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

Citation for published version:
Csiki-Sava, Z, Brusatte, S & Vasile, S 2016, '"Megalosaurus cf. superbus" from southeastern Romania: the oldest known Cretaceous carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous Europe-Gondwana connections' Cretaceous Research, vol. 60, pp. 221-238. DOI: 10.1016/j.cretres.2015.12.004

Digital Object Identifier (DOI):
10.1016/j.cretres.2015.12.004

Published In:
Cretaceous Research

Elsevier Editorial System(tm) for Cretaceous Research
Manuscript Draft

Manuscript Number: YCRES-D-15-00207R2

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

Article Type: Full Length Article

Keywords: Southern Dobrogea; Valanginian; Carcharodontosauridae; cratonic Europe; palaeobiogeography

Corresponding Author: Dr. Zoltan Csiki-Sava, Ph.D.

Corresponding Author's Institution: University of Bucharest

First Author: Zoltan Csiki-Sava, Ph.D.

Order of Authors: Zoltan Csiki-Sava, Ph.D.; Stephen L Brusatte; Ștefan Vasile

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 Hațeg 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 evolved 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 Aptian, illustrating the importance of palaeogeographic ties between these two realms during the largely mysterious early-mid Early Cretaceous.

Dear Editors,

We are submitting here the latest, corrected version of our manuscript about an Early Cretaceous carcharodontosaurid dinosaur from southeastern Romania. We have implemented all the changes suggested by the Handling Associated Editor, as outlined below. In the case of the changes concerning the reference list, we have included two different versions, as explained below, due to uncertainties we have about the correct formatting style. We hope that this revised version is now suitable for publication in Cretaceous Research.

Sincerely,

Zoltan Csiki-Sava (also on behalf of the co-authors)

Editor comments:
Page 1 – email addresses removed from other authors than corresponding author, as instructed.

Page 2 – some of the former keywords were replaced by newly selected ones, as suggested.

Page 3, line 75 – 'in prep.', removed, this work is still ongoing and mentioning it is not entirely necessary.

Page 11, line 258 – 'in part' removed; this is a controversial detail of the local stratigraphy that is of no importance for the economy of this manuscript.

Page 18, line 441 – we have added 3 to 'Figure', thanks for spotting this omission!

Page 22, line 526 – the correct reference is Williamson and Brusatte, 2014, as it is correctly listed in the reference list. We have corrected this reference; again, we are grateful for noting this error.

Page 32, line 786 – '2102' was replaced by '2012'; also, we have updated (here and in the reference list) the reference 'Lü et al., 2014', published in the meantime, to 'Lü et al., 2016'.

Page 36, line 884 – 'see below' was removed from the text, as suggested.

Page 37, line 917 – 'KcKenna' corrected to 'McKenna'

References:
We have checked the latest issue(s) of CR, and are somewhat confused as to the required formatting of the references. We have compared several recently published papers, and have found two different formatting styles, e.g., one that comes from our own recent paper (Csiki-Sava, Z. et al., 2016. The East Side Story - The Transylvanian latest Cretaceous continental

vertebrate record and its implications for understanding Cretaceous-Paleogene boundary events. Cretaceous Research, 57: 662-698. http://dx.doi.org/10.1016/j.cretres.2015.09.003) and one in the still more recent paper of Averianov and Sues (Averianov, A. and Sues, H.-D., 2016. Troodontidae (Dinosauria: Theropoda) from the Upper Cretaceous of Uzbekistan. Cretaceous Research, 59: 98-110. http://dx.doi.org/10.1016/j.cretres.2015.11.005). Accordingly, in our resubmission we have included two different versions of our revised MS, each one following one of the two styles.

In one of the versions, we have retained our original, chronological formatting, that coincides with that used by Averianov and Sues (2016), while the second version follows the formatting implemented in Csiki-Sava et al. (2016) and also suggested by the Handling Editor. In this second version, we have made all of the changes suggested by the Editor, except a few instances such as:

Page 49, lines 1196-1214: Csiki-Sava et al. (2013, 2015) were kept after Csiki and Grigorescu (1998), Csiki et al. (2010), according to the alphabetical order recommended.

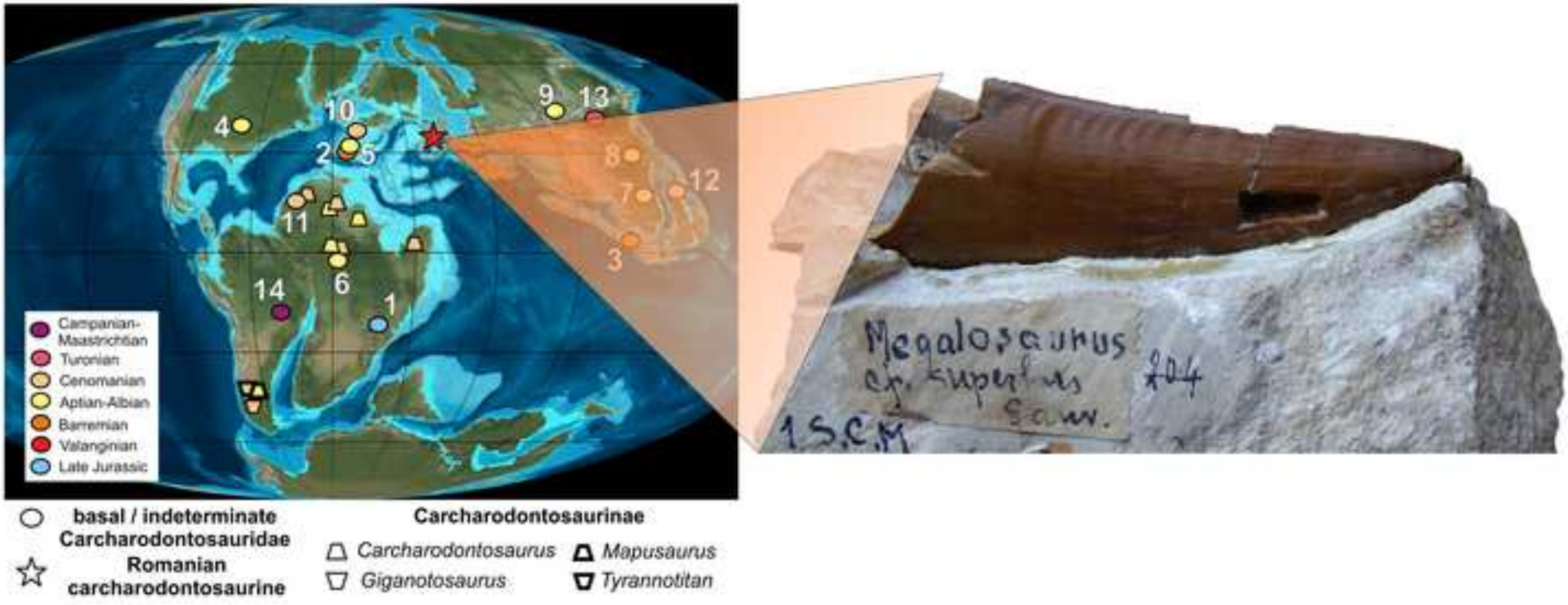
Page 60, lines 1475-1484: Rauhut and Werner (1995) kept before Richter et al. (2013) and Royo Torres et al. (2009), according to the alphabetical ordering we followed.

Highlights

Research highlights

- An isolated, large theropod dinosaur tooth from Romania is referred to Carcharodontosauridae
- The Romanian carcharodontosaurid is Valanginian in age, the oldest Cretaceous record of the clade
- This occurrence supports dispersal from Europe to west-Gondwana during the mid-Early Cretaceous

Graphical Abstract



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

Zoltán Csiki-Sava[1*], Stephen L. Brusatte[2], Ștefan Vasile[1]

[1] Department of Geology, Faculty of Geology and Geophysics, University of Bucharest, 1 Nicolae Bălcescu Boulevard, 010041 Bucharest, Romania~~, zoltan.csiki@g.unibuc.ro, yokozuna_uz@yahoo.com~~

[2] School of GeoSciences, University of Edinburgh, Grant Institute, James Hutton Road, Edinburgh, EH9 3FE, United Kingdom~~, Stephen.Brusatte@ed.ac.uk~~

* Corresponding author

zoltan.csiki@g.unibuc.ro

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 Hațeg 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 evolved 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 Aptian, illustrating the importance of palaeogeographic ties between these two realms during the largely mysterious early–mid Early Cretaceous.

Keywords

~~Romania~~Southern Dobrogea; ~~Lower Cretaceous~~Valanginian; ~~Theropoda;~~ Carcharodontosauridae; cratonic Europe; palaeobiogeography

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 Early Cretaceous bauxite accumulations of Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997; Posmoșanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Hațeg, Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the dinosaur-dominated 'Hațeg 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 ‘Hațeg 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 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~~, in prep.~~; 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 split, but originated earlier, and perhaps in Europe, suggesting faunal interchange between Europe and Gondwana during the ‘dark ages’ of the early Early Cretaceous.

Abbreviations: UAIC – University “Alexandru Ioan Cuza”, Iași, Romania.

2. History of collecting and curation

Only two dinosaurian fossils are currently known from the cratonic areas of Romania: an isolated theropod tooth and an isolated caudal vertebral centrum. Both of these were reported from the Lower Cretaceous deposits of Southern Dobrogea (southeastern Romania; Csiki-Sava et al., 2013, see also below). Unfortunately, exact details of their discovery and places of origin are lost, a fact that can hinder an assessment of their age and interpretation of their phylogenetic and palaeobiogeographic significance. Our aim here is to gather and report all available information concerning the collecting of specimen UAIC (SCM1) 615, that is, the isolated theropod tooth reported by Simionescu (1913; Fig. 2A).

According to the existing information - unpublished museum labels and records, and the preliminary publication of Simionescu (1913) - specimen UAIC (SCM1) 615 was discovered in the surroundings of Cochirleni, a small village south of Cernavodă and close to the right bank of the Danube, in Southern Dobrogea, southeastern Romania (Fig. 1), probably shortly before 1913, the date of its publication by Simionescu (1913).

Although studied and preliminarily described by Simionescu, UAIC (SCM1) 615 was not collected by Simionescu personally. Instead, it was donated by a certain “de Tomas” (also mentioned as ”de Thomas” in the registry of the Hârșova Museum) to V. Cotovu from Hârşova (Central Dobrogea), a local teacher, archaeology and natural history aficionado, and amateur fossil collector (see, e.g., Covacef, 1995). Cotovu, described by Simionescu himself as the “zélé fondateur et directeur du muséum de Hârşova” (*enthusiastic founder and director of the Hârşova Museum*; Simionescu, 1906: p. 2), had previously provided fossil specimens from Southern Dobrogea for study to Simionescu, a nationally acknowledged popular science writer and scientist, whom Cotovu knew personally (Brânzilă, 2010). These circumstances are supported by the fact that in the original description, Simionescu figures the specimen as being accessioned in the “Regional-Museum von Harschowa” (*Hârşova Regional Museum*; Simionescu, 1913: p. 687, fig.1), a designation he also used to refer to other Dobrogean

specimens not collected by him first-hand (e.g., a specimen of '*Nautilus' pseudoelegans* from Cernavodă, or a fragmentary tooth-bearing palatal fragment referred to as '*Coelodus*' sp., also originating from Cochirleni; see Simionescu, 1906). Confirming this deduction, an isolated tooth appears accessioned in the old registry book of the Hârşova Museum (under specimen number 200) as "*Megalosaurus* cf. *superbus*", with the mention that it was "*described by Prof. Simionescu in the Centralblatt f. min. etc*.". This is also the case of the '*Coelodus'* sp. specimen from Cochirleni (specimen number 86), similarly clearly identified as being described by Simionescu in the registry book.

Both of these vertebrate remains from Dobrogea that were formerly part of the Hârşova Museum collections are currently accessioned in the palaeontology collections of the UAIC (Turculeț and Brânzilă, 2012), suggesting that, at one moment, several specimens were transferred there from the Hârşova Museum. Although no details are known about this transfer, it is probable that it took place right before (or when) the Hârşova Museum, including a part of its collections, was burned and largely destroyed during WWI, in 1916, a time when Simionescu still held a position at the UAIC.

After its original description, specimen UAIC (SCM1) 615 underwent a minor amount of damage (see below, Description). Also, at some point between its description in 1913 and the early 1960s (when the specimen was found in its present state in the collections of the UAIC by academic staff members who are still alive today and recall the discovery; I. Turculeț, personal communication, May 2013) it was glued into a limestone matrix holder, while it was obviously completely freed of the surrounding matrix when it was described and figured in 1913 (Fig. 2). The circumstances under which these alterations took place are unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the spring of 1944, the frontline between the German-Romanian and Soviet armies reached the Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

were packed in crates, and moved together with its personnel and other possessions to Zlatna, in the Apuseni Mountains (western Romania), to safeguard them from any potential damage. Mounting the specimen into the limestone stand would have been a quick way to stabilize it, as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă, personal communication, April 2103). If that was indeed the case, the mounting would have taken place without the knowledge of Simionescu, who left Iași and the UAIC in 1929, being invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă, 2010). Then again, however, Simionescu himself or staff of the Hârşova Museum might have re-mounted the tooth after its original description, or else the mounting might have taken place after the return of the collections to Iași, after WWII.

Unfortunately, it is not documented whether the mounting was made using the original matrix, or if a trough corresponding to the tooth outline was carved into a randomly chosen limestone block. The apparently excellent fit between the tooth and the depression housing it (Fig. 2B, 3) suggests that this operation was completed carefully, and accurate carving of a fake holder is difficult to reconcile with the rush accompanying the evacuation of the Iași University, in 1944. Alternatively, the presence of a hand-written old registration number on the specimen holder would support its early re-mounting, while still at the Hârşova Museum. As noted previously, the original Hârşova Museum registration number of the specimen was 200, which does not correspond to that currently written both on the limestone holder and on a paper sticker (204). However, according to the old collection registry of the Hârşova Museum, specimen numbers 201 through 225 were given to a series of “indeterminate (fossil) bone fragments” from the “Cochirleni quarries”. Thus, these specimens (now apparently lost) came from the same locality as the tooth, and they were collected and donated by the same person to the Museum who donated UAIC (SCM1) 615. There is, thus, a (albeit admittedly remote) possibility that the registration numbers were

mixed up during the re-mounting of the specimen, which in this case took place at an early date in the Hârşova Museum. If this is indeed the case, the limestone used as holder could have been the same as the original matrix of the specimen.

To conclude, the history of recovery and curation of the historically important dinosaurian specimen UAIC (SCM1) 615 is rather convoluted and clouded by many uncertainties. The exact date of discovery remains conjectural, and the exact place of the discovery (thus also the original geological context of the tooth) is even more ambiguous. The current state of the specimen, and especially its mounted status, suggest a curatorial history that produced a moderate amount of damage to, but also partially obscured the detailed morphology of the specimen. The convergence of such unfortunate events makes deciphering the age, identity and evolutionary significance of the specimen troublesome, although many lines of evidence, carefully considered, allow us to draw reasonable conclusions (see below).

3. Geological setting

According to the available collecting information, the isolated theropod tooth UAIC (SCM1) 615 was discovered at Cochirleni (sometimes noted more specifically as the "*Cochirleni quarry*" or "*Cokerleni quarry*"). Cochirleni is a small village in southwestern Dobrogea situated close to the right bank of the Danube, and about 9 km south of the main urban center of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).

Southern Dobrogea is a cratonic area corresponding to the southeastern corner of Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984; Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,

2010), researchers agree that it became integrated into the main European Craton towards the end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine: Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001; Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

The Precambrian basement of Southern Dobrogea is overlain by a flat-lying sedimentary cover that begins with the lowermost Palaeozoic and ends with the uppermost Neogene. The sedimentary succession is interrupted by a few major, as well as several less important, sedimentary hiatuses that separate 5 main sedimentary sequences corresponding to the Cambrian–Upper Carboniferous, the Permian–Triassic, the Middle Jurassic–Cretaceous, the Eocene–?Oligocene, and the middle Badenian (middle Miocene)–Upper Pliocene. The Palaeozoic and lower Mesozoic are known only from the subsurface of Southern Dobrogea, but Cretaceous and Cenozoic deposits have limited exposures along the main water courses of the region (Ionesi, 1994; Mutihac and Mutihac, 2010).

The outcropping Cretaceous in Southern Dobrogea is represented mainly by shallow marine, carbonate platform deposits in the lower part of the system, replaced by more open-water, chalky facies towards the later part of the period (e.g., Avram et al., 1993, 1996; Dragastan et al., 1998; Dinu et al., 2007); these crop out only as isolated patches along the main watercourses of the region (Fig. 1).

The Lower Cretaceous Series consists of several lithostratigraphic units with complex, partially overlapping and interfingering relationships (Dragastan et al., 1998, 2014). The lowest (and only artificially) outcropping unit is the Purbeck-type, siliciclastic-evaporitic Upper Kimmeridgian–Lower Berriasian Amara Formation that represents lagoonal to continental environments. This unit is covered by the shallow-marine, richly fossiliferous and locally reefal limestone-dominated Cernavodă Formation (restricted-open lagoonal to

carbonate platform, Upper Berriasian–Lower Hauterivian). A time-correlative unit of the Cernavodă Formation, the limestone-dolomitic Dumbrăveni Formation (Upper Berriasian–Lower Hauterivian), is restricted to the southeastern part of Southern Dobrogea. The Cernavodă and Dumbrăveni formations are covered unconformably by dominantly calcareous deposits with hippuritoid ('pachyodont') coquinas, small reefs and lens-like orbitolinid accumulations, referred to the Barremian–Lower Aptian Ostrov Formation by Dragastan et al. (1998), but to the Ramadan Formation (in part) by Avram et al. (1993, 1996). These deposits, formed in littoral to lagoonal and open reef terrace environments, are in turn capped by the fluvial-lacustrine, siliciclastic deposits of the Gherghina Formation, with Middle–Upper Aptian kaolinitic clays and thin coal intercalations. The Lower Cretaceous succession ends with the transgressive, glauconite-bearing, coastal to sublittoral siliciclastic deposits of the Cochirleni Formation (uppermost Aptian–Albian).

The Upper Cretaceous has a significantly more patchy development, mainly restricted to the eastern part of Southern Dobrogea, excepting the weakly glauconitic, chalky-sandy Peștera Formation (Lower Cenomanian) and the marly Dobromiru Formation (Upper Cenomanian) that cover the western-central parts of the area. The younger Cuza Vodă (Turonian), Murfatlar (Santonian–Lower-Middle Campanian), and Satu Nou (Upper Campanian) formations are dominantly chalky, suggesting the instalment of a relatively deeper, offshore depositional environment; neither of these units is known from western Southern Dobrogea.

In total, the Lower Cretaceous of Southern Dobrogea was deposited in a shallow marine, near-shore setting, fluctuating between carbonate platform, lagoonal, coastal-tidal flat, and continental environments (see Avram et al., 1996; Dragastan et al., 1998). Its main characteristic features, such as the observed lithological variability, the areal distribution of the different units, and the presence of several unconformities within the series, are all linked

to eustatic sea-level changes that affected the Southern Dobrogean territory during the Early Cretaceous (Dragastan et al., 1998). The main emergent land in the area was represented by the Central Dobrogean Massif, lying north of the study area, almost completely subaerially exposed and actively eroding during the Cretaceous. Consequently, shallow-marine to continental deposits are restricted mainly to the northern part of Southern Dobrogea, close to its boundary with the Central Dobrogean Massif (marked by the Capidava-Ovidiu Fault), and are replaced by more open marine deposits southward. As summarized above, several littoral, and even continental, sequences occur in this succession, including deposits in the Amara, Cernavodă, Ramadan (~~in part;~~ Avram et al., 1996) and Cochirleni formations, whereas the Gherghina Formation is purely continental, with occasional minor marine interbeds produced during short-term ingressions of the sea.

In the Cernavodă-Cochirleni area the outcropping Mesozoic is restricted to the Lower Cretaceous, and includes deposits belonging to the Cernavodă, Ostrov (or Ramadan), Gherghina, and Cochirleni formations. While the lower–middle part of the Cernavodă Formation is well exposed and widely distributed in this area, its upper part (the lower Hauterivian Vederoasa Member) is unevenly developed. This member is missing in the classical succession from Cernavodă-Hinog, on the right bank of the Danube (Dragastan et al., 1998), but was recently identified in the more eastern Cernavodă-lock section (Dragastan et al., 2014). Similarly, the Ostrov Formation is represented in the area only by its upper subunit (the Lower Aptian Lipniţa Member; Dragastan et al., 1998), covering unconformably and transgressively the Valanginian Alimanu Member of the Cernavodă Formation in the southern end of the Cernavodă-Hinog section (Dragastan et al., 1998), and the lower Hauterivian Vederoasa Member in the Cernavodă-lock section (Dragastan et al., 2014).

Northward of the Hinog area, Valanginian deposits of the Alimanu Member are overlain directly by the Middle–Upper Aptian continental deposits of the Gherghina

Formation. These continental deposits also cover the *Orbitolina*-bearing calcareous-clayey deposits of the Lipniţa Member towards the south, marking the advancement of emerged areas towards the central parts of Southern Dobrogea, including the Cernavodă-Cochirleni area, during this time interval (Avram et al., 1996). Marine conditions returned in the study area again in the latest Aptian, with a transgression marked by widespread deposition of the glauconitic, siliciclastic coastal to innermost shelf deposits of the Cochirleni Formation. These uppermost Aptian to Albian sands and sandstones cover transgressively all the underlying deposits, belonging to the Cernavodă, Ostrov, or Gherghina formations. Siliciclastic shallow-marine sedimentation continued into the Early Cenomanian, with the chalky-glauconitic deposits of the Peștera Formation.

4. Palaeontology

The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu (1913), who referred it to *Megalosaurus* cf. *superbus*, a taxon erected by Sauvage (1882) from the Gault (‘mid’-Cretaceous: Albian) of the Paris Basin, France. The Gault material described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it and the type species *M. bucklandi*.

The convoluted taxonomic history of *Erectopus superbus* was recently reviewed by Allain (2005), who established that both the isolated teeth first mentioned by Sauvage (1876) and the skeletal elements described by Sauvage (1882) belong to the same taxon, for which the name *Erectopus superbus* was retained. Allain (2005) regarded *Erectopus* as a member of

Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al. (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.” Accordingly, if we are following the original assessment of Simionescu (1913) but updating with contemporary taxonomy, the Cochirleni theropod tooth should now be considered referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to *Erectopus superb*us (or a close relative) was considered to be unsupported by positive evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B, 3), we provide here a detailed description of its morphology followed by a thorough comparative study of this tooth based on large datasets of theropod dental measurements and discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).

We note that in his review of Romanian dinosaurs, Grigorescu (2003) erroneously considered UAIC (SCM1) 615 as being referred by Simionescu to the taxon *Megalosaurus dunkeri* Kohen (sic; actually, *Megalosaurus dunkeri* Dames, 1884). This is clearly a simple misreading of Simionescu’s identification. Additionally, such a referral is also contradicted by the absence of mesial serrations in the holotype tooth of *M. dunkeri*, considered by Carrano et al. (2012) to represent an indeterminate theropod. The Dobrogea tooth, on the other hand, has mesial serrations (see below).

4.1. Age of UAIC (SCM1) 615

The age of UAIC (SCM1) 615 has been contentious, due to the uncertainties concerning its place of origin. Although it is often mentioned as originating from Cochirleni village (e.g., Grigorescu, 2003; Turculeț and Brânzilă, 2012), this has not been definitively established. According to the original report of Simionescu (1913), the tooth came from the upper part of

the Lower Cretaceous limestone succession exposed in the cliffs extending from Cernavodă to Cochirleni along the right bank of the Danube. The corresponding entry from the Hârșova Museum registry states that it was found in the 'Cochirleni quarry', a location that presently cannot be identified precisely. The only rocks to be quarried in the area are the calcareous deposits of either the Cernavodă or Ostrov formations, particularly the ones that crop out in the Danube bank cliffs between Cernavodă-Hinog-Cochirleni. Finally, although the mention 'Cochirleni' is usually considered to refer to Cochirleni village, it should be mentioned that the cliff-forming hill that extends between Cernavodă and Cochirleni is also known by the same name (Fig. 1). Taking all of this evidence into consideration, it is thus reasonable to conclude that the tooth was most likely found in the Lower Cretaceous limestone succession exposed in the Danube cliffs between Cernavodă and Cochirleni.

Based on the location of the discovery, in the upper part of the local limestone succession, and the age of the deposits from Cernavodă-Cochirleni known to him, Simionescu (1913) considered the tooth to be of Barremian age. Subsequently, the age of the tooth was given as Valanginian–Barremian (Weishampel, 1990; Weishampel et al., 2004) or Valanginian (e.g., Grigorescu, 2003), but without any supporting information.

New attempts have been made to more precisely constrain the age of UAIC (SCM1) 615. Dragastan et al. (2014) recently sampled the limestone matrix holder of the tooth, and reported from these samples an assemblage of foraminiferans, ostracods and microproblematicae (=*incertae sedis* microorganisms) that characterize their 'Biozone IX with *Meandrospira favrei*', of latest Valanginian age in the local lithostratigraphic scheme. In parallel, we also sampled the same limestone holder – a yellowish white, friable lime mudstone – that yielded a poor and badly preserved calcareous nannoplankton assemblage with *Watznaueria barnesiae, W. ovata, Nannoconus steinmanni*, *N. kamptneri*, *N. globulus*, *Calcicalathina sp*., *Speetonia colligata* and *Cyclagelosphaera deflandrei* (M. C. Melinte-

Dobrinescu, personal communication, November 2013), an assemblage that suggests a Berriasian–Hauterivian age of the limestone holder.

Since it is not clear if the limestone holder came from the same site as the tooth itself, we managed to take a second sample from the limestone matrix still partly filling the pulp cavity of the tooth, which must definitively be identical with the rocks the tooth was found in. This second, much smaller sample yielded only very scarce specimens of *Watznaueria barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in abundance during the Berriasian and, especially, the Valanginian.

In the nannoplankton succession reported previously by Avram et al. (1993) and derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu Member of the Cernavodă Formation. These assemblages were interpreted to represent the nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous of the Mecsek Mountains, Hungary, by Császár et al. (2000).

Together, all the available evidence (Simionescu’s original account, geographic and geologic records, foraminifera, ostracods, microproblematicae, and calcareous nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member of the Cernavodă Formation, and it is most probably of late Valanginian age.

4.2. Description and comparisons

Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2, 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown

base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is remarkably well preserved, with the enamel in pristine condition. It preserves most of the crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5 mm missing in the apical region.

In its present state, the mesial edge and part of the mesial third of the tooth are embedded in the limestone holder (Fig. 2B), although the tooth was once removed (see above, History of collecting and curation; Fig. 2A). Accordingly, it is exposed so that all faces of the tooth are widely visible, including the root region, except for the mesial surface.

Only the basal-most part of the root is preserved, and it is more complete near the mesial margin (Fig. 3B, C). Here, broken areas around the crown-root contact area (cervix) reveal details of the pulp cavity development, as well as the pattern of the dentine thickness variation (Fig. 3B–D). The crown also exhibits a transverse break at about two-thirds of its length (not present so obviously in the original figure of the specimen in Simionescu, 1913), and adjacent to it, the distal carina is also slightly chipped distal to mid-length. The labial face is superficially split near this break (Fig. 3A), while a more prominent region of damage appears on the lingual face, where a large (13 x 5 mm), slightly triangular wedge is broken off, exposing the deeper parts of the dentine (Fig. 3C). The damage to the lingual side apparently occurred after the original description of the tooth (Fig. 2), an observation that is concordant with the complex curatorial history of the specimen.

The basal-most, exposed part of the mesial face lacks the enamel cover (Fig. 3C, D), suggesting that this area already belongs to the root region. The mesial edge of the preserved crown base appears to be wider than the distal one, and is largely rounded transversely. Accordingly, the basal cross-section is teardrop-shaped (lanceolate); it is rounded mesially, but narrows distally into a small carina (Fig. 3D). As mentioned above, the pulp cavity is

exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B). Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped (Fig. 3D).

The tooth is ziphodont and only very slightly recurved distally. The distal edge is nearly straight across its length, being very mildly concave in its basal half and slightly convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the tooth crown base. The mesial edge, as shown in the original publication of Simionescu (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually compressed (Fig. 3B), with a crown base ratio (CBR=CBW/CBL) of 0.56, within the normal range of variation of most theropods. This differs from the thinner teeth of some, but not all, carcharodontosaurids (CBR<0.50), and the much thicker incrassate teeth of derived tyrannosauroids and conical teeth of spinosaurids (CBR>0.75) (Sereno et al., 1996; Brusatte et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).

The crown cross-section is slightly asymmetrical labiolingually when it is seen in distal view. In this view, when the carina is facing directly distally, one side of the crown has a more pronounced bulge than its counterpart (about 8.5 mm wide, measured from the carina, vs. 6 mm on the other side; Fig. 3B); based on comparisons with the teeth of *Mapusaurus* (Coria and Currie, 2006), the more bulging side can be interpreted as the lingual one. This asymmetry diminishes apically, where both sides become about equally convex. The distal carina itself twists slightly sideways (labially) in apical direction, such that it is located closer

to the labial face where it terminates at the crown apex, and the lingual face of the denticles is exposed distally (Fig. 3B, F). This twist of the distal carina is accompanied by a similar outline of the lingual side; in distal view, this is somewhat convex basally, but becomes flat to slightly concave in the apical two-thirds of the crown. A similar S-shaped curvature of the crown, albeit more pronounced and different in details, was also reported in *Mapusaurus* and *Giganotosaurus* (Coria and Currie, 2006), and in indeterminate carcharodontosaurid teeth from Morocco (Richter et al., 2013).

The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with minute serrations across its entire preserved length; the denticles are proximodistally subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig. 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so it is not possible to determine whether the serrations continued over the apex of the tooth. There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the carina. Serration shape and size remain relatively constant across the carina, although the serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig. 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F). Changes in serration size are gradual across the carina, not sudden or sporadic.

Although they are all more or less rectangular in shape, the apical denticles are relatively shorter proximodistally than the more basal ones. Most of the denticles have slightly rounded, asymmetrically convex triangular tips, instead of being simply squarred-off, and they do not hook as in troodontids and to a lesser extent abelisaurids (Hendrickx and Mateus, 2014). Other denticles near the apex, however, show a faint concavity along their tips, giving them a bilobate aspect, although this is both less conspicuous and far less regularly developed than reported in *Tyrannotitan* (Novas et al., 2005). The denticles are

separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length. The interdenticular space between adjacent denticles is broad, measuring more than a third of the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These sulci are so short and indistinct that they are only visible under low angle light.

Little can be said about the mesial carina, as it is not visible in the current state of the specimen, buried in the limestone matrix. Based on the description of Simionescu (1913), however, it is covered across its length with minute serrations; these decrease in size towards the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles) per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus, 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii* where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*’ *superbus* (Sauvage, 1876, 1882) in this respect.

The external enamel surface exhibits two forms of ornamentation. First, the majority of the labial and lingual faces are covered by relatively smooth enamel that exhibits a subtle form of braided texture visible under low angle light (Fig. 3A, C, E). This texture is made up of a series of very faint, apico-basally running ridges; these are of unequal lengths, starting at different points of the crown height, but none extends the whole length of the crown. The two longest ridges are placed near the distal carina. The enamel is also finely granulated.

Second, near the carinae on both labial and lingual surfaces there are marginal undulations: wrinkles in the enamel that stand out in bas relief (Brusatte et al., 2007). These are much better preserved and visible near the distal carina, where they are so pronounced

that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly developed wrinkles are present along the crown height; in the basal half of the crown, the wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer than twice the space separating each undulation. The wrinkles project obliquely (in the mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal segment on the crown, and curve apically as they approach the carina (at about 45^{o}) with a tendency to become tangential to the distal edge. The wrinkles are especially well developed, prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig. 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm). Apically, however, the wrinkles are somewhat wider and longer, extending over about half of the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the crown in wrinkle development as well, these being better expressed on the more rounded, convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the presumed labial face, only some of the basal-most wrinkles, particularly the second and third one, appear well defined.

Towards the base of the crown a few of the wrinkles continue across the labial and lingual surfaces as very subtle transverse undulations. Most conspicuous of these is a 3.5 mm wide horizontal swelling that crosses the crown, at the level of wrinkles 2 and 3; this swelling is clearly visible on both sides of the crown (Fig. 3. A, C). There are no lateral flutes, apico-basal ridges, or longitudinal grooves on the labial or lingual faces, either in the centre of the tooth or paralleling the carinae. Instead, the labial and lingual faces are uniformly convex, giving the tooth its teardrop-shaped outline in cross section.

5. Discussion

5.1. *Identification of UAIC (SCM1) 615*

The isolated tooth from Cochirleni can be referred to Theropoda based on its large size, recurved and labiolingually compressed morphology, and presence of a continuous series of well-defined serrations on the distal carina.

Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are also known to posess remarkably theropod-like, laterally compressed and serrated teeth, not unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are significantly smaller than the Southern Dobrogean specimen, especially in the case of the Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest, caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615; moreover, these teeth are slightly conical and less laterally compressed than the Southern Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true denticles along their carinae) are reported in Europe only beginning in the Albian (Ősi et al., 2015), and these are both significantly smaller and different in morphology from the Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a theropod tooth.

We used four techniques to identify which type of theropod UAIC (SCM1) 615 likely belongs to (see also Supplementary Material).

First, we conducted a Principal Components Analysis (PCA) based on a large database that includes a broad and representative sample of theropod teeth. This dataset was compiled by Hendrickx et al. (2015a), which built upon the earlier studies of Smith et al.

(2005) and Larson and Currie (2013), and it or a similar version has been used in recent studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, ~~2013~~2014; Brusatte and Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL, CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to this dataset, the data were log-transformed prior to analysis, missing values for measurements were estimated with a mean value for that measurement from across the sample, and then a PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17 (Hammer et al., 2001).

In the resulting two dimensional morphospace (Fig. 4), UAIC (SCM1) 615 plots close to many teeth belonging to carcharodontosaurids, along with some teeth belonging to spinosaurids and tyrannosauroids. It falls within the convex hull (maximum morphospace occupation area) of carcharodontosaurids only, although it is closely outside of the edges of spinosaurid and tyrannosauroid space. It also falls within the 95% confidence interval ellipse for carcharodontosaurids, but not within the ellipse of any other group (Supplementary Information). This exercise indicates that UAIC (SCM1) 615 is most similar to carcharodontosaurids.

Secondly, we used the log-transformed dataset that we also used for the PCA to conduct a clustering analysis. We performed the analysis in PAST v2.17, using the paired group algorithm and the correlation similarity measure. In the resulting dendrogram, UAIC (SCM1) 615 groups with a handful of teeth belonging to carcharodontosaurids, tyrannosauroids, and *Allosaurus* (Supplementary Information).

Third, we used the tooth measurement database to conduct a discriminant analysis in PAST v3.0 (Hammer et al., 2001). This analysis uses pre-determined groups (in this case, taxonomic clusters) to create a morphospace in which these groups are maximally separated.

This allows teeth of unknown affinities, such as UAIC (SCM1) 615, to be classified according to which taxonomic group it is most similar to in this discriminant morphospace. In total, 67.79% of other teeth are classified correctly when they are treated as having uncertain affinities and their measurements are used to classify them in discriminant space, indicating that this exercise returns reasonable results. Our analysis classifies the Romanian tooth as a carcharodontosaurid. Furthermore, the analysis places UAIC (SCM1) 615 within the convex hulls for carcharodontosaurids and tyrannosauroids, and the 95% confidence ellipses for carcharodontosaurids, coelophysoids, and neovenatorids.

Fourth, we ran a phylogenetic analysis by including UAIC (SCM1) 615 in the discrete character dataset of theropod dental features published by Hendrickx and Mateus (2014). The Romanian specimen was scored as a lateral tooth in this analysis. The analysis was conducted in TNT (Goloboff et al., 2008), and resulted in 224 most parsimonious trees (686 steps, consistency index of 0.338, retention index of 0.566). The strict consensus topology is moderately well resolved and places the Romanian tooth as the sister taxon to *Carcharodontosaurus* (Supplementary Material). This sister taxon pair is recovered as the sister clade to a grouping of the derived carcharodontosaurids *Mapusaurus* and *Giganotosaurus*.

Several synapomorphies support the carcharodontosaurid affinities of UAIC (SCM1) 615. The sister group relationship with *Carcharodontosaurus* is supported by two features: a roughly straight distal margin of the crown (character 68) and pronounced marginal undulations in the enamel that are well visible in normal light (character 112). The broader clade of UAIC (SCM1) 615, *Carcharodontosaurus*, *Mapusaurus*, and *Giganotosaurus* (= Carcharodontosaurinae, as defined by Brusatte and Sereno, 2008, and Carrano et al., 2012) is linked by numerous characters, including: large teeth with a crown height greater than 6 cm (character 65), a bowed or sigmoid distal carina in distal view (character 82), marginal

undulations that are at least twice as long mesiodistally as the space separating each undulation (character 111), and marginal undulations present on both mesial and distal sides of the crown (character 113).

The Romanian specimen also lacks many keystone dental synapomorphies of other theropod clades, based on the clade diagnoses of Hendrickx and Mateus (2014) and other cladistic studies that include dental characters. UAIC (SCM1) 615 does not possess the hooked distal denticles of some Abelisauridae, the strongly labially deflected distal carina and pronounced transverse enamel undulations extending across the labial and lingual tooth faces of Ceratosauridae, the incrassate teeth with apicobasal enamel flutes and deeply veined enamel surface texture of Spinosauridae, and the large transverse undulations of some basal allosauroids (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of derived tyrannosauroids (Brusatte et al., 2010a) and the large and strongly hooked (or pointed) denticles of troodontids and therizinosauroids (e.g., Turner et al., 2012; Brusatte et al., 2014; Hendrickx and Mateus, 2014). The large size, as well as recurved and ziphodont shape of UAIC (SCM1) 615 is strikingly different from the non-ziphodont therizinosauroids, ornithomimosaurs, alvarezsauroids, and most troodontids, which have conical, leaf-shaped, or peg-like teeth (when teeth are present) (e.g., Holtz et al., 2004a; Turner et al., 2012; Brusatte et al., 2014). Finally, besides its remarkably large size, the presence of serrations indicates that UAIC (SCM1) 615 does not belong to groups such as alvarezsauroids, oviraptorosaurs, basal troodontids, or avialans, which have unserrated crowns (e.g., Turner et al., 2012; Hendrickx and Mateus, 2014).

In summary, the four analyses all support carcharodontosaurid affinities for UAIC (SCM1) 615. Both overall tooth proportions and discrete phylogenetic characters point to a carcharodontosaurid identification, and the discriminant function analysis and phylogenetic analysis both explicitly recover the tooth as a carcharodontosaurid. For this reason we refer

this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as recovered in our analysis, is congruent with results of previous analyses based on larger sets of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno, 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015), and offers some support for considering the Romanian carcharodontosaurid from Southern Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

Two final notes are worth adding. First, our analyses also incorporated carcharodontosaurids that are usually found to be basal within the clade, such as *Acrocanthosaurus* and *Eocarcharia* (e.g., Harris, 1998; Sereno and Brusatte, 2008; Carrano et al., 2012) as well as a host of other allosauroids, including members of Neovenatoridae (*Neovenator*, *Australovenator* and *Fukuiraptor*), a clade that is often recovered as sister-taxon to carcharodontosaurids within Carcharodontosauria (e.g., Benson et al., 2010; Carrano et al., 2012; but see Novas et al., 2013; Porfiri et al., 2014, for an alternate placement of neovenatorids in general). Both PCA and phylogenetic analysis clearly identified UAIC (SCM1) 615 as more closely comparable morphologically to derived carcharodontosaurids than to either basal carcharodontosaurids or to any other allosauroid subclade.

Second, our datasets also included teeth of *Erectopus*, the genus erected for ‘*Megalosaurus’ superbus* to which UAIC (SCM1) 615 was originally referred. Again, our analyses clearly indicate that there are no close morphological and morphometric similarities between the two, which is in accordance with the suggestion of Carrano et al. (2012) that *Erectopus* represents a non-carcharodontosaurid taxon, while our analysis identifies UAIC

(SCM1) 615 as a carcharodontosaurid. Instead, *Erectopus* groups with abelisauroids in the phylogenetic analysis. This is somewhat surprisingly, as Allain (2005) and Carrano et al. (2012) both identified *Erectopus* as a tetanuran. It should be noted, however, that Albian-aged abelisauroids are known from the same general area (eastern France) as that yielding the material referred to *Erectopus* (Accarie et al., 1995; Carrano and Sampson, 2008), raising the intriguing possibility that this taxon may represent an abelisauroid instead of an allosauroid tetanuran as suggested by Allain (2005) and Carrano et al. (2012). However, it must be remembered that this phylogenetic analysis is based on dental characters only, so it is probably more likely that *Erectopus* is a tetanuran with a dentition convergent to some extent with those of certain abelisauroids.

5.2. Body size of UAIC (SCM1) 615

One of the most salient and remarkable features of UAIC (SCM1) 615 is its large size. In the large and comprehensive sample of theropod teeth from our dataset, tooth size (estimated based on crown height – CH, and used as a rough proxy of body size) ranges from 2.2 mm (in the dromaeosaurid *Saurornitholestes* and the coelurosaur of uncertain affinities *Richardoestesia*) to 117.1 mm in the gigantic tyrannosauroid *Tyrannosaurus*. The Romanian specimen UAIC (SCM1) 615, with a CH of 85.5 mm, is ranked in the 60-80% maximum size (~ CH) range of the sample, and has a CH that is 73% of the largest tyrannosauroid teeth. Most of the teeth in the dataset (over 61% of the 966 measured teeth) are very small to small (less than 25 mm CH), and less than 10% of these fall in the 60-100% CH size categories. Teeth larger than UAIC (SCM1) 615 make up less than 5% of the total sample, and they represent only five taxa: the megalosaurid *Torvosaurus*, the tyrannosauroid *Tyrannosaurus*, the basal carcharodontosaurid *Acrocanthosaurus*, and the derived carcharodontosaurines *Carcharodontosaurus* and *Giganotosaurus*. Compared to other carcharodontosaurids, UAIC

(SCM1) 615 is smaller than the largest teeth of *Acrocanthosaurus* (9% difference), *Carcharodontosaurus* (20%), and *Giganotosaurus* (12.5%) in the dataset, but is 13% bigger than the largest tooth of *Mapusaurus*.

It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Sereno et al., 1996; Calvo and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn, corroborates growing evidence that very large body size was acquired very early in carcharodontosaurid history, since the earliest potential members of the clade are already of relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.

The inferred large body size of the South Dobrogean theropod is also remarkable as virtually all other dinosaur remains reported previously from Romania (both from the Early Cretaceous Cornet assemblage and the much later, end Cretaceous Haţeg Island fauna) are significantly smaller, and many have been interpreted as insular dwarfs (e.g., Weishampel et al., 1993, 2003; Benton et al., 2006, 2010; Stein et al., 2010; Ősi et al., 2014). Although other Romanian theropod dinosaurs were not particularly dwarfed (e.g. Brusatte et al., 2013), they were nonetheless small (Nopcsa, 1902; Csiki and Grigorescu, 1998; Csiki et al., 2010; Brusatte et al., 2013). This bias towards small bodied Romanian theropods was also

interpreted as a consequence of their insular habitat (Csiki and Grigorescu, 1998), as all previously reported theropod remains come from within the Carpathian Orogen, an area with an archipelago-type palaeogeography during the Cretaceous (Dercourt et al., 2000; Csontos and Vörös, 2004; Csiki-Sava et al., 2015). By contrast, UAIC (SCM1) 615 was found in shallow marine deposits bordering the emerged areas of Central Dobrogea, part of the stable cratonic areas of Europe and connected at least intermittently to the Ukrainean Shield since the Late Jurassic (Fig. 5A). Although cratonic Europe was also transformed into an archipelago of islands during much of the Cretaceous, these islands were often both larger in size and more stable in space and time than were the transient emerged areas of the Tethyan archipelagoes. As such, it is conceivable that the Southern Dobrogean carcharodontosaurid was less constrained by space or resource limitations than the Tethyan insular dinosaurs, allowing it to retain a large body size.

5.*3. UAIC (SCM1) 615 and Valanginian dinosaur distribution*

Besides documenting the presence of large-sized mainland carcharodontosaurids in the Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a significant gap in our knowledge on the composition and distribution of the Early Cretaceous dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these being known from the later part (Barremian–Albian) of that epoch; only around a dozen localities were listed from each age of the early part of the Early Cretaceous (Berriasian, Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al., 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards

western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no occurrences are known from the entire central, eastern and southern Europe for the Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).

Our identification of the Romanian tooth as a carcharodontosaurid documents the presence of this clade in Europe in the very early Cretaceous. This is significant, as carcharodontosaurids were widely distributed tens of millions of years later, in the middle Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see below). Despite the recent discoveries documenting that the clade was also present in North America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010; see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than previously thought and were a long-term component of the European mainland Early Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might have been already present between the cratonic, stable European mainland, with a dinosaur fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania (Benton et al., 2006).

This Valanginian carcharodontosaurid represents an important datapoint not only for the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a poorly documented age in dinosaur evolution, with very few precisely dated fossil occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known from Asia, some of which have debatable or controversial dates. These include sites in Japan (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992; Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare dinosaur remains of possible Valanginian (or ‘Neocomian’) age were also reported from southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g., Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli et al., 2014).

As one of the two known reports of Valanginian dinosaurs in Europe east of France, the Southern Dobrogean dinosaur record fills a huge palaeogeographic gap between the western European and the eastern Asian dinosaur faunas. Moreover, none of these early Early Cretaceous dinosaur assemblages from outside Europe include carcharodontosaurids (see below), as theropods are represented by coelurosaurians interpreted either as compsognathids (Gishlick and Gauthier, 2007) or basal ornithomimosaurs (Choiniere et al., 2012) in southern Africa, metriacanthosaurid allosauroids (‘sinraptorids’) in Thailand (Buffetaut and Suteethorn, 2007), and indeterminate allosauroids (Pérez-Moreno et al., 1993), non-

carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz, 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest that carcharodontosaurids had not achieved a wide geographic distribution by this point in time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.

Finally, the presence of the Cochirleni carcharodontosaurid might hint at the presence of palaeobiogeographic provinciality between the western and the eastern parts of Europe, partly mirroring those reported from the later part of the Late Cretaceous (e.g., Le Loeuff and Buffetaut, 1995; Weishampel et al., 2010; Ősi et al., 2012; Csiki-Sava et al., 2015). In the reasonably well sampled, and significantly better known, western European dinosaur faunas, Valanginian large carnivorous dinosaurs include non-carcharodontosaurid tetanurans (*Becklespinax*), as well as indeterminate allosauroids or indeterminate theropods (often described as ‘*Megalosaurus’ dunkeri*, ‘*M.*’ *insignis* or ‘*M.*’ *oweni*), none of which can be referred positively to Carcharodontosauridae (Carrano et al., 2012). The apparently provincial geographic distribution of the large-bodied theropods suggests that some degree of faunal differentiation was occurring within the European mainland, most probably promoted by geographic distance. Notably, this intra-European differentiation in theropod assemblages appears to stand in contrast with the faunal homogeneity reported in the case of the ornithopods from the UK and Romania (e.g., Galton, 2009). It is important, however, to re-emphasize at this point that the Valanginian dinosaur fossil record is both exceedingly poor and patchy, even in Europe. Accordingly, further discoveries are needed to verify and support (or contradict) the presence of such a distribution pattern pointing to palaeobiogeographic provinciality inside Europe, as the one suggested by our carcharodontosaurid identification for UAIC (SCM1) 615.

5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography

Carcharodontosauridae were long considered as an exclusively Gondwanan group of theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996; Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Cau et al., 2013). This view started to change with the identification of the Early Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan one, was further supported by the discovery of definitive carcharodontosaurids in the Lower Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper Cretaceous of China (Brusatte et al., 2009, 2010b, 2~~1~~012; Mo et al., 2014; Lü et al., ~~2014~~2016).

Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin of the carcharodontosaurids, followed by their dispersal across Laurasia and western Gondwana beginning at least by the Aptian (Fig. 5B), a scenario that is concordant with the tentatively suggested presence of early carcharodontosaurids in the Upper Jurassic of Tanzania, which are based on fragmentary specimens (Rauhut, 2011; Carrano et al., 2012). It is also concordant with the widespread appearance of carcharodontosaurids in the fossil record starting with the Aptian, when they are reported in Africa (*Eocarcharia*; Sereno and Brusatte, 2008), South America (Vickers-Rich et al., 1999), North America (*Acrocanthosaurus*; Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000 Eddy and Clarke, 2011), Europe (Canudo and Ruiz-Omeñaca, 2003; Pereda-Suberbiola et al., 2012), and eastern Asia (*Kelmayisaurus*; Brusatte et al., 2012;~~ Lü et al., 2014;~~ Mo et al., 2014; Lü et al., 2016).

During the Albian–Turonian, carcharodontosaurids became especially abundant and diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and South America (*Tyrannotitan*, *Giganotosautus*, *Mapusaurus*, alongside with indeterminate carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005; Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig. 5B). They were still present during this time interval in other continents, as well: in North America with *Acrocanthosaurus* until the Albian (D'Emic et al., 2012), in Europe until the Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).

After dominating terrestrial ecosystems at least in Africa, South America and eastern Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado, 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana. Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-Cenomanian deposits of South America to Carcharodontosaridae (e.g., Canudo et al., 2008; Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were reported to suggest the survival of carcharodontosaurids into the latest Cretaceous (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).

Contrasting with this rich and relatively continuous fossil record of Carcharodontosauridae starting with the Aptian, the first half of its evolutionary history is very poorly documented (Fig. 5B). Prior to the identification of UAIC (SCM1) 615, only two occurrences of pre-Aptian Cretaceous carcharodontosaurids were reported, one from the Barremian of Spain (Ortega et al., 2010; Gasca et al., 2014) and the other from the Barremian of Thailand (Buffetaut and Suteethorn, 2012). The Early Cretaceous *Kelmayisaurus* from Xinjiang, western China, was recognized as a carcharodontosaurid of possibly ?Valanginian to Aptian in age by Brusatte et al. (2012), but the deposits yielding these remains (the Lianmugin, or Lianmuxin, Formation of the Tugulu Group) were dated as Aptian–Albian by Eberth et al. (2001; see also Tong et al., 2009). An important temporal gap – of about 20 to 28 millions of years, according to the dates in Gradstein et al. (2012) – thus stretched between the oldest, tentatively assigned carcharodontosaurids from the Oxfordian–Tithonian of Tanzania, including the formally erected *Veterupristisaurus* (Rauhut, 2011; see also Carrano et al., 2012), and those that started to appear in the fossil record in the Barremian and then spread widely during the Aptian. Referral of UAIC (SCM1) 615 to Carcharodontosauridae partially fills this frustrating gap, effectively halving this shadowy period in the evolutionary history of the group.

Furthermore, our analyses tentatively cluster the Dobrogean theropod with the derived members of the Carcharodontosaurinae to the exclusion of the more basal, but significantly younger non-carcharodontosaurine carcharodontosaurids *Eocarcharia* and *Acrocanthosaurus*. If this placement is correct, then the Romanian tooth indicates that Carcharodontosaurinae diverged from other carcharodontosaurids considerably earlier than hitherto recognized.

