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## Lamniform sharks from the Cenomanian (Upper Cretaceous) of Venezuela

Guinot, Guillaume ; Carrillo-Briceño, Jorge

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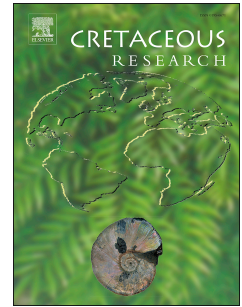
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**Lamniform sharks from the Cenomanian (Upper Cretaceous) of Venezuela**Guillaume GUINOT<sup>a\*</sup>, Jorge CARRILLO-BRICEÑO<sup>b</sup>

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21 **Abstract.** Sampling of Cenomanian fossil-rich horizons within the La Luna Formation of two localities  
22 in the Zulia and Trujillo states (northern Venezuela) yielded numerous shark teeth belonging to  
23 various species within the order Lamniformes (Mackerel sharks). Twelve lamniform species were  
24 identified including three new species (*Squalicorax lalunaensis* sp. nov., *Squalicorax moodyi* sp. nov.,  
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31 Luna Sea but also possible connexions with the Western Interior Seaway. One of the most striking  
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35 marine vertebrates that provided food resources.

36

37 **Keywords.** Chondrichthyes; Anacoracidae; La Luna Formation; South America; Upper Cretaceous.

## 38 1. Introduction

39 Mackerel sharks (Lamniformes) form a clade of mainly marine selachians represented today by  
40 fifteen species included within ten genera (Weigmann, 2016). Despite their relative low diversity,  
41 recent lamniforms display a wide range of marine habitats (from intertidal to bathypelagic zones), a  
42 large array of behaviours (slow-swimming benthopelagic to fast oceanic swimmers) and include a  
43 number of feeding strategies (top predators, filter feeders, opportunistic predators, scavengers).  
44 Analysis of the fossil record indicates that lamniform diversity was much higher in the past, especially  
45 in the Cretaceous-Paleogene interval (Cappetta, 2012; Guinot and Cavin, 2016). This, along with the  
46 large range of morphological disparity (Compagno, 1990) and body size (1 to 10 meters) of modern  
47 representatives of this clade suggest that Recent Mackerel sharks gather derived relic forms of a  
48 formerly flourishing group. One of the key events in the lamniform evolutionary history is their  
49 dramatic mid-Cretaceous (~125 - 90 Ma) diversification (Cappetta, 2012; Guinot et al., 2012; Guinot  
50 and Cavin, 2016; Underwood, 2006) that occurred relatively early after the first appearance of the  
51 group in the fossil record (Valanginian, Rees, 2005). This marked Aptian-Cenomanian radiation  
52 resulted in the rapid apparition of a number of modern and fossil lamniform clades showing a variety  
53 of specialisations and ecological characteristics. These include small nectobenthic predators that  
54 were comparable in size range, dental morphology, ecology and even gross general morphology with  
55 some modern Ground Sharks (Carcharhiniformes) (Siverson et al., 2007; Vullo et al., 2016). Following  
56 this mid-Cretaceous diversification, lamniforms became a major component of chondrichthyan  
57 faunas throughout the Late Cretaceous-Paleogene interval. The abundance and diversity of  
58 lamniform taxa since their mid-Cretaceous diversification suggest that their generic diversity is  
59 relatively well known in comparison to other chondrichthyan groups (Underwood et al., 2016).  
60 However, the Cretaceous lamniform species diversity remains difficult to assess due to poor  
61 definition/illustration of many nominal species and difficulties in assessing intraspecific  
62 morphological variations (Siverson et al., 2007; Siverson et al., 2015). A more general issue is that  
63 our perception of Cretaceous chondrichthyan diversity is mainly based on European, North African

64 and North American localities, whereas data from the southern hemisphere and particularly from  
65 South America is comparatively scarce.

66 The mid-Cretaceous chondrichthyan record in South America is based on a few isolated reports. In  
67 Brazil, the upper Aptian–lower Albian Santana Formation of the Araripe Basin yielded several  
68 articulated specimens of the batomorphs *Iansan beurleni* (Silva Santos, 1968) and *Stahlraja*  
69 *sertanensis* Brito, Leal and Gallo, 2013 and of the hybodont *Tribodus limae* Brito and Ferreira, 1989.  
70 Isolated rostral denticles of the sclerorhynchiform *Atlanticoprists equatorialis* Pereira and Medeiros,  
71 2008 were reported from the lower Cenomanian Alcântara Fm. The Peruvian record is restricted to  
72 the lamniform species *Priscusurus adruptodontus* Kriwet, 2006 from the Albian of northwestern Peru.  
73 Turonian chondrichthyans include *Ptychodus chappelli* Reinhart, 1951 (probably synonymous with *P.*  
74 *mammilaris* Agassiz, 1838, see Cappetta, 2006) and *Onchosaurus* species from Colombia (Parámo  
75 Fonseca, 1997), also reported from Ecuador (Dunkle, 1951). Fossil record of mid-Cretaceous  
76 chondrichthyans from Venezuela is no richer than elsewhere in South America and is restricted to  
77 the Cenomanian-Campanian of La Luna Formation. These reports include *Ptychodus atcoensis* Hamm,  
78 2009, probably from the Coniacian (Carrillo-Briceño and Lucas, 2013), “*Ptychodus decurrens*” Agassiz,  
79 1835 from the Cenomanian-Santonian (Carrillo-Briceño, 2009) and *Ptychodus cyclodontis* Mutter,  
80 Iturralde-Vinent and Carmona, 2005 reported as *Ptychodus* sp. from the Cenomanian-Santonian of La  
81 Luna Fm. (Carrillo-Briceño, 2009) and from an unknown locality (Venezuela or Colombia) tentatively  
82 assigned to La Luna Fm. (Brito and Janvier, 2002). Moody and Maisey (1994) signaled the presence of  
83 *Squalicorax* in the Cenomanian of La Luna Quarry but did not provide illustrations. The presence of  
84 *Squalicorax* from La Luna Quarry represents the only report of non-ptychodontid chondrichthyans  
85 from the mid-Cretaceous of Venezuela (Cenomanian of La Luna Fm.) and one of the two records of  
86 Cretaceous lamniforms from this region along with the Maastrichtian record of *Serratolamna serrata*  
87 from the Andes region (Carrillo-Briceño et al., 2008). Based on the fossil shark specimens of Moody  
88 and Maisey (1994) from the La Luna Quarry (Sierra de Perijá, Zulia state) and additional collected  
89 material from the Cordillera de Mérida (Trujillo state), this paper provides the first description of

90 lamniform sharks from the Cenomanian of Venezuela and adds to the knowledge of the mid-  
91 Cretaceous marine diversity in the northernmost part of South America.

92

## 93 **2. Geographical and geological Settings**

94 The specimens described here come from two different quarry outcrops in western Venezuela (Fig.  
95 1), where rocks of La Luna Formation are extracted for cement production. One of the locations is  
96 the quarry exploited by Cementos Andinos company and located in the Andes range (Cordillera de  
97 Mérida), east of Lake Maracaibo, 10 km to the northeast of Monay city (9° 36.57' 06" N, 70° 24' 14"  
98 W), Candelaria Municipality, Trujillo estate (Chejendé region, Figure 2). The second outcrop is located  
99 in La Luna Quarry, Sierra de Perijá, west of Maracaibo Lake, approximately 20 km to the northwest of  
100 Villa del Rosario town (10° 22' 21" N, 72° 27' 45" W), Rosario de Perijá Municipality, Zulia estate  
101 (Maracaibo Basin, Fig. 2).

102 La Luna Formation (Upper Cretaceous) is characterized by a sequence of marine rocks deposited  
103 under anoxic-dysoxic conditions along the passive margin of northern South America during the  
104 Cenomanian-Campanian (Zapata et al., 2003) and is the most prolific petroleum source rock in  
105 western Venezuela and part of eastern Colombia (Tribovillard et al., 1991; Zapata et al., 2003;  
106 Zumberge, 1984). La Luna Formation is characterized by alternating black or dark-gray limestones  
107 and organic calcareous shales, where calcareous concretions are abundant (Davis et al., 1999; Juana  
108 et al., 1980; Tribovillard et al., 1991) and reaching in some cases very large sizes (e.g. Albino et al.  
109 2016, fig. 3). The unit has been subdivided by Renz (1959) into three members exposed in the  
110 southeast of the Maracaibo basin (Lara and Trujillo states, Cordillera de Mérida): the lower, La  
111 Aguada Member (~ 60 m thick of a dense dark-grey limestones and black shales); the middle,  
112 Chejendé Member (~ 80 m thick of black shales and marls); and the upper, Timbetes Member (~ 90  
113 m thick of laminated limestones and shales).

114 The fossiliferous outcrop of the Cementos Andinos Quarry belongs to the Aguada Member (Fig. 2)  
115 and is characterized by dense dark-grey limestones of up to ~ 60-70 cm thick, intercalated with  
116 compact and laminated black/dark-grey shales. The material reported here was collected from  
117 successive black shale horizons in association with ichnofossils, molluscs (bivalves, gastropods and  
118 cephalopods), bony fishes (Carrillo-Briceño et al., 2012) and marine squamate remains (Albino et al.,  
119 2016). For more details about the stratigraphy of the Cementos Andinos Quarry see Albino et al.  
120 (2016).

121 Specimens from La Luna Quarry were collected from organic calcareous layers made of thin  
122 alternations of compact and light brown siliceous-rich platy limestones and darker shales in the  
123 lowest part of the exposed section in the La Luna Formation, just above the contact with the  
124 underlying Maraca Formation of the Cogollo Group (Moody and Maisey, 1994, p. 2). Shark teeth  
125 were found in association with abundant and mostly disarticulated bony fish remains. A preliminary  
126 report on fossil fishes from the La Luna Quarry was made by Moody and Maisey (1994) who  
127 mentioned one shark taxon (*Squalicorax* sp.) and various osteichthyans (enchodontids,  
128 *Belonostomus*, *Bananogmius* and unidentified teleost scales and bones). A Cenomanian age was  
129 proposed for rocks of La Luna Formation overlaying the Maraca Formation in the Maracaibo Basin  
130 (e.g. Juana et al., 1980, fig. IV-12; Dot et al., 2015, fig. 4). However, other authors (Renz, 1982, fig. 4;  
131 Erlich et al., 1999, figs. 3-4) suggested the existence of a regional hiatus in the Sierra de Perijá at the  
132 base of La Luna Formation where most of the Cenomanian is lacking. Considering the Sierra de Perijá  
133 section suggested by Erlich et al. (1999), the basal section of La Luna Formation in La Luna Quarry  
134 could correspond to a late Cenomanian age.

135

### 136 3. Material and Methods

137 Specimens from La Luna Quarry were surface-collected in the 90s by paleontologist John M. Moody  
138 and other members and collaborators of the Museo de Biología de La Universidad del Zulia

139 Maracaibo, Zulia estate. Surface-collected specimens were extracted from the sediment both  
140 chemically (3% formic acid) and mechanically. About 2 Kg of rock were subsequently bulk-collected  
141 by one of us (JDCB.) from the fossil-rich horizon, processed in 7.5% formic acid and sieved down to  
142 300  $\mu\text{m}$  mesh. This yielded abundant disarticulated osteichthyan microremains but no  
143 chondrichthyans. Selachian specimens are well preserved and show no signs of abrasion but nearly  
144 all specimens are weakly fractured.

145 Specimens from Cementos Andinos Quarry were surface-collected (between 2013 and 2016) by one  
146 of us (JDCB) with the collaboration of the personal of this institution. All specimens are heavily  
147 fractured due to strong sediment compaction and some teeth show weak degree of abrasion.

148 Surface-collected specimens were extracted from the sediment both chemically (3% formic acid) and  
149 mechanically. About 3 Kg of rock were processed in 7.5% formic acid and sieved down to 300  $\mu\text{m}$   
150 mesh. This yielded some small selachian and osteichthyan tooth fragments and distorted  
151 osteichthyan vertebrae.

