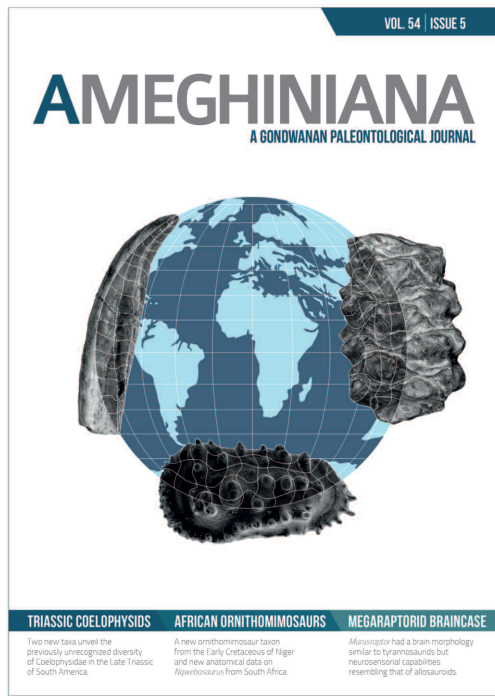




# AMEGHINIANA

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## GONDWANAN PERSPECTIVES: THEROPOD DINOSAURS FROM WESTERN GONDWANA. A BRIEF HISTORICAL OVERVIEW ON THE RESEARCH OF MESOZOIC THEROPODS IN GONDWANA.

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# GONDWANAN PERSPECTIVES: THEROPOD DINOSAURS FROM WESTERN GONDWANA. A BRIEF HISTORICAL OVERVIEW ON THE RESEARCH OF MESOZOIC THEROPODS IN GONDWANA.

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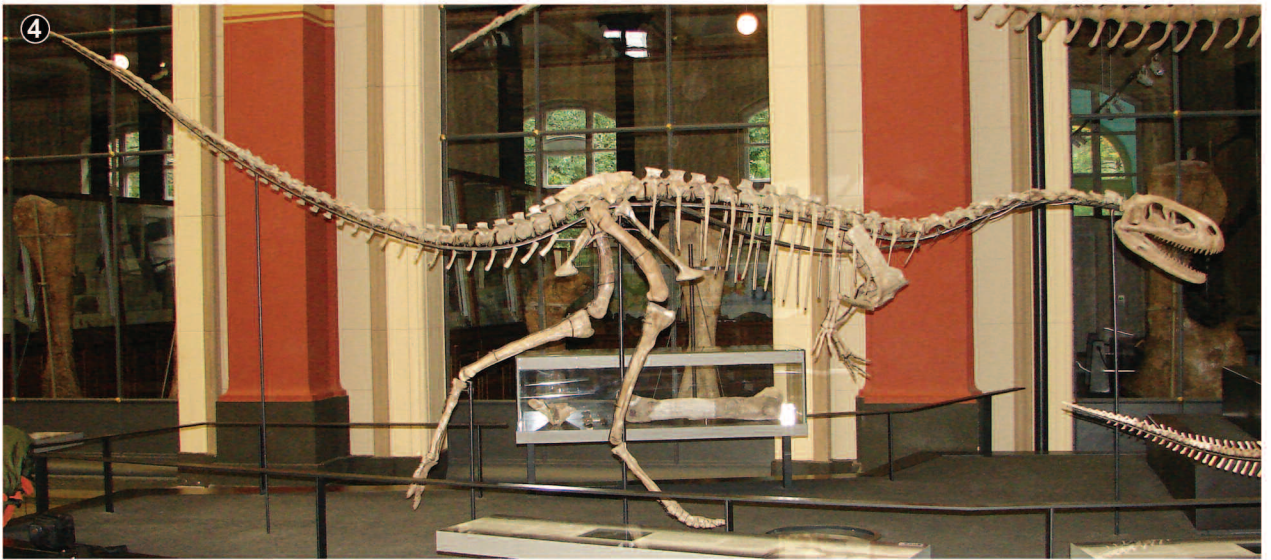
THE study of Gondwanan non-avian theropods has been outstandingly prolific in the last three decades and has shown that the taxonomic and morphological diversity of the group is comparable to that of Laurasia. The Mesozoic Gondwanan neotheropod record is currently composed of coelophysoids, basal averostrans, ceratosaurids, abelisauroids, megalosauroids, carcharodontosaurids, megaraptorans, basal coelurosaurs, compsognathids, alvarezsauroids, unenlagiids, and basal avialans, as well as putative tyrannosauroids, ornithomimosaur-like forms, and troodontids (Novas, 2009; Benson *et al.*, 2012). As a consequence of this diversity, the Gondwanan non-avian theropod record has been crucial to understand the evolution and global biogeography of dinosaurs during the Mesozoic. The contributions of this special issue of *Ameghiniana* enrich the record of some poorly known Gondwanan theropod clades with the description of four new species: two Triassic coelophysoids, a Jurassic basal tetanuran, and a Cretaceous ornithomimosaurian. In addition, in this issue it is described for the first time the cranial endocast of a megaraptoran and the forelimb posture of the enigmatic theropod *Chilesaurus*.

