

1 **Until Panama do us part: new finds from the Pliocene of Ecuador provide insights into**  
2 **the origins of the extant requiem sharks *Carcharhinus acronotus* and *Nasolamia velox***

3

4 (Short title: *Carcharhinus acronotus* from the Pliocene of Ecuador)

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7 With 4 figures

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19

20 **Abstract**

21 The extant blacknose shark *Carcharhinus acronotus* is a small-sized, tropical to warm-  
22 temperate carcharhinid shark occurring along the western Atlantic coasts from North Carolina  
23 (USA) through the Gulf and Caribbean regions to southern Brazil. Here, we report on two  
24 carcharhinid teeth from lower Pliocene (4.07–3.76 Ma) strata of the Upper Onzole Formation

25 exposed in the vicinities of Camarones (northwestern Ecuador). These specimens are  
26 assigned to *C. acronotus*, of which they seemingly represent the first occurrence in the  
27 Pacific Ocean. The blacknose shark is currently regarded as the sister group of the whitenose  
28 shark *Nasolamia velox*, an idiosyncratic carcharhinid that currently inhabits the eastern  
29 Pacific coasts from Baja California (Mexico) to Peru; furthermore, the divergence between  
30 *C. acronotus* and *N. velox* has been recently estimated at about 3.7 Ma, which matches well  
31 the final phases of formation of the Isthmus of Panama. In light of these data, our Ecuadorian  
32 specimens might document an early Pliocene phase in which the newly originated *C.*  
33 *acronotus* occurred West of the then-fading Panamanian Seaway, possibly as a consequence  
34 of occasional dispersal through the latter; alternatively, they might represent the teeth of an as  
35 yet unnamed *C. acronotus*-like carcharhine from which *C. acronotus* and *N. velox* later arose  
36 by vicariance as the Isthmus of Panama rose. A survey of the fossil record of these two taxa  
37 does not falsify either hypothesis. Further research on the fossil chondrichthyans from the  
38 only partly investigated Cenozoic marine successions of Ecuador will hopefully shed new  
39 light on this issue and, more generally, on the role played by the closure of the Panamanian  
40 Seaway as a macroevolutionary trigger in the late Cenozoic marine realm.

41

#### 42 **Keywords**

43 Borbón Basin, Carcharhinidae, Elasmobranchii, evolution, Isthmus of Panama,  
44 palaeobiogeography, Panamanian Seaway, Upper Onzole Formation, vicariance, Zanclean

45 **1. Introduction**

46 The blacknose shark *Carcharhinus acronotus* (POEY, 1860) is a small (up to ca. 1.4 m in total  
47 body length) requiem shark (Elasmobranchii: Carcharhinidae) characterised by a moderately  
48 long and rounded snout, fairly large eyes, a black spot on the underside of the snout tip,  
49 oblique-cusped serrated teeth in both jaws, small pectoral fins, a small first dorsal and a  
50 moderately large second dorsal, and dusky or blackish markings on the second dorsal and  
51 upper caudal tip (GARRICK 1982; COMPAGNO 1984). This diminutive carcharhinid is known as  
52 a coastal, tropical to warm-temperate shark that mainly occurs over sandy and corally sea  
53 bottoms of the continental and insular shelves (MORGAN et al. 2009, and references therein).  
54 It occurs in the western Atlantic Ocean, from North Carolina (eastern USA) southward  
55 throughout the Great and Little Bahama Banks, the Caribbean Sea, west in the Gulf of  
56 Mexico to Louisiana (southern USA), and along the South American coast from Venezuela to  
57 off Rio de Janeiro (southeastern Brasil) (GARRICK 1982; COMPAGNO 1984). *Carcharhinus*  
58 *acronotus* is not an abundant species, and only occurs in remarkable numbers off western  
59 Florida and North Carolina (SCHWARTZ 1984, and references therein). As a consequence of it,  
60 our understanding of the biology of the blacknose shark is still relatively fragmentary, as  
61 fragmentary is also its fossil record, which to date is comprised of two occurrences – one  
62 Pliocene and one Pleistocene – from within the present-day range of this carcharhinid species  
63 (SCUDDER et al. 1995; CARRILLO-BRICEÑO et al. 2018).

64 The present paper reports on two carcharhinid teeth from the Pliocene portion of the  
65 Onzole Formation (Borbón Basin, northwestern Ecuador). Strong similarities are noted  
66 between these teeth and those of the extant blacknose shark *C. acronotus*. The  
67 palaeontological and palaeobiogeographic significance of our finds is then discussed with  
68 special regard to the quest for the evolutionary roots of a rather poorly known genus of

69 Carcharhinidae, *Nasolamia*, whose sole member known to date is the extant Pacific  
70 whitenose shark *Nasolamia velox* (GILBERT in JORDAN & EVERMANN, 1898).

