

1 **DIVERSITY PATTERNS OF NOTOSUCHIA (CROCODYLIFORMES,**  
2 **MESOEUCROCODYLIA) DURING THE CRETACEOUS OF GONDWANA**

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15 RH: POL AND LEARDI: NOTOSUCHIAN DIVERSITY PATTERNS

16

17 **Abstract.** Notosuchia is a diverse clade of Crocodyliformes that achieved a remarkable  
18 diversity during the Cretaceous. This group is particularly abundant in continental  
19 deposits of Gondwana throughout the Cretaceous, especially in South America.  
20 Notosuchia was first recognized as a distinct group by the early work of Gasparini in the  
21 1970's and in the last decades numerous discoveries and studies have increased the  
22 geographical, temporal and taxonomical scope of this clade. Here we analyze the  
23 patterns of diversity of Notosuchia during the Cretaceous, considering their taxic and  
24 phylogenetic diversity, as well as implementing sampling corrections aiming to account  
25 for the uneven fossil record of different stages of the Cretaceous. We identify two  
26 subsequent pulses of diversification in the late Early Cretaceous and the middle Late  
27 Cretaceous, followed by two separate extinction events that occurred during the latest  
28 Cretaceous (Campanian/Maastrichtian). We discuss the contribution of the South  
29 American, African, and Malagasy fossil records to the diversity curves, which indicates  
30 the African fossil record dominates the first pulse of diversification and the South  
31 American fossil record exclusively compose the second pulse of diversification. Finally,  
32 we analyze the patterns of diversity shown by the different subclades of Notosuchia  
33 throughout the Cretaceous, which reveal markedly different evolutionary dynamics of  
34 four major groups of notosuchian crocodyliforms.

35 **Key words.** Notosuchia. Diversity. Radiation. Cretaceous. Gondwana.

36 **Resumen.** PATRONES DE DIVERSIDAD DE NOTOSUCHIA  
37 (CROCODYLIFORMES, MESOEUCROCODYLIA) DURANTE EL CRETÁCICO  
38 DE GONDWANA. Notosuchia es un clado diverso de Crocodyliformes que adquirió  
39 una notable diversidad durante el Cretácico. Este grupo es particularmente abundante en  
40 depósitos continentales de Gondwana a lo largo del Cretácico, especialmente en  
41 América del Sur. Notosuchia fue originalmente reconocido como un grupo distintivo

42 por Gasparini en trabajos durante la década de 1970 y en años recientes numerosos  
43 estudios y descubrimientos han incrementado el rango geográfico, temporal y  
44 taxonómico de este clado. En este trabajo analizamos los patrones de diversidad de  
45 Notosuchia durante el Cretácico, considerando su diversidad taxonómica y filogenética,  
46 así como también implementando correcciones de muestreo que intentan considerar el  
47 dispar registro fósil de los diferentes pisos del Cretácico. Se identifican dos pulsos  
48 sucesivos de diversificación en el Cretácico Temprano tardío y en el Cretácico Tardío  
49 medio, seguidos de dos eventos separados de extinción ocurridos durante el Cretácico  
50 más tardío (Campaniense/Maastrichtiense). Se discuten las contribuciones del registro  
51 fósil de América del Sur, África, y Madagascar a las curvas de diversidad, las cuales  
52 indican que el registro africano domina el primer pulso de diversificación y el registro  
53 sudamericano compone de manera exclusiva el segundo pulso de diversificación.  
54 Finalmente, analizamos los patrones de diversidad de los diferentes subclados de  
55 Notosuchia a través del Cretácico, los cuales revelan una dinámica evolutiva  
56 marcadamente diferente para cuatro grandes grupos de crocodyliformes notosuquios.  
57 **Palabras clave.** Notosuchia. Diversidad. Radiación. Cretácico. Gondwana.

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60 NOTOSUCHIA is the most diverse clade of Gondwanan crocodyliforms that thrived  
61 during the Cretaceous Period (Turner and Sertich, 2010; Pol *et al.*, 2014). Much of the  
62 currently known diversity, including over 70 different species, has been revealed during  
63 the last 25 years through discoveries across most Gondwanan landmasses. The bulk of  
64 this diversity is found in South America, where notosuchian remains have been known  
65 since the latest XIXth century. The description of *Notosuchus terrestris* and  
66 *Cynodontosuchus rothi* from the Late Cretaceous of Patagonia (Woodward, 1896) was  
67 the first contribution to notosuchian diversity in South America. Subsequently, during  
68 the first half of the XXth century the discoveries of *Uruguaysuchus* (Rusconi, 1933) and  
69 five taxa from the Cretaceous of Brazil (Price, 1945, 1950a,b, 1955, 1959) increased the  
70 diversity of the group currently known as Notosuchia. The Brazilian taxa described by  
71 Price included small-bodied forms known from relatively complete remains (*i.e.*,  
72 *Araripesuchus*; Price, 1959), large-bodied taxa with adaptations to hypercarnivory (*i.e.*,  
73 *Baurusuchus*; Price, 1945), and more fragmentary specimens with unusual tooth  
74 morphology (*i.e.*, *Sphagesaurus*, *Itasuchus*, *Peirosaurus*; Price, 1950a,b, 1955).

