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A new basal ornithopod dinosaur from the Barremian of Galve, Spain

*Un nouveau dinosaure ornithopode basal du Barrémien de Galve, Espagne*José Ignacio Ruiz-Omeñaca^{a,*,b,c}, José Ignacio Canudo^{c,1}, Gloria Cuenca-Bescós^c,
Penélope Cruzado-Caballero^c, José Manuel Gasca^c, Miguel Moreno-Azanza^c^a Museo del Jurásico de Asturias (MUJA), Rasa de San Telmo s/n, 33328 Colunga, Asturias, Spain^b Departamento de Geología, Universidad de Oviedo, c/Jesús Arias de Velasco s/n, 33005 Oviedo, Spain^c Grupo Aragosaurus-IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, c/Pedro Cerbuna 12, 50009 Zaragoza, Spain

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This publication honours Mr. José María Herrero, discoverer of the holotype specimen of *Gideonmantellia*, who passed away on May 20, 2012 when the manuscript was still in review.

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ABSTRACT

A partially articulated postcranial skeleton of a small ornithischian dinosaur, *Gideonmantellia amosanjuanae* nov. gen. et sp., from the Early Cretaceous of Galve (Teruel province, Spain) is described. It was recovered in an outcrop of fluvial red clays from the Camarillas Formation, which is Barremian in age. This partial skeleton is recognised as a new ornithopod taxon by the following autapomorphies: (1) postacetabular process of the ilium with a *brevis shelf* that is noticeably medially expanded in its cranial part but narrow and horizontal in its caudal part; (2) rod-like prepubic process with its anterior end twisted and expanded; and (3) L-shaped first chevron. Our phylogenetic analysis indicates that *Gideonmantellia* represents a basal ornithopod taxon more derived than *Orodromeus*, the "Asian clade" (which includes *Haya* and others) and *Hypsilophodon*.

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RÉSUMÉ

Un squelette postcrânien partiellement articulé d'un petit dinosaure ornithischien, *Gideonmantellia amosanjuanae* nov. gen. et sp., du Crétacé inférieur de Galve (province de Teruel, nord-est de l'Espagne) est décrit. Il a été trouvé dans des argiles rouges fluviales de la Formation Camarillas, datée du Barrémien. Ce squelette partiel est reconnu comme appartenant à un nouveau taxon d'ornithopode par les autapomorphies suivantes : (1) processus postacétabulaire de l'ilion avec un *brevis shelf* qui est notablement élargi médialement dans sa partie antérieure mais étroit et horizontal dans sa partie postérieure ;

* Corresponding author. Museo del Jurásico de Asturias (MUJA), Rasa de San Telmo s/n, 33328 Colunga, Asturias, Spain.

E-mail addresses: jigrui@unizar.es (J.I. Ruiz-Omeñaca), jicnudo@unizar.es (J.I. Canudo), cuencag@unizar.es (G. Cuenca-Bescós), penelope@unizar.es (P. Cruzado-Caballero), gascajm@unizar.es (J.M. Gasca), mmazanza@unizar.es (M. Moreno-Azanza).

¹ <http://www.aragosaurus.com>.

(2) processus prépubien en forme de tige avec son extrémité antérieure tordue et élargie ; et (3) premier chevron en forme de L. Notre analyse phylogénétique indique que *Gideonmantellia* représente un taxon d'ornithopode basal plus dérivé qu'*Orodromeus*, le clade « asiatique » (qui inclut *Haya* et d'autres taxons) et *Hypsilophodon*.

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1. Introduction

Ornithischia is a diverse clade of dinosaurs that originated during the Late Triassic and were abundant in many Cretaceous ecosystems (Butler, 2010). In recent years, there has been a remarkable increase in what is known about the phylogenetic relationships and early evolution of ornithischian dinosaurs (Boyd et al., 2009; Butler, 2010; Butler et al., 2011; Makovicky et al., 2011). The phylogenetic hypothesis put forward by Butler et al. (2008) fixed the position of the main clades traditionally recognized (Serenó, 1998). Moreover, it identified the interrelationships of basal Ornithopoda and basal Cerapoda as the most problematic area of ornithischian phylogeny. The most important group of Cretaceous ornithischians was the ornithopods, which include a paraphyletic assemblage of small-bodied basal taxa traditionally named “hypsilophodontids”, the “iguanodontids” and the hadrosaurids. Butler et al. (2008) propose that taxa traditionally considered basal ornithopods are situated outside this clade: for instance, the heterodontosaurids are non-neornithischian basal ornithischians. The basal cerapodans such as *Othnielosaurus* have a more uncertain position, and their relationship within the basal Ornithopoda is poorly resolved (Makovicky et al., 2011). Nor does the proposal of an “Asian clade” comprising the taxa *Haya*, *Jeholosaurus* and *Changchunsaurus* substantially improve the resolution of basal Ornithopoda (Butler et al., 2011; Makovicky et al., 2011). We agree with Butler et al. (2011) that new taxa must be found in order to be able to resolve the relationships in this part of the tree. This continues to be fundamental if progress is to be made in establishing a more robust cladogram.

Relatively frequent in the Early Cretaceous of Spain are fragmentary remains, especially teeth, of small ornithopods that have been classified as “hypsilophodontids” without being able to be more specific (Canudo et al., 2010; Ruiz-Omeñaca et al., 2004b; Sanz et al., 1987). In this article, we describe for the first time a partially articulated postcranial skeleton of a small neornithischian dinosaur from Spain and evaluate its phylogenetic relationships within Ornithischia.

