Mesozoic 002 (4): 302–312
https://www.mapress.com/mz/

Article

ISSN 3021-1859 (print edition)
MESOZOIC
ISSN 3021-1867 (online edition)

https://doi.org/10.11646/mesozoic.2.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:C6B0185D-0CAE-4B39-A812-DD0D6D2083CE

Reassessment of *Iguanodon galvensis* classification

FRANCO SANCARLO[1], DAVIDE MANDORLO[2] & TRACY LEE FORD[3]
[1]*Legambiente Association, Via Carlo Alberto Dalla Chiesa, 8, San Giovanni Rotondo (FG) 71013, Italy*
[2]*Legambiente Association, Via Ugo Foscolo, 20, Garbagnate Milanese (MI) 20024, Italy*
[3]*P. O. Box 1171 Poway, CA 92074, USA*
franco.sancarlo.sgr@gmail.com; https://orcid.org/0009-0009-9285-9755
mandorlod@gmail.com; https://orcid.org/0009-0007-9123-2243
dino.hunter@cox.net; https://orcid.org/0000-0001-7253-0367

Abstract

In this study, we revise the taxonomic status of the styracosternan dinosaur *Iguanodon galvensis*. Initially assigned to the genus *Iguanodon*, subsequent analyses questioned this classification due to key morphological differences. In this study, we reassess the fossil material assigned to *I. galvensis* through detailed comparative analysis with a broader sample of iguanodontid taxa. Particular focus is given to the postcranial skeleton, as well as the dentary and skull. Our findings reveal several autapomorphic features, including fully separated manual digits, a hook-like pollex, a rugose lateral femoral ridge, and a proportionally large distal ischial expansion, none of which are consistent with the diagnostic traits of *Iguanodon bernissartensis* or related genera. These anatomical distinctions support the removal of early Barremian galvensis from late Barremian or early Aptian *Iguanodon*, and the erection of a new genus, *Paulodon* **gen. nov.**, with *Paulodon galvensis* as the type species. This reclassification contributes to a more refined understanding of European iguanodontid diversity during the Early Cretaceous.

Keywords: Iguanodontia, Galve, Styracosterna, dinosaur taxonomy, Barremian, new taxa, European dinosaurs

Introduction

In the mid-2010s, a study described a series of ornithischian dinosaur fossils from the vicinity of Galve, Spain, including both adult and juvenile specimens. This material was compared to other hadrosauroids: *Iguanodon bernissartensis*, *Iguanodon seelyi*, *Mantellisaurus*, *Ouranosaurus*, and *Delapparentia*, as well as North American non-hadrosaurid hadrosauroids like *Eolambia* and *Protohadros*. Based on morphological comparisons, the authors identified a distinct combination of traits supporting the designation of a new species within the genus *Iguanodon*, formally named *Iguanodon galvensis* (Verdu *et al.*, 2015). However, the classification as *Iguanodon* was later challenged by subsequent revaluations defining it unnamed genus *galvensis* (Paul, 2016, 2024).

In the present work, we reassess the classification of *Iguanodon galvensis* by re-evaluating the character set used to characterize the species using, for comparison, a larger set of Iguanodontids taxa than in previous studies. The number of specimens described to date includes 3 adults, 1 juvenile, and 15 perinates (Verdú *et al.*, 2015, 2017; Cobeña *et al.*, 2024).

Material and methods

Institutional abbreviation
SCH: Museo Paleontologico de Galve, Galve, Spain.

MAP: Museo Aragones de Paleontología (Fundacion Conjunto Paleontologico de Teruel-Dinopolis), Teruel, Spain

SC: San Cristóbal site, Galve, Spain

RBINS: Royal Belgian institute of Natural Sciences

MPT: Museo de Teruel, Teruel, Spain

Definition of Iguanodon
In 2012 Norman proposed a classification of *Iguanodon* with a description and diagnostic traits common not only in *Iguanodon* but also in various iguanodontids. Consequently, using this description, different genera could be included in *Iguanodon*, such as: (proposed classifications based on Paul (2007, 2008, 2012, 2016, 2024); Norman (2010, 2012); Verdú *et al*. (2017); and Bonsor (2023).

 Submitted: 27 Jul. 2025; accepted by D.-Y. Huang: 30 Nov. 2025; published: 18 Dec. 2025

Mantellisaurus (Paul, 2007)
Dollodon (Paul, 2008)
Dakotadon (Paul, 2008)
Owenodon (Galton, 2009)
Hypselospinus (Norman, 2010)
Barilium (Norman, 2010)
Darwinsaurus (Paul, 2012)
Mantellodon (Paul, 2012)
Huxleysaurus (Paul, 2012)

The authors of the description of *Iguanodon galvensis* used this classification but on the basis of these premises and analysis of other studies, we could consider the description given by Paul (2008) more representative of the genus classification and useful to better define this species.

In this analysis we analysed and compared the following materials: *Iguanodon galvensis*, MAP-4787 (Holotype) SCH-10 juvenile right dentary, MAP-4902 partially articulated skeleton of a perinate, MAP-4790 perinate pollex, SC-8-100 minority of the skeleton of an adult, *Iguanodon* cf. *galvensis* MPT/I.G.472, *Iguanodon bernissartensis, Mantellisaurus atherfieldensis*, *Brighstoneus simmondsi, Dollodon bampingi, Dakotadon lakotaensis.* All the specimen and taxa were already described (Paul, 2008, 2012; Verdu *et al*., 2015, 2017; Lockwood *et al*., 2021; Bonsor *et al*. 2023; Cobena *et al*., 2024), only the specimens of *Iguanodon galvensis* received additional information and description.

Results

Manus. In their description of *Iguanodon galvensis*, Verdú *et al*. (2015) identified a perinatal specimen attributed to the species, preserving an almost complete manus. Some carpals and the pollex were absent from this individual, and the missing elements were recovered from associated specimens. Despite the relative completeness of the manus, the authors limited their comparative analysis only to the morphology of the pollex. In the present study, we undertake a systematic comparison of the entire manus to better evaluate its taxonomic assignment to *Iguanodon*.

