



## Teeth of embryonic or hatchling sauropods from the Berriasian (Early Cretaceous) of Cherves-de-Cognac, France

PAUL M. BARRETT, JOANE POUÉCH, JEAN-MICHEL MAZIN, and FIONA M. JONES

**The Cherves-de-Cognac site (Charente, France) has yielded a diverse continental microvertebrate fauna of Berriasian (earliest Cretaceous) age. Dinosaur remains are rare, but include three teeth that are referable to an indeterminate sauropod, which might represent either a titanosauriform, a non-titanosauriform macronarian or a non-neosauropod. The small size of these teeth (with a maximum length of 3 mm, as preserved) and the almost complete absence of enamel wrinkling suggests that they pertained to embryonic or hatchling individuals. The Cherves-de-Cognac sauropod represents a rare occurrence of sauropod embryos/hatchlings, a new sauropod record from the poorly-known terrestrial Berriasian and another possible instance of the persistence of non-diplodocoid, non-titanosauriform sauropods into the Cretaceous.**

### Introduction

Sauropod dinosaurs have an extensive fossil record and some taxa, such as *Camarasaurus* and *Diplodocus*, are represented by many individual specimens (Upchurch et al. 2004). However, although the majority of sauropod specimens are subadults juveniles are rare. For example, it has been estimated that juveniles account for approximately one-sixth of the total number of sauropod specimens recovered from the famous Upper Jurassic (Tithonian) exposures of the Morrison Formation in the western USA (Foster 2005). Although recent work on sauropod histology has revealed critical information on their growth rates and life history strategies (e.g., Curry 1999; Sander 2000; Curry Rogers and Erickson 2005; Woodward and Lehman 2009; Sander et al. 2011), the dearth of embryonic, hatchling and juvenile material has hampered a broader understanding of sauropod ontogeny, although some work has revealed substantial age-related differences in morphology and ecology (e.g., Ikejiri et al. 2005; Schwarz et al. 2007; Whitlock et al. 2010).

To date, the only definitive sauropod embryos are those of an unnamed titanosaurid from the Rio Colorado Formation (Coniacian–Campanian) of Neuquén Province, Argentina (Chiappe et al. 1998, 2001) and an unidentified sauropod from the Lameta Formation (Maastrichtian) of Gujarat, India (Wilson et al. 2010), although none of these specimens have yet been described in full. Notable material of baby and juvenile sauropods recovered from the Morrison Formation includes: a complete skeleton of *Camarasaurus* (Gilmore 1925); a *Diplodocus* skull (Whitlock et al. 2010); the holotype specimen of *Brontosaurus* (= *Elosaurus*) *parvus* (Carpenter and McIntosh 1994); a partial skeleton of an unnamed brachiosaurid (Schwarz et al. 2007;

Carballido et al. 2012); and other undescribed diplodocid material (Myers and Storrs 2007). In addition, an assortment of more fragmentary specimens has also been reported from this unit, comprising an isolated premaxilla (Britt and Naylor 1994) and vertebral and limb material (Carpenter and McIntosh 1994; Foster 2005) referred to *Camarasaurus*, postcranial material assigned to *Apatosaurus* (Carpenter and McIntosh 1994; Foster 2005), and taxonomically indeterminate material (Carpenter and McIntosh 1994). Juvenile sauropod specimens from other localities include those referred to *Patagosaurus* (Cañadon Asfalto Formation, Toarcian–Aalenian or Bajocian, Argentina; Bonaparte 1986), *Bellusaurus* (Shishugou Formation, Oxfordian, China; Dong 1990), *Giraffatitan* and *Tornieria* (Tendaguru Beds, Kimmeridgian, Tanzania; Sander 2000), *Astrodon* (Arundel Formation, Aptian, USA; Carpenter and Tidwell 2005), and teeth referred to the titanosaurid *Lirainosaurus* (unnamed formation, late Campanian–early Maastrichtian, Spain; Díez Díaz et al. 2012). Consequently, the discovery of any additional embryonic, hatchling or baby sauropod material has the potential to improve our understanding of their early growth and development.

The lowermost Cretaceous (Berriasian; Colin et al. 2004; El Albani et al. 2004) locality of Cherves-de-Cognac (Charente, southwestern France; Fig. 1) has yielded a diverse macro- and microvertebrate fauna consisting primarily of terrestrial and freshwater taxa (Mazin et al. 2006, 2008; Pouech et al. 2006). The section consists of a lower unit (U1) composed of alternating gypsum and marly horizons, representing hypersaline lagoonal environments, and an upper unit (U2) consisting of alternating clay and marl overlain by limestones at the top of the series, which represents environmental change from brackish lagoonal to freshwater lacustrine conditions (El Albani et al. 2004; Mazin et al. 2006, 2008; Pouech and Mazin 2008a; Pouech et al. 2014). The fauna includes actinopterygians (Pouech et al. 2015), selachians (Rees et al. 2013), stegosaurian (Billon-Bruyat et al. 2010) and sauropod (Le Loeuff et al. 1996) dinosaurs, as well as amphibians, testudines, lepidosaurs, crocodylians, pterosaurs, other dinosaurs and mammals that have yet to be described in full (for additional information see Billon-Bruyat 2003; Pouech et al. 2006; Mazin and Pouech 2008; Mazin et al. 2008; Pouech 2008; Pouech and Mazin 2008b). Here, we describe three sauropod dinosaur teeth from this locality, which have been mentioned in the most recent of these faunal lists (as “Titanosauriformes non-Titanosauria”; see Mazin et al. 2008; Pouech 2008), but not described. These teeth represent a rare occurrence of a lowermost Cretaceous sauropod and pertain to individuals that were either embryos or hatchlings.

