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EVOLUTIONARY CONVERGENCE IN A SMALL CURSORIAL STYRACOSTERNAN ORNITHOPOD DINOSAUR FROM WESTERN EUROPE

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ABSTRACT—A metatarsal IV from a hitherto unknown endemic small-bodied styracosternan is described from uppermost Maastrichtian strata of NE Spain, part of the Ibero-Armorican island of the Late Cretaceous European Archipelago. This element is unique among the fourth metatarsals of all other ornithopods in combining the greatly elongated proportions of basally branching members of the clade with the prominent medial flange seen in other styracosternans. This specimen becomes the holotype of a new genus and species. Histological data indicate that this individual was a late subadult at the time of death, but not far from reaching somatic maturity. By analogy with the elongate metatarsals of lightly built, small-bodied cursorial ornithopods, it is likely that this animal was also capable of rapid locomotion. This is consistent with the differential distribution of intense bone remodeling in metatarsal IV, likely resulting from biomechanical stress produced during rapid hindlimb propelling. Notably, this styracosternan represents an exception to the mediportality and large body size that characterize all other members of the clade. The elongation of metatarsal IV, inferred cursoriality, and small body size constitute a case of evolutionary convergence with the distantly related non-iguanodontian ornithopods and dryosaurid and elasmarian iguanodontians. Unlike other regions of the world where, during the latest stages of the Cretaceous, the small-bodied cursorial herbivore ecological niche was represented by non-iguanodontians and non-hadrosauriforms, in the Ibero-Armorican island this niche was likely occupied by a styracosternan.

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SUPPLEMENTARY FILES—Supplementary files are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Islands have long been recognized as excellent systems for the study of evolution (Darwin, 1859). The isolation and relatively constrained geography of insular settings often impose strong selective pressures on organisms, thereby facilitating the observation and interpretation of evolutionary patterns. Examples of evolutionary phenomena documented on islands include high levels of endemism (Goodman & Benstead, 2005) and evolution of bizarre phenotypes (Csiki et al., 2010b), the occurrence of relict taxa (Millien-

Parra & Jaeger, 1999), dramatic body size changes relative to closely related taxa living in the mainland (the ‘island rule’, Foster, 1964), and changes in evolutionary rates (Millien, 2006). These insular phenomena are well documented in the vertebrate continental faunas that once populated the Late Cretaceous European Archipelago, most notably in dinosaurs. Examples of the latter include large flightless birds (Buffetaut & Angst, 2020), bizarre morphological characters in theropods (Brusatte et al., 2013) and hadrosauroids (Dalla Vecchia, 2020), and dwarfism in sauropods (Sander et al., 2006; Stein et al., 2010) and hadrosauroids (Weishampel et al., 1991; Benton et al., 2010).

Ornithopod dinosaurs form a clade representing one of the most evolutionarily successful radiations of Mesozoic vertebrates (Norman et al., 2004). These herbivores colonized every continent and left a rich fossil record spanning the middle Jurassic (Ruiz-Omeñaca et al., 2007) through the latest Cretaceous (Weishampel et al., 2003; Prieto-Márquez, 2010). One of the main evolutionary trends throughout ornithopod evolution is the progressive increase in body size (Benson et al., 2018). In particular, the earliest ornithopods were relatively small (1–2 m in length), lightly built cursorial bipeds, exemplified by *Hypsilophodon foxii* (Galton, 1974) from the Early Cretaceous of England or *Orodromeus makelai* from the Campanian of the Western

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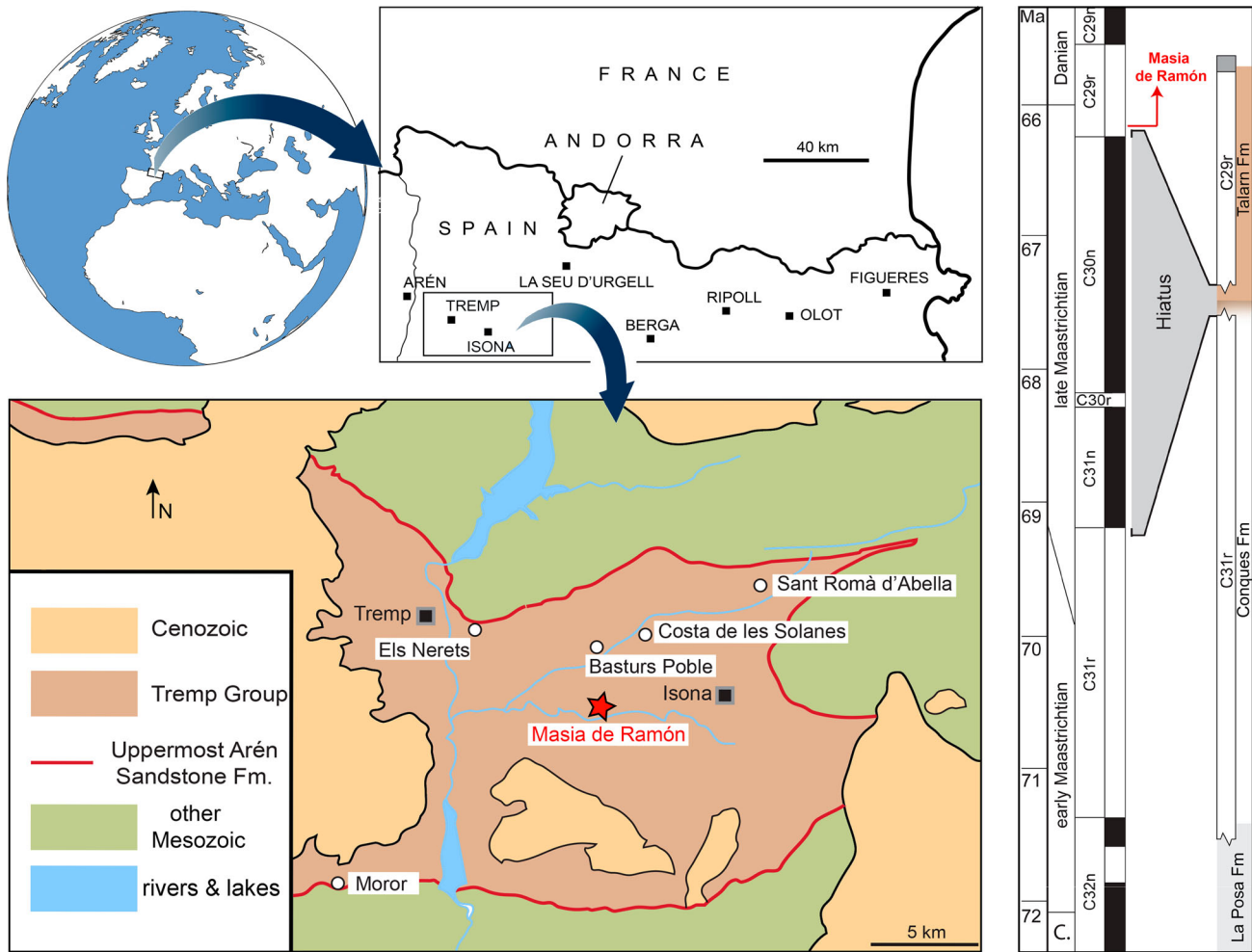


FIGURE 1. Geographic location and stratigraphic position of the type locality of *Calvarius rapidus*, Masía de Ramón. This site is within a few kilometers of major lambeosaurine localities spanning the lower to the upper Maastrichtian, such as Els Nerets, Basturs Poble, Costa de les Solanes (type locality of the lambeosaurine hadrosaurid *Adynomosaurus arcanus*), and Sant Romà d'Abella (type locality of the lambeosaurine hadrosaurid *Pararhabdodon isonensis*) (geologic map based on Fondevilla et al., 2019:fig. 1).

Interior of North America (Horner & Weishampel, 1988). With the evolution of Iguanodontia, and particularly Hadrosauriformes, ornithopods experienced a tenfold increase in body length, and at least 300-fold increase in body mass (Benson et al., 2014). As ornithopods became more massive, they acquired a mediportal mode of locomotion (Coombs, 1978).

Here, we report on a species of styracosternan iguanodontian ornithopod from the Ibero-Armorican domain of south-western Europe (Fig. 1), represented by a single and isolated, highly modified metatarsal IV (Fig. 2) nowhere to be found among ornithopods (Figs. 3–5). The relatively small body size of this dinosaur, together with the morphological attributes of the metatarsal and inferred cursoriality, indicate evolutionary, and possibly ecological, convergence with distantly related clades of non-iguanodontian and early-diverging iguanodontian ornithopods. Further, this animal represents a case of endemic small-bodied insular styracosternan with peculiar adaptations.

MATERIAL AND METHODS

Shape Analysis Using Procrustes Superimposition

We conducted geometric morphometric analyses to quantitatively expose the unique morphology of the metatarsal IV MCD-

8734 in a sample of ornithopod taxa spanning the diversity of the clade. The contour in ventral view of metatarsal IV was digitized using 10 landmarks (Fig. 6B) on photographs by means of the program tpsUtil version 1.68 (Rohlf, 2016a). The files with the landmark coordinates were created in tpsDig2 version 2.26 (Rohlf, 2016b). The Procrustes superimposition technique was then implemented in MorphoJ version 1.06d (Klingenberg, 2011). The method is based on the optimal superimposition of configurations of landmark coordinates using least-squares estimation of translation, rotation and other scaling parameters (Slice, 2007). A covariance matrix was subsequently generated and shape variability was summarized using Principal Components Analysis displayed using bivariate plots using MorphoJ (Fig. 6A, C).