75         The systematic arrangement of these Cretaceous crocodyliforms from South  
76 America was tackled in a series of influential papers by Gasparini (1971, 1972, 1981,  
77 1982), who recognized and created different taxonomic groups for classifying these  
78 forms. One of the most relevant contributions was the creation of Notosuchia  
79 (Gasparini, 1971), a high level group that clustered small-bodied forms such as  
80 *Notosuchus*, *Araripesuchus*, and *Uruguaysuchus*. Within Notosuchia, Gasparini (1971)  
81 restricted Notosuchidae to *Notosuchus* and grouped the latter two species by erecting  
82 the family Uruguaysuchidae. Other contributions of Gasparini were focused on less  
83 diverse groups at that time, such as Sebecosuchia (Gasparini, 1972) and Peirosauridae  
84 (Gasparini, 1982), which were not considered part of Notosuchia until recently (Ortega

85 *et al.*, 2000; Pol, 2003; Turner and Sertich, 2010; Pol *et al.*, 2012, 2014). Within  
86 Sebecosuchia, Gasparini validated the Cretaceous group Baurusuchidae (including  
87 *Baurusuchus* and the fragmentary *Cynodontosuchus*) as related to the Cenozoic  
88 sebecids. Finally, Gasparini erected Peirosauridae (Gasparini, 1982) by recognizing the  
89 distinctness of *Peirosaurus torminni* from all other crocodyliforms, while studying the  
90 type materials of this taxon described originally by Price (1955), and more complete  
91 material discovered in Patagonia. These studies therefore organized the known diversity  
92 of Cretaceous crocodyliforms from South America by recognizing four basic groups:  
93 Notosuchidae, Uruguaysuchidae, Peirosauridae, and Baurusuchidae. These four groups,  
94 recognized by Gasparini on the basis of only six different species, represent adaptive  
95 morphs that differ from each other in a suite of characters of the rostral region,  
96 dentition, and palatal anatomy (Fig. 1).

97         The diversity of Cretaceous crocodyliforms from South America (and other  
98 regions of Gondwana) has remarkably increased since the original studies of Gasparini  
99 in the 1970's and 1980's (Carvalho and Bertini, 1999; Ortega *et al.*, 2000; Campos *et*  
100 *al.*, 2001; Carvalho *et al.*, 2004, 2005, 2007, 2011; Pol and Apesteguía, 2005; Nobre  
101 and Carvalho, 2006; Andrade and Bertini, 2008; Iori and Carvalho, 2009, 2011; Kellner  
102 *et al.*, 2009, 2011a,b; Marinho and Carvalho, 2009; Novas *et al.*, 2009; Nascimento and  
103 Zaher, 2010; Montefeltro *et al.*, 2011; Martinelli *et al.*, 2012; Marinho *et al.*, 2013). The  
104 new discoveries, coupled with the inclusion of both Baurusuchidae and Peirosauridae  
105 within Notosuchia in recent phylogenetic studies (*e.g.*, Turner and Sertich, 2010; Pol *et*  
106 *al.*, 2012, 2014), revealed a previously unsuspected diversity of Notosuchian  
107 crocodyliforms. There has been an almost 4-fold increase in its known diversity during  
108 the last 25 years (Fig. 2). This increase in notosuchian diversity improved our  
109 knowledge on the distribution of this clade, both temporally and geographically. The

110 biochron of most notosuchian clades is restricted to the Cretaceous, and ranges from the  
111 Aptian (Early Cretaceous) to the Maastrichtian (Late Cretaceous), although a lineage of  
112 notosuchians of debated affinities (Sebecidae) is recorded after the K/Pg extinction  
113 event, and survived until the Miocene in South America (Gasparini, 1972, 1996;  
114 Buffetaut, 1982; Kellner *et al.*, 2014).

115         From a biogeographic point of view, recent discoveries are highlighting a  
116 growing number of Cretaceous notosuchians in other Gondwanan landmasses in  
117 addition to South America, such as Africa (Sereno and Larsson, 2009; O'Connor *et al.*,  
118 2010; Sertich and O'Connor, 2014) and Madagascar (Buckley and Brochu, 1999;  
119 Buckley *et al.*, 2000; Simons and Buckley, 2009). Furthermore, fragmentary (but still  
120 informative) remains found in Indo-Pakistan (Wilson *et al.*, 2001; Prasad and de Broin,  
121 2002; Prasad *et al.*, 2013), Central Asia (*Chimaerasuchus*; Wu and Sues, 1996), and  
122 Europe (Company *et al.*, 2005; Dalla Vecchia and Cau, 2011; Rabi and Sebök, 2015)  
123 suggests that the geographic distribution of Notosuchia was broader than previously  
124 thought. The major diversity of Cretaceous notosuchians is, however, still found in  
125 South America, where over 70% of the known species of this group have been  
126 recovered (Fig. 2).

127         These discoveries prompted a growing number of research efforts focused on the  
128 anatomy and systematics of notosuchian crocodyliforms. A strong component of recent  
129 research on notosuchians has been the use of cladistics analysis for testing the  
130 relationships of Notosuchia (Ortega *et al.*, 2000; Pol, 2003; Carvalho *et al.*, 2004;  
131 Turner and Sertich, 2010; Andrade *et al.*, 2011; Montefeltro *et al.*, 2011; Pol *et al.*,  
132 2012, 2014). Many of these studies are now corroborating the monophyly of the four  
133 Cretaceous clades early recognized by Gasparini for South American forms in pioneer  
134 contributions during her early career (*i.e.*, Uruguaysuchidae, Peirosauridae,

135 Baurusuchidae, and a clade allying *Notosuchus* and closely related forms; Gasparini,  
136 1971, 1972, 1982). In this contribution, we analyze the diversity patterns among  
137 notosuchians during the Cretaceous, aiming to evaluate with the currently known  
138 diversity, the radiation and extinction events of this diverse group of crocodyliforms.

## 139 **MATERIALS AND METHODS**

### 140 *Notosuchian diversity*

141 *Notosuchian species.* A list of published species of notosuchian crocodyliforms was  
142 compiled summarizing the diversity and distribution of the group, including age,  
143 geographic and stratigraphic provenance, systematic assignment to five different  
144 subgroups of Notosuchia (see below), and year of publication (see Supplementary  
145 Information).