Growth of the manus. Ontogenetic development plays a key role in the interpretation of the manus morphology, and it is essential to identify unique anatomical traits. In the specimen attributed to *Iguanodon galvensis*, the manus exhibits proportions remarkably similar to those observed in adult individuals of *Iguanodon*. Comparative analysis with perinatal and juvenile hadrosaurids and Iguanodontian, revealed developmental patterns. Specifically, digit V increases in proportional length from the perinatal to the adult stage, with juvenile specimens already approaching adult-like proportions. Conversely, the overall morphology of the manus (except for the digit V) remains relatively conservative throughout growth, with carpals and the metacarpals maintaining consistent relative proportions. These developmental trends are based on the comparisons with well-documented ontogenetic series in hadrosaurids and iguanodontids of multiple genera: *Lambeosaurus* (or *Hypacrosaurus*) *lambei*, *Hypacrosaurus stebingeri*, *Maiasaura* (or *Brachylophosaurus*) *peeblesorum*, *Anatosaurus* (or *Edmontosaurus*) *annectens*, *Tenontosaurus tilletti* (comparisons made on the fossils of the following studies: Osborn, 1912; Park, 1931; Sternberg, 1935; Lull & Wright, 1942; Ostrom, 1970; Currie, 1987; Currie & Horner, 1988; Weishampel, 1988; Rogers, 1991; Horner & Currie, 1994; Carpenter & Alf, 1994; Maxwell, 1995; Maxwell & Ostrom, 1995; Dilkes, 2001; Prieto-Márquez, 2014; Paul, 2010, 2016, 2024; Prieto-Márquez & Guenther, 2018; Frederickson *et al*., 2020).

Manus excluding pollex. As previously noted, the manus undergoes minimal morphological changes during ontogeny. This stability allows meaningful taxonomic comparisons between taxa of the same group. Upon examination, several notable differences emerge between the manus of *Iguanodon bernissartensis* and *Iguanodon galvensis*, as follows:

1) Metacarpal: In *I. bernissartensis*, the metacarpal are tightly articulated, forming a compact unit as illustrated in Paul (2012). In contrast, the manus of *I. galvensis* exhibits fully separated metacarpal (Verdú *et al*., 2015; Paul, 2016, 2024) (Fig. 1). This degree of digital separation has not been documented among congeneric taxa, extinct or extant, suggesting a potentially significant morphological divergence. Given the magnitude of this difference, we propose referring to the Galve material provisionally as *unnamed genus galvensis* (hereafter *ug. galvensis*);

2) Number of bones of digit IV: The manus attributed to *ug. galvensis* possesses an additional bone in digit IV, 3 bones, compared to *Iguanodon bernissartensis*, 2 bones (Paul, 2012; Fig. 1). This variation in digital structure further supports a distinction at anatomical level. This variation in the articulation does not occur;

3) Metacarpal-carpal articulation: In *ug. galvensis*, metacarpal III articulates its proximal end approximately 50% with carpal I and 50% with carpal II. In contrast, reconstructions of *I. bernissartensis* suggest that metacarpal III mainly articulated with carpal II and had only minor contact with carpal III (Paul, 2012). Moreover, in *ug. galvensis*, metacarpal III contacts carpal I with slight extension onto carpal II and this represent a distinct pattern of articulation not seen in *I. bernissartensis* (see Paul, 2016, 2024). All these features can be observed in

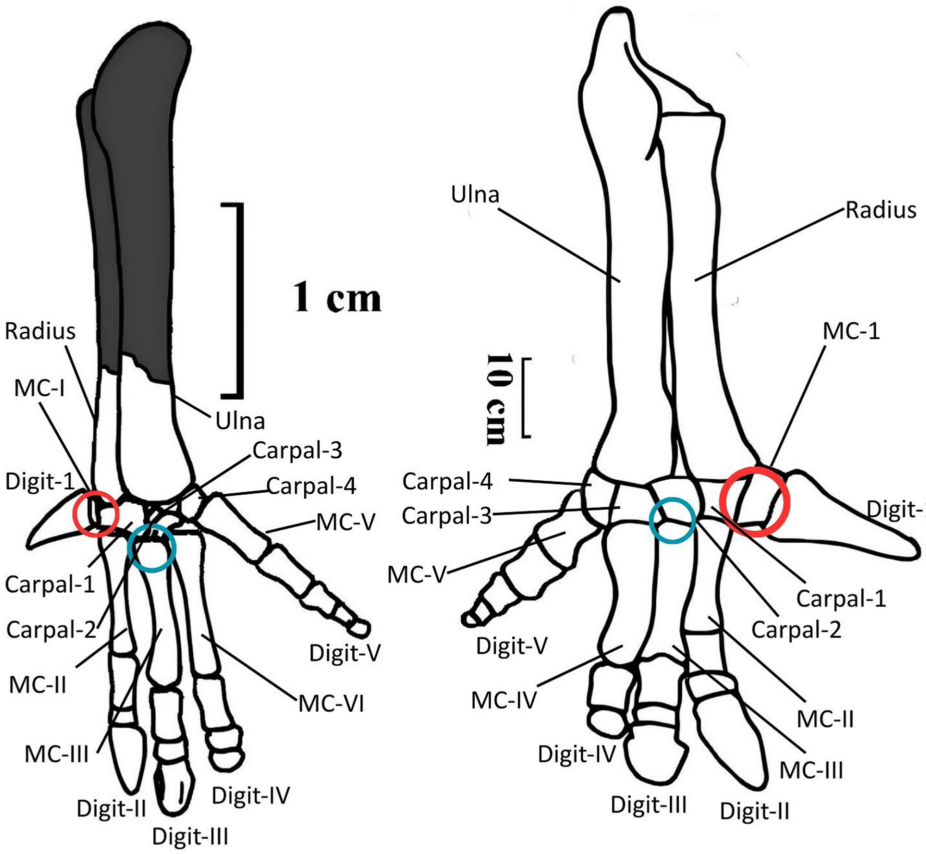

FIGURE 1. Manus and lower arm of perinate MAP-4902 with the pollex of MAP-4790 after Verdu *et al*. 2015 (left). Manus and lower arm of *Iguanodon bernissartensis* holotype after Paul (2012) (right). Blue circles indicate the carpal-metacarpal joint, red circles indicates the 1st metacarpal The grey areas indicate reconstructed portions of the specimen. MC=Metacarpal.

Fig.1. Poole (2022) proposed that *Iguanodon* possessed three phalanges on the fourth digit, based on a referred specimen (RBINS 1558). However, the phalanges of this specimen differ markedly from those of the holotype (Paul, 2012: fig. Bc; Poole, 2022: fig. 11; Fig. 1), and the specimen itself lacks a formal description.

Pollex

Verdú *et al*. (2015) described the pollex of *Iguanodon galvensis* as "long and conical with a slight medial curvature along its length." However, upon closer inspection (see Fig. 2), this description appears inconsistent with the actual morphology. While the pollex is indeed conical, it is not proportionally long, and the medial curvature is not slight but rather pronounced. In *galvensis*, the pollex exhibits a distinct hook-like curvature, a morphology not observed in *Iguanodon bernissartensis* (Paul, 2012). Additionally, the pollex of *ug. galvensis* articulates with a proportionally low and broad metacarpal I, in contrast to *I. bernissartensis*, where it rests upon a proportionally taller and narrow metacarpal. These differences the hypothesis that *ug. galvensis* represents a distinct genus rather than a species within *Iguanodon*. Verdu *et al*. (2017) proposes that the Pollex is straight, although this does not seem to be the case.