2. Previous work

The local amateur palaeontologist José María Herrero found and excavated in 1982 the partially articulated skeleton described here. The fossil was recovered in the locality of “Poyales Barranco Canales” (“Poyales Barranco Hondo” in Sanz et al., 1987). Since the early 1990s, the specimen has been on display in the Palaeontological Museum of Galve. The first reference to the dinosaur was as cf. *Valdosaurus* sp. on the basis of the femora (Sanz et al., 1984; but see Section 5: Comparative description). The left ilium

and left femur were subsequently figured and described as *Hypsilophodon foxii* (Sanz et al., 1987). In 1995, the preparation of the remainder of the skeleton (posterior dorsal, sacral and caudal series, left pelvis and both hindlimbs) by the senior author of the present paper showed characters in some bones of the appendicular skeleton that are not present in *Hypsilophodon*, and it was suggested that these in fact belong to a new unnamed “hypsilophodontid” (Ruiz-Omeñaca and Cuenca-Bescós, 1995). This went on to form part of the senior author's PhD thesis (Ruiz-Omeñaca, 2006). The presence of *H. foxii* in the province of Teruel has been mentioned by subsequent authors (Norman et al., 2004; Weishampel et al., 2004), with references to Galve and the small neornithischian from Galve cited by Sanz et al. (1987). However, the presence of *Hypsilophodon* in Spain cannot be confirmed with the available material (Galton, 2009; Ruiz-Omeñaca, 2001).

3. Geological setting

Galve is a village in the province of Teruel (Aragon, NE Spain), famous for its Latest Jurassic-Early Cretaceous vertebrate fossil record (see geographical location in Ruiz-Omeñaca et al., 2004a: fig. 1). There are more than 50 localities with shark, bony fish, amphibian, squamate, turtle, crocodile, pterosaur, dinosaur and mammal remains (Cuenca-Bescós et al., 2011; Ruiz-Omeñaca, 2011; Ruiz-Omeñaca et al., 2004a; Sanz et al., 1987).

The Early Cretaceous of eastern Teruel is part of the Maestrazgo Basin, which is further divided into seven sub-basins, one of which is the Galve Sub-basin (Salas et al., 2001). The Galve syncline is located in the northwestern part of the Galve Sub-basin. Marine, continental and transitional sediments from the Tithonian (Late Jurassic) to the early Aptian outcrop in this syncline. The lithostratigraphic units that are richest in fossil vertebrates are the Villar del Arzobispo Formation, the El Castellar Formation and the Camarillas Formation, ranging from the late Tithonian to the Barremian (Canudo et al., 2012; Ruiz-Omeñaca et al., 2004a).

The locality of “Poyales Barranco Canales”, from now on referred to as Poyales, was situated in an outcrop of fluvial red clays from the upper part of the Camarillas Formation and was destroyed by the local clay-mining industry (see stratigraphical and cartographical location in Ruiz-Omeñaca et al., 2004a: figs. 2, 3). Besides the ornithopod skeleton, this locality also provided two ungual phalanges from a medium-sized theropod, and bony fish, turtle and crocodile remains identified as *Lepidotestudo* sp., Testudines indet., Mesoeucrocodylia indet. and Neosuchia indet. (Ruiz-Omeñaca, 2006). The skeleton was recovered without an accompanying taphonomic study; nevertheless, the preparation of some remains still in the matrix and the study

of the state of preservation of the bones showed that the skeleton had undergone short transportation and was buried quickly (stage 0 in the indexes both of abrasion and weathering; Cook, 1995).

The Camarillas Formation conformably overlies the El Castellar Formation. It represents a significant lithological change, being composed mainly of red clays and white sands at its base, deposited in a fluvial environment with a certain marine influence. Dating by charophytes allows the upper El Castellar Formation to be considered early Barremian in age and the Camarillas Formation to be considered Barremian in age (early Barremian and lower part of the late Barremian). The upper El Castellar Formation and the Camarillas Formation are included in the *Atopochara trivolvus triquetra* zone (Canudo et al., 2012).

4. Systematic palaeontology

ORNITHISCHIA Seeley, 1887
NEORNITHISCHIA Cooper, 1985
CERAPODA Sereno, 1986
ORNITHOPODA Marsh, 1881
***Gideonmantellia* nov. gen.**

Etymology: in honour of Gideon Algernon Mantell, the first author to describe and to figure “hypsilophodontid” remains, in 1849, as those of a very young *Iguanodon* (subsequently regarded as the paratype of *H. foxii* Huxley, 1869; Galton, 1974a)

Type species: *Gideonmantellia amosanjuanae* nov. sp.
Generic diagnosis: that of the type species.

***Gideonmantellia amosanjuanae* nov. sp.**

Etymology: dedicated to Olga María Amo Sanjuan, a fellow of the Department of Palaeontology at the University of Zaragoza who was doing her thesis on eggshell fragments of vertebrates from the Lower Cretaceous of Galve when she died prematurely in October 2002.

