



Notes on the rising diversity of Iguanodont taxa, and Iguanodonts named after Darwin, Huxley, and evolutionary science

Notas sobre el aumento de la diversidad de taxones de iguanodontes, e iguanodontes descritos después Darwin, Huxley, y la ciencia evolutiva

G. Paul¹

Recibido el 7 de enero de 2011, aceptado el 1 de septiembre de 2011.

(1): 3019 North Calvert Station, Side Apartment, Baltimore, MD 21218-3807, USA, email: GSP1954@aol.com

Abstract

The taxonomic diversity of previously published European iguanodonts is reviewed and analyzed. It is concluded that the diversity was very high, contrary to suggestions that many specimens can be referred to a limited number of genera and species. It is emphasized that specimens usually can be assigned to the same species only when sufficient overlapping material exists and they are stratigraphically similar in time within a given formation. The separation of *Mantellisaurus atherfieldensis* and *Dollodon bampingi* is supported, but redescription of the holotypes is needed before they can be fully diagnosed. Three new genera and two new species are named. A Spanish fossil demonstrates the presence of *Iguanodon* type iguanodonts in the Iberian peninsula somewhat earlier than they have been found in northern Europe.

Key words: iguanodonts, dinosaurs, Early Cretaceous

Resumen

En este trabajo se revisa y analiza la diversidad taxonómica de los iguanodontes europeos publicados hasta el momento. Se concluye que su diversidad fue amplia, contrariamente a las propuestas más usadas de agrupar muchos especímenes en un limitado número de géneros y especies. Lo adecuado es asignar a la misma especie cuando los materiales vengan de los mismos niveles estratigráficos y existan los mismos restos anatómicos para comparar. La separación de *Mantellisaurus atherfieldensis* y *Dollodon bampingi* parece correcta, pero es necesario la redescipción de los holotipos de ambas especies para hacer una diagnosis adecuada. Se describen tres nuevos géneros y dos especies nuevas. Un fósil español demuestra la presencia de iguanodontes tipo *Iguanodon* en la Península Ibérica, de una edad un poco antes de los descritos en el norte de Europa.

Palabras clave: Iguanodontes, dinosaurios, Cretácico Inferior

INTRODUCTION

After about a century and half of the overlumping of iguanodonts spanning most of the Early Cretaceous and the northern hemisphere into the genus *Iguanodon*, the genus is now limited to one or a very few species of a specialized, robust ornithopod so far known only from the late Barremian and/or early Aptian of Europe (Paul, 2007; 2008; Carpenter and Ishida, 2010). Partly as a result, a rapidly growing number of iguanodont genera and species are being designated, many based on material that had been assigned to *Iguanodon* (Paul, 2007; 2008; Naish and Martill, 2008; Galton, 2009; Norman, 2010; Carpenter and Ishida, 2010; McDonald *et al.*, 2010a, b; Ruiz-Omeñaca, 2011), as well as new material (McDonald *et al.*, 2010b). Although the basic diversification of iguanodont taxa out of *Iguanodon* is not being contested, some important details are being disputed, and Norman (2010) is continuing the tendency to consolidate iguanodont taxa by proposing that both in the early and in the later Early Cretaceous there were just two taxa in Europe, one robust and the other gracile; *Barilium dawsoni* and *Hypselospinus fittoni* in the Valanginian, followed by *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* all the way from the Hauterivian up to the early Aptian. McDonald (2012) also supports the documentation of just the two latter iguanodonts in the upper Wealden.

As noted by Paul (2008, 2010) as well as Ryan and Evans (2005), Mallon and Holmes (2006) and Scannella (2010), it is vital to consider stratigraphic information in determining dinosaur taxa, especially at the level of species which can have rapid turnover rates on the order of a few hundred thousand years (Carroll, 1988). If it cannot be demonstrated that specimens are from the same horizon within a formation, and that they are indistinguishable as a species, then assignment to the same species is unwarranted, all the more so if sufficiently overlapping material is not preserved.

The analysis of major iguanodont taxa including some major holotypes is being hindered because of the lack of current access to specimens, or damage during storage. For example the holotypes of *Mantellisaurus* and *Dollodon* can be compared only via the available descriptions (McDonald, 2012) that lack full documentation, high quality photographs of the skulls especially, and some cranial illustrations of the *Dollodon* holotype in Norman (1986) may not be entirely accurate. As a result attempts to accurately diagnose the specimens may have been less reliable than realized, and continue to be imprecise using the available data. This is a review of some of the previously published material and analysis with some additional results. The latter reinforce that iguanodont diversity in Europe was very high, and that the naming of some new taxa is warranted.

SYSTEMATIC PALEONTOLOGY

Ornithischia Seeley, 1887-1888

Ornithopoda Marsh, 1881

Iguanodontia Dollo, 1888

Ankylopollexia Sereno, 1986

Styracosterna Sereno, 1986

Huxleysaurus gen. nov.

Etymology: For Darwin's "Bulldog" and coiner of the term agnostic, Thomas Huxley.

Diagnosis: As for the type and only known species.

Type Species: *Huxleysaurus hollingtoniensis* (Lydekker, 1889)

= *Iguanodon hollingtoniensis* Lydekker 1889

= *Hypselospinus fittoni* Norman 2010

Holotype of Type Species: NHMUK R1148/1629/1632/811/811b/604.

Type horizon, locality, age: Wadhurst Clay Formation, England, early Valanginian.

Diagnosis of Type Species: Femur robust, moderately curved, 4th trochanter pendent.

Comments: The assignment of the basal "*Iguanodon*" *hollingtonensis* to *Hypselospinus fittoni* by Norman (2010) risks creating a multitaxa chimera because of the lack of adequate overlapping material, and because of the failure to demonstrate that they are from the same level of the Wadhurst Clay Formation. Because the latter is up to nearly 80 meters thick (Anonymous, 2010) it is possible that considerable geological time passed during the deposition of the formation, time sufficient to allow significant species and even genus turnover. The "*I.*" *hollingtonensis* ilium is not sufficiently complete to compare to the better preserved element from *Huxleysaurus fittoni*; although the NHMUK R811b ilium appears to be short and deep, because it is split as midlength it could actually be elongated. It is possible that these are two species within the same genus.

Darwinsaurus gen. nov.

Etymology: For Charles Darwin.

Diagnosis: As for the type and only known species.

Darwinsaurus evolutionis sp. nov.

= *Iguanodon fittoni* (Lydekker 1889)

= *Hypselospinus fittoni* (Norman 2010)

Holotype: NHMUK R8131/1833/1835/1836.

Type horizon, locality, age: Wadhurst Clay Formation, England, early Valanginian.

Etymology: In recognition of Darwin's theory, with the diverse iguanodonts standing as an example of complex evolution via rapid speciation.

