Theropod dinosaurs from Argentina

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Abstract. Theropoda includes all the dinosaurs more closely related to birds than to sauropodomorphs (long-necked dinosaurs) and ornithischians (bird-hipped dinosaurs). The oldest members of the group are early Late Triassic in age, and non-avian theropods flourished during the rest of the Mesozoic until they vanished in the Cretaceous-Palaeogene mass extinction. Theropods radiated into two main lineages, Ceratosauria and Tetanurae, which are well represented in Cretaceous rocks from Argentina. Ceratosaurians are the most taxonomically diverse South American non-avian theropods, including small to large-sized species, such as the iconic horned dinosaur Carnotaurus. Argentinean tetanurans are represented by multiple lineages that include some of the largest carnivorous dinosaurs known worldwide (carcharodontosaurids), the enigmatic large-clawed megaraptorans, and small to medium-sized species very closely related to avialans (e.g. unenlagiids). The Argentinean non-avian theropod record has been and is crucial to understand the evolutionary and palaeobiogeographical history of the group in the southern continents during the Mesozoic.

Key words. Dinosauria, Saurischia, phylogeny, evolution, palaeobiogeography.

INTRODUCTION

Theropoda is the clade that includes all the dinosaurs more closely related to birds than to sauropodomorphs (long-necked dinosaurs) and ornithischians (bird-hipped dinosaurs). Most theropods were carnivorous forms, but some were secondarily herbivorous (e.g. Chilesaurus, ornithomimosaurs, therizinosaurs). Theropods appear for the first time in the early Late Triassic (ca. 231 Ma) and flourished during the rest of the Mesozoic. The vast majority of the theropod lineages were vanished away by the Cretaceous-Palaeogene mass extinction event (ca. 66 Ma) and only one clade survives nowadays with approximately 10,000 species, the birds. The evolutionary history of non-avian dinosaurs has been mainly known from the Northern Hemisphere record until the 1960’s and mainly the 1980’s, when the explorations of José F. Bonaparte and subsequently by several Argentinean palaeontologists
resulted in the discovery of an abundant and diverse Jurassic and Cretaceous theropod assemblage, mainly in Patagonian provinces (Novas et al., 2013). Before the exponential sequence of discoveries that started in the late XX century, the theropod record from Argentina was based on the enigmatic Genyodectes serus from the Early Cretaceous of Chubut, which was the first theropod to be described for the country (Woodward, 1901). As a result, beyond some sporadic reports of fragmentary bony specimens (e.g. Unquillosaurus ceibalii) and ichnites (e.g. Sarmientichnus scagliai), the theropod faunas of Argentina remained almost unknown during most of the last century. The discoveries that started during the 1980’s show that the Cretaceous theropod assemblages of South America resembled those from other regions of Gondwana (e.g. India, Africa), but contrast with those from North America and Asia (Bonaparte & Novas, 1985; Bonaparte & Kielan-Jawarowska, 1987). The non-avian theropod record of Argentina spans from the Carnian up to the Maastrichtian, thus documenting the complete 165 Ma of evolutionary history of the group. Here we provide a brief update of our current understanding of the higher-level phylogenetic relationships of theropods, and then a summary of the Argentinean record of the group.


PHYLOGENETIC INTERRELATIONSHIPS OF NON-AVIAN THEROPODS

The phylogenetic relationships of the non-avian theropod dinosaurs have been explored by multiple, independent cladistic analyses in the last 30 years. The vast majority of these analyses have agreed in the recognition of several theropod clades, such as Coelophysoidea, Abelisauroidea (Abelisauroidea + Noasauridae), Spinosauroidea (megalosaurs + spinosaurs), Allosauroidea (allosaurs + carcharodontosaurs) and Coelurosauria, a highly diverse group that includes Megaraptora (but see below), Tyrannosauroidea, Compsognathidae, Ornithomimosauria, Alvarezsauroida, Therizinosauria, Oviraptorosauria, Scansoriopterygidae, Dromaeosauridae, Troodontidae, and Aves (e.g. Carrano et al., 2012; Pol & Rauhut, 2012; Nesbitt & Ezcurra, 2015; Novas et al., 2015; Xu et al., 2015; Brusatte & Carr, 2016) (Fig. 1). However, the interrelationships among all these clades and in some cases their taxonomic content has been matter of considerable debate.

