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

PAUL M. BARRETT, JOANE POUECH, 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 referrable 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 emanel 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 Gujurat, 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 consisiting 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, crocodilians, 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.

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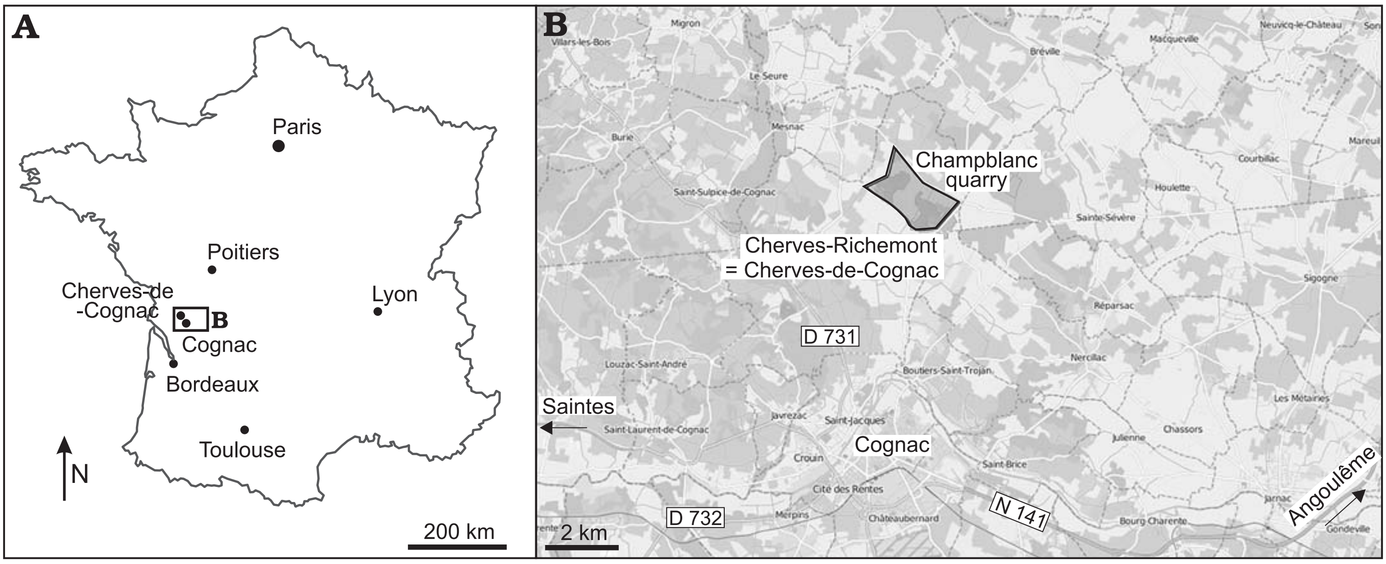

Fig. 1. Location of the Cherves-de-Cognac site near the town of Cognac, Charente, southwestern France (**A**), area of the Champblanc Quarry (**B**, modified from OpenStreetMap.org).

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 μm; 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 an 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 subcircular 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