Diagnosis: Dentary straight, elongated diastema present, dentary shallow ventral to diastema and deeper astride dental battery, anteriormost dentary teeth reduced. Forelimb very robust, olecranon process well developed,

some carpals very large, metacarpals fairly elongated, thumb spike massive.

Comments: Norman (2010) referred a number of specimens including the holotype of *D. evolutionis* to *Hypselospinus fittoni*. Some of these assignments have been questioned (Naish 2010), and Norman (2010) does not provide evidence that the referred specimens are from the same horizon as the holotypes whose species they are assigned to, other than their being from the Wadhurst Clay Formation. It is possible that the exact stratigraphic level that some of the specimens were found is no longer recoverable due to inadequate documentation. Because Norman (2010) assigned NHMUK 1831-36 to *H. fittoni* despite the lack of stratigraphic correlation and overlapping parts the risk that he has created a taxonomic chimera is high.

Norman (2010) challenges the claim by Paul (2008) that the preserved dentary NHMUK 1831 features a very long diastema. Comparing the element as currently preserved to the very detailed illustration of its original condition (Pl. 1, Fig. 1 in Lydekker, 1889) shows that there has been considerable erosion of bone due to lack of modern conservation techniques (Fig. 2C). Norman (2010) asserts that the small complete tooth that was included in the original illustration is an anomaly, giving the false impression of a long diastema. Aside from the lack of an explanation for why the tooth was included in the exquisitely drawn illustration unless it was actually there, there are at least three and perhaps four similarly small roots with broken off crowns shown immediately anterior to the more complete small tooth, these can be hard to spot in a low resolution reproduction but are readily visible in the first, full scale graphic. The damage in the intervening century and a quarter has apparently resulted in the loss of these small teeth, which may still reside in the collections but could be lost. The best evidence of the original condition of the dentary indicates that the dental battery was short and anteriorly terminated by small teeth, posterior to a long diastema comparable in length to those of some hadrosaurs. In some other iguanodonts the anteriormost teeth in the dentary row are smaller than the others, albeit not to the extreme seen in *D. evolutionis* (Fig. 2D, J, K). The unusually strong antero-dorsal pitch of the border between the anterior section of alveolar parapet and alveolar shelf is unusual for iguanodonts, and further indicates that the tooth battery was constricted to a posterior position; Norman (2010) suggests that R8131 is similar to the better preserved and deep dentary of the *Kukufeldia tilgatensis* holotype NHMUK R28660, but they differ too greatly in the form of the alveolar shelf (Fig. 2B, C), as well as stratigraphic level, for the latter to be used to restore the former. Norman (2010) claims that NHMUK R8131 was originally anteriorly deeper than it seems in the original illustration, but there is no evidence of significant loss of depth of the dentary in the original figure, and in hadrosaurs with long diastemas it is common for the

dentary anterior to the dental battery to be shallower than it is astride the teeth, as seems to be true of NHMUK 1831. Although relying on initial illustrations is not ideal, it is sometimes necessary (as per illustrations being the only surviving record of the holotype of *Spinosaurus aegypticus* and *Poekilopleuron bucklandii*).

The forelimb of *D. evolutionis* was massive (Lydekker, 1888), exceeding *I. bernissartensis* in this regard and rivaling that of *Lurdusauru arenatus* (Fig. 1B, a-c). The metacarpals of *D. evolutionis* were elongated in the manner of more derived iguanodonts.

Mantellodon gen. nov.

Etymology: The holotype has long been known as Gideon Mantell's "Mantel-piece."

Diagnosis: As for the type and only known species.

Mantellodon carpenteri sp. nov.

= *Iguanodon atherfieldensis* Hooley 1925

= *Mantellisaurus atherfieldensis* (Paul, 2007)

Holotype: NHMUK R3741.

Type horizon, locality, age: Lower Lower Greensand Formation, England, early Aptian.

Etymology: In recognition of Kenneth Carpenter's work on dinosaurs including iguanodonts.

Diagnosis: Limb elements slender. Ilium deep, anterior process robust, posterior acetabular body short and very triangular, dorsal margin strongly arched.

Comments: Paul (2008) referred NHMUK R3741 to *M. atherfieldensis*, but this is probably incorrect because the specimen is from a younger formation, and Carpenter and Ishida (2010) and Naish (2010) have noted significant morphological differences centering on the ilium (Fig. 1Ce) that indicate that the late appearing NHMUK R3741 may be closer the more derived iguanodonts of the later Cretaceous. Despite problems with making *I. bernissartensis* the type species of the *Iguanodon* (Paul, 2008; Carpenter and Ishida, 2010), the suggestion by Carpenter and Ishida (2010) that the ICZN be petitioned to revive NHMUK R3741 as the type of the genus will create at least as many problems as it solves and is unlikely to occur.

ADDITIONAL EVIDENCE OF EUROIGUANODONT DIVERSITY

Norman's (2010) basic argument that there were just two European iguanodonts in the Valanginian, and then just two more in the next two stages up into the early Aptian, is so simplistic in evolutionary terms that it must be rejected unless future discoveries actually do show that specimens from such long spans of time must be placed in so few taxa. Iguanodontoids (*sensu* Paul, 2010) as well as ceratopsids in the Dinosaur Park Formation show rapid species turnover, with each lineage showing three or four sequential species in the 80 meter thick deposit (Eberth, 2005; Ryan and Evans, 2005; Mallon and Holmes, 2006; Paul 2010). The diversity of iguanodontoids at any

level of the Dinosaur Park Formation is high (Ryan and Evans, 2005; Paul, 2010). Because the cross channel beds containing the Valanginian to Aptian iguanodonts under discussion herein are hundreds of meters deep (Jackson, 2008) and formed over about 20 million years they should contain a long multiplicity of faunas each with distinct and often diverse set of taxa. It follows that *B. dawsoni* and *H. fittoni* were probably limited to the early Valanginian, perhaps to a few hundred thousand years within the formation of the Wadhurst Clay; *Mantellisaurus atherfieldensis* is probably just early Aptian in age, although late Barremian cannot be ruled out; *I. bernissartensis* is from a short span of time in the latter Barremian or early Aptian; more than two iguanodonts may have been extant at the same time and region during some periods; and the total number of European iguanodont species in the early Cretaceous could have been in the many dozens.