Coelophysoidea represents the most basal branch of Neotheropoda (Fig. 1). Current phylogenetic studies found strong evidence favouring the placement of ceratosaurians (Ceratosaurus and abelisaurids) closer to tetanurans than to coelophysoids, resulting in a monophyletic Averostra (i.e. Ceratosauria + Tetanuridae, excluding Coelophysoidea) (Paul, 2002; Rauhut, 2003; Ezcurra, 2006). Within Tetanuridae, most analyses recovered Allosauroidea more closely related to Coelurosauria than to Megalosauroidea (e.g. Carrano et al., 2012). Nevertheless, a recent analysis recovered a monophyletic Carnosauria, being composed of Megalosauroidea and Allosauroidea to the exclusion of other theropods (Rauhut et al., 2012). The phylogenetic position of the Argentinean theropod Megaraptor namunhuaiquii and its kin (e.g. Aerosteon riocoloradensis, Orkoraptor burkei) has been a contentious issue since the discovery of this taxon (Novas, 1998; Benson et al., 2010; Novas et al., 2013, 2015). The recognition of a monophyletic Megaraptora (Benson et al., 2010) has not helped to reach a consensus about the phylogenetic position of the group and in recent analyses they have been alternatively found as deeply nested within Allosauroidea (Benson et al., 2010; Carrano et al., 2012) or Tyrannosauroidea (Novas et al., 2013; Porfiri et al., 2014), or as the most basal coelurosaurids (Novas et al., 2015) (Fig. 1).
Tyrannosauroids (Proceratosauridae + Tyrannosauridae) are generally found as the most basal members of Coelurosauria, being the sister-taxon of Compsognathidae and a clade composed of Ornithomimosauria and more derived forms (e.g. Choiniere et al. 2013). Among these more derived forms, Oviraptorosaurus, Therizinosauroida and Alvarezsaurioidea are frequently recovered as the successive sister-taxa of Avialae and its more closely related clades (e.g. Xu et al., 2015). The position of the closest clade to Avialae has been also matter of considerable debate in recent years.
A monophyletic Deinonychosauria (Dromaeosauridae + Troodontidae) has been repeatedly found as the sister-taxon of *Archaeopteryx lithographica* and its kin during the 1990’s and 2000’s (e.g. Gauthier, 1986; Makovicky et al., 2005). However, Hu et al. (2009) recovered the tiny and presumably arboreal scansoriopterygids as the non-avian theropods most closely related to avialans. Subsequently, Agnolin and Novas (2011, 2013) found scansoriopterygids more closely related to oviraptorosaurs than to other theropods and unenlagiids as the sister-taxon of avialans. The latter hypothesis contrasts with previous results (e.g. Makovicky et al., 2005) but agreed with the early proposal of Novas & Puerta (1997) about the close affinities between *Unenlagia comahuensis* and birds. Xu et al. (2011) recovered *Archaeopteryx lithographica* and its kin as more closely related to dromaeosaurs and troodontids than to birds (i.e. within Deinonychosauria), thus sharply contrasting with the historical view of this species as the most basal bird. By contrast, Xu et al. (2011) found scansoriopterygids as the most basal branch of Avialae. More recently, Xu et al. (2015) recovered a similar result, in which deinonychosaurus (including *Archaeopteryx lithographica*) were more closely related to avialans than to other coelurosaurians, but this time to the exclusion of scansoriopterygids. Finally, Godefroit et al. (2013) found troodontids as more closely related to avialans than to dromaeosaurs.

In conclusion, there is a general consensus in the monophyly of most of the main theropod lineages and the higher-level phylogenetic relationships (i.e. the monophyly of Averostra, Coelurosauria, Maniraptora). However, the placement of Megaraptora and the most immediate sister-taxa to Avialae are still strongly contentious topics (Fig. 1) and will probably attract a considerable amount of research in future years.