152 Specimens from Zulia state (La Luna Quarry) are housed in the collections of the Museo de Biología  
153 de La Universidad del Zulia Maracaibo, Zulia estate (with the acronym MBLUZ-P) and specimens from  
154 Trujillo state (Cementos Andinos Quarry) are housed in the paleontological collection of the Alcaldía  
155 Bolivariana de Urumaco, Venezuela (with the acronym AMU-CURS).

156

#### 157 **4. Systematic Palaeontology**

158 The terminology and systematic framework used here largely follow those of Cappetta (2012).

159

160

Class Chondrichthyes Huxley, 1880

161

Subclass Elasmobranchii Bonaparte, 1838

162 Cohort Euselachii Hay, 1902

163 Subcohort Neoselachii Compagno, 1977

164 Order Lamniformes Berg, 1958

165 Family Anacoracidae Casier, 1947

166 Genus *Nanocorax* Cappetta, 2012

167 cf. *Nanocorax* sp.

168 Figures 3A-B

169

170 *Material.* One tooth (AMU-CURS-906) from Cementos Andinos quarry (Trujillo state).

171

172 *Description.* This small-sized tooth is slightly higher (5.5 mm) than wide (4.5 mm) and occupies an  
173 anterolateral jaw position. The main cusp is bent to the posterior, thin and elongate. The lingual face  
174 of the main cusp is convex while the labial face is flat with the exception of a light median bulge at  
175 the base of the crown. The mesial cutting edge is slightly concave whereas the distal one is straight. A  
176 low mesial heel is present, poorly individualised from the main cusp and oblique. The distal heel is  
177 nearly horizontal. Both mesial and distal heels have abrupt and vertical lateral edges. The cutting  
178 edges are smooth and continuous from the apex of the main cusp until the lateral edges of the heels.  
179 A rather well-developed lingual neck marks the limit between the crown and root. The root is high  
180 and stubby with short, thick and basally-oriented lobes. The distal root lobe is more developed and  
181 narrower than the distal one. The labial root face exhibits a very slight bulge that overhangs a  
182 depressed median region where several large foramina open. A central and two additional foramina  
183 are present on the basal root face.

184

185 *Remarks.* The morphology of this tooth including nearly flat labial face, smooth cutting edges and  
186 heels, stubby root with short lobes is rather uncommon among anacoracid species. The root – and to  
187 a lesser extent the crown – morphologies bear resemblances with those of some *Nanocorax* teeth, in  
188 particular lateral teeth of *Nanocorax crassus* (Cappetta and Case, 1999) from the upper Cenomanian  
189 Woodbine Formation of Texas (Cappetta and Case, 1999, 1975; Welton and Farish, 1993). However,  
190 lateral teeth of *N. crassus* have a more convex labial crown face, more lingually oriented main cusp,  
191 less differentiated mesial heel and more developed mesial cutting edge. *Nanocorax microserratodon*  
192 (Shimada, 2008) described from the ?Coniacian of Kansas and also known from the Santonian to  
193 Campanian of England, France, Belgium and Morocco (see Guinot et al., 2013) is the other nominal  
194 *Nanocorax* species known so far. Teeth of *N. microserratodon* differ from the Venezuelan tooth in  
195 having a wider main cusp with a typical mesiodistal twisting, small serrations unevenly present on  
196 main cusp and heels, more labio-lingually developed crown and root, weak demarcation between  
197 main cusp and mesial heel and stronger labial crown bulge. More material is needed to better assess  
198 the systematic attribution of the Venezuelan specimen, especially considering the heterodonty of  
199 some *Nanocorax* species.

200

201 Genus *Squalicorax* Whitley, 1939202 *Squalicorax moodyi* sp. nov.

203 Figures 3C-H

204

205 *Derivation of name.* The species is named in honour of John M. Moody, who left a valuable legacy in  
206 the study of Mesozoic vertebrate faunas from Venezuela.

207

208 *Holotype.* MBLUZ P-432-C.



209

210 *Material.* Four teeth (MBLUZ P-430, MBLUZ P-432-C, MBLUZ P-432-D and MBLUZ P-881-B) from La  
211 Luna quarry (Zulia state).

212

213 *Type stratum.* Organic calcareous limestone/shales in the lowest part of the La Luna Formation, just  
214 above the contact with the underlying Maraca Formation of the Cogollo Group (see Moody and  
215 Maisey, 1994).

216

217 *Diagnosis.* Anacoracid shark with small teeth not exceeding 8 mm in both width and height. Gradient  
218 monognathic heterodonty. Main cusp triangular, rather wide and inclined distally; strongly convex  
219 lingual crown face; wide lingual neck. No differentiated mesial heel. Distal heel low, convex and  
220 oblique. Apex of main cusp occasionally extends slightly beyond the distal edge of the heel. Cutting  
221 edges and heels serrated; serrations taper near apex and lateral extremities of heels. Basal edge of  
222 labial crown face, scalloped, strongly concave with marked bulge. Root lobes well developed,  
223 separated by deep concavity of basal root edge. Mesial root lobe thin with sharp extremity; distal  
224 lobe wider with rounded extremity. Concave mesial and distal root edges.

225

226 *Description.* Teeth of anteriormost position are slightly higher (8 mm) than wide (6 mm), strongly  
227 mesio-distally compressed and asymmetrical. The triangular main cusp is high and bent distally with  
228 a strongly convex labial face and a flat labial face. The apex of the main cusp is sharp and slightly bent  
229 labially. The mesial cutting edge of the main cusp is convex and connect to a very low, poorly  
230 individualized and strongly oblique mesial heel. The distal cutting edge of the main cusp is slightly  
231 concave in its median region and is separated from the distal heel by a notch. The distal heel is rather  
232 low, convex and moderately oblique. The lateral extremities of both the mesial and distal heels

233 terminate in a thin enamelled blade that is supported by a narrow root protuberance and oriented  
234 labially. A broad lingual neck is present in the basal region of the crown. The basal edge of the labial  
235 crown face exhibits a strong triangular concavity in its median region with a marked bulge that  
236 overhangs the root. Root foramina pierce the enamelled bulge, which confers a scalloped aspect to  
237 the bulge. The labial marginal areas of the basal crown face are flat but oriented labially, whereas the  
238 labial face of the main cusp is vertical. The cutting edges and heels have small and rather regular  
239 serration that diminish in size and taper toward the lateral edge of the heels and near the apex of  
240 the main cusp. The root is bilobate and mesio-distally compressed. The root lobes are well-developed  
241 and separated by a deep and wide concavity of the basal root edge. The lingual root face exhibits a  
242 wide and poorly individualized lingual protuberance that is pierced by a wide nutritive foramen along  
243 with other smaller foramina. Additional rather wide foramina are present on the basal root face of  
244 the lobe. The mesial root lobe is thin with a relatively acute extremity whereas the distal lobe is  
245 much wider with a rounded labial edge. Both the mesial and distal edges of the root are markedly  
246 concave in lingual view. The labial root face is low and bears a marked concavity in its central area.  
247 Large, oval-shaped foramina open near (in lateral regions) or on (in medial region) the crown/root  
248 edge. Teeth from more lateral positions become gradually wider than high with a strongly distally  
249 bent main cusp than can extend slightly beyond the distal edge of the heel. The mesial heel is not  
250 differentiated from the cutting edge of the main cusp whereas the distal heel is similar in shape to  
251 that of anterior teeth but less inclined to the base of the tooth. The mesial cutting edge is slightly  
252 convex whereas the distal one is nearly straight. The shape of the apex varies in teeth from  
253 anterolateral and lateral positions, being either bent to the commissure or erect, but in all teeth  
254 show some degree of labial inclination. The labial concavity of the basal crown edge is wider and less  
255 deep than in anterior teeth. The root is mesio-distally elongate with a flat basal face and a wider  
256 concavity of the basal root edge than in anterior teeth.

257

258 *Remarks.* By the morphology of their asymmetrical root lobes, wide and deep concavity of basal root  
259 edge, broad neck, labially inclined apex, regular serrations and strongly convex labial crown face,  
260 teeth of *Squalicorax moodyi* sp. nov. differ from those of other known mid-Cretaceous anacoracid  
261 species. Several nominal and unnamed small-sized anacoracid species are known from mid-  
262 Cretaceous deposits. The species *Squalicorax volgensis* (Glikman in Glikman and Shvazhaite, 1971)  
263 was described from the lower Cenomanian of Saratov Province (Russia) based on scarce and  
264 incomplete specimens but additional material from the type stratum was figured by Siverson et al.  
265 (2007). Teeth of this species differ from those of *Squalicorax moodyi* sp. nov. by the absence of  
266 serrations, more squared distal root lobe in basal view, absence of marked notches on the mesial and  
267 distal edges of the root and more marked notch between the main cusp and distal heel. *Squalicorax*  
268 *pawpawensis* Siverson, Lindgren and Kelley, 2007 is another mid-Cretaceous anacoracid with small-  
269 sized teeth known from the Albian of Texas. *Squalicorax pawpawensis* can be readily differentiated  
270 from the Venezuelan species by its lower rooted-teeth, more symmetrical root lobes, more  
271 irregularly present serrations, less deep concavity of basal root edge, more mesio-distally elongate  
272 root, absence of serration on distal heel and presence of small short vertical folds on basal edge of  
273 the labial crown face. Siverson (1996; p. 845, pl. 6) described specimens from the upper  
274 Cenomanian–lower Turonian Beedagong Claystone of Western Australia (now referred to as Haycock  
275 Marl) he attributed to *S. volgensis* but were later considered as a separated, unnamed species  
276 (Siverson et al., 2007). This taxon is probably conspecific or closely-related with the tooth reported as  
277 *S. volgensis* from the upper Cenomanian of Kansas (Shimada and Martin, 2008) and with some of the  
278 material published as *S. volgensis* by Cappetta and Case (1999; pl. 5, fig. 1) from the  
279 Turonian/Coniacian boundary of Texas, whereas the remaining of the specimens attributed to *S.*  
280 *volgensis* by Cappetta and Case (1999; pl. 4, figs. 7-8) from the Albian of Texas likely belong to *S.*  
281 *pawpawensis* (see Siverson et al., 2007). This unnamed taxon from Australia and USA differs from  
282 *Squalicorax moodyi* sp. nov. by its incipient serration occasionally present on the median region of  
283 the mesial cutting edge, higher and smooth distal heel, narrower neck and less marked – or absence

284 of – notches on the mesial and distal edges of the root. Teeth of *Squalicorax priscoserratus* Siverson,  
285 Lindgren and Kelley, 2007 from the upper Albian Pawpaw Formation in Texas differ from *Squalicorax*  
286 *moodyi* sp. nov. in having a more gracile and narrower main cusp with more marked and coarser  
287 serrations, more mesio-distally elongate and lower root and less marked concavity of the basal root  
288 edge. A specimen figured by Glikman and Shvazhaite (1971; pl. 1, fig. 10 non figs. 8-9) from the  
289 Cenomanian of Russia (Saratov Province) as *Palaeoanacorax obliquus* (Reuss, 1845) represents a  
290 *Squalicorax* tooth from an anterior position in labial view. Although the species *S. obliquus* is based  
291 on a few poorly preserved teeth (Reuss, 1845; pl. 4, figs. 1-3) (see below), the specimen from Russia  
292 strongly differs from the type material collected from Turonian of Czech Republic. The general  
293 morphology of the Russian specimen could, however, fall within the variation of *Squalicorax moodyi*  
294 sp. nov. but the lack of additional view and poor quality of the line-drawing preclude further  
295 taxonomic assignment. Welton and Farish (1993; p. 120) figured an anterolateral and a posterior  
296 tooth of a *Squalicorax* sp. from the Weno Formation (Albian) of Texas. Teeth of this unnamed species  
297 are comparable in size and general morphology to *Squalicorax moodyi* sp. nov. suggesting that these  
298 two taxon are closely-related. However, the Albian taxon displays morphological differences  
299 including more symmetrical root with less developed distal lobe, less regular and irregularly present  
300 serrations, marked notch between main cusp and distal heel, and presence of vertical folds below  
301 the lingual neck, that differ from the species described here. To date, *Squalicorax moodyi* sp. nov. is  
302 only known from the type locality.

303

304

*Squalicorax lalunaensis* sp. nov.