Indeed, other taxonomically distinctive iguanodont material in addition to Norman's four species from Europe have already come into the light aside from *D. evolutionis*. *Sellacoxa pauli* (Carpenter and Ishida, 2010) is from the Wadhurst Clay, apparently higher than *D. evolutionis* and not necessarily from the same level as *B. dawsoni* and *H. fittoni*. The claim by Norman (2010) that the distinctive ilium of *S. pauli* holotype NHMUK R3788 is distorted is incorrect according to Naish (2010, pers. comm.), description of the other ilium may resolve the dispute. The anatomical and perhaps temporal disparities refute Norman's assignment of the specimen to *B. dawsoni* (Naish and Martill, 2008; Naish 2010). Although naming a taxon based on an isolated dentary is questionable, *Kukufeldia tilgatensis* (McDonald *et al.*, 2010a) indicates the existence of a distinctive taxon from the late Valanginian (Fig. 2B). The elongated MIWG.6344 may be *Dollodon* (Fig. 2I) but its exceptional slenderness is compatible with it being distinct at least at the species level, as does the possibility that it is from a different time than poorly dated *D. bampingi* (Paul, 2008). From the late Barremian Carpenter and Ishida (2010) named *Proplanicoxa galtoni*. The nearly complete isolated ilium 06.34-OT, 13 from the late Barremian or Aptian of Spain (Contreras-Izquierdo *et al.*, 2007) is more posteriorly elongated than that of any other iguanodont, and is probably exceptionally deep posteriorly (Fig. 1Cf). Although too fragmentary to serve as a type, the element represents of distinct taxon and should be considered Iguanodontoidea *incertae sedis*.

Another fragmentary Spanish specimen from the late Hauterivian or early Barremian, the partial scapula PS-TBMV, 1 (Fernandez-Baldor *et al.*, 2006) is notable because the robust element is very similar to that of *Iguanodon* (Fig. 1A, a, b, c), including a dorsally placed, abbreviated, subhorizontal acromion process, and a prominent, overhanging posterior process of the glenoid. The acromion processes of the more gracile scapulae of *Mantellisaurus* and *Dollodon* are more distally placed and slanted, and the glenoid is not as strongly built (Fig. 1Ad,

e; Paul, 2007, 2008). Other elements that may belong to the same specimen as PS-TBMV, 1 are less diagnostic. Because the overall form of the iguanodont that PS-TBMV, 1 belonged to is not known, and especially because the specimens are significantly older than *Iguanodon*, the fossils cannot be assigned to that genus much less *I. bernissartensis*, but they do indicate that the basic type was extant by about the end of the Hauterivian-Barremian boundary and further increase Euroiguanodont diversity. Being from the early Barremian, Spanish *Delapparentia turolensis* has been separated from the later and anatomically distinctive *I. bernissartensis* (Ruiz-Omeñaca, 2011). And an indeterminate but distinctive Spanish iguanodont from the late Hauterivian or early Barremian has been distinguished from the much earlier "*I.*" *fittoni* by Pereda-Suberbiola *et al.* (2011).

Carpenter and Ishida (2010) suggested that *D. bampingi* and "*I.*" *seelyi* are the same taxon, and erected the new combination *Dollodon seelyi*. The ilia of the two holotypes are not similar (Fig. 1Cb, d), and Naish (2010) observed that the robust remains assigned to *I. seelyi* indicate it is within or close to *Iguanodon*, as per Paul (2008) and McDonald (2012). The inability to determine the temporal placement of the holotypes of *D. bampingi* and "*I.*" *seelyi* relative to one another further works against placing them in one taxon. The same issue also bars assigning "*I.*" *seelyi* specifically to *I. bernissartensis*, or even to *Iguanodon* unless sufficient material assignable to "*I.*" *seelyi* shows it belongs to the species or genus. The dissimilarities in the ilium of the holotypes suggest separation at least at the species level (Fig. 1Ca, b). Nor do "*I.*" *seelyi* and *M. atherfieldensis* represent members of the same fauna because they are temporally separated by a few million years.

The splitting of some specimens that were classified under *I. atherfieldensis* into two taxa, *Mantellisaurus atherfieldensis* (Paul, 2007) and *Dollodon bampingi* (Paul, 2008), is disputed by Norman (2010), McDonald *et al.* (2010b) and McDonald (2012) who consider *D. bampingi* to be synonymous with *M. atherfieldensis*. In their works Norman and McDonald seem to presume that the two taxa should be assumed to be the same unless it can be demonstrated otherwise. That position would be viable if the two holotypes were from the same horizon of the same formation. So McDonald (2012) superficially dismisses Paul's (2008) tabulation of characters distinguishing the two taxa and then automatically assumes they are one species, rather than conducting a thorough reanalysis that is needed to refute or confirm the generic and specific separation. But because the specimens are from different formations and probably differ in age it should be presumed they are distinct taxa unless shown otherwise. Below is a critique of McDonald's critique of Paul (2008) with some additional analysis.

McDonald (2012) criticizes using differing rostrum/posterior skull length ratios to distinguish *Mantellisaurus* and *Dollodon* because the NHMUK R5764 skull