**TRIASSIC THEROPODS**

The oldest known dinosaur-bearing beds are recorded in the upper Carnian Ischigualasto Formation of NW Argentina (San Juan and La Rioja provinces) and approximately coeval units of Brazil, India and Zimbabwe. The Ischigualasto dinosaur assemblage includes representatives of Theropoda, namely *Eodromaeus murphi* and probably *Herrerasaurus ischiguaslastensis*. *Eodromaeus murphi* is a small species originally described as a non-neotheropod theropod (Martínez et al., 2011) and subsequent analyses bolstered this result (e.g. Nesbitt & Ezcurra, 2015). The phylogenetic position of *Herrerasaurus ischiguaslastensis* (body length ca. 6 m) and its kin is variable in different analyses, being alternatively recovered as either the most basal saurischians or theropods. In any case, herrerasaurids show cranial...
character-states probably related to predatory habits that resemble the condition in later tetanuran theropods (Sereno & Novas, 1993). *Eoraptor lunensis*, from the same geological unit, has been historically considered a theropod, but recent analyses have found it as a basal sauropodomorph (Martínez et al., 2011).
The lower-middle Norian Los Colorados Formation (La Rioja Province) overlies the Ischigualasto Formation and four theropod specimens have been recovered from this unit. The most complete of them is the holotype and only known specimen of *Zupaysaurus rougieri*, which is represented by a fairly complete skull with a partial postcranium (Fig. 2A). *Zupaysaurus rougieri* is a medium-sized animal (skull length ca. 45 cm) that was originally interpreted as a basal tetanuran (Arcucci & Coria, 2003), but subsequently found as one of the most basal successive sister taxa of Averostra (Nesbitt & Ezcurra, 2015). Other two specimens from the same unit belong to indeterminate theropods, represented by a partial postcranium (Bonaparte, 1972) and a fragmentary femur (Novas, 1993), respectively. The fourth specimen is a tiny theropod (astragalus width 7 mm) currently under description, which is represented by partial hindlimbs and nested within Coelophysidae (MDE unpublished data). In addition, Martínez et al. (2015) preliminary reported the remains of an unnamed coelophysoid from the upper Norian Quebrada del Barro Formation of the Marayes-El Carrízal Basin in San Juan Province.

**JURASSIC THEROPODS**

The Jurassic theropod record of Argentina is restricted to the Lower-Middle Jurassic Cañadón Asfalto and Upper Jurassic Cañadón Calcáreo formations of the Chubut Province. Three named species and an unnamed form currently compose the theropod assemblage of the former unit, namely the ceratosaur *Eoabelisaurus mefi* (Pol & Rauhut, 2012) (Fig. 2H, I), the basal tetanurans *Piatnitzkysaurus floresi* (Fig. 2C–G) and *Condorraptor currumili* (Fig. 2B) (Bonaparte, 1986; Rauhut, 2005), and a still preliminary reported, unnamed basal tetanuran (Rauhut & Pol, 2011). *Eoabelisaurus mefi* is a medium-sized theropod (total length 6–6.5 m) originally interpreted as the most basal member of the Abelisauridae, thus predating the oldest record of the clade by more than 40 Ma (Pol & Rauhut, 2012). By contrast, *Eoabelisaurus mefi* has been recovered more recently as the sister-taxon of Abelisauroidea (i.e. Noasauridae + Abelisauridae) by Tortosa et al. (2014). The other two named species from the Cañadón Asfalto Formation are similar in size to *Eoabelisaurus mefi* and have been found more closely related to each other than to other theropods, within the family Piatnitzkysauridae (Smith et al., 2007; Carrano et al., 2012). This family have been alternatively recovered at the base of Tetanurae (Smith et al., 2007) or at the base of Megalosauroidea (Carrano et al., 2012). The preliminary reported theropod form the Cañadón Asfalto Formation is a large-sized basal tetanuran represented by a rather complete skeleton that awaits for its formal description (Rauhut & Pol, 2011). In addition, a partial skull of a basal tetanuran different from *Piatnitzkysaurus floresi*, an isolated dentary of a possible ceratosaur, and several theropod teeth have been reported from this unit (Rauhut, 2007; Ezcurra & Pol, 2009).

