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

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Title: "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.

Dear Editors,

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

Sincerely,

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

Editor comments:

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

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

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

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

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

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

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

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

Page 37, line 917 – ‘KcKenna’ corrected to ‘McKenna’

References:

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

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

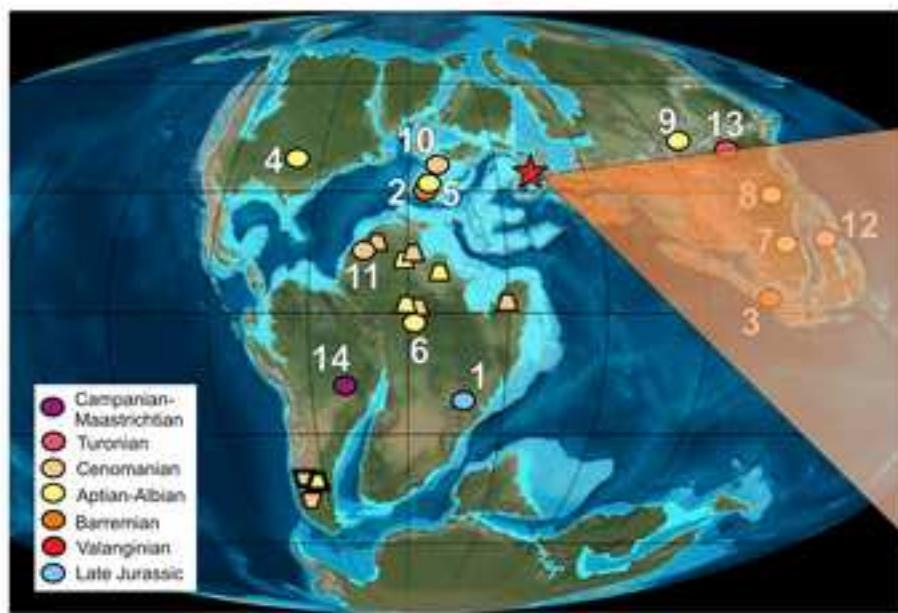
In one of the versions, we have retained our original, chronological formatting, that coincides with that used by Averianov and Sues (2016), while the second version follows the formatting implemented in Csiki-Sava et al. (2016) and also suggested by the Handling Editor. In this second version, we have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

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

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

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



- | | | | | | |
|---|---|---|----------------------------|---|---------------------|
| ○ | basal / indeterminate Carcharodontosauridae | △ | <i>Carcharodontosaurus</i> | ▲ | <i>Mapusaurus</i> |
| ☆ | Romanian carcharodontosaurine | ▽ | <i>Giganotosaurus</i> | ▼ | <i>Tyrannotitan</i> |

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

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15 ABSTRACT

16 Some of the best records of continental vertebrates from the Cretaceous of Europe come from
17 Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant
18 dinosaurs and other taxa that lived on islands (the Cornet and Hațeg Island faunas).
19 Substantially less is known about those vertebrates living in the more stable, cratonic regions
20 of Romania (and Eastern Europe as a whole), particularly during the earliest Cretaceous. We
21 describe one of the few early Early Cretaceous fossils that have ever been found from these
22 regions, the tooth of a large theropod dinosaur from Southern Dobrogea, which was
23 discovered over a century ago but whose age and identification have been controversial. We
24 identify the specimen as coming from the Valanginian stage of the Early Cretaceous, an
25 incredibly poorly sampled interval in global dinosaur evolution, and as belonging to

26 Carcharodontosauridae, a clade of derived, large-bodied apex predators whose earliest
27 Cretaceous history is poorly known. Quantitative analyses demonstrate that the Romanian
28 tooth shows affinities with a derived carcharodontosaurid subgroup, the
29 Carcharodontosaurinae, which until now has been known solely from Gondwana. Our results
30 suggest that this subgroup of colossal predators did not evolved vicariantly as Laurasia split
31 from Gondwana, but originated earlier, perhaps in Europe. The carcharodontosaurine
32 diversification may have been tied to a north-to-south trans-Tethyan dispersal that took place
33 sometime between the Valanginian and Aptian, illustrating the importance of
34 palaeogeographic ties between these two realms during the largely mysterious early–mid
35 Early Cretaceous.

37 Keywords

38 RomaniaSouthern Dobrogea; Lower CretaceousValanginian; Theropoda;
39 Carcharodontosauridae; cratonic Europe; palaeobiogeography

41 1. Introduction

42 Romania boasts one of the best records of continental vertebrate fossils from the Cretaceous
43 of Europe (e.g., Grigorescu, 1992, 2003; Csiki-Sava et al., 2015). The vast majority of fossils
44 come from two well-known occurrences: the Early Cretaceous bauxite accumulations of
45 Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997;
46 Posmoşanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Haţeg,
47 Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the
48 dinosaur-dominated ‘Haţeg Island fauna’ (e.g, Nopcsa, 1923; Weishampel et al., 1991;
49 Benton et al. 2010; Codrea et al., 2010, 2012; Grigorescu, 2010; Vremir, 2010; Vasile and
50 Csiki, 2011; Csiki-Sava et al., 2015). Both of these faunas inhabited islands that were part of

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51 the vast Cretaceous European Archipelago of the Neo-Tethys Ocean. Based on their isolated
52 geological settings and the many dwarfed and morphologically aberrant taxa that make up the
53 faunas, both have been interpreted as insular assemblages that give a unique window into
54 how island environments affected the evolution of long-extinct organisms (e.g., Benton et al.,
55 1997, 2010; Csiki-Sava et al., 2015).

56 The great volume of research on these assemblages over the past century, particularly
57 the ‘Hațeg Island fauna’, has concealed an inconvenient bias: the stable, non-island, cratonic
58 regions of Romania have yielded only extremely rare Mesozoic continental vertebrate
59 remains (i.e., the Moldavian, Moesian and Scythian platforms; Săndulescu, 1984; Mutihac
60 and Mutihac, 2010; Fig. 1). This is mostly because Mesozoic deposits are located in the
61 subsurface in these regions, with only limited subaerial exposures available in the structurally
62 highest-lying parts of the Moesian Platform, in Central and Southern Dobrogea (Middle
63 Jurassic–Upper Cretaceous), as well as in the northeastern-most corner of the Moldavian
64 Platform, along the Prut Valley (lower Upper Cretaceous) (see, e.g., Mutihac and Mutihac,
65 2010). This bias is unfortunate because fossils from these settings could lead to a better
66 understanding of how mainland and island faunas differed during the Cretaceous, and
67 because the cratonic portion of Europe was an important biogeographic stepping stone
68 between the north and south as the continents fragmented and sea levels fluctuated.

69 Although the cratonic regions of Romania have yielded few Cretaceous terrestrial
70 fossils, these deposits are not totally barren. In fact, one of the first Mesozoic continental
71 vertebrates ever recorded from Romania comes from one of these deposits, the Lower
72 Cretaceous shallow marine limestones of Southern Dobrogea (Fig. 1). This specimen—the
73 isolated but well-preserved tooth of a large theropod dinosaur—has often been overlooked. It
74 was described a little over a century ago by Simionescu (1913; Fig. 2A), and until a few
75 recent discoveries of very rare isolated specimens (Stoica and Csiki, 2002; Csiki-Sava et al.,

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76 | 2013, ~~in prep.~~; Dragastan et al., 2014), it remained as the sole published record of Mesozoic
77 terrestrial vertebrates from the cratonic areas of Romania. It has never been comprehensively
78 described and its precise age and taxonomic affinities have yet to be clarified, despite its
79 potential importance as a well-preserved fossil from a poorly sampled area that could have
80 critical evolutionary and biogeographic implications.

81 We here present a comprehensive description of the Dobrogea tooth and discuss its
82 relevance for understanding dinosaur evolution and biogeography. We review the peculiar
83 history of how this specimen was collected and curated, thoroughly document its morphology
84 and age, identify it based on comparison to a broad range of theropods, and outline its
85 importance. It turns out that this specimen, although only a single tooth, has wide-ranging
86 implications. We identify it as coming from the Valanginian stage of the Early Cretaceous,
87 which is incredibly poorly sampled both in Europe and globally (Weishampel et al., 2004),
88 and as belonging to a carcharodontosaurid, a group of derived, large-bodied apex predators
89 whose earliest Cretaceous history is poorly known. Carcharodontosaurids were once thought
90 to be a uniquely Gondwanan group, but recent discoveries show that the basal members of
91 the group were more widespread during the late Early-middle Cretaceous (e.g., Sereno et al.,
92 1996; Brusatte and Sereno, 2008). The Romanian tooth shows affinities with a derived
93 carcharodontosaurid subgroup, the Carcharodontosaurinae, that until now has been known
94 only from Gondwana. It suggests that this subgroup of enormous predators did not evolve
95 vicariantly as Pangaea split, but originated earlier, and perhaps in Europe, suggesting faunal
96 interchange between Europe and Gondwana during the ‘dark ages’ of the early Early
97 Cretaceous.

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

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100 2. History of collecting and curation

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

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

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

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

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

141 After its original description, specimen UAIC (SCM1) 615 underwent a minor
142 amount of damage (see below, Description). Also, at some point between its description in
143 1913 and the early 1960s (when the specimen was found in its present state in the collections
144 of the UAIC by academic staff members who are still alive today and recall the discovery; I.
145 Turculeţ, personal communication, May 2013) it was glued into a limestone matrix holder,
146 while it was obviously completely freed of the surrounding matrix when it was described and
147 figured in 1913 (Fig. 2). The circumstances under which these alterations took place are
148 unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the
149 spring of 1944, the frontline between the German-Romanian and Soviet armies reached the
150 Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

1 151 were packed in crates, and moved together with its personnel and other possessions to Zlatna,
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3 152 in the Apuseni Mountains (western Romania), to safeguard them from any potential damage.
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5 153 Mounting the specimen into the limestone stand would have been a quick way to stabilize it,
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7 154 as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă,
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9 155 personal communication, April 2103). If that was indeed the case, the mounting would have
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11 156 taken place without the knowledge of Simionescu, who left Iași and the UAIC in 1929, being
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13 157 invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă,
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15 158 2010). Then again, however, Simionescu himself or staff of the Hârșova Museum might have
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17 159 re-mounted the tooth after its original description, or else the mounting might have taken
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19 160 place after the return of the collections to Iași, after WWII.
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24 161 Unfortunately, it is not documented whether the mounting was made using the
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26 162 original matrix, or if a trough corresponding to the tooth outline was carved into a randomly
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28 163 chosen limestone block. The apparently excellent fit between the tooth and the depression
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30 164 housing it (Fig. 2B, 3) suggests that this operation was completed carefully, and accurate
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32 165 carving of a fake holder is difficult to reconcile with the rush accompanying the evacuation of
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34 166 the Iași University, in 1944. Alternatively, the presence of a hand-written old registration
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36 167 number on the specimen holder would support its early re-mounting, while still at the
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38 168 Hârșova Museum. As noted previously, the original Hârșova Museum registration number of
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40 169 the specimen was 200, which does not correspond to that currently written both on the
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42 170 limestone holder and on a paper sticker (204). However, according to the old collection
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44 171 registry of the Hârșova Museum, specimen numbers 201 through 225 were given to a series
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46 172 of “indeterminate (fossil) bone fragments” from the “Cochirleni quarries”. Thus, these
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48 173 specimens (now apparently lost) came from the same locality as the tooth, and they were
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50 174 collected and donated by the same person to the Museum who donated UAIC (SCM1) 615.
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52 175 There is, thus, a (albeit admittedly remote) possibility that the registration numbers were
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176 mixed up during the re-mounting of the specimen, which in this case took place at an early
177 date in the Hârșova Museum. If this is indeed the case, the limestone used as holder could
178 have been the same as the original matrix of the specimen.

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

189 190 3. Geological setting

191 According to the available collecting information, the isolated theropod tooth UAIC (SCM1)
192 615 was discovered at Cochirleni (sometimes noted more specifically as the “*Cochirleni*
193 *quarry*” or “*Cokerleni quarry*”). Cochirleni is a small village in southwestern Dobrogea
194 situated close to the right bank of the Danube, and about 9 km south of the main urban center
195 of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of
196 the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous
197 deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).

198 Southern Dobrogea is a cratonic area corresponding to the southeastern corner of
199 Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984;
200 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
202 end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine:
203 Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001;
204 Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from
205 Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

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

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

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

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

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

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

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

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

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

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

287 4. Palaeontology

288 The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova
289 Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu
290 (1913), who referred it to *Megalosaurus cf. superbis*, a taxon erected by Sauvage (1882)
291 from the Gault ('mid'-Cretaceous: Albian) of the Paris Basin, France. The Gault material
292 described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were
293 deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of
294 *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was
295 referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it
296 and the type species *M. bucklandi*.

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

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301 Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al.
302 (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered
303 *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.”
304 Accordingly, if we are following the original assessment of Simionescu (1913) but updating
305 with contemporary taxonomy, the Cochirleni theropod tooth should now be considered
306 referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to
307 *Erectopus superbus* (or a close relative) was considered to be unsupported by positive
308 evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to
309 understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B,
310 3), we provide here a detailed description of its morphology followed by a thorough
311 comparative study of this tooth based on large datasets of theropod dental measurements and
312 discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).

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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

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

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

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

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3 351 Dobrinescu, personal communication, November 2013), an assemblage that suggests a
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5 352 Berriasian–Hauterivian age of the limestone holder.

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7 353 Since it is not clear if the limestone holder came from the same site as the tooth itself,
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9 354 we managed to take a second sample from the limestone matrix still partly filling the pulp
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11 355 cavity of the tooth, which must definitively be identical with the rocks the tooth was found in.
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13 356 This second, much smaller sample yielded only very scarce specimens of *Watznaueria*
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15 357 *barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-
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17 358 Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in
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19 359 abundance during the Berriasian and, especially, the Valanginian.

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22 360 In the nannoplankton succession reported previously by Avram et al. (1993) and
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24 361 derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the
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26 362 concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus*
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28 363 *lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu
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30 364 Member of the Cernavodă Formation. These assemblages were interpreted to represent the
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32 365 nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was
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34 366 assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous
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36 367 of the Mecsek Mountains, Hungary, by Császár et al. (2000).

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39 368 Together, all the available evidence (Simionescu's original account, geographic and
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41 369 geologic records, foraminifera, ostracods, microproblematicae, and calcareous
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43 370 nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member
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45 371 of the Cernavodă Formation, and it is most probably of late Valanginian age.

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52 53 373 *4.2. Description and comparisons*

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56 374 Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2,
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58 375 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown

376 base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of
377 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is
378 remarkably well preserved, with the enamel in pristine condition. It preserves most of the
379 crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5
380 mm missing in the apical region.

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

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

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

1 401 exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of
2 402 the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about
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4 403 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5
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7 404 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes
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9 405 thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but
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11 406 thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B).
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13 407 Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped
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15 408 (Fig. 3D).
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19 409 The tooth is ziphodont and only very slightly recurved distally. The distal edge is
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21 410 nearly straight across its length, being very mildly concave in its basal half and slightly
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23 411 convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the
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25 412 tooth crown base. The mesial edge, as shown in the original publication of Simionescu
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27 413 (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually
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29 414 compressed (Fig. 3B), with a crown base ratio ($CBR=CBW/CBL$) of 0.56, within the normal
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31 415 range of variation of most theropods. This differs from the thinner teeth of some, but not all,
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33 416 carcharodontosaurids ($CBR<0.50$), and the much thicker incrassate teeth of derived
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35 417 tyrannosauroids and conical teeth of spinosaurids ($CBR>0.75$) (Serenó et al., 1996; Brusatte
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37 418 et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).
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43 419 The crown cross-section is slightly asymmetrical labiolingually when it is seen in
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45 420 distal view. In this view, when the carina is facing directly distally, one side of the crown has
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47 421 a more pronounced bulge than its counterpart (about 8.5 mm wide, measured from the carina,
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49 422 vs. 6 mm on the other side; Fig. 3B); based on comparisons with the teeth of *Mapusaurus*
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51 423 (Coria and Currie, 2006), the more bulging side can be interpreted as the lingual one. This
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53 424 asymmetry diminishes apically, where both sides become about equally convex. The distal
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55 425 carina itself twists slightly sideways (labially) in apical direction, such that it is located closer
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426 to the labial face where it terminates at the crown apex, and the lingual face of the denticles is
427 exposed distally (Fig. 3B, F). This twist of the distal carina is accompanied by a similar
428 outline of the lingual side; in distal view, this is somewhat convex basally, but becomes flat
429 to slightly concave in the apical two-thirds of the crown. A similar S-shaped curvature of the
430 crown, albeit more pronounced and different in details, was also reported in *Mapusaurus* and
431 *Giganotosaurus* (Coria and Currie, 2006), and in indeterminate carcharodontosaurid teeth
432 from Morocco (Richter et al., 2013).

433 The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with
434 minute serrations across its entire preserved length; the denticles are proximodistally
435 subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig.
436 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are
437 oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so
438 it is not possible to determine whether the serrations continued over the apex of the tooth.
439 There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the
440 carina. Serration shape and size remain relatively constant across the carina, although the
441 serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig.
442 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F).
443 Changes in serration size are gradual across the carina, not sudden or sporadic.

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

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451 separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length.

452 The interdenticular space between adjacent denticles is broad, measuring more than a third of
453 the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the
454 crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These
455 sulci are so short and indistinct that they are only visible under low angle light.

456 Little can be said about the mesial carina, as it is not visible in the current state of the
457 specimen, buried in the limestone matrix. Based on the description of Simionescu (1913),
458 however, it is covered across its length with minute serrations; these decrease in size towards
459 the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles)
460 per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly
461 smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and
462 Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus,
463 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends
464 towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii*
465 where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*’
466 *superbus* (Sauvage, 1876, 1882) in this respect.

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

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

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476 that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly
477 developed wrinkles are present along the crown height; in the basal half of the crown, the
478 wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer
479 than twice the space separating each undulation. The wrinkles project obliquely (in the
480 mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal
481 segment on the crown, and curve apically as they approach the carina (at about 45°) with a
482 tendency to become tangential to the distal edge. The wrinkles are especially well developed,
483 prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig.
484 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm).
485 Apically, however, the wrinkles are somewhat wider and longer, extending over about half of
486 the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the
487 crown in wrinkle development as well, these being better expressed on the more rounded,
488 convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the
489 presumed labial face, only some of the basal-most wrinkles, particularly the second and third
490 one, appear well defined.

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

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56 499 5. Discussion

58 500 5.1. *Identification of UAIC (SCM1) 615*

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

504 Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert
505 (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are
506 also known to possess remarkably theropod-like, laterally compressed and serrated teeth, not
507 unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are
508 significantly smaller than the Southern Dobrogean specimen, especially in the case of the
509 Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest,
510 caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene
511 *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615;
512 moreover, these teeth are slightly conical and less laterally compressed than the Southern
513 Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia
514 appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly
515 younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true
516 denticles along their carinae) are reported in Europe only beginning in the Albian (Ősi et al.,
517 2015), and these are both significantly smaller and different in morphology from the
518 Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian
519 affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a
520 theropod tooth.

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

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

526 (2005) and Larson and Currie (2013), and it or a similar version has been used in recent
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2 527 studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, ~~2013~~2014; Brusatte
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5 528 and Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL,
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7 529 CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at
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10 530 the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to
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12 531 this dataset, the data were log-transformed prior to analysis, missing values for measurements
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15 532 were estimated with a mean value for that measurement from across the sample, and then a
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17 533 PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17
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19 534 (Hammer et al., 2001).

22 535 In the resulting two dimensional morphospace (Fig. 4), UAIC (SCM1) 615 plots close
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24 536 to many teeth belonging to carcharodontosaurids, along with some teeth belonging to
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27 537 spinosaurids and tyrannosauroids. It falls within the convex hull (maximum morphospace
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29 538 occupation area) of carcharodontosaurids only, although it is closely outside of the edges of
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32 539 spinosaurid and tyrannosauroid space. It also falls within the 95% confidence interval ellipse
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34 540 for carcharodontosaurids, but not within the ellipse of any other group (Supplementary
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37 541 Information). This exercise indicates that UAIC (SCM1) 615 is most similar to
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39 542 carcharodontosaurids.

41 543 Secondly, we used the log-transformed dataset that we also used for the PCA to
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44 544 conduct a clustering analysis. We performed the analysis in PAST v2.17, using the paired
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46 545 group algorithm and the correlation similarity measure. In the resulting dendrogram, UAIC
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49 546 (SCM1) 615 groups with a handful of teeth belonging to carcharodontosaurids,
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51 547 tyrannosauroids, and *Allosaurus* (Supplementary Information).

54 548 Third, we used the tooth measurement database to conduct a discriminant analysis in
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56 549 PAST v3.0 (Hammer et al., 2001). This analysis uses pre-determined groups (in this case,
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59 550 taxonomic clusters) to create a morphospace in which these groups are maximally separated.

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

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

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

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

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

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

601 this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very
602 derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and
603 *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno
604 (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as
605 recovered in our analysis, is congruent with results of previous analyses based on larger sets
606 of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno,
607 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015),
608 and offers some support for considering the Romanian carcharodontosaurid from Southern
609 Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of
610 the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

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

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

626 (SCM1) 615 as a carcharodontosaurid. Instead, *Erectopus* groups with abelisauroids in the
627 phylogenetic analysis. This is somewhat surprisingly, as Allain (2005) and Carrano et al.
628 (2012) both identified *Erectopus* as a tetanuran. It should be noted, however, that Albian-
629 aged abelisauroids are known from the same general area (eastern France) as that yielding the
630 material referred to *Erectopus* (Accarie et al., 1995; Carrano and Sampson, 2008), raising the
631 intriguing possibility that this taxon may represent an abelisauroid instead of an allosauroid
632 tetanuran as suggested by Allain (2005) and Carrano et al. (2012). However, it must be
633 remembered that this phylogenetic analysis is based on dental characters only, so it is
634 probably more likely that *Erectopus* is a tetanuran with a dentition convergent to some extent
635 with those of certain abelisauroids.

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637 5.2. Body size of UAIC (SCM1) 615

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

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

654 It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized
655 carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic
656 carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Serenó et al., 1996; Calvo
657 and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close
658 relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn,
659 corroborates growing evidence that very large body size was acquired very early in
660 carcharodontosaurid history, since the earliest potential members of the clade are already of
661 relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is
662 *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and
663 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more
664 derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the
665 uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see
666 below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized
667 carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.

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

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

688 5.3. UAIC (SCM1) 615 and Valanginian dinosaur distribution

690 Besides documenting the presence of large-sized mainland carcharodontosaurids in the
691 Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a
692 significant gap in our knowledge on the composition and distribution of the Early Cretaceous
693 dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed
694 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these
695 being known from the later part (Barremian–Albian) of that epoch; only around a dozen
696 localities were listed from each age of the early part of the Early Cretaceous (Berriasian,
697 Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous
698 dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al.,
699 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs
700 and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards

1 701 western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no
2 702 occurrences are known from the entire central, eastern and southern Europe for the
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4 703 Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–
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6 704 Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et
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8 705 al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the
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10 706 carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in
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12 707 Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).
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17 708 Our identification of the Romanian tooth as a carcharodontosaurid documents the
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19 709 presence of this clade in Europe in the very early Cretaceous. This is significant, as
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21 710 carcharodontosaurids were widely distributed tens of millions of years later, in the middle
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23 711 Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see
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25 712 below). Despite the recent discoveries documenting that the clade was also present in North
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27 713 America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and
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29 714 Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in
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31 715 Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010;
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33 716 see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older
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35 717 than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than
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37 718 previously thought and were a long-term component of the European mainland Early
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39 719 Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might
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41 720 have been already present between the cratonic, stable European mainland, with a dinosaur
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43 721 fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine
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45 722 areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those
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47 723 described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania
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49 724 (Benton et al., 2006).
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725 This Valanginian carcharodontosaurid represents an important datapoint not only for
726 the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a
727 poorly documented age in dinosaur evolution, with very few precisely dated fossil
728 occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of
729 Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known
730 from Asia, some of which have debatable or controversial dates. These include sites in Japan
731 (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009
732 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these
733 assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age
734 constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible
735 Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992;
736 Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were
737 shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare
738 dinosaur remains of possible Valanginian (or ‘Neocomian’) age were also reported from
739 southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g.,
740 Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli
741 et al., 2014).

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

1 750 carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz,
2 751 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest
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4 752 that carcharodontosaurids had not achieved a wide geographic distribution by this point in
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7 753 time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.
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10 754 Finally, the presence of the Cochirleni carcharodontosaurid might hint at the presence
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12 755 of palaeobiogeographic provinciality between the western and the eastern parts of Europe,
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14 756 partly mirroring those reported from the later part of the Late Cretaceous (e.g., Le Loeuff and
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17 757 Buffetaut, 1995; Weishampel et al., 2010; Ösi et al., 2012; Csiki-Sava et al., 2015). In the
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19 758 reasonably well sampled, and significantly better known, western European dinosaur faunas,
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22 759 Valanginian large carnivorous dinosaurs include non-carcharodontosaurid tetanurans
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24 760 (*Becklespinax*), as well as indeterminate allosauroids or indeterminate theropods (often
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27 761 described as ‘*Megalosaurus*’ *dunkeri*, ‘*M.*’ *insignis* or ‘*M.*’ *oweni*), none of which can be
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29 762 referred positively to Carcharodontosauridae (Carrano et al., 2012). The apparently
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32 763 provincial geographic distribution of the large-bodied theropods suggests that some degree of
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34 764 faunal differentiation was occurring within the European mainland, most probably promoted
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36 765 by geographic distance. Notably, this intra-European differentiation in theropod assemblages
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39 766 appears to stand in contrast with the faunal homogeneity reported in the case of the
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41 767 ornithopods from the UK and Romania (e.g., Galton, 2009). It is important, however, to re-
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44 768 emphasize at this point that the Valanginian dinosaur fossil record is both exceedingly poor
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46 769 and patchy, even in Europe. Accordingly, further discoveries are needed to verify and support
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49 770 (or contradict) the presence of such a distribution pattern pointing to palaeobiogeographic
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51 771 provinciality inside Europe, as the one suggested by our carcharodontosaurid identification
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53 772 for UAIC (SCM1) 615.
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58 774 *5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography*
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775 Carcharodontosauridae were long considered as an exclusively Gondwanan group of
776 theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa
777 (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–
778 Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996;
779 Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte,
780 2008; Cau et al., 2013). This view started to change with the identification of the Early
781 Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal
782 carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and
783 Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic
784 distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan
785 one, was further supported by the discovery of definitive carcharodontosaurids in the Lower
786 Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper
787 Cretaceous of China (Brusatte et al., 2009, 2010b, ~~2012~~; Mo et al., 2014; Lü et al.,
788 ~~2014~~2016).

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

799 | 2012), and eastern Asia (*Kelmaysaurus*; Brusatte et al., 2012; Lü et al., 2014; Mo et al.,
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2 800 | 2014; Lü et al., 2016).

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5 801 | During the Albian–Turonian, carcharodontosaurids became especially abundant and
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7 802 | diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996;
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9 803 | Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and
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11 804 | South America (*Tyrannotitan*, *Giganotosaurus*, *Mapusaurus*, alongside with indeterminate
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13 805 | carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005;
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15 806 | Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig.
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17 807 | 5B). They were still present during this time interval in other continents, as well: in North
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19 808 | America with *Acrocanthosaurus* until the Albian (D’Emic et al., 2012), in Europe until the
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21 809 | Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with
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23 810 | *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).

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29 811 | After dominating terrestrial ecosystems at least in Africa, South America and eastern
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31 812 | Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et
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33 813 | al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the
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35 814 | Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado,
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37 815 | 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large
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39 816 | theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana.
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41 817 | Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-
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43 818 | Cenomanian deposits of South America to Carcharodontosaridae (e.g., Canudo et al., 2008;
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45 819 | Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the
46
47 820 | abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were
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49 821 | reported to suggest the survival of carcharodontosaurids into the latest Cretaceous
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51 822 | (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).

