral margin anteroposteriorly extended (in *Neovenator* and *Allosaurus* the greater trochanter is anteroposteriorly narrow, making the proximal end of femur in proximal view teardrop-shaped; this is not the case in Tyrannosauridae, Therizinosaurioidea, Oviraptorosauria, Troodontidae and Dromaeosauridae; Osborn, 1917; Maleev, 1974; Ostrom, 1976; Barsbold et al., 1990; Russell and Dong, 1993; Currie and Peng, 1993); 6) tibial facet for the reception of the ascending process of the astragalus almost flat (present in *Aerosteon* and *Australovenator*, and differs from the step-like facet seen in *Allosaurus*, *Neovenator* and more basal theropods; Azuma and Currie, 2000; Hocknull et al., 2009; see Rauhut, 2003; Benson, 2010); 7) fibular shaft abruptly narrowed distal to the *M. iliofibularis* tubercle (present in *Tanycolagreus*, *Compsognathus*, *Struthiomimus*, *Deinonychus* and other coelurosaurs, and among megaraptorans it is also present in *Australovenator* and *Aerosteon*; Osborn, 1917; Ostrom, 1969, 1978; Carpenter et al., 2005); 8) astragalus ascending process height more than 0.5 times width of the astragalus body (this condition is present in most coelurosaurs, including tyrannosaurids and the megaraptorans *Fukuiraptor*, *Aerosteon* and *Australovenator*; on the contrary, in more basal theropods including *Allosaurus* and *Mapusaurus* the ascending process of the astragalus is low and transversely narrow; Welles and Long, 1974; Azuma and Currie, 2000; Rauhut, 2003; Coria and Currie, 2006; Hocknull et al., 2009); 9) transverse width of ascending process of the astragalus occupying the total width of the anterior surface of distal tibia (this is a condition present in all known coelurosaurs, including *Aerosteon*, *Fukuiraptor*, and *Australovenator*; Azuma and Currie, 2000; Hocknull et al., 2009); 10) fibular facet of the ascending process of the astragalus reduced and laterally oriented (this condition occurs in tyrannosaurids, ornithomimids, troodontids and dromaeosaurids, as well as the megaraptorans *Aerosteon*, *Australovenator*, and *Fukuiraptor*; but in *Allosaurus* and *Mapusaurus* the fibular facet is cranio-laterally oriented and almost continuous with the anterior surface of the ascending process of the astragalus; Madsen, 1976; Coria and Currie, 2006); 11) distinct anterior development of the lateral condyle of the astragalus body (in *Albertosaurus*, *Troodon*, *Deinonychus*, and ornithomimids the lateral portion of the astragalus is forward projecting, a condition also documented in *Aerosteon*, *Australovenator*, and *Fukuiraptor*; Welles and Long, 1974; Azuma and Currie, 2000; Rauhut, 2003; Hocknull et al., 2009); and 12) metatarsal III slender and elongate (present in most coelurosaurs, as well as *Megaraptor* and *Australovenator*, contrasting with the stouter condition seen in basal tetanuras, including *Allosaurus* and *Neovenator*; Madsen, 1976; Novas, 1998; Brusatte and Sereno, 2008; Hocknull et al., 2009).

As it was mentioned previously, several of the purported apomorphies proposed by Benson et al. (2010a) as uniquely shared by megaraptorans and carcharodontosaurids are also present in tyrannosauroids (see SI parts 2 and 3). Thus, due to the position of Megaraptora within Coelurosauria, several of these features are

parsimoniously optimized as apomorphies shared by megaraptorans and tyrannosauroids, and convergently acquired in Carcharodontosauridae. Accordingly, in the current analysis we found megaraptorans deeply nested within Tyrannosauroida. The apomorphies that megaraptorans share with tyrannosauroids and more inclusive clades include (see SI parts 2 and 3): 1) metacarpal III length <0.75 length of metacarpal II; 2) pubic symphysis interrupted distally by a large median fenestra visible in anterior view; and 3) pneumatic quadrate with a deep anterior recess at the intersection of distal condyles and pterygoid wing. In addition, Megaraptora was recovered as the sister taxon of *Xiongguanlong* + Tyrannosauridae on the basis of several synapomorphies, including: 1) cervical vertebrae with hyposphene–hypantrum accessory articulations (this feature is also present among carcharodontosaurids; Smith et al., 2007; Li et al., 2010); 2) posterior dorsal neural spines ≥ 1.5 taller than long (Zheng et al., 2009; this feature is also present among carcharodontosaurids); 3) pubic shaft anteriorly concave in lateral view (this condition is present in *Aerosteon* and tyrannosaurids, being absent in basal tyrannosauroids such as *Coelurus* and *Guanlong*, in which the shaft is anteriorly convex; Benson et al., 2010a); 4) distal pubic boot with the anterior projection well expanded in comparison to the posterior one; 5) length of the pubic boot $\geq 60\%$ the length of the entire pubis (this condition is shared by the megaraptorid *Aerosteon* and tyrannosauroids, as well as *Neovenator* and carcharodontosaurids; Benson et al., 2010a); 6) lesser trochanter high, near the level to the greater trochanter (Rauhut, 2003; this feature is present in oviraptorids, therizinosaurids, ornithomimosaurids, *Xiongguanlong* and derived tyrannosaurids, being absent in basal tyrannosauroids such as *Coelurus* and *Tanycolagreus*; the high position of the lesser trochanter in megaraptorids contrast with the much lower condition seen in carcharodontosaurids, *Allosaurus* and *Neovenator*; Madsen, 1976; Brusatte and Sereno, 2008; Coria and Currie, 2006); 7) fourth trochanter robust (Rauhut, 2003; this trochanter is reduced to a tiny proximodistally oriented ridge in ornithomimosaurids, oviraptorosaurians, paravians, as well as basal tyrannosauroids, including *Coelurus*, *Tanycolagreus*, and *Ornitholestes*; Carpenter et al., 2005; in contrast, in the megaraptorids *Australovenator* and *Fukuiraptor* and in *Xiongguanlong* and derived tyrannosauroids the fourth trochanter is represented by a stout ridge; Li et al., 2010), 8) tibial lateral malleolus laterally projected, representing more than 5% of tibial total length (within Coelurosauria this feature is absent in ornithomimosaurids, basal paravians such as *Deinonychus*, and basal tyrannosauroids such as *Coelurus* and *Tanycolagreus*; a laterally expanded lateral malleolus of distal tibia is documented in the megaraptorids *Australovenator* and *Aerosteon*, as well as in tyrannosaurids; also present in carcharodontosaurids; Sereno and Brusatte, 2008) (see SI parts 2 and 3).

In addition, megaraptorids are diagnosed by an extensive list of synapomorphies, including: opisthocoelous cervical vertebrae, manual ungual of digit I three times longer than its proximal depth, transversely compressed, and with a dorsoventrally elliptical proximal end, metatarsal III with distal ginglymoid proximally extended and extensor fossa wide and crescent shaped (Fig. 16).

Removing megaraptorids from Carcharodontosauria and Allosauroida allows us to return to the interpretation that these two later clades were absent from terminal Cretaceous ecosystems of South America, and that they were succeeded by large-bodied ceratosaurians (abelisaurids) and coelurosaurians (megaraptorans, unenlagiids) in Late Cretaceous times (see Novas et al., 2009). In addition, megaraptorids have not been recovered so far from the Upper Cretaceous deposits of North America and Asia, both of which preserve tyrannosaurid-dominated faunas (Brusatte et al., 2009, 2010b). Conversely, southern faunas are devoid of the tyrannosaurid theropods.

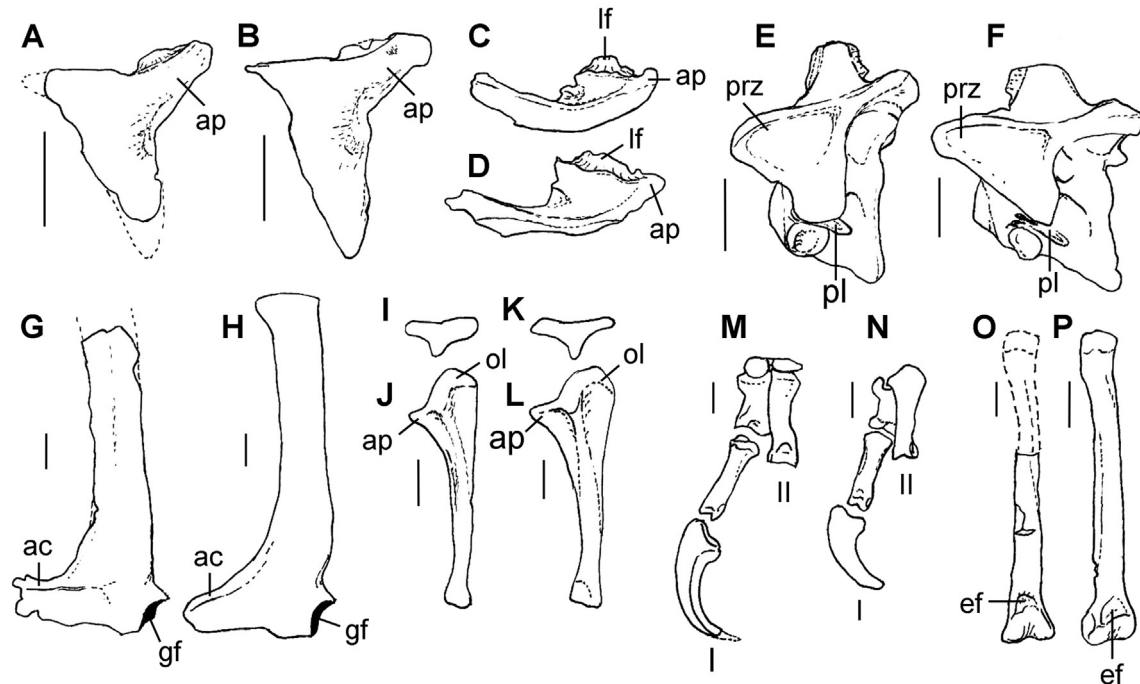


Fig. 16. Selected bones of megaraptorans. (A, C) *Orkoraptor*, (B, D, F, H) *AeroSTEON*, (E, G, K, L, M, O) *Megaraptor* and (I, J, N, P) *Australovenator*. Right postorbital in (A–B) lateral and (C–D) dorsal views, (E–F) mid-cervical vertebrae in left lateral views, (G–H) left scapula in lateral views, left ulna in (I, K) proximal and (J, L) lateral views, (M–N) left metacarpals I and II and digit I in anterior view, and (O–P) right metatarsal III in anterior views. Abbreviations: I–II, first to second manual digit/metacarpal; ac, acromion; ap, anterior process; ef, extensor fossa; gf, glenoid fossa; lf, laterosphenoid facet; ol, olecranon; pl, pleurocoel; prz, prezygapophysis. Scale bar 5 cm. (A, C) redrawn from Novas et al. (2008), (B, D, F) redrawn from Sereno et al. (2008) and (I, J, N, P) redrawn from Hocknull et al. (2009).

Documentation of members of Megaraptoridae in Patagonia has increased in recent years. In addition to the previously known taxa *Megaraptor namunhuaiquii*, *AeroSTEON riocoloradoensis* and *Orkoraptor burkei*, there are other less well known specimens that belong to this clade. Among them, Martínez et al. (2001) and Lamanna et al. (2004) mentioned the presence of a *Megaraptor*-like theropod from the Bajo Barreal Formation (Cenomanian–Turonian) of Chubut province, Argentina. This specimen shows the hypertrophied first manual ungual and pleurocoelous caudal vertebrae, indicating its membership to Megaraptoridae.

Porfiri et al. (2008) described from the Bajo de la Carpa Formation (Santonian), Neuquén province, Argentina, a series of posterior dorsal vertebrae and partial sacrum (composed by 5 vertebrae), ribs and fragments of ilium. This specimen shows complex pneumatic dorsal and sacral vertebrae with tall neural spines inclined forward. This combination of features may indicate that this theropod also belongs to the Megaraptoridae.

The discovery of a yet unnamed large theropod was announced by Coria and Currie (2002b) from the Portezuelo Formation exposed at Sierra Barrosa, Neuquén Province. Based on the information afforded by these authors, we believe that the specimen they described is a megaraptorid. For example, the incomplete skeleton shows complex pneumatic dorsal, sacral and caudal vertebrae with pleurocoels, a hyperpneumatic ilium with pneumatopores at its posterior end, pubis vertically oriented with an expanded pubic boot and a transversely wide cupped fossa (Coria and Currie, 2002b; Coria et al., 2001), which are features present in megaraptorid theropods.

From the same locality and horizon where the holotype of *AeroSTEON* was collected, some associated metatarsals and phalanges were found, including an isolated right manual ungual of the second digit (MCNA-PV-3075) and a single right manual ungual of the first digit (MCNA-PV-3112), both resembling *Megaraptor*. These specimens indicate the presence of more megaraptorid specimens in these strata.

Outside the South American context, megaraptorids are currently well-known from Australia, where the nearly complete skeleton of *Australovenator* was recovered (Hocknull et al., 2009), as well as some fragmentary specimens also referred to as indeterminate megaraptorans (Smith et al., 2008; Benson et al., 2012). Regarding Africa, the pedal unguals reported by Stromer (1934) and Novas et al. (2005a) as belonging to the enigmatic “*Spinosaurus B*” from the Cenomanian of Egypt and Morocco, exhibit a closely similar morphology, albeit not identical, to that of *Australovenator* (Hocknull et al., 2009). As in the latter taxon, “*Spinosaurus B*” exhibits an apomorphic flat ventral surface, which is concave proximally, and sharply defined longitudinal marginal ridges separating the ventral side from the lateral and medial surfaces of the ungual. These features contrast with the bulkier and more rounded lateral keels and shallower longitudinal grooves seen in spinosaurid pedal phalanges (Mateus et al., 2011). The presence of these features in “*Spinosaurus B*” contributed to the historically enigmatic nature of the specimens because they had not been reported in other known theropods. However, their presence in *Australovenator* suggests that at least the pedal unguals of the “*Spinosaurus B*” taxon may belong to Megaraptora, thus supporting the possible presence of this clade in the early Late Cretaceous of Africa.

In terms of stratigraphic range, megaraptorans are currently confined to rocks of Aptian (i.e., *Fukuiraptor*, *Australovenator*) through Coniacian (e.g., *Megaraptor*) and eventually Santonian (e.g., *AeroSTEON*) ages. Novas et al. (2008) provisionally reported a Maastriichtian age for the megaraptoran *Orkoraptor*, leading to the interpretation that the clade survived up to the end of the Cretaceous (Benson et al., 2010a). However, the age of the beds that yielded *Orkoraptor* (i.e., Mata Amarilla Formation, former Pari Aike Formation) seems to be Cenomanian–Santonian (O’Gorman and Varela, 2010; see SI part 3). In this regard, Patagonian megaraptorid remains are currently documented in pre-Campanian Upper Cretaceous beds.

In our interpretation, megaraptorans were basal coelurosaurs that shared the role of top predators with other large theropods such as abelisauroids and carcharodontosauroids. Although most authors have concluded that the Laurasian top predatory dinosaurs were the coelurosaurs (represented by Tyrannosauridae), in clear contrast with archaic-dominated predatory Gondwanan faunas (Sereno, 1999; Holtz, 2004; Brusatte et al., 2010b), the presence and abundance of tyrannosauroid megaraptorans in most Cretaceous southern faunal assemblages suggest that they were also outstanding predators in Gondwana. Megaraptorans considerably improve our knowledge about the scarcely documented basal radiation of Gondwanan coelurosaurs, as well as tyrannosauroids as a whole.

2.3.3. Alvarezsauridae

Alvarezsauridae is a group of maniraptoran theropods originally erected by Bonaparte (1991b) in order to include the highly distinctive genus *Alvarezsaurus*, from the Coniacian–Santonian Bajo de la Carpa Formation of Neuquén province. Posteriorly, several new Patagonian species were included in this family: *Patagonykus puertai* (from the Coniacian Portezuelo beds, Neuquén; Novas, 1996, 1997a), *Achillesaurus manazzoni* (from the Coniacian–Santonian Bajo de la Carpa Formation, Neuquén; Martinelli and Vera, 2007), *Bonapartenykus ultimus* (from the Campanian–Maastriichtian Allen Formation, Río Negro; Agnolín et al., 2006, 2012; Salgado et al., 2009) and *Alnashetri cerropolicensis* (from the upper Cenomanian Candeleros Formation, Río Negro; Makovicky et al., 2012). In addition to the South American forms, the Alvarezsauridae also includes the avian-like clade Parvicursorinae, represented by Cretaceous European, Asiatic and North American taxa such as *Mononykus*, *Shuvuuia* and *Parvicursor* (Perle et al., 1993; Karhu and Rautian, 1996; Chiappe et al., 1998; Hutchinson and Chiappe, 1998; Naish and Dyke, 2004; Alifanov and Barsbold, 2009; Xu et al., 2010a; Nesbitt et al., 2011) [it must be noted that the Late Jurassic *Haplocheirus sollers* was formerly described as the most basal alvarezsaur (Choiniere et al., 2010b) but it was recently reinterpreted as an early ornithomimosaur (Choiniere et al., 2011)].

Alvarezsaurids are highly derived theropods diagnosed by an extensive list of synapomorphies, including a lightly built skull bearing numerous small teeth restricted to the anterior portion of the snout, large and rounded orbits, postorbital and jugal lacking contact, robust humerus with a proximally projected inner tubercle, robust ulna with enlarged olecranon, block-like carpometacarpus, hand with very robust digit I carrying a large and stout claw, and keeled sternum, among other features (Novas, 1996, 1997a, 2009; Chiappe et al., 1998, 2002). A recent phylogenetic analysis (Agnolín et al., 2012) revealed a main dichotomy at the base of Alvarezsauridae (Fig. 17) between the group including the newly named South American clade Patagonykinae (*Bonapartenykus* and *Patagonykus*) and another clade composed of the Patagonian taxon *Alvarezsaurus* and the Parvicursorinae subfamily. The parvicursorines are currently restricted to the northern hemisphere, and include approximately ten different nominal species (Chiappe et al., 2002; Alifanov and Barsbold, 2009; Longrich and Currie, 2009; Xu et al., 2010a, 2011a). Parvicursorines are diagnosed by several bizarre derived traits, such as opisthocoelous cervical and anterior thoracic vertebrae, procoelous synsacrum, a biconvex vertebra uniting the dorsal and sacral vertebral series, procoelous caudal vertebrae, and an opisthopic pelvis with rod-like posteroventrally oriented pubis and ischium, recalling the condition present in derived ornithurine birds (Chiappe et al., 2002). To date no parvicursorine remains have been reported from the southern landmasses. Curiously, in Agnolín et al. (2012) analysis, *Alvarezsaurus* was recovered as the sister taxon of Parvicursorinae, whereas in previous analyses this Patagonian genus was usually

regarded as the most basal alvarezsaurid (e.g. Novas, 1996, 1997a; Chiappe et al., 2002; Longrich and Currie, 2009; Choiniere et al., 2010a,b). The clade encompassing *Alvarezsaurus* and parvicursorines is characterized by bearing shortened phalanges on pedal digit IV, and an ilium completely lacking a *cuppedicus fossa* (Agnolín et al., 2012) (Fig. 17). However, in the most recent analysis dealing with alvarezsaurid phylogeny, Makovicky et al. (2012) again recovered *Alvarezsaurus* as the most basal member of the group and *Patagonykus*, *Bonapartenykus* and the recently described *Alnashetri* within a polytomy together with a monophyletic Parvicursorinae.

Bonapartenykus and *Patagonykus* (i.e. the patagonykines) retain several plesiomorphies that are absent in Parvicursorinae, including: subvertical pubis with extensive distal pubic boot, pubic shaft with pubic apron still present, pubic shaft subtriangular in cross-section, posterior margin of proximal end of pubis devoid of a longitudinal sulcus for the ischium, and hyposphene–hypantrum additional articulations present and well developed on dorsal vertebrae. Agnolín et al. (2012) found the following synapomorphy for Patagonykinae: coracoid with its ventral half medially tilted with respect to the lateral surface of the bone and a profusely sculptured ventral half (Fig. 18A). The sculptured surface is composed of several bumps separated by splitting grooves, probably suggesting some kind of skin cornification. Moreover, the medial tilting of the coracoid and the expected presence of a strongly developed sternum (not preserved), indicate the existence of a wide breast for these South American alvarezsaurids (Agnolín et al., 2012).

Achillesaurus manazzoni was described by Martinelli and Vera (2007) on the basis of a highly incomplete postcranium. The fact that this specimen was found in the same beds and at the same locality where *Alvarezsaurus* was found, together with the incomplete nature of the only known specimen, prompted some authors to propose that *Achillesaurus manazzoni* was of dubious taxonomic validity (Novas, 2009) and likely a junior synonym of *Alvarezsaurus calvoi* (Makovicky et al., 2012). Although *Achillesaurus* may represent a fully grown specimen of *Alvarezsaurus* (currently known by a single juvenile individual; Bonaparte, 1991b) (Makovicky et al., 2012), some anatomical features suggest that *Achillesaurus* may belong to the patagonykines and thus may not be closely related to *Alvarezsaurus*. In fact, *Achillesaurus* resembles *Patagonykus* and *Bonapartenykus* in several features, including the general morphology of the proximal femur, the presence of a subcircular lateral depression on the cranial half of the centrum in the proximal caudals (only known in *Patagonykus*), and a transversely compressed and cranially protruding medial condyle of the astragalus (Martinelli and Vera, 2007). These traits are absent in other alvarezsaurids (e.g. *Alvarezsaurus*, *Shuvuuia*; Bonaparte, 1991b; Chiappe et al., 2002), and a numerical phylogenetic analysis may indicate that they constitute synapomorphies of the Patagonykinae. Accordingly, the presence of *Patagonykus* and other closely related South American taxa demonstrates the survival of basal alvarezsaurids into the latest Cretaceous in Patagonia, while highly derived parvicursorines evolved on the northern continents contemporaneously.