The bizarre basal tetanuran *Chilesaurus diegosuarezi* was recently described from the uppermost Jurassic of southern Chile (Novas et al., 2015). This species is one of the best known Late Jurassic dinosaurs from the Southern Hemisphere and its unique combination of features suggests the presence of an endemic clade of secondarily herbivorous theropods in south-western Gondwana by the end of the Jurassic. The latest Middle–Late Jurassic theropod record of Argentina is represented by the functionally monodactyl ichinites of *Sarmientichnus scagliai* from the La Matilde Formation of the Santa Cruz Province (Casamiquela, 1964) and a preliminary reported basal tetanuran from the Cañadón Calcáreo Formation of the Chubut Province (Rauhut & Pol, 2011).
The Early Cretaceous theropod record from Argentina is restricted to occurrences from Chubut and Neuquén provinces. The oldest Cretaceous theropod-bearing beds of Argentina correspond to those of the Berriasian–Valanginian Bajada Colorada and the upper Valanginian Mulichinco formations (Neuquén Province), which have

**EARLY CRETACEOUS THEROPODS**

The Early Cretaceous theropod record from Argentina is restricted to occurrences from Chubut and Neuquén provinces. The oldest Cretaceous theropod-bearing beds of Argentina correspond to those of the Berriasian–Valanginian Bajada Colorada and the upper Valanginian Mulichinco formations (Neuquén Province), which have
yielded scarce remains of preliminary reported basal tetanurans (Apesteguía & Bonaparte, 2004; Gianechini et al., 2011) and an animal with abelisaur affinities (Coria et al., 2010). Although fragmentary, these theropod remains are particularly important because terrestrial Berriasian–Valanginian tetrapods are very poorly sampled worldwide (Ezcurra & Agnolin, 2012). The late Barremian–early Aptian La Amarga Formation possesses some of the best known Early Cretaceous tetrapods from South America, such as the dicraeosaurid sauropod *Amargasaurus cazaui* and the cladotherian mammal *Vincelestes neuquenianus* (Bonaparte, 1996). The theropod record from this unit is currently limited to the tiny partial postcranium of the abelisauroid *Ligabueino andesi* (femoral length 62.4 mm) (Fig. 3A, C) and several isolated teeth comparable with those of large basal tetanurans (Apesteguía, 2007). *Ligabueino andesi* has been recently found within Noasauridae (Tortosa et al., 2014) and a detailed description of its anatomy is currently under preparation by the senior author. Del Corro (1974) described an isolated tooth crown from the Middle–lowermost Late Cretaceous Castillo Formation of the San Jorge Basin, southern Chubut Province, as the holotype of “*Megalosaurus chubutensis*”, Poblete & Calvo (2004) considered “*Megalosaurus chubutensis*” a nomen vanum and assigned it possibly to the Carcharodontosauridae. This taxonomic assignment is soundly based on the large size (preserved apicobasal length 64.5 mm and mesiodistal width 34.3 mm) of the crown and the presence of wrinkles adjacent to the distal margin, but these features are highly homoplastic among theropods and we agree with these authors in considering the affinities of the specimen as tentative. Martinelli et al. (2007) described isolated teeth and caudal vertebrae of indeterminate theropods from the Albian Cullín Grande Member of the Lohan Cura Formation, Neuquén Province.

The richest diversity of Argentinean Early Cretaceous theropods comes from the Aptian–Albian Cerro Barcino Formation of the Chubut Province. The first theropod specimen described for these beds was the ceratosaur *Genyodectes serus*, which is based on a partial snout of a single specimen (Woodward, 1901; Rauhut, 2004) (Fig. 3G–I). This species has been recently recovered as the sister-taxon of the Late Jurassic North American ceratosaur *Ceratosaurus* (Pol & Rauhut, 2012). More recently, Rauhut et al. (2003) described two anterior caudal vertebrae of an abelisaurian (probably abelisaurid) theropod from the Hauterivian–Barremian La Paloma Member of the same formation (Fig. 3E, F). Novas et al. (2005) erected the new genus and species *Tyrannotitan chubutensis* based on two partial skeletons from the Aptian Cerro Castaño Member of this formation (Fig. 3B, D). The skeletons that compose the hypodigm of *Tyrannotitan chubutensis* belonged to animals with a total body length of around 13 metres and are the most complete Early Cretaceous theropod specimens so far from Argentina.