823 Contrasting with this rich and relatively continuous fossil record of
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2 824 Carcharodontosauridae starting with the Aptian, the first half of its evolutionary history is
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4
5 825 very poorly documented (Fig. 5B). Prior to the identification of UAIC (SCM1) 615, only two
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7 826 occurrences of pre-Aptian Cretaceous carcharodontosaurids were reported, one from the
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9 827 Barremian of Spain (Ortega et al., 2010; Gasca et al., 2014) and the other from the Barremian
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11 828 of Thailand (Buffetaut and Suteethorn, 2012). The Early Cretaceous *Kelmaysaurus* from
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13 829 Xinjiang, western China, was recognized as a carcharodontosaurid of possibly ?Valanginian
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15 830 to Aptian in age by Brusatte et al. (2012), but the deposits yielding these remains (the
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17 831 Lianmugin, or Lianmuxin, Formation of the Tugulu Group) were dated as Aptian–Albian by
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19 832 Eberth et al. (2001; see also Tong et al., 2009). An important temporal gap – of about 20 to
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21 833 28 millions of years, according to the dates in Gradstein et al. (2012) – thus stretched between
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23 834 the oldest, tentatively assigned carcharodontosaurids from the Oxfordian–Tithonian of
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25 835 Tanzania, including the formally erected *Veterupristisaurus* (Rauhut, 2011; see also Carrano
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27 836 et al., 2012), and those that started to appear in the fossil record in the Barremian and then
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29 837 spread widely during the Aptian. Referral of UAIC (SCM1) 615 to Carcharodontosauridae
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31 838 partially fills this frustrating gap, effectively halving this shadowy period in the evolutionary
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33 839 history of the group.
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41 840 Furthermore, our analyses tentatively cluster the Dobrogean theropod with the derived
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43 841 members of the Carcharodontosaurinae to the exclusion of the more basal, but significantly
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45 842 younger non-carcharodontosaurine carcharodontosaurids *Eocarcharia* and *Acrocanthosaurus*.
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47 843 If this placement is correct, then the Romanian tooth indicates that Carcharodontosaurinae
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49 844 diverged from other carcharodontosaurids considerably earlier than hitherto recognized.
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53 845 The previously known fossil record of the clade suggested that Carcharodontosaurinae
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55 846 originated sometime between the Aptian and Albian, as basal carcharodontosaurids
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57 847 (*Acrocanthosaurus*, *Concavenator*, *Eocarcharia*) were moderately diverse in the Barremian–
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1 848 Aptian, followed by the appearance of many fossils of carcharodontosaurines beginning in
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3 849 the Albian (Fig. 5B). The proposed affinities of the oldest carcharodontosaurid material –
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5 850 including isolated teeth referred to as ‘*Megalosaurus*’ *ingens* – from the east African Upper
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7 851 Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut,
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9 852 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC
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11 853 (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with
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13 854 the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very
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15 855 large size and dental morphology characterizing it) well before the Albian, during or even
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17 856 before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and
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19 857 *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the
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21 858 basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.
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26 859 Besides shifting the emergence of the carcharodontosaurines earlier in time,
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28 860 identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting
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30 861 palaeobiogeographic implications. As already noted, recent discoveries show that
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32 862 Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g.,
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34 863 Novas et al., 2005), with the identification of its widespread, Pangaeian distribution during the
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36 864 late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999;
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38 865 Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014).
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40 866 However, within Carcharodontosauridae itself, some palaeogeographic patterns have been
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42 867 widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae
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44 868 is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al.,
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46 869 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as
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48 870 previously all its recognized members were restricted strictly to either Africa (Stromer, 1931;
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50 871 Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995;
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52 872 Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of
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873 Carcharodontosaurinae were still adhering to patterns of continental fragmentation and
874 vicariant evolution, with a basal split between the Albian–Cenomanian African
875 *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian
876 southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if
877 this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

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

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

898 Alternatively, it can be hypothesized that appearance of carcharodontosaurines in
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2 899 Southern Dobrogea is a consequence of southern immigration originating in western
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5 900 Gondwana, often considered the place of origin for this clade. However, this scenario has
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7 901 several potential caveats. Although Europe has been considered as forming part of a larger
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9 902 Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín,
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11 903 2012), and occasional trans-Tethyan faunal connections have been recognized between
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14 904 Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage,
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16 905 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and
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18 906 Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-
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20 907 Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place
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22 908 during the ‘Neocomian’ (Berriasian–Hauterivian) time interval.
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26 909 More recently, some potential evidence has emerged for Gondwana-to-Europe
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28 910 interchange during the ‘Neocomian’. The presence of the basal rebbachisaurid *Histriasaurus*
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30 911 (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as
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32 912 indicative of very early and very rapid northward dispersal of this clade from western
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34 913 Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of
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36 914 this particular dispersal event was even constrained to the Berriasian–Valanginian time
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38 915 interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the
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40 916 Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of
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42 917 the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian
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44 918 Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive
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46 919 transportation mechanism (‘Noah’s Ark’; ~~KeKennaMcKenna~~, 1973) for basal
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48 920 rebbachisaurids after its separation from mainland Africa (e.g., Torcida Fernández-Baldor et
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51 921 al., 2011). Furthermore, the palaeogeographical separation between Africa and Adria (and
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53 922 thus the effective movement of the presumed ark) is considered to be at most an incipient one
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1 923 during the Early Cretaceous by Bossellini (2002) and Zarccone et al. (2010), with spatial
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3 924 continuity still present between the two landmasses, while deep-water basins continued to
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5 925 separate Adria from the European Craton. Accordingly, although the presence of
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7 926 *Histriasaurus* can represent a case of northward range extension of rebbachisaurids during
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9 927 the Berriasian–Valanginian, it took place not strictly speaking into Europe, but only reached
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11 928 the northernmost extremity of Adria, a northerly peninsular extension of the African
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13 929 mainland. It was only starting with the Barremian that rebbachisaurids dispersed as far north
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15 930 as the European cratonic areas, including Iberia and the British Isles (Mannion, 2009;
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17 931 Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011), a time when faunal
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19 932 interchanges between Europe and Africa are considered to have been well underway (e.g.,
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21 933 Gheerbrant and Rage, 2006; Canudo et al., 2009).

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26 934 Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant
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28 935 of the European mainland. It is thus unclear to what extent the example of rebbachisaurid
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30 936 range extension into (present-day) Europe during the early Early Cretaceous, as potentially
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32 937 testified by the discovery of the Croatian taxon, would also be applicable for the Southern
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34 938 Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are
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36 939 very different, and that faunal connections during this time interval are not documented
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38 940 between the African and European cratons as already pointed out by Gheerbrant and Rage
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40 941 (2006).

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45 942 Absence of documented faunal interactions weakens support for a scenario of south-
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47 943 to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the
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49 944 Cretaceous, and would argue instead for a local, European development to explain the
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51 945 presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian
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53 946 presence of carcharodontosaurids in Europe is also consistent with their appearance in the
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55 947 Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the
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1 948 eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in
2 949 North America likely requires the presence of pre-Aptian members of the clade in Europe,
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4 950 since faunal exchanges between these two landmasses are known to have been halted before
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7 951 the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal
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9 952 carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the
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11 953 derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western
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13 954 Gondwana. The causes of these distribution patterns remain as yet unknown, and further
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15 955 support – in the form on new carcharodontosaurid discoveries from the early-middle part of
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17 956 the Early Cretaceous – is required to better uphold such a scenario.

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19 957 We finally reiterate that if the Romanian tooth does not belong to a
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21 958 carcharodontosaurine, but instead is artefactually grouping with them in the phylogenetic
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23 959 analysis because of the very incomplete nature of the material, then the traditional story of
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25 960 Carcharodontosaurinae as a product of vicariant evolution driven by the breakup of Pangea
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27 961 will remain strongly supported. However, even in such case UAIC (SCM1) 615 would still
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29 962 record the presence of early-occurring large carcharodontosaurid theropods with a very
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31 963 characteristic carcharodontosaurine-type dentition in the eastern part of the European craton,
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33 964 adding to known early Early Cretaceous theropod (and dinosaur) diversity, and potentially
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35 965 documenting dinosaur faunal provinciality in Europe and worldwide.

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37 967 6. Conclusions

38 968 We re-describe and interpret the affinities of one of the most significant historical dinosaurian
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40 969 specimens of Romania, an isolated but well-preserved theropod tooth from Southern
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42 970 Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth,
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44 971 while the available evidence – including novel calcareous nannoplankton sampling – supports
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46 972 its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of

1 973 Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a
2 974 collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only
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4 975 two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this
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7 976 record advances our understanding of European dinosaur distribution during the early Early
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9 977 Cretaceous, and also fills an important palaeogeographic gap between Western European and
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11 978 Eastern Asian dinosaurian assemblages of the Valanginian.

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14 979 Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a
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16 980 possible member of Carcharodontosaurinae, a subclade of derived and gigantic
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18 981 carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western
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20 982 Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean
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22 983 specimen documents the emergence of Carcharodontosaurinae earlier than previously
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24 984 recognized, thus also indicating an earlier acquisition of their characteristically large size.

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26 985 Based on currently known palaeogeographic and chronostratigraphic constraints on the
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28 986 evolution of Carcharodontosauridae, it appears that not only did this clade have a wide
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30 987 distribution, but that crucial events of its evolutionary history such as the emergence of the
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32 988 derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of
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34 989 western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia
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36 990 split, as was formerly suggested. In such a case, instead of endemic evolution the emergence
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38 991 of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-
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40 992 to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the
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42 993 Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into
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44 994 western Gondwana adds further support for the presence of important palaeogeographic ties
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46 995 between the two realms during the second half of the Early Cretaceous.

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39 1548 Figure captions
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41 1549 Figure 1. Simplified geological map of the Cernavodă-Cochirleni area; inset shows the
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44 1550 position of the study area within Romania. Legend: 1. Quaternary: a. Holocene alluvia, b.
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46 1551 Pleistocene–Holocene loessoid deposits; 2. Pre-Quaternary Cenozoic (Middle Eocene and
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49 1552 Miocene) deposits; Cretaceous: 3. Peștera Formation, Lower Cenomanian; 4. Cochirleni
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51 1553 Formation; uppermost Aptian–Lower Albian; 5. Gherghina Formation, Middle–Upper
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54 1554 Aptian; 6. Ostrov (= Ramadan) Formation; Barremian–Lower Aptian; 7. Cernavodă
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56 1555 Formation, Alimanu Member, Berriasian–Valanginian; 8. Water courses. (Redrawn after
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58 1556 Dragastan et al., 1998, 2014).
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2 1558 Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from
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5 1559 Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B.
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7 1560 Current state of UAIC (SCM1) 615, mounted in a limestone holder.
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12 1562 Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid
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15 1563 lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B.,
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17 1564 distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina
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19 1565 (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal
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22 1566 part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).
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27 1568 Figure 4. Dental morphospace of the different theropod clades according to the results of the
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29 1569 PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by
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32 1570 Carcharodontosauridae. See further details of this analysis, as well as other quantitative
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34 1571 analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant
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36 1572 function analysis, phylogenetic analysis), in the Supplementary Material.
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41 1574 Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur
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44 1575 occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-
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46 1576 Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the
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49 1577 marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and
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51 1578 palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian
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54 1579 (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615
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56 1580 from Southern Dobrogea. Legend: 1 – *Veterupristisaurus*, ‘*Megalosaurus*’ *ingens*,
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58 1581 Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator*, Spain, Barremian;
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1582 3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern
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2 1583 United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 –
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5 1584 *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China,
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7 1585 Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmayisaurus*,
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10 1586 Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11
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12 1587 – *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan,
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15 1588 Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 –
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17 1589 Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant
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1 “*Megalosaurus cf. superbus*” from southeastern Romania: the oldest known Cretaceous
2 carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous
3 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

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26 Cretaceous history is poorly known. Quantitative analyses demonstrate that the Romanian
27 tooth shows affinities with a derived carcharodontosaurid subgroup, the
28 Carcharodontosaurinae, which until now has been known solely from Gondwana. Our results
29 suggest that this subgroup of colossal predators did not evolved vicariantly as Laurasia split
30 from Gondwana, but originated earlier, perhaps in Europe. The carcharodontosaurine
31 diversification may have been tied to a north-to-south trans-Tethyan dispersal that took place
32 sometime between the Valanginian and Aptian, illustrating the importance of
33 palaeogeographic ties between these two realms during the largely mysterious early–mid
34 Early Cretaceous.

36 Keywords

37 Southern Dobrogea; Valanginian; Carcharodontosauridae; cratonic Europe;
38 palaeobiogeography

40 1. Introduction

41 Romania boasts one of the best records of continental vertebrate fossils from the Cretaceous
42 of Europe (e.g., Grigorescu, 1992, 2003; Csiki-Sava et al., 2015). The vast majority of fossils
43 come from two well-known occurrences: the Early Cretaceous bauxite accumulations of
44 Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997;
45 Posmoşanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Haţeg,
46 Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the
47 dinosaur-dominated ‘Haţeg Island fauna’ (e.g, Nopcsa, 1923; Weishampel et al., 1991;
48 Benton et al. 2010; Codrea et al., 2010, 2012; Grigorescu, 2010; Vremir, 2010; Vasile and
49 Csiki, 2011; Csiki-Sava et al., 2015). Both of these faunas inhabited islands that were part of
50 the vast Cretaceous European Archipelago of the Neo-Tethys Ocean. Based on their isolated

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51 geological settings and the many dwarfed and morphologically aberrant taxa that make up the
52 faunas, both have been interpreted as insular assemblages that give a unique window into
53 how island environments affected the evolution of long-extinct organisms (e.g., Benton et al.,
54 1997, 2010; Csiki-Sava et al., 2015).

55 The great volume of research on these assemblages over the past century, particularly
56 the ‘Hațeg Island fauna’, has concealed an inconvenient bias: the stable, non-island, cratonic
57 regions of Romania have yielded only extremely rare Mesozoic continental vertebrate
58 remains (i.e., the Moldavian, Moesian and Scythian platforms; Săndulescu, 1984; Mutihac
59 and Mutihac, 2010; Fig. 1). This is mostly because Mesozoic deposits are located in the
60 subsurface in these regions, with only limited subaerial exposures available in the structurally
61 highest-lying parts of the Moesian Platform, in Central and Southern Dobrogea (Middle
62 Jurassic–Upper Cretaceous), as well as in the northeastern-most corner of the Moldavian
63 Platform, along the Prut Valley (lower Upper Cretaceous) (see, e.g., Mutihac and Mutihac,
64 2010). This bias is unfortunate because fossils from these settings could lead to a better
65 understanding of how mainland and island faunas differed during the Cretaceous, and
66 because the cratonic portion of Europe was an important biogeographic stepping stone
67 between the north and south as the continents fragmented and sea levels fluctuated.

68 Although the cratonic regions of Romania have yielded few Cretaceous terrestrial
69 fossils, these deposits are not totally barren. In fact, one of the first Mesozoic continental
70 vertebrates ever recorded from Romania comes from one of these deposits, the Lower
71 Cretaceous shallow marine limestones of Southern Dobrogea (Fig. 1). This specimen—the
72 isolated but well-preserved tooth of a large theropod dinosaur—has often been overlooked. It
73 was described a little over a century ago by Simionescu (1913; Fig. 2A), and until a few
74 recent discoveries of very rare isolated specimens (Stoica and Csiki, 2002; Csiki-Sava et al.,
75 2013; Dragastan et al., 2014), it remained as the sole published record of Mesozoic terrestrial

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76 vertebrates from the cratonic areas of Romania. It has never been comprehensively described
77 and its precise age and taxonomic affinities have yet to be clarified, despite its potential
78 importance as a well-preserved fossil from a poorly sampled area that could have critical
79 evolutionary and biogeographic implications.

80 We here present a comprehensive description of the Dobrogea tooth and discuss its
81 relevance for understanding dinosaur evolution and biogeography. We review the peculiar
82 history of how this specimen was collected and curated, thoroughly document its morphology
83 and age, identify it based on comparison to a broad range of theropods, and outline its
84 importance. It turns out that this specimen, although only a single tooth, has wide-ranging
85 implications. We identify it as coming from the Valanginian stage of the Early Cretaceous,
86 which is incredibly poorly sampled both in Europe and globally (Weishampel et al., 2004),
87 and as belonging to a carcharodontosaurid, a group of derived, large-bodied apex predators
88 whose earliest Cretaceous history is poorly known. Carcharodontosaurids were once thought
89 to be a uniquely Gondwanan group, but recent discoveries show that the basal members of
90 the group were more widespread during the late Early-middle Cretaceous (e.g., Sereno et al.,
91 1996; Brusatte and Sereno, 2008). The Romanian tooth shows affinities with a derived
92 carcharodontosaurid subgroup, the Carcharodontosaurinae, that until now has been known
93 only from Gondwana. It suggests that this subgroup of enormous predators did not evolve
94 vicariantly as Pangaea split, but originated earlier, and perhaps in Europe, suggesting faunal
95 interchange between Europe and Gondwana during the ‘dark ages’ of the early Early
96 Cretaceous.

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

98

99 2. History of collecting and curation

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

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

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

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

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

140 After its original description, specimen UAIC (SCM1) 615 underwent a minor
141 amount of damage (see below, Description). Also, at some point between its description in
142 1913 and the early 1960s (when the specimen was found in its present state in the collections
143 of the UAIC by academic staff members who are still alive today and recall the discovery; I.
144 Turculeţ, personal communication, May 2013) it was glued into a limestone matrix holder,
145 while it was obviously completely freed of the surrounding matrix when it was described and
146 figured in 1913 (Fig. 2). The circumstances under which these alterations took place are
147 unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the
148 spring of 1944, the frontline between the German-Romanian and Soviet armies reached the
149 Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

150 were packed in crates, and moved together with its personnel and other possessions to Zlatna,
151 in the Apuseni Mountains (western Romania), to safeguard them from any potential damage.
152 Mounting the specimen into the limestone stand would have been a quick way to stabilize it,
153 as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă,
154 personal communication, April 2103). If that was indeed the case, the mounting would have
155 taken place without the knowledge of Simionescu, who left Iași and the UAIC in 1929, being
156 invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă,
157 2010). Then again, however, Simionescu himself or staff of the Hârșova Museum might have
158 re-mounted the tooth after its original description, or else the mounting might have taken
159 place after the return of the collections to Iași, after WWII.

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

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

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

189 3. Geological setting

190 According to the available collecting information, the isolated theropod tooth UAIC (SCM1)
191 615 was discovered at Cochirleni (sometimes noted more specifically as the “*Cochirleni*
192 *quarry*” or “*Cokerleni quarry*”). Cochirleni is a small village in southwestern Dobrogea
193 situated close to the right bank of the Danube, and about 9 km south of the main urban center
194 of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of
195 the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous
196 deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).

197 Southern Dobrogea is a cratonic area corresponding to the southeastern corner of
198 Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984;
199 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
201 end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine:
202 Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001;
203 Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from
204 Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

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

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

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

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

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

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

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

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

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

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

286 4. Palaeontology

287 The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova
288 Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu
289 (1913), who referred it to *Megalosaurus cf. superbus*, a taxon erected by Sauvage (1882)
290 from the Gault ('mid'-Cretaceous: Albian) of the Paris Basin, France. The Gault material
291 described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were
292 deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of
293 *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was
294 referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it
295 and the type species *M. bucklandi*.

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

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300 Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al.
301 (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered
302 *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.”
303 Accordingly, if we are following the original assessment of Simionescu (1913) but updating
304 with contemporary taxonomy, the Cochirleni theropod tooth should now be considered
305 referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to
306 *Erectopus superbus* (or a close relative) was considered to be unsupported by positive
307 evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to
308 understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B,
309 3), we provide here a detailed description of its morphology followed by a thorough
310 comparative study of this tooth based on large datasets of theropod dental measurements and
311 discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).

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

319 320 4.1. Age of UAIC (SCM1) 615

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

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

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

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

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5 350 Dobrinescu, personal communication, November 2013), an assemblage that suggests a

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7 351 Berriasian–Hauterivian age of the limestone holder.

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9 352 Since it is not clear if the limestone holder came from the same site as the tooth itself,

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11 353 we managed to take a second sample from the limestone matrix still partly filling the pulp

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13 354 cavity of the tooth, which must definitively be identical with the rocks the tooth was found in.

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15 355 This second, much smaller sample yielded only very scarce specimens of *Watznaueria*

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17 356 *barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-

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19 357 Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in

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21 358 abundance during the Berriasian and, especially, the Valanginian.

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23 359 In the nannoplankton succession reported previously by Avram et al. (1993) and

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25 360 derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the

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27 361 concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus*

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29 362 *lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu

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31 363 Member of the Cernavodă Formation. These assemblages were interpreted to represent the

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33 364 nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was

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35 365 assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous

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37 366 of the Mecsek Mountains, Hungary, by Császár et al. (2000).

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39 367 Together, all the available evidence (Simionescu's original account, geographic and

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41 368 geologic records, foraminifera, ostracods, microproblematicae, and calcareous

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43 369 nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member

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45 370 of the Cernavodă Formation, and it is most probably of late Valanginian age.

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49 372 *4.2. Description and comparisons*

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51 373 Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2,

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53 374 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown

375 base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of
376 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is
377 remarkably well preserved, with the enamel in pristine condition. It preserves most of the
378 crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5
379 mm missing in the apical region.

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

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

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

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400 exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of
401 the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about
402 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5
403 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes
404 thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but
405 thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B).
406 Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped
407 (Fig. 3D).

408 The tooth is ziphodont and only very slightly recurved distally. The distal edge is
409 nearly straight across its length, being very mildly concave in its basal half and slightly
410 convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the
411 tooth crown base. The mesial edge, as shown in the original publication of Simionescu
412 (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually
413 compressed (Fig. 3B), with a crown base ratio ($CBR=CBW/CBL$) of 0.56, within the normal
414 range of variation of most theropods. This differs from the thinner teeth of some, but not all,
415 carcharodontosaurids ($CBR<0.50$), and the much thicker incrassate teeth of derived
416 tyrannosauroids and conical teeth of spinosaurids ($CBR>0.75$) (Serenó et al., 1996; Brusatte
417 et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).

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

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

432 The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with
433 minute serrations across its entire preserved length; the denticles are proximodistally
434 subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig.
435 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are
436 oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so
437 it is not possible to determine whether the serrations continued over the apex of the tooth.
438 There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the
439 carina. Serration shape and size remain relatively constant across the carina, although the
440 serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig.
441 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F).
442 Changes in serration size are gradual across the carina, not sudden or sporadic.

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

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450 separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length.

451 The interdenticular space between adjacent denticles is broad, measuring more than a third of
452 the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the
453 crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These
454 sulci are so short and indistinct that they are only visible under low angle light.

455 Little can be said about the mesial carina, as it is not visible in the current state of the
456 specimen, buried in the limestone matrix. Based on the description of Simionescu (1913),
457 however, it is covered across its length with minute serrations; these decrease in size towards
458 the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles)
459 per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly
460 smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and
461 Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus,
462 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends
463 towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii*
464 where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*’
465 *superbus* (Sauvage, 1876, 1882) in this respect.

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

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

1 475 that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly
2 476 developed wrinkles are present along the crown height; in the basal half of the crown, the
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4 477 wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer
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7 478 than twice the space separating each undulation. The wrinkles project obliquely (in the
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10 479 mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal
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12 480 segment on the crown, and curve apically as they approach the carina (at about 45°) with a
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14 481 tendency to become tangential to the distal edge. The wrinkles are especially well developed,
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17 482 prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig.
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19 483 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm).
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21 484 Apically, however, the wrinkles are somewhat wider and longer, extending over about half of
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24 485 the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the
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27 486 crown in wrinkle development as well, these being better expressed on the more rounded,
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29 487 convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the
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32 488 presumed labial face, only some of the basal-most wrinkles, particularly the second and third
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34 489 one, appear well defined.

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36 490 Towards the base of the crown a few of the wrinkles continue across the labial and
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39 491 lingual surfaces as very subtle transverse undulations. Most conspicuous of these is a 3.5 mm
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41 492 wide horizontal swelling that crosses the crown, at the level of wrinkles 2 and 3; this swelling
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44 493 is clearly visible on both sides of the crown (Fig. 3. A, C). There are no lateral flutes, apico-
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46 494 basal ridges, or longitudinal grooves on the labial or lingual faces, either in the centre of the
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49 495 tooth or paralleling the carinae. Instead, the labial and lingual faces are uniformly convex,
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51 496 giving the tooth its teardrop-shaped outline in cross section.

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54 498 5. Discussion

55 499 5.1. *Identification of UAIC (SCM1) 615*

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

503 Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert
504 (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are
505 also known to possess remarkably theropod-like, laterally compressed and serrated teeth, not
506 unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are
507 significantly smaller than the Southern Dobrogean specimen, especially in the case of the
508 Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest,
509 caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene
510 *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615;
511 moreover, these teeth are slightly conical and less laterally compressed than the Southern
512 Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia
513 appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly
514 younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true
515 denticles along their carinae) are reported in Europe only beginning in the Albian (Ösi et al.,
516 2015), and these are both significantly smaller and different in morphology from the
517 Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian
518 affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a
519 theropod tooth.

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

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

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525 (2005) and Larson and Currie (2013), and it or a similar version has been used in recent
526 studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, 2014; Brusatte and
527 Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL,
528 CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at
529 the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to
530 this dataset, the data were log-transformed prior to analysis, missing values for measurements
531 were estimated with a mean value for that measurement from across the sample, and then a
532 PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17
533 (Hammer et al., 2001).

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

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

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

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

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

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

1 575 undulations that are at least twice as long mesiodistally as the space separating each
2 576 undulation (character 111), and marginal undulations present on both mesial and distal sides
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5 577 of the crown (character 113).
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7 578 The Romanian specimen also lacks many keystone dental synapomorphies of other
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9 579 theropod clades, based on the clade diagnoses of Hendrickx and Mateus (2014) and other
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11 580 cladistic studies that include dental characters. UAIC (SCM1) 615 does not possess the
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13 581 hooked distal denticles of some Abelisauridae, the strongly labially deflected distal carina
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15 582 and pronounced transverse enamel undulations extending across the labial and lingual tooth
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17 583 faces of Ceratosauridae, the incrassate teeth with apicobasal enamel flutes and deeply veined
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19 584 enamel surface texture of Spinosauridae, and the large transverse undulations of some basal
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21 585 allosauroids (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of
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23 586 derived tyrannosauroids (Brusatte et al., 2010a) and the large and strongly hooked (or
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25 587 pointed) denticles of troodontids and therizinosauroids (e.g., Turner et al., 2012; Brusatte et
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27 588 al., 2014; Hendrickx and Mateus, 2014). The large size, as well as recurved and ziphodont
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29 589 shape of UAIC (SCM1) 615 is strikingly different from the non-ziphodont therizinosauroids,
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31 590 ornithomimosaur, alvarezsauroids, and most troodontids, which have conical, leaf-shaped, or
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33 591 peg-like teeth (when teeth are present) (e.g., Holtz et al., 2004a; Turner et al., 2012; Brusatte
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35 592 et al., 2014). Finally, besides its remarkably large size, the presence of serrations indicates
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37 593 that UAIC (SCM1) 615 does not belong to groups such as alvarezsauroids, oviraptorosaurs,
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39 594 basal troodontids, or avialans, which have unserrated crowns (e.g., Turner et al., 2012;
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41 595 Hendrickx and Mateus, 2014).
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51 596 In summary, the four analyses all support carcharodontosaurid affinities for UAIC
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53 597 (SCM1) 615. Both overall tooth proportions and discrete phylogenetic characters point to a
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55 598 carcharodontosaurid identification, and the discriminant function analysis and phylogenetic
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57 599 analysis both explicitly recover the tooth as a carcharodontosaurid. For this reason we refer
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600 this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very
601 derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and
602 *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno
603 (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as
604 recovered in our analysis, is congruent with results of previous analyses based on larger sets
605 of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno,
606 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015),
607 and offers some support for considering the Romanian carcharodontosaurid from Southern
608 Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of
609 the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

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

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

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(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.