Femur

The femur was one of the skeletal elements analysed by Verdú *et al*. (2015) to support the assignment of *ug. galvensis* to the genus *Iguanodon*. However, several key morphological differences were not addressed in their assessment:

1) Fourth trochanter (FT) morphology: In *ug. galvensis* (Holotype and perinate specimen perinate MAP-4902) the fourth trochanter forms a prominent shelf-like structure that is clearly separated from the shaft of the femur. This structure closely resembles the one seen in *Dollodon bampingi* and *Ig. seelyi* but in *ug. galvensis* is distinguished from these taxa by a subtle concavity within the shelf itself. In contrast, *Iguanodon bernissartensis* and *Mantellisaurus* exhibit a more integrated fourth trochanter that merges smoothly with the femoral shaft, resulting in a wave-like profile (see Figs 4 and 5);

2) Proximal spur: A small bony spur is present near the femoral head that originate from the lateral

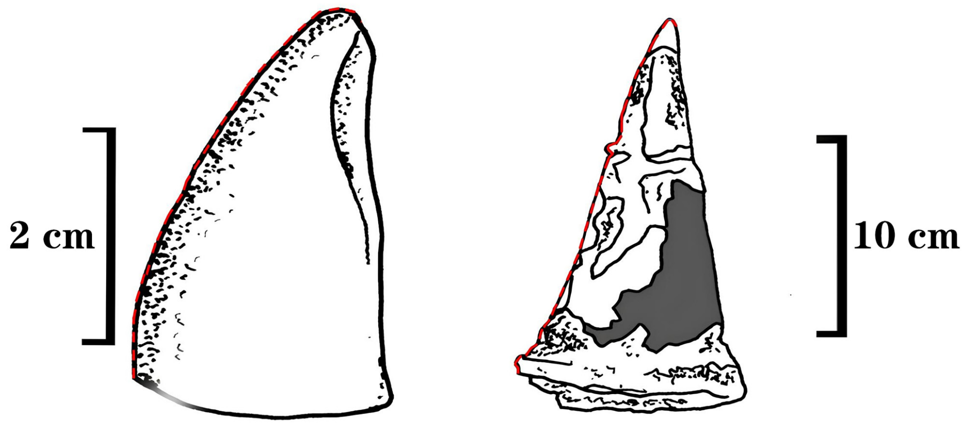

FIGURE 2. Pollex: MAP-4790 after Verdu *et al*., 2015 (left), *Iguanodon bernissartensis* holotype (right). The grey areas indicate reconstructed portions of the specimen. Dotted red lines accentuate the curvature.

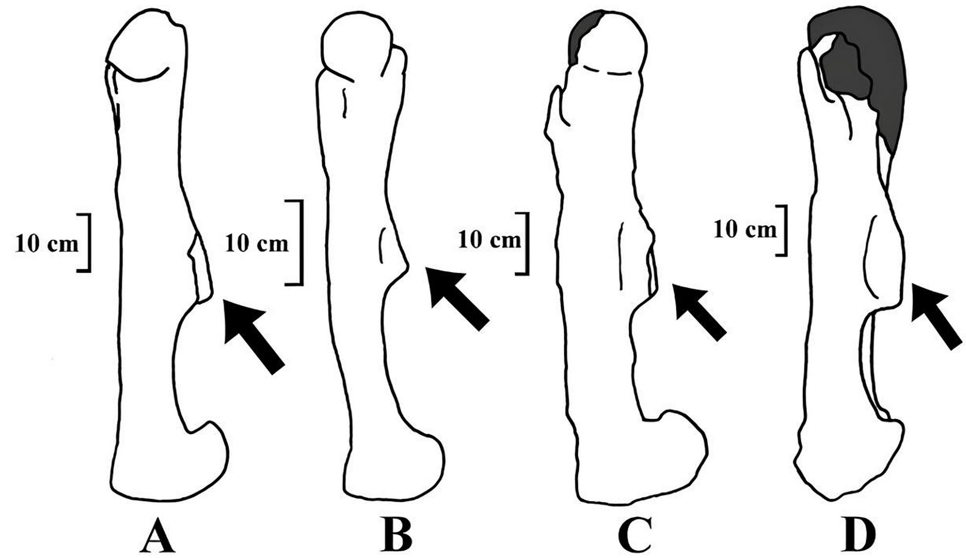

FIGURE 3. Comparison of the femora of different Iguanodontids in lateral view. **A**, *Iguanodon bernissartensis*. **B**, *Mantellisaurus atherfieldensis*. **C**, *Ug galvensis holotype*. **D**, IG (indeterminate genus) *or Dollodon seelyi.* The black arrows point the FT (Fourth trochanter). Modified from Verdu *et al*. (2015). The grey areas indicate reconstructed portions of the specimens.

trochanter in *ug. galvensis* (see Fig. 4), and can be traced even in perinatal individuals. This structure is absent in *Iguanodon* and related taxa, and may represent an autapomorphic feature diagnostic of *ug. galvensis*.

In addition, Verdu *et al*. (2017) described a rugose and inflated ridge on the lateral surface of the femur, and noted that the distal end of the femur is proportionally larger than the one present in *Iguanodon,* comparable in size to large specimens of *Iguanodon*, in fact the distal end appears particularly robust, measuring as wide as, or even wider than, the proximal end. All these observations indicate that the femoral morphology of *ug. galvensis* differs significantly from *Iguanodon bernissartensis*. These features, with differing proportional development, were present also in the perinate holotype of the ug. *galvensis* presenting a better state of femur preservation suggesting that these features are unlikely to be solely attributable as the result of taphonomic modifications related to post-burial diagenetic processes (Verdú *et al*., 2015; Fig. 4).

Ischium

Verdú *et al*. (2015) noted that the distal morphology of the ischium in *ug. galvensis* closely resembles *Iguanodon*. However, they did not consider the overall robustness of the element. With the distal expansion measuring twice the width of the proximal shaft as measured from the García-Cobeña *et al*. (2024). Verdu *et al*. (2017) noted other differences in the ischium, although we believe that distinguishing them in 4 diagnostic points is excessive, in our view a single diagnostic point is enough as it is outlined by Verdu *et al*. (2017) these traits are not

