



AN OVERVIEW OF NON-AVIAN THEROPOD DISCOVERIES AND CLASSIFICATION

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ABSTRACT

Theropods form a taxonomically and morphologically diverse group of dinosaurs that include extant birds. Inferred relationships between theropod clades are complex and have changed dramatically over the past thirty years with the emergence of cladistic techniques. Here, we present a brief historical perspective of theropod discoveries and classification, as well as an overview on the current systematics of non-avian theropods. The first scientifically recorded theropod remains dating back to the 17th and 18th centuries come from the Middle Jurassic of Oxfordshire and most likely belong to the megalosaurid *Megalosaurus*. The latter was the first theropod genus to be named in 1824, and subsequent theropod material found before 1850 can all be referred to megalosauroids. In the fifty years from 1856 to 1906, theropod remains were reported from all continents but Antarctica. The clade Theropoda was erected by Othniel Charles Marsh in 1881, and in its current usage corresponds to an intricate ladder-like organization of 'family' to 'superfamily' level clades. The earliest definitive theropods come from the Carnian of Argentina, and coelophysoids form the first significant theropod radiation from the Late Triassic to their extinction in the Early Jurassic. Most subsequent theropod clades such as ceratosaurs, allosauroids, tyrannosauroids, ornithomimosaurs, therizinosauroids, oviraptorosaurs, dromaeosaurids, and troodontids persisted until the end of the Cretaceous, though the megalosauroid clade did not extend into the Maastrichtian. Current debates are focused on the monophyly of deinonychosaurs, the position of dilophosaurids within coelophysoids, and megaraptorans among neovenatorids. Some recent analyses have suggested a placement of dilophosaurids outside Coelophisoidea, Megaraptora within Tyrannosauroidea, and a paraphyletic Deinonychosauria with troodontids placed more closely to avialans than dromaeosaurids.

Introduction

Theropods form a clade of bipedal tetrapods among which birds and all strictly carnivorous dinosaurs are found (e.g., Gauthier 1986; Sereño 1997; Holtz & Osmólska 2004; Holtz 2012; Naish 2012). Along with sauropodomorph and ornithischian clades, they appeared in the Late Triassic (Figure 1) and rapidly acquired a worldwide distribution, being present on every continent by the Lower Jurassic (Tykoski & Rowe 2004). In the Jurassic (possibly as early as the Middle Jurassic, based on ghost ranges; e.g., Hu et al. 2009; Godefroit et al. 2013a, b), small theropods gave rise to birds, the only dinosaurs to survive the Cretaceous-Paleocene (K-Pg) mass extinction event 66 million years ago (Figure 1). After surviving the K-Pg extinction event, birds radiated into ecological niches left by non-avian dinosaurs (Padian & Chiappe 1998; Chiappe & Witmer 2002; Naish 2012). As a result, theropods are one of the most successful groups of tetrapods, and the most morphologically and taxonomically diverse clade of dinosaurs (Rauhut 2003a; Holtz 2012; Foth & Rauhut 2013).

Non-avian theropods (i.e., Theropoda excluding Avialae) were the dominant terrestrial predators in Jurassic and Cretaceous ecosystems worldwide (Rauhut 2003a; D'Amore 2009). Though their diversity and disparity remained high through the end of the Cretaceous, they became extinct at the end of the Cretaceous concurrent with all other clades of non-avian dinosaurs (Rauhut 2003a; Holtz et al. 2004; Upchurch et al. 2011; Brusatte et al. 2012b, 2015). While non-avian theropods include the majority (if not all) of meat-eating dinosaurs, many theropod clades became secondarily adapted to herbivorous diets (Barrett 2005; Xu et al. 2009b; Zanno et al. 2009; Zanno & Makovicky 2011), and several taxa have been described as omnivores (Holtz et al. 1998; Lee et al. 2014), insectivores (Senter 2005) or filter feeders (Norell et al. 2001). The non-avian theropod body plan underwent relatively little modification during the evolution of the clade, being almost exclusively bipedal and exhibiting, for the large majority of them, elongated necks and a long, horizon-

tally projecting tail (*n.b.*, some theropods such as tyrannosaurids and caudipterids had a short neck and short tail, respectively). Variation in the postcranium mostly occurs in the forelimb, manual and pelvic morphology, hind limbs proportion as well as the vertebral counts, ossification, and elongation of the neural spine. Some theropods like abelisaurids had short stubby arms bearing four short fingers (e.g., Ruiz et al. 2011; Burch & Carrano 2012) whereas others like therizinosaurids possess elongated forelimbs with three slender fingers bearing large claws (Clark et al. 2004; Zanno 2010a). Likewise, although a large majority of theropods exhibit short neural spines, some spinosaurids, allosauroids and deinocheirids have developed hypertrophied spines forming a hump or a sail on the back of these animals (Bailey 1997; Lee et al. 2014). Unlike the postcranial skeleton, there is a tremendous diversity of skull morphology in non-avian theropods, from the elongated skull of spinosaurids showing a terminal spatulate rosette (Charig & Milner 1997; Dal Sasso et al. 2005) to the short parrot-like skull and edentulous jaws of oviraptorids (Xu & Han 2010). Recent discoveries of non-avian theropods such as the rodent-like *Incisivosaurus* (Xu et al. 2002a), the beaked *Limusaurus* (Xu et al. 2009b), the crested *Guanlong* (Xu et al. 2006), the long snouted *Buitreraptor* (Makovicky et al. 2005) and the duck-billed *Deinocheirus* (Lee et al. 2014) indicate a particularly high variety of skull morphologies among theropod dinosaurs (Brusatte et al. 2012c; Foth & Rauhut 2013).

Given such morphological and taxonomic diversity, it is not surprising that theropod classification is particularly complex, with Theropoda currently comprising more than 20 clades at the 'family' and 'super-family' level. With the emergence of cladistic approaches and the discovery of a large number of new theropod taxa, higher-level theropod relationships have also changed dramatically over the past thirty years. This paper aims to present an overview of the current state of knowledge on the systematics of non-avian theropods and a general description of each subclade. A historical perspective of initial discoveries and the evolution of theropod classification are also provided.

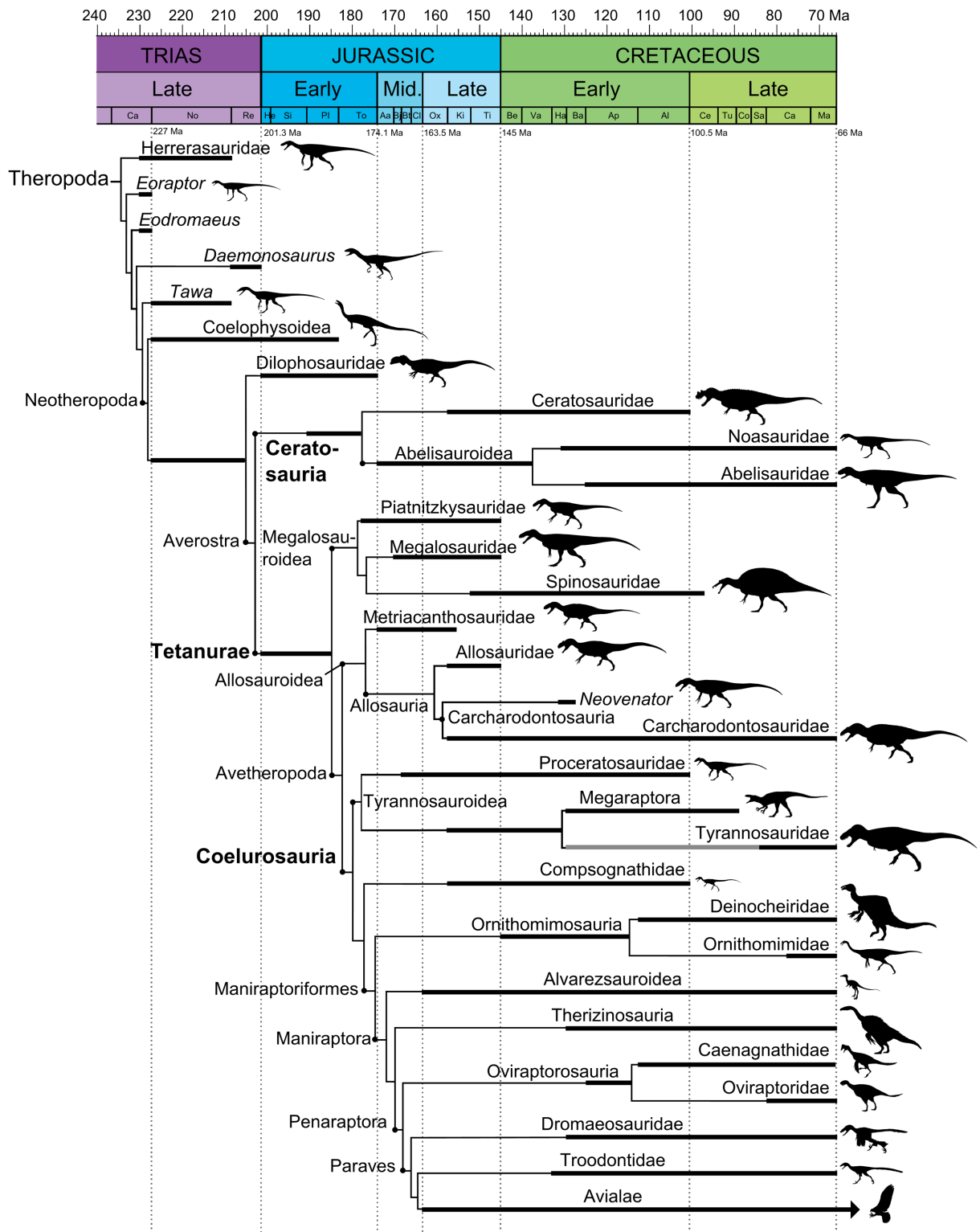


Figure 1. Phylogeny and stratigraphic distribution of theropod clades. The phylogenetic classification of theropods follows the results of the cladistic analyses obtained by Sues *et al.* (2011) for non-neotheropod Theropoda, Smith *et al.* (2007) and Ezcurra & Brusatte (2011) for non-averostran Neotheropoda, Pol & Rauhut (2012) and Tortosa *et al.* (2014) for Ceratosauria, Carrano *et al.* (2012) for non-coelurosaur Tetanurae, Loewen *et al.* (2013), Lü *et al.* (2014) and Porfiri *et al.* (2014) for Tyrannosauroidae, Lee *et al.* (2014) for Ornithomimosauria, Lamanna *et al.* (2014) for Oviraptorosauria, and Turner *et al.* (2012), Godefroit *et al.* (2013a) and Choiniere *et al.* (2014b) for non-tyrannosauroid Coelurosauria. Silhouettes by Michael Bech Hussein (Coelophysoidea, Dilophosauridae, Therizinosauria, and Alvarezsauridae), Jaime Headden (Caenagnathidae), Michael Keesey (Deinocheiridae), William Parker (*Daemonosaurus*), Travis Tischler (Megaraptora), and Scott Hartman (all others).

Historical Background

First Discoveries

The description of the first theropod remains and the first dinosaur material go hand in hand, as the first dinosaur bones and teeth reported in the literature belong to theropods (Lebrun 2004). All theropod material reported in the 17th, 18th, and the first half of the 19th century came from England and France, and has been referred to megalosauroid theropods, with most remains being assigned to Megalosauridae. This coincidence can be explained by two independent factors: 1) the emergence of vertebrate paleontology in the Early modern period and early 19th century in Western Europe, with scientists like Georges Cuvier, Gideon Mantell, and Richard Owen; and 2) the excavation, at that time, of vertebrate remains from Middle Jurassic limestone quarries of Stonesfield (Oxfordshire) and Caen (Normandy), a period of time when megalosauroids were the dominant theropods in Europe.

Theropod fossils were almost certainly found by prescientific societies prior to the 17th century, but the discovery of these unusual remains were interpreted in ways that gave rise to myths and legends (Buffetaut 1994; Lebrun 2004; Spalding & Sarjeant 2012). Theropod tracks from the Lower Cretaceous sandstones of Paraíba in north-eastern Brazil were, for instance, considered by Amerindians to pertain to giant running birds (Leonardi 1984; Mayor & Sarjeant 2001). Likewise, a set of theropod tracks visible on Cenomanian limestone in the south of Algeria was believed by Arabs to belong to a giant ostrich, property of a venerated man buried nearby (Taquet 2010).

The first published record of a theropod bone is of an incomplete left femur described and figured by Robert Plot in his 1677 'Natural History of Oxfordshire' (Figure 2A). The fossil was dug up from a quarry in the Parish of Cornwell, Oxfordshire, and probably pertains to the megalosaurid *Megalosaurus* (Delair & Sarjeant 1975, 2002). Plot (1677) correctly identified the bone as a distal femoral condyle (*capita femoris inferiora*), and wondered whether this partial femur belonged to an elephant brought to Britain by the Romans. Plot (1677), however, noted many differences with the femur of elephants and instead referred the bone to a human giant also brought by the Romans (Evans 2010). This

portion of femur was reillustrated by English naturalist Richard Brookes (1763) who labeled the figure 'Scrotum Humanum', given the superficial similarity of the distal condyle to human testicles (Figure 2B). Although this binomial term was clearly used as a descriptive appellation by Brookes (Spalding & Sarjeant 2012), some have proposed its use as a valid scientific name. That would make 'Scrotum Humanum' the first formal binomial name given to a dinosaur and a senior synonym of *Megalosaurus bucklandii* (Halstead 1970; Delair & Sarjeant 1975), a proposition which was rejected by the International Zoological Commission (Halstead & Sarjeant 1993; Delair & Sarjeant 2002).

Isolated theropod teeth were first described and figured in 1699 by Welsh naturalist Edward Lhuyd in his catalogue of fossils and minerals *Lithophylacii Britannici Ichnographica* (Lhuyd 1699). The specimen number 1328 (Lhuyd 1699, plate 16), originally ascribed to a fish by Lhuyd (1699), corresponds to an isolated tooth from the Middle Jurassic Great Oolite of Stonesfield (Figure 2C). This shed tooth greatly resembles *Megalosaurus* and most likely belongs to that taxon (Delair & Sarjeant 2002). Additional theropod findings reported in the 18th century include a limb bone from Stonesfield labeled specimen a.1 by John Woodward (1729) in his catalogue of British fossils from his personal collection. This section of limb bone is currently preserved in the Sedgwick Museum of Cambridge (specimen D.30.1) and, once again, likely pertains to *Megalosaurus* (Delair & Sarjeant 1975, 2002). It may, therefore, be the earliest-discovered bone that can still be identified as belonging to a theropod with confidence (Delair & Sarjeant 1975, 2002). Later, an incomplete femur described and illustrated by Platt (1758) was identified as belonging to a hippopotamus, a rhinoceros, or an unknown animal of large size (Figure 2D). This large femur, which is also from Stonesfield, was recently referred to *Megalosaurus bucklandii* (Evans 2010).

The first theropod taxon to be recognized as reptilian and formally described in the literature is, in fact, *Megalosaurus*, coined by William Buckland in 1824 (although the generic name was already announced by James Parkinson in 1822). Material originally ascribed to *Megalosaurus* included a right dentary with a well-preserved erupted tooth (Figure 2E), ribs, hind-limb elements, pelvic bones, and sacral

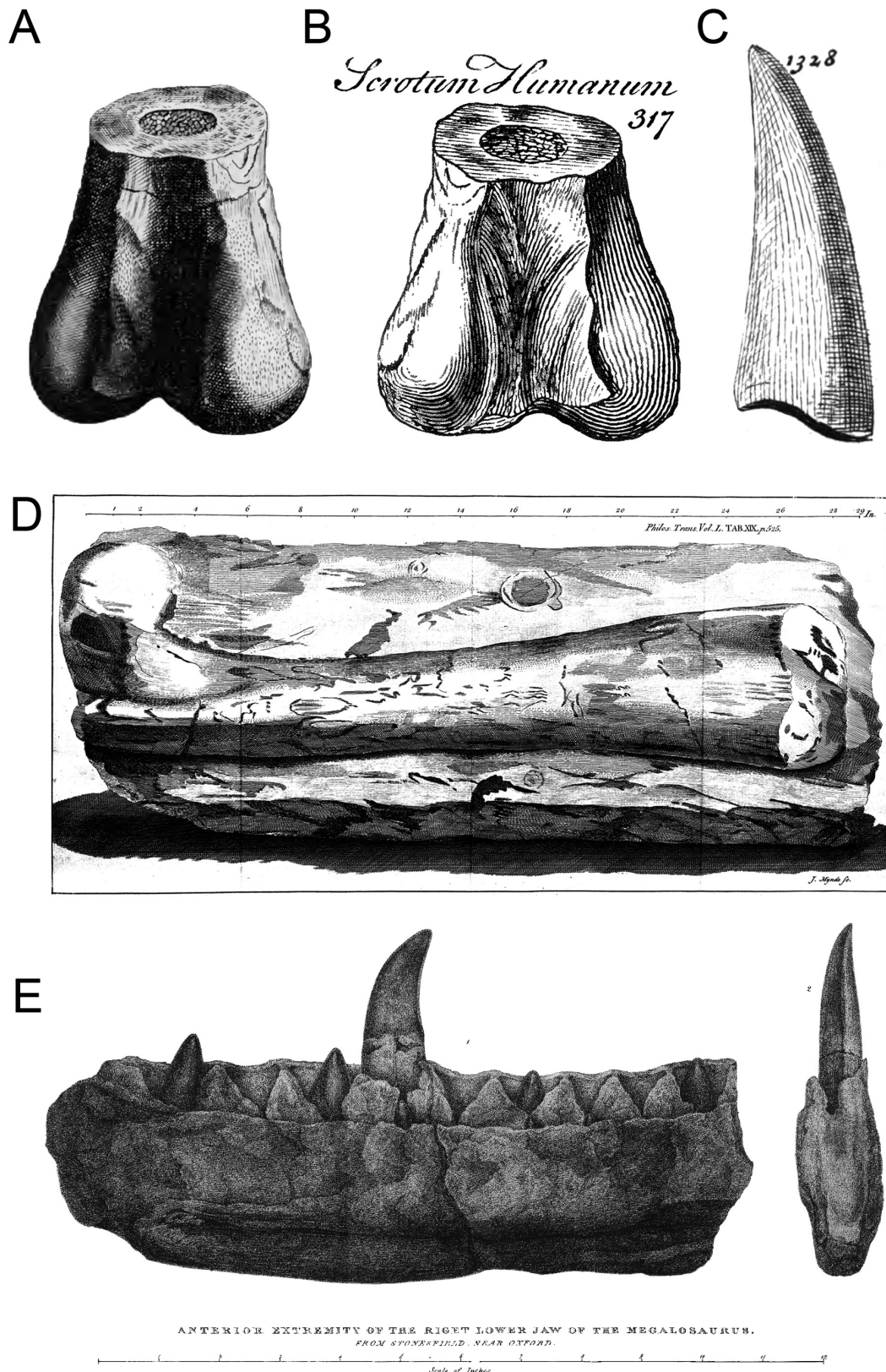


Figure 2. Earliest historical records of theropod remains in the world. A-B) Distal part of a left femur of *Megalosaurus* from Cornwell, U.K., in posterior view, and first reported by Plot (1677); A, illustrations by Plot (1677, table 8, fig.4); and B, Brookes (1763, p. 312, figure 317) showing the label 'Scrotum Humanum'; C) Isolated theropod tooth (likely *Megalosaurus*) from the Stonesfield, U.K., illustrated by Lhuys (1699, table 16, figure 1328); D) Right femur of *Megalosaurus* from Stonesfield, U.K., in anterior view, illustrated by Platt (1758, table 19); E) Right dentary of *Megalosaurus bucklandii* from Stonesfield, U.K., in medial and posterior views, illustrated by Buckland (1824, plate 40).

and caudal vertebrae, all collected in the Taynton Limestone Formation (middle Bathonian) of Stonesfield, Oxfordshire. As Buckland (1824) did not provide a species name for *Megalosaurus*, the type species *Megalosaurus conybeari* was proposed by Ferdinand von Ritgen in 1826 (von Ritgen 1826). This author failed to provide a description and diagnosis for the species, allowing Mantell (1827) to be the first scientist to name and diagnose a theropod species, i.e., *Megalosaurus bucklandii*, which is the name currently accepted by the scientific community.

Streptospondylus altdorfensis (Meyer 1832) and *Poekilopleuron bucklandii* (Eudes-Deslongchamps 1837) from France were the first non-avian theropods to be described in the literature outside England, and the second and third Mesozoic theropods to be formally named. These two megalosauroids, considered valid species (Carrano *et al.* 2012), are only known from post-cranial remains. The material of *Streptospondylus*, discovered in the Callovian Vaches Noires cliffs around 1770, was mixed with crocodylian remains, and interpreted as a crocodile by Cuvier (1808, 1812, 1824). The remains of *Poekilopleuron* from the Calcaire de Caen Formation (middle Bathonian) in Caen, Normandy, were correctly identified as belonging to a large reptile closely related to *Megalosaurus*. Unfortunately, the material was lost during World War II and, besides the original illustrations provided by Eudes-Deslongchamps (1837), only casts of some bones remain (Allain & Chure 2002).

Although Buckland (1824) and Mantell (1827) were the first to give a relatively good description of the dentition of *Megalosaurus*, Richard Owen was the first scientist to exhaustively investigate the tooth anatomy of theropods and many other vertebrates. In his treatise on vertebrate teeth, 'Odontography' (Owen 1840-1845), and his richly illustrated four volume 'A History of British Fossil Reptiles' (Owen 1849-1884), Owen provided a comprehensive description and illustration of the crowns, denticles, and internal structure of the teeth of *Megalosaurus bucklandii* and *Suchosaurus cultridens*. The latter was erected by Owen (1840-1845) based on isolated teeth from the Wealden of Tilgate Forest, near Cuckfield (Sussex). Interestingly, the teeth of *Suchosaurus* were discovered by Mantell, and were first described and illustrated by Mantell (1822) and Cuvier (1824), respectively (Buffetaut 2010). Cuvier (1824), Mantell (1827,

1833), and Owen (1840-1845; 1849-1884) all referred these isolated teeth to crocodylians, yet they closely resemble those of the spinosaurid *Baryonyx walkeri* discovered much later. *Suchosaurus* teeth are now considered as belonging to either *Baryonyx* or an unnamed member of Baryonychinae (Milner 2003; Buffetaut 2007; Mateus *et al.* 2011).

The first non-megalosauroid theropod to be formally described is *Nuthetes destructor* from the Purbeck Formation (Berriasian, Early Cretaceous) of Durlston Bay, Dorset. This tentative dromaeosaurid was erected by Owen (1854) based on an incomplete dentary and some isolated teeth originally assigned to a lizard or a varanid (Milner 2002). A few years later, *Compsognathus longipes* (Wagner 1861), from the Solnhofen Limestone of Germany, was the first non-avian theropod preserving a nearly complete and slightly disarticulated skull and skeleton to be reported in the literature. This theropod was discovered in Germany around 1859 (Wellnhofer 2008) and was reported by Wagner (1859) the same year. It remained one of the most completely known theropods for more than a century (Ostrom 1978).

After Europe, North America became the second continent to yield theropod remains described by paleontologists. The first theropod fossils reported were isolated teeth discovered in 1855 by eminent American scientist Ferdinand Vandiveer Hayden from the Upper Cretaceous of Montana, at the confluence of the Missouri and Judith rivers (Breithaupt 1999). The dental material was briefly described one year later by Leidy (1856) who erected two new species, *Deinodon horridus* based on several fragment of teeth (Figure 3A) and *Troodon formosus* based on a single shed tooth (Figure 3B). *Troodon* and *Deinodon* were originally thought to belong to a 'lacertian' (a large Monitor according to Leidy 1860) and a relative of *Megalosaurus*, respectively (Leidy 1856, 1860). *Troodon* is now considered to be a valid species of troodontid (Currie 1987), whereas *Deinodon* has been recognized as belonging to an unidentified tyrannosaurid, probably *Albertosaurus* known from the same deposits (Breithaupt 1999; Breithaupt & Elizabeth 2008).