71

## 72 **2. Geological and stratigraphic setting**

73 The Borbón Basin is one of the major Cenozoic forearc basins located along the Ecuadorian  
74 coast (MARCAILLOU & COLLOT 2008; HERNÁNDEZ et al. 2020, and references therein). Its fill is  
75 made up by a ~5 km-thick siliciclastic succession of deep-marine strata irregularly  
76 punctuated by minor intercalations of shallow-water sediments that record alternating  
77 episodes of subsidence and uplift producing substantial fluctuations of relative sea-level and  
78 numerous large-scale unconformities.

79 The Onzole Formation (BRISTOW & HOFFSTETTER 1977), spanning the Mio-Pliocene  
80 stratigraphic record of the Borbón Basin fill, overlies the Angostura Formation through an  
81 apparently conformable and transitional contact (CANTALAMESSA et al. 2007). It was  
82 subdivided by EVANS & WHITTAKER (1982) into two main units (namely, the Lower Onzole  
83 Formation and the Upper Onzole Formation) that are separated from each other by a  
84 prominent angular unconformity represented by a regional and complex erosional surface.  
85 The Lower Onzole Formation ranges between 300 and 500 m in thickness and is composed  
86 of outer neritic, silty mudstones with thin and rare sandstone beds. In light of the presence of  
87 *Neogloboquadrina acostaensis* (BLOW, 1959), its base is assigned to Zone N16 in the zonal  
88 scheme of BLOW (1969), and probably to Zone N16B (WHITTAKER 1988). The overlying  
89 Upper Onzole Formation, called the Esmeraldas Formation by HASSON & FISCHER (1986) and  
90 Lower Borbón member by HERNÁNDEZ et al. (2020), consists of 10 to 250 m thick, coarse- to  
91 fine-grained sandstones with pebbly lenses (the Súa Member) at the base, grading upward  
92 into about 1200 m of silty-dominated mudstones interbedded with minor sandstone layers of

93 the Upper Onzole Formation sensu stricto. In the west, the Upper Onzole Formation also  
94 includes about 300 m of resedimented sandstones and mudstones (the Estero Plátano  
95 Member). Based on the occurrence of *Globorotalia tumida* (BRADY, 1877), the Súa Member  
96 is assigned to Zone N18 or younger, whereas the minimum age for the Upper Onzole  
97 Formation is fixed at the early Zone N21 based on the cooccurrence of *Dentoglobigerina*  
98 *altispira* (CUSHMAN & JARVIS, 1936), *Globorotalia tosaensis* TAKAYANAGI & SAITO, 1962 and  
99 *Sphaeroidinellopsis* spp. (WHITTAKER 1988). A micropaleontological study of rock samples  
100 collected from Upper Onzole strata exposed along the coastal belt between Punta Galera and  
101 Camarones (HASSON & FISCHER 1986) suggested that they are of Pliocene age (and probably  
102 largely Zanclean), and that sediments of this unit were accumulated in upper bathyal water  
103 depths.

104 The two specimens documented in this study are part of a larger macrofaunal assemblage  
105 (mainly consisting of molluscs, fish otoliths and elasmobranch teeth) obtained from strata  
106 exposed along the banks of the Estero Camarones stream, in the vicinity of the Camarones  
107 village (LANDINI et al. 1991, in prep.). The foraminiferal assemblage recovered from these  
108 strata includes both planktonic and benthic microfossils, with numerous species being  
109 reminiscent of warm-water environmental conditions. LANDINI et al. (1991) regarded this  
110 assemblage as indicative of an age not younger than the Early Pliocene and suggested  
111 deposition within the Zone N19 of BLOW (1969) or about the *Globorotalia*  
112 *tumida/Sphaeroidinella dehiscens* Zones of JENKINS & ORR (1972). According to LANDINI et  
113 al. (1991), the genus *Pulleniatina* occurs throughout the sampled section with specimens  
114 showing a predominant dextral coiling direction. The preferential coiling direction of  
115 *Pulleniatina* populations switched from dominantly sinistral to dextral during the Pliocene at  
116 about 4.07 (WADE et al. 2011), which represents the maximum age of the foraminiferal

117 assemblage; the minimum age is in turn provided by the occurrence of *Globorotalia*  
118 *plesiotumida* (BANNER & BLOW 1967), which made its last appearance in the global ocean at  
119 about 3.76 Ma (WADE et al. 2011).