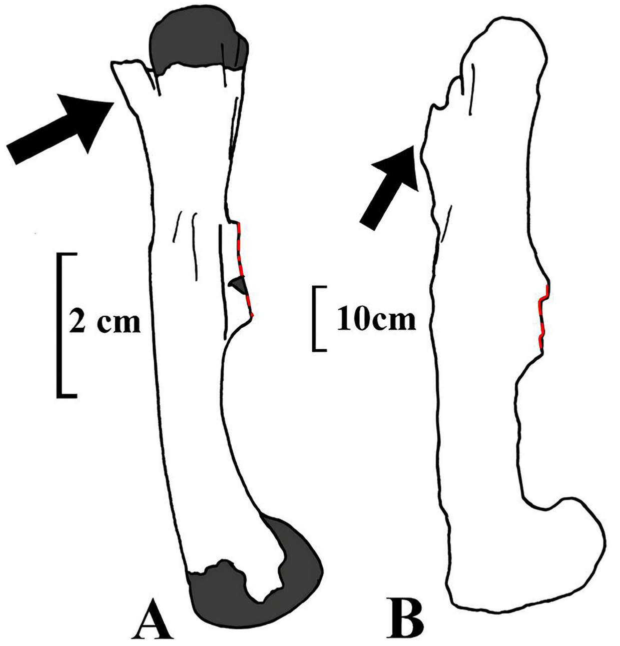

FIGURE 4. Left Femur of *ug galvensis* in lateral view. **A**, Perinate MAP-4902. **B**, Holotype. The arrows point to an atypical spur of the femora above the lateral trochanter. After Verdú *et al*. (2015). The grey areas indicate reconstructed portions of the specimen. Dotted lines show the concavity

independent but rather interrelated components of the same morphological structure. When considered collectively, they support a diagnostic distinction, whereas individually, they lack diagnostic value. This pronounced enlargement of the distal expansion may represent a diagnostic trait permitting also to differentiate *ug. galvensis* from *Iguanodon bernissartensis* for its unique characteristics (Verdu *et al*., 2015, 2017; Fig. 6)

Ilium

The ilium was used by Verdú *et al*. (2015) as a key element supporting the inclusion of *ug. galvensis* within the genus *Iguanodon*. However, this interpretation presents several flaws:

1) The presence of a well-developed brevis shelf is not exclusive to *Iguanodon* and is also observed in other styracosternan taxa such as *Mantellodon* (Paul, 2012) and "*Hypselospinus*" (Norman, 2010);

2) The presence of a lateral ridge is likewise not unique to *Iguanodon*, having been reported in multiple iguanodontid taxa (see Paul, 2008, 2012), reducing its diagnostic value;

3) Ilium morphology is known to be highly variable throughout ontogeny in both hadrosaurids and iguanodontians (see Paul, 2010, 2016, 2024; Frederickson *et al*., 2020) limiting its taxonomic reliability at genus level. Verdú *et al*. (2017) assigned an isolated ilium to *Iguanodon* cf. *galvensis* (MPT/I.G.472). However, subsequent studies have emphasized the limitations of using open nomenclature for species-level taxonomic assignments, as such practices can compromise the

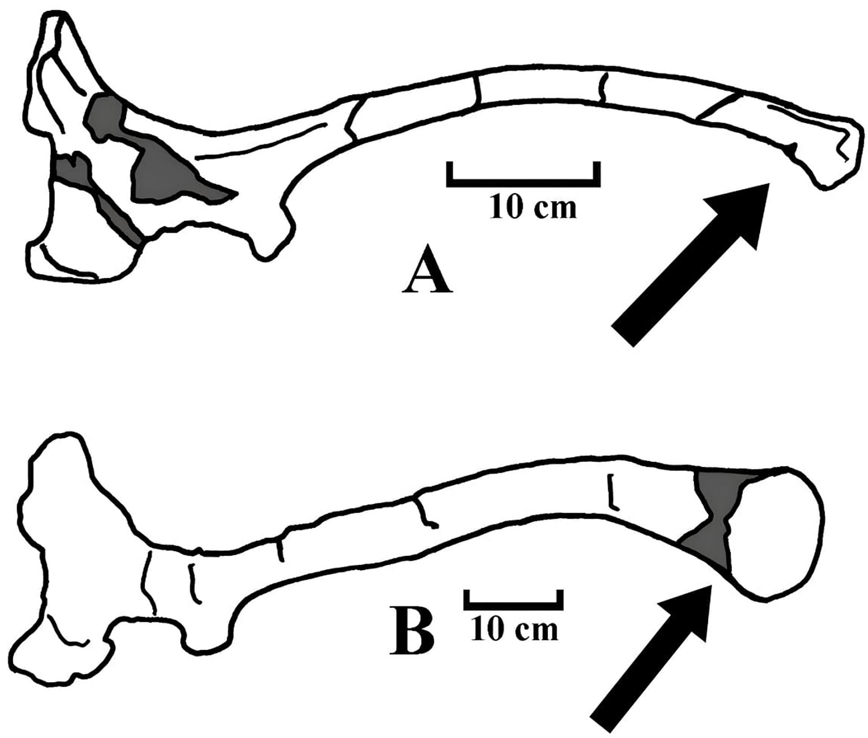

FIGURE 5. Right Ischium in lateral view. **A**, *Iguanodon bernissartensis* holotype. **B**, *Ug. galvensis* holotype. Black arrows point at the distal end. Both after Cobena *et al*. (2024). The grey areas indicate reconstructed portions of the specimen.

reliability of systematic interpretations (Paul, 2012; Lockwood *et al*., 2021). Verdú *et al*. (2017) also referred an adult ilium (SC-8-100) to *I. galvensis*, but this specimen is highly distorted and damaged. As highlighted in previous work, heavily deformed and incomplete material provides an unreliable basis for phylogenetic or taxonomic inferences (Norman, 2010, 2012; Paul, 2012). A comparison of the ilia is presented in Fig. 6.

On the basis of these considerations, the features of the ilium cited by Verdú *et al*. (2015, 2017) did not provide sufficient valid criteria to assign *ug. galvensis* to *Iguanodon*.

Skull

Dentary. Verdú *et al*. (2015) assigned the dentary of *ug. galvensis* to the genus *Iguanodon*, primarily based on its straight morphology and robust construction. However, this interpretation relies heavily on a perinatal reconstruction inferred from the juvenile specimen SCH-10 (see Verdú *et al*., 2015; fig. 6), rather than on the adult morphology. A re-evaluation of the adult dentary (holotype) yields several distinctions that challenge its attribution to *Iguanodon*:

1) Robustness: The adult dentary of *ug. galvensis* is notably less robust than that of *Iguanodon bernissartensis*. Its proportions are more comparable to those of *Dakotadon* or *Comptonatus* (see Figs 7 and 8; Paul, 2008; Lockwood *et al*., 2024.) This suggest a lighter head construction that is inconsistent with the typically robust morphology of *Iguanodon*;

2) Predentary: In *ug. galvensis*, the predentary appears to contact the dentary both dorsally and ventrally (Verdú *et al*., 2015, 2017, Paul, 2016, 2024). This contrasts with *Iguanodon*, where the predentary contacts only the dorsal surface of the dentary (Paul, 2008; see also Fig. 7) determining a clear morphological difference;