Holotype: MPG-PBCH, a partially articulated skeleton housed in the Museo Paleontológico de Galve (MPG), which includes: nine dorsal, three sacral and twenty-one caudal vertebrae, fragments of dorsal ribs, six chevrons, fragments of ossified tendons, left ilium, left prepubic process, fragments of left ischium and postpubis, both femora, tibiae and fibulae, right astragalus, both calcanei, and five metatarsals and nineteen phalanges from both feet.

Locality: Poyales, Galve (Teruel, NE Spain), Galve Subbasin (Maestrazgo Basin, Iberian Range).

Horizon: Upper part of the Camarillas Formation (Barremian).

Diagnosis: small neornithischian dinosaur characterized by the following autapomorphies:

- postacetabular process of the ilium with a brevis shelf that is noticeably medially expanded in its cranial part but narrow and horizontal in its caudal part;

- rod-like prepubic process with its anterior end twisted and expanded;
- L-shaped first chevron.

5. Comparative description

Altogether, 104 remains from the vertebral series, left hip and the two hindlimbs have been identified, all belonging to a single individual (Fig. 1

). This makes it the most complete ornithopod skeleton and one of the most complete dinosaur skeletons found in Spain. The neural arches of the dorsal and anterior caudal vertebrae are suturally separated from the centra and have inflated pedicels, indicating an immature stage in the individual's development (Irmis, 2007). The dorsal surface of these centra and the ventral surface of the pedicels are rugged, indicating that the specimen was not a hatchling (Chure et al., 1994). There are three preserved unfused sacral centra (the first, second and last ones). According to Butler et al. (2011), the lack of neurocentral fusion means that growth had not ceased at the time of death, although estimating the exact ontogenetic stage of this individual is impossible without an osteohistological analysis.

Dorsal vertebrae. There are nine dorsal vertebral centra and six dorsal neural arch fragments. The centra are cylindrical, spool-like and amphiplatyan (Fig. 1A). The dorsal vertebrae are similar to those of other basal ornithischians. Their anterior articular faces are flat, whereas their posterior articular faces are slightly concave, as in *Hypsilophodon* and *Hexinlusaurus* (Galton, 1974a; He and Cai, 1984). The articular faces of the centra have a circular outline (Fig. 1A), except the posterior articular face of the last dorsal centrum, which is heart-shaped. The ventral margins are smoothly rounded, as in other small-bodied ornithischian taxa (Butler, 2010). The transverse width of the articular faces of the centra exceeds their dorsoventral height. Longitudinal fluting and wrinkling is present on the anterior and posterior ends of the lateral and ventral surfaces of the centra, as well as tiny nutrient foramina on the lateral surfaces. In the dorsal neural arches, the transverse processes are short and wide and are situated, forwardly inclined, at the anterior end of the centrum, as in *Hypsilophodon* (Galton, 1974a: fig. 22); the neural spine is vertically placed at the posterior end of the centrum; and the postzygapophyses project slightly behind the centrum.

Dorsal ribs. There are nine small fragments of dorsal ribs. These are shafts that are circular to elliptical in cross-section, and two fragments represent the capitulum and the tuberculum. In general, the dorsal ribs resemble those of other ornithischians.

Sacrum. Three sacral vertebral centra have been preserved. These are the first two (Fig. 1B) and the last one (Fig. 1C). The first centrum is procoelous, with a concave, heart-shaped anterior surface and a U-shaped posterior articular surface. As in *Changchunsaurus*, the first sacral can be interpreted as a dorsosacral, because the succeeding first true sacral vertebra has migrated anteriorly to articulate between the centra of both adjacent vertebrae (Butler et al., 2011). The posterior end of the first centrum is therefore considerably expanded relative to its anterior end, as is often observed in dorsosacrals (e.g. Butler et al., 2011,



fig. 3.D), whereas the anterior end of the second centrum is expanded relative to its posterior end. The first two sacral centra are dorsoventrally compressed, with a broad neural canal, the ventrolateral surfaces gently excavated, and the ventral margin smoothly rounded, but a ventral ridge is absent, as in other basal ornithischians (e.g. *Eocursor*: see Butler, 2010). The last sacral centrum is spool-shaped and less lateromedially expanded than the anterior ones.

Caudal vertebrae and chevrons. There are twenty caudal vertebrae preserved, the first fourteen with transverse processes, and the subsequent six without them. As is typical of basal ornithopods, the proximal centra gradually become lower and proportionately more elongate distally (Norman et al., 2004). In the first eight, the transverse process is suturally separated from both the centrum and the neural arch (Fig. 1D), so there are sutural surfaces for the transverse process on both the centrum and the neural arch, just above the neurocentral suture (stage 1 of character 85 in the matrix from Boyd et al., 2009: appendix 1, 2), as in some ornithopods such as *Parksosaurus* and *Thescelosaurus*. In *Parksosaurus* this occurs in the first twelve caudals (Parks, 1926), in *Thescelosaurus*, only in some caudals (Galton, 1974b). In the last few anterior caudal vertebrae, the transverse process is fused to the centrum (Fig. 1E), and becomes progressively smaller posteriorly, disappearing in caudal fifteen. The mid-caudal vertebrae have a longitudinal ridge on the lateral surface (Fig. 1F), as in other ornithopods (Galton, 1981). The caudal centra are spool-shaped and amphicoelous, have articular surfaces with a subcircular to hexagonal outline, and bear chevron facets on both the cranioventral and caudoventral margins. The ventral margins are concave between the chevron facets, and some of them have longitudinal fluting next to the chevron facets.