One of the most interesting recent discoveries regarding Patagonian alvarezsaurid paleobiology consists of the discovery of the holotype of *Bonapartenykus ultimus* in close association with two partial eggs (Fig. 19). Association of dinosaur eggs with embryos or adult individuals that allow taxonomic identification are scarce, and reports in the literature are restricted to megalosauroids, allosauroids, oviraptorids, therizinosaurids, troodontids and dromaeosaurids (Norell et al., 1994, 1995, 2001; Mateus et al., 1997; Varricchio et al., 1995, 2002; Grellet-Tinner et al., 2006; Kundrát et al., 2008; Weishampel et al., 2008; Bever and Norell, 2009; Araújo et al., 2012). Thus, this specimen of *Bonapartenykus*

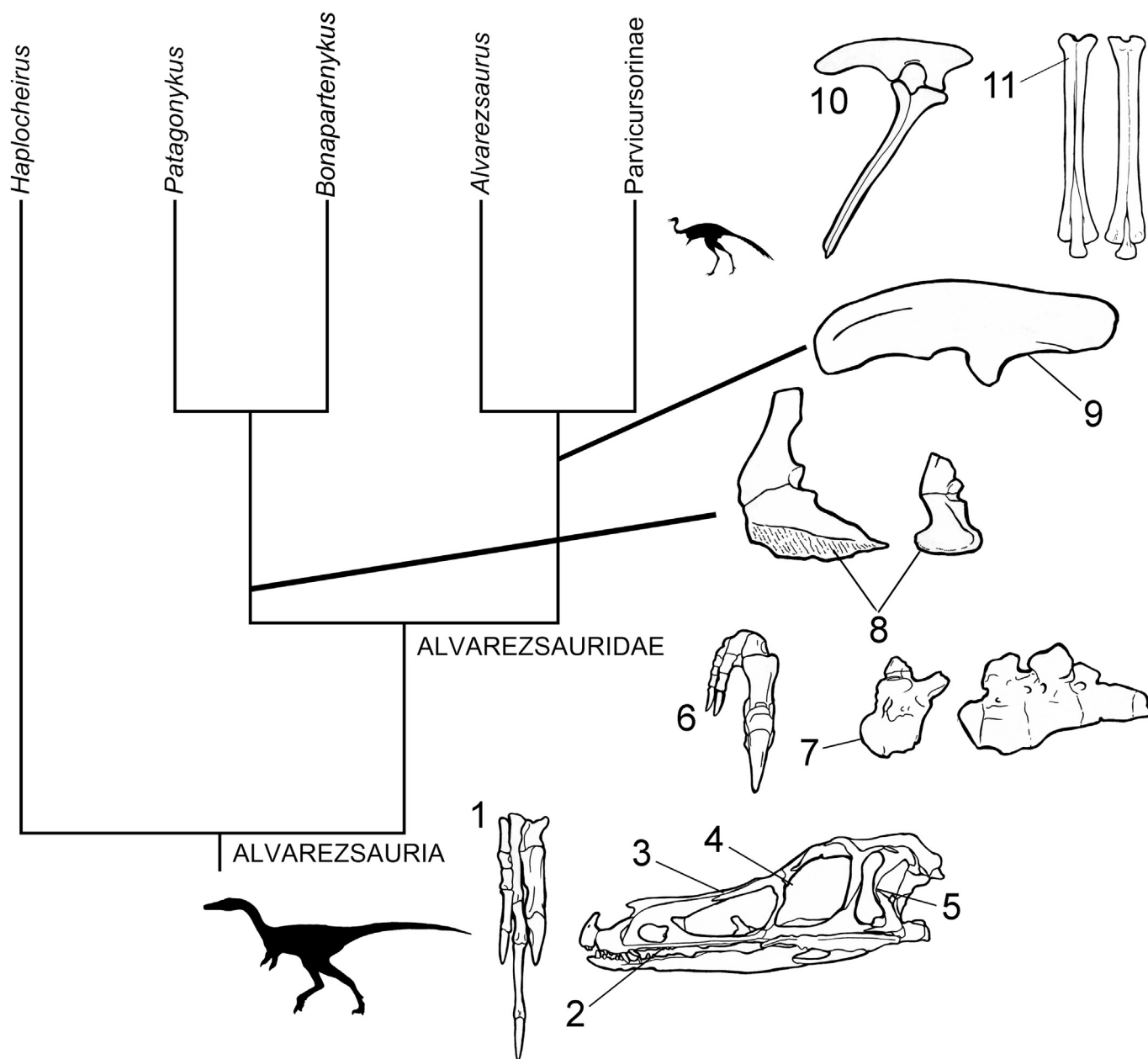


Fig. 17. Time calibrated phylogenetic tree showing the relationships of the main alvarezsaur clades. Node 1 (Alvarezsauria): 1 – hand with large digit I with a very stout unguis claw, 2 – elongate snout with small teeth restricted to the anterior end of muzzle, 3 – expanded anterior process of lacrimal, 4 – large and rounded orbit, 5 – loss of postorbital–jugal contact. Node 2 (Alvarezsauridae): 6 – hand with reduced digits II and III and block-like metacarpals, 7 – opisthocoelous thoracic and sacral vertebrae. Node 3 (*Patagonykus* + *Bonapartenykus*): 8 – medially tilted and ornamented ventral half of coracoid. Node 4 (*Alvarezsaurus* + *Parvicursorinae*): 9 – total absence of *cuppeditica fossa* on ilium. Node 5 (*Parvicursorinae*): 10 – modified bird-like pelvis, 11 – elongate and proximally fused metatarsals.

represents the first direct association of skeletal remains and oological material documented for the Alvarezsauridae. The eggs found near the skeleton of *Bonapartenykus* show an external surface extensively ornamented with ridges and bumps. This morphology resembles eggs previously reported in basal maniraptoriform theropods (e.g., therizinosauroids, oviraptorosaurians; Weishampel et al., 2008) and referred to the elongatoolithid oofamily (Agnolín et al., 2012). In more derived maniraptoran taxa such as the basal paravians *Byronosaurus* and *Troodon*, the external eggshell surface is nearly smooth, with faint longitudinal striations (Norell et al., 1994; Varricchio et al., 2002; Bever and Norell, 2009), as is also the case in living and fossil birds (Schweitzer et al., 2002; Grellet-Tinner and Chiappe, 2004). The presence of a highly

ornamented external surface of the eggshell in Alvarezsauridae, Therizinosauroidae and Oviraptorosauria suggests that this condition is symplesiomorphic for Maniraptoriformes, and that an almost smooth eggshell represents a derived condition for paravians, including birds (Agnolín et al., 2012). Alvarezsaurid eggshells exhibit unique and highly apomorphic features absent in the remaining coelurosaurs that support the erection of a new oofamily Arriagadoolithidae (Agnolín et al., 2012).

2.3.4. *Unenlagiidae*

Paraves is currently considered as the clade encompassing the theropod clades Deinonychosauria (which currently includes Dromaeosauridae and Troodontidae) and Avialae (Gauthier, 1986;

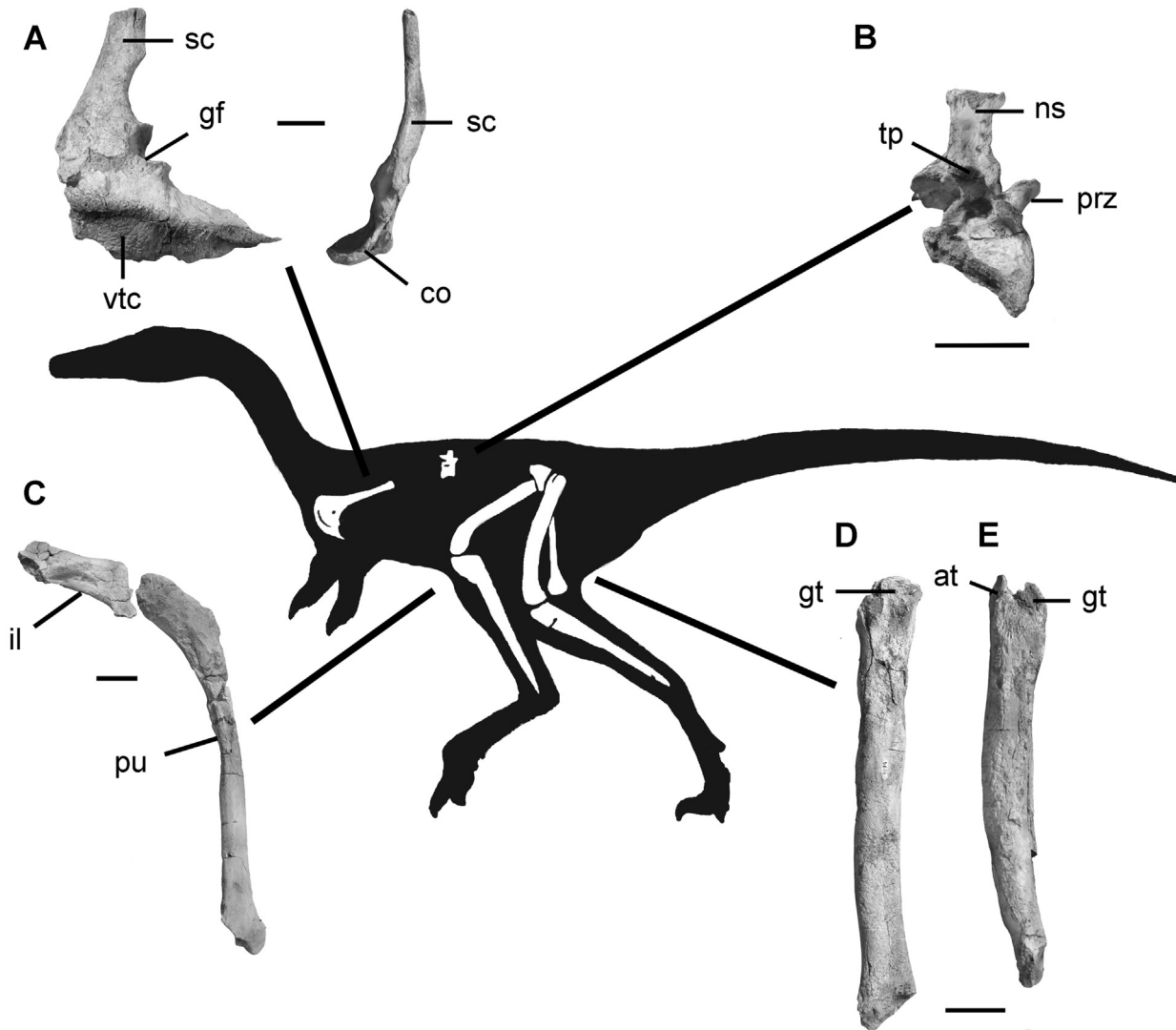


Fig. 18. Selected skeletal pieces of the alvarezsaurid *Bonpartenykus ultimus* (MPCA-1290). (A) Left coracoid in lateral and posterior views, (B) dorsal vertebra in left lateral view, (C) left pelvic elements in left lateral view, (D) left tibia in anterior view and (E) left femur in lateral view. Abbreviations: at, anterior trochanter; co, coracoid; gf, glenoid fossa; gt, greater trochanter; il, ilium; ns, neural spine; prz, prezygapophysis; pu, pubis; sc, scapula; tp, transverse process; vtc, ventral tilting of the coracoid. Scale bar equals 5 cm.

Holtz, 2000). Until recently, the fossil record of basal paravians was geographically restricted to the Northern Hemisphere (Norell and Makovicky, 2004), but recent discoveries have demonstrated that they were also present and highly diversified in the southern landmasses, suggesting that an important adaptive radiation took place in Gondwana during the Cretaceous (Novas and Pol, 2005; Makovicky et al., 2005; Novas et al., 2009). South American paravians are included within the clade Unenlagiidae [in most previous literature this clade was considered as Unenlagiinae, but here we follow the taxonomy employed by Agnolín and Novas (2011) who recovered this group outside Dromaeosauridae], which have been documented from different Cenomanian to Maastrichtian units of northwestern Patagonia (Novas and Puerta, 1997; Calvo et al., 2004a; Novas and Pol, 2005; Makovicky et al., 2005; Novas et al., 2009; Gianechini and Apesteguía, 2011).

Unenlagiidae is phylogenetically defined as the clade that includes all taxa closer to *Unenlagia comahuensis* than to *Velociraptor mongoliensis* and *Microraptor zhaoianus* (Makovicky et al., 2005). The Unenlagiidae includes the Patagonian *Unenlagia comahuensis* (Novas and Puerta, 1997; Novas, 1999, 2004, 2009), *Unenlagia paynemili* (Calvo et al., 2004a), *Neuquenraptor argentinus* (Novas

and Pol, 2005), *Buitreraptor gonzalezorum* (Makovicky et al., 2005) (Fig. 20) and *Austroraptor cabazai* (Novas et al., 2009) (Fig. 21). Recently, the taxon *Pamparaptor micros* was referred to Unenlagiidae on the basis of an incomplete foot collected from beds of the Portezuelo Formation, Neuquén (Porfiri et al., 2011) (but see below for an alternative interpretation). The latest Cretaceous *Rahonavis ostromi* from Madagascar, originally described as a basal bird more derived than *Archaeopteryx* (Forster et al., 1998), was also considered by some authors (e.g., Makovicky et al., 2005; Novas and Pol, 2005; Novas et al., 2009; Turner et al., 2007a,b) as a member of Unenlagiidae. More recently, O'Connor et al. (2011) indicated that the anatomy of *Rahonavis* matches better with that of a derived ornithuran and not an unenlagiid, a conclusion that also was independently reached by Agnolín and Novas (2013). Ezcurra (2009) and Benson et al. (2012) reported the presence of probable unenlagiid fragmentary remains from the Aptian–Albian of Australia and Maastrichtian of Colombia, respectively.

The monophyly of Unenlagiidae is supported by several derived characters, including: elongate anterior portion of maxilla, large number of small and unserrated teeth, vertical pubis, dorsal margin of postacetabular blade of ilium concave, pedal phalanx II-2 with



Fig. 19. Fossil egg associated with the holotype of *Bonapartenykus ultimus* (MPCA-1290). Note the strongly ornamented external surface. Scale bar equals 3 cm.

transversely narrow posteroventral keel, and ischium with deeply concave posterior end (Makovicky et al., 2005; Zheng et al., 2009; Agnolín and Novas, 2011) (Fig. 22). However, higher-level relationships of unenlagiids are still a matter of debate. In its original

description, *Unenlagia* was interpreted closer to birds than to dromaeosaurids (Novas and Puerta, 1997), an interpretation subsequently adhered to by some authors (Forster et al., 1998; Xu et al., 1999; Holtz, 2000; Rauhut, 2003; Novas, 2004). Nevertheless,

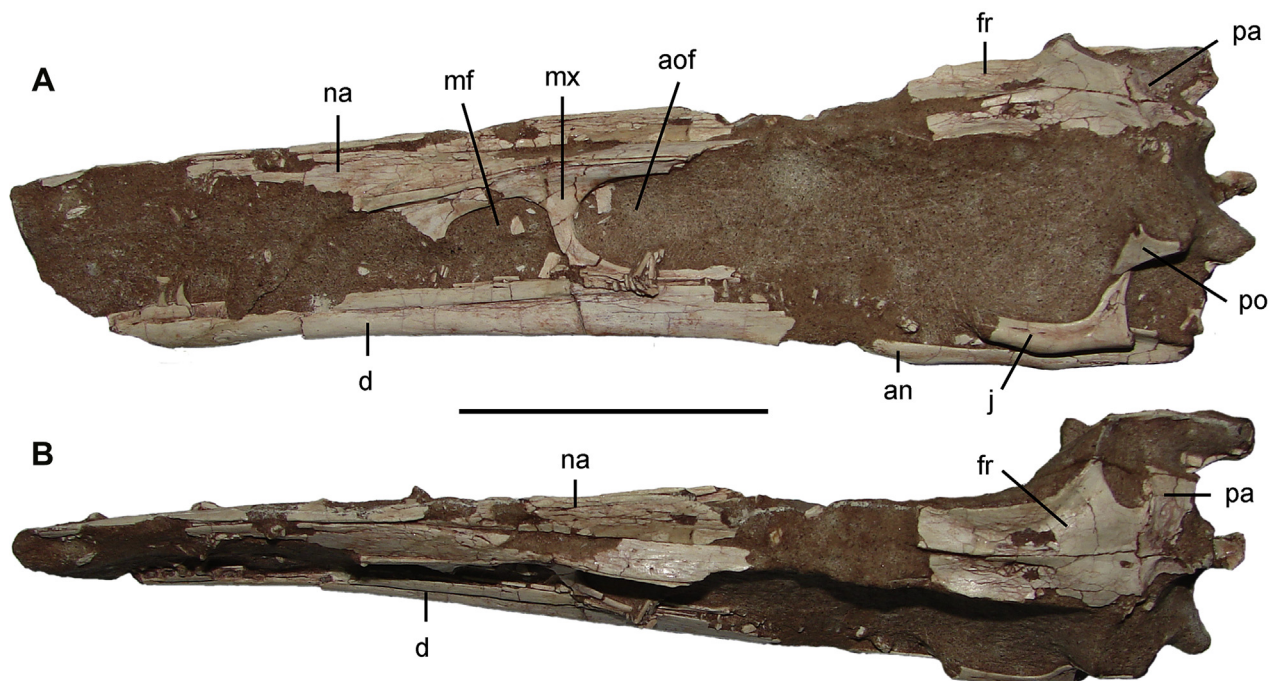


Fig. 20. Skull of *Buitreraptor gonzalezorum* (MPCA-245, holotype) in (A) right lateral and (B) dorsal views. Abbreviations: an, angular; aof, antorbital fenestra; d, dentary; fr, frontal; mf, maxillary fenestra; j, jugal; mx, maxilla; na, nasal; pa, parietal; po, postorbital. Scale bar equals 5 cm.

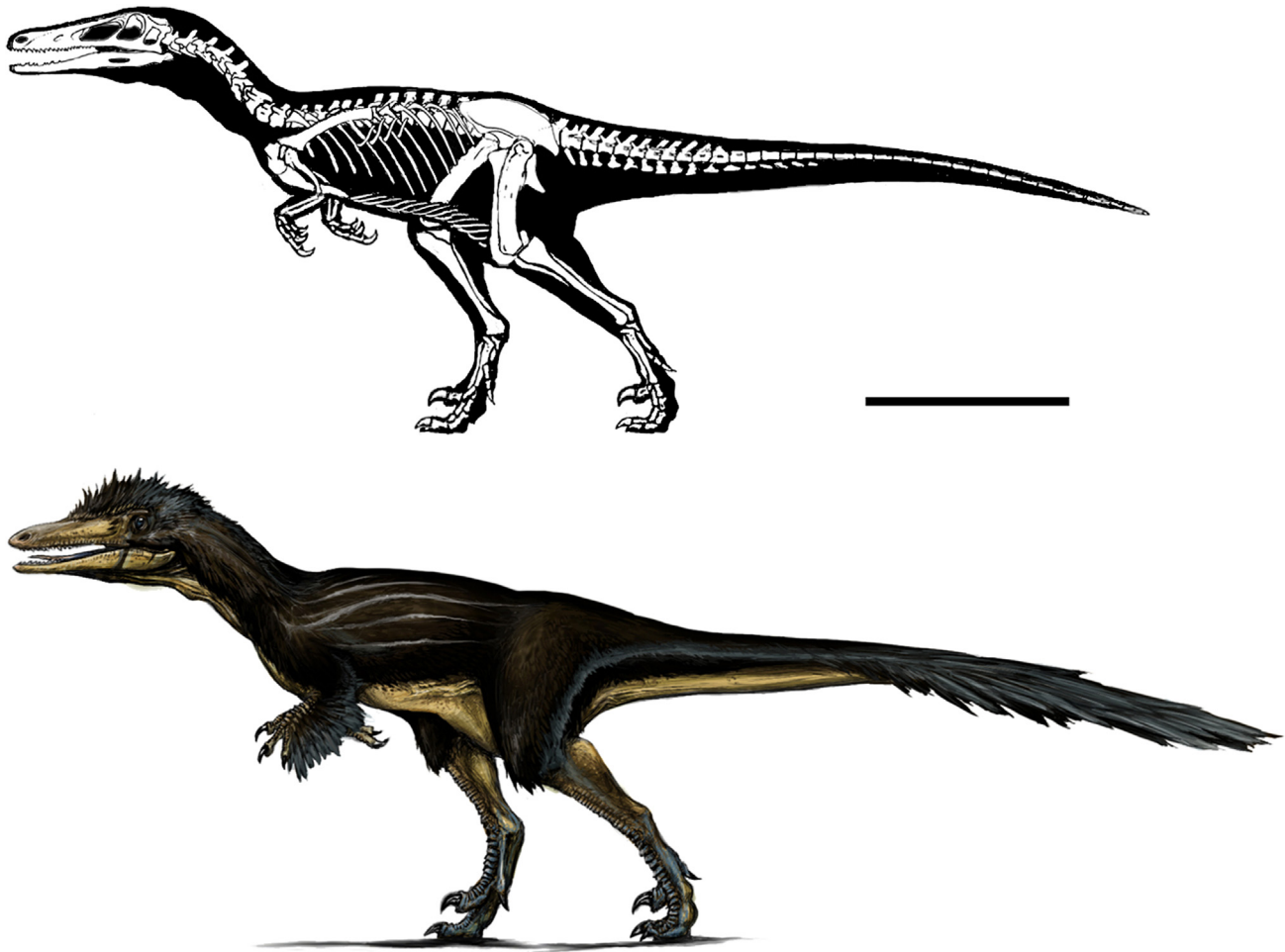


Fig. 21. Life reconstruction of *Austroraptor cabazai*. Scale bar equals 1 m (drawing by R. Vera).

most researchers concluded that *Unenlagia* and its kin were deeply nested within deinonychosaurian dromaeosaurids (Norell and Makovicky, 1999; Novas and Pol, 2005; Makovicky et al., 2005; Longrich and Currie, 2008; Xu et al., 2008; Novas et al., 2009; Hu et al., 2009). In this phylogenetic context, several unenlagiid derived features were viewed as examples of an evolutionary convergence with birds, and particularly the elongated forelimbs of *Rahonavis* (and its inferred potential for flight capability) were accepted as independently evolved from those of birds (Makovicky et al., 2005; Senter, 2007; Novas, 2009). Nevertheless, recent reviews by O'Connor et al. (2011) and Agnolín and Novas (2013) return *Rahonavis* to its previous position as a basal ornithuran and unenlagiids to that as the sister group of birds (Fig. 22). These authors propose that most characters previously employed in order to unite unenlagiids with deinonychosaurians (e.g. Xu et al., 2000, 2008; Makovicky et al., 2005; Novas and Pol, 2005; Norell et al., 2001; Turner et al., 2007a,b; Novas et al., 2009) are more widespread than previously thought (e.g., lacrimal with anterodorsal process much longer than posterior process, nutrient foramina on external surface of the dentary within a deep groove, femur with mound-like posterior trochanter distinctly raised from shaft, subarctometatarsalian metatarsus, large, longitudinal flange along caudal face of metatarsal IV, modified digit II carrying a trenchant ungueal claw) or were not properly observed in available unenlagiid specimens (e.g., dentaries lacking distinct interdental plates, splenial exposed as a broad triangle between dentary and angular). In the same way, Agnolín and Novas (2011) undertook a detailed

reappraisal of the synapomorphies that supported the monophyly of Dromaeosauridae + Unenlagiidae in previous studies and found that most of them were also present in basal birds, such as *Archaeopteryx* and *Jeholornis* (e.g. maxillary fenestra represented by a small and dorsally displaced opening, lacrimal T-shaped in lateral view, extension of supratemporal fossa over most of the ascending process of the postorbital, sinusoidal anterior emargination of supratemporal fossa on frontal, epiphyses of cervical vertebrae placed distally on postzygapophyses, parapophyses of posterior dorsal vertebrae distinctly projected on pedicels, manual unguals with dorsal arch higher than level of dorsal extremity of proximal articular surface, hallucal ungual strongly curved). Available evidence supports, on the contrary, that unenlagiids are closely related to avialans, in agreement with the original proposal (Novas and Puerta, 1997). Derived features in support of this hypothesis include: splenial not exposed on lateral surface of mandible, triangular acromion with apex pointing away from and subparallel to the scapular blade, ischiac peduncle of pubis short being nearly continuous with the lateral surface of pubic shaft, ischidiac shaft with its minimum anteroposterior diameter more than 20% of total length of ischium.