The history of the research of the southern theropods has been heterogeneous in the last century and only in 2004 we reached the 50% of all the valid Gondwanan theropod species currently known (see Supplementary Information).

Here we propose that the history of the Gondwanan theropod research can be divided into the following three stages.

## THE EARLY YEARS (1800s–1914)

The Early Years of the research on Gondwanan non-avian theropods were characterized by patched studies conducted mainly by French and British authors (*e.g.*, Depéret, Hislop, Le Mesle, Lydekker, Peron, Woodward), with the exception of the Argentinean palaeontologist Florentino Ameghino. The first probable fossil theropod remains from Gondwana were discovered in Colombia by the German engineer Carl Degenhardt in 1839, which were represented by "bird-like" footprints (Buffetaut, 2000). However, these footprints were not illustrated and it is not possible to determine if they belonged to ornithopod or theropod dinosaurs (Buffetaut, 2000). The first Gondwanan theropod was named by the French palaeontologist Charles Depéret, close to the end of the XIX Century, as "*Megalosaurus*" *crenatissimus* from the Upper Cretaceous of Madagascar (Depéret, 1896). Nevertheless, several other fragmentary theropod remains were described from India, Africa, and South America during this century and the first years of the XX Century (*e.g.*, Hislop, 1861, 1864; Lydekker, 1879, 1890; Le Mesle and Peron, 1880; Ameghino, 1899; Woodward, 1901) (Fig. 1.1–2). These early discoveries clearly showed the presence of theropods in the southern conti-



nents, but their fragmentary nature forced the authors of the XIX-early XX centuries to interpret them as belonging to the same lineages present in Europe and North America (e.g., Lydekker, 1890; Ameghino, 1899; Woodward, 1901).

### THE EUROPEAN AUTHORS ERA (1915–1962)

This stage continued with the predominance of European authors in the study of Gondwanan theropods. However, we recognized from 1915 a change in the quality and quantity of the discoveries (Fig. 2), including for the first time the publication of very informative partial skeletons, such as those of *Spinosaurus aegyptiacus* and *Elaphrosaurus bambergi* (Stromer, 1915; Janensch, 1920) (Fig. 1.4, 1.6). This period included contributions of several British and French authors (e.g., Lapparent, Lavocat, Lydekker, Matley, Pivetaut, Woodward), but the most relevant Gondwanan theropod discoveries were produced by the work of the German palaeontologists Frederich von Huene, Ernst Stromer, and Werner Janensch before the Second World War. Thus, we consider the span between 1915 and 1933 as the “German Period” of the “European Authors Era”, but during and after the Second World War the influence of the German palaeontology in the research of Gondwanan theropods abruptly declined and there is a plateau in the naming of new species (Fig. 2). After this “German Period”, several contributions, mainly by French palaeontologists, added more novel theropod specimens mainly from Africa and Madagascar (Fig. 1.5). The discoveries conducted during this stage considerably expanded the anatomical knowledge of some Gondwanan theropod clades (e.g., spinosaurids, carcharodontosaurids, abelisaurids), but these groups were still considered members of northern hemisphere lineages,

such as allosaurs, tyrannosaurs, and ornithomimosaurs (Janensch, 1920; Huene, 1929, 1932; Lapparent and Lavocat, 1955).

