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

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Abstract: Some of the best records of continental vertebrates from the Cretaceous of Europe come from Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant dinosaurs and other taxa that lived on islands (the Cornet and 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 evolve vicariantly as Laurasia split from Gondwana, but originated earlier, perhaps in Europe. The carcharodontosaurine diversification may have been tied to a north-to-south trans-Tethyan dispersal that took place sometime between the Valanginian and 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...

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.
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

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ABSTRACT

Some of the best records of continental vertebrates from the Cretaceous of Europe come from Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant dinosaurs and other taxa that lived on islands (the Cornet and 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; Sândulescu, 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.
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 Hârșova (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 Hârșova” (enthusiastic founder and director of the Hârșova 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” (Hârșova 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* pseudelegans’ 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 (Turculeţ 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. Turculeţ, 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 Iaşi, 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 Iaşi 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 Hârșova 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 (Sândulescu, 1984;
Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,
201 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 Vederoaş 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 Vederoaş 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 Peştera Formation.

4. Palaeontology

The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hărşova 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 Cochirileni theropod tooth should now be considered referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to *Erectopus superbus* (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 Cochirileni 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 Cochirlenei along the right bank of the Danube. The corresponding entry from the Hărşova Museum registry states that it was found in the ‘Cochirlenei 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-Cochirlenei. Finally, although the mention ‘Cochirlenei’ is usually considered to refer to Cochirlenei village, it should be mentioned that the cliff-forming hill that extends between Cernavodă and Cochirlenei 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 Cochirlenei.

Based on the location of the discovery, in the upper part of the local limestone succession, and the age of the deposits from Cernavodă-Cochirlenei 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 foraminifers, ostracods and microproblematica ( = 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
tyrranosauroids 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 squared-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 possess 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; 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 tyrannosaurid 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
allosaurs (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of
derived tyrannosaurs (Brusatte et al., 2010a) and the large and strongly hooked (or
pointed) denticles of troodontids and therizinosaurids (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 therizinosaurids,
ornithomimosaurs, alvarezsaurids, 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 alvarezsaurids, 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 carcharodontosaur. 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 Ukrainian 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.,
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
carcharodontosaur 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 carcharodontosaur documents the
presence of this clade in Europe in the very early Cretaceous. This is significant, as
carcharodontosaurs 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 carcharodontosaur 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 ornithomimosaurids (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-
carcharodontosaur 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 carcharodontosaurs 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; Ösi 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 carcharodontosaur 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; Brusatet 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 carcharodontosaurs in the Lower Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper Cretaceous of China (Brusatet et al., 2009, 2010b, 2012; Mo et al., 2014; Lü et al., 2014, 2016).

Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin of the carcharodontosaurs, 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 carcharodontosaurs 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 carcharodontosaurs in the fossil record starting with the Aptian, when they are reported in Africa (Eocarcharia; Sereno and Brusatet, 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., 2014).
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*, *Giganotosaurus*, *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 tyrannosaurs 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-carcharodontosauarine 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 (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 carcharodontosauroids 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 Microlate (= 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
tested 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

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-occurring 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.

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Figure captions
Figure 1. Simplified geological map of the Cernavodă-Cochirleni area; inset shows the

Pleistocene–Holocene loessoid deposits; 2. Pre-Quaternary Cenozoic (Middle Eocene and
Miocene) deposits; Cretaceous: 3. Peștera 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
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

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ABSTRACT

Some of the best records of continental vertebrates from the Cretaceous of Europe come from Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant dinosaurs and other taxa that lived on islands (the Cornet and 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 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; Sândulescu, 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”, Iaşi, 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 Hârșova (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 Hârșova” (enthusiastic founder and director of the Hârșova 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” (Hârșova 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 Hârșova 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 Hârșova 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 Hârșova Museum. Although no details are known about this transfer, it is probable that it took place right before (or when) the Hârșova 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 Iași–Chișinău 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 Hărşova 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 (Sândulescu, 1984;
Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,
200 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
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-glaucnitic deposits of the Peştera Formation.

4. Palaeontology

The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hărşova 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 superbus* (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 microproblematica (=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. kamptoneri, 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 squared-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).
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
devolved 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. 3A, 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 possess 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 tyrannosaurid 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 carcharodontosaur. Furthermore, the analysis places UAIC (SCM1) 615 within the convex hulls for carcharodontosaurs and tyrannosaurids, and the 95% confidence ellipses for carcharodontosaurs, 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 carcharodontosaur 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 therizinosaurids (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 therizinosaurids,
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 carcharodontosaur. 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 carcharodontosaur 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 Hațeg 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; Ösi 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 Ukrainian 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.,
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 carcharodontosaurs 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 carcharodontosaurs 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 ornithomimosaur (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; Ösi 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 carcharodontosaur 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 (*Tyannotitan, Giganotosaurus, 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. 804). 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 tyrannosaurs 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 Carcharodontosauridae (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 carcharodontosaurs
(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 carcharodontosaur 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 Bosselini (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
tested 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

Absence of documented faunal interactions weakens support for a scenario of south-
to-north immigration of derived carcharodontosaurusines 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-occurring 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 nanoplankton 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.