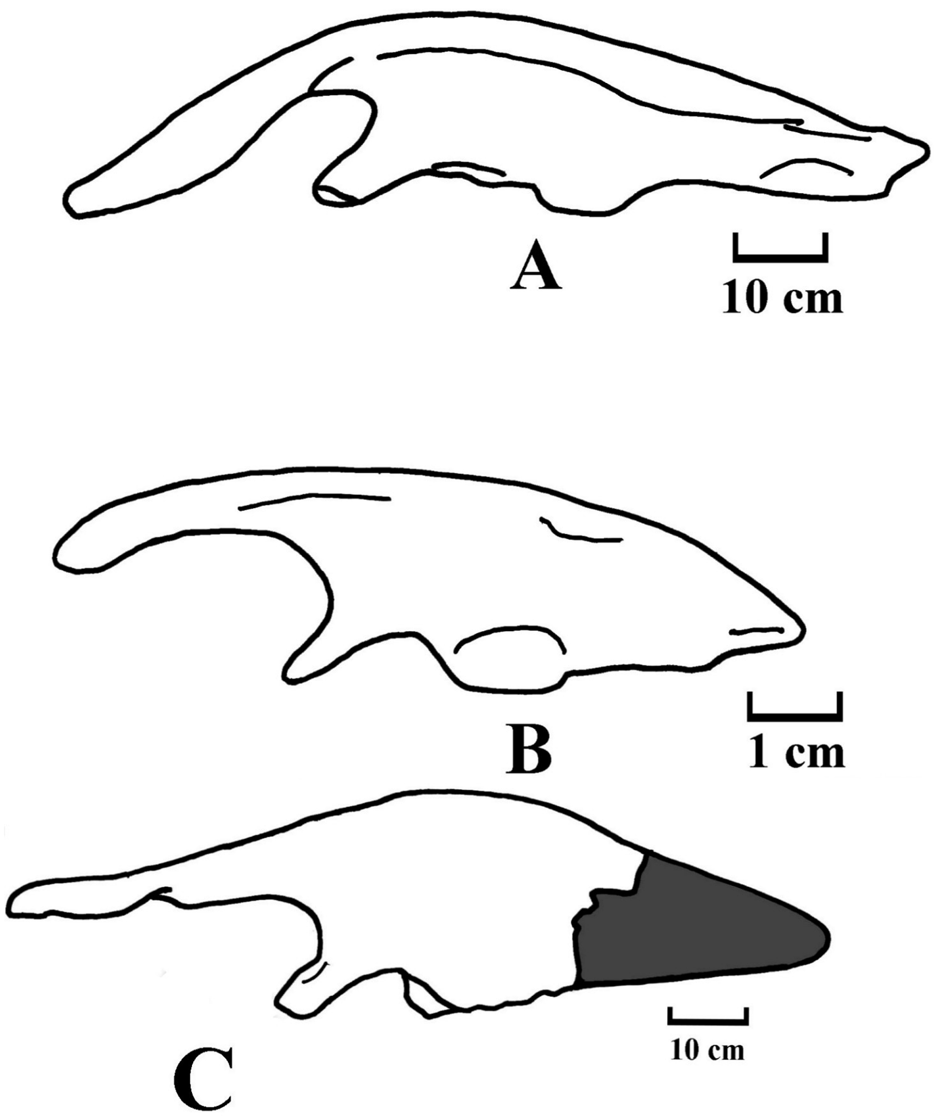

FIGURE 6. Ilia of different iguanodontian in lateral view. **A**, *Iguanodon bernissartensis* holotype. **B**, MAP-4902. **C**, SC-8-100. The grey areas indicate reconstructed portions of the specimen.

3) Coronoid process: The coronoid process in *ug. galvensis* is straighter and proportionally broader than in *Iguanodon* (Verdú *et al*., 2015; Paul, 2008; Figs 7, 8).

These features indicated that the dentary of *ug. galvensis* does not correspond to the diagnostic characteristics of *Iguanodon*, and instead supports its assignment to a separate taxon.

Rest of the skull

The cranial anatomy of *ug. galvensis* (SCH-10), beyond the dentary, provided further taxonomic data. While the dentary shares some similarities with *Dakotadon*, the remainder of the skull exhibits clear differences, allowing *ug. galvensis* to be distinguished from that taxon. Although *Comptonatus* may share certain cranial traits, *ug. galvensis* can be reliably differentiated based on postcranial morphology (Lockwood *et al*., 2024).

Notably, the overall cranial configuration of *ug. galvensis* is more closely aligned with *Iguanodon bernissartensis* than with other styracosternans (Verdú *et al*., 2015).

Based on the morphological evidence presented here, we conclude that *ug. galvensis* represents a distinct genus, diagnosable on the basis of multiple cranial and postcranial features. Accordingly, we propose the new taxonomic combination *Paulodon* gen. nov. *galvensis* (see Systematic Palaeontology below) Based on the palaeospecies terms used for other Styracosternan genera (Paul, 2007, 2008, 2010, 2012, 2016, 2024; Norman, 2010, 2012.)

Temporal separation

Paul (2024) suggested that one of the main criteria for distinguishing the two genera is their stratigraphic distribution: ug. *galvensis* is restricted to the early Barremian, whereas *Iguanodon* is documented from the late Barremian to the early Aptian (Paul, 2008, 2012, 2016, 2024; Verdú *et al*., 2015, 2017; Cobeña *et al*., 2024). This represents a temporal discontinuity of approximately 5–8 million years, which, given the typical duration of iguanodontid palaeogenera, may be sufficient to warrant recognition of a distinct genus (Paul, 2008). On this basis, the available data appear to support, the separation of *Paulodon* from *Iguanodon* at the genus level.