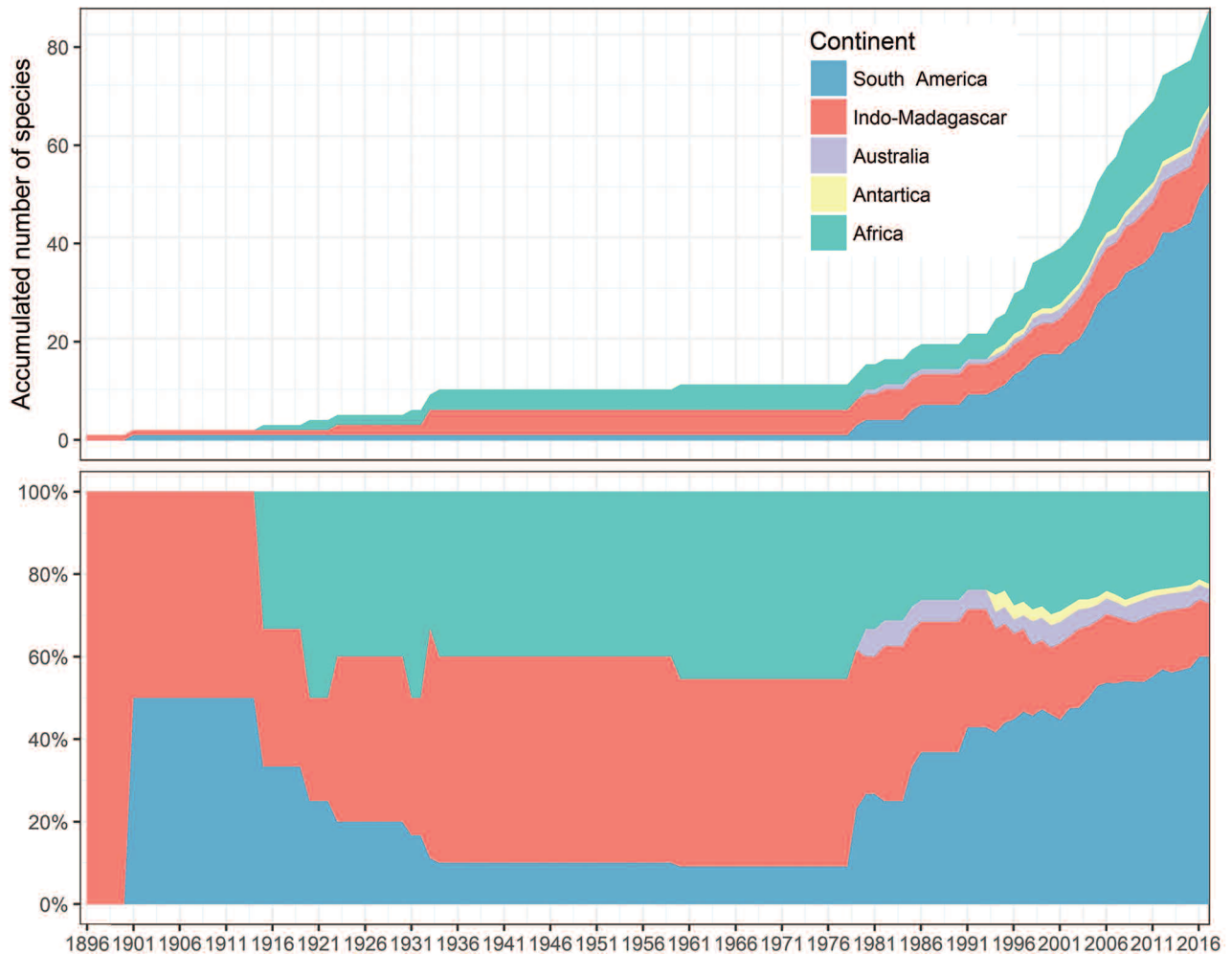
### THE MODERN ERA (1963–PRESENT)

This stage differs from the others in that the research was led by native authors, mainly in South America. By the 1960s, the Argentine biologist Osvaldo Reig, together with Rodolfo Casamiquela and José Bonaparte, began to explore the Mesozoic rocks of Argentina looking for fossil tetrapods. This resulted in the publication of several papers that constituted the seeds of the modern studies in Gondwanan dinosaurs conducted by South American researchers, in which we identify the description of early dinosaurs—including some of the probable oldest known theropods—from north-western Argentina as a starting point (Reig, 1963).