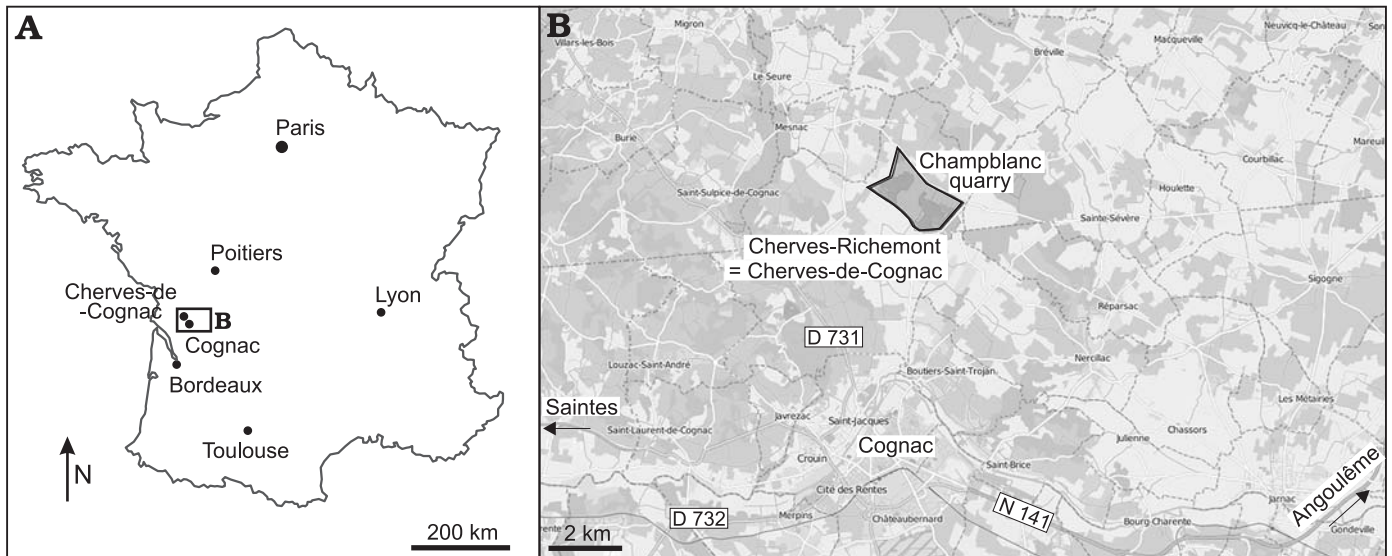


Fig. 1. Location of the Cherves-de-Cognac site near the town of Cognac, Charente, southwestern France (A), area of the Champblanc Quarry (B, modified from OpenStreetMap.org).

*Institutional abbreviations.*—CHV, Museum of Angoulême, Département de la Charente, France.

*Other abbreviations.*—SI, slenderness index.

## Material and methods

The teeth were extracted by screen-washing the marly sediment from level C36 of unit U2, after dissociation by adding oxygen peroxide. Over 300 kg of sediment was screened in total, yielding 10 812 isolated teeth of numerous taxa, of which only three can be referred to Sauropoda. Imaging was carried out using X-Ray microtomography at the European Synchrotron Radiation Facility (ESRF, Grenoble, France), on beamline ID19. Tomographic specifications used were: pixel size, 1.4  $\mu\text{m}$ ; propagation distance, 50 mm; energy, 20 KeV. Data processing and 3D reconstructions were conducted using Octave, Matlab and VGStudioMax 2, under ESRF and MNHN licences.

## Systematic palaeontology

Sauropoda Marsh, 1878

Gen. et sp. indet.

Figs. 2, 3.

*Material.*—CHVm03.561, CHVm03.588, and CHVm03.589, three isolated tooth crowns (Figs. 2, 3), from Level C36, Champblanc Quarry, Cherves-de-Cognac, Charente, France; Berriasian (Lower Cretaceous).