Rahonavis was described as a basal bird by Forster et al. (1998), and although some authors defended its inclusion within Unenlagiidae (e.g., Makovicky et al., 2005; Novas and Pol, 2005; Novas et al., 2009), several others (Zhou and Zhang, 2002; Hwang et al., 2002; Xu et al., 2008; O'Connor et al., 2011) found the Malagasy taxon to be placed within Avialae. Several derived features support

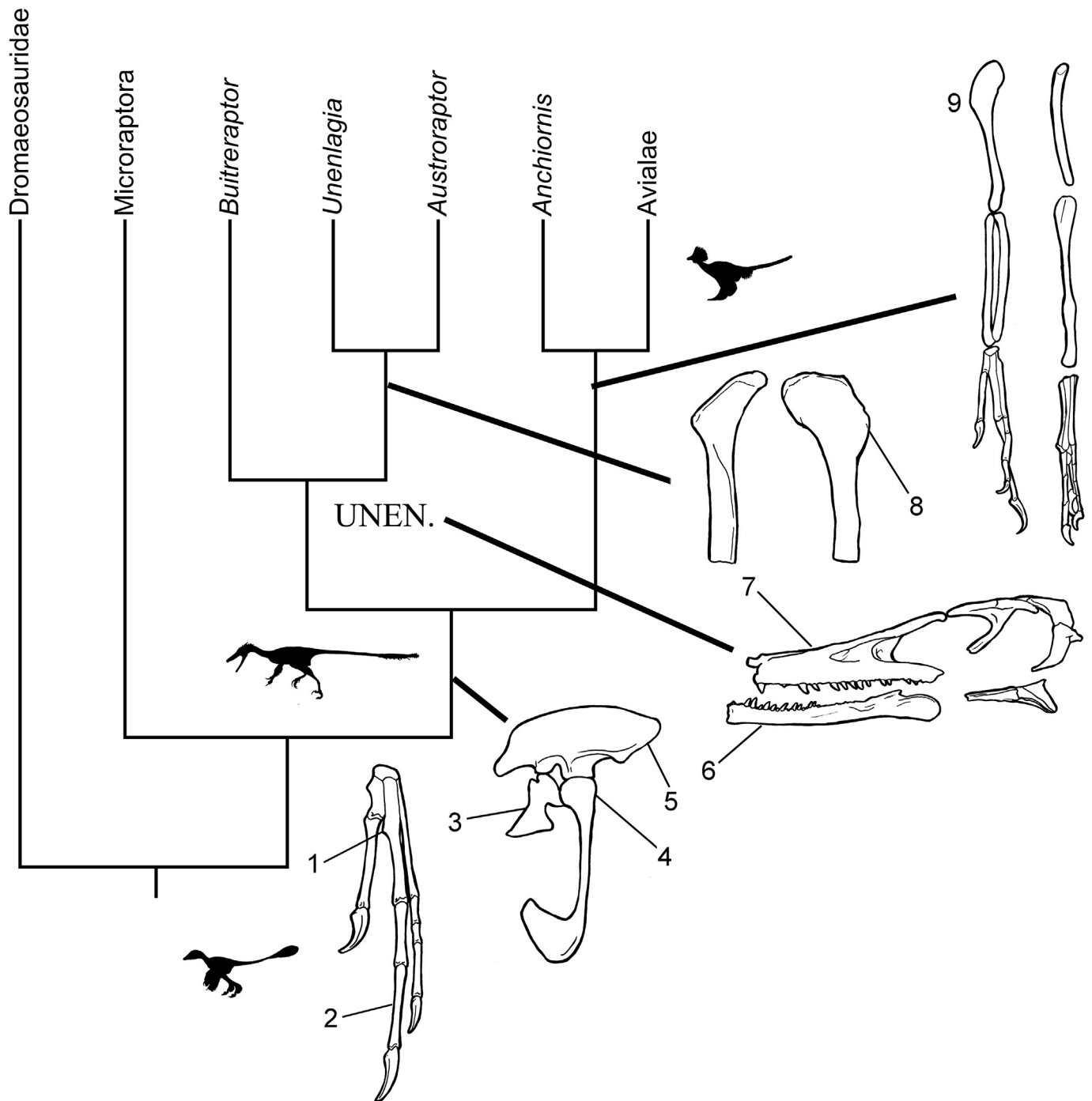


Fig. 22. Time calibrated phylogenetic tree depicting the relationships of the Unenlagiidae. Node 1: 1 – posterolateral flange on manual phalanx II-1, 2 – penultimate manual phalanx elongate and bowed. Node 2: 3 – short and stout ilium, 4 – proximal pubis rounded, 5 – preacetabular blade expanded. Node 3 (Unenlagiidae): 6 – low dentary carrying small unserrated teeth, 7 – elongate muzzle. Node 4 (*Unenlagia* + *Austroraptor*): 8 – reduced deltopectoral crest on humerus. Node 5 (*Anchiornis* + *Avialae*): 9 – elongate humerus and radius/ulna. Abbreviations: UNEN., Unenlagiidae.

Rahonavis as a basal bird more derived than *Archaeopteryx*, and *Rahonavis* shares the following characters with birds, including *Archaeopteryx*: robust scapula with sharply ridged dorsal margin close to its distal end, total length of humerus subequal to femur, radius longer than femur, humeral deltopectoral crest length more than 30% of total humeral length, pubic symphysis length less than 40% of total pubic length, reduced lateral cnemial crest of tibiotarsus, and very large hallux ungual (Agnolín and Novas, 2013). All these features are derived characters absent in more basal taxa,

including unenlagiids and dromaeosaurids, and indicate avialan affinities for *Rahonavis*. This new phylogenetic arrangement suggests that derived features once thought to be evolutionary convergences with birds, including the particularly elongated forelimbs of *Rahonavis* (and its inferred potential for flight capability) did not originate independently from those of birds, being in fact synapomorphies uniting *Rahonavis* and Aves.

Pamparaptor micros was described by Porfiri et al. (2011) and assigned to the Unenlagiidae by these authors based mainly on

several shared characters of the metatarsals (e.g., metatarsal III proximally pinched, metatarsal IV with a caudal longitudinal flange, metatarsal II posteriorly embracing metatarsal III). However, none of these features constitute unambiguous synapomorphies of Unenlagiidae, and all of them are currently considered as diagnostic of more inclusive clades (i.e., Maniraptora, Paraves; Agnolín and Novas, 2011). *Pamparaptor* shares with birds a very elongate metatarsus, and a distally extended metatarsal IV, subequal in distal extension to metatarsal III. Moreover, in *Pamparaptor* metatarsals II and IV lack any sign of a distal ginglymoid, a condition also shared with birds, but absent in dromaeosaurids and unenlagiids (Agnolín and Novas, 2011). In addition, the claw is more elongate and acute than in most deinonychosaurs (Porfiri et al., 2011). Thus we regard the phylogenetic position of *Pamparaptor* as an indeterminate paravian until a detailed description of the holotype specimen became available. Accordingly, the Unenlagiidae is unambiguously composed of *Buitreraptor gonzalezorum*, *Unenlagia comahuensis*, *Unenlagia paynemili* and *Austroraptor cabazai*, all recovered from the Upper Cretaceous of Patagonia, Argentina.

Our phylogenetic framework weakens some previous proposals on early bird distribution and radiation. For example, Xu and Zhang (2005) proposed a Laurasian, or more precisely Asiatic, location for the origin of birds, indicating that most plesiomorphic representatives of Troodontidae and Dromaeosauridae were recorded in Eastern Asia. However, recent evidence favors Unenlagiidae as the immediate sister group of Avialae and all unquestionable unenlagiids come from South America (Makovicky et al., 2005; Novas, 2009). In addition, the oldest known avialan, *Archaeopteryx*, is recorded in Europe, and the basal bird *Rahonavis* comes from another Gondwanan landmass, Madagascar. In view of the extremely incomplete fossil record of basal paravians, it is not possible to confidently establish a center of origin for the Avialae, especially given that their diversification occurred during the Middle Jurassic, when the continents were mostly joined together into a single landmass.

Accordingly, the close relationship between Unenlagiidae and Avialae invites to investigate in more detail their anatomy, which potentially will shed light on questions concerning with the early evolutionary radiation of birds, such as postural activities and flapping abilities related with the origin of flight.

3. Theropod paleobiogeography

Hypotheses concerning the Cretaceous paleobiogeography of the southern continents have strongly relied on information gathered from theropod dinosaurs. Documentation of abelisaurids during the 1980s and 1990s from Cretaceous beds of South America, India and Madagascar suggested that these theropods were abundant, diverse and widespread in Gondwana. This evidence also supports the interpretation (e.g., Bonaparte, 1991a) that Gondwana remained geographically isolated from Laurasia during most of the Cretaceous prior to the Campanian–Maastrichtian. The role of large predators in Gondwana was mainly played by abelisaurids, in sharp contrast with North America and eastern Asia, in which the largest-bodied carnivores were the tyrannosaurids (Bonaparte, 1991a). Discoveries in Patagonia of the chicken-sized *Velocisaurus unicus* (Bonaparte, 1991b) and the even smaller *Ligabueino andesi* (Bonaparte, 1996) demonstrated that the evolutionary radiation of Cretaceous abelisaurids also included small predators. This evidence further differentiated the Gondwanan dinosaur assemblages from those of North America and Asia, in which abelisaurids seem to have been absent, and the role of small carnivores was played by coelurosaurian maniraptorans (Bonaparte and Kielan-Jawarowska, 1987). Similarly, pioneering studies of late Mesozoic paleobiogeography (e.g. Lillegraven et al., 1979; Smith et al., 1981; Bonaparte,

1986; Bonaparte and Kielan-Jawarowska, 1987) have recognized sharp distinctions between the tetrapod assemblages of Laurasia (i.e., North America, Europe and Asia) and Gondwana (i.e., South America, Africa, Antarctica, India, Madagascar and Australia).

However, discoveries of purported Gondwanan lineages (e.g. abelisaurids, spinosaurids, carcharodontosaurians, alvarezsaurids) in Laurasian territories blurred the sharp faunal distinctions once recognized between southern and northern landmasses. Several authors (e.g., Casamiquela, 1964; Sues and Taquet, 1979; Rage, 1981, 2003; Bonaparte et al., 1984; Rich and Vickers-Rich, 1989, 1994; Le Loeuff, 1991; Russell and Dong, 1993; Sereno et al., 2004) attempted to explain these anomalous occurrences, invoking the development of temporary terrestrial landbridges either between Europe–Africa, North America–South America and Asia–Australia, thus allowing north–south faunal interchanges at different moments of the Cretaceous. Such incongruities in faunal distribution lead some authors (see Xu, 2010; Xu et al., 2011a) to express serious doubts regarding the Gondwana–Laurasia paleobiogeographical dichotomy.

More recently, an alternative palaeobiogeographical model, the “Eurogondwanan hypothesis” (sensu Ezcurra and Agnolín (2012b); but see also Le Loeuff (1991) for a different usage of the term “Eurogondwana”), has been presented. This new hypothesis aims to explain not only the presence of ‘Gondwanan’ taxa in Laurasia, but also the absence of northern tetrapod lineages in Gondwana. The model proposes that most of the areas that currently compose the European region had a close biogeographical affinity with Gondwana during the earliest Cretaceous (i.e., Berriasian–Hauterivian times, allowed by a connections through Africa) (Fig. 23).

The recognition of an Eurogondwanan fauna from the Berriasian to Hauterivian is based on the shared presence in Europe and Gondwana of spinosaurid theropods, rebbachisaurid and derived titanosaurian sauropods, basal dryomorph ornithopods, and boreosphenidan, peramurid, and thereuodontid mammals (e.g.; Rage, 1988; Buffetaut, 1989; Le Loeuff, 1991; Russell, 1993; Martill and Hutt, 1996; Charig and Milner, 1997; Sigogneau-Russell and Ensom, 1998; Martill and Naish, 2001; Dalla-Vecchia, 2003; Torcida et al., 2003; Juárez Valieri et al., 2004; Kielan-Jaworowska et al., 2004; Ruiz-Omeñaca et al., 2005; Gheerbrant and Rage, 2006; Canudo et al., 2008, 2009; Coria et al., 2010; Ezcurra and Agnolín, 2012b) (Fig. 23). These tetrapod clades yet remain unrecorded in Asiamerica for the same time-span.

After the Hauterivian, several Eurogondwanan tetrapod clades made their appearance in Asiamerica, including megaraptorans (i.e., *Fukuiraptor*; Azuma and Currie, 2000), carcharodontosaurids (i.e., *Shaochilong*; Brusatte and Sereno, 2008), and spinosaurids (Allain et al., 2012), in conjunction with other amniote groups such as basal titanosauriforms and derived titanosaurians (Wilson and Upchurch, 2009), notosuchian crocodylomorphs (Wu and Sues, 1996), and possibly boreosphenidan mammals (Ezcurra and Agnolín, 2012b). This evidence is interpreted as indicative of the coalescence of Europe with Asiamerica during the Barremian, after a short interval of isolation of the European region with its Eurogondwanan fauna. Thus, during the Barremian probably took part a bidirectional biotic interchange between the European region and Asia, but not implying the dispersal of typical Laurasian taxa into Gondwana.

In our interpretation, Gondwana remained isolated from Laurasia during Barremian to Santonian. During this time of isolation some amniote clades (e.g. unenlagiid and noasaurid theropods, mahajangasuchid and peirosaurid crocodylomorphs, and gondwanatherian mammals) acquired a wide geographic distribution across the southern continents, and their absence in Laurasia indicates that these clades were strict endemics of Gondwana (Krause et al., 1997; Makovicky et al., 2005; Candeiro and Martinelli, 2007;

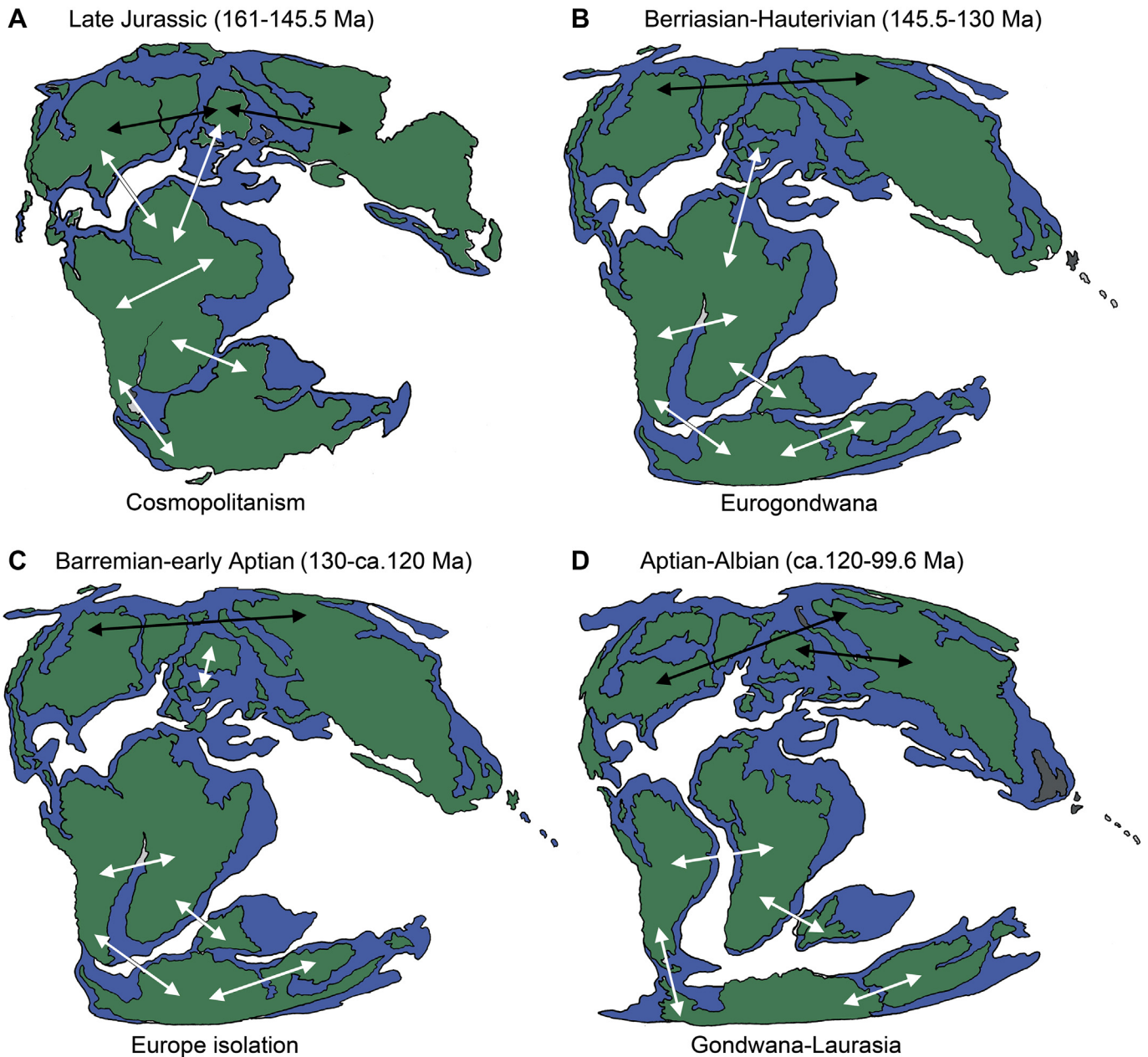


Fig. 23. Global paleogeographic reconstructions showing the main biogeographical model and connections here proposed for the (A) Late Jurassic, (B) Berriasian–Hauterivian, (C) Barremian–earliest Aptian, and (D) Aptian–Albian time-slice. The white arrows depict biogeographical connections among and within southern landmasses and/or Europe and the black arrows between Asia and North America or within Laurasia (modified from Ezcurra and Agnolín, 2012b). (A–D) redrawn from Blakey (2006) and modified following Canudo et al. (2009) regarding the position of the Apulian Plate.

Larsson and Sues, 2007; Carrano and Sampson, 2008; Novas, 2009; Sereno and Larsson, 2009) (Figs. 23, 24).