305

Figure 4

306

307 *Derivation of name.* After the La Luna Formation.

308

309 *Holotype*. AMU-CURS-897.

310

311 *Material*. Twelve teeth (AMU-CURS-894 to 905) from Cementos Andinos quarry (Trujillo state).

312

313 *Type stratum*. Laminated black/dark-grey shales in the basal part of the La Aguada Member, La Luna  
314 Formation.

315

316 *Diagnosis*. Anacoracid shark with small teeth (less than 9 mm high) showing moderate degree of  
317 gradient monognathic and possibly dignathic heterodonty. Main cusp biconvex and triangular with  
318 narrow apical region; main cusp moderately to strongly inclined to the commissure with convex  
319 mesial cutting edge. Mesial heel elongate and well separated from main cusp in lateral teeth. Distal  
320 heel convex and individualized from main cusp by marked notch. Moderately developed basal bulge  
321 at base of labial crown face; basal bulge restricted to median region of crown in anteriors and  
322 laterals, extended to marginal crown edges in posteriors. Cutting edges of heels and main cusp sharp  
323 and well developed, devoid of serrations. Lingual neck of moderate and sub-equal width from mesial  
324 to distal edges. Root bilobate; mesial root lobe thin and elongate; distal lobe short with blunt  
325 extremity, nearly squared in laterals and posteriors. Lingual root face short and convex in profile  
326 view. Marginal edges of root concave in labial/lingual views. Basal root face flat except in anteriors.  
327 Labial root face with foramina of variable shape below basal crown bulge.

328

329 *Description*. Teeth of this species are relatively small, not exceeding 9 mm, and show a moderate  
330 degree of gradient monognathic and possibly dignathic heterodonty. Anterior teeth are higher than

331 wide with a biconvex main cusp inclined to the commissure and sigmoid in lingual/labial views. The  
332 cutting edges of the main cusp and heels are sharp and rather developed. The mesial cutting edge of  
333 the main cusp is convex whereas the distal cutting edge is straight to slightly convex. The mesial heel  
334 is fairly low, short, oblique and separated from the main cusp by a slight concavity. The distal heel is  
335 convex and short, individualized from the main cusp by a notch. A moderately developed basal bulge  
336 is present at the base of the labial crown face but restricted to the median region of the crown,  
337 where it overhangs the root in occlusal view. The lingual crown face exhibits a neck of even width  
338 from its distal to medial extremities. The root is bilobate with labially oriented lobes separated by a  
339 V-shaped basal edge of variable depth and width according to tooth position. The mesial root lobe  
340 tend to be thinner and more elongate than the distal one that is short with a blunt extremity. The  
341 central areas of the basal root face is concave in profile view and bears a narrow and poorly marked  
342 lingual protuberance in anteriormost teeth where a central foramina is present. Other rather large  
343 foramina are present on the basal face of the lobes. The lingual face is fairly low and convex in profile  
344 view. A short vertical protuberance is present on the lingual face, below the lateral edge of the distal  
345 heel, which confers a concave outline of the distal root edge. The labial root face is flat in its marginal  
346 areas and concave in its center where several foramina of variable sizes are present immediately  
347 below the labial protuberance of the crown. Lateral teeth are wider than high and labio-lingually  
348 compressed with a strongly distally bent and sigmoid (in lingual view) main cusp. The mesial crown  
349 heel is high and elongate. The distal heel is well developed, sub-horizontal and separated from the  
350 main cusp by a deep notch. The basal bulge of the labial crown face is thin with an indented basal  
351 edge. The root is mesio-distally expanded with a flat basal face in profile view and concave mesial  
352 and distal edges in lingual/labial views. Posterior teeth have a sub-horizontal and sigmoid main cusp  
353 and vary from wider than high to as high as wide. The basal bulge of the labial crown face reaches  
354 the lateral margins of the crown. The distal root lobe has a nearly squared distal angle whereas the  
355 mesial one is sharp. Short vertical ridges are irregularly present on the labial bulge, below the distal  
356 heel. All teeth have smooth and sharp cutting edges.

357

358 *Remarks.* Teeth of *Squalicorax lalunaensis* sp. nov. differ from those of other anacoracid species by  
359 the combination of smooth and sharp cutting edges, sigmoid main cusp in labial-lingual view, distal  
360 heel separated from main cusp by marked notch, well-developed mesial heel in antero-laterals and  
361 laterals, bilobate and asymmetrical root with mesial root lobe thin and elongate and distal lobe short  
362 with blunt extremity (nearly squared in laterals and posteriors), and presence of short vertical folds  
363 on the labial crown face (below the distal heel). The morphology of posterior teeth (some rather  
364 large ones are mesio-distally short whereas other smaller ones are strongly mesio-distally elongate  
365 are morphologically closer to laterals) may suggest a dignathic heterodonty for this species. The  
366 species *Squalicorax intermedius* (Glikman in Glikman and Shvazhaite, 1971) (originally included in the  
367 genus *Palaeoanacorax*) was based on two poorly figured teeth from the Upper Turonian of Western  
368 Kazakhstan (Mangyshlak) but additional material from the type locality was subsequently attributed  
369 to this species (Glikman, 1980). One of the *S. intermedius* teeth (Glikman, 1980; pl. 12, fig. 6) is a  
370 latero-posterior tooth that exhibits comparable characters to those of *S. lalunaensis* sp. nov. but  
371 differs by its much more marked basal bulge of the labial crown face, wider main cusp, less  
372 differentiated mesial heel, less labio-lingually compressed aspect, and presence of serrations. Vullo  
373 et al. (2007) reported one tooth attributed to *Squalicorax* cf. *intermedius* that can be separated from  
374 those of the species described here by its strong serrations, wider and non-sigmoid main cusp and  
375 more rounded extremities of root lobes; along with its larger size. Glikman (1980, p. 99) erected the  
376 subspecies *Palaeoanacorax obliquus subserratus* based on the single latero-posterior tooth figured  
377 by Glikman (1964; p. 76, pl. 3, fig. 7) as *Palaeoanacorax falcatus* from the Cenomanian of Saratov  
378 (Russia). The cutting edges of this tooth appear smooth although the description reports irregular  
379 serrations on some specimens. In addition, the tooth figured by Glikman (1964) differs from those of  
380 *S. lalunaensis* sp. nov. by its shorter and wider main cusp, less marked convexity of the mesial cutting  
381 edge of main cusp and lower distal heel. *Squalicorax pamiricus* (Glikman in Glikman and Shvazhaite,  
382 1971) was described on the basis of two crown fragments from the lower Turonian (Mammites

383 nodosoides Zone) of Tajikistan but additional material from the type locality was figured by (Glikman,  
384 1980), both under the genus name *Palaeoanacorax*. Teeth of this species bear serrations and can  
385 further be separated from *S. lalunaensis* sp. nov. by their more symmetrical root, wider and less  
386 sigmoid main cusp in lingual/labial views. Teeth of *S. pawpawensis* can be readily separated from  
387 those of *S. lalunaensis* sp. nov. by their less individualised mesial heel, presence of serrated cutting  
388 edges, more flared labial extremities of root lobes and less concave basal bulge of labial crown face  
389 with more numerous and finer indentations. Teeth of a number of nominal and unnamed small-sized  
390 *Squalicorax* species with smooth or irregularly serrated cutting edges may resemble those of *S.*  
391 *lalunaensis* sp. nov. Species of the *S. volgensis* group (including *S. volgensis* and an unnamed species  
392 from the Cenomanian–Turonian of Australia, Texas and upper Cenomanian of Kansas) are  
393 represented by teeth of comparable morphology with those of *S. lalunaensis* sp. nov. and these  
394 taxon are likely closely-related. However, teeth of this group of taxa differ from those of the species  
395 described here by their less mesio-distally expanded laterals, presence of weak and uneven  
396 serrations (see Siverson et al., 2007), smooth labial crown face in posteriors and mesial heel less  
397 individualised from the main cusp. *Squalicorax* aff. *pawpawensis* reported from the Cenomanian of  
398 Canada (Underwood and Cumbaa, 2010) is another small-sized anacoracid that is close to the *S.*  
399 *volgensis* group. This material have a less elongate main cusp and higher mesial heel.

400

401 *Squalicorax* aff. *lalunaensis* sp. nov.

402

Figures 5A-B

403

404 *Material.* One tooth (AMU-CURS-907) from Cementos Andinos quarry (Trujillo state).

405



406 *Remarks.* The single (lateral) tooth referred to this taxon resembles those of *S. lalunaensis* sp. nov.  
407 but differs by its larger size, more robust general aspect, much wider main cusp with convex distal  
408 edge, wider lingual neck, less marked notch separating the main cusp from the distal heel, wider  
409 labial angle between the main cusp and basal root face, higher root and presence of marked and  
410 irregular serrations on the mesial and distal cutting edges of main cusp and distal heel.

411

412 *Squalicorax* sp. 1

413 Figures 5C-I

414

415 *Material.* Three teeth (MBLUZ P-15, MBLUZ P-430-B, MBLUZ P-430-C) from La Luna quarry (Zulia  
416 state).

417

418 *Description.* The anterior tooth of this taxon is higher (8.5 mm) than wide (7.5 mm). The crown is  
419 composed of a fairly low and wide triangular main cusp that is slightly bent to the commissure and  
420 low and short distal heel. The main cusp is strongly convex lingually and flat labially with straight  
421 mesial and distal cutting edges. A thick lingual neck is present. The labial crown face bears a strongly  
422 marked labial bulge in its W-shaped basal edge that protrudes labially. The labial bulge is strongly  
423 scalloped by numerous notches where nutritive foramina of variable size open. Faint thin and short  
424 vertical folds are present on the labial bulge. The root is high and stocky with short and wide root  
425 lobes and slightly concave lateral edges in lingual view. Lateral and latero-posterior teeth are as high  
426 as wide, reaching 12.5 mm in maximum size. The main cusp is moderately inclined to the posterior  
427 with straight to slightly convex mesial cutting edge and straight distal cutting edge. The mesial heel is  
428 elongate and weakly demarcated from the main cusp by a slight concavity in lingual view. The distal  
429 heel is low and elongate. Both heels have their lateral extremities supported by a thin protuberance

430 of the root oriented labially. The basal bulge of the labial crown face is strongly marked, labially  
431 oriented in the marginal regions and scalloped with short folds associated with larger but low  
432 enamelled protuberances. The root is fairly high with a large concavity of the basal edge separating  
433 two labially-oriented lobes. The mesial root lobe is shorter and thicker than the distal one, which  
434 exhibits a sharp mesial extremity. Several labial foramina are present both at the crown/root edge  
435 and below. All teeth bear large and regular serrations on the cutting edges and heels.

436

437 *Remarks.* Teeth of this taxon bear resemblances with those of *Squalicorax* sp. 3 described below but  
438 display differences including a less individualised mesial heel, wider and less labially convex main  
439 cusp, labial folds and more strongly and finely scalloped labial crown bulge and strongly labially  
440 oriented marginal regions of labial bulge. *Squalicorax* sp. 1 can be differentiated from *Squalicorax* sp.  
441 4 by its teeth with higher root, more developed root lobes, straight mesial cutting edge of main cusp  
442 and more indented labial crown bulge. The taxon reported as *Squalicorax* sp. 1 from the upper  
443 Turonian of the Kwanza Basin in Angola by Antunes and Cappetta (2002) might be closely related to  
444 the species described here. However, the Angolan taxon differs in having less marked labial concavity  
445 of the root and narrow notch separating the main cusp from distal heel in lateral teeth and in the  
446 overall morphology of anteriors. This material cannot be assigned to any nominal *Squalicorax* species  
447 and likely represents a separated species.

448

449 *Squalicorax* sp. 2

450

Figures 5J-N

451

452 *Material.* Two teeth (AMU-CURS-892 and AMU-CURS-893) from Cementos Andinos quarry (Trujillo  
453 state).