Shortly after Leidy's description of theropod teeth from North America, the Reverend Stephen Hislop (1861, 1864) reported the discovery of isolated theropod teeth from the Upper

Cretaceous of India. One of them was discovered by Mr. Rawes in the locality of Takli, in the Nagpur area of Maharashtra, and represents the earliest historical record of theropod dinosaurs in Asia (Carrano *et al.* 2010). The shed tooth was sent to the Geological Society's Museum of London (which is now part of the Natural History Museum) and studied and illustrated by English naturalist Richard Lydekker (1879, 1885, 1890; Figure 3C). Although the latter recognized the theropod affinity of the tooth, he assigned it to a new species of basal sauropodomorph, *Masospondylus rawesi* (Lydekker 1890). The tooth was later referred to *Megalosaurus* (Vianey-Liaud *et al.* 1988) and is currently assigned to an indeterminate theropod, almost certainly an abelisaurid (Carrano *et al.* 2010, 2012; C.H. pers. obs.).

In the span of a decade, between the latest part of the 19th century and the first part of the 20th century, theropod skeletal material was reported on three continents of the Southern Hemisphere, Africa, South America and Australia. The French were the first to collect and describe material belonging to Gondwanan theropods. The first definitive theropod skeletal remains to be reported in the Southern Hemisphere, in fact, belong to the well-known abelisaurid *Majungasaurus crenatissimus* unearthed in the Maevarano Formation (Maastrichtian) of Madagascar. The species was erected as *Megalosaurus crenatissimus* by French paleontologist Charles Depéret in 1896, based on fossils collected by Mr. Landillon in the Mahajanga Basin one year before (Depéret 1896a, b; Krause *et al.* 2007). Nevertheless, theropod tracks discovered in Cenomanian limestone in the Jebel Bou-Khail (near the city of Laghouat), Algeria, by French geologist G. Le Mesle were already reported by Le Mesle & Peron (1880; Figure 3D) sixteen years before, and account for the first described theropod material from Africa (Taquet 2010; Chabou *et al.* 2015). Almost twenty years later, a theropod vertebra and isolated teeth assigned to Spinosauridae were discovered in the Djoua country (near Timassanine), Algeria, during a mission led by French officer François Lami and explorer Fernand Foureau in 1898 (Buffetaut 2010; Taquet 2010). Based on the material collected by the latter, French paleontologist Emile Haug (1904, 1905) reported on and illustrated the first skeletal material of a theropod (and a dinosaur) from the Sahara,

though the teeth were interpreted as belonging to an ichthyodectid fish (Buffetaut 2005, 2010).

The first theropod material to be reported in South America was an isolated tooth described by famous Argentinian paleontologist Florentino Ameghino in 1899 (Ameghino 1899; Coria & Salgado 1996; Figure 3E-F). Based on this fragmentary tooth and a partial femur found in the Upper Cretaceous of Par-Aik, Shehuen River, Santa Cruz Province of Argentina, Ameghino erected the taxon *Loncosaurus argentes* which was initially classified as a megalosaurid (Ameghino 1899). Although the partial tooth most likely belongs to a theropod, the femur of *Loncosaurus* is that of an ornithopod (Coria & Salgado 1996). *Genyodectes serus*, named and described by Woodward only two years later, is the first valid theropod (and dinosaur) to be reported from Argentina (Woodward 1901; Rauhut 2004b). Until the 1970s, this ceratosaurid remained one of the most complete theropods known from that continent (Rauhut 2004b).

Theropod material is scarcer in Oceania, yet the first representative fossil was reported in Australia by the beginning of the 20th century (Agnolín *et al.* 2010). Woodward (1906) described a theropod ungual unearthed from Cape Patterson, on the south coast of Victoria (Figure 3G). This claw, the first dinosaur material reported from Australia, was collected by Mr. W. H. Ferguson in the Wonthaggi Formation (early Aptian; Agnolín *et al.* 2010). The pedal ungual was initially thought to be from a taxon closely related to *Megalosaurus*, and sometimes as *Megalosaurus* itself (Woodward 1906; Huene 1926a). It is now considered an indeterminate theropod (Agnolín *et al.* 2010; Carrano *et al.* 2012). Four years later, Woodward (1910) briefly reported the discovery of a tooth and a posterior caudal vertebra of what he assumed to be a small megalosaurian theropod. The material was found by T.C. Wollaston and comes from the Grimman Creek Formation (Albian) of Lightning Ridge near Walgett, New South Wales. Huene (1932) described and referred the vertebra to the new taxon *Walgettosuchus woodwardi*, an indeterminate theropod currently considered a *nomen dubium* (Agnolín *et al.* 2010).

Antarctica is the last continent to have yielded non-avian theropod material. The first discovery of theropod remains occurred in 1988

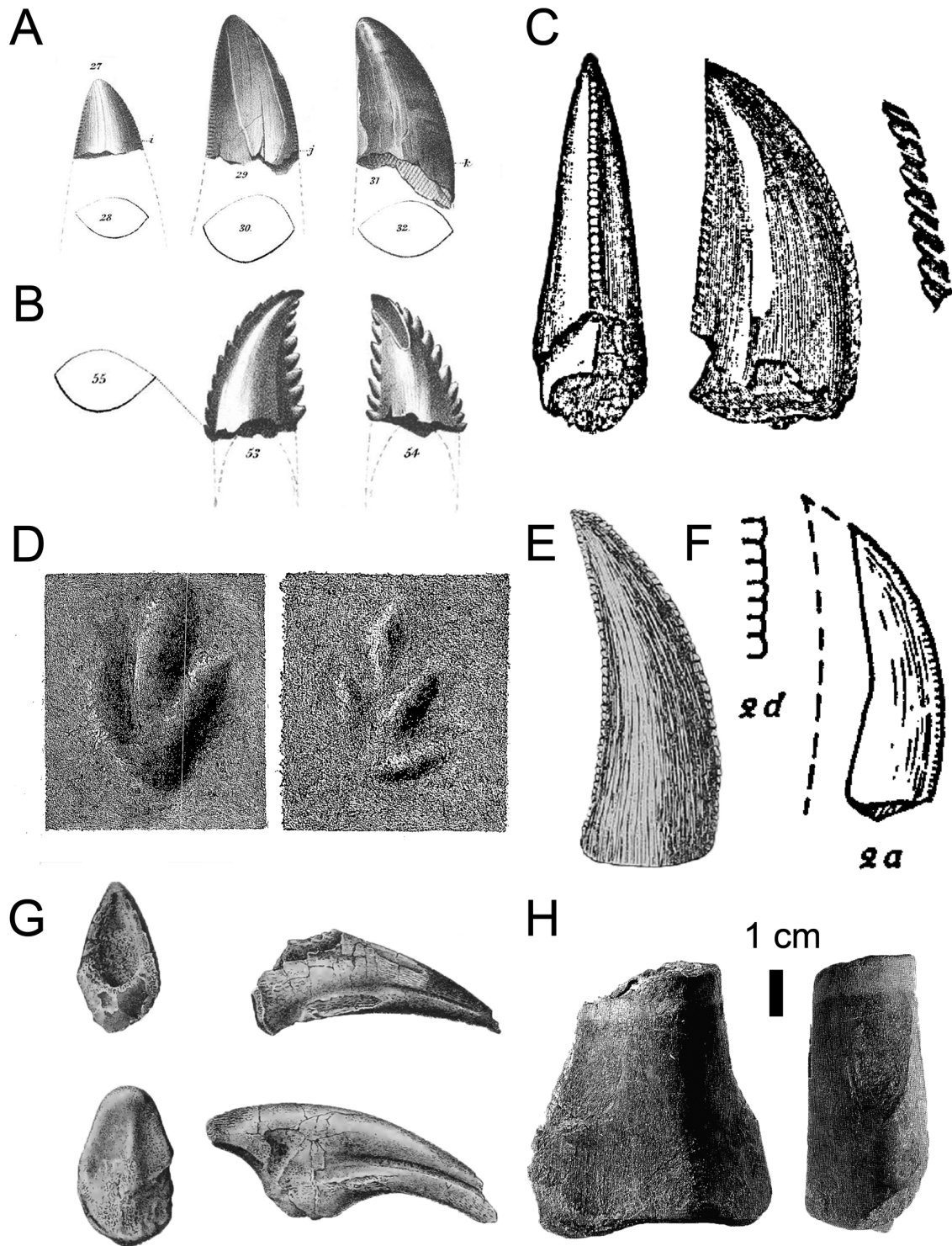


Figure 3. Earliest historical records of theropod remains in A-B, North America; C, Asia; D, Africa; E-F, South America; G, Oceania; and H, Antarctica. Isolated teeth of: A) *Troodon formosus*; and B) *Deinodon horridus* (= *Albertosaurus sarcophagus*) from the Upper Cretaceous Judith River of Colorado and first reported by Leidy (1856; modified from Leidy 1860, plate 9); C) Isolated theropod tooth of '*Massospondylus rawesi*', an abelisaurid from the Upper Cretaceous of India (localities of Takli and Maleri) first reported by Hislop (1861, 1864, illustration by Lydekker 1890, fig. 1); D) Casts of theropod tracks from the Upper Cretaceous of Jebel Bou-Khail, Algeria, and first reported by Le Mesle and Peron (1880; illustration by Mesle & Peron 1880, figures 65 and 66); E-F) Isolated theropod tooth from the Upper Cretaceous of Par-Aik, Argentina, referred to *Loncosaurus argentineus* and first reported by Ameghino (1899); E, illustration by Ameghino (1900, p. 160) and Ameghino (1906, Figure 8); and F, Huene (1929a, plate 41); G) Pedal ungual of an indeterminate theropod from the Upper Cretaceous of Cape Patterson, Australia, and first reported by Woodward (1906); H) Distal part of a tibia of a megalosauroid? theropod from the Upper Cretaceous of Col Crame, Antarctica, discovered in 1988 (modified from Molnar *et al.* 1996).

when Agelandro Lopez Angriman found the distal part of a tibia in the Coniacian-Santonian Hidden Lake Formation of Antarctica (Molnar *et al.* 1996; Figure 3H). The bone, known as the Hidden Lake specimen (Carrano *et al.* 2012), comes from the north of Col Crame in the Cape Lachman region, north-western James Ross Island. This tibia was assigned to an indeterminate tetanuran by Molnar *et al.* (1996), and to a megalosauroid by Carrano *et al.* (2012), which makes it the latest surviving member of this clade found to date. Although the Hidden Lake specimen was the first theropod material to be found in Antarctica, this partial tibia was only described in 1996, and the first theropod to be reported in the literature is, in fact, *Cryolophosaurus ellioti*, described by Hammer and Hickerson (1994) two years earlier. *Cryolophosaurus* material was collected during the 1990-1991 and 2003-2004 field seasons, and this taxon is the most complete theropod from Antarctica, one of the largest from the Early Jurassic, and possibly one of the earliest tetanurans hitherto discovered (Smith *et al.* 2007; Carrano *et al.* 2012).

History of Classification

The clade Dinosauria was erected as a tribe (or a sub-order) by Richard Owen in 1842 to contain three taxa of large reptiles, *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*. Owen (1842) did not include the already named theropods *Poekilopleuron*, *Streptospondylus*, and *Suchosaurus*, all considered to be crocodylian taxa at the time. 'Goniopoda' was the first clade of dinosaurs to gather two valid theropod dinosaurs. This order was erected by Edward Drinker Cope in 1866 to encompass *Laelaps* (now known as *Dryptosaurus*; Brusatte *et al.* 2011) and 'probably' *Megalosaurus*. 'Goniopoda' was, by then, opposed to the 'Orthopoda' consisting of *Scelidosaurus*, *Hylaeosaurus*, *Iguanodon*, and *Hadrosaurus* (Cope 1866).

Although the taxa 'Goniopoda' and 'Orthopoda' were used in Matthew & Brown's (1922) classification of theropods in the 20th century, these two groups were abandoned in favor of clades coined by Othniel Charles Marsh by the end of the 19th century. Marsh (1881) first erected the taxon Theropoda to contain the family Allosauridae, initially represented by the North American genera *Allosaurus*, *Creosaurus*, and *Labrosaurus*. The term 'Theropoda' derived

from the old Greek words *θηρίον*, *thérion* meaning 'wild beast, animal', and *ποδος*, *pous*, *podos* meaning 'foot'. Theropods, with 'beast feet' were, at that time, separated from ornithopods, meaning 'bird feet', and sauropods, meaning 'reptile feet', which were coined by Marsh in 1871 and 1878, respectively. A year after naming the taxon Theropoda, Marsh (1882) already included six 'families' in this clade, namely Megalosauridae, Zancloodontidae, Amphisauridae, Labrosauridae, Coeluridae, and Compsognathidae. A few years later, Seeley (1887) used the orientation and morphology of the pubis to divide the clade of Dinosauria into two major groups, the Saurischia and the Ornithischia. Theropods and sauropodomorphs were grouped among saurischian dinosaurs with reptile-like pelvises, whereas ornithischians with bird-like pelvises included Stegosauria and Ornithopoda. Ironically, saurischian theropods with beast-like feet and a reptile-like pelvis ultimately give rise to birds, instead of the ornithischians with a bird-like pelvis, and the ornithopods with bird-like feet. By the end of the 19th century, four currently valid theropod clades (Ceratosauridae, Megalosauridae, Compsognathidae, Omithomimidae), two sauropodomorph (Plateosauridae, Anchisauridae) and four unrecognized archosaur clades (i.e., Labrosauridae, Dryptosauridae, Coeluridae, and Hallopidae) were gathered into Theropoda by Marsh (1895, 1896).

The classification of theropods was markedly affected by the work of German paleontologist Friedrich von Huene (1909, 1914a, b, 1923, 1926a, b, 1929b, 1932) in the first half of the 20th century. Up until 1932, Huene ignored the name Theropoda and erected two new clades to encompass all saurischian dinosaurs, Coelurosauria and 'Pachypodosauria'. In Huene's earlier classifications, coelurosaurs comprised theropods such as *Coelophysus*, *Ceratosaurus*, *Compsognathus*, *Proceratosaurus*, *Tyrannosaurus*, and *Ornithomimus*, whereas pachypodosaurians included the Carnosauria, consisting of *Megalosaurus*, *Spinosaurus*, and *Allosaurus* (formerly known as *Antrodemus*), as well as the Prosauropoda and the Sauropoda, two clades currently classified as sauropodomorphs. In the 1930s, Huene (1932) modified his view on theropod systematics and abandoned the taxon 'Pachypodosauria'. At that time, saurischian dinosaurs included Coelurosauria, Carnosauria, Prosauropoda, and Sauropoda, and the separa-

tion between coelurosaurs and carnosaurs was mostly based on size (Rauhut 2003a). Among carnivorous saurischians, coelurosaurs were assigned to relatively small, slenderly built, predaceous theropod clades such as Coelophysidae (formerly known as 'Podokesauridae'), Compsognathidae, and Ornithomimidae, whereas carnosaurs encompassed large, heavily built predators with massive skulls such as Megalosauridae, Spinosauridae, Tyrannosauridae (formerly known as 'Dinodontidae'), and Allosauridae (Huene 1932).

In the beginning of the second half of the 20th century, Alfred Sherwood Romer, in his authoritative book 'Osteology of the Reptiles', (1956) proposed a slightly modified version of the saurischian classification. Romer separated saurischian dinosaurs into Theropoda and Sauropoda, and included all bipedal saurischians within theropods, including Prosauropoda, Coelurosauria, and Carnosauria. Romer adopted the size criteria followed by Huene (1932) and restricted carnosaurs to Teratosauridae (now considered to be a clade of rauisuchian archosaurs; e.g., Benton 1986), Megalosauridae (represented at that time by theropods such as *Ceratosaurus*, *Megalosaurus*, *Spinosaurus*, *Allosaurus*, *Carcharodontosaurus*, and *Proceratosaurus*), and Tyrannosauridae. From the 1960s to the beginning of the 1980s, authors working on theropods, including Walker (1964), Colbert (1964), Colbert & Russell (1969), Ostrom (1976a), and Russell (1984) did not deviate significantly from the classification scheme of Romer (1956). Most of them, however, did acknowledge that coelurosaurs and carnosaurs were likely to be grades rather than clades (Thulborn 1984). A few authors like Ostrom (1972), Barsbold (1977), Welles (1984) and Carroll (1988) abandoned the size-based dichotomy between coelurosaurs and carnosaurs, and Barsbold (1977) included newly erected clades such as Oviraptorosauria (with Oviraptoridae), Deinonychosauria (with Dromaeosauridae and Troodontidae, formerly known as 'Saurornithoididae'), and Therizinosauria (formerly known as 'Deinocheirosauria' by Barsbold, 1977, then 'Segnosauria' by Barsbold and Perle, 1980) among theropods.

The adoption in the early 1980s of phylogenetic methodology developed by German entomologist Willi Hennig (1950) in the beginning of the second half of the 20th century, was a major step in the history of theropod systemat-

ics, and the results of those cladistic analyses radically changed prevailing views on theropod phylogeny. Thulborn (1984) was the first to investigate theropod interrelationships through a cladistic approach by addressing the systematics of *Archaeopteryx* and other stem-group birds. Gauthier's (1986) work on saurischian interrelationships was the first to outline the current phylogenetic classification of non-avian theropods. Based on a cladistic analysis performed on a data matrix of 84 characters, the American paleontologist confirmed the monophyly of dinosaurs and corroborated Seeley's idea that Sauropodomorpha and Theropoda were sister-groups within Saurischia. Gauthier (1986) recovered Theropoda as a well-supported clade divided into Ceratosauria and Tetanurae, and provided the modern phylogenetic definition of theropods as birds and all saurischians closer to birds than to sauropodomorphs. He recognized a dichotomy between Carnosauria and Coelurosauria within tetanuran theropods, and erected the clade Maniraptora to encompass coelurosaurs more derived than Ornithomimidae. At that time, Ceratosauria contained *Coelophysis*, *Dilophosaurus*, and *Ceratosaurus*, carnosaurs included *Allosaurus*, *Acrocanthosaurus* and tyrannosaurids, and non-avian coelurosaurs comprised *Compsognathus*, *Ornitholestes*, and the Ornithomimidae, Caenagnathidae, and Deinonychosauria (Gauthier 1986).

Since the pioneering work of Gauthier (1986), the availability of parsimony-based phylogenetic software has enabled a large number of authors to investigate theropod interrelationships via cladistic analysis, resulting in major revisions to theropod systematics. Novas (1992) was the first to include abelisaurids and tyrannosaurids among ceratosaurs and coelurosaurs, respectively (Rauhut 2003a), and Holtz (1994) was the first major phylogenetic analysis that recovered the clade Avetheropoda (erected by Paul 1988 and also known as 'Neotetanurae'; Table 1) to include Allosauridae and Coelurosauria (Figure 4). The same year, Sereno *et al.* (1994) found that Megalosauroidea (formerly known as 'Torvosauroidae' and 'Spinosauroidae') formed the sister group of Avetheropoda and was divided into Megalosauridae (formerly known as 'Torvosauridae') and Spinosauridae (Figure 4). Two years later, Sereno *et al.* (1996) found the new clade Allosauroidae (also termed 'Carnosauria' *sensu* Padian *et al.* 1999), which

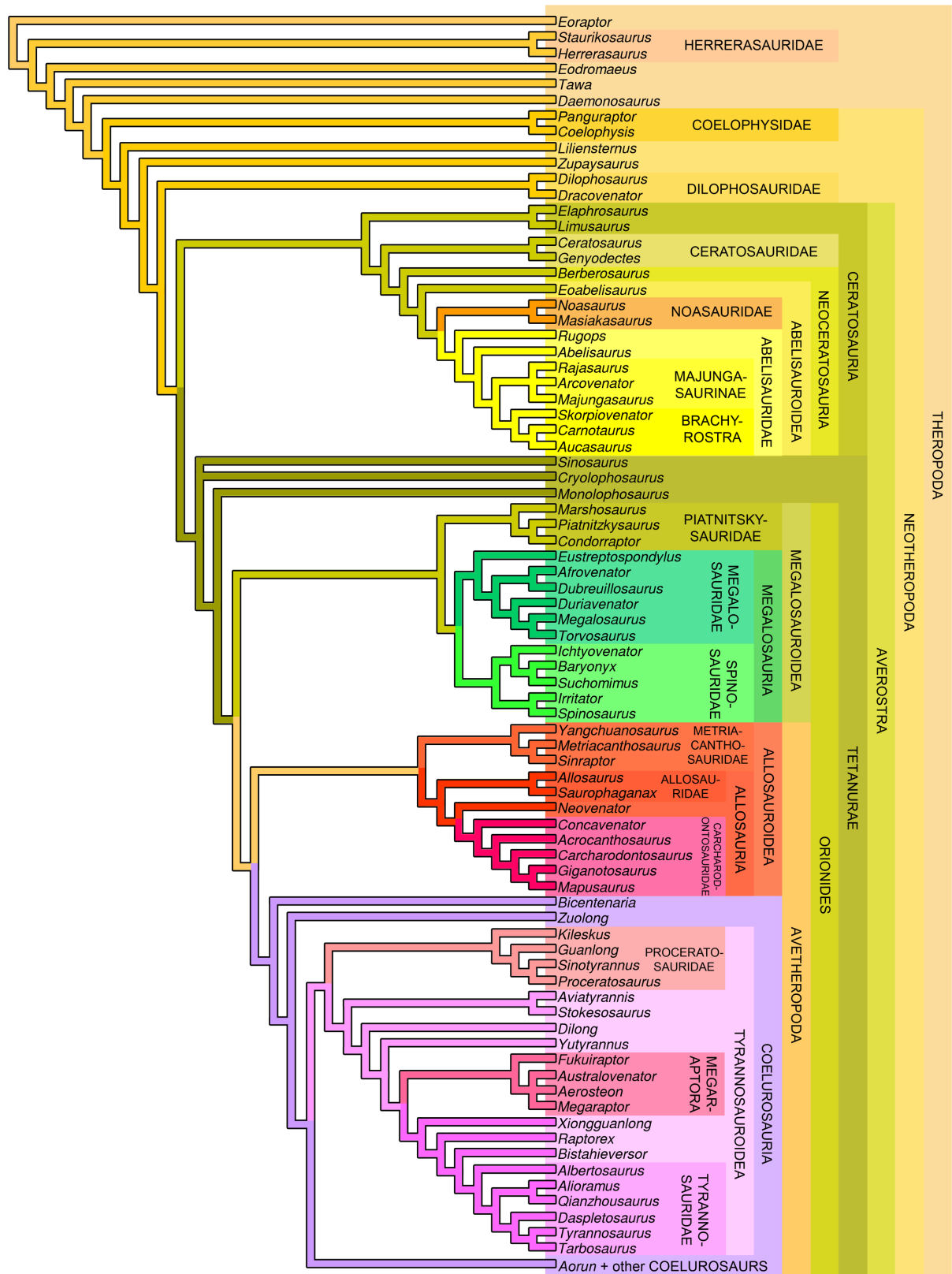


Figure 4. Cladogram of basal Theropoda showing the relationships of tyrannosauroids and non-coelurosaur theropods. The phylogenetic classification follows the results of the cladistic analyses obtained by Sues *et al.* (2011) for non-neotheropod Theropoda, Smith *et al.* (2007) and Ezcurra & Brusatte (2011) for non-averostran Neotheropoda, Pol & Rauhut (2012) and Tortosa *et al.* (2014) for Ceratosauria, Carrano *et al.* (2012) for non-coelurosaur Tetanurae, Loewen *et al.* (2013), Lü *et al.* (2014) and Porfiri *et al.* (2014) for Tyrannosauroidea, and Choiniere *et al.* (2014b) for basalmost Coelurosauria.

gathered *Allosaurus*, Sinraptoridae, and Carcharodontosauridae, to be the sister-group of Coelurosauria. Following these preliminary analyses, Sereno's (1997, 1998, 1999) major phylogenetic analyses of dinosaurs proceeded to define major theropod clades such as Neotheropoda, Coelophysoidea, Megalosauroida, Allosauroida, Tyrannosauroida, Ornithomimosauria ('Ornithomimoidea' *sensu* Sereno 1998), Therizinosauroida, Paraves, and Deinonychosauria (Figure 5).