*Description.*—All of the teeth are generally similar in overall morphology, although there are minor differences between them that may represent positional or taxonomic variation (Figs. 2, 3). Nevertheless, as the teeth are not associated and, as the sample size is so small, it is not possible to distinguish between these alternative hypotheses at present. The crowns

are complete and well-preserved, but the teeth are all broken basally (Figs. 2, 3). CHVm03.588 and CHVm03.589 each possess a small amount of the root and the root-crown junction in these teeth is marked by a slight mesial constriction (present in CHVm03.561 and CHVm03.589, but absent in CHVm03.588), and changes in enamel surface texture and colour (Figs. 2A–C, 3). CHVm03.588 has a slenderness index (SI: sensu Upchurch 1998) of approximately 2.16, and this ratio is 2.02 and 1.6 in CHVm03.561 and CHVm03.589, respectively. As preserved, none of the tooth crowns exceed 3.0 mm in total apicobasal length (inclusive of both the crown and partial root) or 1 mm in mesiodistal width.

All three crowns have a “D”-shaped cross-section with a convex labial surface and shallowly concave lingual surface (Fig. 2D), with the labial convexity more marked distally than mesially, so that the labiolingually thickest part of the crown is offset slightly distal to the tooth long axis. The root has a sub-circular cross-section (Fig. 2E). In labial or lingual view, the crowns are mesiodistally narrow and either unexpanded relative to the root (CHVm03.588), or only very slightly expanded mesially (CHVm03.561 and CHVm03.589). The distal margin of the tooth is almost straight, whereas the mesial margin is gently convex in CHVm03.561 and CHVm03.589 and results in the abovementioned mesial constriction at the root-crown junction (Figs. 2, 3). In all three teeth, the crown margins converge apically to form a bluntly rounded, triangular apex. The tooth apices lack recurvature.

CHVm03.588 and CHVm03.589 lack labial grooves, but very shallow grooves are present adjacent to both the mesial and distal crown margins in CHVm03.561. The lingual concavity houses a low, broad lingual ridge in all three teeth that extends for the full length of the crown (Figs. 2, 3). None of the teeth possess wear facets on their apical, mesial, or distal margins and denticles are absent from all teeth. In general, the enamel is either smooth or exhibits a fine, granular texture that

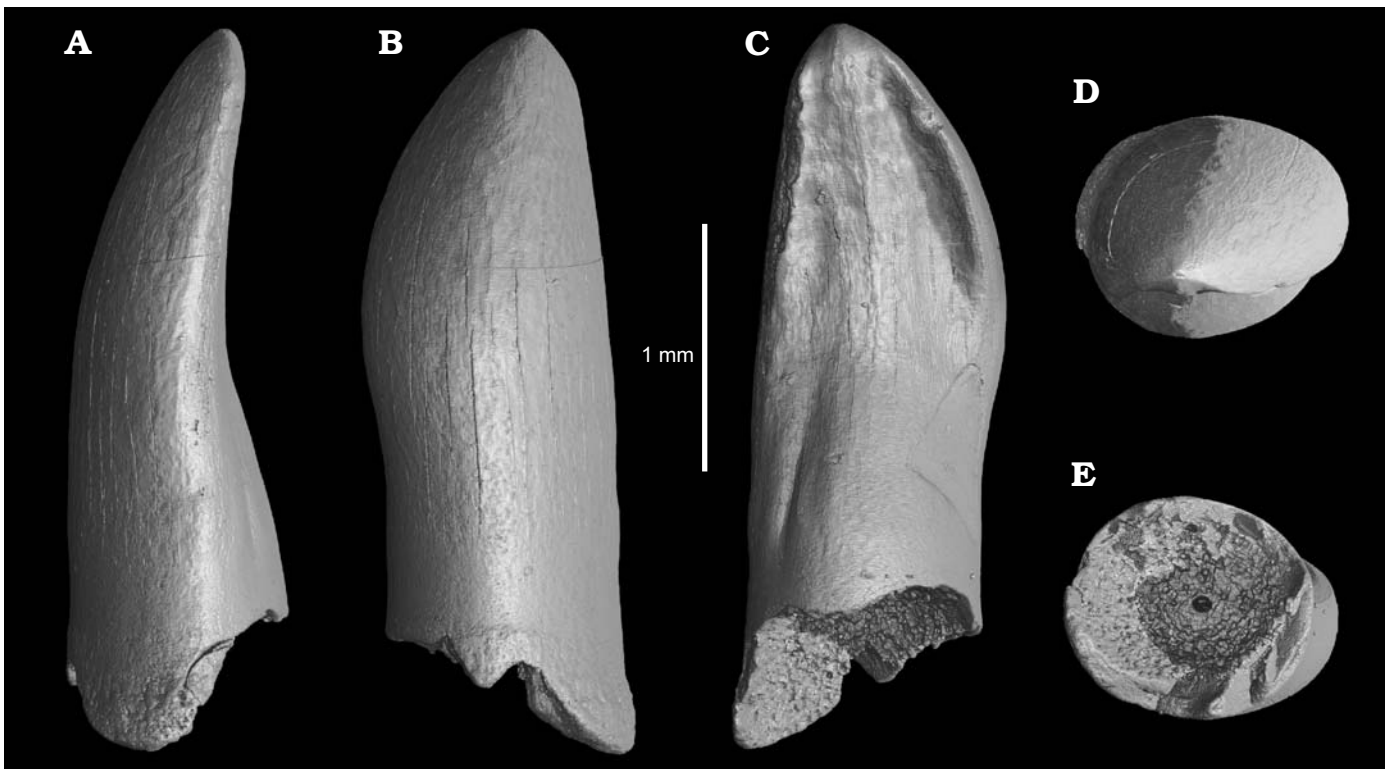


Fig. 2. Isolated tooth (CHVm03.588) of an indeterminate embryonic or hatchling sauropod from the Berriasian (Early Cretaceous) of Cherves-de-Cognac, France; in mesial (A), labial (B), lingual (C), apical (D), and basal (E) views.