120 Paleobathymetric estimates are for the most part based on the depth-distributions of  
121 benthic foraminifera, otoliths and molluscs. The recorded fauna is typical of the bathyal zone,  
122 probably epi-bathyal, with shallow-water forms transported from the shelf by gravity flow  
123 mechanisms or by predators. The unconformity interposed between the Lower Onzole  
124 Formation and the Upper Onzole Formation is interpreted to record a regional-scale uplift  
125 phase that exposed the entire forearc area near the Miocene-to-Pliocene transition. By earliest  
126 Pliocene times, the uplift phase ceased and was followed by regional extension, which  
127 resulted in renewed subsidence, continual rise in relative sea level, and marine transgression,  
128 with initial deposition of the lowest division of the Lower Onzole Formation (the Súa  
129 Member) in a nearshore to mid-shelf depositional setting (CARNEVALE et al. 2011; DI CELMA  
130 et al. 2010), followed by rapid deepening of the continental shelf to bathyal depths and  
131 deposition of the overlying fine-grained turbidites (AALTO & MILLER 1999).

132

### 133 **3. Systematic palaeontology**

134 Chondrichthyes HUXLEY, 1880

135 Elasmobranchii BONAPARTE, 1838

136 Carcharhiniformes COMPAGNO, 1973

137 Carcharhinidae JORDAN & EVERMANN, 1896

138 *Carcharhinus* BLAINVILLE, 1816

139

140 *Carcharhinus acronotus* (POEY, 1860)

141 (Figure 2)

142

143 **Referred material:** Two upper anterolateral teeth, kept at Museo di Storia Naturale  
144 dell'Università di Pisa (=MSNUP) with accession numbers MSNUP I-16951 and MSNUP I-  
145 16952. These specimens have been recovered in 2020 by means of sieving and hand-picking  
146 from bulk sediment samples that were collected at the find locality in 2004 and have since  
147 been stored at Dipartimento di Scienze della Terra dell'Università di Pisa.

148 **Occurrence:** Lower Pliocene (4.07–3.76 Ma) marine deposits exposed in the vicinities of the  
149 village of Camarones, Esmeraldas Province, Ecuador (approximate geographic coordinates:  
150 0°59'34" N; 79°33'49" W). The sediments from which MSNUP I-16951 and MSNUP I-16952  
151 were collected belong to the Upper Onzole Formation of the Borbón Basin.

152 **Comparisons and identification:** MSNUP I-16951 and MSNUP I-16952 are  
153 morphologically reminiscent of teeth of the extant carcharhinid species *Carcharhinus*  
154 *acronotus* and *Nasolamia velox* by virtue of the following combination of characters: 1) size  
155 slightly sub-centimetric; 2) crown provided with an oblique, roughly triangular cusp; 3)  
156 mesial and distal cutting edges finely serrated, without lateral cusplets; 4) distal cutting edge  
157 distinctly notched and convex basally; 5) root bilobed, sub-straight (COMPAGNO & GARRICK  
158 1983; COMPAGNO 1984; VOIGT & WEBER 2011). The observation of a homogeneous serration  
159 throughout and, especially, the presence of a straight rather than convex mesial cutting edge  
160 (which is regarded as a diagnostic character of *N. velox*; COMPAGNO & GARRICK 1983) lead to  
161 attributing these teeth to *C. acronotus* (GARRICK 1982; VOIGT & WEBER 2011).

162

#### 163 **4. Discussion**

164 Relatively few studies have dealt with the Ecuadorian fossil record of fishes. As regards the

165 bony fishes, palaeontological investigations have mostly focused on a few remarkable otolith  
166 assemblages (BIANUCCI et al. 1993, 1997; LANDINI et al. 1991, 2002a, b; AGUILERA et al. 2011;  
167 CARNEVALE et al. 2011; SCHWARZHANS & AGUILERA 2013; AGUILERA et al. 2016). As regards  
168 the cartilaginous fishes, LONGBOTTOM (1979) was the first to report on a chondrichthyan  
169 assemblage from the Miocene portion of the Onzole Formation, whereas AGUILERA et al.  
170 (2011) and CARRILLO-BRICEÑO et al. (2014) documented the presence of additional Mio-  
171 Pleistocene taxa from the Angostura, Onzole and Jama formations. More recently, CARRILLO-  
172 BRICEÑO et al. (2018) have studied a few new specimens from the same units, whereas  
173 CARRILLO-BRICEÑO et al. (2020) have expanded on the elasmobranch diversity from the  
174 Oligo-Miocene Dos Bocas Formation. By introducing a carcharhinid form that has never  
175 been reported from Ecuador, the fossil teeth documented herein constitute a significant  
176 addition to the Ecuadorian fossil record of cartilaginous fishes.