The previously known fossil record of the clade suggested that Carcharodontosaurinae originated sometime between the Aptian and Albian, as basal carcharodontosaurids (*Acrocanthosaurus*, *Concavenator*, *Eocarcharia*) were moderately diverse in the Barremian–

Aptian, followed by the appearance of many fossils of carcharodontosaurines beginning in the Albian (Fig. 5B). The proposed affinities of the oldest carcharodontosaurid material – including isolated teeth referred to as '*Megalosaurus*' *ingens* – from the east African Upper Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut, 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very large size and dental morphology characterizing it) well before the Albian, during or even before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.

Besides shifting the emergence of the carcharodontosaurines earlier in time, identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting palaeobiogeographic implications. As already noted, recent discoveries show that Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g., Novas et al., 2005), with the identification of its widespread, Pangaean distribution during the late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999; Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014). However, within Carcharodontosauridae itself, some palaeogeographic patterns have been widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al., 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as previously all its recognized members were restricted strictly to either Africa (Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995; Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of

Carcharodontosaurinae were still adhering to patterns of continental fragmentation and vicariant evolution, with a basal split between the Albian–Cenomanian African *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

This scenario is now challenged by our finding that the Southern Dobrogean carcharodontosaurid UAIC (SCM1) 615 may nest inside Carcharodontosaurinae. If true, such an affinity would suggest that the origin of Carcharodontosaurinae was not a southern, vicariant by-product of the Gondwana-Laurasia separation, a major palaeogeographic event that is considered to have been well underway by the end of the Jurassic, and essentially completed by the mid-Early Cretaceous (see Weishampel et al., 2010). Indeed, during this time palaeogeographic connections and faunal interactions were virtually non-existent between the northern Tethyan (European) and southern Tethyan (western Gondwanan, but essentially African) areas of the Mediterranean (e.g., Canudo et al., 2009~~; see below~~), which makes a vicariant hypothesis intuitive. However, if the Romanian tooth represents a carcharodontosaurine, then it implies a much more complicated palaeogeographic history of the clade, which is not so clearly linked to continental breakup.

The palaeogeographic position of the Southern Dobrogean carcharodontosaurine in cratonic Europe, north of the Neo-Tethys, together with its significantly older age compared to other carcharodontosaurines, could indicate that separation of the carcharodontosaurine lineage took part in Europe and not in western Gondwana as previously assumed. This would also mean that representatives of this lineage were subsequently – after the Barremian – introduced to Africa and South America via trans-Tethyan dispersal, most probably at a time when faunal interactions between the southern and northern margins of the Mediterranean Tethys were resumed, after the early Barremian (Canudo et al., 2009).

Alternatively, it can be hypothesized that appearance of carcharodontosaurines in Southern Dobrogea is a consequence of southern immigration originating in western Gondwana, often considered the place of origin for this clade. However, this scenario has several potential caveats. Although Europe has been considered as forming part of a larger Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín, 2012), and occasional trans-Tethyan faunal connections have been recognized between Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage, 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place during the 'Neocomian' (Berriasian–Hauterivian) time interval.

More recently, some potential evidence has emerged for Gondwana-to-Europe interchange during the 'Neocomian'. The presence of the basal rebbachisaurid *Histriasaurus* (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as indicative of very early and very rapid northward dispersal of this clade from western Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of this particular dispersal event was even constrained to the Berriasian–Valanginian time interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive transportation mechanism ('Noah's Ark'; ~~KcKenna~~McKenna, 1973) for basal rebbachisaurids after its separation from mainland Africa (e.g., Torcida Fernández-Baldor et al., 2011). Furthermore, the palaeogeographical separation between Africa and Adria (and thus the effective movement of the presumed ark) is considered to be at most an incipient one during the Early Cretaceous by Bossellini (2002) and Zarcone et al. (2010), with spatial continuity still present between the two landmasses, while deep-water basins continued to separate Adria from the European Craton. Accordingly, although the presence of *Histriasaurus* can represent a case of northward range extension of rebbachisaurids during the Berriasian–Valanginian, it took place not strictly speaking into Europe, but only reached the northernmost extremity of Adria, a northerly peninsular extension of the African mainland. It was only starting with the Barremian that rebbachisaurids dispersed as far north as the European cratonic areas, including Iberia and the British Isles (Mannion, 2009; Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011), a time when faunal interchanges between Europe and Africa are considered to have been well underway (e.g., Gheerbrant and Rage, 2006; Canudo et al., 2009).

Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant of the European mainland. It is thus unclear to what extent the example of rebbachisaurid range extension into (present-day) Europe during the early Early Cretaceous, as potentially testified by the discovery of the Croatian taxon, would also be applicable for the Southern Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are very different, and that faunal connections during this time interval are not documented between the African and European cratons as already pointed out by Gheerbrant and Rage (2006).

Absence of documented faunal interactions weakens support for a scenario of south-to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the Cretaceous, and would argue instead for a local, European development to explain the presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian presence of carcharodontosaurids in Europe is also consistent with their appearance in the Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in North America likely requires the presence of pre-Aptian members of the clade in Europe, since faunal exchanges between these two landmasses are known to have been halted before the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western Gondwana. The causes of these distribution patterns remain as yet unknown, and further support – in the form on new carcharodontosaurid discoveries from the early-middle part of the Early Cretaceous – is required to better uphold such a scenario.

We finally reiterate that if the Romanian tooth does not belong to a carcharodontosaurine, but instead is artefactually grouping with them in the phylogenetic analysis because of the very incomplete nature of the material, then the traditional story of Carcharodontosaurinae as a product of vicariant evolution driven by the breakup of Pangea will remain strongly supported. However, even in such case UAIC (SCM1) 615 would still record the presence of early-occuring large carcharodontosaurid theropods with a very characteristic carcharodontosaurine-type dentition in the eastern part of the European craton, adding to known early Early Cretaceous theropod (and dinosaur) diversity, and potentially documenting dinosaur faunal provinciality in Europe and worldwide.

6. Conclusions

We re-describe and interpret the affinities of one of the most significant historical dinosaurian specimens of Romania, an isolated but well-preserved theropod tooth from Southern Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth, while the available evidence – including novel calcareous nannoplankton sampling – supports its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of

Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this record advances our understanding of European dinosaur distribution during the early Early Cretaceous, and also fills an important palaeogeographic gap between Western European and Eastern Asian dinosaurian assemblages of the Valanginian.

Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a possible member of Carcharodontosaurinae, a subclade of derived and gigantic carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean specimen documents the emergence of Carcharodontosaurinae earlier than previously recognized, thus also indicating an earlier acquisition of their characteristically large size. Based on currently known palaeogeographic and chronostratigraphic constraints on the evolution of Carcharodontosauridae, it appears that not only did this clade have a wide distribution, but that crucial events of its evolutionary history such as the emergence of the derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia split, as was formerly suggested. In such a case, instead of endemic evolution the emergence of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into western Gondwana adds further support for the presence of important palaeogeographic ties between the two realms during the second half of the Early Cretaceous.

Acknowledgements

This research was supported by the National Research Council of Romania (CNCS) grant PN-IIID-PCE-2011-3-0381 and a Sepkoski grant of the Paleontological Society for Z.Cs.-S. S.L.B. is supported by a Marie Curie Career Integration Grant EC630652, the Division of Paleontology of the American Museum of Natural History, and the School of GeoSciences of the University of Edinburgh. He thanks Mátyás Vremir, Radu Totoianu, and Mark Norell for many hours of fun discussion on Romanian fossils, and for supporting his work and travel in Romania. We thank Mihai Brânzilă and Paul Ţibuleac (UAIC) for access to the specimen, for allowing us to collect samples for the nannoplankton analyses, and for their help and collegiality during our visit to Iaşi, as well as Ilie Turculeţ for sharing information about the history of the specimen. Mihaela C. Melinte-Dobrinescu has gracefully analyzed the nannoplankton samples derived from UAIC (SCM1) 615; her contribution was essential in assessing the age of the specimen. Finally, we thank the reviewers Eric W.A. Mulder (Denekamp, the Netherlands) and Xabier Pereda-Suberbiola (Bilbao, Spain), as well as Associated Editor Elena Jagt-Yazykova, for their useful comments and suggestions that helped improve ~~a~~ previous versions of the manuscript.

References

Accarie, H., Beaudoin, B., Dejax, J., Friès, G., Michard, J.G., Taquet, P., 1995. Découverte d'un dinosaure théropode nouveau (*Genusaurus sisteronis* n. g., n. sp.) dans l'Albien marin de Sisteron (Alpes-de-Haute-Provence, France) et extension au Crétacé inférieur de la lignée cératosaurienne. Comptes Rendus de l’Académie des Sciences Paris, IIa 320, 327–334.

Allain, R., 2002. Discovery of a megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. Journal of Vertebrate Paleontology 22, 548–563.

Allain, R., 2005. The enigmatic theropod dinosaur *Erectopus superbus* (Sauvage, 1882) from the Lower Albian of Louppy-le-Chateau (Meuse, France). In: Carpenter, K. (Ed.), The Carnivorous Dinosaurs. Indiana University Press, Bloomington, pp. 72–86.

Avram, E., Szasz, L., Antonescu, E., Baltreş, A., Iva, M., Melinte, M., Neagu, T., Rădan, S., Tomescu, C., 1993. Cretaceous terrestrial and shallow marine deposits in northern South Dobrogea (SE Romania). Cretaceous Research 14, 265–305.

Avram, E., Costea, I., Dragastan, O., Muţiu, R., Neagu, T., Şindilar, V., Vinogradov, C.., 1996. Distribution of the Middle-Upper Jurassic and Cretaceous facies in the Romanian eastern part of the Moesian Platform. Revue Roumaine de Géologie 39-40, 3–33.

Azevedo, R.P.F. de, Simbras, F.M., Furtado, M.R., Candeiro, C.R.A., Bergqvist, L.P., 2013. First Brazilian carcharodontosaurid and other new theropod dinosaur fossils from the Campanian-Maastrichtian Presidente Prudente Formation, São Paulo State, southeastern Brazil. Cretaceous Research 40, 131–142.

Benson, R.B.J., Barrett, P.M., Powell, H.P., Norman, D.B., 2008. The taxonomic status of *Megalosaurus bucklandii* (Dinosauria, Theropoda) from the Middle Jurassic of Oxfordshire, UK. Palaeontology 51, 419–424.

Benson, R.B.J., Carrano, M.T., Brusatte, S.L., 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. Naturwissenschaften 97, 71–78.

Benton, M.J., Cook, E., Grigorescu, D., Popa, E., Tallódi, E., 1997. Dinosaurs and other tetrapods in an Early Cretaceous bauxite-filled fissure, northwestern Romania. Palaeogeography, Palaeoclimatology, Palaeoecology 130, 275–292.

Benton, M.J., Minter, N.J., Posmoșanu, E., 2006. Dwarfing in ornithopod dinosaurs from the Early Cretaceous of Romania. In: Csiki, Z. (Ed.), Mesozoic and Cenozoic Vertebrates and

Paleoenvironments; Tributes to the Career of Prof. Dan Grigorescu. Ars Docendi, Bucharest, pp. 79–87.

Benton, M.J., Csiki, Z., Grigorescu, D., Redelstorff, R., Sander, M., Stein, K., Weishampel, D.B., 2010. Dinosaurs and the island rule: the dwarfed dinosaurs from Haţeg Island. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 438–454.

Blows, W.T., Honeysett, K., 2014. First Valanginian *Polacanthus foxii* (Dinosauria, Ankylosauria) from England, from the Lower Cretaceous of Bexhill, Sussex. Proceedings of the Geologists' Association 125, 233–251.

Bosselini, A., 2002. Dinosaurs ‘‘re-write’’ the geodynamics of the eastern Mediterranean and the paleogeography of the Apulia Platform. Earth-Science Reviews 59, 211–234.

Brânzilă, M. (ed.), 2010. Academicianul Ion Simionescu - savant şi dascăl al neamului. Ed. Universităţii "Alexandru Ioan Cuza", Iaşi, 182 pp.

Brusatte, S.L., Sereno, P.C., 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. Journal of Vertebrate Paleontology 27, 902–916.

Brusatte, S.L., Sereno, P.C., 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. Journal of Systematic Palaeontology 6, 155–182.

Brusatte, S. L., Clark, N.D.L., 2015. Theropod dinosaurs from the Middle Jurassic (Bajocian-Bathonian) of Skye, Scotland. Scottish Journal of Geology 51, 157-164. doi: 10.1144/sjg2014-022

Brusatte, S., Benson, R.B.J., Carr, T.D., Williamson, T.E., Sereno, P.C., 2007. The systematic utility of theropod enamel wrinkles. Journal of Vertebrate Paleontology 27, 1052–1056.

Brusatte, S.L., Benson, R.B.J., Chure, D.J., Xu, X., Sullivan, C., Hone, D.W.E., 2009. The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. Naturwissenschaften 96, 1051–1058.Brusatte, S.L., Norell, M.A., Carr, T.D., Erickson, G.M., Hutchinson, J.R., Balanoff, A.M., Bever, G.S., Choiniere, J.N., Makovicky, P.J., Xu, X. , 2010a. Tyrannosaur paleobiology: new research on ancient exemplar organisms. Science 329, 1481–1485.

Brusatte, S., Chure, D.J., Benson, R.B.J., Xu, X., 2010b. The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Asia. Zootaxa 2334, 1–46.

Brusatte, S.L., Benson, R.B.J., Xu, X., 2012. A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China. Acta Palaeontologica Polonica 57, 65–72.

Brusatte, S.L., Vremir, M., Csiki-Sava, Z., Turner, A.H., Watanabe, A., Erickson, G.M., Norell, M.A., 2013. The osteology of *Balaur bondoc,* an island-dwelling dromaeosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Romania. Bulletin of the American Museum of Natural History 374, 3–100. doi: 10.1206/798.1

Brusatte, S.L., Lloyd, G.T., Wang, S.C., Norell, M.A., 2014. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. Current Biology 24, 2386–2392.

Buckland, W., 1824. Notice on the *Megalosaurus* or great fossil lizard of Stonesfield. Transactions of the Geological Society 21, 390–397.

Buffetaut, E., Suteethorn, V., 1998. Early Cretaceous dinosaurs from Thailand and their bearing on the early evolution and biogeographical history of some groups of Cretaceous dinosaurs. In: Lucas, S.G., Kirkland, J.I., Estep, J.W. (Eds.), Lower and Middle Cretaceous Terrestrial Ecosystems, New Mexico Museum of Natural History and Science Bulletin 14, pp. 205–210.

Buffetaut, E., Suteethorn, V., 2007. A sinraptorid theropod (Dinosauria: Saurischia) from the Phu Kradung Formation of northeastern Thailand. Bulletin de la Société Géologique de France 178, 497–502.

Buffetaut, E., Suteethorn, V., 2012. A carcharodontid theropod (Dinosauria, Saurischia) from the Sao Khua Formation (Early Cretaceous, Barremian) of Thailand. In: Royo-Torres, R., Gascó, F., Alcalá, L. (Eds.), 10th Annual Meeting of the European Association of Vertebrate Palaeontologists. ¡Fundamental! 20, Teruel, pp. 27–30.

Calvo, J.O., Coria, A., 1998. New specimen of *Giganotosaurus carolinii* (Coria & Salgado, 1995), supports it as the largest theropod ever found. Gaia 15, 117–122.

Calvo, J.O., Gandossi, P., Porfiri, J.D., 2006. Dinosaur faunal replacement during Cenomanian times in Patagonia, Argentina. In: Evans, S.E., Barrett, P.M. (Eds.), 9th Mesozoic Terrestrial Ecosystems and Biota~~,~~. Manchester, UK, pp. 17–20.

Canale, J.I., Scanferla, C.A., Agnolin, F.L., Novas, F.E., 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. Naturwissenschaften 96, 409–414.

Canale, J.I., Novas, F.E., Pol, D., 2015. Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. Historical Biology 27, 1–32. doi: 10.1080/08912963.2013.861830.

Candeiro, C.R.A., Fanti, F., Therrien, F., Lamanna, M.C., 2011. Continental fossil vertebrates from the mid-Cretaceous (Albian-Cenomanian) Alcântara Formation, Brazil, and their relationship with contemporaneous faunas from North Africa. Journal of African Earth Sciences 60, 79–92.

Canudo, J.I., Ruiz-Omeñaca, J.I., 2003. Los restos directos de dinosaurios terópódos (excluyendo Aves) en España. Ciencias de la Tierra 26, 347–373.

Canudo, J.I., Filippi, L.S., Salgado, L., Garrido, A.C., Cerda, I.A., Garcia, R., Otero, A., 2008. Theropod teeth associated with a sauropod carcass in the Upper Cretaceous (Plottier Formation) of Rincón de los Sauces. In: Colectivo Arqueológico y Paleontológico de Salas de los Infantes (Ed.), Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Salas de los Infantes, Burgos, pp. 321–330.

Canudo, J.I. Barco, J.L., Pereda Suberbiola, X., Ruiz-Omeñ~~n~~aca, J.I., Salgado, L., Torcida Fernández-Baldor, F., Gasulla, J.M., 2009. What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. Bulletin de la Société Géologique de France, 180, 5–11.

Carballido, J.L., Salgado, L., Pol, D., Canudo, J.I., Garrido, A., 2012. A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. Historical Biology 24, 631–654.

Carrano, M.T., Sampson, S.D., 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). Journal of Systematic Palaeontology 6, 183–236.

Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10, 211–300.Carvalho, I.S., Campos, A.C.A., Nobre, P.H., 2005. *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. Gondwana Research 8, 11–30.

Casal, G., Candeiro, C.R.A., Martinez, R., Ivany, E., Ibiricu, L., 2009. Dientes de Theropoda (Dinosauria: Saurischia) de la Formación Bajo Barreal, Cretácico Superior, Provincia del Chubut, Argentina. Géobios 42, 553–560.

Cau, A., Dalla Vecchia, F.M., Fabbri, M., 2013. A thick-skulled theropod (Dinosauria, Saurischia) from the Upper Cretaceous of Morocco with implications for carcharodontosaurid cranial evolution. Cretaceous Research 40, 251–260.

Choiniere, J.N., Forster, C.A., De Klerk, W.J., 2012. New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation in South Africa. Journal of African Earth Sciences 71–72, 1–17.

Chure, D.J., Manabe, M., Tanimoto, M., Tomida, Y., 1999. An unusual theropod tooth from the Mifune Group (Late Cenomanian to Early Turonian), Kumamoto, Japan. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs 15, Tokyo, pp. 291–296.

Cifelli, R.L., Davis, B.M., Sames, B., 2014. Earliest Cretaceous mammals from the western United States. Acta Palaeontologica Polonica 59, 31–52. doi:10.4202/app.2012.0089.

Cobos, A., Royo-Torres, R., Luque, L., Alcalá, L., Mampel, L., 2010. An Iberian stegosaurs paradise: The Villar del Arzobispo Formation (Tithonian–Berriasian) in Teruel (Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 293, 223–236.

Cobos, A., Lockley, M.G., Gascó, F., Royo–Torres, R., Alcalá, L., 2014. Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 399, 31–41. doi: 10.1016/j.palaeo.2014.02.008.

Codrea, V., Vremir, M., Jipa, C., Godefroit, P., Csiki, Z., Smith, T., Fărcaş, C., 2010. More than just Nopcsa's Transylvanian dinosaurs: A look outside the Haţeg Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 391–405. doi: 10.1016/j.palaeo.2009.10.027.

Codrea, V., Godefroit, P., Smith, T., 2012. First discovery of Maastrichtian (latest Cretaceous) terrestrial vertebrates in Rusca Montană Basin (Romania). In: Godefroit, P. (Ed.) Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 570–581.

Colbert, E.H., 1946. *Sebecus*, representative of a peculiar suborder of fossil Crocodilia from Patagonia. Bulletin of the American Museum of Natural History 87(4), 217–270.

Coria, R.A, Salgado, L., 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. Nature 377, 224–226.

Coria, R.A., Salgado, L., 2005. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwartz, E. (Eds.), The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics. Geological Society, London, Special Publications 252, pp. 317–327.

Coria, R.A., Currie, P.J., 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas 28, 71–118.

Covacef, Z., 1995. Pionieri ai culturii românești în Dobrogea; Ioan Cotovu și Vasile Cotovu. Analele Dobrogei I(1), 127–134.

Császár, G., Kollányi, K., Lantos, M., Lelkes, G. and Tardiné Filácz, E., 2000. A Hidasivölgyi Márga Formáció kora és képzõdési környezete. Földtani Közlöny 130(4), 695–723.

Csiki, Z., Grigorescu, D., 1998. Small theropods of the Late Cretaceous of the Haţeg Basin (Western Romania) - an unexpected diversity at the top of the food chain. Oryctos 1, 87–104.

Csiki, Z., Vremir, M., Brusatte, S.L., Norell, M.A., 2010. An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania. Proceedings of the National Academy of Sciences 107, 15357–15361.

Csiki-Sava, Z., Codrea, V., Vasile, Ș., 2013. Early Cretaceous dinosaur remains from Dobrogea (southeastern Romania). In: Picot, L. (Ed.), Abstracts, 11th Annual Meeting of the European Association of Vertebrate Palaeontologists, Villers-sur-Mer, France, pp. 28.

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., Brusatte, S.L., 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. Zookeys 469, 1–161. doi: 10.3897/zookeys.469.8439.

Csontos, L., Vörös, A., 2004. Mesozoic plate tectonic reconstruction of the Carpathian region. Palaeogeography, Palaeoclimatology, Palaeoecology 210, 1–56. doi: 10.1016/j.palaeo.2004.02.033.

Currie, P.J., Carpenter, K., 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. Geodiversitas 22, 207–246.

Currie, P.J., Rigby, J.K., Sloan, R.E., 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter, K., Currie, P.J. (Eds,), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, Boston, pp. 107–125.

Dalla Vecchia, F.M., 1998. Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (Upper Hauterivian/Lower Barremian) limestones of SW Istria (Croatia). Geologia Croatica 5, 105–134.

Dames, W., 1884. *Megalosaurus dunkeri.* Sitzungberichte Gesellschaft Naturforschender Freunde zu Berlin 1884, 186–188.

De Klerk, W.J., Forster, C.A., Sampson, S.D., Chinsamy, A., Ross, C.F., 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. Journal of Vertebrate Paleontology 20, 324–332.

D’Emic, M.D., Melstrom, K.M., Eddy, D.R., 2012. Paleobiology and geographic range of the large-bodied Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. Palaeogeography, Palaeoclimatology, Palaeoecology 333–334, 13–23.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M., Cadet, J.P., Crasquin, S., Săndulescu, M., Eds. (2000) Atlas Peri-Tethys Palaeogeographical Maps. CCGM/CGMW, Paris, 269 pp.

Dinu, C., Grădinaru, E., Stoica, M., Diaconescu, V., 2007. Dobrogea 2007 Field Trip Preparation and Assistance. University of Bucharest, 123 pp.

Dragastan, O., Neagu, T., Bărbulescu, A., Pană, I., 1998. Jurasicul şi Cretacicul din Dobrogea Centrală şi de Sud. Bucharest, 249 pp.

Dragastan, O.N., Antoniade, C., Stoica, M., 2014. Biostratigraphy and zonation of the Lower Cretaceous succession from Cernavodă-lock section, South Dobrogea, eastern part of the Moesian Platform (Romania). Carpathian Journal of Earth and Environmental Sciences 9(1), 231–260.

Dyke, G.J., Benton, M.J., Posmoşanu, E., Naish, D., 2011. Early Cretaceous (Berriasian) birds and pterosaurs from the Cornet bauxite mine, Romania. Palaeontology 54, 79–95.

Eberth, D.A., Brinkman, D.B., Chen, P.-J., Yuan, F.-T., Wu, X.-C., Li, G., Cheng, ~~Xian~~X.-S~~hen, C~~., 2001. Sequence stratigraphy, paleoclimate patterns, and vertebrate fossil preservation in Jurassic–Cretaceous strata of the Juggar Basin, Xinjiang Autonomous Region, People's Republic of China. Canadian Journal of Earth Sciences 38, 1627–1644.

Eddy, D.R., Clarke, J.A., 2011. New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroidea (Dinosauria: Theropoda). PLoS ONE 6(3), e17932. doi:10.1371/journal.pone.0017932.

Evans, S.E., Matsumoto, R., 2015. An assemblage of lizards from the Early Cretaceous of Japan. Palaeontologia Electronica 18.2.36A, 1–36.

Ezcurra, M.D., Agnolín, F.L., 2012. A new global palaeobiogeographical model for the Late Mesozoic and Early Tertiary. Systematic Biology 61, 553–566. doi:10.1093/sysbio/syr115.

Fanti, F., Cau, A., Cantelli, L., Hassine, M., Auditore, M., 2015. New information on *Tataouinea hannibalis* from the Early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. PLoS ONE 10(4), e0123475. doi:10.1371/journal.pone.0123475.

Galton, P.M., 2009. Notes on Neocomian (Lower Cretaceous) ornithopod dinosaurs from England - *Hypsilophodon*, *Valdosaurus*, "*Camptosaurus*", "*Iguanodon*" - and referred specimens from Romania and elsewhere. Revue de Paléobiologie 28, 211–273.

Gardner, J.D., Evans, S.E., Sigogneau-Russell, D., 2003. New albanerpetontid amphibians from the Early Cretaceous of Morocco and Middle Jurassic of England. Acta Palaeontologica Polonica 48, 301–319.

Gasca, J.M., Canudo, J.I., Moreno-Azanza, M., 2014. A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 273, 13–23. doi: 10.1127/0077-7749/2014/0413.

Gheerbrant, E., Rage, J.-C., 2006. Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? Palaeogeography, Palaeoclimatology, Palaeoecology 241, 224–246. doi:10.1016/j.palaeo.2006.03.016.

Gishlick, A.D., Gauthier, J.A., 2007. On the manual morphology of *Compsognathus longipes* and its bearing on the diagnosis of Compsognathidae. Zoological Journal of the Linnean Society 149, 569–581.

Goloboff, P. A., Farris, J. S., Nixon, K. C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786.

Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), 2012. The Geologic Time Scale 2012. Elsevier, Amsterdam, 1144 pp.

Grigorescu, D., 1992. Nonmarine Cretaceous Formations of Romania. In: Matter, N.J., Chen, P.-J. (Eds.), Aspects of Nonmarine Cretaceous Geology. China Ocean Press, Beijing, pp. 142–164.

Grigorescu, D., 2003. Dinosaurs of Romania. Comptes rendus Palevol 2, 97–101.

Grigorescu, D., 2010. The Latest Cretaceous fauna with dinosaurs and mammals from the Haţeg Basin — A historical overview. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 271–282.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 1–9.

Harris, J.D., 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. New Mexico Museum of Natural History and Science Bulletin 13, 1–75.

Hendrickx, C., Mateus, O., 2014. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. Zootaxa 3751(1), 1–74.

Hendrickx, C., Mateus, O., Araújo, R., 2015a. The dentition of megalosaurid theropods. Acta Palaeontologica Polonica 60, 627–642. doi:10.4202/app.00056.2013.

Hendrickx, C., Mateus, O., Araújo, R., 2015b. A proposed terminology of theropod teeth (Dinosauria, Saurischia). Journal of Vertebrate Paleontology 35(5~~):~~), e982797. doi: 10.1080/02724634.2015.982797.

Holtz, T.R., Jr.., Molnar, R.E., Currie, P.J., 2004a. Basal Tetanurae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, Los Angeles, London~~Berkeley, ~~, pp. 71–110.

Holtz, T.R., Chapman, R.E., Lamanna, M.C., 2004b. Mesozoic biogeography of Dinosauria. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. Second Edition.

University of California Press, Berkeley, Los Angeles, London~~Berkeley, Los Angeles~~, pp. 627–642.

Huene, F. von~~.~~, 1923. Carnivorous Saurischia in Europe since the Triassic. Bulletin of the Geological Society of America 34, 449–458.

Hippolyte, J.-C., 2002. Geodynamics of Dobrogea (Romania): new constraints on the evolution of the Tornquist–Teisseyre Line, the Black Sea and the Carpathians. Tectonophysics 357, 33–53.

Ionesi, L., 1994. Geologia unităţilor de platformă şi a orogenului Nord-Dobrogean. Ed. Tehnică, Bucharest, 280 pp.

Jerzykiewicz, T., Russell, D.A., 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. Cretaceous Research 12, 345–377.

Jurcsák, T., 1982. Occurences nouvelles des Sauriens mésozoïques de Roumanie. Vertebrata Hungarica 21, 175–184.

Jurcsák, T., Popa, E., 1979. Dinozaurieni ornithopozi din bauxitele de la Cornet (Munții Pădurea Craiului). Nymphaea 7, 37–75.

Jurcsák, T., Popa, E., 1983. La faune de dinosauriens du Bihor (Roumanie). In: Buffetaut, E., Mazin, J.M., Salmon, E. (Eds.), Actes du Symposium Paléontologique Georges Cuvier. Le Serpentaire, Montbéliard, pp. 325–335.

Kellner, A.W.A., Pinheiro, A.E.P., Campos, D.A., 2014. A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K–Pg boundary. PLoS ONE 9(1), e81386. doi:10.1371/journal.pone.0081386.

Kirkland, J.I., Cifelli, R.L., Britt, B.B., Burge, D.L., DeCourten, F.L., Eaton, J.G., Parrish, J.M., 1999. Distribution of vertebrate faunas in the Cedar Mountain Formation, east-central Utah. Utah Geological Survey Miscellaneous Publication 99-1, 201–217.

Knoll, F., Ruiz-Omeñaca, J.I., 2009. Theropod teeth from the basalmost Cretaceous of Anoual (Morocco) and their palaeobiogeographical significance. Geological Magazine 146, 602–616.

Kusuhashi, N., Matsumoto, A., Murakami, M., Tagami, T., Hirata, T., Iizuka, T., Handa, T., Matsuoka, H., 2006. Zircon U−Pb ages from tuff beds of the upper Mesozoic Tetori Group in the Shokawa district, Gifu Prefecture, central Japan. The Island Arc 15, 378–390.

Lacasa Ruiz, A., 1989. Nuevo genero de ave fosil del yacimiento Neocomiense del Montsec (Provincia de Lerida, España). Estudios geológicos 45(5-6), 417–425.

Larson, D.W., Currie, P.J., 2013. Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time. PLoS ONE 8(1), e54329. doi:10.1371/journal.pone.0054329.

Le Loeuff, J., Buffetaut, E., 1995. The evolution of Late Cretaceous non-marine vertebrate faunas in Europe. In: Sun, A.-L., Wang, Y.-Q. (Eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers. China Ocean Press, Beijing, pp. 181–184.

Le Loeuff, J., Lang, E., Cavin, L., Buffetaut, E., 2012. Between Tendaguru and Bahariya: on the age of the Early Cretaceous dinosaur sites from the Continental Intercalaire and other African formations. Journal of Stratigraphy 36, 486–502.

Lucas, F.A., 1901. A new dinosaur, *Stegosaurus marshi*, from the Lower Cretaceous of South Dakota. Proceedings of the United States National Museum 23(1224), 591–592.

Lucas, S.G., 2006. The *Psittacosaurus* biochron, Early Cretaceous of Asia. Cretaceous Research 27, 189–198.

Lucas, S.G., Estep, J.W., 1998. Vertebrate biostratigraphy and biochronology of the Cretaceous of China. In: Lucas, S.G., Kirkland, J.I., Estep, J.W. (Eds.), Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science Bulletin 14, pp. 1–20.

Lü, J.-C., Xu, L., Pu, H.-Y., Jia, S.-H., Azuma, Y., Chang, H.-L., Zhang, J.-M., ~~2014~~2016. Paleogeographical significance of carcharodontosaurid teeth from the late Early Cretaceous of Ruyang, Henan Province of central China. Historical Biology, 28, 8–13. doi: 10.1080/08912963.2014.947287.

Manabe, M., Hasegawa, Y., 1995. Diapsid fauna and its paleobiogeographical implication, the Neocomian section of the Tetori Group. In: Sun, A., Wang, Y. (Eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers,~~–~~. China Ocean Press, Beijing, pp. 179.

Mannion, P.D., 2009. A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. Cretaceous Research 30, 521–526.

Mannion, P.D., Upchurch, P., Hutt, S., 2011. New rebbachisaurid (Dinosauria: Sauropoda) material from the Wessex Formation (Barremian, Early Cretaceous), Isle of Wight, United Kingdom. Cretaceous Research 32, 774–780.

Matsukawa, M., Ito, M., Nishida, N., Koarai, K., Lockley, M.G., Nichols, D.J., 2006. The Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial ecosystems in Asia. Cretaceous Research 27, 199–225.

McDonald, A.T., 2011. The taxonomy of species assigned to *Camptosaurus* (Dinosauria: Ornithopoda). Zootaxa 2783, 52–68.

McKenna, M.C., 1973. Sweepstakes, filters, corridors, Noah's Arks, and Beached Viking Funeral Ships in palaeogeography. In: Tarling, D.H., Runcorn, S.K. (Eds.), Implications of Continental Drift to the Earth Sciences. Academic Press, New York, pp. 295–308.

Mo, J.-Y., Huang, C.-L., Xie, S.-W., Buffetaut, E., 2014. A megatheropod tooth from the Early Cretaceous of Fusui, Guangxi, Southern China. Acta Geologica Sinica (English Edition) 88, 6–12.

Molnar, R.E., 1990. Problematic Theropoda: "Carnosaurs". In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, Los Angeles, Oxford, pp. 306–317.

Mutihac, V., Mutihac, G., 2010. The geology of Romania, within the Central East European geostructural context. Ed. Didactică şi Pedagogică, Bucharest, 690 pp.

Neagu, T., Dragastan, O., Csiki, Z., 1997. Early Cretaceous shelf paleocommunities of Cernavodă (South Dobrogea, SE Romania). Acta Palaeontologica Romaniae 1, 28–36.

Nopcsa, F., 1902. Notizen über cretacische Dinosaurier. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 111, 93–114.

Nopcsa, F., 1923. On the geological importance of the primitive reptilian fauna of the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotium*). Quarterly Journal of the Geological Society of London 79, 100–116.

Norman, D.B., 2010. A taxonomy of iguanodontians (Dinosauria: Ornithopoda) from the lower Wealden Group (Cretaceous: Valanginian) of southern England. Zootaxa 2489, 47–66.

Norman, D.B., 2013. On the taxonomy and diversity of Wealden iguanodontian dinosaurs (Ornithischia: Ornithopoda). Revue de Paléobiologie 32~~(2)~~, 385–404.

Novas, F.E., de Valais, S., Vickers-Rich, P.A., Rich, T.H., 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. Naturwissenschaften 92, 226–230.

Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. Cretaceous Research 45, 174–215.

Ortega, F., Escaso, F., Sanz, J.L., 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. Nature 467, 203–206.

Ősi, A., Rabi, M., Makádi, L., Szentesi, Z., Botfalvai, G., Gulyás, P., 2012. The Late Cretaceous continental vertebrate fauna from Iharkút (western Hungary): a review. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 533–569.

Ősi, A., Codrea, V., Prondvai, E., Csiki-Sava, Z., 2014. New ankylosaurian material from the Upper Cretaceous of Transylvania. Annales de Paléontologie 100, 257–271. doi: 10.1016/j.annpal.2014.02.001.

Ősi, A., Rabi, M., Makádi, L., 2015. An enigmatic crocodyliform tooth from the bauxites of western Hungary suggests hidden mesoeucrocodylian diversity in the Early Cretaceous European archipelago. PeerJ 3, e1160. doi:10.7717/peerj.1160.

Paolillo, A., Linares, O.J., 2007. Nuevos cocodrilos Sebecosuchia del Cenozoico Suramericano (Mesosuchia: Crocodylia). Paleobiologia Neotropical 3, 1–25.

Pereda-Suberbiola, X., Ruiz-Omeñ~~n~~aca, J.I., Fernandez-Baldor, F.T., Maisch, M.W., Huerta, P., Contreras, R., Izquierdo, L.A., Huerta, D.M., Montero, V.U., Welle, J., 2011. A tall-spined ornithopod dinosaur from the Early Cretaceous of Salas de los Infantes (Burgos, Spain). Comptes Rendus Palevol 10, 551–558.

Pereda-Suberbiola, X., Ruiz-Omeñ~~n~~aca, J.I., Canudo, J.I., Torcida, F., Sanz, J.L., 2012. Dinosaur faunas from the Early Cretaceous (Valanginian–Albian) of Spain. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. ~~Life of the Past.~~ Indiana University Press, Bloomington, pp. 378–407.

Pérez-Moreno, B.P., Sanz, J.L., Sudre, J., Sigé, B., 1993. A theropod dinosaur from the Lower Cretaceous of southern France. Revue de Paléobiologie~~,~~ Volume spéciale 7, 173–188.

Pol, D., Powell, J.E., 2011. A new sebecid mesoeucrocodylian from the Rio Loro Formation (Palaeocene) of north-western Argentina. Zoological Journal of the Linnean Society 163, S7–S36.

Porfiri, J.D., Novas, F.E., Calvo, J.O., Agnolín, F.L., Ezcurra, M.D., Cerda, I.A., 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. Cretaceous Research 51, 35–55. doi:10.1016/j.cretres.2014.04.007.

Posmoşanu, E., 2003. Iguanodontian dinosaurs from the Lower Cretaceous bauxite site from Romania. Acta Palaeontologica Romaniae 4, 431–439.

~~Porfiri, J.D., Novas, F.E., Calvo, J.O., Agnolín, F.L., Ezcurra, M.D., Cerda, I.A., 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. Cretaceous Research, 51, 35–55. doi:10.1016/j.cretres.2014.04.007.~~

Rabi, M., Sebők, N., 2015. A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. Gondwana Research 28, 1197–1211. doi:10.1016/j.gr.2014.09.015.

Racey, A., 2009. Mesozoic red bed sequences from SE Asia and the significance of the Khorat Group of NE Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. ~~The~~ Geological Society, London, Special Publications 315, pp. 41–67. doi: 10.1144/SP315.5.

Racey, A., Goodall, J.G.S., 2009. Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. ~~The~~ Geological Society~~ of~~, London, Special Publications 315, pp. 69–83. doi: 10.1144/SP315.6.

Rauhut, O.W.M., 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). Special Papers in Palaeontology 86, 195–239.

Rauhut, O.W.M., Werner, C., 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan. Paläontologische Zeitschrift 69~~(3/4)~~, 475–489.

Richter, U., Mudroch, A., Buckley, L.G., 2013. Isolated theropod teeth from the Kem Kem Beds (Early Cenomanian) near Taouz, Morocco. Paläontologische Zeitschrift 87, 291–309.

Royo-Torres, R., Cobos, A., Luque, L., Aberasturi, A., Espilez, E., Fierro, I., Gonzales, A., Mampel, L., Alcalá, L., 2009. High European sauropod dinosaur diversity during Jurassic–Cretaceous transition in Riodeva (Teruel, Spain). Palaeontology 52, 1009–1027.

Sachs, S., Hornung, J.J., 2013. Ankylosaur remains from the Early Cretaceous (Valanginian) of Northwestern Germany. PLoS ONE 8(4), e60571. doi:10.1371/journal.pone.0060571.

Salgado, L., Canudo, J.I., Garrido, A.C., Ruiz-Omeñaca, J.I., Garcia, R.A., de la Fuente, M.S., Barco, J.L., Bollati, R., 2009. Upper Cretaceous vertebrates from El Anfiteatro area, Río Negro, Patagonia, Argentina. Cretaceous Research 30, 767–784.

Sames, B., Cifelli, R.L., Schudack, M.E., 2010. The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: New biostratigraphic results from ostracod correlations and early mammals, and their implications for paleontology and geology of the basin—An overview. Earth-Science Reviews 101, 207–224.

Sauvage, H.E., 1876. Notes sur les reptiles fossiles. Bulletin de la Société Géologique de France 4, 435–442.

Sauvage, H.E., 1882. Recherches sur les reptiles trouves dans le Gault de l'est du bassin de Paris. Mémoires de la Société Géologique de France 2, 1–42.

Săndulescu, M., 1984. Geotectonica României. Ed. Tehnică, Bucharest, 329 pp.

Seghedi, A., 2001. The North Dobrogea orogenic belt (Romania): a review. In: Ziegler, P.A., Cavazza, W., Robertson, A.H.F., Crasquin-Soleau, S. (Eds.), Peri-Tethys Memoir 6: Peri-Tethyan Rift/Wrench Basins and Passive Margins. Mémoires de la Musée National d'Histoire Naturelle, Paris, pp. 237–257.

Sereno, P.C., 1999. Dinosaurian biogeography: vicariance, dispersal and regional extinction.

In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs 15, Tokyo, pp. 249–257.

Sereno, P.C., Brusatte, S.L., 2008. Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. Acta Palaeontologica Polonica 53, 15–46.

Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J., Wilson, J.A., 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science 272, 986–991.

Shen, Y.B., Mateer, N.J., 1992. An outline of the Cretaceous system in northern Xinjiang, western China. In: Mateer, N.J., Chen, P.J. (Eds.), Aspects of Nonmarine Cretaceous Geology. China Ocean Press, Beijing, pp. 49–77.

Simionescu, I., 1906. Note sur l'age des calcaires de Cernavoda (Dobrogea). Annales Scientifiques de l'Université de Jassy 4(1), 1–3.

Simionescu, I., 1913. *Megalosaurus* aus der Unterkreide der Dobrogea. Centralblatt für Mineralogie, Geologie und Paläontologie 1913(20), 686–687.

Sissingh, W., 1977. Biostratigraphy of Cretaceous calcareous nannoplankton. Geologie en Mijnbouw 56, 37–65.

Smith, J.B., Vann, D.R., Dodson, P., 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. The Anatomical Record A 285A, 699–736.

Stein, K., Csiki, Z., Curry Rogers, K., Weishampel, D.B., Redelstorff, R., Carballido, J.L., Sander, P.M., 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). Proceedings of the National Academy of Sciences 107, 9258–9263.

Stoica, M., Csiki, Z., 2002. An earliest Cretaceous (Purbeckian) vertebrate fauna from Southern Dobrogea (southeastern Romania). In: Grigorescu, D., Csiki, Z. (Eds.), 7th European Workshop on Vertebrate Palaeontology, Sibiu, Romania~~,~~. Ars Docendi, Bucharest, pp. 34.

Stovall, J.W., Langston, W., Jr., 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. American Midland Naturalist 43, 686–728.

Stromer, E., 1931. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîjestufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematischnaturwissenschaftliche Abteilung~~,~~ Neue Folge 9, 1–23.

Therrien, F., Henderson, D.M., 2007. My theropod is bigger than yours … or not: estimating body size from skull length in theropods. Journal of Vertebrate Paleontology 27, 108–115.

Tong, H., Claude, J., Suteethorn, V., Naksri, W., Buffetaut, E., 2009. Turtle assemblages of the Khorat Group (Late Jurassic–Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. The Geological Society, London, Special Publications 315, pp. 141–151.

Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Montero, D., Pereda Suberbiola, X., Salgado, L., 2011. *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. Acta Palaeontologica Polonica 56, 535–552.

Turculeț, I., Brânzilă, M., 2012. Muzeul colecțiilor paleontologice originale de la Universitatea "Alexandru Ioan Cuza" Iași. Editura Universității "Alexandru Ioan Cuza" Iași, Iași, 173 pp.

Turner, A.H., Sertich, J.J.W., 2010. Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 30(Supplement 1), 177–236.

Turner, A.H., Makovicky, P.J., Norell, M.A., 2012. A review of dromaeosaurid systematics and paravian phylogeny. Bulletin of the American Museum of Natural History 371, 1–206.

Vasile, Ş., Csiki, Z., 2011. New Maastrichtian microvertebrates from the Rusca Montană Basin (Romania). Oltenia. Studii și comunicări. Științele Naturii 27(1), 221–230.

Vickers-Rich, P., Rich, T.H., Lanus, D.R., Rich, L.S.V., Vacca, R., 1999. "Big Tooth" from the Early Cretaceous of Chubut Province, Patagonia: a possible carcharodontosaurid. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs 15, Tokyo, pp. 85–88.

Vremir, M., 2010. New faunal elements from the Late Cretaceous (Maastrichtian) continental deposits of Sebeș area (Transylvania). Terra Sebus. Acta Musei Sabesiensis 2, 635–684.

Vullo, R., Néraudeau, D., Lenglet, T., 2007. Dinosaur teeth from the Cenomanian of Charentes, western France: evidence for a mixed Laurasian-Gondwanan assemblage. Journal of Vertebrate Paleontology 27, 931–943.

Weishampel, D.B., 1990. Dinosaurian distribution. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. California University Press, Berkeley, Los Angeles, Oxford, pp. 63–140.

Weishampel, D.B., Grigorescu, D., Norman, D.B., 1991. The Dinosaurs of Transylvania. National Geographic Research & Exploration 7(2), 196–215.

Weishampel, D.B., Norman, D.B., Grigorescu, D., 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. Palaeontology 36, 361–385.

Weishampel, D.B., Jianu, C.M., Csiki, Z., Norman, D.B., 2003. Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. Journal of Systematic Palaeontology 1, 65–123.

Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X-J., Sahni, A., Gomani, E.M., Noto, C.R., 2004. Dinosaur distribution. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, Los Angeles, London, pp. 517–606.

Weishampel, D.B., Csiki, Z., Benton, M.J., Grigorescu, D., Codrea, V., 2010. Palaeobiogeographic relationships of the Haţeg biota — Between isolation and innovation. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 419–437.

Williamson, T.E., Brusatte, S.L., 2014. Small theropod teeth from the Late Cretaceous of the San Juan Basin, northwestern New Mexico and their implications for understanding latest Cretaceous dinosaur evolution. PLoS ONE 9(4), e93190. doi:10.1371/journal.pone.0093190.

Zarcone, G., Cillari, F.M.P., Stefano, P.D., Guzzetta, D., Nicosia, U., 2010. A possible bridge between Adria and Africa: New palaeobiogeographic and stratigraphic constraints on the Mesozoic palaeogeography of the Central Mediterranean area. Earth-Science Reviews 103, 154–162.

Figure captions

Figure 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).

Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B. Current state of UAIC (SCM1) 615, mounted in a limestone holder.

Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B., distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).

Figure 4. Dental morphospace of the different theropod clades according to the results of the PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by Carcharodontosauridae. See further details of this analysis, as well as other quantitative analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant function analysis, phylogenetic analysis), in the Supplementary Material.

Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615 from Southern Dobrogea. Legend: 1 – *Veterupristisaurus*, ‘*Megalosaurus’ ingens*, Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator*, Spain, Barremian;

3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 – *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China, Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmayisaurus*, Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11 – *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan, Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 – Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant references, see text, *5.4.*). Palaeogeographic maps, courtesy of Ron Blakey (http://cpgeosystems.com/).

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

Zoltán Csiki-Sava[1*], Stephen L. Brusatte[2], Ștefan Vasile[1]
[1] Department of Geology, Faculty of Geology and Geophysics, University of Bucharest, 1 Nicolae Bălcescu Boulevard, 010041 Bucharest, Romania
[2] School of GeoSciences, University of Edinburgh, Grant Institute, James Hutton Road, Edinburgh, EH9 3FE, United Kingdom
* Corresponding author
zoltan.csiki@g.unibuc.ro

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 Hațeg 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 evolved 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 Aptian, illustrating the importance of palaeogeographic ties between these two realms during the largely mysterious early–mid Early Cretaceous.

Keywords

Southern Dobrogea; Valanginian; Carcharodontosauridae; cratonic Europe; palaeobiogeography

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 Early Cretaceous bauxite accumulations of Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997; Posmoșanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Haţeg, Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the dinosaur-dominated 'Hațeg 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 ‘Hațeg 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 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 split, but originated earlier, and perhaps in Europe, suggesting faunal interchange between Europe and Gondwana during the ‘dark ages’ of the early Early Cretaceous.

Abbreviations: UAIC – University “Alexandru Ioan Cuza”, Iași, Romania.

2. History of collecting and curation

Only two dinosaurian fossils are currently known from the cratonic areas of Romania: an isolated theropod tooth and an isolated caudal vertebral centrum. Both of these were reported from the Lower Cretaceous deposits of Southern Dobrogea (southeastern Romania; Csiki-Sava et al., 2013, see also below). Unfortunately, exact details of their discovery and places of origin are lost, a fact that can hinder an assessment of their age and interpretation of their phylogenetic and palaeobiogeographic significance. Our aim here is to gather and report all available information concerning the collecting of specimen UAIC (SCM1) 615, that is, the isolated theropod tooth reported by Simionescu (1913; Fig. 2A).

According to the existing information - unpublished museum labels and records, and the preliminary publication of Simionescu (1913) - specimen UAIC (SCM1) 615 was discovered in the surroundings of Cochirleni, a small village south of Cernavodă and close to the right bank of the Danube, in Southern Dobrogea, southeastern Romania (Fig. 1), probably shortly before 1913, the date of its publication by Simionescu (1913).

Although studied and preliminarily described by Simionescu, UAIC (SCM1) 615 was not collected by Simionescu personally. Instead, it was donated by a certain “de Tomas” (also mentioned as ”de Thomas” in the registry of the Hârșova Museum) to V. Cotovu from Hârşova (Central Dobrogea), a local teacher, archaeology and natural history aficionado, and amateur fossil collector (see, e.g., Covacef, 1995). Cotovu, described by Simionescu himself as the “zélé fondateur et directeur du muséum de Hârşova” (*enthusiastic founder and director of the Hârşova Museum*; Simionescu, 1906: p. 2), had previously provided fossil specimens from Southern Dobrogea for study to Simionescu, a nationally acknowledged popular science writer and scientist, whom Cotovu knew personally (Brânzilă, 2010). These circumstances are supported by the fact that in the original description, Simionescu figures the specimen as being accessioned in the “Regional-Museum von Harschowa” (*Hârşova Regional Museum*; Simionescu, 1913: p. 687, fig.1), a designation he also used to refer to other Dobrogean

specimens not collected by him first-hand (e.g., a specimen of '*Nautilus' pseudoelegans* from Cernavodă, or a fragmentary tooth-bearing palatal fragment referred to as '*Coelodus*' sp., also originating from Cochirleni; see Simionescu, 1906). Confirming this deduction, an isolated tooth appears accessioned in the old registry book of the Hârşova Museum (under specimen number 200) as "*Megalosaurus* cf. *superbus*", with the mention that it was "*described by Prof. Simionescu in the Centralblatt f. min. etc*.". This is also the case of the '*Coelodus'* sp. specimen from Cochirleni (specimen number 86), similarly clearly identified as being described by Simionescu in the registry book.

Both of these vertebrate remains from Dobrogea that were formerly part of the Hârşova Museum collections are currently accessioned in the palaeontology collections of the UAIC (Turculeț and Brânzilă, 2012), suggesting that, at one moment, several specimens were transferred there from the Hârşova Museum. Although no details are known about this transfer, it is probable that it took place right before (or when) the Hârşova Museum, including a part of its collections, was burned and largely destroyed during WWI, in 1916, a time when Simionescu still held a position at the UAIC.