lacks reticulate wrinkled textures (Figs. 2, 3). Nevertheless, very low relief, coarse enamel wrinkling is present on the apical part of the labial crown surface in CHVm03.588. (Fig. 2B).

## Discussion

Referral of the Cherves-de-Cognac teeth to Sauropoda is supported by the presence of a crown with a “D”-shaped cross-section, the presence of a lingual concavity with an associated lingual ridge, and faint indications of enamel wrinkling on one of the teeth (Upchurch 1998; Wilson 2002). The lack of both extreme crown elongation (with SIs that are substantially lower than 4.0) and a cylindrical crown cross-section excludes the teeth from referral to either Diplodocoidea or a derived clade within Titanosauria (Upchurch 1998; Wilson 2002). These teeth also lack the characteristic “heart-shaped” outline of turiasaur tooth crowns (Royo-Torres and Upchurch 2012). The Cherves-de-Cognac teeth were originally referred to “Titanosauriformes non-Titanosauria” (Mazin et al. 2008; Pouech 2008), but no discussion was provided to support this identification. The site has also yielded several skeletal elements of an adult sauropod that has been mentioned as “Camarasauridae” in faunal lists but not been fully described (Le Loeuff et al. 1996; Billon-Bruyat 2003; Mazin et al. 2006, 2008). The teeth described herein are similar to those of both *Camarasaurus* and basal titanosauriforms, in having tooth crowns of subequal mesiodistal width to the roots, retaining a “D”-shaped cross-section with a lingual concavity and ridge, and in possessing subparallel, straight to slightly convex

mesial and distal crown margins (e.g., McIntosh et al. 1996; Barrett et al. 2002; Barrett and Wang 2007). The low SIs of the Cherves-de-Cognac teeth are consistent with the crown proportions seen in *Camarasaurus* (e.g., McIntosh et al. 1996). However, although the presence of elongate tooth crowns is regarded as a titanosauriform synapomorphy (with SIs >3.0; Upchurch 1998), the SIs of basal titanosauriform taxa, such as *Brachiosaurus* and *Astrodon*, vary positionally (ranging from 2.0–4.0; Barrett et al. 2002), so referral to Titanosauriformes cannot be ruled out on this basis. Moreover, some of the dental characters present in the Cherves-de-Cognac teeth, such as parallel-sided tooth crowns and low SIs, are also present in several non-neosauropod taxa (such as *Shunosaurus*; Zhang 1988). Due to the combination of features present, we adopt a conservative approach and regard the Cherves-de-Cognac teeth as referable to an indeterminate sauropod: more material is required to make a definitive identification.

The size of the Cherves-de-Cognac teeth indicates that they belonged to very small individuals. Teeth of the unnamed *Auca Maheuvo* titanosaur embryos reach lengths of approximately 2 mm (Chiappe et al. 1998) and are associated with skulls that are approximately 30 mm long (Chiappe et al. 2001). Consequently, the slightly larger teeth of the Cherves-de-Cognac taxon suggests that they pertained to either a late stage embryo or a hatchling individual. The general absence of wrinkled enamel (the presence of which is usually regarded as a eusauropod synapomorphy: Upchurch 1998; Wilson 2002) in the Cherves-de-Cognac taxon is also indicative of embryonic or juvenile status (Díez Díaz et al. 2012; Holwerda et al. 2015). Unwrinkled