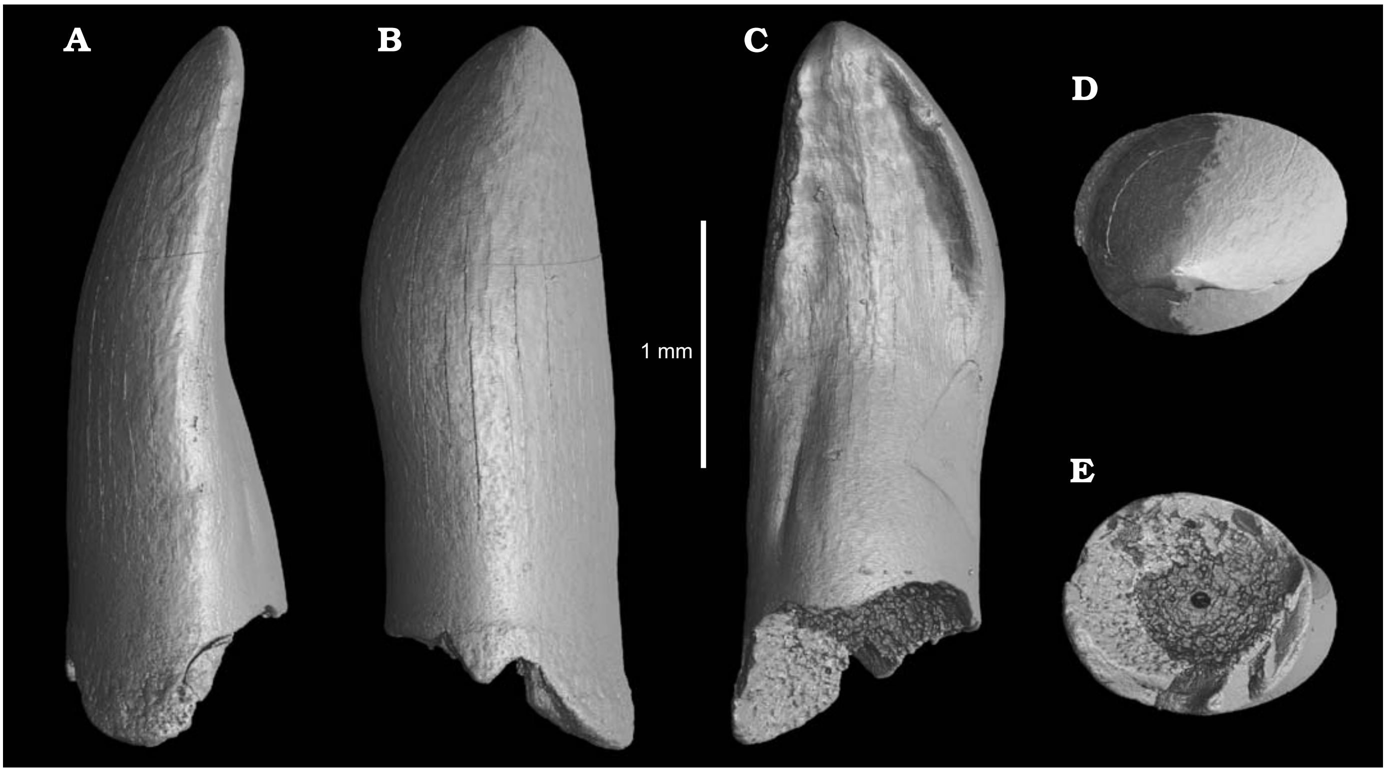

Fig. 2. Isolated tooth (CHVm03.588) of an indeterminate embryonic or hatchling sauropod from the Berriasian (Early Cretaceous) of Cherves-de-Cognac, France; in mesial (**A**), labial (**B**), lingual (**C**), apical (**D**), and basal (**E**) views.

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 referrable 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

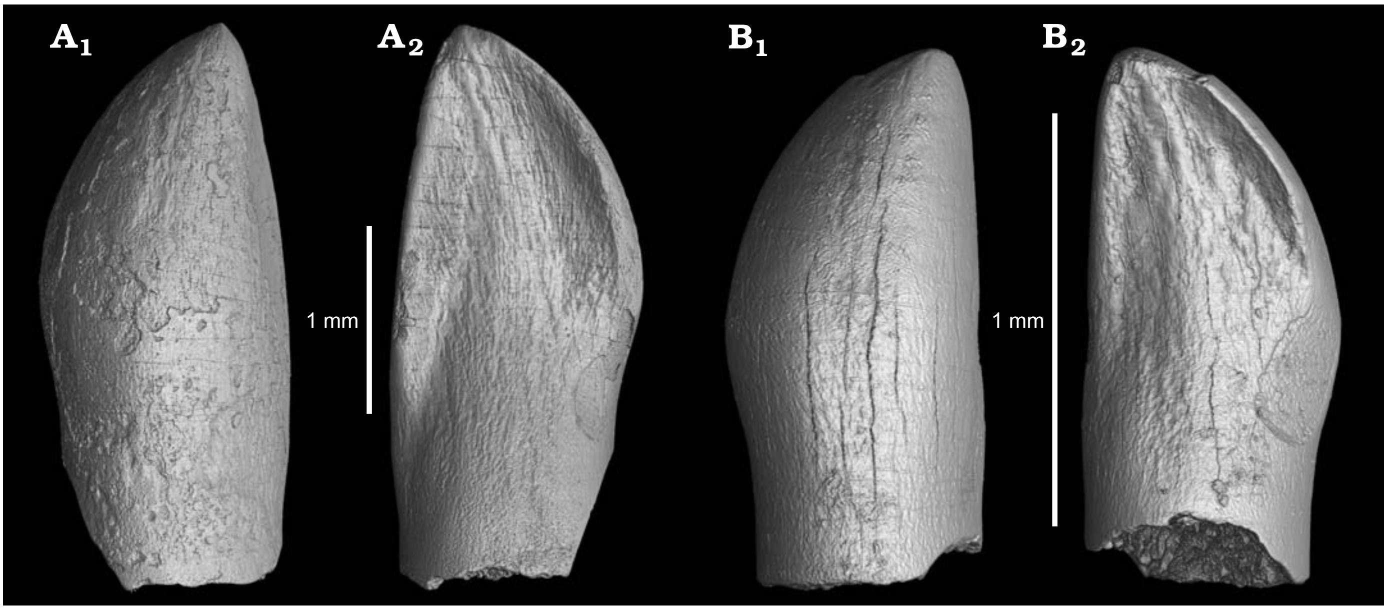

Fig. 3. Isolated teeth (**A**, CHVm03.561; **B**, CHVm03.589) of an indeterminate embryonic or hatchling sauropod from the Berriasian (Early Cretaceous) of Cherves-de-Cognac, France; in labial (A_1, B_1) and lingual (A_2, B_2) views.

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 wrinked 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 occurence 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).

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