635 636 *5.2. Body size of UAIC (SCM1) 615*

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

1 (SCM1) 615 is smaller than the largest teeth of *Acrocanthosaurus* (9% difference),
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3 651 *Carcharodontosaurus* (20%), and *Giganotosaurus* (12.5%) in the dataset, but is 13% bigger
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5 652 than the largest tooth of *Mapusaurus*.
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7 653 It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized
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9 654 carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic
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11 655 carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Serenó et al., 1996; Calvo
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13 656 and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close
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15 657 relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn,
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17 658 corroborates growing evidence that very large body size was acquired very early in
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19 659 carcharodontosaurid history, since the earliest potential members of the clade are already of
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21 660 relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is
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23 661 *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and
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25 662 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more
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27 663 derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the
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29 664 uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see
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31 665 below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized
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33 666 carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.
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36 667 The inferred large body size of the South Dobrogean theropod is also remarkable as
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38 668 virtually all other dinosaur remains reported previously from Romania (both from the Early
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40 669 Cretaceous Cornet assemblage and the much later, end Cretaceous Hațeg Island fauna) are
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42 670 significantly smaller, and many have been interpreted as insular dwarfs (e.g., Weishampel et
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44 671 al., 1993, 2003; Benton et al., 2006, 2010; Stein et al., 2010; Ósi et al., 2014). Although other
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46 672 Romanian theropod dinosaurs were not particularly dwarfed (e.g. Brusatte et al., 2013), they
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48 673 were nonetheless small (Nopcsa, 1902; Csiki and Grigorescu, 1998; Csiki et al., 2010;
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50 674 Brusatte et al., 2013). This bias towards small bodied Romanian theropods was also
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1 675 interpreted as a consequence of their insular habitat (Csiki and Grigorescu, 1998), as all
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3 676 previously reported theropod remains come from within the Carpathian Orogen, an area with
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5 677 an archipelago-type palaeogeography during the Cretaceous (Dercourt et al., 2000; Csontos
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7 678 and Vörös, 2004; Csiki-Sava et al., 2015). By contrast, UAIC (SCM1) 615 was found in
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9 679 shallow marine deposits bordering the emerged areas of Central Dobrogea, part of the stable
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11 680 cratonic areas of Europe and connected at least intermittently to the Ukrainian Shield since
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13 681 the Late Jurassic (Fig. 5A). Although cratonic Europe was also transformed into an
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15 682 archipelago of islands during much of the Cretaceous, these islands were often both larger in
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17 683 size and more stable in space and time than were the transient emerged areas of the Tethyan
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19 684 archipelagoes. As such, it is conceivable that the Southern Dobrogean carcharodontosaurid
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21 685 was less constrained by space or resource limitations than the Tethyan insular dinosaurs,
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23 686 allowing it to retain a large body size.
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30 31 688 *5.3. UAIC (SCM1) 615 and Valanginian dinosaur distribution*

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33 689 Besides documenting the presence of large-sized mainland carcharodontosaurids in the
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35 690 Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a
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37 691 significant gap in our knowledge on the composition and distribution of the Early Cretaceous
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39 692 dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed
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41 693 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these
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43 694 being known from the later part (Barremian–Albian) of that epoch; only around a dozen
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45 695 localities were listed from each age of the early part of the Early Cretaceous (Berriasian,
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47 696 Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous
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49 697 dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al.,
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51 698 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs
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53 699 and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards
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1 700 western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no
2 701 occurrences are known from the entire central, eastern and southern Europe for the
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4 702 Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–
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6 703 Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et
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8 704 al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the
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10 705 carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in
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12 706 Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).
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17 707 Our identification of the Romanian tooth as a carcharodontosaurid documents the
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19 708 presence of this clade in Europe in the very early Cretaceous. This is significant, as
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21 709 carcharodontosaurids were widely distributed tens of millions of years later, in the middle
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23 710 Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see
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25 711 below). Despite the recent discoveries documenting that the clade was also present in North
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27 712 America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and
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29 713 Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in
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31 714 Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010;
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33 715 see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older
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35 716 than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than
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37 717 previously thought and were a long-term component of the European mainland Early
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39 718 Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might
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41 719 have been already present between the cratonic, stable European mainland, with a dinosaur
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43 720 fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine
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45 721 areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those
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47 722 described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania
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49 723 (Benton et al., 2006).
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724 This Valanginian carcharodontosaurid represents an important datapoint not only for
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2 725 the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a
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5 726 poorly documented age in dinosaur evolution, with very few precisely dated fossil
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7 727 occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of
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10 728 Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known
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12 729 from Asia, some of which have debatable or controversial dates. These include sites in Japan
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14 730 (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009
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16 731 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these
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18 732 assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age
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20 733 constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible
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22 734 Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992;
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24 735 Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were
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26 736 shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare
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28 737 dinosaur remains of possible Valanginian (or ‘Neocomian’) age were also reported from
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30 738 southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g.,
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32 739 Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli
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34 740 et al., 2014).

41 741 As one of the two known reports of Valanginian dinosaurs in Europe east of France,
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43 742 the Southern Dobrogean dinosaur record fills a huge palaeogeographic gap between the
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45 743 western European and the eastern Asian dinosaur faunas. Moreover, none of these early Early
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47 744 Cretaceous dinosaur assemblages from outside Europe include carcharodontosaurids (see
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49 745 below), as theropods are represented by coelurosaurians interpreted either as compsognathids
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51 746 (Gishlick and Gauthier, 2007) or basal ornithomimosaurids (Choiniere et al., 2012) in southern
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53 747 Africa, metriacanthosaurid allosauroids (‘sinraptorids’) in Thailand (Buffetaut and
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55 748 Suteethorn, 2007), and indeterminate allosauroids (Pérez-Moreno et al., 1993), non-

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749 carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz,
750 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest
751 that carcharodontosaurids had not achieved a wide geographic distribution by this point in
752 time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.

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

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773 *5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography*

774 Carcharodontosauridae were long considered as an exclusively Gondwanan group of
775 theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa
776 (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–
777 Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996;
778 Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte,
779 2008; Cau et al., 2013). This view started to change with the identification of the Early
780 Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal
781 carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and
782 Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic
783 distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan
784 one, was further supported by the discovery of definitive carcharodontosaurids in the Lower
785 Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper
786 Cretaceous of China (Brusatte et al., 2009, 2010b, 2012; Mo et al., 2014; Lü et al., 2016).

787 Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin
788 of the carcharodontosaurids, followed by their dispersal across Laurasia and western
789 Gondwana beginning at least by the Aptian (Fig. 5B), a scenario that is concordant with the
790 tentatively suggested presence of early carcharodontosaurids in the Upper Jurassic of
791 Tanzania, which are based on fragmentary specimens (Rauhut, 2011; Carrano et al., 2012). It
792 is also concordant with the widespread appearance of carcharodontosaurids in the fossil
793 record starting with the Aptian, when they are reported in Africa (*Eocarcharia*; Sereno and
794 Brusatte, 2008), South America (Vickers-Rich et al., 1999), North America
795 (*Acrocanthosaurus*; Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000
796 Eddy and Clarke, 2011), Europe (Canudo and Ruiz-Omeñaca, 2003; Pereda-Suberbiola et al.,
797 2012), and eastern Asia (*Kelmaysaurus*; Brusatte et al., 2012; Mo et al., 2014; Lü et al.,
798 2016).

799 During the Albian–Turonian, carcharodontosaurids became especially abundant and
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2 800 diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996;
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4 801 Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and
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6 802 South America (*Tyrannotitan*, *Giganotosaurus*, *Mapusaurus*, alongside with indeterminate
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9 803 carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005;
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11 804 Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig.
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14 805 5B). They were still present during this time interval in other continents, as well: in North
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16 806 America with *Acrocanthosaurus* until the Albian (D’Emic et al., 2012), in Europe until the
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18 807 Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with
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21 808 *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).

24 809 After dominating terrestrial ecosystems at least in Africa, South America and eastern
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26 810 Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et
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28 811 al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the
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30 812 Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado,
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32 813 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large
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34 814 theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana.
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36 815 Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-
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38 816 Cenomanian deposits of South America to Carcharodontosauridae (e.g., Canudo et al., 2008;
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40 817 Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the
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42 818 abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were
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44 819 reported to suggest the survival of carcharodontosaurids into the latest Cretaceous
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48 820 (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).

53 821 Contrasting with this rich and relatively continuous fossil record of
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55 822 Carcharodontosauridae starting with the Aptian, the first half of its evolutionary history is
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57 823 very poorly documented (Fig. 5B). Prior to the identification of UAIC (SCM1) 615, only two
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824 occurrences of pre-Aptian Cretaceous carcharodontosaurids were reported, one from the
825 Barremian of Spain (Ortega et al., 2010; Gasca et al., 2014) and the other from the Barremian
826 of Thailand (Buffetaut and Suteethorn, 2012). The Early Cretaceous *Kelmaysaurus* from
827 Xinjiang, western China, was recognized as a carcharodontosaurid of possibly ?Valanginian
828 to Aptian in age by Brusatte et al. (2012), but the deposits yielding these remains (the
829 Lianmugin, or Lianmuxin, Formation of the Tugulu Group) were dated as Aptian–Albian by
830 Eberth et al. (2001; see also Tong et al., 2009). An important temporal gap – of about 20 to
831 28 millions of years, according to the dates in Gradstein et al. (2012) – thus stretched between
832 the oldest, tentatively assigned carcharodontosaurids from the Oxfordian–Tithonian of
833 Tanzania, including the formally erected *Veterupristisaurus* (Rauhut, 2011; see also Carrano
834 et al., 2012), and those that started to appear in the fossil record in the Barremian and then
835 spread widely during the Aptian. Referral of UAIC (SCM1) 615 to Carcharodontosauridae
836 partially fills this frustrating gap, effectively halving this shadowy period in the evolutionary
837 history of the group.

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

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

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849 Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut,
850 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC
851 (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with
852 the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very
853 large size and dental morphology characterizing it) well before the Albian, during or even
854 before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and
855 *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the
856 basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.

857 Besides shifting the emergence of the carcharodontosaurines earlier in time,
858 identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting
859 palaeobiogeographic implications. As already noted, recent discoveries show that
860 Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g.,
861 Novas et al., 2005), with the identification of its widespread, Pangaeian distribution during the
862 late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999;
863 Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014).
864 However, within Carcharodontosauridae itself, some palaeogeographic patterns have been
865 widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae
866 is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al.,
867 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as
868 previously all its recognized members were restricted strictly to either Africa (Stromer, 1931;
869 Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995;
870 Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of
871 Carcharodontosaurinae were still adhering to patterns of continental fragmentation and
872 vicariant evolution, with a basal split between the Albian–Cenomanian African
873 *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian

1 874 southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if
2 875 this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

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5 876 This scenario is now challenged by our finding that the Southern Dobrogean
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7 877 carcharodontosaurid UAIC (SCM1) 615 may nest inside Carcharodontosaurinae. If true, such
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9 878 an affinity would suggest that the origin of Carcharodontosaurinae was not a southern,
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11 879 vicariant by-product of the Gondwana-Laurasia separation, a major palaeogeographic event
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13 880 that is considered to have been well underway by the end of the Jurassic, and essentially
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15 881 completed by the mid-Early Cretaceous (see Weishampel et al., 2010). Indeed, during this
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17 882 time palaeogeographic connections and faunal interactions were virtually non-existent
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19 883 between the northern Tethyan (European) and southern Tethyan (western Gondwanan, but
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21 884 essentially African) areas of the Mediterranean (e.g., Canudo et al., 2009), which makes a
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23 885 vicariant hypothesis intuitive. However, if the Romanian tooth represents a
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25 886 carcharodontosaurine, then it implies a much more complicated palaeogeographic history of
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27 887 the clade, which is not so clearly linked to continental breakup.

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34 888 The palaeogeographic position of the Southern Dobrogean carcharodontosaurine in
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36 889 cratonic Europe, north of the Neo-Tethys, together with its significantly older age compared
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38 890 to other carcharodontosaurines, could indicate that separation of the carcharodontosaurine
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40 891 lineage took part in Europe and not in western Gondwana as previously assumed. This would
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42 892 also mean that representatives of this lineage were subsequently – after the Barremian –
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44 893 introduced to Africa and South America via trans-Tethyan dispersal, most probably at a time
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46 894 when faunal interactions between the southern and northern margins of the Mediterranean
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48 895 Tethys were resumed, after the early Barremian (Canudo et al., 2009).

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53 896 Alternatively, it can be hypothesized that appearance of carcharodontosaurines in
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55 897 Southern Dobrogea is a consequence of southern immigration originating in western
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57 898 Gondwana, often considered the place of origin for this clade. However, this scenario has

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899 several potential caveats. Although Europe has been considered as forming part of a larger
900 Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín,
901 2012), and occasional trans-Tethyan faunal connections have been recognized between
902 Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage,
903 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and
904 Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-
905 Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place
906 during the ‘Neocomian’ (Berriasian–Hauterivian) time interval.

907 More recently, some potential evidence has emerged for Gondwana-to-Europe
908 interchange during the ‘Neocomian’. The presence of the basal rebbachisaurid *Histriasaurus*
909 (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as
910 indicative of very early and very rapid northward dispersal of this clade from western
911 Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of
912 this particular dispersal event was even constrained to the Berriasian–Valanginian time
913 interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the
914 Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of
915 the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian
916 Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive
917 transportation mechanism (‘Noah’s Ark’; McKenna, 1973) for basal rebbachisaurids after its
918 separation from mainland Africa (e.g., Torcida Fernández-Baldor et al., 2011). Furthermore,
919 the palaeogeographical separation between Africa and Adria (and thus the effective
920 movement of the presumed ark) is considered to be at most an incipient one during the Early
921 Cretaceous by Bossellini (2002) and Zarccone et al. (2010), with spatial continuity still present
922 between the two landmasses, while deep-water basins continued to separate Adria from the
923 European Craton. Accordingly, although the presence of *Histriasaurus* can represent a case

1 924 of northward range extension of rebbachisaurids during the Berriasian–Valanginian, it took
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3 925 place not strictly speaking into Europe, but only reached the northernmost extremity of Adria,
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5 926 a northerly peninsular extension of the African mainland. It was only starting with the
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7 927 Barremian that rebbachisaurids dispersed as far north as the European cratonic areas,
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9 928 including Iberia and the British Isles (Mannion, 2009; Mannion et al., 2011; Torcida
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11 929 Fernández-Baldor et al., 2011), a time when faunal interchanges between Europe and Africa
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13 930 are considered to have been well underway (e.g., Gheerbrant and Rage, 2006; Canudo et al.,
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15 931 2009).

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19 932 Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant
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21 933 of the European mainland. It is thus unclear to what extent the example of rebbachisaurid
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23 934 range extension into (present-day) Europe during the early Early Cretaceous, as potentially
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25 935 testified by the discovery of the Croatian taxon, would also be applicable for the Southern
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27 936 Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are
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29 937 very different, and that faunal connections during this time interval are not documented
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31 938 between the African and European cratons as already pointed out by Gheerbrant and Rage
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33 939 (2006).

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39 940 Absence of documented faunal interactions weakens support for a scenario of south-
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41 941 to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the
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43 942 Cretaceous, and would argue instead for a local, European development to explain the
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45 943 presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian
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47 944 presence of carcharodontosaurids in Europe is also consistent with their appearance in the
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49 945 Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the
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51 946 eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in
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53 947 North America likely requires the presence of pre-Aptian members of the clade in Europe,
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55 948 since faunal exchanges between these two landmasses are known to have been halted before
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949 the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal
950 carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the
951 derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western
952 Gondwana. The causes of these distribution patterns remain as yet unknown, and further
953 support – in the form on new carcharodontosaurid discoveries from the early-middle part of
954 the Early Cretaceous – is required to better uphold such a scenario.

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

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965 6. Conclusions

966 We re-describe and interpret the affinities of one of the most significant historical dinosaurian
967 specimens of Romania, an isolated but well-preserved theropod tooth from Southern
968 Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth,
969 while the available evidence – including novel calcareous nannoplankton sampling – supports
970 its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of
971 Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a
972 collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only
973 two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this

1 974 record advances our understanding of European dinosaur distribution during the early Early
2 975 Cretaceous, and also fills an important palaeogeographic gap between Western European and
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5 976 Eastern Asian dinosaurian assemblages of the Valanginian.
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7 977 Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a
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9 978 possible member of Carcharodontosaurinae, a subclade of derived and gigantic
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12 979 carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western
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14 980 Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean
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17 981 specimen documents the emergence of Carcharodontosaurinae earlier than previously
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19 982 recognized, thus also indicating an earlier acquisition of their characteristically large size.
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22 983 Based on currently known palaeogeographic and chronostratigraphic constraints on the
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24 984 evolution of Carcharodontosauridae, it appears that not only did this clade have a wide
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26 985 distribution, but that crucial events of its evolutionary history such as the emergence of the
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29 986 derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of
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32 987 western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia
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34 988 split, as was formerly suggested. In such a case, instead of endemic evolution the emergence
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36 989 of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-
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39 990 to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the
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41 991 Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into
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44 992 western Gondwana adds further support for the presence of important palaeogeographic ties
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46 993 between the two realms during the second half of the Early Cretaceous.
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14 1542 Figure captions
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16
17 1543 Figure 1. Simplified geological map of the Cernavodă-Cochirleni area; inset shows the
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19 1544 position of the study area within Romania. Legend: 1. Quaternary: a. Holocene alluvia, b.
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21
22 1545 Pleistocene–Holocene loessoid deposits; 2. Pre-Quaternary Cenozoic (Middle Eocene and
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24 1546 Miocene) deposits; Cretaceous: 3. Peștera Formation, Lower Cenomanian; 4. Cochirleni
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27 1547 Formation; uppermost Aptian–Lower Albian; 5. Gherghina Formation, Middle–Upper
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29 1548 Aptian; 6. Ostrov (= Ramadan) Formation; Barremian–Lower Aptian; 7. Cernavodă
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32 1549 Formation, Alimanu Member, Berriasian–Valanginian; 8. Water courses. (Redrawn after
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34 1550 Dragastan et al., 1998, 2014).
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36 1551
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39 1552 Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from
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41 1553 Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B.
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44 1554 Current state of UAIC (SCM1) 615, mounted in a limestone holder.
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46 1555
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49 1556 Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid
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51 1557 lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B.,
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54 1558 distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina
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56 1559 (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal
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58 1560 part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).
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2 1562 Figure 4. Dental morphospace of the different theropod clades according to the results of the
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5 1563 PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by
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7 1564 Carcharodontosauridae. See further details of this analysis, as well as other quantitative
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9
10 1565 analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant
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12 1566 function analysis, phylogenetic analysis), in the Supplementary Material.
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15 1567
16
17 1568 Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur
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19 1569 occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-
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22 1570 Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the
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24 1571 marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and
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26
27 1572 palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian
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29 1573 (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615
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31
32 1574 from Southern Dobrogea. Legend: 1 – *Veterupristisaurus*, ‘*Megalosaurus*’ *ingens*,
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34 1575 Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator*, Spain, Barremian;
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36 1576 3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern
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39 1577 United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 –
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41 1578 *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China,
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44 1579 Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmaysaurus*,
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46 1580 Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11
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49 1581 – *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan,
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51 1582 Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 –
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54 1583 Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant
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56 1584 references, see text, 5.4.). Palaeogeographic maps, courtesy of Ron Blakey
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58 1585 (<http://cpgeosystems.com/>).
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2 1 “*Megalosaurus cf. superbis*” from southeastern Romania: the oldest known Cretaceous
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4 2 carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous
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6 3 Europe-Gondwana connections
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12 6 Zoltán Csiki-Sava^{1*}, Stephen L. Brusatte², Ștefan Vasile¹

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30
31 15 ABSTRACT

32
33 16 Some of the best records of continental vertebrates from the Cretaceous of Europe come from

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35 17 Romania, particularly two well-known occurrences of dwarfed and morphologically aberrant

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37 18 dinosaurs and other taxa that lived on islands (the Cornet and Hațeg Island faunas).

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39 19 Substantially less is known about those vertebrates living in the more stable, cratonic regions

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41 20 of Romania (and Eastern Europe as a whole), particularly during the earliest Cretaceous. We

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43 21 describe one of the few early Early Cretaceous fossils that have ever been found from these

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45 22 regions, the tooth of a large theropod dinosaur from Southern Dobrogea, which was

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47 23 discovered over a century ago but whose age and identification have been controversial. We

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49 24 identify the specimen as coming from the Valanginian stage of the Early Cretaceous, an

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51 25 incredibly poorly sampled interval in global dinosaur evolution, and as belonging to

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2 26 Carcharodontosauridae, a clade of derived, large-bodied apex predators whose earliest
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4 27 Cretaceous history is poorly known. Quantitative analyses demonstrate that the Romanian
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6 28 tooth shows affinities with a derived carcharodontosaurid subgroup, the
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8 29 Carcharodontosaurinae, which until now has been known solely from Gondwana. Our results
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10 30 suggest that this subgroup of colossal predators did not evolved vicariantly as Laurasia split
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12 31 from Gondwana, but originated earlier, perhaps in Europe. The carcharodontosaurine
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14 32 diversification may have been tied to a north-to-south trans-Tethyan dispersal that took place
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16 33 sometime between the Valanginian and Aptian, illustrating the importance of
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18 34 palaeogeographic ties between these two realms during the largely mysterious early–mid
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21 35 Early Cretaceous.

22 36

23 37 Keywords

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25 38 ~~Romania~~Southern Dobrogea; ~~Lower Cretaceous~~Valanginian; ~~Theropoda~~;

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27 39 Carcharodontosauridae; cratonic Europe; palaeobiogeography

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31 41 1. Introduction

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33 42 Romania boasts one of the best records of continental vertebrate fossils from the Cretaceous
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35 43 of Europe (e.g., Grigorescu, 1992, 2003; Csiki-Sava et al., 2015). The vast majority of fossils
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37 44 come from two well-known occurrences: the Early Cretaceous bauxite accumulations of
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39 45 Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997;
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41 46 Posmoşanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Haţeg,
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43 47 Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the
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45 48 dinosaur-dominated ‘Haţeg Island fauna’ (e.g., Nopcsa, 1923; Weishampel et al., 1991;
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47 49 Benton et al. 2010; Codrea et al., 2010, 2012; Grigorescu, 2010; Vremir, 2010; Vasile and
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49 50 Csiki, 2011; Csiki-Sava et al., 2015). Both of these faunas inhabited islands that were part of

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2 51 the vast Cretaceous European Archipelago of the Neo-Tethys Ocean. Based on their isolated
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4 52 geological settings and the many dwarfed and morphologically aberrant taxa that make up the
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6 53 faunas, both have been interpreted as insular assemblages that give a unique window into
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8 54 how island environments affected the evolution of long-extinct organisms (e.g., Benton et al.,
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10 55 1997, 2010; Csiki-Sava et al., 2015).

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12 56 The great volume of research on these assemblages over the past century, particularly
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14 57 the ‘Hațeg Island fauna’, has concealed an inconvenient bias: the stable, non-island, cratonic
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16 58 regions of Romania have yielded only extremely rare Mesozoic continental vertebrate
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18 59 remains (i.e., the Moldavian, Moesian and Scythian platforms; Săndulescu, 1984; Mutihac
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20 60 and Mutihac, 2010; Fig. 1). This is mostly because Mesozoic deposits are located in the
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22 61 subsurface in these regions, with only limited subaerial exposures available in the structurally
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24 62 highest-lying parts of the Moesian Platform, in Central and Southern Dobrogea (Middle
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26 63 Jurassic–Upper Cretaceous), as well as in the northeastern-most corner of the Moldavian
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28 64 Platform, along the Prut Valley (lower Upper Cretaceous) (see, e.g., Mutihac and Mutihac,
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30 65 2010). This bias is unfortunate because fossils from these settings could lead to a better
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32 66 understanding of how mainland and island faunas differed during the Cretaceous, and
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34 67 because the cratonic portion of Europe was an important biogeographic stepping stone
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36 68 between the north and south as the continents fragmented and sea levels fluctuated.

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39 69 Although the cratonic regions of Romania have yielded few Cretaceous terrestrial
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41 70 fossils, these deposits are not totally barren. In fact, one of the first Mesozoic continental
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43 71 vertebrates ever recorded from Romania comes from one of these deposits, the Lower
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45 72 Cretaceous shallow marine limestones of Southern Dobrogea (Fig. 1). This specimen—the
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47 73 isolated but well-preserved tooth of a large theropod dinosaur—has often been overlooked. It
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49 74 was described a little over a century ago by Simionescu (1913; Fig. 2A), and until a few
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51 75 recent discoveries of very rare isolated specimens (Stoica and Csiki, 2002; Csiki-Sava et al.,
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2 76 | 2013, ~~in prep.~~; Dragastan et al., 2014), it remained as the sole published record of Mesozoic
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4 77 terrestrial vertebrates from the cratonic areas of Romania. It has never been comprehensively
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6 78 described and its precise age and taxonomic affinities have yet to be clarified, despite its
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8 79 potential importance as a well-preserved fossil from a poorly sampled area that could have
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10 80 critical evolutionary and biogeographic implications.

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12 81 We here present a comprehensive description of the Dobrogea tooth and discuss its
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14 82 relevance for understanding dinosaur evolution and biogeography. We review the peculiar
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16 83 history of how this specimen was collected and curated, thoroughly document its morphology
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18 84 and age, identify it based on comparison to a broad range of theropods, and outline its
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20 85 importance. It turns out that this specimen, although only a single tooth, has wide-ranging
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22 86 implications. We identify it as coming from the Valanginian stage of the Early Cretaceous,
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24 87 which is incredibly poorly sampled both in Europe and globally (Weishampel et al., 2004),
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26 88 and as belonging to a carcharodontosaurid, a group of derived, large-bodied apex predators
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28 89 whose earliest Cretaceous history is poorly known. Carcharodontosaurids were once thought
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30 90 to be a uniquely Gondwanan group, but recent discoveries show that the basal members of
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32 91 the group were more widespread during the late Early-middle Cretaceous (e.g., Sereno et al.,
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34 92 1996; Brusatte and Sereno, 2008). The Romanian tooth shows affinities with a derived
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36 93 carcharodontosaurid subgroup, the Carcharodontosaurinae, that until now has been known
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38 94 only from Gondwana. It suggests that this subgroup of enormous predators did not evolve
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40 95 vicariantly as Pangaea split, but originated earlier, and perhaps in Europe, suggesting faunal
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42 96 interchange between Europe and Gondwana during the ‘dark ages’ of the early Early
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44 97 Cretaceous.

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47 98 *Abbreviations:* UAIC – University “Alexandru Ioan Cuza”, Iași, Romania.
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51
52 100 2. History of collecting and curation
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2 101 Only two dinosaurian fossils are currently known from the cratonic areas of Romania: an
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4 102 isolated theropod tooth and an isolated caudal vertebral centrum. Both of these were reported
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6 103 from the Lower Cretaceous deposits of Southern Dobrogea (southeastern Romania; Csiki-
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8 104 Sava et al., 2013, see also below). Unfortunately, exact details of their discovery and places
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10 105 of origin are lost, a fact that can hinder an assessment of their age and interpretation of their
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12 106 phylogenetic and palaeobiogeographic significance. Our aim here is to gather and report all
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14 107 available information concerning the collecting of specimen UAIC (SCM1) 615, that is, the
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16 108 isolated theropod tooth reported by Simionescu (1913; Fig. 2A).

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19 109 According to the existing information - unpublished museum labels and records, and
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21 110 the preliminary publication of Simionescu (1913) - specimen UAIC (SCM1) 615 was
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23 111 discovered in the surroundings of Cochirleni, a small village south of Cernavodă and close to
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25 112 the right bank of the Danube, in Southern Dobrogea, southeastern Romania (Fig. 1), probably
26
27 113 shortly before 1913, the date of its publication by Simionescu (1913).

28
29 114 Although studied and preliminarily described by Simionescu, UAIC (SCM1) 615 was not
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31 115 collected by Simionescu personally. Instead, it was donated by a certain “de Tomas” (also
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33 116 mentioned as “de Thomas” in the registry of the Hârşova Museum) to V. Cotovu from
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35 117 Hârşova (Central Dobrogea), a local teacher, archaeology and natural history aficionado, and
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37 118 amateur fossil collector (see, e.g., Covacef, 1995). Cotovu, described by Simionescu himself
38
39 119 as the “zélé fondateur et directeur du muséum de Hârşova” (*enthusiastic founder and director*
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41 120 *of the Hârşova Museum*; Simionescu, 1906: p. 2), had previously provided fossil specimens
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43 121 from Southern Dobrogea for study to Simionescu, a nationally acknowledged popular science
44
45 122 writer and scientist, whom Cotovu knew personally (Brânzilă, 2010). These circumstances
46
47 123 are supported by the fact that in the original description, Simionescu figures the specimen as
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49 124 being accessioned in the “Regional-Museum von Harschowa” (*Hârşova Regional Museum*;
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51 125 Simionescu, 1913: p. 687, fig.1), a designation he also used to refer to other Dobrogean

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2 126 specimens not collected by him first-hand (e.g., a specimen of ‘*Nautilus*’ *pseudoelegans* from
3
4 127 Cernavodă, or a fragmentary tooth-bearing palatal fragment referred to as ‘*Coelodus*’ sp.,
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6 128 also originating from Cochirleni; see Simionescu, 1906). Confirming this deduction, an
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8 129 isolated tooth appears accessioned in the old registry book of the Hârşova Museum (under
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10 130 specimen number 200) as “*Megalosaurus* cf. *superbus*”, with the mention that it was
11
12 131 “described by Prof. Simionescu in the *Centralblatt f. min. etc.*”. This is also the case of the
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14 132 ‘*Coelodus*’ sp. specimen from Cochirleni (specimen number 86), similarly clearly identified
15
16 133 as being described by Simionescu in the registry book.