177 As anticipated above, the fossil record of *Carcharhinus acronotus* is to date limited to two  
178 occurrences from the lower Pliocene of the Bocas del Toro archipelago of Atlantic Panama  
179 (CARRILLO-BRICEÑO et al. 2018; geological age after COATES et al. 2005), and the upper lower  
180 Pleistocene (Calabrian) of Florida, USA (SCUDDER et al. 1995) (Fig. 3). Both these records  
181 are based on teeth that were neither described nor figured. In addition, teeth and vertebrae  
182 referred to *C. acronotus* have been reported from several Holocene archaeological sites of  
183 Florida and southeastern Brasil (e.g., KOZUCH 1998; WALKER 2000; HUTCHINSON et al. 2016;  
184 LOPES et al. 2016; MENDES et al. 2018) (Fig. 3). All these occurrences come from within the  
185 present-day range of *C. acronotus*, which largely corresponds to the equatorial and tropical  
186 coastal waters of the western Atlantic Ocean (GARRICK 1982; COMPAGNO 1984). Conversely,  
187 the herein reported Ecuadorian fossils seemingly comprise the first occurrence of *C.*  
188 *acronotus* from the Pacific realm as well as one of its geologically oldest records (Fig. 3).



189 COMPAGNO & GARRICK (1983) instituted the genus *Nasolamia* for the poorly known  
190 *Carcharhinus velox*. Found in the tropical and sub-tropical waters of the eastern Pacific  
191 Ocean (from Baja California, Mexico to Peru, including the Gulf of California; POLLOM et al.  
192 2020), this coastal shark could be regarded as a sort of amphi-Panamanian equivalent of *C.*  
193 *acronotus*. Indeed, while *Nasolamia velox* clearly differs from all other carcharhinids in  
194 having very wide, transversely oriented nostrils that are placed very close to each other along  
195 a narrow conical snout, as observed by COMPAGNO & GARRICK (1983),  
196 “in dentition, vertebral counts, and general external morphology *Nasolamia velox* seems  
197 closest to *Carcharhinus acronotus* (POEY, 1860).”  
198 A general comparison of the body outlines and dental designs of *C. acronotus* and the  
199 similarly sized *N. velox* is here proposed in Figure 4. With respect to *Nasolamia*, COMPAGNO  
200 (1984) further stated that  
201 “[i]ts only species, *Nasolamia velox*, is close to *Carcharhinus acronotus* in dentition and  
202 other features and may be a sister species to it by common ancestry. However, [*C.*]  
203 *acronotus* lacks the derived peculiarities of [*N.*] *velox* and is retained in *Carcharhinus*. The  
204 aggregation of odd rostral and cranial characters of *N. velox* is reminiscent of incipient  
205 stages of the teratogenic continuum of cyclopia in vertebrates. It is tempting to speculate  
206 that *Nasolamia* is derived from an [*C.*] *acronotus*-like ancestry in *Carcharhinus* by  
207 stabilization of a complex of incipient, cyclopic abnormalities that gave *N. velox* a  
208 selective advantage over normal [*C.*] *acronotus*-like *Carcharhinus*.”  
209 A sister group relationship between *C. acronotus* and *N. velox* has recently been supported by  
210 NAYLOR et al. (2012) and subsequently detected by the time-calibrated molecular  
211 phylogenetic analysis performed by SORENSON et al. (2013), who also proposed a divergence  
212 date estimate of ca. 3.7 Ma (with a confidence interval of ca. 7.2–0.9 Ma) for these two taxa.

213 This is very suggestive of a vicariance event due to the rise of the Isthmus of Panama and the  
214 consequent separation of the eastern Pacific and western Atlantic marine equatorial biotas.  
215 The exact timing of the definitive closure of the Panamanian Seaway is at present a debated  
216 topic, having been alternatively estimated at 2.8 Ma (e.g., O'DEA et al. 2017), ca. 3 Ma (e.g.,  
217 COATES & STALLARD 2013), or not later than 3.5 Ma (e.g., JARAMILLO 2018). Regardless for  
218 these uncertainties, across the Panama region, the number of diverging marine species  
219 peaked after ca. 4 Ma (O'DEA et al. 2017), at a time when salinity and carbonate accumulation  
220 rates had already started to diverge (JARAMILLO et al. 2017). Before that time, some species of  
221 *Carcharhinus* [including the copper shark *Carcharhinus brachyurus* (GÜNTHER, 1870)] had  
222 indeed a trans-Panamanian distribution that was subsequently lost with the eventual  
223 establishment of the Isthmus of Panama (LANDINI et al. in press).