During the Campanian–Maastrichtian Europe renewed its faunal connections with the southern landmasses, rather than with Asiamerica (Fig. 24) (Le Loeuff, 1991; Ezcurra and Agnolín, 2012b). This paleobiogeographical signal is based on the common presence of basal didelphoids and ungulatormorph mammals, podocnemidoid turtles, madtsoiid and boid snakes, baurusuchid and trematochampsid crocodylomorphs, carnosaurine theropods, and derived titanosaurian sauropods in Europe and southern landmasses (de Broin, 1977, 1980; Lavocat, 1977; Rage, 1981, 1996; Crochet and Sigé, 1983; Buffetaut, 1985, 1989; Astibia et al., 1990; Le Loeuff, 1991, 1993, 1995; Lapparent de Broin and Murelaga, 1996; Allain and Pereda Suberbiola, 2003; Kielan-Jaworowska et al.,

2004; Company et al., 2005; Rasmusson and Buckley, 2009; Cadena et al., 2010; Williamson et al., 2010; Ezcurra and Agnolín, 2012b). The re-connection of the European region and South America via Africa during the Campanian–Maastrichtian is supported by the presence of Laurasian tetrapod lineages in the Campanian–Maastrichtian of South America and Antarctica (e.g., lambeosaurine and ankylosaurian ornithischians, and ungulatormorphs and basal didelphoid mammals; Ezcurra and Agnolín, 2012b) (Fig. 24). This model constitutes an alternative to the traditional hypothesis of a dispersal event between North America and South America via a terrestrial bridge during the latest Cretaceous (Rage, 1981; Bonaparte, 1984, 1986). This Panamerican connection rests on weak and controversial paleogeographic evidence (Schmidt-Effing, 1979; Rage, 1981; Pitman et al., 1993) and

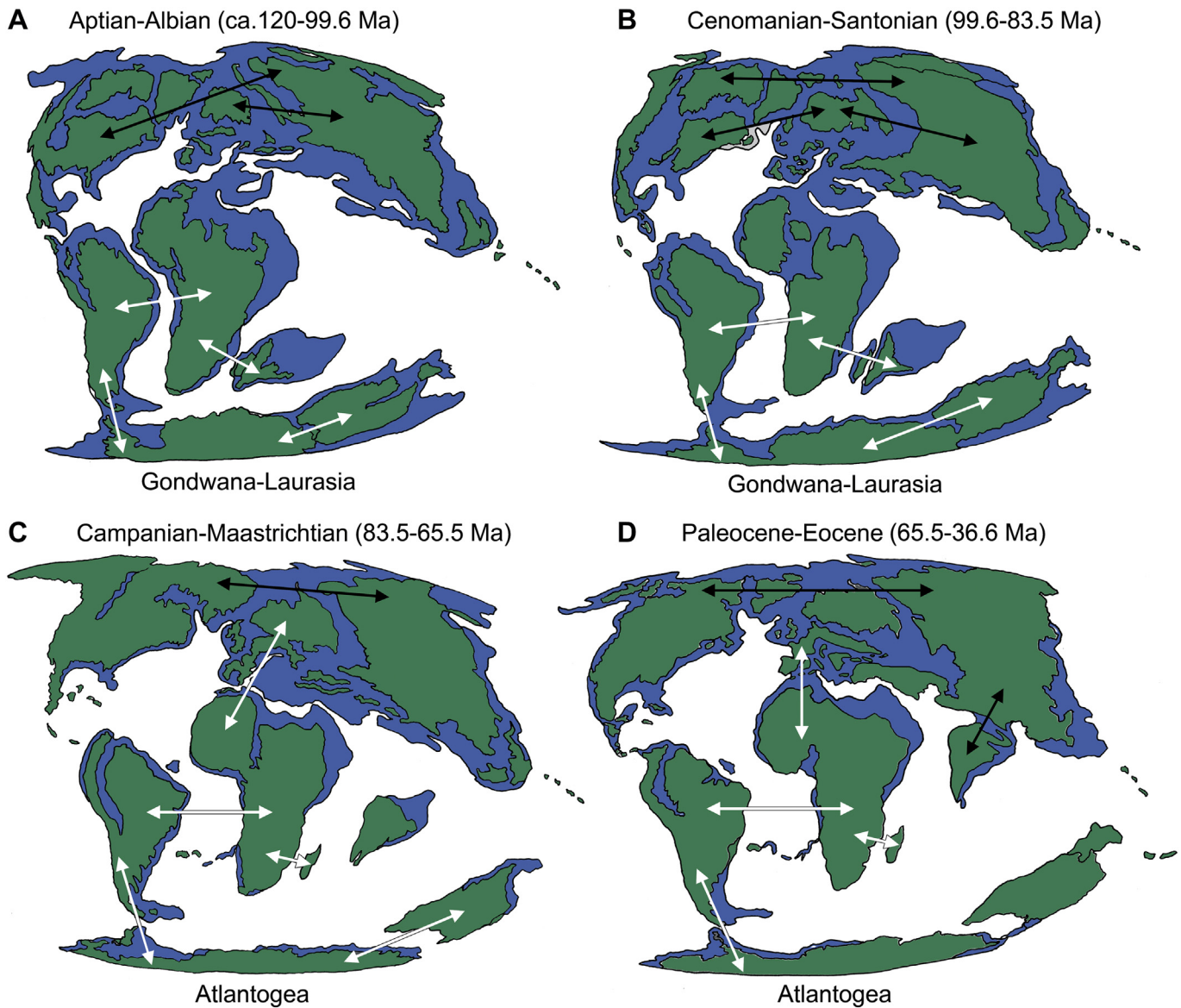


Fig. 24. Global paleogeographic reconstructions showing the main biogeographical model and connections here proposed for the (A) Aptian–Albian, (B) Cenomanian–Santonian, (C) Campanian–Maastrichtian, and (D) Paleocene–Eocene time-slices. The white arrows depict biogeographical connections within Gondwana and Atlantogea and the black arrows within Laurasia and Asiamerica (modified from Ezcurra and Agnolín, 2012b). (A–D) redrawn from Blakey (2006) and modified following Oliveira et al. (2010) regarding the South Atlantic paleogeography.

most recent paleogeographic reconstructions do not depict such a land bridge (Scotese, 2001; Blakey, 2006). On the other hand, available geological evidence strongly suggests that South America and Africa still remained connected during the latest Cretaceous through the Rio Grande Rise and Walvis Ridge (Le Pichon and Hayes, 1971; O'Connor and Duncan, 1990; Parrish, 1993; Ferrari and Riccomini, 1999; Schettino and Scotese, 2005). Paleobathymetric and geological evidence supports the presence of an island chain allowing the establishment of paleobiogeographical connections between these two southern landmasses across the South Atlantic, from the Campanian to Eocene (Oliveira et al., 2010). Moreover, the absence of the most abundant North American Campanian–Maastrichtian tetrapod lineages in the latest Cretaceous of South America (e.g., anguimorph lizards, tyrannosaurid, troodontid, therizinosaurid, oviraptorosaurid, and velociraptorine theropods, and marginocephalian ornithischians; Ezcurra and Agnolín, 2012b) constitutes an incongruent pattern under the

Panamerican land bridge model. Accordingly, since these abundant North American taxa are also absent in latest Cretaceous beds of Europe, the dispersal of Laurasian forms (e.g., hadrosaurids, ankylosaurids) to South America is considered here more likely to have occurred from Europe via Africa rather than from North America directly to South America. These evidence led Ezcurra and Agnolín (2012b) to propose the new biogeographic paleoprovince of Atlantogea, composed of the European territories, Africa, South America, Antarctica and Australia from the Campanian–Maastrichtian to the Eocene.

4. Analysis of Australian theropods in view of Patagonian evidence

As indicated above, the Patagonian theropod fossil record currently constitutes the best source of information to allow identification of carnivorous dinosaurs recorded in other regions of

Gondwana. In particular, the paleobiogeographic relationships of dinosaur assemblages of Australasia constitute a topic of heated debate (Rich and Vickers-Rich, 1994, 2003; Vickers-Rich and Rich, 1997; Smith et al., 2008; Hocknull et al., 2009; Agnolín et al., 2010; Benson et al., 2010b; Barrett et al., 2011; Fitzgerald et al., 2012). Agnolín et al. (2010) recently proposed that the Australian dinosaur faunas were very similar to those of other Gondwanan regions, especially South America. On the other hand, Barrett et al. (2011), Benson et al. (2012) and Fitzgerald et al. (2012), based on the theropod record from the Early Cretaceous of southern Australia, proposed a different paleobiogeographic model, which may be termed as the “Cosmopolitanism Hypothesis”. These authors pointed out that the Cretaceous Australian assemblages were part of a cosmopolitan global dinosaur fauna which acquired distinctive taxonomical features through regional extinctions. They proposed that most of the higher clades of Theropoda (e.g., Spinosauridae, Ceratosauria, Tyrannosauroida, Ornithomimosauria, Maniraptora) were present in Australia by the end of the Early Cretaceous. Barrett et al. (2011), Benson et al. (2012) and Fitzgerald et al. (2012) stated that the currently known Australian dinosaur record undermines previous hypotheses which considered the Cretaceous faunas of this continent as endemic (Rich and Vickers-Rich, 1994, 2003; Vickers-Rich and Rich, 1997) or predominantly Gondwanan in composition (Agnolín et al., 2010).

With the aim to evaluate the paleobiogeographic relationships of the Cretaceous dinosaur assemblages from Australia, we examine the evidence supporting the presence of spinosaurids, ornithomimosaurids, tyrannosauroids, and ceratosaurians on this continent. These fossils, consisting of isolated pieces, most of them incomplete and deformed, come from the Aptian–Albian Eumeralla and Wonthaggi formations, cropping out in diverse localities of the Victoria County, southeastern Australia (Benson et al., 2012). Among the several theropod specimens there collected, four of them have been considered pivotal in discussing the paleobiogeography of Cretaceous Australian dinosaurs: a spinosaurid cervical vertebra (Barrett et al., 2011; Benson et al., 2012), an ornithomimid caudal vertebra (Benson et al., 2012), a tyrannosauroid pubis (Benson et al., 2010b, 2012) and a ceratosaurian astragalocalcaneum (Fitzgerald et al., 2012). A summary review of these specimens follows.

4.1. *Spinosaurid cervical (NMV P221081)*

Barrett et al. (2011) reported the presence of Spinosauridae in Australia based on a partial anterior cervical vertebra collected in the Early Cretaceous Eumeralla Formation. Barrett et al. (2011) supported the assignment of the specimen to Tetanurae based on the presence of an opisthocoelous centrum, a camerate internal structure, a single pair of anteriorly situated pneumatic foramina (pleurocoel), and a space between the prezygapophyses wider than the neural canal. However, most of these features seem to be also present among non-tetanuran theropods (for example, abelisauroids; Bonaparte et al., 1990; Sereno et al., 2004; Carrano et al., 2011; see SI part 6). Moreover, Barrett et al. (2011) proposed spinosaurid affinities for the specimen NMV P221081 particularly on the basis on the elongate vertebral centrum and a pleurocoel divided internally by a fine, subvertical lamina, that these authors judged to be “identical to *Baryonyx*” (Benson et al., 2012:4). In regard to this latter feature, it must be noted that the morphology of the pleurocoel of the purported spinosaurid cervical is low and elongate, and divided by a lamina that is posterodorsally inclined, thus clearly differing from that of *Baryonyx* (see SI), in which the pleurocoel is rounded and its internal lamina is anterodorsally inclined. No other theropods with divided anterior pleurocoels (e.g., carcharodontosaurids, megaraptorids, tyrannosauroids) exhibit the

unusual morphology seen in the Australian specimen. NMV P221081 exhibits a moderately convex cranial articular surface of the centrum, differing from the ball-shaped surface characteristic of spinosaurids (e.g., *Baryonyx*, *Spinosaurus*; Stromer, 1915; Russell, 1996; Charig and Milner, 1997) and other basal tetanurans (e.g., *Allosaurus*, carcharodontosaurids). NMV P221081 exhibits a camerate internal structure present in disparate tetanuran clades, such as spinosaurids and in a yet undescribed juvenile specimen of *Megaraptor namunhuaiquii*. The unusual pleurocoel of NMV P221081, in conjunction with the moderately convex cranial articular surface of the centrum, and its camerate internal structure, present a combination of features not seen in post-axial cervicals of other theropods, including spinosaurids, megaraptorids, and carcharodontosaurids. Thus there is no firm anatomical evidence in support of the referral of NMV P221081 to Spinosauridae; on the contrary, anatomical characteristics afforded by this fragmentary vertebra lead us to refer this specimen as an indeterminate avostran or tetanuran, at best.

4.2. *Ornithomimosaur caudal (NMV P186168)*

Benson et al. (2012) indicated the presence of an indeterminate ornithomimosaur in Australia on the basis of a partial proximal caudal vertebra. These authors based their identification on the proplatycoelous centrum and a sheet-like anteroposteriorly expanded transverse processes subequal to the anteroposterior length of the neural spine. Both features are not unique to ornithomimosaurids and are widely present among basal abelisauroids, such as *Elaphrosaurus* and *Masiakasaurus* (MB unnumbered; Novas et al., 2004; Carrano et al., 2002, 2011). Another feature cited in support of ornithomimosaurian affinities for the caudal vertebra is the internal structure of the neural arch, consisting of numerous irregularly-shaped chambers, which resemble the ornithomimosaur *Archaeornithomimus*. However, the distribution of this feature is poorly known within Theropoda. General proportions of this vertebra have been also cited to support an ornithomimosaur relationship, but similar proportions of centrum and transverse processes are also exhibited in theropods other than ornithomimosaurids (for example, the ceratosaurians *Ceratosaurus* and *Majungasaurus*; Gilmore, 1920; O'Connor, 2007). In sum, NMV P186168 exhibits general characteristics that are widely present among theropods, and referral to Ornithomimosauria is questionable.

4.3. *Tyrannosauroid pubis (NMV P186046)*

Regarding the presence of “stem”-tyrannosauroids, Benson et al. (2010b, 2012) described a distorted, broken and partially preserved pair of pubes, that was assigned to a “stem”-tyrannosauroid. The specimen was re-interpreted by Herne et al. (2010) as an indeterminate neotetanuran, but Benson et al. (2010c, 2012) offered new evidence that this bone belongs to a tyrannosauroid coelurosaurian. Features recognized by Benson et al. (2010c, 2012) in support of their interpretation include the presence of a prominent and laterally rugose, flange-like tubercle on the proximal pubis, a transversely narrow pubic apron, and a transversely narrow and parallel-sided distal pubic boot. However, direct observation of the specimen NMV P186046 reveals that each of these regions of pubes is badly damaged and deformed, as was previously noted by Herne et al. (2010). The right pubis exhibits a similar profile (in side view) as in tyrannosauroids and megaraptorids (e.g., *Aerosteon*, *Megaraptor*), with an anteriorly convex flange-like prominence. The pubic shaft is certainly narrow (in anterior aspect), resembling coelurosaurians (Benson et al., 2012), but the left pubis of specimen NMV P186046 reveals that the pubic apron was wider than that preserved on the right pubis. A strongly anteroposteriorly

expanded distal pubic boot is a feature that NMV P186046 shares with tyrannosaurids, but also with carcharodontosaurids and megaraptorids. Direct study of the specimen reveals that the distal end of the pubis has lost most of its lateral and distal surfaces, thus a transversely narrow boot constitutes a preservational artifact, and not a true coelurosaurian synapomorphy. It is noteworthy that in NMV P186046 the surface of the anterior extension of the distal pubic foot is fused, almost flattened, and with a slight median ridge. In contrast, in tyrannosaurids and megaraptorids the dorsal surface of the anterior extension of the pubic boot is grooved. This condition may represent an autapomorphic feature of NMV P186046, not recognized in previous work (Benson et al., 2010b, c, 2012; Herne et al., 2010). Overall, general morphology of NMV P186046 is congruent with tyrannosaurids and megaraptorids, the later ones being well documented in Cretaceous beds of Australia (Smith et al., 2008; Hocknull et al., 2009), thus the referral of NMV P186046 to this family clade may represent the best supported option.

4.4. *Ceratosaurian astragalocalcaneum* (NMV P221202)

Fitzgerald et al. (2012) reported the presence of Ceratosauria on the basis of an isolated and distorted fused astragalocalcaneum from Early Cretaceous beds of the Wonthaggi Formation, San Remo, southeast Australia. The specimen was regarded as a ceratosaurian due to the presence of a combination of characters, including: coossified astragalus and calcaneum, ascending process of astragalus with parallel-sided base, distinct fossa at the base of the ascending process of the astragalus that is not associated with the transverse groove of astragalar body. However, this combination of characters is not unique of Ceratosauria, but it is also present in most members of the coelurosaurian clade Alvarezsauridae (e.g., *Alvarezsaurus*, *Mononykus*, *Patagonykus*; Novas, 1996). Fitzgerald et al. (2012) indicated that the Australian specimen shares with *Masiakasaurus*, and differs from remaining ceratosaurians, a pair of pits into an oval fossa at the base of the ascending process, and a distinct eminence on the medial edge of the ascending process. It is worth mentioning that these two characters are also documented in the alvarezsaurids *Patagonykus* and *Mononykus* (Novas, 1996). Moreover, the morphology of the medial edge of the ascending process of the astragalus has been previously considered as diagnostic of Alvarezsauridae (Novas, 1996). However, the presence of an ascending process restricted to the lateral three-quarters of the astragalar body clearly contrasts with the condition observed in alvarezsaurids, megaraptorids and other coelurosaurs. The ascending process of the astragalus exhibits a vertical groove on its posterior surface (NMV P221202), which was previously documented in the megaraptorids *Aerosteon* and NMV P150070 (formerly *Allosaurus* sp.). Furthermore, the base of the ascending process of NMV P221202 is distinctly asymmetric in posterior view, with the lateral margin being considerably more ventrally extended than the medial one, thereby strongly constricting anteroposteriorly the tibial facet at the level of the lateral margin of the ascending process. This condition was only observed in megaraptorids (i.e., NMV P150070, *Aerosteon*, *Australovenator*). The calcaneum of the Australian specimen exhibits a well developed and obliquely oriented postedorsal notch for the articulation with the tibia, a condition synapomorphic of Tetanurae (i.e., Spinosauroidae + Avetheropoda; Holtz et al., 2004), thus weakening the affinities originally proposed with Ceratosauria, in which this notch is absent. In summary, we consider that the evidence to support the assignment of the astragalocalcaneum NMV P221202 to Ceratosauria is weak and it may be preferable to identify it as an indeterminate averostran.

Overall, taxonomic allocations of the most relevant theropod specimens from Victoria are far from conclusive, meaning that the paleobiogeographic signals they provide are ambiguous and

preventing any convincing statement about the cosmopolitan nature of the Cretaceous dinosaur fauna from being made. We consider that the current evidence favors Gondwanan affinities for the Australian theropod assemblages (see SI, part 6, for a quantitative analysis), as evidenced by the most complete theropod specimen from Australia, *Australovenator* from the Winton Formation (Hocknull et al., 2009), which is phylogenetically close to the Patagonian megaraptorids, as demonstrated in the present paper. In congruence with this interpretation, a number of other specimens from Victoria are also assignable to Megaraptora, including an isolated ulna (NMV P186076; Smith et al., 2008), isolated vertebrae, as well as an abundant collection of shed teeth (Benson et al., 2012). We thus conclude that the theropod assemblages from Australia can be comfortably interpreted within a Gondwanan faunal realm.

5. Theropods as evidence of provincialism across Gondwana

Because southern landmasses were joined and/or in close proximity during the Cretaceous, the dinosaur assemblages from Gondwana have been usually considered to have been uniformly distributed across the entire supercontinent. It is clear that the Aptian–Cenomanian continental faunas from northern Africa and Brazil closely resemble each other (Calvo, 1999), and those from Madagascar, India and Patagonia are also very similar in composition (Bonaparte, 1986, 1999). However, the available fossil record suggests that Cretaceous dinosaur distribution in Gondwana was not uniform, but rather that notable distinctions emerge when comparing the reptile assemblages from the Sahara, Brazil, Patagonia and Australia (Novas et al., 2005; Novas, 2009; Benson et al., 2012). Such distinctions may be explained as having been due to paleoclimatic and paleoecological conditions which impacted both plant and animal distributions. In fact, some differences become apparent when dinosaurian faunas from northern Gondwana (i.e., Sahara + northern South America) are compared with those from southern Gondwana (i.e., Patagonia + Australasia), and in a palaeobiogeographic analysis presented here, northern Gondwana and southern Gondwana appear as separated monophyletic clades (see SI, part 6). In fact, northern South America exhibits several similarities with the fossil faunas of Saharan Africa, including the common presence of arganodontid and ceratodontid-like dipnoans, dominance of podocnemidoid pleurodire turtles, presence of anhanguerid pterosaurs, and among theropods, the presence of top-predatory spinosaurid and sigilmassosaurid taxa (Apesteguía, 2002; Novas et al., 2005, 2009; Agnolín, 2010; Kellner et al., 2011; previous reports of isolated spinosaurid teeth from Patagonia were dismissed by Bertini, 2010). On the contrary, southern Gondwanan faunas, including those of Argentina and Australasia, are marked by the common presence of basal dipnoans, predominance of chelid pleurodiran turtles, and among theropods a great diversity and abundance of megaraptorids (Apesteguía, 2002; Smith et al., 2008; Agnolín, 2010; de la Fuente et al., 2011; see Méndez et al., 2012).