Both the chevrons and neural spines are short (Fig. 1D, G), as in the majority of basal Ornithopoda (Galton, 1974a; fig. 28). The first chevron is situated between the first two caudals, as in *Dryosaurus*, *Hypsilophodon* and *Othnielosaurus* (Galton, 1974a, 1981; Galton and Jensen, 1973); in *Thescelosaurus* there is no chevron between the first two caudals (Galton, 1974b). This first chevron is bent at a right angle (Fig. 1G), unlike in other basal ornithischians, which have chevrons that are straight (e.g. *Othnielosaurus*) or somewhat curved and directed backwards (e.g. *Haya*). This unusual shape of the first chevron is not the result of breakage or diagenetic distortion, and there are no marks of thickening, fractures or osseous growth associated with pathology. In other ornithopods, such as *Iguanodon* (Norman, 1980), the first chevrons incline strongly

downwards, but these do not have a distal blade that is bent as in *Gideonmantellia*; in *Hypsilophodon*, the first chevron is fragmented but seems very small; in *Othnielosaurus*, this chevron is straight and elongated, and is directed downwards.

Ilium. The left ilium is well preserved and almost complete (Fig. 1H). The preacetabular process is broken and incomplete cranially, whereas only a small part of the postacetabular process and caudal margin of the brevis shelf has been lost by breakage. In general, the ilium of *Gideonmantellia* broadly resembles that of *Hypsilophodon* and *Othnielosaurus* (Galton, 1974a; Galton and Jensen, 1973), but it differs in some characters that seem to be diagnostic for *Gideonmantellia*. The dorsal margin of the ilium is gently convex – almost straight in its caudal half – in lateral view, as in other basal ornithischians (e.g. *Parksosaurus*, *Hypsilophodon*). The main body of the ilium is in general transversely compressed, with a thin iliac blade that increases in thickness somewhat in its lower part. The base of the preacetabular process is lateromedially compressed. A medial flange above the acetabulum, which emerges from the pubic peduncle, is present as in some basal ornithischians, but a well-developed supracetabular flange is absent, unlike in basal ornithischians such as *Eocursor* (Butler, 2010). The pubic peduncle projects cranioventrally and is relatively short when compared to the ischial peduncle, as in *Hypsilophodon* and unlike in other basal ornithischians (e.g. *Heterodontosaurus*: Santa Luca, 1980). The ischial peduncle, which projects ventrally, is long and narrow and is remarkably delicate (Fig. 1H), without a robust base as in the rest of the ornithopods. The brevis shelf, located ventromedially on the elongate, subrectangular postacetabular process, is nearly horizontal and differs from that of other basal ornithischians such as *Othnielosaurus* and *Hypsilophodon*, which have a postacetabular process that is directed slightly medioventrally or even more strongly ventrally (e.g. *Lesothosaurus*: Butler, 2010). The brevis shelf is wider than in *Hypsilophodon* but narrower than in *Othnielosaurus*, and much narrower than in *Dryosaurus* and *Valdosaurus* (Galton, 1974a, 1983; Galton and Jensen, 1973). The morphology of the brevis shelf, medially expanded in its cranial part but narrow and horizontal in its caudal part (Fig. 1H, see also Ruiz-Omeñaca, 2006: appendix III.1, fig. 4.37), is exclusive to *Gideonmantellia*.

Pubis. Only the left prepubis (Fig. 1I) and a small fragment of the rod-like postpubic shaft are preserved. The prepubis is rod-shaped and anteroposteriorly curved, with the concavity outside, as in *Hypsilophodon* and dryosaurids

Fig. 1. Holotype specimen of *Gideonmantellia amosanjuanae* nov. gen. et sp. (MPG-PBCH) from the Early Cretaceous of Galve, Spain. A. Dorsal vertebra. B. Last dorsal and the first two sacral vertebrae. C. Last sacral vertebra. D–F. Caudal vertebrae. G. Chevrons. H. Left ilium. I. Left prepubis. J. Right femur. K. Left femur. L. Right fibula. M. Left tibia. N. Right calcaneum and astragalus. O. Right pes; in anterior (A3, E2, F1, K2, L2), posterior (A1, G2, M1), dorsal (A2, B, C, E1, I3, O), lateral (A4, D, E3, F2, G1, H2, I2, J, M2), medial (H1, I1, K1, L1) and proximal (N) views. Scale bars: 5 cm (s1: A–G; s2: H–I, s3: J–O). The white arrows indicate the autapomorphies.

Fig. 1. Holotype de *Gideonmantellia amosanjuanae* nov. gen. et sp. (MPG-PBCH) du Crétacé inférieur de Galve, Espagne. A. vertèbre dorsale. B. Dernière vertèbre dorsale et deux premières vertèbres sacrées. C. Dernière vertèbre sacrée. D–F. Vertèbres caudales. G. Chevrons. H. Ilium gauche. I. Processus prépubien gauche. J. Fémur droit. K. Fémur gauche. L. Fibula droite. M. Tibia gauche. N. Calcaneum et astragale droits. O. Pied droit ; en vues antérieure (A3, E2, F1, K2, L2), postérieure (A1, G2, M1), dorsale (A2, B, C, E1, I3, O), latérale (A4, D, E3, F2, G1, H2, I2, J, M2), médiale (H1, I1, K1, L1) et proximale (N). Barres d'échelle : 5 cm (s1 : A–G ; s2 : H–I, s3 : J–O). Les flèches blanches indiquent les autapomorphies.