Subsequent studies on theropod systematics, whose results are summarized by Holtz (1998), Rauhut (2003a), Senter (2007), Carrano & Sampson (2008) and Carrano *et al.* (2012), better resolved the relationships of non-avian theropods and defined additional clades such as Noasauridae (Coria & Salgado 1998), Piatnitzkysauridae (Carrano *et al.* 2012), Megaraptora (Benson *et al.* 2010), and Proceratosauridae (Rauhut *et al.* 2010; Figures 4-5). In 2015, the current consensus on non-avian theropod classification is based on the results of the most recent large scaled phylogenetic analyses obtained by Sues *et al.* (2011) for non-neotheropod Theropoda, Smith *et al.* (2007) and Ezcurra & Brusatte (2011) for non-averostran Neotheropoda, Pol & Rauhut (2012) and Tortosa *et al.* (2014) for Ceratosauria, Carrano *et al.* (2012) for non-coelurosaur Tetanurae, Loewen *et al.* (2013), Lü *et al.* (2014; which is based on Brusatte *et al.*, 2010d) and Porfiri *et al.* (2014) for Tyrannosauroida, and Godefroit *et al.* (2013a), Choiniere *et al.* (2014b) and Brusatte *et al.* (2014; the most updated version of the Theropod Working Group (TWIG) dataset) for non-tyrannosauroid Coelurosauria (Figures 4-5).

As noted by Turner *et al.* (2012), Theropoda is now comprised of numerous well-supported 'family' or 'super-family'-level subclades that form a pectinate, ladder-like organization, with each rung corresponding to a node-based clade that has not always received a name. Although the relationships between most theropod clades are currently well understood, several aspects of theropod systematics remain controversial. Current debate occurs over the phylogenetic placement of *Eoraptor* and/or herrerasaurids within non-theropod saurischians (*e.g.*, Langer & Benton 2006; Alcober & Martinez 2010; Ezcurra 2010; Martinez *et al.* 2011; Sereno *et al.* 2013) or at the base of Theropoda (Nesbitt *et al.* 2009; Ezcurra & Brusatte 2011; Nesbitt 2011;

Sues *et al.* 2011; Langer & Ferigolo 2013; Figure 4), and over the monophyly or paraphyly of Coelophysoidea (*i.e.*, Coelophysidae + Dilophosauridae; *e.g.*, Tykoski 2005; Yates 2005; Ezcurra & Cuny 2007; Ezcurra & Novas 2007; Smith *et al.* 2007; Nesbitt *et al.* 2009; Ezcurra & Brusatte 2011; Xing 2012), and Deinonychosauria (*i.e.*, Dromaeosauridae + Troodontidae; *e.g.*, Senter 2011; Turner *et al.* 2012; Godefroit *et al.* 2013a, b; Brusatte *et al.* 2014; Choiniere *et al.* 2014b; Foth *et al.* 2014; Tsuihiji *et al.* 2014). Recent debate also focuses on the position of megaraptorans within neovenatorid allosauroids (Benson *et al.* 2010; Carrano *et al.* 2012) or among tyrannosauroid coelurosaurs (Novas *et al.* 2013; Porfiri *et al.* 2014; Figure 4).

Current Classification

First Theropods

Theropoda can be defined as the most inclusive clade containing the house sparrow *Passer domesticus* (Linnaeus 1758) but not the titanosaurid sauropod *Saltasaurus loricatus* Bonaparte & Powell 1980 (Sereno 2005; Table 1 [see appendix]). Regardless of the status of inclusion of *Eoraptor* and herrerasaurids within Theropoda, the oldest definitive theropod remains come from the mid-Carnian (early Late Triassic; ~231 Ma) of Argentina (Figure 1). Similar in age to *Eoraptor lunensis* (Sereno *et al.* 2013; Figure 6A) and the herrerasaurids *Herrerasaurus ischigualastensis* (Sereno & Novas 1994; Figure 6B) and *Sanjuansaurus gordilloi* (Alcober & Martinez 2010), the oldest unquestioned theropod taxon *Eodromaeus murphi* (Martinez *et al.* 2011) is from the Ischigualasto Formation of San Juan Province. *Eodromaeus*, *Eoraptor* and herrerasaurids were small to large sized (1-6m long; Sereno & Novas 1992) bipedal saurischians with relatively elongated skulls. These primitive saurischians retained the ancestral dinosauriform habit of obligate bipedality and the ziphodont dentition present in more primitive archosauriforms (Holtz *et al.* 1998; Barrett *et al.* 2010; Holtz 2012), leading to their consideration as carnivorous dinosaurs. Nevertheless, *Eoraptor*, recently interpreted to be a basal sauropodomorph (Martinez *et al.* 2011; Sereno *et al.* 2013), exhibits constricted crowns and pointed denticles that suggest that this primitive saurischian, as well as the first dinosaurs, might have been omnivorous (Barrett *et*

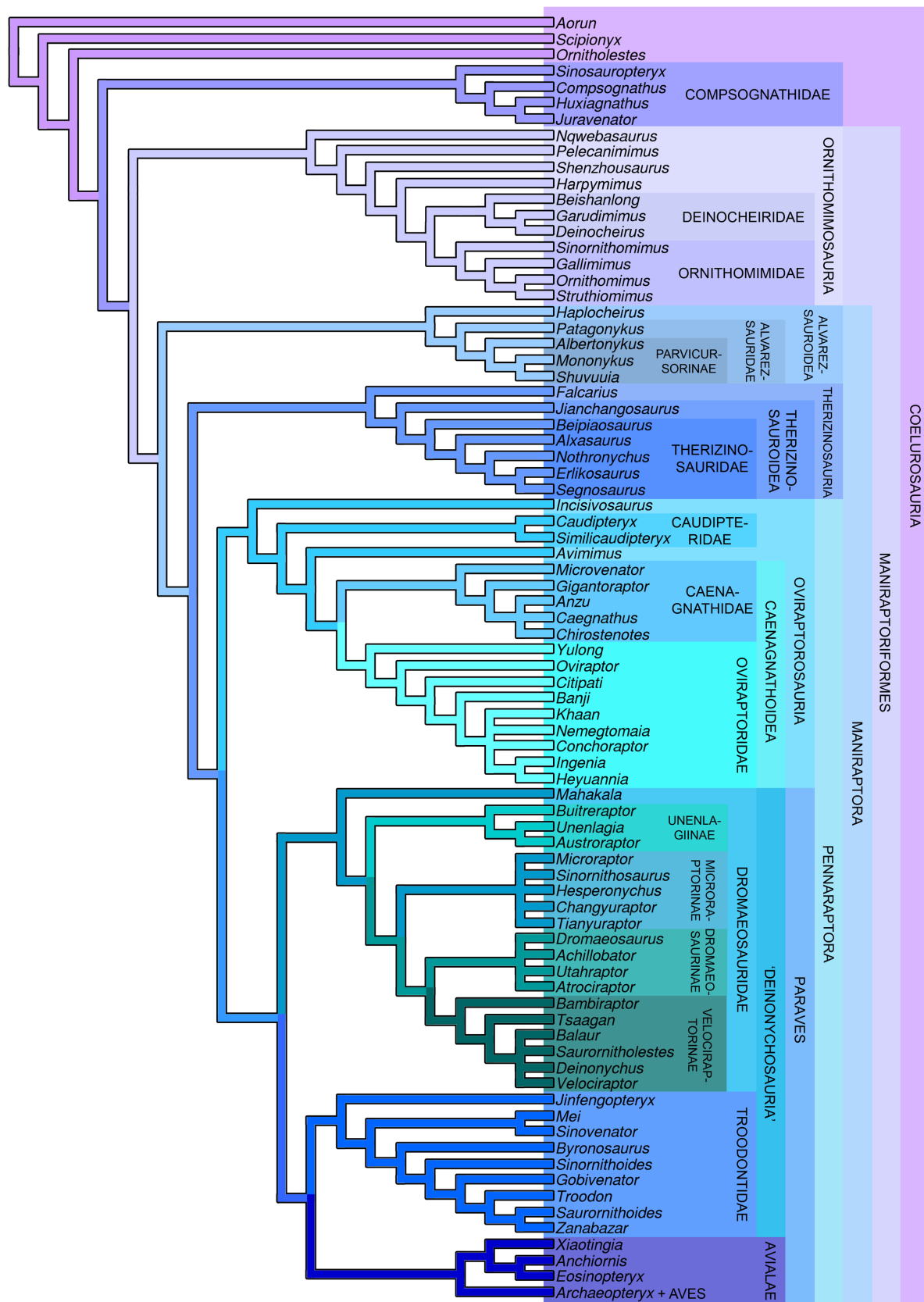


Figure 5. Cladogram of non-tyrannosauroid Coelurosauria showing the relationships of compsognathids and maniraptoriforms. The phylogenetic classification follows the results of the cladistic analyses obtained by Choiniere *et al.* (2014b) for basalmost Coelurosauria and Compsognathidae, Longrich & Currie (2009a) and Choiniere *et al.* (2010b) for Alvarezsauridae, Lee *et al.* (2014) for Ornithomimosauria, Senter *et al.* (2012a) and Pu *et al.* (2013) for Therizinosauria, Lamanna *et al.* (2014) for Oviraptorosauria, Turner *et al.* (2012) for Paraves, and Foth *et al.* (2014) for Avialae.

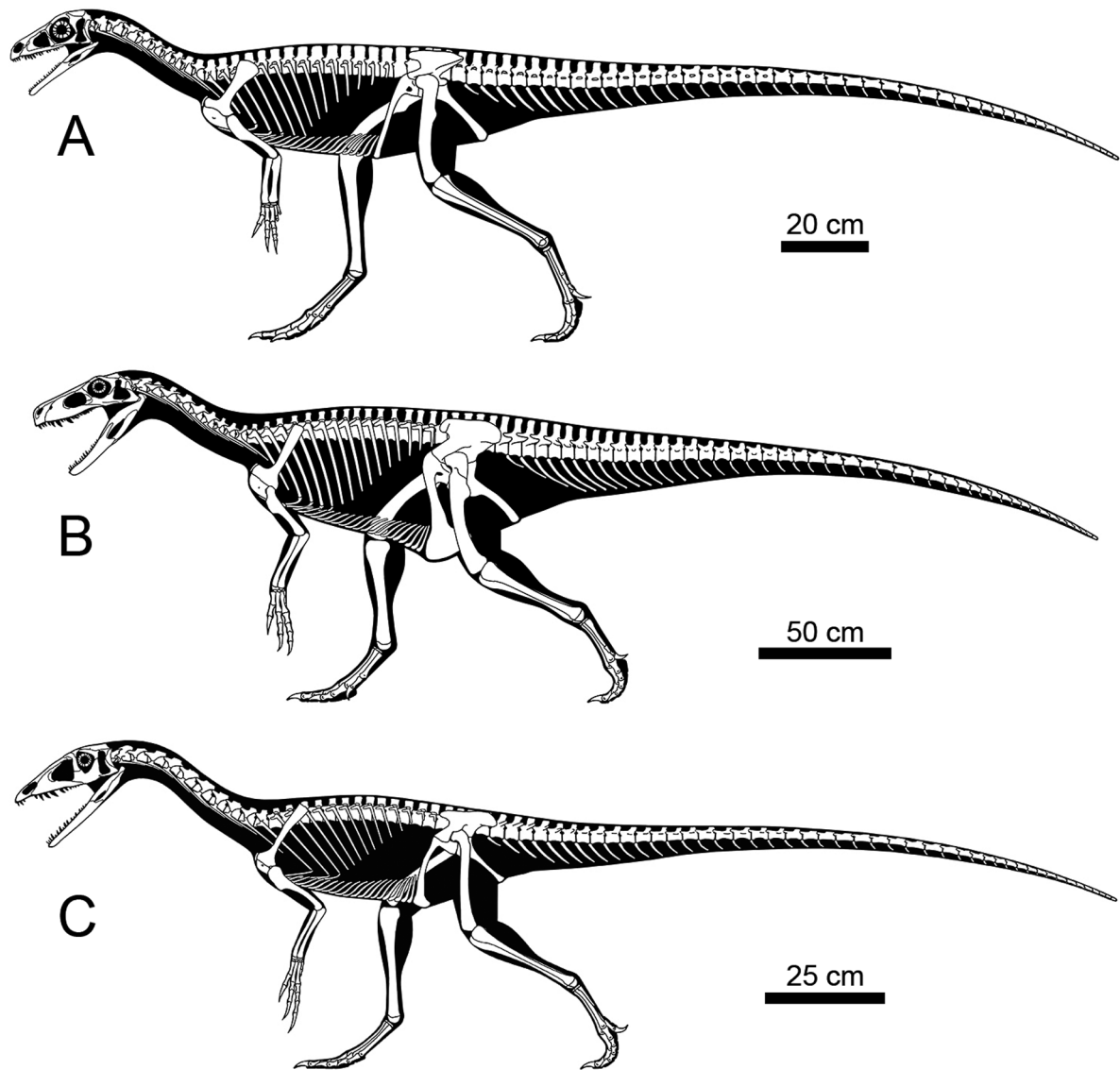


Figure 6. Skeletal reconstructions of three non-neotheropod saurischians (and possibly three basalmost theropods). A) The possible primitive sauropodomorph *Eoraptor lunensis*; B) The herrerasaurid *Herrerasaurus ischigualastensis*; C) The very basal theropod *Tawa hallae*. Reconstructions by Scott Hartman.

al. 2010; Langer et al. 2010; Sereno et al. 2013). *Tawa hallae* (Nesbitt et al. 2009; Figure 6C) and *Daemonosaurus chauliodus* (Sues et al. 2011) from the Norian and possibly Rhaetian of New Mexico, respectively, are currently recovered between *Eodromaeus* and neotheropods (Figure 4). Unlike *Eoraptor*, these two recently reported taxa possess the short subnarial gap present in basal neotheropods and an antorbital fossa restricted to the vicinity of the antorbital fenestra, as seen in *Herrerasaurus* (Nesbitt et al. 2009; Sues et al. 2011; Langer 2014). This condition

contrasts with the expanded antorbital fossa of *Eoraptor* and *Eodromaeus*. *Daemonosaurus* is unique in having a short and tall skull filled with procumbent premaxillary and dentary teeth (Sues et al. 2011). *Tawa* is closer to coelophysoids than *Daemonosaurus* and other primitive theropods in having an elongated snout and a more gracile body. *Tawa* shares with *Daemonosaurus* greatly enlarged maxillary teeth as well as pneumatic fossae (pleurocoels) in the cervical vertebrae (Nesbitt et al. 2009; Sues et al. 2011).

Coelophysoidea and Dilophosauridae

Neotheropoda (Bakker 1986), the least inclusive clade containing *Coelophysis bauri* (Cope 1889) and *Passer domesticus* (Linnaeus 1758) (Serenó 2005), currently comprises theropods more derived than *Tawa* (Nesbitt *et al.* 2009; Nesbitt 2011; Sues *et al.* 2011). Among their derived features, neotheropods are characterized by an intramandibular joint and a hinge between the dentary and the postdentary bones (Holtz 2012). Current consensus on basal theropod phylogeny suggests that neotheropods encompass a basal clade that can be referred to Coelophysoidea and a slightly more derived clade named Dilophosauridae (*sensu* Charig & Milner 1990; Figure 4; the clade Dilophosauridae is here defined phylogenetically for the first time, see Table 1). *Dilophosaurus* is thought to belong to Coelophysoidea by some authors (*e.g.*, Carrano *et al.* 2005; Tykoski 2005; Ezcurra & Cuny 2007; Ezcurra & Novas 2007; Xing 2012). However, results of more recent and/or larger scale analyses recover Dilophosauridae as a more derived clade of neotheropods, and the sister-group of *Averostra* (*e.g.*, Smith *et al.* 2007; Nesbitt *et al.* 2009; Ezcurra & Brusatte 2011; Sues *et al.* 2011; Ezcurra 2012). Consequently, though the phylogenetic relationships of dilophosaurids remains unresolved, these basal theropods seem to be more derived than coelophysoids.

Coelophysoidea (*sensu* Sereno 2005; Table 1) encompasses small to medium sized theropods (2-6m long) with slender skulls, and lightly built, gracile, and elongated bodies characterized by elongated cervical centra (Tykoski & Rowe 2004; Brusatte *et al.* 2010c; Holtz 2012). The first coelophysoids are already present in the Norian of Europe (*Procompsognathus triassicus*, *Camposaurus arizonensis*; Sereno & Wild 1992; Rauhut & Hungerbühler 1998; Ezcurra & Brusatte 2011) and North America (*Coelophysis bauri*; Colbert 1989; Figure 7A). Although coelophysoids form the first radiation of neotheropods, they were not apex terrestrial predators in the Late Triassic, as pseudosuchian carnivores such as rauisuchians and phytosaurs were larger and more abundant at that time (Brusatte *et al.* 2010c; Holtz 2012). Unlike most large pseudosuchian archosaurs, coelophysoids survived the Triassic/Jurassic boundary, and Jurassic coelophysoids are known from the Hettangian-Pliensbachian of China (*Panguraptor lufengensis*; You *et al.* 2014), South Africa (*Coelophysis*

rhodesiensis; Raath 1969, 1977; Bristowe & Raath 2004), and North America (*Coelophysis kayentakatae*; Rowe 1989; *n.b.*, this taxon was originally coined 'Syntarsus' by Rowe, 1989; it is also referred to as *Megapnosaurus* by some authors as the genus name 'Syntarsus' was preoccupied by a beetle, and the entomologists Ivie *et al.* 2001 replaced it with *Megapnosaurus*; 'Syntarsus' is thought to be a junior synonym of *Coelophysis* by many authors such as Downs 2000, Bristowe & Raath 2004 and Carrano *et al.* 2012). *Zupaysaurus rougieri* (Arcucci & Coria 2003; Ezcurra 2007) and *Liliensternus liliensterini* (Huene 1934) from the Norian of Argentina and Germany, respectively, are either classified as coelophysoids (*e.g.*, You *et al.* 2014) or recovered as more derived neotheropods positioned between Coelophysoidea and Dilophosauridae (Nesbitt *et al.* 2009; Ezcurra & Brusatte 2011; Sues *et al.* 2011; Ezcurra 2012; Figure 4).

Dilophosauridae is a poorly supported clade that may contain medium to large sized (4-7m long) theropods, such as *Dilophosaurus wetherilli* (Welles 1984; Figure 7B) and *Dracovenator regenti* (Yates 2005) from the Early Jurassic of North America and South Africa, respectively. Similar to coelophysoids, these two taxa possess a subnarial gap and anteriormost maxillary teeth facing anteroventrally, yet they share with averostrans a promaxillary fenestra and a reduced number of maxillary teeth (Holtz 2012). The clade has been recovered by some authors (Yates 2005; Smith *et al.* 2007; Xu *et al.* 2009b); however, an over-atomization of cranial crest characters may have been leading phylogenetic analyses to artificially find such a dilophosaurid clade (Brusatte *et al.* 2010a). In fact, '*Dilophosaurus*' *sinensis* (Hu 1993), considered to be a synonym junior of *Sinosaurus triassicus* (Dong 2003; Xing *et al.* 2013a, 2014), and *Cryolophosaurus ellioti* (Smith *et al.* 2007) from the Early Jurassic of China and Antarctica, respectively, were formerly interpreted as dilophosaurid taxa and are now classified among basal tetanurans (Benson 2010a; Brusatte *et al.* 2010c; Carrano *et al.* 2012; Xing 2012). The cranial crest of *Dilophosaurus*, *Cryolophosaurus*, and '*Dilophosaurus*' *sinensis* was convergently acquired in these taxa and evolved independently in dilophosaurids and basal tetanurans (Brusatte *et al.* 2010a; Xing 2012), or was a derived feature present in the common ancestor of dilophosaurids and basal averostrans. Although relatively common

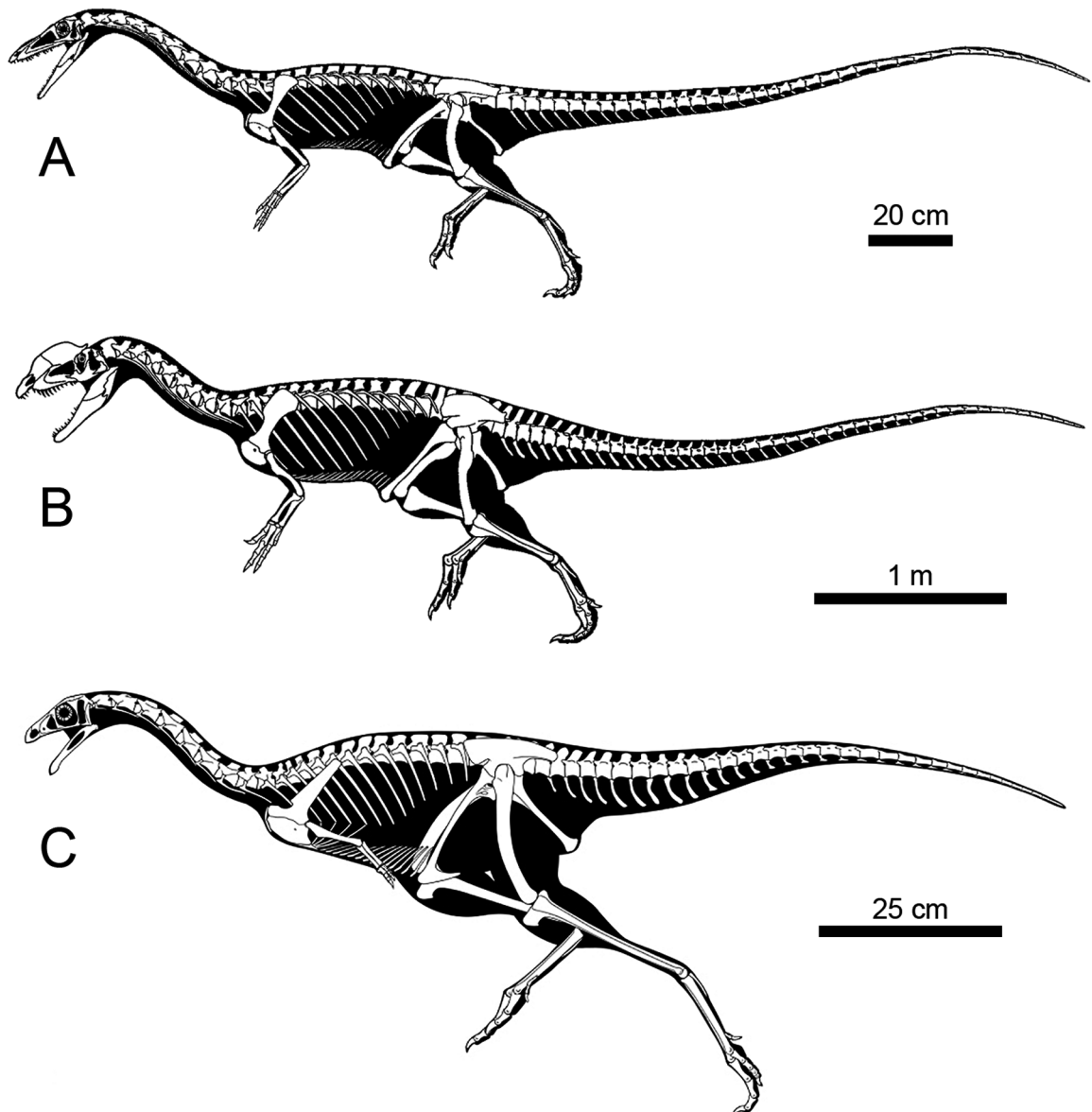


Figure 7. Skeletal reconstructions of two non-averostran neotheropods and one basal ceratosaur. A) The coelophysoid *Coelophysis bauri*; B) The dilophosaurid *Dilophosaurus wetherilli*; C) The 'elaphrosaur' *Limusaurus inextricabilis*. Reconstructions by Gregory Paul for *Coelophysis* and *Dilophosaurus* (modified), and Ville Sinkkonen for *Limusaurus* (modified).

and diverse entering the Jurassic, coelophysoids and dilophosaurids became extinct at or near the end of Early Jurassic (Carrano & Sampson 2004; Ezcurra & Novas 2007; Langer *et al.* 2010).