Taxonomically, the Cretaceous dinosaur fauna of Australia is similar to the rest of Gondwana. Evidence to support this includes the fossil assemblage recently documented in the Winton Formation, which is composed of a megaraptorid and two titanosaurian taxa (Hocknull et al., 2009; Agnolín et al., 2010; Benson et al., 2010a). This faunistic composition is similar to typically Patagonian faunas, in which both megaraptorids and titanosaurians are recorded together. Similar assemblages remain unrecorded in other southern and northern landmasses. The main differences between Patagonian and Australian faunas relate to the relative abundance of certain theropod groups, as in the case of the materials collected from the Eumeralla Formation (late Aptian–early Albian), Otway Group of the Otway ranges, southwest of Melbourne, in which no remains unambiguously referable to Abelisauroidae have been

identified so far. This is in sharp contrast with Patagonia, in which abelisauroids are notably abundant and diverse (Novas, 2009). Australia is known to have been home to megaraptorids during the Aptian–Albian at least, as demonstrated by the discovery of an isolated, but diagnostic ulna from Flat Rock locality (Smith et al., 2008; Agnolín et al., 2010), the well preserved remains of *Australovenator* (Hocknull et al., 2009) which shares outstanding

apomorphies with Patagonian megaraptorans, and an abundant collection of more than a hundred teeth collected by Tom Rich and collaborators in the Flat Rocks locality recently interpreted as belonging to Megaraptora (Benson et al., 2012). The morphology of these teeth fits well with the morphology described for the Patagonian *Orkoraptor* (Novas et al., 2008) and *Australovenator* (Hocknull et al., 2009), in which the tooth crown shows an eight-

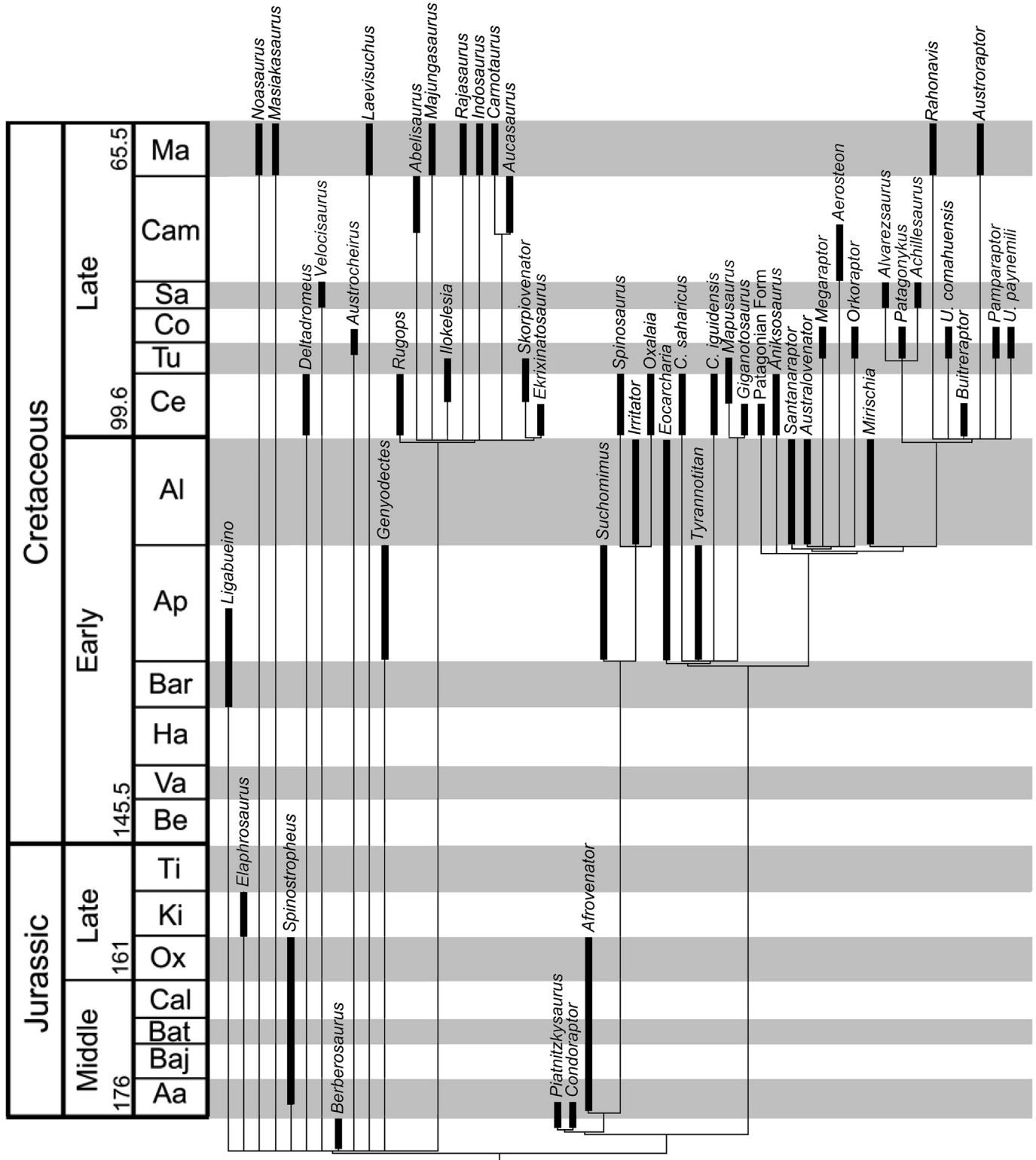


Fig. 25. Temporally calibrated Gondwanan theropod tree showing their phylogenetic relationships and temporal occurrences.

shaped cross-section at its base, strongly reduced mesial denticles, and strongly curved mesial and distal margins of the teeth. Overall, these fossil specimens reveal a predominance of megaraptorids in Australia which is not seen in the remaining southern continents. This evidence, taken in joint with the apparent absence of abelisauroids in Australia, may be explained as evidence of certain degree of provincialism in the context of the Gondwanan realm.

6. Tempo and mode of the Patagonian Cretaceous theropod macroevolution

Most, if not all, of the theropod lineages that inhabited Patagonia and the rest of Gondwana during the Cretaceous originated during the Jurassic (Makovicky et al., 2005; Zhang et al., 2008; Hu et al., 2009) (Figs. 25, 26). The Gondwanan Jurassic theropod

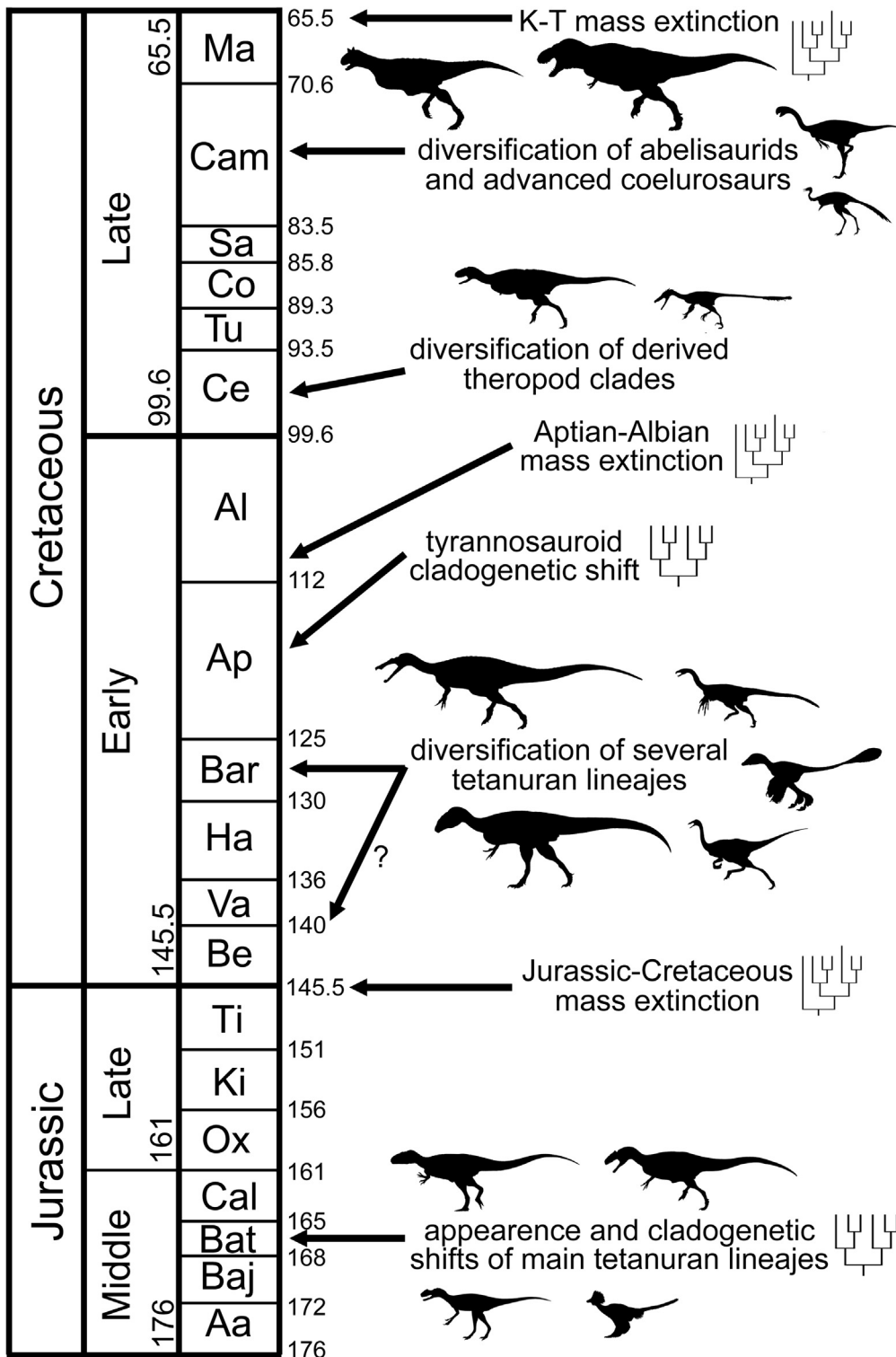


Fig. 26. Global macroevolutionary patterns of theropod dinosaurs along the Late Mesozoic.

record is strongly biased and represented by a small number of widely dispersed assemblages of disparate age: the latest Early Jurassic–early Middle Jurassic Cañadon Asfalto Formation, the Kimmeridgian Tendaguru beds, and the Early Jurassic Toundoute series (Janensch, 1925; Bonaparte, 1986; Rauhut, 2005, 2011; Weishampel et al., 2004; Allain et al., 2007). These Jurassic Gondwanan assemblages have yielded basal tetanurans (e.g. *Piatnitzky-saurus*, *Condorraptor*), basal ceratosaurians (e.g. *Elaphrosaurus*, *Eoabelisaurus*, *Berberosaurus*) and basal allosauroids (e.g. “*Allosaurus tendagurensis*”, *Veterupristisaurus*) (Janensch, 1925; Bonaparte, 1986; Rauhut, 2005, 2011). To date, no coelurosaurian remains have been reported from the Jurassic of the southern continents. In contrast, the Jurassic Laurasian record is taxonomically richer and includes basal ceratosaurians, basal tetanurans, plus a wide array of coelurosaurian clades (e.g., tyrannosauroids, compognathids, scansoriopterygids, archaeopterygids; Rauhut, 2003; Zhang et al., 2008; Xu et al., 2011a). This rich Laurasian record allows recognition of a peak in origination index at the Bathonian (Fig. 27). At this age a disparate set of tetanuran lineages is recorded for the first time, as represented by basal tyrannosauroids (i.e., *Proceratosaurus*; Rauhut, 2005; Rauhut et al., 2010), bizarre oviraptorosaurs (e.g., *Epidendrosaurus*; Agnolín and Novas, 2013), and basal avialans (*Anchiornis*; Agnolín and Novas, 2013), indicating that an overall theropod phylogenetic branching was well underway since the Bathonian at least (Figs. 25, 26, 28). Additionally, the Laurasian record suggests a significant extinction event occurred at the Jurassic–Cretaceous boundary ($p < 0.001$), which is in agreement with a mass extinction event recognized for other continental and marine biotas (Raup and Sepkoski, 1984) (Fig. 27). The poor Gondwanan theropod record does indicate extinction events similar to those in Laurasia ($p = 0.785$, it does not depart from background extinction levels) (Table 1).

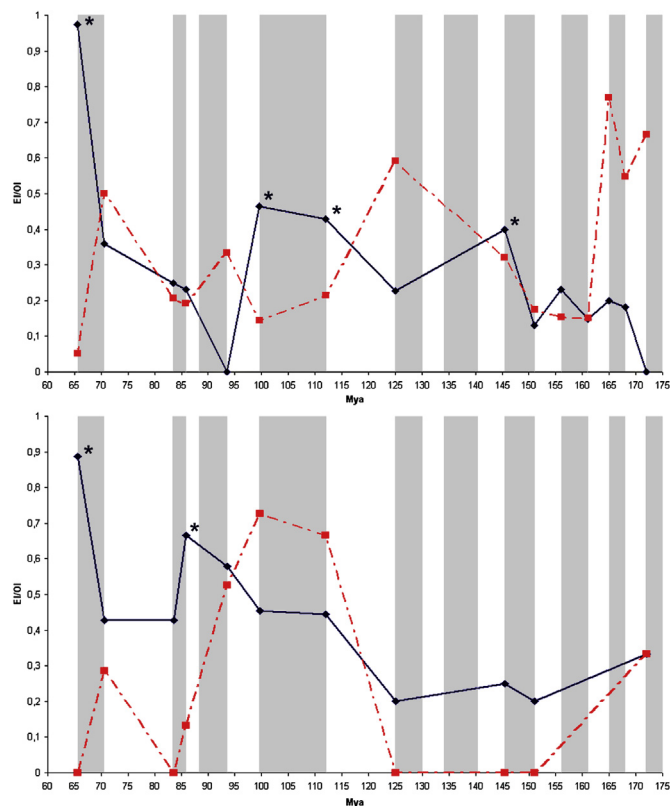


Fig. 27. Comparative graphic showing origination (red) and extinction (blue) indexes of theropods in Laurasia (top) and Gondwana (bottom). The asterisks depict extinction events significantly differing from background extinction levels after bootstrapping.

The theropod record in Gondwana is also poor during the start of the Early Cretaceous (i.e. Berriasian–Barremian; Fig. 25). In Patagonia, two sedimentary units yielded theropod remains from this epoch: the Valanginian Bajada Colorada Formation, which provided scarce remains of basal tetanurans (Apesteguiá and Bonaparte, 2004; Gianechini et al., 2011a), and the late Barremian–early Aptian La Amarga Formation, which yielded the basal abelisauroid *Ligabueino* and some indeterminate theropod teeth (Bonaparte, 1996). Thus, knowledge of the Gondwanan theropod assemblages from this time interval is not sufficient to allow reliable recognition of macroevolutionary patterns. However, the richer Laurasian record indicates a peak in the theropod origination index for the Berriasian–Barremian (Fig. 26; see SI part 1). This peak corresponds to the taxonomic diversification of several tetanuran clades during the Barremian, including spinosaurids, carcharodontosauroids, ornithomimosaurs, therizinosaurs, oviraptorosaurs, troodontids, dromaeosaurids and ornithurines. Nevertheless, it should be noted that the ghost lineages of these clades and the oldest body fossil remains suggest Middle Jurassic origins (e.g., Makovicky et al., 2005; Hu et al., 2009; Choiniere et al., 2010b; Rauhut, 2011) (Figs. 25, 27).

The Aptian–Albian record from Gondwana reveals a diverse theropod fauna composed of ceratosauroids, spinosaurids, carcharodontosauroids and basal coelurosauroids (Bonaparte, 1986; Sereno et al., 1996, 1998; Leanza et al., 2004; Novas, 2009) (Fig. 28). Nevertheless, the Patagonian record is still restricted to a small number of specimens, including the purported ceratosauroid *Genyodectes* (Rauhut, 2004), the carcharodontosauroid *Tyrannotitan* (Novas et al., 2005), and two isolated abelisauroid caudal vertebrae (Rauhut et al., 2003). Thus the major predatory lineages that dominated early Late Cretaceous terrestrial ecosystems in Patagonia first appear in the terminal Early Cretaceous. It should be noted that a high origination peak is recorded for the Aptian–Cenomanian in Gondwana (Fig. 27). However, this peak seems to be an artifact resulting from the almost unknown southern theropod record prior to the Aptian–Albian (Weishampel et al., 2004). In Laurasia we observe a significant extinction event in the Aptian–Albian ($p = 0.001$ and $p < 0.001$ for the Aptian and Albian, respectively), which is not recorded in the southern record ($p = 0.545$ and $p = 0.727$). The available Aptian–Albian theropod record from Gondwana suggests that the extinction observed in Laurasia may constitute a regional event (Table 1). All major theropod lineages known from the mid-Cretaceous of Gondwana (e.g., ceratosaurians, spinosaurids, carcharodontosauroids, megaraptorids) are also recorded in the early Late Cretaceous (Novas, 2009).

In the Cenomanian–Coniacian we recognize high extinction indices in Gondwana (0.58 and 0.67), but only the Turonian–Coniacian value significantly departs from background extinction levels ($p = 0.048$) (Table 1). In the Cenomanian the spinosaurids and some basal coelurosauroids went extinct along with basal abelisauroids and carcharodontosauroids (Novas et al., 2005) (Figs. 27, 28). A similar faunal extinction and replacement may be seen in other vertebrate groups such as dipnoans (Apesteguiá et al., 2007; Agnolín, 2010), rebbachisauroid sauropods (Apesteguiá, 2002; Novas et al., 2005; Salgado and Coria, 2005), crocodylomorphs and turtles. In the case of turtles, the early and mid-Cretaceous record appears to be dominated by *Prochelidella*-like chelids, whereas in post-Cenomanian beds they are replaced by larger more modern chelids and podocnemidoids (Lapparent de Broin and de la Fuente, 2001; de la Fuente et al., 2011). Regarding crocodylomorphs, species of *Araripesuchus* numerically dominate Aptian–Turonian beds of Argentina and Brazil (Price, 1959; Ortega et al., 2000; Pol and Apesteguiá, 2005), but they are replaced by more derived notosuchians by Turonian–Santonian times (Bonaparte, 1991b). The Gondwanan Turonian–Coniacian theropod record is almost

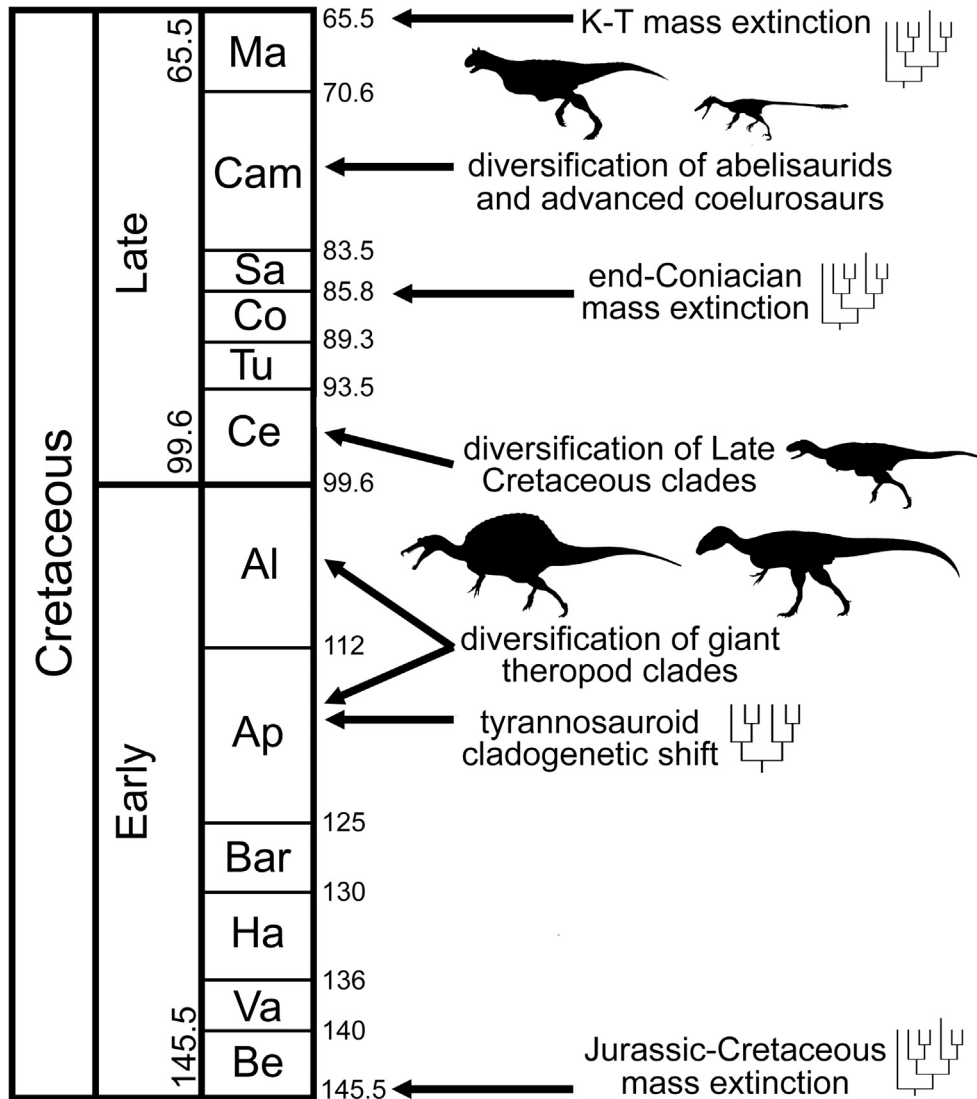


Fig. 28. Macroevolutionary patterns of theropod dinosaurs in the Late Mesozoic of Gondwana.

represented by Patagonian forms. At this stage the Patagonian theropod assemblages suffered high extinction rates, including the last record of carcharodontosaurids (Novas, 2009). In addition, abelisaurids, megaraptorids, and unenlagiids lost several of their genera (Fig. 25). Aside from theropods, diplodocimorphs went extinct by the end of the Cenomanian, and most non-saltasaurine titanosaurs vanished by the end of the Turonian–Coniacian (Coria and Salgado, 2003; Salgado and Coria, 2005). In this regard, the different taxonomic selectivity between the Cenomanian and Turonian–Coniacian events suggests that they were caused by different processes acting over several million years, rather than a single extinction event. In contrast, the Cenomanian–Coniacian time span exhibited a strong fall in the values of origination indices (Fig. 27). In our analysis, focused on theropod dinosaurs, no Cenomanian or Turonian–Coniacian extinctions are evident in the fossil record of the northern continents (Table 1) (Weishampel et al., 2004). However, it must be noted that some authors have documented important changes in terrestrial vertebrate faunal composition in Laurasia by Cenomanian times (Jacobs and Winkler, 1998). In addition, and also contrasting with the southern theropod faunas, a peak in the origination index is observed for the Laurasian faunas after the Aptian–Albian mass extinction, due to the diversification of derived therizinosaurids and ornithomimids.