**Figure 4** (Next page). The Late Cretaceous abelisauroids *Carnotaurus sastrei* (A, B), *Noasaurus leali* (C), *Abelisaurus comahuensis* (D) and *Skorpiovenator bustingorryi* (E), the carcharodontosaurid *Giganotosaurus carolinii* (F), and the megaraptorans *Aerosteon rioloradensis* (G) and *Megaraptor namunhuaiquii* (H). Reconstruction of the skeleton (preserved bones in white) in right lateral view (A), skulls in right lateral (B, E) and left lateral (D) views; left maxilla in lateral view (C), left dentary in lateral view (F), partial pre-caudal postcranium in left lateral view (G), and manual ungual I-1 in lateral view (H). Abbreviations: anfe, antorbital fenestra; anfo, antorbital fossa; bf, brevis fossa; b/f, brevis fossa; co, coracoid; d, dentary; db, distal boot; emf, external mandibular fenestra; en, external naris; fu, furcula; gf, glenoid fossa; gr, groove; ho, horn; ip, ischial peduncle; itf, infratemporal fenestra; la, lacrimal; mx, maxilla; ns, neural spine; or, orbit; paf, posterior articular facet; pl, pleurocoel; po, postorbital; pop, postacetabular process; prp, preacetabular process; pu, pubis; qj, quadratojugal; sa, surangular; sc, scapula; so, supraoccipital eminence; sq, squamosal. Scale bars equal 50 cm in (A), 10 cm in (B, E, F), 1 cm in (C), 5 cm in (H), and 20 cm in (D, G).
LATE CRETACEOUS THEROPODS

The Late Cretaceous theropod record from Argentina is considerably richer than those from older Mesozoic outcrops of the country and represents the richest theropod sample from Gondwana in terms of quantity and quality of specimens (Novas et al.,
The most comprehensive knowledge of an early Late Cretaceous theropod assemblage comes from the Cenomanian Candeleros Formation of the Neuquén Basin (Neuquén Province). This unit yielded the remains of abelisaurids (*Ekrixinatosaurus novasi*), carcharodontosaurs (*Giganotosaurus carolinii*; Fig. 4F), basal coelurosaurs (*Bicentenaria argentina*; Fig. 5A−C), alvarezsaurids (*Alnashetri cerropoliciensis*) and unenlagiids (*Buitreraptor gonzalezorum*; Fig. 5I, J; Coria & Salgado, 1995; Calvo et al., 2004; Makovicky et al., 2005, 2012; Novas et al., 2012). Thus, the Candeleros Formation includes the oldest records of alvarezsaurids, unenlagiids, and probably carcharodontosaurs (depending on the affinities of "Megalosaurus chubutensis") for Argentina. The upper Cenomanian−lower Turonian Huincul Formation directly overlies the Candeleros Formation and preserves a theropod assemblage composed of abelisaurids (*Ilokelesia aguadLegrandensis, Skorpiovenator bustingorryi*: Fig. 4E) and carcharodontosaurs (*Mapusaurus roseae*; Coria & Salgado, 2000; Coria & Currie, 2006; Canale et al., 2009).

Cenomanian abelisaurids (*Xenotarsosaurus bonapartei*), probable carcharodontosaurs (based on isolated teeth), megaraptorans (a preliminary reported form), basal coelurosaurs (e.g. *Anikosaurus darwini*: Fig. 5E, G, H) and putative dromaeosaurs (based on isolated teeth) have been also described for the lower member of the Bajo Barreal Formation of the San Jorge Basin (Chubut Province) (Martínez et al., 1986; Martínez & Novas, 2006; Coria & Currie, 2002; Casal et al., 2009). Isolated theropod tooth crowns found in the Cenomanian Bayo Overo Member of the Cerro Barcino Formation represent the hypodigm of "Megalosaurus inexpectatus" (del Corro, 1966). These tooth crowns possess a continuously convex mesial margin and a straight distal one, lacking ornamentation on the enamel (MACN-Pv 18172; but two of the original set of four teeth are currently lost). This combination of features suggests that this species could be an abelisaurid and based on the absence of a unique combination of character-states among abelisaurids, "Megalosaurus inexpectatus" is here considered a nomen vanum.

