

SPECIAL

On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species

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The species *Allosaurus fragilis*, from the Morrison Formation of North America (Kimmeridgian–Tithonian, Upper Jurassic), is one of the best known members of the Theropoda, the group including all predatory non-avian dinosaurs and birds. Here, we report on the first diagnostic theropod remains discovered from the Jurassic of the Iberian Peninsula. The specimen is the first evidence of *A. fragilis* outside North America. Thus, this taxon represents the first dinosaur species found on two different continents, and suggests the existence of a ‘land bridge’ between North America and Europe during the Late Jurassic.

Keywords: Upper Jurassic, Dinosauria, Theropoda, *Allosaurus*, Palaeobiogeography.

O. C. Marsh (1877) named the type species *Allosaurus fragilis* from fragmentary remains from the Upper Jurassic (Kimmeridgian–Tithonian, Kowallis *et al.* 1998) Morrison Formation of Colorado, and the genus has been well documented from the western United States. Subsequently, specimens from Africa, Europe and Australia have been referred to *Allosaurus*. However, none of these specimens shows diagnostic features of this genus (Chure 1998). Moreover, none of the theropods described as allosaurids from Europe over the last century can be referred to the family Allosauridae. A theropod from Montmirat (Gard, Southern France) found in 1965 in marine Valanginian (Lower Cretaceous) sediments, was recognized as being more closely related to *Allosaurus fragilis* than to other theropods (Pérez-Moreno *et al.* 1993). However, the

incompleteness of the skeleton, lacking diagnostic features, precluded formal taxonomic placement of the specimen. In a preliminary description, *Neovenator salerii* (Hutt *et al.* 1996), a theropod from the Barremian (Lower Cretaceous) of the Isle of Wight (United Kingdom), was claimed to be the first European allosaurid. Others have claimed it is more closely related to carcharodontosaurids (Harris 1998). Until a detailed description and a phylogenetic analysis appears, its referral to the Allosauridae must be viewed cautiously.

We report here on a new specimen, found in 1988 in Upper Jurassic sediments of the Lourinhã Formation (Lusitanian Basin), Upper Kimmeridgian–Tithonian (Upper Jurassic) (Wilson *et al.* 1989), near the village of Andrés (District of Leiria, west-central Portugal), about 135 km NNE of Lisbon. The Lourinhã Formation is mainly represented by micaceous sandstones (as occur in Andrés), fine sands and silts, and was deposited in a fluvial meandering environment with subsidiary deltaic and marginal marine environments (Wilson *et al.* 1989). The specimen (MNHNUL/AND.001; Museu Nacional de História Natural, Universidade de Lisboa. Andrés collection) is a partial skeleton that includes part of the right quadrate, several vertebrae and chevrons, several dorsal ribs and gastralia, a partial pelvis, parts of the hind limbs and several indeterminate fragments (Fig. 1).

Only the ventral articular end of the quadrate is preserved. It has two well-developed oblique condyles, with the lateral one more than two thirds the maximum transverse length of the medial one. None of the vertebrae of the specimen have pleurocoels (pneumatic foramina) and all articular surfaces are weakly concave. The only preserved proximal caudal is nearly identical to the 4th caudal of *Allosaurus fragilis* (Madsen 1976). The five distal caudal vertebrae are the most complete vertebrae of the specimen. The centra are elongate and low, and the prezygapophyses project about two thirds of the length of the centrum beyond the cranial articular surface. The large pubic peduncle of the ilium is longer than wide, and is much longer than the ischiadic peduncle. The distal end of the ischium is absent, but a distal expansion was present, and was probably more developed caudally than cranially (Fig. 2). The obturator process is large and tapering and projects cranially to the level of the puboischadic contact. Although this obturator process appears to be unique in its morphology, identical obturator processes are present in undescribed specimens of *Allosaurus* (AMNH 813—American Museum of Natural History; BYU 5524—Brigham Young University; DINO 11541—Dinosaur National Monument) (Fig. 2). A small notch separates the caudodistal margin of the obturator process from the ischiadic shaft. The ventral surface of the obturator process is slightly concave, whereas the dorsal one is nearly straight. The pubis has a ventral notch in the ischiadic peduncle. On the medial surface of the pubic shaft, distal to the obturator notch, there is a caudally directed, subtriangular crest, nearly identical to that of *Allosaurus fragilis* (Madsen 1976). It is interpreted as the reduced ventral part of the obturator process of the pubis. There is a large distal foot with a well developed cranial part that is shorter, higher and stouter than the caudal one. The cranial part is consistent in height, while the caudal one becomes lower caudally. Only the left femur is present and it is partly covered by the pelvic elements, so little morphological information is available. It has a deep, large depression on the craniodistal surface that is delineated medially by a strong longitudinal crest. The right tibia is almost complete, and is nearly identical to that of *Allosaurus*