By the end of the Late Cretaceous, both Gondwanan and Laurasian theropod assemblages shared a similar macroevolutionary pattern, consisting of a continuous increase of extinction levels (Fig. 27; Table 1) until reaching the KT boundary, and a peak in species origination by the end of the Campanian. Gondwana exhibits a dinosaur faunal composition during the Santonian–Maastrichtian differing from those previous to the Turonian–Coniacian extinction event, including a diversification of “noasaurids”, derived abelisaurids, alvarezsaurids and birds (Bonaparte, 1991a, 1999; Novas, 1997a; Apesteguía, 2002; Agnolín and Martinelli, 2009). During the Santonian, the last megaraptorids are recorded in Patagonia (Porfiri et al., 2008; Gianechini et al., 2011b) and during the Maastrichtian the unenlagiids reached the position of top predators alongside abelisaurids in northern Patagonia (Novas et al., 2009). The composition of the ornithischian faunas underwent major change in Patagonia at the Santonian–Campanian boundary. Small to medium-sized basal euiguanodontids usually recovered in Cenomanian and Santonian beds were replaced in the Campanian–Maastrichtian by larger and abundant hadrosauriforms and basal ankylosaurians (Brett-Surman, 1979; Bonaparte, 1984; Salgado and Coria, 1996).

In conclusion, theropod faunas from Gondwana underwent macroevolutionary pathways seemingly differing from those from Laurasia, with a lack of synchronicity in origination peaks and

Table 1
Extinction indexes and results of the non-parametric statistical analyses for the Gondwanan and Laurasian theropod semi-strict supertrees.

Time-slice	Extinction index	P-value	Upper boundary
Laurasia			
Aalenian	0.0000	0.001*	172
Bajocian	0.1818	0.982	168
Bathonian	0.2000	0.759	165
Callovian	0.1481	0.512	161
Oxfordian	0.2308	0.485	156
Kimmeridgian	0.1304	0.219	151
Tithonian	0.4000	<0.001*	145.5
Berriasian–Barremian	0.2273	0.973	125
Aptian	0.4286	0.001*	112
Albian	0.4643	<0.001*	99.6
Cenomanian	0.0000	<0.001*	93.5
Turonian–Coniacian	0.2308	0.271	85.8
Santonian	0.2500	0.393	83.5
Campanian	0.3600	0.500	70.6
Maastrichtian	0.9737	<0.001*	65.5
Gondwana			
Aalenian	0.3333	0.334	172
Bajocian–Kimmeridgian	0.2000	0.524	151
Tithonian	0.2500	0.785	145.5
Berriasian–Barremian	0.2000	0.250	125
Aptian	0.4444	0.545	112
Albian	0.4545	0.727	99.6
Cenomanian	0.5789	0.232	93.5
Turonian–Coniacian	0.6667	0.048*	85.8
Santonian	0.4286	0.635	83.5
Campanian	0.4286	0.336	70.6
Maastrichtian	0.8889	0.005*	65.5

Bold letter indicates time-slices with high extinction indexes. Asterisks indicate high P-value.

extinction events occurring on both supercontinents (Fig. 27). Gondwana lacks evidence of an extinction event that affected Laurasia during Aptian–Albian times (Table 1), as well as the high origination peak during the Cenomanian in Laurasia. Additionally, the extinction event recognized in Gondwana for the Cenomanian and Turonian–Coniacian, is not evidenced in Laurasia.

7. Conclusions

7.1. Abelisauroida is the best represented theropod clade in the Cretaceous beds of Patagonia. The monophyly of Noasauridae and the intrarelationships among basal abelisauroids and derived abelisauroids remain an open question. Recent work agrees regarding the monophyly of Abelisauridae, and Canale et al. (2009) have recognized the Brachyrostra as a less inclusive clade of South American abelisauroids.

7.2. Carcharodontosaurid theropods played the role of top predators in Patagonia and Africa from Aptian through Coniacian times, but apparently attained their maximum diversity during the Cenomanian. The carcharodontosaurids achieved a global distribution during the mid-Cretaceous and their presence has been recently documented in Asia. The clade Giganotosaurinae includes a suite of giant South American forms.

7.3. Recent interpretations allow recognition of Megaraptora as a clade of mid- to large-bodied cosmopolitan allosauroid theropods (e.g., Brusatte and Sereno, 2008; Hocknull et al., 2009; Benson et al., 2010a). However, we recover megaraptorans not only inside Coelurosauria, but also as probable members of Tyrannosauroida. This phylogenetic hypothesis lends support to the interpretation that Patagonia, and probably also the rest of Gondwana, was a cradle for the evolutionary radiation of a wide variety of basal coelurosaurians.

7.4. The alvarezsaurids were a group of small coelurosaurians, recorded in latest Cretaceous beds of Patagonia. The Patagonian forms are plesiomorphic with respect to those recovered in

northern continents. A recent phylogenetic analysis has found a monophyletic clade of South American forms, including the Turonian *Patagonykus* and the Maastrichtian *Bonapartenykus*, both from northwestern Patagonia.

7.5. The unenlagiids seem to represent an endemic clade of South American derived coelurosaurians. They ranged from small to large forms with a disparate forelimb anatomy and proportions. Although they were interpreted as members of Dromaeosauridae, recent phylogenetic analyses have recovered them as basal avialans closely related to birds.

7.6. The Patagonian Cretaceous theropod record has contributed to the understanding of the global historical paleobiogeography. Late Mesozoic paleobiogeography has been characterized by a distinction between the northern territories of Laurasia and the southern landmasses of Gondwana. The repeated discovery of Gondwanan lineages in some of the Laurasian continents has led to alternative scenarios explaining these anomalous occurrences. In order to explain these paleobiogeographic patterns, a new model has been recently proposed, in which Europe and ‘Gondwanan’ territories possessed a common Eurogondwanan fauna during the earliest Cretaceous. Subsequently, following the Hauterivian, the European territories severed from Africa and after isolation then connected to Asiamerica resulting in a faunal interchange. This model explains the presence of ‘Gondwanan’ taxa in Laurasia and the absence of Laurasian forms in the southern territories during the Cretaceous.

7.7. The Gondwanan theropod record suggests the presence of provincialism in the southern landmasses during the Cretaceous. Northern South America presents closer biogeographic affinities with Africa and southern South America with Australasia. However, the Australasian theropod assemblage differs from that of other Gondwanan areas in its abundance of megaraptorids and probable absence of abelisauroids, carcharodontosaurids and spinosaurids.

7.8. The Late Cretaceous macroevolutionary patterns observed in Gondwana differ from those recorded in the northern continents. These differences include the occurrence of extinction events during the Cenomanian and Turonian–Coniacian in Gondwana that are not recorded in northern dinosaur assemblages. Although the theropod assemblages of Gondwana and Laurasia were distinctly different to each other, assemblages from both continents show a common macroevolutionary pattern during post-Coniacian times.

Acknowledgments

We thank the editors of Cretaceous Research for their kind invitation to submit this contribution. A. Martinelli, A. Scanferla, N. Chimento and S. Bogan for their comments and suggestions. M. Charnelli for her help in producing illustrations and drawings. O. Rauhut for his insightful comments on an early draft and for sharing unpublished information. The comments and suggestions of R. Benson improved the quality of the present manuscript. R. Sookias help to improve the grammar of the manuscript. Special thanks to T. Rich, P. Rich and S. Hocknull for funding FEN to his visit to Australia. The Jurassic Foundation and the Doris and Samuel Welles Fund of the UCMP supported partially the research of MDE. We acknowledge the following people for allowing access theropod specimens under their care: A. Kramarz, E. Ruigómez, J. Calvo, R. Coria, S. Devinenzi Gonzáles, D. Schwarz-Wings, L. Steel, P. Barrett, S. Chapman, J. Powell, M. Brett-Surman, T. Rich, P. Rich, D. Pickering, E. Fitzgerald and S. Hocknull. This research has been funded with a grant from the Agencia Nacional de Promoción Científica y Técnica (Buenos Aires, PICTs 2006-058 and 2010-066 to FEN). MDE is supported by Ph.D. funding from the Emmy Noether Programme of the DFG (grant BU 2587/3-1 to Richard Butler).

References

- Agnolín, F.L., 2010. A new species of the genus *Atlantoceratodus* (Dipnoiformes: Ceratodontoidei) from the Uppermost Cretaceous of Patagonia and a brief overview of fossil dipnoans from the Cretaceous and Paleogene of South America. *Brazilian Geographical Journal: Geosciences and Humanities Research Medium* 12, 162–210.
- Agnolín, F.L., Chiarelli, P., 2010. The position of the claws in Noasauridae (Dinosauria: Abelisauroida) and its implications for abelisauroid morph evolution. *Palaeontologische Zeitschrift* 84, 293–300.
- Agnolín, F.L., Martinelli, A.G., 2009. Fossil birds from the Late Cretaceous Los Alamitos Formation, Río Negro Province, Argentina. *Journal of South American Earth Sciences* 27, 42–49.
- Agnolín, F.L., Novas, F.E., 2011. Unenlagiid theropods: are they members of Dromaeosauridae (Theropoda, Maniraptor). *Anais Academia Brasileira de Ciências* 83, 117–162.
- Agnolín, F.L., Novas, F.E., 2013. Avian ancestors: a review of the phylogenetic relationships of the theropods Unenlagiidae, Microraptorina, *Anchiornis*, and Scansoriopterygidae. In: Lohmann, G., Mysak, L.A., Notholt, J., Rabassa, J., Unnithan, V. (Eds.), *SpringerBriefs South America and the Southern Hemisphere*. Springer Verlag, Dordrecht, Heidelberg, New York, London, pp. 1–96.
- Agnolín, F.L., Powell, J.E., Novas, F.E., 2006. Discovery of Maastrichtian alvarezsaurid theropods in NW Patagonia, Argentina. *Jornadas Argentinas de Paleontología de Vertebrados* 22, 6.
- Agnolín, F.L., Ezcurra, M.D., Pais, D.F., Salisbury, S.W., 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology* 8, 257–300.
- Agnolín, F.L., Powell, J.E., Novas, F.E., Kundrát, M., 2012. New alvarezsaurid (Dinosauria, Theropoda) from uppermost Cretaceous of north-western Patagonia with associated eggs. *Cretaceous Research* 35, 33–56.
- Alifanov, V.R., Barsbold, R., 2009. *Ceratomykus oculatus* gen. et sp. nov., a new dinosaur (Theropoda, Alvarezsauria) from the Late Cretaceous of Mongolia. *Paleontological Journal* 43, 94–106.
- Allain, R., Pereda Suberbiola, X., 2003. Dinosaurs of France. *Comptes Rendus Palevol* 2, 27–44.
- Allain, R., Tykoski, R.S., Aquesbi, N., Jalil, N.-E., Monbaron, M., Russell, D.A., Taquet, P., 2007. An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurs. *Journal of Vertebrate Paleontology* 27, 610–624.
- Allain, R., Xaisanavong, T., Richir, P., Khentavong, B., 2012. The first definitive Asian spinosaurid (Dinosauria: Theropoda) from the early cretaceous of Laos. *Naturwissenschaften* 99, 369–377.
- Apesteguía, S., 2002. Successional structure in continental tetrapods faunas from Argentina along the Cretaceous. In: *Boletim do VIº Simpósio sobre o Cretáceo do Brasil - IIº Simposio sobre el Cretáceo de América del Sur (Sao Pedro, Brasil)*, Abstracts, pp. 135–141.
- Apesteguía, S., Bonaparte, J.F., 2004. Bajada Colorada (Valanginian) dinosaurs from Neuquén: note on the oldest Cretaceous dinosaurs from the Neuquén basin. *Ameghiniana* 41, 34R.
- Apesteguía, S., Agnolín, F.L., Claeson, K., 2007. Review of Cretaceous dipnoans from Argentina (Sarcopterygii: Dipnoi) with description of new species. *Revista del Museo Argentino de Ciencias Naturales* 9, 27–40.
- Araújo, R., Castanhinha, R., Mateus, O., Martins, R., 2012. Late Jurassic theropod embryos from Porto Das Barcas, Lourinha Formation, Portugal. *Journal of Vertebrate Paleontology* 32, 57A.
- Astibia, H., Buffetaut, E., Buscalioni, A.D., Cappelletta, H., Corral, C., Estes, R., Garcia-Garmilla, F., Jaeger, J.J., Jimenez-Fuentes, E., Le Loeuff, J., Mazin, J.M., Orue-Etxebarria, X., Pereda-Suberbiola, J., Powell, J.E., Rage, J.C., Rodríguez-Lazaro, J., Sanz, J.L., Tong, H., 1990. The fossil vertebrates from Laño (Basque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. *Terra Nova* 2, 460–466.
- Azuma, Y., Currie, P.J., 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences* 37, 1735–1753.
- Barrett, P.M., Benson, R.B.J., Rich, T.H., Vickers-Rich, P., 2011. First spinosaurid dinosaur from Australia and the cosmopolitanism of Cretaceous dinosaur faunas. *Biology Letters* 7, 933–936.
- Barsbold, R., Maryanska, T.H., Osmólska, H., 1990. *Oviraptorosauria*. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*. University of California Press, Berkeley, pp. 249–258.
- Benson, R.B.J., 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society of London* 158, 882–935.
- Benson, R.B.J., Xu, X., 2008. The anatomy and systematic position of the theropod dinosaur *Chilantaisaurus tashuikouensis* Hu, 1964 from the Early Cretaceous of Alanshan, People's Republic of China. *Geological Magazine* 145, 778–789.
- Benson, R.B.J., Carrano, M.T., Brusatte, S.L., 2010a. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroida) that survived to the latest Mesozoic. *Naturwissenschaften* 97, 71–78.
- Benson, R.B.J., Barrett, P.M., Rich, T.H., Vickers-Rich, P., 2010b. A southern tyrant reptile. *Science* 327, 1613.
- Benson, R.B.J., Barrett, P.M., Rich, T.H., Vickers-Rich, P., Pickering, D., Holland, T., 2010c. Response to comment on "A Southern Tyrant Reptile". *Science* 329, 1013.
- Benson, R.B.J., Rich, T.H., Vickers-Rich, P., Hall, M., 2012. Theropod fauna from Southern Australia indicates high Polar Diversity and Climate-Driven dinosaur provinciality. *PLoS One* 7 (5), e37122.
- Bertini, T., 2010. A catalogue of material and review of the Spinosauridae. *PalArch Journal of Vertebrate Paleontology* 7, 1–39.
- Bever, G., Norell, M.A., 2009. The perinate skull of *Byronosaurus* (Troodontidae) with observations on the cranial ontogeny of paravian theropods. *American Museum Novitates* 3657, 1–51.
- Blakey, R.H., 2006. *Global Paleogeography*. <http://jan.ucc.nau.edu>.
- Bonaparte, J.F., 1984. El intercambio faunístico de vertebrados continentales entre América del Sur y del Norte a fines del Cretácico. *Memória do III Congresso Latinoamericano de Paleontología*, 438–450.
- Bonaparte, J.F., 1986. History of the terrestrial Cretaceous vertebrates of Gondwana. *IV Congreso Argentino de Paleontología y Bioestratigrafía* 2, 63–95.
- Bonaparte, J.F., 1991a. The Gondwanan theropod families Abelisauridae and Noasauridae. *Historical Biology* 5, 1–25.
- Bonaparte, J.F., 1991b. Los vertebrados fósiles de la Formación Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico Superior, Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 4, 17–123.
- Bonaparte, J.F., 1996. Cretaceous tetrapods of Argentina. *Münchener Geowissenschaftliche Abhandlungen* 30, 73–130.
- Bonaparte, J.F., 1999. Tetrapod faunas from South America and India: a palaeobiogeographic interpretation. *Proceeding of the India Academy of Sciences* 65, 427–437.
- Bonaparte, J.F., Coria, R.A., 1993. Un nuevo y gigantesco saurópodo Titanosaurio de la Formación Río Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. *Ameghiniana* 30, 271–282.
- Bonaparte, J.F., Kielan-Jawarowska, Z., 1987. Late Cretaceous dinosaur and mammal faunas of Laurasia and Gondwana. In: Currie, P.M., Koster, E.H. (Eds.), *Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Tyrrell Museum of Paleontology Occasional Papers, Drumheller, pp. 24–29.
- Bonaparte, J.F., Powell, J., 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda - Coelurosauria - Carnosauria - Aves). *Société Géologique de France* 139, 19–28.
- Bonaparte, J.F., Franchi, M.R., Powell, J.E., Sepúlveda, E.G., 1984. La Formación Los Alamitos (Campaniano-Maastrichtiano) del sudeste de Río Negro, con descripción de *Kritosaurus australis* n. sp. (Hadrosauridae) Significado paleogeográfico de los vertebrados. *Revista de la Asociación Geológica Argentina* 39, 284–299.
- Bonaparte, J.F., Novas, F.E., Coria, R.A., 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the middle Cretaceous of Patagonia. *Contributions in Science*. Natural History Museum of Los Angeles County 416, 1–42.
- Brett-Surman, M.K., 1979. Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. *Nature* 277, 560–562.
- Brochu, C.A., 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology Memoir* 7, 1–138.
- Brusatte, S.L., Sereno, P.C., 2008. Phylogeny of Allosauroida (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Paleontology* 6, 155–182.
- Brusatte, S.L., Benson, R.B.J., Chure, D.J., Xu, X., Sullivan, C., Hone, D.W.E., 2009. The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. *Naturwissenschaften* 96, 1051–1058.
- Brusatte, S.L., Norell, M.A., Carr, T.D., Erickson, G.M., Hutchinson, J.R., Balanoff, A.M., Bever, G.S., Choiniere, J.N., Makovicky, P.J., Xu, X., 2010a. Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science* 329, 1481–1485.
- Brusatte, S.L., Benson, B.J., Xu, X., 2010b. The evolution of large-bodied theropod dinosaurs during the Mesozoic in Asia. *Journal of Iberian Geology* 36, 275–296.
- Brusatte, S.L., Benson, B.J., Xu, X., 2012. A reassessment of *Kelmaysaurus petroliticus*, a large theropod dinosaur from the Early Cretaceous of China. *Acta Paleontologica Polonica* 57, 65–72.
- Buffetaut, E., 1985. Presence de Trematochampsidae (Crocodylia, Mesosuchia) dans le Crétacé supérieur du Brésil. Implications paléobiogéographiques. *Comptes Rendus de l'Académie des Sciences* 301, 1221–1224.
- Buffetaut, E., 1989. A new ziphodont mesosuchian crocodile from the Eocene of Algeria. *Palaeontographica, Abteilung A* 208, 1–10.
- Burch, S.H., Carrano, M.T., 2012. An articulated pectoral girdle and forelimb of the abelisaurid theropod *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 32, 1–16.
- Cadena, E., Bloch, J., Jaramillo, C., 2010. New podocnemidid turtle (Testudines: Pleurodira) from the middle-upper Paleocene of South America. *Journal of Vertebrate Paleontology* 30, 367–372.
- Calvo, J.O., 1999. Dinosaurs and other vertebrates of the Lake Ezequiel Ramos Mexía Area, Neuquén-Patagonia, Argentina. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium*. National Science Museum Monographs, 15, pp. 13–45.
- Calvo, J.O., Coria, R.A., 2000. New specimen of *Giganotosaurus carolinii* (Coria and Salgado, 1995), supports it as the largest theropod ever found. *Gaia* 15, 117–122.
- Calvo, J.O., Porfiri, J.D., Kellner, A.W.A., 2004a. On a new maniraptoran dinosaur (Theropoda) from the Upper Cretaceous of Neuquén, Patagonia, Argentina. *Archivos do Museo Nacional* 62, 549–566.
- Calvo, J.O., Porfiri, J.D., Veralli, C., Novas, F.E., Poblete, F., 2004b. Phylogenetic status of *Megaraptor namunhuaiquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. *Ameghiniana* 41, 565–575.
- Canale, J.I., Scanferla, C.A., Agnolín, F., Novas, F.E., 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften* 96, 409–414.