224 In light of these considerations, the herein reported Ecuadorian fossils might document an  
225 early Pliocene phase in which the newly originated *C. acronotus* occurred West of the then-  
226 fading Panamanian Seaway, possibly as a consequence of occasional dispersal through the  
227 latter, which would have acted as a marine “filter bridge” (SIMPSON 1940). This interpretation  
228 would obviously imply a divergence date older than the geological age of the Camarones  
229 deposits (i.e., 4.07–3.76 Ma) for *C. acronotus* and *N. velox*. In this respect, it must be noted  
230 that vicariance events related to the rise of the Isthmus of Panama seem to have occurred in  
231 the marine realm as early as around 12 Ma (JARAMILLO et al. 2017, and references therein),  
232 whereas the confidence interval reported by SORENSON et al. (2013) for the *C. acronotus*–*N.*  
233 *velox* divergence extends back to ca. 7.2 Ma. Post-speciation, cross-Panamanian events of  
234 dispersal might have been possible until the final closure of the Isthmus of Panama, possibly  
235 resulting in the foundation of ephemeral populations of *C. acronotus* within the present-day  
236 range of *N. velox*. Indirect support to this hypothetical scenario might come from the

237 observation that teeth of *C. acronotus* are present in the lower Pliocene of Panama, i.e., at the  
238 margins of the purported filter bridge area (CARRILLO-BRICEÑO et al. 2018).

239 That said, some further considerations might suggest that our attribution of MSNUP I-  
240 16951 and MSNUP I-16952 to *C. acronotus*, though well supported by morphological  
241 observations, might be not univocal, thus leading to the elaboration of an alternative  
242 palaeobiogeographic scenario. Considering that i) the eastern Pacific fossil teeth described in  
243 the present work are dated to 4.07–3.76 Ma and ii) their morphology indicates the  
244 morphologically conservative *C. acronotus* rather than the more derived *N. velox*, these finds  
245 might represent the teeth of an as yet unnamed *C. acronotus*-like carcharhine from which *C.*  
246 *acronotus* and *N. velox* originated allopatrically due to the closure of the Panamanian Seaway  
247 around 3.7 Ma. In light of this hypothesis, the existence of such an ancient trans-Panamanian  
248 population would be witnessed not only by our Ecuadorian finds, but also by teeth consistent  
249 with *C. acronotus* from the lower Pliocene deposits of Atlantic Panama (CARRILLO-BRICEÑO  
250 et al. 2018). Whether or not such an hypothetical ancestral population should necessarily be  
251 assigned to another species compared to the less derived of its present-day descendants (in  
252 our case, *C. acronotus*) is a nomenclatural vexata quaestio that falls well beyond the scope of  
253 the present paper (e.g., BELL 1979; MEIER & WILLMANN 2000; WILEY & LIEBERMAN 2011).  
254 The persistence of ancestral sister species is commonly admitted, though somewhat  
255 implicitly, by most shark palaeontologists: for example, the purported latest Miocene origin  
256 of *Carcharodon* from within the radiation of *Cosmopolitodus* is not regarded as having  
257 implied the disappearance of the ancestral species (identified as either *Cosmopolitodus*  
258 *hastalis* or *Cosmopolitodus plicatilis*; CIONE et al. 2012; EHRET et al. 2012; KENT 2018),  
259 whose teeth have in turn been reported from several Pliocene (and even lower Pleistocene)  
260 localities worldwide (e.g., PURDY et al. 2001; MARSILI 2006; EBERSOLE et al. 2017). On the

261 other hand, this might partly reflect the fact that dealing solely with dental and dermal  
262 remains (which comprise the largest part of the fossil record of cartilaginous fishes) is not  
263 always sufficient for discriminating between different species; as a consequence of it, some  
264 binomial taxa of elasmobranchs that are based on fossil teeth (including the rostral “teeth” of  
265 pristid sawfishes) might indeed include different genera [e.g., *Cretolamna appendiculata*  
266 (AGASSIZ, 1835) and *Pristis lathamii* GALEOTTI, 1837; CAPPETTA 2012; CAPPETTA & CASE  
267 2016]. With respect to Carcharhinidae, some genera (e.g., *Scoliodon* and *Loxodon*) are hardly  
268 distinguishable on the basis of the teeth alone (CAPPETTA 2012), and some species of  
269 *Carcharhinus* (e.g., *C. brachyurus*) possess a more taxonomically diagnostic dentition than  
270 others (PURDY et al. 2001; MARSILI 2007). As far as our study is concerned, the Ecuadorian  
271 fossil teeth MSNUP I-16951 and MSNUP I-16952 have been identified phenetically as  
272 consistent with those of the extant blacknose shark; thus, in light of the morphological  
273 species concept that sustains the palaeontological research on shark teeth (e.g., WARD &  
274 BONAVIA 2001; TAPANILA & PRUITT 2019), they could be assigned straightforward to *C.*  
275 *acronotus*. That said, considering also the minor differences observed between the dentitions  
276 of *N. velox* and *C. acronotus*, teeth that compare favourably with those of the blacknose shark  
277 (rather than with the morphologically more derived whitenose shark) are expectable in the  
278 putative carcharhine that is ancestral to both the aforementioned extant species. Thus,  
279 MSNUP I-16951 and MSNUP I-16952 could be conservatively regarded as belonging to  
280 either the extant blacknose shark or the most recent common ancestor of the latter and *N.*  
281 *velox*. Whether or not this hypothetical ancestor and the living *C. acronotus* might comprise a  
282 single biological entity pertains to the controversy over the persistence of ancestral species,  
283 and as such, it remains an open philosophical question (WILEY & MAIDEN 2000) of only  
284 marginal relevance to the very issue dealt with herein.