146 *Notosuchian phylogeny.* The systematic arrangement of notosuchian species was based  
147 on recent phylogenetic analyses published by Pol *et al.* (2014), with subsequent addition  
148 of two taxa made by Leardi *et al.* (2015). These studies were chosen as they are the  
149 most comprehensive analyses, in terms of both taxon and character sampling, of  
150 notosuchian crocodyliforms performed to date and agree in many aspects to other  
151 studies published in recent years (Sereno and Larsson, 2009; Turner and Sertich, 2010;  
152 Andrade *et al.*, 2011; Montefeltro *et al.*, 2013; Sertich and O'Connor, 2014). The  
153 topologies from these phylogenetic analyses were used for two main purposes. Firstly,  
154 the topology served for establishing the clade assignment for each terminal taxon into  
155 five major clades recognized within Notosuchia during the Cretaceous (see below).  
156 Secondly, the topologies served to perform a phylogenetic correction of diversity based  
157 on the inferences of ghost lineages (Norell, 1992) at each period of time (see below).  
158 Some notosuchian species were not included in the data matrices published by Pol *et al.*  
159 (2014) and Leardi *et al.* (2015) and therefore have been excluded from the diversity

160 analyses conducted here, because their absence in the used phylogenetic hypotheses  
161 precluded assessing their impact on the phylogenetically corrected diversity measures.  
162 These, however, are limited to 18 out of the 77 known species, may not alter the  
163 diversity trends discussed in this paper.

164 ***Notosuchian clades.*** Most recent phylogenetic analyses have recovered a large clade  
165 clustering most Cretaceous crocodyliforms from Gondwana (Turner and Sertich, 2010;  
166 Andrade *et al.*, 2011; Montefeltro *et al.*, 2013; Pol *et al.*, 2012, 2014; Sertich and  
167 O'Connor, 2014), creating a relatively recent but broad consensus on the monophyly of  
168 Notosuchia and its taxonomic content. The taxonomic content of Notosuchia has been  
169 enlarged in comparison with the one original proposal by Gasparini (1971; restricted to  
170 Notosuchidae+Uruguaysuchidae) and currently includes the Cenozoic Sebecidae and  
171 the Cretaceous Peirosauridae (and related forms; Turner and Sertich, 2010; Pol *et al.*,  
172 2012). Although some discrepancies still exist among published phylogenies (*e.g.*, the  
173 exclusion of Peirosauridae from Notosuchia), we have based our study on the  
174 phylogenetic results of Pol *et al.* (2014) and for the purpose of assessing diversity  
175 patterns we recognize here five major groups of Cretaceous notosuchians (Fig. 3), four  
176 of which represent monophyletic clades. These four clades correspond to the four basic  
177 taxonomic groups originally identified by Gasparini (although with some differences in  
178 their taxonomic content).

179         The first of them, Uruguaysuchidae (Fig. 3), includes *Uruguaysuchus*, the now  
180 highly diverse *Araripesuchus* (including six species distributed from the Albian to the  
181 Campanian–Maastrichtian; Price, 1959; Buffetaut, 1981; Ortega *et al.*, 2000; Pol and  
182 Apesteguía, 2005; Turner, 2006), as well as the bizarrely broad snouted *Anatosuchus*  
183 (Sereno *et al.*, 2003). The second clade, Peirosauridae, includes a variety of Late  
184 Cretaceous South American taxa (*e.g.*, *Peirosaurus*, *Lomasuchus*, *Gasparinisuchus*,



185 *Uberabasuchus*, *Montealtosuchus*; Price, 1955; Gasparini *et al.*, 1991; Carvalho *et al.*,  
186 2004, 2007; Martinelli *et al.*, 2012) but also closely related African species from the  
187 “mid” Cretaceous (*e.g.*, *Hamadasuchus*, *Stolokrosuchus*; Larsson and Gado, 2000;  
188 Larsson and Sues, 2007). We have included in this group the bizarre but closely related  
189 clade Mahajangasuchidae (Fig. 3), recorded in the Cenomanian of Africa and the  
190 Campanian–Maastrichtian of Madagascar (Serenio and Larsson, 2009). The third group,  
191 here referred as basal ziphosuchians, does not represent a clade but a number of taxa  
192 mainly recorded in the “middle” Cretaceous of Africa (*Libycosuchus*, *Malawisuchus*,  
193 *Pakasuchus*; Stromer, 1914; Gomani, 1997; O’Connor *et al.*, 2010), South America  
194 (*Candidodon*; Carvalho, 1994), and some relictual forms in the Late Cretaceous  
195 (*Neuquensuchus*, *Simosuchus*; Buckley *et al.*, 2000; Fiorelli and Calvo, 2007). These  
196 forms are clearly closer to advanced notosuchians and sebecosuchians than to  
197 uruguaysuchids and peirosaurids but are placed basally within Ziphosuchia. The fourth  
198 clade, advanced notosuchians (*sensu* Pol *et al.*, 2014), is recorded in the Late  
199 Cretaceous of South America and includes its basal members (*Morrinhosuchus*,  
200 *Notosuchus*, *Mariliasuchus*; Woodward, 1896; Carvalho and Bertini, 1999; Iori and  
201 Carvalho, 2009) and the diverse Sphagesauridae (Fig. 3). The fifth clade,  
202 Baurusuchidae, is mainly recorded in two formations from the middle Late Cretaceous  
203 of Argentina (*Cynodontosuchus*, *Wargosuchus*; Woodward, 1896; Martinelli and Pais,  
204 2008) and Brazil (*Baurusuchus*, *Campinasuchus*, *Pissarrachampsia*, *Aplestosuchus*,  
205 *Gondwanasuchus*; Price, 1945; Carvalho *et al.*, 2011; Montefeltro *et al.*, 2011; Godoy  
206 *et al.*, 2014; Marinho *et al.*, 2013), with the possible addition of *Pabwehshi* (Wilson *et*  
207 *al.*, 2001) a fragmentary form found in the Maastrichtian of Pakistan. Finally, although  
208 our focus is centered in the Cretaceous, we have grouped the Cenozoic Sebecidae and

209 allies from other regions (*e.g.*, *Iberosuchus*, *Bergisuchus*, *Doratodon*; Kuhn, 1968;  
210 Antunes, 1975; Company *et al.*, 2005; Rabi and Sebök, 2015) in a separate group.