Phylogenetic Analysis

The phylogenetic position of MCD-8734 was inferred via parsimony, using the taxon/character state matrix of Párraga and Prieto-Márquez (2019), which was based on the matrix of Madzia et al. (2018). We choose to infer the relationships of MCD-8734 within ornithopods because the morphology of this metatarsal IV is most similar to that of iguanodontian

ornithopods, particularly the more morphologically derived types such as hadrosaurids and other styracosternans. This primarily regards the trapezoidal distal articular surface with gently convex dorsal and concave medial and ventral margins (Fig. 4O–W), the thick prominent flange protruding from the medial surface of the metatarsal that lies nearer the proximal end of the bone (Figs. 3E–N, 4B–L), and the broad D-shaped (variably more or less crescentic) proximal articular surface. This combination of attributes is not observed in the metatarsal IV of other dinosaurian clades recorded in Upper Cretaceous strata of Europe, which include titanosaur sauropods (Le Loeuff, 1995; Sanz et al., 1999; García et al., 2010; Csiki et al., 2010a; Díez Díaz et al., 2016; Vila et al., 2022), abelisauroid (Huene, 1932; Le Loeuff & Buffetaut, 1991; Tortosa et al., 2014), alvarezsaurid (Harrison & Walker, 1975) and paravian (Antunes & Broin, 1988; Le Loeuff & Buffetaut, 1998; Allain & Taquet, 2000; Csiki et al., 2010b; Sellés et al., 2021) theropods, nodosaurid ankylosaurs (Huxley, 1867; Seeley, 1881; Pereda Suberbiola & Galton, 2001; García & Pereda Suberbiola, 2003), and early-diverging ceratopsians (Godefroit & Lambert, 2007; Ōsi, 2005; Ōsi et al., 2010).

Thus, titanosaur metatarsals IV possess shafts that are more mediolaterally constricted than those of ornithopods and lack the thick and large medial flange present in styracosternans (e.g., D’Emic et al., 2016:fig. 23; Gorscak & O’Connor, 2019:fig. 26S–U). Further, MCD-8734 is too gracile and elongate to belong to a titanosaur. Within theropods, paravians display metatarsals IV that are even more elongate (e.g., *Troodon formosus* MOR 553S, or *Deinonychus antirrhopus*, Ostrom, 1969:fig. 73) than in MCD-8734 and other ornithopods. When observed, the medial flange is less prominent and much longer, extending along most of the length of the metatarsal’s shaft (e.g., *Velociraptor mongoliensis*, Norell & Makovicky, 1999: fig. 16); in other instances (e.g., *Troodon formosus* MOR 553S) no medial flange is seen. Similarly, alvarezsaurids display metatarsals IV that exhibit even more extremely elongate proportions than MCD-8734 and also lack a medial flange (e.g., the holotype of *Kolghuva*, Turner et al., 2009:fig. 2). Relatively large abelisauroids, exemplified by *Majungasaurus crenatissimus* (Carrano, 2007:fig. 10), display a metatarsal IV that is overall more curved laterally and with a medial flange that is also much wider than in styracosternans, extending along a more extensive segment of the shaft. In other abelisauroids, such as the small-sized *Masiakasaurus knopfleri*, no medial flange is observed in metatarsal IV and the bone displays much elongate proportions than the metatarsal IV of *Calvarius rapidus* (Carrano et al., 2002:fig. 20). The distal surface in the metatarsal IV of *M. knopfleri* (Carrano et al., 2002:fig. 20) and also that of paravians such as *T. formosus* (e.g., *T. formosus* MOR 553S) also differs from that of ornithopods, particularly styracosternans, in being more triangular than trapezoidal.

Among ornithischians, the metatarsal IV of basally branching ceratopsians such as *Yinlong downsi* (Han et al., 2018:fig. 14B) and even that of some basally branching coronosaurians such as *Protoceratops andrewsi* (Brown & Schlaikjer, 1940:fig. 33) may be similar in length/width proportions to early-diverging ornithopods and *Calvarius rapidus*, but the former do not show the prominent and thick medial flange of MCD-8734 and other styracosternan ornithopods. Finally, the metatarsal IV of nodosaurid ankylosaurs is proportionately shorter, nearly straight, and more constricted mediolaterally along the central shaft, with a more hourglass shape in dorsal view (e.g., right pes of *Edmontonia rugosidens*, AMNH 5665) than in ornithopods.

The taxonomic sample included *Lesothosaurus diagnosticus* as outgroup taxon and 55 ornithopod species spanning the morphological and taxonomic diversity of the clade. The data set consisted of 144 discrete morphological characters (94 cranial and 50 postcranial; Supplementary File 1) of which 134 are from Madzia et al. (2018) and six other characters are from Párraga

and Prieto-Márquez (2019). The NEXUS and TNT files of the data set are provided as Supplementary Files 2 and 3, respectively. We added four new discrete characters capturing the main morphological variation present in the metatarsal IV of ornithopod taxa (Supplementary File 1). Multistate characters containing states that are not mutually exclusive, following a natural morphocline, were ordered; these ordered characters accounted for 26 of the 144 characters. A traditional search of 10,000 replicates using random addition sequences, with branch swapping using tree bisection reconnection (TBR) holding 10 trees per replicate was performed in TNT version 1.5 (Goloboff & Catalano, 2016). After the first round, a second round of TBR was performed with trees from RAM.

Bremer support (Bremer, 1988) was assessed by computing decay indices (Donoghue et al., 1992) using TNT (Fig. 7). Bootstrap proportions (Felsenstein 1985) were also calculated using TNT, setting the analysis for 5,000 replicates using heuristic searches, in which each search was conducted using random additional sequences with branch-swapping by subtree pruning and regrafting and 25 replicates (Fig. 7).

Osteohistological Analysis

We sampled the mid-shaft of MCD-8734 (Figs. 2E, 8A). The cut surface was exposed using a Buehler Isomet low speed saw and subsequently polished on a glass sheet coated with carborundum powder, using a decreasing particle size of 600, 800, and 1000 grit. The bone sample was fixed to a frosted glass slide using ultraviolet curing glue Loctite 358. The ground section was then prepared with a Buehler PetroThin diamond saw to a final thickness of approximately 100 μm . The thin section was polished with 800 and 1200 grit carborundum gradients. The slice was dehydrated through a graded series of alcohol baths, cleared in Histo-Clear II for 5 minutes and finally mounted in a DPX mounting medium. Finally, the thin section was observed under transmitted and polarized light using a petrographic microscope Nikon® Eclipse E400 POL connected to a digital camera Nikon® DS-FI3. The paleohistological nomenclature used in this study follows Słowiak et al. (2020) and Woodward et al. (2015).

Institutional Abbreviations—**AEHM**, Amur Natural History Museum, Blagoveschensk, Russia; **AMNH FARB**, American Museum of Natural History, Fossil Amphibians and Reptiles collection, New York, NY, U.S.A.; **ANSP**, Academy of Natural Sciences of Philadelphia, Philadelphia, PA, U.S.A.; **CM**, Carnegie Museum of Natural History, Pittsburgh, PA, U.S.A.; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **CPC**, Colección Paleontológica de Coahuila (Paleontological Collection of Coahuila), Saltillo, Mexico; **CUST**, Changchun University of Sciences and Technology, Changchun, China; **GDF**, field acronym for the Gadofaoua locality, Niger; casts of this material housed at the Muséum national d’Histoire naturelle, Paris, France, were used in this study; **IGM**, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People’s Republic of China; **JLUM**, Jilin University Geological Museum, Changchun, China; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, CA, U.S.A.; **MCD**, Museo de la Conca Dellà, Isona, Spain; **MOR**, Museum of the Rockies, Bozeman, MT, U.S.A.; **NHMUK**, Natural History Museum, London, U.K.; **MB**, Naturkundemuseum, Berlin, Germany; **NMV**, National Museum of Victoria, Melbourne, Australia; **PU**, Princeton University, Princeton, NJ, U.S.A.; **ROM**, Royal Ontario Museum, Toronto, Canada; **SHN**, Sociedade de Historia Natural, Torres Vedras, Portugal; **TCMI**, The Children’s Museum of Indianapolis, Indianapolis, IN, U.S.A.; **UTEP**, Centennial Museum at the University of Texas El Paso, El Paso, TX, U.S.A.; **YPM-PU**, Yale Peabody Museum of Natural History, Princeton University collection, New Haven, CT,

U.S.A.; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
 ORNITHISCHIA Seeley, 1887
 ORNITHOPODA Marsh, 1881
 IGUANODONTIA Baur, 1891
 STYRACOSTERNA Sereno, 1986
CALVARIUS RAPIDUS, gen. et sp. nov.
 (Figs. 2 and 7)

Type [and Only] Species—*Calvarius rapidus*.

Holotype and Only Known Material—MCD-8734, a left metatarsal IV.

Etymology—The genus name refers to a nearby hill known as Serrat del Calvari. It is also a derivation of the Catalan ‘calvari’ (‘suffering’), alluding to the chronostratigraphic proximity of MCD-8734 to the K-Pg extinction event. The species name means ‘quick’ or ‘fast’ in Latin, referring to the likely cursorial adaptations of this animal.