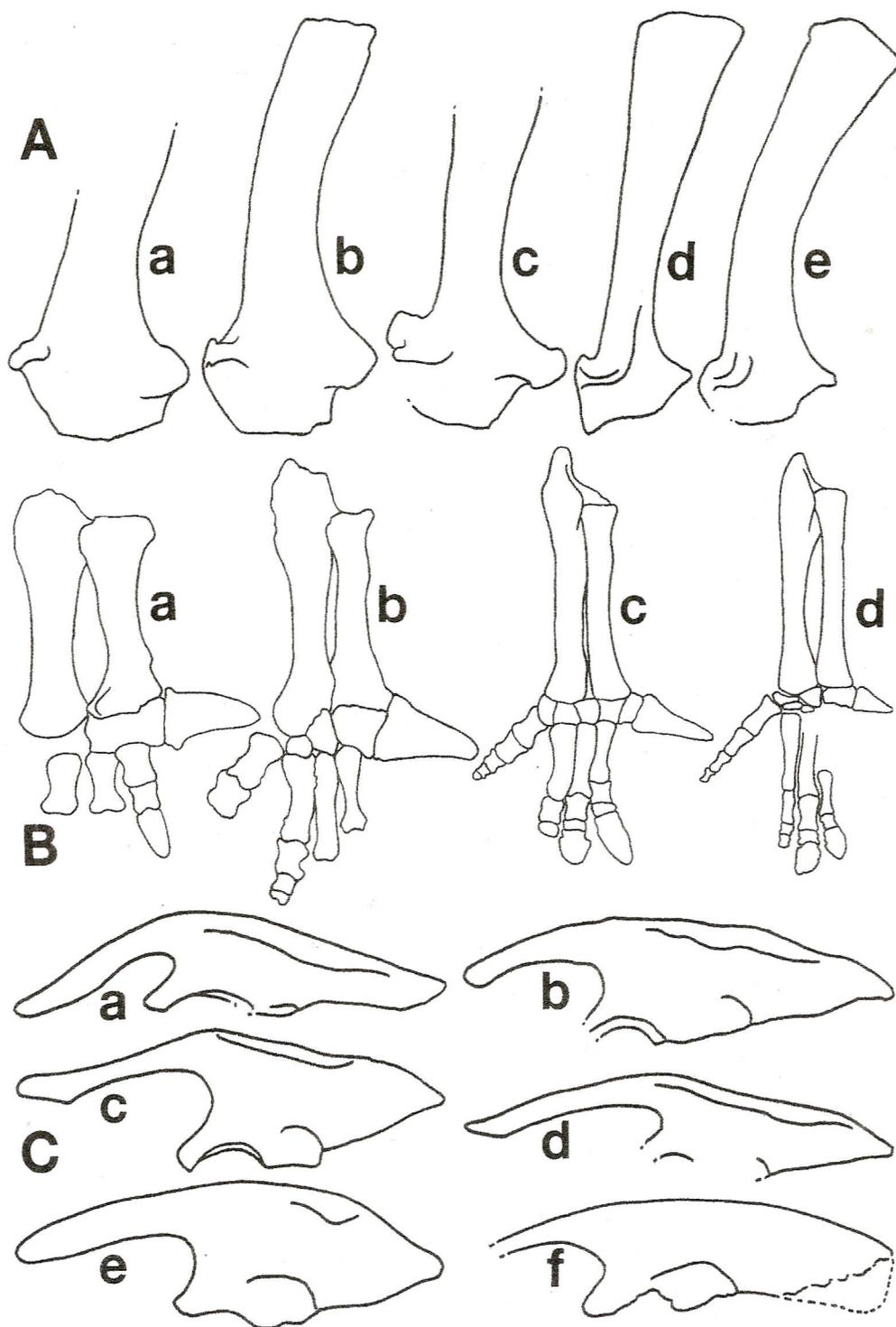


FIGURE 1. A-C: constant size comparisons of European iguanodont elements, all shown as lefts. A: scapulae in lateral view, a: PS-TBMV,1, b: *Iguanodon bernissartensis* lectotype, c: "Iguanodon" sp. GPI-D.559, d: *Mantellisaurus atherfieldensis* holotype, e: *Dollodon bampingi* holotype. B: distal forelimbs, a: *Lurdusaurus arenatus* holotype, b: *Darwinsaurus evolutionis* gen. nov. sp. nov. holotype, c: *Iguanodon bernissartensis*, d: *Mantellisaurus atherfieldensis* holotype. C: Ilii in lateral view, a: *Iguanodon bernissartensis* lectotype, b: "Iguanodon" *seelyi* holotype, c: *Mantellisaurus atherfieldensis* holotype, d: *Dollodon bampingi* holotype. E: *Mantellodon carpenteri* sp. nov. holotype. F: 06.34-OT,13.

restoration (Fig. 3B) is supposedly “subjective.” Utilizing the short rostrum of the disarticulated NHMUK R5764 for taxonomic purposes is no more subjective than is using the short holotype maxilla of *Atrociraptor* to help taxonomically distinguish it from the long snouted articulated holotype skull of *Velociraptor* (Currie and Varricchio, 2004). The rostrum of NHMUK R5764 is definitely markedly less elongated than that of IRSNB 1551 primarily because the former’s maxilla anterior to the antorbital fenestra is shorter relative to the posterior section, and because the mandible of NHMUK R5764 is not as long relative to the posterior skull from the anterior rim of the orbit to the paroccipital process tip. The short rostrum of the NHMUK R5764 restoration matches that of the mounted skull, it is abjectly impossible to further elongate the rostrum to approach or match that of IRSNB 1551, and any who contend it is possible for NHMUK R5764 to have a rostrum as remarkably elongated as IRSNB 1551 must produce a plausible skull restoration to that effect. If that cannot be done then the exceptionally long rostrum of IRSNB 1551 is a highly diagnostic character vis-à-vis more typically proportioned NHMUK R5764. Restoring the skull of *M. atherfieldensis* by combining elements from NHMUK R5764 and IRSNB 1551 (as per Fig. 3 in Norman, 1986) risks taxonomic confusion by obscuring the differences between the two crania, thereby producing a multitaxa chimera.

McDonald (2012) disputes that it has been established that NHMUK R5764 lacks the kind of diastema present in IRSNB 1551. In the former the oral rims of both dentaries plunge strongly ventrally immediately anterior to the first tooth position (Fig. 4I, Pl. I in Hooley, 1925). This is like iguanodonts in which the dorso-posterior corner of the predentary nearly reaches the first tooth position, precluding the existence of a diastema. If a diastema was present then the posteriormost oral cutting edge of the predentary was well below that of the tooth row. In illustrations of IRSNB 1551 the oral rim of both dentaries continue in a nearly straight, subhorizontal line along the dental battery and anterior to the first tooth position for about 100 mm until they reach the dorso-posterior corners of the predentary (see Fig. 6 in Norman, 1986; Pl. VI Fig. 3 in Dollo 1884). The result is a well-developed diastema with at least the posteriormost cutting edge of the predentary only a little below the cutting edge of the lower dental battery. However, this has not been confirmed by detailed description or high quality photographs of both sides of IRSNB 1551. Nor has the presumption by Norman (1986) that the two holotypes share the same tooth family count been verified because the mouth of IRSNB 1551 remains closed (and apparently must remain so according to Norman [1986]). Figure 3 in Plate VI in Dollo (1884) suggests that the latter has two or three more tooth positions than NHMUK R5764, but figure 6 in Norman (1986) implies otherwise. Again no photograph of sufficient resolution to help

clarify the matter appears to be available. Note that if the dental battery extends further anteriorly than has been illustrated then IRSNB 1551 almost certainly must have a higher tooth family count than NHMUK R5764, a reflection of its longer rostrum. One way or another, the oral configuration of the two specimens differs too much to support taxonomic synonymy.

The jugal and squamosal contributions to the borders of the lateral temporal fenestra are markedly smaller in area in IRSNB 1551 than in NHMUK R5764, so demonstrating that the latter does not have a larger fenestra (McDonald, 2012) again requires producing a plausible skull restoration to that effect. Because the skull length of NHMUK R5764 is accurately restored it does have a lower skull/quadrangle length ratio than IRSNB 1551.