(Sues and Norman, 1990), whereas in iguanodontians, it is blade-shaped, laterally flattened and dorsoventrally deep (Norman, 2004; see also Ruiz-Omeñaca, 2011). The anterior end is not broken but has suffered some erosion; the posterior end is certainly broken and would have merged with the main body of the pubis. The prepubis of *Gideonmantellia* is characteristic in that its anterior end is expanded and twisted, so the lateral surface turns into the dorsal (Fig. 11). This torsion in the prepubis has only been cited in *Parksosaurus* and *Thescelosaurus* (Galton, 1974b; Parks, 1926). However, in combination with its distal expansion, it is unique to *Gideonmantellia*. The prepubis is relatively larger than in *Parksosaurus*, *Hypsilophodon*, *Othnielosaurus* and *Thescelosaurus*, being similar in size to that in *Tenontosaurus* (Forster, 1990; Galton, 1974a; Galton and Jensen, 1973; Gilmore, 1915; Parks, 1926).

Ischium. Only two possible fragments of the left ischial shaft are preserved. The big fragment, subcircular to sigmoid and elliptical in cross-section, belongs to the middle part of the ischium. It has a medially twisted part where the obturator process has broken off. The other fragment, elliptical in cross-section, belongs to the proximal part of the shaft.

Femur. Both femora are almost completely preserved, especially the left one (Fig. 1K), which is only lacking a fragment of the medial condyle at the distal end and part of the fourth trochanter. The femur is similar to that in *Othnielosaurus* (Galton, 1983). The shaft of the femur is bowed cranially, and the femoral head is perpendicular to the shaft, as in most basal ornithopods (Makovicky et al., 2011). A well-developed constriction separates the head from the greater trochanter. The lesser trochanter is offset cranially from the greater trochanter (Fig. 1J), and they are separated by a deep cleft as in *Othnielosaurus* (Galton and Jensen, 1973) and dryosaurids (e.g. *Valdosaurus*: Barrett et al., 2011) and unlike in *Hypsilophodon* (Galton, 1974a), which presents a shallow cleft. The lesser trochanter is positioned rather distally on the shaft relative to the proximal surface of the femoral head. The proximal surface is trapezoid-shaped, with the craniocaudal width being greater laterally than medially as in other ornithopods (e.g. *Hypsilophodon*).

At midlength, the femoral shaft is subcircular to subquadrate in cross-section. The fourth trochanter, positioned on the caudomedial surface of the femoral shaft in the proximal half of the femur, is incomplete in both femora. A low, rounded ridge extends from the distal end of the base of the fourth trochanter, connecting to the lateral condyle distally, as in other ornithischians (e.g. *Eocursor*). The lateromedial width of the distal end of the femur is slightly greater than its craniocaudal width, as in some ornithopods (e.g. *Hypsilophodon*) and in contrast to basal ornithischians (Butler, 2010). A broad intercondylar fossa is present between the medial and lateral condyles; it is U-shaped in distal view, as in other ornithischians such as *Hypsilophodon* (Galton, 1974a). The cranial surface of the distal femur shows no evidence of an intercondylar groove, as in basal ornithischians and in contrast to derived ornithischians. This precludes the original assignment of the femora to *Valdosaurus* by Sanz et al. (1984),

as dryosaurids have a deep anterior intercondylar groove (Barrett et al., 2011; Galton, 2009).

Tibia. The left tibia is preserved nearly complete (Fig. 1M), whereas only the distal end of the right tibia is known. The two tibiae differ slightly in size, the right one being lateromedially wider (11%) than the left one, but morphologically concordant. The area of the distal section in the left tibia is 16% less than in the right one. It is difficult to determine whether this difference in size is due to differential taphonomic deformation or to the two tibiae belonging to different individuals. This is indeed an open – but not a significant – question. However, in the light of the lack of field data, the taphonomic deformation in some bones, and the absence of a repeated bone-record, here we follow the previously adopted measure (Ruiz-Omeñaca, 2006) of including both the tibiae within the type material. The tibia is longer than the femur, as is usual in “hypsilophodontids” (Thulborn, 1972). Elongation of the tibia relative to the femur appears to represent the plesiomorphic condition for Ornithischia (Butler, 2010). The proximal end is strongly expanded craniocaudally, whereas the distal end is expanded transversely. The tibia has a twisted diaphysis (Fig. 1M), with an angle of 78°; in ornithischians this torsion ranges from 40° in *Parksosaurus* (Parks, 1926) to 90° in *Pisanosaurus* (Bonaparte, 1976). The proximal end is more craniocaudally expanded than in *Hypsilophodon* (Galton, 1974a) and other basal ornithopods (e.g. *Changchunsaurus*: Butler et al., 2011), being more similar to *Eocursor* (Butler, 2010). However, this feature could be influenced by some degree of taphonomic deformation in the case of *Gideonmantellia*. The pronounced, sharp cnemial crest projects cranially and is separated from the fibular condyle by the *incisura tibialis*. A small accessory condyle (Thulborn, 1972) is present between the fibular condyle and the cnemial crest, as in *Hypsilophodon*. The fibular and inner condyles are separated by a deep notch, as is typical in ornithischians (Butler, 2010). In *Gideonmantellia*, the fibular condyle is prominent, as in *Valdosaurus* (Barrett et al., 2011) and unlike in *Hypsilophodon* (Galton, 1974a). The cnemial crest and inner condyle are unusually expanded in *Gideonmantellia* (Fig. 1M), unlike in other ornithopods (e.g. *Hypsilophodon*), but this is probably increased by lateromedial taphonomic compression. The proximal articular surface is caudally inclined, as in other ornithischians.