After its original description, specimen UAIC (SCM1) 615 underwent a minor amount of damage (see below, Description). Also, at some point between its description in 1913 and the early 1960s (when the specimen was found in its present state in the collections of the UAIC by academic staff members who are still alive today and recall the discovery; I. Turculeț, personal communication, May 2013) it was glued into a limestone matrix holder, while it was obviously completely freed of the surrounding matrix when it was described and figured in 1913 (Fig. 2). The circumstances under which these alterations took place are unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the spring of 1944, the frontline between the German-Romanian and Soviet armies reached the Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

were packed in crates, and moved together with its personnel and other possessions to Zlatna, in the Apuseni Mountains (western Romania), to safeguard them from any potential damage. Mounting the specimen into the limestone stand would have been a quick way to stabilize it, as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă, personal communication, April 2103). If that was indeed the case, the mounting would have taken place without the knowledge of Simionescu, who left Iaşi and the UAIC in 1929, being invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă, 2010). Then again, however, Simionescu himself or staff of the Hârşova Museum might have re-mounted the tooth after its original description, or else the mounting might have taken place after the return of the collections to Iași, after WWII.

Unfortunately, it is not documented whether the mounting was made using the original matrix, or if a trough corresponding to the tooth outline was carved into a randomly chosen limestone block. The apparently excellent fit between the tooth and the depression housing it (Fig. 2B, 3) suggests that this operation was completed carefully, and accurate carving of a fake holder is difficult to reconcile with the rush accompanying the evacuation of the Iași University, in 1944. Alternatively, the presence of a hand-written old registration number on the specimen holder would support its early re-mounting, while still at the Hârşova Museum. As noted previously, the original Hârşova Museum registration number of the specimen was 200, which does not correspond to that currently written both on the limestone holder and on a paper sticker (204). However, according to the old collection registry of the Hârşova Museum, specimen numbers 201 through 225 were given to a series of “indeterminate (fossil) bone fragments” from the “Cochirleni quarries”. Thus, these specimens (now apparently lost) came from the same locality as the tooth, and they were collected and donated by the same person to the Museum who donated UAIC (SCM1) 615. There is, thus, a (albeit admittedly remote) possibility that the registration numbers were

mixed up during the re-mounting of the specimen, which in this case took place at an early date in the Hârşova Museum. If this is indeed the case, the limestone used as holder could have been the same as the original matrix of the specimen.

To conclude, the history of recovery and curation of the historically important dinosaurian specimen UAIC (SCM1) 615 is rather convoluted and clouded by many uncertainties. The exact date of discovery remains conjectural, and the exact place of the discovery (thus also the original geological context of the tooth) is even more ambiguous. The current state of the specimen, and especially its mounted status, suggest a curatorial history that produced a moderate amount of damage to, but also partially obscured the detailed morphology of the specimen. The convergence of such unfortunate events makes deciphering the age, identity and evolutionary significance of the specimen troublesome, although many lines of evidence, carefully considered, allow us to draw reasonable conclusions (see below).

3. Geological setting

According to the available collecting information, the isolated theropod tooth UAIC (SCM1) 615 was discovered at Cochirleni (sometimes noted more specifically as the "*Cochirleni quarry*" or "*Cokerleni quarry*"). Cochirleni is a small village in southwestern Dobrogea situated close to the right bank of the Danube, and about 9 km south of the main urban center of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).

Southern Dobrogea is a cratonic area corresponding to the southeastern corner of Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984; Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,

2010), researchers agree that it became integrated into the main European Craton towards the end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine: Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001; Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

The Precambrian basement of Southern Dobrogea is overlain by a flat-lying sedimentary cover that begins with the lowermost Palaeozoic and ends with the uppermost Neogene. The sedimentary succession is interrupted by a few major, as well as several less important, sedimentary hiatuses that separate 5 main sedimentary sequences corresponding to the Cambrian–Upper Carboniferous, the Permian–Triassic, the Middle Jurassic–Cretaceous, the Eocene–?Oligocene, and the middle Badenian (middle Miocene)–Upper Pliocene. The Palaeozoic and lower Mesozoic are known only from the subsurface of Southern Dobrogea, but Cretaceous and Cenozoic deposits have limited exposures along the main water courses of the region (Ionesi, 1994; Mutihac and Mutihac, 2010).

The outcropping Cretaceous in Southern Dobrogea is represented mainly by shallow marine, carbonate platform deposits in the lower part of the system, replaced by more open-water, chalky facies towards the later part of the period (e.g., Avram et al., 1993, 1996; Dragastan et al., 1998; Dinu et al., 2007); these crop out only as isolated patches along the main watercourses of the region (Fig. 1).

The Lower Cretaceous Series consists of several lithostratigraphic units with complex, partially overlapping and interfingering relationships (Dragastan et al., 1998, 2014). The lowest (and only artificially) outcropping unit is the Purbeck-type, siliciclastic-evaporitic Upper Kimmeridgian–Lower Berriasian Amara Formation that represents lagoonal to continental environments. This unit is covered by the shallow-marine, richly fossiliferous and locally reefal limestone-dominated Cernavodă Formation (restricted-open lagoonal to

carbonate platform, Upper Berriasian–Lower Hauterivian). A time-correlative unit of the Cernavodă Formation, the limestone-dolomitic Dumbrăveni Formation (Upper Berriasian–Lower Hauterivian), is restricted to the southeastern part of Southern Dobrogea. The Cernavodă and Dumbrăveni formations are covered unconformably by dominantly calcareous deposits with hippuritoid (‘pachyodont’) coquinas, small reefs and lens-like orbitolinid accumulations, referred to the Barremian–Lower Aptian Ostrov Formation by Dragastan et al. (1998), but to the Ramadan Formation (in part) by Avram et al. (1993, 1996). These deposits, formed in littoral to lagoonal and open reef terrace environments, are in turn capped by the fluvial-lacustrine, siliciclastic deposits of the Gherghina Formation, with Middle–Upper Aptian kaolinitic clays and thin coal intercalations. The Lower Cretaceous succession ends with the transgressive, glauconite-bearing, coastal to sublittoral siliciclastic deposits of the Cochirleni Formation (uppermost Aptian–Albian).

The Upper Cretaceous has a significantly more patchy development, mainly restricted to the eastern part of Southern Dobrogea, excepting the weakly glauconitic, chalky-sandy Peștera Formation (Lower Cenomanian) and the marly Dobromiru Formation (Upper Cenomanian) that cover the western-central parts of the area. The younger Cuza Vodă (Turonian), Murfatlar (Santonian–Lower-Middle Campanian), and Satu Nou (Upper Campanian) formations are dominantly chalky, suggesting the instalment of a relatively deeper, offshore depositional environment; neither of these units is known from western Southern Dobrogea.

In total, the Lower Cretaceous of Southern Dobrogea was deposited in a shallow marine, near-shore setting, fluctuating between carbonate platform, lagoonal, coastal-tidal flat, and continental environments (see Avram et al., 1996; Dragastan et al., 1998). Its main characteristic features, such as the observed lithological variability, the areal distribution of the different units, and the presence of several unconformities within the series, are all linked

to eustatic sea-level changes that affected the Southern Dobrogean territory during the Early Cretaceous (Dragastan et al., 1998). The main emergent land in the area was represented by the Central Dobrogean Massif, lying north of the study area, almost completely subaerially exposed and actively eroding during the Cretaceous. Consequently, shallow-marine to continental deposits are restricted mainly to the northern part of Southern Dobrogea, close to its boundary with the Central Dobrogean Massif (marked by the Capidava-Ovidiu Fault), and are replaced by more open marine deposits southward. As summarized above, several littoral, and even continental, sequences occur in this succession, including deposits in the Amara, Cernavodă, Ramadan (Avram et al., 1996) and Cochirleni formations, whereas the Gherghina Formation is purely continental, with occasional minor marine interbeds produced during short-term ingressions of the sea.

In the Cernavodă-Cochirleni area the outcropping Mesozoic is restricted to the Lower Cretaceous, and includes deposits belonging to the Cernavodă, Ostrov (or Ramadan), Gherghina, and Cochirleni formations. While the lower–middle part of the Cernavodă Formation is well exposed and widely distributed in this area, its upper part (the lower Hauterivian Vederoasa Member) is unevenly developed. This member is missing in the classical succession from Cernavodă-Hinog, on the right bank of the Danube (Dragastan et al., 1998), but was recently identified in the more eastern Cernavodă-lock section (Dragastan et al., 2014). Similarly, the Ostrov Formation is represented in the area only by its upper subunit (the Lower Aptian Lipniţa Member; Dragastan et al., 1998), covering unconformably and transgressively the Valanginian Alimanu Member of the Cernavodă Formation in the southern end of the Cernavodă-Hinog section (Dragastan et al., 1998), and the lower Hauterivian Vederoasa Member in the Cernavodă-lock section (Dragastan et al., 2014).

Northward of the Hinog area, Valanginian deposits of the Alimanu Member are overlain directly by the Middle–Upper Aptian continental deposits of the Gherghina

Formation. These continental deposits also cover the *Orbitolina*-bearing calcareous-clayey deposits of the Lipniţa Member towards the south, marking the advancement of emerged areas towards the central parts of Southern Dobrogea, including the Cernavodă-Cochirleni area, during this time interval (Avram et al., 1996). Marine conditions returned in the study area again in the latest Aptian, with a transgression marked by widespread deposition of the glauconitic, siliciclastic coastal to innermost shelf deposits of the Cochirleni Formation. These uppermost Aptian to Albian sands and sandstones cover transgressively all the underlying deposits, belonging to the Cernavodă, Ostrov, or Gherghina formations. Siliciclastic shallow-marine sedimentation continued into the Early Cenomanian, with the chalky-glauconitic deposits of the Peștera Formation.

4. Palaeontology

The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu (1913), who referred it to *Megalosaurus* cf. *superbus*, a taxon erected by Sauvage (1882) from the Gault ('mid'-Cretaceous: Albian) of the Paris Basin, France. The Gault material described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it and the type species *M. bucklandi*.

The convoluted taxonomic history of *Erectopus superbus* was recently reviewed by Allain (2005), who established that both the isolated teeth first mentioned by Sauvage (1876) and the skeletal elements described by Sauvage (1882) belong to the same taxon, for which the name *Erectopus superbus* was retained. Allain (2005) regarded *Erectopus* as a member of

Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al. (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.” Accordingly, if we are following the original assessment of Simionescu (1913) but updating with contemporary taxonomy, the Cochirleni theropod tooth should now be considered referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to *Erectopus superb*us (or a close relative) was considered to be unsupported by positive evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B, 3), we provide here a detailed description of its morphology followed by a thorough comparative study of this tooth based on large datasets of theropod dental measurements and discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).

We note that in his review of Romanian dinosaurs, Grigorescu (2003) erroneously considered UAIC (SCM1) 615 as being referred by Simionescu to the taxon *Megalosaurus dunkeri* Kohen (sic; actually, *Megalosaurus dunkeri* Dames, 1884). This is clearly a simple misreading of Simionescu’s identification. Additionally, such a referral is also contradicted by the absence of mesial serrations in the holotype tooth of *M. dunkeri*, considered by Carrano et al. (2012) to represent an indeterminate theropod. The Dobrogea tooth, on the other hand, has mesial serrations (see below).

4.1. Age of UAIC (SCM1) 615

The age of UAIC (SCM1) 615 has been contentious, due to the uncertainties concerning its place of origin. Although it is often mentioned as originating from Cochirleni village (e.g., Grigorescu, 2003; Turculeț and Brânzilă, 2012), this has not been definitively established. According to the original report of Simionescu (1913), the tooth came from the upper part of

the Lower Cretaceous limestone succession exposed in the cliffs extending from Cernavodă to Cochirleni along the right bank of the Danube. The corresponding entry from the Hârșova Museum registry states that it was found in the 'Cochirleni quarry', a location that presently cannot be identified precisely. The only rocks to be quarried in the area are the calcareous deposits of either the Cernavodă or Ostrov formations, particularly the ones that crop out in the Danube bank cliffs between Cernavodă-Hinog-Cochirleni. Finally, although the mention 'Cochirleni' is usually considered to refer to Cochirleni village, it should be mentioned that the cliff-forming hill that extends between Cernavodă and Cochirleni is also known by the same name (Fig. 1). Taking all of this evidence into consideration, it is thus reasonable to conclude that the tooth was most likely found in the Lower Cretaceous limestone succession exposed in the Danube cliffs between Cernavodă and Cochirleni.

Based on the location of the discovery, in the upper part of the local limestone succession, and the age of the deposits from Cernavodă-Cochirleni known to him, Simionescu (1913) considered the tooth to be of Barremian age. Subsequently, the age of the tooth was given as Valanginian–Barremian (Weishampel, 1990; Weishampel et al., 2004) or Valanginian (e.g., Grigorescu, 2003), but without any supporting information.

New attempts have been made to more precisely constrain the age of UAIC (SCM1) 615. Dragastan et al. (2014) recently sampled the limestone matrix holder of the tooth, and reported from these samples an assemblage of foraminiferans, ostracods and microproblematicae (=*incertae sedis* microorganisms) that characterize their 'Biozone IX with *Meandrospira favrei*', of latest Valanginian age in the local lithostratigraphic scheme. In parallel, we also sampled the same limestone holder – a yellowish white, friable lime mudstone – that yielded a poor and badly preserved calcareous nannoplankton assemblage with *Watznaueria barnesiae, W. ovata, Nannoconus steinmanni*, *N. kamptneri*, *N. globulus*, *Calcicalathina sp*., *Speetonia colligata* and *Cyclagelosphaera deflandrei* (M. C. Melinte-

Dobrinescu, personal communication, November 2013), an assemblage that suggests a Berriasian–Hauterivian age of the limestone holder.

Since it is not clear if the limestone holder came from the same site as the tooth itself, we managed to take a second sample from the limestone matrix still partly filling the pulp cavity of the tooth, which must definitively be identical with the rocks the tooth was found in. This second, much smaller sample yielded only very scarce specimens of *Watznaueria barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in abundance during the Berriasian and, especially, the Valanginian.

In the nannoplankton succession reported previously by Avram et al. (1993) and derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu Member of the Cernavodă Formation. These assemblages were interpreted to represent the nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous of the Mecsek Mountains, Hungary, by Császár et al. (2000).

Together, all the available evidence (Simionescu's original account, geographic and geologic records, foraminifera, ostracods, microproblematicae, and calcareous nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member of the Cernavodă Formation, and it is most probably of late Valanginian age.

4.2. Description and comparisons

Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2, 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown

base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is remarkably well preserved, with the enamel in pristine condition. It preserves most of the crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5 mm missing in the apical region.

In its present state, the mesial edge and part of the mesial third of the tooth are embedded in the limestone holder (Fig. 2B), although the tooth was once removed (see above, History of collecting and curation; Fig. 2A). Accordingly, it is exposed so that all faces of the tooth are widely visible, including the root region, except for the mesial surface.

Only the basal-most part of the root is preserved, and it is more complete near the mesial margin (Fig. 3B, C). Here, broken areas around the crown-root contact area (cervix) reveal details of the pulp cavity development, as well as the pattern of the dentine thickness variation (Fig. 3B–D). The crown also exhibits a transverse break at about two-thirds of its length (not present so obviously in the original figure of the specimen in Simionescu, 1913), and adjacent to it, the distal carina is also slightly chipped distal to mid-length. The labial face is superficially split near this break (Fig. 3A), while a more prominent region of damage appears on the lingual face, where a large (13 x 5 mm), slightly triangular wedge is broken off, exposing the deeper parts of the dentine (Fig. 3C). The damage to the lingual side apparently occurred after the original description of the tooth (Fig. 2), an observation that is concordant with the complex curatorial history of the specimen.

The basal-most, exposed part of the mesial face lacks the enamel cover (Fig. 3C, D), suggesting that this area already belongs to the root region. The mesial edge of the preserved crown base appears to be wider than the distal one, and is largely rounded transversely. Accordingly, the basal cross-section is teardrop-shaped (lanceolate); it is rounded mesially, but narrows distally into a small carina (Fig. 3D). As mentioned above, the pulp cavity is

exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B). Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped (Fig. 3D).

The tooth is ziphodont and only very slightly recurved distally. The distal edge is nearly straight across its length, being very mildly concave in its basal half and slightly convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the tooth crown base. The mesial edge, as shown in the original publication of Simionescu (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually compressed (Fig. 3B), with a crown base ratio (CBR=CBW/CBL) of 0.56, within the normal range of variation of most theropods. This differs from the thinner teeth of some, but not all, carcharodontosaurids (CBR<0.50), and the much thicker incrassate teeth of derived tyrannosauroids and conical teeth of spinosaurids (CBR>0.75) (Sereno et al., 1996; Brusatte et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).

The crown cross-section is slightly asymmetrical labiolingually when it is seen in distal view. In this view, when the carina is facing directly distally, one side of the crown has a more pronounced bulge than its counterpart (about 8.5 mm wide, measured from the carina, vs. 6 mm on the other side; Fig. 3B); based on comparisons with the teeth of *Mapusaurus* (Coria and Currie, 2006), the more bulging side can be interpreted as the lingual one. This asymmetry diminishes apically, where both sides become about equally convex. The distal carina itself twists slightly sideways (labially) in apical direction, such that it is located closer

to the labial face where it terminates at the crown apex, and the lingual face of the denticles is exposed distally (Fig. 3B, F). This twist of the distal carina is accompanied by a similar outline of the lingual side; in distal view, this is somewhat convex basally, but becomes flat to slightly concave in the apical two-thirds of the crown. A similar S-shaped curvature of the crown, albeit more pronounced and different in details, was also reported in *Mapusaurus* and *Giganotosaurus* (Coria and Currie, 2006), and in indeterminate carcharodontosaurid teeth from Morocco (Richter et al., 2013).

The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with minute serrations across its entire preserved length; the denticles are proximodistally subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig. 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so it is not possible to determine whether the serrations continued over the apex of the tooth. There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the carina. Serration shape and size remain relatively constant across the carina, although the serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig. 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F). Changes in serration size are gradual across the carina, not sudden or sporadic.

Although they are all more or less rectangular in shape, the apical denticles are relatively shorter proximodistally than the more basal ones. Most of the denticles have slightly rounded, asymmetrically convex triangular tips, instead of being simply squarred-off, and they do not hook as in troodontids and to a lesser extent abelisaurids (Hendrickx and Mateus, 2014). Other denticles near the apex, however, show a faint concavity along their tips, giving them a bilobate aspect, although this is both less conspicuous and far less regularly developed than reported in *Tyrannotitan* (Novas et al., 2005). The denticles are

separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length. The interdenticular space between adjacent denticles is broad, measuring more than a third of the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These sulci are so short and indistinct that they are only visible under low angle light.

Little can be said about the mesial carina, as it is not visible in the current state of the specimen, buried in the limestone matrix. Based on the description of Simionescu (1913), however, it is covered across its length with minute serrations; these decrease in size towards the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles) per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus, 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii* where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*’ *superbus* (Sauvage, 1876, 1882) in this respect.

The external enamel surface exhibits two forms of ornamentation. First, the majority of the labial and lingual faces are covered by relatively smooth enamel that exhibits a subtle form of braided texture visible under low angle light (Fig. 3A, C, E). This texture is made up of a series of very faint, apico-basally running ridges; these are of unequal lengths, starting at different points of the crown height, but none extends the whole length of the crown. The two longest ridges are placed near the distal carina. The enamel is also finely granulated.

Second, near the carinae on both labial and lingual surfaces there are marginal undulations: wrinkles in the enamel that stand out in bas relief (Brusatte et al., 2007). These are much better preserved and visible near the distal carina, where they are so pronounced

that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly developed wrinkles are present along the crown height; in the basal half of the crown, the wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer than twice the space separating each undulation. The wrinkles project obliquely (in the mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal segment on the crown, and curve apically as they approach the carina (at about 45°) with a tendency to become tangential to the distal edge. The wrinkles are especially well developed, prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig. 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm). Apically, however, the wrinkles are somewhat wider and longer, extending over about half of the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the crown in wrinkle development as well, these being better expressed on the more rounded, convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the presumed labial face, only some of the basal-most wrinkles, particularly the second and third one, appear well defined.

Towards the base of the crown a few of the wrinkles continue across the labial and lingual surfaces as very subtle transverse undulations. Most conspicuous of these is a 3.5 mm wide horizontal swelling that crosses the crown, at the level of wrinkles 2 and 3; this swelling is clearly visible on both sides of the crown (Fig. 3. A, C). There are no lateral flutes, apico-basal ridges, or longitudinal grooves on the labial or lingual faces, either in the centre of the tooth or paralleling the carinae. Instead, the labial and lingual faces are uniformly convex, giving the tooth its teardrop-shaped outline in cross section.

5. Discussion

5.1. *Identification of UAIC (SCM1) 615*

The isolated tooth from Cochirleni can be referred to Theropoda based on its large size, recurved and labiolingually compressed morphology, and presence of a continuous series of well-defined serrations on the distal carina.

Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are also known to posess remarkably theropod-like, laterally compressed and serrated teeth, not unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are significantly smaller than the Southern Dobrogean specimen, especially in the case of the Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest, caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615; moreover, these teeth are slightly conical and less laterally compressed than the Southern Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true denticles along their carinae) are reported in Europe only beginning in the Albian (Ősi et al., 2015), and these are both significantly smaller and different in morphology from the Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a theropod tooth.

We used four techniques to identify which type of theropod UAIC (SCM1) 615 likely belongs to (see also Supplementary Material).

First, we conducted a Principal Components Analysis (PCA) based on a large database that includes a broad and representative sample of theropod teeth. This dataset was compiled by Hendrickx et al. (2015a), which built upon the earlier studies of Smith et al.

(2005) and Larson and Currie (2013), and it or a similar version has been used in recent studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, 2014; Brusatte and Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL, CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to this dataset, the data were log-transformed prior to analysis, missing values for measurements were estimated with a mean value for that measurement from across the sample, and then a PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17 (Hammer et al., 2001).

In the resulting two dimensional morphospace (Fig. 4), UAIC (SCM1) 615 plots close to many teeth belonging to carcharodontosaurids, along with some teeth belonging to spinosaurids and tyrannosauroids. It falls within the convex hull (maximum morphospace occupation area) of carcharodontosaurids only, although it is closely outside of the edges of spinosaurid and tyrannosauroid space. It also falls within the 95% confidence interval ellipse for carcharodontosaurids, but not within the ellipse of any other group (Supplementary Information). This exercise indicates that UAIC (SCM1) 615 is most similar to carcharodontosaurids.

Secondly, we used the log-transformed dataset that we also used for the PCA to conduct a clustering analysis. We performed the analysis in PAST v2.17, using the paired group algorithm and the correlation similarity measure. In the resulting dendrogram, UAIC (SCM1) 615 groups with a handful of teeth belonging to carcharodontosaurids, tyrannosauroids, and *Allosaurus* (Supplementary Information).

Third, we used the tooth measurement database to conduct a discriminant analysis in PAST v3.0 (Hammer et al., 2001). This analysis uses pre-determined groups (in this case, taxonomic clusters) to create a morphospace in which these groups are maximally separated.

This allows teeth of unknown affinities, such as UAIC (SCM1) 615, to be classified according to which taxonomic group it is most similar to in this discriminant morphospace. In total, 67.79% of other teeth are classified correctly when they are treated as having uncertain affinities and their measurements are used to classify them in discriminant space, indicating that this exercise returns reasonable results. Our analysis classifies the Romanian tooth as a carcharodontosaurid. Furthermore, the analysis places UAIC (SCM1) 615 within the convex hulls for carcharodontosaurids and tyrannosauroids, and the 95% confidence ellipses for carcharodontosaurids, coelophysoids, and neovenatorids.

Fourth, we ran a phylogenetic analysis by including UAIC (SCM1) 615 in the discrete character dataset of theropod dental features published by Hendrickx and Mateus (2014). The Romanian specimen was scored as a lateral tooth in this analysis. The analysis was conducted in TNT (Goloboff et al., 2008), and resulted in 224 most parsimonious trees (686 steps, consistency index of 0.338, retention index of 0.566). The strict consensus topology is moderately well resolved and places the Romanian tooth as the sister taxon to *Carcharodontosaurus* (Supplementary Material). This sister taxon pair is recovered as the sister clade to a grouping of the derived carcharodontosaurids *Mapusaurus* and *Giganotosaurus*.

Several synapomorphies support the carcharodontosaurid affinities of UAIC (SCM1) 615. The sister group relationship with *Carcharodontosaurus* is supported by two features: a roughly straight distal margin of the crown (character 68) and pronounced marginal undulations in the enamel that are well visible in normal light (character 112). The broader clade of UAIC (SCM1) 615, *Carcharodontosaurus*, *Mapusaurus*, and *Giganotosaurus* (= Carcharodontosaurinae, as defined by Brusatte and Sereno, 2008, and Carrano et al., 2012) is linked by numerous characters, including: large teeth with a crown height greater than 6 cm (character 65), a bowed or sigmoid distal carina in distal view (character 82), marginal

undulations that are at least twice as long mesiodistally as the space separating each undulation (character 111), and marginal undulations present on both mesial and distal sides of the crown (character 113).

The Romanian specimen also lacks many keystone dental synapomorphies of other theropod clades, based on the clade diagnoses of Hendrickx and Mateus (2014) and other cladistic studies that include dental characters. UAIC (SCM1) 615 does not possess the hooked distal denticles of some Abelisauridae, the strongly labially deflected distal carina and pronounced transverse enamel undulations extending across the labial and lingual tooth faces of Ceratosauridae, the incrassate teeth with apicobasal enamel flutes and deeply veined enamel surface texture of Spinosauridae, and the large transverse undulations of some basal allosauroids (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of derived tyrannosauroids (Brusatte et al., 2010a) and the large and strongly hooked (or pointed) denticles of troodontids and therizinosauroids (e.g., Turner et al., 2012; Brusatte et al., 2014; Hendrickx and Mateus, 2014). The large size, as well as recurved and ziphodont shape of UAIC (SCM1) 615 is strikingly different from the non-ziphodont therizinosauroids, ornithomimosaurs, alvarezsauroids, and most troodontids, which have conical, leaf-shaped, or peg-like teeth (when teeth are present) (e.g., Holtz et al., 2004a; Turner et al., 2012; Brusatte et al., 2014). Finally, besides its remarkably large size, the presence of serrations indicates that UAIC (SCM1) 615 does not belong to groups such as alvarezsauroids, oviraptorosaurs, basal troodontids, or avialans, which have unserrated crowns (e.g., Turner et al., 2012; Hendrickx and Mateus, 2014).

In summary, the four analyses all support carcharodontosaurid affinities for UAIC (SCM1) 615. Both overall tooth proportions and discrete phylogenetic characters point to a carcharodontosaurid identification, and the discriminant function analysis and phylogenetic analysis both explicitly recover the tooth as a carcharodontosaurid. For this reason we refer

this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as recovered in our analysis, is congruent with results of previous analyses based on larger sets of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno, 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015), and offers some support for considering the Romanian carcharodontosaurid from Southern Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

Two final notes are worth adding. First, our analyses also incorporated carcharodontosaurids that are usually found to be basal within the clade, such as *Acrocanthosaurus* and *Eocarcharia* (e.g., Harris, 1998; Sereno and Brusatte, 2008; Carrano et al., 2012) as well as a host of other allosauroids, including members of Neovenatoridae (*Neovenator*, *Australovenator* and *Fukuiraptor*), a clade that is often recovered as sister-taxon to carcharodontosaurids within Carcharodontosauria (e.g., Benson et al., 2010; Carrano et al., 2012; but see Novas et al., 2013; Porfiri et al., 2014, for an alternate placement of neovenatorids in general). Both PCA and phylogenetic analysis clearly identified UAIC (SCM1) 615 as more closely comparable morphologically to derived carcharodontosaurids than to either basal carcharodontosaurids or to any other allosauroid subclade.

Second, our datasets also included teeth of *Erectopus*, the genus erected for ‘*Megalosaurus’ superbus* to which UAIC (SCM1) 615 was originally referred. Again, our analyses clearly indicate that there are no close morphological and morphometric similarities between the two, which is in accordance with the suggestion of Carrano et al. (2012) that *Erectopus* represents a non-carcharodontosaurid taxon, while our analysis identifies UAIC

(SCM1) 615 as a carcharodontosaurid. Instead, *Erectopus* groups with abelisauroids in the phylogenetic analysis. This is somewhat surprisingly, as Allain (2005) and Carrano et al. (2012) both identified *Erectopus* as a tetanuran. It should be noted, however, that Albian-aged abelisauroids are known from the same general area (eastern France) as that yielding the material referred to *Erectopus* (Accarie et al., 1995; Carrano and Sampson, 2008), raising the intriguing possibility that this taxon may represent an abelisauroid instead of an allosauroid tetanuran as suggested by Allain (2005) and Carrano et al. (2012). However, it must be remembered that this phylogenetic analysis is based on dental characters only, so it is probably more likely that *Erectopus* is a tetanuran with a dentition convergent to some extent with those of certain abelisauroids.

5.2. Body size of UAIC (SCM1) 615

One of the most salient and remarkable features of UAIC (SCM1) 615 is its large size. In the large and comprehensive sample of theropod teeth from our dataset, tooth size (estimated based on crown height – CH, and used as a rough proxy of body size) ranges from 2.2 mm (in the dromaeosaurid *Saurornitholestes* and the coelurosaur of uncertain affinities *Richardoestesia*) to 117.1 mm in the gigantic tyrannosauroid *Tyrannosaurus*. The Romanian specimen UAIC (SCM1) 615, with a CH of 85.5 mm, is ranked in the 60-80% maximum size (~ CH) range of the sample, and has a CH that is 73% of the largest tyrannosauroid teeth. Most of the teeth in the dataset (over 61% of the 966 measured teeth) are very small to small (less than 25 mm CH), and less than 10% of these fall in the 60-100% CH size categories. Teeth larger than UAIC (SCM1) 615 make up less than 5% of the total sample, and they represent only five taxa: the megalosaurid *Torvosaurus*, the tyrannosauroid *Tyrannosaurus*, the basal carcharodontosaurid *Acrocanthosaurus*, and the derived carcharodontosaurines *Carcharodontosaurus* and *Giganotosaurus*. Compared to other carcharodontosaurids, UAIC

(SCM1) 615 is smaller than the largest teeth of *Acrocanthosaurus* (9% difference), *Carcharodontosaurus* (20%), and *Giganotosaurus* (12.5%) in the dataset, but is 13% bigger than the largest tooth of *Mapusaurus*.

It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Sereno et al., 1996; Calvo and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn, corroborates growing evidence that very large body size was acquired very early in carcharodontosaurid history, since the earliest potential members of the clade are already of relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.

The inferred large body size of the South Dobrogean theropod is also remarkable as virtually all other dinosaur remains reported previously from Romania (both from the Early Cretaceous Cornet assemblage and the much later, end Cretaceous Haţeg Island fauna) are significantly smaller, and many have been interpreted as insular dwarfs (e.g., Weishampel et al., 1993, 2003; Benton et al., 2006, 2010; Stein et al., 2010; Ősi et al., 2014). Although other Romanian theropod dinosaurs were not particularly dwarfed (e.g. Brusatte et al., 2013), they were nonetheless small (Nopcsa, 1902; Csiki and Grigorescu, 1998; Csiki et al., 2010; Brusatte et al., 2013). This bias towards small bodied Romanian theropods was also

interpreted as a consequence of their insular habitat (Csiki and Grigorescu, 1998), as all previously reported theropod remains come from within the Carpathian Orogen, an area with an archipelago-type palaeogeography during the Cretaceous (Dercourt et al., 2000; Csontos and Vörös, 2004; Csiki-Sava et al., 2015). By contrast, UAIC (SCM1) 615 was found in shallow marine deposits bordering the emerged areas of Central Dobrogea, part of the stable cratonic areas of Europe and connected at least intermittently to the Ukrainean Shield since the Late Jurassic (Fig. 5A). Although cratonic Europe was also transformed into an archipelago of islands during much of the Cretaceous, these islands were often both larger in size and more stable in space and time than were the transient emerged areas of the Tethyan archipelagoes. As such, it is conceivable that the Southern Dobrogean carcharodontosaurid was less constrained by space or resource limitations than the Tethyan insular dinosaurs, allowing it to retain a large body size.

5.*3. UAIC (SCM1) 615 and Valanginian dinosaur distribution*

Besides documenting the presence of large-sized mainland carcharodontosaurids in the Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a significant gap in our knowledge on the composition and distribution of the Early Cretaceous dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these being known from the later part (Barremian–Albian) of that epoch; only around a dozen localities were listed from each age of the early part of the Early Cretaceous (Berriasian, Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al., 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards

western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no occurrences are known from the entire central, eastern and southern Europe for the Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).

Our identification of the Romanian tooth as a carcharodontosaurid documents the presence of this clade in Europe in the very early Cretaceous. This is significant, as carcharodontosaurids were widely distributed tens of millions of years later, in the middle Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see below). Despite the recent discoveries documenting that the clade was also present in North America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010; see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than previously thought and were a long-term component of the European mainland Early Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might have been already present between the cratonic, stable European mainland, with a dinosaur fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania (Benton et al., 2006).

This Valanginian carcharodontosaurid represents an important datapoint not only for the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a poorly documented age in dinosaur evolution, with very few precisely dated fossil occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known from Asia, some of which have debatable or controversial dates. These include sites in Japan (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992; Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare dinosaur remains of possible Valanginian (or ‘Neocomian’) age were also reported from southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g., Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli et al., 2014).

As one of the two known reports of Valanginian dinosaurs in Europe east of France, the Southern Dobrogean dinosaur record fills a huge palaeogeographic gap between the western European and the eastern Asian dinosaur faunas. Moreover, none of these early Early Cretaceous dinosaur assemblages from outside Europe include carcharodontosaurids (see below), as theropods are represented by coelurosaurians interpreted either as compsognathids (Gishlick and Gauthier, 2007) or basal ornithomimosaurs (Choiniere et al., 2012) in southern Africa, metriacanthosaurid allosauroids (‘sinraptorids’) in Thailand (Buffetaut and Suteethorn, 2007), and indeterminate allosauroids (Pérez-Moreno et al., 1993), non-

carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz, 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest that carcharodontosaurids had not achieved a wide geographic distribution by this point in time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.

Finally, the presence of the Cochirleni carcharodontosaurid might hint at the presence of palaeobiogeographic provinciality between the western and the eastern parts of Europe, partly mirroring those reported from the later part of the Late Cretaceous (e.g., Le Loeuff and Buffetaut, 1995; Weishampel et al., 2010; Ősi et al., 2012; Csiki-Sava et al., 2015). In the reasonably well sampled, and significantly better known, western European dinosaur faunas, Valanginian large carnivorous dinosaurs include non-carcharodontosaurid tetanurans (*Becklespinax*), as well as indeterminate allosauroids or indeterminate theropods (often described as '*Megalosaurus' dunkeri*, '*M.*' *insignis* or '*M.*' *oweni*), none of which can be referred positively to Carcharodontosauridae (Carrano et al., 2012). The apparently provincial geographic distribution of the large-bodied theropods suggests that some degree of faunal differentiation was occurring within the European mainland, most probably promoted by geographic distance. Notably, this intra-European differentiation in theropod assemblages appears to stand in contrast with the faunal homogeneity reported in the case of the ornithopods from the UK and Romania (e.g., Galton, 2009). It is important, however, to re-emphasize at this point that the Valanginian dinosaur fossil record is both exceedingly poor and patchy, even in Europe. Accordingly, further discoveries are needed to verify and support (or contradict) the presence of such a distribution pattern pointing to palaeobiogeographic provinciality inside Europe, as the one suggested by our carcharodontosaurid identification for UAIC (SCM1) 615.

5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography

Carcharodontosauridae were long considered as an exclusively Gondwanan group of theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996; Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Cau et al., 2013). This view started to change with the identification of the Early Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan one, was further supported by the discovery of definitive carcharodontosaurids in the Lower Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper Cretaceous of China (Brusatte et al., 2009, 2010b, 2012; Mo et al., 2014; Lü et al., 2016).

Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin of the carcharodontosaurids, followed by their dispersal across Laurasia and western Gondwana beginning at least by the Aptian (Fig. 5B), a scenario that is concordant with the tentatively suggested presence of early carcharodontosaurids in the Upper Jurassic of Tanzania, which are based on fragmentary specimens (Rauhut, 2011; Carrano et al., 2012). It is also concordant with the widespread appearance of carcharodontosaurids in the fossil record starting with the Aptian, when they are reported in Africa (*Eocarcharia*; Sereno and Brusatte, 2008), South America (Vickers-Rich et al., 1999), North America (*Acrocanthosaurus*; Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000 Eddy and Clarke, 2011), Europe (Canudo and Ruiz-Omeñaca, 2003; Pereda-Suberbiola et al., 2012), and eastern Asia (*Kelmayisaurus*; Brusatte et al., 2012; Mo et al., 2014; Lü et al., 2016).

During the Albian–Turonian, carcharodontosaurids became especially abundant and diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and South America (*Tyrannotitan*, *Giganotosautus*, *Mapusaurus*, alongside with indeterminate carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005; Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig. 5B). They were still present during this time interval in other continents, as well: in North America with *Acrocanthosaurus* until the Albian (D'Emic et al., 2012), in Europe until the Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).

After dominating terrestrial ecosystems at least in Africa, South America and eastern Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado, 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana. Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-Cenomanian deposits of South America to Carcharodontosaridae (e.g., Canudo et al., 2008; Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were reported to suggest the survival of carcharodontosaurids into the latest Cretaceous (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).

Contrasting with this rich and relatively continuous fossil record of Carcharodontosauridae starting with the Aptian, the first half of its evolutionary history is very poorly documented (Fig. 5B). Prior to the identification of UAIC (SCM1) 615, only two occurrences of pre-Aptian Cretaceous carcharodontosaurids were reported, one from the Barremian of Spain (Ortega et al., 2010; Gasca et al., 2014) and the other from the Barremian of Thailand (Buffetaut and Suteethorn, 2012). The Early Cretaceous *Kelmayisaurus* from Xinjiang, western China, was recognized as a carcharodontosaurid of possibly ?Valanginian to Aptian in age by Brusatte et al. (2012), but the deposits yielding these remains (the Lianmugin, or Lianmuxin, Formation of the Tugulu Group) were dated as Aptian–Albian by Eberth et al. (2001; see also Tong et al., 2009). An important temporal gap – of about 20 to 28 millions of years, according to the dates in Gradstein et al. (2012) – thus stretched between the oldest, tentatively assigned carcharodontosaurids from the Oxfordian–Tithonian of Tanzania, including the formally erected *Veterupristisaurus* (Rauhut, 2011; see also Carrano et al., 2012), and those that started to appear in the fossil record in the Barremian and then spread widely during the Aptian. Referral of UAIC (SCM1) 615 to Carcharodontosauridae partially fills this frustrating gap, effectively halving this shadowy period in the evolutionary history of the group.

Furthermore, our analyses tentatively cluster the Dobrogean theropod with the derived members of the Carcharodontosaurinae to the exclusion of the more basal, but significantly younger non-carcharodontosaurine carcharodontosaurids *Eocarcharia* and *Acrocanthosaurus*. If this placement is correct, then the Romanian tooth indicates that Carcharodontosaurinae diverged from other carcharodontosaurids considerably earlier than hitherto recognized.

The previously known fossil record of the clade suggested that Carcharodontosaurinae originated sometime between the Aptian and Albian, as basal carcharodontosaurids (*Acrocanthosaurus, Concavenator*, *Eocarcharia*) were moderately diverse in the Barremian–Aptian, followed by the appearance of many fossils of carcharodontosaurines beginning in the Albian (Fig. 5B). The proposed affinities of the oldest carcharodontosaurid material – including isolated teeth referred to as ‘*Megalosaurus*’ *ingens* – from the east African Upper

Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut, 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very large size and dental morphology characterizing it) well before the Albian, during or even before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.

Besides shifting the emergence of the carcharodontosaurines earlier in time, identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting palaeobiogeographic implications. As already noted, recent discoveries show that Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g., Novas et al., 2005), with the identification of its widespread, Pangaean distribution during the late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999; Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014). However, within Carcharodontosauridae itself, some palaeogeographic patterns have been widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al., 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as previously all its recognized members were restricted strictly to either Africa (Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995; Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of Carcharodontosaurinae were still adhering to patterns of continental fragmentation and vicariant evolution, with a basal split between the Albian–Cenomanian African *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

This scenario is now challenged by our finding that the Southern Dobrogean carcharodontosaurid UAIC (SCM1) 615 may nest inside Carcharodontosaurinae. If true, such an affinity would suggest that the origin of Carcharodontosaurinae was not a southern, vicariant by-product of the Gondwana-Laurasia separation, a major palaeogeographic event that is considered to have been well underway by the end of the Jurassic, and essentially completed by the mid-Early Cretaceous (see Weishampel et al., 2010). Indeed, during this time palaeogeographic connections and faunal interactions were virtually non-existent between the northern Tethyan (European) and southern Tethyan (western Gondwanan, but essentially African) areas of the Mediterranean (e.g., Canudo et al., 2009), which makes a vicariant hypothesis intuitive. However, if the Romanian tooth represents a carcharodontosaurine, then it implies a much more complicated palaeogeographic history of the clade, which is not so clearly linked to continental breakup.

The palaeogeographic position of the Southern Dobrogean carcharodontosaurine in cratonic Europe, north of the Neo-Tethys, together with its significantly older age compared to other carcharodontosaurines, could indicate that separation of the carcharodontosaurine lineage took part in Europe and not in western Gondwana as previously assumed. This would also mean that representatives of this lineage were subsequently – after the Barremian – introduced to Africa and South America via trans-Tethyan dispersal, most probably at a time when faunal interactions between the southern and northern margins of the Mediterranean Tethys were resumed, after the early Barremian (Canudo et al., 2009).

Alternatively, it can be hypothesized that appearance of carcharodontosaurines in Southern Dobrogea is a consequence of southern immigration originating in western Gondwana, often considered the place of origin for this clade. However, this scenario has several potential caveats. Although Europe has been considered as forming part of a larger Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín, 2012), and occasional trans-Tethyan faunal connections have been recognized between Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage, 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place during the 'Neocomian' (Berriasian–Hauterivian) time interval.

More recently, some potential evidence has emerged for Gondwana-to-Europe interchange during the 'Neocomian'. The presence of the basal rebbachisaurid *Histriasaurus* (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as indicative of very early and very rapid northward dispersal of this clade from western Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of this particular dispersal event was even constrained to the Berriasian–Valanginian time interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive transportation mechanism ('Noah's Ark'; McKenna, 1973) for basal rebbachisaurids after its separation from mainland Africa (e.g., Torcida Fernández-Baldor et al., 2011). Furthermore, the palaeogeographical separation between Africa and Adria (and thus the effective movement of the presumed ark) is considered to be at most an incipient one during the Early Cretaceous by Bossellini (2002) and Zarcone et al. (2010), with spatial continuity still present between the two landmasses, while deep-water basins continued to separate Adria from the European Craton. Accordingly, although the presence of *Histriasaurus* can represent a case of northward range extension of rebbachisaurids during the Berriasian–Valanginian, it took place not strictly speaking into Europe, but only reached the northernmost extremity of Adria, a northerly peninsular extension of the African mainland. It was only starting with the Barremian that rebbachisaurids dispersed as far north as the European cratonic areas, including Iberia and the British Isles (Mannion, 2009; Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011), a time when faunal interchanges between Europe and Africa are considered to have been well underway (e.g., Gheerbrant and Rage, 2006; Canudo et al., 2009).

Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant of the European mainland. It is thus unclear to what extent the example of rebbachisaurid range extension into (present-day) Europe during the early Early Cretaceous, as potentially testified by the discovery of the Croatian taxon, would also be applicable for the Southern Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are very different, and that faunal connections during this time interval are not documented between the African and European cratons as already pointed out by Gheerbrant and Rage (2006).

Absence of documented faunal interactions weakens support for a scenario of south-to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the Cretaceous, and would argue instead for a local, European development to explain the presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian presence of carcharodontosaurids in Europe is also consistent with their appearance in the Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in North America likely requires the presence of pre-Aptian members of the clade in Europe, since faunal exchanges between these two landmasses are known to have been halted before the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western Gondwana. The causes of these distribution patterns remain as yet unknown, and further support – in the form on new carcharodontosaurid discoveries from the early-middle part of the Early Cretaceous – is required to better uphold such a scenario.

We finally reiterate that if the Romanian tooth does not belong to a carcharodontosaurine, but instead is artefactually grouping with them in the phylogenetic analysis because of the very incomplete nature of the material, then the traditional story of Carcharodontosaurinae as a product of vicariant evolution driven by the breakup of Pangea will remain strongly supported. However, even in such case UAIC (SCM1) 615 would still record the presence of early-occuring large carcharodontosaurid theropods with a very characteristic carcharodontosaurine-type dentition in the eastern part of the European craton, adding to known early Early Cretaceous theropod (and dinosaur) diversity, and potentially documenting dinosaur faunal provinciality in Europe and worldwide.

6. Conclusions

We re-describe and interpret the affinities of one of the most significant historical dinosaurian specimens of Romania, an isolated but well-preserved theropod tooth from Southern Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth, while the available evidence – including novel calcareous nannoplankton sampling – supports its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this record advances our understanding of European dinosaur distribution during the early Early Cretaceous, and also fills an important palaeogeographic gap between Western European and Eastern Asian dinosaurian assemblages of the Valanginian.

Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a possible member of Carcharodontosaurinae, a subclade of derived and gigantic carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean specimen documents the emergence of Carcharodontosaurinae earlier than previously recognized, thus also indicating an earlier acquisition of their characteristically large size. Based on currently known palaeogeographic and chronostratigraphic constraints on the evolution of Carcharodontosauridae, it appears that not only did this clade have a wide distribution, but that crucial events of its evolutionary history such as the emergence of the derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia split, as was formerly suggested. In such a case, instead of endemic evolution the emergence of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into western Gondwana adds further support for the presence of important palaeogeographic ties between the two realms during the second half of the Early Cretaceous.

Acknowledgements

This research was supported by the National Research Council of Romania (CNCS) grant PN-IIID-PCE-2011-3-0381 and a Sepkoski grant of the Paleontological Society for Z.Cs.-S.

S.L.B. is supported by a Marie Curie Career Integration Grant EC630652, the Division of Paleontology of the American Museum of Natural History, and the School of GeoSciences of the University of Edinburgh. He thanks Mátyás Vremir, Radu Totoianu, and Mark Norell for many hours of fun discussion on Romanian fossils, and for supporting his work and travel in Romania. We thank Mihai Brânzilă and Paul Țibuleac (UAIC) for access to the specimen, for allowing us to collect samples for the nannoplankton analyses, and for their help and collegiality during our visit to Iași, as well as Ilie Turculeț for sharing information about the history of the specimen. Mihaela C. Melinte-Dobrinescu has gracefully analyzed the nannoplankton samples derived from UAIC (SCM1) 615; her contribution was essential in assessing the age of the specimen. Finally, we thank the reviewers Eric W.A. Mulder (Denekamp, the Netherlands) and Xabier Pereda-Suberbiola (Bilbao, Spain), as well as Associated Editor Elena Jagt-Yazykova, for their useful comments and suggestions that helped improve previous versions of the manuscript.

References

Accarie, H., Beaudoin, B., Dejax, J., Friès, G., Michard, J.G., Taquet, P., 1995. Découverte d'un dinosaure théropode nouveau (*Genusaurus sisteronis* n. g., n. sp.) dans l'Albien marin de Sisteron (Alpes-de-Haute-Provence, France) et extension au Crétacé inférieur de la lignée cératosaurienne. Comptes Rendus de l’Académie des Sciences Paris, IIa 320, 327–334.

Allain, R., 2002. Discovery of a megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. Journal of Vertebrate Paleontology 22, 548–563.

Allain, R., 2005. The enigmatic theropod dinosaur *Erectopus superbus* (Sauvage, 1882) from the Lower Albian of Louppy-le-Chateau (Meuse, France). In: Carpenter, K. (Ed.), The Carnivorous Dinosaurs. Indiana University Press, Bloomington, pp. 72–86.

Avram, E., Szasz, L., Antonescu, E., Baltreş, A., Iva, M., Melinte, M., Neagu, T., Rădan, S., Tomescu, C., 1993. Cretaceous terrestrial and shallow marine deposits in northern South Dobrogea (SE Romania). Cretaceous Research 14, 265–305.

Avram, E., Costea, I., Dragastan, O., Muţiu, R., Neagu, T., Şindilar, V., Vinogradov, C.., 1996. Distribution of the Middle-Upper Jurassic and Cretaceous facies in the Romanian eastern part of the Moesian Platform. Revue Roumaine de Géologie 39-40, 3–33.

Azevedo, R.P.F. de, Simbras, F.M., Furtado, M.R., Candeiro, C.R.A., Bergqvist, L.P., 2013. First Brazilian carcharodontosaurid and other new theropod dinosaur fossils from the Campanian-Maastrichtian Presidente Prudente Formation, São Paulo State, southeastern Brazil. Cretaceous Research 40, 131–142.

Benson, R.B.J., Barrett, P.M., Powell, H.P., Norman, D.B., 2008. The taxonomic status of *Megalosaurus bucklandii* (Dinosauria, Theropoda) from the Middle Jurassic of Oxfordshire, UK. Palaeontology 51, 419–424.

Benson, R.B.J., Carrano, M.T., Brusatte, S.L., 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. Naturwissenschaften 97, 71–78.

Benton, M.J., Cook, E., Grigorescu, D., Popa, E., Tallódi, E., 1997. Dinosaurs and other tetrapods in an Early Cretaceous bauxite-filled fissure, northwestern Romania. Palaeogeography, Palaeoclimatology, Palaeoecology 130, 275–292.

Benton, M.J., Minter, N.J., Posmoșanu, E., 2006. Dwarfing in ornithopod dinosaurs from the Early Cretaceous of Romania. In: Csiki, Z. (Ed.), Mesozoic and Cenozoic Vertebrates and Paleoenvironments; Tributes to the Career of Prof. Dan Grigorescu. Ars Docendi, Bucharest, pp. 79–87.

Benton, M.J., Csiki, Z., Grigorescu, D., Redelstorff, R., Sander, M., Stein, K., Weishampel, D.B., 2010. Dinosaurs and the island rule: the dwarfed dinosaurs from Haţeg Island. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 438–454.

Blows, W.T., Honeysett, K., 2014. First Valanginian *Polacanthus foxii* (Dinosauria, Ankylosauria) from England, from the Lower Cretaceous of Bexhill, Sussex. Proceedings of the Geologists' Association 125, 233–251.

Bosselini, A., 2002. Dinosaurs ''re-write'' the geodynamics of the eastern Mediterranean and the paleogeography of the Apulia Platform. Earth-Science Reviews 59, 211–234.

Brânzilă, M. (ed.), 2010. Academicianul Ion Simionescu - savant şi dascăl al neamului. Ed. Universităţii "Alexandru Ioan Cuza", Iaşi, 182 pp.

Brusatte, S.L., Sereno, P.C., 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. Journal of Vertebrate Paleontology 27, 902–916.

Brusatte, S.L., Sereno, P.C., 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. Journal of Systematic Palaeontology 6, 155–182.

Brusatte, S. L**.**, Clark, N.D.L., 2015. Theropod dinosaurs from the Middle Jurassic (Bajocian-Bathonian) of Skye, Scotland. Scottish Journal of Geology 51, 157-164. doi: 10.1144/sjg2014-022

Brusatte, S., Benson, R.B.J., Carr, T.D., Williamson, T.E., Sereno, P.C., 2007. The systematic utility of theropod enamel wrinkles. Journal of Vertebrate Paleontology 27, 1052–1056.