The Mata Amarilla Formation of the Austral Basin (Santa Cruz Province) has been interpreted as upper Campanian-lower Maastrichtian in age on the basis of its micropalaeontological content, but an older age (Cenomanian) was subsequently proposed on the basis of its dinosaurian and dipnoan content (Novas et al., 2002) and a recent radioisotopic dating yielded a middle Cenomanian age for this unit (Varela et al., 2012). The theropod assemblage of the Mata Amaerilla Formation (referred to as Pari Aike Formation in some previous contributions) is composed of an abelisaurid (*Austrocheirus isasii*) and a megaraptoran (*Orkoraptor burkei*) (Novas et al., 2008; Ezcurra et al., 2010).

The middle Turonian Cerro Lisandro Formation directly overlies the Huincul Formation and has a theropod record limited to an indeterminate, medium-sized abelisaurid (Coria et al., 2006). Immediately overlying this unit, the Portezuelo Formation is dated as late Turonian−early Coniacian in age and preserves a very good sample of middle Late Cretaceous theropods. The carnivorous dinosaur assemblage of this unit includes abelisaurids (an unnamed form), megaraptorans (*Megaraptor namunhuaiqüi*: Fig. 4H), alvarezsaurids (*Patagonykus puertai*), and unenlagiids (*Neuquenraptor argentinus, Pamparaptor micros, Unenlagia comahuensis*: Fig. 5D, *Unenlagia paynemili*), thus closely resembling the taxonomic richness and composition of the older Candeleros Formation.

The holotype and only known specimen of the megaraptoran *Aerosteon riocoloradensis* (Sereno et al., 2008; Fig. 4G) and isolated tooth crowns of a cf. Carcharodontosauridae and an indeterminate maniraptoran (Canudo et al., 2009) come from the upper Coniacian−lower Santonian Plottier Formation (Neuquén and Mendoza provinces) of the Neuquén Basin (Novas et al., 2013). This geological
Figure 5. The Late Cretaceous small to medium-sized coelurosaurs *Bicentenaria argentina* (A−C), *Unenlagia comahuensis* (D), *Aniksosaurus darwini* (E, G, H), *Bonapartenykus ultimus* (F), and *Buitreraptor gonzalezorum* (I, J). Posterior half of the skull in left lateral view (A), right astragalus in anterior view (B), reconstruction of the skeleton (preserved bones in white) in left lateral view (C), right hemipelvis in lateral view (D), left ilium in lateral view (E), left scapula and coracoid in lateral view (F), right femur in posterior view (G), partial right foot in anterior view (H), and skull in left lateral (I) and dorsal (J) views. Abbreviations: I−IV, pedal digits I−IV; ac, acetabulum; anfe, antorbital fenestra; ap, acromial process; asp, ascending process; bs, brevis shelf; cf, cuppedicus fossa; co, coracoid; db, pubic boot; de, dentary; fh, femoral head; fr, frontal; ft, fourth trochanter; gf, glenoid fossa; gt, greater trochanter; hm, hemimandible; ip, ischial peduncle; is, ischium; if, infratemporal fenestra; ju, jugal; mf, maxillary fenestra; mx, maxilla; na, nasal; or, orbit; pa, parietal; pf, popliteal fossa; po, postorbital; pop, postacetabular process; pp, pubic peduncle; prp, preacetabular process; pu, pubis; sa, surangular; sc, scapula; sn, scapular notch; tc, tibial condyle; tfc, tibiofibular crest; vtc, ventral tilting of coracoid. Scale bars equal 1 cm in (A), 5 mm in (B), 20 cm in (C), 5 cm in (D, F), and 2 cm in (E, G, H−J). Skeletal reconstruction (C) made by Emilio L. Rolandi, and photograph (D) courtesy of F. Brissón Egli.
unit is directly overlaid by the middle—upper Santonian Bajo de la Carpa Formation (Río Negro and Neuquén provinces), which is worldwide known for its diverse non-dinosaurian fauna (Bonaparte, 1991). The non-avian theropod record of the Bajo de la Carpa Formation is composed of noasaurids (*Velocisaurus unicus*), abelisaurids (e.g. *Viavenator exxoni*), a preliminary reported possible carcharodontosaurid, and alvarezsaurids (*Alvarezsaurus calvoi*, *Achillesaurus manazzonei*) (Bonaparte, 1991; Martinelli & Vera, 2007; Porfiri et al., 2008; Fillipi et al., 2016). The early Campanian beds of the Neuquén Basin crop out as the Anacleto Formation (Río Negro and Neuquén provinces), which has a theropod assemblage represented by medium to large-sized abelisaurids (e.g. *Abelisaurus comahuensis*: Fig. 4D, *Aucasaurus garridoi*) (Bonaparte & Novas, 1985; Coria et al., 2002).