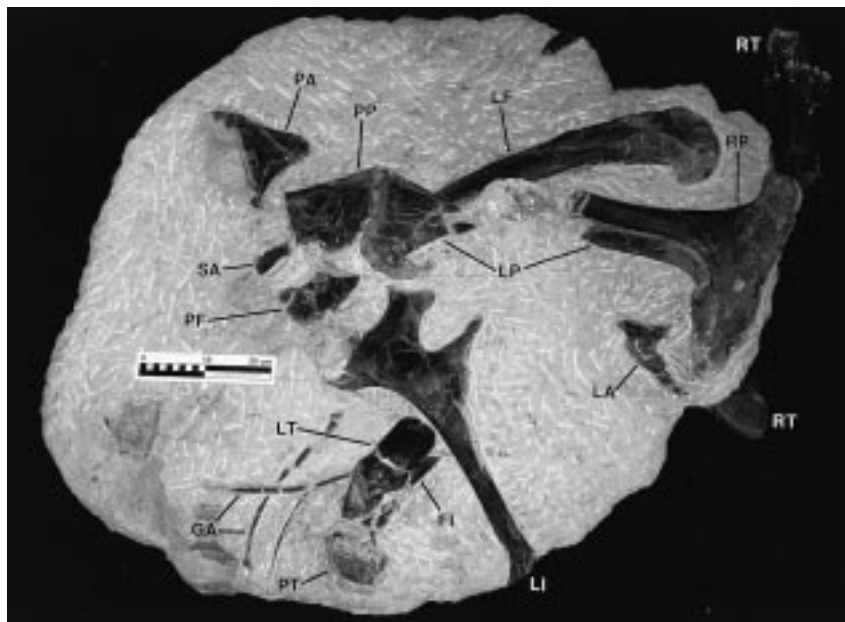


Fig. 1. Main block of MNHNUL/AND.001 (Museu Nacional de História Natural da Universidade de Lisboa, Andrés collection), *Allosaurus fragilis*. The complete specimen is composed by the articular end of the right quadrate, some vertebrae (the last dorsal, first sacral and part of the second one, one anterior caudal, one midcaudal and five posterior ones), some thoracic ribs, gastralia and chevrons, part of the pelvic girdle (part of the left ilium, the left ischium and both pubis), part of the left hindlimb (femur, tibia, fibula and second metatarsal) and the tibia and fibula of the right one, and several indeterminate fragments. Scale in centimetres. Abbreviations: FI, left fibula?; GA, gastralia; LA, lacrimal?; LF, left femur; LI, left ischium; LP, left pubis; LT, left tibia?; PA, preacetabular blade of the left ilium; PF, proximal end of the left femur; PP, pubic peduncle of the left ilium; PT, left proximal tarsals?; RP, right pubis; RT, right tibia; SA, supracetabular crest of the left ilium.

fragilis. Although the astragalus is missing, the astragalular scar on the tibia indicates a moderately high ascending process of the astragalus, a feature unique to *Allosaurus* among known