Brusatte, S.L., Benson, R.B.J., Chure, D.J., Xu, X., Sullivan, C., Hone, D.W.E., 2009. The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. Naturwissenschaften 96, 1051–1058.Brusatte, S.L., Norell, M.A., Carr, T.D., Erickson, G.M., Hutchinson, J.R., Balanoff, A.M., Bever, G.S., Choiniere, J.N., Makovicky, P.J., Xu, X. , 2010a. Tyrannosaur paleobiology: new research on ancient exemplar organisms. Science 329, 1481–1485.

Brusatte, S., Chure, D.J., Benson, R.B.J., Xu, X., 2010b. The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Asia. Zootaxa 2334, 1–46.

Brusatte, S.L., Benson, R.B.J., Xu, X., 2012. A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China. Acta Palaeontologica Polonica 57, 65–72.

Brusatte, S.L., Vremir, M., Csiki-Sava, Z., Turner, A.H., Watanabe, A., Erickson, G.M., Norell, M.A., 2013. The osteology of *Balaur bondoc*, an island-dwelling dromaeosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Romania. Bulletin of the American Museum of Natural History 374, 3–100. doi: 10.1206/798.1

Brusatte, S.L., Lloyd, G.T., Wang, S.C., Norell, M.A., 2014. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. Current Biology 24, 2386–2392.

Buckland, W., 1824. Notice on the *Megalosaurus* or great fossil lizard of Stonesfield. Transactions of the Geological Society 21, 390–397.

Buffetaut, E., Suteethorn, V., 1998. Early Cretaceous dinosaurs from Thailand and their bearing on the early evolution and biogeographical history of some groups of Cretaceous dinosaurs. In: Lucas, S.G., Kirkland, J.I., Estep, J.W. (Eds.), Lower and Middle Cretaceous Terrestrial Ecosystems, New Mexico Museum of Natural History and Science Bulletin 14, pp. 205–210.

Buffetaut, E., Suteethorn, V., 2007. A sinraptorid theropod (Dinosauria: Saurischia) from the Phu Kradung Formation of northeastern Thailand. Bulletin de la Société Géologique de France 178, 497–502.

Buffetaut, E., Suteethorn, V., 2012. A carcharodontid theropod (Dinosauria, Saurischia) from the Sao Khua Formation (Early Cretaceous, Barremian) of Thailand. In: Royo-Torres, R., Gascó, F., Alcalá, L. (Eds.), 10th Annual Meeting of the European Association of Vertebrate Palaeontologists. ¡Fundamental! 20, Teruel, pp. 27–30.

Calvo, J.O., Coria, A., 1998. New specimen of *Giganotosaurus carolinii* (Coria & Salgado, 1995), supports it as the largest theropod ever found. Gaia 15, 117–122.

Calvo, J.O., Gandossi, P., Porfiri, J.D., 2006. Dinosaur faunal replacement during Cenomanian times in Patagonia, Argentina. In: Evans, S.E., Barrett, P.M. (Eds.), 9th Mesozoic Terrestrial Ecosystems and Biota. Manchester, UK, pp. 17–20.

Canale, J.I., Scanferla, C.A., Agnolin, F.L., Novas, F.E., 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. Naturwissenschaften 96, 409–414.

Canale, J.I., Novas, F.E., Pol, D., 2015. Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. Historical Biology 27, 1–32. doi: 10.1080/08912963.2013.861830.

Candeiro, C.R.A., Fanti, F., Therrien, F., Lamanna, M.C., 2011. Continental fossil vertebrates from the mid-Cretaceous (Albian-Cenomanian) Alcântara Formation, Brazil, and their relationship with contemporaneous faunas from North Africa. Journal of African Earth Sciences 60, 79–92.

Canudo, J.I., Ruiz-Omeñaca, J.I.**,** 2003. Los restos directos de dinosaurios teropódos (excluyendo Aves) en España. Ciencias de la Tierra 26, 347–373.

Canudo, J.I., Filippi, L.S., Salgado, L., Garrido, A.C., Cerda, I.A., Garcia, R., Otero, A., 2008. Theropod teeth associated with a sauropod carcass in the Upper Cretaceous (Plottier Formation) of Rincón de los Sauces. In: Colectivo Arqueológico y Paleontológico de Salas de los Infantes (Ed.), Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Salas de los Infantes, Burgos, pp. 321–330.

Canudo, J.I. Barco, J.L., Pereda Suberbiola, X., Ruiz-Omeñaca, J.I., Salgado, L., Torcida Fernández-Baldor, F., Gasulla, J.M., 2009. What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. Bulletin de la Société Géologique de France, 180, 5–11.

Carballido, J.L., Salgado, L., Pol, D., Canudo, J.I., Garrido, A., 2012. A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. Historical Biology 24, 631–654.

Carrano, M.T., Sampson, S.D., 2008. The phylogeny of Ceratosauria (Dinosauria: Theropoda). Journal of Systematic Palaeontology 6, 183–236.

Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10, 211–300.Carvalho, I.S., Campos, A.C.A., Nobre, P.H., 2005. *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. Gondwana Research 8, 11–30.

Casal, G., Candeiro, C.R.A., Martinez, R., Ivany, E., Ibiricu, L., 2009. Dientes de Theropoda (Dinosauria: Saurischia) de la Formación Bajo Barreal, Cretácico Superior, Provincia del Chubut, Argentina. Géobios 42, 553–560.

Cau, A., Dalla Vecchia, F.M., Fabbri, M., 2013. A thick-skulled theropod (Dinosauria, Saurischia) from the Upper Cretaceous of Morocco with implications for carcharodontosaurid cranial evolution. Cretaceous Research 40, 251–260.

Choiniere, J.N., Forster, C.A., De Klerk, W.J., 2012. New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation in South Africa. Journal of African Earth Sciences 71–72, 1–17.

Chure, D.J., Manabe, M., Tanimoto, M., Tomida, Y., 1999. An unusual theropod tooth from the Mifune Group (Late Cenomanian to Early Turonian), Kumamoto, Japan. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs 15, Tokyo, pp. 291–296.

Cifelli, R.L., Davis, B.M., Sames, B., 2014. Earliest Cretaceous mammals from the western United States. Acta Palaeontologica Polonica 59, 31–52. doi:10.4202/app.2012.0089.

Cobos, A., Royo-Torres, R., Luque, L., Alcalá, L., Mampel, L., 2010. An Iberian stegosaurs paradise: The Villar del Arzobispo Formation (Tithonian–Berriasian) in Teruel (Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 293, 223–236.

Cobos, A., Lockley, M.G., Gascó, F., Royo–Torres, R., Alcalá, L., 2014. Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 399, 31–41. doi: 10.1016/j.palaeo.2014.02.008.

Codrea, V., Vremir, M., Jipa, C., Godefroit, P., Csiki, Z., Smith, T., Fărcaş, C., 2010. More than just Nopcsa's Transylvanian dinosaurs: A look outside the Haţeg Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 391–405. doi: 10.1016/j.palaeo.2009.10.027.

Codrea, V., Godefroit, P., Smith, T., 2012. First discovery of Maastrichtian (latest Cretaceous) terrestrial vertebrates in Rusca Montană Basin (Romania). In: Godefroit, P. (Ed.) Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 570–581.

Colbert, E.H., 1946. *Sebecus*, representative of a peculiar suborder of fossil Crocodilia from Patagonia. Bulletin of the American Museum of Natural History 87(4), 217–270.

Coria, R.A, Salgado, L., 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. Nature 377, 224–226.

Coria, R.A., Salgado, L., 2005. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. In: Veiga, G.D., Spalletti, L.A., Howell, J.A., Schwartz, E. (Eds.), The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics. Geological Society, London, Special Publications 252, pp. 317–327.

Coria, R.A., Currie, P.J., 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas 28, 71–118.

Covacef, Z., 1995. Pionieri ai culturii românești în Dobrogea; Ioan Cotovu și Vasile Cotovu. Analele Dobrogei I(1), 127–134.

Császár, G., Kollányi, K., Lantos, M., Lelkes, G. and Tardiné Filácz, E., 2000. A Hidasivölgyi Márga Formáció kora és képzõdési környezete. Földtani Közlöny 130(4), 695–723.

Csiki, Z., Grigorescu, D., 1998. Small theropods of the Late Cretaceous of the Haţeg Basin (Western Romania) - an unexpected diversity at the top of the food chain. Oryctos 1, 87–104.

Csiki, Z., Vremir, M., Brusatte, S.L., Norell, M.A., 2010. An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania. Proceedings of the National Academy of Sciences 107, 15357–15361.

Csiki-Sava, Z., Codrea, V., Vasile, Ș., 2013. Early Cretaceous dinosaur remains from Dobrogea (southeastern Romania). In: Picot, L. (Ed.), Abstracts, 11th Annual Meeting of the European Association of Vertebrate Palaeontologists, Villers-sur-Mer, France, pp. 28.

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., Brusatte, S.L., 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. Zookeys 469, 1–161. doi: 10.3897/zookeys.469.8439.

Csontos, L., Vörös, A., 2004. Mesozoic plate tectonic reconstruction of the Carpathian region. Palaeogeography, Palaeoclimatology, Palaeoecology 210, 1–56. doi: 10.1016/j.palaeo.2004.02.033.

Currie, P.J., Carpenter, K., 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. Geodiversitas 22, 207–246.

Currie, P.J., Rigby, J.K., Sloan, R.E., 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter, K., Currie, P.J. (Eds,), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, Boston, pp. 107–125.

Dalla Vecchia, F.M., 1998. Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (Upper Hauterivian/Lower Barremian) limestones of SW Istria (Croatia). Geologia Croatica 5, 105–134.

Dames, W., 1884. *Megalosaurus dunkeri.* Sitzungberichte Gesellschaft Naturforschender Freunde zu Berlin 1884, 186–188.

De Klerk, W.J., Forster, C.A., Sampson, S.D., Chinsamy, A., Ross, C.F., 2000. A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. Journal of Vertebrate Paleontology 20, 324–332.

D'Emic, M.D., Melstrom, K.M., Eddy, D.R., 2012. Paleobiology and geographic range of the large-bodied Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. Palaeogeography, Palaeoclimatology, Palaeoecology 333–334, 13–23.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M., Cadet, J.P., Crasquin, S., Săndulescu, M., Eds. (2000) Atlas Peri-Tethys Palaeogeographical Maps. CCGM/CGMW, Paris, 269 pp.

Dinu, C., Grădinaru, E., Stoica, M., Diaconescu, V., 2007. Dobrogea 2007 Field Trip Preparation and Assistance. University of Bucharest, 123 pp.

Dragastan, O., Neagu, T., Bărbulescu, A., Pană, I., 1998. Jurasicul şi Cretacicul din Dobrogea Centrală şi de Sud. Bucharest, 249 pp.

Dragastan, O.N., Antoniade, C., Stoica, M., 2014. Biostratigraphy and zonation of the Lower Cretaceous succession from Cernavodă-lock section, South Dobrogea, eastern part of the Moesian Platform (Romania). Carpathian Journal of Earth and Environmental Sciences 9(1), 231–260.

Dyke, G.J., Benton, M.J., Posmoșanu, E., Naish, D., 2011. Early Cretaceous (Berriasian) birds and pterosaurs from the Cornet bauxite mine, Romania. Palaeontology 54, 79–95.

Eberth, D.A., Brinkman, D.B., Chen, P.-J., Yuan, F.-T., Wu, X.-C., Li, G., Cheng, X.-S., 2001. Sequence stratigraphy, paleoclimate patterns, and vertebrate fossil preservation in Jurassic–Cretaceous strata of the Juggar Basin, Xinjiang Autonomous Region, People's Republic of China. Canadian Journal of Earth Sciences 38, 1627–1644.

Eddy, D.R., Clarke, J.A., 2011. New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroidea (Dinosauria: Theropoda). PLoS ONE 6(3), e17932. doi:10.1371/journal.pone.0017932.

Evans, S.E., Matsumoto, R., 2015. An assemblage of lizards from the Early Cretaceous of Japan. Palaeontologia Electronica 18.2.36A, 1–36.

Ezcurra, M.D., Agnolín, F.L., 2012. A new global palaeobiogeographical model for the Late Mesozoic and Early Tertiary. Systematic Biology 61, 553–566. doi:10.1093/sysbio/syr115.

Fanti, F., Cau, A., Cantelli, L., Hassine, M., Auditore, M., 2015. New information on *Tataouinea hannibalis* from the Early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. PLoS ONE 10(4), e0123475. doi:10.1371/journal.pone.0123475.

Galton, P.M., 2009. Notes on Neocomian (Lower Cretaceous) ornithopod dinosaurs from England - *Hypsilophodon*, *Valdosaurus*, “*Camptosaurus*”, “*Iguanodon*” - and referred specimens from Romania and elsewhere. Revue de Paléobiologie 28, 211–273.

Gardner, J.D., Evans, S.E., Sigogneau-Russell, D., 2003. New albanerpetontid amphibians from the Early Cretaceous of Morocco and Middle Jurassic of England. Acta Palaeontologica Polonica 48, 301–319.

Gasca, J.M., Canudo, J.I., Moreno-Azanza, M., 2014. A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 273, 13–23. doi: 10.1127/0077-7749/2014/0413.

Gheerbrant, E., Rage, J.-C., 2006. Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? Palaeogeography, Palaeoclimatology, Palaeoecology 241, 224–246. doi:10.1016/j.palaeo.2006.03.016.

Gishlick, A.D., Gauthier, J.A., 2007. On the manual morphology of *Compsognathus longipes* and its bearing on the diagnosis of Compsognathidae. Zoological Journal of the Linnean Society 149, 569–581.

Goloboff, P. A., Farris, J. S., Nixon, K. C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786.

Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), 2012. The Geologic Time Scale 2012. Elsevier, Amsterdam, 1144 pp.

Grigorescu, D., 1992. Nonmarine Cretaceous Formations of Romania. In: Matter, N.J., Chen, P.-J. (Eds.), Aspects of Nonmarine Cretaceous Geology. China Ocean Press, Beijing, pp. 142–164.

Grigorescu, D., 2003. Dinosaurs of Romania. Comptes rendus Palevol 2, 97–101.

Grigorescu, D., 2010. The Latest Cretaceous fauna with dinosaurs and mammals from the Hațeg Basin — A historical overview. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 271–282.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 1–9.

Harris, J.D., 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. New Mexico Museum of Natural History and Science Bulletin 13, 1–75.

Hendrickx, C., Mateus, O., 2014. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. Zootaxa 3751(1), 1–74.

Hendrickx, C., Mateus, O., Araújo, R., 2015a. The dentition of megalosaurid theropods. Acta Palaeontologica Polonica 60, 627–642. doi:10.4202/app.00056.2013.

Hendrickx, C., Mateus, O., Araújo, R., 2015b. A proposed terminology of theropod teeth (Dinosauria, Saurischia). Journal of Vertebrate Paleontology 35(5), e982797. doi: 10.1080/02724634.2015.982797.

Holtz, T.R., Jr.., Molnar, R.E., Currie, P.J., 2004a. Basal Tetanurae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, Los Angeles, London, pp. 71–110.

Holtz, T.R., Chapman, R.E., Lamanna, M.C., 2004b. Mesozoic biogeography of Dinosauria. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, Los Angeles, London, pp. 627–642.

Huene, F. von, 1923. Carnivorous Saurischia in Europe since the Triassic. Bulletin of the Geological Society of America 34, 449–458.

Hippolyte, J.-C., 2002. Geodynamics of Dobrogea (Romania): new constraints on the evolution of the Tornquist–Teisseyre Line, the Black Sea and the Carpathians. Tectonophysics 357, 33–53.

Ionesi, L., 1994. Geologia unităţilor de platformă şi a orogenului Nord-Dobrogean. Ed. Tehnică, Bucharest, 280 pp.

Jerzykiewicz, T., Russell, D.A., 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. Cretaceous Research 12, 345–377.

Jurcsák, T., 1982. Occurences nouvelles des Sauriens mésozoïques de Roumanie. Vertebrata Hungarica 21, 175–184.

Jurcsák, T., Popa, E., 1979. Dinozaurieni ornithopozi din bauxitele de la Cornet (Munții Pădurea Craiului). Nymphaea 7, 37–75.

Jurcsák, T., Popa, E., 1983. La faune de dinosauriens du Bihor (Roumanie). In: Buffetaut, E., Mazin, J.M., Salmon, E. (Eds.), Actes du Symposium Paléontologique Georges Cuvier. Le Serpentaire, Montbéliard, pp. 325–335.

Kellner, A.W.A., Pinheiro, A.E.P., Campos, D.A., 2014. A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K–Pg boundary. PLoS ONE 9(1), e81386. doi:10.1371/journal.pone.0081386.

Kirkland, J.I., Cifelli, R.L., Britt, B.B., Burge, D.L., DeCourten, F.L., Eaton, J.G., Parrish, J.M., 1999. Distribution of vertebrate faunas in the Cedar Mountain Formation, east-central Utah. Utah Geological Survey Miscellaneous Publication 99-1, 201–217.

Knoll, F., Ruiz-Omeñaca, J.I., 2009. Theropod teeth from the basalmost Cretaceous of Anoual (Morocco) and their palaeobiogeographical significance. Geological Magazine 146, 602–616.

Kusuhashi, N., Matsumoto, A., Murakami, M., Tagami, T., Hirata, T., Iizuka, T., Handa, T., Matsuoka, H., 2006. Zircon U−Pb ages from tuff beds of the upper Mesozoic Tetori Group in the Shokawa district, Gifu Prefecture, central Japan. The Island Arc 15, 378–390.

Lacasa Ruiz, A., 1989. Nuevo genero de ave fosil del yacimiento Neocomiense del Montsec (Provincia de Lerida, España). Estudios geológicos 45(5-6), 417–425.

Larson, D.W., Currie, P.J., 2013. Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time. PLoS ONE 8(1), e54329. doi:10.1371/journal.pone.0054329.

Le Loeuff, J., Buffetaut, E., 1995. The evolution of Late Cretaceous non-marine vertebrate faunas in Europe. In: Sun, A.-L., Wang, Y.-Q. (Eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers. China Ocean Press, Beijing, pp. 181–184.

Le Loeuff, J., Lang, E., Cavin, L., Buffetaut, E., 2012. Between Tendaguru and Bahariya: on the age of the Early Cretaceous dinosaur sites from the Continental Intercalaire and other African formations. Journal of Stratigraphy 36, 486–502.

Lucas, F.A., 1901. A new dinosaur, *Stegosaurus marshi*, from the Lower Cretaceous of South Dakota. Proceedings of the United States National Museum 23(1224), 591–592.

Lucas, S.G., 2006. The *Psittacosaurus* biochron, Early Cretaceous of Asia. Cretaceous Research 27, 189–198.

Lucas, S.G., Estep, J.W., 1998. Vertebrate biostratigraphy and biochronology of the Cretaceous of China. In: Lucas, S.G., Kirkland, J.I., Estep, J.W. (Eds.), Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science Bulletin 14, pp. 1–20.

Lü, J.-C., Xu, L., Pu, H.-Y., Jia, S.-H., Azuma, Y., Chang, H.-L., Zhang, J.-M., 2016. Paleogeographical significance of carcharodontosaurid teeth from the late Early Cretaceous of Ruyang, Henan Province of central China. Historical Biology, 28, 8–13. doi: 10.1080/08912963.2014.947287.

Manabe, M., Hasegawa, Y., 1995. Diapsid fauna and its paleobiogeographical implication, the Neocomian section of the Tetori Group. In: Sun, A., Wang, Y. (Eds.), Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers. China Ocean Press, Beijing, pp. 179.

Mannion, P.D., 2009. A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. Cretaceous Research 30, 521–526.

Mannion, P.D., Upchurch, P., Hutt, S., 2011. New rebbachisaurid (Dinosauria: Sauropoda) material from the Wessex Formation (Barremian, Early Cretaceous), Isle of Wight, United Kingdom. Cretaceous Research 32, 774–780.

Matsukawa, M., Ito, M., Nishida, N., Koarai, K., Lockley, M.G., Nichols, D.J., 2006. The Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial ecosystems in Asia. Cretaceous Research 27, 199–225.

McDonald, A.T., 2011. The taxonomy of species assigned to *Camptosaurus* (Dinosauria: Ornithopoda). Zootaxa 2783, 52–68.

McKenna, M.C., 1973. Sweepstakes, filters, corridors, Noah’s Arks, and Beached Viking Funeral Ships in palaeogeography. In: Tarling, D.H., Runcorn, S.K. (Eds.), Implications of Continental Drift to the Earth Sciences. Academic Press, New York, pp. 295–308.

Mo, J.-Y., Huang, C.-L., Xie, S.-W., Buffetaut, E., 2014. A megatheropod tooth from the Early Cretaceous of Fusui, Guangxi, Southern China. Acta Geologica Sinica (English Edition) 88, 6–12.

Molnar, R.E., 1990. Problematic Theropoda: "Carnosaurs". In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, Los Angeles, Oxford, pp. 306–317.

Mutihac, V., Mutihac, G., 2010. The geology of Romania, within the Central East European geostructural context. Ed. Didactică şi Pedagogică, Bucharest, 690 pp.

Neagu, T., Dragastan, O., Csiki, Z., 1997. Early Cretaceous shelf paleocommunities of Cernavodă (South Dobrogea, SE Romania). Acta Palaeontologica Romaniae 1, 28–36.

Nopcsa, F., 1902. Notizen über cretacische Dinosaurier. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 111, 93–114.

Nopcsa, F., 1923. On the geological importance of the primitive reptilian fauna of the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotium*). Quarterly Journal of the Geological Society of London 79, 100–116.

Norman, D.B., 2010. A taxonomy of iguanodontians (Dinosauria: Ornithopoda) from the lower Wealden Group (Cretaceous: Valanginian) of southern England. Zootaxa 2489, 47–66.

Norman, D.B., 2013. On the taxonomy and diversity of Wealden iguanodontian dinosaurs (Ornithischia: Ornithopoda). Revue de Paléobiologie 32, 385–404.

Novas, F.E., de Valais, S., Vickers-Rich, P.A., Rich, T.H., 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. Naturwissenschaften 92, 226–230.

Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. Cretaceous Research 45, 174–215.

Ortega, F., Escaso, F., Sanz, J.L., 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. Nature 467, 203–206.

Ősi, A., Rabi, M., Makádi, L., Szentesi, Z., Botfalvai, G., Gulyás, P., 2012. The Late Cretaceous continental vertebrate fauna from Iharkút (western Hungary): a review. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 533–569.

Ősi, A., Codrea, V., Prondvai, E., Csiki-Sava, Z., 2014. New ankylosaurian material from the Upper Cretaceous of Transylvania. Annales de Paléontologie 100, 257–271. doi: 10.1016/j.annpal.2014.02.001.

Ősi, A., Rabi, M., Makádi, L., 2015. An enigmatic crocodyliform tooth from the bauxites of western Hungary suggests hidden mesoeucrocodylian diversity in the Early Cretaceous European archipelago. PeerJ 3, e1160. doi:10.7717/peerj.1160.

Paolillo, A., Linares, O.J., 2007. Nuevos cocodrilos Sebecosuchia del Cenozoico Suramericano (Mesosuchia: Crocodylia). Paleobiologia Neotropical 3, 1–25.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Fernandez-Baldor, F.T., Maisch, M.W., Huerta, P., Contreras, R., Izquierdo, L.A., Huerta, D.M., Montero, V.U., Welle, J., 2011. A tall-spined ornithopod dinosaur from the Early Cretaceous of Salas de los Infantes (Burgos, Spain). Comptes Rendus Palevol 10, 551–558.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Canudo, J.I., Torcida, F., Sanz, J.L., 2012. Dinosaur faunas from the Early Cretaceous (Valanginian–Albian) of Spain. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 378–407.

Pérez-Moreno, B.P., Sanz, J.L., Sudre, J., Sigé, B., 1993. A theropod dinosaur from the Lower Cretaceous of southern France. Revue de Paléobiologie Volume spéciale 7, 173–188.

Pol, D., Powell, J.E., 2011. A new sebecid mesoeucrocodylian from the Rio Loro Formation (Palaeocene) of north-western Argentina. Zoological Journal of the Linnean Society 163, S7–S36.

Porfiri, J.D., Novas, F.E., Calvo, J.O., Agnolín, F.L., Ezcurra, M.D., Cerda, I.A., 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. Cretaceous Research 51, 35–55. doi:10.1016/j.cretres.2014.04.007.

Posmoșanu, E., 2003. Iguanodontian dinosaurs from the Lower Cretaceous bauxite site from Romania. Acta Palaeontologica Romaniae 4, 431–439.

Rabi, M., Sebők, N., 2015. A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. Gondwana Research 28, 1197–1211. doi:10.1016/j.gr.2014.09.015.

Racey, A., 2009. Mesozoic red bed sequences from SE Asia and the significance of the Khorat Group of NE Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. Geological Society, London, Special Publications 315, pp. 41–67. doi: 10.1144/SP315.5.

Racey, A., Goodall, J.G.S., 2009. Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. Geological Society, London, Special Publications 315, pp. 69–83. doi: 10.1144/SP315.6.

Rauhut, O.W.M., 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). Special Papers in Palaeontology 86, 195–239.

Rauhut, O.W.M., Werner, C., 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan. Paläontologische Zeitschrift 69, 475–489.

Richter, U., Mudroch, A., Buckley, L.G., 2013. Isolated theropod teeth from the Kem Kem Beds (Early Cenomanian) near Taouz, Morocco. Paläontologische Zeitschrift 87, 291–309.

Royo-Torres, R., Cobos, A., Luque, L., Aberasturi, A., Espilez, E., Fierro, I., Gonzales, A., Mampel, L., Alcalá, L., 2009. High European sauropod dinosaur diversity during Jurassic–Cretaceous transition in Riodeva (Teruel, Spain). Palaeontology 52, 1009–1027.

Sachs, S., Hornung, J.J., 2013. Ankylosaur remains from the Early Cretaceous (Valanginian) of Northwestern Germany. PLoS ONE 8(4), e60571. doi:10.1371/journal.pone.0060571.

Salgado, L., Canudo, J.I., Garrido, A.C., Ruiz-Omeñaca, J.I., Garcia, R.A., de la Fuente, M.S., Barco, J.L., Bollati, R., 2009. Upper Cretaceous vertebrates from El Anfiteatro area, Río Negro, Patagonia, Argentina. Cretaceous Research 30, 767–784.

Sames, B., Cifelli, R.L., Schudack, M.E., 2010. The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: New biostratigraphic results from ostracod correlations and early mammals, and their implications for paleontology and geology of the basin—An overview. Earth-Science Reviews 101, 207–224.

Sauvage, H.E., 1876. Notes sur les reptiles fossiles. Bulletin de la Société Géologique de France 4, 435–442.

Sauvage, H.E., 1882. Recherches sur les reptiles trouves dans le Gault de l'est du bassin de Paris. Mémoires de la Société Géologique de France 2, 1–42.

Săndulescu, M., 1984. Geotectonica României. Ed. Tehnică, Bucharest, 329 pp.

Seghedi, A., 2001. The North Dobrogea orogenic belt (Romania): a review. In: Ziegler, P.A., Cavazza, W., Robertson, A.H.F., Crasquin-Soleau, S. (Eds.), Peri-Tethys Memoir 6: Peri-Tethyan Rift/Wrench Basins and Passive Margins. Mémoires de la Musée National d'Histoire Naturelle, Paris, pp. 237–257.

Sereno, P.C., 1999. Dinosaurian biogeography: vicariance, dispersal and regional extinction. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs 15, Tokyo, pp. 249–257.

Sereno, P.C., Brusatte, S.L., 2008. Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. Acta Palaeontologica Polonica 53, 15–46.

Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J., Wilson, J.A., 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science 272, 986–991.

Shen, Y.B., Mateer, N.J., 1992. An outline of the Cretaceous system in northern Xinjiang, western China. In: Mateer, N.J., Chen, P.J. (Eds.), Aspects of Nonmarine Cretaceous Geology. China Ocean Press, Beijing, pp. 49–77.

Simionescu, I., 1906. Note sur l'age des calcaires de Cernavoda (Dobrogea). Annales Scientifiques de l'Université de Jassy 4(1), 1–3.

Simionescu, I., 1913. *Megalosaurus* aus der Unterkreide der Dobrogea. Centralblatt für Mineralogie, Geologie und Paläontologie 1913(20), 686–687.

Sissingh, W., 1977. Biostratigraphy of Cretaceous calcareous nannoplankton. Geologie en Mijnbouw 56, 37–65.

Smith, J.B., Vann, D.R., Dodson, P., 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. The Anatomical Record A 285A, 699–736.

Stein, K., Csiki, Z., Curry Rogers, K., Weishampel, D.B., Redelstorff, R., Carballido, J.L., Sander, P.M., 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). Proceedings of the National Academy of Sciences 107, 9258–9263.

Stoica, M., Csiki, Z., 2002. An earliest Cretaceous (Purbeckian) vertebrate fauna from Southern Dobrogea (southeastern Romania). In: Grigorescu, D., Csiki, Z. (Eds.), 7th European Workshop on Vertebrate Palaeontology, Sibiu, Romania. Ars Docendi, Bucharest, pp. 34.

Stovall, J.W., Langston, W., Jr., 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. American Midland Naturalist 43, 686–728.

Stromer, E., 1931. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîjestufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematischnaturwissenschaftliche Abteilung Neue Folge 9, 1–23.

Therrien, F., Henderson, D.M., 2007. My theropod is bigger than yours … or not: estimating body size from skull length in theropods. Journal of Vertebrate Paleontology 27, 108–115.

Tong, H., Claude, J., Suteethorn, V., Naksri, W., Buffetaut, E., 2009. Turtle assemblages of the Khorat Group (Late Jurassic–Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (Eds.), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. The Geological Society, London, Special Publications 315, pp. 141–151.

Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Montero, D., Pereda Suberbiola, X., Salgado, L., 2011. *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. Acta Palaeontologica Polonica 56, 535–552.

Turculeț, I., Brânzilă, M., 2012. Muzeul colecțiilor paleontologice originale de la Universitatea "Alexandru Ioan Cuza" Iași. Editura Universității "Alexandru Ioan Cuza" Iași, Iași, 173 pp.

Turner, A.H., Sertich, J.J.W., 2010. Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 30(Supplement 1), 177–236.

Turner, A.H., Makovicky, P.J., Norell, M.A., 2012. A review of dromaeosaurid systematics and paravian phylogeny. Bulletin of the American Museum of Natural History 371, 1–206.

Vasile, Ş., Csiki, Z., 2011. New Maastrichtian microvertebrates from the Rusca Montană Basin (Romania). Oltenia. Studii și comunicări. Științele Naturii 27(1), 221–230.

Vickers-Rich, P., Rich, T.H., Lanus, D.R., Rich, L.S.V., Vacca, R., 1999. "Big Tooth" from the Early Cretaceous of Chubut Province, Patagonia: a possible carcharodontosaurid. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs 15, Tokyo, pp. 85–88.

Vremir, M., 2010. New faunal elements from the Late Cretaceous (Maastrichtian) continental deposits of Sebeș area (Transylvania). Terra Sebus. Acta Musei Sabesiensis 2, 635–684.

Vullo, R., Néraudeau, D., Lenglet, T., 2007. Dinosaur teeth from the Cenomanian of Charentes, western France: evidence for a mixed Laurasian-Gondwanan assemblage. Journal of Vertebrate Paleontology 27, 931–943.

Weishampel, D.B., 1990. Dinosaurian distribution. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. California University Press, Berkeley, Los Angeles, Oxford, pp. 63–140.

Weishampel, D.B., Grigorescu, D., Norman, D.B., 1991. The Dinosaurs of Transylvania. National Geographic Research & Exploration 7(2), 196–215.

Weishampel, D.B., Norman, D.B., Grigorescu, D., 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. Palaeontology 36, 361–385.

Weishampel, D.B., Jianu, C.M., Csiki, Z., Norman, D.B., 2003. Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. Journal of Systematic Palaeontology 1, 65–123.

Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X-J., Sahni, A., Gomani, E.M., Noto, C.R., 2004. Dinosaur distribution. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, Los Angeles, London, pp. 517–606.

Weishampel, D.B., Csiki, Z., Benton, M.J., Grigorescu, D., Codrea, V., 2010. Palaeobiogeographic relationships of the Haţeg biota — Between isolation and innovation. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 419–437.

Williamson, T.E., Brusatte, S.L., 2014. Small theropod teeth from the Late Cretaceous of the San Juan Basin, northwestern New Mexico and their implications for understanding latest Cretaceous dinosaur evolution. PLoS ONE 9(4), e93190. doi:10.1371/journal.pone.0093190.

Zarcone, G., Cillari, F.M.P., Stefano, P.D., Guzzetta, D., Nicosia, U., 2010. A possible bridge between Adria and Africa: New palaeobiogeographic and stratigraphic constraints on the Mesozoic palaeogeography of the Central Mediterranean area. Earth-Science Reviews 103, 154–162.

Figure captions

Figure 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).

Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B. Current state of UAIC (SCM1) 615, mounted in a limestone holder.

Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B., distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).

Figure 4. Dental morphospace of the different theropod clades according to the results of the PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by Carcharodontosauridae. See further details of this analysis, as well as other quantitative analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant function analysis, phylogenetic analysis), in the Supplementary Material.

Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615 from Southern Dobrogea. Legend: 1 – *Veterupristisaurus*, ‘*Megalosaurus’ ingens*, Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator,* Spain, Barremian; 3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 – *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China, Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmayisaurus*, Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11 – *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan, Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 – Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant references, see text, *5.4.*). Palaeogeographic maps, courtesy of Ron Blakey (http://cpgeosystems.com/).

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

Zoltán Csiki-Sava[1*], Stephen L. Brusatte[2], Ştefan Vasile[1]

[1] Department of Geology, Faculty of Geology and Geophysics, University of Bucharest, 1 Nicolae Bălcescu Boulevard, 010041 Bucharest, Romania~~, zoltan.csiki@g.unibuc.ro, yokozuna_uz@yahoo.com~~

[2] School of GeoSciences, University of Edinburgh, Grant Institute, James Hutton Road, Edinburgh, EH9 3FE, United Kingdom~~, Stephen.Brusatte@ed.ac.uk~~

* Corresponding author

zoltan.csiki@g.unibuc.ro

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 evolved 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 Aptian, illustrating the importance of palaeogeographic ties between these two realms during the largely mysterious early–mid Early Cretaceous.

Keywords

~~Romania~~Southern Dobrogea; ~~Lower Cretaceous~~Valanginian;~~ Theropoda;~~ Carcharodontosauridae; cratonic Europe; palaeobiogeography

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 Early Cretaceous bauxite accumulations of Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997; Posmoșanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Haţeg, Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the dinosaur-dominated ‘Hațeg 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 ‘Hațeg 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 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~~, in prep.~~; 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 split, but originated earlier, and perhaps in Europe, suggesting faunal interchange between Europe and Gondwana during the ‘dark ages’ of the early Early Cretaceous.

Abbreviations: UAIC – University “Alexandru Ioan Cuza”, Iași, Romania.

2. History of collecting and curation

Only two dinosaurian fossils are currently known from the cratonic areas of Romania: an isolated theropod tooth and an isolated caudal vertebral centrum. Both of these were reported from the Lower Cretaceous deposits of Southern Dobrogea (southeastern Romania; Csiki-Sava et al., 2013, see also below). Unfortunately, exact details of their discovery and places of origin are lost, a fact that can hinder an assessment of their age and interpretation of their phylogenetic and palaeobiogeographic significance. Our aim here is to gather and report all available information concerning the collecting of specimen UAIC (SCM1) 615, that is, the isolated theropod tooth reported by Simionescu (1913; Fig. 2A).

According to the existing information - unpublished museum labels and records, and the preliminary publication of Simionescu (1913) - specimen UAIC (SCM1) 615 was discovered in the surroundings of Cochirleni, a small village south of Cernavodă and close to the right bank of the Danube, in Southern Dobrogea, southeastern Romania (Fig. 1), probably shortly before 1913, the date of its publication by Simionescu (1913).

Although studied and preliminarily described by Simionescu, UAIC (SCM1) 615 was not collected by Simionescu personally. Instead, it was donated by a certain “de Tomas” (also mentioned as ”de Thomas” in the registry of the Hârșova Museum) to V. Cotovu from Hârşova (Central Dobrogea), a local teacher, archaeology and natural history aficionado, and amateur fossil collector (see, e.g., Covacef, 1995). Cotovu, described by Simionescu himself as the “zélé fondateur et directeur du muséum de Hârşova” (*enthusiastic founder and director of the Hârşova Museum*; Simionescu, 1906: p. 2), had previously provided fossil specimens from Southern Dobrogea for study to Simionescu, a nationally acknowledged popular science writer and scientist, whom Cotovu knew personally (Brânzilă, 2010). These circumstances are supported by the fact that in the original description, Simionescu figures the specimen as being accessioned in the “Regional-Museum von Harschowa” (*Hârşova Regional Museum*; Simionescu, 1913: p. 687, fig.1), a designation he also used to refer to other Dobrogean

specimens not collected by him first-hand (e.g., a specimen of '*Nautilus' pseudoelegans* from Cernavodă, or a fragmentary tooth-bearing palatal fragment referred to as '*Coelodus*' sp., also originating from Cochirleni; see Simionescu, 1906). Confirming this deduction, an isolated tooth appears accessioned in the old registry book of the Hârşova Museum (under specimen number 200) as "*Megalosaurus* cf. *superbus*", with the mention that it was "*described by Prof. Simionescu in the Centralblatt f. min. etc*.". This is also the case of the '*Coelodus'* sp. specimen from Cochirleni (specimen number 86), similarly clearly identified as being described by Simionescu in the registry book.

Both of these vertebrate remains from Dobrogea that were formerly part of the Hârşova Museum collections are currently accessioned in the palaeontology collections of the UAIC (Turculeț and Brânzilă, 2012), suggesting that, at one moment, several specimens were transferred there from the Hârşova Museum. Although no details are known about this transfer, it is probable that it took place right before (or when) the Hârşova Museum, including a part of its collections, was burned and largely destroyed during WWI, in 1916, a time when Simionescu still held a position at the UAIC.

After its original description, specimen UAIC (SCM1) 615 underwent a minor amount of damage (see below, Description). Also, at some point between its description in 1913 and the early 1960s (when the specimen was found in its present state in the collections of the UAIC by academic staff members who are still alive today and recall the discovery; I. Turculeț, personal communication, May 2013) it was glued into a limestone matrix holder, while it was obviously completely freed of the surrounding matrix when it was described and figured in 1913 (Fig. 2). The circumstances under which these alterations took place are unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the spring of 1944, the frontline between the German-Romanian and Soviet armies reached the Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

were packed in crates, and moved together with its personnel and other possessions to Zlatna, in the Apuseni Mountains (western Romania), to safeguard them from any potential damage. Mounting the specimen into the limestone stand would have been a quick way to stabilize it, as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă, personal communication, April 2103). If that was indeed the case, the mounting would have taken place without the knowledge of Simionescu, who left Iaşi and the UAIC in 1929, being invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă, 2010). Then again, however, Simionescu himself or staff of the Hârşova Museum might have re-mounted the tooth after its original description, or else the mounting might have taken place after the return of the collections to Iași, after WWII.

Unfortunately, it is not documented whether the mounting was made using the original matrix, or if a trough corresponding to the tooth outline was carved into a randomly chosen limestone block. The apparently excellent fit between the tooth and the depression housing it (Fig. 2B, 3) suggests that this operation was completed carefully, and accurate carving of a fake holder is difficult to reconcile with the rush accompanying the evacuation of the Iași University, in 1944. Alternatively, the presence of a hand-written old registration number on the specimen holder would support its early re-mounting, while still at the Hârşova Museum. As noted previously, the original Hârşova Museum registration number of the specimen was 200, which does not correspond to that currently written both on the limestone holder and on a paper sticker (204). However, according to the old collection registry of the Hârşova Museum, specimen numbers 201 through 225 were given to a series of “indeterminate (fossil) bone fragments” from the “Cochirleni quarries”. Thus, these specimens (now apparently lost) came from the same locality as the tooth, and they were collected and donated by the same person to the Museum who donated UAIC (SCM1) 615. There is, thus, a (albeit admittedly remote) possibility that the registration numbers were

mixed up during the re-mounting of the specimen, which in this case took place at an early date in the Hârşova Museum. If this is indeed the case, the limestone used as holder could have been the same as the original matrix of the specimen.

To conclude, the history of recovery and curation of the historically important dinosaurian specimen UAIC (SCM1) 615 is rather convoluted and clouded by many uncertainties. The exact date of discovery remains conjectural, and the exact place of the discovery (thus also the original geological context of the tooth) is even more ambiguous. The current state of the specimen, and especially its mounted status, suggest a curatorial history that produced a moderate amount of damage to, but also partially obscured the detailed morphology of the specimen. The convergence of such unfortunate events makes deciphering the age, identity and evolutionary significance of the specimen troublesome, although many lines of evidence, carefully considered, allow us to draw reasonable conclusions (see below).

3. Geological setting

According to the available collecting information, the isolated theropod tooth UAIC (SCM1) 615 was discovered at Cochirleni (sometimes noted more specifically as the "*Cochirleni quarry*" or "*Cokerleni quarry*"). Cochirleni is a small village in southwestern Dobrogea situated close to the right bank of the Danube, and about 9 km south of the main urban center of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).

Southern Dobrogea is a cratonic area corresponding to the southeastern corner of Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984; Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,

2010), researchers agree that it became integrated into the main European Craton towards the end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine: Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001; Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

The Precambrian basement of Southern Dobrogea is overlain by a flat-lying sedimentary cover that begins with the lowermost Palaeozoic and ends with the uppermost Neogene. The sedimentary succession is interrupted by a few major, as well as several less important, sedimentary hiatuses that separate 5 main sedimentary sequences corresponding to the Cambrian–Upper Carboniferous, the Permian–Triassic, the Middle Jurassic–Cretaceous, the Eocene–?Oligocene, and the middle Badenian (middle Miocene)–Upper Pliocene. The Palaeozoic and lower Mesozoic are known only from the subsurface of Southern Dobrogea, but Cretaceous and Cenozoic deposits have limited exposures along the main water courses of the region (Ionesi, 1994; Mutihac and Mutihac, 2010).

The outcropping Cretaceous in Southern Dobrogea is represented mainly by shallow marine, carbonate platform deposits in the lower part of the system, replaced by more open-water, chalky facies towards the later part of the period (e.g., Avram et al., 1993, 1996; Dragastan et al., 1998; Dinu et al., 2007); these crop out only as isolated patches along the main watercourses of the region (Fig. 1).

The Lower Cretaceous Series consists of several lithostratigraphic units with complex, partially overlapping and interfingering relationships (Dragastan et al., 1998, 2014). The lowest (and only artificially) outcropping unit is the Purbeck-type, siliciclastic-evaporitic Upper Kimmeridgian–Lower Berriasian Amara Formation that represents lagoonal to continental environments. This unit is covered by the shallow-marine, richly fossiliferous and locally reefal limestone-dominated Cernavodă Formation (restricted-open lagoonal to

carbonate platform, Upper Berriasian–Lower Hauterivian). A time-correlative unit of the Cernavodă Formation, the limestone-dolomitic Dumbrăveni Formation (Upper Berriasian–Lower Hauterivian), is restricted to the southeastern part of Southern Dobrogea. The Cernavodă and Dumbrăveni formations are covered unconformably by dominantly calcareous deposits with hippuritoid ('pachyodont') coquinas, small reefs and lens-like orbitolinid accumulations, referred to the Barremian–Lower Aptian Ostrov Formation by Dragastan et al. (1998), but to the Ramadan Formation (in part) by Avram et al. (1993, 1996). These deposits, formed in littoral to lagoonal and open reef terrace environments, are in turn capped by the fluvial-lacustrine, siliciclastic deposits of the Gherghina Formation, with Middle–Upper Aptian kaolinitic clays and thin coal intercalations. The Lower Cretaceous succession ends with the transgressive, glauconite-bearing, coastal to sublittoral siliciclastic deposits of the Cochirleni Formation (uppermost Aptian–Albian).

The Upper Cretaceous has a significantly more patchy development, mainly restricted to the eastern part of Southern Dobrogea, excepting the weakly glauconitic, chalky-sandy Peştera Formation (Lower Cenomanian) and the marly Dobromiru Formation (Upper Cenomanian) that cover the western-central parts of the area. The younger Cuza Vodă (Turonian), Murfatlar (Santonian–Lower-Middle Campanian), and Satu Nou (Upper Campanian) formations are dominantly chalky, suggesting the instalment of a relatively deeper, offshore depositional environment; neither of these units is known from western Southern Dobrogea.

In total, the Lower Cretaceous of Southern Dobrogea was deposited in a shallow marine, near-shore setting, fluctuating between carbonate platform, lagoonal, coastal-tidal flat, and continental environments (see Avram et al., 1996; Dragastan et al., 1998). Its main characteristic features, such as the observed lithological variability, the areal distribution of the different units, and the presence of several unconformities within the series, are all linked

to eustatic sea-level changes that affected the Southern Dobrogean territory during the Early Cretaceous (Dragastan et al., 1998). The main emergent land in the area was represented by the Central Dobrogean Massif, lying north of the study area, almost completely subaerially exposed and actively eroding during the Cretaceous. Consequently, shallow-marine to continental deposits are restricted mainly to the northern part of Southern Dobrogea, close to its boundary with the Central Dobrogean Massif (marked by the Capidava-Ovidiu Fault), and are replaced by more open marine deposits southward. As summarized above, several littoral, and even continental, sequences occur in this succession, including deposits in the Amara, Cernavodă, Ramadan (~~in part;~~ Avram et al., 1996) and Cochirleni formations, whereas the Gherghina Formation is purely continental, with occasional minor marine interbeds produced during short-term ingressions of the sea.

In the Cernavodă-Cochirleni area the outcropping Mesozoic is restricted to the Lower Cretaceous, and includes deposits belonging to the Cernavodă, Ostrov (or Ramadan), Gherghina, and Cochirleni formations. While the lower–middle part of the Cernavodă Formation is well exposed and widely distributed in this area, its upper part (the lower Hauterivian Vederoasa Member) is unevenly developed. This member is missing in the classical succession from Cernavodă-Hinog, on the right bank of the Danube (Dragastan et al., 1998), but was recently identified in the more eastern Cernavodă-lock section (Dragastan et al., 2014). Similarly, the Ostrov Formation is represented in the area only by its upper subunit (the Lower Aptian Lipniţa Member; Dragastan et al., 1998), covering unconformably and transgressively the Valanginian Alimanu Member of the Cernavodă Formation in the southern end of the Cernavodă-Hinog section (Dragastan et al., 1998), and the lower Hauterivian Vederoasa Member in the Cernavodă-lock section (Dragastan et al., 2014).

Northward of the Hinog area, Valanginian deposits of the Alimanu Member are overlain directly by the Middle–Upper Aptian continental deposits of the Gherghina

Formation. These continental deposits also cover the *Orbitolina*-bearing calcareous-clayey deposits of the Lipniţa Member towards the south, marking the advancement of emerged areas towards the central parts of Southern Dobrogea, including the Cernavodă-Cochirleni area, during this time interval (Avram et al., 1996). Marine conditions returned in the study area again in the latest Aptian, with a transgression marked by widespread deposition of the glauconitic, siliciclastic coastal to innermost shelf deposits of the Cochirleni Formation. These uppermost Aptian to Albian sands and sandstones cover transgressively all the underlying deposits, belonging to the Cernavodă, Ostrov, or Gherghina formations. Siliciclastic shallow-marine sedimentation continued into the Early Cenomanian, with the chalky-glauconitic deposits of the Peștera Formation.

4. Palaeontology

The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu (1913), who referred it to *Megalosaurus* cf. *superbus*, a taxon erected by Sauvage (1882) from the Gault (‘mid’-Cretaceous: Albian) of the Paris Basin, France. The Gault material described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it and the type species *M. bucklandi*.

The convoluted taxonomic history of *Erectopus superbus* was recently reviewed by Allain (2005), who established that both the isolated teeth first mentioned by Sauvage (1876) and the skeletal elements described by Sauvage (1882) belong to the same taxon, for which the name *Erectopus superbus* was retained. Allain (2005) regarded *Erectopus* as a member of

Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al. (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.” Accordingly, if we are following the original assessment of Simionescu (1913) but updating with contemporary taxonomy, the Cochirleni theropod tooth should now be considered referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to *Erectopus superb*us (or a close relative) was considered to be unsupported by positive evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B, 3), we provide here a detailed description of its morphology followed by a thorough comparative study of this tooth based on large datasets of theropod dental measurements and discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).

We note that in his review of Romanian dinosaurs, Grigorescu (2003) erroneously considered UAIC (SCM1) 615 as being referred by Simionescu to the taxon *Megalosaurus dunkeri* Kohen (sic; actually, *Megalosaurus dunkeri* Dames, 1884). This is clearly a simple misreading of Simionescu’s identification. Additionally, such a referral is also contradicted by the absence of mesial serrations in the holotype tooth of *M. dunkeri*, considered by Carrano et al. (2012) to represent an indeterminate theropod. The Dobrogea tooth, on the other hand, has mesial serrations (see below).

4.1. Age of UAIC (SCM1) 615

The age of UAIC (SCM1) 615 has been contentious, due to the uncertainties concerning its place of origin. Although it is often mentioned as originating from Cochirleni village (e.g., Grigorescu, 2003; Turculeț and Brânzilă, 2012), this has not been definitively established. According to the original report of Simionescu (1913), the tooth came from the upper part of

the Lower Cretaceous limestone succession exposed in the cliffs extending from Cernavodă to Cochirleni along the right bank of the Danube. The corresponding entry from the Hârșova Museum registry states that it was found in the 'Cochirleni quarry', a location that presently cannot be identified precisely. The only rocks to be quarried in the area are the calcareous deposits of either the Cernavodă or Ostrov formations, particularly the ones that crop out in the Danube bank cliffs between Cernavodă-Hinog-Cochirleni. Finally, although the mention 'Cochirleni' is usually considered to refer to Cochirleni village, it should be mentioned that the cliff-forming hill that extends between Cernavodă and Cochirleni is also known by the same name (Fig. 1). Taking all of this evidence into consideration, it is thus reasonable to conclude that the tooth was most likely found in the Lower Cretaceous limestone succession exposed in the Danube cliffs between Cernavodă and Cochirleni.

Based on the location of the discovery, in the upper part of the local limestone succession, and the age of the deposits from Cernavodă-Cochirleni known to him, Simionescu (1913) considered the tooth to be of Barremian age. Subsequently, the age of the tooth was given as Valanginian–Barremian (Weishampel, 1990; Weishampel et al., 2004) or Valanginian (e.g., Grigorescu, 2003), but without any supporting information.

New attempts have been made to more precisely constrain the age of UAIC (SCM1) 615. Dragastan et al. (2014) recently sampled the limestone matrix holder of the tooth, and reported from these samples an assemblage of foraminiferans, ostracods and microproblematicae (=*incertae sedis* microorganisms) that characterize their 'Biozone IX with *Meandrospira favrei*', of latest Valanginian age in the local lithostratigraphic scheme. In parallel, we also sampled the same limestone holder – a yellowish white, friable lime mudstone – that yielded a poor and badly preserved calcareous nannoplankton assemblage with *Watznaueria barnesiae*, *W. ovata*, *Nannoconus steinmanni*, *N. kamptneri, N. globulus, Calcicalathina sp.*, *Speetonia colligata* and *Cyclagelosphaera deflandrei* (M. C. Melinte-

Dobrinescu, personal communication, November 2013), an assemblage that suggests a Berriasian–Hauterivian age of the limestone holder.