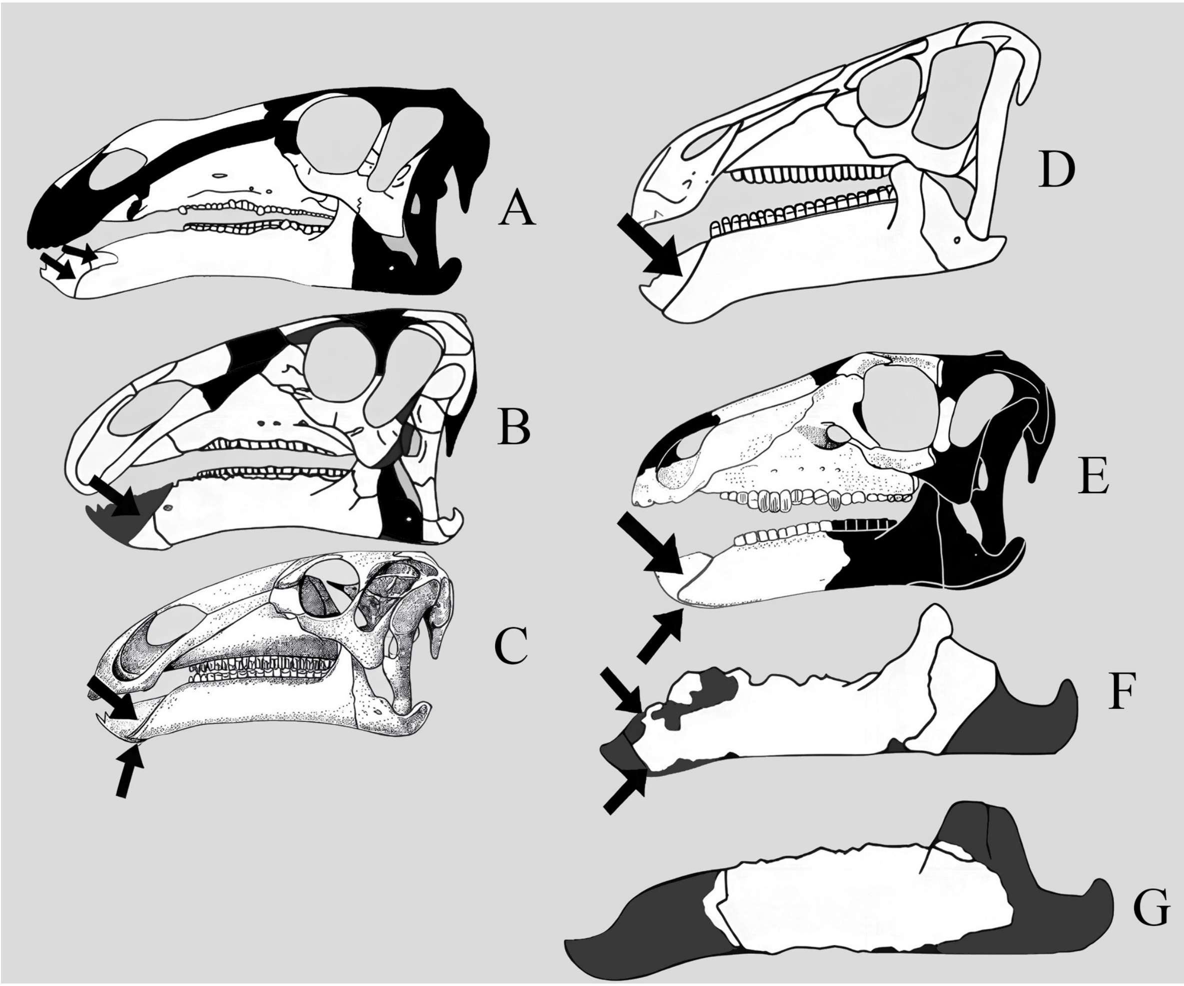

FIGURE 7. Iguanodontidae heads in lateral view. **A**, *Brighstoneus*. **B**, *Mantellisaurus*. **C**, *Dollodon*. **D**, *Iguanodon bernissartensis*. **E**, *Dakotadon*. F, dentary of perinate of *ug galvensis*. **H**, dentary of the type of *ug galvensis*. The black arrows indicate the points where the predentary would have attached. The grey areas indicate reconstructed portions of the specimens.

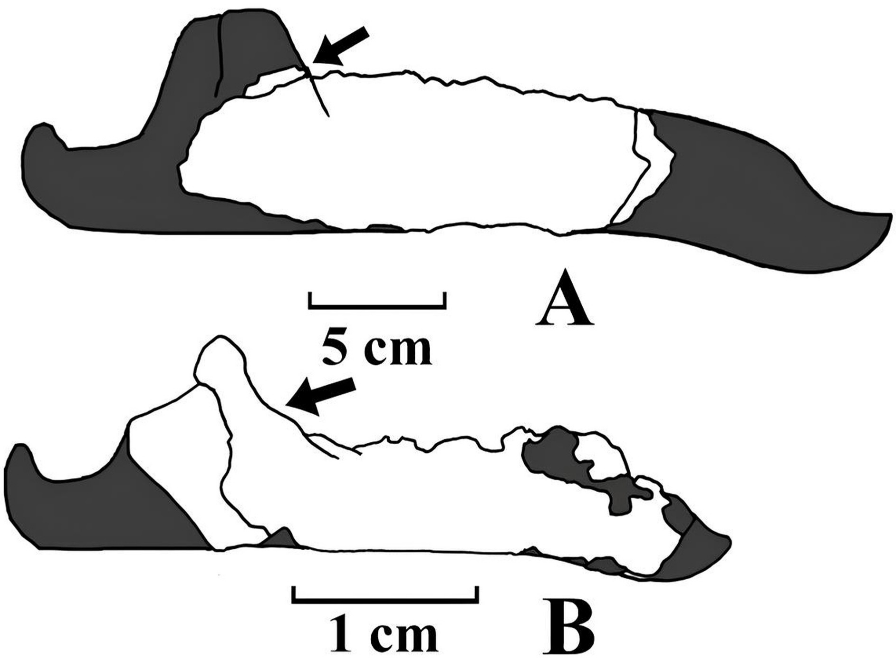

FIGURE 8. Dentaries in lateral view of *ug galvensis*. **A**, Type. **B**, Perinate. Both after Verdu *et al*. (2015). Black arrows indicate the coronoid process. The grey areas indicate reconstructed portions of the specimens.

Phylogentics

We conducted a phylogenetic analysis using TNT v.1.6 (Goloboff & Morales, 2023), based on the morphological dataset of Xu *et al*. (2018), implementing the same parameters used by Bonsor *et al*. (2023), 123 characters, with the matrix from Bonsor *et al*. (2023). This dataset was selected because it represents a large and widely tested matrix that has proven reliable in several previous studies (Xu *et al*., 2018; Bonsor *et al*., 2023).

Data for ug. *galvensis* were compiled from Verdú *et al*. (2015, 2017) and Cobeña *et al*. (2024)

All the ilia were excluded from the analysis because they belong to juvenile individuals, specimens of uncertain affinities, or highly distorted material. For perinatal individuals, only the manus was included in the data analysis, as it undergoes minimal ontogenetic variation.

The results indicate that *Paulodon* is phylogenetically distant from *Iguanodon* showing instead a closer affinity with *Proa* and *Lanzhousaurus* (Fig. 9). Our results, differ from those of previous studies (Verdú *et al*., 2015, 2017), where the results shows that ug. *galvensis* is a sister taxon with *Iguanodon,* for the following reasons: we employed a more comprehensive and updated character dataset, and we also incorporated the manus of perinatal individuals, which had not been considered previously due to uncertainties regarding its ontogenetic variation.

Coding of the species:
Paulodon_galvensis ???????0?????????????????????????
??????????????????0??0?????????????????????2201???
?00111??10101101???????30000110120411???

