



ERRATUM ON “AN OVERVIEW OF NON-AVIAN THEROPOD DISCOVERIES AND CLASSIFICATION”

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Christophe Hendrickx & Matthew T. Carrano. 2016. Erratum on “An overview of Non-Avian Theropod Discoveries and Classification”. - PalArch's Journal of Vertebrate Palaeontology 13, 2 (2016), 1-7. ISSN 1567-2158. 7 pages + 1 figure, 1 table.

Keywords: Theropoda, Discovery, Dilophosauridae

ABSTRACT

In their recent publication on an overview of theropod discoveries and classification, Hendrickx and colleagues mistakenly attributed the earliest historical reports of non-avian theropods in North America and South America to Joseph Leidy in 1856 and Florentino Ameghino in 1899, respectively. Yet, theropod tracks from Massachusetts had already been reported by Hitchcock in 1836, and isolated theropod centra from Patagonia were described by Lydekker in 1893. We here provide additional information on the earliest theropod discoveries in Asia, America and Oceania. We also credit Thomas Holtz as being the first author to give a phylogenetic definition for the clade Dilophosauridae, and correct the phylogenetic definitions of the clades Allosauroidea and Megalosauria.

Historical Background

Hendrickx *et al.* (2015) recently investigated the current status of non-avian theropod classification, as well as the earliest historical records of this group of dinosaurs on each continent. In their chapter on the first discoveries, they noted that the first reports in the literature were by Plot (1677) for Europe, Leidy (1856) for North America, Hislop (1861) for Asia, Le Mesle and Peron (1880) for Africa, Ameghino (1899) for South America, Woodward (1910) for Oceania, and Molnar *et al.* (1996) for Antarctica (Hendrickx *et al.* 2015). Yet theropod remains from both North and South America had been published prior to the description of isolated theropod teeth from the Missouri and Judith rivers of Montana by Joseph Leidy (1856), and the single theropod tooth referred to '*Loncosaurus argentinus*' by Florentino Ameghino (1899) from the Chubut Province of Argentina, respectively.

In North America, theropod footprints from the banks of the Connecticut River in Massachusetts were reported by Edward Hitchcock (1836), President of Amherst College, twenty years prior to Leidy's (1856) descriptions. The latter seems to be the first report of theropod skeletal material from the New World, while Hitchcock's (1836) publication accounts for the first description of dinosaur footprints in the New World (Olsen *et al.* 1998). The discovery of these footprints was made in the south part of Montague in early 1835 by Dexter Marsh, a workman from Greenfield. The same year, he informed his neighbour James Deane of his finding (Herbert 2012, 2014). Deane purchased two of the tracks and wrote about them to Hitchcock in March 1835, identifying them as the tracks of prehistoric birds "probably of the turkey species" (Herbert 2012: 32). Hitchcock (1836) comprehensively described the footprints and erected several ichnospecies thought to belong to different taxa of early birds. One of them, *Ornithichnites giganteus* (figure 1A), now referred to *Eubrontes giganteus* (see Olsen *et al.* (1998) for a nomenclatural history of this ichnospecies), is currently considered to record the footsteps of large non-avian theropods from the Early Jurassic (Olsen *et al.* 1998). According to Hitchcock (1844), one of the many footprints illustrated in his final report on the geology of Massachusetts (Hitchcock 1841: plate 48, fig. 55) was found by a boy named Pliny Moody Jr.

of South Hadley around 1802, which accounts for the earliest historical discovery of non-avian theropod material outside Europe. Interestingly, Elihu Dwight, who purchased the fossilized trackway and kept it for nearly thirty years before selling it to Hitchcock's Cabinet in 1839, thought that the tracks were probably those of 'Noah's raven' (Hitchcock 1844).