Since it is not clear if the limestone holder came from the same site as the tooth itself, we managed to take a second sample from the limestone matrix still partly filling the pulp cavity of the tooth, which must definitively be identical with the rocks the tooth was found in. This second, much smaller sample yielded only very scarce specimens of *Watznaueria barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in abundance during the Berriasian and, especially, the Valanginian.

In the nannoplankton succession reported previously by Avram et al. (1993) and derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu Member of the Cernavodă Formation. These assemblages were interpreted to represent the nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous of the Mecsek Mountains, Hungary, by Császár et al. (2000).

Together, all the available evidence (Simionescu's original account, geographic and geologic records, foraminifera, ostracods, microproblematicae, and calcareous nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member of the Cernavodă Formation, and it is most probably of late Valanginian age.

4.2. Description and comparisons

Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2, 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown

base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is remarkably well preserved, with the enamel in pristine condition. It preserves most of the crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5 mm missing in the apical region.

In its present state, the mesial edge and part of the mesial third of the tooth are embedded in the limestone holder (Fig. 2B), although the tooth was once removed (see above, History of collecting and curation; Fig. 2A). Accordingly, it is exposed so that all faces of the tooth are widely visible, including the root region, except for the mesial surface.

Only the basal-most part of the root is preserved, and it is more complete near the mesial margin (Fig. 3B, C). Here, broken areas around the crown-root contact area (cervix) reveal details of the pulp cavity development, as well as the pattern of the dentine thickness variation (Fig. 3B–D). The crown also exhibits a transverse break at about two-thirds of its length (not present so obviously in the original figure of the specimen in Simionescu, 1913), and adjacent to it, the distal carina is also slightly chipped distal to mid-length. The labial face is superficially split near this break (Fig. 3A), while a more prominent region of damage appears on the lingual face, where a large (13 x 5 mm), slightly triangular wedge is broken off, exposing the deeper parts of the dentine (Fig. 3C). The damage to the lingual side apparently occurred after the original description of the tooth (Fig. 2), an observation that is concordant with the complex curatorial history of the specimen.

The basal-most, exposed part of the mesial face lacks the enamel cover (Fig. 3C, D), suggesting that this area already belongs to the root region. The mesial edge of the preserved crown base appears to be wider than the distal one, and is largely rounded transversely. Accordingly, the basal cross-section is teardrop-shaped (lanceolate); it is rounded mesially, but narrows distally into a small carina (Fig. 3D). As mentioned above, the pulp cavity is

exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B). Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped (Fig. 3D).

The tooth is ziphodont and only very slightly recurved distally. The distal edge is nearly straight across its length, being very mildly concave in its basal half and slightly convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the tooth crown base. The mesial edge, as shown in the original publication of Simionescu (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually compressed (Fig. 3B), with a crown base ratio (CBR=CBW/CBL) of 0.56, within the normal range of variation of most theropods. This differs from the thinner teeth of some, but not all, carcharodontosaurids (CBR<0.50), and the much thicker incrassate teeth of derived tyrannosauroids and conical teeth of spinosaurids (CBR>0.75) (Sereno et al., 1996; Brusatte et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).

The crown cross-section is slightly asymmetrical labiolingually when it is seen in distal view. In this view, when the carina is facing directly distally, one side of the crown has a more pronounced bulge than its counterpart (about 8.5 mm wide, measured from the carina, vs. 6 mm on the other side; Fig. 3B); based on comparisons with the teeth of *Mapusaurus* (Coria and Currie, 2006), the more bulging side can be interpreted as the lingual one. This asymmetry diminishes apically, where both sides become about equally convex. The distal carina itself twists slightly sideways (labially) in apical direction, such that it is located closer

to the labial face where it terminates at the crown apex, and the lingual face of the denticles is exposed distally (Fig. 3B, F). This twist of the distal carina is accompanied by a similar outline of the lingual side; in distal view, this is somewhat convex basally, but becomes flat to slightly concave in the apical two-thirds of the crown. A similar S-shaped curvature of the crown, albeit more pronounced and different in details, was also reported in *Mapusaurus* and *Giganotosaurus* (Coria and Currie, 2006), and in indeterminate carcharodontosaurid teeth from Morocco (Richter et al., 2013).

The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with minute serrations across its entire preserved length; the denticles are proximodistally subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig. 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so it is not possible to determine whether the serrations continued over the apex of the tooth. There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the carina. Serration shape and size remain relatively constant across the carina, although the serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig. 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F). Changes in serration size are gradual across the carina, not sudden or sporadic.

Although they are all more or less rectangular in shape, the apical denticles are relatively shorter proximodistally than the more basal ones. Most of the denticles have slightly rounded, asymmetrically convex triangular tips, instead of being simply squarred-off, and they do not hook as in troodontids and to a lesser extent abelisaurids (Hendrickx and Mateus, 2014). Other denticles near the apex, however, show a faint concavity along their tips, giving them a bilobate aspect, although this is both less conspicuous and far less regularly developed than reported in *Tyrannotitan* (Novas et al., 2005). The denticles are

separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length. The interdenticular space between adjacent denticles is broad, measuring more than a third of the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These sulci are so short and indistinct that they are only visible under low angle light.

Little can be said about the mesial carina, as it is not visible in the current state of the specimen, buried in the limestone matrix. Based on the description of Simionescu (1913), however, it is covered across its length with minute serrations; these decrease in size towards the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles) per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus, 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii* where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*’ *superbus* (Sauvage, 1876, 1882) in this respect.

The external enamel surface exhibits two forms of ornamentation. First, the majority of the labial and lingual faces are covered by relatively smooth enamel that exhibits a subtle form of braided texture visible under low angle light (Fig. 3A, C, E). This texture is made up of a series of very faint, apico-basally running ridges; these are of unequal lengths, starting at different points of the crown height, but none extends the whole length of the crown. The two longest ridges are placed near the distal carina. The enamel is also finely granulated.

Second, near the carinae on both labial and lingual surfaces there are marginal undulations: wrinkles in the enamel that stand out in bas relief (Brusatte et al., 2007). These are much better preserved and visible near the distal carina, where they are so pronounced

that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly developed wrinkles are present along the crown height; in the basal half of the crown, the wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer than twice the space separating each undulation. The wrinkles project obliquely (in the mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal segment on the crown, and curve apically as they approach the carina (at about 45^{o}) with a tendency to become tangential to the distal edge. The wrinkles are especially well developed, prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig. 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm). Apically, however, the wrinkles are somewhat wider and longer, extending over about half of the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the crown in wrinkle development as well, these being better expressed on the more rounded, convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the presumed labial face, only some of the basal-most wrinkles, particularly the second and third one, appear well defined.

Towards the base of the crown a few of the wrinkles continue across the labial and lingual surfaces as very subtle transverse undulations. Most conspicuous of these is a 3.5 mm wide horizontal swelling that crosses the crown, at the level of wrinkles 2 and 3; this swelling is clearly visible on both sides of the crown (Fig. 3. A, C). There are no lateral flutes, apico-basal ridges, or longitudinal grooves on the labial or lingual faces, either in the centre of the tooth or paralleling the carinae. Instead, the labial and lingual faces are uniformly convex, giving the tooth its teardrop-shaped outline in cross section.

5. Discussion

5.1. *Identification of UAIC (SCM1) 615*

The isolated tooth from Cochirleni can be referred to Theropoda based on its large size, recurved and labiolingually compressed morphology, and presence of a continuous series of well-defined serrations on the distal carina.

Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are also known to posess remarkably theropod-like, laterally compressed and serrated teeth, not unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are significantly smaller than the Southern Dobrogean specimen, especially in the case of the Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest, caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615; moreover, these teeth are slightly conical and less laterally compressed than the Southern Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true denticles along their carinae) are reported in Europe only beginning in the Albian (Ősi et al., 2015), and these are both significantly smaller and different in morphology from the Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a theropod tooth.

We used four techniques to identify which type of theropod UAIC (SCM1) 615 likely belongs to (see also Supplementary Material).

First, we conducted a Principal Components Analysis (PCA) based on a large database that includes a broad and representative sample of theropod teeth. This dataset was compiled by Hendrickx et al. (2015a), which built upon the earlier studies of Smith et al.

(2005) and Larson and Currie (2013), and it or a similar version has been used in recent studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, ~~2013~~2014; Brusatte and Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL, CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to this dataset, the data were log-transformed prior to analysis, missing values for measurements were estimated with a mean value for that measurement from across the sample, and then a PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17 (Hammer et al., 2001).

In the resulting two dimensional morphospace (Fig. 4), UAIC (SCM1) 615 plots close to many teeth belonging to carcharodontosaurids, along with some teeth belonging to spinosaurids and tyrannosauroids. It falls within the convex hull (maximum morphospace occupation area) of carcharodontosaurids only, although it is closely outside of the edges of spinosaurid and tyrannosauroid space. It also falls within the 95% confidence interval ellipse for carcharodontosaurids, but not within the ellipse of any other group (Supplementary Information). This exercise indicates that UAIC (SCM1) 615 is most similar to carcharodontosaurids.

Secondly, we used the log-transformed dataset that we also used for the PCA to conduct a clustering analysis. We performed the analysis in PAST v2.17, using the paired group algorithm and the correlation similarity measure. In the resulting dendrogram, UAIC (SCM1) 615 groups with a handful of teeth belonging to carcharodontosaurids, tyrannosauroids, and *Allosaurus* (Supplementary Information).

Third, we used the tooth measurement database to conduct a discriminant analysis in PAST v3.0 (Hammer et al., 2001). This analysis uses pre-determined groups (in this case, taxonomic clusters) to create a morphospace in which these groups are maximally separated.

This allows teeth of unknown affinities, such as UAIC (SCM1) 615, to be classified according to which taxonomic group it is most similar to in this discriminant morphospace. In total, 67.79% of other teeth are classified correctly when they are treated as having uncertain affinities and their measurements are used to classify them in discriminant space, indicating that this exercise returns reasonable results. Our analysis classifies the Romanian tooth as a carcharodontosaurid. Furthermore, the analysis places UAIC (SCM1) 615 within the convex hulls for carcharodontosaurids and tyrannosauroids, and the 95% confidence ellipses for carcharodontosaurids, coelophysoids, and neovenatorids.

Fourth, we ran a phylogenetic analysis by including UAIC (SCM1) 615 in the discrete character dataset of theropod dental features published by Hendrickx and Mateus (2014). The Romanian specimen was scored as a lateral tooth in this analysis. The analysis was conducted in TNT (Goloboff et al., 2008), and resulted in 224 most parsimonious trees (686 steps, consistency index of 0.338, retention index of 0.566). The strict consensus topology is moderately well resolved and places the Romanian tooth as the sister taxon to *Carcharodontosaurus* (Supplementary Material). This sister taxon pair is recovered as the sister clade to a grouping of the derived carcharodontosaurids *Mapusaurus* and *Giganotosaurus*.

Several synapomorphies support the carcharodontosaurid affinities of UAIC (SCM1) 615. The sister group relationship with *Carcharodontosaurus* is supported by two features: a roughly straight distal margin of the crown (character 68) and pronounced marginal undulations in the enamel that are well visible in normal light (character 112). The broader clade of UAIC (SCM1) 615, *Carcharodontosaurus*, *Mapusaurus*, and *Giganotosaurus* (= Carcharodontosaurinae, as defined by Brusatte and Sereno, 2008, and Carrano et al., 2012) is linked by numerous characters, including: large teeth with a crown height greater than 6 cm (character 65), a bowed or sigmoid distal carina in distal view (character 82), marginal

undulations that are at least twice as long mesiodistally as the space separating each undulation (character 111), and marginal undulations present on both mesial and distal sides of the crown (character 113).

The Romanian specimen also lacks many keystone dental synapomorphies of other theropod clades, based on the clade diagnoses of Hendrickx and Mateus (2014) and other cladistic studies that include dental characters. UAIC (SCM1) 615 does not possess the hooked distal denticles of some Abelisauridae, the strongly labially deflected distal carina and pronounced transverse enamel undulations extending across the labial and lingual tooth faces of Ceratosauridae, the incrassate teeth with apicobasal enamel flutes and deeply veined enamel surface texture of Spinosauridae, and the large transverse undulations of some basal allosauroids (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of derived tyrannosauroids (Brusatte et al., 2010a) and the large and strongly hooked (or pointed) denticles of troodontids and therizinosauroids (e.g., Turner et al., 2012; Brusatte et al., 2014; Hendrickx and Mateus, 2014). The large size, as well as recurved and ziphodont shape of UAIC (SCM1) 615 is strikingly different from the non-ziphodont therizinosauroids, ornithomimosaurs, alvarezsauroids, and most troodontids, which have conical, leaf-shaped, or peg-like teeth (when teeth are present) (e.g., Holtz et al., 2004a; Turner et al., 2012; Brusatte et al., 2014). Finally, besides its remarkably large size, the presence of serrations indicates that UAIC (SCM1) 615 does not belong to groups such as alvarezsauroids, oviraptorosaurs, basal troodontids, or avialans, which have unserrated crowns (e.g., Turner et al., 2012; Hendrickx and Mateus, 2014).

In summary, the four analyses all support carcharodontosaurid affinities for UAIC (SCM1) 615. Both overall tooth proportions and discrete phylogenetic characters point to a carcharodontosaurid identification, and the discriminant function analysis and phylogenetic analysis both explicitly recover the tooth as a carcharodontosaurid. For this reason we refer

this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as recovered in our analysis, is congruent with results of previous analyses based on larger sets of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno, 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015), and offers some support for considering the Romanian carcharodontosaurid from Southern Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

Two final notes are worth adding. First, our analyses also incorporated carcharodontosaurids that are usually found to be basal within the clade, such as *Acrocanthosaurus* and *Eocarcharia* (e.g., Harris, 1998; Sereno and Brusatte, 2008; Carrano et al., 2012) as well as a host of other allosauroids, including members of Neovenatoridae (*Neovenator*, *Australovenator* and *Fukuiraptor*), a clade that is often recovered as sister-taxon to carcharodontosaurids within Carcharodontosauria (e.g., Benson et al., 2010; Carrano et al., 2012; but see Novas et al., 2013; Porfiri et al., 2014, for an alternate placement of neovenatorids in general). Both PCA and phylogenetic analysis clearly identified UAIC (SCM1) 615 as more closely comparable morphologically to derived carcharodontosaurids than to either basal carcharodontosaurids or to any other allosauroid subclade.

Second, our datasets also included teeth of *Erectopus*, the genus erected for ‘*Megalosaurus’ superbus* to which UAIC (SCM1) 615 was originally referred. Again, our analyses clearly indicate that there are no close morphological and morphometric similarities between the two, which is in accordance with the suggestion of Carrano et al. (2012) that *Erectopus* represents a non-carcharodontosaurid taxon, while our analysis identifies UAIC

(SCM1) 615 as a carcharodontosaurid. Instead, *Erectopus* groups with abelisauroids in the phylogenetic analysis. This is somewhat surprisingly, as Allain (2005) and Carrano et al. (2012) both identified *Erectopus* as a tetanuran. It should be noted, however, that Albian-aged abelisauroids are known from the same general area (eastern France) as that yielding the material referred to *Erectopus* (Accarie et al., 1995; Carrano and Sampson, 2008), raising the intriguing possibility that this taxon may represent an abelisauroid instead of an allosauroid tetanuran as suggested by Allain (2005) and Carrano et al. (2012). However, it must be remembered that this phylogenetic analysis is based on dental characters only, so it is probably more likely that *Erectopus* is a tetanuran with a dentition convergent to some extent with those of certain abelisauroids.

5.2. Body size of UAIC (SCM1) 615

One of the most salient and remarkable features of UAIC (SCM1) 615 is its large size. In the large and comprehensive sample of theropod teeth from our dataset, tooth size (estimated based on crown height – CH, and used as a rough proxy of body size) ranges from 2.2 mm (in the dromaeosaurid *Saurornitholestes* and the coelurosaur of uncertain affinities *Richardoestesia*) to 117.1 mm in the gigantic tyrannosauroid *Tyrannosaurus*. The Romanian specimen UAIC (SCM1) 615, with a CH of 85.5 mm, is ranked in the 60-80% maximum size (~ CH) range of the sample, and has a CH that is 73% of the largest tyrannosauroid teeth. Most of the teeth in the dataset (over 61% of the 966 measured teeth) are very small to small (less than 25 mm CH), and less than 10% of these fall in the 60-100% CH size categories. Teeth larger than UAIC (SCM1) 615 make up less than 5% of the total sample, and they represent only five taxa: the megalosaurid *Torvosaurus*, the tyrannosauroid *Tyrannosaurus*, the basal carcharodontosaurid *Acrocanthosaurus*, and the derived carcharodontosaurines *Carcharodontosaurus* and *Giganotosaurus*. Compared to other carcharodontosaurids, UAIC

(SCM1) 615 is smaller than the largest teeth of *Acrocanthosaurus* (9% difference), *Carcharodontosaurus* (20%), and *Giganotosaurus* (12.5%) in the dataset, but is 13% bigger than the largest tooth of *Mapusaurus*.

It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Sereno et al., 1996; Calvo and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn, corroborates growing evidence that very large body size was acquired very early in carcharodontosaurid history, since the earliest potential members of the clade are already of relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.

The inferred large body size of the South Dobrogean theropod is also remarkable as virtually all other dinosaur remains reported previously from Romania (both from the Early Cretaceous Cornet assemblage and the much later, end Cretaceous Haţeg Island fauna) are significantly smaller, and many have been interpreted as insular dwarfs (e.g., Weishampel et al., 1993, 2003; Benton et al., 2006, 2010; Stein et al., 2010; Ősi et al., 2014). Although other Romanian theropod dinosaurs were not particularly dwarfed (e.g. Brusatte et al., 2013), they were nonetheless small (Nopcsa, 1902; Csiki and Grigorescu, 1998; Csiki et al., 2010; Brusatte et al., 2013). This bias towards small bodied Romanian theropods was also

interpreted as a consequence of their insular habitat (Csiki and Grigorescu, 1998), as all previously reported theropod remains come from within the Carpathian Orogen, an area with an archipelago-type palaeogeography during the Cretaceous (Dercourt et al., 2000; Csontos and Vörös, 2004; Csiki-Sava et al., 2015). By contrast, UAIC (SCM1) 615 was found in shallow marine deposits bordering the emerged areas of Central Dobrogea, part of the stable cratonic areas of Europe and connected at least intermittently to the Ukrainean Shield since the Late Jurassic (Fig. 5A). Although cratonic Europe was also transformed into an archipelago of islands during much of the Cretaceous, these islands were often both larger in size and more stable in space and time than were the transient emerged areas of the Tethyan archipelagoes. As such, it is conceivable that the Southern Dobrogean carcharodontosaurid was less constrained by space or resource limitations than the Tethyan insular dinosaurs, allowing it to retain a large body size.

5.*3. UAIC (SCM1) 615 and Valanginian dinosaur distribution*

Besides documenting the presence of large-sized mainland carcharodontosaurids in the Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a significant gap in our knowledge on the composition and distribution of the Early Cretaceous dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these being known from the later part (Barremian–Albian) of that epoch; only around a dozen localities were listed from each age of the early part of the Early Cretaceous (Berriasian, Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al., 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards

western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no occurrences are known from the entire central, eastern and southern Europe for the Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).

Our identification of the Romanian tooth as a carcharodontosaurid documents the presence of this clade in Europe in the very early Cretaceous. This is significant, as carcharodontosaurids were widely distributed tens of millions of years later, in the middle Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see below). Despite the recent discoveries documenting that the clade was also present in North America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010; see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than previously thought and were a long-term component of the European mainland Early Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might have been already present between the cratonic, stable European mainland, with a dinosaur fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania (Benton et al., 2006).

This Valanginian carcharodontosaurid represents an important datapoint not only for the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a poorly documented age in dinosaur evolution, with very few precisely dated fossil occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known from Asia, some of which have debatable or controversial dates. These include sites in Japan (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992; Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare dinosaur remains of possible Valanginian (or 'Neocomian') age were also reported from southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g., Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli et al., 2014).

As one of the two known reports of Valanginian dinosaurs in Europe east of France, the Southern Dobrogean dinosaur record fills a huge palaeogeographic gap between the western European and the eastern Asian dinosaur faunas. Moreover, none of these early Early Cretaceous dinosaur assemblages from outside Europe include carcharodontosaurids (see below), as theropods are represented by coelurosaurians interpreted either as compsognathids (Gishlick and Gauthier, 2007) or basal ornithomimosaurs (Choiniere et al., 2012) in southern Africa, metriacanthosaurid allosauroids ('sinraptorids') in Thailand (Buffetaut and Suteethorn, 2007), and indeterminate allosauroids (Pérez-Moreno et al., 1993), non-

carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz, 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest that carcharodontosaurids had not achieved a wide geographic distribution by this point in time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.

Finally, the presence of the Cochirleni carcharodontosaurid might hint at the presence of palaeobiogeographic provinciality between the western and the eastern parts of Europe, partly mirroring those reported from the later part of the Late Cretaceous (e.g., Le Loeuff and Buffetaut, 1995; Weishampel et al., 2010; Ősi et al., 2012; Csiki-Sava et al., 2015). In the reasonably well sampled, and significantly better known, western European dinosaur faunas, Valanginian large carnivorous dinosaurs include non-carcharodontosaurid tetanurans (*Becklespinax*), as well as indeterminate allosauroids or indeterminate theropods (often described as ‘*Megalosaurus’ dunkeri*, ‘*M.*’ *insignis* or ‘*M.*’ *oweni*), none of which can be referred positively to Carcharodontosauridae (Carrano et al., 2012). The apparently provincial geographic distribution of the large-bodied theropods suggests that some degree of faunal differentiation was occurring within the European mainland, most probably promoted by geographic distance. Notably, this intra-European differentiation in theropod assemblages appears to stand in contrast with the faunal homogeneity reported in the case of the ornithopods from the UK and Romania (e.g., Galton, 2009). It is important, however, to re-emphasize at this point that the Valanginian dinosaur fossil record is both exceedingly poor and patchy, even in Europe. Accordingly, further discoveries are needed to verify and support (or contradict) the presence of such a distribution pattern pointing to palaeobiogeographic provinciality inside Europe, as the one suggested by our carcharodontosaurid identification for UAIC (SCM1) 615.

5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography

Carcharodontosauridae were long considered as an exclusively Gondwanan group of theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996; Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Cau et al., 2013). This view started to change with the identification of the Early Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan one, was further supported by the discovery of definitive carcharodontosaurids in the Lower Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper Cretaceous of China (Brusatte et al., 2009, 2010b, 2~~1~~012; Mo et al., 2014; Lü et al., ~~2014~~2016).

Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin of the carcharodontosaurids, followed by their dispersal across Laurasia and western Gondwana beginning at least by the Aptian (Fig. 5B), a scenario that is concordant with the tentatively suggested presence of early carcharodontosaurids in the Upper Jurassic of Tanzania, which are based on fragmentary specimens (Rauhut, 2011; Carrano et al., 2012). It is also concordant with the widespread appearance of carcharodontosaurids in the fossil record starting with the Aptian, when they are reported in Africa (*Eocarcharia*; Sereno and Brusatte, 2008), South America (Vickers-Rich et al., 1999), North America (*Acrocanthosaurus*; Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000 Eddy and Clarke, 2011), Europe (Canudo and Ruiz-Omeñaca, 2003; Pereda-Suberbiola et al., 2012), and eastern Asia (*Kelmayisaurus*; Brusatte et al., 2012; ~~Lü et al., 2014;~~ Mo et al., 2014; Lü et al., 2016).

During the Albian–Turonian, carcharodontosaurids became especially abundant and diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and South America (*Tyrannotitan*, *Giganotosautus*, *Mapusaurus*, alongside with indeterminate carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005; Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig. 5B). They were still present during this time interval in other continents, as well: in North America with *Acrocanthosaurus* until the Albian (D'Emic et al., 2012), in Europe until the Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).

After dominating terrestrial ecosystems at least in Africa, South America and eastern Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado, 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana. Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-Cenomanian deposits of South America to Carcharodontosaridae (e.g., Canudo et al., 2008; Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were reported to suggest the survival of carcharodontosaurids into the latest Cretaceous (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).

Contrasting with this rich and relatively continuous fossil record of Carcharodontosauridae starting with the Aptian, the first half of its evolutionary history is very poorly documented (Fig. 5B). Prior to the identification of UAIC (SCM1) 615, only two occurrences of pre-Aptian Cretaceous carcharodontosaurids were reported, one from the Barremian of Spain (Ortega et al., 2010; Gasca et al., 2014) and the other from the Barremian of Thailand (Buffetaut and Suteethorn, 2012). The Early Cretaceous *Kelmayisaurus* from Xinjiang, western China, was recognized as a carcharodontosaurid of possibly ?Valanginian to Aptian in age by Brusatte et al. (2012), but the deposits yielding these remains (the Lianmugin, or Lianmuxin, Formation of the Tugulu Group) were dated as Aptian–Albian by Eberth et al. (2001; see also Tong et al., 2009). An important temporal gap – of about 20 to 28 millions of years, according to the dates in Gradstein et al. (2012) – thus stretched between the oldest, tentatively assigned carcharodontosaurids from the Oxfordian–Tithonian of Tanzania, including the formally erected *Veterupristisaurus* (Rauhut, 2011; see also Carrano et al., 2012), and those that started to appear in the fossil record in the Barremian and then spread widely during the Aptian. Referral of UAIC (SCM1) 615 to Carcharodontosauridae partially fills this frustrating gap, effectively halving this shadowy period in the evolutionary history of the group.

Furthermore, our analyses tentatively cluster the Dobrogean theropod with the derived members of the Carcharodontosaurinae to the exclusion of the more basal, but significantly younger non-carcharodontosaurine carcharodontosaurids *Eocarcharia* and *Acrocanthosaurus*. If this placement is correct, then the Romanian tooth indicates that Carcharodontosaurinae diverged from other carcharodontosaurids considerably earlier than hitherto recognized.

The previously known fossil record of the clade suggested that Carcharodontosaurinae originated sometime between the Aptian and Albian, as basal carcharodontosaurids (*Acrocanthosaurus*, *Concavenator*, *Eocarcharia*) were moderately diverse in the Barremian–

Aptian, followed by the appearance of many fossils of carcharodontosaurines beginning in the Albian (Fig. 5B). The proposed affinities of the oldest carcharodontosaurid material – including isolated teeth referred to as '*Megalosaurus*' *ingens* – from the east African Upper Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut, 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very large size and dental morphology characterizing it) well before the Albian, during or even before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.

Besides shifting the emergence of the carcharodontosaurines earlier in time, identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting palaeobiogeographic implications. As already noted, recent discoveries show that Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g., Novas et al., 2005), with the identification of its widespread, Pangaean distribution during the late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999; Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014). However, within Carcharodontosauridae itself, some palaeogeographic patterns have been widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al., 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as previously all its recognized members were restricted strictly to either Africa (Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995; Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of

Carcharodontosaurinae were still adhering to patterns of continental fragmentation and vicariant evolution, with a basal split between the Albian–Cenomanian African *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

This scenario is now challenged by our finding that the Southern Dobrogean carcharodontosaurid UAIC (SCM1) 615 may nest inside Carcharodontosaurinae. If true, such an affinity would suggest that the origin of Carcharodontosaurinae was not a southern, vicariant by-product of the Gondwana-Laurasia separation, a major palaeogeographic event that is considered to have been well underway by the end of the Jurassic, and essentially completed by the mid-Early Cretaceous (see Weishampel et al., 2010). Indeed, during this time palaeogeographic connections and faunal interactions were virtually non-existent between the northern Tethyan (European) and southern Tethyan (western Gondwanan, but essentially African) areas of the Mediterranean (e.g., Canudo et al., 2009~~; see below~~), which makes a vicariant hypothesis intuitive. However, if the Romanian tooth represents a carcharodontosaurine, then it implies a much more complicated palaeogeographic history of the clade, which is not so clearly linked to continental breakup.

The palaeogeographic position of the Southern Dobrogean carcharodontosaurine in cratonic Europe, north of the Neo-Tethys, together with its significantly older age compared to other carcharodontosaurines, could indicate that separation of the carcharodontosaurine lineage took part in Europe and not in western Gondwana as previously assumed. This would also mean that representatives of this lineage were subsequently – after the Barremian – introduced to Africa and South America via trans-Tethyan dispersal, most probably at a time when faunal interactions between the southern and northern margins of the Mediterranean Tethys were resumed, after the early Barremian (Canudo et al., 2009).

Alternatively, it can be hypothesized that appearance of carcharodontosaurines in Southern Dobrogea is a consequence of southern immigration originating in western Gondwana, often considered the place of origin for this clade. However, this scenario has several potential caveats. Although Europe has been considered as forming part of a larger Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín, 2012), and occasional trans-Tethyan faunal connections have been recognized between Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage, 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place during the 'Neocomian' (Berriasian–Hauterivian) time interval.

More recently, some potential evidence has emerged for Gondwana-to-Europe interchange during the 'Neocomian'. The presence of the basal rebbachisaurid *Histriasaurus* (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as indicative of very early and very rapid northward dispersal of this clade from western Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of this particular dispersal event was even constrained to the Berriasian–Valanginian time interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive transportation mechanism ('Noah's Ark'; ~~KcKenna~~McKenna, 1973) for basal rebbachisaurids after its separation from mainland Africa (e.g., Torcida Fernández-Baldor et al., 2011). Furthermore, the palaeogeographical separation between Africa and Adria (and thus the effective movement of the presumed ark) is considered to be at most an incipient one during the Early Cretaceous by Bossellini (2002) and Zarcone et al. (2010), with spatial continuity still present between the two landmasses, while deep-water basins continued to separate Adria from the European Craton. Accordingly, although the presence of *Histriasaurus* can represent a case of northward range extension of rebbachisaurids during the Berriasian–Valanginian, it took place not strictly speaking into Europe, but only reached the northernmost extremity of Adria, a northerly peninsular extension of the African mainland. It was only starting with the Barremian that rebbachisaurids dispersed as far north as the European cratonic areas, including Iberia and the British Isles (Mannion, 2009; Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011), a time when faunal interchanges between Europe and Africa are considered to have been well underway (e.g., Gheerbrant and Rage, 2006; Canudo et al., 2009).

Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant of the European mainland. It is thus unclear to what extent the example of rebbachisaurid range extension into (present-day) Europe during the early Early Cretaceous, as potentially testified by the discovery of the Croatian taxon, would also be applicable for the Southern Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are very different, and that faunal connections during this time interval are not documented between the African and European cratons as already pointed out by Gheerbrant and Rage (2006).

Absence of documented faunal interactions weakens support for a scenario of south-to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the Cretaceous, and would argue instead for a local, European development to explain the presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian presence of carcharodontosaurids in Europe is also consistent with their appearance in the Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in North America likely requires the presence of pre-Aptian members of the clade in Europe, since faunal exchanges between these two landmasses are known to have been halted before the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western Gondwana. The causes of these distribution patterns remain as yet unknown, and further support – in the form on new carcharodontosaurid discoveries from the early-middle part of the Early Cretaceous – is required to better uphold such a scenario.

We finally reiterate that if the Romanian tooth does not belong to a carcharodontosaurine, but instead is artefactually grouping with them in the phylogenetic analysis because of the very incomplete nature of the material, then the traditional story of Carcharodontosaurinae as a product of vicariant evolution driven by the breakup of Pangea will remain strongly supported. However, even in such case UAIC (SCM1) 615 would still record the presence of early-occuring large carcharodontosaurid theropods with a very characteristic carcharodontosaurine-type dentition in the eastern part of the European craton, adding to known early Early Cretaceous theropod (and dinosaur) diversity, and potentially documenting dinosaur faunal provinciality in Europe and worldwide.

6. Conclusions

We re-describe and interpret the affinities of one of the most significant historical dinosaurian specimens of Romania, an isolated but well-preserved theropod tooth from Southern Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth, while the available evidence – including novel calcareous nannoplankton sampling – supports its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of

Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this record advances our understanding of European dinosaur distribution during the early Early Cretaceous, and also fills an important palaeogeographic gap between Western European and Eastern Asian dinosaurian assemblages of the Valanginian.

Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a possible member of Carcharodontosaurinae, a subclade of derived and gigantic carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean specimen documents the emergence of Carcharodontosaurinae earlier than previously recognized, thus also indicating an earlier acquisition of their characteristically large size. Based on currently known palaeogeographic and chronostratigraphic constraints on the evolution of Carcharodontosauridae, it appears that not only did this clade have a wide distribution, but that crucial events of its evolutionary history such as the emergence of the derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia split, as was formerly suggested. In such a case, instead of endemic evolution the emergence of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into western Gondwana adds further support for the presence of important palaeogeographic ties between the two realms during the second half of the Early Cretaceous.

Acknowledgements

This research was supported by the National Research Council of Romania (CNCS) grant PN-IIID-PCE-2011-3-0381 and a Sepkoski grant of the Paleontological Society for Z.Cs.-S. S.L.B. is supported by a Marie Curie Career Integration Grant EC630652, the Division of Paleontology of the American Museum of Natural History, and the School of GeoSciences of the University of Edinburgh. He thanks Mátyás Vremir, Radu Totoianu, and Mark Norell for many hours of fun discussion on Romanian fossils, and for supporting his work and travel in Romania. We thank Mihai Brânzilă and Paul Ţibuleac (UAIC) for access to the specimen, for allowing us to collect samples for the nannoplankton analyses, and for their help and collegiality during our visit to Iași, as well as Ilie Turculeț for sharing information about the history of the specimen. Mihaela C. Melinte-Dobrinescu has gracefully analyzed the nannoplankton samples derived from UAIC (SCM1) 615; her contribution was essential in assessing the age of the specimen. Finally, we thank the reviewers Eric W.A. Mulder (Denekamp, the Netherlands) and Xabier Pereda-Suberbiola (Bilbao, Spain), as well as Associated Editor Elena Jagt-Yazykova, for their useful comments and suggestions that helped improve ~~a~~ previous versions of the manuscript.

References

Accarie, H., Beaudoin, B., Dejax, J., Friès, G., Michard, J. G., & Taquet, P~~.,~~. (1995). Découverte d'un dinosaure théropode nouveau (*Genusaurus sisteronis* n. g., n. sp.) dans l'Albien marin de Sisteron (Alpes-de-Haute-Provence, France) et extension au Crétacé inférieur de la lignée cératosaurienne. *Comptes Rendus de l'Académie des Sciences Paris, IIa 320*, 327–334.

Allain, R~~.,~~. (2002). Discovery of a megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology*, *22*, 548–563.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Allain, R~~.,~~. (2005). The enigmatic theropod dinosaur *Erectopus superbus* (Sauvage, 1882) from the Lower Albian of Louppy-le-Chateau (Meuse, France). In K.~~:~~ Carpenter~~, K.~~ (Ed.), *The Carnivorous Dinosaurs* (pp. 72–86).~~ Indiana University Press,~~ Bloomington: Indiana University Press~~, pp. 72–86~~.

Avram, E., Costea, I., Dragastan, O., Muţiu, R., Neagu, T., Şindilar, V., & Vinogradov, C. (1996). Distribution of the Middle-Upper Jurassic and Cretaceous facies in the Romanian eastern part of the Moesian Platform. *Revue Roumaine de Géologie*, *39-40*, 3–33.

Avram, E., Szasz, L., Antonescu, E., Baltreş, A., Iva, M., Melinte, M., Neagu, T., Rădan, S., & Tomescu, C~~.,~~. (1993). Cretaceous terrestrial and shallow marine deposits in northern South Dobrogea (SE Romania). *Cretaceous Research*, *14*, 265–305.

~~Avram, E., Costea, I., Dragastan, O., Muţiu, R., Neagu, T., Şindilar, V., Vinogradov, C.., 1996. Distribution of the Middle-Upper Jurassic and Cretaceous facies in the Romanian eastern part of the Moesian Platform. *Revue Roumaine de Géologie 39-40*, 3–33.~~

Azevedo, R. P. F. de, Simbras, F. M., Furtado, M. R., Candeiro, C. R. A., & Bergqvist, L. P.~~,~~ (2013). First Brazilian carcharodontosaurid and other new theropod dinosaur fossils from the Campanian-Maastrichtian Presidente Prudente Formation, São Paulo State, southeastern Brazil. *Cretaceous Research*, *40*, 131–142.

Benson, R. B. J., Barrett, P. M., Powell, H. P., & Norman, D. B~~.,~~. (2008). The taxonomic status of *Megalosaurus bucklandii* (Dinosauria, Theropoda) from the Middle Jurassic of Oxfordshire, UK. *Palaeontology*, *51*, 419–424.

Benson, R. B. J., Carrano, M. T., & Brusatte, S. L.~~,~~ (2010). A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften*, *97*, 71–78.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Benton, M. J., Cook, E., Grigorescu, D., Popa, E., & Tallódi, E~~.,~~. (1997). Dinosaurs and other tetrapods in an Early Cretaceous bauxite-filled fissure, northwestern Romania. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *130*, 275–292.

Benton, M. J., Csiki, Z., Grigorescu, D., Redelstorff, R., Sander, M., Stein, K., & Weishampel, D. B. (2010). Dinosaurs and the island rule: the dwarfed dinosaurs from Haţeg Island. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *293*, 438–454.

Benton, M. J., Minter, N. J., & Posmoşanu, E.~~,~~ (2006). Dwarfing in ornithopod dinosaurs from the Early Cretaceous of Romania. In~~:~~ Z. Csiki~~, Z.~~ (Ed.), *Mesozoic and Cenozoic Vertebrates and Paleoenvironments; Tributes to the Career of Prof. Dan Grigorescu* (pp. 79–87).~~ Ars Docendi,~~ Bucharest: Ars Docendi~~, pp. 79–87~~.

~~Benton, M.J., Csiki, Z., Grigorescu, D., Redelstorff, R., Sander, M., Stein, K., Weishampel, D.B., 2010. Dinosaurs and the island rule: the dwarfed dinosaurs from Haţeg Island. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 438–454.~~

Blows, W. T., & Honeysett, K.~~,~~ (2014). First Valanginian *Polacanthus foxii* (Dinosauria, Ankylosauria) from England, from the Lower Cretaceous of Bexhill, Sussex. *Proceedings of the Geologists' Association*, *125*, 233–251.

Bosselini, A.~~,~~ (2002). Dinosaurs ''re-write'' the geodynamics of the eastern Mediterranean and the paleogeography of the Apulia Platform. *Earth-Science Reviews*, *59*, 211–234.

Brânzilă, M. (ed.)~~,~~ (2010). *Academicianul Ion Simionescu - savant şi dascăl al neamului* (p. 182). Iaşi: Ed. Universităţii "Alexandru Ioan Cuza"~~, Iaşi, 182 pp~~.

~~Brusatte, S.L., Sereno, P.C., 2007. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. Journal of Vertebrate Paleontology 27, 902–916.~~

~~Brusatte, S.L., Sereno, P.C., 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. Journal of Systematic Palaeontology 6, 155–182.~~

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

~~Brusatte, S. L., Clark, N.D.L., 2015. Theropod dinosaurs from the Middle Jurassic (Bajocian-Bathonian) of Skye, Scotland. *Scottish Journal of Geology 51*, 157164. doi: 10.1144/sjg2014-022~~

Brusatte, S., Benson, R. B. J., Carr, T. D., Williamson, T. E., & Sereno, P. C~~.,~~. (2007). The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology*, *27*, 1052–1056.

Brusatte, S. L., Benson, R. B. J., Chure, D. J., Xu, X., Sullivan, C., & Hone, D. W. E~~.,~~. (2009). The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. *Naturwissenschaften*, *96*, 1051–1058.

Brusatte, S. L., Benson, R. B. J., & Xu, X. (2012). A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China. *Acta Palaeontologica Polonica*, *57*, 65–72.

Brusatte, S. L., & Clark, N. D. L. (2015). Theropod dinosaurs from the Middle Jurassic (Bajocian-Bathonian) of Skye, Scotland. *Scottish Journal of Geology*, *51*, 157–164. doi: 10.1144/sjg2014-022

Brusatte, S., Chure, D. J., Benson, R. B. J., & Xu, X. (2010b). The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Asia. *Zootaxa*, *2334*, 1–46.

Brusatte, S. L., Lloyd, G. T., Wang, S. C., & Norell, M. A. (2014). Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology*, *24*, 2386–2392.

Brusatte, S. L., Norell, M. A., Carr, T. D., Erickson, G. M., Hutchinson, J. R., Balanoff, A. M., Bever, G. S., Choiniere, J. N., Makovicky, P. J., & Xu, X. ~~,~~(2010a). Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science*, *329*, 1481–1485.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Adjust space between Latin and Asian text, Adjust space between Asian text and numbers

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

~~Brusatte, S., Chure, D.J., Benson, R.B.J., Xu, X., 2010b. The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Asia. Zootaxa 2334, 1–46.~~

~~Brusatte, S.L., Benson, R.B.J., Xu, X., 2012. A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China. Acta Palaeontologica Polonica 57, 65–72.~~

~~Brusatte, S.L., Vremir, M., Csiki-Sava, Z., Turner, A.H., Watanabe, A., Erickson, G.M., Norell, M.A., 2013. The osteology of *Balaur bondoc*, an island-dwelling dromaeosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Romania. Bulletin of the American Museum of Natural History 374, 3–100. doi: 10.1206/798.1~~

~~Brusatte, S.L., Lloyd, G.T., Wang, S.C., Norell, M.A., 2014. Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. Current Biology 24, 2386–2392.~~

Brusatte, S. L., & Sereno, P. C. (2007). A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology*, *27*, 902–916.

Brusatte, S. L., & Sereno, P. C. (2008). Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Palaeontology*, *6*, 155–182.

Brusatte, S. L., Vremir, M., Csiki-Sava, Z., Turner, A. H., Watanabe, A., Erickson, G. M., & Norell, M. A. (2013). The osteology of *Balaur bondoc*, an island-dwelling dromaeosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Romania. *Bulletin of the American Museum of Natural History*, *374*, 3–100. doi: 10.1206/798.1

Buckland, W.~~,~~ (1824). Notice on the *Megalosaurus* or great fossil lizard of Stonesfield. *Transactions of the Geological Society*, *21*, 390–397.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Adjust space between Latin and Asian text, Adjust space between Asian text and numbers

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Buffetaut, E., & Suteethorn, V~~.,~~. (1998). Early Cretaceous dinosaurs from Thailand and their bearing on the early evolution and biogeographical history of some groups of Cretaceous dinosaurs. In~~:~~ ~~Lucas,~~ S. G. Lucas, ~~Kirkland,~~ J. I. Kirkland, ~~Estep,~~ & J. W. Estep (Eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems* (pp. 205–210), New Mexico Museum of Natural History and Science Bulletin, 14~~, pp. 205–210~~.

Buffetaut, E., & Suteethorn, V~~.,~~. (2007). A sinraptorid theropod (Dinosauria: Saurischia) from the Phu Kradung Formation of northeastern Thailand. *Bulletin de la Société Géologique de France*, *178*, 497–502.

Buffetaut, E., & Suteethorn, V~~.,~~. (2012). A carcharodontid theropod (Dinosauria, Saurischia) from the Sao Khua Formation (Early Cretaceous, Barremian) of Thailand. In~~:~~ ~~Royo-Torres,~~ R. Royo-Torres, ~~Gascó,~~ F. Gascó, & ~~Alcalá,~~ L. Alcalá (Eds.), *10th Annual Meeting of the European Association of Vertebrate Palaeontologists* (pp. 27–30). Teruel: ¡Fundamental!, 20~~, pp. 27–30~~.

Calvo, J. O., & Coria, A~~.,~~. (1998). New specimen of *Giganotosaurus carolinii* (Coria & Salgado, 1995), supports it as the largest theropod ever found. *Gaia*, *15*, 117–122.

Calvo, J. O., Gandossi, P., & Porfiri, J. D~~.,~~. (2006). Dinosaur faunal replacement during Cenomanian times in Patagonia, Argentina. In: ~~Evans,~~ S. E. Evans, & ~~Barrett,~~ P. M. Barrett (Eds.), *9th Mesozoic Terrestrial Ecosystems and Biota*~~,~~ (pp. 17–20). Manchester, UK~~, pp. 17–20~~.

Canale, J. I., Scanferla, C. A., Agnolin, F. L., & Novas, F. E~~.,~~. (2009). New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften*, *96*, 409–414.

Canale, J. I., Novas, F. E., & Pol, D~~.,~~. (2015). Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda:

Formatted: Font: Italic

Formatted: Font: Not Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. *Historical Biology*, *27*, 1–32. doi: 10.1080/08912963.2013.861830.

Candeiro, C. R. A., Fanti, F., Therrien, F., & Lamanna, M. C~~.,~~. (2011). Continental fossil vertebrates from the mid-Cretaceous (Albian-Cenomanian) Alcântara Formation, Brazil, and their relationship with contemporaneous faunas from North Africa. *Journal of African Earth Sciences*, *60*, 79–92.

Canudo, J. I. Barco, J. L., Pereda Suberbiola, X., Ruiz-Omeñaca, J. I., Salgado, L., Torcida Fernández-Baldor, F., & Gasulla, J. M. (2009). What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. *Bulletin de la Société Géologique de France*, *180*, 5–11.

Canudo, J. I., Filippi, L. S., Salgado, L., Garrido, A. C., Cerda, I. A., Garcia, R., & Otero, A. (2008). Theropod teeth associated with a sauropod carcass in the Upper Cretaceous (Plottier Formation) of Rincón de los Sauces. In Colectivo Arqueológico y Paleontológico de Salas de los Infantes (Ed.), *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno* (pp. 321–330). Salas de los Infantes, Burgos.

Canudo, J. I., & Ruiz-Omeñaca, J. I~~.,~~. (2003). Los restos directos de dinosaurios terópódos (excluyendo Aves) en España. *Ciencias de la Tierra 26*, 347–373.

~~Canudo, J.I., Filippi, L.S., Salgado, L., Garrido, A.C., Cerda, I.A., Garcia, R., Otero, A., 2008. Theropod teeth associated with a sauropod carcass in the Upper Cretaceous (Plottier Formation) of Rincón de los Sauces. In: Colectivo Arqueológico y Paleontológico de Salas de los Infantes (Ed.), Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Salas de los Infantes, Burgos, pp. 321–330.~~

~~Canudo, J.I. Barco, J.L., Pereda Suberbiola, X., Ruiz-Omenaca, J.I., Salgado, L., Torcida Fernández-Baldor, F., Gasulla, J.M., 2009. What Iberian dinosaurs reveal about the bridge~~

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: (Default) Times New Roman

Formatted: Font: Italic

~~said to exist between Gondwana and Laurasia in the Early Cretaceous. Bulletin de la Société Géologique de France, 180, 5–11.~~

Carballido, J. L., Salgado, L., Pol, D., Canudo, J. I., & Garrido, A.~~, ~~. (2012). A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. *Historical Biology*, *24*, 631–654.

Carrano, M. T., Benson, R. B. J., & Sampson, S. D. (2012). The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, *10*, 211–300.

Carrano, M. T., & Sampson, S. D.~~, ~~. (2008). The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, *6*, 183–236.

~~Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10, 211–300.~~

Carvalho, I. S., Campos, A. C. A., & Nobre, P. H.~~, ~~. (2005). *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research*, *8*, 11–30.

Casal, G., Candeiro, C. R. A., Martinez, R., Ivany, E., & Ibiricu, L.~~, ~~. (2009). Dientes de Theropoda (Dinosauria: Saurischia) de la Formación Bajo Barreal, Cretácico Superior, Provincia del Chubut, Argentina. *Géobios*, *42*, 553–560.

Cau, A., Dalla Vecchia, F. M., & Fabbri, M.~~, ~~. (2013). A thick-skulled theropod (Dinosauria, Saurischia) from the Upper Cretaceous of Morocco with implications for carcharodontosaurid cranial evolution. *Cretaceous Research*, *40*, 251–260.

Choiniere, J. N., Forster, C. A., & De Klerk, W. J.~~, ~~. (2012). New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation in South Africa. *Journal of African Earth Sciences*, *71–72*, 1–17.

Chure, D. J., Manabe, M., Tanimoto, M., & Tomida, Y.~~, ~~. (1999). An unusual theropod tooth from the Mifune Group (Late Cenomanian to Early Turonian), Kumamoto, Japan. In~~:~~

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

~~Tomida, ~~Y. Tomida, ~~Rich, ~~T. H. Rich, & ~~Vickers-Rich, ~~P. Vickers-Rich (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium* (pp. 291–296). Tokyo: National Science Museum Monographs, 15~~, Tokyo, pp. 291–296~~.

Formatted: Font: Italic

Cifelli, R. L., Davis, B. M., & Sames, B~~.,~~. (2014). Earliest Cretaceous mammals from the western United States. *Acta Palaeontologica Polonica*, *59*, 31–52. doi:10.4202/app.2012.0089.

Formatted: Font: Italic

Cobos, A., Lockley, M. G., Gascó, F., Royo–Torres, R., & Alcalá, L. (2014). Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *399*, 31–41. doi: 10.1016/j.palaeo.2014.02.008.

Formatted: Font: Italic

Formatted: Font: Italic

Cobos, A., Royo-Torres, R., Luque, L., Alcalá, L., & Mampel, L~~.,~~. (2010). An Iberian stegosaurs paradise: The Villar del Arzobispo Formation (Tithonian–Berriasian) in Teruel (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *293*, 223–236.

Formatted: Font: Italic

Formatted: Font: Italic

~~Cobos, A., Lockley, M.G., Gascó, F., Royo–Torres, R., Alcalá, L., 2014. Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 399, 31–41. doi: 10.1016/j.palaeo.2014.02.008.~~

Codrea, V., Godefroit, P., & Smith, T. (2012). First discovery of Maastrichtian (latest Cretaceous) terrestrial vertebrates in Rusca Montană Basin (Romania). In P. Godefroit (Ed.) *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems* (pp. 570–581). Bloomington: Indiana University Press.

Formatted: Font: Italic

Codrea, V., Vremir, M., Jipa, C., Godefroit, P., Csiki, Z., Smith, T., & Fărcaş, C~~.,~~. (2010). More than just Nopcsa's Transylvanian dinosaurs: A look outside the Haţeg Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology 293*, 391–405. doi: 10.1016/j.palaeo.2009.10.027.

Formatted: Font: Italic

~~Codrea, V., Godefroit, P., Smith, T., 2012. First discovery of Maastrichtian (latest Cretaceous) terrestrial vertebrates in Rusca Montană Basin (Romania). In: Godefroit, P. (Ed.) Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 570–581.~~

Colbert, E. H. (~~,~~1946). *Sebecus*, representative of a peculiar suborder of fossil Crocodilia from Patagonia. *Bulletin of the American Museum of Natural History, 87(4)*, 217–270.

Coria, R. A., & Currie, P. J. (2006). A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas, 28*, 71–118.

Coria, R. A, & Salgado, L~~.,~~. (1995). A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature, 377*, 224–226.

Coria, R. A., & Salgado, L~~.,~~. (2005). Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. In~~: Veiga,~~ G. D. Veiga, ~~Spalletti,~~ L. A. Spalletti, ~~Howell,~~ J. A. Howell, & ~~Schwartz,~~ E. Schwartz (Eds.), *The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics* (pp. 317–327). Geological Society, London, Special Publications, 252~~, pp. 317–327~~.