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19 134 Both of these vertebrate remains from Dobrogea that were formerly part of the
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21 135 Hârşova Museum collections are currently accessioned in the palaeontology collections of the
22
23 136 UAIC (Turculeţ and Brânzilă, 2012), suggesting that, at one moment, several specimens were
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25 137 transferred there from the Hârşova Museum. Although no details are known about this
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27 138 transfer, it is probable that it took place right before (or when) the Hârşova Museum,
28
29 139 including a part of its collections, was burned and largely destroyed during WWI, in 1916, a
30
31 140 time when Simionescu still held a position at the UAIC.

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33 141 After its original description, specimen UAIC (SCM1) 615 underwent a minor
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35 142 amount of damage (see below, Description). Also, at some point between its description in
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37 143 1913 and the early 1960s (when the specimen was found in its present state in the collections
38
39 144 of the UAIC by academic staff members who are still alive today and recall the discovery; I.
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41 145 Turculeţ, personal communication, May 2013) it was glued into a limestone matrix holder,
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43 146 while it was obviously completely freed of the surrounding matrix when it was described and
44
45 147 figured in 1913 (Fig. 2). The circumstances under which these alterations took place are
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47 148 unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the
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49 149 spring of 1944, the frontline between the German-Romanian and Soviet armies reached the
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51 150 Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

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2 151 were packed in crates, and moved together with its personnel and other possessions to Zlatna,
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4 152 in the Apuseni Mountains (western Romania), to safeguard them from any potential damage.
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6 153 Mounting the specimen into the limestone stand would have been a quick way to stabilize it,
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8 154 as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă,
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10 155 personal communication, April 2103). If that was indeed the case, the mounting would have
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12 156 taken place without the knowledge of Simionescu, who left Iași and the UAIC in 1929, being
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14 157 invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă,
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16 158 2010). Then again, however, Simionescu himself or staff of the Hârșova Museum might have
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18 159 re-mounted the tooth after its original description, or else the mounting might have taken
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21 160 place after the return of the collections to Iași, after WWII.

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23 161 Unfortunately, it is not documented whether the mounting was made using the
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25 162 original matrix, or if a trough corresponding to the tooth outline was carved into a randomly
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27 163 chosen limestone block. The apparently excellent fit between the tooth and the depression
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29 164 housing it (Fig. 2B, 3) suggests that this operation was completed carefully, and accurate
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31 165 carving of a fake holder is difficult to reconcile with the rush accompanying the evacuation of
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33 166 the Iași University, in 1944. Alternatively, the presence of a hand-written old registration
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35 167 number on the specimen holder would support its early re-mounting, while still at the
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37 168 Hârșova Museum. As noted previously, the original Hârșova Museum registration number of
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39 169 the specimen was 200, which does not correspond to that currently written both on the
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41 170 limestone holder and on a paper sticker (204). However, according to the old collection
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43 171 registry of the Hârșova Museum, specimen numbers 201 through 225 were given to a series
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45 172 of “indeterminate (fossil) bone fragments” from the “Cochirleni quarries”. Thus, these
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47 173 specimens (now apparently lost) came from the same locality as the tooth, and they were
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49 174 collected and donated by the same person to the Museum who donated UAIC (SCM1) 615.
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51
52 175 There is, thus, a (albeit admittedly remote) possibility that the registration numbers were

1
2 176 mixed up during the re-mounting of the specimen, which in this case took place at an early
3
4 177 date in the Hârșova Museum. If this is indeed the case, the limestone used as holder could
5
6 178 have been the same as the original matrix of the specimen.
7

8 179 To conclude, the history of recovery and curation of the historically important
9
10 180 dinosaurian specimen UAIC (SCM1) 615 is rather convoluted and clouded by many
11
12 181 uncertainties. The exact date of discovery remains conjectural, and the exact place of the
13
14 182 discovery (thus also the original geological context of the tooth) is even more ambiguous.
15
16 183 The current state of the specimen, and especially its mounted status, suggest a curatorial
17
18 184 history that produced a moderate amount of damage to, but also partially obscured the
19
20
21 185 detailed morphology of the specimen. The convergence of such unfortunate events makes
22
23 186 deciphering the age, identity and evolutionary significance of the specimen troublesome,
24
25 187 although many lines of evidence, carefully considered, allow us to draw reasonable
26
27 188 conclusions (see below).
28

29 189
30
31 190 3. Geological setting
32

33 191 According to the available collecting information, the isolated theropod tooth UAIC (SCM1)
34
35 192 615 was discovered at Cochirleni (sometimes noted more specifically as the “*Cochirleni*
36
37 193 *quarry*” or “*Cokerleni quarry*”). Cochirleni is a small village in southwestern Dobrogea
38
39 194 situated close to the right bank of the Danube, and about 9 km south of the main urban center
40
41 195 of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of
42
43 196 the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous
44
45 197 deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).
46
47

48 198 Southern Dobrogea is a cratonic area corresponding to the southeastern corner of
49
50 199 Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984;
51
52 200 Ionesi, 1994), or a distinct craton (the South-Dobrogean Platform; Mutihac and Mutihac,
53

1
2 201 2010), researchers agree that it became integrated into the main European Craton towards the
3
4 202 end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine;
5
6 203 Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001;
7
8 204 Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from
9
10 205 Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

12 206 The Precambrian basement of Southern Dobrogea is overlain by a flat-lying
13
14 207 sedimentary cover that begins with the lowermost Palaeozoic and ends with the uppermost
15
16 208 Neogene. The sedimentary succession is interrupted by a few major, as well as several less
17
18 209 important, sedimentary hiatuses that separate 5 main sedimentary sequences corresponding to
19
20 210 the Cambrian–Upper Carboniferous, the Permian–Triassic, the Middle Jurassic–Cretaceous,
21
22 211 the Eocene–?Oligocene, and the middle Badenian (middle Miocene)–Upper Pliocene. The
23
24 212 Palaeozoic and lower Mesozoic are known only from the subsurface of Southern Dobrogea,
25
26 213 but Cretaceous and Cenozoic deposits have limited exposures along the main water courses
27
28 214 of the region (Ionesi, 1994; Mutihac and Mutihac, 2010).

31 215 The outcropping Cretaceous in Southern Dobrogea is represented mainly by shallow
32
33 216 marine, carbonate platform deposits in the lower part of the system, replaced by more open-
34
35 217 water, chalky facies towards the later part of the period (e.g., Avram et al., 1993, 1996;
36
37 218 Dragastan et al., 1998; Dinu et al., 2007); these crop out only as isolated patches along the
38
39 219 main watercourses of the region (Fig. 1).

41 220 The Lower Cretaceous Series consists of several lithostratigraphic units with
42
43 221 complex, partially overlapping and interfingering relationships (Dragastan et al., 1998, 2014).
44
45 222 The lowest (and only artificially) outcropping unit is the Purbeck-type, siliciclastic-evaporitic
46
47 223 Upper Kimmeridgian–Lower Berriasian Amara Formation that represents lagoonal to
48
49 224 continental environments. This unit is covered by the shallow-marine, richly fossiliferous and
50
51 225 locally reefal limestone-dominated Cernavodă Formation (restricted-open lagoonal to
52

1
2 226 carbonate platform, Upper Berriasian–Lower Hauterivian). A time-correlative unit of the
3
4 227 Cernavodă Formation, the limestone-dolomitic Dumbrăveni Formation (Upper Berriasian–
5
6 228 Lower Hauterivian), is restricted to the southeastern part of Southern Dobrogea. The
7
8 229 Cernavodă and Dumbrăveni formations are covered unconformably by dominantly
9
10 230 calcareous deposits with hippuritoid (‘pachyodont’) coquinas, small reefs and lens-like
11
12 231 orbitolinid accumulations, referred to the Barremian–Lower Aptian Ostrov Formation by
13
14 232 Dragastan et al. (1998), but to the Ramadan Formation (in part) by Avram et al. (1993, 1996).
15
16 233 These deposits, formed in littoral to lagoonal and open reef terrace environments, are in turn
17
18 234 capped by the fluvial-lacustrine, siliciclastic deposits of the Gherghina Formation, with
19
20
21 235 Middle–Upper Aptian kaolinitic clays and thin coal intercalations. The Lower Cretaceous
22
23 236 succession ends with the transgressive, glauconite-bearing, coastal to sublittoral siliciclastic
24
25 237 deposits of the Cochirleni Formation (uppermost Aptian–Albian).

26
27 238 The Upper Cretaceous has a significantly more patchy development, mainly restricted
28
29 239 to the eastern part of Southern Dobrogea, excepting the weakly glauconitic, chalky-sandy
30
31 240 Peștera Formation (Lower Cenomanian) and the marly Dobromiru Formation (Upper
32
33 241 Cenomanian) that cover the western-central parts of the area. The younger Cuza Vodă
34
35 242 (Turonian), Murfatlar (Santonian–Lower-Middle Campanian), and Satu Nou (Upper
36
37 243 Campanian) formations are dominantly chalky, suggesting the instalment of a relatively
38
39 244 deeper, offshore depositional environment; neither of these units is known from western
40
41
42 245 Southern Dobrogea.

43
44 246 In total, the Lower Cretaceous of Southern Dobrogea was deposited in a shallow
45
46 247 marine, near-shore setting, fluctuating between carbonate platform, lagoonal, coastal-tidal
47
48 248 flat, and continental environments (see Avram et al., 1996; Dragastan et al., 1998). Its main
49
50 249 characteristic features, such as the observed lithological variability, the areal distribution of
51
52 250 the different units, and the presence of several unconformities within the series, are all linked

1
2 251 to eustatic sea-level changes that affected the Southern Dobrogean territory during the Early
3
4 252 Cretaceous (Dragastan et al., 1998). The main emergent land in the area was represented by
5
6 253 the Central Dobrogean Massif, lying north of the study area, almost completely subaerially
7
8 254 exposed and actively eroding during the Cretaceous. Consequently, shallow-marine to
9
10 255 continental deposits are restricted mainly to the northern part of Southern Dobrogea, close to
11
12 256 its boundary with the Central Dobrogean Massif (marked by the Capidava-Ovidiu Fault), and
13
14 257 are replaced by more open marine deposits southward. As summarized above, several littoral,
15
16 258 and even continental, sequences occur in this succession, including deposits in the Amara,
17
18
19 259 Cernavodă, Ramadan (~~in part;~~ Avram et al., 1996) and Cochirleni formations, whereas the
20
21 260 Gherghina Formation is purely continental, with occasional minor marine interbeds produced
22
23 261 during short-term incursions of the sea.

24
25 262 In the Cernavodă-Cochirleni area the outcropping Mesozoic is restricted to the Lower
26
27 263 Cretaceous, and includes deposits belonging to the Cernavodă, Ostrov (or Ramadan),
28
29 264 Gherghina, and Cochirleni formations. While the lower–middle part of the Cernavodă
30
31 265 Formation is well exposed and widely distributed in this area, its upper part (the lower
32
33 266 Hauterivian Vederoasa Member) is unevenly developed. This member is missing in the
34
35 267 classical succession from Cernavodă-Hinog, on the right bank of the Danube (Dragastan et
36
37 268 al., 1998), but was recently identified in the more eastern Cernavodă-lock section (Dragastan
38
39 269 et al., 2014). Similarly, the Ostrov Formation is represented in the area only by its upper
40
41 270 subunit (the Lower Aptian Lipnița Member; Dragastan et al., 1998), covering unconformably
42
43 271 and transgressively the Valanginian Alimanu Member of the Cernavodă Formation in the
44
45 272 southern end of the Cernavodă-Hinog section (Dragastan et al., 1998), and the lower
46
47 273 Hauterivian Vederoasa Member in the Cernavodă-lock section (Dragastan et al., 2014).

48
49
50 274 Northward of the Hinog area, Valanginian deposits of the Alimanu Member are
51
52 275 overlain directly by the Middle–Upper Aptian continental deposits of the Gherghina

1
2 276 Formation. These continental deposits also cover the *Orbitolina*-bearing calcareous-clayey
3
4 277 deposits of the Lipnița Member towards the south, marking the advancement of emerged
5
6 278 areas towards the central parts of Southern Dobrogea, including the Cernavodă-Cochirleni
7
8 279 area, during this time interval (Avram et al., 1996). Marine conditions returned in the study
9
10 280 area again in the latest Aptian, with a transgression marked by widespread deposition of the
11
12 281 glauconitic, siliciclastic coastal to innermost shelf deposits of the Cochirleni Formation.
13
14 282 These uppermost Aptian to Albian sands and sandstones cover transgressively all the
15
16 283 underlying deposits, belonging to the Cernavodă, Ostrov, or Gherghina formations.
17
18 284 Siliciclastic shallow-marine sedimentation continued into the Early Cenomanian, with the
19
20 285 chalky-glauconitic deposits of the Peștera Formation.
21
22
23 286
24

25 287 4. Palaeontology

26
27 288 The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova
28
29 289 Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu
30
31 290 (1913), who referred it to *Megalosaurus* cf. *superbus*, a taxon erected by Sauvage (1882)
32
33 291 from the Gault ('mid'-Cretaceous: Albian) of the Paris Basin, France. The Gault material
34
35 292 described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were
36
37 293 deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of
38
39 294 *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was
40
41 295 referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it
42
43 296 and the type species *M. bucklandi*.

44
45 297 The convoluted taxonomic history of *Erectopus superbus* was recently reviewed by
46
47 298 Allain (2005), who established that both the isolated teeth first mentioned by Sauvage (1876)
48
49 299 and the skeletal elements described by Sauvage (1882) belong to the same taxon, for which
50
51 300 the name *Erectopus superbus* was retained. Allain (2005) regarded *Erectopus* as a member of

1
2 301 Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al.
3
4 302 (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered
5
6 303 *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.”
7
8 304 Accordingly, if we are following the original assessment of Simionescu (1913) but updating
9
10 305 with contemporary taxonomy, the Cochirleni theropod tooth should now be considered
11
12 306 referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to
13
14 307 *Erectopus superbus* (or a close relative) was considered to be unsupported by positive
15
16 308 evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to
17
18 309 understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B,
19
20 310 3), we provide here a detailed description of its morphology followed by a thorough
21
22 311 comparative study of this tooth based on large datasets of theropod dental measurements and
23
24 312 discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).
25
26
27 313 We note that in his review of Romanian dinosaurs, Grigorescu (2003) erroneously
28
29 314 considered UAIC (SCM1) 615 as being referred by Simionescu to the taxon *Megalosaurus*
30
31 315 *dunkeri* Kohen (sic; actually, *Megalosaurus dunkeri* Dames, 1884). This is clearly a simple
32
33 316 misreading of Simionescu’s identification. Additionally, such a referral is also contradicted
34
35 317 by the absence of mesial serrations in the holotype tooth of *M. dunkeri*, considered by
36
37 318 Carrano et al. (2012) to represent an indeterminate theropod. The Dobrogea tooth, on the
38
39 319 other hand, has mesial serrations (see below).
40

41 42 320 43 44 321 *4.1. Age of UAIC (SCM1) 615*

45
46 322 The age of UAIC (SCM1) 615 has been contentious, due to the uncertainties concerning its
47
48 323 place of origin. Although it is often mentioned as originating from Cochirleni village (e.g.,
49
50 324 Grigorescu, 2003; Turculeț and Brânzilă, 2012), this has not been definitively established.
51
52 325 According to the original report of Simionescu (1913), the tooth came from the upper part of
53

1
2 326 the Lower Cretaceous limestone succession exposed in the cliffs extending from Cernavodă
3
4 327 to Cochirleni along the right bank of the Danube. The corresponding entry from the Hârșova
5
6 328 Museum registry states that it was found in the ‘Cochirleni quarry’, a location that presently
7
8 329 cannot be identified precisely. The only rocks to be quarried in the area are the calcareous
9
10 330 deposits of either the Cernavodă or Ostrov formations, particularly the ones that crop out in
11
12 331 the Danube bank cliffs between Cernavodă-Hinog-Cochirleni. Finally, although the mention
13
14 332 ‘Cochirleni’ is usually considered to refer to Cochirleni village, it should be mentioned that
15
16 333 the cliff-forming hill that extends between Cernavodă and Cochirleni is also known by the
17
18 334 same name (Fig. 1). Taking all of this evidence into consideration, it is thus reasonable to
19
20
21 335 conclude that the tooth was most likely found in the Lower Cretaceous limestone succession
22
23 336 exposed in the Danube cliffs between Cernavodă and Cochirleni.

24
25 337 Based on the location of the discovery, in the upper part of the local limestone
26
27 338 succession, and the age of the deposits from Cernavodă-Cochirleni known to him,
28
29 339 Simionescu (1913) considered the tooth to be of Barremian age. Subsequently, the age of the
30
31 340 tooth was given as Valanginian–Barremian (Weishampel, 1990; Weishampel et al., 2004) or
32
33 341 Valanginian (e.g., Grigorescu, 2003), but without any supporting information.

34
35 342 New attempts have been made to more precisely constrain the age of UAIC (SCM1)
36
37 343 615. Dragastan et al. (2014) recently sampled the limestone matrix holder of the tooth, and
38
39 344 reported from these samples an assemblage of foraminiferans, ostracods and
40
41 345 microproblematicae (= *incertae sedis* microorganisms) that characterize their ‘Biozone IX
42
43 346 with *Meandrospira favrei*’, of latest Valanginian age in the local lithostratigraphic scheme. In
44
45 347 parallel, we also sampled the same limestone holder – a yellowish white, friable lime
46
47 348 mudstone – that yielded a poor and badly preserved calcareous nannoplankton assemblage
48
49 349 with *Watznaueria barnesiae*, *W. ovata*, *Nannoconus steinmanni*, *N. kamptneri*, *N. globulus*,
50
51 350 *Calcicalathina sp.*, *Speetonia colligata* and *Cyclagelosphaera deflandrei* (M. C. Melinte-

1
2 351 Dobrinescu, personal communication, November 2013), an assemblage that suggests a
3
4 352 Berriasian–Hauterivian age of the limestone holder.
5
6 353 Since it is not clear if the limestone holder came from the same site as the tooth itself,
7
8 354 we managed to take a second sample from the limestone matrix still partly filling the pulp
9
10 355 cavity of the tooth, which must definitively be identical with the rocks the tooth was found in.
11
12 356 This second, much smaller sample yielded only very scarce specimens of *Watznaueria*
13
14 357 *barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-
15
16 358 Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in
17
18 359 abundance during the Berriasian and, especially, the Valanginian.
19
20

21 360 In the nannoplankton succession reported previously by Avram et al. (1993) and
22
23 361 derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the
24
25 362 concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus*
26
27 363 *lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu
28
29 364 Member of the Cernavodă Formation. These assemblages were interpreted to represent the
30
31 365 nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was
32
33 366 assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous
34
35 367 of the Mecsek Mountains, Hungary, by Császár et al. (2000).
36

37 368 Together, all the available evidence (Simionescu's original account, geographic and
38
39 369 geologic records, foraminifera, ostracods, microproblematicae, and calcareous
40
41 370 nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member
42
43 371 of the Cernavodă Formation, and it is most probably of late Valanginian age.
44

45
46 372

47 48 373 *4.2. Description and comparisons*

49
50 374 Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2,
51
52 375 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown
53

1
2 376 base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of
3
4 377 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is
5
6 378 remarkably well preserved, with the enamel in pristine condition. It preserves most of the
7
8 379 crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5
9
10 380 mm missing in the apical region.

11
12 381 In its present state, the mesial edge and part of the mesial third of the tooth are
13
14 382 embedded in the limestone holder (Fig. 2B), although the tooth was once removed (see
15
16 383 above, History of collecting and curation; Fig. 2A). Accordingly, it is exposed so that all
17
18 384 faces of the tooth are widely visible, including the root region, except for the mesial surface.

19
20
21 385 Only the basal-most part of the root is preserved, and it is more complete near the
22
23 386 mesial margin (Fig. 3B, C). Here, broken areas around the crown-root contact area (cervix)
24
25 387 reveal details of the pulp cavity development, as well as the pattern of the dentine thickness
26
27 388 variation (Fig. 3B–D). The crown also exhibits a transverse break at about two-thirds of its
28
29 389 length (not present so obviously in the original figure of the specimen in Simionescu, 1913),
30
31 390 and adjacent to it, the distal carina is also slightly chipped distal to mid-length. The labial
32
33 391 face is superficially split near this break (Fig. 3A), while a more prominent region of damage
34
35 392 appears on the lingual face, where a large (13 x 5 mm), slightly triangular wedge is broken
36
37 393 off, exposing the deeper parts of the dentine (Fig. 3C). The damage to the lingual side
38
39 394 apparently occurred after the original description of the tooth (Fig. 2), an observation that is
40
41 395 concordant with the complex curatorial history of the specimen.

42
43 396 The basal-most, exposed part of the mesial face lacks the enamel cover (Fig. 3C, D),
44
45 397 suggesting that this area already belongs to the root region. The mesial edge of the preserved
46
47 398 crown base appears to be wider than the distal one, and is largely rounded transversely.
48
49
50 399 Accordingly, the basal cross-section is teardrop-shaped (lanceolate); it is rounded mesially,
51
52 400 but narrows distally into a small carina (Fig. 3D). As mentioned above, the pulp cavity is

1
2 401 exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of
3
4 402 the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about
5
6 403 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5
7
8 404 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes
9
10 405 thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but
11
12 406 thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B).
13
14 407 Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped
15
16 408 (Fig. 3D).
17

18
19 409 The tooth is ziphodont and only very slightly recurved distally. The distal edge is
20
21 410 nearly straight across its length, being very mildly concave in its basal half and slightly
22
23 411 convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the
24
25 412 tooth crown base. The mesial edge, as shown in the original publication of Simionescu
26
27 413 (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually
28
29 414 compressed (Fig. 3B), with a crown base ratio ($CBR=CBW/CBL$) of 0.56, within the normal
30
31 415 range of variation of most theropods. This differs from the thinner teeth of some, but not all,
32
33 416 carcharodontosaurids ($CBR<0.50$), and the much thicker incrassate teeth of derived
34
35 417 tyrannosauroids and conical teeth of spinosaurids ($CBR>0.75$) (Sereno et al., 1996; Brusatte
36
37 418 et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).
38

39
40 419 The crown cross-section is slightly asymmetrical labiolingually when it is seen in
41
42 420 distal view. In this view, when the carina is facing directly distally, one side of the crown has
43
44 421 a more pronounced bulge than its counterpart (about 8.5 mm wide, measured from the carina,
45
46 422 vs. 6 mm on the other side; Fig. 3B); based on comparisons with the teeth of *Mapusaurus*
47
48 423 (Coria and Currie, 2006), the more bulging side can be interpreted as the lingual one. This
49
50 424 asymmetry diminishes apically, where both sides become about equally convex. The distal
51
52 425 carina itself twists slightly sideways (labially) in apical direction, such that it is located closer
53

1
2 426 to the labial face where it terminates at the crown apex, and the lingual face of the denticles is
3
4 427 exposed distally (Fig. 3B, F). This twist of the distal carina is accompanied by a similar
5
6 428 outline of the lingual side; in distal view, this is somewhat convex basally, but becomes flat
7
8 429 to slightly concave in the apical two-thirds of the crown. A similar S-shaped curvature of the
9
10 430 crown, albeit more pronounced and different in details, was also reported in *Mapusaurus* and
11
12 431 *Giganotosaurus* (Coria and Currie, 2006), and in indeterminate carcharodontosaurid teeth
13
14 432 from Morocco (Richter et al., 2013).

16
17 433 The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with
18
19 434 minute serrations across its entire preserved length; the denticles are proximodistally
20
21 435 subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig.
22
23 436 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are
24
25 437 oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so
26
27 438 it is not possible to determine whether the serrations continued over the apex of the tooth.
28
29 439 There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the
30
31 440 carina. Serration shape and size remain relatively constant across the carina, although the
32
33 441 serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig.
34
35 442 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F).
36
37 443 Changes in serration size are gradual across the carina, not sudden or sporadic.

39 444 Although they are all more or less rectangular in shape, the apical denticles are
40
41 445 relatively shorter proximodistally than the more basal ones. Most of the denticles have
42
43 446 slightly rounded, asymmetrically convex triangular tips, instead of being simply squared-off,
44
45 447 and they do not hook as in troodontids and to a lesser extent abelisaurids (Hendrickx and
46
47 448 Mateus, 2014). Other denticles near the apex, however, show a faint concavity along their
48
49 449 tips, giving them a bilobate aspect, although this is both less conspicuous and far less
50
51 450 regularly developed than reported in *Tyrannotitan* (Novas et al., 2005). The denticles are
52

1
2 451 separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length.
3
4 452 The interdenticular space between adjacent denticles is broad, measuring more than a third of
5
6 453 the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the
7
8 454 crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These
9
10 455 sulci are so short and indistinct that they are only visible under low angle light.

11
12 456 Little can be said about the mesial carina, as it is not visible in the current state of the
13
14 457 specimen, buried in the limestone matrix. Based on the description of Simionescu (1913),
15
16 458 however, it is covered across its length with minute serrations; these decrease in size towards
17
18 459 the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles)
19
20
21 460 per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly
22
23 461 smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and
24
25 462 Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus,
26
27 463 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends
28
29 464 towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii*
30
31 465 where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*
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33 466 *superbus* (Sauvage, 1876, 1882) in this respect.

34
35 467 The external enamel surface exhibits two forms of ornamentation. First, the majority
36
37 468 of the labial and lingual faces are covered by relatively smooth enamel that exhibits a subtle
38
39 469 form of braided texture visible under low angle light (Fig. 3A, C, E). This texture is made up
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41 470 of a series of very faint, apico-basally running ridges; these are of unequal lengths, starting at
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43 471 different points of the crown height, but none extends the whole length of the crown. The two
44
45 472 longest ridges are placed near the distal carina. The enamel is also finely granulated.

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48 473 Second, near the carinae on both labial and lingual surfaces there are marginal
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50 474 undulations: wrinkles in the enamel that stand out in bas relief (Brusatte et al., 2007). These
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52 475 are much better preserved and visible near the distal carina, where they are so pronounced

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2 476 that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly
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4 477 developed wrinkles are present along the crown height; in the basal half of the crown, the
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6 478 wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer
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8 479 than twice the space separating each undulation. The wrinkles project obliquely (in the
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10 480 mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal
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12 481 segment on the crown, and curve apically as they approach the carina (at about 45°) with a
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14 482 tendency to become tangential to the distal edge. The wrinkles are especially well developed,
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16 483 prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig.
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18 484 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm).
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21 485 Apically, however, the wrinkles are somewhat wider and longer, extending over about half of
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23 486 the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the
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25 487 crown in wrinkle development as well, these being better expressed on the more rounded,
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27 488 convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the
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29 489 presumed labial face, only some of the basal-most wrinkles, particularly the second and third
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31 490 one, appear well defined.

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33 491 Towards the base of the crown a few of the wrinkles continue across the labial and
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35 492 lingual surfaces as very subtle transverse undulations. Most conspicuous of these is a 3.5 mm
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37 493 wide horizontal swelling that crosses the crown, at the level of wrinkles 2 and 3; this swelling
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39 494 is clearly visible on both sides of the crown (Fig. 3. A, C). There are no lateral flutes, apico-
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41 495 basal ridges, or longitudinal grooves on the labial or lingual faces, either in the centre of the
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43 496 tooth or paralleling the carinae. Instead, the labial and lingual faces are uniformly convex,
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45 497 giving the tooth its teardrop-shaped outline in cross section.
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50 499 5. Discussion

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52 500 5.1. *Identification of UAIC (SCM1) 615*

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2 501 The isolated tooth from Cochirleni can be referred to Theropoda based on its large size,
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4 502 recurved and labiolingually compressed morphology, and presence of a continuous series of
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6 503 well-defined serrations on the distal carina.
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8 504 Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert
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10 505 (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are
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12 506 also known to possess remarkably theropod-like, laterally compressed and serrated teeth, not
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14 507 unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are
15
16 508 significantly smaller than the Southern Dobrogean specimen, especially in the case of the
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18 509 Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest,
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20 510 caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene
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22 511 *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615;
23
24 512 moreover, these teeth are slightly conical and less laterally compressed than the Southern
25
26 513 Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia
27
28 514 appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly
29
30 515 younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true
31
32 516 denticles along their carinae) are reported in Europe only beginning in the Albian (Ósi et al.,
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34 517 2015), and these are both significantly smaller and different in morphology from the
35
36 518 Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian
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38 519 affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a
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40 520 theropod tooth.
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42
43 521 We used four techniques to identify which type of theropod UAIC (SCM1) 615 likely
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45 522 belongs to (see also Supplementary Material).
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47
48 523 First, we conducted a Principal Components Analysis (PCA) based on a large
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50 524 database that includes a broad and representative sample of theropod teeth. This dataset was
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52 525 compiled by Hendrickx et al. (2015a), which built upon the earlier studies of Smith et al.
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1
2 526 (2005) and Larson and Currie (2013), and it or a similar version has been used in recent
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4 527 studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, ~~2013~~2014; Brusatte
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6 528 and Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL,
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8 529 CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at
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10 530 the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to
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12 531 this dataset, the data were log-transformed prior to analysis, missing values for measurements
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14 532 were estimated with a mean value for that measurement from across the sample, and then a
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16 533 PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17
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19 534 (Hammer et al., 2001).