The theropod assemblages immediately before the Cretaceous-Palaeogene mass extinction (i.e. Campanian-Maastrichtian) are widely represented in Patagonia and northern Argentina. The Maastrichtian Allen Formation of the Neuquén Basin (Río Negro Province) has a diverse tetrapod fauna that includes abelisaurids (*Quilmesaurus curriei*), alvarezsaurids (e.g. *Bonapartenykus ultimus*: Fig. 5F), and large-sized unenlagiids (*Austroraptor cabazai*) (Coria, 2001; Novas et al., 2009; Agnolin et al., 2012). The Maastrichtian La Colonia Formation of the Chubut Province has yielded the most complete and well preserved theropod known so far from Gondwana, the abelisaurid *Carnotaurus sastrei* (Bonaparte, 1985) (Fig. 4A, B). In northern Argentina, the large maniraptoran *Unquilloptrosaurus ceballi* comes from the Campanian Los Blanquitos Formation (Powell, 1979) and the small noasaurid *Noasaurus leali* from the Campanian-Maastrichtian Lecho Formation (Fig. 4C), both from Salta Province (Bonaparte & Powell, 1980).

A recently and preliminary reported theropod assemblage from the Upper Cretaceous Los Llanos Formation of the Bermejo Basin (La Rioja Province) includes abelisaurids, maniraptorans, and an indeterminate averostran (Fiorelli et al., 2014). A large partial tooth crown of an indeterminate theropod was described for the Puerto Yeruá Formation (Entre Ríos Province), but the age of the unit is poorly constrained as Cretaceous (de Valais et al., 2003).

**MACROEVOLUTIONARY HISTORY OF THE GROUP BASED ON THE GONDWANAN RECORD**

The oldest known Argentinean predatory dinosaurs, recovered in the Ischigualasto Formation (e.g. *Eodromaeus*, *Herrerasaurus*), distinctly differ morphologically from the approximately 10−15 million years younger Triassic theropods of the Los Colorados Formation (*Zupaysaurus rougieri*, a still unnamed coelophysoid). This difference implies a replacement in the composition of the carnivorous dinosaur faunas before the Triassic-Jurassic mass extinction, resembling the pattern observed in coeval beds of India (Novas et al., 2011). The vast majority, if not all, of the averostran lineages should have originated during the Early-Middle Jurassic, but the Jurassic theropod record of Gondwana is currently restricted to non-coelurosaurians averostrans (e.g. abelisauroids, piatnitzkysaurids). By contrast, the Jurassic Laurasian record is taxonomically richer and includes basal ceratosaurians, basal tetanurans, and several coelurosaurian clades (e.g., tyrannosauroid, compsoagnathids, scansioniopterygids, archaeopterygids).