454

455 *Description.* The two lateral teeth of this taxon are slightly wider than high, reaching maximum width  
456 of 12 mm. The triangular main cusp is large and bent to the commissure with a strongly convex  
457 lingual face and a slight convex labial face. The lower part of the labial face of main cusp bears a  
458 shallow vertical depression in its median region. The mesial cutting edge is slightly convex in lingual  
459 view whereas the distal cutting edge is straight. The mesial heel is elongate but low and  
460 undifferentiated from the cutting edge except by a light concavity. The distal heel is well developed  
461 and sub-horizontal with an uneven straight to slightly convex outline in lingual view. A very broad  
462 triangular-shaped lingual neck delimits the crown from the root. The basal region of the labial crown  
463 face bears a moderately developed bulge that tapers towards the marginal regions. The labial bulge  
464 is concave in its median part and indented by depressions where large labial foramina open. Cutting  
465 edges of the main cusp and heels bear thin, irregular and marked serrations that penetrate deep into  
466 the crown. The root is fairly low, mesio-distally developed and bilobate. The mesial root lobe is  
467 rather short with a sharp extremity whereas the distal lobe is more developed, thicker, with a blunt  
468 extremity. Both lobes are separated by a wide concavity of the basal root edge. The lingual crown  
469 face is low and exhibits a narrow and shallow central protuberance. A central foramina is present on  
470 the flat basal face, along with other foramina randomly located and of variable size.

471

472 *Remarks.* The overall tooth morphology of this taxon is relatively common among large mid-  
473 Cretaceous *Squalicorax* and the scarcity of the material recovered from La Luna Formation precludes  
474 finer taxonomic assignment. Most mid-Cretaceous *Squalicorax* teeth with comparable general  
475 morphology (e.g. relatively large teeth with strong serrations and fairly wide main cusp) were placed  
476 within - or put in close relationship within - either *Squalicorax curvatus* (Williston, 1900) or  
477 *Squalicorax falcatus* (Agassiz, 1843). This situation was in great parts due to the quality of the type  
478 series of both species, being represented by scarce incomplete specimens for the former and by

479 drawings of a heterogenous series for the latter (see Siverson et al. 2007 for illustrations of the  
480 lectotype of *S. falcatus*). In addition, morphologies of these two taxa appear to be quite distinct  
481 when type materials are compared but teeth from some *Squalicorax* populations were frequently  
482 included, despite morphological differences, into one or both of these taxa (see Underwood and  
483 Cumbaa, 2010). Teeth of *Squalicorax* sp. 2 can be differentiated from those of *S. falcatus* by their  
484 narrower main cusp with straight distal cutting edge, less convex contact between the lingual crown  
485 face and root, more marked labial crown bulge and lower root with more developed lobes. Teeth of  
486 *S. curvatus* have a lower and much broader main cusp, higher heels with the mesial one being  
487 generally more individualised than in *Squalicorax* sp. 2. Specimens figured in Welton and Farish  
488 (1993, p. 116, figs. 1-2) as *S. curvatus* from the Cenomanian (Lewisville Member of the Woodbine  
489 Formation) of Texas fall outside of the range of variation of *S. curvatus* and are morphologically close  
490 to those of *Squalicorax* sp. 2. However, differences including less developed root lobes with  
491 shallower concavity of the basal root edge and higher lingual root face in the North American  
492 material separate both taxa. *Squalicorax obliquus* (Reuss, 1845) and *Squalicorax heterodon* (Reuss,  
493 1845) are two species described from the Turonian of Czech Republic. In the original description of *S.*  
494 *heterodon*, Reuss (1845; p. 3, pl. 3, figs. 49-71) considered that all *Corax* (the former name of  
495 *Squalicorax*) species described by Agassiz (1843) excepted *Corax pristodontus* and *Corax*  
496 *appendiculatus* (with the exception of pl. 26 fig. 3) should be lumped into a single taxon. [It should be  
497 noted that parts of the material on which Agassiz based his species *C. appendiculatus* corresponds to  
498 the squaliform genus *Centrophoroides* (pl. 26a, figs. 18-20, non figs. 16-17, pl. 26, fig. 3 as *Galeus*  
499 *appendiculatus*), whereas the remaining specimens belong to the genus *Squalicorax*]. Consequently,  
500 he erected the species *S. heterodon* to accommodate this lumping, clearly stating that some of his  
501 material (pl. 3, figs 49-50, 52-53, 55-63, 65-68) corresponds to *S. falcatus*, others (pl. 3, figs. 51, 54) to  
502 *S. kaupi*, some specimens (pl. 3, figs. 64, 70) to *C. affinis* (now in the genus *Pseudocorax*), whereas he  
503 considered the remaining teeth (pl. 3, figs. 64, 70) to be close to *C. appendiculatus*. Although it is  
504 clear that the type series of *S. heterodon* is heterogeneous, the different species lumped into this

505 taxon name do not correspond to those mentioned by Reuss and only a thorough re-examination of  
506 Reuss's material will allow the assessment of the identity of the species figured under the name *S.*  
507 *heterodon*. The species name *S. heterodon* cannot be considered valid and must be considered  
508 *nomen neglectum*. The species *S. obliquus* is based on three specimens (pl. 4, figs 1-3) from the  
509 Turonian of Czech Republic but Reuss himself indicated (Reuss, 1845; p. 4) that one specimen (pl. 4,  
510 fig. 2) might belong to a different species. Assessing the degree of morphological variation of this  
511 species is complicated as the material (pl. 4, figs 1, 3) is incomplete and might be morphologically  
512 close to some specimens figured in *S. heterodon*. Teeth of *Squalicorax* sp. 2 are morphologically close  
513 to the Reuss's specimen (pl. 4, fig. 2) but differ by their shorter distal heel. The crown of the  
514 incomplete most lateral tooth of *Squalicorax* sp. 2 but the root morphology of *S. obliquus* teeth is not  
515 known.

516

517 *Squalicorax* sp. 3

518 Figures 50-S

519 ? 1927 *Squalicorax baharijensis*; Stromer, pl. 1, fig. 26 *non* pl. 1, figs 25, 27.520 ? 1989 *Squalicorax baharijensis* Stromer; Werner, pl. 15, fig. 1 *non* pl. 14, figs 1-9 & pl. 15, figs 2-3.

521

522 *Material*. Two teeth (MBLUZ P-881 and MBLUZ P-430-D) from La Luna quarry (Zulia state).

523

524 *Description*. The anterior tooth is higher (10 mm) than wide (7.5 mm). The triangular main cusp is  
525 erect though slightly bent to the commissure with a nearly straight distal cutting edge and a slightly  
526 convex mesial cutting edge in its median region. The mesial heel is short, oblique, and poorly  
527 individualised from the main cusp. The distal heel is convex, fairly low and oblique, which contrasts

528 with the vertical distal edge of main cusp. The lingual face of main cusp is strongly convex whereas  
529 the labial face is flat. A very wide lingual neck is present, reaching its maximum width in its median  
530 region. The lower area of the labial crown face is oriented labially and exhibits a marked labial bulge  
531 that overhangs the root in its central part. The basal edge of the labial crown face shows a fairly  
532 narrow and concave median area that bears five notches corresponding to the openings of labial root  
533 foramina. The labial marginal areas of the basal crown edge are convex. The cutting edges of main  
534 cups and heels bear relatively coarse serrations with the exception of the smooth lateral edges of the  
535 heels. The root is bilobate and V-shaped in basal view with a marked concavity of the basal edge of  
536 the labial crown face. The distal root lobe is wider with a more rounded distal edge in basal view. A  
537 central foramen is present on the basal face, along with other smaller foramina over the basal  
538 surface. Large, oval-shaped labial foramina are present at (median area) or below (marginal areas)  
539 the root/crown edge. The lateral tooth is more mesio-distally elongate than the anterior and slightly  
540 higher (11 mm) than wide (10 mm). The mesial and distal cutting edges of the main cusp are fairly  
541 straight. A well-developed mesial heel is present, slightly oblique and fairly low. The distal heel is sub-  
542 horizontal, low and separated from the main cusp by a notch. The labial crown face is similar to that  
543 of the anterior tooth though more mesio-distally elongate with a less deep median concavity and  
544 more numerous notches where large labial foramina open. The root lobes are oriented laterally and  
545 form a shallow and wide concavity of basal root edge. The distal root lobe is shorter and wider than  
546 the mesial one. The basal root face is fairly flat. The mesial edge of the root is straight and oblique  
547 whereas the distal one bears a shallow notch below the crown/root edge. Below the labial crown  
548 bulge, the large oval-shaped foramina opening at the crown-root edge bear a thin veil of  
549 osteodentine over the enamelled edges. Other large and smaller foramina are present on the labial  
550 face.

551

552 *Remarks.* This taxon is represented by scarce material but exhibits tooth characters that differ from  
553 other *Squalicorax* species reported here. *Squalicorax* sp. 3 is morphologically close to *Squalicorax* sp.  
554 1 described here from the same locality but differs by its more developed and individualised mesial  
555 heel (in laterals), narrower main cusp, labial crown face with less marked basal bulge and less labially  
556 oriented marginal areas, basal edge of labial crown face devoid of vertical folds. The size and  
557 morphology of the lateral tooth of *Squalicorax* sp. 3 is comparable to the specimen figured in the  
558 original description of *Squalicorax baharijensis* (Stromer, 1927) by Stromer (1927; pl. 1, fig. 26) and  
559 refigured by Werner (1989; pl. 15, fig. 1) from the upper Cenomanian of the Gebel Dist Member of  
560 the Bahariya Formation in Egypt, although the latter likely corresponds to a more lateral tooth file. As  
561 already noted by Siverson et al. (2007) the specimen illustrated by Werner (1989) strongly contrasts  
562 from the topotypic material of *S. baharijensis* she illustrated and probably represents a different  
563 species. Based on the scarce material from Egypt and Venezuela, it is preferable to leave this species  
564 in open nomenclature.

565

566 *Squalicorax* sp. 4

567 Figures 5T-V

568

569 *Material.* Two teeth (MBLUZ P-432 and MBLUZ P-432-B) from La Luna quarry (Zulia state).

570

571 *Description.* These lateral teeth is wider (11 mm) than high (8.5 mm) and exhibit a triangular main  
572 cusp bent to the posterior. The main cusp is biconvex but strongly labio-lingually compressed. The  
573 mesial edge of the main cusp is slightly convex and undifferentiated from the low mesial heel. The  
574 distal heel is low, convex and sub-horizontal with a marked demarcation from the main cusp. A  
575 rather large lingual neck is present. The basal edge of the labial crown face is concave in its median

576 region where it bears a labial bulge, whereas the marginal edges are convex and less protruded.  
577 Rather coarse but irregular serrations are present on cutting edges and heels of the crown.  
578 Serrations reach maximum width in the lower part of the cutting edges and proximal part of the  
579 heels and taper near the apex of the main cusp. The root is low with fairly narrow lobes oriented  
580 laterally. The basal face is weakly concave in labial view and bears a central foramen and other  
581 foramina of variable sizes. The mesial and distal root edges are concave. The labial root face is  
582 pierced by several foramina, some of them being situated in very shallow notches of the labial crown  
583 bulge.

584  
585 *Remarks.* This material shares features with teeth of *Squalicorax* sp. 2 from Cementos Andinos  
586 quarry. However, teeth of *Squalicorax* sp. 4 differ in having a more convex labial face of main cusp,  
587 marked labial angle between distal heel and main cusp, lower root (in labial view) with more  
588 symmetrical root lobes and thinner basal labial bulge of the crown. In addition to their smaller size,  
589 teeth of *Squalicorax* sp. 4 bear serrations that differ from those of *Squalicorax* sp. 2. In the latter (Fig.  
590 5M), serrations penetrate deep into the crown in labial view and are thin, irregular and separated by  
591 rather wide depressed areas. Serrations of teeth of *Squalicorax* sp. 4 are rather large, blunt and  
592 separated by narrow notches (Fig. 5V). Teeth of *Squalicorax* sp. 4 differ from the laterals of  
593 *Squalicorax* sp. 3 from the same locality in being more labio-lingually compressed with no  
594 differentiated mesial heel, lower root, more convex labial face of main cusp, more symmetrical root  
595 lobes, more convex and oblique distal heel and less scalloped labial bulge. Teeth of *Squalicorax* sp. 4  
596 have a more convex mesial cutting edge than laterals of *Squalicorax* sp. 1, lower root with thinner  
597 and less developed root lobes. The morphology of teeth of *Squalicorax* sp. 4 does not fall into the  
598 range of variation of any nominal or unnamed species published so far.