- Candeiro, C.R.A., Martinelli, A.G., 2007. Paleogeographical and chronostratigraphical distribution of mesoeucrocodylian species from the Upper Cretaceous beds from Bauru (Brazil) and Neuquén (Argentina) Groups, Southern South America. *Journal of South American Earth Sciences* 22, 116–129.
- Canudo, J.I., Royo-Torres, R., Cuenca-Bescós, G., 2008. A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology* 28, 712–731.
- Canudo, J.I., Barco, J.L., Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Salgado, L., Torcida Fernández-Baldor, F., Gasulla, J.M., 2009. What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. *Bulletin de la Société géologique de France* 180, 5–11.
- Carpenter, K., Miles, C., Cloward, K., 2005. New small theropod from the Upper Jurassic Morrison Formation of Wyoming. In: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington, pp. 23–48.
- Carrano, M.T., Sampson, S., 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 6, 183–236.
- Carrano, M.T., Sampson, S.D., Forster, C.A., 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 22, 510–534.
- Carrano, M.T., Loewen, M.A., Sertich, J.J.W., 2011. New materials of *Masiakasaurus knopfleri* Sampson, Carrano, and Forster, 2001, and implications for the morphology of the Noasauridae (Theropoda: Ceratosauria). *Smithsonian Contributions to Paleobiology* 95, 1–53.
- Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Paleontology* 10, 211–300.
- Casamiquela, R.M., 1964. Sobre un dinosaurio hadrosaurídeo de la Argentina. *Ameghiniana* 3, 285–308.
- Charig, A.J., Milner, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London* 53, 11–70.
- Chiappe, L.M., Norell, M.A., Clark, J.M., 1998. The skull of a new relative of *Mononykus*. *Nature* 392, 275–278.
- Chiappe, L.M., Norell, M.A., Clark, J.M., 2002. The Cretaceous, short-armed Alvarezsauridae. *Mononykus* and its kin. In: Chiappe, L.M., Witmer, L.M. (Eds.), *Mesozoic birds: above the heads of dinosaurs*. Berkeley University Press, Berkeley, pp. 87–120.
- Choiniere, J.N., Clark, J.M., Forster, C.A., Xu, X., 2010a. A basal coelurosaur (Dinosauria: Theropoda) from the Late Jurassic (Oxfordian) of the Shishugou Formation in Wucuiwan, People's Republic of China. *Journal of Vertebrate Paleontology* 30, 1773–1796.
- Choiniere, J.N., Xu, X., Clark, J.M., Forster, C.A., Guo, Y., Han, F., 2010b. A basal alvarezsaurid theropod from the Early Late Jurassic of Xinjiang, China. *Science* 327, 571–574.
- Choiniere, J.N., Norell, M., Dyke, G., 2011. The anatomy of the parvicursorine braincase and its implications for alvarezsaurid systematics and evolution. *Journal of Vertebrate Paleontology* 31, 89A.
- Choiniere, J.N., Forster, C.A., De Klerk, W.J., 2012. New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous (Hauterivian?) Kirkwood Formation in South Africa. *Journal of African Earth Sciences*. <http://dx.doi.org/10.1016/j.jafrearsci.2012.05.005>.
- Company, J., Suberbiola, X.P., Ruiz-Omeñaca, J.I., Buscalioni, A.D., 2005. A new species of *Doratodon* (Crocodyliformes: Ziphosuchia) from the Late Cretaceous of Spain. *Journal of Vertebrate Paleontology* 25, 343–353.
- Coria, R.A., Currie, P.J., 2002a. The braincase of *Giganotosaurus carolinii*, (Dinosauria: Theropoda) from the Upper Cretaceous of Argentina. *Journal of Vertebrate Paleontology* 4, 802–811.
- Coria, R.A., Currie, P.J., 2002b. Un gran terópodo celurosaurio en el Cretácico Superior de Neuquén. *Ameghiniana* 39, 9R.
- Coria, R.A., Currie, P.J., 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28, 71–118.
- Coria, R.A., Salgado, L., 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377, 224–226.
- Coria, R.A., Salgado, L., 2000. A Basal Abelisauria Novas, 1992 (Theropoda-Ceratosauria) from the Cretaceous of Patagonia, Argentina. *Gaia* 15, 89–102.
- Coria, R.A., Salgado, L., 2003. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. In: Veiga, G.D., Spalletti, L.A., Howell, S.E. (Eds.), *The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics*. Geological Society of London Special Publication, 252, pp. 317–327.
- Coria, R.A., Currie, P.J., Eberth, D., Garrido, A., Koppelhus, E., 2001. Nuevos vertebrados fósiles del Cretácico Superior de Neuquén. *Ameghiniana* 38, 6–7R.
- Coria, R.A., Chiappe, L.M., Dingus, L., 2002. A new close relative of *Carnotaurus sastrei* Bonaparte, 1985 (Theropoda:Abelisauridae) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 22, 460–465.
- Coria, R.A., Currie, P.J., Koppelhus, E., Braun, A., Cerda, I., 2010. First record of a Valanginian (Early Cretaceous) dinosaur association from South America. *Journal of Vertebrate Paleontology* 28, 35A.
- Crochet, J.Y., Sigé, B., 1983. Les mammifères montiens de Hainin (Paléocène moyen de Belgique). Part III: Marsupiaux. *Palaeovertebrata* 13, 51–64.
- Currie, P.J., Carpenter, K., 2000. A new specimen of *Acrocantanosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas* 22, 207–246.
- Currie, P.J., Peng, J.H., 1993. A juvenile specimen of *Sauromithoides mongoliensis* from the upper Cretaceous of northern China. *Canadian Journal of Earth Sciences* 30, 2224–2230.
- Currie, P.J., Zhao, X., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30, 2037–2081.
- Dalla-Vecchia, F.M., 2003. Observations on the presence of plant-eating dinosaurs in an oceanic carbonate platform. *Natura Nascosta* 27, 14–27.
- de Broin, F., 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. *Mémoires du Muséum d'Histoire Naturelle* 38, 1–366.
- de Broin, F., 1980. Les tortues de Gadoufaoua (Aptien du Niger): aperçu sur la paléogéographie des Pelomedusidae (Pleurodira). *Mémoires de la Société géologique de France* 139, 39–46.
- de Klerk, W.J., Forster, C.A., Sampson, S.D., Chinsamy, A., Ross, C.F., 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. *Journal of Vertebrate Paleontology* 20, 324–332.
- de la Fuente, M.S., Umazano, A.M., Sterli, J., Carballido, J.L., 2011. New chelid turtles of the lower section of the Cerro Barco Formation (Aptian-Albian?), Patagonia, Argentina. *Cretaceous Research* 32, 527–537.
- Eddy, D., Clarke, J., 2011. New Information on the Cranial Anatomy of *Acrocantanosaurus atokensis* and Its Implications for the Phylogeny of Allosauroida (Dinosauria: Theropoda). *PLoS One* 6, e17932.
- Evers, S., Rauhut, O.W.M., Milner, A.C., 2012. Was Stromer right? The affinities of *Sigilmassasaurus brevicollis* (Theropoda, Tetanurae). *Journal of Vertebrate Paleontology* 32, 91A.
- Ezcurra, M.D., 2009. Theropod remains from the latest Cretaceous of Colombia and their implications on the palaeozoogeography of western Gondwana. *Cretaceous Research* 30, 1339–1344.
- Ezcurra, M.D., Agnolín, F.L., 2012a. An abelisauroid dinosaur from the Middle Jurassic of Laurasia and its implications on theropod palaeobiogeography and evolution. *Proceedings of the Geologists' Association* 123, 500–507.
- Ezcurra, M.D., Agnolín, F.L., 2012b. A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. *Systematic Biology* 61, 553–566.
- Ezcurra, M.D., Agnolín, F.L., Novas, F.E., 2010. An abelisauroid dinosaur with a non-atrophied manus from the Late Cretaceous Pari Aike Formation of southern Patagonia. *Zootaxa* 2450, 1–25.
- Ferrari, A.L., Riccomini, C., 1999. Campo de esforços plio-pleistocênico na Ilha de Trindade (oceano Atlântico Sul, Brasil) e sua relação com a tectônica regional. *Revista Brasileira de Geociências* 29, 195–202.
- Fitzgerald, E.M., Carrano, M.T., Holland, T., Wagstaff, B.E., Pickering, D., Rich, T.H., Vickers-Rich, P., 2012. First ceratosaurian dinosaur from Australia. *Naturwissenschaften* 99, 397–405.
- Forster, C.A., 1999. Gondwanan dinosaur evolution and biogeographic analysis. *Journal of African Earth Sciences* 28, 169–185.
- Forster, C., Sampson, S., Chiappe, L.M., Krause, D., 1998. The Theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279, 1915–1919.
- Gauthier, J.A., 1986. Saurischian monophyly and the origin of birds. In: Padian, K. (Ed.), *The Origin of Birds and the Evolution of Flight*. *Memoirs of the California Academy of Sciences*, 8, pp. 1–55.
- Gheerbrant, E., Rage, J.C., 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology* 241, 224–246.
- Gianechini, F.A., Apesteguía, S., 2011. Unenlagiinae revisited: dromaeosaurid theropods from South America. *Anais da Academia Brasileira de Ciências* 83, 163–197.
- Gianechini, F., Apesteguía, S., Canale, J., Haluza, A., 2011a. New dinosaur remains from the Bajada Colorado Fm (Berrislian-Valanginian): notes on the earliest Cretaceous dinosaurs from the Neuquén Basin, Patagonia, Argentina. In: IV Congreso Latinoamericano de Paleontología de Vertebrados, R14.
- Gianechini, F.A., Lio, G.L., Apesteguía, S., 2011b. Isolated archosaurian teeth from "La Bonita" locality (Late Cretaceous, Santonian-Campanian), Río Negro province, Argentina. *Historia Natural* 1, 5–16.
- Gilmore, C.W., 1920. Osteology of the carnivorous Dinosauria in the United States; National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum* 110, 1–154.
- Grellet-Tinner, G., Chiappe, L.M., 2004. Dinosaur eggs and nestings: implications for understanding the origin of birds. In: Currie, P.J., Koppelhus, E.B., Shugar, M.A., Wright, J.L. (Eds.), *Feathered dragons: Studies on the transition from Dinosaurs to Birds*. Indiana University Press, pp. 185–214.
- Grellet-Tinner, G., Chiappe, L.M., Norell, M., Bottjer, D., 2006. Dinosaur eggs and nesting behaviours: a paleobiological investigation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232, 294–321.
- Harris, J.D., 1998. A reanalysis of *Acrocantanosaurus atokensis*, its phylogenetic status and paleobiogeographic implications, based on a new specimen from Texas. *Bulletin New Mexico Museum of Natural History and Science* 13, 1–75.
- Herne, M.C., Nair, J.P., Salisbury, S.W., 2010. Comment on "A Southern Tyrant Reptile". *Science* 329, 1013.
- Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., Elliott, D.A., 2009. New Mid-Cretaceous (Latest Albian) Dinosaurs from Winton, Queensland, Australia. *PLoS One* 4, e6190.
- Holtz T.R., Jr., 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* 68, 1100–1117.
- Holtz T.R., Jr., 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia* 15, 5–61.
- Holtz T.R., Jr., 2004. Tyrannosauroida. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, pp. 111–136.

- Holtz T.R., Jr., Rey, L.V., 2007. Dinosaurs. The most complete, up-to-date encyclopedia for dinosaur lovers of all ages. Random House, New York, pp. 1–427.
- Holtz, T.R., Molnar, R.E., Currie, P.J., 2004. Basal Tetanurae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, Second ed. California University Press, pp. 71–110.
- Hu, D., Hou, L., Zhang, L., Xu, X., 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461, 640–643.
- Hutchinson, J.R., Chiappe, L.M., 1998. The first known Alvarezsaurid (Theropoda: Aves) from North America. *Journal of Vertebrate Paleontology* 18, 447–450.
- Hutt, S., Martill, D.M., Barker, M.J., 1996. The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group). *Neues Jahrbuch für Geologie und Paläontologie* 10, 635–644.
- Hwang, S.H., Norell, M.A., Qiang, J., Keqin, G., 2002. New specimens of *Microraptor zhaonianus* (Theropoda: Dromaeosauridae) from Northeastern China. *American Museum Novitates* 3381, 1–44.
- Jacobs, L.L., Winkler, D.A., 1998. Mammals, archosaurs, and the Early to Late Cretaceous transition in North-Central Texas. In: Tomida, Y., Flynn, L.J., Jacobs, L.L. (Eds.), *Advances in Vertebrate Paleontology and Geochronology*. National Science Museum Monographs, 14, pp. 253–280.
- Janensch, W., 1920. Über *Elaphrosaurus bambergi* und die Megalosaurier aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* 1920, 225–235.
- Janensch, W., 1925. Die Coelurosaurier und Theropoden der Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica Supplement* 7, 1–100.
- Juárez Valieri, R.D., Fiorelli, L.E., Salinas, G.C., 2004. Los saurópodos titanosauriformes del Cretácico y sus implicancias biogeográficas. *Ameghiniana* 41, 14R.
- Juárez Valieri, R.D., Porfiri, J.D., Calvo, J.O., 2011. New information on *Ekrixinatosaurus novasi* Calvo et al, 2004, a giant and massively-constructed Abelisaurid from the “Middle Cretaceous” of Patagonia. In: Calvo, J.O., Gonzalez-Riga, B., Porfiri, J.D., Dos Santos, D. (Eds.), *Paleontología y Dinosaurios en América Latina*, pp. 161–169.
- Juárez Vallieri, R.D., Fiorelli, L.E., Cruz, L.E., 2007. *Quilmesaurus curriei* Coria, 2001 (Dinosauria, Theropoda). Su validez taxonómica y relaciones filogenéticas. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* 9, 59–66.
- Karhu, A.A., Rautian, A.S., 1996. A new family of Maniraptora (Dinosauria: Saurischia) from the Late Cretaceous of Mongolia. *Paleontological Journal* 30, 583–592.
- Kellner, A.W.A., 1999. Short note on a new dinosaur (Theropoda, Coelurosauria) from the Santana Formation (Romualdo Member, Albian), Northeastern Brasil. *Boletim do Museu Nacional, Geologia* 49, 1–8.
- Kellner, A.W.A., Azevedo, S.A.K., Machado, E.B., Carvalho, L.B., Henriques, D.D.R., 2011. A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. *Anais da Academia Brasileira de Ciências* 83, 99–108.
- Kielan-Jaworowska, Z., Cifelli, R.L., Luo, Z.-X., 2004. Mammals from the age of dinosaurs: origins, evolution, and structure. Columbia University Press, New York, pp. 1–700.
- Krause, D.W., Prasad, G.V.R., von Koenigswald, W., Sahni, A., Grine, F.E., 1997. Cosmopolitanism among gondwanan Late Cretaceous mammals. *Nature* 390, 504–507.
- Krause, D.W., Sampson, S.D., Carrano, M.T., O’Connor, P.M., 2007. Overview of the history of discovery, taxonomy, phylogeny, and biogeography of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology Memoir* 8, 1–20.
- Kundrát, M., Cruickshank, A.R.L., Manning, T.W., Nudds, J., 2008. Embryos of therizinosaurid theropods from the Upper Cretaceous of China: diagnosis and analysis of ossification patterns. *Acta Zoologica* 89, 231–251.
- Lamanna, M., Martínez, R., Luna, M., Casal, G., Ibiricu, L., Ivany, E., 2004. New specimens of the problematic large theropod dinosaur *Megaraptor* from the Late Cretaceous of central Patagonia. *Journal of Vertebrate Paleontology* 64, 252A.
- Lapparent de Broin, F., de la Fuente, M.S., 2001. Oldest world Cheloniidae (Chelonii, Pleurodira), from the Cretaceous of Patagonia, Argentina. *Comptes Rendus Académie Sciences Paris. Sciences de la Terre et des planètes* 333, 463–467.
- Lapparent de Broin, F., Murelaga, X., 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. *Comptes Rendus de l’Académie des Sciences* 323, 729–735.
- Larson, P.L., 1991. The Black Hills Institute *Tyrannosaurus*: a preliminary report. *Journal of Vertebrate Paleontology* 11, 41A–42A.
- Larsson, H.C.E., Sues, H.-D., 2007. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society* 149, 533–567.
- Lavocat, R., 1977. Sur l’origine des faunes sud-américaines de mammifères du Mésozoïque terminal et du Cénozoïque ancien. *Comptes Rendus de l’Académie des Sciences Paris* 285, 1423–1426.
- Le Loeuff, J., 1991. The Campano-Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world; palaeobiogeographical implications. *Cretaceous Research* 12, 93–114.
- Le Loeuff, J., 1993. European titanosaurids. *Revue Paléobiologie* 7, 105–117.
- Le Loeuff, J., 1995. *Ampelosaurus atasis* (nov. gen., nov. sp.), un nouveau Titanosauridae (Dinosauria, Sauropoda) du Crétacé supérieur de la Haute Vallée de l’Aude (France). *Comptes Rendus de l’Académie des Sciences* 321, 693–699.
- Le Pichon, X., Hayes, D.E., 1971. Marginal offsets fracture zones, and the early opening of the South Atlantic. *Journal of Geophysical Research* 76, 6283–6293.
- Leanza, H.A., Apesteguía, S., Novas, F.E., de la Fuente, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research* 25, 61–87.
- Li, D., Norell, M.A., Gao, K.Q., Smith, N.D., Makovicky, P.J., 2010. A longirostre tyrannosaurid from the Early Cretaceous of China. *Proceedings of the Royal Society B* 277, 183–190.
- Lillegraven, J.A., Kraus, M.J., Bown, T.M., 1979. Paleogeography of the World of the Mesozoic. In: Lillegraven, J.A., Kielan-Jaworowska, Z., Clemens, W.A. (Eds.), *Mesozoic mammals: the first two-thirds of mammalian history*. University of California Press, Berkeley, pp. 277–308.
- Longrich, N.R., Currie, P.J., 2008. A microraptorine (Dinosauria-Dromaeosauridae) from the Late Cretaceous of North America. *Proceedings of the National Academy of Sciences* 106, 5002–5007.
- Longrich, N.R., Currie, P.J., 2009. *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the Early Maastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretaceous Research* 30, 239–252.
- Madsen J.H., Jr., 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineralogical Survey Bulletin* 109, 3–163.
- Madsen J.H., Jr., Welles, S.P., 2000. *Ceratosaurus* (Dinosauria, Theropoda) a revised osteology. *Miscellaneous Publication Utah Geological Survey*, pp. 1–80.
- Makovicky, P.J., Apesteguía, S., Agnolín, F.H., 2005. The earliest dromaeosaurid theropod from South America. *Nature* 437, 1007–1011.
- Makovicky, P.J., Apesteguía, S.N., Gianechini, F.A., 2012. A New Coelurosaurian Theropod from the La Buitrera Fossil Locality of Río Negro, Argentina. *Fieldiana Life and Earth Sciences* 5, 90–98.
- Maleev, E.A., 1974. Gigantic carnosaur of the family Tyrannosauridae. The Joint Soviet-Mongolian Paleontological Expedition Transactions 1, 132–191 (in Russian).
- Martill, D.M., Hutt, S., 1996. Possible baryonychid dinosaur teeth from the Wessex formation (Lower Cretaceous, Barremian) of the Isle of Wight. *Proceedings of the Geologists’ Association* 107, 81–84.
- Martill, D.M., Naish, D., 2001. Dinosaurs of the Isle of Wight. In: *Field Guides to Fossils Series* 10. London.
- Martill, D.M., Frey, E., Sues, H.-D., Cruickshank, A.R.L., 2000. Skeletal remains of the small theropod dinosaur with associated soft structures from the Lower Cretaceous Santana Formation of northeastern Brazil. *Canadian Journal of Earth Sciences* 37, 891–900.
- Martinelli, A.G., Vera, E.I., 2007. *Achillesaurus manazzoni*, a new alvarezsaurid theropod (Dinosauria) from the Late Cretaceous Bajo de la Carpa Formation, Río Negro Province, Argentina. *Zootaxa* 1582, 1–17.
- Martínez, R.D., Novas, F.E., 2006. New coelurosaurian theropod from the Early Late Cretaceous of Central Patagonia, Argentina. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* 8, 2243–2259.
- Martínez, R.D., Lamanna, M., Casal, G., Luna, M., Dodson, P., Tiedemann, C., Koprovsky, A., 2001. Dinosaurios de la Formación Bajo Barreal, Cretácico Superior Temprano del sur de Chubut. *Ameghiniana* 38, 12–13R.
- Mateus, I., Mateus, H., Antunes, M.T., Mateus, O., Taquet, P., Ribeiro, V., Manuppella, G., 1997. Couvée, oeufs et embryons d’un dinosaure théropode du Jurassique supérieur de Lourinha (Portugal). *Comptes Rendus d’la Académie Sciences Paris* 325, 71–78.
- Mateus, O., Araújo, R., Natário, C., Castaninha, R., 2011. A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa* 2827, 54–68.
- Matley, C.A., 1923. Note on an armoured dinosaur from the Lameta beds of Jabulpore. *Records of the Geological Survey of India* 55, 105–109.
- Méndez, A.H., Novas, F.E., Chatterjee, S., 2010. An abelisaurid humerus from the Upper Cretaceous of India. *Palaeontologische Zeitschrift* 84, 421–425.
- Méndez, A.H., Novas, F.E., Iori, F.V., 2012. First record of Megaraptora (Theropoda, Neovenatoridae) from Brazil. *Comptes Rendus Palevol* 11, 251–256.
- Naish, D., Dyke, G.D., 2004. *Heptasteornis* was no ornithomimid, troodontid, dromaeosaurid or owl: the first alvarezsaurid (Dinosauria: Theropoda) from Europe. *Neues Jahrbuch für Geologie und Paläontologie* 7, 385–401.
- Nesbitt, S.J., Clarke, J.A., Turner, A.H., Norell, M.A., 2011. A small alvarezsaurid from the Eastern Gobi Desert offers insight into evolutionary patterns in the Alvarezsauridae. *Journal of Vertebrate Paleontology* 31, 144–153.
- Norell, M.A., Makovicky, P.J., 1999. Important features of the dromaeosaur skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates* 3282, 1–45.
- Norell, M.A., Makovicky, P.J., 2004. Dromaeosauridae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, Berkeley, pp. 196–209.
- Norell, M.A., Clark, J.M., Dashzeveg, D., Barsbold, R., Chiappe, L.M., Davidson, A.R., McKenna, M.C., Novacek, M.J., 1994. A theropod dinosaur embryo, and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266, 779–782.
- Norell, M.A., Clark, J.M., Chiappe, L.M., Dashzeveg, D., 1995. A nesting dinosaur. *Nature* 378, 774–776.
- Norell, M.A., Clark, J.M., Makovicky, P., 2001. Phylogenetic relationships among coelurosaurian theropods. In: Gauthier, J., Gall, L.F. (Eds.), *New perspectives on the origin and Early Evolution of Birds*. Proceedings of the International Symposium in Honor of John H. Ostrom. Peabody Museum of Natural History, New Haven, pp. 69–98.
- Novas, F.E., 1996. Alvarezsauridae, Late Cretaceous maniraptorans from Patagonia and Mongolia. In: Novas, F.E., Molnar, R.E. (Eds.), *Proceedings of the Gondwanan Dinosaur Symposium*. *Memoirs of the Queensland Museum*, 39, pp. 675–702.