Systematic palaeontology

Magnorder Ornithischia Seeley, 1887–1888
Microrder Ornithopoda Marsh, 1881
Order Iguanodontia Dollo, 1888
Suborder Ankylopollexia Sereno, 1986
Infraorder Styracosterna Sereno, 1986

***Paulodon* gen. nov.**

Referred specimens. As listed by Verdú *et al*. (2017) and Cobeña *et al*. (2024).

Holotype. MAP-4787. Premaxilla, dentary, postorbital, quadrate, maxillary teeth, atlas arch, cervical remains, a sacral vertebra, ribs, coracoid, scapula, part of both pubis, part of both ischia, and a right femur of an adult.

Etymology. In honor of iguanodont researcher Gregory S. Paul.

Paratypes. SCH-10 is a juvenile right dentary, MAP-4902 Partially articulated skeleton of a perinate, MAP-4790 perinate pollex.

FIGURE 9. Most Parsimonious tree of tree of Iguanodontia. We used for the analysis the same settings and number of trees as for Bonsor *et al*. (2023).

Diagnosis. As for the type and only known species.

***Paulodon galvensis* Verdu *et al.*, 2015**

=*Iguanodon galvensis* Verdu *et al*., 2015

Etymology. Galvensis, meaning from Galve, the Spanish locality where the holotype was found.

Diagnosis (autapomorphic characters=*)**.** Fully separated digits; *metacarpal III articulates approximately 50% with carpal I and 50% with carpal II; pollex proportionally short and conical; pronounced medial curvature form a hook-like shape that articulates with a proportionally low and broad metacarpal I; *a rugose and inflated ridge appears on the lateral side of the femur shaft near to the lateral condyle; *the lateral trochanter forms a bony spur; *a prominent tuberosity (like a bump) on the articular surface of the iliac peduncle of the ischium; the ischiatic peduncle forms a step on the lateral face of ilium; shaft of the ischium is 'D-shaped' in cross section close to the distal end, where the ischium forms a rounded expansion which is relatively large compared to the proximal end (ratio 0.45–0.50); dentary straight, averagely constructed compared to iguanodontids; *dentary with dorsal margin close to the symphyseal region with a short, abrupt and marked convexity.

Locality and horizon. The site SC-1 lies within the SIBELCO EUROPE clay mine in Galve , Province of Teruel, Aragon, Spain (Universal Transverse Mercator grid coordinates 678925,96 and 4501598,87). SC-1 and SC-2 are located close to one another but present different levels of the Camarillas Formation (lower Barremian) of the Galve sub-basin (Maestrazgo Basin).

Remarks. The proximal end of the ulna of *Paulodon* is comparatively rounder than that of *Iguanodon*, which exhibits a more pointed morphology associated with a more complex olecranon process (Paul, 2012; Cobeña *et al*., 2024).

Conclusion

Our reassessment of the Galve fossil material, previously assigned to *Iguanodon galvensis* (Verdú *et al*., 2015), demonstrates that it represents a distinct genus, here designated as *Paulodon* gen. nov. This conclusion is grounded in a comprehensive anatomical review which reveals a suite of significant morphological differences when compared to *Iguanodon bernissartensis* and other closely related iguanodontid taxa. Notably, our comparative analysis highlights clear divergences in both cranial and postcranial regions, including the structure of the manus, the curvature and articulation of the pollex, the development and morphology of the femur (particularly the fourth trochanter and lateral spur), the robust distal expansion of the ischium, and the configuration of the dentary and predentary contact. These combined features are not consistent with the diagnostic criteria of *Iguanodon* sensu stricto, but instead support the recognition of a separate lineage within Styracosterna. Consequently, the establishment of *Paulodon galvensis* provides a refined and more accurate taxonomic framework for interpreting iguanodontid diversity in the Early Cretaceous of Europe, particularly within the Barremian faunal assemblages of the Galve region.

Acknowledgments

We thank Joe Bonsor for his help in understanding the phylogenetic analyses. We also would like to thank the two reviewers for their comments and important advice.

References

Bonsor, J.A. (2023) *The taxonomy and systematics of the iguanodontian dinosaurs*. PhD thesis, University of Bath, 1–423.

Bonsor, J.A., Lockwood, J.A.F., Leite, J.V., Scott-Murray, A. & Maidment, S.C.R. (2023) The osteology of the holotype of the British Iguanodontian dinosaur Mantellisaurus atherfieldensis. *Monographs of the Palaeontographical Society*, 177, 1–63. https://doi.org/10.1080/02693445.2023.2234156

Carpenter, K. & Alf, R.M. (1994) Global distribution of dinosaur eggs, nests, and babies. *In*: Carpenter, K., Hirsch, K. & Horner, J. (Eds), *Dinosaur Eggs and Babies*. Cambridge University Press, Cambridge, pp. 15–30.

Currie, P.J. (1987). *In dinosaurs past and present (Vol. 2)*. University of Washington Press, Seattle and London, pp. 100–117.

Currie, P.J. & Horner, J.R. (1988) Lambeosaurine hadrosaur embryos (Reptilia; *Ornithischia*). *Journal of Vertebrate Paleontology*, 8, 13A.

Dilkes, D. (2001) An ontogenetic perspective on locomotion in the Late Cretaceous dinosaur *Maiasaura peeblesorum* (Ornithischia: Hadrosauridae). *Canadian Journal of Earth Sciences*, 38 (8), 1205–1227. https://doi.org/10.1139/e01-016

Dollo, L. (1888) Iguanodontidae et Camptonotidae. *Comptes Rendus de l'Académie des Sciences (Paris)*, 106, 775–777.

Frederickson, J.A., Engel, M.H. & Cifelli, R.L. (2020) Ontogenetic dietary shifts in *Deinonychus antirrhopus* (Theropoda; Dromaeosauridae): Insights into the ecology and social behavior of raptorial dinosaurs through stable isotope analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 552, 109780. https://doi.org/10.1016/j.palaeo.2020.109780

Galton, P.M. (2009) Notes on Neocomian (Late Cretaceous) ornithopod dinosaurs from England—*Hypsilophodon*, *Valdosaurus*, "Camptosaurus", *Iguanodon*—and referred specimens from Romania and elsewhere. *Revue de Paléobiologie*, 28 (1), 211–273.

García-Cobeña, J., Verdú, F.J. & Cobos, A. (2024) Systematic of a massively constructed specimen of *Iguanodon galvensis* (Ornithopoda, Iguanodontidae) from the Early Barremian (Early Cretaceous) of eastern Spain. *Diversity*, 16 (9), 586, 1–22. https://doi.org/10.3390/d16090586

Goloboff, P.A. & Morales, M.A. (2023) TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel, Cladistics. The Willi Hennig Society, 39 (2), 144–153. https://doi.org/10.1111/cla.12524

Horner, J.R. & Weishampel, D. (1988) A comparative embryological study of two ornithischian dinosaurs. *Nature*, 332, 256–257. https://doi.org/10.1038/332256a0

Horner, J.R. & Currie, P.J. (1994) Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia: Lambeosauridae) from Montana and Alberta. *In*: Carpenter, K., Hirsch, K. & Horner, J. (Eds), *Dinosaur eggs and babies*, pp. 312–336.