Ceratosauria

Averostra (Paul 2002), the least inclusive clade containing *Ceratosaurus nasicornis* Marsh 1884a and *Passer domesticus* (Linnaeus 1758) (Allain *et al.* 2012; Table 1), radiated into two main clades, Ceratosauria and Tetanurae (Figure 4). Basal averostrans are characterized by the oreinirostral condition of their head, de-

fined as a transversally narrow and dorsoventrally high skull (Holtz 2012). According to Carrano *et al.* (2012), the derived features shared by averostrans include a reduced prefrontal which remains unfused to the postorbital in adults, the moderate size of the acromion process of the scapula, a ridge-like medial epicondyle on the femur, an interpubic fenestra, the subtriangular morphology of the distal end of the ischium, and a centrally positioned fibular fossa on the medial surface of the fibula. The first averostrans are known from the Early Jurassic and are distributed widely across the globe

with remains found in China ('*Dilophosaurus sinensis*'; Hu 1993), Antarctica (*Cryolophosaurus ellioti*; Smith *et al.* 2007), Africa (*Berberosaurus liassicus*; Allain *et al.* 2007), South America (*Tachiraptor admirabilis*; Langer *et al.* 2014), and possibly Europe ('*Saltriosaurus*'; Dal Sasso 2003; Benson 2010b). Ceratosaurs currently include a basal clade informally referred to as 'elaphrosaur', a more derived family named Ceratosauridae, and a major clade known as the Abelisauroida (Wilson *et al.* 2003; Sereno *et al.* 2004; Carrano & Sampson 2008; Pol & Rauhut 2012; Tortosa *et al.* 2014). 'Elaphrosaur' are a poorly known group of primitive ceratosaurs including *Elaphrosaurus bambergi* from the Kimmeridgian-Tithonian of Tendaguru (Carrano & Sampson 2008), *Limusaurus inextricabilis* from the Oxfordian of China (Xu *et al.* 2009b; Figure 7C), and *Spinostropheus gauthieri* from the Middle Jurassic of Niger (Carrano & Sampson 2008; Rauhut and López-Arbarello 2009; Remes *et al.* 2009). The 'elaphrosaur' clade was retrieved in all recent cladistic analyses on ceratosaurs (Xu *et al.* 2009b; Pol & Rauhut 2012; Farke & Sertich 2013; Tortosa *et al.* 2014) and always gathers the taxa *Elaphrosaurus* and *Limusaurus*. The latter is the only 'elaphrosaur' known from cranial material and the only non-maniraptoriform theropod to possess an edentulous skull convergent with that of ornithomimids (Figure 7C). Although recovered as 'elaphrosaur' in all recent large scaled cladistic analyses on ceratosaurs (Pol & Rauhut 2012; Tortosa *et al.* 2014), *Elaphrosaurus* and *Limusaurus* have also been suggested to belong to Noosauridae (Canale *et al.* 2009; Stiegler *et al.* 2014).

Ceratosauridae only contains two taxa, the eponymous *Ceratops* from the Kimmeridgian-Tithonian of North America (*C. nasicornis*; Gilmore 1920; Madsen & Welles 2000; Carrano & Sampson 2008; Figure 8A) and Europe (*Ceratops* sp.; Mateus & Antunes 2000; Malafaia *et al.* 2015), and *Genyodectes serus* from the Aptian-Albian of Argentina (Rauhut 2004b). Ceratosaurs were large theropods (6-8m long) characterized by strongly elongated maxillary teeth longer than the dentary height, and at least *Ceratops* showed a fused nasal horn, two lacrimal horns, and osteoderms on the dorsal midline of the animal (Marsh 1884a; Gilmore 1920; Madsen & Welles 2000; Rauhut 2004b). Along with megalosaurids and allosaurids, ceratosaurs were apex predators in the Late

Jurassic (Kimmeridgian-Tithonian) ecosystems of Europe, North America, and possibly South America and Africa (Henderson 1998; Bakker & Bir 2004; Soto & Perea 2008; Rauhut 2011).

Abelisauroida falls into two divergent subclades, the Noosauridae and Abelisauridae (Wilson *et al.* 2003; Sereno *et al.* 2004; Carrano & Sampson 2008; Pol & Rauhut 2012; Tortosa *et al.* 2014; Figure 4). Noosaurids form a relatively poorly known group of small, slender abelisauroids with forelimbs bearing well-developed claws (Bonaparte 1991a; Carrano & Sampson 2008; Agnolín & Chiarelli 2010; Carrano *et al.* 2011). They are only known from the Cretaceous and may have already been present in the Barremian-early Aptian of Argentina (*Ligabueino andesi*; Bonaparte 1996; Carrano & Sampson 2008). Noosaurids are well-known in the latest part of the Cretaceous of Gondwana, having been unearthed in Santonian-Maastrichtian deposits in Argentina (*Noosaurus leali*, *Velocisaurus unicus*; Bonaparte & Powell 1980; Bonaparte 1991b, 1996), Madagascar (*Masiakasaurus knopfleri*; Carrano *et al.* 2002, 2011) and India (*Laevisuchus*; Huene & Matley 1933). *Masiakasaurus knopfleri* (Figure 8B), the best known noosaurid taxon, shows the peculiarity of having procumbent dentary teeth with a constriction at the crown base and flutes on the lingual surface (Carrano *et al.* 2002, 2011).

Abelisauridae is a well-supported clade of medium to large (5-9m long) stubby-armed theropods with short rounded snouts, deep, heavily sculptured skulls bearing bony protuberances and weakly recurved teeth (Bonaparte 1991a; Wilson *et al.* 2003; Carrano & Sampson 2008; Canale *et al.* 2009; Pol & Rauhut 2012). The inclusion of *Eoabelisaurus mafi* (Pol & Rauhut 2012) from the Aalenian-Bajocian of Patagonia within abelisaurids is subject of debate (Pol & Rauhut 2012; Tortosa *et al.* 2014) and the first definitive Abelisauridae, *Kryptops palaios*, comes from the Aptian-Albian of North Africa (Sereno and Brusatte 2008). Abelisaurids were not the dominant predators in Gondwanian ecosystems in the Early Cretaceous and early Late Cretaceous of South America and North Africa, as they were dominated by the larger spinosaurids and carcharodontosaurids during that time (Holtz 2012; Novas *et al.* 2013). Following the extinction and/or decline of Spinosauridae and Carcharodontosauridae after the Cenomanian-Turonian transition, abelisaurids

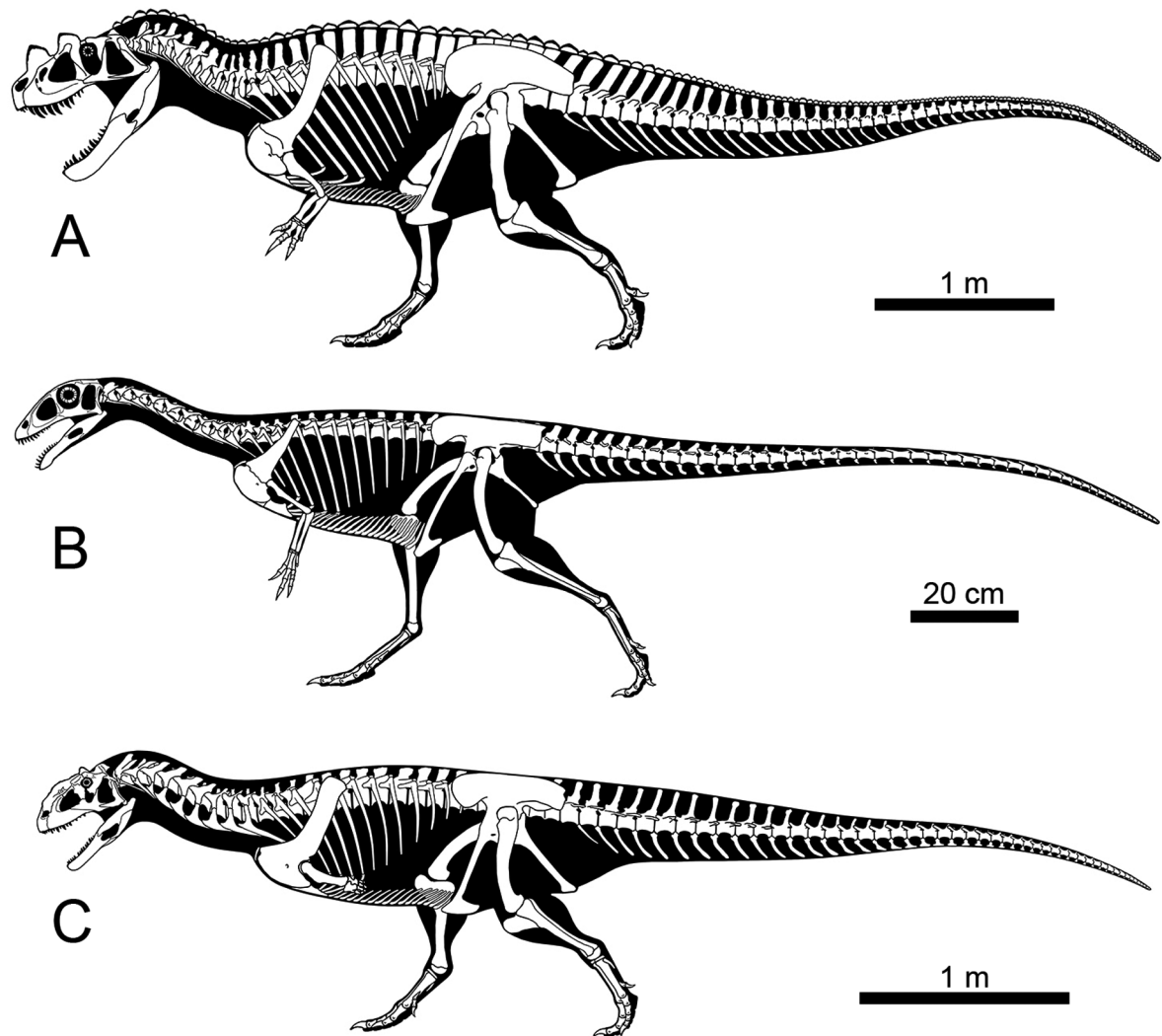


Figure 8. Skeletal reconstructions of three ceratosaurs. A) The ceratosaurid *Ceratosaurus nasicornis*; B) The noasaurid *Masiakasaurus knopfleri*; C) The abelisaurid *Majungasaurus crenatissimus*. Reconstructions by Scott Hartman.

became apex predators in Africa, Western Europe, and South America in the latest part of the Cretaceous (Buffetaut *et al.* 2005; Candeiro & Martinelli 2005; Carrano *et al.* 2012; Novas *et al.* 2013; Tortosa *et al.* 2014; Csiki-Sava *et al.* 2015). The best-known taxa are from the Campanian-Maastrichtian of Europe and Gondwana, including *Majungasaurus crenatissimus* (Sampson *et al.* 1998; Sampson & Witmer 2007; Figure 8C) from Madagascar, *Aucasaurus garridoi* (Coria *et al.* 2002), *Skorpiovenator bustingorryi* (Canale *et al.* 2009) and *Carnotaurus sastrei* (Bonaparte *et al.* 1990; Carabajal 2011) from Argentina, *Rajasaurus narmadensis* (Wilson *et al.* 2003) from India, and *Arcovenator escotae* (Tortosa *et al.* 2014) from France.

Megalosauroida

Tetanurae (Gauthier 1986), the most inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Ceratosaurus nasicornis* Marsh 1884a (Allain *et al.* 2012; Table 1), is diagnosed by an antorbital tooth row, a moderately extended anterior ramus of the maxilla, a maxillary fenestra piercing the lateral wall of the maxilla, separated interdental plates, and a prominent deltopectoral crest of the humerus (Carrano *et al.* 2012). Several relatively complete basal tetanurans are known from the Early and Middle Jurassic of China and Antarctica (i.e., '*Dilophosaurus*' *sinensis*, *Cryolophosaurus*, and *Monolophosaurus*). These primitive tetanurans are recovered between basal averostrans and the recent clade Orionides which comprises two major radiations, the Megalosauroida and Avethero-

poda (Carrano *et al.* 2012). The first one, Megalosauroida, currently gathers three subclades, namely the Piatnitzkysauridae, Megalosauridae, and Spinosauridae (Figure 4). Piatnitzkysauridae is the sister group of Megalosauria, which is divided into Megalosauridae and Spinosauridae. Piatnitzkysaurids as currently known comprise medium sized (5-6m long) American forms such as *Marshosaurus bicentesimus* (Madsen 1976a; Figure 9A) from the Kimmeridgian-Tithonian of North-America, and *Piatnitzkysaurus floresi* (Bonaparte 1986; Rauhut 2004a) and *Condorraptor currumili* (Rauhut 2005) from the Toarcian-Bajocian of Argentina (Cúneo *et al.* 2013). These basal megalosauroids are characterized by a maxilla with a short anterior ramus and vertically ridged interdental plates (Carrano *et al.* 2012).

Megalosauridae is a diverse clade of theropods restricted to the Middle to Late Jurassic, which suggests they went extinct at the Jurassic-Cretaceous boundary (Carrano *et al.* 2012). Megalosaurids are medium to very large (4-10m long) theropods exhibiting relatively elongate skulls that lack cranial protuberances, and powerful arms possibly bearing a large claw at digit one (Hendrickx *et al.* 2015; Sadelir *et al.* 2008; Benson 2010a; Allain *et al.* 2012; Carrano *et al.* 2012). The most primitive and one of the oldest theropod embryos, found to date, from the Late Kimmeridgian-Early Tithonian of Portugal have been ascribed to this clade (Araújo *et al.* 2013). Megalosaurids are known as early as the Bajocian of England (*Magnosaurus nethercombensis*, *Duriavenator hesperis*; Benson 2008a, 2010b) and include forms from the Bajocian-Callovian of England and France (*Megalosaurus bucklandii*, Figure 9B; *Dubreuillosaurus valesdunensis*; Allain 2002; Benson *et al.* 2008; Benson 2010a), the Middle Jurassic of Africa (*Afrovenator abakensis*; Sereno *et al.* 1996), the Late Jurassic of China (*Leshansaurus qianweiensis*; Li *et al.* 2009), and the Kimmeridgian-Tithonian of North-America and Portugal (*Torvosaurus tanneri*, *Torvosaurus gurneyi*; Britt 1991; Hendrickx & Mateus 2014a). *Sciurumimus albersdoerferi*, a possible megalosaurid from the Kimmeridgian of Germany, is the most complete megalosauroid discovered so far (Rauhut *et al.* 2012). It is also currently the most primitive theropod preserved with direct evidence of filamentous integument, indicating that protofeathers were already covering some tetanurans early in their evolution (Rauhut *et al.* 2012).

Spinosauridae, the sister group of Megalosauridae, is a well-supported clade of highly specialized theropods united by an elongated crocodile-like skull, spatulate snout with sigmoid alveolar margins, fluted conical teeth with minute or no denticles, and an hypertrophied manual ungual (Charig & Milner 1997; Sereno *et al.* 1998; Sues *et al.* 2002; Bertin 2010; Allain *et al.* 2012; Ibrahim *et al.* 2014). These derived anatomical features, associated with computer modeling of the skull (Rayfield *et al.* 2007; Cuff & Rayfield 2013), oxygen isotope ratios (Amiot *et al.* 2010), morphofunctional analysis of the mandibular articulation (Hendrickx *et al.* 2008) and gut contents (Charig & Milner 1997; Buffetaut *et al.* 2004), suggest that spinosaurids were at least partially piscivorous, while also feeding on dinosaurs and pterosaurs. Spinosaurids were large to very large theropods (8-17m long) and include the largest terrestrial predators discovered hitherto. They were also characterized by elongated neural spines which evolved into a bony sail in some members (*e.g.*, *Spinosaurus aegyptiacus*, *Ichthyovenator laosensis*; Stromer 1915; Allain *et al.* 2012; Ibrahim *et al.* 2014). Spinosaurid teeth seem to be already present in the Kimmeridgian-Tithonian of Tanzania (Buffetaut 2011; but for a different opinion see Rauhut 2011), yet the earliest definitive spinosaurid is currently *Baryonyx walkeri* (Figure 9C) from the Barremian of England and Portugal (Charig & Milner 1986, 1997; Mateus *et al.* 2011). Spinosauridae are also known from the Aptian and/or Albian of Niger (*Suchomimus tenerensis*; Sereno *et al.* 1998; *n.b.*, *Suchomimus tenerensis* most likely represents the same animal as the non-diagnostic *Cristatusaurus lapparenti* Taquet & Russell 1998 from the same deposits; Carrano *et al.* 2012), Brazil (*Angaturama limai*, *Irritator challengeri*; Kellner & Campos 1996; Sues *et al.* 2002; *n.b.*, these two taxa known from non-overlapping cranial material recovered from the same deposits may in fact represent the same taxon/individual; Sereno *et al.* 1998; Sues *et al.* 2002; Dal Sasso *et al.* 2005) and South-eastern Asia (*Ichthyovenator laosensis*; Allain *et al.* 2012). The most derived spinosaurid, *Spinosaurus aegyptiacus*, comes from the Albian-Cenomanian of North Africa (*e.g.*, Stromer 1915; Taquet & Russell 1998; Buffetaut & Ouaja 2002; Dal Sasso *et al.* 2005; Ibrahim *et al.* 2014). Recent studies have shown that this taxon had many adaptations for a semi-aquatic

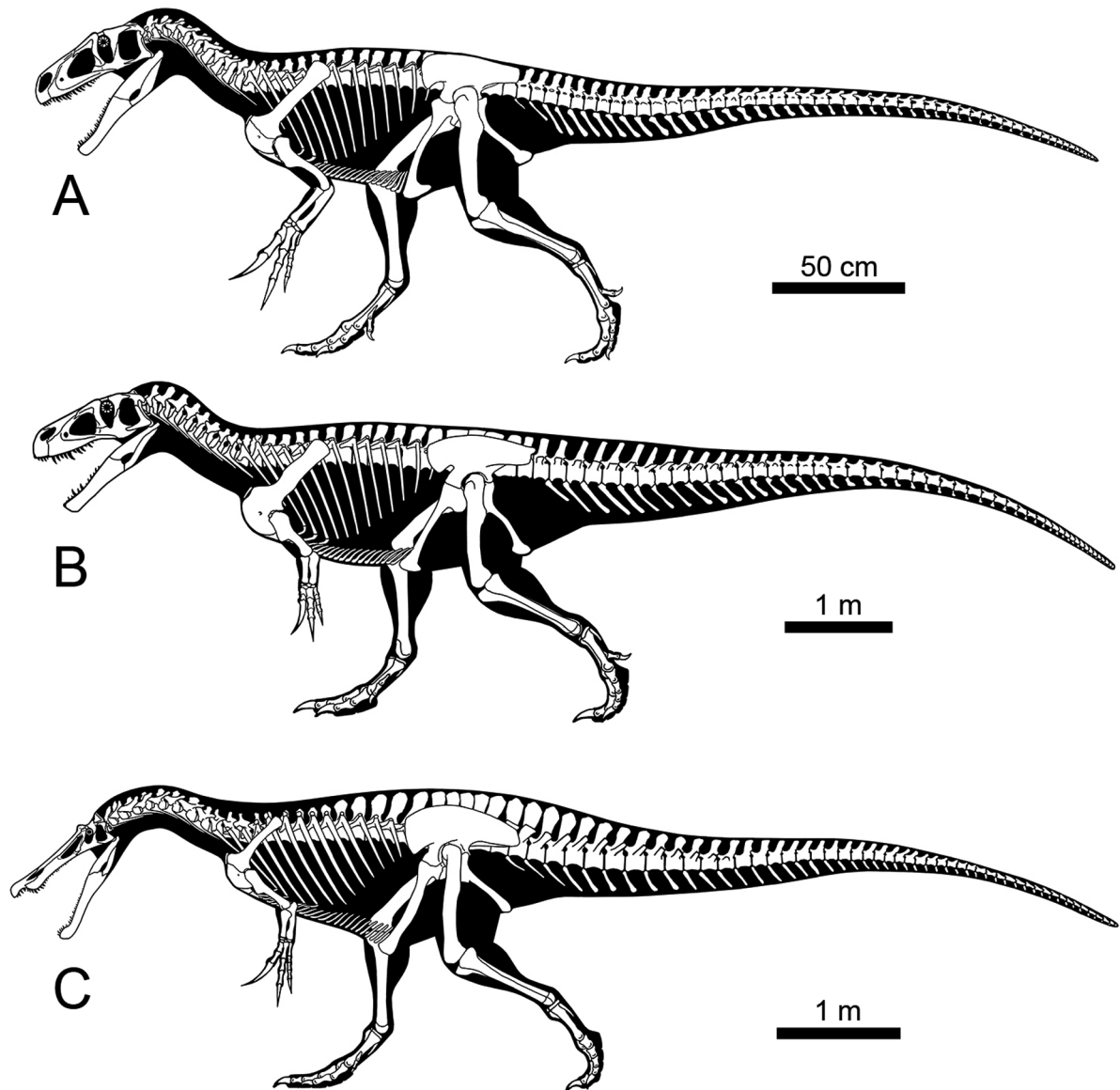


Figure 9. Skeletal reconstructions of three megalosauroids. A) The piatnitzkysaurid *Marshosaurus bicentissimus*; B) The megalosauroid *Megalosaurus bucklandii*; C) The spinosaurid *Baryonyx walkeri*. Reconstructions by Scott Hartman.

lifestyle, including short hind-limbs, downsized pelvic girdle, flat-bottomed pedal claws and solid long bones (Ibrahim *et al.* 2014).

Despite the presence of the tetanuran *Chilantaisaurus* from the Turonian (or younger stage) of China and considered to be a spinosaurid by Allain *et al.* (2012; *n.b.*, *Chilantaisaurus* is recovered as a neovenatorid allosauroid by Benson *et al.* 2010 and Carrano *et al.* 2012) as well as isolated teeth tentatively assigned to Spinosauridae from post-Cenomanian deposits of South America and Asia (Salgado *et al.* 2009; Hone *et al.* 2010; for a different opinion see Hasegawa *et al.* 2010), spinosaurids seem to go extinct in the early Late Cretaceous.

Allosauroides

Avetheropoda (also known as 'Neotetanurae'; *e.g.*, Sereno *et al.* 1994; Sereno 1998, 1999; Allain *et al.* 2012; Table 1), the least inclusive clade containing *Allosaurus fragilis* Marsh 1877 and *Passer domesticus* (Linnaeus 1758) (Allain *et al.* 2012), is comprised of two major subclades: the Allosauroides, and the Coelurosauria (Figure 4). According to Carrano *et al.* (2012), avetheropods differ from more primitive theropods by possessing strongly curved chevrons, a poorly developed ridge on the medial surface of the ilium, and a subtriangular flange-like accessory trochanter on the femur. Allosauroids were dominant terrestrial predators in the Late

Jurassic, Early Cretaceous, and early Late Cretaceous worldwide. Allosauroids are currently divided into four subclades: the Metriacanthosauridae, Allosauridae, Neovenatoridae, and Carcharodontosauridae (Figure 4). Metriacanthosauridae (formerly known as 'Sinraptoridae'; Carrano *et al.* 2012) is the most primitive and contains forms from the Middle and Late Jurassic of China such as *Sinraptor dongi* (Currie & Zhao 1993a), '*Yangchuanosaurus*' *hepingensis*, and *Yangchuanosaurus shangyouensis* (Dong *et al.* 1983). These taxa, which are known from exceptionally well-preserved skeletons, share a maxilla with a promaxillary fenestra larger than the maxillary fenestra, a pneumatic recess on the lateral surface of the ascending ramus, and the absence of an anterior ramus (Currie & Zhao 1993a; Carrano *et al.* 2012). *Metriacanthosaurus parkeri* (Huene 1923) from the Oxfordian of England is the only definitive non-Asian metriacanthosaurid reported to date (though *Lourinhanosaurus antunesi* from the Kimmeridgian-Tithonian of Portugal may also be referred to this clade; see Benson 2010a), and *Siamotyrannus isanensis* (Buffetaut *et al.* 1996) from the Barremian-Aptian of Thailand is the only known metriacanthosaurid that survived into the Cretaceous (Carrano *et al.* 2012).

Allosauridae, a more derived clade of allosauroids and the sister-clade of Carcharodontosauria, is a small group of Kimmeridgian-Tithonian tetanurans comprising several North American and Portuguese taxa, namely *Allosaurus fragilis* (Gilmore 1920; Madsen 1976b; Chure 2000; Loewen 2010; Figure 10A), *Allosaurus europaeus* (Mateus *et al.* 2006), *Allosaurus* n. sp. (*Allosaurus jimmadsemi sensu* Chure 2000; Chure *et al.* 2006; Loewen 2010), and *Sauropogonax maximus* (Chure 1995). Allosaurids were medium to large (8-10m long) theropods with thin and dorsally-developed lacrimal horns, and were one of the dominant predators in Late Jurassic ecosystems of North America and Europe (Chure 2000; Loewen 2010).