599

600



601 Genus *Cretoxyrhina* Glikman, 1958

602 *Cretoxyrhina mantelli* (Agassiz, 1843)

603 Figures 6A-B

604

605 *Material.* One incomplete tooth (MBLUZ P-41) from La Luna quarry (Zulia).

606

607 *Description.* This tooth is cuspidate with a broad main cusp inclined distally. The labial cusp face is  
608 almost flat whereas the lingual face is markedly convex. A pair of oblique lateral heels is present, the  
609 distal one being less inclined and higher than the distal one. The heels bear no cusplets, although the  
610 mesial one is damaged, and the cutting edges are continuous from the main cusp to the lateral  
611 extremity of the heels. The crown lacks ornament but bears a faint central vertical fold at the base of  
612 the labial crown face. The labial crown very weakly overhangs the root in occlusal view. The base of  
613 the lingual crown face is marked by a rather thick neck that reaches its maximum thickness in its  
614 median part. The root is wide (25 mm), bilobate and asymmetrical with a more elongate, more  
615 oblique and thinner mesial lobe. The basal edge of the root is strongly concave. The lingual root face  
616 bears an acute lingual protuberance that is pierced by a central foramen. The lingual face of the  
617 distal extremity of the root lobes is nearly flat. Numerous oval-shaped labial foramina open below  
618 the basal edge of the crown and others are randomly situated over the labial face of the root lobes.  
619 Lingual foramina are present on the marginal faces, below the basal crown edge.

620

621 *Remarks.* The species *Cretoxyrhina mantelli* is known from a large number of Upper Cretaceous  
622 localities worldwide, but the specimen reported here represents the first record of the genus in  
623 South America. Numerous associated tooth sets have been described (Bourdon and Everhart, 2011;  
624 Shimada, 1997a; Welton and Farish, 1993) and the dentition and range of variation of this species is

625 relatively well known. The specimen described here agrees with the morphology of *C. mantelli* and  
626 probably represents an upper lateral tooth. *Cretoxyrhina denticulata* (Glikman, 1957) is another  
627 species of this genus that occurs in the Cenomanian of Russia and North America (Underwood and  
628 Cumbaa, 2010), France (Vullo, 2015) and England (Guinot et al., 2013). This differs from *C. mantelli* in  
629 having lateral and posterior teeth of adult specimens with lateral cusplets and being smaller with a  
630 more stubby general aspect.

631

632 Family Odontaspidae Müller and Henle, 1839

633 Genus *Microcarcharias* gen. nov.

634

635 *Derivation of name.* After the small size of the teeth and their overall resemblance to the teeth of the  
636 modern lamniform shark *Carcharias* Rafinesque, 1810.

637

638 *Type species.* *Odontaspis saskatchewanensis* Case, Tokaryk and Baird, 1990 from the lower Turonian  
639 of Canada. The age of the type stratum was initially indicated as Coniacian in original publication but  
640 was subsequently revised to early Turonian (Cumbaa and Tokaryk, 1999; Underwood and Cumbaa,  
641 2010).

642

643 *Diagnosis.* Odontaspidid possessing small (less than 6 mm high) and gracile teeth with gradient  
644 monognathic and dignathic heterodonty. Main cusp slender, biconvex, triangular and bent lingually.  
645 Pair of erect lateral cusplets in labial position relative to main cusp; wide and bulbous lower region of  
646 cusplets overhanging the root in marginal area; thin and needle-like in upper region, straight to  
647 slightly diverging. Cutting edges of main cusp thin and low, sometimes discontinuous with those of

648 cusplets. Basal region of crown overhanging the root labially in occlusal view. Main cups with median  
649 vertical ridge occasionally present in lower region of labial face, connected to a slight bulge at the  
650 basal crown edge. Faint short vertical ridges on basal edge of labial crown face. Root holaulacorhize  
651 and bilobate with flared distal region of root branches. Strong lingual root protuberance with wide  
652 and deep nutritive groove pierced by large central foramen. Numerous large foramina on labial root  
653 face. Upper lateral teeth more inclined to the posterior, rarely with an additional mesial cusplet.  
654 Lower laterals with wider crown. Posterior teeth low with short and mesio-distally oriented root  
655 branches; basal root face flat. Lateral cusplets wide and short. Labial crown ornament of more or less  
656 pronounced vertical ridges on main cusp and cusplets.

657

658 *Remarks.* This genus adds to the diversity of small mid-Cretaceous lamniform sharks and can be  
659 separated from those by the following association of tooth characters: small size of teeth (the  
660 smallest of all known odontaspids), marked lingual root protuberance, peculiar morphology of  
661 lateral cusplets, labial bulge of basal crown face and labial crown ornamentation. Teeth of the  
662 odontaspid genus *Cenocarcharias* Cappetta and Case, 1999 are close in size and morphology to  
663 those of *Microcarcharias* gen. nov. but differ in their thicker main cusp with peculiar lingual wrinkles,  
664 wide lingual neck and wider and stouter lateral cusplets that not protrude labially relatively to the  
665 main cusp. Teeth of *Rouletia* Vullo, Cappetta and Néraudeau, 2007 can be differentiated from to  
666 those of *Microcarcharias* gen. nov. by their larger size, more robust general aspect, wide lower  
667 region of main cup, lack of labial crown overhang, poorly individualized cusplets and absence of  
668 crown ornamentation. *Johnlongia* Siverson, 1996 is another mid-Cretaceous odontaspid genus  
669 whose teeth show a strong lingual protuberance and gracile and elongate main cusp. However, teeth  
670 of *Johnlongia* can be easily distinguished by their extremely developed lingual root protuberance  
671 with a rectangular shape in basal view, very high crown heels, rectilinear basal edge of the labial  
672 crown face and typical foraminifera on the margino-lingual root faces. Teeth of a few non-

673 odontaspids may resemble some of *Microcarcharias* gen. nov. Among them, the tentative  
674 archaeolamnid genus *Dallasiella* Cappetta and Case, 1999 has teeth that differ from *Microcarcharias*  
675 gen. nov. by their flatter labial crown face, lower and wider cusplets not protruding labially, less  
676 marked nutritive groove and thicker root lobes. *Haimirichia* Vullo, Guinot and Barbe, 2016 is another  
677 small mid-Cretaceous lamniform included in the family Haimirichiidae. Teeth of *Haimirichia* are easily  
678 separated from those of *Microcarcharias* gen. nov. less marked lingual root protuberance and  
679 nutritive groove, flat basal edge of the labial crown face, wide and developed root lobes in laterals  
680 with flat basal face with wider and shorter cusplets.

681

682 *Microcarcharias saskatchewanensis* (Case, Tokaryk and Baird, 1990) comb. nov.

683 Figures 6C-O

684

685 1974 *Odontaspis applegatei* Meyer, p. 201-202, fig. 64.

686 1990 *Odontaspis saskatchewanensis* Case, Tokaryk and Baird, p. 1085, figs 4-5.

687 1990 *Synodontaspis lilliae* Case, Tokaryk and Baird, p. 1085, fig. 6.

688 1993 *Carcharias* sp. A; Welton and Farish, p. 91, figs 1-6.

689 2001a *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Cicimurri, p. 36, fig. 7n;

690 2001b *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Cicimurri, p. 188, fig. 5q.

691 2006 *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Shimada et al., p. 11, figs 9.3-9.4.

692 2006 *Carcharias tenuiplicatus* (Cappetta and Case, 1975); Shimada et al., p. 13, figs 9.5-9.6.

693 2008 *Carcharias saskatchewanensis* (Case, Tokaryk and Baird); Shimada and Martin, p. 92, fig. 5H.

694

695 *Material.* Two teeth (AMU-CURS-890 and AMU-CURS-891) from Cementos Andinos quarry (Trujillo  
696 state) and three teeth (MBLUZ P-14, MBLUZ P-433 and MBLUZ P-14-B) from La Luna quarry (Zulia  
697 state).

698

699 *Description.* Teeth of this species are small, not exceeding 6 mm high. Teeth from the anterior files  
700 are sub-symmetrical with a narrow triangular main cup that is erect and bent lingually. The main cusp  
701 is biconvex and bears very thin and low cutting edges that become very thin or fade out on the heels.  
702 The heels are strongly inclined basally and bear a pair of lateral cusplets. Lateral cusplets are erect or  
703 slightly diverging, oriented lingually and conical with a wide lower region that thins out in the upper  
704 half. Cusplets are well separated from the main cusp and in labial position relatively to the main  
705 cusp. The basal edge of the labial crown face bears a bulge that is more marked below the heels than  
706 in its central part. A thin lingual neck separates the lingual crown face from the root. The root is  
707 holaulacorhize and bilobate with well-developed root branches that are inclined basally. Root  
708 branches become thinner distally and largely overtake the labial edge of the heels. The lingual root  
709 protuberance is marked and separated by a wide nutritive groove that is pierced by a large central  
710 foramen. The marginal regions of the lingual root face bear numerous foramina that are aligned just  
711 below the crown/root edge. The labial root face is high, abrupt, and pierced by several wide foramina  
712 including a large central foramen. Teeth from antero-lateral files are more asymmetrical in upper  
713 files than in lower files. Teeth from these files can show a narrower and more protruding lingual  
714 protuberance of the root. The distal extremity of the root lobes is slightly bent basally. The mesial  
715 root lobe is shorter and wider than the distal one. The labial face of the main cusp can show a thin  
716 median vertical ridge in lower region ending in a slight bulge at the basal edge of the crown. Some  
717 faint labial vertical ridges are irregularly distributed below the distal edge of the cusplets and poorly  
718 marked folds can be present on the basal edge of the labial crown face, on both sides of the labial  
719 buldge.

720

721 *Remarks.* In addition to the description of the species *Microcarcharias saskatchewanensis* comb.  
722 nov., Case et al. (1990) described the species *Synodontaspis lilliae* Case, Tokaryk and Baird, 1990 on  
723 the basis of two teeth from the same locality. The authors only figured the holotype represented by a  
724 lateral tooth. Comparing this specimen with laterals of *M. saskatchewanensis* comb. nov.  
725 subsequently reported from the Cenomanian of Texas (Welton and Farish, 1993) and Colorado  
726 (Shimada et al., 2006 as *Cenocarcharias tenuiplicatus*) indicate that the holotype of *S. lilliae* is a  
727 lateral tooth of *M. saskatchewanensis* comb. nov. Consequently, we consider the species *S. lilliae* a  
728 junior synonym of *M. saskatchewanensis* comb. nov. This species has been reported from a number  
729 of Cenomanian to lower Turonian localities in the Western Interior Seaway: lower Turonian of  
730 Canada (Case et al., 1990), Cenomanian (Eagle Ford Group, Britton Formation) of Texas (Welton and  
731 Farrish, 1993: p. 91; Meyer 1974), Colorado (Shimada et al., 2006), Kansas (Shimada and Martin  
732 2008) and S. Dakota (Cicimurri, 2001a, 2001b). The material reported here represents the  
733 southernmost record of this species and the first outside the WIS.

734

735 Family Otodontidae Glikman, 1964

736 Genus *Cretolamna* Glikman, 1958737 *Cretolamna* sp.

738 Fig. 6P

739

740 *Material.* One incomplete tooth (MBLUZ P-86) from La Luna quarry (Zulia state).

741

742 *Description.* The single specimen recovered is an incomplete tooth embedded in matrix with only the  
743 labial face being observable. The tooth is wider (14 mm) than high, although the apex of the crown is  
744 lacking. The main cusp is triangular and inclined to the posterior with a convex labial face except in  
745 its central region where a vertical concavity is present at the base of the cusp. A pair of low and  
746 broad lateral cusplets is present, separated from the cutting edges of the main cusp by a narrow  
747 notch. The mesial cusplet is diverging and bears an incipient secondary cusplets in its mesial edge.  
748 The distal cusplet is incomplete but both mesial and distal marginal cusplets bear a blade-like  
749 extension of enameloid that exceeds the lateral edges of the root. The basal edge of the labial crown  
750 face is flat except in the median region where a slight bulge is present. The labial crown face is  
751 devoid of ornamentation apart from very faint and short vertical folds at the basal edge of the crown.  
752 The labial root face is flat to slightly concave in profile view shows two large and triangular-shaped  
753 lobes separated by a narrow v-shaped notch. Both lobes bear a protuberance on the angle between  
754 their lateral and basal root edges. Numerous large and oval-shaped foramina open on the labial root  
755 face.