The first putative non-avian theropod fossils to be reported in the Southern Hemisphere were also footprints, found in Lower Cretaceous rocks near Oiva, Colombia, by Carl Degenhardt in 1839, and reported by Mahlmann (1840) one year later (Buffetaut 2000). Although Mahlmann (1840) erroneously reported that they had been discovered in Mexico, these probable theropod footprints were recently revealed to have been found in Socorro Province, Colombia, on a red sandstone at the summit of the Cuchilla de las Pesuñas del Venado ridge, 5000 feet above sea level (Buffetaut 2000). However, the first definitive theropod body fossils to be reported from South America are two vertebral centra (figure 1B) described and illustrated by Lydekker (1893) six years before the description of *Loncosaurus* by Ameghino (1899). The material was unearthed by Swiss paleontologist Santiago Roth near Neuquén, Patagonia, between 1882 and 1887 (Huene 1929), along with many sauropod bones assigned to the then-new genus *Titanosaurus* by Lydekker (1893). They are still accessible in the collection of the Museo de la Plata, and the dorsal centrum may belong to a neovenatorid allosauroid (MTC, pers. obs.). It is unknown when the theropod tooth described by Ameghino (1899) and recovered by his brother Carlos Ameghino in Pari Aike (n.b., spelled 'Par-Aik' by Ameghino (1906) and Hendrickx *et al.* (2015); see Griffin & Varela 2012) was found. Nonetheless, the discovery of this isolated tooth probably predates that of *Genyodectes serus* material by Roth in Chubut Province in 1898 (Huene 1929).

Stephen Hislop (1861, 1864) published the first report of theropod material from Asia (Carrano *et al.* 2010; Hendrickx *et al.* 2015), but the isolated theropod tooth found by Rawes in Takli, India that he mentioned may not be the first theropod fossil to be discovered in Asia. Only one year after Hislop's (1861) Remarks on the Geology of Nágpur, Henry F. Blanford (1862) reported the discovery of an isolated tooth and a few more badly preserved bones that