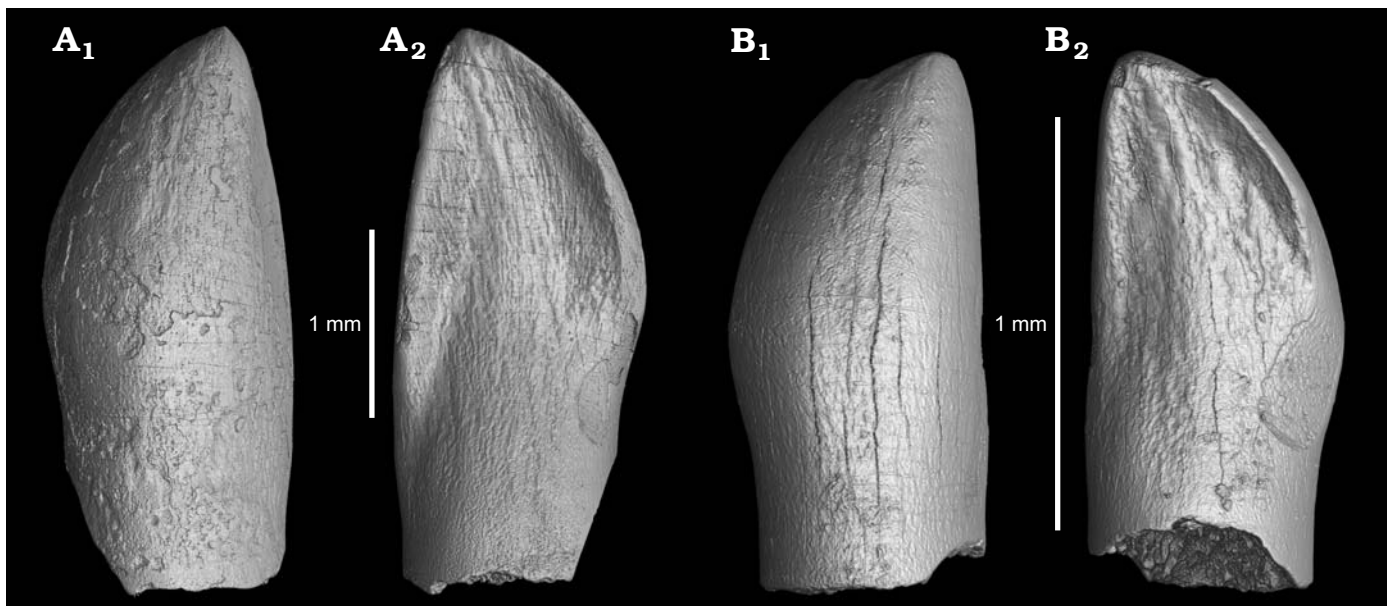


Fig. 3. Isolated teeth (A, CHVm03.561; B, CHVm03.589) of an indeterminate embryonic or hatchling sauropod from the Berriasian (Early Cretaceous) of Cherves-de-Cognac, France; in labial (A<sub>1</sub>, B<sub>1</sub>) and lingual (A<sub>2</sub>, B<sub>2</sub>) views.

enamel is present on the teeth of the Auca Mahuevo titanosaur (Chiappe et al. 2001) and the juvenile teeth of *Lirainosaurus* (Díez Díaz et al. 2012), although wrinkled enamel is present on larger teeth of the latter taxon and so its presence/absence seems to be under ontogenetic control. However, other embryonic and juvenile sauropods, such as specimens of *Camarasaurus* and an unnamed diplodocid, possess wrinkled enamel (Britt and Naylor 1994; Holwerda et al. 2015).

Sauropods underwent a major faunal turnover over the Jurassic–Cretaceous boundary (e.g., Upchurch and Barrett 2005; Mannion et al. 2011), but localities yielding earliest Cretaceous sauropods are relatively rare (e.g., Weishampel et al. 2004; Upchurch et al. 2015; McPhee et al. 2016). Consequently, the material from Cherves-de-Cognac adds another useful datum in understanding sauropod distributions at this important time in their history and also offers the potential for future discoveries that may provide additional insights into faunal changes across the boundary. Moreover, although the Cherves-de-Cognac teeth are taxonomically indeterminate, it is possible that they represent a non-titanosauriform macronarian sauropod or a non-neosauropod (see above). This is significant in the light of other recent discoveries, which suggest that non-diplodocoid and non-titanosauriform taxa were more common in earliest Cretaceous ecosystems than previously appreciated (Upchurch et al. 2015; McPhee et al. 2016).

Finally, it is interesting to speculate that western European “Purbeckian” localities, which exhibit similar lagoonal/sabkha-type environments, might have been important as nesting sites, due to the associated occurrence of microvertebrate remains with eggshell fragments. The Purbeck Limestone Group of southern England has a sauropod record that includes the teeth of embryonic/hatchling individuals, possible sauropod eggshell fragments and a putative nest (Ensom 2002; Barrett et al. 2010). Reptile eggshell has also been reported from

Cherves-de-Cognac (Grellet-Tinner et al. 2008), although none has been identified as sauropod thus far and no nests have been identified. By contrast macrovertebrate remains are rare at both sites, and the scarcity of large dinosaur remains may either reflect taphonomic bias or might indicate that adult dinosaurs were only transient residents in these environments (Wright et al. 1998; Norman and Barrett 2002).

**Acknowledgements.**—PMB thanks JMM and JP for their invitation to work on this material. We thank Alex Ball (NHM Image and Analysis Centre, London, UK) for help with SEM imaging. The translation of Dong (1990) was provided by the late Will Downs and can be downloaded from The Polyglot Paleontologist (<http://paleoglot.org>). The authors are especially grateful to Paul Tafforeau (European Synchrotron Radiation Facility, Grenoble, France) for imaging. X-Ray imaging was partly supported by ESRF grant EC531. Field investigations were supported by French Public Councils (Municipalité de Cherves-Richemont, Communauté de Communes de Cognac, Département de la Charente), the quarrying company Groupe Garandeau and the Musée d’Angoulême. We thank John Whitlock (Mount Aloysius College, Cresson, USA) and Femke Holwerda (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany) for helpful reviews of this article and Stephen Brusatte (School of GeoSciences, University of Edinburgh, UK) for editorial assistance.

