CONCLUSIONS: *Implications of giant Ichnotaxa for Dinosaurian size Distribution*

Giant-sized dinosaur trace fossils are known from various temporal and geographical locations throughout the mesozoic and on several continents.

In some strata, they greatly expand the known size ranges (eg. lower Jurassic, Poland/Upper Jurassic, Portugal/North Africa) of the ecosystem's palaeofauna, in others, they confirm sizes known from (often fragmentary) body fossils (eg. upper Cretaceous, USA/Upper Jurassic, France).

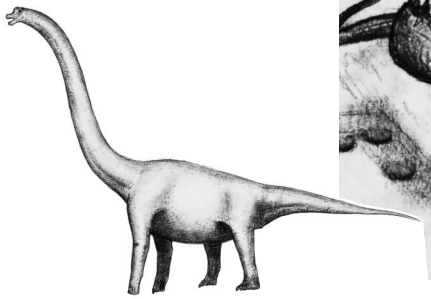
It has often been argued footprints were an unreliable predictor of size and of limited use for scientific conclusions, which is only true in part.

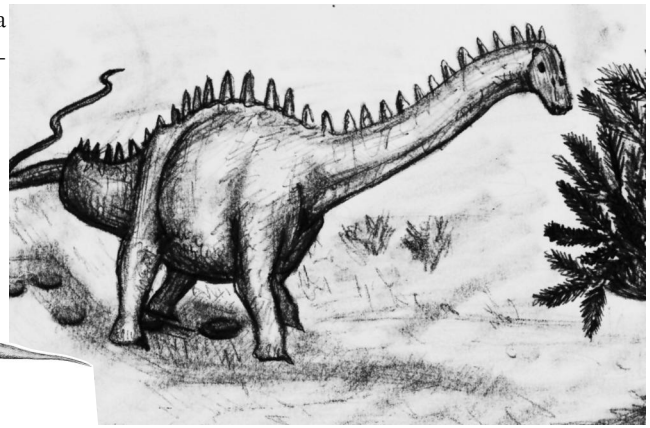
Precise body size figures are difficult to conclude, as with all fragmentary findings, due to the incertainity in soft-tissue reconstruction and phylogenetic assignment. However the mere general size of some ichnotaxa justifies approximate estimates on the trackmakers. While there is the possibility of artificial enlargement of pes prints, depending on geological conditions, many factors can also make them smaller than the foot that left them, or at least appear so, for example toemark collapse, roofing, erosion and infilling with sediments (Farlow et al., 2012).

Ichnotaxa are an important factor to consider for size evolution because they often record extraordinarly large animals whose bodies may not fossilise due to preservation bias.

Accordingly, several dinosaurian ichnotaxa are among the largest recorded for their respective clades; For example, the upper Jurassic sauropod trackmakers from Plagne appear to reach sizes rivalling even the largest whales. Upper Jurassic footprints from Iberia and North Africa indicate giant theropods in these ecosystems which were on par with, or larger than their Cretaceous equivalents, and significantly larger than contemporaries known from body fossils.

Ichnology can give important clues in this regard when we lack other sufficient material, and many poorly known ichnotaxa are thus of extraordinaly importance.





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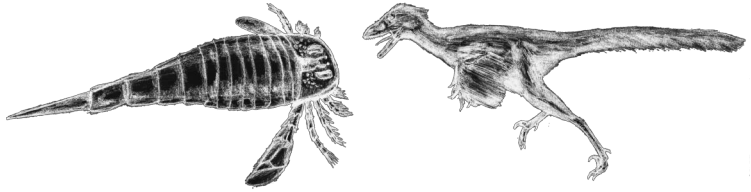
Prehistoric



Nature

Mega-Footprints: *Implications for Gigantism in Dinosaurs*

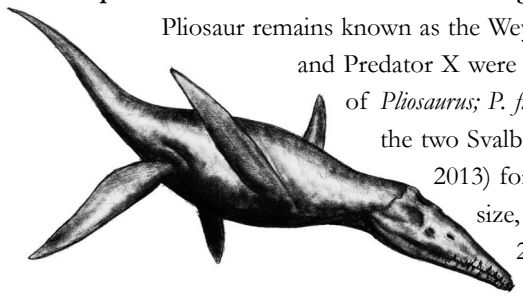
"When the last forest is cleared, the last river poisoned, and the last bison killed, then you will realise biology is the most important subject."