Carcharodontosauria falls into two subclades, the Neovenatoridae and the Carcharodontosauridae (Carrano *et al.* 2012). It has been debated whether Neovenatoridae is a monospecific clade including the taxon *Neovenator salerii* (Brusatte *et al.* 2008; Figure 10B) from the Hauterivian-Barremian of England (Novas *et al.* 2013; Porfiri *et al.* 2014), or a more

inclusive clade including *Neovenator* and megaraptorans (Benson *et al.* 2010; Carrano *et al.* 2012; Zanno & Makovicky 2013). According to Benson *et al.* (2010), neovenatorids are united by postcranial synapomorphies such as a short and broad scapula and a pneumatic ilium. The recent discovery of a relatively well-preserved megaraptoran with cranial material, however, seems to suggest a placement of Megaraptora within Tyrannosauroida (Porfiri *et al.* 2014). Though this is still an active debate in theropod systematics, megaraptorans will be described in the next section.

Carcharodontosauridae, on the other hand, forms a well-supported clade comprising medium to very large theropods (6-14m long) characterized by a massive and deep skull with sculptured facial bones, and cranial protuberances on the lacrimals and postorbitals (Novas *et al.* 2005, 2013; Coria & Currie 2006; Brusatte & Sereno 2007; Ortega *et al.* 2010; Cau *et al.* 2013). The earliest carcharodontosaurid is currently *Veterupristisaurus milneri* (Rauhut 2011) known from caudal vertebrae from the Kimmeridgian-Tithonian of Tanzania. In the Cretaceous, carcharodontosaurids became a diversified clade of allosauroids distributed worldwide. Due to their very large sized, carcharodontosaurids were at the apex of the food chain in most 'mid' Cretaceous ecosystems. The best preserved carcharodontosaurids are *Concavenator corcovatus* (Ortega *et al.* 2010) from the Barremian of Spain, *Acrocanthosaurus atokensis* (Harris 1998; Currie & Carpenter 2000; Eddy and Clarke 2011) and *Tyrannotitan chubutensis* (Novas *et al.* 2005; Canale *et al.* 2015) from the Aptian-Albian of North America and Argentina, respectively, *Carcharodontosaurus saharicus* (Rauhut 1995; Brusatte & Sereno 2007) from the Cenomanian of North Africa, *Giganotosaurus carolinii* (Coria & Salgado 1995; Calvo and Coria 1998; Figure 10C) and *Mapusaurus roseae* (Coria & Currie 2006) from the Cenomanian-Santonian of Argentina, and *Shaochilong maortuensis* (Brusatte *et al.* 2009, 2010b) from the Turonian of China (Carrano *et al.* 2012). The carcharodontosaurid lineage may have extended to the latest part of the Cretaceous in South America as material assigned to Carcharodontosauridae have been reported from the Campanian-Maastrichtian of Brazil (*e.g.*, Candeiro *et al.* 2012; Azevedo *et al.* 2013).

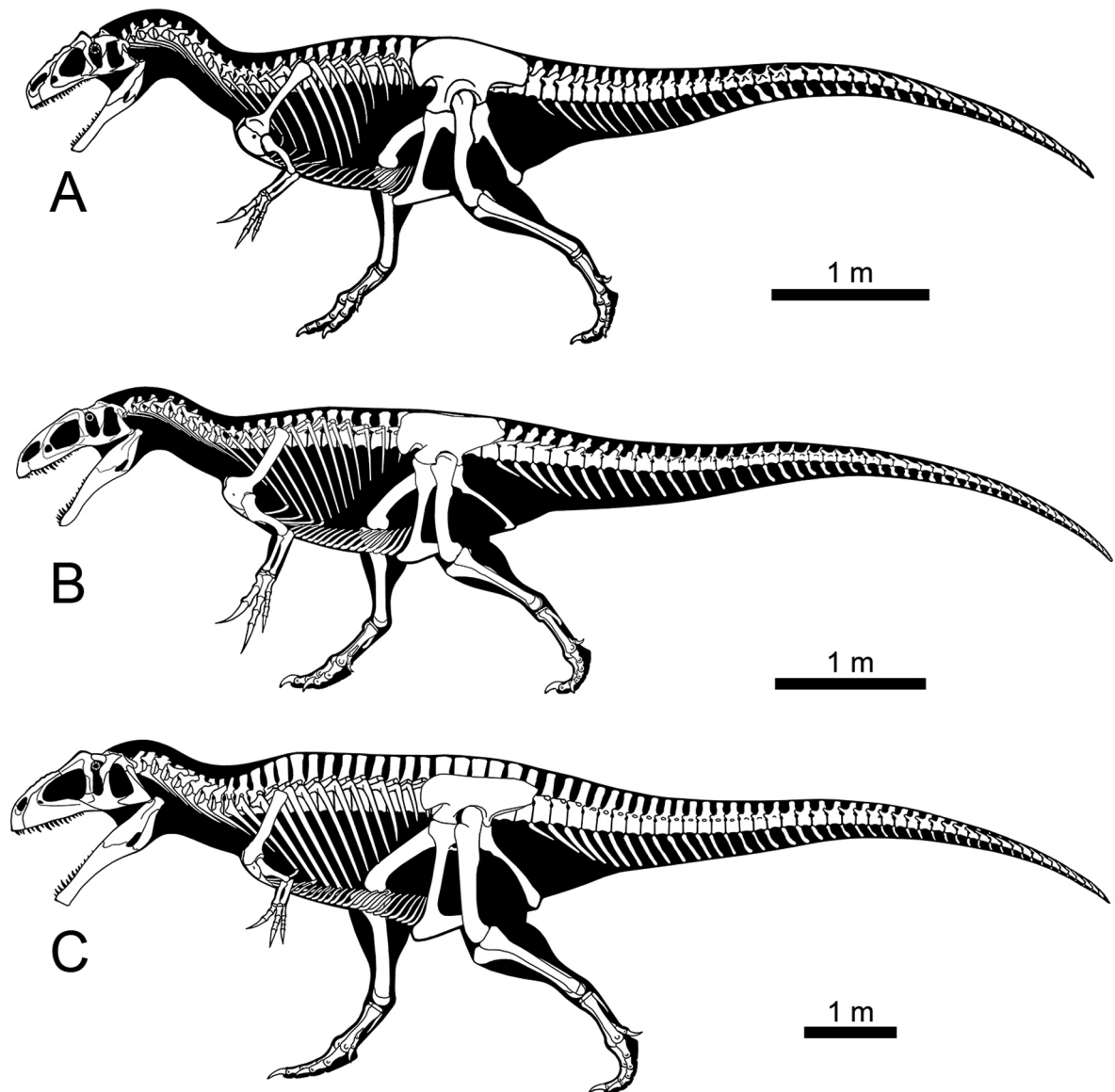


Figure 10. Skeletal reconstructions of three allosauroids. A) The allosaurid *Allosaurus 'jimmadseni'*; B) The neovenatorid *Neovenator salerii*; C) The carcharodontosaurid *Giganotosaurus carolinii*. Reconstructions by Scott Hartman.

Basal Coelurosauria and Tyrannosauoidea

Coelurosauria (Huene 1914a), the most inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Allosaurus fragilis* Marsh 1877, *Sinraptor dongi* Currie & Zhao 1993a, and *Carcharodontosaurus saharicus* (Depéret & Sarronin 1927) (Sereno 2005), is a well-supported clade that contains a large diversity of herbivorous and carnivorous non-avian theropods as well as living birds. According to Turner *et al.* (2012), members of this group differ from more basal theropods by possessing a well-developed medial shelf on the maxilla, a reversed L-shape quadratojugal, and amphiplatyan cervical and anterior dorsal vertebrae. Coelurosaur interre-

lationships are complex, including several well-defined coelurosaur groups nested in different subclades (Figures 4-5). The oldest definite coelurosaur is known from the Bathonian of Eurasia (Averianov *et al.* 2010; Rauhut *et al.* 2010), though putative coelurosaur remains have been described from the Early Jurassic of China (Zhao & Xu 1998; Barrett 2009). The majority of recent cladistic analyses on coelurosaurians recovered Tyrannosauoidea as the basal-most clade of Coelurosauria (*e.g.*, Dal Sasso & Maganuco 2011; Senter *et al.* 2012b; Turner *et al.* 2012; Godefroit *et al.* 2013a; Loewen *et al.* 2013; Brusatte *et al.* 2014; Choiniere *et al.* 2014b; *n.b.*, Tyrannosauoidea are found more

derived than Compsognathidae in Zanno *et al.* 2009, Rauhut *et al.* 2010 and Novas *et al.* 2013). There are, however, several coelurosaur taxa that fall outside Tyrannosauroidea, at the very base of Coelurosauria (Figure 4). These include *Aorun zhaoi* (Choiniere *et al.* 2014b) and *Zuolong sallei* (Choiniere *et al.* 2010a) from the Oxfordian-Callovian of China, *Bicentenaria argentina* from the Cenomanian of Argentina (Novas *et al.* 2012), and possibly *Tanycolagreus topwilsoni* from the Kimmeridgian-Tithonian of Wyoming and *Tugulusaurus faciles* from the ?Valanginian-Albian of China (Rauhut & Xu 2005). The latter two are also recovered as sister-taxa among the Coeluridae, a clade recovered at the base of Coelurosauria by Li *et al.* (2010), but also at the base of the tyrannosauroid clade (*e.g.*, Dal Sasso & Maganuco 2011; Novas *et al.* 2012; Senter *et al.* 2012b; Brusatte *et al.* 2014), or slightly more derived than tyrannosauroids (Choiniere *et al.* 2014b).

Due to the iconic status of *Tyrannosaurus rex* and numerous tyrannosauroid specimens, tyrannosauroids are the most studied and best known non-avian theropods (Brusatte *et al.* 2010d). The recent discovery of a large number of basal and derived tyrannosauroids has dramatically increased the known diversity of this group, resulting in a well-characterized phylogenetic sequence. Tyrannosauroids encompass small to very large-bodied theropods (3-13m long) diagnosed by premaxillary teeth significantly smaller than anterior maxillary teeth and with a U-shaped cross-section, small premaxillae with elongated nasal and maxillary (subnarial) processes, and fused nasals (Holtz 2004, 2012; Brusatte *et al.* 2010d). The discovery of several well-preserved tyrannosauroids from China has revealed that small to large bodied primitive forms such as *Dilong paradoxus* (Xu *et al.* 2004) and *Yutyranus huali* (Xu *et al.* 2012) were covered with filamentous integument. Some recent phylogenetic analyses of Tyrannosauroidea suggest that three main subclades radiated independently: the Proceratosauridae, Megaraptora, and Tyrannosauridae (Figure 4).

The most basal clade, the Proceratosauridae, comprises small-bodied tyrannosauroids characterized by elaborated cranial crests (Brusatte *et al.* 2010d; Figure 11A). Proceratosaurids originated in the Middle Jurassic of Eurasia, including the taxa *Proceratosaurus bradleyi* (Rauhut *et al.* 2010) and *Kileskus aristotocus* (Averianov

et al. 2010) from the Bathonian of England and Siberia, respectively. Proceratosaurids are also known from the Oxfordian of China (*Guanlong wucaii*; Xu *et al.* 2006; Figure 11A), and the youngest member is *Sinotyrannus kazuoensis* (Ji *et al.* 2009) from the Aptian of China (Brusatte *et al.* 2010d).

Primitive non-proceratosaurid tyrannosauroids (*i.e.*, non-proceratosaurid tyrannosauroids more basal than Tyrannosauridae) encompass several small to medium sized forms from the Late Jurassic of Europe (*Aviatyrannis jurassica*, *Juratyran langhami*; Rauhut 2003b; Benson 2008b; Brusatte & Benson 2013) and North America (*Stokesosaurus clevelandi*; Benson 2008b; Brusatte & Benson 2013), and the Early Cretaceous of Europe (*Eotyrannus lengi*; Hutt *et al.* 2001) and China (*Dilong paradoxus*, *Yutyranus huali*, *Xiongguanlong baimoensis*; Xu *et al.* 2004, 2012; Li *et al.* 2010). They are also known in the Late Cretaceous of North America (*e.g.*, *Dryptosaurus aquilunguis*, *Appalachiosaurus montgomeriensis*, *Bistahieversor sealeyi*; Carr *et al.* 2005; Carr & Williamson 2010; Brusatte *et al.* 2011) and Asia (*e.g.*, *Raptorex kriegsteini*, *Alectrosaurus olseni*; Mader & Bradley 1989; Sereno *et al.* 2009).

Based on the recent description of a relatively complete juvenile specimen of *Megaraptor namunhuaiquii*, megaraptorans are thought to have evolved from primitive tyrannosauroids more derived than proceratosaurids (Novas *et al.* 2013; Porfiri *et al.* 2014). Megaraptorans are gracile theropods characterized by an elongated skull, and elongated and robust forelimbs with enlarged thumb claws on digits I and II (Benson *et al.* 2010; Porfiri *et al.* 2014). They were distributed widely across the globe as they encompass *Fukuiraptor kitadaniensis* (Azuma & Currie 2000; Currie & Azuma 2006) from the Barremian of Japan, *Australovenator wintonensis* (Hocknull *et al.* 2009) from the Albian of Australia, and *Aerosteon riocoloradensis* (Sereno *et al.* 2008) from the Campanian of North Argentina. Megaraptorans seem also to extend to the end of the Cretaceous, with *Orkoraptor burkei* (Novas *et al.* 2008) from the Maastrichtian of Patagonia as the most recent member of this clade.

Tyrannosaurids are the most derived and the largest tyrannosauroids. Within Tyrannosauroidea, they show the derived features of large body size (6-13m long), robust and broad

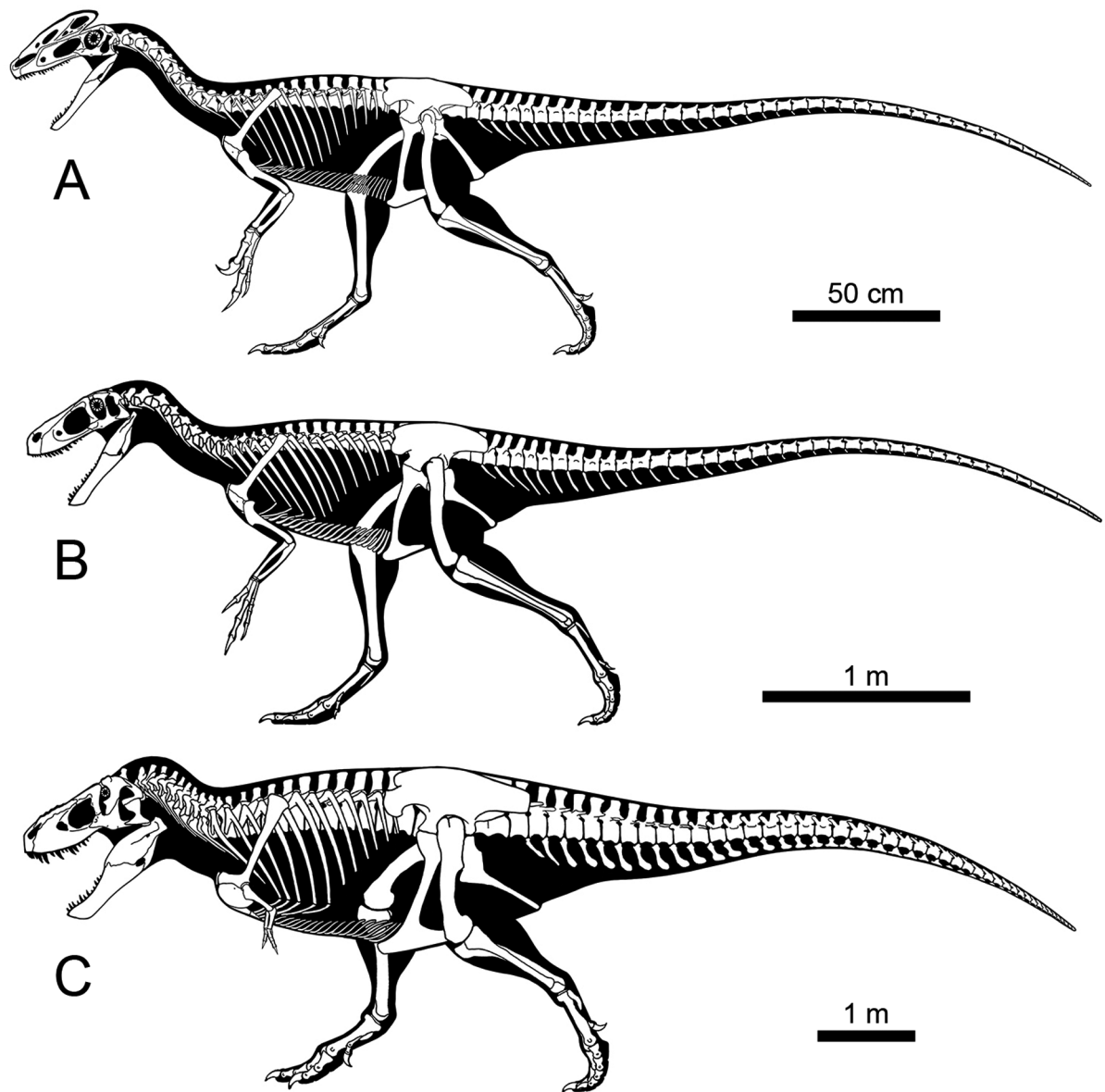


Figure 11. Skeletal reconstructions of three tyrannosauroids. A) The proceratosaurid *Guanlong wucaii*; B) The basal tyrannosauroid *Eotyrannus lengi*; C) The tyrannosauroid *Tyrannosaurus rex*. Reconstructions by Scott Hartman.

skulls with powerful jaws bearing incassate teeth with long roots, and reduced forelimbs ending in two functional fingers (the third digit is vestigial and does not carry phalanges; Currie 2003; Holtz 2004, 2012; Brusatte *et al.* 2010d). Tyrannosaurids were apex predators in all Late Cretaceous ecosystems of North America and Asia. They were hypercarnivores and were able to produce extremely powerful bite forces capable of crushing bone (Erickson *et al.* 1996; Bates and Falkingham 2012). Tyrannosaurids also possessed a higher degree of stereoscopic vision than other non-avian theropods, and their olfactory ratios are particularly high, suggestive of a keen sense of smell (Stevens 2006;

Witmer & Ridgely 2009; Zelenitsky *et al.* 2009). Studies have shown that they had accelerated grow rates and underwent well-characterized changes during ontogeny (Carr 1999; Erickson *et al.* 2004; Horner & Padian 2004). The best known tyrannosaurids are from the Campanian-Maastrichtian of Asia and North-America and include *Albertosaurus sarcophagus*, *Gorgosaurus libratus*, *Daspletosaurus torosus*, and *Tyrannosaurus rex* (Figure 11C) from USA and Canada (*e.g.*, Russell 1970; Molnar 1991; Brochu 2003; Currie 2003), and *Alioramus altai* and *Tarbosaurus baatar* from Mongolia (*e.g.*, Hurum & Sabath 2003; Tsuihiji *et al.* 2011; Brusatte *et al.* 2012a).

Compsognathidae and Ornithomimosauria

Compsognathidae and Ornithomimosauria are typically recovered as more derived than Tyrannosauroidae and more basal than Alvarezsauroidae, Therizinosauria, and Oviraptorosauria. Several recent large scale cladistic analyses have placed Compsognathidae and Ornithomimosauria as the second and third basalmost clades of coelurosaurs, respectively (e.g., Csiki et al. 2010; Senter 2011; Turner et al. 2012; Godefroit et al. 2013a; Choiniere et al. 2014b; Figure 5). Compsognathids are characterized by small body size (1-2.5m long), a gracile and slender body, and an elongated skull with slender jaws bearing ziphodont teeth (Figure 12A). Many specimens are immature individuals retaining a primitive and unspecialized anatomy, and Compsognathidae have sometimes been thought to be paraphyletic, with some compsognathid taxa recovered outside the clade in phylogenetic analyses by Butler & Upchurch (2007), Godefroit et al. (2013a), Choiniere et al. (2014b) and others. Nevertheless, the clade is strongly supported (i.e., united by 18 unambiguous synapomorphies in Brusatte et al., 2014), which is currently the largest and most recent cladistic analyses performed on coelurosaurs. According to Brusatte et al. (2014), compsognathids are diagnosed by a dentition with some unserrated teeth, premaxillary teeth with a subcircular cross-section, the presence of an anterior ramus on the maxilla, a vertically oriented pubis shaft, and ossified sternal plates. In this study, compsognathids include *Juravenator starki* (Chiappe & Göhlich 2010) and *Compsognathus longipes* (Bidar et al. 1972; Ostrom 1978; Peyer 2006; Figure 12A) from the Kimmeridgian-Tithonian of Germany and France, respectively, *Mirischia asymmetrica* (Naish et al. 2004) from the Albian of Brazil, as well as *Huxiagnathus orientalis* (Hwang et al. 2004), *Sinocalliopteryx gigas* (Ji et al. 2007a) and *Sinosauropteryx prima* (Currie & Chen 2001; Ji et al. 2007b) from the Barremian-early Aptian Yixian Formation of China. *Aristosuchus pusillus*, from the Barremian of England, and *Scipionyx samniticus*, from the Albian of Italy, are also considered as compsognathids by some authors (e.g., Naish 2002, 2011; Dal Sasso & Maganuco 2011; Loewen et al. 2013; Choiniere et al. 2014b). The latter taxon is remarkable for being a hatchling specimen preserving exquisitely fossilized soft tissues and internal organs such as intestines,

muscles, and blood vessels (Dal Sasso & Maganuco 2011). Compsognathid feeding behavior is among the best known in non-avian theropods, as stomach contents are preserved in both specimens of *Compsognathus* (Bidar et al. 1972; Ostrom 1976a; Evans 1994; Peyer 2006), *Huxiagnathus* (Hwang et al. 2004), *Scipionyx* (Dal Sasso & Maganuco 2011), and two specimens of *Sinosauropteryx* (Currie & Chen 2001; Ji et al. 2007b) and *Sinocalliopteryx* (Xing et al. 2012). These reveal that compsognathids ingested gastroliths and had an extremely diverse diet composed of fish, lizards, non-avian theropods (dromaeosaurids), primitive birds, and mammals. Similar to more basal tetanurans, evidences of filamentous integument in well-preserved compsognathids such as *Sinosauropteryx* (Currie & Chen 2001) and *Juravenator* (Chiappe & Göhlich 2010) suggest that protofeathers partially or extensively covered the body of these basal coelurosaurs. A recent study on the fossilized melanosomes in *Sinosauropteryx* has also revealed that the tail of this animal had stripes which exhibited chestnut to rufous (reddish-brown) tones (Zhang et al. 2010).