### 211 ***Diversity analysis***

212         The diversity analyses performed here are based on establishing the number of  
213 notosuchian lineages present at different periods of time during the Cretaceous. The  
214 most basic and raw estimate is the taxic diversity (Levinton, 1988) at a given period of  
215 time (*i.e.*, number of species known from that time slice). Different corrections that aim  
216 to minimize the bias introduced by the vagaries of the fossil record have been proposed  
217 for establishing diversity patterns across time. Here we have explored the use of two  
218 commonly used corrections, one that aim to minimize the influence of the uneven  
219 distribution of fossiliferous rocks for different periods of time (sampling correction) and  
220 other that corrects diversity counts based on lineages inferred from the phylogenetic  
221 analysis (phylogenetic correction; Norell and Novacek, 1992a,b).

222 ***Time bins.*** Diversity curves are not only affected by the granularity of the taxonomy  
223 (hierarchical taxonomic level) but also by the precision of age assignment for each  
224 fossil species. This depends on the nature of the available chronostratigraphic  
225 information as well as the questions being tested. Here we have chosen to assign ages  
226 based on the geological stages recognized by the International Chronostratigraphic  
227 Chart (Cohen *et al.*, 2012). This follows the procedures of recent studies on the  
228 diversity dynamics of mesozoic vertebrates (Barrett *et al.*, 2009; Butler *et al.*, 2009;  
229 Mannion *et al.*, 2011) and is based on the fact that the age of most Cretaceous  
230 continental units from Gondwana is only constrained to one geological stage, at best.  
231 Several lithostratigraphic units have uncertain age assignment and assigned to various  
232 contiguous stages (*e.g.*, Aptian–Albian, Turonian–Santonian). These diversity counts  
233 for these units have been counted for the stages included in the uncertainty range rather

234 than choosing an arbitrary midpoint age assignment. These may create plateaus in the  
235 diversity curves that should be interpreted as chronostratigraphic uncertainty rather than  
236 stasis of diversity levels through time.

237 ***Sampling correction.*** The geological record heavily influences our perception of the  
238 fossil diversity, in particular limiting the findings of the taxa of interest. It has been  
239 demonstrated that the amount of taxa known for a particular time bin is correlated with  
240 the number of fossil-bearing formations available (*e.g.*, Behrensmeyer *et al.*, 2000;  
241 Miller, 2000; Alroy *et al.*, 2001, 2008). A typical correction used in diversity studies  
242 implies the recognition of the fossil-bearing formations for the particular case of study  
243 (*e.g.*, Barrett *et al.*, 2009; Butler *et al.*, 2009; Irmis, 2011; Mannion *et al.*, 2011), and  
244 afterwards normalizing the diversity curves. In our case, we recognized the  
245 notosuchian-bearing formations (NBFs) for each time bin (see Supplementary  
246 Information), and the resulting diversity for that period of time was divided by the  
247 number NBFs.

248 ***Phylogenetic correction.*** The number of species known for each period of time (taxic  
249 diversity) is a minimum estimate on the true diversity due to the incompleteness of the  
250 fossil record. Phylogenetic trees provide hypotheses on the existence of lineages prior to  
251 their first appearance in the fossil record (ghost lineages *sensu* Norell, 1992). A ghost  
252 lineage extending throughout a period of time implies an undetected lineage that can be  
253 added to the known (taxic) diversity, which is the basic rationale of the phylogenetic  
254 correction of diversity curves (Norell and Novacek, 1992a,b). Here we have counted an  
255 additional lineage to the diversity counts when the phylogenetic topology implied a  
256 lineage that spans at least throughout an entire geological stage.

257 **RESULTS**

258           The diversity of notosuchians varied significantly along the Cretaceous. We  
259 show first the patterns of overall diversity through time for the clade Notosuchia.  
260 Afterwards, we decompose the curves to evaluate the contribution of the different  
261 geographic areas and phylogenetic clades to the total diversity of Notosuchia.

262 ***Notosuchian diversity curves***

263 ***Taxic and phylogenetic diversity.*** The number of notosuchian species known for each  
264 period of time increases in two distinct pulses during the Cretaceous. The first pulse  
265 (Fig. 4.1) represents the Aptian radiation of basal notosuchians (see Pol *et al.*, 2014).  
266 The notosuchian diversity remains stable during the Aptian–Cenomanian, a stasis that is  
267 likely affected by the chronostratigraphic uncertainty of notosuchian bearing formations  
268 of the “middle” Cretaceous of South America (*e.g.*, Itapecurú, Guichón) or Africa (Kem  
269 Kem, Gadoufaua, Galula). After this stasis, the second pulse of diversification (Fig. 4.1)  
270 occurs later during the Late Cretaceous, presumably between the Turonian and  
271 Santonian, where the highest peak of notosuchian diversity is achieved (Turonian–  
272 Santonian radiation *sensu* Pol *et al.*, 2014). The precise timing of this radiation depends  
273 on the age of certain formations from South America (*e.g.*, Adamantina, Bajo de la  
274 Carpa; see Pol *et al.*, 2014 and Discussion below). Drastic drops in diversity are  
275 recorded at the end Cretaceous (most likely Campanian–Maastrichtian) that reduced the  
276 diversity of Cretaceous notosuchians, of which only one lineage (sebecids) survives the  
277 K/Pg extinction event.

278           The phylogenetic correction shows that the periods of time in which there are  
279 more unsampled lineages are precisely the timespan during which most notosuchians  
280 are known (Aptian–Santonian; light grey curve in Fig. 4.1). This indicates that both the  
281 Aptian and the Turonian–Santonian radiation events were larger than what the direct  
282 reading of the fossil record (*i.e.*, taxic diversity) implies. In our analysis, the

283 phylogenetic correction almost does not make any difference before the Aptian or after  
284 the Santonian, implying that our phylogenetic tree does not indicate that unsampled  
285 lineages are biasing the estimates of low notosuchian diversity outside the Aptian–  
286 Santonian timespan.