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Figure captions


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 Corne 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

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ABSTRACT

Some of the best records of continental vertebrates from the Cretaceous of Europe come from Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant dinosaurs and other taxa that lived on islands (the Cornet and 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

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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 ‘Hateg 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; Sândulescu, 1984; Mutihac
and Mutihac, 2010; Fig. 1). This is mostly because Mesozoic deposits are located in the
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 Hârșova (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 Hârșova” (enthusiastic founder and director of the Hârșova 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” (Hârșova 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 (Turculeţ 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. Turculeţ, 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 2013). 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 Hărşova 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 Iaşi, 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 Iaşi 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 Hărşova Museum. As noted previously, the original Hărşova 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 Hărşova 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 Hârșova 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 (Sândulescu, 1984;
Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,
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
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 Lipnița 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 superbus* (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 Watznauieria 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 (Simionscă’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 squared-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 *Tyrannosaurus* (Novas et al., 2005). The denticles are
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, 2013; 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 tyrannosaurids. It falls within the convex hull (maximum morphospace occupation area) of carcharodontosaurids only, although it is closely outside of the edges of spinosaurid and tyrannosaurid 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, tyrannosaurids, 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
allosaurs (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 carcharodontosaurs (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 carcharodontosaur from Southern
Dobrogea as more closely related to the African Carcharodontosaurus than to the clade of
the South American giant carcharodontosaurs 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 carcharodontosaurs 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 carcharodontosaurs 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; Ósi 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 Ukrainian 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.,
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
carcharodontosaur 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 carcharodontosaur 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 compsgnathids (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 carcharodontosaurs 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 carcharodontosaur 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; Ösi 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., 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, Saurognathos*; 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, Giganotosaurus, 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 tyrannosauroids in parts of Laurasia and abelisauroids in parts of Gondwana. Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-Cenomanian deposits of South America to Carcharodontosauridae (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–Maasrichtian) 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 carcharodontosaurs 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-carcharodontosauine carcharodontosaurs Eocarcharia and Acrocanthosaurus. If this placement is correct, then the Romanian tooth indicates that Carcharodontosaurinae diverged from other carcharodontosaurs considerably earlier than hitherto recognized.

The previously known fossil record of the clade suggested that Carcharodontosaurinae (Acrocanthosaurus, Concavenator, Eocarcharia) were moderately diverse in the Barremian–
Aptian, followed by the appearance of many fossils of carcharodontosaurusines 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 carcharodontosaurusines 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 carcharodontosaurusids (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 \textit{Carcharodontosaurus} and the Giganotosaurini, uniting the similarly Albian–Cenomanian southern South American \textit{Giganotosaurus} and \textit{Mapusaurus} (together with \textit{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 carcharodontosaurs in Southern Dobrogea is a consequence of southern immigration originating in western Gondwan, 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’; KeKenna, 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
tested 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

Absence of documented faunal interactions weakens support for a scenario of south-
to-north immigration of derived carcharodontosauines 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 carcharodontosauroids 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-occurring 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.

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Figure captions

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*,

Aptian, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11

– *Saurognathus*, 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

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ABSTRACT

Some of the best records of continental vertebrates from the Cretaceous of Europe come from Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant dinosaurs and other taxa that lived on islands (the Cornet and 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 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; Sândulescu, 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”, Iaşi, 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 Hârşova Museum) to V. Cotovu from Hârșova (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 Hârșova” (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” (Hârșova 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 Coimirilen; 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 Coimirileni (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 Iaşi, 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 Iaşi 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 Co chirleni (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 (Șândulescu, 1984;
Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,
200 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
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 (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 Lipnița 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-glaucnitic 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 superbus* (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* Kohn (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 microproblematica (=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. kampfneri, 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 squared-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 possess 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 tyrannosaurids. It falls within the convex hull (maximum morphospace
occupation area) of carcharodontosaurids only, although it is closely outside of the edges of
spinosaurid and tyrannosaurid 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 tyrannosaurids (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,
ornithomimosurs, 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 carcharodontosaur. 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 carcharodontosaurs *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 carcharodontosaurs) (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 carcharodontosaurs 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 Hațeg 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).
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 Ukrainian 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.,
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
carcharodontosaur 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 carcharodontosaur documents the
presence of this clade in Europe in the very early Cretaceous. This is significant, as
carcharodontosaurs 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 carcharodontosaurs 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 fossils 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 ornithomimosaurids (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 carcharodontosaurs 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; Ösi 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 carcharodontosaur 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), 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*, *Giganotosaurus*, *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 tyrannosaurs 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 Carcharodontosauridae (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 *Kelmaysaurus* 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-carcharodontosauine 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 carcharodontosaurs
(*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 Bosselini (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
tested 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

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-occurring 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.

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Figure captions


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/).
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