Fig. 2. (a) Medial view of the left ischium of MNHNUL/AND.001 (Museu Nacional de História Natural da Universidade de Lisboa, Andrés collection), *Allosaurus fragilis*. (b) Lateral view of the right ischium of DINO 11541 (Dinosaur National Monument, Utah), *Allosaurus* n. sp., from the Salt Wash Member of the Morrison Formation (Dinosaur National Monument). Both of them show a very large obturator process, a diagnostic character of the genus *Allosaurus*. Scale bars: 5 cm. Abbreviations: A, acetabulum; IF, ischiadic foot; IP, iliac peduncle; OP, obturator process; PP, pubic peduncle; VN, ventral notch.

allosauroids. The right fibula lacks its distal end. The proximal end is craniocaudally expanded, and has a conspicuous medial longitudinal fossa, extending into the shaft, where a cranial knob appears. In proximal view, the articular surface of the second metatarsal possesses a caudal process that is separated laterally from the main body of the bone by a conspicuous cleft. This feature is also present in *Allosaurus* (Gilmore 1920) and *Acrocanthosaurus* (Stovall & Langston 1950).

The genus *Allosaurus* contains two species, *A. fragilis* and a new species currently under study by D.J.C. (DINO 11541). The only difference between these two species that can be compared with the Portuguese material is in the morphology of the proximal end of the pubis. *A. fragilis* has a craniocaudally short proximal end with a small obturator notch. The new species has a craniocaudally long proximal end with a wide and open obturator notch. While it is unclear as to which condition is primitive, MNHNUL/AND.001 exhibits the morphology seen in *A. fragilis* and on that basis we refer the specimen to that species. Both species have the peculiarly-shaped obturator process seen in the Portuguese specimen (Fig. 2).

MNHNUL/AND.001 represents the first diagnostic Jurassic theropod remains known from the Iberian Peninsula. Sediments of this age are exceptionally rare in Spain, where there are abundant Cretaceous beds. Fragmentary remains have been described from the Upper Jurassic of Portugal, and were assigned to the *nomina dubia* *Megalosaurus pombali* and *M. insignis* (Lapparent & Zbyszewski 1957). Recently, a well-preserved clutch with eggs containing embryonic remains of a large theropod has been reported from the Upper Kimmeridgian–Lower Tithonian of Lourinhã (Portugal), along with adult remains from the same area (Mateus *et al.* 1997). Whether the embryos can be assigned or not to *A. fragilis* await detailed description of both adult and embryonic specimens.

Most of the known specimens of *Allosaurus fragilis* come from the continental interior and the coastline area of the

Sundance Sea (Colorado, Montana, Utah, New Mexico, Oklahoma and Wyoming). The presence of *A. fragilis* (MNHNUL/AND.001) in Portugal suggests it was also probably present in the eastern part of North America. Unfortunately, rocks of Mid- and Late Jurassic age are absent from eastern United States (Weishampel & Young 1996). Nevertheless, the present specimen implies the existence of a connection between the North American continent and western Europe during Late Jurassic times, casting doubts on most palaeogeographic reconstructions where a fully open North Atlantic appears.

The hypothesis of the existence of a connection between North America and Europe in the Late Jurassic has been proposed previously by several authors. Galton (1980a, b) and Galton & Powell (1980) addressed this question based on the presence of the ornithomimid genus *Camptosaurus* Marsh, on the Upper Jurassic of North America and England, which they used in support of a land connection between Europe and North America during the early Late Jurassic (Oxfordian). Cox (1980), in his discussion of the palaeobiogeography of the Mesozoic world, stressed that the Jurassic flora of western North America was very similar to the Eurasian one. According to this author, the seaway between these two continents '(...) was too narrow to act as a barrier to the dispersal of these Jurassic plants', but he suggests it may have been more effective as a barrier for the dinosaur and other terrestrial faunas at that time (Cox 1980, p. 76).