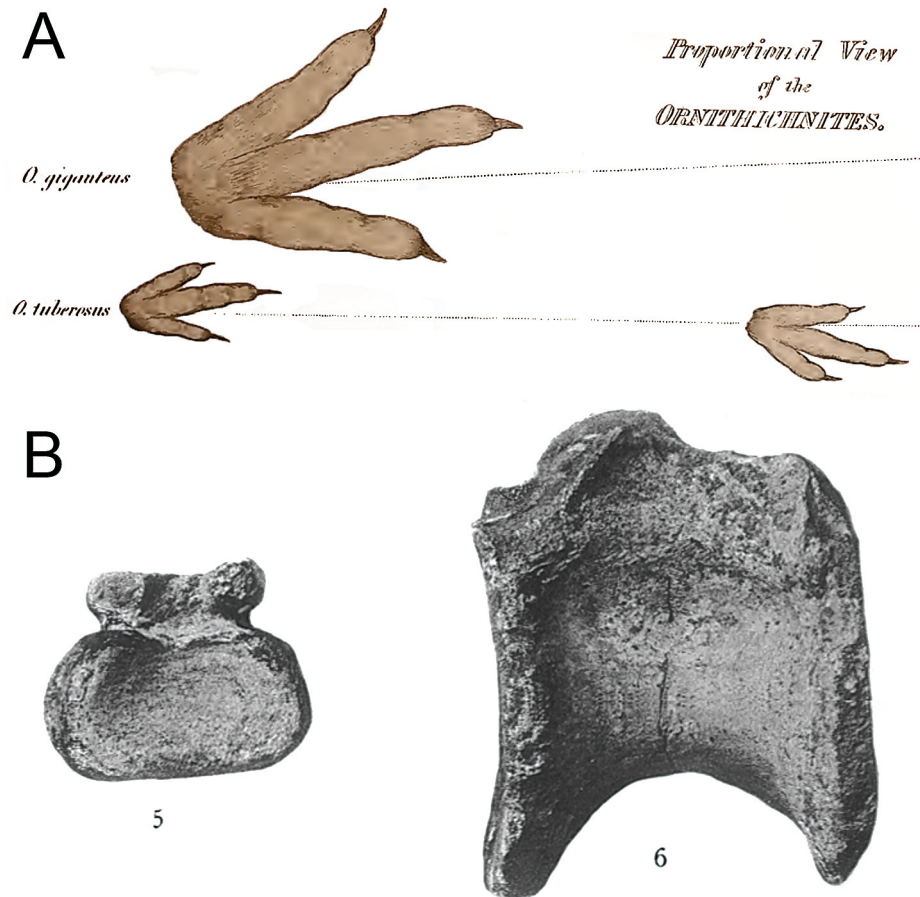


Figure 1. Earliest historical records of theropod remains in North America (A) and South America (B). A) Theropod footprints referred to the ichnospecies *Ornithichnites giganteus* and *O. tuberosus* from the Lower Jurassic of the Connecticut River, Massachusetts, and first reported and illustrated by Hitchcock (1836: plate appended "Proportional view of the Ornithichnites"; modified); B) Caudal centrum of a theropod ('5') and dorsal centrum of a ?neovenatorid theropod ('6'), from the Upper Cretaceous of the Neuquén region, Argentina, and first described and illustrated by Lydekker (1893: plate 3).

he referred to *Megalosaurus*. He found these remains in the Trichinopoly District, India, between 1857 and 1860 (Blanford 1862), possibly prior to Rawes's discovery in Takli, which took place between 1858 and 1861 (Hislop 1861).

In Australia, the theropod unguis described by Woodward (1906) not only accounts for the earliest historical report of a non-avian theropod in Oceania, but also for the first theropod fossil to be discovered on that continent. This unguis was collected by W. H. Ferguson in Cape Patterson, Victoria, in 1903, two years before the discovery of theropod remains in Lightning Ridge, New South Wales, by T. C. Wollaston in 1905 (Rich & Vickers-Rich 2000) that were described by Woodward (1910). Contra Hendrickx *et al.* (2015), the material from Lightning Ridge was referred to two theropods by Huene (1932), the indeterminate taxon *Walgettosuchus woodwardi* (caudal vertebral centrum; Molnar

1990) and the possible megaraptoran *Rapator ornitholestoides* (left metacarpal I; Agnolin *et al.* 2010; White *et al.* 2013). The distal part of a femur from the same locality was also ascribed by Huene (1932) to a new species of coelurosaur, *Fulgurotherium australe*, although this taxon is now recognized to be an ornithomimid (Molnar & Galton 1986).

Current Classification

Hendrickx *et al.* (2015) also provided a list of phylogenetic definitions for each main clade and subclade of non-avian theropods, and here we correct several errors that were introduced in that publication. Corrected versions of these definitions are provided in table 1.

Hendrickx *et al.* (2015) thought they had offered the first phylogenetic definition of the clade Dilophosauridae, but Holtz (2012: 352)

had already defined this clade as “*Dilophosaurus wetherilli* and all taxa sharing a more recent common ancestor with it than with *Coelophysis bauri*, *Ceratosaurus nasicornis*, and *Allosaurus fragilis*.” Likewise, the first phylogenetic definition provided by Allain *et al.* (2012: Electronic supplementary material) for Megalosauria is not “the most inclusive clade containing *Spinosaurus aegyptiacus* and *Torvosaurus tanneri* but not *Allosaurus fragilis*, and *Passer domesticus*” but “the most inclusive clade containing *Dubreuillosaurus valesdunensis* and *Eustrepsodylus oxoniensis* but not *Allosaurus fragilis*, *Spinosaurus aegyptiacus*, *Passer domesticus*.” In addition, Paul (1988) is the nominal author of the clade Metriacanthosaurinae, on which Metriacanthosauridae was based, as corrected by Carrano *et al.* (2012a). The latter clade was coined by Carrano *et al.* (2012b) and defined by Hendrickx *et al.* (2015), and not by Sereno (2005), contra Hendrickx *et al.* (2015). Likewise, Hendrickx *et al.*'s (2015) definition of Allosauroida *sensu* Sereno (2005) in table 1 does not correspond to the description provided in the text and in the classification illustrated in figure 4. Allosauroida, as defined by Sereno (2005), is indeed similar to the clade Allosauridae defined by Hendrickx *et al.* (2015). Consequently, a new stem-based definition for the allosauroid clade is provided here, *i.e.*, the most inclusive clade containing *Allosaurus fragilis* and *Sinraptor dongi* but not *Passer domesticus*, which is a modified version of the definition given by Holtz *et al.* (2004).