Šuŋgmánitu Maka Ob'wačhi/Dances-with-Skunks (Peter Nachbaur)

Aurornis xui and new Views on Paravian Phylogeny

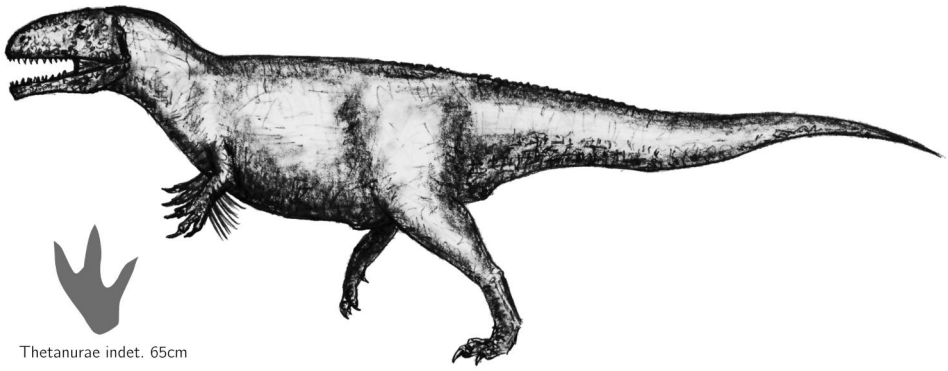
Potentially the most important finding of the year, this early Paravian dinosaur from China can, depending on the definition, be considered the first bird. The type and only specimen of *A. xui* from the upper Bathonian stage of the Late Middle Jurassic was named by Godefroid et al. in 2013, and found to be the basalmost Avialan (using a stem based definition as all animals closer to Neornithes than to Troodontids or Dromaeosaurs) in a subsequent phylogenetic analysis, also establishing *Anchiornis* and *Xiaotingia* as birds. It mostly resembles other basal Avialans or Troodontids, the latter found to be the sister taxon of Avialae, in morphology, but differs in its relatively short metatarsals which rather resemble derived members of Dromaeosauria. It was a small creature of only about 50cm in lenght, with a large skull, large eyes, and a moderately long tail.

New species of Pliosaurus and a review of giant Pliosaur specimens



Pliosaur remains known as the Weymouth Bay Pliosaur, the Svalbard monster and Predator X were described and assigned to two new species of *Pliosaurus; P. funkei* (Knutsen et al., 2012), compromising the two Svalbard specimens, and *P. kevani* (Benson et al., 2013) for the Dorset skull. Both are of comparable size, with a maximum skull lenght in excess of 2m, a probable total lenght of 10-11m and a weight of 10-13t. With the exception of *Pliosaurus macromerus* this puts them among the largest known pliosaurs known from reasonably complete remains. Some other giant remains, like hinted 45cm long teeth (R. Forrest, website), a huge vertebra and other fragments, may be indicative of even larger animals, but precise size figures are hard to establish due to lacking description of the already incomplete material.

theropod origin, as demonstrated by the preserved hallux and clawmarks, however the total lenght is greater than the usual lenght of the foot-pad would have been, due to preservation of a metatarsal impression.