287 ***Sampling correction.*** The sampling correction provides an overall similar pattern of  
288 diversity, with two pulses of diversification (Aptian and Turonian–Santonian) and a  
289 drastic drop in diversity at the latest Cretaceous (Fig. 4.2). However, there are two most  
290 notable differences with respect to the diversity curves uncorrected for uneven  
291 sampling. The first of them is that the first diversification pulse reaches a peak by the  
292 Aptian but then is followed by a decrease in diversity (corrected by sampling) during  
293 the Albian and Cenomanian (Fig. 4.2) rather than a diversity stasis. This drop is caused  
294 by the fact that there are a similar number of notosuchian taxa (or lineages) known for  
295 these three stages, but there are more notosuchian bearing formations for the  
296 Cenomanian (nine) than for the Aptian (seven) so that the diversity relative to the  
297 number of sampling units is lower. The second difference is found in the diversity  
298 dynamics across the K/Pg mass extinction event. When the diversity is uncorrected by  
299 sampling there is a drastic drop in diversity between the Maastrichtian and the  
300 Paleocene (Fig. 4.1) whereas there is only a minor decrease in diversity across the K/Pg  
301 boundary when the diversity is corrected by uneven sampling (Fig. 4.2). The end  
302 Cretaceous known diversity is indeed higher than in the Paleocene (11 species versus 4  
303 species) but the number of units for these two periods of time is also markedly different.  
304 The apparent insensitivity of notosuchians to the mass extinction event inferred from  
305 the diversity curve corrected by sampling is nonetheless a byproduct of lumping all  
306 notosuchians within a single taxonomical category (see below).

307 ***Diversity patterns of Notosuchia across Gondwana***

308           As noted above, although close to 75% of the known notosuchian diversity is  
309 found in South America (Fig. 2), there is a large number of notosuchian species known  
310 from Africa, Madagascar, and other regions of the world. The diversity of Notosuchia  
311 varies not only across time but also across space. The geographically split diversity  
312 curves aim to show the different contributions of Gondwanan landmasses during the  
313 Cretaceous (Fig. 5.1).

314           The first diversification event (Aptian radiation) is largely formed by the African  
315 fossil record (Fig. 5.1), which accounts for more than half the known notosuchian  
316 diversity in the Early Cretaceous. The large African contribution to this radiation is  
317 surely influenced by the numerous notosuchians discovered in highly fossiliferous  
318 deposits of Niger (Sereno and Larsson, 2009) but also in other regions of Africa (*e.g.*,  
319 Tanzania, Malawi, Egypt, Morocco; Stromer, 1914; Gomani, 1997; Sereno and Larsson,  
320 2009; O'Connor *et al.*, 2010; Sertich and O'Connor, 2014). The contribution of the  
321 South American fossil record to the first diversification pulse is second to the African  
322 contribution and increases towards the Cenomanian. The record in other landmasses is  
323 limited to the Aptian–Albian *Chimaerasuchus paradoxus* from China (Wu *et al.*, 1995).

324           The second diversification pulse (referred as the Turonian–Santonian radiation)  
325 is exclusively formed by the South American fossil record (Fig. 5.1), which accounts  
326 for the major diversity peak in the history of Notosuchia. This is undoubtedly  
327 influenced by the remarkable diversity of notosuchians in the Adamantina Formation in  
328 Brazil and the Neuquén Group in northwestern Patagonia (see Pol *et al.*, 2014), which  
329 represents a major radiation not only in terms of the number of taxa but also in the  
330 ecological diversity of the group known from these units (Godoy *et al.*, 2014). As noted  
331 above, some authors regard the age of this unit as younger than Turonian–Santonian

332 (e.g., Gobbo-Rodrigues *et al.*, 1999; Fernandes and Coimbra, 2000) and therefore this  
333 diversity peak may be displaced slightly later, towards the Campanian (see below).

334 By the latest Cretaceous (Campanian–Maastrichtian), notosuchian diversity falls  
335 to half the number of species known from the preceding diversity peak. Although the  
336 decrease in South American diversity is steep, this landmass still contributes to more  
337 than half of the known diversity in the latest Cretaceous (Fig. 5.1). An important  
338 contribution to the Campanian–Maastrichtian diversity is found in Madagascar  
339 (Maevarano Formation; Buckley and Brochu, 1999; Buckley *et al.*, 2000; Turner, 2006;  
340 Rasmusson Simons and Buckley, 2009). Other regions have provided records of  
341 ziphodont crocodyliforms by the end Cretaceous linked to different groups of  
342 notosuchians, such as Europe (Company *et al.*, 2005) or Pakistan (Wilson *et al.*, 2001).  
343 After the K/Pg extinction event the diversity of notosuchians is mainly restricted to  
344 South America, with minor contributions from other regions (Fig. 5.1), such as Europe  
345 (e.g., *Iberosuchus*, *Bergisuchus*; Antunes, 1975; Ortega *et al.*, 1996; Ortega, 2004)  
346 although possible notosuchian remains have also been reported from the Paleogene of  
347 Africa (*Eremosuchus*; Buffetaut, 1989).

#### 348 ***Diversity patterns of notosuchian subclades***

349 The diversity of Notosuchia as a whole varies markedly during the Cretaceous,  
350 and this variation responds to the sum of evolutionary dynamics of the different  
351 notosuchian subclades. The taxic diversity curves of the five major groups of  
352 Cretaceous notosuchians reveal that different clades diversify and become extinct at  
353 different times (Fig. 5.2). Three of the five groups (basal members of Ziphosuchia,  
354 uruguaysuchids, and peirosaurids) show a similar pattern of taxic diversity: they early  
355 diversify and form the first pulse of diversification during the “middle” Cretaceous  
356 (Aptian–Cenomanian), followed by a period of low diversity in the Turonian–

357 Santonian, a minor diversity peak during the latest Cretaceous (Campanian–  
358 Maastrichtian), and a complete extinction by the end of the Mesozoic (Fig. 5.2). The  
359 two other groups (advanced notosuchians and baurusuchids) differ markedly from this  
360 pattern of diversification, but their diversity curves closely resemble to each other.  
361 These two groups form the major diversification peak of Notosuchia (Turonian–  
362 Santonian) but have extremely low taxic diversity before and after this period.

