



Current knowledge of Late Jurassic ornithopod dinosaurs from Europe



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Journal webpage:

<http://cienciasdaterra.novaidfct.pt/>

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ISSN: 0254 - 055X

eISSN: 2183 - 4431

Abstract

The ornithopod skeletal fossil record from the Upper Jurassic of Europe is more scarce and fragmentary than in North America, but showing a similar diversity. In Europe, most of the knowledge about this group of dinosaurs comes from finding in Portugal, Spain, UK, France, and Germany. In this work we concisely review the main discoveries in these regions. As result, we determined that Late Jurassic European ornithopod faunas were mainly composed by dryosaurids, non-styracosternan ankylopollexians, and perhaps other derived species.

Keywords: diversity, Dinosauria, Ornithopoda, Europe, Late Jurassic.

1. Introduction

Late Jurassic ornithopods are well known thanks to many skeletal fossils from the Morrison Fm (lower Kimmeridgian-Tithonian) of USA and Tendaguru Fm (Callovian-Hauterivian) of Tanzania. In the former lithostratigraphic unit, species as the dryosaurids *Dryosaurus altus* (Galton, 1981) and *Dryosaurus elderae* (Carpenter & Galton, 2018), or the basal ankylopollexians *Camptosaurus dispar* (Gilmore, 1909) and *Uteodon* (= *Camptosaurus*) *aphanoecetes* (Carpenter & Wilson, 2008) have been described for first time. In the Tendaguru Fm, several skeletons of the dryosaurid *Dysalotosaurus lettowvorbecki* have been found (Hübner, 2010). This situation contrast with those in other regions, as is the case of Europe where ornithopod specimens are less complete and frequent (Fig. 1). The aim of this work is to update the current knowledge on the ornithopod diversity during the Late Jurassic, focused on outcrops from different parts of Europe.

Portugal

Some of the most important findings of Europe concentrate in the Lusitanian Basin. To date, here

two species have been described: the dryosaurid *Eousdryosaurus nanohallucis* whose type specimen is the posterior part of a skeleton from the Alcobaça Fm (upper Kimmeridgian) (Escaso *et al.*, 2014) and the probable non-styracosternan ankylopollexian *Draconyx loureoi* which was defined based on a partial skeleton composed by two teeth and fragmentary postcranial remains from the Bombarral Fm (Tithonian) (Mateus & Antunes, 2001). Furthermore, Escaso (2014) describes other scarce but well-preserved postcranial fossils remains from the Praia da Amoreira-Porto Novo Fm (upper Kimmeridgian-lower Tithonian) which were referred to the North American non-styracosternan ankylopollexian *Uteodon* (= *Camptosaurus*) *aphanoecetes*. Additionally, Rotatori *et al.* (2019) studied a few postcranial fossils from the Lourinhã Fm (Kimmeridgian-Tithonian) which might belong to a large-sized ornithopod resembling those typical of the Early Cretaceous. Moreover, several fragmentary cranial and postcranial remains from the Kimmeridgian-Tithonian have been referred to Ornithopoda indet. (scarce and fragmentary axial and appendicular elements; Escaso, 2014), Iguanodontia indet. (a partial skeleton, Dantas *et al.*, 2000; and three

teeth, Rauhut, 2001), *Dryomorpha* indet. (two dentary teeth, Rotatori *et al.*, 2018a), *Dryosauridae* indet. (three phalanges and a dorsal vertebra, Malafaia *et al.*, 2010; two different femora, Escaso, 2014; a dentary, a parietal, two femora, two tibia, Rotatori *et al.*, 2018a, b), and *Ankylopollexia* indet. (isolated teeth, Malafaia *et al.*, 2010; two different femora, Escaso, 2014; a set of caudal vertebrae, Escaso *et al.*, 2018).

Spain

The Spanish record is represented by the Ibero-Levantine (or South Iberian) Basin, Cameros Basin, and Gijón-Villaviciosa Basin fossils. In the former, the Villar del Arzobispo Fm (Kimmeridgian-Berriasian?) has yielded fossils ascribed to *Ornithopoda* indet. such as several vertebrae (Pereda-Suberbiola *et al.*, 2009), and a tooth (Suñer & Martín, 2009) from the

