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"*Megalosaurus* cf. *superbus*" from southeastern Romania: The oldest known Cretaceous carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous Europe-Gondwana connections

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ABSTRACT

Some of the best records of continental vertebrates from the Cretaceous of Europe come from Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant dinosaurs and other taxa that lived on islands (the Cornet and Haţeg Island faunas). Substantially less is known about those vertebrates living in the more stable, cratonic regions of Romania (and Eastern Europe as a whole), particularly during the earliest Cretaceous. We describe one of the few early Early Cretaceous fossils that have ever been found from these regions, the tooth of a large theropod dinosaur from Southern Dobrogea, which was discovered over a century ago but whose age and identification have been controversial. We identify the specimen as coming from the Valanginian stage of the Early Cretaceous, an incredibly poorly sampled interval in global dinosaur evolution, and as belonging to Carcharodontosauridae, a clade of derived, large-bodied apex predators whose earliest Cretaceous history is poorly known. Quantitative analyses demonstrate that the Romanian tooth shows affinities with a derived carcharodontosaurid subgroup, the Carcharodontosaurinae, which until now has been known solely from Gondwana. Our results suggest that this subgroup of colossal predators did not evolve vicariantly as Laurasia split from Gondwana, but originated earlier, perhaps in Europe. The carcharodontosaurine diversification may have been tied to a north-to-south trans-Tethyan dispersal that took place sometime between the Valanginian and the Aptian, illustrating the importance of palaeogeographic ties between these two realms during the largely mysterious early–mid Early Cretaceous.

1. Introduction

Romania boasts one of the best records of continental vertebrate fossils from the Cretaceous of Europe (e.g., Grigorescu, 1992, 2003; Csiki-Sava et al., 2015). The vast majority of fossils come from two well-known occurrences: the Lower Cretaceous bauxite accumulations of Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997; Posmoşanu, 2003; Dyke et al., 2011), and the famous uppermost Cretaceous beds of the Haţeg, Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the dinosaur-dominated 'Haţeg Island fauna' (e.g., Nopcsa, 1923; Weishampel et al., 1991; Benton et al., 2010; Codrea et al., 2010, 2012; Grigorescu, 2010; Vremir, 2010; Vasile and Csiki, 2011; Csiki-Sava et al., 2015). Both of these faunas inhabited islands that were part of the vast Cretaceous European Archipelago of the Neo-Tethys Ocean. Based on their isolated geological settings and the many dwarfed and morphologically aberrant taxa that make up the faunas, both have been interpreted as insular assemblages that give a unique window into how island environments affected the evolution of long-extinct organisms (e.g., Benton et al., 1997, 2010; Csiki-Sava et al., 2015).

The great volume of research on these assemblages over the past century, particularly the 'Haţeg Island fauna', has concealed an inconvenient bias: the stable, non-island, cratonic regions of Romania have yielded only extremely rare Mesozoic continental vertebrate remains (i.e., the Moldavian, Moesian and Scythian platforms; Săndulescu, 1984; Mutihac and Mutihac, 2010; Fig. 1). This is mostly because Mesozoic deposits are located in the subsurface in these regions, with only limited subaerial exposures available in the structurally highest-lying parts of the Moesian

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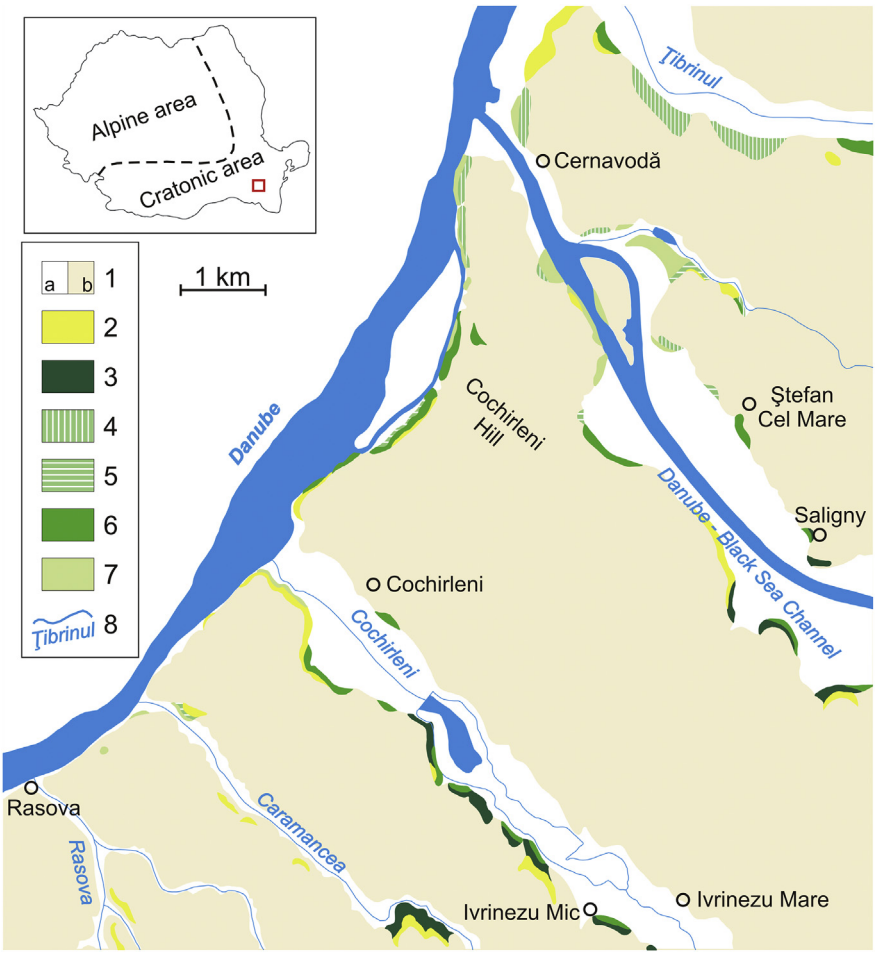