The considerably richer Late Cretaceous Gondwanan non-avian theropod record, when compared with that from the Triassic to Early Cretaceous, allowed Novas et al. (2013) to explore the late macroevolutionary history of the clade. These authors found high extinction indices in the Cenomanian-Coniacian time span, but only the index for the Turonian-Coniacian boundary significantly departed from background
extinction levels. In the Cenomanian-Turonian spinosaurids, carcharodontosaurids, and several basal abelisaurid and coelurosaurians lineages went extinct, which is part of a faunal turnover also observed in other vertebrate groups (e.g. dipnoans, rebbachisaurid sauropods, crocodylomorphs, turtles) (Novas et al., 2005). A different taxonomic selectivity between the Cenomanian and Turonian-Coniacian turnovers suggests that they were different processes acting over several million years, rather than a single extinction event. No Cenomanian or Turonian-Coniacian extinctions are evident in the theropod record of the northern continents, but some authors have documented important changes in the terrestrial vertebrate assemblages of Laurasia by Cenomanian times (e.g. Jacobs & Winkler, 1998). By the end of the Late Cretaceous, both Gondwanan and Laurasian theropod assemblages share a similar macroevolutionary pattern, consisting of a continuous increase of extinction levels until reaching the Cretaceous-Palaeogene boundary, and a peak in species origination by the end of the Campanian. Gondwana possesses a Santonian-Maastrichtian dinosaur faunal composition that clearly differs from that previous to the Turonian-Coniacian extinction event, including the presence of abelisaurids and unenlagiids as the top predators of these latest Cretaceous assemblages in Argentina (Coria, 2001; Novas et al., 2009).

THEROPOD PALAEOBIOGEOGRAPHY

The description 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 (Bonaparte, 1996). This evidence supported the interpretation that Gondwana remained geographically isolated from Laurasia during most of the Cretaceous prior to the Campanian-Maastrichtian (Bonaparte & Kielan-Jawarowska, 1987). However, discoveries of purported Gondwanan lineages (e.g. abelisaurids, spinosaurids, carcharodontosaurids) in Laurasian territories blurred the sharp faunal distinctions once recognized between southern and northern landmasses. Several authors attempted to explain these anomalous occurrences describing the presence 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. Ezcurra & Agnolín (2012) proposed the Eurogondwanan hypothesis, in which the European region had a close biogeographical affinity with Gondwana during the Berriasian-Hauterivian time-span, allowed by a connection through Africa. After the Hauterivian, several Eurogondwanan tetrapod clades made their appearance in Asiamerica (e.g. megaraptorans, carcharodontosaurids, spinosaurids). This biogeographic pattern was interpreted as evidence for the coalescence of the European region with Asiamerica during the Barremian. These authors proposed that this purported European-Asiameiran faunistic interchange occurred after a short interval of biogeographical isolation of the European region from Gondwana, thus allowing the dispersal of Eurogondwanan taxa into Asiamerica but preventing the immigration of Laurasian taxa into Gondwana.

Ezcurra & Agnolín (2012) found that Europe possessed closer biogeographical affinities with the southern landmasses during the Campanian-Maastrichtian rather than with Asiamerica. The biogeographical 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. hadrosaurid ornithischians). 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 (Bonaparte,
1984). Future palaeogeographic research and work on the latest Cretaceous terrestrial faunas of South America may shed light on the provenance of the supposed Laurasian immigrant taxa into the southern continents.

FUTURE DIRECTIONS

The intensive discovery and description of theropod dinosaurs in Argentina is relatively recent in comparison with more than 150 years of continuous research in the Northern Hemisphere. The Late Cretaceous record of theropods, mainly in Patagonia, has considerably increased in the last 20 years and multiple ceratosaurs, allosauroids and coelurosaurids are currently known from these beds. By contrast, the Triassic, Jurassic and Early Cretaceous neotheropod record is still scarce. The discovery of new specimens from this temporal span (e.g. Los Colorados, Laguna Colorada, Cañadón Calcáreo, Bajada Colorada, La Amarga formations), but in parallel with further sampling in Upper Cretaceous beds, seems to be imperative to nourish a more comprehensive understanding of the evolutionary history of Theropoda in the southern continents, including the early evolution of clades such as Carcharodontosauridae, Megaraptora and Unenlagiidae. Such discoveries may become also relevant to shed light on currently contentious phylogenetic issues, including the higher-level relationships of megaraptorans around the allosauroid-coelurosaur dichotomy and the identity of the closest relatives to avialans. In addition, the sampling in poorly prospected regions of the country (e.g. La Rioja, Santa Cruz provinces) will probably add interesting information about more regional patterns that characterized the evolution of the carnivorous dinosaurs in the southern continents. Beyond new discoveries, the revision of already collected specimens using traditional and modern techniques (e.g. CT-scans) is a symptom of a dynamic and healthy line of research that has considerably contributed to increase our knowledge of the South American theropods and should continue in subsequent decades.

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