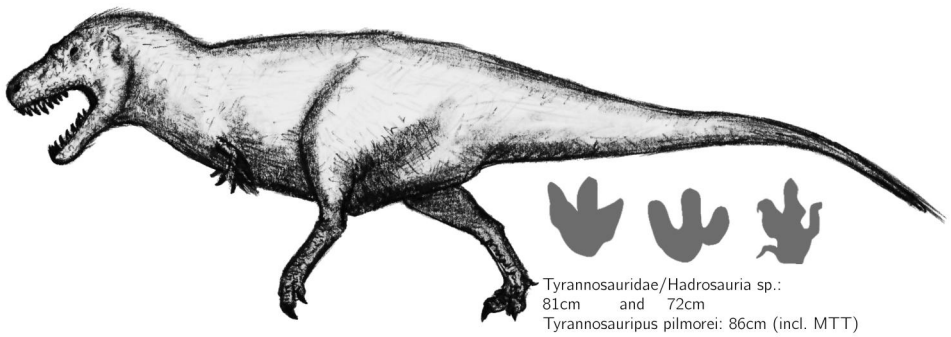
Two large theropod trackways are also known from the lower Cretaceous of Peru and Chile, the Peruvian track averaging 59cm and 47cm in ichnite lenght and width respectively and ranging up to 65 and 54cm, and the Chilean tracksite averaging slightly lower at the same maximum lenght of the prints (Moreno et al., 2012). The size of these imprints is consistent with large Allosaurs or Spinosaurs, which were the dominant large predators in Gondwanan ecosystems of this time. A taxon that may be close in age and size is the Aptian Carcharodontosaur *Tyrannotitan chubutensis* (Novas et al., 2005).

ICHNOLOGICAL EVIDENCE FOR "GIGAPODS"

The very largest, enigmatic sauropods (eg. *Amphicoelias fragillimus*, *"Brachiosaurus" nougaredi*), often referred to as "gigapods", have left behind little fossil evidence of their existence. This can be explained by their rarity and the vanishingly small probability of suitable conditions for preservation of such huge animals. Some confirmation of their size and presence in mesozoic environments can be found in ichnotaxa like those from Cretaceous Broome, Australia (Thulborn, 2012), Jurassic Plagne, France (Wedel, 2009, SVPOW) or tracks referred to *Parabrontopodus distercii*, 1,7m, 1,5-2m and 1,48-1,65m long respectively. Matt Wedel (blog post) gave speculative body size estimates (plausibly 2 times the linear dimensions of the *Giraffatitan* holotype specimen and accordingly 8 times the weight) for the Plagne trackmaker, supporting it as one of the largest, if not the largest animal ever to exist. Several other large tracks have been found, including the famous *Breviparopus*, and some of the aforementioned ichnotaxa, but none approach the size of the largest Broome, Plagne and *Parabrontopodus* tracks, which all measure in excess of 1,5m long.

um sized genera *Camptosaurus* and *Draconyx*. The Sauropod footprints, the majority of which measures roughly 1m (max.: 1,05m), belonged to intermediate or large-sized animals, possibly *Dinheirosaurus*. The largest Stegosaurian ichnites, referred to *Deltapodus*, reach 42cm. Theropod tracks range from 30 to 79cm (max. including Metatarsal impression: 96cm) in lenght and reflect a diverse fauna of medium to huge predators in the ecosystem. In addition, many non-dinosaurian trace fossils from the location are known, and the contemporary Asturias ichnofauna contains similar traces, some of them gigantic (largest theropod track: 82cm, incl. MTT 103cm).