The intact neural spines of the anterior dorsals of IRSNB 1551 appear to be taller than those of NHMUK R5764, suggesting that the prominent dorsosacral neural spines of *D. bampingi* were deeper than those of *M. atherfieldensis*; future specimens unambiguously referable to the latter species are required to clarify this matter. The scapular acromion processes of the holotypes need to be better documented before proper comparison. Although the majority of what is preserved of the left ilium of IRSNB 1551 is dorso-ventrally flattened, the claim that similar crushing of the right ilium produces an illusion that it is proportionally shallower than the ilium of NHMUK R5764 has not been verified. Metatarsal II is proportionally much shorter in NHMUK R5764 than IRSNB 1551 (Fig. 3C). McDonald (2012) contends that the fore and hindlimb proportional differences between NHMUK R5764 and IRSNB 1551 are not taxonomically useful. A brachiosaurid with a forelimb 5-10% shorter relative to the hindlimb than that of *Brachiosaurus altithorax* would not be attributed to the same species, or even genus. More importantly, Paul (2008) found that the combination of the shorter forelimb and shorter dorsal series relative to the hindlimb makes it difficult to pose NHMUK R5764 in a quadrupedal walk or run, while the proportionally longer forelimbs and trunk of IRSNB 1551 allowed it to easily move quadrupedally, a major functional divergence indicative of generic separation. Refuting this conclusion requires presenting skeletal diagrams showing that NHMUK R5764 could be quadrupedal as readily as IRSNB 1551. Proportional differentiations have the most taxonomic significance if they result in functional differentiations. Note that using the holotype skeleton of *D. bampingi* as representative of *M. atherfieldensis* rather than the actual holotype of the latter is technically inappropriate and risks contributing to taxonomic confusion, so if a single *M. atherfieldensis* skeleton is used to represent the species it must be a photograph or restoration of the only good specimen that undoubtedly is *M. atherfieldensis*, NHMUK R5764, rather than IRSNB 1551 that is so divergent from that species.

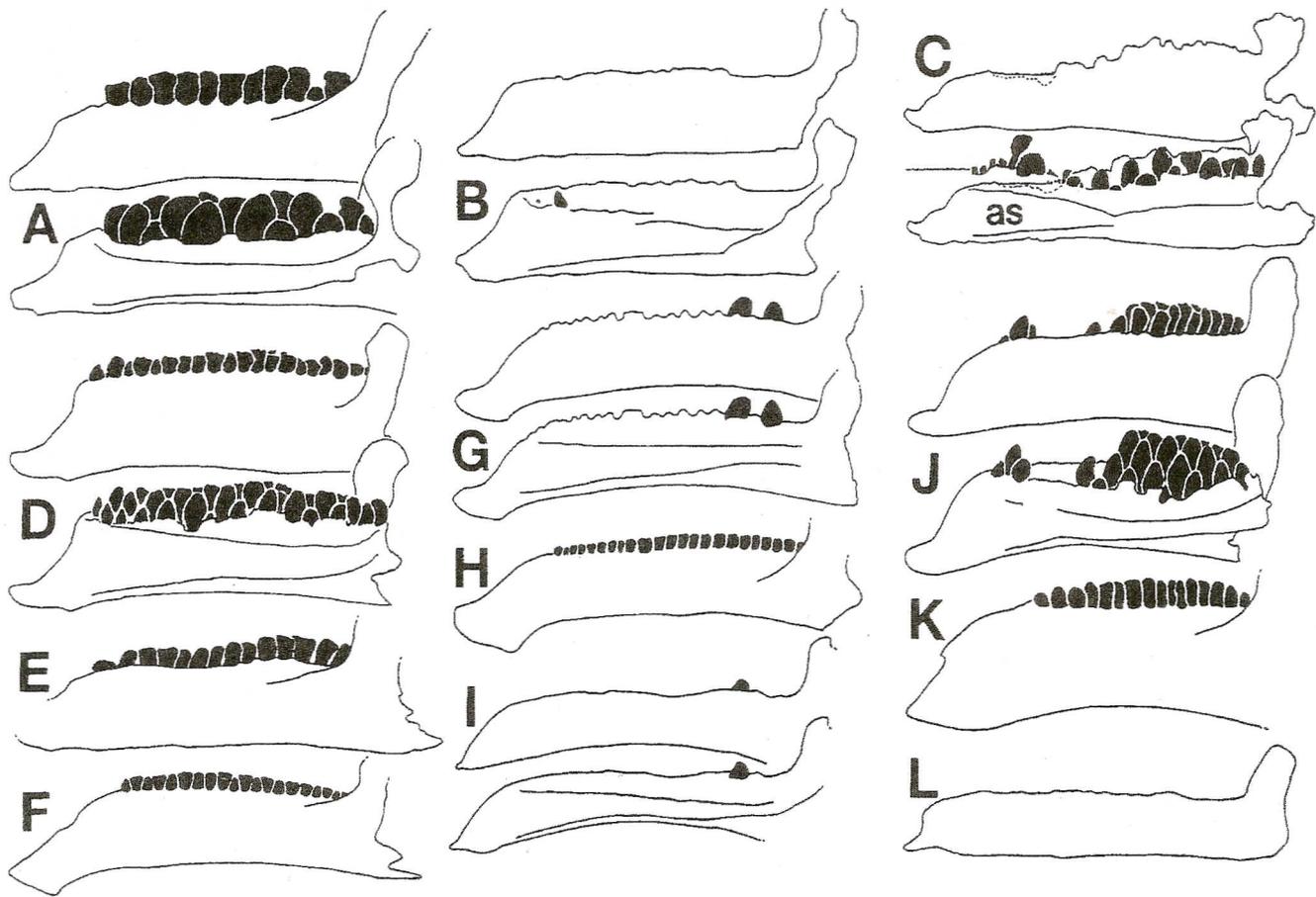


FIGURE 2. Constant size comparison of iguanodont dentaries in lateral (top) and/or medial (bottom) views. A: *Lanzhousaurus magnidens* holotype. B: *Kukufeldia tilgatensis* holotype. C: *Darwinsaurus evolutionis* gen. nov. sp. nov. holotype as originally preserved, dashed lines show erosion, inset magnifies anteriormost tooth crowns and roots. D: *Iguanodon bernissartensis* lectotype. E: *Jinzhousaurus yangi* holotype. F: *Altirhinus kurzanovi* holotype. G: *Mantellisaurus atherfieldensis* holotype. H: *Dolloodon bampingi* holotype. I: MIWG.6344. J: *Proactrosaurus gobiensis* PIN 2232/42-1. K: *Equijubus normani* holotype. L: *Ouranosaurus nigeriensis* holotype. as - alveolar shelf.

A comparison of the skeletal restorations (Fig. 3A) of the two holotypes shows that the differences between them are markedly greater than those that separate other iguanodontoid genera (Fig. 3D).