~~Coria, R.A., Currie, P.J., 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas 28, 71–118.~~

Covacef, Z~~.,~~. (1995). Pionieri ai culturii românești în Dobrogea; Ioan Cotovu și Vasile Cotovu. *Analele Dobrogei, I(1)*, 127–134.

Császár, G., Kollányi, K., Lantos, M., Lelkes, G., ~~and~~ & Tardiné Filácz, E~~.,~~. (2000). A Hidasivölgyi Márga Formáció kora és képzõdési környezete. *Földtani Közlöny, 130~~(4)~~*, 695–723.

Csiki, Z., & Grigorescu, D~~.,~~. (1998). Small theropods of the Late Cretaceous of the Haţeg Basin (Western Romania) - an unexpected diversity at the top of the food chain. *Oryctos, 1*, 87–104.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Csiki, Z., Vremir, M., Brusatte, S. L., & Norell, M. A~~.,~~. (2010). An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania. *Proceedings of the National Academy of Sciences*, *107*, 15357–15361.

~~Csiki-Sava, Z., Codrea, V., Vasile, Ș., 2013. Early Cretaceous dinosaur remains from Dobrogea (southeastern Romania). In: Picot, L. (Ed.), Abstracts, 11th Annual Meeting of the European Association of Vertebrate Palaeontologists, Villers-sur-Mer, France, pp. 28.~~

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., & Brusatte, S. L~~.,~~. (2015). Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *Zookeys*, *469*, 1–161. doi: 10.3897/zookeys.469.8439.

Csiki-Sava, Z., Codrea, V., & Vasile, Ș. (2013). Early Cretaceous dinosaur remains from Dobrogea (southeastern Romania). In L. Picot (Ed.), *Abstracts, 11th Annual Meeting of the European Association of Vertebrate Palaeontologists* (pp. 28). Villers-sur-Mer, France.

Csontos, L., & Vörös, A~~.,~~. (2004). Mesozoic plate tectonic reconstruction of the Carpathian region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *210*, 1–56. doi: 10.1016/j.palaeo.2004.02.033.

Currie, P. J., & Carpenter, K~~.,~~. (2000). A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, *22*, 207–246.

Currie, P. J., Rigby, J. K., & Sloan, R. E~~.,~~. (1990). Theropod teeth from the Judith River Formation of southern Alberta, Canada. In~~: Carpenter,~~ K. Carpenter, & ~~Currie,~~ P. J. Currie (Eds~~.),~~.), *Dinosaur Systematics: Approaches and Perspectives* (pp. 107–125). Cambridge, Boston: Cambridge University Press~~, pp. 107–125~~.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Dalla Vecchia, F. M.~~,~~ (1998). Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (Upper Hauterivian/Lower Barremian) limestones of SW Istria (Croatia). *Geologia Croatica*, *5*, 105–134.

Dames, W.~~,~~ (1884). *Megalosaurus dunkeri*. *Sitzungberichte Gesellschaft Naturforschender Freunde zu Berlin*, *1884*, 186–188.

De Klerk, W. J., Forster, C. A., Sampson, S. D., Chinsamy, A., & Ross, C. F. (2000). A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. *Journal of Vertebrate Paleontology*, *20*, 324–332.

D'Emic, M. D., Melstrom, K. M., & Eddy, D. R~~.,~~. (2012). Paleobiology and geographic range of the large-bodied Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *333–334*, 13–23.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M., Cadet, J. P., Crasquin, S., & Săndulescu, M~~.,~~. (Eds.) (2000). *Atlas Peri-Tethys Palaeogeographical Maps* (269 p). Paris: CCGM/CGMW~~, Paris, 269 pp~~.

Dinu, C., Grădinaru, E., Stoica, M., & Diaconescu, V~~.,~~. (2007). *Dobrogea 2007 Field Trip Preparation and Assistance* (123 p.). University of Bucharest~~, 123 pp~~.

Dragastan, O. N., Antoniade, C., & Stoica, M. (2014). Biostratigraphy and zonation of the Lower Cretaceous succession from Cernavodă-lock section, South Dobrogea, eastern part of the Moesian Platform (Romania). *Carpathian Journal of Earth and Environmental Sciences*, *9*, 231–260.

Dragastan, O., Neagu, T., Bărbulescu, A., & Pană, I~~.,~~. (1998). *Jurasicul şi Cretacicul din Dobrogea Centrală şi de Sud* (249 p.). Bucharest~~, 249 pp~~.

~~Dragastan, O.N., Antoniade, C., Stoica, M., 2014. Biostratigraphy and zonation of the Lower Cretaceous succession from Cernavodă-lock section, South Dobrogea, eastern part of the~~

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

~~Moesian Platform (Romania). Carpathian Journal of Earth and Environmental Sciences 9(1), 231–260.~~

Dyke, G. J., Benton, M. J., Posmoşanu, E., & Naish, D~~.,~~. (2011). Early Cretaceous (Berriasian) birds and pterosaurs from the Cornet bauxite mine, Romania. *Palaeontology*, *54*, 79–95.

Formatted: Font: Italic

Eberth, D. A., Brinkman, D. B., Chen, P.-J., Yuan, F.-T., Wu, X.-C., Li, G., & Cheng, ~~Xian~~X.-S~~hen, C.,~~. (2001). Sequence stratigraphy, paleoclimate patterns, and vertebrate fossil preservation in Jurassic–Cretaceous strata of the Juggar Basin, Xinjiang Autonomous Region, People's Republic of China. *Canadian Journal of Earth Sciences*, *38*, 1627–1644.

Formatted: Font: Italic

Formatted: Font: Italic

Eddy, D. R., & Clarke, J. A~~.,~~. (2011). New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroidea (Dinosauria: Theropoda). *PLoS ONE*, *6(3)*, e17932. doi:10.1371/journal.pone.0017932.

Formatted: Font: Italic

Formatted: Font: Italic

Evans, S. E., & Matsumoto, R~~.,~~. (2015). An assemblage of lizards from the Early Cretaceous of Japan. *Palaeontologia Electronica*, *18.2.36A*, 1–36.

Formatted: Font: Italic

Ezcurra, M. D., & Agnolín, F. L~~.,~~. (2012). A new global palaeobiogeographical model for the Late Mesozoic and Early Tertiary. *Systematic Biology*, *61*, 553–566. doi:10.1093/sysbio/syr115.

Formatted: Font: Italic

Formatted: Font: Italic

Fanti, F., Cau, A., Cantelli, L., Hassine, M., & Auditore, M~~.,~~. (2015). New information on *Tataouinea hannibalis* from the Early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. *PLoS ONE*, *10(4)*, e0123475. doi:10.1371/journal.pone.0123475.

Formatted: Font: Italic

Formatted: Font: Italic

Galton, P. M~~.,~~. (2009). Notes on Neocomian (Lower Cretaceous) ornithopod dinosaurs from England - *Hypsilophodon*, *Valdosaurus*, "*Camptosaurus*", "*Iguanodon*" - and referred specimens from Romania and elsewhere. *Revue de Paléobiologie*, *28*, 211–273.

Formatted: Font: Italic

Formatted: Font: Italic

Gardner, J. D., Evans, S. E., & Sigogneau-Russell, D~~.,~~. (2003). New albanerpetontid amphibians from the Early Cretaceous of Morocco and Middle Jurassic of England. *Acta Palaeontologica Polonica*, *48*, 301–319.

Gasca, J. M., Canudo, J. I., & Moreno-Azanza, M~~.,~~. (2014). A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, *273*, 13–23. doi: 10.1127/0077-7749/2014/0413.

Gheerbrant, E., & Rage, J.-C~~.,~~. (2006). Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *241*, 224–246. doi:10.1016/j.palaeo.2006.03.016.

Gishlick, A. D., & Gauthier, J. A~~.,~~. (2007). On the manual morphology of *Compsognathus longipes* and its bearing on the diagnosis of Compsognathidae. *Zoological Journal of the Linnean Society*, *149*, 569–581.

Goloboff, P. A., Farris, J. S., & Nixon, K. C~~.,~~. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, *24*, 774–786.

Gradstein, F. M., Ogg, J. G., Schmitz, M. D., & Ogg, G. M. (Eds~~.),~~.) (2012). *The Geologic Time Scale 2012* (1144 p.). Amsterdam: Elsevier~~, 1144 pp~~.

Grigorescu, D.~~,~~ (1992). Nonmarine Cretaceous Formations of Romania. In~~: Matter,~~ N. J. Matter, & ~~Chen,~~ P.-J. Chen (Eds.), *Aspects of Nonmarine Cretaceous Geology* (pp. 142–164). Beijing: China Ocean Press~~, Beijing, pp. 142–164~~.

Grigorescu, D.~~,~~ (2003). Dinosaurs of Romania. *Comptes ~~rendus~~ Rendus Palevol*, *2*, 97–101.

Grigorescu, D.~~,~~ (2010). The Latest Cretaceous fauna with dinosaurs and mammals from the Hațeg Basin — A historical overview. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, *293*, 271–282.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Hammer, O., Harper, D. A. T., & Ryan, P. D~~.,~~. (2001). Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica, 4*, 1–9.

Harris, J. D~~.,~~. (1998). A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science Bulletin, 13*, 1–75.

Hendrickx, C., & Mateus, O~~.,~~. (2014). Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa, 3751(1)*, 1–74.

Hendrickx, C., Mateus, O., & Araújo, R~~.,~~. (2015a). The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica, 60*, 627–642. doi:10.4202/app.00056.2013.

Hendrickx, C., Mateus, O., & Araújo, R~~.,~~. (2015b). A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology, 35(5*~~):~~), e982797. doi: 10.1080/02724634.2015.982797.

Holtz, T. R., Chapman, R. E., & Lamanna, M. C. (2004b). Mesozoic biogeography of Dinosauria. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria. Second Edition* (pp. 627–642). Berkeley, Los Angeles, London: University of California Press.

Holtz, T. R., Jr.., Molnar, R. E., & Currie, P. J~~.,~~. (2004a). Basal Tetanurae. In~~:~~ D. B. Weishampel, P. Dodson, & H. Osmólska~~Weishampel, D.B., Dodson, P., Osmólska, H.~~ (Eds.), *The Dinosauria. Second Edition* (pp. 71–110).~~ University of California Press,~~ Berkeley, Los Angeles, London: University of California Press~~ pp. 71–110~~.

~~Holtz, T.R., Chapman, R.E., Lamanna, M.C., 2004b. Mesozoic biogeography of Dinosauria. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, Los Angeles, pp. 627–642.~~

Huene, F. von~~.~~ (1923). Carnivorous Saurischia in Europe since the Triassic. *Bulletin of the Geological Society of America*, *34*, 449–458.

Hippolyte, J.-C.~~,~~ (2002). Geodynamics of Dobrogea (Romania): new constraints on the evolution of the Tornquist–Teisseyre Line, the Black Sea and the Carpathians. *Tectonophysics*, *357*, 33–53.

Ionesi, L.~~,~~ (1994). *Geologia unităţilor de platformă şi a orogenului Nord-Dobrogean* (p. 280). ~~Ed. Tehnică,~~ Bucharest: Ed. Tehnică~~, 280 pp~~.

Jerzykiewicz, T., & Russell, D. A~~., –~~. (1991). Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research*, *12*, 345–377.

Jurcsák, T.~~,~~ (1982). Occurences nouvelles des Sauriens mésozoïques de Roumanie. *Vertebrata Hungarica*, *21*, 175–184.

Jurcsák, T., & Popa, E.~~,~~ (1979). Dinozaurieni ornithopozi din bauxitele de la Cornet (Munții Pădurea Craiului). *Nymphaea*, *7*, 37–75.

Jurcsák, T., & Popa, E~~., –~~. (1983). La faune de dinosauriens du Bihor (Roumanie). In~~:~~ ~~Buffetaut,~~ E. Buffetaut, ~~Mazin,~~ J. M. Mazin, ~~Salmon,~~ E. Salmon (Eds.), *Actes du Symposium Paléontologique Georges Cuvier* (pp. 325–335). ~~Le Serpentaire,~~ Montbéliard: Le Serpentaire~~, pp. 325–335~~.

Kellner, A. W. A., Pinheiro, A. E. P., & Campos, D. A~~., –~~. (2014). A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K–Pg boundary. *PLoS ONE*, *9(1)*, e81386. doi:10.1371/journal.pone.0081386.

Kirkland, J. I., Cifelli, R. L., Britt, B. B., Burge, D. L., DeCourten, F. L., Eaton, J. G., & Parrish, J. M~~., –~~. (1999). Distribution of vertebrate faunas in the Cedar Mountain Formation, east-central Utah. *Utah Geological Survey Miscellaneous Publication*, *99-1*, 201–217.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Knoll, F., & Ruiz-Omeñaca, J. I~~., ~~. (2009). Theropod teeth from the basalmost Cretaceous of Anoual (Morocco) and their palaeobiogeographical significance. *Geological Magazine, 146*, 602–616.

Kusuhashi, N., Matsumoto, A., Murakami, M., Tagami, T., Hirata, T., Iizuka, T., Handa, T., & Matsuoka, H~~., ~~. (2006). Zircon U−Pb ages from tuff beds of the upper Mesozoic Tetori Group in the Shokawa district, Gifu Prefecture, central Japan. *The Island Arc, 15*, 378–390.

Lacasa Ruiz, A.~~,~~ (1989). Nuevo genero de ave fosil del yacimiento Neocomiense del Montsec (Provincia de Lerida, España). *Estudios geológicos, 45(5-6)*, 417–425.

Larson, D. W., & Currie, P. J~~., ~~. (2013). Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time. *PLoS ONE, 8(1)*, e54329. doi:10.1371/journal.pone.0054329.

Le Loeuff, J., & Buffetaut, E. ~~,~~(1995). The evolution of Late Cretaceous non-marine vertebrate faunas in Europe. In~~: Sun,~~ A.-L. Sun, & ~~Wang,~~ Y.-Q. Wang (Eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers* (pp. 181–184). ~~China Ocean Press,~~ Beijing~~,~~: China Ocean Press~~ pp. 181–184~~.

Le Loeuff, J., Lang, E., Cavin, L., & Buffetaut, E~~., ~~. (2012). Between Tendaguru and Bahariya: on the age of the Early Cretaceous dinosaur sites from the Continental Intercalaire and other African formations. *Journal of Stratigraphy, 36*, 486–502.

Lucas, F. A~~., ~~. (1901). A new dinosaur, *Stegosaurus marshi*, from the Lower Cretaceous of South Dakota. *Proceedings of the United States National Museum, 23(1224)*, 591–592.

Lucas, S. G~~., ~~. (2006). The *Psittacosaurus* biochron, Early Cretaceous of Asia. *Cretaceous Research, 27*, 189–198.

Lucas, S. G., & Estep, J. W~~., ~~. (1998). Vertebrate biostratigraphy and biochronology of the Cretaceous of China. In ~~Lucas,~~ S. G. Lucas, ~~Kirkland,~~ J. I. Kirkland, ~~Estep,~~ J. W. Estep

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

(Eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems* (pp. 1–20). New Mexico Museum of Natural History and Science Bulletin, 14~~, pp. 1–20~~.

Lü, J.-C., Xu, L., Pu, H.-Y., Jia, S.-H., Azuma, Y., Chang, H.-L., & Zhang, J.-M~~., ~~. (~~2014~~2016). Paleogeographical significance of carcharodontosaurid teeth from the late Early Cretaceous of Ruyang, Henan Province of central China. *Historical Biology*, 28, 8–13. doi: 10.1080/08912963.2014.947287.

Manabe, M., & Hasegawa, Y~~., ~~. (1995). Diapsid fauna and its paleobiogeographical implication, the Neocomian section of the Tetori Group. In~~: Sun, ~~A. Sun, & ~~Wang, ~~Y. Wang (Eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*~~,~~ (pp. 179). Beijing: China Ocean Press~~, pp. 179~~.

Mannion, P. D. ~~,~~(2009). A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. *Cretaceous Research*, *30*, 521–526.

Mannion, P. D., Upchurch, P., & Hutt, S~~., ~~. (2011). New rebbachisaurid (Dinosauria: Sauropoda) material from the Wessex Formation (Barremian, Early Cretaceous), Isle of Wight, United Kingdom. *Cretaceous Research*, *32*, 774–780.

Matsukawa, M., Ito, M., Nishida, N., Koarai, K., Lockley, M. G., Nichols, D. J. ~~,~~(2006). The Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial ecosystems in Asia. *Cretaceous Research*, *27*, 199–225.

McDonald, A. T~~., ~~. (2011). The taxonomy of species assigned to *Camptosaurus* (Dinosauria: Ornithopoda). *Zootaxa*, *2783*, 52–68.

McKenna, M. C~~., ~~. (1973). Sweepstakes, filters, corridors, Noah's Arks, and Beached Viking Funeral Ships in palaeogeography. In~~: Tarling, ~~D. H. Tarling, ~~Runcorn, ~~S. K. Runcorn (Eds.), *Implications of Continental Drift to the Earth Sciences* (pp. 295–308). ~~Academic Press, ~~New York~~,~~: Academic Press~~pp. 295–308~~.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Mo, J.-Y., Huang, C.-L., Xie, S.-W., & Buffetaut, E~~.,~~. (2014). A megatheropod tooth from the Early Cretaceous of Fusui, Guangxi, Southern China. *Acta Geologica Sinica (English Edition)*, *88*, 6–12.

Molnar, R. E~~.,~~. (1990). Problematic Theropoda: "Carnosaurs". In~~:~~ ~~Weishampel,~~ D. B. Weishampel, ~~Dodson,~~ P. Dodson, & ~~Osmólska,~~ H. Osmólska (Eds.), *The Dinosauria* (pp. 306–317). ~~University of California Press,~~ Berkeley, Los Angeles, Oxford~~,~~: University of California Press~~pp. 306–317~~.

Mutihac, V., & Mutihac, G~~.,~~. (2010). *The geology of Romania, within the Central East European geostructural context* (p. 690). ~~Ed. Didactică şi Pedagogică,~~ Bucharest: Ed. Didactică şi Pedagogică~~, 690 pp~~.

Neagu, T., Dragastan, O., & Csiki, Z~~.,~~. (1997). Early Cretaceous shelf paleocommunities of Cernavodă (South Dobrogea, SE Romania). *Acta Palaeontologica Romaniae*, *1*, 28–36.

Nopcsa, F~~.,~~. (1902). Notizen über cretacische Dinosaurier. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*, *111*, 93–114.

Nopcsa, F~~.,~~. (1923). On the geological importance of the primitive reptilian fauna of the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotium*). *Quarterly Journal of the Geological Society of London*, *79*, 100–116.

Norman, D. B~~.,~~. (2010). A taxonomy of iguanodontians (Dinosauria: Ornithopoda) from the lower Wealden Group (Cretaceous: Valanginian) of southern England. *Zootaxa*, *2489*, 47–66.

Norman, D. B~~.,~~. (2013). On the taxonomy and diversity of Wealden iguanodontian dinosaurs (Ornithischia: Ornithopoda). *Revue de Paléobiologie*, *32*~~(2)~~, 385–404.

Novas, F. E., Agnolín, F. L., Ezcurra, M. D., Porfiri, J., & Canale, J. I. (2013). Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Research*, *45*, 174–215.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Novas, F. E., de Valais, S., Vickers-Rich, P. A., & Rich, T. H~~.,~~. (2005). A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften*, *92*, 226–230.

~~Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. Cretaceous Research 45, 174–215.~~

Ortega, F., Escaso, F., & Sanz, J. L~~.,~~. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature*, *467*, 203–206.

Ősi, A., Codrea, V., Prondvai, E., & Csiki-Sava, Z. (2014). New ankylosaurian material from the Upper Cretaceous of Transylvania. *Annales de Paléontologie*, *100*, 257–271. doi: 10.1016/j.annpal.2014.02.001.

Ősi, A., Rabi, M., Makádi, L., Szentesi, Z., Botfalvai, G., & Gulyás, P.~~,~~ (2012). The Late Cretaceous continental vertebrate fauna from Iharkút (western Hungary): a review. In~~:~~ ~~Godefroit,~~ P. Godefroit (Ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems* (pp. 533–569). ~~Indiana University Press,~~ Bloomington~~,~~: Indiana University Press~~pp. 533–569~~.

~~Ősi, A., Codrea, V., Prondvai, E., Csiki-Sava, Z., 2014. New ankylosaurian material from the Upper Cretaceous of Transylvania. Annales de Paléontologie 100, 257–271. doi: 10.1016/j.annpal.2014.02.001.~~

Ősi, A., Rabi, M., & Makádi, L~~.,~~. (2015). An enigmatic crocodyliform tooth from the bauxites of western Hungary suggests hidden mesoeucrocodylian diversity in the Early Cretaceous European archipelago. *PeerJ*, *3*, e1160. doi:10.7717/peerj.1160.

Paolillo, A., & Linares, O. J~~.,~~. (2007). Nuevos cocodrilos Sebecosuchia del Cenozoico Suramericano (Mesosuchia: Crocodylia). *Paleobiologia Neotropical*, *3*, 1–25.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Pereda-Suberbiola, X., Ruiz-Omeñaca, J. I., Canudo, J. I., Torcida, F., & Sanz, J. L. (2012). Dinosaur faunas from the Early Cretaceous (Valanginian–Albian) of Spain. In P. Godefroit (Ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems* (pp. 378–407). Bloomington: Indiana University Press.

Formatted: Font: Italic

Pereda-Suberbiola, X., Ruiz-Omeñ~~n~~aca, J. I., Fernandez-Baldor, F. T., Maisch, M. W., Huerta, P., Contreras, R., Izquierdo, L. A., Huerta, D. M., Montero, V. U., & Welle, J~~.,~~. (2011). A tall-spined ornithopod dinosaur from the Early Cretaceous of Salas de los Infantes (Burgos, Spain). *Comptes Rendus Palevol*, *10*, 551–558.

Formatted: Font: Italic

Formatted: Font: Italic

~~Pereda-Suberbiola, X., Ruiz-Omenaca, J.I., Canudo, J.I., Torcida, F., Sanz, J.L., 2012. Dinosaur faunas from the Early Cretaceous (Valanginian–Albian) of Spain. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Life of the Past. Indiana University Press, Bloomington, pp. 378–407.~~

Pérez-Moreno, B. P., Sanz, J. L., Sudre, J., & Sigé, B~~.,~~. (1993). A theropod dinosaur from the Lower Cretaceous of southern France. *Revue de Paléobiologie*, *Volume spéciale 7*, 173–188.

Formatted: Font: Italic

Formatted: Font: Italic

Pol, D., & Powell, J. E~~.,~~. (2011). A new sebecid mesoeucrocodylian from the Rio Loro Formation (Palaeocene) of north-western Argentina. *Zoological Journal of the Linnean Society*, *163*, S7–S36.

Formatted: Font: Italic

Formatted: Font: Italic

Porfiri, J. D., Novas, F. E., Calvo, J. O., Agnolín, F. L., Ezcurra, M. D., & Cerda, I. A. (2014). Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. *Cretaceous Research*, *51*, 35–55. doi:10.1016/j.cretres.2014.04.007.

Formatted: Font: Italic

Formatted: Font: Italic

Posmoșanu, E~~.,~~. (2003). Iguanodontian dinosaurs from the Lower Cretaceous bauxite site from Romania. *Acta Palaeontologica Romaniae*, *4*, 431–439.

Formatted: Font: Italic

Formatted: Font: Italic

~~Porfiri, J.D., Novas, F.E., Calvo, J.O., Agnolín, F.L., Ezcurra, M.D., Cerda, I.A., 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. Cretaceous Research, 51, 35--55. doi:10.1016/j.cretres.2014.04.007.~~

Rabi, M., & Sebők, N~~.,~~. (2015). A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. *Gondwana Research*, *28*, 1197–1211. doi:10.1016/j.gr.2014.09.015.

Racey, A~~.,~~. (2009). Mesozoic red bed sequences from SE Asia and the significance of the Khorat Group of NE Thailand. In~~:~~ ~~Buffetaut,~~ E. Buffetaut, ~~Cuny,~~ G. Cuny, ~~Le Loeuff,~~ J. Le Loeuff, & ~~Suteethorn,~~ V. Suteethorn (Eds.), *Late Palaeozoic and Mesozoic Ecosystems in SE Asia* (pp. 41–67). ~~The~~ Geological Society, London, Special Publications, 315~~, pp. 41–67~~. doi: 10.1144/SP315.5.

Racey, A., & Goodall, J. G. S~~.,~~. (2009). Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. In~~:~~ ~~Buffetaut,~~ E. Buffetaut, ~~Cuny,~~ G. Cuny, ~~Le Loeuff,~~ J. Le Loeuff, & ~~Suteethorn,~~ V. Suteethorn (Eds.), *Late Palaeozoic and Mesozoic Ecosystems in SE Asia* (pp. 69–83). ~~The~~ Geological Society ~~of~~, London, Special Publications, 315~~, pp. 69–83~~. doi: 10.1144/SP315.6.

Rauhut, O. W. M~~.,~~. (2011). Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology*, *86*, 195–239.

Rauhut, O. W. M., & Werner, C~~.,~~. (1995). First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan. *Paläontologische Zeitschrift*, *69*~~(3/4)~~, 475–489.

Richter, U., Mudroch, A., & Buckley, L. G~~.,~~. (2013). Isolated theropod teeth from the Kem Kem Beds (Early Cenomanian) near Taouz, Morocco. *Paläontologische Zeitschrift*, *87*, 291–309.

Formatted: Left, Adjust space between Latin and Asian text, Adjust space between Asian text and numbers

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Royo-Torres, R., Cobos, A., Luque, L., Aberasturi, A., Espilez, E., Fierro, I., Gonzales, A., Mampel, L., & Alcalá, L~~., ~~. (2009). High European sauropod dinosaur diversity during Jurassic–Cretaceous transition in Riodeva (Teruel, Spain). *Palaeontology*, *52*, 1009–1027.

Sachs, S., & Hornung, J. J~~., ~~. (2013). Ankylosaur remains from the Early Cretaceous (Valanginian) of Northwestern Germany. *PLoS ONE*, *8(4)*, e60571. doi:10.1371/journal.pone.0060571.

Salgado, L., Canudo, J. I., Garrido, A. C., Ruiz-Omeñaca, J. I., Garcia, R. A., de la Fuente, M. S., Barco, J. L., & Bollati, R~~., ~~. (2009). Upper Cretaceous vertebrates from El Anfiteatro area, Río Negro, Patagonia, Argentina. *Cretaceous Research*, *30*, 767–784.

Sames, B., Cifelli, R. L., & Schudack, M. E~~., ~~. (2010). The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: New biostratigraphic results from ostracod correlations and early mammals, and their implications for paleontology and geology of the basin—An overview. *Earth-Science Reviews*, *101*, 207–224.

Sauvage, H. E~~., ~~. (1876). Notes sur les reptiles fossiles. *Bulletin de la Société Géologique de France*, *4*, 435–442.

Sauvage, H. E~~., ~~. (1882). Recherches sur les reptiles trouves dans le Gault de l'est du bassin de Paris. *Mémoires de la Société Géologique de France*, *2*, 1–42.

Săndulescu, M~~., ~~. (1984). *Geotectonica României* (p. 329). ~~Ed. Tehnică, ~~Bucharest~~, 329 pp:~~ Ed. Tehnică.

Seghedi, A~~., ~~. (2001). The North Dobrogea orogenic belt (Romania): a review. In~~: Ziegler, ~~P. A. Ziegler, ~~Cavazza, ~~W. Cavazza, ~~Robertson, ~~A. H. F. Robertson, & ~~Crasquin-Soleau, ~~S. Crasquin-Soleau (Eds.), *Peri-Tethys Memoir 6: Peri-Tethyan Rift/Wrench Basins and Passive Margins* (pp. 237–257). Paris: Mémoires de la Musée National d'Histoire Naturelle~~, Paris, pp. 237–257~~.

Sereno, P. C~~., ~~. (1999). Dinosaurian biogeography: vicariance, dispersal and regional

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

extinction. In~~:~~ ~~Tomida,~~ Y. Tomida, ~~Rich,~~ T. H. Rich, & ~~Vickers-Rich,~~ P. Vickers-Rich (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium* (pp. 249–257). Tokyo: National Science Museum Monographs, 15~~, Tokyo, pp. 249–257~~.

Sereno, P. C., & Brusatte, S. L~~.,~~. (2008). Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontologica Polonica*, *53*, 15–46.

Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., Sidor, C. A., Varricchio, D. J., & Wilson, J. A~~.,~~. (1996). Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, *272*, 986–991.

Shen, Y. B., & Mateer, N. J~~.,~~. (1992). An outline of the Cretaceous system in northern Xinjiang, western China. In~~:~~ ~~Mateer,~~ N. J. Mateer, & ~~Chen,~~ P. J. Chen (Eds.), *Aspects of Nonmarine Cretaceous Geology* (pp. 49–77).~~ China Ocean Press,~~ Beijing: China Ocean Press~~, pp. 49–77~~.

Simionescu, I.~~,~~ (1906). Note sur l'age des calcaires de Cernavoda (Dobrogea). *Annales Scientifiques de l'Université de Jassy*, *4(1)*, 1–3.

Simionescu, I.~~,~~ (1913). *Megalosaurus* aus der Unterkreide der Dobrogea. *Centralblatt für Mineralogie, Geologie und Paläontologie*, *1913(20)*, 686–687.

Sissingh, W.~~,~~ (1977). Biostratigraphy of Cretaceous calcareous nannoplankton. *Geologie en Mijnbouw*, *56*, 37–65.

Smith, J. B., Vann, D. R., & Dodson, P~~.,~~. (2005). Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record A*, *285A*, 699–736.

Stein, K., Csiki, Z., Curry Rogers, K., Weishampel, D. B., Redelstorff, R., Carballido, J. L., & Sander, P. M~~.,~~. (2010). Small body size and extreme cortical bone remodeling indicate

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences*, *107*, 9258–9263.

Stoica, M., & Csiki, Z~~.,~~. (2002). An earliest Cretaceous (Purbeckian) vertebrate fauna from Southern Dobrogea (southeastern Romania). In~~:~~ ~~Grigorescu,~~ D. Grigorescu, & ~~Csiki,~~ Z. Csiki (Eds.), *7th European Workshop on Vertebrate Palaeontology, Sibiu, Romania*~~,~~ (pp. 34). Bucharest: Ars Docendi.

Stovall, J. W., & Langston, W., Jr~~.,~~. (1950). *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *American Midland Naturalist*, *43*, 686–728.

Stromer, E~~.,~~. (1931). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîjestufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematischnaturwissenschaftliche Abteilung, Neue Folge 9*, 1–23.

Therrien, F., & Henderson, D. M~~.,~~. (2007). My theropod is bigger than yours … or not: estimating body size from skull length in theropods. *Journal of Vertebrate Paleontology*, *27*, 108–115.

Tong, H., Claude, J., Suteethorn, V., Naksri, W., & Buffetaut, E~~.,~~. (2009). Turtle assemblages of the Khorat Group (Late Jurassic–Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. In ~~Buffetaut,~~ E. Buffetaut, ~~Cuny,~~ G. Cuny, ~~Le Loeuff,~~ J. Le Loeuff, & ~~Suteethorn,~~ V. Suteethorn (Eds.), *Late Palaeozoic and Mesozoic Ecosystems in SE Asia* (pp. 141–151). ~~The~~ Geological Society, London, Special Publications, 315~~, pp. 141–151~~.

Torcida Fernández-Baldor, F., Canudo, J. I., Huerta, P., Montero, D., Pereda Suberbiola, X., & Salgado, L~~.,~~. (2011). *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. *Acta Palaeontologica Polonica*, *56*, 535–552.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Turculeț, I., & Brânzilă, M~~.,~~. (2012). *Muzeul colecțiilor paleontologice originale de la Universitatea "Alexandru Ioan Cuza" Iași* (p. 173). ~~Editura Universității "Alexandru Ioan Cuza" Iași,~~ Iași~~,~~: Editura Universităţii "Alexandru Ioan Cuza" Iaşi~~173 pp~~.

Turner, A. H., Makovicky, P. J., & Norell, M. A. (2012). A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History*, *371*, 1–206.

Turner, A. H., & Sertich, J. J. W~~.,~~. (2010). Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, *30(Supplement 1)*, 177–236.

~~Turner, A.H., Makovicky, P.J., Norell, M.A., 2012. A review of dromaeosaurid systematics and paravian phylogeny. Bulletin of the American Museum of Natural History 371, 1–206.~~

Vasile, Ș., & Csiki, Z~~.,~~. (2011). New Maastrichtian microvertebrates from the Rusca Montană Basin (Romania). *Oltenia. Studii și comunicări. Științele Naturii*, *27(1)*, 221–230.

Vickers-Rich, P., Rich, T. H., Lanus, D. R., Rich, L. S. V., & Vacca, R~~.,~~. (1999). "Big Tooth" from the Early Cretaceous of Chubut Province, Patagonia: a possible carcharodontosaurid. In~~:~~ ~~Tomida,~~ Y. Tomida, ~~Rich,~~ T. H. Rich, ~~Vickers-Rich, &~~ P. Vickers-Rich (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium* (pp. 85–88). Tokyo: National Science Museum Monographs, 15~~, Tokyo, pp. 85–88~~.

Vremir, M~~.,~~. (2010). New faunal elements from the Late Cretaceous (Maastrichtian) continental deposits of Sebeș area (Transylvania). *Terra Sebus. Acta Musei Sabesiensis*, *2*, 635–684.

Vullo, R., Néraudeau, D., & Lenglet, T~~.,~~. (2007). Dinosaur teeth from the Cenomanian of Charentes, western France: evidence for a mixed Laurasian-Gondwanan assemblage. *Journal of Vertebrate Paleontology*, *27*, 931–943.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Weishampel, D. B.~~,~~ (1990). Dinosaurian distribution. In~~: Weishampel,~~ D. B. Weishampel, ~~Dodson,~~ P. Dodson, ~~Osmólska,~~ & H. Osmólska (Eds.), *The Dinosauria* (pp. 63–140). ~~California University Press,~~ Berkeley, Los Angeles, Oxford~~Berkeley,~~: California University Press~~ pp. 63–140~~.

Formatted: Font: Italic

Weishampel, D. B., Barrett, P. M., Coria, R. A., Le Loeuff, J., Xu, X., Zhao, X-J., Sahni, A., Gomani, E. M., & Noto, C. R. (2004). Dinosaur distribution. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria. Second Edition* (pp. 517–606). Berkeley, Los Angeles, London: University of California Press.

Formatted: Font: Italic

Weishampel, D. B., Csiki, Z., Benton, M. J., Grigorescu, D., & Codrea, V. (2010). Palaeobiogeographic relationships of the Haţeg biota — Between isolation and innovation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *293*, 419–437.

Formatted: Font: Italic

Formatted: Font: Italic

Weishampel, D. B., Grigorescu, D., & Norman, D. B~~.,~~. (1991). The Dinosaurs of Transylvania. *National Geographic Research & Exploration*, *7(2)*, 196–215.

Formatted: Font: Italic

Formatted: Font: Italic

Weishampel, D. B., Jianu, C. M., Csiki, Z., & Norman, D. B. (2003). Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. *Journal of Systematic Palaeontology*, *1*, 65–123.

Formatted: Font: Italic

Formatted: Font: Italic

Weishampel, D. B., Norman, D. B., & Grigorescu, D~~.,~~. (1993). *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. *Palaeontology*, *36*, 361–385.

Formatted: Font: Italic

Formatted: Font: Italic

~~Weishampel, D.B., Jianu, C.M., Csiki, Z., Norman, D.B., 2003. Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. Journal of Systematic Palaeontology 1, 65–123.~~

~~Weishampel, D.B., Barrett, P.M., Coria, R.A., Le Loeuff, J., Xu, X., Zhao, X-J., Sahni, A., Gomani, E.M., Noto, C.R., 2004. Dinosaur distribution. In: Weishampel, D.B., Dodson, P.,~~

~~Osmólska, H. (Eds.), The Dinosauria. Second Edition. University of California Press, Berkeley, Los Angeles, London, pp. 517–606.~~

~~Weishampel, D.B., Csiki, Z., Benton, M.J., Grigorescu, D., Codrea, V., 2010. Palaeobiogeographic relationships of the Haţeg biota — Between isolation and innovation. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 419–437.~~

Williamson, T. E., & Brusatte, S. L~~.,~~. (2014). Small theropod teeth from the Late Cretaceous of the San Juan Basin, northwestern New Mexico and their implications for understanding latest Cretaceous dinosaur evolution. *PLoS ONE, 9(4)*, e93190. doi:10.1371/journal.pone.0093190.

Zarcone, G., Cillari, F. M. P., Stefano, P. D., Guzzetta, D., & Nicosia, U~~.,~~. (2010). A possible bridge between Adria and Africa: New palaeobiogeographic and stratigraphic constraints on the Mesozoic palaeogeography of the Central Mediterranean area. *Earth-Science Reviews, 103*, 154–162.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

Figure captions

Figure 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).

Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B. Current state of UAIC (SCM1) 615, mounted in a limestone holder.

Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B., distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).

Figure 4. Dental morphospace of the different theropod clades according to the results of the PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by Carcharodontosauridae. See further details of this analysis, as well as other quantitative analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant function analysis, phylogenetic analysis), in the Supplementary Material.

Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615 from Southern Dobrogea. Legend: 1 – *Veterupristisaurus*, ‘*Megalosaurus’ ingens*, Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator,* Spain, Barremian; 3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern

United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 – *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China, Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmayisaurus*, Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11 – *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan, Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 – Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant references, see text, *5.4.*). Palaeogeographic maps, courtesy of Ron Blakey (http://cpgeosystems.com/).

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

Zoltán Csiki-Sava[1*], Stephen L. Brusatte[2], Ștefan Vasile[1]

[1] Department of Geology, Faculty of Geology and Geophysics, University of Bucharest, 1 Nicolae Bălcescu Boulevard, 010041 Bucharest, Romania

[2] School of GeoSciences, University of Edinburgh, Grant Institute, James Hutton Road, Edinburgh, EH9 3FE, United Kingdom

* Corresponding author

zoltan.csiki@g.unibuc.ro

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 Hațeg 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 evolved 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 Aptian, illustrating the importance of palaeogeographic ties between these two realms during the largely mysterious early–mid Early Cretaceous.

Keywords

Southern Dobrogea; Valanginian; Carcharodontosauridae; cratonic Europe; palaeobiogeography

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 Early Cretaceous bauxite accumulations of Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997; Posmoșanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Haţeg, Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the dinosaur-dominated 'Hațeg 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 ‘Hațeg 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 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 split, but originated earlier, and perhaps in Europe, suggesting faunal interchange between Europe and Gondwana during the ‘dark ages’ of the early Early Cretaceous.

Abbreviations: UAIC – University “Alexandru Ioan Cuza”, Iași, Romania.

2. History of collecting and curation

Only two dinosaurian fossils are currently known from the cratonic areas of Romania: an isolated theropod tooth and an isolated caudal vertebral centrum. Both of these were reported from the Lower Cretaceous deposits of Southern Dobrogea (southeastern Romania; Csiki-Sava et al., 2013, see also below). Unfortunately, exact details of their discovery and places of origin are lost, a fact that can hinder an assessment of their age and interpretation of their phylogenetic and palaeobiogeographic significance. Our aim here is to gather and report all available information concerning the collecting of specimen UAIC (SCM1) 615, that is, the isolated theropod tooth reported by Simionescu (1913; Fig. 2A).

According to the existing information - unpublished museum labels and records, and the preliminary publication of Simionescu (1913) - specimen UAIC (SCM1) 615 was discovered in the surroundings of Cochirleni, a small village south of Cernavodă and close to the right bank of the Danube, in Southern Dobrogea, southeastern Romania (Fig. 1), probably shortly before 1913, the date of its publication by Simionescu (1913).

Although studied and preliminarily described by Simionescu, UAIC (SCM1) 615 was not collected by Simionescu personally. Instead, it was donated by a certain “de Tomas” (also mentioned as ”de Thomas” in the registry of the Hârșova Museum) to V. Cotovu from Hârşova (Central Dobrogea), a local teacher, archaeology and natural history aficionado, and amateur fossil collector (see, e.g., Covacef, 1995). Cotovu, described by Simionescu himself as the “zélé fondateur et directeur du muséum de Hârşova” (*enthusiastic founder and director of the Hârşova Museum*; Simionescu, 1906: p. 2), had previously provided fossil specimens from Southern Dobrogea for study to Simionescu, a nationally acknowledged popular science writer and scientist, whom Cotovu knew personally (Brânzilă, 2010). These circumstances are supported by the fact that in the original description, Simionescu figures the specimen as being accessioned in the “Regional-Museum von Harschowa” (*Hârşova Regional Museum*; Simionescu, 1913: p. 687, fig.1), a designation he also used to refer to other Dobrogean

specimens not collected by him first-hand (e.g., a specimen of '*Nautilus' pseudoelegans* from Cernavodă, or a fragmentary tooth-bearing palatal fragment referred to as '*Coelodus*' sp., also originating from Cochirleni; see Simionescu, 1906). Confirming this deduction, an isolated tooth appears accessioned in the old registry book of the Hârşova Museum (under specimen number 200) as "*Megalosaurus* cf. *superbus*", with the mention that it was "*described by Prof. Simionescu in the Centralblatt f. min. etc*.". This is also the case of the '*Coelodus'* sp. specimen from Cochirleni (specimen number 86), similarly clearly identified as being described by Simionescu in the registry book.

Both of these vertebrate remains from Dobrogea that were formerly part of the Hârşova Museum collections are currently accessioned in the palaeontology collections of the UAIC (Turculeț and Brânzilă, 2012), suggesting that, at one moment, several specimens were transferred there from the Hârşova Museum. Although no details are known about this transfer, it is probable that it took place right before (or when) the Hârşova Museum, including a part of its collections, was burned and largely destroyed during WWI, in 1916, a time when Simionescu still held a position at the UAIC.

After its original description, specimen UAIC (SCM1) 615 underwent a minor amount of damage (see below, Description). Also, at some point between its description in 1913 and the early 1960s (when the specimen was found in its present state in the collections of the UAIC by academic staff members who are still alive today and recall the discovery; I. Turculeț, personal communication, May 2013) it was glued into a limestone matrix holder, while it was obviously completely freed of the surrounding matrix when it was described and figured in 1913 (Fig. 2). The circumstances under which these alterations took place are unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the spring of 1944, the frontline between the German-Romanian and Soviet armies reached the Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

were packed in crates, and moved together with its personnel and other possessions to Zlatna, in the Apuseni Mountains (western Romania), to safeguard them from any potential damage. Mounting the specimen into the limestone stand would have been a quick way to stabilize it, as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă, personal communication, April 2103). If that was indeed the case, the mounting would have taken place without the knowledge of Simionescu, who left Iaşi and the UAIC in 1929, being invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă, 2010). Then again, however, Simionescu himself or staff of the Hârşova Museum might have re-mounted the tooth after its original description, or else the mounting might have taken place after the return of the collections to Iași, after WWII.

Unfortunately, it is not documented whether the mounting was made using the original matrix, or if a trough corresponding to the tooth outline was carved into a randomly chosen limestone block. The apparently excellent fit between the tooth and the depression housing it (Fig. 2B, 3) suggests that this operation was completed carefully, and accurate carving of a fake holder is difficult to reconcile with the rush accompanying the evacuation of the Iași University, in 1944. Alternatively, the presence of a hand-written old registration number on the specimen holder would support its early re-mounting, while still at the Hârşova Museum. As noted previously, the original Hârşova Museum registration number of the specimen was 200, which does not correspond to that currently written both on the limestone holder and on a paper sticker (204). However, according to the old collection registry of the Hârşova Museum, specimen numbers 201 through 225 were given to a series of “indeterminate (fossil) bone fragments” from the “Cochirleni quarries”. Thus, these specimens (now apparently lost) came from the same locality as the tooth, and they were collected and donated by the same person to the Museum who donated UAIC (SCM1) 615. There is, thus, a (albeit admittedly remote) possibility that the registration numbers were

mixed up during the re-mounting of the specimen, which in this case took place at an early date in the Hârşova Museum. If this is indeed the case, the limestone used as holder could have been the same as the original matrix of the specimen.

To conclude, the history of recovery and curation of the historically important dinosaurian specimen UAIC (SCM1) 615 is rather convoluted and clouded by many uncertainties. The exact date of discovery remains conjectural, and the exact place of the discovery (thus also the original geological context of the tooth) is even more ambiguous. The current state of the specimen, and especially its mounted status, suggest a curatorial history that produced a moderate amount of damage to, but also partially obscured the detailed morphology of the specimen. The convergence of such unfortunate events makes deciphering the age, identity and evolutionary significance of the specimen troublesome, although many lines of evidence, carefully considered, allow us to draw reasonable conclusions (see below).

3. Geological setting

According to the available collecting information, the isolated theropod tooth UAIC (SCM1) 615 was discovered at Cochirleni (sometimes noted more specifically as the "*Cochirleni quarry*" or "*Cokerleni quarry*"). Cochirleni is a small village in southwestern Dobrogea situated close to the right bank of the Danube, and about 9 km south of the main urban center of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).

Southern Dobrogea is a cratonic area corresponding to the southeastern corner of Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984; Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,

2010), researchers agree that it became integrated into the main European Craton towards the end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine: Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001; Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

The Precambrian basement of Southern Dobrogea is overlain by a flat-lying sedimentary cover that begins with the lowermost Palaeozoic and ends with the uppermost Neogene. The sedimentary succession is interrupted by a few major, as well as several less important, sedimentary hiatuses that separate 5 main sedimentary sequences corresponding to the Cambrian–Upper Carboniferous, the Permian–Triassic, the Middle Jurassic–Cretaceous, the Eocene–?Oligocene, and the middle Badenian (middle Miocene)–Upper Pliocene. The Palaeozoic and lower Mesozoic are known only from the subsurface of Southern Dobrogea, but Cretaceous and Cenozoic deposits have limited exposures along the main water courses of the region (Ionesi, 1994; Mutihac and Mutihac, 2010).

The outcropping Cretaceous in Southern Dobrogea is represented mainly by shallow marine, carbonate platform deposits in the lower part of the system, replaced by more open-water, chalky facies towards the later part of the period (e.g., Avram et al., 1993, 1996; Dragastan et al., 1998; Dinu et al., 2007); these crop out only as isolated patches along the main watercourses of the region (Fig. 1).

The Lower Cretaceous Series consists of several lithostratigraphic units with complex, partially overlapping and interfingering relationships (Dragastan et al., 1998, 2014). The lowest (and only artificially) outcropping unit is the Purbeck-type, siliciclastic-evaporitic Upper Kimmeridgian–Lower Berriasian Amara Formation that represents lagoonal to continental environments. This unit is covered by the shallow-marine, richly fossiliferous and locally reefal limestone-dominated Cernavodă Formation (restricted-open lagoonal to

carbonate platform, Upper Berriasian–Lower Hauterivian). A time-correlative unit of the Cernavodă Formation, the limestone-dolomitic Dumbrăveni Formation (Upper Berriasian–Lower Hauterivian), is restricted to the southeastern part of Southern Dobrogea. The Cernavodă and Dumbrăveni formations are covered unconformably by dominantly calcareous deposits with hippuritoid (‘pachyodont’) coquinas, small reefs and lens-like orbitolinid accumulations, referred to the Barremian–Lower Aptian Ostrov Formation by Dragastan et al. (1998), but to the Ramadan Formation (in part) by Avram et al. (1993, 1996). These deposits, formed in littoral to lagoonal and open reef terrace environments, are in turn capped by the fluvial-lacustrine, siliciclastic deposits of the Gherghina Formation, with Middle–Upper Aptian kaolinitic clays and thin coal intercalations. The Lower Cretaceous succession ends with the transgressive, glauconite-bearing, coastal to sublittoral siliciclastic deposits of the Cochirleni Formation (uppermost Aptian–Albian).

The Upper Cretaceous has a significantly more patchy development, mainly restricted to the eastern part of Southern Dobrogea, excepting the weakly glauconitic, chalky-sandy Peștera Formation (Lower Cenomanian) and the marly Dobromiru Formation (Upper Cenomanian) that cover the western-central parts of the area. The younger Cuza Vodă (Turonian), Murfatlar (Santonian–Lower-Middle Campanian), and Satu Nou (Upper Campanian) formations are dominantly chalky, suggesting the instalment of a relatively deeper, offshore depositional environment; neither of these units is known from western Southern Dobrogea.

In total, the Lower Cretaceous of Southern Dobrogea was deposited in a shallow marine, near-shore setting, fluctuating between carbonate platform, lagoonal, coastal-tidal flat, and continental environments (see Avram et al., 1996; Dragastan et al., 1998). Its main characteristic features, such as the observed lithological variability, the areal distribution of the different units, and the presence of several unconformities within the series, are all linked

to eustatic sea-level changes that affected the Southern Dobrogean territory during the Early Cretaceous (Dragastan et al., 1998). The main emergent land in the area was represented by the Central Dobrogean Massif, lying north of the study area, almost completely subaerially exposed and actively eroding during the Cretaceous. Consequently, shallow-marine to continental deposits are restricted mainly to the northern part of Southern Dobrogea, close to its boundary with the Central Dobrogean Massif (marked by the Capidava-Ovidiu Fault), and are replaced by more open marine deposits southward. As summarized above, several littoral, and even continental, sequences occur in this succession, including deposits in the Amara, Cernavodă, Ramadan (Avram et al., 1996) and Cochirleni formations, whereas the Gherghina Formation is purely continental, with occasional minor marine interbeds produced during short-term ingressions of the sea.

In the Cernavodă-Cochirleni area the outcropping Mesozoic is restricted to the Lower Cretaceous, and includes deposits belonging to the Cernavodă, Ostrov (or Ramadan), Gherghina, and Cochirleni formations. While the lower–middle part of the Cernavodă Formation is well exposed and widely distributed in this area, its upper part (the lower Hauterivian Vederoasa Member) is unevenly developed. This member is missing in the classical succession from Cernavodă-Hinog, on the right bank of the Danube (Dragastan et al., 1998), but was recently identified in the more eastern Cernavodă-lock section (Dragastan et al., 2014). Similarly, the Ostrov Formation is represented in the area only by its upper subunit (the Lower Aptian Lipniţa Member; Dragastan et al., 1998), covering unconformably and transgressively the Valanginian Alimanu Member of the Cernavodă Formation in the southern end of the Cernavodă-Hinog section (Dragastan et al., 1998), and the lower Hauterivian Vederoasa Member in the Cernavodă-lock section (Dragastan et al., 2014).

Northward of the Hinog area, Valanginian deposits of the Alimanu Member are overlain directly by the Middle–Upper Aptian continental deposits of the Gherghina

Formation. These continental deposits also cover the *Orbitolina*-bearing calcareous-clayey deposits of the Lipniţa Member towards the south, marking the advancement of emerged areas towards the central parts of Southern Dobrogea, including the Cernavodă-Cochirleni area, during this time interval (Avram et al., 1996). Marine conditions returned in the study area again in the latest Aptian, with a transgression marked by widespread deposition of the glauconitic, siliciclastic coastal to innermost shelf deposits of the Cochirleni Formation. These uppermost Aptian to Albian sands and sandstones cover transgressively all the underlying deposits, belonging to the Cernavodă, Ostrov, or Gherghina formations. Siliciclastic shallow-marine sedimentation continued into the Early Cenomanian, with the chalky-glauconitic deposits of the Peștera Formation.