## References

- Barrett, P.M. and Wang, X.-L. 2007. Basal titanosauriform (Dinosauria, Sauropoda) teeth from the Lower Cretaceous Yixian Formation of Liaoning Province, China. *Palaeworld* 16: 265–271.
- Barrett, P.M., Benson, R.B.J., and Upchurch, P. 2010. Dinosaurs of Dorset: Part II, the sauropod dinosaurs (Saurischia: Sauropoda) with additional comments on the theropods. *Proceedings of the Dorset Natural History and Archaeological Society* 131: 113–126.
- Barrett, P.M., Hasegawa, Y., Manabe, M., Isaji, S., and Matsuoka, H. 2002. Sauropod dinosaurs from the Lower Cretaceous of eastern Asia: taxonomic and biogeographical implications. *Palaontology* 45: 1197–1217.
- Billon-Bruyat, J.-P. 2003. *Les écosystèmes margino-littoraux du Juras-*

- sique terminal et du Crétacé basal d'Europe occidentale: biodiversité, biogéochimie et l'événement biotique de al limite Jurassique/Crétacé.* 254 pp. Ph.D. Dissertation, Université de Poitiers, Poitiers.
- Billon-Bruyat, J.-P., Mazin, J.-M., and Pouech, J. 2010. A stegosaur tooth (Dinosauria: Ornithischia) from the Early Cretaceous of southwestern France. *Swiss Journal of Geosciences* 103: 143–153.
- Bonaparte, J.F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétoosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie* 72: 325–386.
- Britt, B.B. and Naylor, B.G. 1994. An embryonic *Camarasaurus* (Dinosauria, Sauropoda) from the Upper Jurassic Morrison Formation (Dry Mesa Quarry, Colorado). In: K. Carpenter, K.F. Hirsch, and J.R. Horner (eds.), *Dinosaur Eggs and Babies*, 256–264. Cambridge University Press, Cambridge.
- Carballido, J.L., Marpmann, J.S., Schwarz-Wings, D., and Pabst, B. 2012. New information on a juvenile sauropod specimen from the Morrison Formation and the reassessment of its systematic position. *Palaeontology* 55: 567–528.
- Carpenter, K. and McIntosh, J. 1994. Upper Jurassic sauropod babies from the Morrison Formation. In: K. Carpenter, K.F. Hirsch, and J.R. Horner (eds.), *Dinosaur Eggs and Babies*, 265–278. Cambridge University Press, Cambridge.
- Carpenter, K. and Tidwell, V. 2005. Reassessment of the Early Cretaceous sauropod *Astrodon johnsoni* Leidy 1865 (Titanosauriformes). In: V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*, 78–114. Indiana University Press, Bloomington.
- Chiappe, L.M., Salgado, L., and Coria, R.A. 2001. Embryonic skulls of titanosaur sauropod dinosaurs. *Science* 293: 2444–2446.
- Chiappe, L.M., Coria, R.A., Dingus, L., Jackson, F., Chinsamy, A., and Fox, M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* 396: 258–261.
- Colin, J.-P., El Albani, A., Fürsich, F.T., Martín-Closas, C., Mazin, J.-M., and Billon-Bruyat, J.-P. 2004. Le gisement "Purbeckien" de vertébrés de Cherves-de-Cognac, Charente (SW France): nouvelles données biostratigraphiques. *Comptes Rendus Palevol* 3: 9–16.
- Curry, K.A. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *Journal of Vertebrate Paleontology* 19: 654–665.
- Curry Rogers, K. and Erickson, G.M. 2005. Sauropod histology: microscopic views on the lives of giants. In: K.A. Curry Rogers and J.A. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*, 303–326. University of California Press, Berkeley.
- Diez Díaz, V., Pereda Suberbiola, X., and Sanz, J.L. 2012. Juvenile and adult teeth of the titanosaurian dinosaur *Lirainosaurus* (Sauropoda) from the Late Cretaceous of Iberia. *Geobios* 45: 265–274.
- Dong, Z.M. 1990. Sauropoda from the Kelameili Region of the Junggar Basin, Xinjiang Autonomous Region [in Chinese]. *Vertebrata Palaeoasiatica* 28: 43–58.
- El Albani, A., Fürsich, F.T., Colin, J.-P., Meunier, A., Hochuli, P., Martín-Closas, C., Mazin, J.-M., and Billon-Bruyat, J.-P. 2004. Palaeoenvironmental reconstruction of the basal Cretaceous vertebrate bearing beds in the northern part of the Aquitaine Basin (SW France): sedimentological and geochemical evidence. *Facies* 50: 195–215.
- Ensom, P.C. 2002. Reptile eggshell, tiny vertebrate remains and globular calcified cartilage from the Purbeck Limestone Group of southern England. *Special Papers in Paleontology* 68: 221–240.
- Foster, J.R. 2005. New juvenile sauropod material from western Colorado, and the record of juvenile sauropods from the Upper Jurassic Morrison Formation. In: V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*, 141–153. Indiana University Press, Bloomington.