The distal end is transversely expanded and triangular in distal view, as in all basal ornithischians (Norman et al., 2004). The distal end has a ventral notch for the posterior part of the astragalus. The medial malleolus is thicker than the lateral malleolus, as is typical in ornithischians (e.g. *Hypsilophodon*), whereas the lateral malleolus is more developed and transversely expanded than in *Hypsilophodon* (Galton, 1974a).

Fibula. The right fibula is apparently complete (Fig. 1L), whereas the left fibula has lost a small distal portion. The fibula is slender, with its proximal end strongly craniocaudally expanded, and weakly concave in the medial surface. The shaft is transversely compressed. The distal end is slightly thickened and craniocaudally expanded. The fibulae of *Gideonmantellia* are similar to those of *Othnielosaurus* (Galton and Jensen, 1973) and *Hypsilophodon*

(Galton, 1974a), but, unlike in these genera, in *Gideonmantellia* the fibula is twisted and is shorter than the tibia, as in *Thescelosaurus garbanii* Morris, 1976 (Boyd et al., 2009). However, the validity of this feature – fibula shorter than tibia – in the *Gideonmantellia* material is doubtful due to the breakage present in the shaft of both fibulae, which are composed of several glued pieces, and the variation in size between the two tibiae, which is discussed above.

Astragalus. The astragalus (Fig. 1N), only the right one of which is preserved, is lateromedially expanded. The ascending process is shallower than in *Othnielosaurus* (Galton and Jensen, 1973) and bears a laterally placed tooth-like structure (Galton, 1974a; “articular cone” of Bakker et al., 1990) similar to that in *Hypsilophodon*. The posterior process is poorly developed.

Calcaneum. Both calcanei are partially preserved, the right one being nearly complete (Fig. 1N). Its dorsal margin is subdivided into a large and deeply excavated facet for the tibia caudally and a reduced facet for the fibula cranially, unlike other basal ornithopods, which have subequal facets in dorsal view (e.g. *Valdosaurus*: Barrett et al., 2011). The facet for the fibula is positioned proximally to that for the tibia. The ventral margin is convex, with a shallow horizontal groove in the caudoventral margin that is continuous with a gentle groove in the astragalus located on the caudal side below the ascending process.

Metatarsus/Pes. The right pes (Fig. 1O), with three metatarsals and twelve phalanges, is more complete than the left one, which has two metatarsals and seven phalanges. Metatarsals I, III and IV (MT1, MT3, MT4) have been preserved, as have the proximal, intermediate and ungual phalanges of digits I, II, III and IV.

MT1 of *Gideonmantellia* is smaller than MT3 and MT4 but has phalanges associated with it, as in other “hypsilophodontids” (Galton, 1981). MT1 is 55% the length of MT3, similar to *Hypsilophodon* (54%: Galton, 1974a). In other ornithopods with MT1, this ratio varies between 10% (*Dryosaurus*: Galton, 1981) and 65% (*Tenontosaurus*: Forster, 1990). MT1 of *Gideonmantellia* is splint-shaped and twisted, as is the case in *Lesothosaurus* (Thulborn, 1972). MT1 is shorter in *Hypsilophodon* and has a wider proximal end (Galton, 1974a). The proximal end of MT1 in *Gideonmantellia* is thin and lacks an articular surface, so it would not contribute to the tarsometatarsal articulation. Both the proximal and the distal ends of MT1 are similar to *Othnielosaurus* (Galton and Jensen, 1973); in *Hypsilophodon*, the proximal end is thicker (Galton, 1974a).

MT3 is the longest of the preserved metatarsals (Fig. 1O). Galton and Powell (1980) used the “maximum anteroposterior width/length of MT3” ratio to distinguish genera. This ratio is 0.35 in *Cumnoria*, between 0.39–0.46 in *Campylosaurus*, 0.15 in *Hypsilophodon*, 0.26 in *Dryosaurus*, 0.27 in *Ouranosaurus* and between 0.34–0.51 in *Iguanodon*. In *Gideonmantellia*, it is 0.20, similar to *Hypsilophodon*. MT3 of *Gideonmantellia* is straight, and MT4 curves laterally, so the two metatarsals are not in contact distally, as in *Lesothosaurus* and *Eocursor* (Butler, 2010). In *Gideonmantellia*, the medial surface of MT4 is excavated for contact with MT3, as in *Parksosaurus* (Parks, 1926). The proximal end of MT4 is triangular, as in other primitive ornithopods (Galton, 1981). This proximal end has an excavated ventral

face, which might have served to articulate with metatarsal V. The distal end of MT4 is similar to that in *Dryosaurus* (Galton, 1981). There is a thin, sharp crest on the lateral margin, as in *Lesothosaurus* (Thulborn, 1972). In distal view, MT4 of *Gideonmantellia* is similar to that of the holotype of *Othnielosaurus* (Galton, 1983).