- Novas, F.E., 1997a. Anatomy of *Patagonykus puertai* (Theropoda, Avialae, Alvarezsauridae), from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 17, 137–166.
- Novas, F.E., 1998. *Megaraptor namunhuaiquii* gen. et. sp. nov., a large-clawed, Late Cretaceous Theropod from Argentina. *Journal of Vertebrate Paleontology* 18, 4–9.
- Novas, F.E., 1999. Dinosaur. McGraw-Hill Yearbook of Science and Technology, pp. 133–135.
- Novas, F.E., 2004. Avian traits in the ilium of *Unenlagia comahuensis* (Maniraptor, Avialae). In: Currie, P.J., Koppelhus, E.B., Shugar, M.A., Wright, J.L. (Eds.), Feathered Dragons: Studies on the Transition from Dinosaurs to Birds. Indiana University Press, Bloomington, pp. 150–166.
- Novas, F.E., 2009. The Age of Dinosaurs in South America. Indiana University Press, Indiana, pp. 1–536.
- Novas, F.E., Bandyopadhyay, S., 1999. New approaches on the Cretaceous theropods from India. VII International Symposium on Mesozoic Terrestrial Ecosystems (Buenos Aires). Asociación Paleontológica Argentina, Special Publication, 7, pp. 46–47.
- Novas, F.E., Bandyopadhyay, S., 2001. Abelisaurid pedal unguals from the Late Cretaceous of India. Asociación Paleontológica Argentina, Special Publication 7, 145–149.
- Novas, F.E., Pol, D., 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. *Nature* 433, 858–861.
- Novas, F.E., Puerta, P., 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. *Nature* 387, 390–392.
- Novas, F.E., Agnolín, F., Bandyopadhyay, S., 2004. Cretaceous Theropods from India: a review of specimens described by Huene and Matley (1933). *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* 6, 67–103.
- Novas, F.E., de Valais, S., Vickers-Rich, P., Rich, T., 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften* 92, 226–230.
- Novas, F.E., Ezcurra, M.D., Lecuona, A., 2008. *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Research* 29, 468–480.
- Novas, F.E., Pol, D., Canale, J.I., Porfiri, J.D., Calvo, J.O., 2009. A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proceedings of the Royal Society of London B* 276, 1101–1107.
- Novas, F.E., Chatterjee, S., Rudra, D.K., Datta, P.M., 2010. *Rahiolisaurus gujaratensis*, n. gen. n. sp., a new abelisaurid theropod from the Late Cretaceous of India. In: Bandyopadhyay, S. (Ed.), *New aspects of Mesozoic biodiversity*. Lecture Notes in Earth Science, 132. Springer, Heidelberg, pp. 45–62.
- Novas, F.E., Ezcurra, M.D., Agnolín, F.L., Pol, D., Ortíz, R., 2012. New Patagonian Cretaceous theropods shed light about the early radiation of Coelurosauria. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* 14, 57–81.
- O'Connor, P.M., 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: Sampson, S.D., Krause, D.W. (Eds.), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir, 8, pp. 127–162.
- O'Connor, J.M., Duncan, R.A., 1990. Evolution of the Walvis Ridge-Rio Grande Rise hot spot system: Implications for African and South American plate motions over plumes. *Journal of Geophysical Research* 95, 17475–17502.
- O'Connor, J.M., Chiappe, L.M., Bell, A., 2011. Pre-modern Birds: Avian Divergences in the Mesozoic. In: Dyke, G., Kaiser, G. (Eds.), *Living Dinosaurs: The Evolutionary History of Modern Birds*, first ed. Wiley, Hoboken, New Jersey, pp. 39–114.
- O'Gorman, J.P., Varela, A.N., 2010. The oldest lower Upper Cretaceous plesiosaurs (Reptilia, Sauropterygia) from southern Patagonia, Argentina. *Ameghiniana* 47, 1–13.
- Oliveira, F.B., Cassola Molina, E., Marroig, G., 2010. Paleogeography of the South Atlantic: a Route for Primates and Rodents into the NewWorld? In: Garber, P.A., Estrada, A., Bicca-Marques, J.C., Heymann, E.W., Strier, K.B. (Eds.), *South American Primates, Developments in Primatology: Progress and Prospects*. Springer Science, pp. 55–68.
- Ortega, F.J., Gasparini, Z.B., Buscalioni, A.D., Calvo, J.O., 2000. A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). *Journal of Vertebrate Paleontology* 20, 57–76.
- Ortega, F.J., Escaso, F., Sanz, J.L., 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature* 467, 203–206.
- Osborn, H.F., 1917. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. *Bulletin of the American Museum of Natural History* 35, 733–771.
- Ostrom, J.H., 1969. A new theropod dinosaur from the Lower Cretaceous of Montana. *Postilla* 128, 1–17.
- Ostrom, J.H., 1976. *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean Society* 8, 91–182.
- Ostrom, J.H., 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana* 4, 73–118.
- Parrish, J.T., 1993. The palaeogeography of the opening South Atlantic. In: George, W., Lavocat, R. (Eds.), *The Africa-South America Connection*. Clarendon Press, Oxford, pp. 8–27.
- Perle, A., Norell, M.A., Chiappe, L.M., Clark, J.M., 1993. Flightless bird from the Cretaceous of Mongolia. *Nature* 362, 623–626.
- Pitman, W.C.I., Cande, S., LaBrecque, J., Pindell, J., 1993. Fragmentation of Gondwana: the separation of Africa from South America. In: Goldblatt, P. (Ed.), *Biological Relationships Between Africa and South America*. Yale University Press, New Haven, pp. 15–34.
- Pol, D., Apesteguía, S., 2005. New *Araripesuchus* remains from the early Late Cretaceous (Cenomanian-Turonian) of Patagonia. *American Museum Novitates* 3940, 1–38.
- Pol, D., Rauhut, O.W.M., 2012. A Middle Jurassic abelisaurid from Patagonia and the Early diversification of theropod dinosaurs. *Proceedings of the Royal Society B*. <http://dx.doi.org/10.1098/rspb.2012.0660>.
- Porfiri, J.D., Calvo, J.O., Juárez Valieri, R.D., Santos, D., 2008. A new large theropod dinosaur from the Bajo de La Carpa Formation (Late Cretaceous) of Neuquén, Patagonia. In: III Congreso Latinoamericano de Paleontología de Vertebrados, R202.
- Porfiri, J.D., Calvo, J.O., Dos Santos, D., 2011. A new small deinonychosaur (Dinosauria: Theropoda) from the Late Cretaceous of Patagonia, Argentina. *Anais da Academia Brasileira de Ciências* 83, 109–116.
- Price, L.I., 1959. Sobre um crocodilídeo notossuquido do Cretácico Brasileiro. *Boletim Divisao de Geologia e Mineralogia Rio de Janeiro* 118, 1–55.
- Rage, J.C., 1981. Les continents péri-atlantiques au Crétacé supérieur: Migrations des faunes continentales et problèmes paléogéographiques. *Cretaceous Research* 2, 65–68.
- Rage, J.C., 1988. Gondwana, Tethys, and terrestrial vertebrates during the Mesozoic and Cainozoic. In: Audley-Charles, M.G., Hallam, A. (Eds.), *Gondwana and Tethys*. Geology Society Special Paper 37, pp. 235–273.
- Rage, J.C., 1996. Les Madtsoiidae (Reptilia, Serpentes) du Crétacé supérieur d'Europe: témoins gondwaniens d'une dispersion transéthysienne. *Comptes Rendus de l'Académie des Sciences de Paris* 322, 603–608.
- Rage, J.C., 2003. Relationships of the Malagasy fauna during the Late Cretaceous: Northern or Southern routes? *Acta Paleontologica Polonica* 48, 661–662.
- Rasmuson, E.L., Buckley, G.A., 2009. New material of “*Trematochampsia*” *oblita* (Crocodyliformes, Trematochampsidae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 29, 599–604.
- Rauhut, O.W.M., 2003. Interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Paleontology* 69, 1–215.
- Rauhut, O.W.M., 2004. Provenance and anatomy of *Genyodectes serus*, a large-toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. *Journal of Vertebrate Paleontology* 24, 894–902.
- Rauhut, O.W.M., 2005. Postcranial remains of “coelurosaur” (Dinosauria, Theropoda) from the Late Jurassic of Tanzania. *Geological Magazine* 142, 97–107.
- Rauhut, O.W.M., 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Paleontology* 86, 195–239.
- Rauhut, O.W.M., 2012. A reappraisal of a putative record of abelisauroid theropod dinosaur from the Middle Jurassic of England. *Proceedings of the Geologists' Association* 123, 779–786.
- Rauhut, O.W.M., Cladera, G., Vickers-Rich, P., Rich, T.H.V., 2003. Dinosaur remains from the Lower Cretaceous of the Chubut Group, Argentina. *Cretaceous Research* 24, 487–497.
- Rauhut, O.W.M., Milner, A.C., Moore-Fay, S., 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society* 158, 155–195.
- Raup, D.M., Sepkoski, J.J., 1984. Periodicity of extinction in the geological past. *Proceedings of the National Academy of Sciences* 81, 801–805.
- Rich, T.H., Vickers-Rich, P., 1989. Polar dinosaurs and the biotas of Early Cretaceous of southeastern Australia. *National Geographic Research Explorations* 5, 15–53.
- Rich, T.H., Vickers-Rich, P., 1994. Neoceratopsians and ornithomimosaurs: dinosaurs of Gondwana origin? *National Geographic Research Explorations* 10, 129–131.
- Rich, T.H., Vickers-Rich, P., 2003. Protoceratopsian? Ulnae from Australia. *Records of the Queen Victoria Museum* 113, 1–12.
- Ruiz, J., Torices, A., Serrano, H., López, V., 2011. The hand structure of *Carnotaurus sastrei* (Theropoda, Abelisauridae): implications for hand evolution in abelisaurids. *Palaeontology* 54, 1271–1277.
- Ruiz-Omeñaca, J.I., Canudo, J.I., Cruzado-Caballero, P., Infante, P., Moreno-Azanza, M., 2005. Baryonychine teeth (Theropoda: Spinosauridae) from the Lower Cretaceous of La Cantalera (Josa, NE Spain). *Kaupia* 14, 59–63.
- Russell, D.A., 1993. The role of Central Asia in dinosaurian biogeography. *Canadian Journal of Earth Sciences* 30, 2002–2012.
- Russell, D.A., 1996. Isolated dinosaur bones from the middle Cretaceous of the Tafilalet, Morocco. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série* 4 18, 349–402.
- Russell, D.A., Dong, Z.-M., 1993. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 30, 2107–2127.
- Salgado, L., Coria, R., 1996. First evidence of an armoured ornithischian dinosaur in the late Cretaceous of North Patagonia, Argentina. *Ameghiniana* 33, 367–371.
- Salgado, L., Coria, R., 2005. Sauropods of Patagonia: systematic update and notes on global sauropod evolution. In: Tidwell, V., Carpenter, K. (Eds.), *Thunder-Lizards: The sauropodomorph dinosaurs*. Indiana University Press, Indiana, pp. 430–452.
- Salgado, L., Coria, R.A., Arcucci, A.B., Chiappe, L.M., 2009. Restos de Alvarezsauridae (Theropoda, Coelurosauria) en la Formación Allen (Campaniano-Maastrichtiano), en Salitral Ojo de Agua, Provincia de Río Negro, Argentina. *Andean Geology* 36, 67–80.
- Sampson, S.D., Witmer, L.M., Forster, C.A., Krause, D.W., O'Connor, P.M., Dodson, P., Ravoavy, F., 1998. Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. *Science* 280, 1048–1051.
- Sampson, S.D., Carrano, M.T., Forster, C.A., 2001. A theropod dinosaur with bizarre dentition from the late Cretaceous of Madagascar. *Nature* 409, 504–506.

- Schettino, A., Scotese, C.R., 2005. Apparent polar wander paths for the major continents (200Ma-present day): A paleomagnetic reference frame for global plate tectonic reconstructions. *Geophysical Journal* 163, 727–759.
- Schmidt-Effing, R., 1979. Alter ung genese des Nicoya-klomplexes, einer ozeanischen Paläokruste (Oberjura bis Eozän im südlichen zentralamerika. *Geol Rundschau* 68, 457–494.
- Schweitzer, M.H., Jackson, F.D., Chiappe, L.M., Schmitt, J.G., Calvo, J.O., Rubilar, D.E., 2002. Late Cretaceous avian eggs with embryos from Argentina. *Journal of Vertebrate Paleontology* 22, 191–195.
- Scotese, C.R., 2001. Atlas of Earth History. PALEOMAP Project, Arlington, Texas.
- Senter, P., 2007. A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 5, 429–463.
- Senter, P., 2009. Vestigial skeletal structures in dinosaurs. *Journal of Zoology* 280, 60–71.
- Sereno, P.C., 1999. The evolution of dinosaurs. *Science* 284, 2137–2147.
- Sereno, P.C., 2005. The Logical Basis of Phylogenetic Taxonomy. *Systematic Biology* 54, 595–619.
- Sereno, P.C., 2010. Noasaurid (Theropod:Abelisauroidea) skeleton from Africa shows derived skeletal proportions and function. *Journal of Vertebrate Paleontology* 30, 162A.
- Sereno, P.C., Brusatte, S.L., 2008. Basal abelisauroid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation (Aptian-Albian) of Niger. *Acta Palaeontologica Polonica* 53, 15–46.
- Sereno, P.C., Larsson, H.C.E., 2009. Cretaceous Crocodyliiformes from the Sahara. *ZooKeys* 28, 1–143.
- Sereno, P.C., Duthheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Hagwene, P.M., Sidor, C.A., Varricchio, D.J., Wilson, J.A., 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* 272, 986–991.
- Sereno, P.C., Beck, A.L., Duthheil, D.B., Gado, B., Larsson, H.C.E., Lyon, G.H., Marcot, J.D., Rauhut, O.W.M., Sadleir, R.W., Sidor, C.A., Varricchio, D.D., Wilson, G.P., Wilson, J.A., 1998. A long-snouted predatory dinosaur from Africa and the evolution of Spinosaurids. *Science* 282, 1298–1302.
- Sereno, P.C., Wilson, J.A., Conrad, J.L., 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings of the Royal Society of London B* 271, 1325–1330.
- Sereno, P.C., Martínez, R.N., Wilson, J.A., Varricchio, D.J., Alcober, O.A., 2008. Evidence for Avian Intrathoracic Air Sacs in a New Predatory Dinosaur from Argentina. *PLoS One* 3, e3303.
- Sigogneau-Russell, D., Ensom, P., 1998. *Thereuodon* (Theria, Symmetrodonta) from the Lower Cretaceous of North Africa and Europe, and a brief review of symmetrodonts. *Cretaceous Research* 19, 445–470.
- Smith, A.G., Hurlley, A.M., Briden, J.C., 1981. Phanerozoic paleocontinental world maps. Cambridge University Press, Cambridge, pp. 1–346.
- Smith, J.B., Lamanna, M.C., Lacovara, K.J., Dodson, P., Smith, J.R., Poole, J.C., Giegengack, R., Attia, Y., 2001. A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. *Science* 292, 1704–1706.
- Smith, N.D., Makovicky, P.J., Hammer, W.R., Currie, P.J., 2007. Osteology of *Cryolophosaurus elliotti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society* 151, 377–421.
- Smith, N.D., Makovicky, P.J., Agnolín, F.L., Ezcurra, M.D., Pais, D.F., Salisbury, S.W., 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous. *Proceedings of the Royal Society of London B* 275, 2085–2090.
- Smith, J.B., Lamanna, M.C., Askar, A.S., Bergig, K.A., Tshakreen, S.O., Abugares, M.M., Rasmussen, D.T., 2010. A large abelisauroid theropod dinosaur from the Early Cretaceous of Lybia. *Journal of Paleontology* 84, 927–934.
- Stromer, E., 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse* 28, 1–32.
- Stromer, E., 1934. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe. 13 Dinosauria. *Abhandlungen Bayerische Akademie Wissenschafte Atheilung-naturwissenschaften Abteilung Neue Folge* 22, 1–79.
- Sues, H.-D., Taquet, P., 1979. A pachycephalosaurid dinosaur from Madagascar and a Laurasia–Gondwanaland connection in the Cretaceous. *Nature* 279, 633–635.
- Torcida, F., Izquierdo Montero, L.A., Huerta Hurtado, P., Montero Huerta, D., Pérez Martínez, G., 2003. Dientes de dinosaurios (Theropoda, Sauropoda), en el Cretácico Inferior de Burgos (España). In: Pérez-Lorente, F. (Ed.), *Dinosaurios y otros reptiles mesozoicos de España*. Instituto de Estudios Riojanos, Logroño, pp. 335–346.
- Turner, A.H., Pol, D., Clarke, J.A., Erickson, G.M., Norell, M.A., 2007a. A basal dromaeosaurid and size evolution preceding avian flight. *Science* 317, 1378–1381.
- Turner, A.H., Hwang, S.H., Norell, M.A., 2007b. A small derived theropod from Öösh, Early Cretaceous, Baykhangor Mongolia. *American Museum Novitates* 3557, 1–27.
- Varricchio, D.J., Jackson, F.D., Borkowski, J.J., Horner, J.R., 1995. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* 385, 247–250.
- Varricchio, D.J., Horner, J.R., Jackson, F.D., 2002. Embryos and eggs for the Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* 22, 564–576.
- Vickers-Rich, P., Rich, T.H., 1997. The polar dinosaurs of southeastern Australia. In: Wolberg, D.L., Stump, E., Rosenberg, G.D. (Eds.), *Proceedings of the 1997 Dinofest International*. Academy of Natural Sciences, Philadelphia, pp. 253–257.
- Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X., Sahni, A., Gomani, E.M.P., Noto, C.R., 2004. *Dinosaur Distribution*. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, Berkeley, pp. 517–606.
- Weishampel, D.B., Fastovsky, D.E., Watabe, M., Varricchio, D., Jackson, F., Tsogtbataar, K., Barsbold, R., 2008. New oviraptorid embryos from Bugin.Tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habitat and growth. *Journal of Vertebrate Paleontology* 28, 1110–1119.
- Welles, S.P., Long, R.A., 1974. The tarsus of theropod dinosaurs. *Annals of the South African Museum* 64, 191–218.
- Williamson, T., Brusatte, S., Weil, A., 2010. Phylogeny of Cretaceous–Paleocene metatherians: implications for the metatherian radiation and survivorship of lineages across the K/Pg boundary. *Journal of Vertebrate Paleontology* 28, 188A.
- Wilson, J.A., Upchurch, P., 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Palaeontology* 7, 199–239.
- Wilson, J.A., Sereno, P.C., Srivastava, S., Bhatt, D.K., Khosla, A., Sahni, A., 2003. A new abelisauroid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. *Contributions from the Museum of Paleontology, University of Michigan* 31, 1–42.
- Wu, X.C., Sues, H.-D., 1996. Anatomy and Phylogenetic Relationships of *Chimaerasuchus paradoxus*, an Unusual Crocodyliiform Reptile from the Lower Cretaceous of Hubei, China. *Journal of Vertebrate Paleontology* 16, 688–702.
- Xu, X., 2010. Biogeography: Horned dinosaurs venture abroad. *Nature* 465, 431–432.
- Xu, X., Zhang, F., 2005. A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* 92, 173–177.
- Xu, X., Wang, X.-L., Wu, X.-C., 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* 401, 262–266.
- Xu, X., Zhou, Z., Wang, X., 2000. The smallest known non-avian theropod dinosaur. *Nature* 408, 705–708.
- Xu, X., Zhao, Q., Norell, M.A., Sullivan, C., Hone, D., Erickson, P.G., Wang, X., Han, F., Guo, Y., 2008. A new feathered dinosaur fossil that fills a morphological gap in avian origin. *Chinese Science Bulletin* 54, 430–435.
- Xu, X., Clark, J.M., Mo, J., Choiniere, J., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C., Han, F., Guo, Y., 2009. A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature* 459, 940–944.
- Xu, X., Wang, D.Y., Sullivan, C., Hone, D.W.E., Han, F.L., Yan, R.H., Du, F.M., 2010a. A basal parvicursorine (Theropoda: Alvarezsauridae) from the Upper Cretaceous of China. *Zootaxa* 2413, 1–19.
- Xu, X., Sullivan, C., Pittman, M., Choiniere, J.N., Hone, D., Upchurch, P., Tan, Q., Xiao, D., Tan, L., Han, F., 2010b. A monodactyl nonavian dinosaur and the complex evolution of alvarezsaurid hand. *Proceedings of the National Academy of Sciences* 108, 2338–2342.
- Zhang, F., Zhou, Z., Xu, X., Wang, X., Sullivan, C., 2008. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature* 455, 1105–1108.
- Zheng, X., Xu, X., You, H., Zhao, Q., Dong, Z., 2009. A short-armed dromaeosaurid from the Jehol Group of China with implications for early dromaeosaurid evolution. *Proceedings of the Royal Society of London B* 277, 211–217.
- Zhou, Z.H., Zhang, F.C., 2002. A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* 418, 405–409.
- Ősi, A., Buffetaut, E., 2011. Additional non-avian theropod and bird remains from the early Late Cretaceous (Santonian) of Hungary and a review of the European abelisauroid record. *Annales de Paleontologie* 97, 35–49.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cretres.2013.04.001>