363         Uruguaysuchids have an initial diversity represented by the *Araripesuchus*  
364 species from South America and Africa and the African *Anatosuchus*. This group  
365 apparently becomes extinct throughout Gondwana, except for Madagascar, where a  
366 lineage of *Araripesuchus* survived until the latest Cretaceous (*A. tsangatsangana*;  
367 Turner, 2006). The age of *Uruguaysuchus* from South America, however, is uncertain  
368 (Soto *et al.*, 2011) and precludes defining the mid-Cretaceous extinction of  
369 uruguaysuchids in South America more confidently.

370         The basal ziphosuchians follow a similar pattern of diversity as uruguaysuchids  
371 (Fig. 5.2), having a high initial diversification that is broadly distributed, but dominated  
372 by the “middle” Cretaceous African record (*Libycosuchus*, *Pakasuchus*, *Malawisuchus*).  
373 Subsequently basal ziphosuchians become extinct, except in Madagascar where a  
374 surviving lineage is represented by the aberrant *Simosuchus* in the latest Cretaceous  
375 (Buckley *et al.*, 2000; Turner and Sertich, 2010).

376         Peirosaurids (and closely related forms) also have their initial diversity in the  
377 Aptian and through the “middle” Cretaceous, being recorded in South America  
378 (*Barcinosuchus*; Leardi and Pol, 2009) and Africa (*Hamadasuchus*, *Stolokrosuchus*,  
379 *Kaprosuchus*; Larsson and Gado, 2000; Larsson and Sues, 2007; Sereno and Larsson,  
380 2009). However, they differ slightly from the two previous groups in that they are  
381 recorded in South America throughout the rest of the Cretaceous, during the Turonian–



382 Santonian (*Lomasuchus*, *Gasparinisuchus*, *Montealtosuchus*; Gasparini *et al.*, 1991;  
383 Carvalho *et al.*, 2007; Martinelli *et al.*, 2012) and the latest Cretaceous (*Peirosaurus*,  
384 *Uberabasuchus*; Price 1955; Carvalho *et al.*, 2004). The latest Cretaceous diversity of  
385 the group is also present in Madagascar, contributing to their higher diversity at the end-  
386 Cretaceous in comparison with their initial peak of diversity in the Early Cretaceous  
387 (Fig. 5.2).

388           Advanced notosuchians (the group to which *Notosuchus* belongs) are  
389 exclusively known from South America and are virtually unknown prior to the  
390 Turonian–Santonian. The only pre-Turonian record is *Coringasuchus anisodontis* from  
391 the Cenomanian of Brazil (Kellner *et al.*, 2009), a taxon known from fragmentary  
392 remains and of uncertain affinities within the clade of advanced notosuchians (Pol *et al.*,  
393 2014). This group has a remarkable diversity during the Turonian–Santonian in South  
394 America (over half of the notosuchian taxic diversity known from this period of time;  
395 Fig. 5.2). This diversity is dominated by the numerous species of sphagesaurids known  
396 from the Adamantina Formation of Brazil (Pol *et al.*, 2014). After their diversity acme,  
397 advanced notosuchians are rare and the only known advanced notosuchian from the  
398 latest Cretaceous is *Labidiosuchus amicum* (Kellner *et al.*, 2011b), a taxon known from  
399 partial dentary remains from the Marilia Formation (Campanian–Maastrichtian) of  
400 Brazil. The precise age of this diversity peak is slightly uncertain as there are authors  
401 that propose the Adamantina Formation is younger in age than Turonian–Santonian (see  
402 below) and because two other advanced notosuchians have been found in units with  
403 poorly constrained ages (*e.g.*, Late Cretaceous) of Bolivia (*Yacararani*; Novas *et al.*,  
404 2009) and Argentina (*Notosuchus* n. sp.; Fiorelli *et al.*, 2014). Therefore the diversity  
405 peak of this group interpreted here as the Turonian–Santonian acme could be slightly

406 younger (toward the Campanian). As all other groups, advanced notosuchians become  
407 completely extinct by the end of the Cretaceous.

408         Baurusuchids are also known exclusively from South America and they are  
409 completely absent from the fossil record prior to the Turonian–Santonian (Fig. 5.2).  
410 Their sudden appearance occurs with high diversity levels, accounting for  
411 approximately 30% of the taxic diversity known from this period of time. As in the case  
412 of advanced notosuchians, this diversity is also dominated by the records from the  
413 Adamantina of Brazil (*Baurusuchus* spp., *Campinasuchus*, *Pissarachampsa*,  
414 *Gondwanasuchus*), with the addition some records from the Santonian (*sensu* Garrido,  
415 2010) Bajo de la Carpa Formation of Patagonia (Fig. 5.2). After their diversity peak,  
416 there are no definitive baurusuchids known in the fossil record. The two possible  
417 exceptions are *Pehuenchesuchus enderi* from Patagonia (Campanian *sensu* Garrido,  
418 2010) and *Pabwehshi pakistanensis* from Pakistan (Maastrichtian; Wilson *et al.*, 2001),  
419 but the former has uncertain affinities within Sebecosuchia (Pol *et al.*, 2014) and the  
420 latter has been retrieved as a peirosaurid by some phylogenetic analyses (*e.g.*, Larsson  
421 and Sues, 2007). Despite their possible survival until the end Cretaceous there are no  
422 remains of this clade after the K/Pg boundary.

## 423 **DISCUSSION**

424         The diversity patterns shown above reveal the complex dynamics of notosuchian  
425 evolution during the Cretaceous, which highlights the components across space of two  
426 successive diversification pulses followed by two distinct extinction events that shaped  
427 the diversity curves of this clade. Despite the implemented phylogenetic and sampling  
428 corrections, these increases and drops in diversity are undoubtedly affected by the  
429 vagaries of the fossil record. Here we discuss these four events considering first the  
430 radiations and then the extinction events.