285 How does the palaeontological data regarding *Nasolamia* fit the above hypotheses?  
286 Among the extant shark genera, *Nasolamia* is known for its particularly 'shallow'  
287 chronostratigraphic range (PAILLARD et al. in press). The fossil record of Pacific South  
288 America seemingly includes two occurrences of *N. velox*, from Baja California, northwestern  
289 Mexico (GONZÁLES-BARBA & THIES 2000) and northwestern Peru (GONZÁLES-BARBA &  
290 MARTÍNEZ 2010), respectively (Fig. 3). The Mexican occurrence was referred to the Pliocene  
291 (Zanclean or Piacenzian) by GONZÁLES-BARBA & THIES (2000); however, it lacks precise  
292 stratigraphic whereabouts and is apparently not featured in the recent review of the Mexican  
293 fossil record of fishes provided by GONZÁLEZ-RODRÍGUEZ et al. (2013). The Peruvian  
294 occurrence was reported as originating from strata of the Miramar Formation exposed at the  
295 localities of Cerro Amarillo and Chuchal (GONZÁLES-BARBA & THIES 2000). GONZÁLES-  
296 BARBA & THIES (2000) did not provide detailed stratigraphic information about these sites,  
297 reporting instead the chronostratigraphic range of the Miramar Formation as “upper Miocene  
298 – lower Pliocene(?)”. A maximum Piacenzian age for the shark tooth-bearing Cerro Amarillo  
299 and Chuchal exposures is supported by the occurrence of teeth of the white shark  
300 *Carcharodon carcharias*, which is believed to have originated in earliest Pliocene times from  
301 the late Miocene species *Carcharodon hubbelli* (EHRET et al. 2012). Furthermore, elsewhere  
302 along the northwestern coast of Peru, the Miramar Formation is thought to include an upper  
303 portion that is younger than 3.4 Ma (TIMOTEO et al. 2017), that is, younger than both the early  
304 Pliocene Ecuadorian finds (dated to 4.07–3.76 Ma) and the ca. 3.7 Ma age estimate reported  
305 by SORENSON et al. (2013) for the divergence between *C. acronotus* and *N. velox*. In light of  
306 these considerations, whereas the presence of the whitenose shark in some Pliocene deposits  
307 of Mexico and Peru can be regarded as ascertained, there is no strong suggestion of the  
308 presence of *N. velox* in the tropical and sub-tropical waters of the eastern Pacific Ocean or

309 elsewhere before 3.8-3.7 Ma.

310

## 311 **5. Conclusions**

312 We reported on two carcharhinid teeth, assigned to the blacknose shark *Carcharhinus*  
313 *acronotus*, from lower Pliocene (4.07–3.76 Ma) strata of the Upper Onzole Formation  
314 exposed in the vicinities of Camarones (northwestern Ecuador). Nowadays, *C. acronotus* is  
315 regarded as the sister group of *Nasolamia velox*, an idiosyncratic Pacific carcharhinid (known  
316 as the whitenose shark) whose origin has been recently approximated at about 3.7 Ma (an age  
317 estimate that matches well the final phases of closure of the Panamanian Seaway). In light of  
318 these data, the fossil specimens from Camarones might testify to an early Pliocene phase in  
319 which the newly originated *C. acronotus* occurred on the Pacific side of the then-fading  
320 Panamanian Seaway, likely as a consequence of occasional dispersal through the latter;  
321 alternatively, they might document an as yet unnamed *C. acronotus*-like carcharhine from  
322 which *C. acronotus* and *N. velox* later arose allopatrically due to the eventual closure of the  
323 Panamanian Seaway. An overview of the fossil record of *C. acronotus* and *N. velox* does not  
324 falsify either hypothesis. Furthermore, our results encourage the quest for fossil  
325 chondrichthyans from the still underinvestigated Cenozoic marine successions of Ecuador,  
326 suggesting that such an effort might shed new light on the role of the closure of the  
327 Panamanian Seaway as a macroevolutionary trigger in the late Cenozoic marine realm.

