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Individual variation in the postcranial skeleton of the Early Cretaceous *Iguanodon bernissartensis* (Dinosauria: Ornithopoda)



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ABSTRACT

At the end of nineteenth century, approximately thirty nearly complete skeletons of the ornithopod dinosaur *Iguanodon bernissartensis* were discovered in Lower Cretaceous deposits in Bernissart (Belgium). Because most of the specimens are approximately the same size, they offer a unique opportunity for studying individual variation (i.e., differences among individuals of the same or roughly the same age) in iguanodontians. Here, we report the results of a study combining both morphometric and visual analyses of the postcranial skeleton of the Bernissart specimens. We found significant individual variation in the morphology of the axis, sacrum, caudal vertebrae, scapula, humerus, pollex, ilium, ischium, femur, and tibia. No definitive evidence of sexual dimorphism was identified in *I. bernissartensis*. Individual variation in *I. bernissartensis* has significant implications for phylogenetic and ontogenetic studies as well as for evaluating diagnostic characters in *Iguanodon* and other iguanodontians. For example, the status of the basal styracosternan '*Delapparentia turolensis*' from the lower Barremian of Spain is discussed; given the individual variation in the postcranial skeleton of *I. bernissartensis*, it is in fact impossible to distinguish '*Delapparentia*' from *Iguanodon* species based on the available material.

1. Introduction

Intraspecific variability can be defined as those differences occurring among individuals of the same species regardless of type (morphological, behavioral, ecological, genetic, etc.). Two sources of intraspecific variations can be distinguished: ontogenetic variability (age-dependent) and individual variability (age-independent). Individuals of different ages are subject to both ontogenetic and individual variation; thus, individual variation can only be studied in individuals of approximately the same age and development stage. In non-hadrosaurid ornithopods, studies of morphological ontogenetic variation are rare but usually rather detailed (e.g., Galton, 1974; Norman, 1980; Grigorescu and Csiki, 2006; Hübner and Rauhut, 2010; Prieto-Márquez, 2011; Guenther, 2014; Zheng et al., 2014; Verdú et al., 2015). In contrast, studies of individual variation are even scarcer and less detailed (e.g., Galton, 1974; Norman, 1980; Weishampel et al., 2003; Carpenter and Wilson, 2008; Godefroit et al., 2009; McDonald, 2012a;

Carpenter and Lamanna, 2015), including some attempts to identify sexual dimorphism (Nopcsa, 1929; Galton, 1974; Weishampel et al., 2003), despite the importance of individual variation in systematic, phylogenetic and ontogenetic studies in dinosaurs.

The main problem in studies of individual variation in nonhadrosaurid ornithopods is the usually low number of comparable individuals discovered of a single species; thus, the results cannot be considered statistically significant. The Early Cretaceous (late Barremian-earliest Aptian) styracosternan Iguanodon bernissartensis Boulenger in Van Beneden 1881 is represented by an exceptional series of subcomplete specimens from a single locality. In 1878, miners discovered a large number of skeletons in a coal mine in Bernissart (southern Belgium; Godefroit et al., 2012); Norman (1986) estimated that at least 37-38 specimens of I. bernissartensis were unearthed from this 'Iguanodon Sinkhole'. Most of them are approximately the same size and can be considered 'adults', while three smaller specimens may represent 'subadults'. All these skeletons appeared to be clustered into four stratigraphically separated, dinosaur bone beds in an 8-m-thick clay layer (Baele et al., 2012). Accounting for both the stratigraphic and taphonomic data in the 'Iguanodon Sinkhole', the most likely



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scenario for the formation of these four bone bed deposits is a periodic mass-death event (perhaps an intoxication) occurring seasonally in an Early Cretaceous paleolake (Baele et al., 2012). Hence, this high number of specimens from Bernissart is a unique opportunity to study the morphological variation in the skeleton of non-hadrosaurid ornithopods. Furthermore, *I. bernissartensis* fossils have also been found in other areas of Europe, including the United Kingdom, France, Germany, and Spain (Norman, 2012).

As part of his extensive and detailed monograph about *I. bernissartensis*, Norman (1980) briefly described some variations in its cranial and postcranial skeleton. Here, we report the results of a more detailed study of the individual variation in the postcranial skeleton of the larger, similarly sized *I. bernissartensis* specimens from Bernissart (Belgium). However, the smaller 'sub-adult' specimens were also examined, and any ontogenetic variation is discussed. These observations are evaluated against those of other specimens of this taxon from other regions of Europe. Moreover, the implications of this work for systematic, phylogenetic, and ontogenetic studies in Iguanodontia are explored. Finally, we discuss the importance of individual variation in *I. bernissartensis* for evaluating the validity of the early Barremian basal styracosternan '*Delapparentia turolensis*' Ruiz-Omeñaca 2011 from Spain, which is considered a potential *nomen dubium* by Norman (2015).

1.1. Institutional and other abbreviations

AR – Mina Santa María de Ariño site, Ariño, Spain (the material is currently housed at the *Museo Aragonés de Paleontología* in Teruel, Spain).

CMP – Cantera Más de la Parreta site, Morella, Spain (the material is currently housed at the *Museo de la Valltorta* in Tirig, Spain, and the *Museo Paleontológico de Elche* in Elche, Spain [*sensu* Gasulla, 2015]).

GPI – Geologisches und Paläontologisches Institute, Münster, Germany.

MAP – Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis), Teruel, Spain.

M-MR – Mas de Romeu site, Morella, Spain (the material is currently housed at the *Museu Temps de Dinosaures*, Morella, Spain).

MNHN – Muséum National d'Histoire Naturelle, Paris, France.

MPT – Museo Provincial de Teruel, Teruel, Spain.

M-TA – Tejería Azuví site (currently Cantera Azuví), Morella, Spain (the material is currently housed at the *Museu Temps de Dinosaures*, Morella, Spain).

NHMUK – Natural History Museum, London, U.K.

RBINS – *Royal Belgian Institute of Natural Sciences*, Brussels, Belgium.

SC – San Cristóbal sites, Galve, Teruel, Spain (the material is currently housed at the *Museo Aragonés de Paleontología*, Teruel, Spain).

USNM – National Museum of Natural History, Washington D.C., U.S.

2. Materials and methods

2.1. Materials

The *I. bernissartensis* specimens studied in this work were unearthed from the lacustrine facies of the Sainte-Barbe Clay Formation (upper Barremian-lowermost Aptian) in the 'Iguanodon Sinkhole' in Bernissart (Belgium) (Yans et al., 2012). These specimens were described in detail by Norman (1980), and although they are all deposited in the paleontological collections of the *Royal Belgian Institute of Natural Science* (RBINS), specimen RBINS R343 is currently on exhibit in the *Musée de l'Iguanodon* in Bernissart (Belgium). Almost all the specimens listed by Norman (1980) have been examined, practically in their totality (Supplementary information), and the majority of the material corresponds to more or less complete skeletons that are currently mounted and on exhibit disposed in either in-life gait (bipedal) or 'en gisement' (Fig. 1). However, other disarticulated and incomplete material



Fig. 1. Different dispositions of Iguanodon bernissartensis specimens in the exhibition room at the RBINS, bipedal gait (left, RBINS R52) and 'en gisement' (right, RBINS R347).

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