Two options for trying to maintain the two holotypes in the same taxon despite the considerable anatomical variation between them is ontogenetic or sexual variation within the species. *M. atherfieldensis* NHMUK R5764 is not an adult because the neural arches are not fused to the centra (Hooley, 1925). *D. bampingi* IRSNB 1551 is mature, but it too is not particularly large by iguanodont standards, it is not much larger than NHMUK R5764 (Fig. 3A), and portions of the latter are absolutely as large or larger than those of IRSNB 1551. The skulls of the two specimens are nearly identical in length, but while the elongated rostrum

of IRSNB 1551 is much longer than that of NHMUK R5764, the posterior skull of the latter is significantly larger than that of the former (Fig. 3B). If the right ilium of IRSNB 1551 is not significantly dorso-ventrally crushed then it is shallower in absolute measurement than that of NHMUK R5764. The unusually elongated 3rd phalanx of pedal digit 4 is longer in NHMUK R5764 than in IRSNB 1551, while some of the elements of digit 3 are similar in length in the two specimens (Fig. 3C). These patterns are not indicative of NHMUK R5764 and IRSNB 1551 being growth stages within the same taxon, all the more so because some elements would actually have to decrease in size. The skull and skeletal differences between the two holotypes exceed those present in hadrosaur genera when their cranial crests are excluded

(Fig. 3D), iguanodontoids have not been shown to exhibit well developed sexual morphs, and even the sexual dimorphism of lambeosaurines appears to have been more minimal than thought prior to the Ryan and Evans (2005) study. Ontogeny or dimorphism as explanations for all the differences between the two holotypes would be most plausible but still problematic even if they were from the same horizon of the same formation, and would require a large sample of specimens to verify the hypothesis. Because NHMUK R5764 and IRSNB 1551 probably differ in age using them to try to establish exceptional sexual dimorphism in an iguanodont species would be highly inappropriate.

Specifically, it cannot be shown that the Vectis Formation's NHMUK R5764 and Sainte-Barbe Clays Formation's IRSNB 1551 are from the same stratigraphic level because it is not possible, at least at this time, to date the fissure fill sediments that the latter was found in to closer than three to four million years (Yans *et al.*, 2006; Paul 2008; Schnyder *et al.*, 2009), and it is statistically most probable that IRSNB 1551 is late Barremian and older than the probably early Aptian NHMUK R5764. McDonald (2012) also inappropriately refers to *M. atherfieldensis* a number of insufficiently complete Wessex Formation specimens that are a few million years older than the holotype. The assignment of some Wessex Formation ilia to *cf. Mantellisaurus* by McDonald (2012) is less temporally problematic, but is anatomically open to question because they have longer anterior processes relative to the main body than NHMUK R5764, and the main body of MIWG 6344 is exceptionally deep.

To put it another way, those who wish to unite a number of specimens from different time stages and several formations think it taxonomically appropriate to consider a short snouted, short trunked and short armed and correspondingly more strongly bipedal and bigger hipped iguanodont probably from the lower Aptian the same genus and even species as an unusually long snouted, long trunked and longer armed correspondingly more strongly quadrupedal bipedal, and smaller hipped iguanodont that probably dates a couple of million years earlier from the Barremian, and despite additional differences including in the anterior oral apparatus. The ontogenetic variation required between animals so similar in size, and/or the sexual dimorphism, is well beyond that seen in other iguanodontoids. As a researcher who opines that many dinosaur genera are over split (Paul, 2010) I am unable to defend placing NHMUK R5764 and IRSNB 1551 in the same taxon. Because of the probable temporal separation, and especially because specific and the cumulative anatomical divergences between *M. atherfieldensis* and *D. bampingi* is markedly greater than that between other iguanodontoid genera such as *Corythosaurus* and *Lambeosaurus* and broadly similar to that between the latter and *Parasaurolophus*, the taxonomic separation remains valid. Even in the improbable case that *M.*

atherfieldensis and *D. bampingi* are congeneric, it is unlikely that they are conspecific. Note that cladistic processing that places *M. atherfieldensis* and *D. bampingi* as sister taxa does not necessarily indicate they are congeneric, because generic designations are inherently partly gradistic as explained in Paul (2008). For example, if *Iguanodon* and *Mantellisaurus* were the only known iguanodonts they would not be placed in one genus even though they would be cladistic sister taxa because they are so divergent. Nor is the referral of Wessex specimens to much later *M. atherfieldensis* justified by the current data, or likely to be in the future. However, it is not possible to more properly diagnose the taxa until the skulls are dismantled and then documented and redescribed in as much detail as possible.

CONCLUSIONS

Because simplistic schemes of iguanodont diversity in Europe are improbable, the high level of species diversity among European iguanodonts requires a careful anatomical and stratigraphic review of the assignment of numerous specimens to just the three taxa *B. dawsoni*, *H. fittoni* and *M. atherfieldensis* by Norman (2010) and McDonald (2012). Iguanodont specimens that are not yet types should be assigned to a previously established specific species only under certain circumstances. The optimal situation is when the potentially referable specimen is reasonably complete, shares significant overlapping material with the type or with one or more specimens that shares sufficient overlap with the type, stratigraphic information is sufficient to show that the potentially referable fossil is from the same narrow time zone as the type, and other similar species are not known from well-sampled sediments of that time zone. In the latter case it may not be necessary for specimens to be well preserved for taxonomic referral. For example the only giant ceratopsid known from the latest Maastrichtian just below the K/P boundary of western North America after decades of sampling of skulls is *Triceratops prorsus* (Scannella, 2010), so all large ceratopsid remains regardless of quality from that horizon can be assigned to that species unless they are distinctive from the type and confidently referred specimens, or future discoveries reveal additional related taxa are sufficiently abundant to potentially absorb a portion of the specimens. If one or more similar species are known from the same time zone and geographic neighborhood of the type then the referring specimens to a particular species becomes much more problematic. For example, many Dinosaur Park Formation lambeosaurine fossils that lack a cranial crest for one reason or another and probably belong to a species of *Corythosaurus*, *Lambeosaurus* or *Hypacrosaurus* cannot be assigned to a specific species, including complete juveniles because they appear to be nearly identical between the taxa (Currie and Russell, 2005). In such a situation a potentially referable specimen should be assigned to