Locality, Horizon, and Age—MCD-8734 comes from the Masia de Ramón site, which is located 2.6 km south of Figuerola d’Orcau, a small village near the municipality of Isona i Conca Dellà (Pallars Jussà county, Lleida province, north-western Catalonia; Fig. 1). This locality was discovered in 2019 by a team of paleontologists from the MCD and the Institut Català de Paleontologia Miquel Crusafont while prospecting for fossils between the hills of Les Masies and Lo Riu, in the central region of the Tremp Basin (south-central Pyrenees of north-eastern Spain). The stratigraphic horizon at Masia de Ramón that yielded MCD-8734 crops out at the top of the cliffs of the northern bank of the Conques River. Within this fossiliferous horizon, MCD-8734 was found lying on top of a 50-cm-thick grayish marl layer and underneath a 2.5-meter-thick lenticular coarse sandstone channel, which are all part of a 10-m-thick sedimentary sequence related to the development of a fluvial meandering channel (Vila et al., 2013). Masia de Ramón falls within the upper part of the fluvial Talarn Formation of the Tremp Group and isotopic, magnetostratigraphic, and biochronological calibrations indicate that the locality correlates with the middle part of the C29r magnetochron (latest Maastrichtian) (Vila et al., 2013; Fontdevilla et al., 2019). Notably, Masia de Ramón occurs 25 m below the local K-Pg boundary, thus placing it within the last 100,000 years of the Maastrichtian (Fontdevilla et al., 2019). Apart from MCD-8734, Masia de Ramón only yielded a crocodylian vertebra and various unidentified bone fragments that were found invading the base of the sandstone channel, suggesting the allochthonous origin of these remains and the type specimen of *Calvarius rapidus*.

Diagnosis—Styracosternan iguanodontian ornithopod dinosaur having a metatarsal IV with the following autapomorphies: maximum length/mediolateral width at mid-length ratio greater than nine; segment distal to medial flange longer than combined length of medial flange and proximal extent of metatarsal; prominent medial flange that is dorsoplantarly compressed and with a prominent plantar component in its medioplantar projection; and relatively enlarged medially projected dorsomedial corner of distal surface.

RESULTS

Osteological Description

MCD-8734 is nearly completely preserved, missing only parts of the lateral, medial, and plantar margins of the proximal end (Fig. 2). It is 155.8 mm in length and 17.1 mm wide mediolaterally

at mid-shaft. These dimensions indicate a remarkably slender and elongate metatarsal, more than nine times longer than it is wide at mid-length. This proportions are closer to those exhibited by the metatarsal IV of basally branching ornithischians such as *Hypsilophodon foxii* (Galton, 1974) or *Haya griva* (Makovicky et al., 2011), as well as early-diverging Dryomorpha such as *Dysalotosaurus lettowvorbecki* (Janensch, 1955), but are unlike the stout metatarsals of styracosternan iguanodontians such as *Iguanodon bernissartensis* (Norman, 1980), *Hypselospinus fittoni* (Norman, 2015), *Bactrosaurus johnsoni* (Prieto-Márquez, 2011a), or *Gryposaurus notabilis* (Parks, 1920) (Supplementary File 1 and 2). The great length/width ratio of MCD-8734 is primarily caused by elongation of the segment distal to the medial flange. Specifically, this segment is longer than the combined length of the flange and the proximal region of the metatarsal (Fig. 3Q), whereas in other styracosternans the segment distal to the flange is shorter than the combined length of the flange and proximal region (Fig. 3O, P). The shaft of MCD-8734 is thinnest at mid-length, from which it gradually expands near both the proximal and distal ends. The latter are substantially much more expanded dorsoplantarly than mediolaterally.

Enough is preserved of the proximal facet to observe the crescentic profile typically present among ornithopods (e.g., *D. lettowvorbecki*, MBR.1409; *Mantellisaurus atherfieldensis*, NMHUK R11521; *Hypacrosaurus altispinus*, AMNH FARB 5272). However, unlike earlier diverging ornithopods such as *Orodromeus makelai* (e.g., PU 23246) and dryomorphans such as *D. lettowvorbecki* (e.g., MBR.1409), the crescentic proximal profile of MCD-8734 is taller than wide, as in the morphologically more derived iguanodontians such as *Hypselospinus fittoni* (e.g., NHMUK R1834). The distal surface of MCD-8734 displays a medially skewed trapezoidal profile, which is also typically observed in ornithopods. However, in early-diverging ornithischians and early-diverging dryomorphans the medial and lateral margins of the distal facet are nearly straight (e.g., *D. lettowvorbecki*, MBR.1409; Fig. 4M). In contrast, in styracosternan iguanodontians, including MCD-8734 (Fig. 4W), the medial or lateral margins (both in most taxa) of the distal facet are strongly concave (Fig. 4O–W). The latter are associated to deeper concavities in the medial (e.g., Fig. 4B–L) and lateral surfaces of the distal ends of these taxa. In this regard, MCD-8734 is unique among ornithopods in having a distal end with an even more excavated medial surface caused by a medial projection of its dorsomedial corner (Fig. 4W).

Unlike the thick medial flanges of the metatarsal IV of styracosternan iguanodontians, in MCD-8734 the medial flange is strongly compressed dorsoplantarly. Furthermore, while the medial flange is also only slightly projected plantarly in styracosternan iguanodontians, in MCD-8734 the flange is strongly projected plantarly as well as medially (Fig. 4L). This flange is absent in non-iguanodontian ornithopods such as *Hypsilophodon foxii* (Fig. 3A) or *Jeholosaurus shangyuanensis* (Han et al., 2011), and early-diverging Dryomorpha (Galton, 1977, 1981) (see also Figs. 3C, 4A). In these forms the medial surface of the shaft exhibits a gentle convexity, instead of the flange present in styracosternan iguanodontians (Fig. 3G–N). The dorsal and plantar surfaces of the flange in MCD-8734 are deeply carved with longitudinal striations (Fig. 2).

Phylogenetic Relationships of *Calvarius rapidus*

The phylogenetic analysis resulted in 940 most parsimonious trees (Supplementary File 4) of 486 steps each (C.I. = 0.25, R.I. = 0.52), a best score that was hit 878 times out of the 10,000 replicates. MCD-8734 was positioned within styracosternan iguanodontian ornithopods, forming a large polytomy with most of the included members of this clade, except *Uteodon aphanoeetes* and *Cumnoria prestwichii* (Fig. 7). MCD-8734 shares with

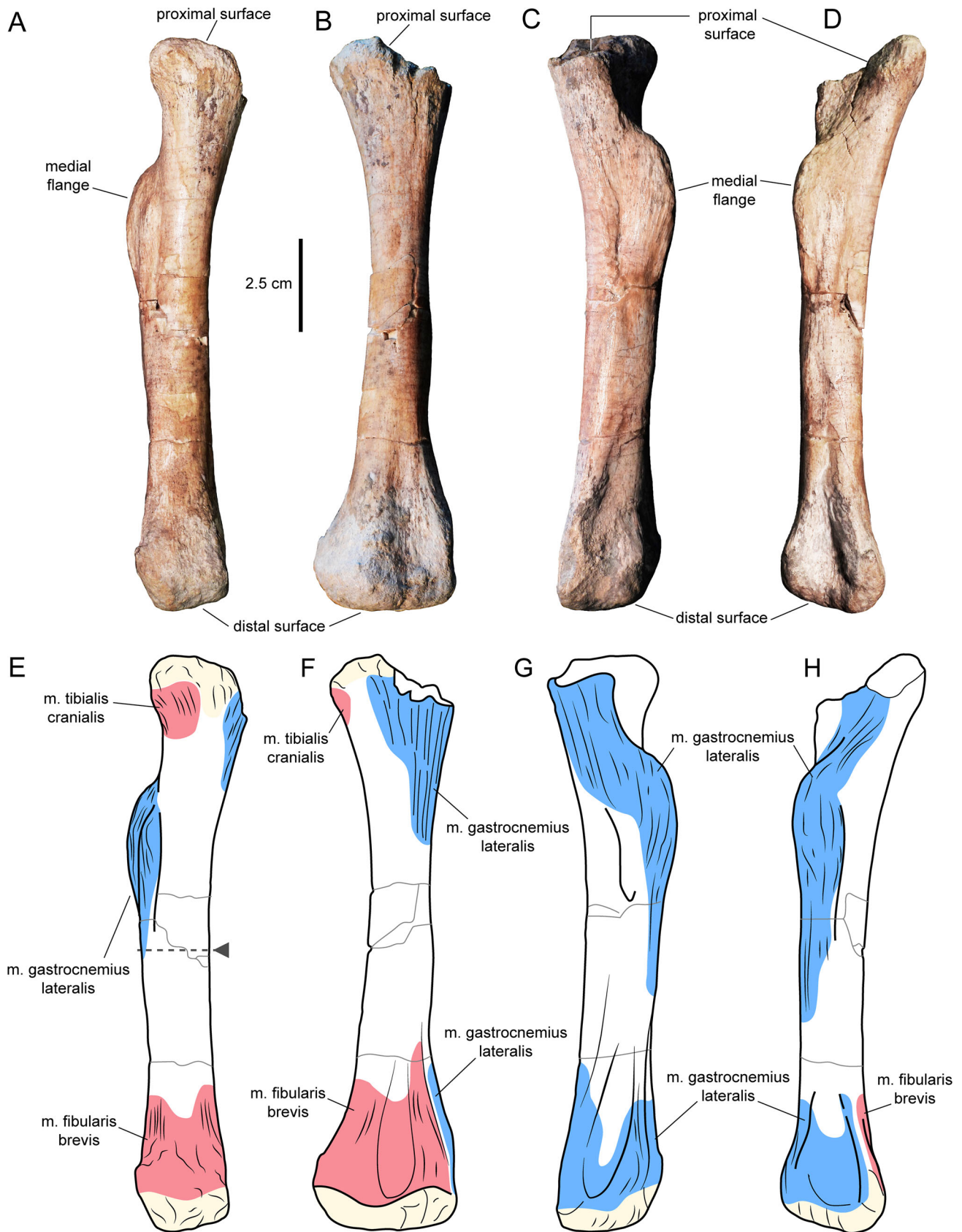


FIGURE 2. The holotype left metatarsal IV (MCD-8734) of *Calvarius rapidus* in **A**, dorsal, **B**, lateral, **C**, plantar, and **D**, medial views. Reconstructed myological map of MCD-8734 in **E**, dorsal, **F**, lateral, **G**, plantar, and **H**, medial views. Insertion areas of flexor and extensor muscles of the ankle joint are also indicated. Areas of insertion of articular cartilages are indicated in yellow. The transverse discontinuous line and arrowhead at mid-shaft in (**E**) indicate where the bone was thin sectioned for the histomorphology shown in Figure 7.