4. Palaeontology

The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu (1913), who referred it to *Megalosaurus* cf. *superbus*, a taxon erected by Sauvage (1882) from the Gault (‘mid’-Cretaceous: Albian) of the Paris Basin, France. The Gault material described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it and the type species *M. bucklandi*.

The convoluted taxonomic history of *Erectopus superbus* was recently reviewed by Allain (2005), who established that both the isolated teeth first mentioned by Sauvage (1876) and the skeletal elements described by Sauvage (1882) belong to the same taxon, for which the name *Erectopus superbus* was retained. Allain (2005) regarded *Erectopus* as a member of

Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al. (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.” Accordingly, if we are following the original assessment of Simionescu (1913) but updating with contemporary taxonomy, the Cochirleni theropod tooth should now be considered referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to *Erectopus superb*us (or a close relative) was considered to be unsupported by positive evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B, 3), we provide here a detailed description of its morphology followed by a thorough comparative study of this tooth based on large datasets of theropod dental measurements and discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).

We note that in his review of Romanian dinosaurs, Grigorescu (2003) erroneously considered UAIC (SCM1) 615 as being referred by Simionescu to the taxon *Megalosaurus dunkeri* Kohen (sic; actually, *Megalosaurus dunkeri* Dames, 1884). This is clearly a simple misreading of Simionescu’s identification. Additionally, such a referral is also contradicted by the absence of mesial serrations in the holotype tooth of *M. dunkeri*, considered by Carrano et al. (2012) to represent an indeterminate theropod. The Dobrogea tooth, on the other hand, has mesial serrations (see below).

4.1. Age of UAIC (SCM1) 615

The age of UAIC (SCM1) 615 has been contentious, due to the uncertainties concerning its place of origin. Although it is often mentioned as originating from Cochirleni village (e.g., Grigorescu, 2003; Turculeț and Brânzilă, 2012), this has not been definitively established. According to the original report of Simionescu (1913), the tooth came from the upper part of

the Lower Cretaceous limestone succession exposed in the cliffs extending from Cernavodă to Cochirleni along the right bank of the Danube. The corresponding entry from the Hârșova Museum registry states that it was found in the 'Cochirleni quarry', a location that presently cannot be identified precisely. The only rocks to be quarried in the area are the calcareous deposits of either the Cernavodă or Ostrov formations, particularly the ones that crop out in the Danube bank cliffs between Cernavodă-Hinog-Cochirleni. Finally, although the mention 'Cochirleni' is usually considered to refer to Cochirleni village, it should be mentioned that the cliff-forming hill that extends between Cernavodă and Cochirleni is also known by the same name (Fig. 1). Taking all of this evidence into consideration, it is thus reasonable to conclude that the tooth was most likely found in the Lower Cretaceous limestone succession exposed in the Danube cliffs between Cernavodă and Cochirleni.

Based on the location of the discovery, in the upper part of the local limestone succession, and the age of the deposits from Cernavodă-Cochirleni known to him, Simionescu (1913) considered the tooth to be of Barremian age. Subsequently, the age of the tooth was given as Valanginian–Barremian (Weishampel, 1990; Weishampel et al., 2004) or Valanginian (e.g., Grigorescu, 2003), but without any supporting information.

New attempts have been made to more precisely constrain the age of UAIC (SCM1) 615. Dragastan et al. (2014) recently sampled the limestone matrix holder of the tooth, and reported from these samples an assemblage of foraminiferans, ostracods and microproblematicae (=*incertae sedis* microorganisms) that characterize their 'Biozone IX with *Meandrospira favrei*', of latest Valanginian age in the local lithostratigraphic scheme. In parallel, we also sampled the same limestone holder – a yellowish white, friable lime mudstone – that yielded a poor and badly preserved calcareous nannoplankton assemblage with *Watznaueria barnesiae, W. ovata, Nannoconus steinmanni*, *N. kamptneri*, *N. globulus*, *Calcicalathina sp*., *Speetonia colligata* and *Cyclagelosphaera deflandrei* (M. C. Melinte-

Dobrinescu, personal communication, November 2013), an assemblage that suggests a Berriasian–Hauterivian age of the limestone holder.

Since it is not clear if the limestone holder came from the same site as the tooth itself, we managed to take a second sample from the limestone matrix still partly filling the pulp cavity of the tooth, which must definitively be identical with the rocks the tooth was found in. This second, much smaller sample yielded only very scarce specimens of *Watznaueria barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in abundance during the Berriasian and, especially, the Valanginian.

In the nannoplankton succession reported previously by Avram et al. (1993) and derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu Member of the Cernavodă Formation. These assemblages were interpreted to represent the nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous of the Mecsek Mountains, Hungary, by Császár et al. (2000).

Together, all the available evidence (Simionescu's original account, geographic and geologic records, foraminifera, ostracods, microproblematicae, and calcareous nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member of the Cernavodă Formation, and it is most probably of late Valanginian age.

4.2. Description and comparisons

Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2, 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown

base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is remarkably well preserved, with the enamel in pristine condition. It preserves most of the crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5 mm missing in the apical region.

In its present state, the mesial edge and part of the mesial third of the tooth are embedded in the limestone holder (Fig. 2B), although the tooth was once removed (see above, History of collecting and curation; Fig. 2A). Accordingly, it is exposed so that all faces of the tooth are widely visible, including the root region, except for the mesial surface.

Only the basal-most part of the root is preserved, and it is more complete near the mesial margin (Fig. 3B, C). Here, broken areas around the crown-root contact area (cervix) reveal details of the pulp cavity development, as well as the pattern of the dentine thickness variation (Fig. 3B–D). The crown also exhibits a transverse break at about two-thirds of its length (not present so obviously in the original figure of the specimen in Simionescu, 1913), and adjacent to it, the distal carina is also slightly chipped distal to mid-length. The labial face is superficially split near this break (Fig. 3A), while a more prominent region of damage appears on the lingual face, where a large (13 x 5 mm), slightly triangular wedge is broken off, exposing the deeper parts of the dentine (Fig. 3C). The damage to the lingual side apparently occurred after the original description of the tooth (Fig. 2), an observation that is concordant with the complex curatorial history of the specimen.

The basal-most, exposed part of the mesial face lacks the enamel cover (Fig. 3C, D), suggesting that this area already belongs to the root region. The mesial edge of the preserved crown base appears to be wider than the distal one, and is largely rounded transversely. Accordingly, the basal cross-section is teardrop-shaped (lanceolate); it is rounded mesially, but narrows distally into a small carina (Fig. 3D). As mentioned above, the pulp cavity is

exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B). Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped (Fig. 3D).

The tooth is ziphodont and only very slightly recurved distally. The distal edge is nearly straight across its length, being very mildly concave in its basal half and slightly convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the tooth crown base. The mesial edge, as shown in the original publication of Simionescu (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually compressed (Fig. 3B), with a crown base ratio (CBR=CBW/CBL) of 0.56, within the normal range of variation of most theropods. This differs from the thinner teeth of some, but not all, carcharodontosaurids (CBR<0.50), and the much thicker incrassate teeth of derived tyrannosauroids and conical teeth of spinosaurids (CBR>0.75) (Sereno et al., 1996; Brusatte et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).

The crown cross-section is slightly asymmetrical labiolingually when it is seen in distal view. In this view, when the carina is facing directly distally, one side of the crown has a more pronounced bulge than its counterpart (about 8.5 mm wide, measured from the carina, vs. 6 mm on the other side; Fig. 3B); based on comparisons with the teeth of *Mapusaurus* (Coria and Currie, 2006), the more bulging side can be interpreted as the lingual one. This asymmetry diminishes apically, where both sides become about equally convex. The distal carina itself twists slightly sideways (labially) in apical direction, such that it is located closer

to the labial face where it terminates at the crown apex, and the lingual face of the denticles is exposed distally (Fig. 3B, F). This twist of the distal carina is accompanied by a similar outline of the lingual side; in distal view, this is somewhat convex basally, but becomes flat to slightly concave in the apical two-thirds of the crown. A similar S-shaped curvature of the crown, albeit more pronounced and different in details, was also reported in *Mapusaurus* and *Giganotosaurus* (Coria and Currie, 2006), and in indeterminate carcharodontosaurid teeth from Morocco (Richter et al., 2013).

The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with minute serrations across its entire preserved length; the denticles are proximodistally subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig. 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so it is not possible to determine whether the serrations continued over the apex of the tooth. There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the carina. Serration shape and size remain relatively constant across the carina, although the serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig. 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F). Changes in serration size are gradual across the carina, not sudden or sporadic.

Although they are all more or less rectangular in shape, the apical denticles are relatively shorter proximodistally than the more basal ones. Most of the denticles have slightly rounded, asymmetrically convex triangular tips, instead of being simply squarred-off, and they do not hook as in troodontids and to a lesser extent abelisaurids (Hendrickx and Mateus, 2014). Other denticles near the apex, however, show a faint concavity along their tips, giving them a bilobate aspect, although this is both less conspicuous and far less regularly developed than reported in *Tyrannotitan* (Novas et al., 2005). The denticles are

separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length. The interdenticular space between adjacent denticles is broad, measuring more than a third of the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These sulci are so short and indistinct that they are only visible under low angle light.

Little can be said about the mesial carina, as it is not visible in the current state of the specimen, buried in the limestone matrix. Based on the description of Simionescu (1913), however, it is covered across its length with minute serrations; these decrease in size towards the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles) per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus, 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii* where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*’ *superbus* (Sauvage, 1876, 1882) in this respect.

The external enamel surface exhibits two forms of ornamentation. First, the majority of the labial and lingual faces are covered by relatively smooth enamel that exhibits a subtle form of braided texture visible under low angle light (Fig. 3A, C, E). This texture is made up of a series of very faint, apico-basally running ridges; these are of unequal lengths, starting at different points of the crown height, but none extends the whole length of the crown. The two longest ridges are placed near the distal carina. The enamel is also finely granulated.

Second, near the carinae on both labial and lingual surfaces there are marginal undulations: wrinkles in the enamel that stand out in bas relief (Brusatte et al., 2007). These are much better preserved and visible near the distal carina, where they are so pronounced

that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly developed wrinkles are present along the crown height; in the basal half of the crown, the wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer than twice the space separating each undulation. The wrinkles project obliquely (in the mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal segment on the crown, and curve apically as they approach the carina (at about 45^{o}) with a tendency to become tangential to the distal edge. The wrinkles are especially well developed, prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig. 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm). Apically, however, the wrinkles are somewhat wider and longer, extending over about half of the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the crown in wrinkle development as well, these being better expressed on the more rounded, convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the presumed labial face, only some of the basal-most wrinkles, particularly the second and third one, appear well defined.

Towards the base of the crown a few of the wrinkles continue across the labial and lingual surfaces as very subtle transverse undulations. Most conspicuous of these is a 3.5 mm wide horizontal swelling that crosses the crown, at the level of wrinkles 2 and 3; this swelling is clearly visible on both sides of the crown (Fig. 3. A, C). There are no lateral flutes, apico-basal ridges, or longitudinal grooves on the labial or lingual faces, either in the centre of the tooth or paralleling the carinae. Instead, the labial and lingual faces are uniformly convex, giving the tooth its teardrop-shaped outline in cross section.

5. Discussion

5.1. *Identification of UAIC (SCM1) 615*

The isolated tooth from Cochirleni can be referred to Theropoda based on its large size, recurved and labiolingually compressed morphology, and presence of a continuous series of well-defined serrations on the distal carina.

Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are also known to posess remarkably theropod-like, laterally compressed and serrated teeth, not unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are significantly smaller than the Southern Dobrogean specimen, especially in the case of the Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest, caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615; moreover, these teeth are slightly conical and less laterally compressed than the Southern Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true denticles along their carinae) are reported in Europe only beginning in the Albian (Ősi et al., 2015), and these are both significantly smaller and different in morphology from the Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a theropod tooth.

We used four techniques to identify which type of theropod UAIC (SCM1) 615 likely belongs to (see also Supplementary Material).

First, we conducted a Principal Components Analysis (PCA) based on a large database that includes a broad and representative sample of theropod teeth. This dataset was compiled by Hendrickx et al. (2015a), which built upon the earlier studies of Smith et al.

(2005) and Larson and Currie (2013), and it or a similar version has been used in recent studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, 2014; Brusatte and Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL, CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to this dataset, the data were log-transformed prior to analysis, missing values for measurements were estimated with a mean value for that measurement from across the sample, and then a PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17 (Hammer et al., 2001).

In the resulting two dimensional morphospace (Fig. 4), UAIC (SCM1) 615 plots close to many teeth belonging to carcharodontosaurids, along with some teeth belonging to spinosaurids and tyrannosauroids. It falls within the convex hull (maximum morphospace occupation area) of carcharodontosaurids only, although it is closely outside of the edges of spinosaurid and tyrannosauroid space. It also falls within the 95% confidence interval ellipse for carcharodontosaurids, but not within the ellipse of any other group (Supplementary Information). This exercise indicates that UAIC (SCM1) 615 is most similar to carcharodontosaurids.

Secondly, we used the log-transformed dataset that we also used for the PCA to conduct a clustering analysis. We performed the analysis in PAST v2.17, using the paired group algorithm and the correlation similarity measure. In the resulting dendrogram, UAIC (SCM1) 615 groups with a handful of teeth belonging to carcharodontosaurids, tyrannosauroids, and *Allosaurus* (Supplementary Information).

Third, we used the tooth measurement database to conduct a discriminant analysis in PAST v3.0 (Hammer et al., 2001). This analysis uses pre-determined groups (in this case, taxonomic clusters) to create a morphospace in which these groups are maximally separated.

This allows teeth of unknown affinities, such as UAIC (SCM1) 615, to be classified according to which taxonomic group it is most similar to in this discriminant morphospace. In total, 67.79% of other teeth are classified correctly when they are treated as having uncertain affinities and their measurements are used to classify them in discriminant space, indicating that this exercise returns reasonable results. Our analysis classifies the Romanian tooth as a carcharodontosaurid. Furthermore, the analysis places UAIC (SCM1) 615 within the convex hulls for carcharodontosaurids and tyrannosauroids, and the 95% confidence ellipses for carcharodontosaurids, coelophysoids, and neovenatorids.

Fourth, we ran a phylogenetic analysis by including UAIC (SCM1) 615 in the discrete character dataset of theropod dental features published by Hendrickx and Mateus (2014). The Romanian specimen was scored as a lateral tooth in this analysis. The analysis was conducted in TNT (Goloboff et al., 2008), and resulted in 224 most parsimonious trees (686 steps, consistency index of 0.338, retention index of 0.566). The strict consensus topology is moderately well resolved and places the Romanian tooth as the sister taxon to *Carcharodontosaurus* (Supplementary Material). This sister taxon pair is recovered as the sister clade to a grouping of the derived carcharodontosaurids *Mapusaurus* and *Giganotosaurus*.

Several synapomorphies support the carcharodontosaurid affinities of UAIC (SCM1) 615. The sister group relationship with *Carcharodontosaurus* is supported by two features: a roughly straight distal margin of the crown (character 68) and pronounced marginal undulations in the enamel that are well visible in normal light (character 112). The broader clade of UAIC (SCM1) 615, *Carcharodontosaurus*, *Mapusaurus*, and *Giganotosaurus* (= Carcharodontosaurinae, as defined by Brusatte and Sereno, 2008, and Carrano et al., 2012) is linked by numerous characters, including: large teeth with a crown height greater than 6 cm (character 65), a bowed or sigmoid distal carina in distal view (character 82), marginal

undulations that are at least twice as long mesiodistally as the space separating each undulation (character 111), and marginal undulations present on both mesial and distal sides of the crown (character 113).

The Romanian specimen also lacks many keystone dental synapomorphies of other theropod clades, based on the clade diagnoses of Hendrickx and Mateus (2014) and other cladistic studies that include dental characters. UAIC (SCM1) 615 does not possess the hooked distal denticles of some Abelisauridae, the strongly labially deflected distal carina and pronounced transverse enamel undulations extending across the labial and lingual tooth faces of Ceratosauridae, the incrassate teeth with apicobasal enamel flutes and deeply veined enamel surface texture of Spinosauridae, and the large transverse undulations of some basal allosauroids (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of derived tyrannosauroids (Brusatte et al., 2010a) and the large and strongly hooked (or pointed) denticles of troodontids and therizinosauroids (e.g., Turner et al., 2012; Brusatte et al., 2014; Hendrickx and Mateus, 2014). The large size, as well as recurved and ziphodont shape of UAIC (SCM1) 615 is strikingly different from the non-ziphodont therizinosauroids, ornithomimosaurs, alvarezsauroids, and most troodontids, which have conical, leaf-shaped, or peg-like teeth (when teeth are present) (e.g., Holtz et al., 2004a; Turner et al., 2012; Brusatte et al., 2014). Finally, besides its remarkably large size, the presence of serrations indicates that UAIC (SCM1) 615 does not belong to groups such as alvarezsauroids, oviraptorosaurs, basal troodontids, or avialans, which have unserrated crowns (e.g., Turner et al., 2012; Hendrickx and Mateus, 2014).

In summary, the four analyses all support carcharodontosaurid affinities for UAIC (SCM1) 615. Both overall tooth proportions and discrete phylogenetic characters point to a carcharodontosaurid identification, and the discriminant function analysis and phylogenetic analysis both explicitly recover the tooth as a carcharodontosaurid. For this reason we refer

this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as recovered in our analysis, is congruent with results of previous analyses based on larger sets of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno, 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015), and offers some support for considering the Romanian carcharodontosaurid from Southern Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

Two final notes are worth adding. First, our analyses also incorporated carcharodontosaurids that are usually found to be basal within the clade, such as *Acrocanthosaurus* and *Eocarcharia* (e.g., Harris, 1998; Sereno and Brusatte, 2008; Carrano et al., 2012) as well as a host of other allosauroids, including members of Neovenatoridae (*Neovenator*, *Australovenator* and *Fukuiraptor*), a clade that is often recovered as sister-taxon to carcharodontosaurids within Carcharodontosauria (e.g., Benson et al., 2010; Carrano et al., 2012; but see Novas et al., 2013; Porfiri et al., 2014, for an alternate placement of neovenatorids in general). Both PCA and phylogenetic analysis clearly identified UAIC (SCM1) 615 as more closely comparable morphologically to derived carcharodontosaurids than to either basal carcharodontosaurids or to any other allosauroid subclade.

Second, our datasets also included teeth of *Erectopus*, the genus erected for ‘*Megalosaurus’ superbus* to which UAIC (SCM1) 615 was originally referred. Again, our analyses clearly indicate that there are no close morphological and morphometric similarities between the two, which is in accordance with the suggestion of Carrano et al. (2012) that *Erectopus* represents a non-carcharodontosaurid taxon, while our analysis identifies UAIC

(SCM1) 615 as a carcharodontosaurid. Instead, *Erectopus* groups with abelisauroids in the phylogenetic analysis. This is somewhat surprisingly, as Allain (2005) and Carrano et al. (2012) both identified *Erectopus* as a tetanuran. It should be noted, however, that Albian-aged abelisauroids are known from the same general area (eastern France) as that yielding the material referred to *Erectopus* (Accarie et al., 1995; Carrano and Sampson, 2008), raising the intriguing possibility that this taxon may represent an abelisauroid instead of an allosauroid tetanuran as suggested by Allain (2005) and Carrano et al. (2012). However, it must be remembered that this phylogenetic analysis is based on dental characters only, so it is probably more likely that *Erectopus* is a tetanuran with a dentition convergent to some extent with those of certain abelisauroids.

5.2. Body size of UAIC (SCM1) 615

One of the most salient and remarkable features of UAIC (SCM1) 615 is its large size. In the large and comprehensive sample of theropod teeth from our dataset, tooth size (estimated based on crown height – CH, and used as a rough proxy of body size) ranges from 2.2 mm (in the dromaeosaurid *Saurornitholestes* and the coelurosaur of uncertain affinities *Richardoestesia*) to 117.1 mm in the gigantic tyrannosauroid *Tyrannosaurus*. The Romanian specimen UAIC (SCM1) 615, with a CH of 85.5 mm, is ranked in the 60-80% maximum size (~ CH) range of the sample, and has a CH that is 73% of the largest tyrannosauroid teeth. Most of the teeth in the dataset (over 61% of the 966 measured teeth) are very small to small (less than 25 mm CH), and less than 10% of these fall in the 60-100% CH size categories. Teeth larger than UAIC (SCM1) 615 make up less than 5% of the total sample, and they represent only five taxa: the megalosaurid *Torvosaurus*, the tyrannosauroid *Tyrannosaurus*, the basal carcharodontosaurid *Acrocanthosaurus*, and the derived carcharodontosaurines *Carcharodontosaurus* and *Giganotosaurus*. Compared to other carcharodontosaurids, UAIC

(SCM1) 615 is smaller than the largest teeth of *Acrocanthosaurus* (9% difference), *Carcharodontosaurus* (20%), and *Giganotosaurus* (12.5%) in the dataset, but is 13% bigger than the largest tooth of *Mapusaurus*.

It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Sereno et al., 1996; Calvo and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn, corroborates growing evidence that very large body size was acquired very early in carcharodontosaurid history, since the earliest potential members of the clade are already of relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.

The inferred large body size of the South Dobrogean theropod is also remarkable as virtually all other dinosaur remains reported previously from Romania (both from the Early Cretaceous Cornet assemblage and the much later, end Cretaceous Haţeg Island fauna) are significantly smaller, and many have been interpreted as insular dwarfs (e.g., Weishampel et al., 1993, 2003; Benton et al., 2006, 2010; Stein et al., 2010; Ősi et al., 2014). Although other Romanian theropod dinosaurs were not particularly dwarfed (e.g. Brusatte et al., 2013), they were nonetheless small (Nopcsa, 1902; Csiki and Grigorescu, 1998; Csiki et al., 2010; Brusatte et al., 2013). This bias towards small bodied Romanian theropods was also

interpreted as a consequence of their insular habitat (Csiki and Grigorescu, 1998), as all previously reported theropod remains come from within the Carpathian Orogen, an area with an archipelago-type palaeogeography during the Cretaceous (Dercourt et al., 2000; Csontos and Vörös, 2004; Csiki-Sava et al., 2015). By contrast, UAIC (SCM1) 615 was found in shallow marine deposits bordering the emerged areas of Central Dobrogea, part of the stable cratonic areas of Europe and connected at least intermittently to the Ukrainean Shield since the Late Jurassic (Fig. 5A). Although cratonic Europe was also transformed into an archipelago of islands during much of the Cretaceous, these islands were often both larger in size and more stable in space and time than were the transient emerged areas of the Tethyan archipelagoes. As such, it is conceivable that the Southern Dobrogean carcharodontosaurid was less constrained by space or resource limitations than the Tethyan insular dinosaurs, allowing it to retain a large body size.

5*.3. UAIC (SCM1) 615 and Valanginian dinosaur distribution*

Besides documenting the presence of large-sized mainland carcharodontosaurids in the Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a significant gap in our knowledge on the composition and distribution of the Early Cretaceous dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these being known from the later part (Barremian–Albian) of that epoch; only around a dozen localities were listed from each age of the early part of the Early Cretaceous (Berriasian, Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al., 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards

western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no occurrences are known from the entire central, eastern and southern Europe for the Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).

Our identification of the Romanian tooth as a carcharodontosaurid documents the presence of this clade in Europe in the very early Cretaceous. This is significant, as carcharodontosaurids were widely distributed tens of millions of years later, in the middle Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see below). Despite the recent discoveries documenting that the clade was also present in North America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010; see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than previously thought and were a long-term component of the European mainland Early Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might have been already present between the cratonic, stable European mainland, with a dinosaur fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania (Benton et al., 2006).

This Valanginian carcharodontosaurid represents an important datapoint not only for the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a poorly documented age in dinosaur evolution, with very few precisely dated fossil occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known from Asia, some of which have debatable or controversial dates. These include sites in Japan (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992; Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare dinosaur remains of possible Valanginian (or ‘Neocomian’) age were also reported from southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g., Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli et al., 2014).

As one of the two known reports of Valanginian dinosaurs in Europe east of France, the Southern Dobrogean dinosaur record fills a huge palaeogeographic gap between the western European and the eastern Asian dinosaur faunas. Moreover, none of these early Early Cretaceous dinosaur assemblages from outside Europe include carcharodontosaurids (see below), as theropods are represented by coelurosaurians interpreted either as compsognathids (Gishlick and Gauthier, 2007) or basal ornithomimosaurs (Choiniere et al., 2012) in southern Africa, metriacanthosaurid allosauroids (‘sinraptorids’) in Thailand (Buffetaut and Suteethorn, 2007), and indeterminate allosauroids (Pérez-Moreno et al., 1993), non-

carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz, 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest that carcharodontosaurids had not achieved a wide geographic distribution by this point in time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.

Finally, the presence of the Cochirleni carcharodontosaurid might hint at the presence of palaeobiogeographic provinciality between the western and the eastern parts of Europe, partly mirroring those reported from the later part of the Late Cretaceous (e.g., Le Loeuff and Buffetaut, 1995; Weishampel et al., 2010; Ősi et al., 2012; Csiki-Sava et al., 2015). In the reasonably well sampled, and significantly better known, western European dinosaur faunas, Valanginian large carnivorous dinosaurs include non-carcharodontosaurid tetanurans (*Becklespinax*), as well as indeterminate allosauroids or indeterminate theropods (often described as '*Megalosaurus' dunkeri*, '*M.*' *insignis* or '*M.*' *oweni*), none of which can be referred positively to Carcharodontosauridae (Carrano et al., 2012). The apparently provincial geographic distribution of the large-bodied theropods suggests that some degree of faunal differentiation was occurring within the European mainland, most probably promoted by geographic distance. Notably, this intra-European differentiation in theropod assemblages appears to stand in contrast with the faunal homogeneity reported in the case of the ornithopods from the UK and Romania (e.g., Galton, 2009). It is important, however, to re-emphasize at this point that the Valanginian dinosaur fossil record is both exceedingly poor and patchy, even in Europe. Accordingly, further discoveries are needed to verify and support (or contradict) the presence of such a distribution pattern pointing to palaeobiogeographic provinciality inside Europe, as the one suggested by our carcharodontosaurid identification for UAIC (SCM1) 615.

5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography

Carcharodontosauridae were long considered as an exclusively Gondwanan group of theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996; Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Cau et al., 2013). This view started to change with the identification of the Early Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan one, was further supported by the discovery of definitive carcharodontosaurids in the Lower Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper Cretaceous of China (Brusatte et al., 2009, 2010b, 2012; Mo et al., 2014; Lü et al., 2016).

Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin of the carcharodontosaurids, followed by their dispersal across Laurasia and western Gondwana beginning at least by the Aptian (Fig. 5B), a scenario that is concordant with the tentatively suggested presence of early carcharodontosaurids in the Upper Jurassic of Tanzania, which are based on fragmentary specimens (Rauhut, 2011; Carrano et al., 2012). It is also concordant with the widespread appearance of carcharodontosaurids in the fossil record starting with the Aptian, when they are reported in Africa (*Eocarcharia*; Sereno and Brusatte, 2008), South America (Vickers-Rich et al., 1999), North America (*Acrocanthosaurus*; Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000 Eddy and Clarke, 2011), Europe (Canudo and Ruiz-Omeñaca, 2003; Pereda-Suberbiola et al., 2012), and eastern Asia (*Kelmayisaurus*; Brusatte et al., 2012; Mo et al., 2014; Lü et al., 2016).

During the Albian–Turonian, carcharodontosaurids became especially abundant and diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and South America (*Tyrannotitan*, *Giganotosautus*, *Mapusaurus*, alongside with indeterminate carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005; Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig. 5B). They were still present during this time interval in other continents, as well: in North America with *Acrocanthosaurus* until the Albian (D'Emic et al., 2012), in Europe until the Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).

After dominating terrestrial ecosystems at least in Africa, South America and eastern Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado, 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana. Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-Cenomanian deposits of South America to Carcharodontosaridae (e.g., Canudo et al., 2008; Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were reported to suggest the survival of carcharodontosaurids into the latest Cretaceous (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).

Contrasting with this rich and relatively continuous fossil record of Carcharodontosauridae starting with the Aptian, the first half of its evolutionary history is very poorly documented (Fig. 5B). Prior to the identification of UAIC (SCM1) 615, only two occurrences of pre-Aptian Cretaceous carcharodontosaurids were reported, one from the Barremian of Spain (Ortega et al., 2010; Gasca et al., 2014) and the other from the Barremian of Thailand (Buffetaut and Suteethorn, 2012). The Early Cretaceous *Kelmayisaurus* from Xinjiang, western China, was recognized as a carcharodontosaurid of possibly ?Valanginian to Aptian in age by Brusatte et al. (2012), but the deposits yielding these remains (the Lianmugin, or Lianmuxin, Formation of the Tugulu Group) were dated as Aptian–Albian by Eberth et al. (2001; see also Tong et al., 2009). An important temporal gap – of about 20 to 28 millions of years, according to the dates in Gradstein et al. (2012) – thus stretched between the oldest, tentatively assigned carcharodontosaurids from the Oxfordian–Tithonian of Tanzania, including the formally erected *Veterupristisaurus* (Rauhut, 2011; see also Carrano et al., 2012), and those that started to appear in the fossil record in the Barremian and then spread widely during the Aptian. Referral of UAIC (SCM1) 615 to Carcharodontosauridae partially fills this frustrating gap, effectively halving this shadowy period in the evolutionary history of the group.

Furthermore, our analyses tentatively cluster the Dobrogean theropod with the derived members of the Carcharodontosaurinae to the exclusion of the more basal, but significantly younger non-carcharodontosaurine carcharodontosaurids *Eocarcharia* and *Acrocanthosaurus*. If this placement is correct, then the Romanian tooth indicates that Carcharodontosaurinae diverged from other carcharodontosaurids considerably earlier than hitherto recognized.

The previously known fossil record of the clade suggested that Carcharodontosaurinae originated sometime between the Aptian and Albian, as basal carcharodontosaurids (*Acrocanthosaurus*, *Concavenator*, *Eocarcharia*) were moderately diverse in the Barremian–Aptian, followed by the appearance of many fossils of carcharodontosaurines beginning in the Albian (Fig. 5B). The proposed affinities of the oldest carcharodontosaurid material – including isolated teeth referred to as '*Megalosaurus*' *ingens* – from the east African Upper

Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut, 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very large size and dental morphology characterizing it) well before the Albian, during or even before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.

Besides shifting the emergence of the carcharodontosaurines earlier in time, identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting palaeobiogeographic implications. As already noted, recent discoveries show that Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g., Novas et al., 2005), with the identification of its widespread, Pangaean distribution during the late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999; Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014). However, within Carcharodontosauridae itself, some palaeogeographic patterns have been widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al., 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as previously all its recognized members were restricted strictly to either Africa (Stromer, 1931; Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995; Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of Carcharodontosaurinae were still adhering to patterns of continental fragmentation and vicariant evolution, with a basal split between the Albian–Cenomanian African *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

This scenario is now challenged by our finding that the Southern Dobrogean carcharodontosaurid UAIC (SCM1) 615 may nest inside Carcharodontosaurinae. If true, such an affinity would suggest that the origin of Carcharodontosaurinae was not a southern, vicariant by-product of the Gondwana-Laurasia separation, a major palaeogeographic event that is considered to have been well underway by the end of the Jurassic, and essentially completed by the mid-Early Cretaceous (see Weishampel et al., 2010). Indeed, during this time palaeogeographic connections and faunal interactions were virtually non-existent between the northern Tethyan (European) and southern Tethyan (western Gondwanan, but essentially African) areas of the Mediterranean (e.g., Canudo et al., 2009), which makes a vicariant hypothesis intuitive. However, if the Romanian tooth represents a carcharodontosaurine, then it implies a much more complicated palaeogeographic history of the clade, which is not so clearly linked to continental breakup.

The palaeogeographic position of the Southern Dobrogean carcharodontosaurine in cratonic Europe, north of the Neo-Tethys, together with its significantly older age compared to other carcharodontosaurines, could indicate that separation of the carcharodontosaurine lineage took part in Europe and not in western Gondwana as previously assumed. This would also mean that representatives of this lineage were subsequently – after the Barremian – introduced to Africa and South America via trans-Tethyan dispersal, most probably at a time when faunal interactions between the southern and northern margins of the Mediterranean Tethys were resumed, after the early Barremian (Canudo et al., 2009).

Alternatively, it can be hypothesized that appearance of carcharodontosaurines in Southern Dobrogea is a consequence of southern immigration originating in western Gondwana, often considered the place of origin for this clade. However, this scenario has several potential caveats. Although Europe has been considered as forming part of a larger Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín, 2012), and occasional trans-Tethyan faunal connections have been recognized between Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage, 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place during the 'Neocomian' (Berriasian–Hauterivian) time interval.

More recently, some potential evidence has emerged for Gondwana-to-Europe interchange during the 'Neocomian'. The presence of the basal rebbachisaurid *Histriasaurus* (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as indicative of very early and very rapid northward dispersal of this clade from western Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of this particular dispersal event was even constrained to the Berriasian–Valanginian time interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive transportation mechanism ('Noah's Ark'; McKenna, 1973) for basal rebbachisaurids after its separation from mainland Africa (e.g., Torcida Fernández-Baldor et al., 2011). Furthermore, the palaeogeographical separation between Africa and Adria (and thus the effective movement of the presumed ark) is considered to be at most an incipient one during the Early Cretaceous by Bossellini (2002) and Zarcone et al. (2010), with spatial continuity still present between the two landmasses, while deep-water basins continued to separate Adria from the European Craton. Accordingly, although the presence of *Histriasaurus* can represent a case of northward range extension of rebbachisaurids during the Berriasian–Valanginian, it took place not strictly speaking into Europe, but only reached the northernmost extremity of Adria, a northerly peninsular extension of the African mainland. It was only starting with the Barremian that rebbachisaurids dispersed as far north as the European cratonic areas, including Iberia and the British Isles (Mannion, 2009; Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011), a time when faunal interchanges between Europe and Africa are considered to have been well underway (e.g., Gheerbrant and Rage, 2006; Canudo et al., 2009).

Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant of the European mainland. It is thus unclear to what extent the example of rebbachisaurid range extension into (present-day) Europe during the early Early Cretaceous, as potentially testified by the discovery of the Croatian taxon, would also be applicable for the Southern Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are very different, and that faunal connections during this time interval are not documented between the African and European cratons as already pointed out by Gheerbrant and Rage (2006).

Absence of documented faunal interactions weakens support for a scenario of south-to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the Cretaceous, and would argue instead for a local, European development to explain the presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian presence of carcharodontosaurids in Europe is also consistent with their appearance in the Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in North America likely requires the presence of pre-Aptian members of the clade in Europe, since faunal exchanges between these two landmasses are known to have been halted before the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western Gondwana. The causes of these distribution patterns remain as yet unknown, and further support – in the form on new carcharodontosaurid discoveries from the early-middle part of the Early Cretaceous – is required to better uphold such a scenario.

We finally reiterate that if the Romanian tooth does not belong to a carcharodontosaurine, but instead is artefactually grouping with them in the phylogenetic analysis because of the very incomplete nature of the material, then the traditional story of Carcharodontosaurinae as a product of vicariant evolution driven by the breakup of Pangea will remain strongly supported. However, even in such case UAIC (SCM1) 615 would still record the presence of early-occuring large carcharodontosaurid theropods with a very characteristic carcharodontosaurine-type dentition in the eastern part of the European craton, adding to known early Early Cretaceous theropod (and dinosaur) diversity, and potentially documenting dinosaur faunal provinciality in Europe and worldwide.

6. Conclusions

We re-describe and interpret the affinities of one of the most significant historical dinosaurian specimens of Romania, an isolated but well-preserved theropod tooth from Southern Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth, while the available evidence – including novel calcareous nannoplankton sampling – supports its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this record advances our understanding of European dinosaur distribution during the early Early Cretaceous, and also fills an important palaeogeographic gap between Western European and Eastern Asian dinosaurian assemblages of the Valanginian.

Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a possible member of Carcharodontosaurinae, a subclade of derived and gigantic carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean specimen documents the emergence of Carcharodontosaurinae earlier than previously recognized, thus also indicating an earlier acquisition of their characteristically large size. Based on currently known palaeogeographic and chronostratigraphic constraints on the evolution of Carcharodontosauridae, it appears that not only did this clade have a wide distribution, but that crucial events of its evolutionary history such as the emergence of the derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia split, as was formerly suggested. In such a case, instead of endemic evolution the emergence of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into western Gondwana adds further support for the presence of important palaeogeographic ties between the two realms during the second half of the Early Cretaceous.

Acknowledgements

This research was supported by the National Research Council of Romania (CNCS) grant PN-IIID-PCE-2011-3-0381 and a Sepkoski grant of the Paleontological Society for Z.Cs.-S.

S.L.B. is supported by a Marie Curie Career Integration Grant EC630652, the Division of Paleontology of the American Museum of Natural History, and the School of GeoSciences of the University of Edinburgh. He thanks Mátyás Vremir, Radu Totoianu, and Mark Norell for many hours of fun discussion on Romanian fossils, and for supporting his work and travel in Romania. We thank Mihai Brânzilă and Paul Țibuleac (UAIC) for access to the specimen, for allowing us to collect samples for the nannoplankton analyses, and for their help and collegiality during our visit to Iași, as well as Ilie Turculeț for sharing information about the history of the specimen. Mihaela C. Melinte-Dobrinescu has gracefully analyzed the nannoplankton samples derived from UAIC (SCM1) 615; her contribution was essential in assessing the age of the specimen. Finally, we thank the reviewers Eric W.A. Mulder (Denekamp, the Netherlands) and Xabier Pereda-Suberbiola (Bilbao, Spain), as well as Associated Editor Elena Jagt-Yazykova, for their useful comments and suggestions that helped improve previous versions of the manuscript.

References

Accarie, H., Beaudoin, B., Dejax, J., Friès, G., Michard, J. G., & Taquet, P. (1995). Découverte d'un dinosaure théropode nouveau (*Genusaurus sisteronis* n. g., n. sp.) dans l'Albien marin de Sisteron (Alpes-de-Haute-Provence, France) et extension au Crétacé inférieur de la lignée cératosaurienne. *Comptes Rendus de l'Académie des Sciences Paris, IIa 320*, 327–334.

Allain, R. (2002). Discovery of a megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology, 22*, 548–563.

Allain, R. (2005). The enigmatic theropod dinosaur *Erectopus superbus* (Sauvage, 1882) from the Lower Albian of Louppy-le-Chateau (Meuse, France). In K. Carpenter (Ed.), *The Carnivorous Dinosaurs* (pp. 72–86). Bloomington: Indiana University Press.

Avram, E., Costea, I., Dragastan, O., Muţiu, R., Neagu, T., Şindilar, V., & Vinogradov, C. (1996). Distribution of the Middle-Upper Jurassic and Cretaceous facies in the Romanian eastern part of the Moesian Platform. *Revue Roumaine de Géologie, 39-40*, 3–33.

Avram, E., Szasz, L., Antonescu, E., Baltreș, A., Iva, M., Melinte, M., Neagu, T., Rădan, S., & Tomescu, C. (1993). Cretaceous terrestrial and shallow marine deposits in northern South Dobrogea (SE Romania). *Cretaceous Research, 14*, 265–305.

Azevedo, R. P. F. de, Simbras, F. M., Furtado, M. R., Candeiro, C. R. A., & Bergqvist, L. P. (2013). First Brazilian carcharodontosaurid and other new theropod dinosaur fossils from the Campanian-Maastrichtian Presidente Prudente Formation, São Paulo State, southeastern Brazil. *Cretaceous Research, 40*, 131–142.

Benson, R. B. J., Barrett, P. M., Powell, H. P., & Norman, D. B. (2008). The taxonomic status of *Megalosaurus bucklandii* (Dinosauria, Theropoda) from the Middle Jurassic of Oxfordshire, UK. *Palaeontology, 51*, 419–424.

Benson, R. B. J., Carrano, M. T., & Brusatte, S. L. (2010). A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften, 97*, 71–78.

Benton, M. J., Cook, E., Grigorescu, D., Popa, E., & Tallódi, E. (1997). Dinosaurs and other tetrapods in an Early Cretaceous bauxite-filled fissure, northwestern Romania. *Palaeogeography, Palaeoclimatology, Palaeoecology, 130*, 275–292.

Benton, M. J., Csiki, Z., Grigorescu, D., Redelstorff, R., Sander, M., Stein, K., & Weishampel, D. B. (2010). Dinosaurs and the island rule: the dwarfed dinosaurs from Haţeg Island. *Palaeogeography, Palaeoclimatology, Palaeoecology, 293*, 438–454.

Benton, M. J., Minter, N. J., & Posmoșanu, E. (2006). Dwarfing in ornithopod dinosaurs from the Early Cretaceous of Romania. In Z. Csiki (Ed.), *Mesozoic and Cenozoic Vertebrates and Paleoenvironments; Tributes to the Career of Prof. Dan Grigorescu* (pp. 79–87). Bucharest: Ars Docendi.

Blows, W. T., & Honeysett, K. (2014). First Valanginian *Polacanthus foxii* (Dinosauria, Ankylosauria) from England, from the Lower Cretaceous of Bexhill, Sussex. *Proceedings of the Geologists' Association*, *125*, 233–251.

Bosselini, A. (2002). Dinosaurs ‘‘re-write’’ the geodynamics of the eastern Mediterranean and the paleogeography of the Apulia Platform. *Earth-Science Reviews*, *59*, 211–234.

Brânzilă, M. (ed.) (2010). *Academicianul Ion Simionescu - savant şi dascăl al neamului* (p. 182). Iaşi: Ed. Universităţii "Alexandru Ioan Cuza".

Brusatte, S., Benson, R. B. J., Carr, T. D., Williamson, T. E., & Sereno, P. C. (2007). The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology, 27,* 1052–1056.

Brusatte, S. L., Benson, R. B. J., Chure, D. J., Xu, X., Sullivan, C., & Hone, D. W. E. (2009). The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. *Naturwissenschaften, 96,* 1051–1058.

Brusatte, S. L., Benson, R. B. J., & Xu, X. (2012). A reassessment of *Kelmayisaurus petrolicus*, a large theropod dinosaur from the Early Cretaceous of China. *Acta Palaeontologica Polonica*, *57*, 65–72.

Brusatte, S. L**.**, & Clark, N. D. L. (2015). Theropod dinosaurs from the Middle Jurassic (Bajocian-Bathonian) of Skye, Scotland. *Scottish Journal of Geology*, *51*, 157–164. doi: 10.1144/sjg2014-022

Brusatte, S., Chure, D. J., Benson, R. B. J., & Xu, X. (2010b). The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Asia. *Zootaxa*, *2334*, 1–46.

Brusatte, S. L., Lloyd, G. T., Wang, S. C., & Norell, M. A. (2014). Gradual assembly of avian body plan culminated in rapid rates of evolution across the dinosaur-bird transition. *Current Biology*, *24*, 2386–2392.

Brusatte, S. L., Norell, M. A., Carr, T. D., Erickson, G. M., Hutchinson, J. R., Balanoff, A. M., Bever, G. S., Choiniere, J. N., Makovicky, P. J., & Xu, X. (2010a). Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science*, *329*, 1481–1485.

Brusatte, S. L., & Sereno, P. C. (2007). A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology*, *27*, 902–916.

Brusatte, S. L., & Sereno, P. C. (2008). Phylogeny of Allosauroidea (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Palaeontology*, *6*, 155–182.

Brusatte, S. L., Vremir, M., Csiki-Sava, Z., Turner, A. H., Watanabe, A., Erickson, G. M., & Norell, M. A. (2013). The osteology of *Balaur bondoc*, an island-dwelling dromaeosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Romania. *Bulletin of the American Museum of Natural History*, *374*, 3–100. doi: 10.1206/798.1

Buckland, W. (1824). Notice on the *Megalosaurus* or great fossil lizard of Stonesfield. *Transactions of the Geological Society*, *21*, 390–397.

Buffetaut, E., & Suteethorn, V. (1998). Early Cretaceous dinosaurs from Thailand and their bearing on the early evolution and biogeographical history of some groups of Cretaceous dinosaurs. In S. G. Lucas, J. I. Kirkland, & J. W. Estep (Eds.), *Lower and Middle Cretaceous*

Terrestrial Ecosystems (pp. 205–210), New Mexico Museum of Natural History and Science Bulletin, 14.

Buffetaut, E., & Suteethorn, V. (2007). A sinraptorid theropod (Dinosauria: Saurischia) from the Phu Kradung Formation of northeastern Thailand. *Bulletin de la Société Géologique de France*, *178*, 497–502.

Buffetaut, E., & Suteethorn, V. (2012). A carcharodontid theropod (Dinosauria, Saurischia) from the Sao Khua Formation (Early Cretaceous, Barremian) of Thailand. In R. Royo-Torres, F. Gascó, & L. Alcalá (Eds.), *10th Annual Meeting of the European Association of Vertebrate Palaeontologists* (pp. 27–30). Teruel: ¡Fundamental!, 20.

Calvo, J. O., & Coria, A. (1998). New specimen of *Giganotosaurus carolinii* (Coria & Salgado, 1995), supports it as the largest theropod ever found. *Gaia*, *15*, 117–122.

Calvo, J. O., Gandossi, P., & Porfiri, J. D. (2006). Dinosaur faunal replacement during Cenomanian times in Patagonia, Argentina. In: S. E. Evans, & P. M. Barrett (Eds.), *9th Mesozoic Terrestrial Ecosystems and Biota* (pp. 17–20). Manchester, UK.

Canale, J. I., Scanferla, C. A., Agnolin, F. L., & Novas, F. E. (2009). New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften, 96*, 409–414.

Canale, J. I., Novas, F. E., & Pol, D. (2015). Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. *Historical Biology*, *27*, 1–32. doi: 10.1080/08912963.2013.861830.

Candeiro, C. R. A., Fanti, F., Therrien, F., & Lamanna, M. C. (2011). Continental fossil vertebrates from the mid-Cretaceous (Albian-Cenomanian) Alcântara Formation, Brazil, and their relationship with contemporaneous faunas from North Africa. *Journal of African Earth Sciences, 60*, 79–92.

Canudo, J. I. Barco, J. L., Pereda Suberbiola, X., Ruiz-Omeñaca, J. I., Salgado, L., Torcida Fernández-Baldor, F., & Gasulla, J. M. (2009). What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. *Bulletin de la Société Géologique de France, 180*, 5–11.

Canudo, J. I., Filippi, L. S., Salgado, L., Garrido, A. C., Cerda, I. A., Garcia, R., & Otero, A. (2008). Theropod teeth associated with a sauropod carcass in the Upper Cretaceous (Plottier Formation) of Rincón de los Sauces. In Colectivo Arqueológico y Paleontológico de Salas de los Infantes (Ed.), *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno* (pp. 321–330). Salas de los Infantes, Burgos.

Canudo, J. I., & Ruiz-Omeñaca, J. I. **(**2003). Los restos directos de dinosaurios teropódos (excluyendo Aves) en España. *Ciencias de la Tierra 26*, 347–373.

Carballido, J. L., Salgado, L., Pol, D., Canudo, J. I., & Garrido, A. (2012). A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. *Historical Biology*, *24*, 631–654.

Carrano, M. T., Benson, R. B. J., & Sampson, S. D. (2012). The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, *10*, 211–300.

Carrano, M. T., & Sampson, S. D. (2008). The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology, 6*, 183–236.

Carvalho, I. S., Campos, A. C. A., & Nobre, P. H. (2005). *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research*, *8,* 11–30.

Casal, G., Candeiro, C. R. A., Martinez, R., Ivany, E., & Ibiricu, L. (2009). Dientes de Theropoda (Dinosauria: Saurischia) de la Formación Bajo Barreal, Cretácico Superior, Provincia del Chubut, Argentina. *Géobios*, *42*, 553–560.

Cau, A., Dalla Vecchia, F. M., & Fabbri, M. (2013). A thick-skulled theropod (Dinosauria, Saurischia) from the Upper Cretaceous of Morocco with implications for carcharodontosaurid cranial evolution. *Cretaceous Research*, *40*, 251–260.

Choiniere, J. N., Forster, C. A., & De Klerk, W. J. (2012). New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation in South Africa. *Journal of African Earth Sciences*, *71–72*, 1–17.

Chure, D. J., Manabe, M., Tanimoto, M., & Tomida, Y. (1999). An unusual theropod tooth from the Mifune Group (Late Cenomanian to Early Turonian), Kumamoto, Japan. In Y. Tomida, T. H. Rich, & P. Vickers-Rich (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium* (pp. 291–296). Tokyo: National Science Museum Monographs, 15.

Cifelli, R. L., Davis, B. M., & Sames, B. (2014). Earliest Cretaceous mammals from the western United States. *Acta Palaeontologica Polonica, 59,* 31–52. doi:10.4202/app.2012.0089.

Cobos, A., Lockley, M. G., Gascó, F., Royo–Torres, R., & Alcalá, L. (2014). Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology, 399,* 31–41. doi: 10.1016/j.palaeo.2014.02.008.

Cobos, A., Royo-Torres, R., Luque, L., Alcalá, L., & Mampel, L. (2010). An Iberian stegosaurs paradise: The Villar del Arzobispo Formation (Tithonian–Berriasian) in Teruel (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology, 293*, 223–236.

Codrea, V., Godefroit, P., & Smith, T. (2012). First discovery of Maastrichtian (latest Cretaceous) terrestrial vertebrates in Rusca Montană Basin (Romania). In P. Godefroit (Ed.) *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems* (pp. 570–581). Bloomington: Indiana University Press.

Codrea, V., Vremir, M., Jipa, C., Godefroit, P., Csiki, Z., Smith, T., & Fărcaş, C. (2010). More than just Nopcsa's Transylvanian dinosaurs: A look outside the Haţeg Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology 293*, 391–405. doi: 10.1016/j.palaeo.2009.10.027.

Colbert, E. H. (1946). *Sebecus,* representative of a peculiar suborder of fossil Crocodilia from Patagonia. *Bulletin of the American Museum of Natural History, 87(4),* 217–270.

Coria, R. A., & Currie, P. J. (2006). A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, *28*, 71–118.

Coria, R. A, & Salgado, L. (1995). A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature*, *377*, 224–226.

Coria, R. A., & Salgado, L. (2005). Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. In G. D. Veiga, L. A. Spalletti, J. A. Howell, & E. Schwartz (Eds.), *The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics* (pp. 317–327). Geological Society, London, Special Publications, 252.

Covacef, Z. (1995). Pionieri ai culturii românești în Dobrogea; Ioan Cotovu și Vasile Cotovu. *Analele Dobrogei*, *I(1)*, 127–134.

Császár, G., Kollányi, K., Lantos, M., Lelkes, G., & Tardiné Filácz, E. (2000). A Hidasivölgyi Márga Formáció kora és képzõdési környezete. *Földtani Közlöny*, *130*, 695–723.

Csiki, Z., & Grigorescu, D. (1998). Small theropods of the Late Cretaceous of the Haţeg Basin (Western Romania) - an unexpected diversity at the top of the food chain. *Oryctos*, *1*, 87–104.

Csiki, Z., Vremir, M., Brusatte, S. L., & Norell, M. A. (2010). An aberrant island-dwelling theropod dinosaur from the Late Cretaceous of Romania. *Proceedings of the National Academy of Sciences*, *107*, 15357–15361.

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., & Brusatte, S. L. (2015). Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *Zookeys, 469*, 1–161. doi: 10.3897/zookeys.469.8439.