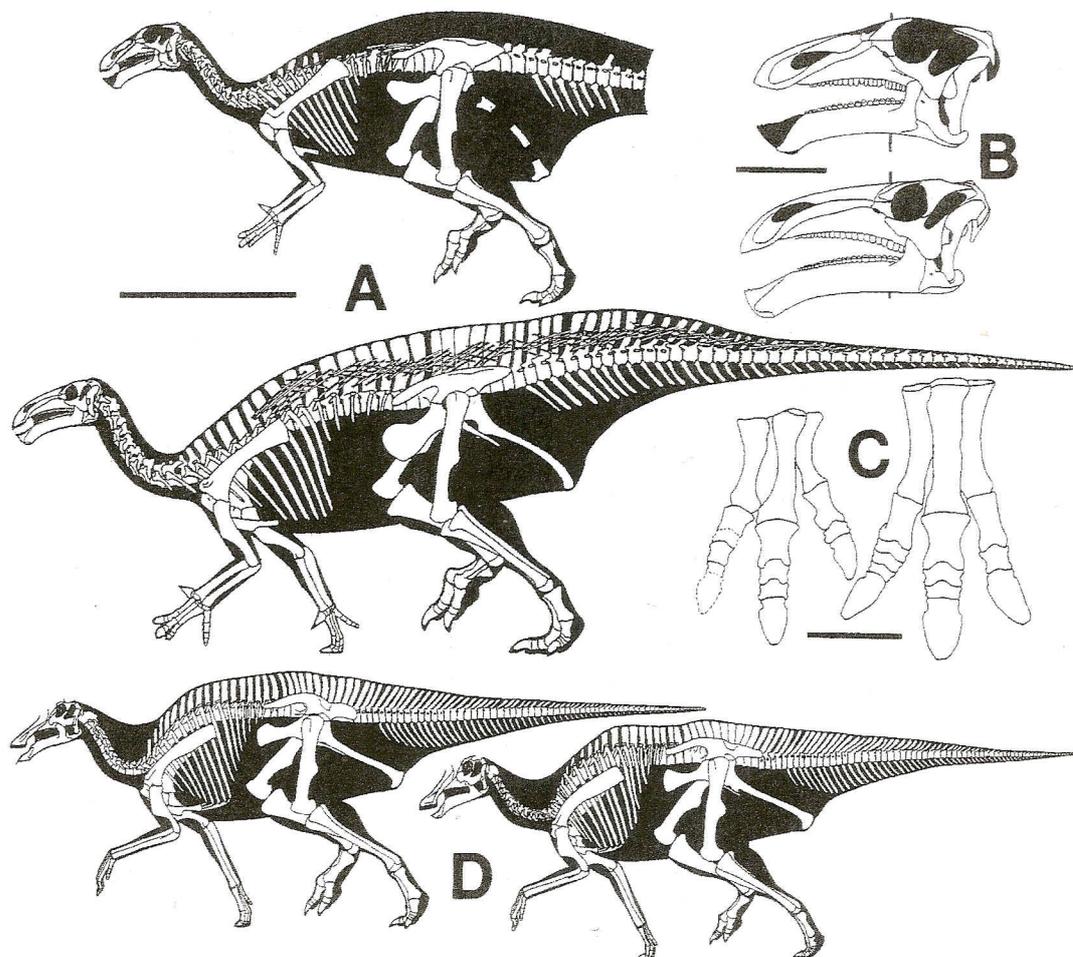


FIGURE 3. A-C: a series of same scale comparisons of *Mantellisaurus atherfieldensis* holotype (on the top or left) and *Dolloodon bampingi* holotype. A: Skeletons, scale bar equals 1 m. B: Skulls as preserved, vertical line divides rostrum from posterior section, scale bar equals 200 mm. C: Right pes, elements in R5764 substituted from left pes by Hooley (1925) dashed, also after Norman (1986), scale bar equals 200 mm. D: Skeletons of *Corythosaurus intermedius* ROM 845 (left) and *Lambeosaurus lambei* ROM 1218 without cranial crests to emphasize similarity of the rest of the crania and the postcrania.

the same species as a particular type only if abundant morphological data based on a sufficiently complete type and similarly well-preserved nontype specimen supports the synonymy. The sharing of just a few elements between the type and potentially referable specimen is unlikely to be sufficient for a referral unless it is a particularly distinctive element such as a cranial crest. If a specimen is from a significantly different horizon than a type then it should be referred to the same species only if abundant morphological data based on a largely complete type and similarly well-preserved nontype specimen compels the synonymy. Even then the possibility that the long time separated fossils were distinct biospecies, the differences being limited to soft tissue, is high. If the above criteria cannot be met and the specimen is sufficiently diagnostic it can be assigned its own taxon. If the material is

insufficiently diagnostic it should be left indeterminate, this lowers the risk of giving a false impression of a fauna that is more or less diverse than it actually is.

As emphasized by Paul (2007, 2008) no iguanodont specimens whether they are skeletal or trace in nature should be assigned to *Iguanodon* unless they are sufficiently complete and clearly match the distinctive characteristics of the genus, and assigning fragmentary remains to *I. bernissartensis* is all the more inappropriate, especially if the remains cannot be shown to be from the same age as the Bernissart quarry material. There is a serious need for more extensive stratigraphic work on the level of origin of many English specimens. The diagnosable characters that distinguish a species should be based only on those found in the type specimen, and in reasonably complete specimens from the same horizon that can be confidently

assigned to the species - in the case of *M. atherfieldensis* this means the upper Vectis Formation. Doing otherwise hazards creating chimeras that blend characters from two or more taxa, perhaps from differing times, as Norman (1986) and McDonald (2012) risked when using IRSNB 1551 to diagnose *M. atherfieldensis*. *Dollodon* cannot not be fully diagnosed at this time, and redescription of it and the *Mantellisaurus* holotypes without the presumption that they are the same taxon are needed so they can be more thoroughly diagnosed and their relationship further tested. A direct on-site comparison of casts of NHMUK R5764 to the skull of IRSNB 1551 would be especially productive, as would be remote scanning of the latter. The high diversity of large iguanodonts within Early Cretaceous Europe may have been facilitated by the high rates of reproduction of large dinosaurs (Paul, 1994).

ACKNOWLEDGMENTS

Thanks go to Darren Naish, Kenneth Carpenter, James Kirkland, Peter Galton, Kris Kripchak, Pascal Godefroit and especially to Pedro Huerta, Fidel Torcida and José Ignacio Canudo for their generous invitation to participate in the enjoyable and productive 2010 symposium.