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21 535 In the resulting two dimensional morphospace (Fig. 4), UAIC (SCM1) 615 plots close
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23 536 to many teeth belonging to carcharodontosaurids, along with some teeth belonging to
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25 537 spinosaurids and tyrannosauroids. It falls within the convex hull (maximum morphospace
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27 538 occupation area) of carcharodontosaurids only, although it is closely outside of the edges of
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29 539 spinosaurid and tyrannosauroid space. It also falls within the 95% confidence interval ellipse
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31 540 for carcharodontosaurids, but not within the ellipse of any other group (Supplementary
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33 541 Information). This exercise indicates that UAIC (SCM1) 615 is most similar to
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35 542 carcharodontosaurids.

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37 543 Secondly, we used the log-transformed dataset that we also used for the PCA to
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39 544 conduct a clustering analysis. We performed the analysis in PAST v2.17, using the paired
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41 545 group algorithm and the correlation similarity measure. In the resulting dendrogram, UAIC
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43 546 (SCM1) 615 groups with a handful of teeth belonging to carcharodontosaurids,
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46 547 tyrannosauroids, and *Allosaurus* (Supplementary Information).

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48 548 Third, we used the tooth measurement database to conduct a discriminant analysis in
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50 549 PAST v3.0 (Hammer et al., 2001). This analysis uses pre-determined groups (in this case,
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52 550 taxonomic clusters) to create a morphospace in which these groups are maximally separated.
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1
2 551 This allows teeth of unknown affinities, such as UAIC (SCM1) 615, to be classified
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4 552 according to which taxonomic group it is most similar to in this discriminant morphospace. In
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6 553 total, 67.79% of other teeth are classified correctly when they are treated as having uncertain
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8 554 affinities and their measurements are used to classify them in discriminant space, indicating
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10 555 that this exercise returns reasonable results. Our analysis classifies the Romanian tooth as a
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12 556 carcharodontosaurid. Furthermore, the analysis places UAIC (SCM1) 615 within the convex
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14 557 hulls for carcharodontosaurids and tyrannosauroids, and the 95% confidence ellipses for
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16 558 carcharodontosaurids, coelophysoids, and neovenatorids.

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19 559 Fourth, we ran a phylogenetic analysis by including UAIC (SCM1) 615 in the discrete
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21 560 character dataset of theropod dental features published by Hendrickx and Mateus (2014). The
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23 561 Romanian specimen was scored as a lateral tooth in this analysis. The analysis was conducted
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25 562 in TNT (Goloboff et al., 2008), and resulted in 224 most parsimonious trees (686 steps,
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27 563 consistency index of 0.338, retention index of 0.566). The strict consensus topology is
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29 564 moderately well resolved and places the Romanian tooth as the sister taxon to
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31 565 *Carcharodontosaurus* (Supplementary Material). This sister taxon pair is recovered as the
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33 566 sister clade to a grouping of the derived carcharodontosaurids *Mapusaurus* and
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35 567 *Giganotosaurus*.

37 568 Several synapomorphies support the carcharodontosaurid affinities of UAIC (SCM1)
38
39 569 615. The sister group relationship with *Carcharodontosaurus* is supported by two features: a
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41 570 roughly straight distal margin of the crown (character 68) and pronounced marginal
42
43 571 undulations in the enamel that are well visible in normal light (character 112). The broader
44
45 572 clade of UAIC (SCM1) 615, *Carcharodontosaurus*, *Mapusaurus*, and *Giganotosaurus* (=
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47 573 Carcharodontosaurinae, as defined by Brusatte and Sereno, 2008, and Carrano et al., 2012) is
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49 574 linked by numerous characters, including: large teeth with a crown height greater than 6 cm
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51 575 (character 65), a bowed or sigmoid distal carina in distal view (character 82), marginal
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2 576 undulations that are at least twice as long mesiodistally as the space separating each
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4 577 undulation (character 111), and marginal undulations present on both mesial and distal sides
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6 578 of the crown (character 113).

8 579 The Romanian specimen also lacks many keystone dental synapomorphies of other
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10 580 theropod clades, based on the clade diagnoses of Hendrickx and Mateus (2014) and other
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12 581 cladistic studies that include dental characters. UAIC (SCM1) 615 does not possess the
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14 582 hooked distal denticles of some Abelisauridae, the strongly labially deflected distal carina
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16 583 and pronounced transverse enamel undulations extending across the labial and lingual tooth
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18 584 faces of Ceratosauridae, the incrassate teeth with apicobasal enamel flutes and deeply veined
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20 585 enamel surface texture of Spinosauridae, and the large transverse undulations of some basal
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22 586 allosauroids (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of
23
24 587 derived tyrannosauroids (Brusatte et al., 2010a) and the large and strongly hooked (or
25
26 588 pointed) denticles of troodontids and therizinosauroids (e.g., Turner et al., 2012; Brusatte et
27
28 589 al., 2014; Hendrickx and Mateus, 2014). The large size, as well as recurved and ziphodont
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30 590 shape of UAIC (SCM1) 615 is strikingly different from the non-ziphodont therizinosauroids,
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32 591 ornithomimosaurs, alvarezsauroids, and most troodontids, which have conical, leaf-shaped, or
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34 592 peg-like teeth (when teeth are present) (e.g., Holtz et al., 2004a; Turner et al., 2012; Brusatte
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36 593 et al., 2014). Finally, besides its remarkably large size, the presence of serrations indicates
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38 594 that UAIC (SCM1) 615 does not belong to groups such as alvarezsauroids, oviraptorosaurs,
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40 595 basal troodontids, or avialans, which have unserrated crowns (e.g., Turner et al., 2012;
41
42 596 Hendrickx and Mateus, 2014).

45 597 In summary, the four analyses all support carcharodontosaurid affinities for UAIC
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47 598 (SCM1) 615. Both overall tooth proportions and discrete phylogenetic characters point to a
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49 599 carcharodontosaurid identification, and the discriminant function analysis and phylogenetic
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51 600 analysis both explicitly recover the tooth as a carcharodontosaurid. For this reason we refer

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2 601 this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very
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4 602 derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and
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6 603 *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno
7
8 604 (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as
9
10 605 recovered in our analysis, is congruent with results of previous analyses based on larger sets
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12 606 of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno,
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14 607 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015),
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16 608 and offers some support for considering the Romanian carcharodontosaurid from Southern
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18 609 Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of
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20
21 610 the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

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23 611 Two final notes are worth adding. First, our analyses also incorporated
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25 612 carcharodontosaurids that are usually found to be basal within the clade, such as
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27 613 *Acrocanthosaurus* and *Eocarcharia* (e.g., Harris, 1998; Sereno and Brusatte, 2008; Carrano
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29 614 et al., 2012) as well as a host of other allosauroids, including members of Neovenatoridae
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31 615 (*Neovenator*, *Australovenator* and *Fukuiraptor*), a clade that is often recovered as sister-
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33 616 taxon to carcharodontosaurids within Carcharodontosauria (e.g., Benson et al., 2010; Carrano
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35 617 et al., 2012; but see Novas et al., 2013; Porfiri et al., 2014, for an alternate placement of
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37 618 neovenatorids in general). Both PCA and phylogenetic analysis clearly identified UAIC
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39 619 (SCM1) 615 as more closely comparable morphologically to derived carcharodontosaurids
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41 620 than to either basal carcharodontosaurids or to any other allosauroid subclade.

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43
44 621 Second, our datasets also included teeth of *Erectopus*, the genus erected for
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46 622 ‘*Megalosaurus*’ *superbus* to which UAIC (SCM1) 615 was originally referred. Again, our
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48 623 analyses clearly indicate that there are no close morphological and morphometric similarities
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50 624 between the two, which is in accordance with the suggestion of Carrano et al. (2012) that
51
52 625 *Erectopus* represents a non-carcharodontosaurid taxon, while our analysis identifies UAIC

1
2 626 (SCM1) 615 as a carcharodontosaurid. Instead, *Erectopus* groups with abelisauroids in the
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4 627 phylogenetic analysis. This is somewhat surprisingly, as Allain (2005) and Carrano et al.
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6 628 (2012) both identified *Erectopus* as a tetanuran. It should be noted, however, that Albian-
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8 629 aged abelisauroids are known from the same general area (eastern France) as that yielding the
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10 630 material referred to *Erectopus* (Accarie et al., 1995; Carrano and Sampson, 2008), raising the
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12 631 intriguing possibility that this taxon may represent an abelisauroid instead of an allosauroid
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14 632 tetanuran as suggested by Allain (2005) and Carrano et al. (2012). However, it must be
15
16 633 remembered that this phylogenetic analysis is based on dental characters only, so it is
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18 634 probably more likely that *Erectopus* is a tetanuran with a dentition convergent to some extent
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21 635 with those of certain abelisauroids.
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23 636 24 25 637 5.2. Body size of UAIC (SCM1) 615 26

27 638 One of the most salient and remarkable features of UAIC (SCM1) 615 is its large size. In the
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29 639 large and comprehensive sample of theropod teeth from our dataset, tooth size (estimated
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31 640 based on crown height – CH, and used as a rough proxy of body size) ranges from 2.2 mm (in
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33 641 the dromaeosaurid *Saurornitholestes* and the coelurosaur of uncertain affinities
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35 642 *Richardoestesia*) to 117.1 mm in the gigantic tyrannosauroid *Tyrannosaurus*. The Romanian
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37 643 specimen UAIC (SCM1) 615, with a CH of 85.5 mm, is ranked in the 60-80% maximum size
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39 644 (~ CH) range of the sample, and has a CH that is 73% of the largest tyrannosauroid teeth.
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41 645 Most of the teeth in the dataset (over 61% of the 966 measured teeth) are very small to small
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43 646 (less than 25 mm CH), and less than 10% of these fall in the 60-100% CH size categories.
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45 647 Teeth larger than UAIC (SCM1) 615 make up less than 5% of the total sample, and they
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47 648 represent only five taxa: the megalosaurid *Torvosaurus*, the tyrannosauroid *Tyrannosaurus*,
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49 649 the basal carcharodontosaurid *Acrocanthosaurus*, and the derived carcharodontosaurines
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51 650 *Carcharodontosaurus* and *Giganotosaurus*. Compared to other carcharodontosaurids, UAIC
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2 651 (SCM1) 615 is smaller than the largest teeth of *Acrocanthosaurus* (9% difference),
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4 652 *Carcharodontosaurus* (20%), and *Giganotosaurus* (12.5%) in the dataset, but is 13% bigger
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6 653 than the largest tooth of *Mapusaurus*.
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8 654 It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized
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10 655 carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic
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12 656 carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Serenó et al., 1996; Calvo
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14 657 and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close
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16 658 relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn,
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18 659 corroborates growing evidence that very large body size was acquired very early in
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21 660 carcharodontosaurid history, since the earliest potential members of the clade are already of
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23 661 relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is
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25 662 *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and
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27 663 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more
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29 664 derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the
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31 665 uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see
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33 666 below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized
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35 667 carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.
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37 668 The inferred large body size of the South Dobrogean theropod is also remarkable as
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39 669 virtually all other dinosaur remains reported previously from Romania (both from the Early
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41 670 Cretaceous Cornet assemblage and the much later, end Cretaceous Hațeg Island fauna) are
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43 671 significantly smaller, and many have been interpreted as insular dwarfs (e.g., Weishampel et
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45 672 al., 1993, 2003; Benton et al., 2006, 2010; Stein et al., 2010; Ósi et al., 2014). Although other
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47 673 Romanian theropod dinosaurs were not particularly dwarfed (e.g. Brusatte et al., 2013), they
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49 674 were nonetheless small (Nopcsa, 1902; Csiki and Grigorescu, 1998; Csiki et al., 2010;
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51 675 Brusatte et al., 2013). This bias towards small bodied Romanian theropods was also
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2 676 interpreted as a consequence of their insular habitat (Csiki and Grigorescu, 1998), as all
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4 677 previously reported theropod remains come from within the Carpathian Orogen, an area with
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6 678 an archipelago-type palaeogeography during the Cretaceous (Dercourt et al., 2000; Csontos
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8 679 and Vörös, 2004; Csiki-Sava et al., 2015). By contrast, UAIC (SCM1) 615 was found in
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10 680 shallow marine deposits bordering the emerged areas of Central Dobrogea, part of the stable
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12 681 cratonic areas of Europe and connected at least intermittently to the Ukrainian Shield since
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14 682 the Late Jurassic (Fig. 5A). Although cratonic Europe was also transformed into an
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16 683 archipelago of islands during much of the Cretaceous, these islands were often both larger in
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18 684 size and more stable in space and time than were the transient emerged areas of the Tethyan
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21 685 archipelagoes. As such, it is conceivable that the Southern Dobrogean carcharodontosaurid
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23 686 was less constrained by space or resource limitations than the Tethyan insular dinosaurs,
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25 687 allowing it to retain a large body size.

26 27 688 28 29 689 *5.3. UAIC (SCM1) 615 and Valanginian dinosaur distribution* 30

31 690 Besides documenting the presence of large-sized mainland carcharodontosaurids in the
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33 691 Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a
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35 692 significant gap in our knowledge on the composition and distribution of the Early Cretaceous
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37 693 dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed
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39 694 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these
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41 695 being known from the later part (Barremian–Albian) of that epoch; only around a dozen
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43 696 localities were listed from each age of the early part of the Early Cretaceous (Berriasian,
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45 697 Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous
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48 698 dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al.,
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50 699 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs
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52 700 and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards

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2 701 western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no
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4 702 occurrences are known from the entire central, eastern and southern Europe for the
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6 703 Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–
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8 704 Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et
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10 705 al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the
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12 706 carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in
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14 707 Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).

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17 708 Our identification of the Romanian tooth as a carcharodontosaurid documents the
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19 709 presence of this clade in Europe in the very early Cretaceous. This is significant, as
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21 710 carcharodontosaurids were widely distributed tens of millions of years later, in the middle
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23 711 Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see
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25 712 below). Despite the recent discoveries documenting that the clade was also present in North
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27 713 America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and
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29 714 Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in
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31 715 Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010;
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33 716 see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older
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35 717 than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than
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37 718 previously thought and were a long-term component of the European mainland Early
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39 719 Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might
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41 720 have been already present between the cratonic, stable European mainland, with a dinosaur
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43 721 fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine
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45 722 areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those
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47 723 described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania
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49 724 (Benton et al., 2006).

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2 725 This Valanginian carcharodontosaurid represents an important datapoint not only for
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4 726 the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a
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6 727 poorly documented age in dinosaur evolution, with very few precisely dated fossil
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8 728 occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of
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10 729 Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known
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12 730 from Asia, some of which have debatable or controversial dates. These include sites in Japan
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14 731 (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009
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16 732 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these
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18 733 assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age
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20 734 constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible
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22 735 Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992;
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24 736 Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were
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26 737 shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare
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28 738 dinosaur remains of possible Valanginian (or ‘Neocomian’) age were also reported from
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30 739 southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g.,
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32 740 Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli
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34 741 et al., 2014).

37 742 As one of the two known reports of Valanginian dinosaurs in Europe east of France,
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39 743 the Southern Dobrogean dinosaur record fills a huge palaeogeographic gap between the
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41 744 western European and the eastern Asian dinosaur faunas. Moreover, none of these early Early
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43 745 Cretaceous dinosaur assemblages from outside Europe include carcharodontosaurids (see
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45 746 below), as theropods are represented by coelurosaurians interpreted either as compsognathids
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47 747 (Gishlick and Gauthier, 2007) or basal ornithomimosaurids (Choiniere et al., 2012) in southern
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49 748 Africa, metriacanthosaurid allosauroids (‘sinraptorids’) in Thailand (Buffetaut and
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51 749 Suteethorn, 2007), and indeterminate allosauroids (Pérez-Moreno et al., 1993), non-

1
2 750 carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz,
3
4 751 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest
5
6 752 that carcharodontosaurids had not achieved a wide geographic distribution by this point in
7
8 753 time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.
9

10 754 Finally, the presence of the Cochirleani carcharodontosaurid might hint at the presence
11
12 755 of palaeobiogeographic provinciality between the western and the eastern parts of Europe,
13
14 756 partly mirroring those reported from the later part of the Late Cretaceous (e.g., Le Loeuff and
15
16 757 Buffetaut, 1995; Weishampel et al., 2010; Ősi et al., 2012; Csiki-Sava et al., 2015). In the
17
18 758 reasonably well sampled, and significantly better known, western European dinosaur faunas,
19
20
21 759 Valanginian large carnivorous dinosaurs include non-carcharodontosaurid tetanurans
22
23 760 (*Becklespinax*), as well as indeterminate allosauroids or indeterminate theropods (often
24
25 761 described as '*Megalosaurus dunkeri*', '*M. insignis*' or '*M. oweni*'), none of which can be
26
27 762 referred positively to Carcharodontosauridae (Carrano et al., 2012). The apparently
28
29 763 provincial geographic distribution of the large-bodied theropods suggests that some degree of
30
31 764 faunal differentiation was occurring within the European mainland, most probably promoted
32
33 765 by geographic distance. Notably, this intra-European differentiation in theropod assemblages
34
35 766 appears to stand in contrast with the faunal homogeneity reported in the case of the
36
37 767 ornithopods from the UK and Romania (e.g., Galton, 2009). It is important, however, to re-
38
39 768 emphasize at this point that the Valanginian dinosaur fossil record is both exceedingly poor
40
41
42 769 and patchy, even in Europe. Accordingly, further discoveries are needed to verify and support
43
44 770 (or contradict) the presence of such a distribution pattern pointing to palaeobiogeographic
45
46 771 provinciality inside Europe, as the one suggested by our carcharodontosaurid identification
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48 772 for UAIC (SCM1) 615.

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52 774 *5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography*

1
2 775 Carcharodontosauridae were long considered as an exclusively Gondwanan group of
3
4 776 theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa
5
6 777 (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–
7
8 778 Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996;
9
10 779 Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte,
11
12 780 2008; Cau et al., 2013). This view started to change with the identification of the Early
13
14 781 Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal
15
16 782 carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and
17
18 783 Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic
19
20 784 distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan
21
22 785 one, was further supported by the discovery of definitive carcharodontosaurids in the Lower
23
24 786 Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper
25
26 787 Cretaceous of China (Brusatte et al., 2009, 2010b, ~~2012~~; Mo et al., 2014; Lü et al.,
27
28 ~~2014~~2016).
29 788
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31 789 Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin
32
33 790 of the carcharodontosaurids, followed by their dispersal across Laurasia and western
34
35 791 Gondwana beginning at least by the Aptian (Fig. 5B), a scenario that is concordant with the
36
37 792 tentatively suggested presence of early carcharodontosaurids in the Upper Jurassic of
38
39 793 Tanzania, which are based on fragmentary specimens (Rauhut, 2011; Carrano et al., 2012). It
40
41 794 is also concordant with the widespread appearance of carcharodontosaurids in the fossil
42
43 795 record starting with the Aptian, when they are reported in Africa (*Eocarcharia*; Sereno and
44
45 796 Brusatte, 2008), South America (Vickers-Rich et al., 1999), North America
46
47 797 (*Acrocanthosaurus*; Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000
48
49 798 Eddy and Clarke, 2011), Europe (Canudo and Ruiz-Omeñaca, 2003; Pereda-Suberbiola et al.,
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2 799 | 2012), and eastern Asia (*Kelmayisaurus*; Brusatte et al., 2012; ~~Lü et al., 2014~~; Mo et al.,
3
4 800 | 2014; [Lü et al., 2016](#)).
5
6 801 | During the Albian–Turonian, carcharodontosaurids became especially abundant and
7
8 802 | diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996;
9
10 803 | Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and
11
12 804 | South America (*Tyrannotitan*, *Giganotosaurus*, *Mapusaurus*, alongside with indeterminate
13
14 805 | carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005;
15
16 806 | Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig.
17
18 807 | 5B). They were still present during this time interval in other continents, as well: in North
19
20 808 | America with *Acrocanthosaurus* until the Albian (D’Emic et al., 2012), in Europe until the
21
22 809 | Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with
23
24 810 | *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).
25
26 811 | After dominating terrestrial ecosystems at least in Africa, South America and eastern
27
28 812 | Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et
29
30 813 | al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the
31
32 814 | Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado,
33
34 815 | 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large
35
36 816 | theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana.
37
38 817 | Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-
39
40 818 | Cenomanian deposits of South America to Carcharodontosaridae (e.g., Canudo et al., 2008;
41
42 819 | Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the
43
44 820 | abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were
45
46 821 | reported to suggest the survival of carcharodontosaurids into the latest Cretaceous
47
48 822 | (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).
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1
2 848 Aptian, followed by the appearance of many fossils of carcharodontosaurines beginning in
3
4 849 the Albian (Fig. 5B). The proposed affinities of the oldest carcharodontosaurid material –
5
6 850 including isolated teeth referred to as ‘*Megalosaurus*’ *ingens* – from the east African Upper
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8 851 Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut,
9
10 852 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC
11
12 853 (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with
13
14 854 the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very
15
16 855 large size and dental morphology characterizing it) well before the Albian, during or even
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18 856 before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and
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20
21 857 *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the
22
23 858 basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.

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25 859 Besides shifting the emergence of the carcharodontosaurines earlier in time,
26
27 860 identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting
28
29 861 palaeobiogeographic implications. As already noted, recent discoveries show that
30
31 862 Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g.,
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33 863 Novas et al., 2005), with the identification of its widespread, Pangaeian distribution during the
34
35 864 late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999;
36
37 865 Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014).
38
39 866 However, within Carcharodontosauridae itself, some palaeogeographic patterns have been
40
41 867 widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae
42
43 868 is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al.,
44
45 869 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as
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47
48 870 previously all its recognized members were restricted strictly to either Africa (Stromer, 1931;
49
50 871 Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995;
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52 872 Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of

1
2 873 Carcharodontosaurinae were still adhering to patterns of continental fragmentation and
3
4 874 vicariant evolution, with a basal split between the Albian–Cenomanian African
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6 875 *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian
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8 876 southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if
9
10 877 this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

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12 878 This scenario is now challenged by our finding that the Southern Dobrogean
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14 879 carcharodontosaurid UAIC (SCM1) 615 may nest inside Carcharodontosaurinae. If true, such
15
16 880 an affinity would suggest that the origin of Carcharodontosaurinae was not a southern,
17
18 881 vicariant by-product of the Gondwana-Laurasia separation, a major palaeogeographic event
19
20 882 that is considered to have been well underway by the end of the Jurassic, and essentially
21
22 883 completed by the mid-Early Cretaceous (see Weishampel et al., 2010). Indeed, during this
23
24 884 time palaeogeographic connections and faunal interactions were virtually non-existent
25
26 885 between the northern Tethyan (European) and southern Tethyan (western Gondwanan, but
27
28 886 essentially African) areas of the Mediterranean (e.g., Canudo et al., 2009; ~~see below~~), which
29
30 887 makes a vicariant hypothesis intuitive. However, if the Romanian tooth represents a
31
32 888 carcharodontosaurine, then it implies a much more complicated palaeogeographic history of
33
34 889 the clade, which is not so clearly linked to continental breakup.

35
36 890 The palaeogeographic position of the Southern Dobrogean carcharodontosaurine in
37
38 891 cratonic Europe, north of the Neo-Tethys, together with its significantly older age compared
39
40 892 to other carcharodontosaurines, could indicate that separation of the carcharodontosaurine
41
42 893 lineage took part in Europe and not in western Gondwana as previously assumed. This would
43
44 894 also mean that representatives of this lineage were subsequently – after the Barremian –
45
46 895 introduced to Africa and South America via trans-Tethyan dispersal, most probably at a time
47
48 896 when faunal interactions between the southern and northern margins of the Mediterranean
49
50 897 Tethys were resumed, after the early Barremian (Canudo et al., 2009).

1
2 898 Alternatively, it can be hypothesized that appearance of carcharodontosaurines in
3
4 899 Southern Dobrogea is a consequence of southern immigration originating in western
5
6 900 Gondwana, often considered the place of origin for this clade. However, this scenario has
7
8 901 several potential caveats. Although Europe has been considered as forming part of a larger
9
10 902 Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín,
11
12 903 2012), and occasional trans-Tethyan faunal connections have been recognized between
13
14 904 Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage,
15
16 905 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and
17
18 906 Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-
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20
21 907 Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place
22
23 908 during the ‘Neocomian’ (Berriasian–Hauterivian) time interval.

24
25 909 More recently, some potential evidence has emerged for Gondwana-to-Europe
26
27 910 interchange during the ‘Neocomian’. The presence of the basal rebbachisaurid *Histriasaurus*
28
29 911 (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as
30
31 912 indicative of very early and very rapid northward dispersal of this clade from western
32
33 913 Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of
34
35 914 this particular dispersal event was even constrained to the Berriasian–Valanginian time
36
37 915 interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the
38
39 916 Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of
40
41 917 the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian
42
43 918 Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive
44
45 919 transportation mechanism (‘Noah’s Ark’; ~~KeKenna~~McKenna, 1973) for basal
46
47 920 rebbachisaurids after its separation from mainland Africa (e.g., Torcida Fernández-Baldor et
48
49 921 al., 2011). Furthermore, the palaeogeographical separation between Africa and Adria (and
50
51 922 thus the effective movement of the presumed ark) is considered to be at most an incipient one
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1
2 923 during the Early Cretaceous by Bossellini (2002) and Zarccone et al. (2010), with spatial
3
4 924 continuity still present between the two landmasses, while deep-water basins continued to
5
6 925 separate Adria from the European Craton. Accordingly, although the presence of
7
8 926 *Histriasaurus* can represent a case of northward range extension of rebbachisaurids during
9
10 927 the Berriasian–Valanginian, it took place not strictly speaking into Europe, but only reached
11
12 928 the northernmost extremity of Adria, a northerly peninsular extension of the African
13
14 929 mainland. It was only starting with the Barremian that rebbachisaurids dispersed as far north
15
16 930 as the European cratonic areas, including Iberia and the British Isles (Mannion, 2009;
17
18 931 Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011), a time when faunal
19
20 932 interchanges between Europe and Africa are considered to have been well underway (e.g.,
21
22 933 Gheerbrant and Rage, 2006; Canudo et al., 2009).

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24
25 934 Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant
26
27 935 of the European mainland. It is thus unclear to what extent the example of rebbachisaurid
28
29 936 range extension into (present-day) Europe during the early Early Cretaceous, as potentially
30
31 937 testified by the discovery of the Croatian taxon, would also be applicable for the Southern
32
33 938 Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are
34
35 939 very different, and that faunal connections during this time interval are not documented
36
37 940 between the African and European cratons as already pointed out by Gheerbrant and Rage
38
39 941 (2006).

40
41 942 Absence of documented faunal interactions weakens support for a scenario of south-
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43 943 to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the
44
45 944 Cretaceous, and would argue instead for a local, European development to explain the
46
47 945 presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian
48
49 946 presence of carcharodontosaurids in Europe is also consistent with their appearance in the
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51 947 Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the
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1
2 948 eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in
3
4 949 North America likely requires the presence of pre-Aptian members of the clade in Europe,
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6 950 since faunal exchanges between these two landmasses are known to have been halted before
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8 951 the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal
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10 952 carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the
11
12 953 derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western
13
14 954 Gondwana. The causes of these distribution patterns remain as yet unknown, and further
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16 955 support – in the form on new carcharodontosaurid discoveries from the early-middle part of
17
18 956 the Early Cretaceous – is required to better uphold such a scenario.

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21 957 We finally reiterate that if the Romanian tooth does not belong to a
22
23 958 carcharodontosaurine, but instead is artefactually grouping with them in the phylogenetic
24
25 959 analysis because of the very incomplete nature of the material, then the traditional story of
26
27 960 Carcharodontosaurinae as a product of vicariant evolution driven by the breakup of Pangea
28
29 961 will remain strongly supported. However, even in such case UAIC (SCM1) 615 would still
30
31 962 record the presence of early-occurring large carcharodontosaurid theropods with a very
32
33 963 characteristic carcharodontosaurine-type dentition in the eastern part of the European craton,
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35 964 adding to known early Early Cretaceous theropod (and dinosaur) diversity, and potentially
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37 965 documenting dinosaur faunal provinciality in Europe and worldwide.