Maniraptoriformes (Holtz 1995), the least inclusive clade containing *Passer domesticus* (Linnaeus 1758) and *Ornithomimus velox* Marsh 1890 (Maryńska et al. 2002), is largely composed of non-strictly-carnivorous theropods that are partially or fully edentulous and/or possess reduced lanceolate crowns, with a few derived maniraptoriforms (i.e., dromaeosaurids) being secondarily carnivorous (Holtz 2012). The first radiation of non-strictly carnivorous (i.e., herbivorous to omnivorous; see Barrett 2005; Zanno & Makovicky 2011; Lee et al. 2014) coelurosaurs were ornithomimosaurids. The latter are small to very large (2-10m long) lightly to heavily built theropods characterized by a low and delicate skull, slender neck, elongate forehands bearing three non-raptorial clawed fingers, and in the ostrich-like ornithomimids long powerful legs that were adapted for rapid locomotion (Russell 1972; Nicholls & Russell 1981; Makovicky et al. 2004; Barrett 2005; Kobayashi & Barsbold 2005a; Liyong et al. 2012; Figure 12B). The jaws of basal ornithomimosaurids bear a large number of small conical teeth, intermediate taxa possess small teeth restricted to the anterior extremity of the dentary and derived forms are fully edentulous, possessing only a rhamphotheca (some

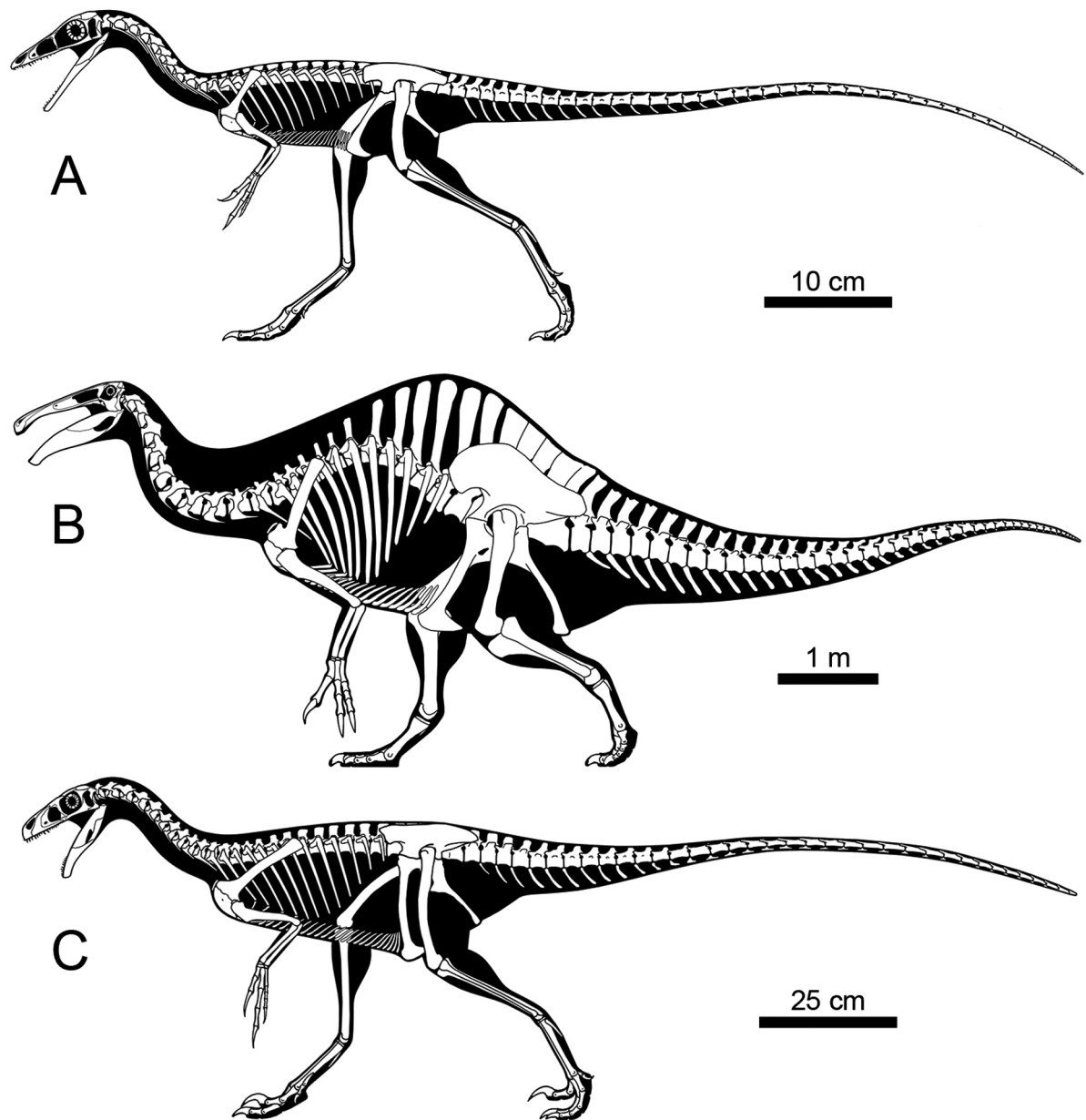


Figure 12. Skeletal reconstructions of three basal maniraptoriforms. A) The compsognathid *Compsognathus longipes*; B) The ornithomimosaur *Deinocheirus mirificus*; C) The basal maniraptoran *Ornitholestes hermanni*. Reconstructions by Scott Hartman.

exhibit columnar structures that may have been used as a filter-feeding system; Norell *et al.* 2001; for an alternative hypothesis, see Barrett 2005). Some derived ornithomimids possessed filamentous protofeathers and possibly long shafted feathers (pennibrachium) on the forearms, forming wings (Zelenitsky *et al.* 2012; for a different opinion see Foth *et al.* 2014). Ornithomimosaur originated in the earliest part of the Cretaceous and the oldest and basalmost member of the clade is *Nqwebasaurus thwazi* from the Berriasian-Valanginian of South Africa (Choiniere *et al.* 2012). *Pelecanimimus poly-*

odon (Pérez-Moreno *et al.* 1994), another basal ornithomimosaur taxon from the Hauterivian of Spain, possessed more than 200 unserrated teeth on the jaws, which makes it the theropod bearing the largest number of teeth. More derived ornithomimosaur with dentulous lower jaws are mostly known from the Valanginian-Albian of China such as *Hexing qingyi* (Liyong *et al.* 2012), *Beishanlong grandis* (Makovicky *et al.* 2010), *Shenzhousaurus orientalis* (Ji *et al.* 2003), and *Harpymimus okladnikovi* (Kobayashi & Barsbold 2005b). Edentulous ornithomimosaur are only known from the Upper Creta-

ceous of Asia and North America, and the best known taxa are *Garudimimus brevipes* (Kobayashi & Barsbold 2005a) and *Sinornithomimus dongi* (Kobayashi and Lü 2003) from the early Late Cretaceous of China, *Ornithomimus edmontonicus* and *Struthiomimus altus* (Russell 1972) from the Campanian-Maastrichtian of Canada, and *Gallimimus bullatus* (Osmólska et al. 1972) and *Deinocheirus mirificus* (Lee et al. 2014; Figure 12B) from the Maastrichtian of Mongolia. The latter was recently revealed to be a very large omnivorous ornithomimosaur with a deep jaw, tall neural spines, elongated forelimbs and short hind limbs. It was recovered as a derived member of a new lineage of Asian ornithomimosaur known as Deinocheiridae (Lee et al. 2014). Deinocheirids, which include *Beishanlong*, *Garudimimus* and *Deinocheirus*, do not seem to be adapted for speed, in contrast to cursorial ornithomimids such as *Gallimimus*, *Struthiomimus* and *Ornithomimus* that are widely interpreted as fast runners (Russell 1972; Thulborn 1990; Lee et al. 2014).

Therizinosauria, Alvarezsauroidea and Oviraptorosauria

Maniraptora (Gauthier 1986), the most-inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Ornithomimus edmontonicus* Marsh 1890 (Maryńska et al. 2002), includes theropods characterized by a well-developed lateral process of the quadrate, a large bony sternum with co-ossified sternal plates, and a semilunate carpal (Holtz 2012; Turner et al. 2012). Many maniraptorans convergently acquired a retroverted pubis superficially similar to ornithischians (Holtz 2012). *Ornitholestes hermanni* (Osborn 1903; Carpenter et al. 2005; Figure 12C) from the Upper Jurassic of North America is either recovered as the basalmost maniraptoran (e.g., Dal Sasso & Maganuco 2011; Novas et al. 2012; Senter et al. 2012b; Turner et al. 2012; Foth et al. 2014) or as a basal coelurosaur closely related to some compsognathids (e.g., Godefroit et al. 2013a; Choiniere et al. 2014b). The basalmost clade within Maniraptora is the Alvarezsauroidea (Figure 5). Alvarezsauroids were small (1-2.5m long) coelurosaurs characterized by a gracile and low skull with large cranial openings, elongate rostrum, and slender jaws bearing a large number of teeth that are, at least for some crowns, lanceolate (Figure 13A). The forelimbs of alvarezsau-

roids bear three fingers in which digit II and III are reduced in size and were even lost in some derived taxa (Perle et al. 1993; Chiappe et al. 1998; Longrich & Currie 2009a; Choiniere et al. 2010b, 2014a; Nesbitt et al. 2011; Xu et al. 2011b). The basalmost member is *Haplocheirus sollers* from the Oxfordian of China; all alvarezsauroids more derived than *Haplocheirus* belong to Alvarezsauridae (Choiniere et al. 2010a, 2014a). Alvarezsaurids are restricted to the Late Cretaceous of North-America, South-America, Asia, and Europe (Naish and Dyke 2004; Longrich & Currie 2009a; Agnolín et al. 2012; Xu et al. 2013). They comprise taxa with a large number of minute and lanceolate crowns, short forelimbs bearing either a single first digit, or a hypertrophied thumb, in both case ended by a massive claw used for digging, a pubis oriented backward, and elongated hind limbs adapted for cursoriality. The best known members are *Patagonykus puertai* (Novas 1997a) from the Turonian-Coniacian of Argentina, and the parvicursorines *Xixianykus zhengi* (Xu et al. 2010b) and *Linhenykus monodactylus* (Xu et al. 2011b, 2013) from the Coniacian-Santonian and Campanian of China, respectively, and *Mononykus olecranus* (Perle et al. 1993, 1994), *Shuvuuia deserti* (Chiappe et al. 1998; Suzuki et al. 2002; Figure 13A), and *Ceratonykus oculatus* (Alifanov & Barsbold 2009) from the Campanian-Maastrichtian of Mongolia. At least one member of this group (i.e., *Shuvuuia*) possessed filamentous integuments similar to those of more primitive tetanurans (Schweitzer et al. 1999).

Therizinosauroids are small to very large (2-10m long) 'prosauropod'-like theropods characterized by a small head bearing reduced and basally constricted crowns, an elongated neck, long and robust arms terminated by large claws, broad abdomen and pelvis, and a relatively vertical position of the body (Barsbold & Perle 1980; Clark et al. 2004; Zanno 2010a, b; Lautenschlager et al. 2014; Figure 13B). Therizinosauroids seem to be restricted to North America and Asia in the Cretaceous, yet the therizinosauroid *Eshanosaurus deguchiianus*, said to be found in the Lower Lufeng Formation of the Yunnan Province, China, may attest to the presence of the clade back to the Lower Jurassic (Zhao & Xu 1998; Xu et al. 2001a). However, given the fact that the time separating this taxon from the most basal therizinosauroid is anomalous, an Early Jurassic age of *Eshanosaurus* requires confirma-

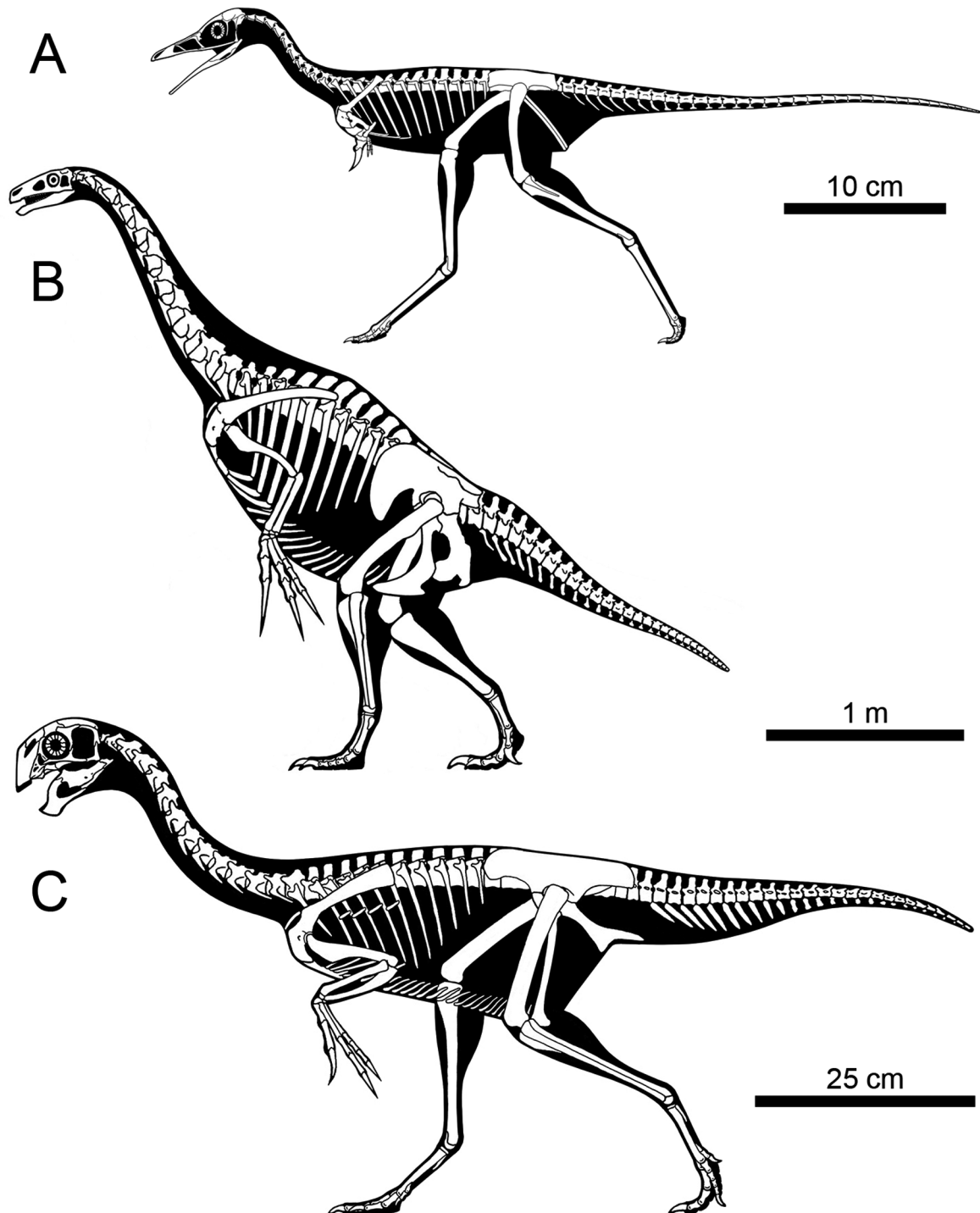


Figure 13. Skeletal reconstructions of three basal maniraptorans. A) The alvarezsauroid *Shuvuuia deserti*; B) The therizinosauroid *Nothronychus graffami*; C) The oviraptorosaur *Khaan mangas*. Reconstructions by Scott Hartman.

tion (Kirkland *et al.* 2005; Barrett 2009). The most primitive known member is currently *Falcaricus utahensis* (Zanno 2006, 2010b) from the Barremian of Utah. *Jianchangosaurus yixianensis* (Pu *et al.* 2013) and *Beipiaosaurus inexpectus* (Xu *et al.* 1999a) are two basal therizinosauroids from the Early Cretaceous (Barremian?) of Chi-

na that are slightly more derived than *Falcaricus*. The body of these two primitive therizinosauroids was covered with filamentous integument (Xu *et al.* 2009a; Pu *et al.* 2013), which suggests that most, if not all, therizinosauroids had protofeathers. Therizinosauroid taxa more derived than *Jianchangosaurus* form the clade Therizinosau-

roidea (Pu *et al.* 2013). *Jianchangosaurus* and therizinosauroids share a downturned anterior extremity of the dentary, large apically inclined denticles of the crowns, and an edentulous premaxilla bearing a rhamphotheca (which may not be present in *Falcarius*). Derived therizinosauroids (therizinosaurids *sensu* Zanno *et al.* 2009; Table 1) possess important basicranial pneumaticity, long scythe-like manual unguals, and a flattened pubic shaft (Zanno 2010a). The best known therizinosauroids are *Alxasaurus elesitaiensis* (Russell & Dong 1993) from the Albian of China, *Nothronychus graffami* (Zanno *et al.* 2009; Figure 13B) from the Turonian of Utah, *Erlikosaurus andrewsi* and *Segnosaurus galbinensis* (Barsbold & Perle 1980; Barsbold 1983; Clark *et al.* 1994; Lautenschlager *et al.* 2014) from the Cenomanian-Turonian of Mongolia, and *Neimongosaurus yangi* (Zhang *et al.* 2001) from the Campanian-Maastrichtian of China (Zanno 2010a).

The clade containing theropods more derived than therizinosauroids, including Oviraptorosauria and Paraves, has recently been named Pennaraptora based on definitive evidence of pennaceous feathers in multiple pennaraptoran taxa (Foth *et al.* 2014). Oviraptorosauria is a well-supported clade of small to large (1–8m long) theropods easily recognized by their short skulls with parrot-like beaks, forelimbs with elongated manual fingers, and short tails (Clark *et al.* 2001; Osmólska *et al.* 2004; Balanoff *et al.* 2009; Longrich *et al.* 2010; Balanoff & Norell 2012; Lamanna *et al.* 2014; Figure 13C). Oviraptorosaurs are restricted to the Cretaceous of Asia, North America and possibly South America (Frey & Martill 1995; Frankfurt & Chiappe 1999; for a different opinion, see Agnolín & Martinelli 2007), and most taxa come from Campanian-Maastrichtian deposits. Members of this clade were partially to strictly herbivorous coelurosaurs who adopted an avian-like brooding posture on their nests (Clark *et al.* 1999; Varricchio *et al.* 2008; Zanno & Makovicky 2011). Similar to ornithomimosaurs, basal oviraptorosaurs retained teeth that were subsequently lost in more derived taxa; the majority of oviraptorosaur taxa, which form the clade Caenagnathoidea, were edentulous. The basal-most oviraptorosaur is currently *Incisivosaurus gauthieri* from the Aptian of China (Balanoff *et al.* 2009). *Incisivosaurus* shows the primitive condition of having dentulous maxillae

and dentaries, and the peculiarity of bearing premaxillary teeth that are much larger than the lateral teeth (Xu *et al.* 2002a; Balanoff *et al.* 2009). Contemporaneous, yet more derived, non-caenagnathoid oviraptorosaurs such as *Caudipteryx zoui* and *Similicaudipteryx yixianensis* from China retained only premaxillary teeth, and several well-preserved specimens possessed branching feathers such as remiges on the forelimbs, and rectrices on the caudal vertebrae (Ji *et al.* 1998; Zhou *et al.* 2000; He *et al.* 2008; Xu *et al.* 2010a). This suggests that some, if not all oviraptorosaurs had feathered bodies and wings, yet they appear entirely flightless. Caenagnathoidea is divided into two main subclades, Oviraptoridae and Caenagnathidae (Osmólska *et al.* 2004; Longrich *et al.* 2013; Lamanna *et al.* 2014). Caenagnathids are characterized by fused dentaries and long, shallow pneumatized mandibles, whereas oviraptorids had deep lower jaws and an external naris extending back and over the antorbital fenestra (Longrich *et al.* 2013). Oviraptorids such as *Khaan mckennai* (Clark *et al.* 1999; Balanoff & Norell 2012; Figure 13C) inhabited xeric environments (i.e., deserts) whereas caenagnathids occurred in fluvial-dominated and coastal floodplain environments (Longrich *et al.* 2013). Taxa from both clades convergently acquired cranial crests, as shown in *Citipati osmolskae* (Clark *et al.* 2002), *Nemegtomaia barsboldi* (Lü *et al.* 2004), and *Anzu wyliei* (Lamanna *et al.* 2014).

Paraves

The remaining maniraptorans, comprising birds and two non-avian theropod clades traditionally labeled deinonychosaurs, are grouped within Paraves (Figure 5). The latter is defined as the most inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Oviraptor philoceratops* (Holtz & Osmólska 2004). Deinonychosauria, on the other hand, is either defined as a node-based clade containing the last common ancestor of *Troodon formosus* and *Velociraptor mongoliensis* and all of its descendants (Turner *et al.* 2012), or the most-inclusive clade containing *Dromaeosaurus albertensis* but not *Passer domesticus* (Linnaeus 1758) (Godefroit *et al.* 2013a). Deinonychosaurs are typically divided into Dromaeosauridae and Troodontidae, theropods that share a raptorial sickle-shaped claw on the hyperextendable pedal digit II (Holtz 2012; Turner *et al.* 2012). Deinonychosauria was con-

sidered a well-supported clade until recently (e.g., Turner *et al.* 2012), but newly discovered basal paravians and the description of additional specimens of *Archaeopteryx* (Mayr *et al.* 2005; Foth *et al.* 2014) have led to analyses that find troodontids more closely related to avialans than to dromaeosaurids, rendering the taxon Deinonychosauria paraphyletic or equivalent to Dromaeosauridae, depending on the phylogenetic definition given to this clade (e.g., Godefroit *et al.* 2013a; Brusatte *et al.* 2014; Choiniere *et al.* 2014b; Foth *et al.* 2014; Figure 5).

Dromaeosaurids are the only definitively carnivorous maniraptoriforms (with perhaps the exception of *Ornitholestes*). They share unconstricted ziphodont teeth and a hinge joint (ginglymus) on the distal end of metatarsal II that permits an extended range of motion in the second toe and its hypertrophied and highly modified claw (Norell & Makovicky 2004; Turner *et al.* 2012). Dromaeosaurids are a widespread group of very small to large bodied (0.6-7m long) paravians that were present on all continents by the Late Cretaceous. Although isolated teeth from the Late Jurassic of Europe have been assigned to members of this clade (e.g., Zinke 1998; Lubbe *et al.* 2009; Hendrickx & Mateus 2014b) and the presence of dromaeosaurids in the Jurassic is evidenced by the appearance of closely related paravians in the Late Jurassic (Figure 1), definitive dromaeosaurids currently range from the Barremian (China) to the Maastrichtian (North America). A large array of evidence indicates that some, and most likely all Dromaeosauridae were covered with filamentous integuments, and at least two dromaeosaurid taxa (i.e., *Microraptor* and *Changyuraptor*) possessed four wings (i.e., pennaceous fore- and hind limbs) with branching feathers like those seen in extant birds (Xu *et al.* 1999b, 2001b, 2003; Ji *et al.* 2001; Turner *et al.* 2007; Han *et al.* 2014). The majority of recent phylogenetic analyses performed on paravians typically recover three dromaeosaurid subclades: Unenlagiinae, Microraptorinae, and Eudromaeosauria (e.g., Senter *et al.* 2012b; Turner *et al.* 2012; Brusatte *et al.* 2014; Choiniere *et al.* 2014b; Foth *et al.* 2014). A different topology was obtained by Agnolín & Novas (2013) who found Microraptorinae and Unenlagiinae outside Dromaeosauridae and gathered within the new clade 'Averaptora' with Avialae, a configuration not recovered by other theropod workers.

Although Agnolín & Novas (2011, 2013) have defended an avialan affinity of unenlagiines, it is commonly accepted that Unenlagiinae was the first dromaeosaurid radiation and is the most basal lineage of Dromaeosauridae. These primitive dromaeosaurids are characterized by an elongate rostrum, unserrated teeth, and a vertically oriented pubis (Gianechini & Apesteguía 2011; Gianechini *et al.* 2011; Turner *et al.* 2012; Figure 14A). They are exclusively found in the Upper Cretaceous of Gondwana, and are mostly known from South America. The best preserved forms are *Buitreraptor gonzalezorum* from the Cenomanian (Makovicky *et al.* 2005; Figure 13A), *Unenlagia comahuensis* from the Turonian-Coniacian (Novas & Puerta 1997), *Austroraptor cabazai* from the Maastrichtian of Argentina (Novas *et al.* 2009), and *Rahonavis ostromi* from the Maastrichtian of Madagascar (Forster *et al.* 1998; Turner *et al.* 2012).