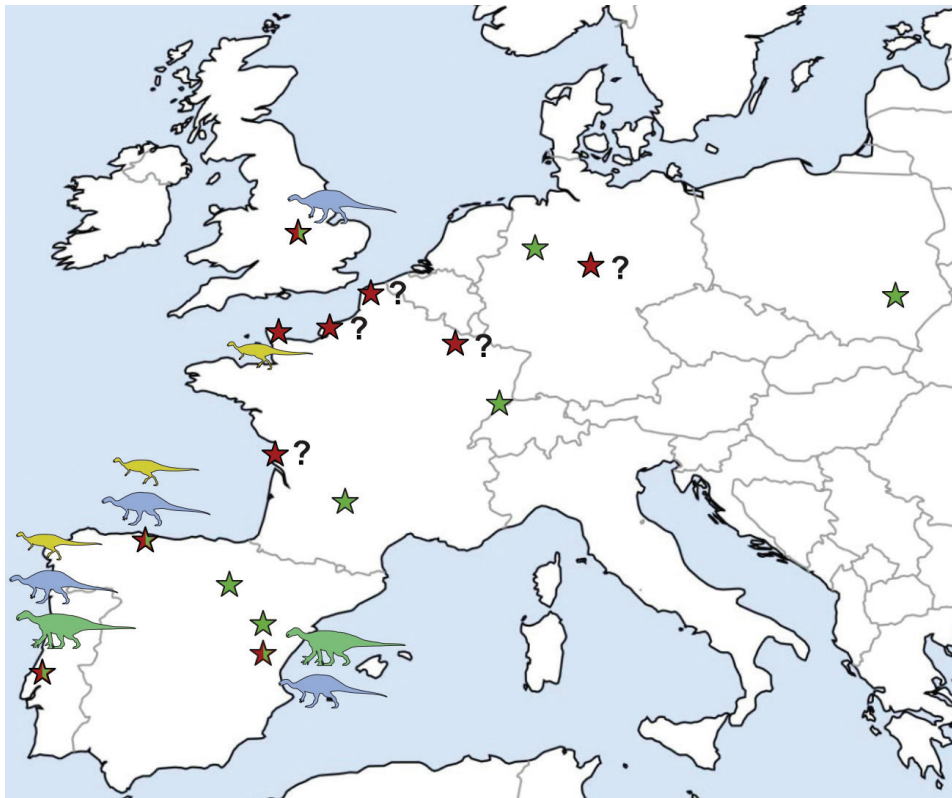


Fig. 1. -Upper Jurassic European localities with ornithopod fossils (bones and footprints, red and green stars respectively). Silhouettes represent the diverse ornithopods recorded (yellow = dryosaurid, blue = non-styracosternan ankylopollexian, green = styracosternan). ? = isolated and fragmentary remains with dubious assignments.

municipality of Alpuente (Valencia Province). As well, several vertebrae and a fragment of a humerus from the same municipality (Sánchez-Fenollosa *et al.*, 2019), and a tooth and a hindlimb from Riodeva (Teruel Province) (Gascó *et al.*, 2013) have been referred to *Ankylopollexia* indet. In the Cameros Basin, a jugal, a quadrate, several vertebrae, ribs, and chevrons, a scapula, and part of the pelvic girdle of an indeterminate basal *Styracosterna* from the Ciria Fm (Tithonian-Berriasian?) in Berdejo (Zaragoza Province) have been also described (Royo-Torres *et al.*, 2012). Regarding to Gijón-Villaviciosa Basin, the ornithopod remains reported from these Jurassic outcrops come from several localities in the Villaviciosa municipality (Asturias Province), most of them from the Lastres Fm (Kimmeridgian). They were referred to: *Ornithopoda* indet. (a dorsal centrum), *Dryomorpha* indet. (a

maxillary tooth), *Dryosauridae*? indet. (a fragment of a right pubis), and *Ankylopollexia* indet. (three cervical vertebrae, three anterior caudal vertebrae, a distal half of a right ischium, and a possible ossified tendon) (Ruiz-Omeñaca *et al.*, 2012 and references therein). Remains from Tereñes Fm (Kimmeridgian) in the same municipality consist of two dorsal centra which were referred to *Ankylopollexia* indet. (Ruiz-Omeñaca *et al.*, 2012 and references therein).

United Kingdom

In the Purbeck Group (Tithonian-Berriasian), a metatarsal from Hartwall, a pes phalanx from Buckinghamshire, and other isolated remains with strictly Tithonian age were referred to *Iguanodontia* indet. by Weishampel *et al.* (2004 and references therein). However, the most complete Upper

Jurassic European ornithopod fossil is the type specimen of the non-styracosternan ankylopollexian *Cumnoria* (= *Camptosaurus*) *prestwichii*, which was discovered in the lower part of Kimmeridge Clay Fm (Kimmeridgian-Berriasian) (Galton & Powell, 1980).

France

The French record is based on isolated remains, such as two ornithopod teeth from Boulonnais (Cuny *et al.*, 1991). Among this fragmentary material, an isolated femur from Marnes de Bleville Fm (lower Kimmeridgian) that was referred to *Dryosaurus* sp. by Buffetaut & Cacheleux (1997) is the most significant finding. Moreover, Vullo *et al.* (2014) referred to *Iguanodontia* indet. a few worn teeth and to small ornithopods several vertebrae from the early Tithonian of Chassiron.

Germany

Finally, Windolf (1998) reported from Lower Saxony (Süntel Fm, Kimmeridgian) the presence of an isolated fragment of a tibia referred to *Iguanodontidae*? indet.

2. Discussion and conclusions

Despite some Upper Jurassic ornithopod specimens described in Europe are well known, the most part of the materials consist of isolated and/or fragmentary postcranial remains. This has consequences for establishing confidently the taxonomic and phylogenetic affinities of such remains, being that valuable morphological characters commonly used in ornithopods data matrices are mainly concentrated in the cranium (e.g., 85 of 134 characters in McDonald *et al.*, 2017 dataset). For these reasons, the phylogenetic affinities of some of the specimens are, currently, not easy to establish as it is the case of *Draconyx loureoi*.

However, it can be confidently determined that Late Jurassic European faunas of ornithopods are composed by dryosaurids and camptosaurus-like non-styracosternan ankylopollexians as reported by other authors (e.g., Ruiz-Omeñaca *et al.*, 2012; Escaso, 2014), with some evidence of the presence of probable more derived ornithopods (i.e., basal Styracosterna, Royo-Torres *et al.*, 2012; Rotatori *et al.*, 2019). The observed ornithopod diversity is in accordance with the ichnological record (tridactyl dinosaur tracks are relatively frequent in the Late Jurassic of Europe, see Castanera *et al.*, 2018 and

references therein) and also with the faunistic composition known from other areas in both North America and Africa, pointing to a biogeographic relationship among these landmasses (e.g., Galton, 1981; Escaso, 2014).

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