431 ***Aptian Radiation***

432 As shown above the first pulse of diversification in Notosuchia involves the  
433 sudden appearance in the Aptian in the fossil record of three major clades,  
434 Uruguaysuchidae, Peirosauridae (and allies), and basal lineages of Ziphosuchia (Fig.  
435 5.2). These clades are the three most basal lineages of Notosuchia and their initial  
436 diversification implies the existence of multiple ghost lineages during the Early  
437 Cretaceous (Fig. 2), which led the proposal of this event as the Aptian radiation by Pol  
438 *et al.* (2014). A problematic point related to this diversification event is the almost  
439 exclusive absence of notosuchians during the earliest Cretaceous (Berriasian–  
440 Barremian), which hampers our understanding of the evolutionary dynamics of this  
441 event (Pol *et al.*, 2014). The absence of pre-Aptian notosuchians is most likely  
442 influenced by the overall scarce fossil record of continental crocodyliforms during the  
443 earliest Cretaceous, which contrasts with the denser sampling available for the Aptian–  
444 Albian (*e.g.*, eight notosuchian bearing formations). Such situations may create an  
445 artificial pattern of sudden radiation even when the diversification of these groups was  
446 much more gradual and scattered through time. The only evidence suggesting this  
447 indeed may be the case is *Amargasuchus minor* (Chiappe, 1988), known from a  
448 fragmentary maxillary found at the Puesto Antigüal Member of the La Amarga  
449 Formation (Barremian). *Amargasuchus* was originally described as a member of  
450 Trematochampsidae, a group of questioned validity but usually regarded as closely  
451 related to or nested within Peirosauridae (Gasparini *et al.*, 1991; Sertich and O’Connor,  
452 2014). Furthermore, Gasparini *et al.* (1991) noted similarities between this fragmentary  
453 form and the peirosaurid *Lomasuchus*. The putative existence of a peirosaurid, or even a  
454 taxon closely related to this clade, in the Barremian would push the initial split of the  
455 basal notosuchian lineages back to this stage. Furthermore, this would decouple the

456 diversification of peirosaurids from that of uruguaysuchids and basal ziphosuchians,  
457 therefore questioning the existence of an Aptian radiation event. New information of the  
458 earliest Cretaceous can easily influence current hypotheses on the initial diversification  
459 of Notosuchia, even if they are based on fragmentary material such as the case of the  
460 possible notosuchian *Amargasuchus*.

#### 461 ***Turonian–Santonian Radiation***

462         The major peak of notosuchian diversity is interpreted here as representing the  
463 Turonian–Santonian radiation (Fig. 4), and the diversity curves split by geography and  
464 subclades show this is largely formed by two South American groups: advanced  
465 notosuchians and baurusuchids (Fig. 5). The well-sampled pre-Turonian units of  
466 different regions of Gondwana, in which these two groups are absent, provide support  
467 for interpreting this peak of diversity as a true radiation event during the Late  
468 Cretaceous (Turner and Sertich, 2010; Pol *et al.*, 2014). As noted by several authors  
469 (*e.g.*, Montefeltro *et al.*, 2011; Pol *et al.*, 2014; Martinelli and Teixeira, 2015), there is  
470 some uncertainty related to the age of the Adamantina Formation, which provides over  
471 80% of the known taxic diversity of advanced notosuchians and baurusuchids. Such  
472 uncertainty may imply this radiation event occurred in South America during the  
473 Santonian–Campanian rather than during the Turonian–Santonian. Despite these  
474 uncertainties, it seems clear the existence of a remarkable radiation of baurusuchids and  
475 advanced notosuchians (especially sphagesaurids) that shaped dynamics of the  
476 terrestrial ecosystems in the middle Late Cretaceous in South America (*e.g.*, Godoy *et*  
477 *al.*, 2014), especially in warm and dry (or seasonal) environments (Carvalho *et al.*,  
478 2010).

479         Whereas the existence of this radiation in South America is robustly supported,  
480 its endemic nature to South America cannot be adequately tested by the currently

481 available fossil record. Notosuchian remains from other regions during the Turonian–  
482 Santonian are extremely scarce, partly because there are no fossiliferous units of this  
483 age in Africa, Madagascar, or other regions of Gondwana. Although not included in our  
484 analysis, there are fragmentary remains of alleged notosuchian affinities from Europe  
485 (Dalla Vecchia and Cau, 2011; Rabi and Sebök, 2015) but these most likely do not  
486 belong to the groups that radiated in South American during this time (*i.e.*, advanced  
487 notosuchians and baurusuchids). The absence of relevant fossil and rock record  
488 therefore precludes determining with certainty if advanced notosuchians or  
489 baurusuchids were present in other regions of Gondwana during the middle Late  
490 Cretaceous. Data from the latest Cretaceous (Campanian–Maastrichtian) of other  
491 regions of Gondwana could provide hints regarding this point, but the available  
492 information is inconclusive. On the one hand, the absence of advanced notosuchians or  
493 baurusuchids in the diverse crocodyliform fauna of the latest Cretaceous Maevarano  
494 Formation of Madagascar (Krause *et al.*, 2006) suggests the South American endemism  
495 of these two groups may be real, given that this unit records survival lineages of all  
496 other notosuchian clades (*e.g.*, uruguaysuchids, peirosaurids, basal ziphosuchians). On  
497 the other hand, if the possible baurusuchid affinities of *Pabwehshi* from the  
498 Maastrichtian of Pakistan are corroborated by more complete remains (*e.g.*, preserving  
499 the choanal region), it would significantly expand the geographic scope of this clade  
500 across Gondwana. New data and crocodyliform remains from the middle Late  
501 Cretaceous of Africa, Madagascar, and other regions of Gondwana will be critical for  
502 adequately testing the South American endemism of the major radiation in the history  
503 of Notosuchia.

504 ***Extinction patterns in Notosuchia***

505 **Campanian event.** The first marked drop in diversity in the history of Notosuchia is  
506 recorded at the beginning of the Campanian (Figs. 4–5) and is caused by the complete  
507 extinction of baurusuchids and the drastic decrease in diversity of advanced  
508 notosuchians in South America (Fig. 5). This decrease, at least in South America, seems  
509 to be a real extinction event given that other groups of crocodyliforms are recorded in  
510 the same geographic regions (*e.g.*, southern Brazil, northwestern Patagonia). The above-  
511 mentioned uncertainty regarding the age of the Adamantina Formation and its impact on  
512 the timing of the middle Late Cretaceous diversity peak also affects the timing of this  
513 extinction event. If this formation is indeed younger than Turonian–Santonian as  
514 proposed by some researchers (Gobbo-Rodrigues *et al.*, 1999; Fernandes and Coimbra,  
515 2000), this extinction event would have occurred later than the Campanian but before  
516 the end of the Cretaceous Period. From a stratigraphic perspective, and given the  
517 dominance of the Bauru Group in the notosuchian diversity curves, the extinction event  
518 is nonetheless placed at the transition between the Adamantina and the Marilia  
519 formations. The extent of this extinction event in other regions of Gondwana is largely  
520 unknown due to the above-mentioned lack of Turonian–Santonian crocodyliform  
521 record.