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41 967 6. Conclusions

43 968 We re-describe and interpret the affinities of one of the most significant historical dinosaurian
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45 969 specimens of Romania, an isolated but well-preserved theropod tooth from Southern
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47
48 970 Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth,
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50 971 while the available evidence – including novel calcareous nannoplankton sampling – supports
51
52 972 its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of

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2 973 Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a
3
4 974 collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only
5
6 975 two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this
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8 976 record advances our understanding of European dinosaur distribution during the early Early
9
10 977 Cretaceous, and also fills an important palaeogeographic gap between Western European and
11
12 978 Eastern Asian dinosaurian assemblages of the Valanginian.

14 979 Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a
15
16 980 possible member of Carcharodontosaurinae, a subclade of derived and gigantic
17
18 981 carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western
19
20 982 Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean
21
22 983 specimen documents the emergence of Carcharodontosaurinae earlier than previously
23
24 984 recognized, thus also indicating an earlier acquisition of their characteristically large size.
25
26 985 Based on currently known palaeogeographic and chronostratigraphic constraints on the
27
28 986 evolution of Carcharodontosauridae, it appears that not only did this clade have a wide
29
30 987 distribution, but that crucial events of its evolutionary history such as the emergence of the
31
32 988 derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of
33
34 989 western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia
35
36 990 split, as was formerly suggested. In such a case, instead of endemic evolution the emergence
37
38 991 of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-
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40 992 to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the
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42 993 Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into
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44 994 western Gondwana adds further support for the presence of important palaeogeographic ties
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46 995 between the two realms during the second half of the Early Cretaceous.
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35 1666 Figure 1. Simplified geological map of the Cernavodă-Cochirleni area; inset shows the
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37 1667 position of the study area within Romania. Legend: 1. Quaternary: a. Holocene alluvia, b.
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39 1668 Pleistocene–Holocene loessoid deposits; 2. Pre-Quaternary Cenozoic (Middle Eocene and
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41 1669 Miocene) deposits; Cretaceous: 3. Peștera Formation, Lower Cenomanian; 4. Cochirleni
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43 1670 Formation; uppermost Aptian–Lower Albian; 5. Gherghina Formation, Middle–Upper
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45 1671 Aptian; 6. Ostrov (= Ramadan) Formation; Barremian–Lower Aptian; 7. Cernavodă
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47 1672 Formation, Alimanu Member, Berriasian–Valanginian; 8. Water courses. (Redrawn after
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49 1673 Dragastan et al., 1998, 2014).
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2 1675 Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from
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4 1676 Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B.
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6 1677 Current state of UAIC (SCM1) 615, mounted in a limestone holder.
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10 1679 Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid
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12 1680 lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B.,
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14 1681 distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina
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16 1682 (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal
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18 1683 part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).
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23 1685 Figure 4. Dental morphospace of the different theropod clades according to the results of the
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25 1686 PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by
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27 1687 Carcharodontosauridae. See further details of this analysis, as well as other quantitative
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29 1688 analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant
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31 1689 function analysis, phylogenetic analysis), in the Supplementary Material.
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35 1691 Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur
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37 1692 occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-
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39 1693 Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the
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41 1694 marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and
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43 1695 palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian
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45 1696 (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615
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47 1697 from Southern Dobrogea. Legend: 1 – *Veterupristisaurus*, ‘*Megalosaurus*’ *ingens*,
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50 1698 Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator*, Spain, Barremian;
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52 1699 3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern
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2 1700 United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 –
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4 1701 *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China,
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6 1702 Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmaysaurus*,
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8 1703 Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11
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10 1704 – *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan,
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12 1705 Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 –
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14 1706 Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant
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16 references, see text, 5.4.). Palaeogeographic maps, courtesy of Ron Blakey
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1 “*Megalosaurus cf. superbus*” from southeastern Romania: the oldest known Cretaceous
2 carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous
3 Europe-Gondwana connections

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32 ABSTRACT

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

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39 Substantially less is known about those vertebrates living in the more stable, cratonic regions
40 of Romania (and Eastern Europe as a whole), particularly during the earliest Cretaceous. We
41 describe one of the few early Early Cretaceous fossils that have ever been found from these
42 regions, the tooth of a large theropod dinosaur from Southern Dobrogea, which was
43 discovered over a century ago but whose age and identification have been controversial. We
44 identify the specimen as coming from the Valanginian stage of the Early Cretaceous, an
45 incredibly poorly sampled interval in global dinosaur evolution, and as belonging to
46 Carcharodontosauridae, a clade of derived, large-bodied apex predators whose earliest
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26 Cretaceous history is poorly known. Quantitative analyses demonstrate that the Romanian
27 tooth shows affinities with a derived carcharodontosaurid subgroup, the
28 Carcharodontosaurinae, which until now has been known solely from Gondwana. Our results
29 suggest that this subgroup of colossal predators did not evolved vicariantly as Laurasia split
30 from Gondwana, but originated earlier, perhaps in Europe. The carcharodontosaurine
31 diversification may have been tied to a north-to-south trans-Tethyan dispersal that took place
32 sometime between the Valanginian and Aptian, illustrating the importance of
33 palaeogeographic ties between these two realms during the largely mysterious early–mid
34 Early Cretaceous.

36 Keywords

37 Southern Dobrogea; Valanginian; Carcharodontosauridae; cratonic Europe;
38 palaeobiogeography

40 1. Introduction

41 Romania boasts one of the best records of continental vertebrate fossils from the Cretaceous
42 of Europe (e.g., Grigorescu, 1992, 2003; Csiki-Sava et al., 2015). The vast majority of fossils
43 come from two well-known occurrences: the Early Cretaceous bauxite accumulations of
44 Cornet, in the northern Apuseni Mountains (e.g., Jurcsák, 1982; Benton et al., 1997;
45 Posmoşanu, 2003; Dyke et al., 2011), and the famous latest Cretaceous beds of the Haţeg,
46 Rusca Montană and western Transylvanian basins of Transylvania, which have yielded the
47 dinosaur-dominated ‘Haţeg Island fauna’ (e.g, Nopcsa, 1923; Weishampel et al., 1991;
48 Benton et al. 2010; Codrea et al., 2010, 2012; Grigorescu, 2010; Vremir, 2010; Vasile and
49 Csiki, 2011; Csiki-Sava et al., 2015). Both of these faunas inhabited islands that were part of
50 the vast Cretaceous European Archipelago of the Neo-Tethys Ocean. Based on their isolated

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51 geological settings and the many dwarfed and morphologically aberrant taxa that make up the
52 faunas, both have been interpreted as insular assemblages that give a unique window into
53 how island environments affected the evolution of long-extinct organisms (e.g., Benton et al.,
54 1997, 2010; Csiki-Sava et al., 2015).

55 The great volume of research on these assemblages over the past century, particularly
56 the ‘Hațeg Island fauna’, has concealed an inconvenient bias: the stable, non-island, cratonic
57 regions of Romania have yielded only extremely rare Mesozoic continental vertebrate
58 remains (i.e., the Moldavian, Moesian and Scythian platforms; Săndulescu, 1984; Mutihac
59 and Mutihac, 2010; Fig. 1). This is mostly because Mesozoic deposits are located in the
60 subsurface in these regions, with only limited subaerial exposures available in the structurally
61 highest-lying parts of the Moesian Platform, in Central and Southern Dobrogea (Middle
62 Jurassic–Upper Cretaceous), as well as in the northeastern-most corner of the Moldavian
63 Platform, along the Prut Valley (lower Upper Cretaceous) (see, e.g., Mutihac and Mutihac,
64 2010). This bias is unfortunate because fossils from these settings could lead to a better
65 understanding of how mainland and island faunas differed during the Cretaceous, and
66 because the cratonic portion of Europe was an important biogeographic stepping stone
67 between the north and south as the continents fragmented and sea levels fluctuated.

68 Although the cratonic regions of Romania have yielded few Cretaceous terrestrial
69 fossils, these deposits are not totally barren. In fact, one of the first Mesozoic continental
70 vertebrates ever recorded from Romania comes from one of these deposits, the Lower
71 Cretaceous shallow marine limestones of Southern Dobrogea (Fig. 1). This specimen—the
72 isolated but well-preserved tooth of a large theropod dinosaur—has often been overlooked. It
73 was described a little over a century ago by Simionescu (1913; Fig. 2A), and until a few
74 recent discoveries of very rare isolated specimens (Stoica and Csiki, 2002; Csiki-Sava et al.,
75 2013; Dragastan et al., 2014), it remained as the sole published record of Mesozoic terrestrial

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76 vertebrates from the cratonic areas of Romania. It has never been comprehensively described
77 and its precise age and taxonomic affinities have yet to be clarified, despite its potential
78 importance as a well-preserved fossil from a poorly sampled area that could have critical
79 evolutionary and biogeographic implications.

80 We here present a comprehensive description of the Dobrogea tooth and discuss its
81 relevance for understanding dinosaur evolution and biogeography. We review the peculiar
82 history of how this specimen was collected and curated, thoroughly document its morphology
83 and age, identify it based on comparison to a broad range of theropods, and outline its
84 importance. It turns out that this specimen, although only a single tooth, has wide-ranging
85 implications. We identify it as coming from the Valanginian stage of the Early Cretaceous,
86 which is incredibly poorly sampled both in Europe and globally (Weishampel et al., 2004),
87 and as belonging to a carcharodontosaurid, a group of derived, large-bodied apex predators
88 whose earliest Cretaceous history is poorly known. Carcharodontosaurids were once thought
89 to be a uniquely Gondwanan group, but recent discoveries show that the basal members of
90 the group were more widespread during the late Early-middle Cretaceous (e.g., Sereno et al.,
91 1996; Brusatte and Sereno, 2008). The Romanian tooth shows affinities with a derived
92 carcharodontosaurid subgroup, the Carcharodontosaurinae, that until now has been known
93 only from Gondwana. It suggests that this subgroup of enormous predators did not evolve
94 vicariantly as Pangaea split, but originated earlier, and perhaps in Europe, suggesting faunal
95 interchange between Europe and Gondwana during the ‘dark ages’ of the early Early
96 Cretaceous.

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

98

99 2. History of collecting and curation

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

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

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

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

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

140 After its original description, specimen UAIC (SCM1) 615 underwent a minor
141 amount of damage (see below, Description). Also, at some point between its description in
142 1913 and the early 1960s (when the specimen was found in its present state in the collections
143 of the UAIC by academic staff members who are still alive today and recall the discovery; I.
144 Turculeţ, personal communication, May 2013) it was glued into a limestone matrix holder,
145 while it was obviously completely freed of the surrounding matrix when it was described and
146 figured in 1913 (Fig. 2). The circumstances under which these alterations took place are
147 unclear. It is a distinct possibility that they occurred sometimes during WWII, when, in the
148 spring of 1944, the frontline between the German-Romanian and Soviet armies reached the
149 Iaşi–Chişinău line. At this moment, the geological-palaeontological collections of the UAIC

150 were packed in crates, and moved together with its personnel and other possessions to Zlatna,
151 in the Apuseni Mountains (western Romania), to safeguard them from any potential damage.
152 Mounting the specimen into the limestone stand would have been a quick way to stabilize it,
153 as it appears that packaging and transport of the specimens was done in haste (M. Brânzilă,
154 personal communication, April 2103). If that was indeed the case, the mounting would have
155 taken place without the knowledge of Simionescu, who left Iași and the UAIC in 1929, being
156 invited to become a professor of Palaeontology at the University of Bucharest (Brânzilă,
157 2010). Then again, however, Simionescu himself or staff of the Hârșova Museum might have
158 re-mounted the tooth after its original description, or else the mounting might have taken
159 place after the return of the collections to Iași, after WWII.

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

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

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

189 3. Geological setting

190 According to the available collecting information, the isolated theropod tooth UAIC (SCM1)
191 615 was discovered at Cochirleni (sometimes noted more specifically as the “*Cochirleni*
192 *quarry*” or “*Cokerleni quarry*”). Cochirleni is a small village in southwestern Dobrogea
193 situated close to the right bank of the Danube, and about 9 km south of the main urban center
194 of the region, Cernavodă (Fig. 1). The geology of the area has been well studied, because of
195 the unique outcropping conditions and rich fossiliferous nature of the Lower Cretaceous
196 deposits (reviewed in Avram et al., 1996; Neagu et al., 1997; Dragastan et al., 1998).

197 Southern Dobrogea is a cratonic area corresponding to the southeastern corner of
198 Romania. Whether it is considered part of the larger Moesian Platform (Săndulescu, 1984;
199 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
201 end of the Jurassic, at the latest, with the consolidation of the Cimmerian (Early Alpine:
202 Triassic–earliest Cretaceous) North Dobrogean fold-and-thrust belt (Seghedi, 2001;
203 Hyppolite, 2002). The age of its basement is also controversial, with estimates ranging from
204 Archaic–Early Proterozoic (Mutihac and Mutihac, 2010) to latest Proterozoic (Ionesi, 1994).

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

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

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

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

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

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

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

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

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

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

4. Palaeontology

287 The isolated theropod tooth UAIC (SCM1) 615 (formerly in the collections of the Hârșova
288 Museum, registered with no. 200; Fig. 2A) was described in a short note by Simionescu
289 (1913), who referred it to *Megalosaurus cf. superbus*, a taxon erected by Sauvage (1882)
290 from the Gault ('mid'-Cretaceous: Albian) of the Paris Basin, France. The Gault material
291 described by Sauvage (1882; see also Sauvage, 1876) includes several isolated teeth that were
292 deemed by Simionescu (1913) to be more similar to the Cochirleni tooth than are the teeth of
293 *Megalosaurus bucklandi* (Buckland, 1824). Subsequently, the French Gault material was
294 referred to the new genus *Erectopus* by Huene (1923), who also noted differences between it
295 and the type species *M. bucklandi*.

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

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300 Carnosauria (= basal Tetanurae), an opinion also shared by Molnar (1990) and Holtz et al.
301 (2004a), whereas the latest review of the Tetanurae (Carrano et al., 2012, p. 254) considered
302 *Erectopus superbus* “a non-carcharodontosaurian allosauroid, possibly a metriacanthosaurid.”
303 Accordingly, if we are following the original assessment of Simionescu (1913) but updating
304 with contemporary taxonomy, the Cochirleni theropod tooth should now be considered
305 referable to the basal tetanuran *Erectopus superbus*. However, the referral of this tooth to
306 *Erectopus superbus* (or a close relative) was considered to be unsupported by positive
307 evidence by Molnar (1990) and Holtz et al. (2004a). In order to re-assess this referral and to
308 understand the exact taxonomic and phylogenetic affinities of UAIC (SCM1) 615 (Fig. 2B,
309 3), we provide here a detailed description of its morphology followed by a thorough
310 comparative study of this tooth based on large datasets of theropod dental measurements and
311 discrete characters compiled by Hendrickx and Mateus (2014) and Hendrickx et al. (2015a).

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

319 320 4.1. Age of UAIC (SCM1) 615

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

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

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

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

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5 350 Dobrinescu, personal communication, November 2013), an assemblage that suggests a

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10 351 Berriasian–Hauterivian age of the limestone holder.

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15 352 Since it is not clear if the limestone holder came from the same site as the tooth itself,

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20 353 we managed to take a second sample from the limestone matrix still partly filling the pulp

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25 354 cavity of the tooth, which must definitively be identical with the rocks the tooth was found in.

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30 355 This second, much smaller sample yielded only very scarce specimens of *Watznaueria*

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35 356 *barnesiae*, *Cyclagelosphaera margerelii* and *Diazomatolithus lehmanni* (M. C. Melinte-

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40 357 Dobrinescu, personal communication, November 2013), the latter two taxa having a peak in

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45 358 abundance during the Berriasian and, especially, the Valanginian.

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50 359 In the nannoplankton succession reported previously by Avram et al. (1993) and

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55 360 derived from a systematic sampling of the Southern Dobrogean Lower Cretaceous, the

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60 361 concurrent presence of *Speetonia colligata*, *Calcicalathina oblongata*, *Diazomatolithus*

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65 362 *lehmanni* and *Nannoconus steinmanni* was noted in samples derived from the Alimanu

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70 363 Member of the Cernavodă Formation. These assemblages were interpreted to represent the

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75 364 nannoplankton zone CC3 of Sissingh (1977), of late Valanginian age. A comparable age was

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80 365 assigned to a roughly similar nannoplankton assemblage reported from the Lower Cretaceous

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85 366 of the Mecsek Mountains, Hungary, by Császár et al. (2000).

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90 367 Together, all the available evidence (Simionescu's original account, geographic and

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95 368 geologic records, foraminifera, ostracods, microproblematicae, and calcareous

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100 369 nannoplankton) thus suggests that UAIC (SCM1) 615 originates from the Alimanu Member

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105 370 of the Cernavodă Formation, and it is most probably of late Valanginian age.

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111 112 113 114 115 372 4.2. Description and comparisons

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120 373 Specimen UAIC (SCM1) 615 is a large (total length, as preserved, is about 100 mm; Figs. 2,

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125 374 3) lateral tooth of a theropod dinosaur, with a crown base length (CBL) of 29 mm, crown

375 base width (CBW) of 16.25 mm, crown height (CH) of 85.5 mm, and apical length (AL) of
376 91 mm (terminology following Smith et al., 2005 and Hendrickx et al., 2015b). It is
377 remarkably well preserved, with the enamel in pristine condition. It preserves most of the
378 crown and a small basal part of the root, but the crown tip is broken off, with an estimated 5
379 mm missing in the apical region.

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

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

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

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400 exposed basally, being partly filled with a whitish-light gray limestone that is reminiscent of
401 the matrix holder lithology. The pulp cavity narrows rapidly towards the cervix, as it is about
402 7.1 mm wide (labiolingually) at the apical-most part of the preserved root, but only about 4.5
403 mm wide at the base of the crown. In parallel, the enamel-dentine wall of the tooth becomes
404 thicker: it is 3.5 mm thick in the apical-most part, 4.4 mm at the base of the crown, but
405 thickens to 5.0–5.8 mm near the apical-most part of the basal break of the crown (Fig. 3B).
406 Mirroring the outside cross-section, the contour of the pulp cavity is also teardrop-shaped
407 (Fig. 3D).

408 The tooth is ziphodont and only very slightly recurved distally. The distal edge is
409 nearly straight across its length, being very mildly concave in its basal half and slightly
410 convex near its apex (Fig. 2, 3A). Thus, the apex is placed roughly at the distal margin of the
411 tooth crown base. The mesial edge, as shown in the original publication of Simionescu
412 (1913), is strongly convex across its entire length (Fig. 2A). The tooth is labiolingually
413 compressed (Fig. 3B), with a crown base ratio ($CBR=CBW/CBL$) of 0.56, within the normal
414 range of variation of most theropods. This differs from the thinner teeth of some, but not all,
415 carcharodontosaurids ($CBR<0.50$), and the much thicker incrassate teeth of derived
416 tyrannosauroids and conical teeth of spinosaurids ($CBR>0.75$) (Serenó et al., 1996; Brusatte
417 et al., 2010a; Hendrickx and Mateus, 2014; Hendrickx et al., 2015a).

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

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

432 The distal carina extends along the entire tooth height (Fig. 3A–C). It is covered with
433 minute serrations across its entire preserved length; the denticles are proximodistally
434 subrectangular, with a mesiodistal long axis that is greater than the apicobasal long axis (Fig.
435 3E–H). They are either roughly perpendicular to the tooth margin, or their long axes are
436 oriented obliquely, such that they point slightly apically. The tip of the apex is broken off, so
437 it is not possible to determine whether the serrations continued over the apex of the tooth.
438 There are approximately 12.5 serrations (denticles) per 5 millimetres at the midpoint of the
439 carina. Serration shape and size remain relatively constant across the carina, although the
440 serrations near the midpoint and closer to the base of the carina (12 denticles per 5 mm; Fig.
441 3G, H) are slightly smaller than those near the apex (9 denticles per 5 mm; Fig. 3E, F).
442 Changes in serration size are gradual across the carina, not sudden or sporadic.

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

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450 separated by simple, linear grooves (interdenticular slits or sulcae) along their entire length.

451 The interdenticular space between adjacent denticles is broad, measuring more than a third of
452 the apicobasal width of a denticle (Fig. 3E, G). This space continues onto the surface of the
453 crown as a very short interdenticular sulcus (“blood groove” of Currie et al., 1990). These
454 sulci are so short and indistinct that they are only visible under low angle light.

455 Little can be said about the mesial carina, as it is not visible in the current state of the
456 specimen, buried in the limestone matrix. Based on the description of Simionescu (1913),
457 however, it is covered across its length with minute serrations; these decrease in size towards
458 the base of the crown. Simionescu (1913) reported approximately 15 serrations (denticles)
459 per 5 millimetres at the midpoint of the carina, meaning that the mesial denticles are slightly
460 smaller than those on the distal carina. The denticle size difference index (DSDI: Rauhut and
461 Werner, 1995) is 1.2, within the range of variation of most theropods (Hendrickx and Mateus,
462 2014). As Simionescu (1913) already pointed out, the presence of a mesial carina that extends
463 towards the base of the crown sets apart UAIC (SCM1) 615 from *Megalosaurus bucklandii*
464 where this stops well above the cervix (Benson et al., 2008), and it is instead similar to ‘*M.*’
465 *superbus* (Sauvage, 1876, 1882) in this respect.

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

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

1 475 that they are clearly observable in normal light (Fig. 3A–C, G, H). Here, about 17 unevenly
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3 476 developed wrinkles are present along the crown height; in the basal half of the crown, the
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5 477 wrinkles extend about 6.5 mm onto the crown. These are elongate, such that they are longer
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7 478 than twice the space separating each undulation. The wrinkles project obliquely (in the
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10 479 mesiobasal direction) relative to the carina. They are apically concave, with a near-horizontal
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12 480 segment on the crown, and curve apically as they approach the carina (at about 45°) with a
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14 481 tendency to become tangential to the distal edge. The wrinkles are especially well developed,
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16 482 prominent and closely spaced in the basal part of the crown (about 7 wrinkles/16 mm; Fig.
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19 483 3C, G)), but become more widely spaced and indistinct apically (about 3 wrinkles/16 mm).
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21 484 Apically, however, the wrinkles are somewhat wider and longer, extending over about half of
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23 485 the crown fore-aft length. Again, a slight asymmetry is present between the two sides of the
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26 486 crown in wrinkle development as well, these being better expressed on the more rounded,
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29 487 convex lingual face, but less well expressed on the flatter labial face (Fig. 3A, C, H). On the
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31 488 presumed labial face, only some of the basal-most wrinkles, particularly the second and third
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34 489 one, appear well defined.

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36 490 Towards the base of the crown a few of the wrinkles continue across the labial and
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39 491 lingual surfaces as very subtle transverse undulations. Most conspicuous of these is a 3.5 mm
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41 492 wide horizontal swelling that crosses the crown, at the level of wrinkles 2 and 3; this swelling
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43 493 is clearly visible on both sides of the crown (Fig. 3. A, C). There are no lateral flutes, apico-
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46 494 basal ridges, or longitudinal grooves on the labial or lingual faces, either in the centre of the
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49 495 tooth or paralleling the carinae. Instead, the labial and lingual faces are uniformly convex,
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51 496 giving the tooth its teardrop-shaped outline in cross section.

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54 498 5. Discussion

55 56 499 5.1. *Identification of UAIC (SCM1) 615*

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

503 Besides theropods, certain derived crocodyliforms – the sebecosuchians of Colbert
504 (1946; see also Turner and Sertich, 2010; Pol and Powell, 2011; Rabi and Sebők, 2015) – are
505 also known to possess remarkably theropod-like, laterally compressed and serrated teeth, not
506 unlike the morphology shown by UAIC (SCM1) 615. However, most sebecosuchian teeth are
507 significantly smaller than the Southern Dobrogean specimen, especially in the case of the
508 Cretaceous members of the clade (e.g. *Baurusuchus*; Carvalho et al., 2005). Even the largest,
509 caniniform teeth of the largest representatives of Sebecosuchia, such as the Miocene
510 *Barinasuchus* (Paolillo and Linares, 2007), are somewhat smaller than UAIC (SCM1) 615;
511 moreover, these teeth are slightly conical and less laterally compressed than the Southern
512 Dobrogean tooth. Finally, it should be noted that the oldest known members of Sebecosuchia
513 appear beginning in the Late Cretaceous (e.g. Kellner et al., 2014), and are thus significantly
514 younger than UAIC (SCM1) 615. Similarly, ziphodont crocodyliform teeth (i.e. with true
515 denticles along their carinae) are reported in Europe only beginning in the Albian (Ősi et al.,
516 2015), and these are both significantly smaller and different in morphology from the
517 Dobrogean tooth. Taken together, these suggest that the hypothesis of sebecosuchian
518 affinities of UAIC (SCM1) 615 can be discarded with confidence, and it indeed represents a
519 theropod tooth.

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

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

1 525 (2005) and Larson and Currie (2013), and it or a similar version has been used in recent
2 526 studies to identify isolated theropod teeth (e.g., Williamson and Brusatte, 2014; Brusatte and
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4 527 Clark, 2015). It comprises nearly 1000 theropod teeth scored for six measurements (CBL,
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7 528 CBW, CH, AL, MC, and DC, the latter two measuring the density of serrations per 5 mm at
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9 529 the midpoint of the mesial and distal carina, respectively). UAIC (SCM1) 615 was added to
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11 530 this dataset, the data were log-transformed prior to analysis, missing values for measurements
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13 531 were estimated with a mean value for that measurement from across the sample, and then a
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16 532 PCA was run using a correlation matrix. The analysis was conducted in PAST v2.17
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19 533 (Hammer et al., 2001).

22 534 In the resulting two dimensional morphospace (Fig. 4), UAIC (SCM1) 615 plots close
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24 535 to many teeth belonging to carcharodontosaurids, along with some teeth belonging to
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26 536 spinosaurids and tyrannosauroids. It falls within the convex hull (maximum morphospace
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28 537 occupation area) of carcharodontosaurids only, although it is closely outside of the edges of
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30 538 spinosaurid and tyrannosauroid space. It also falls within the 95% confidence interval ellipse
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33 539 for carcharodontosaurids, but not within the ellipse of any other group (Supplementary
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35 540 Information). This exercise indicates that UAIC (SCM1) 615 is most similar to
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38 541 carcharodontosaurids.

41 542 Secondly, we used the log-transformed dataset that we also used for the PCA to
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43 543 conduct a clustering analysis. We performed the analysis in PAST v2.17, using the paired
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45 544 group algorithm and the correlation similarity measure. In the resulting dendrogram, UAIC
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47 545 (SCM1) 615 groups with a handful of teeth belonging to carcharodontosaurids,
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50 546 tyrannosauroids, and *Allosaurus* (Supplementary Information).

54 547 Third, we used the tooth measurement database to conduct a discriminant analysis in
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56 548 PAST v3.0 (Hammer et al., 2001). This analysis uses pre-determined groups (in this case,
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58 549 taxonomic clusters) to create a morphospace in which these groups are maximally separated.