FIGURE 3. Plantar and dorsal views of a sample of ornithomimid metatarsals IV. **A**, *Hypsilophodon foxii*, NHMUK R196 (reversed); **B**, *Haya griva* IGM 100/2013 (reversed); **C**, *Dysalotosaurus lettowvorbecki* MB.R.1409; **D**, *Hypselospinus fittoni* NHMUK R1834 (reversed); **E**, cf. *Iguanodon bernissartensis* NHMUK R28645 (reversed); **F**, *Mantellisaurus atherfieldensis* NMHUK R11521; **G**, *Gilmoreosaurus mongoliensis*, AMNH FARB 30756 (reversed); **H**, *Gryposaurus notabilis* AMNH FARB 5350; **I**, *Edmontosaurus annectens* LACM 23502 (reversed); **J**, *Maiasaura peeblesorum* ROM 44770; **K**, *Hypacrosaurus stebingeri*, MOR 548 (neonate); **L**, *H. altispinus*, AMNH FARB 5272; **M**, *Adynomosaurus arcanus*, MCD-7137; **N**, *Calvarijs rapidus* MCD-8734; **O**, *Bactrosaurus johnsoni*, AMNH FARB 6553; **P**, *G. notabilis*, AMNH FARB 5350; **Q**, MCD-8734, MCD-8734. The metatarsals in **A** through **N** are shown in plantar view, whereas those in **O** through **Q** appear in dorsal view. **Abbreviations** in **O** through **Q**: **dsfl**, length of the segment distal to the medial flange; **fl**, length of the medial flange; **pxfl**, length of the segment proximal to the medial flange. Arrows point to the medial flange. All scale bars equal 2.5 cm.

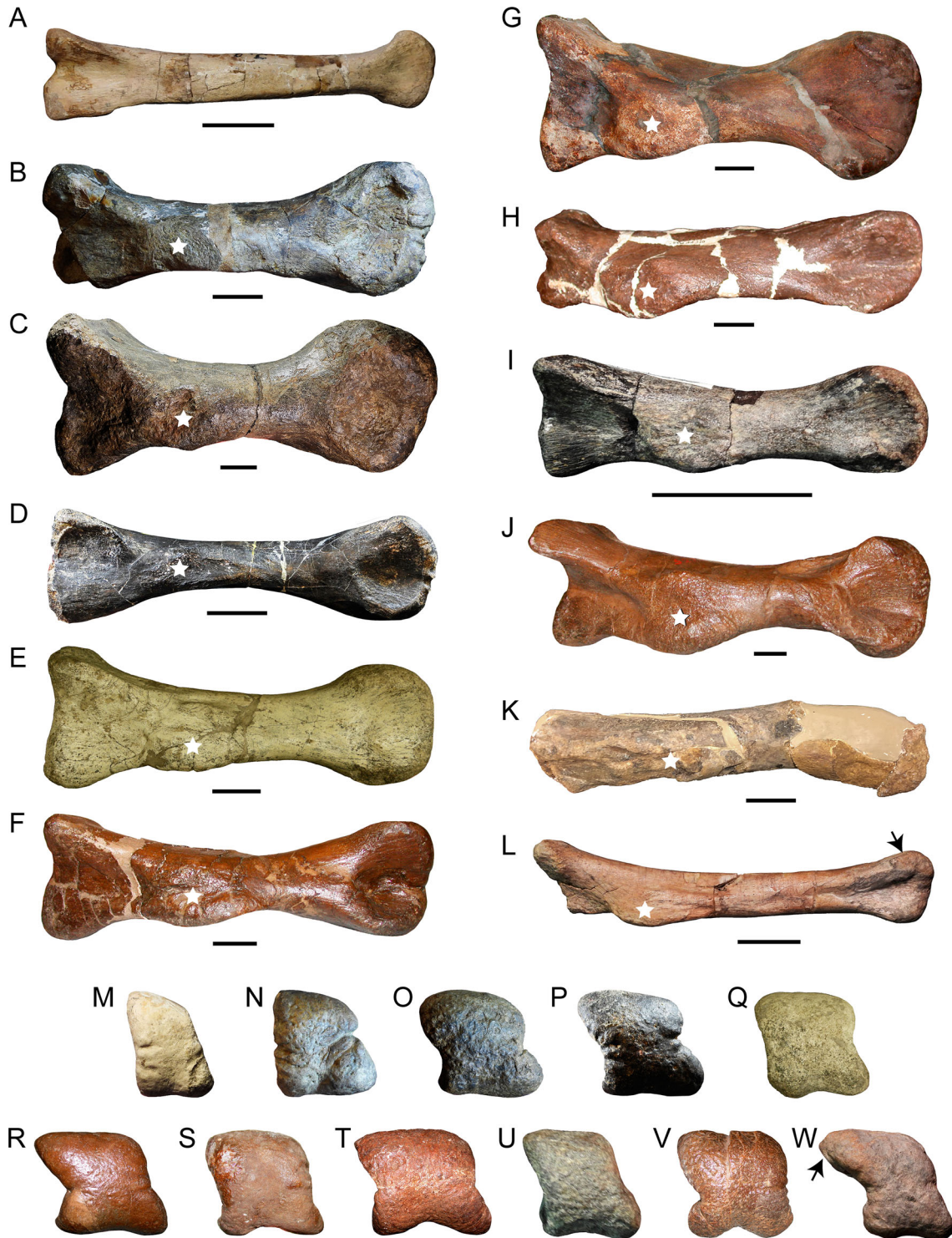


FIGURE 4. Medial and distal views of a sample of ornithopod metatarsals IV. **A**, *Dysalotosaurus lettowvorbecki*, MB.R.1409, left medial view; **B**, *Hypselospinus fittoni*, NHMUK R1834, right medial view (reversed); **C**, cf. *Iguanodon bernissartensis*, NHMUK R28645, right medial view (reversed); **D**, *Mantellisaurus atherfieldensis*, NMHUK R11521, left medial view; **E**, *Gilmoreosaurus mongoliensis*, AMNH FARB 30756, right medial view (reversed); **F**, *Gryposaurus notabilis*, AMNH FARB 5350, left medial view; **G**, *Edmontosaurus annectens*, LACM 23502, right medial view (reversed); **H**, *Maiasaura peeblesorum*, ROM 44770, left medial view; **I**, *Hypacrosaurus stebingeri*, MOR 548, left medial view (neonate); **J**, *Hypacrosaurus altispinus*, AMNH FARB 5272, left medial view; **K**, *Adynomosaurus arcanus*, MCD-7137, left medial view; **L**, *Calvarius rapidus* MCD-8734, left medial view; **M**, *D. lettowvorbecki*, MB.R.1409, distal view; **N**, *H. fittoni*, NHMUK R1834, distal view (reversed); **O**, cf. *I. bernissartensis*, NHMUK R28645, distal view (reversed); **P**, *M. atherfieldensis*, NMHUK R11521, distal view; **Q**, *G. mongoliensis*, AMNH FARB 30756, distal view (reversed); **R**, *G. notabilis*, AMNH FARB 5350, distal view; **S**, *E. annectens*, LACM 23502, distal view (reversed); **T**, *M. peeblesorum*, ROM 44770, distal view; **U**, *H. stebingeri*, MOR 548, distal view; **V**, *H. altispinus*, AMNH FARB 5272, distal view; **W**, MCD-8734, distal view. Stars indicate the medial flanges; the black arrows point to the distinctive prominent dorsal mediiodistal flange. Scale bars equal 2.5 cm.