The North and South American Trackways of the Cretaceous

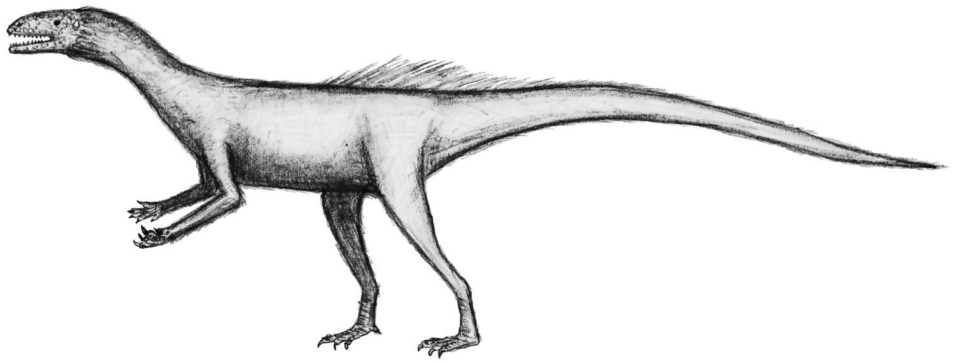


The infamous Paluxy tracksite from the Albian Glen Rose Formation of the USA preserves tridactyl Theropod tracks (avg. 45-60cm) and Sauropod ichnites (avg. 90cm) in what must have once been fine-grained mud (Farlow et al., 2012). The trackway seems to document a lone, large theropod, perhaps Acrocanthosaurus, chasing a large sauropod (maybe Paluxysaurus or Sauroposeidon). Several giant pes prints are known from the Maastrichtian of North America. Giant Hadrosaur (59-94cm long and 53-87cm wide) tracks attributed to *Caririchnium* are known from the late Campanian Fruitland Formation of New Mexico (Lucas et al., 2011). These prints may have been slightly enlarged but are estimated to have belonged to animals of around 2,4-3,8m in hip height, as opposed to the more typical 2-2,5m for North American Hadrosaurs from the same time period. Even larger Hadrosaur tracks are known from the Campanian of Colorado (up to 102cm, Lockley et al., 1983).

Ichnites attributed to theropods have proven problematic as regards assignment and estimation of size. A specimen from Hell Creek measuring 72cm in lenght, was referred to *Tyrannosaurus rex* (Manning et al., 2008); however the proportions of the ichnite (lenght/width ratio: 0,95) and the absence of any indication of claws may suggest it could also be of Hadrosaurian origin. Campanian *Tyrannosauropus petersoni* from Utah is another large (81cm) ichnotaxon of uncertain origin, possibly Theropod or Hadrosaurian (Boutakiout et al., 2009). *Tyrannosauripus pilmorei* on the other hand measures 86cm long in total and is obviously of

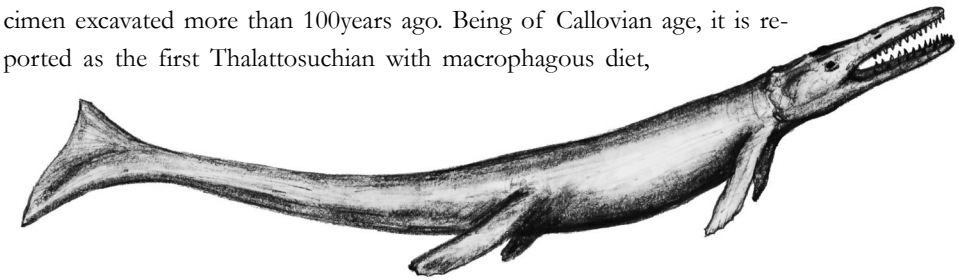
Nyasasaurus parringtoni, the closest known contender for the basalmost Dinosaur

Fossils collected in the 1930s and inofficially named in the late 60s were formally named and described (Nesbitt et al., 2013) as a genus and species of early Dinosauriform or Dinosaur, *Nyasasaurus parringtoni*, from the Anisian Manda Formation in Tanzania. It compromises the original type specimen, NHMUK R6856, and that of *Thecodontosaurus alophos*, SAM-PK-K10654. The holotype consists of a proximal humerus and three dorsal and sacral vertebrae respectively, while the referred specimen compromises three cervical and two dorsal vertebrae. While the two specimens share no autapomorphies, their assignment is supported by their positions in the performed phylogenetic analysis. A position as a basal Ornithischian, Saurischian or the sister taxon of Dinosauria is suggested, making it the closest relative of the common ancestor of all Dinosaurs yet discovered. Assuming a phylogenetic position as an early Dinosaur, it is furthermore the oldest known member of the group. The vascular structure observed on the humerus closely resembles basal dinosaurs, more so than other ornithodirans. Nyasasaurus is estimated to have measured ~2-3m in lenght. Little about its morphology can be inferred, which probably resembled related early Dinosauriforms like *Asilisaurus kongwe*.