Finally, the silhouette of Oviraptoridae in figure 1 should have been attributed to Matthew Martyniuk.

Acknowledgements

We thank Thomas Holtz, Jr., Mickey Mortimer, and Matthew Martyniuk for pointing out the errors in the current classification section of Hendrickx *et al.* (2015). CH warmly thanks Matthew Martyniuk for providing his artwork on Phylopic (<http://phylopic.org/>). This research was supported by the postdoctoral fellowship grant PPD2015/17 provided by the Center of Excellence in Palaeosciences for C. Hendrickx. This is Paleobiology Database publication No. 257.

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Submitted: 24 January 2016
Published: 23 February 2016

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Taxon	First definition- al author	First phylogenetic definition	Definition type	Definition	Definitional author
Allosauroidea (Marsh 1878) Currie & Zhao 1993	Padian & 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> and <i>Sinraptor dongi</i> but not <i>Passer domesticus</i>	Modified from Holtz <i>et al.</i> 2004
Dilophosauridae (Paul 1988) Charig & Milner 1990	Holtz 2012	<i>Dilophosaurus wetherilli</i> and all taxa sharing a more recent common ancestor with it than with <i>Coelophysis</i> <i>bauri</i> , <i>Ceratosaurus nasicornis</i> , and <i>Allosaurus fragilis</i>	Stem-based	The most inclusive clade containing <i>Dilophosaurus</i> <i>wetherilli</i> but not <i>Coelophysis</i> <i>bauri</i> , <i>Ceratosaurus nasicornis</i> and <i>Passer domesticus</i>	Modified from Holtz 2012
Megalosauria (Fitzinger 1843) Bonaparte 1850	Allain <i>et al.</i> 2012	The most inclusive clade containing <i>Dubreuillosaurus</i> <i>valesdunensis</i> and <i>Eustrepto-</i> <i>spondylus oxoniensis</i> but not <i>Allosaurus fragilis</i> , <i>Spinosa-</i> <i>saurus aegyptiacus</i> , <i>Passer</i> <i>domesticus</i>	Stem-based	The most inclusive clade containing <i>Megalosaurus</i> <i>bucklandii</i> and <i>Spinosaurus</i> <i>aegyptiacus</i> but not <i>Piatnitz-</i> <i>kysaurus floresi</i>	New
Metriacanthosauridae (Paul 1988) Carrano <i>et al.</i> 2012b	Padian & Hutchinson 1997	<i>Sinraptor</i> and all Allosau- roidea closer to it than to <i>Allosaurus</i> (definition given to Sinraptoridae)	Stem-based	The most inclusive clade con- taining <i>Metriacanthosaurus</i> <i>parkeri</i> but not <i>Allosaurus</i> <i>fragilis</i> , <i>Carcharodontosaurus</i> <i>saharicus</i> , or <i>Passer domes-</i> <i>ticus</i>	Modified from Sereno 2005
Metriacanthosaurinae Paul 1988	Carrano <i>et al.</i> 2012b	All metriacanthosaurids more closely related to <i>Metriacanthosaurus</i> than to <i>Yangchuanosaurus</i>	Stem-based	The most inclusive clade con- taining <i>Metriacanthosaurus</i> <i>parkeri</i> but not <i>Yangchuanosa-</i> <i>saurus shangyouensis</i>	Modified from Carrano <i>et al.</i> 2012b