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

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

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

1 575 undulations that are at least twice as long mesiodistally as the space separating each
2 576 undulation (character 111), and marginal undulations present on both mesial and distal sides
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5 577 of the crown (character 113).
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7 578 The Romanian specimen also lacks many keystone dental synapomorphies of other
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9 579 theropod clades, based on the clade diagnoses of Hendrickx and Mateus (2014) and other
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11 580 cladistic studies that include dental characters. UAIC (SCM1) 615 does not possess the
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13 581 hooked distal denticles of some Abelisauridae, the strongly labially deflected distal carina
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15 582 and pronounced transverse enamel undulations extending across the labial and lingual tooth
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17 583 faces of Ceratosauridae, the incrassate teeth with apicobasal enamel flutes and deeply veined
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19 584 enamel surface texture of Spinosauridae, and the large transverse undulations of some basal
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21 585 allosauroids (Hendrickx and Mateus, 2014). It also lacks the thickened incrassate teeth of
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23 586 derived tyrannosauroids (Brusatte et al., 2010a) and the large and strongly hooked (or
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25 587 pointed) denticles of troodontids and therizinosauroids (e.g., Turner et al., 2012; Brusatte et
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27 588 al., 2014; Hendrickx and Mateus, 2014). The large size, as well as recurved and ziphodont
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29 589 shape of UAIC (SCM1) 615 is strikingly different from the non-ziphodont therizinosauroids,
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31 590 ornithomimosaur, alvarezsauroids, and most troodontids, which have conical, leaf-shaped, or
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33 591 peg-like teeth (when teeth are present) (e.g., Holtz et al., 2004a; Turner et al., 2012; Brusatte
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35 592 et al., 2014). Finally, besides its remarkably large size, the presence of serrations indicates
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37 593 that UAIC (SCM1) 615 does not belong to groups such as alvarezsauroids, oviraptorosaurs,
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39 594 basal troodontids, or avialans, which have unserrated crowns (e.g., Turner et al., 2012;
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41 595 Hendrickx and Mateus, 2014).
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51 596 In summary, the four analyses all support carcharodontosaurid affinities for UAIC
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53 597 (SCM1) 615. Both overall tooth proportions and discrete phylogenetic characters point to a
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55 598 carcharodontosaurid identification, and the discriminant function analysis and phylogenetic
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57 599 analysis both explicitly recover the tooth as a carcharodontosaurid. For this reason we refer
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600 this tooth to Carcharodontosauridae. Moreover, it appears to belong to a clade that unites very
601 derived and large-sized carcharodontosaurids (*Carcharodontosaurus*, *Giganotosaurus*, and
602 *Mapusaurus*), separated as such and named Carcharodontosaurinae by Brusatte and Sereno
603 (2008) and Carrano et al. (2012). The well-resolved internal topology of this clade, as
604 recovered in our analysis, is congruent with results of previous analyses based on larger sets
605 of characters from across the skeleton (e.g., Coria and Currie, 2006; Brusatte and Sereno,
606 2008; Brusatte et al., 2009; Ortega et al., 2010; Eddy and Clarke, 2011; Canale et al., 2015),
607 and offers some support for considering the Romanian carcharodontosaurid from Southern
608 Dobrogea as more closely related to the African *Carcharodontosaurus* than to the clade of
609 the South American giant carcharodontosaurids *Giganotosaurus* or *Mapusaurus*.

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

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

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(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.

636 5.2. Body size of UAIC (SCM1) 615

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

1 (SCM1) 615 is smaller than the largest teeth of *Acrocanthosaurus* (9% difference),
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3 651 *Carcharodontosaurus* (20%), and *Giganotosaurus* (12.5%) in the dataset, but is 13% bigger
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5 652 than the largest tooth of *Mapusaurus*.
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7 653 It is thus reasonable to conclude that UAIC (SCM1) 615 belonged to a large-sized
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9 654 carcharodontosaurid, comparable to, even if somewhat smaller than, the truly gigantic
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11 655 carcharodontosaurines *Giganotosaurus* and *Carcharodontosaurus* (Serenó et al., 1996; Calvo
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13 656 and Coria, 1998; Therrien and Henderson, 2007), taxa that were recovered as possible close
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15 657 relatives of the Romanian carcharodontosaurid by our phylogenetic analysis. This, in turn,
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17 658 corroborates growing evidence that very large body size was acquired very early in
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19 659 carcharodontosaurid history, since the earliest potential members of the clade are already of
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21 660 relatively large size (Rauhut, 2011). The oldest potential carcharodontosaurid is
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23 661 *Veterupristisaurus*, represented by isolated vertebrae that indicate an animal between 8.5 and
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25 662 10 meters in total body length (compared to 11.5+ meters in *Acrocanthosaurus* and more
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27 663 derived carcharodontosaurids) (Rauhut, 2011). These specimens are known from the
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29 664 uppermost Jurassic of Tanzania, eastern Africa (Rauhut, 2011; Carrano et al., 2012; see
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31 665 below), predating at most ~18 million years (Mya) the occurrence of likely even larger-sized
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33 666 carcharodontosaurids in the Valanginian of Southern Dobrogea, Romania.
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36 667 The inferred large body size of the South Dobrogean theropod is also remarkable as
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38 668 virtually all other dinosaur remains reported previously from Romania (both from the Early
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40 669 Cretaceous Cornet assemblage and the much later, end Cretaceous Hațeg Island fauna) are
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42 670 significantly smaller, and many have been interpreted as insular dwarfs (e.g., Weishampel et
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44 671 al., 1993, 2003; Benton et al., 2006, 2010; Stein et al., 2010; Ósi et al., 2014). Although other
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46 672 Romanian theropod dinosaurs were not particularly dwarfed (e.g. Brusatte et al., 2013), they
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48 673 were nonetheless small (Nopcsa, 1902; Csiki and Grigorescu, 1998; Csiki et al., 2010;
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50 674 Brusatte et al., 2013). This bias towards small bodied Romanian theropods was also
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1 675 interpreted as a consequence of their insular habitat (Csiki and Grigorescu, 1998), as all
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3 676 previously reported theropod remains come from within the Carpathian Orogen, an area with
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5 677 an archipelago-type palaeogeography during the Cretaceous (Dercourt et al., 2000; Csontos
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7 678 and Vörös, 2004; Csiki-Sava et al., 2015). By contrast, UAIC (SCM1) 615 was found in
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9 679 shallow marine deposits bordering the emerged areas of Central Dobrogea, part of the stable
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11 680 cratonic areas of Europe and connected at least intermittently to the Ukrainian Shield since
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13 681 the Late Jurassic (Fig. 5A). Although cratonic Europe was also transformed into an
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15 682 archipelago of islands during much of the Cretaceous, these islands were often both larger in
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17 683 size and more stable in space and time than were the transient emerged areas of the Tethyan
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19 684 archipelagoes. As such, it is conceivable that the Southern Dobrogean carcharodontosaurid
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21 685 was less constrained by space or resource limitations than the Tethyan insular dinosaurs,
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23 686 allowing it to retain a large body size.
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31 688 *5.3. UAIC (SCM1) 615 and Valanginian dinosaur distribution*

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33 689 Besides documenting the presence of large-sized mainland carcharodontosaurids in the
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35 690 Lower Cretaceous of Romania, UAIC (SCM1) 615 is also important in that it fills a
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37 691 significant gap in our knowledge on the composition and distribution of the Early Cretaceous
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39 692 dinosaurs in Europe. In their review of dinosaur occurrences, Weishampel et al. (2004) listed
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41 693 83 Early Cretaceous dinosaur localities spread throughout Europe, more than half of these
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43 694 being known from the later part (Barremian–Albian) of that epoch; only around a dozen
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45 695 localities were listed from each age of the early part of the Early Cretaceous (Berriasian,
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47 696 Valanginian, and Hauterivian). Even despite a significant increase in Early Cretaceous
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49 697 dinosaur discoveries in Europe in recent years (e.g., Royo-Torres et al., 2009; Cobos et al.,
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51 698 2010, 2014; Galton, 2009; Norman, 2010, 2013; Pereda-Suberbiola et al., 2011, 2012; Sachs
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53 699 and Hornung, 2013; Blows and Honeysett, 2014), these remain very strongly biased towards
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1 700 western and southwestern Europe (especially the UK, France and Spain). Frustratingly, no
2 701 occurrences are known from the entire central, eastern and southern Europe for the
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4 702 Berriasian–Hauterivian time interval except for two from Romania: the Berriasian–
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6 703 Valanginian locality of Cornet (e.g., Jurcsák and Popa, 1979, 1983; Jurcsák, 1982; Benton et
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8 704 al., 1997) in the northern Apuseni Mountains of northwestern Romania, and the
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10 705 carcharodontosaurid tooth (Simionescu, 1913) from the Valanginian of Cochirleni, in
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12 706 Southern Dobrogea, southeastern Romania we are describing here (Fig. 5A).
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17 707 Our identification of the Romanian tooth as a carcharodontosaurid documents the
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19 708 presence of this clade in Europe in the very early Cretaceous. This is significant, as
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21 709 carcharodontosaurids were widely distributed tens of millions of years later, in the middle
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23 710 Cretaceous (Aptian to Cenomanian), in western Gondwana (Africa and South America, see
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25 711 below). Despite the recent discoveries documenting that the clade was also present in North
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27 712 America and Asia during the middle Cretaceous (e.g., Sereno et al., 1996; Currie and
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29 713 Carpenter, 2000; Brusatte et al., 2009, 2012), there has been only very few occurrences in
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31 714 Europe, most importantly the Barremian-aged *Concavenator* from Spain (Ortega et al., 2010;
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33 715 see below). The carcharodontosaurid tooth from Southern Dobrogea is substantially older
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35 716 than *Concavenator*, demonstrating that carcharodontosaurids appeared in Europe earlier than
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37 717 previously thought and were a long-term component of the European mainland Early
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39 718 Cretaceous faunas. It also suggests that habitat-related palaeobiological differentiation might
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41 719 have been already present between the cratonic, stable European mainland, with a dinosaur
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43 720 fauna made up of normal-sized (even very large) taxa, and the islands from the mobile Alpine
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45 721 areas of the Mediterranean Neo-Tethys, with by now dwarfed dinosaurs such as those
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47 722 described from the Berriasian–Valanginian Cornet assemblage in northwestern Romania
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49 723 (Benton et al., 2006).
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724 This Valanginian carcharodontosaurid represents an important datapoint not only for
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2 725 the Romanian Lower Cretaceous, but also for that of wider Eurasia. The Valanginian is a
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5 726 poorly documented age in dinosaur evolution, with very few precisely dated fossil
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7 727 occurrences from anywhere in the world (e.g., Weishampel et al., 2004). The best record of
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10 728 Valanginian dinosaurs is from Europe, with fewer and less well dated occurrences known
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12 729 from Asia, some of which have debatable or controversial dates. These include sites in Japan
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14 730 (e.g., Manabe and Hasegawa, 1995; Matsukawa et al., 2006; but see Kusuhashi et al., 2009
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16 731 and Evans and Matsumoto, 2015, supporting an alternative, younger age of these
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18 732 assemblages) and in Thailand (e.g., Buffetaut and Suteethorn, 1998, 2007, with age
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20 733 constraints according to Racey, 2009; Racey and Goodall, 2009). Occurrences of possible
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22 734 Valanginian age from China (e.g., Jerzykiewicz and Russell, 1991; Shen and Mateer, 1992;
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24 735 Lucas and Estep, 1998) are either poorly constrained as early Early Cretaceous, or were
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26 736 shown subsequently to be younger than Valanginian (Lucas, 2006; Tong et al., 2009). Rare
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28 737 dinosaur remains of possible Valanginian (or ‘Neocomian’) age were also reported from
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30 738 southern Africa (e.g., De Klerk et al., 2000) and, tentatively, from North America (e.g.,
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32 739 Lucas, 1901; McDonald, 2011, with age assignments according to Sames et al., 2010; Cifelli
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34 740 et al., 2014).

41 741 As one of the two known reports of Valanginian dinosaurs in Europe east of France,
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43 742 the Southern Dobrogean dinosaur record fills a huge palaeogeographic gap between the
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45 743 western European and the eastern Asian dinosaur faunas. Moreover, none of these early Early
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47 744 Cretaceous dinosaur assemblages from outside Europe include carcharodontosaurids (see
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49 745 below), as theropods are represented by coelurosaurians interpreted either as compsognathids
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51 746 (Gishlick and Gauthier, 2007) or basal ornithomimosaurids (Choiniere et al., 2012) in southern
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53 747 Africa, metriacanthosaurid allosauroids (‘sinraptorids’) in Thailand (Buffetaut and
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55 748 Suteethorn, 2007), and indeterminate allosauroids (Pérez-Moreno et al., 1993), non-

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749 carcharodontosaurid tetanurans (Carrano et al., 2012) or enantiornithine birds (Lacasa Ruiz,
750 1989), besides indeterminate taxa (Carrano et al., 2012), in western Europe. This may suggest
751 that carcharodontosaurids had not achieved a wide geographic distribution by this point in
752 time, and that their more cosmopolitan distribution came later, during the middle Cretaceous.

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

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773 *5.4. UAIC (SCM1) 615 and carcharodontosaurid evolution and palaeobiogeography*

774 Carcharodontosauridae were long considered as an exclusively Gondwanan group of
775 theropods (e.g., Allain, 2002; Novas et al., 2005) since their first discovery in northern Africa
776 (e.g., Stromer, 1931), and subsequent description of a host of referred taxa from the Aptian–
777 Cenomanian of Africa and South America (Coria and Salgado, 1995; Sereno et al., 1996;
778 Novas et al., 2005; Coria and Currie, 2006; Brusatte and Sereno, 2007; Sereno and Brusatte,
779 2008; Cau et al., 2013). This view started to change with the identification of the Early
780 Cretaceous (Aptian–Albian) *Acrocanthosaurus* from North America as a basal
781 carcharodontosaurid (e.g., Sereno et al., 1996; Harris, 1998; Sereno 1999; Brusatte and
782 Sereno, 2008), suggesting that the clade had a wider, Neopangean palaeobiogeographic
783 distribution by the mid–late Early Cretaceous. Such a wide distribution, even a cosmopolitan
784 one, was further supported by the discovery of definitive carcharodontosaurids in the Lower
785 Cretaceous of Europe (Ortega et al., 2010), and in the upper Lower to lower Upper
786 Cretaceous of China (Brusatte et al., 2009, 2010b, 2012; Mo et al., 2014; Lü et al., 2016).

787 Together, the available evidence pointed to an early, pre-mid Early Cretaceous origin
788 of the carcharodontosaurids, followed by their dispersal across Laurasia and western
789 Gondwana beginning at least by the Aptian (Fig. 5B), a scenario that is concordant with the
790 tentatively suggested presence of early carcharodontosaurids in the Upper Jurassic of
791 Tanzania, which are based on fragmentary specimens (Rauhut, 2011; Carrano et al., 2012). It
792 is also concordant with the widespread appearance of carcharodontosaurids in the fossil
793 record starting with the Aptian, when they are reported in Africa (*Eocarcharia*; Sereno and
794 Brusatte, 2008), South America (Vickers-Rich et al., 1999), North America
795 (*Acrocanthosaurus*; Stovall and Langston, 1950; Harris, 1998; Currie and Carpenter, 2000
796 Eddy and Clarke, 2011), Europe (Canudo and Ruiz-Omeñaca, 2003; Pereda-Suberbiola et al.,
797 2012), and eastern Asia (*Kelmaysaurus*; Brusatte et al., 2012; Mo et al., 2014; Lü et al.,
798 2016).

799 During the Albian–Turonian, carcharodontosaurids became especially abundant and
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2 800 diverse in Africa (*Carcharodontosaurus*, *Sauroniops*; Stromer, 1931; Sereno et al., 1996;
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4 801 Brusatte and Sereno, 2007; Le Loeuff et al., 2012; Cau et al., 2013; Richter et al., 2013) and
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6 802 South America (*Tyrannotitan*, *Giganotosaurus*, *Mapusaurus*, alongside with indeterminate
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9 803 carcharodontosaurids; Coria and Salgado, 1995; Calvo and Coria, 1998; Novas et al., 2005;
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11 804 Coria and Currie, 2006; Casal et al., 2009; Candeiro et al., 2011; Canale et al., 2015; Fig.
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14 805 5B). They were still present during this time interval in other continents, as well: in North
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16 806 America with *Acrocanthosaurus* until the Albian (D’Emic et al., 2012), in Europe until the
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18 807 Cenomanian (Vullo et al., 2007; Csiki-Sava et al., 2015), and in Eastern Asia with
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21 808 *Shaochilong* until the Turonian (Brusatte et al., 2009, 2010b; see also Chure et al., 1999).
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24 809 After dominating terrestrial ecosystems at least in Africa, South America and eastern
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26 810 Asia during the Albian–Turonian (Brusatte et al., 2009; Coria and Salgado, 2005; Novas et
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28 811 al., 2013), carcharodontosaurids were considered to disappear from the fossil record after the
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30 812 Turonian in both Asia (Brusatte et al., 2009) and South America (e.g., Coria and Salgado,
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32 813 2005; Calvo et al., 2006; Novas et al., 2013), to be replaced by other groups of large
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34 814 theropods such as tyrannosaurids in parts of Laurasia and abelisaurids in parts of Gondwana.
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36 815 Canale et al. (2009) even cautioned against assigning isolated theropod teeth from post-
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38 816 Cenomanian deposits of South America to Carcharodontosauridae (e.g., Canudo et al., 2008;
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40 817 Casal et al., 2009; Salgado et al., 2009) due to their morphological similarity to those of the
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42 818 abelisaurid *Skorpiovenator*. Recently, however, more diagnostic cranial remains were
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44 819 reported to suggest the survival of carcharodontosaurids into the latest Cretaceous
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49 820 (Campanian–Maastrichtian) in Brazil (Azevedo et al., 2013).
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53 821 Contrasting with this rich and relatively continuous fossil record of
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55 822 Carcharodontosauridae starting with the Aptian, the first half of its evolutionary history is
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57 823 very poorly documented (Fig. 5B). Prior to the identification of UAIC (SCM1) 615, only two
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824 occurrences of pre-Aptian Cretaceous carcharodontosaurids were reported, one from the
825 Barremian of Spain (Ortega et al., 2010; Gasca et al., 2014) and the other from the Barremian
826 of Thailand (Buffetaut and Suteethorn, 2012). The Early Cretaceous *Kelmayisaurus* from
827 Xinjiang, western China, was recognized as a carcharodontosaurid of possibly ?Valanginian
828 to Aptian in age by Brusatte et al. (2012), but the deposits yielding these remains (the
829 Lianmugin, or Lianmuxin, Formation of the Tugulu Group) were dated as Aptian–Albian by
830 Eberth et al. (2001; see also Tong et al., 2009). An important temporal gap – of about 20 to
831 28 millions of years, according to the dates in Gradstein et al. (2012) – thus stretched between
832 the oldest, tentatively assigned carcharodontosaurids from the Oxfordian–Tithonian of
833 Tanzania, including the formally erected *Veterupristisaurus* (Rauhut, 2011; see also Carrano
834 et al., 2012), and those that started to appear in the fossil record in the Barremian and then
835 spread widely during the Aptian. Referral of UAIC (SCM1) 615 to Carcharodontosauridae
836 partially fills this frustrating gap, effectively halving this shadowy period in the evolutionary
837 history of the group.

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

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

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849 Jurassic, considered to be reminiscent of the Aptian–Albian *Acrocanthosaurus* (Rauhut,
850 2011), was also consistent with this evolutionary scenario. Now, our identification of UAIC
851 (SCM1) 615 as a carcharodontosaurid dinosaur sharing important dental apomorphies with
852 the derived Carcharodontosaurinae advocates the emergence of this clade (or at least the very
853 large size and dental morphology characterizing it) well before the Albian, during or even
854 before the Valanginian, and relegates taxa such as *Eocarcharia*, *Acrocanthosaurus* and
855 *Concavenator* (the dentition of *Shaochilong* is unknown) as late-surviving members of the
856 basal carcharodontosaurid radiation, with a relatively plesiomorphic dentition.

857 Besides shifting the emergence of the carcharodontosaurines earlier in time,
858 identification of UAIC (SCM1) 615 as a carcharodontosaurid also has interesting
859 palaeobiogeographic implications. As already noted, recent discoveries show that
860 Carcharodontosauridae is not an endemic Gondwanan clade as was once proposed (e.g.,
861 Novas et al., 2005), with the identification of its widespread, Pangaeian distribution during the
862 late Early Cretaceous (Sereno et al., 1996; Harris, 1998; Chure et al., 1999; Sereno, 1999;
863 Brusatte and Sereno, 2008; Ortega et al., 2010; Brusatte et al., 2009, 2012; Mo et al., 2014).
864 However, within Carcharodontosauridae itself, some palaeogeographic patterns have been
865 widely accepted. For example, it has been widely acknowledged that Carcharodontosaurinae
866 is a endemic subclade of Gondwanan carcharodontosaurids (e.g., Sereno 1999; Holtz et al.,
867 2004b; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008; Novas et al., 2013), as
868 previously all its recognized members were restricted strictly to either Africa (Stromer, 1931;
869 Sereno et al., 1996; Brusatte and Sereno, 2007) or South America (Coria and Salgado, 1995;
870 Novas et al., 2005; Coria and Currie, 2006). Moreover, intra-clade relationships of
871 Carcharodontosaurinae were still adhering to patterns of continental fragmentation and
872 vicariant evolution, with a basal split between the Albian–Cenomanian African
873 *Carcharodontosaurus* and the Giganotosaurini, uniting the similarly Albian–Cenomanian

1 874 southern South American *Giganotosaurus* and *Mapusaurus* (together with *Tyrannotitan*, if
2 875 this taxon is also recovered within Carcharodontosaurinae; e.g., Novas et al., 2005, 2013).

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5 876 This scenario is now challenged by our finding that the Southern Dobrogean
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7 877 carcharodontosaurid UAIC (SCM1) 615 may nest inside Carcharodontosaurinae. If true, such
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9 878 an affinity would suggest that the origin of Carcharodontosaurinae was not a southern,
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11 879 vicariant by-product of the Gondwana-Laurasia separation, a major palaeogeographic event
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13 880 that is considered to have been well underway by the end of the Jurassic, and essentially
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15 881 completed by the mid-Early Cretaceous (see Weishampel et al., 2010). Indeed, during this
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17 882 time palaeogeographic connections and faunal interactions were virtually non-existent
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19 883 between the northern Tethyan (European) and southern Tethyan (western Gondwanan, but
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21 884 essentially African) areas of the Mediterranean (e.g., Canudo et al., 2009), which makes a
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23 885 vicariant hypothesis intuitive. However, if the Romanian tooth represents a
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25 886 carcharodontosaurine, then it implies a much more complicated palaeogeographic history of
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27 887 the clade, which is not so clearly linked to continental breakup.

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33 888 The palaeogeographic position of the Southern Dobrogean carcharodontosaurine in
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35 889 cratonic Europe, north of the Neo-Tethys, together with its significantly older age compared
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37 890 to other carcharodontosaurines, could indicate that separation of the carcharodontosaurine
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39 891 lineage took part in Europe and not in western Gondwana as previously assumed. This would
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41 892 also mean that representatives of this lineage were subsequently – after the Barremian –
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43 893 introduced to Africa and South America via trans-Tethyan dispersal, most probably at a time
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45 894 when faunal interactions between the southern and northern margins of the Mediterranean
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47 895 Tethys were resumed, after the early Barremian (Canudo et al., 2009).

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49 896 Alternatively, it can be hypothesized that appearance of carcharodontosaurines in
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51 897 Southern Dobrogea is a consequence of southern immigration originating in western
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53 898 Gondwana, often considered the place of origin for this clade. However, this scenario has

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899 several potential caveats. Although Europe has been considered as forming part of a larger
900 Eurogondwanan palaeobioprovince during the early Early Cretaceous (Ezcurra and Agnolín,
901 2012), and occasional trans-Tethyan faunal connections have been recognized between
902 Africa and Europe during Late Jurassic to Early Cretaceous times (e.g., Gheerbrant and Rage,
903 2006), these interchanges either pre-dated the Berriasian (e.g., Gardner et al., 2003; Knoll and
904 Ruiz-Omeñaca, 2009), or post-dated the Barremian (Canudo et al., 2009; Torcida Fernández-
905 Baldor et al., 2011), with no positive evidence for actual faunal exchanges taking place
906 during the ‘Neocomian’ (Berriasian–Hauterivian) time interval.

907 More recently, some potential evidence has emerged for Gondwana-to-Europe
908 interchange during the ‘Neocomian’. The presence of the basal rebbachisaurid *Histriasaurus*
909 (Dalla Vecchia, 1998) in the upper Hauterivian–lower Barremian of Croatia has been cited as
910 indicative of very early and very rapid northward dispersal of this clade from western
911 Gondwana (southern South America; Carballido et al., 2012; Fanti et al., 2015). Timing of
912 this particular dispersal event was even constrained to the Berriasian–Valanginian time
913 interval (Fanti et al., 2015), which makes it roughly contemporaneous with the record of the
914 Southern Dobrogean carcharodontosaurine. It was also suggested, however, that dispersal of
915 the line leading to *Histriasaurus* was mediated by the northward drift of the Apulian
916 Microplate (= Adria; see Bosselini, 2002), a continental sliver acting as a passive
917 transportation mechanism (‘Noah’s Ark’; McKenna, 1973) for basal rebbachisaurids after its
918 separation from mainland Africa (e.g., Torcida Fernández-Baldor et al., 2011). Furthermore,
919 the palaeogeographical separation between Africa and Adria (and thus the effective
920 movement of the presumed ark) is considered to be at most an incipient one during the Early
921 Cretaceous by Bossellini (2002) and Zarccone et al. (2010), with spatial continuity still present
922 between the two landmasses, while deep-water basins continued to separate Adria from the
923 European Craton. Accordingly, although the presence of *Histriasaurus* can represent a case

1 924 of northward range extension of rebbachisaurids during the Berriasian–Valanginian, it took
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3 925 place not strictly speaking into Europe, but only reached the northernmost extremity of Adria,
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5 926 a northerly peninsular extension of the African mainland. It was only starting with the
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7 927 Barremian that rebbachisaurids dispersed as far north as the European cratonic areas,
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9 928 including Iberia and the British Isles (Mannion, 2009; Mannion et al., 2011; Torcida
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11 929 Fernández-Baldor et al., 2011), a time when faunal interchanges between Europe and Africa
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13 930 are considered to have been well underway (e.g., Gheerbrant and Rage, 2006; Canudo et al.,
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15 931 2009).

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19 932 Unlike *Histriasaurus*, the taxon represented by UAIC (SCM1) 615 was an inhabitant
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21 933 of the European mainland. It is thus unclear to what extent the example of rebbachisaurid
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23 934 range extension into (present-day) Europe during the early Early Cretaceous, as potentially
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25 935 testified by the discovery of the Croatian taxon, would also be applicable for the Southern
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27 936 Dobrogean carcharodontosaurine. The available evidence suggests that these two cases are
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29 937 very different, and that faunal connections during this time interval are not documented
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31 938 between the African and European cratons as already pointed out by Gheerbrant and Rage
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33 939 (2006).

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39 940 Absence of documented faunal interactions weakens support for a scenario of south-
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41 941 to-north immigration of derived carcharodontosaurines in Europe at the very beginning of the
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43 942 Cretaceous, and would argue instead for a local, European development to explain the
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45 943 presence of a Valanginian carcharodontosaurine in Southern Dobrogea. The pre-Barremian
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47 944 presence of carcharodontosaurids in Europe is also consistent with their appearance in the
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49 945 Barremian–Aptian fossil record of Eastern Asia, with Europe acting as a stepping stone in the
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51 946 eastward dispersal of the clade. Similarly, the presence of Aptian carcharodontosaurids in
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53 947 North America likely requires the presence of pre-Aptian members of the clade in Europe,
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55 948 since faunal exchanges between these two landmasses are known to have been halted before
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949 the Aptian (e.g., Kirkland et al., 1999). Interestingly, it appears that only basal
950 carcharodontosaurids were able to spread into the northern Laurasian landmasses, while the
951 derived carcharodontosaurines dispersed exclusively across the Neo-Tethys, into western
952 Gondwana. The causes of these distribution patterns remain as yet unknown, and further
953 support – in the form on new carcharodontosaurid discoveries from the early-middle part of
954 the Early Cretaceous – is required to better uphold such a scenario.