REFERENCES

- Anonymous (2010): Wadhurst Clay Formation. British Geological Survey, www.bgs.ac.uk/lexicon.cfm?pub+WDC.
- Carpenter, K. and Ishida, Y. (2010): Early and "Middle" Cretaceous iguanodonts in time and space. *Journal of Iberian Geology*, 36: 145-164.
- Carroll, R. (1988): *Vertebrate Paleontology and Evolution*. Freeman and Company, New York, 698 p.
- Contreras, R., Cruzado-Caballero, P., Torcida Fernández-Baldor, F., Huerta, P., Izquierdo, L.A., Montero Huerta, D., Pérez Martínez, G. and Urién Montero, V. (2007): Un ilion de un dinosaurio "Iguanodontido" procedente del Cretacico Inferior de Burgos (España). En: *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno* (P. Hurtado and F. Fernandez-Baldor, Eds). Colectivo Arqueológico y Paleontológico de Salas, Salas de los Infantes, 187-195.
- Currie, P. and Russell, D. (2005): The Geographic and Stratigraphic Distribution of Articulated and Associated Dinosaur Remains. En: *Dinosaur Provincial Park: A Spectacular Ecosystem Revealed* (P. Currie, and E. Koppelhus, Eds). Indiana University Press, Bloomington and Indianapolis, 537-569.
- Currie, P. and Varricchio, D. (2004). A new dromaeosaurid from the Horseshoe Canyon Formation of Alberta, Canada. En: *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds* (P. Currie, E. Koppelhus, M. Shugar and J. Wright, Eds). Indiana University Press, Bloomington and Indianapolis, 112-132.
- Dollo, L. (1884): Cinquieme note sur les dinosauriens de Bernissart. *Bulletin de Museum Royal de Histoire Naturelles de Belgique* 3: 120-140.
- Dollo, L. (1888): Iguanodontidae et Camptonotidae. *Comptes Rendus de Academie des Sciences (Paris)*, 106: 775-777.
- Eberth, D. (2005): The Geology. En: *Dinosaur Provincial Park: A Spectacular Ecosystem Revealed* (P. Currie, P. and E. Koppelhus, Eds). Indiana University Press, Bloomington and Indianapolis, 54-82.
- Galton, P. (2009): Notes on Neocomian Ornithomimid Dinosaurs from England, and referred specimens from Romania and elsewhere. *Revue de Paleobiologie*, 28: 211-272.
- Hooley, R. (1925): On the skeleton of *Iguanodon atherfieldensis* sp. nov., from the Wealden shales of Atherfield. *Quarterly Journal of the Geological Society of London*, 81: 1-61.
- Jackson, A. (2008): *Bedrock Geology UK South*. Nottingham, British Geological Survey.
- Lydekker, R. (1888): Note on a new Wealden iguanodont and other dinosaurs. *Quarterly Journal of the Geological Society of London*, 44: 46-61.
- Lydekker, R. (1889): Notes on new and other dinosaurian remains. *Geological Magazine*, 6: 352-356.
- Mallon, J. and Holmes, R. (2006): A Reevaluation of Sexual Dimorphism in the Postcranium of the Chasmosaurine Ceratopsid *Chasmosaurus belli*. *The Canadian Field-Naturalist*, 120: 403-412.
- Marsh, O. (1881): Classification of The Dinosauria. *American Journal of Science (ser. 3)*, 23: 81-86.
- McDonald, A. (2012). The status of *Dollodon* and other basal iguanodonts from the upper Wealden beds of Europe. *Cretaceous Research*, 33: 1-3.
- McDonald, A., Barrett, P. and Chapman, S. (2010a): A New Basal Iguanodont from the Wealden of England. *Zootaxa*, 2569: 1-43.
- McDonald, A.T., Kirkland, J.I., DeBlieux, D.D., Madsen, S.K., Cavin, J., Milner, A.R.C. and Panzarin, L. (2010b): New Basal Iguanodonts from the Cedar Mountain Formation of Utah and the Evolution of Thumb-Spiked Dinosaurs. *PLoS One*, 5: e14075.
- Naish, D. (2010): The *Iguanodon* Explosion, parts 1-3. *Scientific American*, www.scientificamerican.com/blog/post.cfm?id=the-explosion-of-iguanodon-part-i-2010-11-15.
- Naish, D. and Martill, D. (2008): Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery. *Journal of the Geological Society, London*, 165: 613-623.
- Norman, D. (1986): On the anatomy of *Iguanodon atherfieldensis*. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 56: 281-372.

- Norman, D. (2010): A Taxonomy of iguanodontians from the Lower Wealden Group of Southern England. *Zootaxa*, 2489: 47-66.
- Paul, G. (1994): Dinosaur Reproduction in the Fast Lane: Implications for Size, Success, and Extinction. En: *Dinosaur Eggs and Babies* (K. Carpenter, K. Hirsch and J. Horner, Eds). Cambridge University Press, Cambridge, 244-255.
- Paul, G. (2007): Turning the old into the new: a separate genus for the gracile Iguanodont from the Wealden of England. En: *Horns and Beaks: Ceratopsian and Ornithomimid Dinosaurs* (K. Carpenter, Ed). Indiana University Press, Bloomington, 69-77.
- Paul, G. (2008): A revised taxonomy of the iguanodont dinosaur genera and species. *Cretaceous Research*, 29: 192-216.
- Paul, G. (2010): *The Princeton Field Guide to Dinosaurs*. Princeton University Press, Princeton, 320 p.
- Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Torcida Fernández-Baldor, F., Maisch, M.W., Huerta, P., Contreras, R., Izquierdo, L.A., Montero Huerta, D., Urién Montero, V., Welle, J. (2011): A tall-spined ornithomimid dinosaur from the Early Cretaceous of Salas de los Infantes (Burgos, Spain). *Comptes Rendus Palevol*, 10: 551-558.
- Ruiz-Omeñaca, J. (2011): *Delapparentia turolensis* nov. gen et sp., un nuevo iguanodontoideo en el Cretácico Inferior de Galve. *Estudios geológicos*, 67: 83-110
- Ryan, M. and Evans, D. (2005): Ornithischian Dinosaurs. En: *Dinosaur Provincial Park: A spectacular Ecosystem Revealed* (P. Currie, and E. Koppelhus, Eds). Indiana University Press, Bloomington and Indianapolis, 312-348.
- Scannella, J. (2010): *Triceratops*: A model organism for deciphering dinosaur heterochrony. En: *70th Anniversary Meeting. Society of Vertebrate Paleontology. Program and Abstracts*: 158A.
- Schnyder, J., Dejax, J., Keppens, E., Nguyen Tu, T. T., Spagna, P., Boulila, S., Galbrun, B., Riboulleau, A., Tshibangu, J.-P. y Yans, J. (2009). An Early Cretaceous lacustrine record: organic matter and organic carbon isotopes at Bernissart. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 281: 79-91.
- Seeley, H.G. (1887-1888): On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society London*, 43: 165-171.
- Sereno, P.C. (1986): Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research*, 2: 234-256.
- Torcida Fernández-Baldor, F., Izquierdo Montero, L.A., Contreras Izquierdo, R., Huerta, P., Montero Huerta, D., Pérez Martínez, G. and Urén Montero, V. (2006): Un dinosaurio "iguanodóntido" del Cretácico Inferior de Burgos (España). En: *Actas de las III Jornadas Internacionales sobre Paleontología Dinosaurios y su Entorno* (F. Fernandez-Baldor and P. Hurtado, Eds).
- Colectivo Arqueológico y Paleontológico de Salas, Salas de los Infantes, 349-363.
- Yans, J., Dejax J., Pons D., Taverne, L. and Bultynck, P. (2006): The Iguanodons of Bernissart are Middle Barremian to Earliest Aptian in Age. *Bulletin Institut Sciences Naturelles Belgique*, 76: 91-95.