Portuguese Upper Jurassic dinosaur faunas are still poorly known. The large majority of forms need taxonomic and phylogenetic revision. These faunas comprise theropods, sauropods, ornithomimids, stegosaurians and primitive ankylosaurians (Nodosauridae) (Dantas 1990; Weishampel 1990), and are globally comparable to those from the Morrison Formation of North America, the Kadzi Formation of Zimbabwe (Raath & McIntosh 1987), and the Tendaguru Formation of Tanzania. These three areas (western Europe, North America and eastern Africa) present closely related dinosaurian forms which do not appear in any other part of the world (Weishampel 1990; Russell 1993), suggesting some sort of gene flow between them: the genera *Dryosaurus*, *Camptosaurus* and *Brachiosaurus*, among others, are classical examples of this faunal similarity. The African and North American *Dryosaurus* species (*D. letowvorbecki* Virchow and *D. altus* Marsh, respectively) are almost conspecific, implying (after Galton 1980a) the presence of a land connection between the two areas at some time during the Kimmeridgian. On the other hand, the North American and European species of *Camptosaurus* (*C. dispar* Marsh and *C. prestwichii* Hulke, respectively) differ in several respects. According to Galton (1980a, b) and Galton & Powell (1980), these dissimilarities suggest the existence of an earlier Northern Atlantic connection between these two continents, at some time during the Oxfordian. Studies currently in progress will also try to confirm the presence of a *Camptosaurus* species on the Lourinhã Formation and the Kimmeridgian–Tithonian of Torres Vedras from Portugal (Galton 1980a, b; Galton & Powell 1980; Dantas 1990; Weishampel 1990; Norman & Weishampel 1990) and to determine to which form—*C. dispar* Marsh or *C. amplius* Marsh from the western North America or *C. prestwichii* Hulke from Oxford, England—it has stronger affinities. Although undoubtedly present in Africa and North America during the Late Jurassic, the presence of the sauropod *Brachiosaurus* Riggs in the Lourinhã Formation (Lapparent & Zbyszewski 1957; McIntosh 1990a; Weishampel 1990) still

needs to be confirmed (Dantas 1990; McIntosh 1990b; Wilson & Sereno 1998). However, the remains of the Portuguese species ?*B. atalaiensis* Lapparent & Zbyszewski 1957 most probably belong to a brachiosaurid.

In conclusion, a direct North America–Africa connection has been already proposed through Central and South America (e.g. Cox 1980; Galton 1980a, b; Galton & Powell 1980) in order to explain the faunal similarities between the Morrison and Tendaguru Formations. Nevertheless, the intercontinental distribution of the nonavian theropod *A. fragilis* is a stronger evidence for a land route between North America and Eurasia, and probably also with Africa (although not necessarily at the same time), during the Upper Jurassic. The presence of *A. fragilis* in the Lourinhã Formation suggests the re-instatement of a Northern Atlantic 'land bridge' connection sometime during the Kimmeridgian–Tithonian. Palaeoenvironmental reconstructions of the North Atlantic during the Late Jurassic show that western Europe and the Grand Banks region were already separated by deep water masses (Fourcade *et al.* 1991). In contrast, Golonka *et al.* (1996) show broad land connections between North America and Europe in the Bajocian–Bathonian and a narrow band of shallow water of continental shelf depth between the continents in the Oxfordian–Kimmeridgian. These conflicting reconstructions should be re-evaluated based on the evidence presented here.

Dinosaur faunas of Portugal, together with other vertebrate terrestrial groups such as Mammalia and Lacertilia (*sensu lato*), are of crucial importance for understanding the Late Jurassic paleobiogeography of the North Atlantic region. In this context, the revision and further research of these faunas, namely its evolutionary affinities with those from the Morrison and Tendaguru Formations, currently in progress, is of major importance in providing relevant arguments to this general question.

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