Csiki-Sava, Z., Codrea, V., & Vasile, Ș. (2013). Early Cretaceous dinosaur remains from Dobrogea (southeastern Romania). In L. Picot (Ed.), *Abstracts, 11th Annual Meeting of the European Association of Vertebrate Palaeontologists* (pp. 28). Villers-sur-Mer, France.

Csontos, L., & Vörös, A. (2004). Mesozoic plate tectonic reconstruction of the Carpathian region. *Palaeogeography, Palaeoclimatology, Palaeoecology, 210,* 1–56. doi: 10.1016/j.palaeo.2004.02.033.

Currie, P. J., & Carpenter, K. (2000). A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas, 22*, 207–246.

Currie, P. J., Rigby, J. K., & Sloan, R. E. (1990). Theropod teeth from the Judith River Formation of southern Alberta, Canada. In K. Carpenter, & P. J. Currie (Eds.), *Dinosaur Systematics: Approaches and Perspectives* (pp. 107–125). Cambridge, Boston: Cambridge University Press.

Dalla Vecchia, F. M. (1998). Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (Upper Hauterivian/Lower Barremian) limestones of SW Istria (Croatia). *Geologia Croatica, 5*, 105–134.

Dames, W. (1884). *Megalosaurus dunkeri. Sitzungberichte Gesellschaft Naturforschender Freunde zu Berlin, 1884*, 186–188.

De Klerk, W. J., Forster, C. A., Sampson, S. D., Chinsamy, A., & Ross, C. F. (2000). A new coelurosaurian dinosaur from the Early Cretaceous of South Africa. *Journal of Vertebrate Paleontology, 20*, 324–332.

D'Emic, M. D., Melstrom, K. M., & Eddy, D. R. (2012). Paleobiology and geographic range of the large-bodied Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *333–334*, 13–23.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M., Cadet, J. P., Crasquin, S., & Săndulescu, M. (Eds.) (2000). *Atlas Peri-Tethys Palaeogeographical Maps* (269 p). Paris: CCGM/CGMW .

Dinu, C., Grădinaru, E., Stoica, M., & Diaconescu, V. (2007). *Dobrogea 2007 Field Trip Preparation and Assistance* (123 p.). University of Bucharest.

Dragastan, O. N., Antoniade, C., & Stoica, M. (2014). Biostratigraphy and zonation of the Lower Cretaceous succession from Cernavodă-lock section, South Dobrogea, eastern part of the Moesian Platform (Romania). *Carpathian Journal of Earth and Environmental Sciences, 9*, 231–260.

Dragastan, O., Neagu, T., Bărbulescu, A., & Pană, I. (1998). *Jurasicul şi Cretacicul din Dobrogea Centrală şi de Sud* (249 p.). Bucharest.

Dyke, G. J., Benton, M. J., Posmoșanu, E., & Naish, D. (2011). Early Cretaceous (Berriasian) birds and pterosaurs from the Cornet bauxite mine, Romania. *Palaeontology*, *54*, 79–95.

Eberth, D. A., Brinkman, D. B., Chen, P.-J., Yuan, F.-T., Wu, X.-C., Li, G., & Cheng, X.-S. (2001). Sequence stratigraphy, paleoclimate patterns, and vertebrate fossil preservation in Jurassic–Cretaceous strata of the Juggar Basin, Xinjiang Autonomous Region, People's Republic of China. *Canadian Journal of Earth Sciences*, *38*, 1627–1644.

Eddy, D. R., & Clarke, J. A. (2011). New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroidea (Dinosauria: Theropoda). *PLoS ONE*, *6(3)*, e17932. doi:10.1371/journal.pone.0017932.

Evans, S. E., & Matsumoto, R. (2015). An assemblage of lizards from the Early Cretaceous of Japan. *Palaeontologia Electronica*, *18.2.36A*, 1–36.

Ezcurra, M. D., & Agnolín, F. L. (2012). A new global palaeobiogeographical model for the Late Mesozoic and Early Tertiary. *Systematic Biology*, *61*, 553–566. doi:10.1093/sysbio/syr115.

Fanti, F., Cau, A., Cantelli, L., Hassine, M., & Auditore, M. (2015). New information on *Tataouinea hannibalis* from the Early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. *PLoS ONE*, *10(4)*, e0123475. doi:10.1371/journal.pone.0123475.

Galton, P. M. (2009). Notes on Neocomian (Lower Cretaceous) ornithopod dinosaurs from England - *Hypsilophodon*, *Valdosaurus*, “*Camptosaurus*”, “*Iguanodon*” - and referred specimens from Romania and elsewhere. *Revue de Paléobiologie*, *28*, 211–273.

Gardner, J. D., Evans, S. E., & Sigogneau-Russell, D. (2003). New albanerpetontid amphibians from the Early Cretaceous of Morocco and Middle Jurassic of England. *Acta Palaeontologica Polonica*, *48*, 301–319.

Gasca, J. M., Canudo, J. I., & Moreno-Azanza, M. (2014). A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, *273*, 13–23. doi: 10.1127/0077-7749/2014/0413.

Gheerbrant, E., & Rage, J.-C. (2006). Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology*, *241*, 224–246. doi:10.1016/j.palaeo.2006.03.016.

Gishlick, A. D., & Gauthier, J. A. (2007). On the manual morphology of *Compsognathus longipes* and its bearing on the diagnosis of Compsognathidae. *Zoological Journal of the Linnean Society*, *149*, 569–581.

Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, *24*, 774–786.

Gradstein, F. M., Ogg, J. G., Schmitz, M. D., & Ogg, G. M. (Eds.) (2012). *The Geologic Time Scale 2012* (1144 p.). Amsterdam: Elsevier.

Grigorescu, D. (1992). Nonmarine Cretaceous Formations of Romania. In N. J. Matter, & P.-J. Chen (Eds.), *Aspects of Nonmarine Cretaceous Geology* (pp. 142–164). Beijing: China Ocean Press .

Grigorescu, D. (2003). Dinosaurs of Romania. *Comptes Rendus Palevol*, *2*, 97–101.

Grigorescu, D. (2010). The Latest Cretaceous fauna with dinosaurs and mammals from the Haţeg Basin — A historical overview. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *293*, 271–282.

Hammer, O., Harper, D. A. T., & Ryan, P. D. (2001). Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, *4*, 1–9.

Harris, J. D. (1998). A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science Bulletin*, *13*, 1–75.

Hendrickx, C., & Mateus, O. (2014). Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa, 3751(1)*, 1–74.

Hendrickx, C., Mateus, O., & Araújo, R. (2015a). The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica*, *60*, 627–642. doi:10.4202/app.00056.2013.

Hendrickx, C., Mateus, O., & Araújo, R. (2015b). A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology*, *35(5)*, e982797. doi: 10.1080/02724634.2015.982797.

Holtz, T. R., Chapman, R. E., & Lamanna, M. C. (2004b). Mesozoic biogeography of Dinosauria. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria. Second Edition* (pp. 627–642). Berkeley, Los Angeles, London: University of California Press.

Holtz, T. R., Jr.., Molnar, R. E., & Currie, P. J. (2004a). Basal Tetanurae. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria. Second Edition* (pp. 71–110). Berkeley, Los Angeles, London: University of California Press.

Huene, F. von (1923). Carnivorous Saurischia in Europe since the Triassic. *Bulletin of the Geological Society of America*, *34*, 449–458.

Hippolyte, J.-C. (2002). Geodynamics of Dobrogea (Romania): new constraints on the evolution of the Tornquist–Teisseyre Line, the Black Sea and the Carpathians. *Tectonophysics*, *357*, 33–53.

Ionesi, L. (1994). *Geologia unităţilor de platformă şi a orogenului Nord-Dobrogean* (p. 280). Bucharest: Ed. Tehnică.

Jerzykiewicz, T., & Russell, D. A. (1991). Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research*, *12*, 345–377.

Jurcsák, T. (1982). Occurences nouvelles des Sauriens mésozoïques de Roumanie. *Vertebrata Hungarica*, *21*, 175–184.

Jurcsák, T., & Popa, E. (1979). Dinozaurieni ornithopozi din bauxitele de la Cornet (Munții Pădurea Craiului). *Nymphaea*, *7*, 37–75.

Jurcsák, T., & Popa, E. (1983). La faune de dinosauriens du Bihor (Roumanie). In E. Buffetaut, J. M. Mazin, E. Salmon (Eds.), *Actes du Symposium Paléontologique Georges Cuvier* (pp. 325–335). Montbéliard: Le Serpentaire.

Kellner, A. W. A., Pinheiro, A. E. P., & Campos, D. A. (2014). A new sebecid from the Paleogene of Brazil and the crocodyliform radiation after the K–Pg boundary. *PLoS ONE*, *9(1)*, e81386. doi:10.1371/journal.pone.0081386.

Kirkland, J. I., Cifelli, R. L., Britt, B. B., Burge, D. L., DeCourten, F. L., Eaton, J. G., & Parrish, J. M. (1999). Distribution of vertebrate faunas in the Cedar Mountain Formation, east-central Utah. *Utah Geological Survey Miscellaneous Publication*, *99-1*, 201–217.

Knoll, F., & Ruiz-Omeñaca, J. I. (2009). Theropod teeth from the basalmost Cretaceous of Anoual (Morocco) and their palaeobiogeographical significance. *Geological Magazine*, *146*, 602–616.

Kusuhashi, N., Matsumoto, A., Murakami, M., Tagami, T., Hirata, T., Iizuka, T., Handa, T., & Matsuoka, H. (2006). Zircon U−Pb ages from tuff beds of the upper Mesozoic Tetori Group in the Shokawa district, Gifu Prefecture, central Japan. *The Island Arc*, *15*, 378–390.

Lacasa Ruiz, A. (1989). Nuevo genero de ave fosil del yacimiento Neocomiense del Montsec (Provincia de Lerida, España). *Estudios geológicos*, *45(5-6)*, 417–425.

Larson, D. W., & Currie, P. J. (2013). Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time. *PLoS ONE*, *8(1)*, e54329. doi:10.1371/journal.pone.0054329.

Le Loeuff, J., & Buffetaut, E. (1995). The evolution of Late Cretaceous non-marine vertebrate faunas in Europe. In A.-L. Sun, & Y.-Q. Wang (Eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers* (pp. 181–184). Beijing: China Ocean Press.

Le Loeuff, J., Lang, E., Cavin, L., & Buffetaut, E. (2012). Between Tendaguru and Bahariya: on the age of the Early Cretaceous dinosaur sites from the Continental Intercalaire and other African formations. *Journal of Stratigraphy*, *36*, 486–502.

Lucas, F. A. (1901). A new dinosaur, *Stegosaurus marshi*, from the Lower Cretaceous of South Dakota. *Proceedings of the United States National Museum*, *23(1224)*, 591–592.

Lucas, S. G. (2006). The *Psittacosaurus* biochron, Early Cretaceous of Asia. *Cretaceous Research*, *27*, 189–198.

Lucas, S. G., & Estep, J. W. (1998). Vertebrate biostratigraphy and biochronology of the Cretaceous of China. In S. G. Lucas, J. I. Kirkland, J. W. Estep (Eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems* (pp. 1–20). New Mexico Museum of Natural History and Science Bulletin, 14.

Lü, J.-C., Xu, L., Pu, H.-Y., Jia, S.-H., Azuma, Y., Chang, H.-L., & Zhang, J.-M. (2016). Paleogeographical significance of carcharodontosaurid teeth from the late Early Cretaceous of Ruyang, Henan Province of central China. *Historical Biology*, 28, 8–13. doi: 10.1080/08912963.2014.947287.

Manabe, M., & Hasegawa, Y. (1995). Diapsid fauna and its paleobiogeographical implication, the Neocomian section of the Tetori Group. In A. Sun, & Y. Wang (Eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, *Short Papers* (pp. 179). Beijing: China Ocean Press.

Mannion, P. D. (2009). A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. *Cretaceous Research*, *30*, 521–526.

Mannion, P. D., Upchurch, P., & Hutt, S. (2011). New rebbachisaurid (Dinosauria: Sauropoda) material from the Wessex Formation (Barremian, Early Cretaceous), Isle of Wight, United Kingdom. *Cretaceous Research*, *32*, 774–780.

Matsukawa, M., Ito, M., Nishida, N., Koarai, K., Lockley, M. G., Nichols, D. J. (2006). The Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial ecosystems in Asia. *Cretaceous Research*, *27*, 199–225.

McDonald, A. T. (2011). The taxonomy of species assigned to *Camptosaurus* (Dinosauria: Ornithopoda). *Zootaxa*, *2783*, 52–68.

McKenna, M. C. (1973). Sweepstakes, filters, corridors, Noah's Arks, and Beached Viking Funeral Ships in palaeogeography. In D. H. Tarling, S. K. Runcorn (Eds.), *Implications of Continental Drift to the Earth Sciences* (pp. 295–308). New York: Academic Press.

Mo, J.-Y., Huang, C.-L., Xie, S.-W., & Buffetaut, E. (2014). A megatheropod tooth from the Early Cretaceous of Fusui, Guangxi, Southern China. *Acta Geologica Sinica (English Edition)*, *88*, 6–12.

Molnar, R. E. (1990). Problematic Theropoda: "Carnosaurs". In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria* (pp. 306–317). Berkeley, Los Angeles, Oxford: University of California Press.

Mutihac, V., & Mutihac, G. (2010). *The geology of Romania, within the Central East European geostructural context* (p. 690). Bucharest: Ed. Didactică şi Pedagogică.

Neagu, T., Dragastan, O., & Csiki, Z. (1997). Early Cretaceous shelf paleocommunities of Cernavodă (South Dobrogea, SE Romania). *Acta Palaeontologica Romaniae*, *1*, 28–36.

Nopcsa, F. (1902). Notizen über cretacische Dinosaurier. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*, *111*, 93–114.

Nopcsa, F. (1923). On the geological importance of the primitive reptilian fauna of the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotium*). *Quarterly Journal of the Geological Society of London*, *79*, 100–116.

Norman, D. B. (2010). A taxonomy of iguanodontians (Dinosauria: Ornithopoda) from the lower Wealden Group (Cretaceous: Valanginian) of southern England. *Zootaxa*, *2489*, 47–66.

Norman, D. B. (2013). On the taxonomy and diversity of Wealden iguanodontian dinosaurs (Ornithischia: Ornithopoda). *Revue de Paléobiologie, 32*, 385–404.

Novas, F. E., Agnolín, F. L., Ezcurra, M. D., Porfiri, J., & Canale, J. I. (2013). Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Research*, *45*, 174–215.

Novas, F. E., de Valais, S., Vickers-Rich, P. A., & Rich, T. H. (2005). A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften*, *92*, 226–230.

Ortega, F., Escaso, F., & Sanz, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature*, *467,* 203–206.

Ősi, A., Codrea, V., Prondvai, E., & Csiki-Sava, Z. (2014). New ankylosaurian material from the Upper Cretaceous of Transylvania. *Annales de Paléontologie*, *100,* 257–271. doi: 10.1016/j.annpal.2014.02.001.

Ősi, A., Rabi, M., Makádi, L., Szentesi, Z., Botfalvai, G., & Gulyás, P. (2012). The Late Cretaceous continental vertebrate fauna from Iharkút (western Hungary): a review. In P. Godefroit (Ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems* (pp. 533–569). Bloomington: Indiana University Press.

Ősi, A., Rabi, M., & Makádi, L. (2015). An enigmatic crocodyliform tooth from the bauxites of western Hungary suggests hidden mesoeucrocodylian diversity in the Early Cretaceous European archipelago. *PeerJ*, *3,* e1160. doi:10.7717/peerj.1160.

Paolillo, A., & Linares, O. J. (2007). Nuevos cocodrilos Sebecosuchia del Cenozoico Suramericano (Mesosuchia: Crocodylia). *Paleobiologia Neotropical*, *3*, 1–25.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J. I., Canudo, J. I., Torcida, F., & Sanz, J. L. (2012). Dinosaur faunas from the Early Cretaceous (Valanginian–Albian) of Spain. In P. Godefroit

(Ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems* (pp. 378–407). Bloomington: Indiana University Press.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J. I., Fernandez-Baldor, F. T., Maisch, M. W., Huerta, P., Contreras, R., Izquierdo, L. A., Huerta, D. M., Montero, V. U., & Welle, J. (2011). A tall-spined ornithopod dinosaur from the Early Cretaceous of Salas de los Infantes (Burgos, Spain). *Comptes Rendus Palevol*, *10*, 551–558.

Pérez-Moreno, B. P., Sanz, J. L., Sudre, J., & Sigé, B. (1993). A theropod dinosaur from the Lower Cretaceous of southern France. *Revue de Paléobiologie, Volume spéciale 7*, 173–188.

Pol, D., & Powell, J. E. (2011). A new sebecid mesoeucrocodylian from the Rio Loro Formation (Palaeocene) of north-western Argentina. *Zoological Journal of the Linnean Society*, *163*, S7–S36.

Porfiri, J. D., Novas, F. E., Calvo, J. O., Agnolín, F. L., Ezcurra, M. D., & Cerda, I. A. (2014). Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. *Cretaceous Research*, *51*, 35–55. doi:10.1016/j.cretres.2014.04.007.

Posmoșanu, E. (2003). Iguanodontian dinosaurs from the Lower Cretaceous bauxite site from Romania. *Acta Palaeontologica Romaniae*, *4*, 431–439.

Rabi, M., & Sebők, N. (2015). A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. *Gondwana Research*, *28*, 1197–1211. doi:10.1016/j.gr.2014.09.015.

Racey, A. (2009). Mesozoic red bed sequences from SE Asia and the significance of the Khorat Group of NE Thailand. In E. Buffetaut, G. Cuny, J. Le Loeuff, & V. Suteethorn (Eds.), *Late Palaeozoic and Mesozoic Ecosystems in SE Asia* (pp. 41–67). Geological Society, London, Special Publications, 315. doi: 10.1144/SP315.5.

Racey, A., & Goodall, J. G. S. (2009). Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. In E. Buffetaut, G. Cuny, J. Le Loeuff, & V. Suteethorn (Eds.), *Late Palaeozoic and Mesozoic Ecosystems in SE Asia* (pp. 69–83). Geological Society, London, Special Publications, 315. doi: 10.1144/SP315.6.

Rauhut, O. W. M. (2011). Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology, 86*, 195–239.

Rauhut, O. W. M., & Werner, C. (1995). First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan. *Paläontologische Zeitschrift, 69*, 475–489.

Richter, U., Mudroch, A., & Buckley, L. G. (2013). Isolated theropod teeth from the Kem Kem Beds (Early Cenomanian) near Taouz, Morocco. *Paläontologische Zeitschrift*, *87*, 291–309.

Royo-Torres, R., Cobos, A., Luque, L., Aberasturi, A., Espilez, E., Fierro, I., Gonzales, A., Mampel, L., & Alcalá, L. (2009). High European sauropod dinosaur diversity during Jurassic–Cretaceous transition in Riodeva (Teruel, Spain). *Palaeontology*, *52*, 1009–1027.

Sachs, S., & Hornung, J. J. (2013). Ankylosaur remains from the Early Cretaceous (Valanginian) of Northwestern Germany. *PLoS ONE*, *8(4)*, e60571. doi:10.1371/journal.pone.0060571.

Salgado, L., Canudo, J. I., Garrido, A. C., Ruiz-Omeñaca, J. I., Garcia, R. A., de la Fuente, M. S., Barco, J. L., & Bollati, R. (2009). Upper Cretaceous vertebrates from El Anfiteatro area, Río Negro, Patagonia, Argentina. *Cretaceous Research*, *30*, 767–784.

Sames, B., Cifelli, R. L., & Schudack, M. E. (2010). The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: New biostratigraphic results from ostracod correlations and early mammals, and their implications for paleontology and geology of the basin—An overview. *Earth-Science Reviews*, *101*, 207–224.

Sauvage, H. E. (1876). Notes sur les reptiles fossiles. *Bulletin de la Société Géologique de France*, *4*, 435–442.

Sauvage, H. E. (1882). Recherches sur les reptiles trouves dans le Gault de l'est du bassin de Paris. *Mémoires de la Société Géologique de France*, *2*, 1–42.

Săndulescu, M. (1984). *Geotectonica României* (p. 329). Bucharest: Ed. Tehnică.

Seghedi, A. (2001). The North Dobrogea orogenic belt (Romania): a review. In P. A. Ziegler, W. Cavazza, A. H. F. Robertson, & S. Crasquin-Soleau (Eds.), *Peri-Tethys Memoir 6: Peri-Tethyan Rift/Wrench Basins and Passive Margins* (pp. 237–257). Paris: Mémoires de la Musée National d'Histoire Naturelle .

Sereno, P. C. (1999). Dinosaurian biogeography: vicariance, dispersal and regional extinction. In Y. Tomida, T. H. Rich, & P. Vickers-Rich (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium* (pp. 249–257). Tokyo: National Science Museum Monographs, 15 .

Sereno, P. C., & Brusatte, S. L. (2008). Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontologica Polonica*, *53*, 15–46.

Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., Sidor, C. A., Varricchio, D. J., & Wilson, J. A. (1996). Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, *272*, 986–991.

Shen, Y. B., & Mateer, N. J. (1992). An outline of the Cretaceous system in northern Xinjiang, western China. In N. J. Mateer, & P. J. Chen (Eds.), *Aspects of Nonmarine Cretaceous Geology* (pp. 49–77). Beijing: China Ocean Press.

Simionescu, I. (1906). Note sur l'age des calcaires de Cernavoda (Dobrogea). *Annales Scientifiques de l'Université de Jassy*, *4(1)*, 1–3.

Simionescu, I. (1913). *Megalosaurus* aus der Unterkreide der Dobrogea. *Centralblatt für Mineralogie, Geologie und Paläontologie*, *1913(20)*, 686–687.

Sissingh, W. (1977). Biostratigraphy of Cretaceous calcareous nannoplankton. *Geologie en Mijnbouw*, *56*, 37–65.

Smith, J. B., Vann, D. R., & Dodson, P. (2005). Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record A*, *285A*, 699–736.

Stein, K., Csiki, Z., Curry Rogers, K., Weishampel, D. B., Redelstorff, R., Carballido, J. L., & Sander, P. M. (2010). Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences*, *107*, 9258–9263.

Stoica, M., & Csiki, Z. (2002). An earliest Cretaceous (Purbeckian) vertebrate fauna from Southern Dobrogea (southeastern Romania). In D. Grigorescu, & Z. Csiki (Eds.), *7th European Workshop on Vertebrate Palaeontology, Sibiu, Romania* (pp. 34). Bucharest: Ars Docendi.

Stovall, J. W., & Langston, W., Jr. (1950). *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *American Midland Naturalist*, *43*, 686–728.

Stromer, E. (1931). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharîjestufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematischnaturwissenschaftliche Abteilung*, *Neue Folge 9*, 1–23.

Therrien, F., & Henderson, D. M. (2007). My theropod is bigger than yours … or not: estimating body size from skull length in theropods. *Journal of Vertebrate Paleontology*, *27*, 108–115.

Tong, H., Claude, J., Suteethorn, V., Naksri, W., & Buffetaut, E. (2009). Turtle assemblages of the Khorat Group (Late Jurassic–Early Cretaceous) of NE Thailand and their palaeobiogeographical significance. In E. Buffetaut, G. Cuny, J. Le Loeuff, & V. Suteethorn (Eds.), *Late Palaeozoic and Mesozoic Ecosystems in SE Asia* (pp. 141–151). Geological Society, London, Special Publications, 315.

Torcida Fernández-Baldor, F., Canudo, J. I., Huerta, P., Montero, D., Pereda Suberbiola, X., & Salgado, L. (2011). *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. *Acta Palaeontologica Polonica*, *56*, 535–552.

Turculeț, I., & Brânzilă, M. (2012). *Muzeul colecțiilor paleontologice originale de la Universitatea "Alexandru Ioan Cuza" Iași* (p. 173). Iași: Editura Universității "Alexandru Ioan Cuza" Iași.

Turner, A. H., Makovicky, P. J., & Norell, M. A. (2012). A review of dromaeosaurid systematics and paravian phylogeny. *Bulletin of the American Museum of Natural History*, *371*, 1–206.

Turner, A. H., & Sertich, J. J. W. (2010). Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology, 30(Supplement 1)*, 177–236.

Vasile, Ș., & Csiki, Z. (2011). New Maastrichtian microvertebrates from the Rusca Montană Basin (Romania). *Oltenia. Studii și comunicări. Științele Naturii*, *27(1)*, 221–230.

Vickers-Rich, P., Rich, T. H., Lanus, D. R., Rich, L. S. V., & Vacca, R. (1999). "Big Tooth" from the Early Cretaceous of Chubut Province, Patagonia: a possible carcharodontosaurid. In Y. Tomida, T. H. Rich, & P. Vickers-Rich (Eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium* (pp. 85–88). Tokyo: National Science Museum Monographs, 15.

Vremir, M. (2010). New faunal elements from the Late Cretaceous (Maastrichtian) continental deposits of Sebeș area (Transylvania). *Terra Sebus. Acta Musei Sabesiensis*, *2*, 635–684.

Vullo, R., Néraudeau, D., & Lenglet, T. (2007). Dinosaur teeth from the Cenomanian of Charentes, western France: evidence for a mixed Laurasian-Gondwanan assemblage. *Journal of Vertebrate Paleontology*, *27*, 931–943.

Weishampel, D. B. (1990). Dinosaurian distribution. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria* (pp. 63–140). Berkeley, Los Angeles, Oxford: California University Press.

Weishampel, D. B., Barrett, P. M., Coria, R. A., Le Loeuff, J., Xu, X., Zhao, X-J., Sahni, A., Gomani, E. M., & Noto, C. R. (2004). Dinosaur distribution. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria. Second Edition* (pp. 517–606). Berkeley, Los Angeles, London: University of California Press.

Weishampel, D. B., Csiki, Z., Benton, M. J., Grigorescu, D., & Codrea, V. (2010). Palaeobiogeographic relationships of the Hațeg biota — Between isolation and innovation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *293*, 419–437.

Weishampel, D. B., Grigorescu, D., & Norman, D. B. (1991). The Dinosaurs of Transylvania. *National Geographic Research & Exploration*, *7(2)*, 196–215.

Weishampel, D. B., Jianu, C. M., Csiki, Z., & Norman, D. B. (2003). Osteology and phylogeny of *Zalmoxes* (n. g.), an unusual euornithopod dinosaur from the latest Cretaceous of Romania. *Journal of Systematic Palaeontology*, *1*, 65–123.

Weishampel, D. B., Norman, D. B., & Grigorescu, D. (1993). *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. *Palaeontology*, *36*, 361–385.

Williamson, T. E., & Brusatte, S. L. (2014). Small theropod teeth from the Late Cretaceous of the San Juan Basin, northwestern New Mexico and their implications for understanding latest Cretaceous dinosaur evolution. *PLoS ONE, 9(4)*, e93190. doi:10.1371/journal.pone.0093190.

Zarcone, G., Cillari, F. M. P., Stefano, P. D., Guzzetta, D., & Nicosia, U. (2010). A possible bridge between Adria and Africa: New palaeobiogeographic and stratigraphic constraints on the Mesozoic palaeogeography of the Central Mediterranean area. *Earth-Science Reviews, 103*, 154–162.

Figure captions

Figure 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).

Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B. Current state of UAIC (SCM1) 615, mounted in a limestone holder.

Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B., distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).

Figure 4. Dental morphospace of the different theropod clades according to the results of the PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by Carcharodontosauridae. See further details of this analysis, as well as other quantitative analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant function analysis, phylogenetic analysis), in the Supplementary Material.

Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615 from Southern Dobrogea. Legend: 1 – *Veteruprisitisaurus*, ‘*Megalosaurus’ ingens*, Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator,* Spain, Barremian; 3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 – *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China, Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmayisaurus*, Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11

– *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan, Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 – Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant references, see text, *5.4.*). Palaeogeographic maps, courtesy of Ron Blakey (http://cpgeosystems.com/).

Figure 1 color

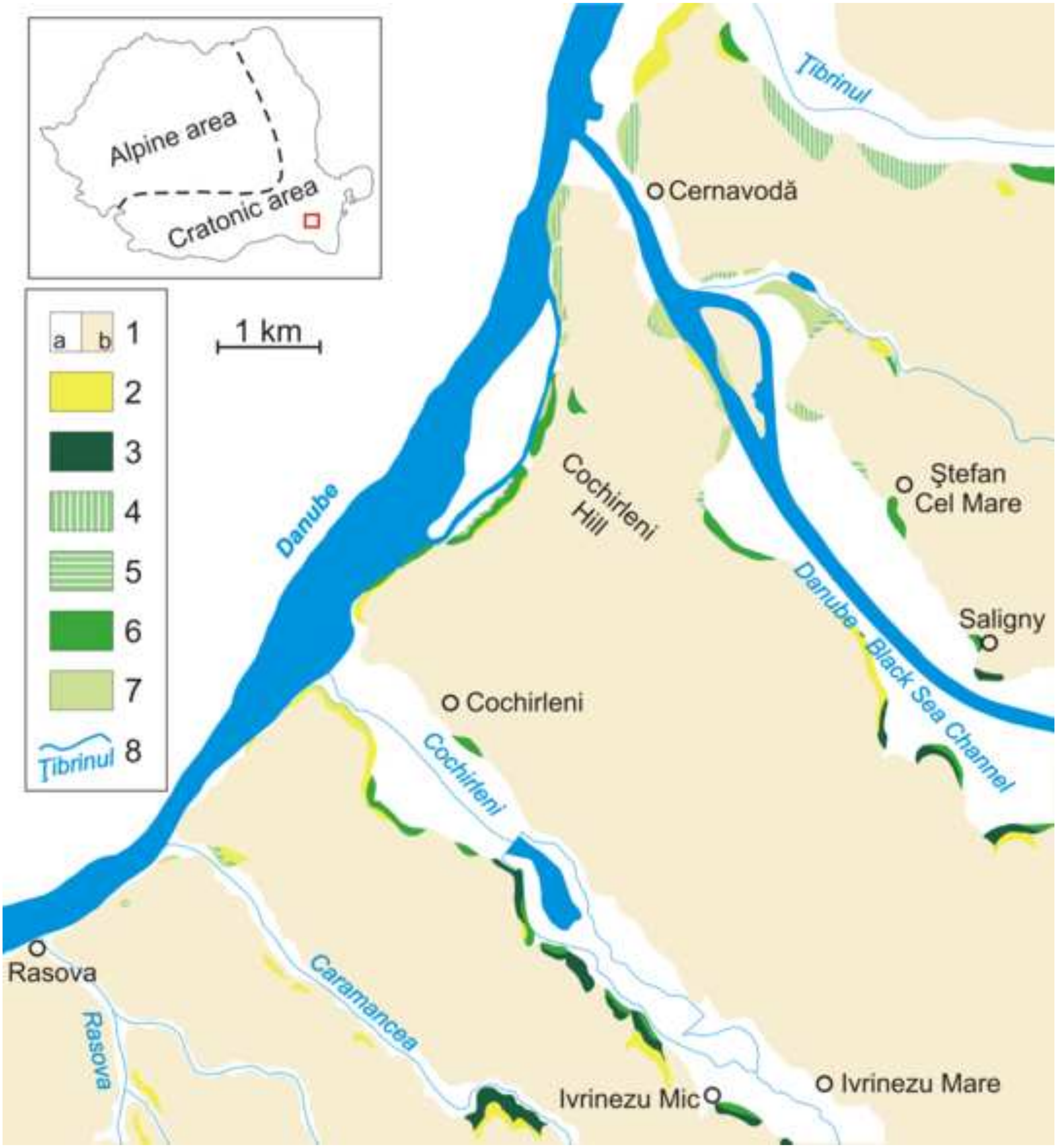


Figure 2 color

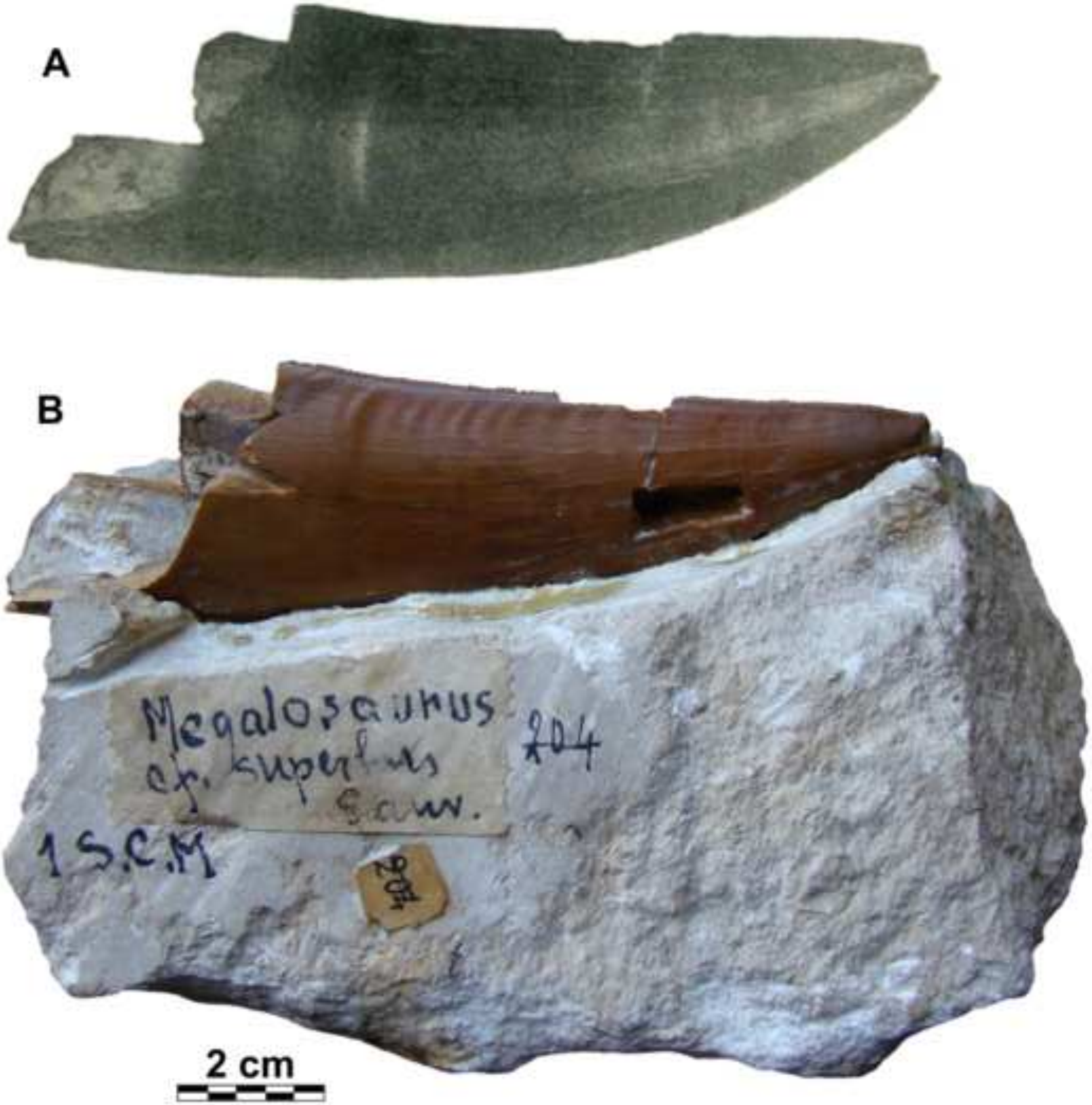


Figure 3 color

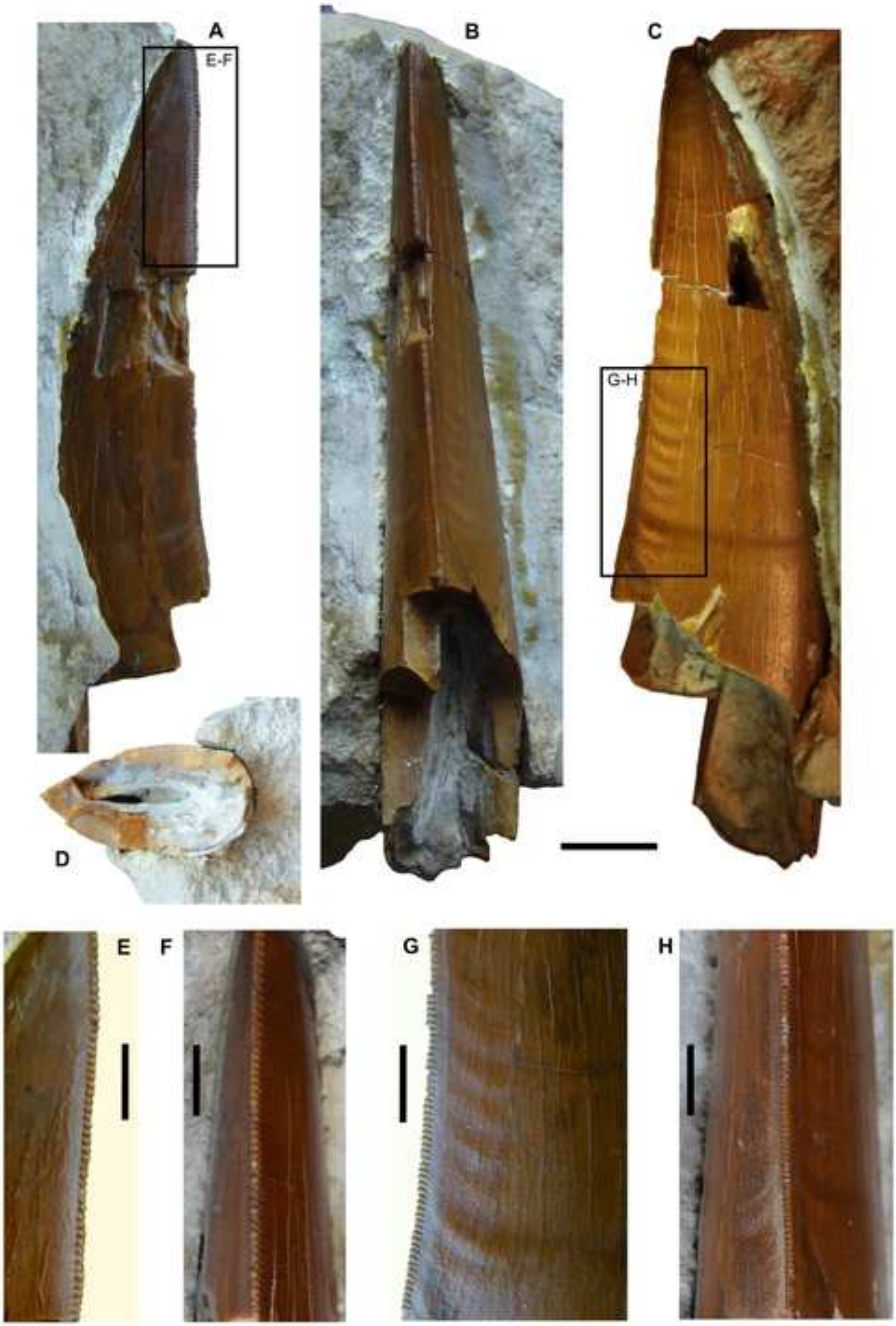


Figure 4 color

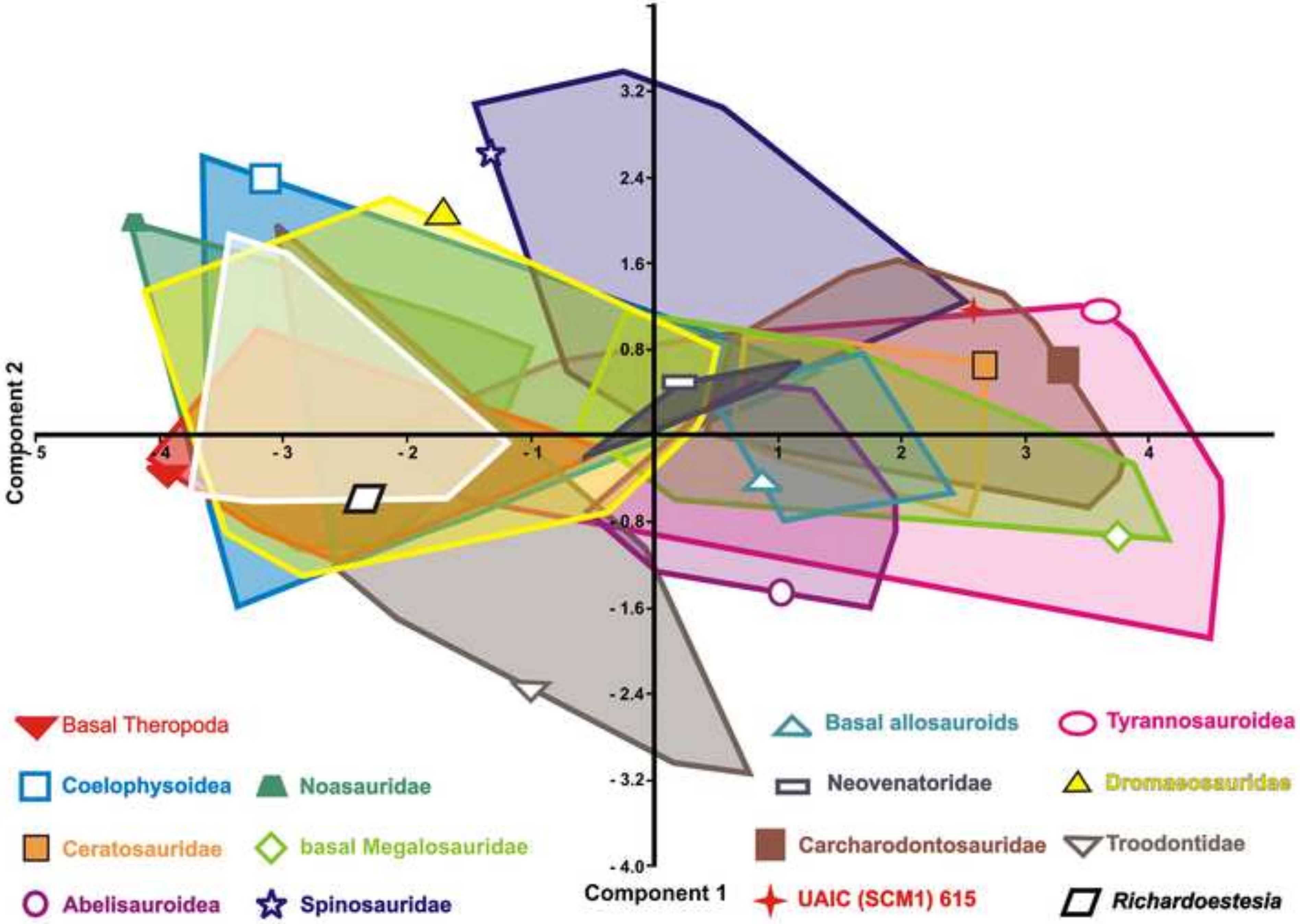
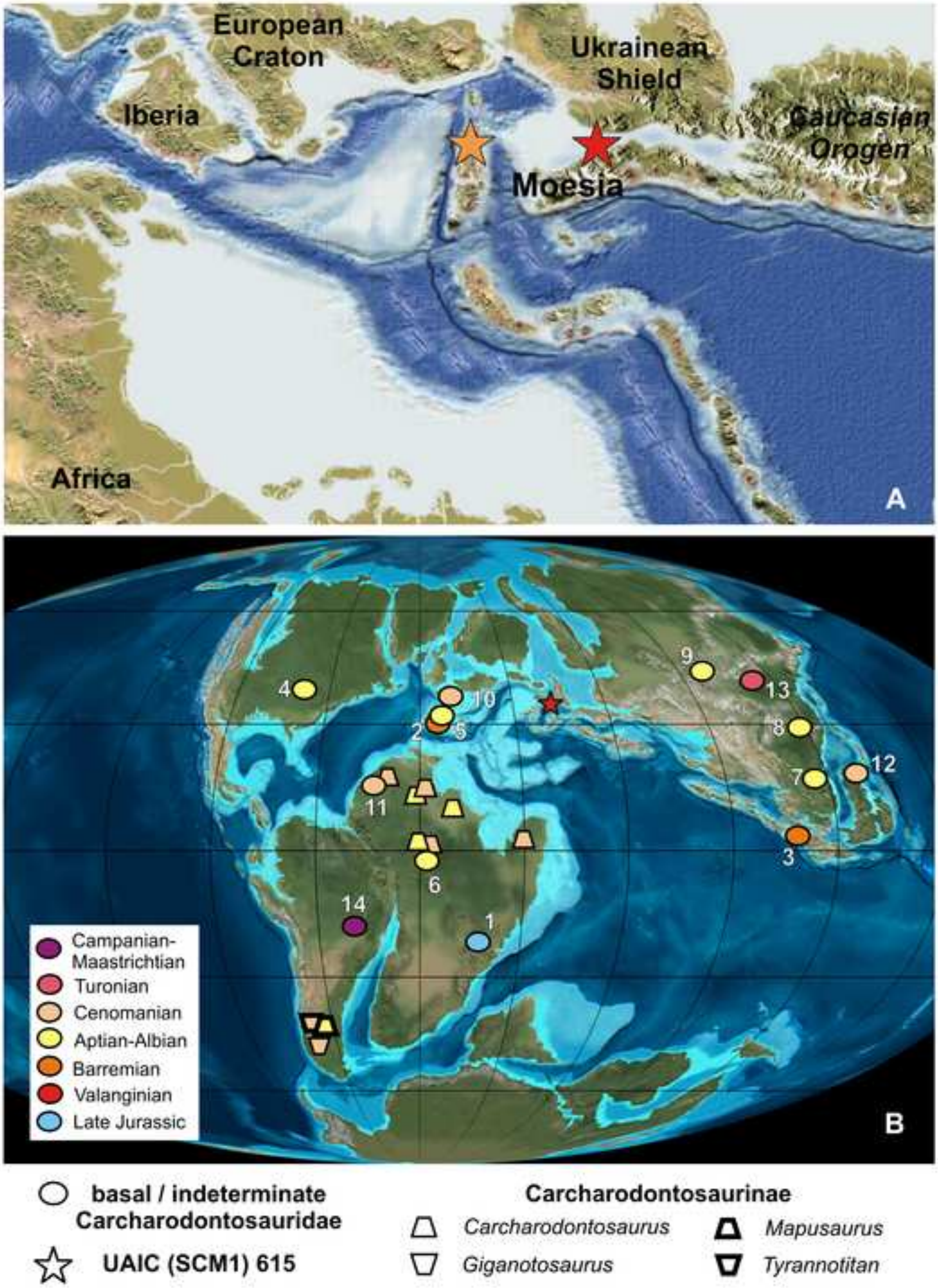


Figure 5 color



Supplementary Material

Taxon	Side	Position	Specimen	Source fro	CBL	CBW	CH
ROMANIAN TOOTH			SCM1 615		29	16.25	85.5
Eoraptor	Left	pmx2	PVSJ 512	Pers. Obser	2.5	1.62	6.74
Eoraptor	Left	pmx3	PVSJ 512	Pers. Obser	1.97	2.35	5.92
Eoraptor	Left	pmx4	PVSJ 512	Pers. Obser	2.19	1.74	6.52
Eoraptor	Right	pmx2	PVSJ 512	Pers. Obser	2.17	1.56	5.01
Eoraptor	Right	pmx4	PVSJ 512	Pers. Obser	2.08	1.61	4.17
Eoraptor	Left	mx2	PVSJ 512	Pers. Obser	2.69	1.82	5.55
Eoraptor	Left	mx4	PVSJ 512	Pers. Obser	3.03	1.48	5.65
Eoraptor	Left	mx5	PVSJ 512	Pers. Obser	3.56	1.69	5.48
Eoraptor	Left	mx9	PVSJ 512	Pers. Obser	2.49	1.75	5.11
Eoraptor	Left	mx10	PVSJ 512	Pers. Obser	2.7	1.22	4.58
Eoraptor	Left	mx11	PVSJ 512	Pers. Obser	2.32	1.42	2.34
Eoraptor	Left	pm02	PVSJ 512	Smith & La	2.88	1.85	7.15
Eoraptor	Left	pm03	PVSJ 512	Smith & La	1.98	1.48	5.73
Eoraptor	Left	pm04	PVSJ 512	Smith & La	1.89	1.55	6.12
Eoraptor	Right	pm02	PVSJ 512	Smith & La	2.32	1.8	5.19
Eoraptor	Left	mx02	PVSJ 512	Smith & La	2.11	1.51	5.71
Eoraptor	Left	mx04	PVSJ 512	Smith & La	3.04	1.97	6.58
Eoraptor	Left	mx06	PVSJ 512	Smith & La	2.9	1.74	5.44
Eoraptor	Left	mx07	PVSJ 512	Smith & La	2.71	1.58	6.17
Eoraptor	Left	mx09	PVSJ 512	Smith & La	2.67	1.82	4.99
Eoraptor	Left	mx10	PVSJ 512	Smith & La	2.56	1.69	4.72
Eoraptor	Right	mx02	PVSJ 512	Smith & La	2.94	1.87	5.32
Eoraptor	Right	mx04	PVSJ 512	Smith & La	2.54	1.55	6.5
Eoraptor	Right	mx05	PVSJ 512	Smith & La	3.33	1.82	6.76
Eoraptor	Right	mx07	PVSJ 512	Smith & La	2.86	1.6	4.83
Eoraptor	Right	mx08	PVSJ 512	Smith & La	2.8	1.5	4.71
Ischisaurus	Right	pmx1	MACN 18.0	Pers. Obser	8.16	4.7	14.62
Ischisaurus	Right	pmx2	MACN 18.0	Pers. Obser	7.48	4.43	14.5
Eodromaeus	Left	mx3	PVSJ 561	Pers. Obser	3.61	1.59	9.67
Coelophysis	Left	pmx2	CM 82931	Pers. Obser	1.7	0.54	4
Coelophysis	Left	pmx3	CM 82931	Pers. Obser	1.8	1.03	6.8
Coelophysis	Left	mx1	CM 81765	Pers. Obser	3	1.49	8.2
Coelophysis	Left	mx2	CM 81765	Pers. Obser	4.1	1.37	8.9
Coelophysis	Left	mx4	CM 81765	Pers. Obser	4.4	1.63	11.6
Coelophysis	Left	mx6	CM 81765	Pers. Obser	5.5	1.71	9.7
Coelophysis	Left	mx8	CM 81765	Pers. Obser	5.9	1.79	9.3
Coelophysis	Left	mx9	CM 81765	Pers. Obser	5.4	1.74	8.6
Coelophysis	Left	mx11	CM 81765	Pers. Obser	5.4	1.85	7.5
Coelophysis	Left	mx13	CM 81765	Pers. Obser	4.7	1.58	5.5
Coelophysis	Left	mx14	CM 81765	Pers. Obser	5.2	1.7	6.2
Coelophysis	Left	mx15	CM 81765	Pers. Obser	3.9	1.49	5.4
Coelophysis	Left	mx16	CM 81765	Pers. Obser	3.3	1.14	5
Coelophysis	Left	mx17	CM 81765	Pers. Obser	3.5	1.63	4.1
Coelophysis	Left	mx19	CM 81765	Pers. Obser	3.35	1.86	3.3
Coelophysis	Left	mx21	CM 81765	Pers. Obser	3.54	0.93	3.45