The phalangeal formula for the pes in *Gideonmantellia* is 2:3:4:5:0, which is common in basal ornithopods (Sues and Norman, 1990) and different from that of iguanodontoids, which is 0:3:4:5:0 (Norman, 2004). The phalanges of the pes in *Gideonmantellia* are very similar to those in *Hypsilophodon* and *Othnielosaurus*. The phalanges of other ornithischians are more elongate (e.g. *Lesothosaurus*), or thicker and more robust (e.g. *Thescelosaurus*, *Iguanodon*). Digit I would hardly touch the ground in the locomotion of *Gideonmantellia*, and would probably be non-functional. The first phalanx of digit I of *Gideonmantellia* is very similar to that of *Othnielosaurus* (Bakker et al., 1990), although the first phalanx of digit III of *Othnielosaurus* differs from that of *Gideonmantellia* in that its proximal end is not biconcave, with depressed areas on either side separated by an incipient dorsal process. As in other basal ornithischians, the preserved ungual phalanges are long, moderately curved and bear grooves.

6. Phylogenetic analysis and discussion

To investigate the phylogenetic relationships of *Gideonmantellia*, it was included in the modified version of the data set from Butler et al. (2011) used by Makovicky et al. (2011). The resulting data matrix included 52 taxa that were scored for 227 osteological characters and analysed with Mesquite 2.74 (Maddison and Maddison, 2010). The scores for *Gideonmantellia* are provided in Appendix 1. In the current analysis, character 193 (shape of the prepubic process) has been modified adding a new state (4. Prepubic process rod-like, twisted along length – mediolaterally compressed at its base whereas the lateral surface faces dorsally at its cranial end). Within the current data matrix *Parksosaurus*, *Thescelosaurus* and *Gideonmantellia* have been scored as 4 for this character.

The resulting matrix was analysed with TNT (Goloboff et al., 2008), maintaining the search settings used by Makovicky et al. (2011): branches with a minimum length of zero were collapsed (the “-amb” option); characters 112, 135, 137, 138 and 174 were treated as ordered; all characters were equally weighted; and multistate taxa were treated as polymorphisms. Five thousand replicates of TBR branch swapping were conducted, holding 10 most parsimonious trees for each replicate. A total of 10 040 most parsimonious trees (MPT) of 563 steps were recovered (CI=0.451, RI=0.705, RC=0.318). As in previous analyses, the strict consensus shows almost no resolution, with only the major groups within Ornithischia recovered as monophyletic. Only minor differences were observed, including *Pisanosaurus* being basal to all other ornithischians, and the collapsing of the node ((*Parksosaurus* + *Gasparinisaura*) + Ornithopoda). *Gideonmantellia* is here recovered as an ornithopod, but no more precise determination can be made. The six maximum agreement subtrees include 39 taxa, with one of these combinations