756

757 *Remarks.* The genus *Cretolamna* is amongst the most commonly reported lamniforms in post-Aptian  
758 Cretaceous deposits. Most Cretaceous records of this genus (and several younger records) were  
759 assigned to the species *Cretolamna appendiculata* (Agassiz, 1843). Yet, this species was based on a  
760 heterogeneous series that lumped several different species and genera with unclear stratigraphic  
761 and precise geographic details, which led Siverson (1999) to designate a lectotype. A much needed  
762 revision of Late Cretaceous *Cretolamna* (Siversson et al., 2015) untangled a large part of the  
763 taxonomic lumping within this genus and concluded that the species *C. appendiculata sensu stricto*  
764 should be restricted to the material from the type area (Cenomanian-Coniacian of Lewes, England)  
765 and lower Turonian of France (Bettrechies). Because of the difficulties in identifying *Cretolamna*

766 material at species level even based on numerous well-preserved specimens, we prefer to leave the  
767 specimen described here in open nomenclature.

768 Although Upper Cretaceous records of *Cretolamna* are frequent worldwide (see Cappetta, 2012),  
769 reports of this genus from South America are scarce. Previous reports include an abraded tooth from  
770 the Maastrichtian of Argentina attributed to *C. appendiculata* (Bogan and Agnolin, 2010) and  
771 *Cretolamna biauriculata* (Wanner, 1902), from the Maastrichtian of Brazil (Rebouças and Silva  
772 Santos, 1956). The tooth described here indicates the presence of the genus *Cretolamna* from South  
773 America as soon as in the earliest Late Cretaceous.

774

775 Lamniformes *incet. sedis*

776 Genus *Acutalamna* gen. nov.

777

778 *Derivation of name.* From the latin *acutus* (sharp, pointed) in allusion to the elongated and sharp  
779 morphology of the crown.

780

781 *Type species.* *Acutalamna karsteni* gen. et sp. nov.

782

783 *Diagnosis.* Lamniform with gradient monognathic heterodonty. Cuspidate teeth higher than wide.  
784 Slender main cusp weakly (anterior teeth) to strongly (laterals) bent distally, devoid of lateral  
785 cusplets; main cup sigmoid in labial and profile views. Lateral heels oblique in anterior teeth; mesial  
786 heel incipient to absent in more lateral tooth files. Cutting edges smooth, low and thin. Large crown  
787 neck. U-shaped root of anaulacorhize stage. Root bilobate, asymmetrical with more developed and  
788 thinner mesial lobe; strong and protruding lingual protuberance with central foramen. Labial root



789 face with variable number of foramina below the crown/root edge. More lateral teeth strongly  
790 asymmetrical with short and stubby mesial root lobe and incipient or no mesial crown heel; basal  
791 root edge curved and wide. Heels absent in latero-posterior teeth.

792

793 *Remarks.* The genus *Priscusurus* Kriwet, 2006 was erected on the type species *Priscusurus*  
794 *adruptodontus* Kriwet, 2006 from the ?middle Albian (Muerto Limestone Fm.) of northwestern Peru.  
795 Yet, the type series mainly includes incomplete teeth and appears to be heterogeneous. The  
796 holotype (BMNH P. 36287) of *P. adruptodontus* is a complete tooth embedded in matrix of which  
797 only the lingual face is observable. This tooth shows characters of anacoracid lamniforms (flat basal  
798 face of the root, poorly differentiated root lobes, labio-lingually compressed root, concave marginal  
799 areas of the lingual root face and triangular-shaped crown) that are typically found in *Squalicorax*  
800 species. Other teeth (?Fig 2B-C and Fig. 3J) also belong to the genus *Squalicorax*. Consequently, as  
801 the holotype is the bearer of the scientific name a species-group taxon (ICZN Art. 72.10), the species  
802 *adruptodontus* must be transferred to the genus *Squalicorax*. However, since the holotype of *S.*  
803 *adruptodontus* comb. nov. (Kriwet, 2006) is embedded in matrix and represents a species of  
804 *Squalicorax*, an extremely diverse genus comprising 53 nominal species (Cappetta et al., 2014) with  
805 high variability in tooth morphologies, the figured specimens are not sufficient to justify the validity  
806 of the species. Accordingly, *S. adruptodontus* comb. nov. (Kriwet, 2006) should be considered *nomen*  
807 *dubium*. In the absence of type species for the genus *Priscusurus*, this genus name should be  
808 considered *nomen nudum* and the non-*Squalicorax* teeth of the original type series of *Priscusurus*  
809 *adruptodontus* should be included in an unnamed species of the genus *Acutalamna* gen. nov. (see  
810 below).

811

812 *Additional species.* Excluding the specimens originally assigned to *Priscusurus adruptodontus* from  
813 the Albian of Peru (Kriwet, 2006) that correspond to the *nomen dubium* species *S. adruptodontus*

814 comb. nov. results in a series (Fig. 2B-C *non* Fig. 2A & ?Fig 2B-C, Fig. 3A-I *non* Fig. 3J) composed of  
815 fragmentary specimens that make difficult the identification of the material at the species level.  
816 Consequently, although the morphology of these teeth corresponds to an *Acutalamna* species, it is  
817 preferred to leave it in open nomenclature. Cappetta (2012) figured two teeth attributed to  
818 *Priscusurus adruptodontus* from the upper Albian of Ecuador. The material was originally said to  
819 come from Peru but was actually collected from the Napo Fm. (Western Oriente Basin) of Ecuador  
820 (Cappetta pers. com. 2017) and reported as “undetermined lamniform probably representing a new  
821 genus” (Jaillard, 1997; p. 58). While the material from Peru (Kriwet, 2006) here attributed to  
822 *Acutalamna* sp. corresponds to lateral to latero-posterior teeth, specimens from Ecuador are  
823 represented by anterior and antero-lateral teeth. Hence, it is possible that they correspond to the  
824 same taxon but the lack of comparable specimens between the two localities and the fragmentary  
825 state of preservation of the Peruvian material precludes certain judgement. Biddle (1993) figured  
826 two teeth (pl. 4, figs. 19-20) as ?*Microcorax* sp. from the middle Albian of France. These show a bulky  
827 and asymmetrical root with a strong lingual protuberance and wide lingual neck as well as a sigmoid  
828 main cusp with wide lower part. These characters allow the attribution of these specimens to the  
829 genus *Acutalamna* gen. nov. However, teeth from France differ from the other Albian specimens by  
830 their more robust general morphology and probably correspond to a different, unnamed species.  
831 Cappetta (2012) proposed that the material figured by Dalinkevičius (1935, p. pl. 5, figs. 114-118) as  
832 *Oxyrhina* (?) *primaeva* from the Albian of Lithuania might be included in the genus *Priscusurus* (now  
833 *Acutalamna* gen. nov.). Yet, one of these specimens (pl. 5, fig. 118) was designated by Landemaine  
834 (1991) as the holotype of the species *Squalicorax primigenius* Landemaine, 1991 whereas the  
835 remaining specimens (pl. 5, figs. 114-117) present characters typical of the genus *Acrolamna*  
836 Zhelezko, 1990 (labio-lingually compressed teeth with no lingual root protuberance, wide and short  
837 root lobes, wide triangular main cusp) and should be included within this genus. The genus  
838 *Acutalamna* gen. nov. described here includes a single nominal species (*Acutalamna karsteni* gen. et  
839 sp. nov.) and ranges from the Albian to the Cenomanian.

840

841

*Acutalamna karsteni* gen. et sp. nov.

842

Fig. 7

843

844 *Derivation of name.* In honour of Hermann Karsten a 19<sup>th</sup> century German naturalist who conducted  
845 a pioneer exploration in northern South America and collected a number of palaeontological material  
846 from the Cretaceous and Pleistocene of Colombia and Venezuela (Carrillo-Briceño et al., 2016).

847

848 *Holotype.* AMU-CURS-908.

849

850 *Type stratum.* Laminated black/dark-grey shales in the basal part of the La Aguada Member, La Luna  
851 Formation.

852

853 *Material.* Six teeth (AMU-CURS-908 to AMU-CURS-913) from Cementos Andinos Quarry (Trujillo  
854 state) and one tooth (MBLUZ P-431) from La Luna Quarry (Zulia state).

855

856 *Diagnosis.* As for genus.

857

858 *Description.* Anterior teeth are cuspidate, higher (10 mm) than wide (5 mm), slender and gracile. The  
859 crown is composed of an elongate and lingually-inclined main cusp that is slightly bent distally and a  
860 pair of lateral heels. The lingual face of the cusp is strongly convex whereas the labial face is slightly  
861 convex to nearly flat with an incipient basal bulge. The crown heels are inclined basally with the

862 mesial heel being more oblique than the distal one. Cutting edges are thin but sharp and run  
863 continuously from the apex of the main cusp to the lateral margins of the heels. The upper part of  
864 the crown is bent labially and shows a slight twisting, which confers a sigmoid shape to the main cusp  
865 in profile view. The crown/root edge of the lingual face bears by a thick neck. The root is  
866 anaulacorhize, bilobate and U-shaped in lingual/labial view with a concave basal face in profile view.  
867 Root branches are individualized and oriented labially. The mesial root lobe is slenderer and more  
868 elongate than the distal one. The lingual root face bears a strong and wide lingual bulge that is  
869 pierced by a wide central foramen. Numerous small foramina open on the lingual root face,  
870 immediately below the neck. The labial root face bears a few foramina in central position and others  
871 more irregularly open on the lingual face of the root lobes. Teeth from more lateral files have a more  
872 robust general morphology. The main cusp is wider in its lower part and has a more marked sigmoid  
873 outline in both lingual and profile views. The labial crown face is convex with a basal bulge. The distal  
874 heel is incipient or absent whereas the mesial heel is low and less oblique than in anterior teeth. The  
875 root is compact with strongly asymmetrical lobes that are well separated by an arched basal edge.  
876 The lingual root bulge is wide and strongly protrudes lingually but is less differentiated from the root  
877 lobes than in anterior teeth. The mesial root lobe is elongate whereas the distal one is short and  
878 stubby, sometimes poorly differentiated from the rest of the root. A series of foramina underline the  
879 labial crown bulge, sometimes associated with more irregularly situated foramina near the basal root  
880 edge. Latero-posterior teeth are low with incipient distal root lobe and no differentiated crown heels.

881

882 *Remarks.* Teeth of *Acutalamna karsteni* gen. et sp. nov. differ from the unnamed species from  
883 Ecuador (Cappetta, 2012) by their more marked and more individualized lingual protuberance. The  
884 specimens reported from the Albian of France (Biddle, 1993) differ from *Acutalamna karsteni* gen. et  
885 sp. nov. by their more robust general aspect, more mesio-distally compressed root and less elongate  
886 main cusp with a wider basal region. The single (antero-lateral) tooth recovered from La Luna Quarry

887 is a museum specimen that could not be extracted from the sediment, nonetheless the observable  
888 features present on the lingual face allows attribution of this specimen to *A. karsteni* gen. et sp. nov.  
889 The material described here represents the last occurrence of the genus which is otherwise known  
890 only from the upper Albian of Ecuador (Cappetta, 2012) and ?middle Albian of Peru (Kriwet, 2006)  
891 and middle Albian of France (Biddle, 1993).