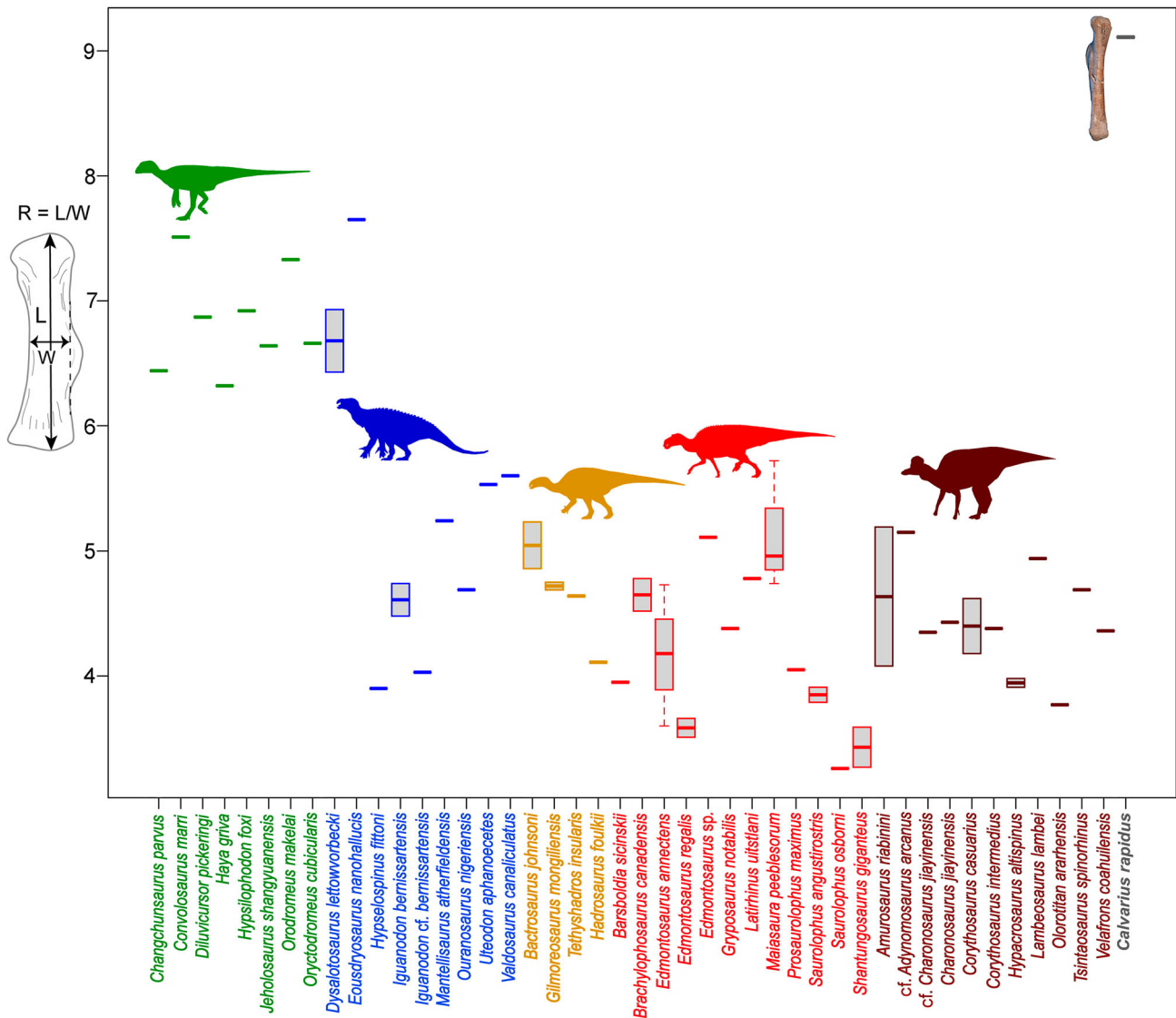


FIGURE 5. Metatarsal IV length/width ratios from a sample of ornithopod taxa. The silhouettes illustrating the different groups were downloaded from <http://phylopic.org> and drawn by Mathew Wedel (<https://creativecommons.org/licenses/by/3.0/>), Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>), Pete Buchholz (<https://creativecommons.org/licenses/by-sa/3.0/>), Scott Hartman (<https://creativecommons.org/licenses/by-nc-sa/3.0/>), and Craig Dylke (<https://creativecommons.org/publicdomain/zero/1.0/>). The silhouettes indicate, from left to right: non-iguanodontian ornithopods, non-hadrosauroid iguanodontians, non-saurolophid hadrosauroids, saurolophine and lambeosaurine hadrosaurids. **Abbreviations:** L, maximum proximal length of metatarsal IV; **R**, ratio L/W; **W**, mid-length mediolateral width of metatarsal IV (excluding the medial flange). Specimens and measurements are in Supplementary File 5.

Camptosaurus dispar and styracosternans a metatarsal IV with medial flange and a distal surface with a trapezoidal profile that is at least as broad dorsally as it is ventrally.

Histomorphological Description

The transverse thin-section from the mid-shaft of MCD-8734 exhibits a moderately expanded oval medullary cavity that is, however, poorly defined due to recrystallized calcite and fragmented cancellous bone (Fig. 8A, B). No evidence of endosteal lamellar bone is observed surrounding the medullary cavity. The cortical bone is primarily composed of a well-vascularized fibrolamellar tissue, although reticulate and longitudinally oriented primary vascular canals are also observed throughout the cortex (Fig. 8E, F). Seven lines of arrested growth (LAGs)

can be seen in the cortex, which decrease in thickness outwards (Fig. 8E, F). While the growth sequence in the inner and mid-cortex is composed of primary laminar and reticulate fibrolamellar tissue, the periosteal sequence shows more abundant longitudinal fibrolamellar tissue (Fig. 8F). Secondary osteons are abundant in the deep cortex, which are developed into two to three different generations of heterometric osteons (Fig. 8B). The degree of bone remodeling, and thus the number of secondary osteons, rapidly decreases outwards, although scattered secondary osteons can reach the outer cortex.

Remarkable differences in the aforementioned histological configuration are observed in two regions of the sample (Fig. 8B, C, D). Those areas are characterized by the extensive development of Haversian tissue, resulting in an extreme bone remodeling that obliterates any trace of the primary bone structure. In those