- Gilmore, C.W. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument. *Memoirs of the Carnegie Museum* 10: 347–384.
- Grellet-Tinner, G., Pouech, J., and Mazin, J.-M. 2008. Exquisitely preserved reptile eggshell fragments from the Berriasian site of Cherves-de-Cognac (Charente): paleobiological implications. In: J.-M. Mazin, J. Pouech, P. Hantzpergue, and V. Lacombe (eds.), *Mid-Mesozoic Life and Environments. Documents des Laboratoires de Géologie Lyon* 164: 46–49.
- Holwerda, F.M., Pol, D., and Rauhut, O.W.M. 2015. Using dental enamel wrinkling to define sauropod tooth morphotypes from the Cañadón Asfalto Formation, Patagonia, Argentina. *PLoS ONE* 10 (2): e0118100.
- Ikejiri, T., Tidwell, V., and Trexler, D.L. 2005. New adult specimens of *Camarasaurus lentus* highlight ontogenetic variation within the species. In: V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*, 154–179. Indiana University Press, Bloomington.
- Le Loeuff, J., Buffetaut, E., and Merser, C. 1996. Découverte d'un dinosaure sauropode tithonien dans la région de Cognac (Charente). *Géologie de la France* 2: 79–81.
- Mannion, P.D., Upchurch, P., Carrano, M.T., and Barrett, P.M. 2011. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews* 86: 157–181.
- Marsh, O.C. 1878. Principal characters of the American Jurassic dinosaurs, Part I. *American Journal of Science (Series 3)* 16: 411–416.
- Mazin, J.-M. and Pouech, J. 2008. Crocodylomorph microremains from Champblanc (Berriasian, Cherves-de-Cognac, Charente, France). In: J.-M. Mazin, J. Pouech, P. Hantzpergue, and V. Lacombe (eds.), *Mid-Mesozoic Life and Environments. Documents des Laboratoires de Géologie Lyon* 164: 65–67.
- Mazin, J.-M., Billon-Bruyat, J.-P., Pouech, J., and Hantzpergue, P. 2006. The Purbeckian site of Cherves-de-Cognac (Berriasian, Early Cretaceous, southwest France): a continental ecosystem accumulated in an evaporitic littoral depositional environment. In: P.M. Barrett and S.E. Evans (eds.), *Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota, Abstracts and Proceedings*, 84–88. Natural History Museum, London.
- Mazin, J.-M., Pouech, J., Hantzpergue, P., and Lenglet, T. 2008. The Purbeckian site of Cherves-de-Cognac (Berriasian, Early Cretaceous, SW France): a first synthesis. In: J.-M. Mazin, J. Pouech, P. Hantzpergue, and V. Lacombe (eds.), *Mid-Mesozoic Life and Environments. Documents des Laboratoires de Géologie Lyon* 164: 68–71.
- McIntosh, J.S., Miles, C.A., Cloward, K.C., and Parker, J.R. 1996. A new nearly complete skeleton of *Camarasaurus*. *Bulletin of the Gunma Museum of Natural History* 1: 1–87.
- McPhee, B.W., Mannion, P.D., de Klerk, W.J., and Choiniere, J.N. 2016. High diversity in the sauropod dinosaur fauna of the Lower Cretaceous Kirkwood Formation of South Africa: implications for the Jurassic–Cretaceous transition. *Cretaceous Research* 59: 228–248.
- Myers, T.S. and Storrs, G.W. 2007. Taphonomy of the Mother's Day Quarry, Upper Jurassic Morrison Formation, south-central Montana, USA. *Palaiois* 22: 651–666.
- Norman, D.B. and Barrett, P.M. 2002. Ornithischian dinosaurs from the Lower Cretaceous (Berriasian) of England. *Special Papers in Palaeontology* 68: 161–189.
- Pouech, J. 2008. *Position des mammifères dans les écosystèmes mésozoïques d'Europe Occidentale: le gisement de Cherves-de-Cognac (Berriasian, Charente, France)*. 274 pp. Ph.D. Dissertation, Université Claude Bernard Lyon 1, Lyon.
- Pouech, J. and Mazin, J.-M. 2008a. Correlation Between Microvertebrates Biodiversity and Conditions of Deposition Along a Sedimentary Series (Berriasian, Cherves-de-Cognac, France). *Berichte der Geologischen Bundesanstalt, Wien* 74: 81–82.
- Pouech, J. and Mazin, J.-M. 2008b. Mammalian diversity: the position of Cherves-de-Cognac in the west European record. In: J.-M. Mazin, J. Pouech, P. Hantzpergue, and V. Lacombe (eds.), *Mid-Mesozoic Life and Environments. Documents des Laboratoires de Géologie Lyon* 164: 74–76.
- Pouech, J., Mazin, J.-M., and Billon-Bruyat, J.-P. 2006. Microvertebrate diversity from Cherves-de-Cognac (Lower Cretaceous, Berriasian: Charente, France). In: P.M. Barrett and S.E. Evans (eds.), *Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota, Abstracts and Proceedings*, 96–100. Natural History Museum, London.