892

## 893 5. Discussion

### 894 5.1. Stratigraphy and palaeobiogeography

895 The specimens described here were sampled from two horizons within the La Luna Formation: one  
896 from the Aguada Member (Cementos Andinos Quarry, Trujillo state) and the other from just above  
897 the contact between the Maraca Formation (Cogollo Group) and the La Luna Formation (La Luna  
898 Quarry, Zulia state). While a Cenomanian age was proposed for the Aguada Member based on  
899 foraminifera and ammonites (Renz, 1959), the presence of horizons of Cenomanian age in the  
900 Maracaibo Basin, from which the La Luna Quarry samples originate, has been controversial (Dot et  
901 al., 2015; Erlich et al., 1999; Renz, 1982). The two sampled localities have distinct (and rich)  
902 anacoracid composition but they share two taxa: *M. saskatchewanensis* and *A. karsteni*. Despite its  
903 small-sized teeth, *M. saskatchewanensis* was collected from various Cenomanian fossil-rich horizons  
904 in the Western Interior Seaway (WIS) as well as from one lower Turonian locality in the WIS (see  
905 above). *Acutalamna* remains were so far known exclusively from the middle-upper Albian by at least  
906 two unnamed species groups (one from South America represented by two closely-related, if not  
907 conspecific, morphs and one from France). In addition, the La Luna quarry also yielded the species  
908 *Squalicorax* sp. 3, to which some material from the upper Cenomanian of Egypt has been referred  
909 (see above). Although the Cementos Andinos quarry and the La Luna quarry faunas are probably not  
910 contemporaneous, the presence of *M. saskatchewanensis* and *A. karsteni* in both localities and of  
911 *Squalicorax* sp. 3 in the Maracaibo Basin suggest a Cenomanian age for the base of the La Luna

912 Formation in this region. This is consistent with the suspected presence of upper Cenomanian strata  
913 forming the base of the La Luna Formation in the northwestern and central parts of the Maracaibo  
914 Basin, where rocks of La Luna Formation unconformably rest on upper Albian rocks (Erlich et al.,  
915 2000, 1999).

916 *Microcarcharias saskatchewanensis* was a small, probably nectobenthic shark typical of the Western  
917 Interior Seaway fauna and its presence in Venezuela suggests marine connexions between the WIS  
918 and the La Luna Sea. In addition, *Squalicorax moodyi* sp. nov. (La Luna quarry) is morphologically  
919 close to *Squalicorax* sp. from the upper Albian of Texas Welton and Farish (1993; p. 120) and *S.*  
920 *lalunaensis* sp. nov. (Cementos Andinos quarry) is close to the *S. volgensis* group (upper Cenomanian  
921 of Australia and Kansas) and to *Squalicorax* aff. *pawpawensis* from the Cenomanian of Canada  
922 (Underwood and Cumbaa, 2010). Although *C. mantelli* and *Cretolamna* species are very common in  
923 the Cenomanian of North America, these are cosmopolitan taxa that might not be reliable for  
924 palaeobiogeographic interpretations. However, the ichthyodectiform fish *Xiphactinus* Leidy, 1870  
925 reported from Cementos Andinos quarry (Carrillo-Briceño et al., 2012) is another taxon typically  
926 found in the WIS. These occurrences suggests more affinities in fauna composition with the North  
927 American WIS than with African assemblages (see Antunes and Cappetta, 2002) although the  
928 *Squalicorax* sp. 3 specimen from La Luna Formation is morphologically close to the Cenomanian  
929 taxon reported from Egypt (Stromer, 1927; pl. 1, fig. 26). The lamniform assemblage reported here  
930 shows little similarities with taxa reported from other Southern Continents. An early Cenomanian  
931 selachian assemblage from South India (Underwood et al., 2011) yielded a single *Squalicorax* species  
932 (*Squalicorax* aff. *baharijensis*) that does not compare with the La Luna *Squalicorax* species along with  
933 teeth belonging to the cosmopolitan *Cretolamna appendiculata* group. Most other lamniform and  
934 non-lamniform sharks present in the Indian assemblage have anti-tropical distributions, which  
935 suggests that temperature, along with endemism, might explain differences in lamniform  
936 composition between these assemblages. Higher latitudes may also explain the differences in  
937 lamniform composition of selachian assemblages from Australia (Siverson, 1999, 1997, 1996) that

938 comprise a high taxic diversity but very few anacoracids including representatives of the *S. volgensis*  
939 group. According to Erlich et al. (2000) the La Luna Sea was situated in a restricted basin surrounded  
940 by topographic highs that restricted connexions excepted in the north/northeast part. The lamniform  
941 material described here indicates some degree of endemism (anacoracids) that agrees with the  
942 restricted conditions of the sea and also indicates some connexions with northern seas. These marine  
943 connexions with northern oceans were certainly continuous through most of the Late Cretaceous as  
944 some other taxa reported from younger parts of the La Luna Formation such as the probably  
945 Coniacian *Ptychodus atcoensis* (Carrillo-Briceño and Lucas, 2013) and the Cenomanian-Santonian  
946 *Ptychodus cyclodontis* (Carrillo-Briceño, 2009) are known from the Coniacian of North America  
947 (Hamm, 2009) and the Turonian of the Caribbean (Mutter et al., 2005), respectively.

948

#### 949 5.2. Palaeoenvironment and palaeoecology

950 La Luna Formation has been interpreted as a typical marine environment where laminated organic-  
951 rich intervals suggest a deposition in the mid-shelf to upper continental slope under anoxic or poorly  
952 oxygenated conditions (e.g. Bralower and Lorente, 2003; Erlich et al., 1999; Macellari and De Vries,  
953 1987; Zapata et al., 2003). According to Tribovillard et al. (1991), the rich organic matter of the  
954 sediments in the La Aguada Member (Andes of Trujillo and Lara states) is of algal origin. González de  
955 Juana et al. (1980) suggested that the La Aguada Member could be considered as a transitional  
956 environment between the shallow waters of the Maraca formation (or La Puya Member according to  
957 Renz, 1968, 1959) and the pelagic facies of the La Luna Formation. Erlich et al. (1999) and Méndez  
958 (1981) suggested that the anoxic conditions of the La Luna Formation during the late Albian-early  
959 Cenomanian transgression were not due to water depth but to pre-existing anoxic conditions in the  
960 slope zone. On basis of benthic and planktonic foraminifera, Méndez (1981) recognized an increase  
961 in the submersion of the platform, but probably with depths that did not exceed 50 m.

962 Strata of the Aguada Member in Cementos Andinos quarry, especially the laminated black/dark-grey  
963 shales, yielded abundant bony fish remains represented by scales and isolated and semi-articulated  
964 cranial and postcranial elements of *Xiphactinus* (Carrillo-Briceño et al., 2012), other  
965 ichthyodectiforms, enchodontids and small indeterminate fishes. Marine sauropsids are represented  
966 in the locality by a single taxon, *Lunaophis aquaticus* Albino, Carrillo-Briceño and Neenan, 2016, a  
967 marine snake that exploited tropical environments. According to our own observations, benthic  
968 invertebrates are scarce in the shales of the Cementos Andinos quarry with only small bivalve moulds  
969 in the limestones (along with undetermined ammonites) and some inoceramids in the calcareous  
970 concretions. This could suggest periods of better oxygenated conditions on the sea floor for the La  
971 Aguada Member or may indicate that these organisms were tolerant to anoxic environments, as  
972 suggested for other sections of the La Luna Formation (e.g., Tribovillard et al., 1991). Although it is  
973 somewhat difficult to suggest a specific palaeoenvironment for this section of the La Aguada  
974 Member using the known vertebrate assemblage, the abundant fish remains may suggest well-  
975 oxygenated surface waters being part of a stratified water column. In La Luna Quarry, Moody and  
976 Maisey (1994) reported abundant fish remains (e.g. enchodontids, *Belonostomus*, *Bananogmius* and  
977 unidentified teleost scales and bones), and our sample from dissolved rocks yielded abundant  
978 disarticulated osteichthyan microremains. Although there is no clear environmental definition for  
979 this section using fossil assemblages, the Cenomanian rocks of the La Luna Formation in the Sierra de  
980 Perijá were considered representative of outer shelf to upper slope deposits (Erlich et al., 1999).

981 The most striking feature of the lamniform assemblages reported here is the high diversity of this  
982 group in the Cenomanian La Luna Sea with 12 species representing five families. In addition, a semi-  
983 complete (1.2 metres long), articulated vertebral column of a possible lamniform shark was also  
984 found *in situ* in the Cementos Andinos quarry. However, this specimen has been destroyed by quarry  
985 workers before being studied and only photographs were available to us. Nevertheless, one  
986 specimen figured here (CURS-893) and referred to *Squalicorax* sp. 2 was collected from the same  
987 layer, less than 20 cm from the vertebrae, which possibly indicates that the articulated vertebral



988 column might belonged to a *Squalicorax*. While the palaeoecology of *Acutalamna* is not well known  
989 (although its tooth morphology suggests a nectobenthic predator or scavenger), the remaining taxa  
990 recovered represent various habits. The tooth morphology and anatomy of *Cretoxyrhina mantelli*  
991 suggest that this shark was an active pelagic predator feeding on large vertebrate preys (Shimada,  
992 1997b), whereas there are numerous evidences of scavenging of large marine vertebrates  
993 (plesiosaurs, mosasaurs, turtles, large actinopterygians) by different *Squalicorax* species in the Late  
994 Cretaceous (Dortangs et al., 2002; Everhart, 2005; Schwimmer et al., 1997; Strganac et al., 2015).  
995 Feeding habits of *Cretalamna* species are more difficult to assess as the species diversity of this genus  
996 with a long stratigraphic range is probably underestimated. However, a report of numerous teeth of  
997 "*C. appendiculata*" around an elasmosaurid carcass from the Santonian of Japan (Shimada et al.,  
998 2010) suggests that at least some of the *Cretalamna* species happened to prey on dead carcasses,  
999 either occasionally or exclusively. *Microcarcharias saskatchewanensis* exhibits very small teeth of  
1000 tearing type, which indicate a small nectobenthic predator probably feeding on small bony fishes and  
1001 invertebrates. The dominance of anacoracids in La Luna quarry (four *Squalicorax* species) and  
1002 Cementos Andinos quarry (three *Squalicorax* and one probable *Nanocorax* species) is correlated with  
1003 the apparent high diversity of medium to large marine vertebrates found in association, which is  
1004 consistent with their probable opportunistic feeding strategy (active predation and scavenging).  
1005 Comparably high anacoracid diversity is known in mid-Cretaceous chondrichthyan assemblages from  
1006 the WIS (Bice and Shimada, 2016; Cappetta and Case, 1999; Siverson et al., 2007; Welton and Farish,  
1007 1993), which also generally co-occur with large marine vertebrates. However, WIS assemblages  
1008 mostly represent shallow to inner shelf epicontinental marine environments that contrast with the  
1009 palaeoenvironments suggested for the La Luna Sea in the Cenomanian. The anacoracid material  
1010 reported here indicates that the outer shelf/upper slope environments of the La Luna Sea were  
1011 favorable to these sharks during the earliest Late Cretaceous. Previous reports of anacoracids from  
1012 deep marine environments were restricted to the uppermost Cretaceous of Angola (Antunes and  
1013 Cappetta, 2002) and Israel (Lewy and Cappetta, 1989). The assemblages described here indicate that

1014 anacoracids were adapted to outer shelf/slope marine environments early in their evolutionary  
1015 history. The contrast in palaeoenvironments between the La Luna Sea and the WIS (although some  
1016 species present in both regions are closely related, see above) might partly explain the differences in  
1017 anacoracid composition of respective assemblages. However, this may also be due to differences in  
1018 stratigraphic origins of these assemblages, suggesting that anacoracid evolutionary rates were high  
1019 in the mid-Cretaceous. This is a likely possibility given the large number of unnamed species from the  
1020 North American mid-Cretaceous.

1021

## 1022 **6. Conclusions**

1023 This contribution is the first report of chondrichthyans from the mid-Cretaceous of Venezuela and  
1024 one of the few records of this group from the Cenomanian of South America. Two sampled sites  
1025 within the La Luna Formation yielded twelve lamniform species including a number of new taxa.  
1026 Comparisons between these assemblages and others suggests a Cenomanian age for the base of the  
1027 La Luna Formation in the Maracaibo Basin. The composition of these assemblages indicates some  
1028 degree of endemism in the La Luna Sea that agrees with the restricted environmental conditions  
1029 proposed for this sea, but also suggests more probable connexions with the Western Interior Seaway  
1030 than with Southern Continent seas. The anacoracid diversity of these assemblages is strikingly high  
1031 (eight species in total) despite the outer shelf/upper slope palaeoenvironments of the La Luna  
1032 Formation. The high diversity of these opportunistic predators is probably related to the high  
1033 diversity of large marine vertebrates reported from these localities, which provided abundant food  
1034 resources.