The remaining dromaeosaurids are distributed among three subclades, Microraptorinae ('Microraptoria' *sensu* Senter *et al.* 2004, 2012b), Velociraptorinae and Dromaeosaurinae (Turner *et al.* 2012; Figure 5). As suggested by the etymology, microraptorines were small to very small (0.6-2m long) dromaeosaurids thought to have aerial or subaerial abilities (i.e., gliding, powered flight, or other semi-aerial locomotion) that are known from the Early to Late Cretaceous of China and North America (Xu *et al.* 2003; Longrich & Currie 2009b; Han *et al.* 2014). The best preserved members of this clade, all from the Early Cretaceous of Liaoning in China, are *Microraptor* sp. (Hwang *et al.* 2002; Xu *et al.* 2003; O'Connor *et al.* 2011; Xing *et al.* 2013b), *Sinornithosaurus millenii* (Xu *et al.* 1999b; Xu and Wu 2001; Gong *et al.* 2010), *Tianyuraptor ostromi* (Zheng *et al.* 2010), and *Changyuraptor yangi* (Han *et al.* 2014). *Hesperonychus elizabethae*, from the Campanian of Alberta, is the youngest known microraptorine, and the only one found outside China (Longrich & Currie 2009b). Velociraptorinae includes North American, Asian and possibly European dromaeosaurids, which are characterized by pleurocoels in all dorsal vertebrae (Turner *et al.* 2012). Velociraptorines encompass the famous theropods *Velociraptor mongoliensis* from the Campanian of Mongolia (Sues 1977; Norell & Makovicky 1997, 1999; Barsbold and Osmólska 1999), *Deinonychus antirrhopus* from the Aptian-Albian of Montana (Ostrom 1969, 1976b), and *Bambi-*

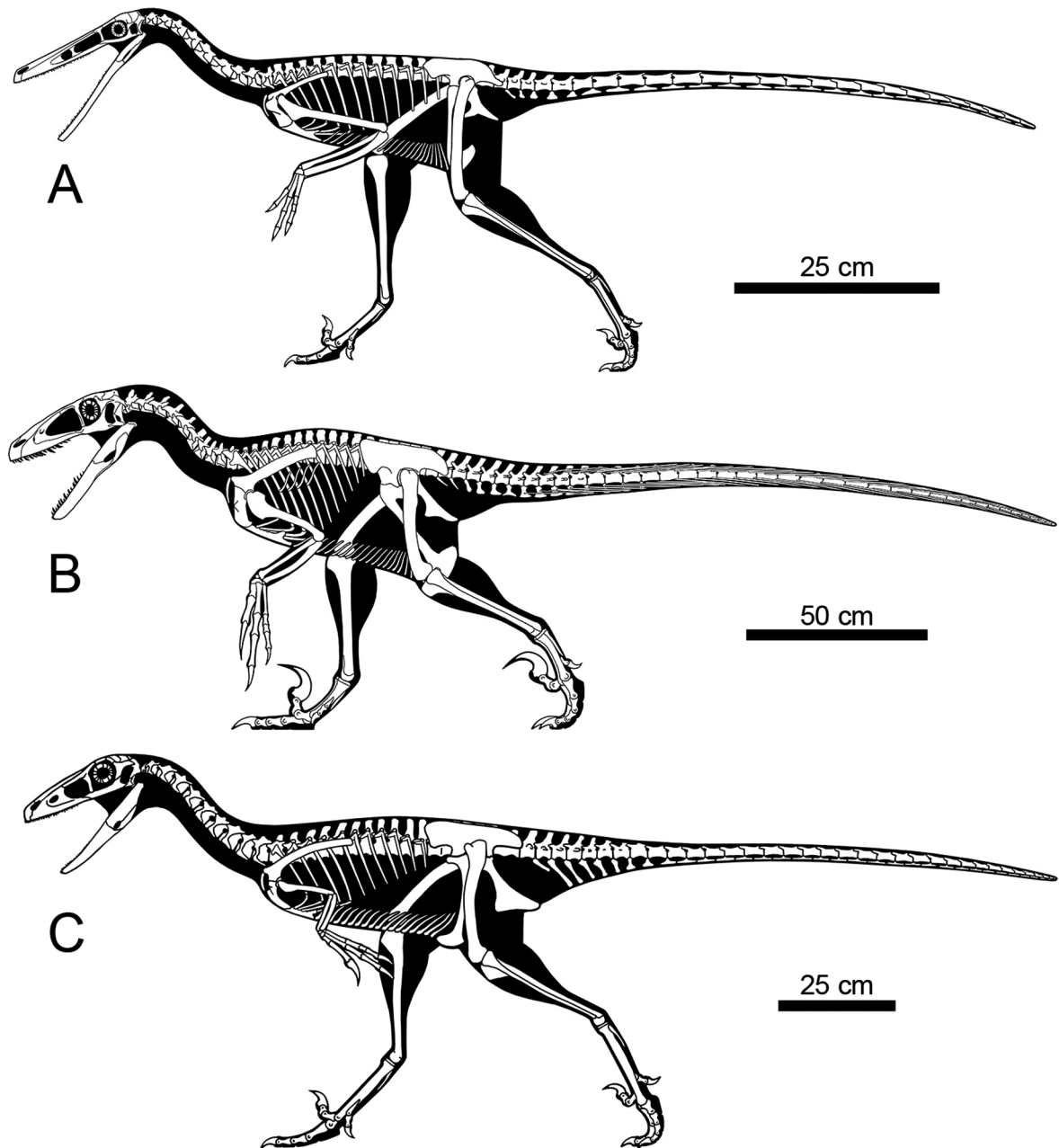


Figure 14. Skeletal reconstructions of three basal paravians. A) The unenlagiine dromaeosaurid *Buitreraptor gonzalezorum*; B) The velociraptorine dromaeosaurid *Deinonychus antirrhopus*; C) The troodontid *Troodon formosus*. Reconstructions by Scott Hartman.

raptor feinbergi from the Campanian of Montana (Burnham *et al.* 2000; Burnham 2004). While *Balaur bondoc*, from the Maastrichtian of Romanian, may represent the only definitive velociraptorine from Europe (Csiki *et al.* 2010; Brusatte *et al.* 2013, 2014), two recent large scale phylogenetic analyses on coelurosaurs recovered it as a basal avialan (i.e., Godefroit *et al.* 2013a; Foth *et al.* 2014) and the position of this taxon among paravians remains unclear. Dromaeosaurinae, the remaining subclade of

dromaeosaurids, includes small to large-sized theropods with a lateral dentition bearing mesial denticles, a ventrodorsally tall jugal process of the maxilla, and a vertically oriented pubis (Turner *et al.* 2012). This clade is mostly comprised by North American dromaeosaurid taxa such as *Utahraptor ostrommaysi* from the Barremian of Utah (Kirkland *et al.* 1993), *Dromaeosaurus albertensis* (Colbert & Russell 1969; Currie 1995; Figure 14B) and *Atrociraptor marshalli* (Currie & Varricchio 2004) from the Campanian

of Alberta. *Achillobator gigantibus* (Perle et al. 1999) from the Cenomanian-Santonian of Mongolia also attests the presence of dromaeosaurines in central Asia in the Late Cretaceous.

Troodontidae is a clade of lightly built non-avian maniraptorans with taxa that rank among the smallest non-avian body sizes and the highest encephalization quotients (Makovicky & Norell 2004; Lü et al. 2010; Zanno et al. 2011; Tsuihiji et al. 2014). Troodontids share an anteroventrally inclined quadrate and jaws with a large number of small, constricted teeth set in an open groove in the dentary (Makovicky & Norell 2004; Turner et al. 2012). The crowns are unserrated in basalmost forms and bear very large hooked denticles in derived taxa, which suggests an herbivorous diet in primitive troodontids and a carnivorous or omnivorous diet in advanced forms bearing serrated teeth (Currie 1987; Holtz et al. 1998; Currie & Dong 2001; Lü et al. 2010; Zanno & Makovicky 2011). Troodontids are known from the Cretaceous of Asia, North America, Europe, and possibly from the Late Jurassic of China, depending on the troodontid affinities of newly discovered forms such as *Anchiornis*, *Xiaotingia*, and *Eosinopteryx* (Makovicky & Norell 2004; Hu et al. 2009; Vullo & Néraudeau 2010; Xu et al. 2011a; Turner et al. 2012; Godefroit et al. 2013b; Brusatte et al. 2014). Isolated teeth from the Late Jurassic of North America and Portugal, and the Late Cretaceous of India, have also been assigned to Troodontidae (Chure 1994; Zinke 1998; Goswami et al. 2013). If *Troodon formosus* from the Campanian of Canada is the most famous troodontid and the first to be discovered (Russell 1948; Currie 1985, 1987; Currie & Zhao 1993b; Figure 14C), the best preserved troodontid taxa all come from the Cretaceous of Asia. They include *Sinuso nasus magnodens* (Xu & Wang 2004), *Mei long* (Xu & Norell 2004; Gao et al. 2012), and *Sinovenator changii* (Xu et al. 2002b) from the Early Cretaceous of China, and *Byronosaurus jaffei* (Norell et al. 2000; Makovicky et al. 2003), *Gobivenator mongoliensis* (Tsuihiji et al. 2014), *Saurornithoides mongoliensis* and *Zanabazar junior* (Barsbold 1974; Norell et al. 2009) from the Campanian of Mongolia.

The recent discovery of a large number of paravian taxa closely related to birds such as *Anchiornis huxleyi* (Hu et al. 2009; Figure 15A), *Xiaotingia zhengi* (Xu et al. 2011a), *Aurornis xui* (Godefroit et al. 2013a), and *Eosinopteryx brevi-*

penna (Godefroit et al. 2013b), all from the Middle to Late Jurassic of the Tiaojishan Formation of China, have brought new data to bear on the relationships of the earliest avian theropods. According to two of the most recent phylogenetic analyses (e.g., Godefroit et al. 2013a; Foth et al. 2014), the latter taxa are gathered within Avialae, the most-inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Dromaeosaurus albertensis* Matthew & Brown 1922 or *Troodon formosus* Leidy 1856 (Godefroit et al. 2013a). Yet, these taxa were recovered in the same clade at the base of Troodontidae in another large scaled phylogenetic analyses (i.e., Brusatte et al. 2014), and their exact position among paravians remains unsettled. For decades, the most basal and earliest avialan taxon was considered to be *Archaeopteryx* sp. (Figure 15B), but with the inclusion of these recently reported paravians from the Tiaojishan Formation into cladistic analyses, *Archaeopteryx*'s systematic position has become uncertain. Currently, *Archaeopteryx* is either recovered as the basalmost avialan (e.g., Turner et al. 2012; Agnolín & Novas 2013; Brusatte et al. 2014a; Choiniere et al. 2014b), a deinonychosaur closely related to troodontids and dromaeosaurids (e.g., Xu et al. 2011a; Godefroit et al. 2013b; Xu & Pol 2014), or an avialan theropod more derived than the basalmost avialans *Aurornis* and *Anchiornis* (e.g., Godefroit et al. 2013a; Foth et al. 2014). The anatomical distinctions between non-avian and avian theropods are, therefore, particularly subtle and vary according to the phylogenetic analysis performed by authors. For instance, in one of the largest and most recent cladistic analyses provided by Foth et al. (2014) on coelurosaurs, avialan synapomorphies include the presence of roots of dentary teeth subcircular in cross-section, extensive contact between pubes, humerus and femur subequal in thickness, and dorsal margin of the antorbital fossa formed by lacrimal and nasal. In another large scaled phylogenetic analysis on coelurosaurs performed by Brusatte et al. (2014a), Avialae are diagnosed by asymmetrical feathers on forelimbs, unfused parietals, less than 26 caudal vertebrae, a dorsal margin of the antorbital fossa formed by lacrimal and nasal, and a humerus longer than the femur.

A similar situation occurs with Scansoriopterygidae and their unsettled phylogenetic position within Pennaraptora. Scansoriopterygids

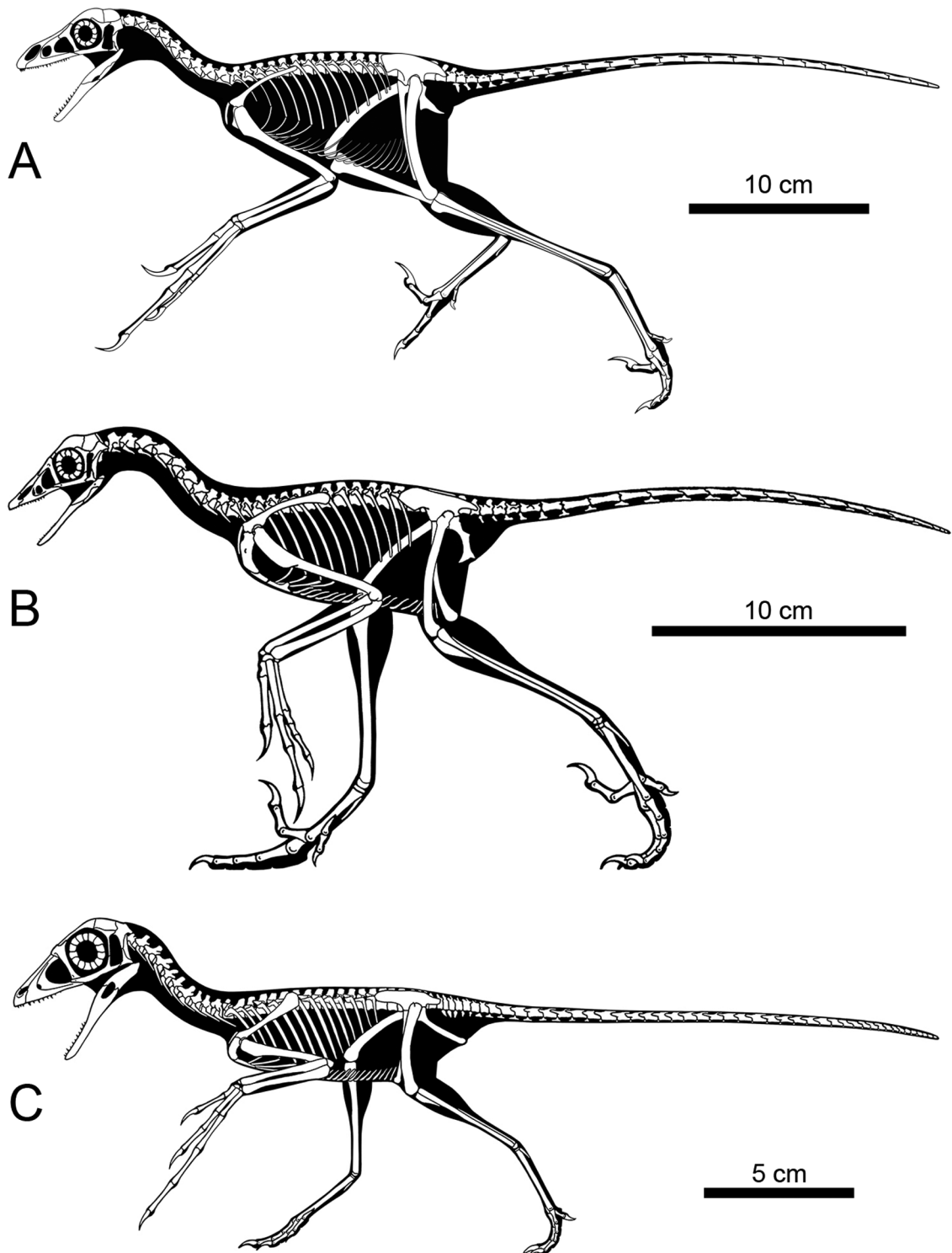


Figure 15. Skeletal reconstructions of three basal avialan? theropods. A) The basal avialan *Anchiornis huxleyi*; B) The archaeopterygid *Archaeopteryx* sp.; C) The scansoriopterygid *Epidendrosaurus ninchengensis*. Reconstructions by Ville Sinkkonen for *Anchiornis* and Scott Hartman for *Archaeopteryx* and *Epidendrosaurus*.

form an aberrant subclade of very small-sized maniraptorans (the only subadult specimen of Scansoriopterygidae has a body length of less than 30 centimeters; Zhang *et al.* 2008) characterized by a short and high skull, a small number of procumbent teeth restricted to the anterior portion of the jaws, propubic pelvis, and elongated ribbon-like tail-feathers (Zhang *et al.* 2002, 2008; Agnolín & Novas 2013). Their distinctive feature is, however, the slender and hypertrophied manual digit III which suggests climbing ability and arboreal habits (Zhang *et al.* 2008) or gathering strategy (as the living Ayes Ayes which uses its elongated fingers to pull bugs out of trees; Lhota *et al.* 2008). This clade currently includes two or three taxa from the Middle Jurassic Daohugou beds (Tiaojishan Formation; Zhou *et al.* 2013) of Ningcheng, Inner Mongolia, China: *Epidendrosaurus nинchen-gensis* (= *Scansoriopteryx heilmanni*; Padian 2004; Figure 15C) known from a partial skeleton (Zhang *et al.* 2002), *Epidexipteryx hui*, the most complete scansoriopterygid preserving a complete skull (Zhang *et al.* 2008), and possibly *Pedopenna daohugouensis* known from a partial right leg covered with pennaceous feathers (Xu and Zhang 2005). Scansoriopterygids are currently recovered as basal Oviraptorosauria (Agnolín & Novas 2013; Brusatte *et al.* 2014), basal Paraves (Godefroit *et al.* 2013a, b), and basal Avialae (Zhang *et al.* 2008; Choiniere *et al.* 2010b; Novas *et al.* 2012; Senter *et al.* 2012b). The clade is also found unresolved by some workers (*e.g.*, Turner *et al.* 2012).

Conclusions

Theropod dinosaurs form one of the most successful and morphologically diverse groups of tetrapods, surviving the Cretaceous-Paleogene extinction event and radiating as birds in the Cenozoic. Even before the K-Pg extinction non-avian theropods were an extremely diverse group of archosaurs with complex interrelationships. The adoption of cladistic techniques in the 1980s was a major step in the study of theropod phylogenetics; modern analyses currently recover around 25 non-

avian theropod subclades, most in a ladder-like organization. While a consensus of higher-level theropod relationships has emerged and the systematics of non-avian theropods seems to be relatively well understood, some significant points of contention remain. Newly discovered non-avian theropods will hopefully shed light on the systematic position of herrerasaurids within saurischians, megaraptorans within avetheropods, scansoriopterygids within pennaraptorans, and troodontids within paravians. Though one might expect few major changes in theropod relationships in the future, large portions of theropod phyletic history remain obscure; future discoveries of theropods in the Jurassic of Australia or the Cretaceous of Antarctica, where theropod faunas are almost unknown, may change the current view of non-avian theropod systematics dramatically.

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Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Abelosauridae Bonaparte and Novas 1985	Novas 1997b	<i>Abelisaurus comahuensis</i> , <i>Carnotaurus sastrei</i> , <i>Xenotarsosaurus bonapartei</i> , <i>Indosaurus matleyi</i> , <i>Indosuchus raptorius</i> , <i>Majungasaurus crenatissimus</i> and all descendants of their common ancestor	Stem-based	The most inclusive clade containing <i>Carnotaurus sastrei</i> but not <i>Noasaurus leali</i>	Wilson et al. 2003
Abelisauroidea (Bonaparte and Novas 1985) Bonaparte 1991a	Holtz 1994	Abelisauroids and those members of the <i>Ceratosaurs</i> -Abelosauridae clade which shared a more recent common ancestry than with the North American genus [<i>Ceratosaurs</i>]	Node-based	The least inclusive clade containing <i>Carnotaurus sastrei</i> and <i>Noasaurus leali</i>	Sereno 2005
Afrovenatorinae Carrano et al. 2012	Carrano et al. 2012	All megalosaurids more closely related to <i>Afrovenator</i> than to <i>Megalosaurus</i>	Stem-based	The most inclusive clade containing <i>Afrovenator abakensis</i> but not <i>Megalosaurus bucklandii</i>	Carrano et al. 2012
Allosauria (Marsh 1878) Paul 1988	/	/	Stem-based	The most inclusive clade containing <i>Allosaurus fragilis</i> and <i>Carcharodontosaurus saharicus</i> but not <i>Sinraptor dongi</i>	New
Allosauridae Marsh 1878	Padian and Hutchinson 1997	<i>Allosaurus</i> and all Allosauroidea closer to it than to <i>Sinraptor</i>	Stem-based	The most inclusive clade containing <i>Allosaurus fragilis</i> but not <i>Sinraptor dongi</i> , <i>Carcharodontosaurus saharicus</i> , and <i>Passer domesticus</i>	Sereno 2005
Allosauroidea (Marsh 1878) Currie & Zhao 1993a	Padian and Hutchinson 1997	<i>Allosaurus</i> and <i>Sinraptor</i> and all descendants of their most recent common ancestor (Node-based definition)	Stem-based	The most inclusive clade containing <i>Allosaurus fragilis</i> but not <i>Passer domesticus</i>	Sereno 2005

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Alvarezsauridae Bonaparte 1991b	Sereno 1998	All ornithomimosaurids closer to <i>Shuvuuia</i> than to <i>Ornithomimus</i> (Stem-based definition)	Node-based	The least inclusive clade containing <i>Alvarezsaurus cabvoi</i> and <i>Mononykus olecranus</i>	Modified from Choiniere et al. 2010b
Alvarezsauridae Bonaparte 1991b	Livezey and Zusi 2007	Clade containing <i>Patagonykus</i> , <i>Alvarezsaurus</i> and <i>Mononykus</i>	Stem-based	The most inclusive clade containing <i>Alvarezsaurus cabvoi</i> but not <i>Passer domesticus</i>	Modified from Choiniere et al. 2010b
Averostra Paul 2002 (<i>sensu</i> Ezcurra 2006)	Paul 2002	[All] ceratosaurs, megalosaurs, and abelisaurids	Node-based	The least inclusive clade containing <i>Ceratopsaurus nasicornis</i> and <i>Passer domesticus</i>	Allain et al. 2012
Avetheropoda Paul 1988	Padian et al. 1999	The most recent common ancestor of Neornithes and <i>Allosaurus</i> and all descendants of that ancestor.	Node-based	The least inclusive clade containing <i>Allosaurus fragilis</i> and <i>Passer domesticus</i>	Modified from Holtz et al. 2004
Avialae Gauthier 1986	Gauthier 1986	Ornithurae plus all extinct maniraptorans that are closer to Ornithurae than they are to Deinonychosauria	Stem-based	The most-inclusive clade containing <i>Passer domesticus</i> but not <i>Dromaeosaurus albertensis</i> or <i>Troodon formosus</i>	Maryńska et al. 2002
Baryonychinae (Charig & Milner 1986) Sereno et al. 1998	Sereno et al. 1998	All spinosaurids that are more closely related to <i>Baryonyx</i> than to <i>Spinosaurus</i>	Stem-based	The most inclusive clade containing <i>Baryonyx walkeri</i> but not <i>Spinosaurus aegyptiacus</i>	Holtz et al. 2004
Brachyrostra Canale et al. 2009	Canale et al. 2009	All the abelisaurids more closely related to <i>Carnotaurus sastrei</i> than to <i>Majungasaurus crenatissimus</i>	Stem-based	The most inclusive clade containing <i>Carnotaurus sastrei</i> but not <i>Majungasaurus crenatissimus</i>	Modified from Canale et al. 2009

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Caenagnathidae Sternberg 1940	Sues 1997	<i>Caenagnathus pergracilis</i> , <i>Chirostenotes elegans</i> , " <i>Elmisaurus rarus</i> ", <i>Caenagnathasia martinsoni</i> , and the most recent common ancestor of the aforementioned taxa (Node-based definition)	Stem-based	The most inclusive clade containing <i>Caenagnathus collinsi</i> but not <i>Oviraptor philoceratops</i>	Maryńska et al. 2002
Caenagnathinae (Sternberg 1940) Paul 1988	Longrich et al. 2013	All species closer to <i>Caenagnathus collinsi</i> than either <i>Caenagnathasia martinsoni</i> or <i>Elmisaurus elegans</i>	Stem-based	The most inclusive clade containing <i>Caenagnathus collinsi</i> but not <i>Elmisaurus rarus</i>	Modified from Longrich et al. 2013
Caenagnathoidea (Sternberg 1940) Sereno 1998	Sereno 1998	Oviraptor, <i>Caenagnathus</i> , their most recent common ancestor and all descendants	Node-based	The least inclusive clade containing <i>Oviraptor philoceratops</i> and <i>Caenagnathus collinsi</i>	Modified from Sereno 2005
Carcharodontosauria (Stromer 1931) Benson et al. 2010	Benson et al. 2010	The most inclusive clade comprising <i>Carcharodontosaurus saharicus</i> and <i>Neovenator salerii</i> but not <i>Allosaurus fragilis</i> or <i>Sinraptor dongi</i>	Stem-based	The most inclusive clade containing <i>Carcharodontosaurus saharicus</i> and <i>Neovenator salerii</i> but not <i>Allosaurus fragilis</i> or <i>Sinraptor dongi</i>	Benson et al. 2010
Carcharodontosauridae Stromer 1931	Sereno 1998	All allosauroids closer to <i>Carcharodontosaurus</i> than to either <i>Allosaurus</i> , <i>Monolophosaurus</i> , <i>Cryolophosaurus</i> , or <i>Sinraptor</i>	Stem-based	The most inclusive clade containing <i>Carcharodontosaurus saharicus</i> but not <i>Neovenator dongi</i> , <i>Allosaurus fragilis</i> or <i>Sinraptor dongi</i>	Benson et al. 2010
Carcharodontosaurinae (Stromer 1931) Carrano et al. 2012	Brusatte & Sereno 2008	The least inclusive clade containing <i>Carcharodontosaurus saharicus</i> and <i>Giganotosaurus carolinii</i>	Node-based	The least inclusive clade containing <i>Carcharodontosaurus saharicus</i> and <i>Giganotosaurus carolinii</i>	Brusatte & Sereno 2008