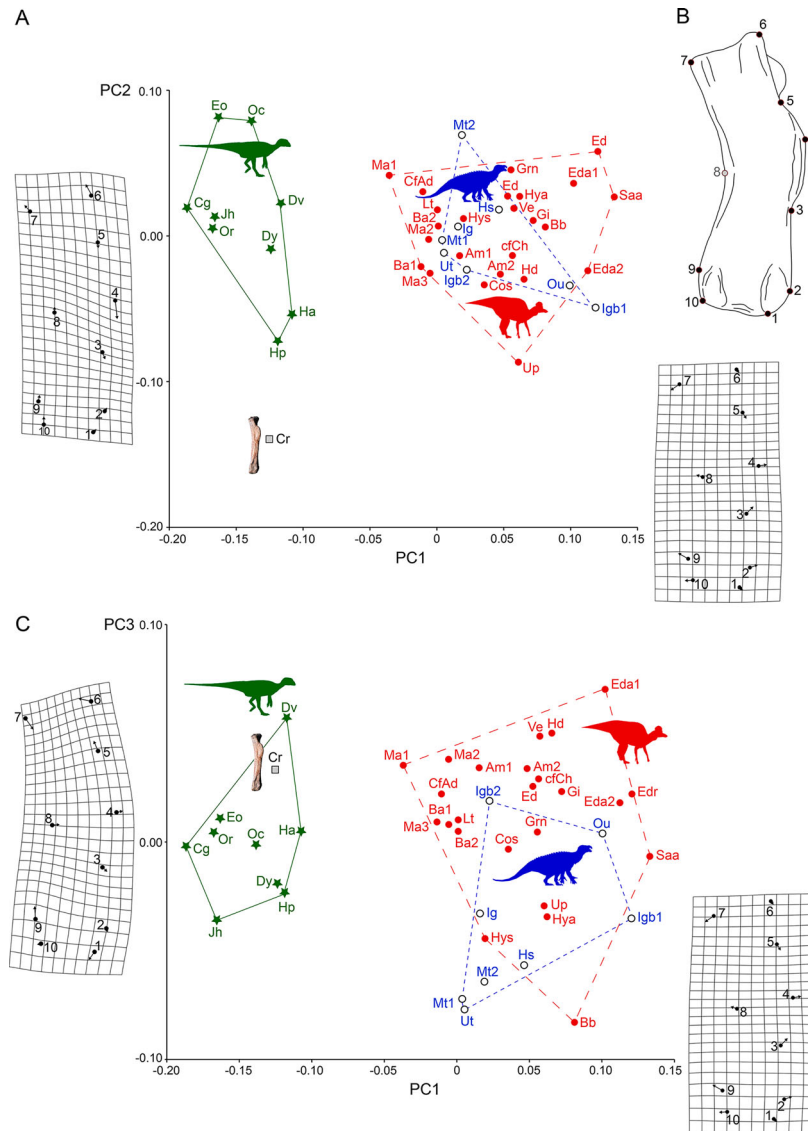


FIGURE 6. Results of the Procrustes superimposition analysis of the ventral outline of metatarsal IV for a sample of ornithopod dinosaurs. **A**, PCA bivariate plot summarizing the results of the analysis for PC1 and PC2. **B**, drawing of an idealized styracosternan metatarsal IV in ventral view, showing the location of the landmarks. **C**, PCA bivariate plot for PC1 and PC3. **Abbreviations in A and C** are as follows: **Am1**, *Amurosaurus riabinini* cast of AEHM unknown catalog number (smaller individual in the *Amurosaurus* sample, likely subadult); **Am2**, *Amurosaurus riabinini* cast of AEHM unknown catalog number (specimen larger than Am1, uncertain ontogenetic stage); **Ba1**, *Bactrosaurus johnsoni* AMNH FARB 6577 (juvenile; Prieto-Márquez 2011a); **Ba2**, *B. johnsoni* AMNH FARB 6553 (largest individual in the *Bactrosaurus* sample, uncertain ontogenetic stage; Prieto-Márquez 2011a); **Bb**, *Barsboldia sicinskii* ZPAL MgD-I 110 (remarkably large specimen, likely adult; Prieto-Márquez 2011b); **cfAd**, cf. *Adynomosaurus arcanus* MCD-7396 (unpublished, likely subadult given that it is substantially smaller than the holotype; Prieto-Márquez et al., 2019); **cfCh**, cf. *Charonosaurus jiyinensis* CUST JI1212 (uncertain ontogenetic stage); **Cg**, *Changchunsaurus parvus* JLUM L0403-j-Zn2 (this specimen might be a subadult; Butler et al., 2011); **Cos**, *Corythosaurus casuaris* CMN 8676 (subadult; Bell 2014); **Cr**, *Calvarius rapidus* MCD-8734 (subadult); **Dv**, *Diluvicursor pickeringi* NMV P221080 (uncertain ontogenetic stage); **Dy**, *Dysalotosaurus lettowvorbecki* M.B.R. 1409 (uncertain ontogenetic stage); **Ed**, *Edmontosaurus* sp. AMNH FARB 5863 (uncertain ontogenetic stage); **Eda1**, *E. annectens* LACM 23504 (subadult; Prieto-Márquez 2014); **Eda2**, *E. annectens* LACM 23502 (likely adult; Prieto-Márquez 2014); **Edr**, *E. regalis* CMN 2289 (adult; Mori et al., 2016); **Eo**, *Eousdryosaurus nanohallucis* SHN(JJS)-170 (uncertain ontogenetic stage); **Gi**, *Gilmoresaurus mongoliensis* AMNH FARB 30756 (uncertain ontogenetic stage); **Gm**, *Gryposaurus notabilis* AMNH FARB 5350 (uncertain ontogenetic stage); **Ha**, *Haya griva* IGM 100/2013 (uncertain ontogenetic stage); **Hd**, *Hadrosaurus foulkii* ANSP 10005 (possibly adult; Prieto-Márquez et al., 2006); **Hp**, *Hypsilophodon foxii* NHMUK R196 (subadult; Bakker & Carpenter 1990); **Hs**, *Hypselospinus fittoni* HMUK R1834 (uncertain ontogenetic stage); **Hya**, *Hypacrosaurus altispinus* AMNH FARB 5272 (uncertain ontogenetic stage); **Hys**, *H. stebingeri* MOR 548 (nestling; Brink et al., 2011); **Ig**, *Iguanodon* cf. *bernissartensis* NHMUK R2536 (uncertain ontogenetic stage); **Igb1**, *I. bernissartensis* NHMUK R28645 (uncertain ontogenetic stage); **Igb2**, *I. bernissartensis* NHMUK R132 (uncertain ontogenetic stage); **Jh**, *Jeholosaurus shangyuanensis* IVPP V15939 (uncertain ontogenetic stage); **Lt**, *Latirhinus uitsilani* IGM 6583 (uncertain ontogenetic stage); **Ma1**, *Maiasaura peeblesorum* YPM-PU 22400 (possibly adult; Prieto-Márquez & Guenther 2018); **Ma2**, *Ma. peeblesorum* TCM1 2001.89.2 (possibly adult; Prieto-Márquez & Guenther 2018); **Ma3**, *Ma. peeblesorum* ROM 44770 (possibly adult; Prieto-Márquez & Guenther 2018); **Mt1**, *Mantellisaurus atherfieldensis* NHMUK R11521 (uncertain ontogenetic stage); **Mt2**, *Mt. atherfieldensis* NHMUK R1829 (uncertain ontogenetic stage); **Oc**, *Oryctodromeus cubicularis* MOR 1642 (adult; Krumeacker 2017); **Or**, *Orodromeus makelai* PU 23246 (uncertain ontogenetic stage); **Ou**, *Ouranosaurus nigeriensis* GDF 300 (subadult; Bertozzo et al., 2017); **Saa**, *Saurolophus angustirostris* ZPAL MgD-I 157 (adult; Maryanska & Osmólska 1984); **Up**, UTEP P.37.7.226-227; **Ut**, *Uteodon aphanoeetes* CM 11337 (uncertain ontogenetic stage); **Ve**, *Velafrons coahuilensis* CPC-59 (subadult; Gates et al., 2007). In the **A** and **C** PCA plots, stars represent non-styracosternan ornithopods, circles indicate styracosternan ornithopods (empty circles for non-hadrosauroid styracosternans and solid circles for hadrosauroids), and *Calvarius rapidus* is represented by a gray square. Silhouettes were downloaded from <http://phylopic.org> and drawn by Mathew Wedel (<https://creativecommons.org/licenses/by/3.0/>), Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>), Pete Buchholz (<https://creativecommons.org/licenses/by-sa/3.0/>), Scott Hartman (<https://creativecommons.org/licenses/by-nc-sa/3.0/>), and Craig Dylke (<https://creativecommons.org/publicdomain/zero/1.0/>).

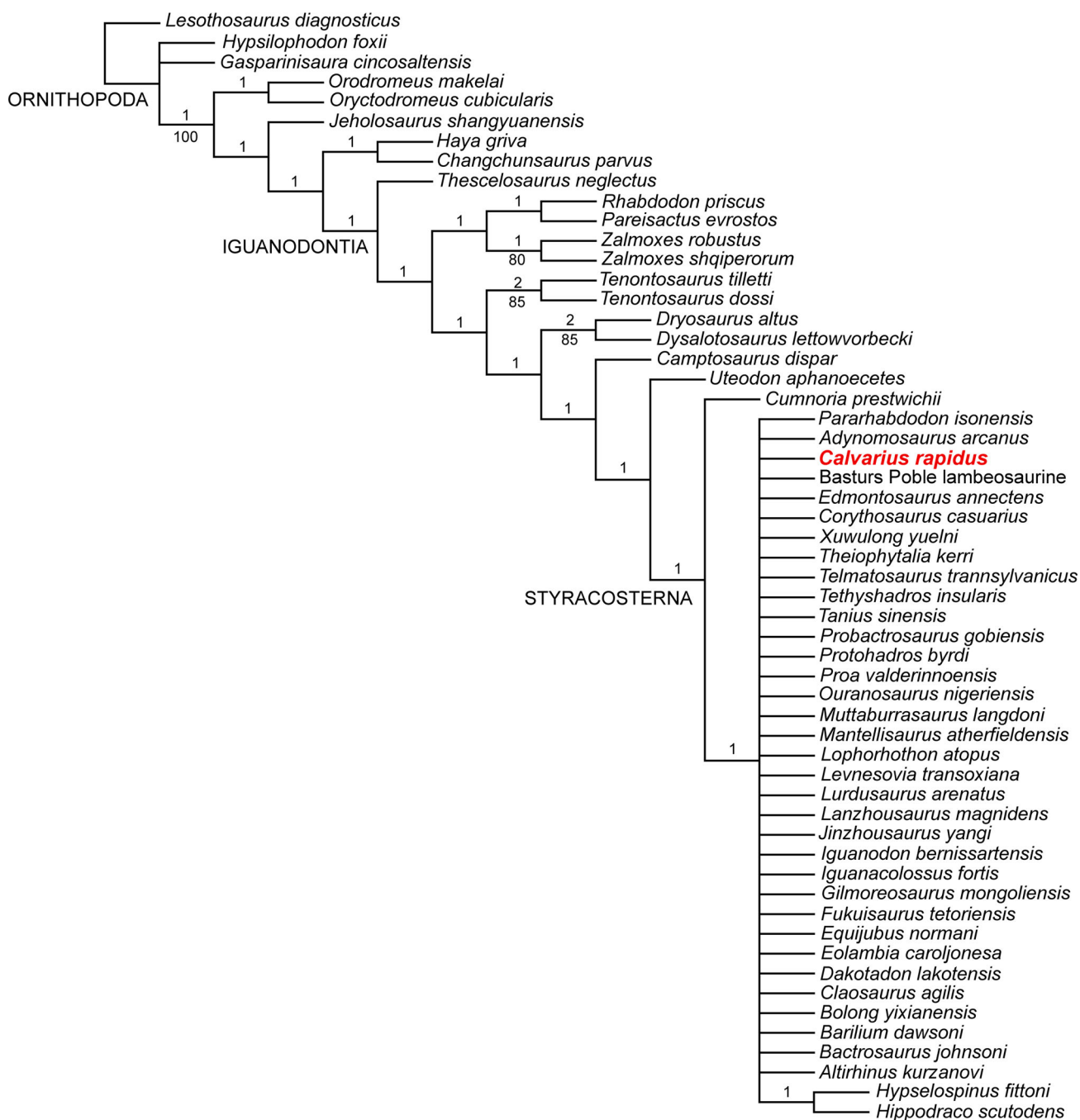


FIGURE 7. Strict consensus tree of the 940 most parsimonious trees resulting from the parsimony phylogenetic analysis of 55 ornithopod species, recovering *Calvarius rapidus* within styracosternan iguanodontian ornithopods. Numbers above branches are Decay indices (Bremer support), whereas those below indicate Bootstrap proportions (only absolute frequencies of 50% and above are reported).

regions, secondary osteons of different size and shape overlap each other in, at least, five consecutive generations (Fig. 8D). No evidence of an external fundamental system (EFS) is observed.

DISCUSSION

Cursoriality

Animals capable of rapid locomotion typically display, among other attributes, limb bones that are long relative to body size (Christiansen, 2002; Persons & Currie, 2014). Relevant here is

the metatarsus/femur ratio ('cursoriality index'), that has been used as a reflection of the elongation of the distal elements of the hindlimb in relation to the length of the proximal elements and as an indicator of cursorial abilities (Garland & Janis, 1993). Within Ornithopoda, non-iguanodontian ornithopods and dryosaurid iguanodontians exhibit the more elongate metatarsals (Figs. 3–6A, C; Supplementary File 5) and the highest metatarsal IV length/femur length ratios (Galton 1971) (Fig. S1 in Supplementary File 6, and Supplementary File 7). Although the femur is unknown in *Calvarius rapidus*, the elongation of its metatarsal IV is even greater than in the proportionately