Since 1985, the naming of new Gondwanan theropod species showed an exponential increase mainly due to the efforts of the Argentine palaeontologist José Bonaparte (Fig. 2). The discoveries of Bonaparte and his collaborators resulted in the recognition of a different evolutionary history of the southern theropods from that of their northern counterparts (Bonaparte, 1986; Bonaparte and Kielan-Jaworowska, 1987). As a result of several seminal contributions, Bonaparte produced a revolution in the knowledge and understanding of the Gondwanan Mesozoic tetrapods, including theropod dinosaurs. The subsequent two next generations of palaeontologists after Bonaparte<sup>3</sup>—most of them direct disciples—contributed to the description of a large number of new taxa and provided novel interpretations, which placed South America as the Gondwanan continent with the most theropod species currently known (Fig. 2).

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**Figure 1.** Historical Gondwanan theropod specimens. **1**, Snout of the ceratosaurian *Genyodectes serus* (Museo de La Plata 26-39, holotype) from the Lower Cretaceous of the Argentinean Patagonia (Woodward, 1901); **2**, isolated tooth crown of an indeterminate theropod (Museo Argentino de Ciencias Naturales, Colección Ameghino 10985) formerly referred to “*Loncosaurus argentinus*” from the Upper Cretaceous of the Argentinean Patagonia (Ameghino, 1899); **3**, right tibia of the averostran *Kakuru kujani* (South Australia Museum P17926, holotype) from the Lower Cretaceous of Australia (Molnar and Pledge, 1980); **4**, postcranial skeleton of the ceratosaurian *Elaphrosaurus bambergi* (Museum für Naturkunde 4960, holotype) from the Upper Jurassic of Tanzania (Janensch, 1920); **5**, right dentary of the abelisaurid *Majungasaurus crenatissimus* (Muséum National d’Histoire Naturelle MAJ 1, holotype) from the Upper Cretaceous of Madagascar (Lavocat, 1955); **6**, cast of the partial braincase of the abelisaurid *Indosaurus matleyi* (cast in the Paläontologische Sammlung der Universität Tübingen) from the Upper Cretaceous of India (Huene and Matley, 1933) (photograph courtesy of M.B. von Baczko). Scale bars = 5 cm in **(1, 3)**, 5 mm in **(2)**, 3 cm in **(5)**, and 2 cm in **(6)**. Total length of the skeleton = 5–5.5 m in **(4)**.



**Figure 2.** New Gondwanan neotheropod species named through time. Accumulated number of species per continent (top) and percentage of named species per continent (bottom). Raw data in Supplementary Information.

In other Gondwanan continents, the research of authors from the Northern Hemisphere and several native and currently active palaeontologists have been continuously increasing the knowledge of the southern theropods (Fig. 2). Several discoveries and research have expanded considerably the knowledge of the theropod assemblages of northern Africa during the last three decades, some of them representing new specimens of species originally described by German palaeontologists during the “The European authors Era”. The information currently available of the theropods of southern Africa is more limited and has been mainly as a result of sporadic contributions. New

specimens have increased the list of Indian theropods in the last decades, but the diversity of the group is still mostly limited to abelisaurids. The non-avian theropod record of Antarctica is based on fossils collected in the last three decades and is restricted to some unnamed fragmentary remains (basal tetanurans and a derived coelurosaur) and the Early Jurassic basal averostran *Cryolophosaurus*. The knowledge of the theropod assemblage of Madagascar has increased considerably in the last decades and includes one of the best currently known Gondwanan theropods, the abelisaurid *Majungasaurus*. The Mesozoic theropod record of Australasia has also increased significantly in the last

years and the better known species is the megaraptoran *Australovenator*. Multiple fragmentary and isolated bones from Lower Cretaceous rocks have also provided important information to understand the Australasian theropod assemblage and the palaeobiogeographic history of the group during the final severing of Gondwana.

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**Supplementary Information.** Spreadsheets including each of the currently valid Gondwanan neotheropod species erected through time and the number and percentages of the erected new species in each continent through time.