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

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965 6. Conclusions

966 We re-describe and interpret the affinities of one of the most significant historical dinosaurian
967 specimens of Romania, an isolated but well-preserved theropod tooth from Southern
968 Dobrogea. Our extensive analyses suggest carcharodontosaurid relationships for this tooth,
969 while the available evidence – including novel calcareous nannoplankton sampling – supports
970 its Valanginian age. The Southern Dobrogean theropod tooth represents the oldest record of
971 Carcharodontosauridae in the Cretaceous, and the second oldest globally, eclipsed only by a
972 collection of isolated specimens from the Upper Jurassic of eastern Africa. As one of the only
973 two known Valanginian dinosaurian occurrences from Central and Eastern Europe, this

1 974 record advances our understanding of European dinosaur distribution during the early Early
2 975 Cretaceous, and also fills an important palaeogeographic gap between Western European and
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5 976 Eastern Asian dinosaurian assemblages of the Valanginian.
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7 977 Based on dental apomorphies, our analyses further identify UAIC (SCM1) 615 as a
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9 978 possible member of Carcharodontosaurinae, a subclade of derived and gigantic
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12 979 carcharodontosaurids formerly known to be restricted to the Albian–Cenomanian of western
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14 980 Gondwana (Africa and South America). If this finding is correct, the Southern Dobrogean
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17 981 specimen documents the emergence of Carcharodontosaurinae earlier than previously
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19 982 recognized, thus also indicating an earlier acquisition of their characteristically large size.
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22 983 Based on currently known palaeogeographic and chronostratigraphic constraints on the
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24 984 evolution of Carcharodontosauridae, it appears that not only did this clade have a wide
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26 985 distribution, but that crucial events of its evolutionary history such as the emergence of the
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29 986 derived carcharodontosaurines took place north of the Tethys, in cratonic Europe, instead of
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32 987 western Gondwana and as the result of vicariant evolution driven by the Gondwana-Laurasia
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34 988 split, as was formerly suggested. In such a case, instead of endemic evolution the emergence
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36 989 of the western Gondwanan mid-Cretaceous carcharodontosaurines was the result of a north-
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39 990 to-south trans-Tethyan dispersal that took place somewhere between the Valanginian and the
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41 991 Aptian. Recognizing a potential carcharodontosaurine dispersal event from Europe into
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44 992 western Gondwana adds further support for the presence of important palaeogeographic ties
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46 993 between the two realms during the second half of the Early Cretaceous.
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24 1560 Figure captions

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27 1561 Figure 1. Simplified geological map of the Cernavodă-Cochirleni area; inset shows the
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29 1562 position of the study area within Romania. Legend: 1. Quaternary: a. Holocene alluvia, b.
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31 1563 Pleistocene–Holocene loessoid deposits; 2. Pre-Quaternary Cenozoic (Middle Eocene and
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34 1564 Miocene) deposits; Cretaceous: 3. Peștera Formation, Lower Cenomanian; 4. Cochirleni
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36 1565 Formation; uppermost Aptian–Lower Albian; 5. Gherghina Formation, Middle–Upper
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39 1566 Aptian; 6. Ostrov (= Ramadan) Formation; Barremian–Lower Aptian; 7. Cernavodă
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41 1567 Formation, Alimanu Member, Berriasian–Valanginian; 8. Water courses. (Redrawn after
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44 1568 Dragastan et al., 1998, 2014).
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49 1570 Figure 2. Specimen UAIC (SCM1) 615, indeterminate carcharodontosaurid lateral tooth from
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51 1571 Cochirleni, Southern Dobrogea. A. UAIC (SCM1) 615, as figured by Simionescu (1913); B.
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53 1572 Current state of UAIC (SCM1) 615, mounted in a limestone holder.
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1574 Figure 3. Detailed morphology of UAIC (SCM1) 615, an indeterminate carcharodontosaurid
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2 1575 lateral tooth from Cochirleni, Southern Dobrogea. UAIC (SCM1) 615 in A. labial? side; B.,
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4 1576 distal; C., lingual? side, and D., basal (mesial to the right) views. Details of the distal carina
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7 1577 (marked with boxes in A, respectively C): apical part in E., labial? and F. distal views; basal
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10 1578 part in G., lingual? and H., distal views. Scale bar: 1 cm (A–D), 5 mm (E–H).

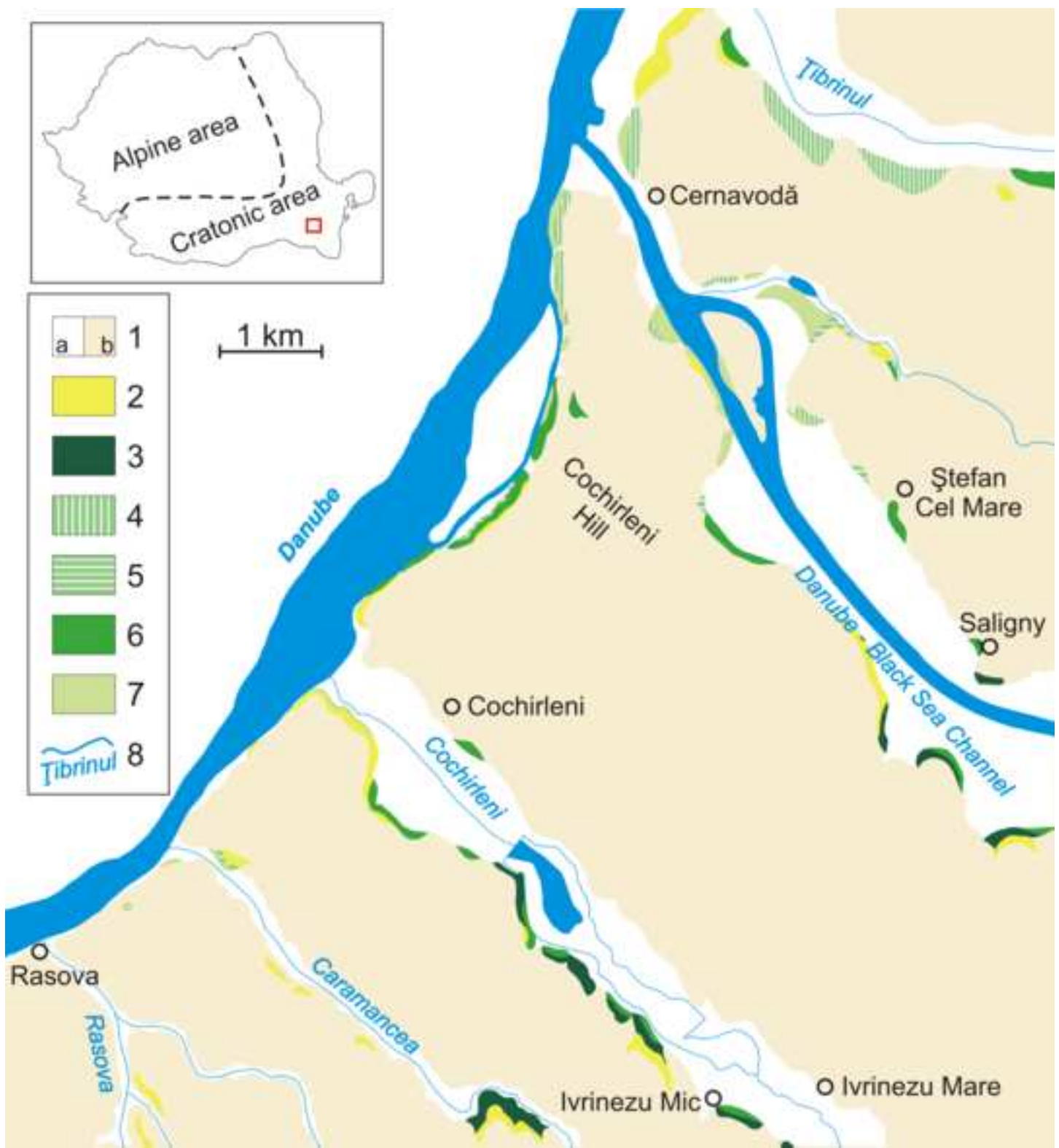
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12 1579
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14 1580 Figure 4. Dental morphospace of the different theropod clades according to the results of the
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17 1581 PCA analysis; UAIC (SCM1) 615 (red star) plots within the morphospace occupied by
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19 1582 Carcharodontosauridae. See further details of this analysis, as well as other quantitative
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21
22 1583 analyses used to identify the tooth that deliver similar results (cluster analysis, discriminant
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24 1584 function analysis, phylogenetic analysis), in the Supplementary Material.

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29 1586 Figure 5. A. Palaeogeographic setting of the two early Early Cretaceous Romanian dinosaur
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31 1587 occurrences: the Berriasian–Valanginian Cornet locality (orange star), located on a Neo-
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34 1588 Tethyan archipelago island, and the Valanginian Cochirleni locality (red star), situated on the
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36 1589 marginal areas of the Eastern European cratonic mainland. B. Global chronostratigraphic and
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39 1590 palaeobiogeographic distribution of the Carcharodontosauridae, plotted on Middle Aptian
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41 1591 (approx. 120 Mya) palaeogeographic map; red star marks the position of UAIC (SCM1) 615
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43 1592 from Southern Dobrogea. Legend: 1 – *Veterupristisaurus*, ‘*Megalosaurus*’ *ingens*,
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46 1593 Carcharodontosauridae indet., Tanzania, Late Jurassic; 2 – *Concavenator*, Spain, Barremian;
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49 1594 3 – Carcharodontosauridae indet., Thailand, Barremian; 4 – *Acrocanthosaurus*, southeastern
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51 1595 United States, Aptian–Albian; 5 – Carcharodontosauridae indet., Spain, Aptian; 6 –
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53 1596 *Eocarcharia*, Niger, Aptian–Albian; 7 – Carcharodontosauridae indet., Guangxi, China,
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56 1597 Aptian; 8 – Carcharodontosauridae indet., Henan, China, Aptian; 9 – *Kelmaysaurus*,
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58 1598 Xinjiang, China, Aptian–Albian; 10 – Carcharodontosauridae indet., France, Cenomanian; 11

- 1599 – *Sauroniops*, Morocco, Cenomanian; 12 – Carcharodontosauridae indet., Japan,
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2 1600 Cenomanian–early Turonian; 13 – *Shaochilong*, Inner Mongolia, China, Turonian; 14 –
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5 1601 Carcharodontosauridae indet., São Paulo, Brazil, Campanian–Maastrichtian (for relevant
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Figure 1 color
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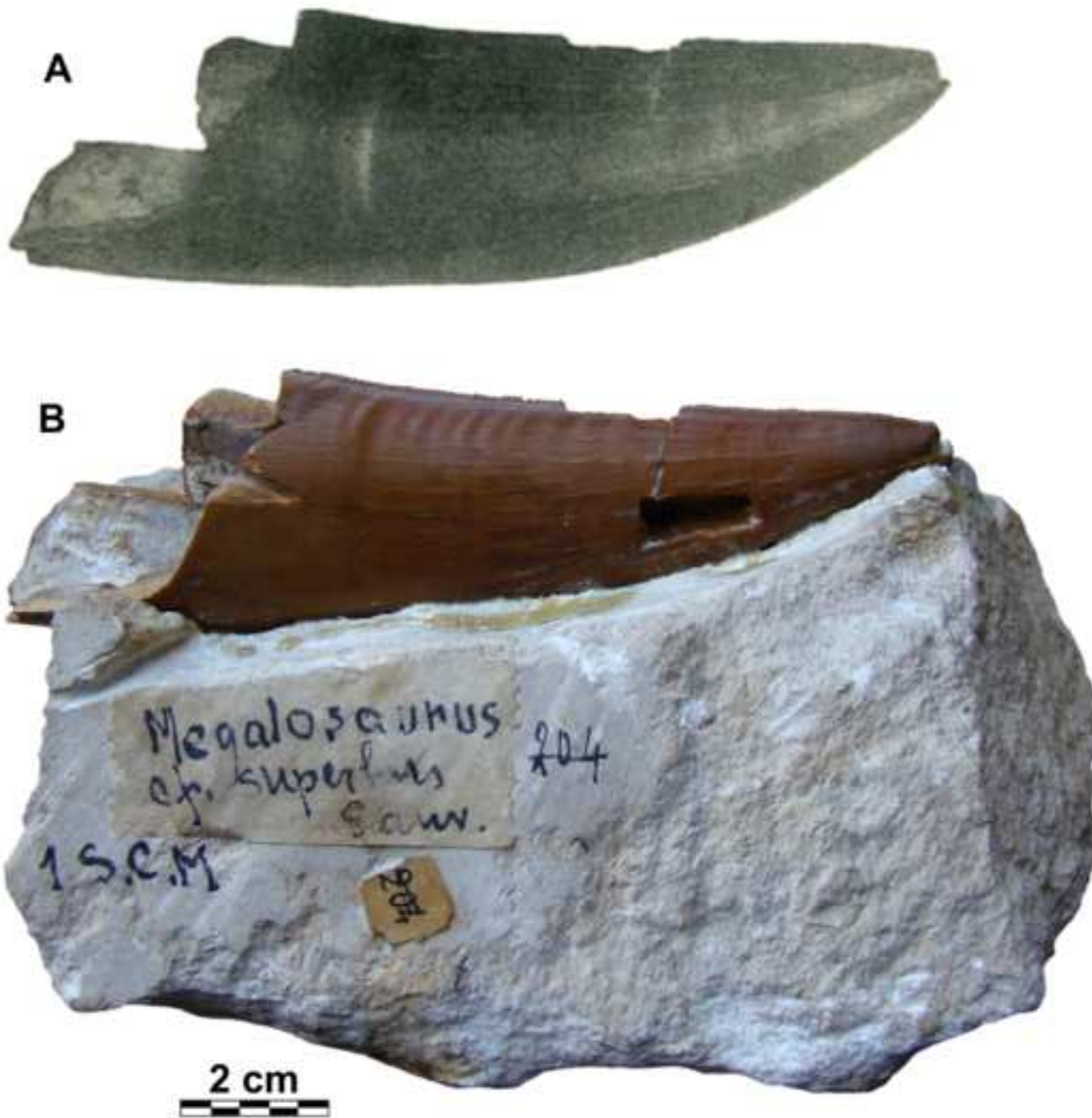


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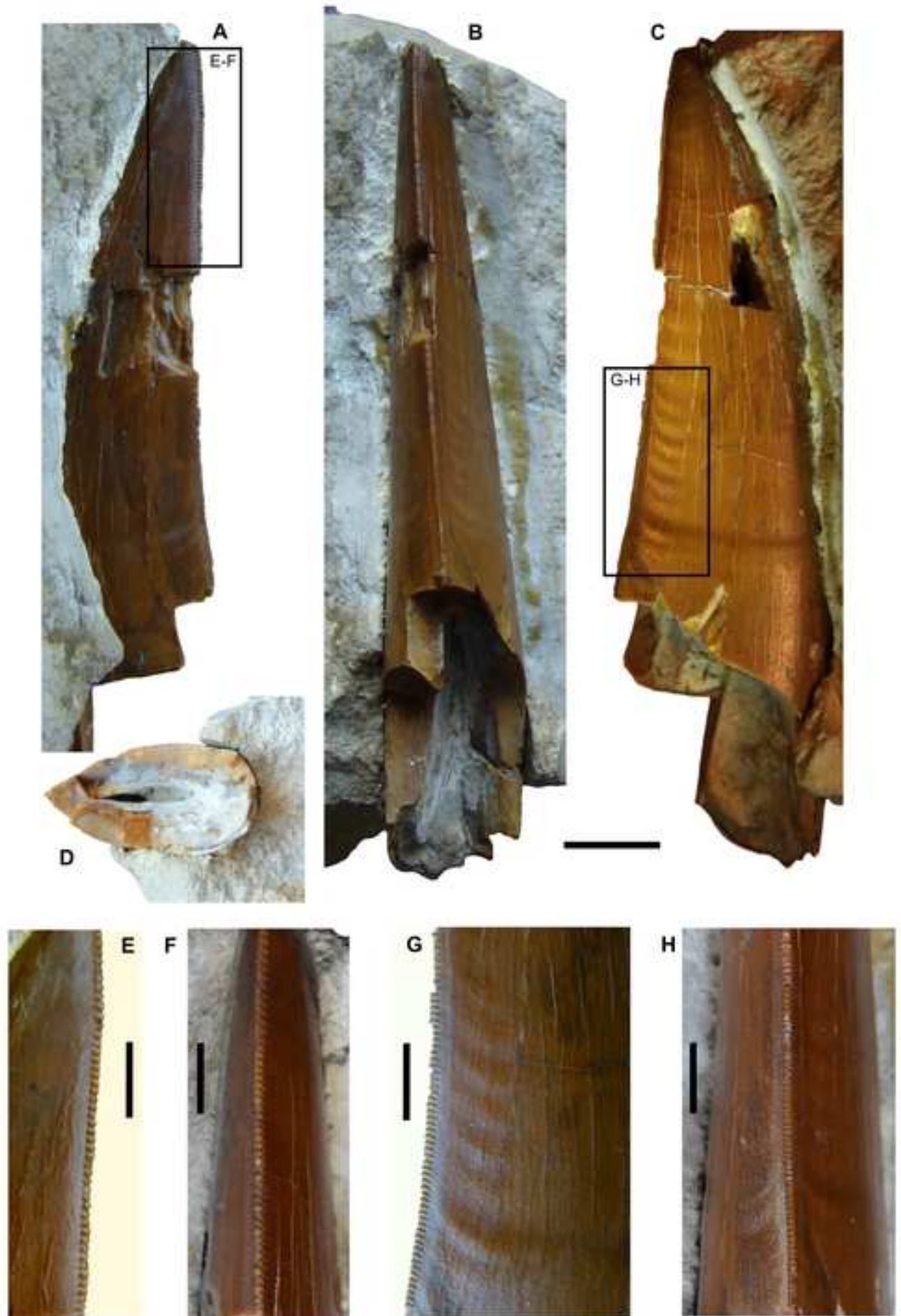


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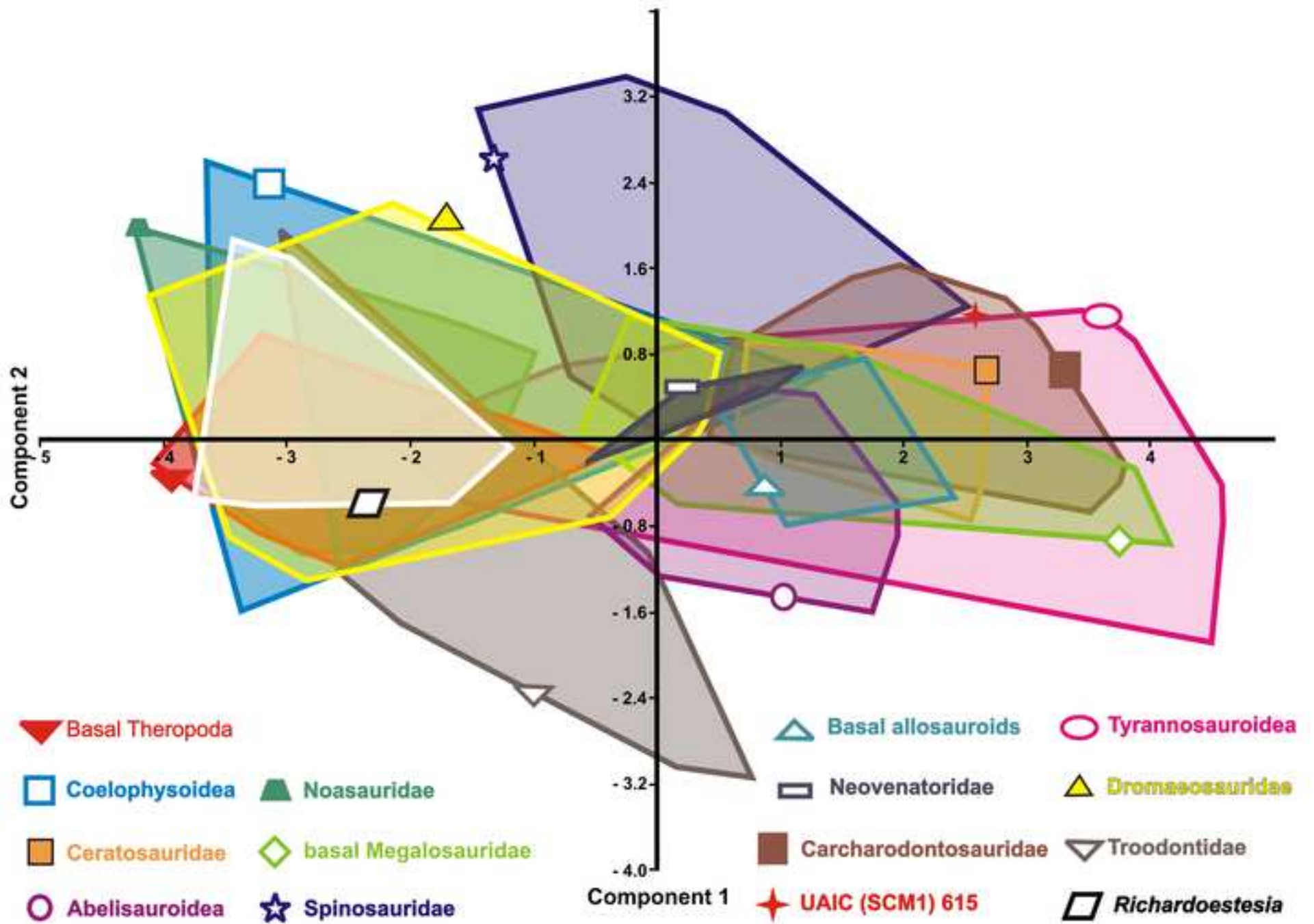
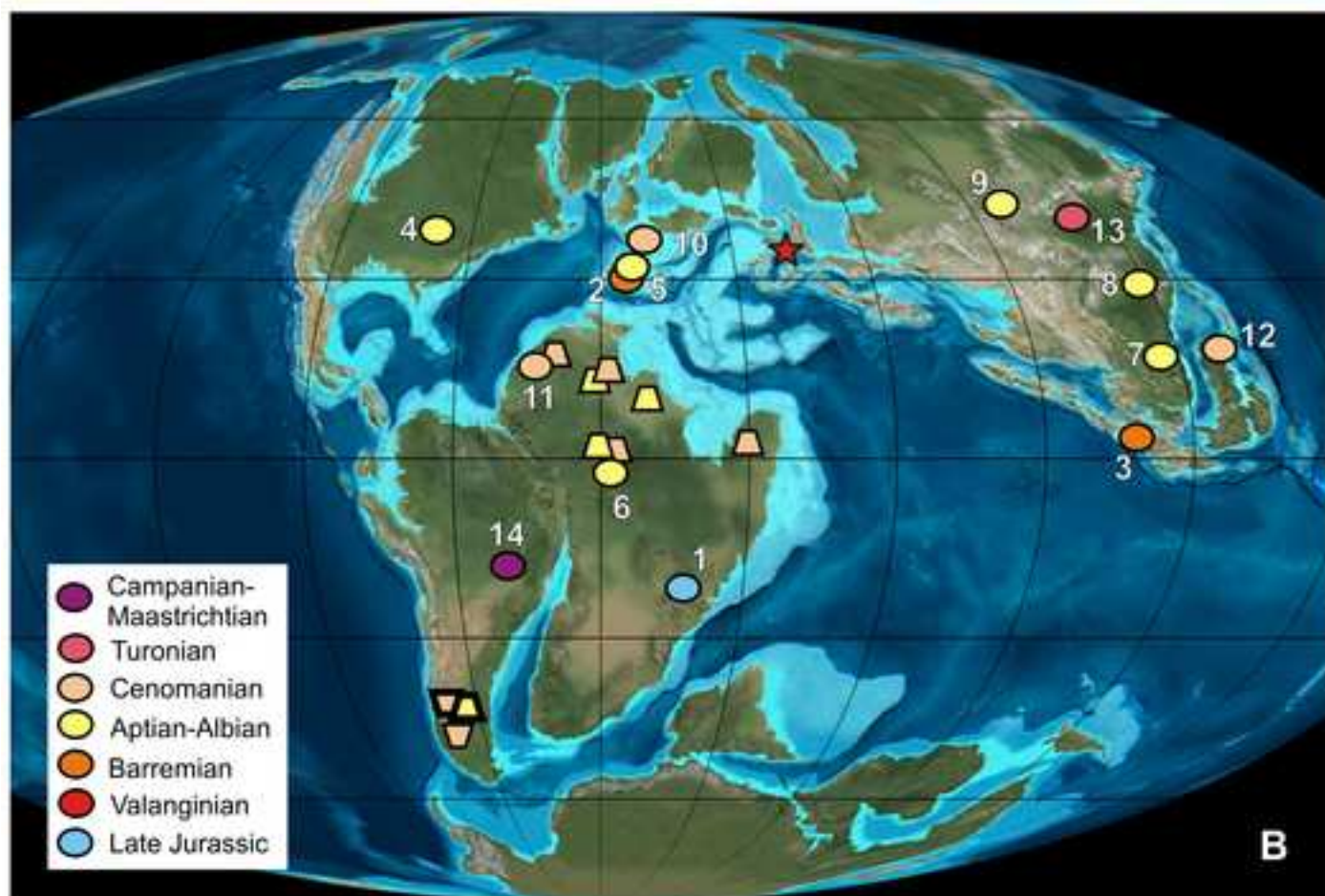


Figure 5 color

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○ basal / indeterminate
Carcharodontosauridae

☆ UAIC (SCM1) 615

Carcharodontosaurinae

△ *Carcharodontosaurus*

▽ *Giganotosaurus*

△ *Mapusaurus*

▽ *Tyrannotitan*

Supplementary Material

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Taxon	Side	Position	Specimen	Source from	CBL	CBW	CH	
ROMANIAN TOOTH			SCM1 615			29	16.25	85.5
Eoraptor	Left	pmx2	PVSJ 512	Pers. Obsei		2.5	1.62	6.74
Eoraptor	Left	pmx3	PVSJ 512	Pers. Obsei		1.97	2.35	5.92
Eoraptor	Left	pmx4	PVSJ 512	Pers. Obsei		2.19	1.74	6.52
Eoraptor	Right	pmx2	PVSJ 512	Pers. Obsei		2.17	1.56	5.01
Eoraptor	Right	pmx4	PVSJ 512	Pers. Obsei		2.08	1.61	4.17
Eoraptor	Left	mx2	PVSJ 512	Pers. Obsei		2.69	1.82	5.55
Eoraptor	Left	mx4	PVSJ 512	Pers. Obsei		3.03	1.48	5.65
Eoraptor	Left	mx5	PVSJ 512	Pers. Obsei		3.56	1.69	5.48
Eoraptor	Left	mx9	PVSJ 512	Pers. Obsei		2.49	1.75	5.11
Eoraptor	Left	mx10	PVSJ 512	Pers. Obsei		2.7	1.22	4.58
Eoraptor	Left	mx11	PVSJ 512	Pers. Obsei		2.32	1.42	2.34
Eoraptor	Left	pm02	PVSJ 512	Smith & La		2.88	1.85	7.15
Eoraptor	Left	pm03	PVSJ 512	Smith & La		1.98	1.48	5.73
Eoraptor	Left	pm04	PVSJ 512	Smith & La		1.89	1.55	6.12
Eoraptor	Right	pm02	PVSJ 512	Smith & La		2.32	1.8	5.19
Eoraptor	Left	mx02	PVSJ 512	Smith & La		2.11	1.51	5.71
Eoraptor	Left	mx04	PVSJ 512	Smith & La		3.04	1.97	6.58
Eoraptor	Left	mx06	PVSJ 512	Smith & La		2.9	1.74	5.44
Eoraptor	Left	mx07	PVSJ 512	Smith & La		2.71	1.58	6.17
Eoraptor	Left	mx09	PVSJ 512	Smith & La		2.67	1.82	4.99
Eoraptor	Left	mx10	PVSJ 512	Smith & La		2.56	1.69	4.72
Eoraptor	Right	mx02	PVSJ 512	Smith & La		2.94	1.87	5.32
Eoraptor	Right	mx04	PVSJ 512	Smith & La		2.54	1.55	6.5
Eoraptor	Right	mx05	PVSJ 512	Smith & La		3.33	1.82	6.76
Eoraptor	Right	mx07	PVSJ 512	Smith & La		2.86	1.6	4.83
Eoraptor	Right	mx08	PVSJ 512	Smith & La		2.8	1.5	4.71
Ischisaurus	Right	pmx1	MACN 18.C	Pers. Obsei		8.16	4.7	14.62
Ischisaurus	Right	pmx2	MACN 18.C	Pers. Obsei		7.48	4.43	14.5
Eodromaeus	Left	mx3	PVSJ 561	Pers. Obsei		3.61	1.59	9.67
Coelophysis	Left	pmx2	CM 82931	Pers. Obsei		1.7	0.54	4
Coelophysis	Left	pmx3	CM 82931	Pers. Obsei		1.8	1.03	6.8
Coelophysis	Left	mx1	CM 81765	Pers. Obsei		3	1.49	8.2
Coelophysis	Left	mx2	CM 81765	Pers. Obsei		4.1	1.37	8.9
Coelophysis	Left	mx4	CM 81765	Pers. Obsei		4.4	1.63	11.6
Coelophysis	Left	mx6	CM 81765	Pers. Obsei		5.5	1.71	9.7
Coelophysis	Left	mx8	CM 81765	Pers. Obsei		5.9	1.79	9.3
Coelophysis	Left	mx9	CM 81765	Pers. Obsei		5.4	1.74	8.6
Coelophysis	Left	mx11	CM 81765	Pers. Obsei		5.4	1.85	7.5
Coelophysis	Left	mx13	CM 81765	Pers. Obsei		4.7	1.58	5.5
Coelophysis	Left	mx14	CM 81765	Pers. Obsei		5.2	1.7	6.2
Coelophysis	Left	mx15	CM 81765	Pers. Obsei		3.9	1.49	5.4
Coelophysis	Left	mx16	CM 81765	Pers. Obsei		3.3	1.14	5
Coelophysis	Left	mx17	CM 81765	Pers. Obsei		3.5	1.63	4.1
Coelophysis	Left	mx19	CM 81765	Pers. Obsei		3.35	1.86	3.3
Coelophysis	Left	mx21	CM 81765	Pers. Obsei		3.54	0.93	3.45