Lockwood, J.A.F., Martill, D.M. & Maidment, S.C.R. (2021) A new hadrosauriform dinosaur from the Wessex Formation, Wealden Group (Early Cretaceous), of the Isle of Wight,

southern England. *Journal of Systematic Palaeontology*, 19 (12), 847–888.
https://doi.org/10.1080/14772019.2021.1978005

Lockwood, J.A.F., Martill, D.M. & Maidment, S.C.R. (2024) *Comptonatus chasei*, a new iguanodontian dinosaur from the Lower Cretaceous Wessex Formation of the Isle of Wight, southern England. *Journal of Systematic Palaeontology*, 22 (1), 1–87.
https://doi.org/10.1080/14772019.2024.2346573

Lull, R.S. & Wright, N.E. (1942) Hadrosaurian dinosaurs of North America. *Geological Society of America Special Paper*, 40, 1–208.
https://doi.org/10.1130/SPE40-p1

Marsh, O.C. (1881) Classification of the Dinosauria. *American Journal of Science (ser. 3)*, 23, 81–86.
https://doi.org/10.2475/ajs.s3-23.133.81

Maxwell, W. (1995) Cranial osteology of *Tenontosaurus* (Dinosauria: Ornithischia). *Journal of Vertebrate Paleontology*, 15, 44A.

Maxwell, W. & Ostrom, J. (1995) Taphonomy and paleobiological implications of *Tenontosaurus—Deinonychus* associations. *Journal of Vertebrate Paleontology*, 15 (4), 707–712.
https://doi.org/10.1080/02724634.1995.10011256

Norman, D.B. (2010) A taxonomy of iguanodontians (Dinosauria: Ornithopoda) from the Lower Wealden Group (Cretaceous: Valanginian) of southern England. *Zootaxa*, 2489 (1), 47–66.
https://doi.org/10.11646/zootaxa.2489.1.3

Norman, D.B. (2012) Iguanodontian taxa (Dinosauria: Ornithischia) from the lower cretaceous of England and Belgium. *In:* Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. *Indiana University Press, Bloomington*, pp. 175–212.

Osborn, H.F. (1912) Integument of the iguanodont dinosaur *Trachodon*. *Memoirs of the American Museum of Natural History*, 1–54.

Ostrom, J. (1970) *Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana*. Peabody Museum of Natural History Bulletin, 35, 1–234.

Parks, W.A. (1931) A new genus and two new species of trachodont dinosaurs from the Belly River Formation of Alberta. *University of Toronto Studies, Geological Series*, 31, 1–11.

Paul, G.S. (2007) Turning the old into the new: A separate genus for the gracile iguanodont from the Wealden of England. *In*: Carpenter, K. (Ed.), *Horns and beaks*, pp. 69–77.

Paul, G.S. (2008) A revised taxonomy of the iguanodont dinosaur genera and species. *Cretaceous Research*, 29, 192–216.
https://doi.org/10.1016/j.cretres.2007.04.009

Paul, G.S. (2010) *The princeton field guide to dinosaurs*. Princeton University Press, 320 pp.
https://doi.org/10.1515/9781400836154

Paul, G.S. (2012) Notes on the rising diversity of iguanodont taxa, and iguanodonts named after Darwin, Huxley, and evolutionary science. *In*: *Actas de v jornadas internacionales sobre paleontología de dinosaurios y su entorno, salas de los infantes (Burgos)*, pp. 121–131.

Paul, G.S. (2016) *The Princeton Field Guide to Dinosaurs* (2nd Ed.). Princeton University Press, 360 pp.
https://doi.org/10.1515/9781400883141

Paul, G.S. (2024) *The Princeton Field Guide to Dinosaurs* (3rd Ed.). Princeton University Press, 384 pp.
https://doi.org/10.1515/9780691253336

Prieto-Márquez, A. (2014) A juvenile *Edmontosaurus* from the Late Maastrichtian (Cretaceous) of North America: Implications for ontogeny and phylogenetic inference in saurolophine dinosaurs. *Cretaceous Research*, 50, 282–303.
https://doi.org/10.1016/j.cretres.2014.05.003

Poole, K.E. (2022) Phylogeny of iguanodontian dinosaurs and the evolution of quadrupedality. *Palaeontologia Electronica*, 25 (3), 1–42.
https://doi.org/10.26879/702

Prieto-Márquez, A. & Guenther, M.F. (2018) Perinatal specimens of *Maiasaura* from the Upper Cretaceous of Montana (USA): Insights into the early ontogeny of saurolophine hadrosaurid dinosaurs. *PeerJ*, 6, e4734.
https://doi.org/10.7717/peerj.4734

Rogers, R.R. (1991) Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: Evidence for drought-related mortality. *Palaios*, 5 (5), 394–413.
https://doi.org/10.2307/3514834

Seeley, H.G. (1887) On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, 43, 165–171.
https://doi.org/10.1098/rspl.1887.0117

Sereno, P.C. (1986) Phylogeny of the bird-hipped dinosaurs. *National Geographic Research*, 2, 234–256.

Sternberg, R. (1935) Hooded hadrosaurs of the Belly River Series of the Upper Cretaceous. *Canada Department of Mines Bulletin, Geological Series*, 52 (77), 1–37.
https://doi.org/10.4095/105051

Verdú, F.J., Royo-Torres, R., Cobos, A. & Alcalá, L. (2015) Perinates of a new species of *Iguanodon* (Ornithischia: Ornithopoda) from the Lower Barremian of Galve (Teruel, Spain). *Cretaceous Research*, 56, 250–264.
https://doi.org/10.1016/j.cretres.2015.05.010

Verdú, F.J., Royo-Torres, R., Cobos, A. & Alcalá, L. (2017) New systematic and phylogenetic data about the Early Barremian *Iguanodon galvensis* (Ornithopoda: Iguanodontoidea) from Spain. *Historical Biology*, 437–474.
https://doi.org/10.1080/08912963.2017.1287179

Xu, X., Tan, Q., Gao, Y., Bao, Z., Yin, Z., Guo, B., Wang, J., Tan, L., Zhang, Y. & Xing, H. (2018) A large-sized basal ankylopollexian from East Asia, shedding light on early biogeographic history of Iguanodontia. *Science Bulletin*, 63 (9), 556–563.
https://doi.org/10.1016/j.scib.2018.03.016