Tyrannoneustes lythrodectikos, a macrophagous metriorhynchid from the middle Jurassic

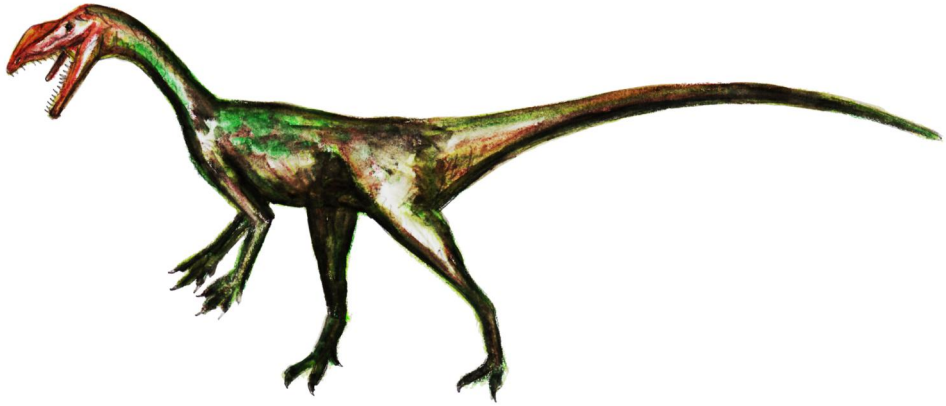
Based on a partial specimen including a 65cm+ mandibular ramus and large, ziphodont teeth, *T. lythrodectikos* was named by Young et al., 2013 on the basis of GLAHM V1436, a specimen excavated more than 100years ago. Being of Callovian age, it is reported as the first Thalattosuchian with macrophagous diet,



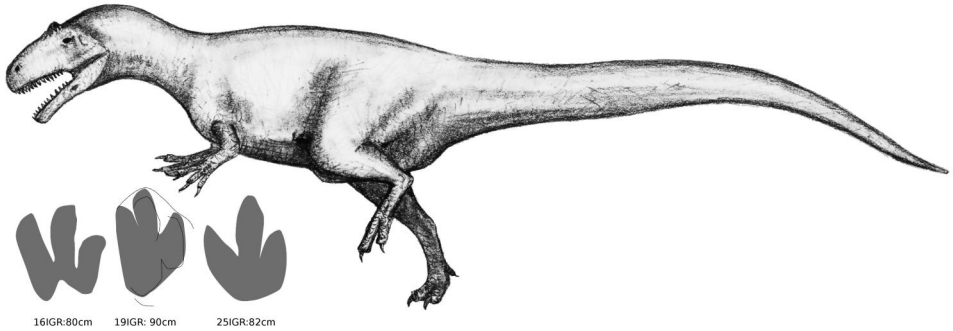
similar to the later genera *Dakosaurus*, *Torvoneustes* and *Plesiosuchus*, as indicated by its dental morphology. The animal itself probably measured 3-4m in total lenght and swam the European seas together with other large sea reptiles like Pliosaurs and Ichthyosaurs.

The Earliest Evidence for Giant Theropods: A Footprint

Several large Triassic and Lower Jurassic Dinosaurs are only known based on ichnological evidence, greatly extending variation in body size of taxa from these strata. Two tridactyl, digitigrade ichnites from the Norian or Raetian of Brazil, measuring 43cm in lenght, 39cm in width and preserving clawmarks whave been referred to *Eubrontes sp.* (Silva et al., 2012) and indicate relatively large theropod dinosaurs from this period. Other footprints of subequal size from various locations were assigned to the same ichnogenus, the Brazilian specimens being the largest known Triassic theropod prints and indicating animals of at least 6-7m in size. An even bigger (54cm long) specimen, Muz.PIG 1661.II from Poland, referred to *Megalosauripus* was discovered in the lower Jurassic of Poland (Gierlinski et al., 2001), and indicates *Allosaurus*-sized theropods from this period. These Ichnotaxa are the first substantial evidence for large predatory dinosaurs from these biota.