- Pouech, J., Mazin, J.-M., Cavin, L., and Poyato-Ariza, F.J. 2015. A Berriasian actinopterygian fauna from Cherves-de-Cognac, France: biodiversity and palaeoenvironmental implications. *Cretaceous Research* 55: 32–43.
- Pouech, J., Amiot, R., Léuyer, C., Mazin, J.-M., Martineau, F., and Fourrel, F. 2014. Oxygen isotope composition of vertebrate phosphates from Cherves-de-Cognac (Berriasian, France): environmental and ecological significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410: 290–299.
- Rees, J., Cuny, G., Pouech, J., and Mazin, J.-M. 2013. Non-marine selachians from the basal Cretaceous of Charente, SW France. *Cretaceous Research* 44: 122–131.
- Royo-Torres, R. and Upchurch, P. 2012. Cranial anatomy of the sauropod *Turiasaurus riodevensis* and implications for its phylogenetic relationships. *Journal of Systematic Palaeontology* 10: 553–583.
- Sander, P.M. 2000. Long bone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology* 26: 466–488.
- Sander, P.M., Klein, N., Stein, N., and Wings, O. 2011. Sauropod bone histology and its implications for sauropod biology. In: N. Klein, K. Remes, C.T. Gee, and P.M. Sander (eds.), *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*, 276–302. Indiana University Press, Bloomington.
- Schwarz, D., Ikejiri, T., Breithaupt, B.H., Sander, P.M., and Klein, N. 2007. A nearly complete skeleton of an early juvenile diplodocid (Dinosauria: Sauropoda) from the lower Morrison Formation (Late Jurassic) of north central Wyoming and its implications for early ontogeny and pneumaticity in sauropods. *Historical Biology* 19: 225–253.
- Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society of London* 124: 43–103.
- Upchurch, P. and Barrett, P.M. 2005. Phylogenetic and taxic perspectives on sauropod diversity. In: K.A. Curry-Rogers and J.A. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*, 104–124. University of California Press, Berkeley.
- Upchurch, P., Barrett, P.M., Dodson, P. 2004. Sauropoda. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria* (Second Edition), 259–322. University of California Press, Berkeley.
- Upchurch, P., Mannion, P.D., and Taylor, M.P. 2015. The anatomy and phylogenetic relationships of “*Pelorosaurus*” *becklesii* (Neosauropoda, Macronaria) from the Early Cretaceous of England. *PLoS ONE* 10 (6): e0125819.
- Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X.-J., Sahní, A., Goman, E.M.P., and Noto, C.R. 2004. Dinosaur Distribution. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria* (Second Edition), 517–606. University of California Press, Berkeley.
- Wilson, J.A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society of London* 136: 217–276.
- Wilson, J.A., Mohabey, S.M., Peters, S.E., and Head, J.J. 2010. Predation upon hatchling dinosaurs by a new snake from the Late Cretaceous of India. *PLoS Biology* 8 (3): e1000322.
- Whitlock, J.A., Wilson, J.A., and Lamanna, M.C. 2010. Description of a nearly complete juvenile skull of *Diplodocus* (Sauropoda: Diplodocoidea) from the Late Jurassic of North America. *Journal of Vertebrate Paleontology* 30: 442–457.
- Woodward, H.N. and Lehman, T.M. 2009. Bone histology and microanatomy of *Alamosaurus sanjuanensis* (Sauropoda; Titanosauria) from the Maastrichtian of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology* 29: 807–821.
- Wright, J.L., Barrett, P.M., Lockley, M.G., and Cook, E. 1998. A review of the Early Cretaceous terrestrial vertebrate track-bearing strata of England and Spain. *New Mexico Museum of Natural History and Science Bulletin* 14: 143–153.
- Zhang, Y.-H. 1988. *The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong Sichuan. Volume II. Sauropod dinosaur (1)*. *Shunosaurus* [in Chinese, with English summary]. 1–89. Sichuan Publishing House of Science and Technology, Chengdu.

Paul M. Barrett [p.barrett@nhm.ac.uk], Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Joane Pouech [joane.pouech@upmc.fr], UMR 7207-UPMC-MNHN-CNRS-Sorbonne Universités, Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements, Université Pierre et Marie Curie Paris 6, 4 place Jussieu, 75005 Paris, France.

Jean-Michel Mazin [jean-michel.mazin@univ-lyon1.fr], UMR 5276-CNRS/ENS, Université Lyon1, Campus de la Doua, 2 rue Dubois, Bâtiment Géode, 69622 Villeurbanne Cedex, France.

Fiona M. Jones [fiona.jones@gtc.ox.ac.uk], Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

Received 27 February 2016, accepted 30 March 2016, available online 5 April 2016.

Copyright © 2016 P.M. Barrett et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see <http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.