328

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334

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576 **Figure captions**

577

578 **Fig. 1.** Geographic and stratigraphic framework. A) Geographic location of the find locality  
579 (marked by a star) in northwestern Ecuador. B) Neogene litho- and chronostratigraphy of the  
580 sedimentary fill of the Borbón Basin of northwestern Ecuador, with the indication of the  
581 stratigraphic position of the deposits exposed at the find locality. Panel B modified from  
582 CARRILLO-BRICEÑO et al. (2014), after an original sketch by LANDAU et al. (2012).

583

584 **Fig. 2.** MSNUP I-16951 and MSNUP I-16952, teeth of *Carcharhinus acronotus* from the  
585 lower Pliocene Upper Onzole strata exposed in the vicinities of Camarones (northwestern  
586 Ecuador). A,B) MSNUP I-16951, upper left anterolateral tooth in A) lingual and B) labial  
587 views. C,D) MSNUP I-16952, upper right anterolateral tooth in A) lingual and B) labial  
588 views.

589

590 **Fig. 3.** General comparison of the body outlines (A,B) and dental designs (C,D) of  
591 *Carcharhinus acronotus* and *Nasolamia velox*. A,C) *Carcharhinus acronotus*, after GARRICK  
592 (1982). B,D) *Nasolamia velox*, after COMPAGNO & GARRICK (1983). The teeth in panels C and  
593 D are upper right anterolaterals from comparable tooth positions; they are depicted in labial  
594 view.

595

596 **Fig. 4.** *Carcharhinus acronotus* and *Nasolamia velox*, present-day ranges and Neogene–  
597 Quaternary records. The extant distributions are from wikimedia.org, after the original maps  
598 by COMPAGNO (1984). The data sources for the Neogene–Quaternary records are as follows:  
599 1–this work; 2–CARRILLO-BRICEÑO et al. (2018); 3–SCUDDER et al. (1995); 4–KOZUCH (1998);

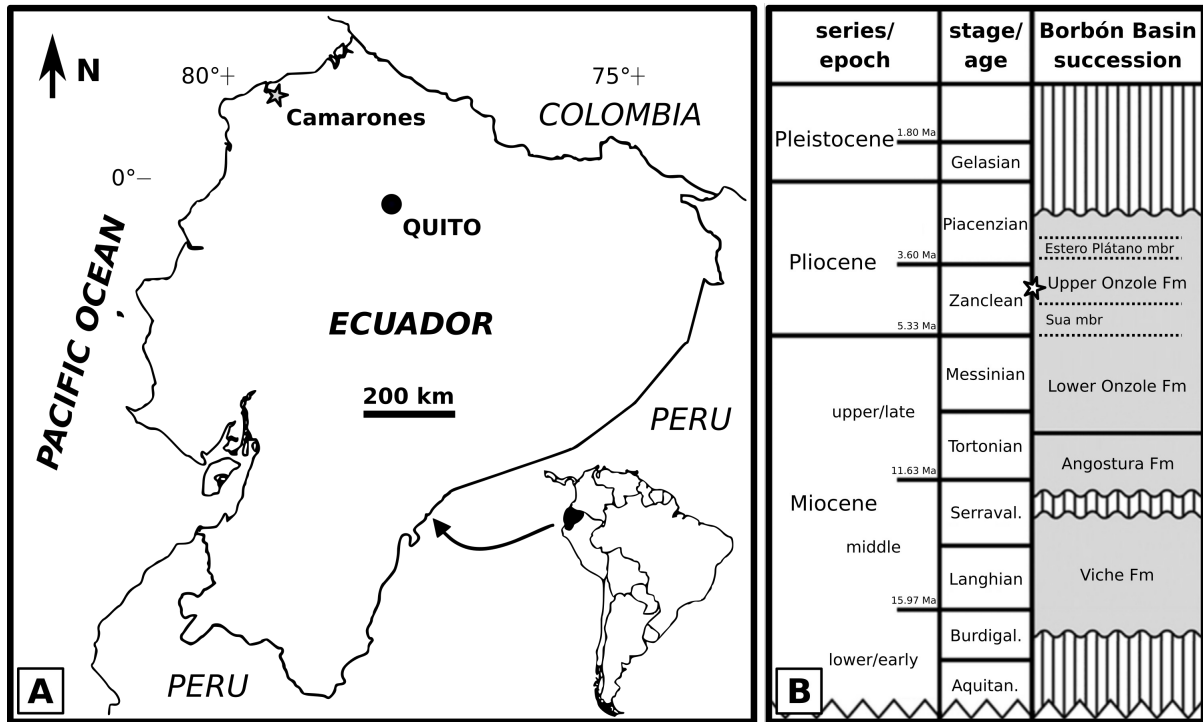
600 5–WALKER (2000); 6–HUTCHINSON et al., 2016; 7–LOPES et al. (2016); 8–MENDES et al.  
601 (2018); 9–GONZÁLES-BARBA & MARTÍNEZ (2010); 10–GONZÁLES-BARBA & THIES (2000). Note  
602 that many of the fossil and subfossil records are based on remains that were neither figured  
603 nor described, and some of them have tenuous provenance (see the main text for further  
604 details).