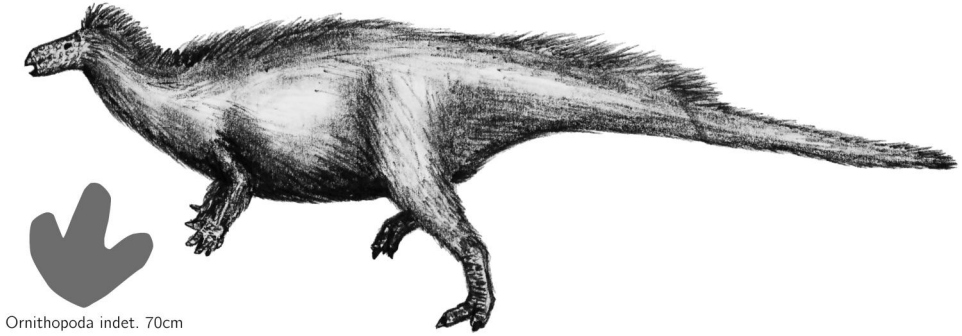


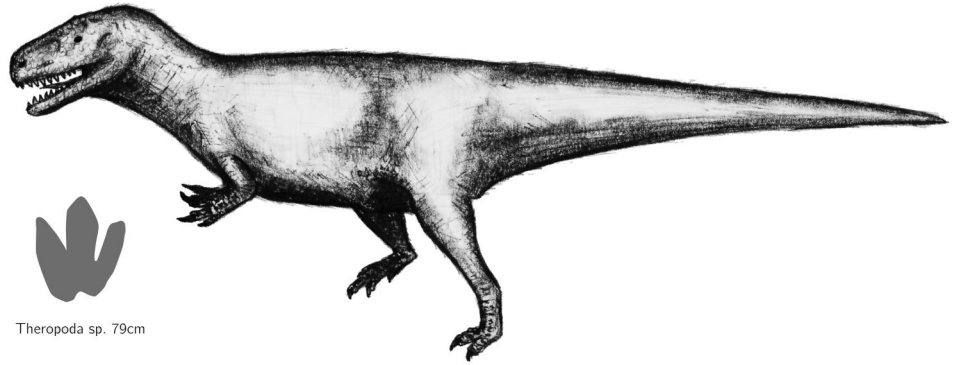
The giant Trackmakers of Morocco; Biggest of the big Jurassic theropods?



A number of gigantic tracks from the Moroccan Iouaridène syncline (Oxfordian-Kimmeridgian), the largest consisting of a single, isolated, tridactyl pes print, were described by Boutakiout et al., 2009. The three sets of footprints average 75, 77 and 90cm respectively, showing no obvious signs of deformation as described. The largest ichnites in each trackway, 16IGR, 25IGR and 19IGR, measure 80, 82 and 90cm long, making them not only the largest known Jurassic theropod prints, but also perhaps the largest in the world, when excluding deformed prints or metatarsal impressions. The trackmakers can be arbitrarily referred to Allosauria incertae sedis, based on age, size and abundance of these animals. Their dimensions point out to Jurassic predators at least equaling, possibly exceeding the largest Cretaceous carnosaurs and tyrannosaurs in overall size; as given by the authors 3,4-4,4m tall at the hip and 10-19m long, and arguably in the 14-15m range.

Lourhinha Formation; A Diverse Upper Jurassic Ichnofauna





Mateus and colleagues (2008/2010) report several large Ichnotaxa from the Tithonian-Kimmeridgian Lourhinha Formation of Portugal, referred to Thyreophora, Sauropoda, Ornithopoda and Theropoda. Among many smaller specimens, a giant tridactyle ichnite referred to Ornithopoda indet. measures 70cm long and 69cm wide, indicating an animal 3-4m tall at the hip, the first record of a giant-sized Ornithopod from the Jurassic, as compared to the medi-