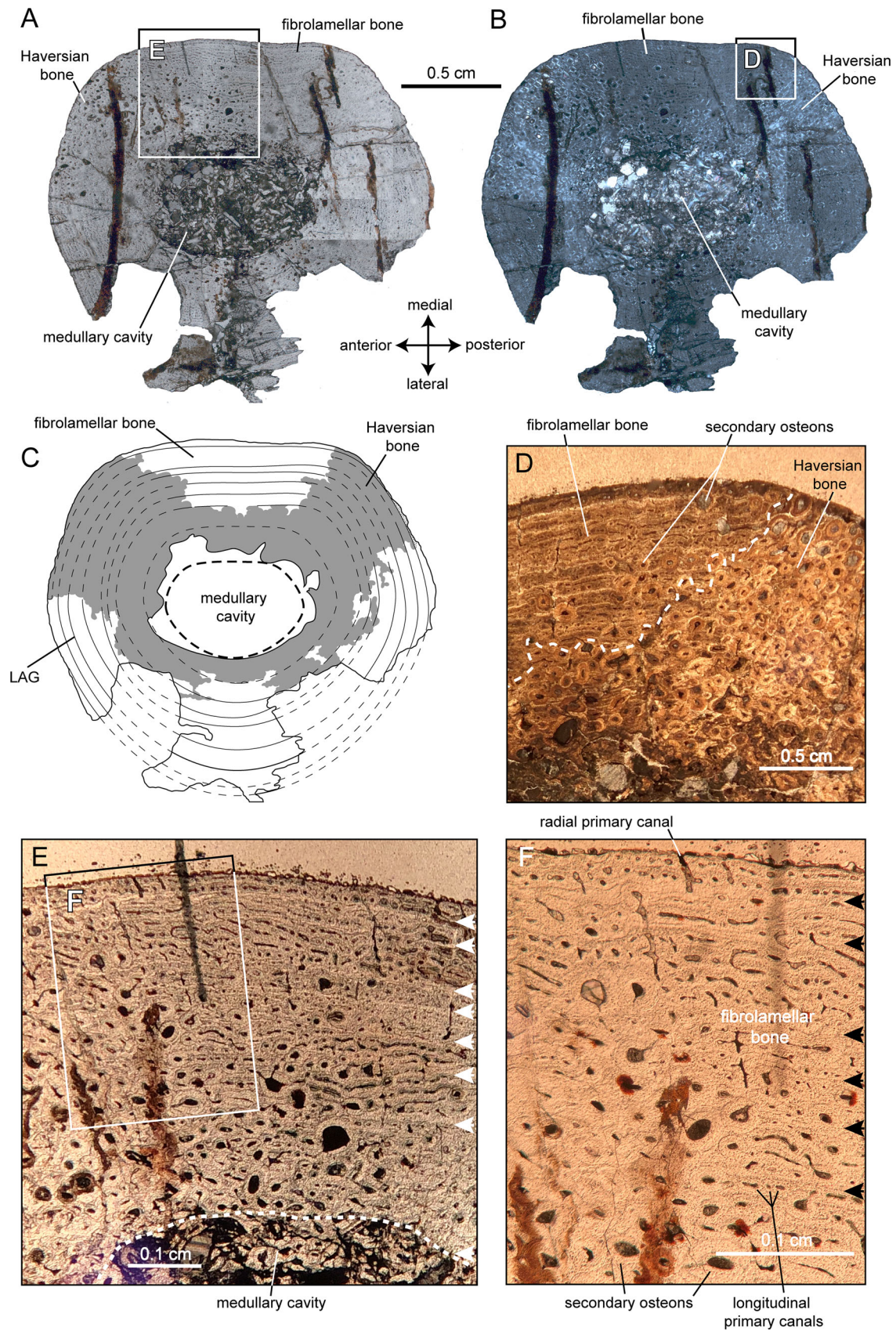


FIGURE 8. Histomorphology of the holotype left metatarsal IV (MCD-8734) of *Calvarius rapidus*. Thin section shown under transmitted, **A**, and **B**, polarized light, accompanied by an interpretative drawing, **C** displaying reconstructed lines of arrested growth (LAGs, as thin dashed lines), the initial size of the medullary cavity (bold dashed line) and the distribution of the Haversian tissue (gray areas). Areas shown in greater magnification appear in **D**, **E**, and **F**, where in **E** and **F** arrowheads indicate the location of LAGs.

long metatarsals of non-iguanodontian ornithopods and dryosaurid iguanodontians. These ornithopod taxa are lightly built bipeds that are thought to have been swift animals (Galton, 1971; Coombs, 1978; Norman et al., 2004). By analogy with these forms, it is likely that *C. rapidus* was also capable of rapid locomotion and it is even within the realm of possibility that its body plan mimicked those of the early members of Ornithopoda.

Another adaptation for cursoriality in vertebrates consists of the compression, reduction, or loss of the lateral elements of the metapodium (Garland & Janis, 1993). In this regard, the exaggerated projection of the mediodorsal corner of the distal end of metatarsal IV in *Calvarius rapidus* (Fig. 4W) increased the area where this region of the bone lapped onto the laterodistal margin of metatarsal III. This configuration would have enhanced compression of the metatarsus by having these two metatarsals more closely appressed to each other, at least distally, contributing to the hypothetical cursorial abilities of this species.

Cursoriality in *Calvarius rapidus* is further supported by some inferred myological attributes. As in other dinosaurs (Dilkes, 2000; Carrano & Hutchinson, 2002; Hutchinson et al., 2005; Fechner, 2009; Piechowski & Tañanda, 2020), the m. gastrocnemius lateralis (an extensor of the ankle joint and flexor of the knee; Piechowski & Tañanda, 2020) may have originated on the posterior side of the distal femur and inserted on the dorsal surface of the medial flange (Fig. 2E) and much of the proximolateral, plantar, and medial surfaces of metatarsal IV (Fig. 2F–H). These areas are carved with a dense array of fine and longitudinally oriented short ridges (Fig. 2). The ridges on the dorsal surface of the medial flange are divided into two zones by a thicker and more continuous longitudinal ridge (Fig. 2A, E). This sculpturing of the medial flange of MCD-8734 (Fig. 2A, C) is more prominent than in other ornithopods such as *Maiasaura peeblesorum* (Dilkes, 2000), *Uteodon aphanocetes* (Carpenter and Wilson 2008), *Parksosaurus warreni* (Parks, 1926), or *Tenontosaurus tilletti* (Forster, 1990), suggesting that in MCD-8734 the m. gastrocnemius lateralis may have played a more significant role in flexing the knee and extending the ankle joint than in other ornithopods. Additional areas with a similar rugose texture are present on the dorsal and part of the lateral surfaces of the proximal end (interpreted as the insertion region of m. tibialis cranialis; Fig. 2E, F) and on the dorsal and lateral surfaces of the distal region (interpreted as the insertion of m. fibularis brevis; Fig. 2E, F). The latter two muscles are the primary flexors of the ankle joint (Piechowski & Tañanda, 2020). Although Dilkes (2000) interpreted a single point of insertion of m. tibialis cranialis in the metatarsal III of *M. peeblesorum*, many other dinosaurs possess insertion areas in both metatarsals II and IV (Carrano & Hutchinson, 2002; Hutchinson et al., 2005; Fechner, 2009; Piechowski & Tañanda, 2020). Notably, the surface covered by m. tibialis cranialis and m. fibularis brevis in MCD-8734 is much larger than in the quadrupedal *M. peeblesorum* (Dilkes 2000) and the bipedal *Dryosaurus altus* (Galton, 1981), *Oryctodromeus cubicularis* (Krumenacker, 2017; e.g., MOR 1642), and *Parksosaurus warreni* (Parks, 1926).

Finally, the histomorphology provided additional information on the potential cursoriality of MCD-8734. As stated above, both the dorsal and plantar regions of the studied thin section display extensive bone remodeling. While the remodeling observed in the plantar region can be directly related to the plantar expansion of the medial flange of the metatarsal and to the stress produced by insertion of m. gastrocnemius lateralis, the development of Haversian tissue in the dorsal side of the metatarsal cannot be correlated to any particular skeletal structure. Thus, the latter was likely produced as a consequence of biomechanical stress. In this regard, the pattern observed in the metatarsal IV of MCD-8734 greatly resembles that of equids

(Martínez-Maza et al., 2014), in which both the dorsal and plantar regions of the metatarsals display the most intense bone remodeling. In horses, the Haversian distribution in the metatarsals is interpreted as the result of biomechanical stress produced during rapid hindlimb propelling on hard ground. Assuming a similar biomechanical response to similar locomotion type, these observations add further support to the hypothesis that MCD-8734 was a cursorial animal.

The inferred adaptations for speed in MCD-8734 contrast with the locomotory mode of other styracosternans, consisting of quadrupedal or facultative quadrupedal forms hypothesized to have exhibited subcursorial to mediportal adaptations (Coombs, 1978; Becerra & Ramírez, 2018), with the more morphologically derived members of the clade being adapted for a slower but sustained locomotion style (Persons & Currie, 2014).

Ontogeny

Despite the abundant literature on ornithopod osteohistology (Bailleul et al., 2019), few studies have focused on the histological characterization of metatarsals. Overall, metatarsals exhibit a medullary cavity surrounded by endosteal lamellar bone and a cortex consisting of well-vascularized fibrolamellar bone tissue. This configuration is common in both basally branching (Cerdeña & Chinsamy, 2012; García-Marsa et al., 2020) and more derived members of the group (Horner et al., 2000), as in MCD-8734.

Dinosaurs are aged on the basis of the number of LAGs (Bailleul et al., 2019). Although LAG counts are usually obtained from the femur and tibia, metatarsals may also offer a record of growth rings (Horner et al., 2000). Seven LAGs are counted along the cortex of MCD-8734, but the intense bone remodeling occurring in the deep cortex may have obliterated the innermost lines. In order to reconstitute the missing number of LAGs, we implemented the growth trajectory determined for the indeterminate styracosternan hadrosaurid from the lower Maastrichtian Basturs Poble locality (Fondevilla et al., 2018) in our sample. This led us to establish that only one LAG was erased by bone remodeling, concluding that there were up to eight LAGs in MCD-8734 at the time of death (Fig. 8C).