605 **Figures**

606

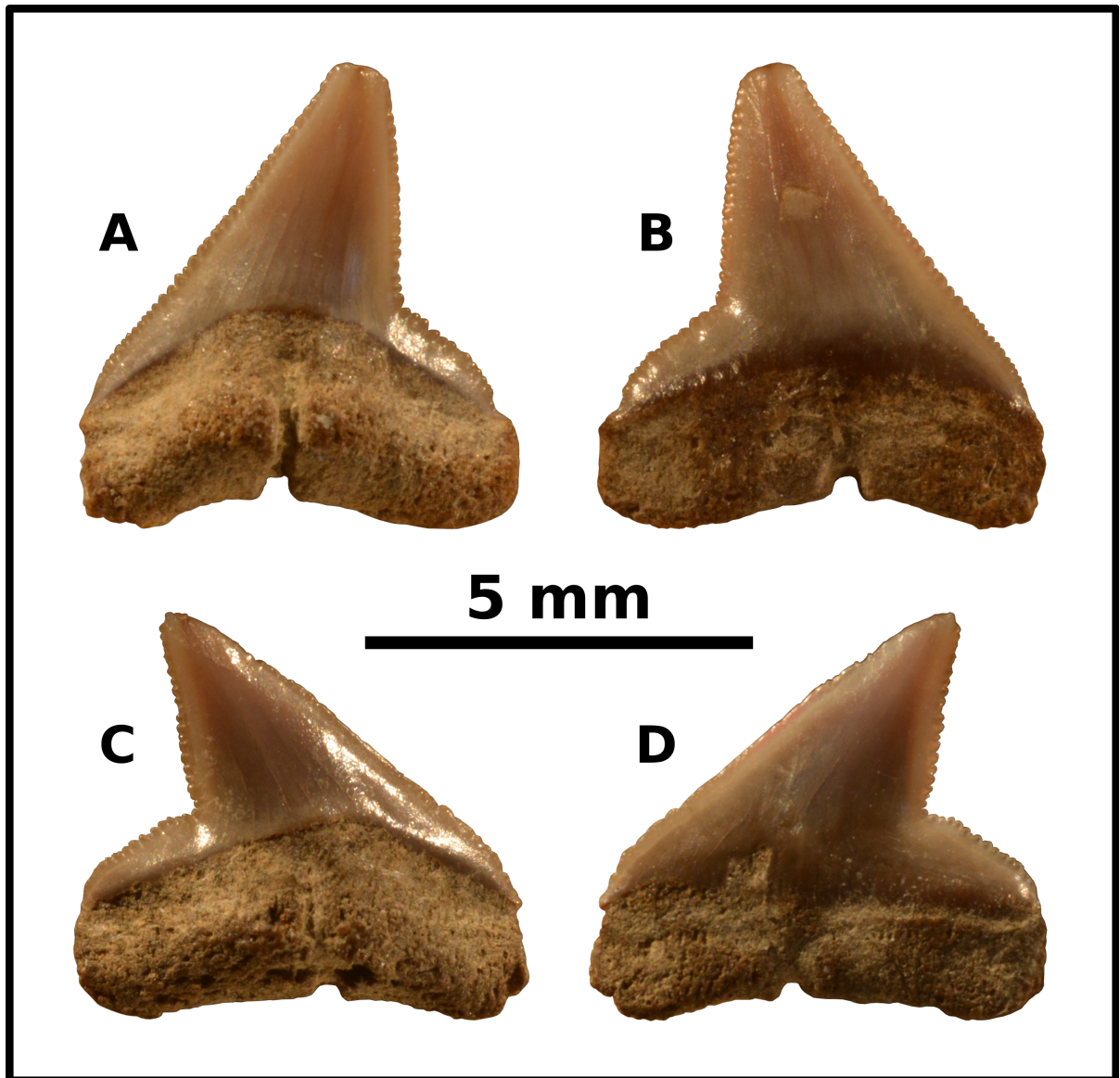
607 **Figure 1**

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609 **Figure 2**

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611 **Figure 3**

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