Fig. 1. Simplified geological map of the Cernavodă-Cochirleni area; inset shows the position of the study area within Romania. Legend: 1. Quaternary: a. Holocene alluvia, b. Pleistocene–Holocene loessoid deposits; 2. Pre-Quaternary Cenozoic (Middle Eocene and Miocene) deposits; Cretaceous: 3. Peştera Formation, Lower Cenomanian; 4. Cochirleni Formation; uppermost Aptian–Lower Albian; 5. Gherghina Formation, Middle–Upper Aptian; 6. Ostrov (=Ramadan) Formation; Barremian–Lower Aptian; 7. Cernavodă Formation, Alimanu Member, Berriasian–Valanginian; 8. Water courses. (Redrawn after Dragastan et al., 1998, 2014.)

Platform, in Central and Southern Dobrogea (Middle Jurassic–Upper Cretaceous), as well as in the northeastern-most corner of the Moldavian Platform, along the Prut Valley (lower Upper Cretaceous) (see, e.g., Mutihac and Mutihac, 2010). This bias is unfortunate because fossils from these settings could lead to a better understanding of how mainland and island faunas differed during the Cretaceous, and because the cratonic portion of Europe was an important biogeographic stepping stone between the north and south as the continents fragmented and sea levels fluctuated.

Although the cratonic regions of Romania have yielded few Cretaceous terrestrial fossils, these deposits are not totally barren. In fact, one of the first Mesozoic continental vertebrates ever recorded from Romania comes from one of these deposits, the Lower Cretaceous shallow marine limestones of Southern Dobrogea (Fig. 1). This specimen—the isolated but well-preserved tooth of a large theropod dinosaur—has often been overlooked. It was described a little over a century ago by Simionescu (1913; Fig. 2A), and until a few recent discoveries of very rare isolated specimens (Stoica and Csiki, 2002; Csiki-Sava et al., 2013; Dragastan et al., 2014), it remained as the sole published record of Mesozoic terrestrial vertebrates from the cratonic areas of Romania. It has never been comprehensively described and its precise age and taxonomic affinities have yet to be clarified, despite its potential importance as a well-preserved fossil from a poorly sampled area that could have critical evolutionary and biogeographic implications.

We here present a comprehensive description of the Dobrogea tooth and discuss its relevance for understanding dinosaur evolution and biogeography. We review the peculiar history of how this specimen was collected and curated, thoroughly document its morphology and age, identify it based on comparison to a broad range of theropods, and outline its importance. It turns out that this specimen, although only a single tooth, has wide-ranging implications. We identify it as coming from the Valanginian stage of the Early Cretaceous, which is incredibly poorly sampled both in Europe and globally (Weishampel et al., 2004), and as belonging to a carcharodontosaurid, a group of derived, large-bodied apex predators whose earliest Cretaceous history is poorly known. Carcharodontosaurids were once thought to be a uniquely Gondwanan group, but recent discoveries show that the basal members of the group were more widespread during the late Early–middle Cretaceous (e.g., Sereno et al., 1996; Brusatte and Sereno, 2008). The Romanian tooth shows affinities with a derived carcharodontosaurid subgroup, the Carcharodontosaurinae, that until now has been known only from Gondwana. It suggests that this subgroup of enormous predators did not evolve vicariantly as Pangaea