The combination of different histomorphological patterns in MCD-8734 (moderate expansion of the medullary cavity, limited development of secondary osteons, primary fibrolamellar bone dominating the cortex, and the absence of EFS) is consistent with the subadult stage established for the saurolophine hadrosaurid *Maiasaura peeblesorum* (Horner et al., 2000). The absence of EFS in the studied sample also indicates that MCD-8734 did not reach somatic maturity.

The two regions showing abundant Haversian tissue (Fig. 8B, C) warrant further discussion. Haversian substitution occurs early in ontogeny in styracosternans such as hadrosauroids. In particular, metatarsals exhibit an extensive bone resorption and reconstruction by Haversian tissue in certain areas related to substantial biomechanical stress (Horner et al., 2000). This seems to be also the case in MCD-8734, in which both the anteriomedial and posteromedial regions of the analyzed section display a remarkable development of Haversian tissue but differ from the metatarsal histology of some heterodontosaurids (Becerra et al., 2016).

The observed growth pattern in MCD-8734 adds to the variety of growth patterns seen among the European styracosternans for which there are osteohistological studies available. Thus, on one hand Maastrichtian Ibero-Armorican lambeosaurine hadrosaurids *Pararhabdodon isonensis* (Serrano et al., 2020) and the species from Basturs Poble (Fondevilla et al., 2018) display an almost uninterrupted growth (Słowiak et al., 2020), where each growth cycle is bounded by annuli rather than LAGs. In contrast, a seasonal growth in MCD-8734 is indicated by well-developed

LAGs, as in *Iguanodon bernissartensis* (Stein et al., 2017), the insular early-diverging hadrosauroid *Telmatosaurus transsylvanicus* from the Maastrichtian Hateg Basin of Romania (Benton et al., 2010) and the indeterminate diminutive hadrosaurid from the late Maastrichtian from the Tremp Formation of Huesca Province in the south-central Pyrenees (Company et al., 2015). Outside the Late Cretaceous European archipelago, growth patterns among styracosternans are also variable. For example, no lines of arrested growth were observed in the non-hadrosauroid styracosternan *Choyrodon barsboldi* from middle to late Albian strata of the Khuren Dukh Formation of eastern Mongolia (Gates et al., 2018). Within Hadrosauridae, some species such as brachylophosaurins *Maiasaura peeblesorum* (Woodward et al., 2015) and *Probrachylophosaurus bergei* (Freedman Fowler & Horner, 2015) and the lambeosaurine *Hypacrosaurus stebingeri* (Horner et al., 1999) display lines of arrested growth, whereas members of the Saurolophini tribe lack LAGs and display uninterrupted growth (Słowiak et al., 2020). According to Słowiak et al., (2020), the absence of LAGs would be related to the evolution of larger body sizes. In this context, the presence of LAGs in MCD-8734 would be consistent with Słowiak et al.'s (2020) hypothesis given the particularly small size of the Masía de Ramón species.

Body Size

Studies on the histology and life history of styracosternans such as *Maiasaura peeblesorum* (Woodward et al., 2015) and *Probrachylophosaurus bergei* (Freedman Fowler & Horner, 2015) show growth curves where these animals reach skeletal maturity at approximately 8–10 years of age. Because of the inferred phylogenetic position of MCD-8734 as a member of Styracosterna, we expect the development of this species to conform to a growth curve similar to that of members of this clade. Accordingly, at 8 years of age at the time of death MCD-8734 would have not been far from reaching somatic maturity. It is therefore unlikely that the length of the metatarsal IV of an adult individual of the Masía de Ramón species would be substantially greater than that of MCD-8734 (155.8 mm in length). Because no femur is preserved for MCD-8734, we can only use the dimensions of metatarsal IV as proxy for body size comparisons with other styracosternans. Standard metatarsal IV lengths for adult individuals of other styracosternan species typically range between 185–380 mm (Supplementary File 5). These data imply that MCD-8734 is one of the smaller styracosternans known so far and adds to the record of lineages that evolved a decrease in body size in the context of Styracosterna. Other examples of small-bodied styracosternans are the European insular species *Telmatosaurus transsylvanicus* (Weishampel et al., 1993), *Tethyshadros insularis* (Dalla Vecchia, 2009), and the fragmentary diminutive hadrosaurid from Serraduy del Pon and Beranuy in Huesca province, NE Spain (Martínez-Maza et al., 2014). Of these, only *T. insularis* preserves the fourth metatarsal. In *T. insularis*, metatarsal IV is comparable in length (153 mm; Dalla Vecchia, 2009) to that of MCD-8734 (yet, with a length/width ratio of 4.64, the metatarsal IV of *T. insularis* lacks the slender proportions of that of MCD-8734).

Evolutionary Convergence and Paleoeological Implications

The Masía de Ramón styracosternan represents an exception to the subcursoriality and mediportality, and relatively large body size that characterize styracosternan dinosaurs, particularly members of Hadrosauriformes (sensu Sereno, 2005, i.e., the least inclusive clade containing *Iguanodon bernissartensis* Boulenger in van Beneden, 1881 and *Parasaurolophus walkeri* Parks, 1922, such as those reported in Hu, 1972; Coombs, 1978; Horner et al., 2004). The extreme elongation of metatarsal IV, inferred

cursoriality and relatively small body size in MCD-8734 constitute a rare instance of evolutionary convergence within Ornithopoda, with the distantly related early-diverging ornithischians and basally branching iguanodontians such as dryosaurids and elasmarians. This indicates that the postcranial skeleton of these animals was capable of substantial morphological plasticity.

During the latest stages of the Cretaceous (Santonian-Maastrichtian), the small-bodied cursorial herbivore ecological niche was represented by non-iguanodontian and non-styracosternan ornithopods. Examples include the basally branching ornithischians *Orodromeus makelai* (Horner & Weishampel, 1988) and *Parksosaurus warreni* (Parks, 1926) in Laramidia, the elasmarians *Gasparinisaura cincosaltensis* (Coria & Salgado, 1996) and *Isasicursor santacrucensis* (Novas et al., 2019) in South America, the early-diverging ornithischians *Haya griva* (Makovicky et al., 2011) and *Koreanosaurus boseongensis* (Hun et al., 2019) in Asia, elasmarians *Trinisaura santamartaensis* (Coria et al., 2013) and *Morrosaurus antarcticus* (Rozadilla et al., 2016) in Antarctica, and rhabdodontids *Zalmoxes robustus* (Weishampel et al., 2003) and *Mochlodon vorosi* (Ösi et al., 2012) in the Tisia-Dacia block of the Late Cretaceous European Archipelago. Unlike elsewhere in the world, however, in the Ibero-Armorican island of the Late Cretaceous European Archipelago this ecological niche was represented by a styracosternan.

CONCLUSION

We describe a new genus and species of a relatively small styracosternan iguanodontian ornithopod from the Ibero-Armorican domain of south-western Europe. This animal is represented by a highly modified metatarsal IV nowhere to be found among ornithopods. The fossil comes from the Masía de Ramón locality, corresponding to uppermost Maastrichtian strata of the Talarn Formation, Lleida province, NE Spain. Within Ornithopoda, this metatarsal IV is unique in combining the greatly elongated proportions of early-diverging members of the clade with the prominent medial flange seen in more derived styracosternans such as hadrosaurids. Histological data indicate that this specimen was a late subadult at the time of death, approaching somatic maturity. By analogy with the elongate metatarsals of lightly built, small-bodied cursorial ornithopods, it is likely that this animal was also capable of rapid locomotion. This is consistent with the differential distribution of intense bone remodeling in metatarsal IV, likely resulting from biomechanical stress produced during rapid hindlimb propelling.

As a styracosternan, *Calvarius rapidus* represents an exception to the subcursoriality and mediportality, as well as the relatively large body size, that characterize other members of the clade. The elongation of metatarsal IV, inferred cursoriality, and relatively small body size led us to hypothesize that this species evolved convergently in relation to the distantly related non-iguanodontian ornithopods and dryosaurid and elasmarian iguanodontians. This also suggests that the postcranial skeleton of these animals was capable of substantial morphological plasticity. In contrast to other regions of the world during the latest Cretaceous, where the small-bodied cursorial herbivore ecological niche was represented by non-iguanodontians and non-hadrosauriforms, in the Ibero-Armorican island of the Late Cretaceous European Archipelago this niche was occupied by a styracosternan. *C. rapidus* is also probably another case of endemism in an insular terrestrial environment.

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AUTHOR CONTRIBUTIONS

APM and AGS designed and drafted the manuscript. APM gathered and analyzed the comparative osteological and phylogenetic character data. AS gathered and analyzed the osteohistological data. Both authors edited the manuscript.

LIST OF SUPPLEMENTARY FILES

Supplementary File 1: list of the characters used in the phylogenetic analysis.

Supplementary File 2: taxon-character matrix used in the phylogenetic analysis in NEXUS format.

Supplementary File 3: taxon-character matrix used in the phylogenetic analysis in NEXUS format.

Supplementary File 4: the most parsimonious trees resulting from the phylogenetic analysis.

Supplementary File 5: measurements used for calculating the ratio between the length and width (at mid-length) of the metatarsal IV of a sample of ornithopod species.

Supplementary File 6: boxplot showing the metatarsal IV length/femur length ratios ('cursoriality index') from a sample of ornithopod taxa.

Supplementary File 7: measurements used for calculating the ratio between the length of metatarsal IV and that of the femur for a sample of ornithopod species.

Supplementary File 8: full resolution brightfield image of the histological cross-section at mid-shaft of the holotype metatarsal IV of *Calvarius rapidus*, MCD-8734, appearing in Fig. 8A.

Supplementary File 9: full resolution polarized image of the histological cross-section at mid-shaft of the holotype metatarsal IV of *Calvarius rapidus*, MCD-8734, appearing in Fig. 8B.

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