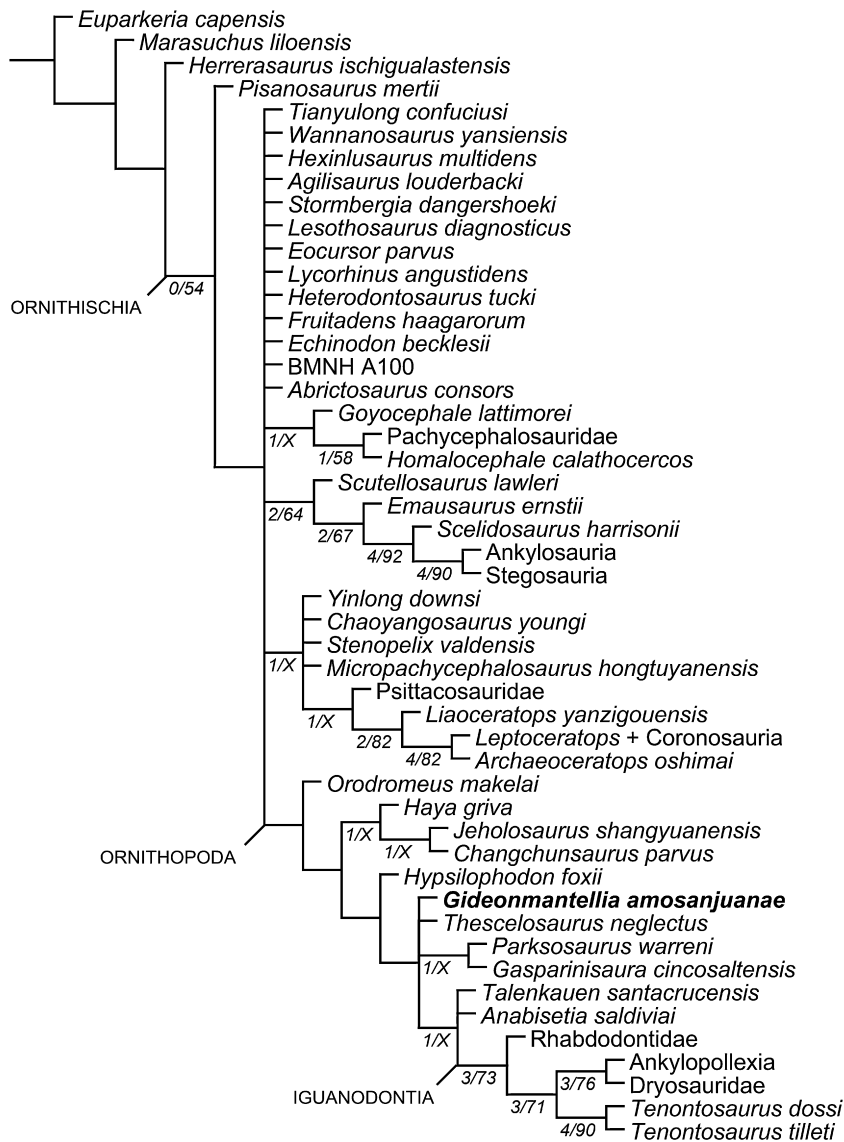


Fig. 2. Strict reduced consensus number 10 (SRC-10) of 10040 most parsimonious trees (CI=0.451, RI=0.705, RC=0.318), based on an updated version of the data set from Butler et al. (2011), modified by Makovicky et al. (2011) and with the addition of the new taxon *Gideonmantellia amosanjuananae* and the modification of character 193 (Appendix 1) on the dataset, after the a posteriori deletion of *Othnielosaurus*, *Yandusaurus* and *Zephyrosaurus*. Numbers below nodes indicate Bremer support/bootstraps values over 50% after 1000 replicates. X indicates a bootstrap recovery rate of less than 50%.

Fig. 2. Consensus réduit strict numéro 10 (SRC-10) des 10040 arbres les plus parcimonieux (CI=0.451, RI=0.705, RC=0.318), basé sur une version de l'ensemble des données de Butler et al. (2011), modifiée par Makovicky et al. (2011), avec l'addition du nouveau taxon *Gideonmantellia amosanjuananae* et la modification du caractère 193 (Annexe 1) sur l'ensemble de données, après la suppression a posteriori de *Othnielosaurus*, *Yandusaurus* et *Zephyrosaurus*. Les numéros en dessous des nœuds indiquent les valeurs du support de Bremer/bootstraps de plus de 50% après 1000 répétitions. X indique un taux de recouvrement de bootstrap inférieur à 50%.

reproducing the exact topology of the one published by Makovicky et al. (2011). None of the maximum agreement subtrees include *Gideonmantellia*, probably due to the large quantity of missing data.

In order to improve the resolution of the consensus, we calculated a strict reduced consensus, SRC (Butler and Upchurch, 2007; Wilkinson, 1994, 1995). This method allows the safe a posteriori deletion of terminal taxa in order to improve the resolution. To determine the most unstable taxa, we used the software REDCON 3.0 (Wilkinson, 2001). The software identified a profile

of twelve consensus trees, including the strict consensus and eleven SRC, which excluded one or more “wildcard taxa” to improve resolution. SRC-10 (Fig. 2) is produced after the a posteriori deletion of *Othnielosaurus*, *Yandusaurus* and *Zephyrosaurus*, all of them taxa that have proved to be problematic in other analyses (Butler et al., 2011). In this SRC, *Gideonmantellia* is placed in a polytomy with *Thescelosaurus*, the clade (*Parksosaurus*+*Gasparinisaura*) and the clade (*Talenkauen*+*Anabisetia*+*Iguanodontia*), with *Hypsilophodon* as their sister group. To analyse the robustness of the

consensus, Bremer support and bootstrap indices after 1000 replicates were calculated.

According to the phylogenetic proposal shown in SCR 10 (Fig. 2), Ornithopoda is supported by three unambiguous cranial synapomorphies (34, 61, and 62), and *Orodromeus*, the Asian clade (i.e. *Haya* + (*Jeholosaurus* + *Changchunsaurus*)) and *Hypsilophodon* are the only ornithopods more basal than *Gideonmantellia*. Taking the available material into account, the Barremian ornithopod *Hypsilophodon* and the Late Jurassic ornithischian *Othnielosaurus* – previously reported to be non-cerapodan (Butler et al., 2011) and deleted a posteriori from SCR 10 – are the only two taxa that share all the character states present in *Gideonmantellia* except character 193 (concerning to the morphology of the prepubic process). *Hypsilophodon* is differentiated from the *Gideonmantellia*-bearing clade by two cranial apomorphies (characters 23 and 109).

Within the polytomy where *Gideonmantellia* is placed, the rest of the taxa are supported by unambiguous synapomorphies. *Thescelosaurus* is distinguished by the ventral projection of the ischial peduncle of the ilium (character 177); the clade (*Parksosaurus* + *Gasparinisaura*) by the strong distal expansion of chevrons (character 144); and the clade (*Talenkauen* + *Anabisetia* + *Iguanodontia*) by the shape of the prepubic process, which is compressed mediolaterally with its dorsoventral height exceeding the mediolateral width (character 193).

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Appendix 1.

Character scorings for *G. amosanjuanae* added to the matrix of Butler et al. (2011), and modified by Makovicky et al. (2011). Character 193 has been modified, to include a new character state (4, scored for *Parksosaurus*, *Thescelosaurus* and *Gideonmantellia*). With the modification used in this paper, the character is as follows:

193. Prepubic process: 0. Compressed mediolaterally, dorsoventral height exceeds mediolateral width; 1. Rod-like, mediolateral width exceeds dorsoventral height; 2. Dorsoventrally compressed; 3. Twisted along length – dorsoventrally compressed at its base and transversely compressed distally; 4. Rod-like, twisted along length – mediolaterally compressed at its base whereas the lateral surface faces dorsally at its cranial end.

Gideonmantellia.amosanjuanae

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