522 **K/Pg event.** Although the major decrease of notosuchian diversity occurred well before  
523 the end of the Cretaceous Period, the K/Pg mass extinction event certainly affected  
524 notosuchians. The five groups of Cretaceous notosuchians analyzed here (with the  
525 possible exception of Baurusuchidae) were still present during the latest Cretaceous  
526 (Fig. 5.2) but became completely extinct by the end of the Mesozoic. The only  
527 notosuchians that survive this mass extinction event are sebecids (and related forms  
528 recorded in the Paleogene of Europe and Africa; Buffetaut, 1989; Ortega *et al.*, 1996;  
529 Ortega, 2004). This group has been phylogenetically allied either to baurusuchids

530 (forming the clade Sebecosuchia; see Pol and Powell, 2011) or to peirosaurids (forming  
531 the clade Sebecia; see Larsson and Sues, 2007). Irrespective of their debated affinities,  
532 this distinct clade of notosuchians has its closest relatives in the Cretaceous and  
533 therefore must have been originated prior to the K/Pg boundary. This is the only  
534 notosuchian lineage that survived the mass extinction event (Gasparini, 1972, 1996;  
535 Buffetaut, 1982; Kellner *et al.*, 2014) and subsequently became abundant during the  
536 Paleogene, especially in South America (Fig. 5.1–2).

### 537 **CONCLUSIONS**

538           The analysis of notosuchian diversity patterns reveals four basic episodes that  
539 shaped the evolutionary dynamics of this group, involving two successive  
540 diversification events and two consecutive extinction events that wiped out the  
541 outstanding diversity of the group by the latest Cretaceous. The currently available  
542 fossil record indicates the first diversification pulse (Aptian radiation) was  
543 geographically widespread across Gondwana (and possibly other regions of the globe)  
544 and involved the basal lineages of Notosuchia (Uruguaysuchidae, Peirosauridae and  
545 allies, and basal forms of Ziphosuchia). However, the remarkably scarce record of pre-  
546 Aptian crocodyliforms suggests this may have not been a simultaneous event. In  
547 contrast, the second pulse of diversification during the middle Late Cretaceous (possibly  
548 Turonian–Santonian) is likely a true and outstanding radiation event (at least in South  
549 America) of the highly diverse advanced notosuchians and baurusuchids.

550           Two consecutive but distinct extinction events are inferred to occur during the  
551 latest Cretaceous (Campanian–Maastrichtian). The former of which records the almost  
552 complete disappearance of advanced notosuchians and baurusuchids, leaving a  
553 depauperated taxic diversity of notosuchians during the latest Cretaceous that were  
554 subsequently affected by the end-Cretaceous mass extinction.

555 Different regions of Gondwana have provided critical evidence for  
556 understanding the evolutionary pattern of Notosuchia at different periods of time during  
557 the Cretaceous. South America dominates the notosuchian fossil record and basically  
558 shapes the diversity curve during the entire Late Cretaceous. Most of what we currently  
559 know about notosuchian evolution and diversity would be just impossible to infer  
560 without the contribution of the South American fossil record. The African fossil record  
561 has been pivotal for understanding the initial diversification of the basal lineages of  
562 Notosuchia and shapes the diversity curves during the “middle” Cretaceous (Aptian–  
563 Cenomanian). Finally, the latest Cretaceous record of Madagascar is relevant as it  
564 shows the survival of lineages (*i.e.*, uruguaysuchids and basal ziphosuchians) that  
565 became extinct in other regions of Gondwana earlier during the Cretaceous.

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883

#### 884 **Figure captions**

885 **Figure 1.** Skull reconstruction of four groups of Cretaceous notosuchians. **1**,  
886 Uruguaysuchidae (*Araripesuchus gomesii*); **2**, Peirosauridae (*Hamadasuchus*  
887 *rebouliei*); **3**, Notosuchidae (*Notosuchus terrestris*); **4**, Baurusuchidae (*Baurusuchus*  
888 *salgadoensis*). Modified from Pol and Larsson (2007).

889

890 **Figure 2.** Number of notosuchian species discovered through time (blue curve). The pie  
891 charts show the relative geographical distribution of the known diversity in 1974, 1994,  
892 and 2014, classified for major landmasses. References: blue: South America, red:  
893 Africa, green: Madagascar; purple: other regions (China, Europe, Pakistan).

894

895 **Figure 3.** Calibrated phylogeny of Notosuchia based on Pol *et al.* (2014) and Leardi *et*  
896 *al.* (2015). P\* indicates the clade formed by Peirosauridae and allies (*i.e.*,  
897 Mahajangasuchidae).

898

899 **Figure 4.** Diversity curves of Notosuchia through time. **1**, Taxic diversity (dark grey)  
900 and phylogenetically corrected diversity counting ghost lineages (light grey), with  
901 vertical axis representing total number of species (taxic) or species plus ghost lineages  
902 (phylogenetic correction) per period of time. **2**, Taxic (dark brown) and  
903 phylogenetically corrected (light brown) diversity corrected by sampling of fossiliferous  
904 units, with vertical axis representing the taxic or phylogenetic diversity divided by the  
905 number of notosuchian bearing formations per unit of time.

906

907 **Figure 5.** Taxic diversity of Notosuchia split by **1**, geographical regions and **2**, different  
908 notosuchian groups across time. For each period of time the different contributions of  
909 each region or clade are on top of each other so that the sum equals the taxic diversity  
910 shown in Figure 4.1.