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Carnosaurinae Sereno 1998	Sereno 1998	All abelisaurids closer to <i>Carnotaurus</i> than to <i>Abelisaurus</i>	Stem-based	The most inclusive clade containing <i>Carnotaurus sastrei</i> but not <i>Skorpiovenator bustingorryi</i>	Modified from Sereno 1998
Caudipteridae Zhou and Wang 2000	/	/	Stem-based	The most inclusive clade containing <i>Caudipteryx zouii</i> but not <i>Oviraptor philoceratops</i> and <i>Caenagnathus collinsi</i>	New
Ceratosauria Marsh 1884b	Rowe and Gauthier 1990	The group including <i>Ceratopsaurus nasicornis</i> , <i>Dilophosaurus wetherilli</i> , <i>Liliensternus liliensis</i> , <i>Coelophysis bauri</i> , <i>Syntarsus rhodesiensis</i> , <i>Syntarsus kayentakatae</i> , <i>Segisaurus halli</i> , <i>Sarcosaurus woodi</i> , and all other taxa stemming from their most recent common ancestor	Stem-based	The most inclusive clade containing <i>Ceratopsaurus nasicornis</i> but not <i>Passer domesticus</i>	Sereno 2005 <i>sensu</i> Holtz and Padian 1995
Ceratosauridae Marsh 1884b	Rauhut 2004b	Clade containing all ceratosaurs that are more closely related to <i>Ceratopsaurus</i> than to abelisaurids	Stem-based	The most inclusive clade containing <i>Ceratopsaurus nasicornis</i> but not <i>Carnotaurus sastrei</i> and <i>Noasaurus leali</i>	Modified from Rauhut 2004b
Coelophysidae (Nopcsa 1928) Paul 1988	Sereno 1998	<i>Coelophysis</i> , <i>Procompsognathus</i> , their most recent common ancestor and all descendants	Node-based	The least inclusive clade containing <i>Coelophysis bauri</i> and <i>Procompsognathus triassicus</i>	Sereno 1998
Coelophysoidea (Nopcsa 1928) Holtz 1994	Sereno 1998	All ceratosaurs closer to <i>Coelophysis</i> than to <i>Carnotaurus</i>	Stem-based	The most inclusive clade containing <i>Coelophysis bauri</i> but not <i>Carnotaurus sastrei</i> , <i>Ceratopsaurus nasicornis</i> , and <i>Passer domesticus</i>	Sereno 2005

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Coeluridae Marsh 1881	/	/	Stem-based	The most inclusive clade containing <i>Coelurus fragilis</i> but not <i>Proceratosaurus bradleyi</i> , <i>Tyrannosaurus rex</i> , <i>Allosaurus fragilis</i> , <i>Compsognathus longipes</i> , <i>Ornithomimus edmontonicus</i> and <i>Deinonychus antirrhopus</i>	New
Coelurosauria Huene 1914c	Gauthier 1986	Birds and all other theropods that are closer to birds than they are to Carnosauria	Stem-based	The most inclusive clade containing <i>Passer domesticus</i> but not <i>Allosaurus fragilis</i> , <i>Sinraptor dongi</i> and <i>Carcharodontosaurus saharicus</i>	Sereno 2005
Compsognathidae Cope 1871	Holtz et al. 2004	<i>Compsognathus longipes</i> and all taxa sharing a more recent common ancestor with it than with <i>Passer domesticus</i>	Stem-based	The most inclusive clade containing <i>Compsognathus longipes</i> but not <i>Passer domesticus</i>	Holtz et al. 2004
Deinocheiridae Osmólska and Roniewicz 1970	Lee et al. 2014	<i>Deinocheirus mirificus</i> and all taxa sharing a more recent common ancestor with it than with <i>Ornithomimus velox</i>	Stem-based	The most inclusive clade containing <i>Deinocheirus mirificus</i> but not <i>Ornithomimus velox</i>	Lee et al. 2014
Deinonychosauria Colbert & Russell 1969	Padian 1997	All maniraptorans closer to <i>Deinonychus</i> than to birds (Stem-based definition)	Node-based	The least inclusive clade containing <i>Troodon formosus</i> and <i>Velociraptor mongoliensis</i> but not <i>Passer domesticus</i>	Modified from Sereno 2005

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Dilophosauridae (Paul 1988) Charig & Milner 1990	/	/	Stem-based	The most inclusive clade containing <i>Dilophosaurus wetherilli</i> but not <i>Coelophysis bauri</i> , <i>Ceratosaurus nasicornis</i> and <i>Passer domesticus</i>	New
Dromaeosauridae (Matthew & Brown 1922) Colbert & Russell 1969	Sereno 1998	All deinonychosaurs closer to <i>Velociraptor</i> than to <i>Troodon</i>	Stem-based	The most inclusive clade containing <i>Dromaeosaurus albertensis</i> but not <i>Troodon formosus</i> , <i>Ornithomimus edmontonicus</i> , and <i>Passer domesticus</i>	Sereno 2005
Dromaeosaurinae Matthew & Brown 1922	Sereno 1998	All dromaeosaurids closer to <i>Dromaeosaurus</i> than to <i>Velociraptor</i>	Stem-based	The most inclusive clade containing <i>Dromaeosaurus albertensis</i> but not <i>Velociraptor mongoliensis</i> , <i>Microaptor zhaotianus</i> , <i>Unenlagia comahuensis</i> and <i>Passer domesticus</i>	Sereno 2005
Elmisaurinae (Osmólska 1981) Currie 2000	/	/	Stem-based	The most inclusive clade containing <i>Elmisaurus rarus</i> but not <i>Caenagnathus colinsi</i>	New
Eudromaeosauria Longrich & Currie 2009b	Turner et al. 2012	The node-based monophyletic group containing the last common ancestor of <i>Saurornitholestes langstoni</i> , <i>Deinonychus antirrhopus</i> , <i>Dromaeosaurus albertensis</i> , and <i>Velociraptor mongoliensis</i> , and all its descendants	Node-based	The least inclusive clade containing <i>Saurornitholestes langstoni</i> , <i>Deinonychus antirrhopus</i> , <i>Dromaeosaurus albertensis</i> , and <i>Velociraptor mongoliensis</i>	Modified from Turner et al. 2012

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Herrerasauridae Benedetto 1973	Novas 1992	<i>Herrerasaurus</i> and <i>Staurikosaurus</i> and their most recent common ancestor	Stem-based	The most inclusive clade containing <i>Herrerasaurus ischigualastensis</i> but not <i>Passer domesticus</i>	Sereno 2005
Jinfengopteryginae Turner et al. 2012	Turner et al. 2012	A stem-based monophyletic group containing <i>Jinfengopteryx elegans</i> , and all coelurosaurs closer to it than to <i>Troodon formosus</i> , <i>Passer domesticus</i> , and <i>Sinovenator changii</i>	Stem-based	The most inclusive clade containing <i>Jinfengopteryx elegans</i> but not <i>Troodon formosus</i> , <i>Sinovenator changii</i> and <i>Passer domesticus</i>	Modified from Turner et al. 2012
Majungasaurinae Tortosa et al. 2014	Tortosa et al. 2014	All the abelisaurids more closely related to <i>Majungasaurus crenatissimus</i> than to <i>Carnotaurus sastrei</i>	Stem-based	The most inclusive clade containing <i>Majungasaurus crenatissimus</i> but not <i>Carnotaurus sastrei</i>	Modified from Tortosa et al. 2014
Maniraptora Gauthier 1986	Gauthier 1986	All coelurosaurs that are closer to birds than they are to Ornithomimidae	Stem-based	The most-inclusive clade containing <i>Passer domesticus</i> but not <i>Ornithomimus velox</i>	Maryńska et al. 2002
Maniraptoriformes Holtz 1995	Holtz 1996	The most recent common ancestor of <i>Ornithomimus</i> and birds (i.e., The most recent common ancestor of Arctometatarsalia and Maniraptora), and all descendants of that common ancestor	Node-based	The least-inclusive clade containing <i>Passer domesticus</i> and <i>Ornithomimus velox</i>	Maryńska et al. 2002
Megalosauria (Fitzinger 1843) Bonaparte 1850	Allain et al. 2012	The most inclusive clade containing <i>Spinosaurus aegyptiacus</i> and <i>Torvosaurus tanneri</i> but not <i>Allosaurus fragilis</i> , and <i>Passer domesticus</i> (Stem-based definition)	Node-based	The least inclusive clade containing <i>Megalosaurus bucklandii</i> and <i>Spinosaurus aegyptiacus</i>	Modified from Allain et al. 2012
Megalosauridae (Fitzinger 1843) Bonaparte 1850	Allain 2002	<i>Poekilopleuron? valesdunensis</i> , <i>Torvosaurus</i> and <i>Afrovenator</i> , and all descendants of their common ancestor (Node-based definition)	Stem-based	The most inclusive clade containing <i>Megalosaurus bucklandii</i> but not <i>Allosaurus fragilis</i> , <i>Spinosaurus aegyptiacus</i> , and <i>Passer domesticus</i>	Holtz et al. 2004

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Megalosaurinae (Fitzinger 1843) Carrano et al. 2012	Carrano et al. 2012	All megalosaurids closer to <i>Megalosaurus</i> than to <i>Afrovenator</i>	Stem-based	The most inclusive clade containing <i>Megalosaurus bucklandii</i> but not <i>Afrovenator abakensis</i>	Carrano et al. 2012
Megaloauoidea (Fitzinger 1843) Walker 1964	Sereno 1998	<i>Spinosaurus</i> , <i>Torvosaurus</i> , their most recent common ancestor and all descendants (Definition given to Spinosauoidea)	Stem-based	The most inclusive clade containing <i>Megalosaurus bucklandii</i> but not <i>Passer domesticus</i>	Modified from Holtz et al. 2004
Megaraptora Benson et al. 2010	Benson et al. 2010	The most inclusive clade comprising <i>Megaraptor namunhuaiquii</i> but not <i>Chilantaisaurus tashuikouensis</i> , <i>Neovenator salerii</i> , <i>Carcharodontosaurus saharicus</i> or <i>Allosaurus fragilis</i>	Stem-based	The most inclusive clade containing <i>Megaraptor namunhuaiquii</i> but not <i>Chilantaisaurus tashuikouensis</i> , <i>Neovenator salerii</i> , <i>Carcharodontosaurus saharicus</i> or <i>Allosaurus fragilis</i>	Benson et al. 2010
Megaraptoridae (Benson et al. 2010) Novas et al. 2013	Novas et al. 2013	A stem based clade including all theropods closer to <i>Megaraptor namunhuaiquii</i> than to <i>Fukuiraptor kitadaniensis</i> , <i>Chilantaisaurus tashuikouensis</i> , <i>Neovenator salerii</i> , <i>Carcharodontosaurus saharicus</i> , <i>Allosaurus fragilis</i> , <i>Baryonyx walkeri</i> , <i>Tyrannosaurus rex</i> , and <i>Passer domesticus</i>	Stem-based	The most inclusive clade containing <i>Megaraptor namunhuaiquii</i> but not <i>Fukuiraptor kitadaniensis</i> , <i>Chilantaisaurus tashuikouensis</i> , <i>Neovenator salerii</i> , <i>Carcharodontosaurus saharicus</i> , <i>Allosaurus fragilis</i> , <i>Baryonyx walkeri</i> , <i>Tyrannosaurus rex</i> , and <i>Passer domesticus</i>	Modified from Novas et al. 2013
Metriacanthosauridae Paul 1988	Padian and Hutchinson 1997	<i>Sinraptor</i> and all Allosauoidea closer to it than to <i>Allosaurus</i> (Definition given to Sinraptoridae)	Stem-based	The most inclusive clade containing <i>Metriacanthosaurus parkeri</i> but not <i>Allosaurus fragilis</i> , <i>Carcharodontosaurus saharicus</i> , or <i>Passer domesticus</i>	Modified from Sereno 2005

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Metriacanthosaurinae (Paul 1988) Carrano et al. 2012	Carrano et al. 2012	All metriacanthosaurids more closely related to <i>Metriacanthosaurus</i> than to <i>Yangchuanosaurus</i>	Stem-based	The most inclusive clade containing <i>Metriacanthosaurus parkeri</i> but not <i>Yangchuanosaurus shangyouensis</i>	Modified from Carrano et al. 2012
Microraptorinae Senter et al. 2004	Sereno 2005	The most inclusive clade containing <i>Microraptor zhaoianus</i> but not <i>Dromaeosaurus albertensis</i> , <i>Velociraptor mongoliensis</i> , <i>Unenlagia comahuensis</i> , <i>Passer domesticus</i>	Stem-based	The most inclusive clade containing <i>Microraptor zhaoianus</i> but not <i>Dromaeosaurus albertensis</i> , <i>Velociraptor mongoliensis</i> , <i>Unenlagia comahuensis</i> , and <i>Passer domesticus</i>	Sereno 2005
Mononykinae Chiappe et al. 1998	Chiappe et al. 1998	The common ancestor of <i>Mononykus</i> , <i>Shuvuuia</i> , and <i>Parvicursor</i> , plus all their descendants	Node-based	The least inclusive clade containing <i>Mononykus oleranus</i> and <i>Shuvuuia deserti</i>	Sereno 2005
Neoceratosauria Novas 1991	Holtz 1994	The most recent common ancestor of <i>Ceratosaurus</i> and <i>Abelisauridae</i> and all of its descendants	Node-based	The least inclusive clade containing <i>Ceratosaurus nasicornis</i> and <i>Carnotaurus sastrei</i>	Modified from Holtz 1994
Neotheropoda Bakker 1986	Sereno 1998	<i>Coelophysis</i> , Neornithes, their most recent common ancestor and all descendants	Node-based	The least inclusive clade containing <i>Coelophysis bauri</i> and <i>Passer domesticus</i>	Sereno 2005
Neovenatoridae Benson et al. 2010	Benson et al. 2010	The most inclusive clade comprising <i>Neovenator salerii</i> but not <i>Carcharodontosaurus sahariensis</i> , <i>Allosaurus fragilis</i> or <i>Sinraptor dongi</i>	Stem-based	The most inclusive clade containing <i>Neovenator salerii</i> but not <i>Carcharodontosaurus saharicus</i> , <i>Allosaurus fragilis</i> or <i>Sinraptor dongi</i>	Benson et al. 2010
Noasauridae Bonaparte & Powell 1980	Wilson et al. 2003	The most inclusive clade containing <i>Noasaurus leali</i> but not <i>Carnotaurus sastrei</i>	Stem-based	The most inclusive clade containing <i>Noasaurus leali</i> but not <i>Carnotaurus sastrei</i>	Wilson et al. 2003

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Orionides Carrano <i>et al.</i> 2012	Carrano <i>et al.</i> 2012	Megalosauroidae, Avetheropoda, their most recent common ancestor, and all its descendants	Node-based	The least-inclusive clade containing <i>Megalosaurus bucklandii</i> , <i>Allosaurus fragilis</i> and <i>Passer domesticus</i>	Modified from Carrano <i>et al.</i> 2012
Ornithomimidae Marsh 1890	Sereno 1998	All ornithomimosaurs closer to <i>Ornithomimus</i> than to <i>Erlingosaurus</i>	Stem-based	The most inclusive clade containing <i>Ornithomimus velox</i> but not <i>Deinocheirus mirificus</i>	Lee <i>et al.</i> 2014
Ornithomimosauria (Marsh 1890) Barsbold 1976a	Osmólska 1997	All bullatosauroids closer to <i>Ornithomimus</i> than to <i>Troodon</i>	Stem-based	The most inclusive clade containing <i>Ornithomimus velox</i> but not <i>Allosaurus fragilis</i> , <i>Tyrannosaurus rex</i> , <i>Compsognathus longipes</i> , <i>Alvarezsaurus calvoi</i> , <i>Therizinosaurus cheloniformis</i> , <i>Deinonychus antirrhopus</i> , <i>Troodon formosus</i> , and <i>Passer domesticus</i>	Lee <i>et al.</i> 2014
Oviraptoridae Barsbold 1976b	Sereno 1998	All oviraptorosaurs closer to <i>Oviraptor</i> than to <i>Caenagnathus</i>	Stem-based	The most inclusive clade containing <i>Oviraptor philoceratops</i> but not <i>Caenagnathus collinsi</i>	Maryńska <i>et al.</i> 2002
Oviraptorinae (Barsbold 1976b) (Barsbold 1981)	Osmólska <i>et al.</i> 2004	<i>Oviraptor philoceratops</i> , <i>Citipati osmólskiae</i> , their most recent common ancestor, and all descendants.	Node-based	The least inclusive clade containing <i>Oviraptor philoceratops</i> and <i>Citipati osmólskiae</i>	Osmólska <i>et al.</i> 2004
Oviraptorosauria Barsbold 1976a	Barsbold 1997	Oviraptoridae and all taxa closer to <i>Oviraptor</i> than to birds	Stem-based	The most-inclusive clade containing <i>Oviraptor philoceratops</i> but not <i>Passer domesticus</i>	Maryńska <i>et al.</i> 2002

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Paraves Sereno 1997	Sereno 1998	All maniraptorans closer to Neornithes than to <i>Oviraptor</i>	Stem-based	The most inclusive clade containing <i>Passer domesticus</i> but not <i>Oviraptor philoceras</i>	Holtz & Osmólska 2004
Parvicursorinae Karhu and Rautian 1996	Choiniere et al. 2010b	The least inclusive clade containing <i>Parvicursor</i> , <i>Mononykus</i> and their most recent common ancestor (Node-based definition)	Stem-based	The most inclusive clade containing <i>Parvicursor remotus</i> but not <i>Patagonykus puertai</i>	Xu et al. 2011b
Pennaraptora Foth et al. 2014	Foth et al. 2014	Clade including <i>Oviraptor philoceras</i> , <i>Deinonychus antirrhopus</i> and <i>Passer domesticus</i> and all descendants of their most recent common ancestor	Node-based	The least inclusive clade containing <i>Oviraptor philoceras</i> , <i>Deinonychus antirrhopus</i> and <i>Passer domesticus</i>	Foth et al. 2014
Piatnitzkysauridae Carrano et al. 2012	Carrano et al. 2012	All megalosauroids more closely related to <i>Piatnitzkysaurus</i> than to either <i>Spinosaurus</i> or <i>Megalosaurus</i>	Stem-based	The most inclusive clade containing <i>Piatnitzkysaurus floresii</i> but not <i>Spinosaurus aegyptiacus</i> and <i>Megalosaurus bucklandii</i>	Carrano et al. 2012
Proceratosauridae Rauhut et al. 2010	Rauhut et al. 2010	All theropods that are more closely related to <i>Proceratosaurus</i> than to <i>Tyrannosaurus</i> , <i>Allosaurus</i> , <i>Compsognathus</i> , <i>Coelurus</i> , <i>Ornithomimus</i> , or <i>Deinonychus</i>	Stem-based	The most inclusive clade containing <i>Proceratosaurus bradleyi</i> but not <i>Tyrannosaurus rex</i> , <i>Allosaurus fragilis</i> , <i>Compsognathus longipes</i> , <i>Coelurus fragilis</i> , <i>Ornithomimus edmontonicus</i> and <i>Deinonychus antirrhopus</i>	Rauhut et al. 2010
Scansoriopterygidae Czerkas and Yuan 2002	Zhang et al. 2008	The least-inclusive clade containing <i>Epidendrosaurus ningchengensis</i> and <i>Epidexipteryx hui</i>	Node-based	The least-inclusive clade containing <i>Epidendrosaurus ningchengensis</i> and <i>Epidexipteryx hui</i>	Zhang et al. 2008

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Spinosauridae Stromer 1915	Sereno 1998	All spinosaurids closer to <i>Spinosaurus</i> than to <i>Torvosaurus</i>	Stem-based	The most inclusive clade containing <i>Spinosaurus aegyptiacus</i> but not <i>Torvosaurus tanneri</i> , <i>Allosaurus fragilis</i> , and <i>Passer domesticus</i>	Sereno 2005
Spinosaurinae (Stromer 1915) Sereno et al. 1998	Holtz et al. 2004	<i>Spinosaurus aegyptiacus</i> and all taxa sharing a more recent common ancestor with it than with <i>Baryonyx walkeri</i>	Stem-based	The most inclusive clade containing <i>Spinosaurus aegyptiacus</i> but not <i>Baryonyx walkeri</i>	Holtz et al. 2004
Tetanurae Gauthier 1986	Gauthier 1986	Birds and all other theropods closer to birds than they are to Ceratosauria	Stem-based	The most inclusive clade containing <i>Passer domesticus</i> but not <i>Ceratosaurus nasicornis</i>	Allain et al. 2012
Therizinosauria (Maleev 1954) Russell 1997	Russell 1997	<i>Alxasaurus</i> , <i>Enigmosaurus</i> , <i>Erikosaurus</i> , <i>Nanshiungosaurus</i> , <i>Segnosaurus</i> , <i>Therizinosaurus</i> and all others closer to them than to oviraptorosaurs, ornithomimids, and troodontids	Stem-based	The most inclusive clade containing <i>Therizinosaurus cheloniformis</i> but not <i>Tyrannosaurus rex</i> , <i>Ornithomimus edmontonicus</i> , <i>Mononykus olecranus</i> , <i>Oviraptor philoceratops</i> or <i>Troodon formosus</i>	Zanno 2010b
Therizinosauridae Maleev 1954	Sereno 1998	All ornithomimosaurids closer to <i>Erikosaurus</i> than to <i>Ornithomimus</i> (Stem-based definition)	Node-based	The least inclusive clade containing <i>Nothronychus graffami</i> , <i>Segnosaurus galbinensis</i> , <i>Erikosaurus andrewsi</i> and <i>Therizinosaurus cheloniformis</i>	Modified from Zanno et al. 2009
Therizinosaurioidea (Maleev 1954) Russell & Dong 1993	Zhang et al. 2001	All coelurosaurs closer to <i>Therizinosaurus</i> than to either <i>Ornithomimus</i> , <i>Oviraptor</i> , <i>Velociraptor</i> , or Neornithes (Stem-based definition)	Node-based	The least inclusive clade containing <i>Beipiaosaurus inexpectus</i> and <i>Therizinosaurus cheloniformis</i>	Clark et al. 2004

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Theropoda Marsh 1881	Gauthier 1986	Birds and all saurischians that are closer to birds than they are to sauropodomorphs	Stem-based	The most inclusive clade containing <i>Passer domesticus</i> but not <i>Saltausaurus loricatus</i>	Sereno 2005
Troodontidae Gilmore 1924	Varricchio 1997	<i>Troodon</i> , <i>Sinornithoides</i> , <i>Saurornithoides</i> , <i>Borogovia</i> , and all coelurosaurs closer to them than to ornithomimids, oviraptorosaurs, or other well-defined taxa	Stem-based	The most inclusive clade containing <i>Troodon formosus</i> but not <i>Velociraptor mongoliensis</i> , <i>Ornithomimus edmontonicus</i> , and <i>Passer domesticus</i>	Sereno 2005
Tyrannosauridae Osborn 1906	Holtz 2001	All descendants of the most recent common ancestor of <i>Tyrannosaurus</i> and <i>Aublysodon</i>	Node-based	The least inclusive clade containing <i>Tyrannosaurus rex</i> , <i>Gorgosaurus libratus</i> and <i>Albertosaurus sarcophagus</i>	Sereno 2005
Tyrannosaurinae (Osborn 1906) Matthew & Brown 1922	Sereno 1998	All tyrannosaurids closer to <i>Tyrannosaurus</i> than to either <i>Albertosaurus</i> , <i>Daspletosaurus</i> , or <i>Gorgosaurus</i>	Stem-based	The most inclusive clade containing <i>Tyrannosaurus rex</i> but not <i>Gorgosaurus libratus</i> and <i>Albertosaurus sarcophagus</i>	Sereno 2005
Tyrannosauroidae (Osborn 1906) Walker 1964	Sereno 1998	All maniraptorans closer to <i>Tyrannosaurus</i> than to Neornithes	Stem-based	The most inclusive clade containing <i>Tyrannosaurus rex</i> but not <i>Ornithomimus edmontonicus</i> , <i>Troodon formosus</i> , or <i>Velociraptor mongoliensis</i>	Sereno 2005

Taxon	First definitional author	First phylogenetic definition	Definition type	Definition	Definitional author
Uenlagiinae Bonaparte 1999	Makovicky <i>et al.</i> 2005	All taxa closer to <i>Uenlagia comahuensis</i> than to <i>Velociraptor mongoliensis</i>	Stem-based	The most inclusive clade containing <i>Uenlagia comahuensis</i> but not <i>Velociraptor mongoliensis</i> , <i>Dromaeosaurus albertensis</i> , <i>Microaptor zhaoianus</i> and <i>Passer domesticus</i>	Sereno 2005