1035

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1046

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1310

**1311 Figure Captions**

1312 Figure 1. Location map of the Cementos Andinos and La Luna quarries, Venezuela.

1313

1314 Figure 2. Cretaceous lithostratigraphic units and stratigraphic sections of La Luna and Cementos  
1315 Andinos quarries. The Sierra de Perijá section is based on Renz (1982) and Erlich et al. (1999). The

1316 fossiliferous horizon in La Luna Quarry is based on Moody and Maisey (1994, p. 2). The Chejendé  
1317 region section is based on Renz (1959) and González de Juana et al. (1980). Stratigraphic section of  
1318 the Aguada Member in the Cementos Andinos quarry is modified after Albino et al. (2016).

1319

1320 Figure 3. **A-B**, *Nanocorax* sp., anterolateral tooth (AMU-CURS-906) in **A**, lingual and **B**, labial views. **C-**  
1321 **H**, *Squalicorax moodyi* sp. nov. **C-D**, anterior tooth (MBLUZ P-430) in **C**, lingual and **D**, labial views. **E-**  
1322 **F**, lateral tooth (MBLUZ P-432-C) in **E**, lingual and **F**, labial views, **holotype**. **G-H**, anterolateral tooth  
1323 (MBLUZ P-432-D) in **G**, lingual and **H**, labial views. All scale bars equal 2 mm.

1324

1325 Figure 4. **A-S**, *Squalicorax lalunaensis* sp. nov. **A-B**, anterior tooth (AMU-CURS-894) in **A**, lingual and  
1326 **B**, labial views. **C-D**, anterolateral tooth (AMU-CURS-895) in **C**, lingual and **D**, labial views. **E-F**,  
1327 anterolateral tooth (AMU-CURS-896) in **E**, lingual and **F**, labial views. **G-H**, lateral tooth (AMU-CURS-  
1328 897) in **G**, lingual and **H**, labial views, **holotype**. **I-J**, anterolateral tooth (AMU-CURS-898) in **I**, lingual  
1329 and **J**, labial views. **K-L**, lateral tooth (AMU-CURS-899) in **K**, lingual and **L**, labial views. **M-N**,  
1330 lateroposterior tooth (AMU-CURS-900) in **M**, lingual and **N**, labial views. **O-P**, lateroposterior tooth  
1331 (AMU-CURS-901) in **O**, lingual and **P**, labial views. **Q-R**, posterior tooth (AMU-CURS-902) in **Q**, lingual  
1332 view, **R**, labial view and **S**, close-up on the labial ornament. All scale bar equal 2 mm except S (1 mm).

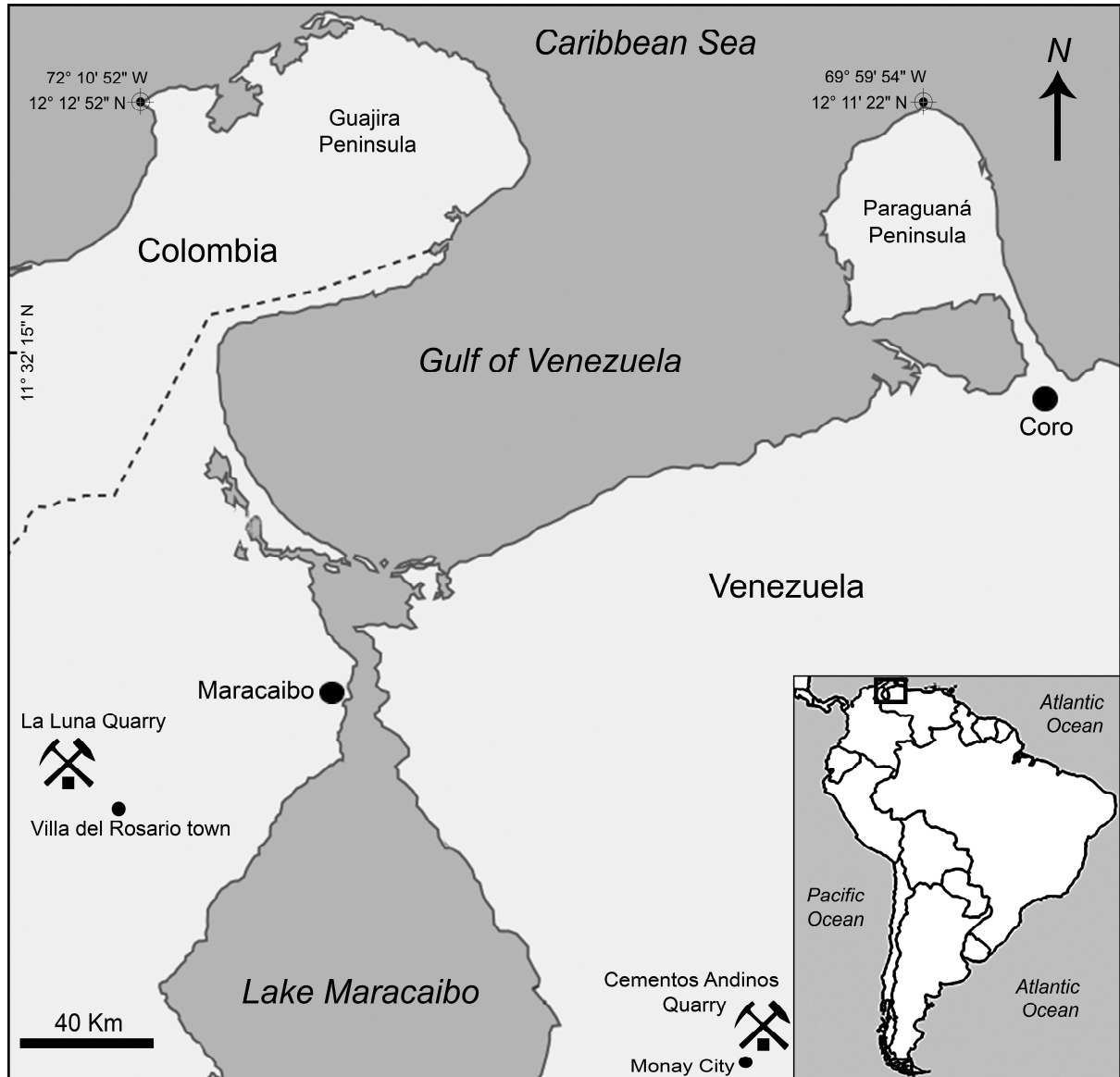
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1334 Figure 5. **A-B**, *Squalicorax* aff. *lalunaensis* sp. nov., lateral tooth (AMU-CURS-907) in **A**, lingual and **B**,  
1335 labial views. **C-I**, *Squalicorax* sp. 1. **C-D**, anterior tooth (MBLUZ P-430-B) in **C**, lingual and **D**, labial  
1336 views. **E-G**, lateroposterior tooth (MBLUZ P-430-C) in **E**, lingual view, **F**, close-up on the labial  
1337 foramina and **G**, labial view. **H-I**, lateral tooth (MBLUZ P-15) in **H**, labial and **I**, lingual views. **J-N**,  
1338 *Squalicorax* sp. 2. **J-K**, lateroposterior tooth (AMU-CURS-892) in **J**, labial and **K**, lingual views. **L-N**,  
1339 lateral tooth (AMU-CURS-893) in **L**, lingual, **M**, close-up on serrations of the median area of the

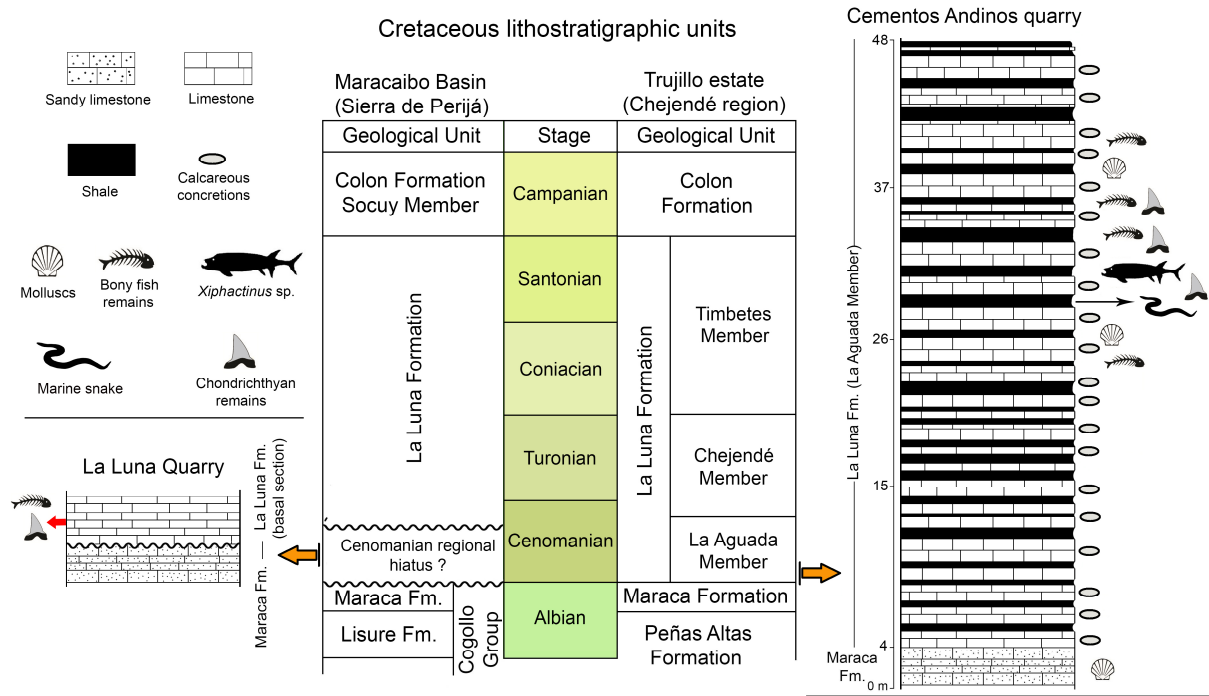
1340 mesial cutting edge of main cusp in labial view and **N**, labial views. **O-S**, *Squalicorax* sp. 3. **O-P**,  
1341 anterior tooth (MBLUZ P-881) in **O**, lingual and **P**, labial views. **Q-S**, lateral tooth (MBLUZ P-430-D) in  
1342 **Q**, lingual view, **R**, labial view and **S**, close-up on the labial foramina. **T-V**, *Squalicorax* sp. 4, lateral  
1343 tooth (MBLUZ P-432-B) in **T**, lingual and **U**, labial views and **V**, close-up on serrations of the median  
1344 area of the mesial cutting edge of main cusp in labial view. All scale bars equal 2 mm except F, M and  
1345 V (1 mm), and R (500  $\mu$ m).

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1347 Figure 6. **A-B**, *Cretoxyrhina mantelli*, lateral tooth (MBLUZ P-41) in **A**, lingual and **B**, labial views. **C-O**,  
1348 *Microcarcharias saskatchewanensis*. **C-D**, anterolateral tooth (MBLUZ P-14) in **C**, lingual and **D**, labial  
1349 views. **E-H**, anterior tooth (AMU-CURS-890) in **E**, lingual, **F**, labial, **G**, profile and **H**, labial views. **I-L**,  
1350 anterior tooth (AMU-CURS-891) in **I**, lingual, **J**, labial, **K**, profile and **L**, labial views. **M-O**, lateral tooth  
1351 (MBLUZ P-14-B) in **M**, lingual, **N**, labial and **O**, labial views. **P**, *Cretolamna* sp., lateral tooth (MBLUZ P-  
1352 86) in labial view. All scale bars equal 1 mm except A-B (5 mm) and P (2 mm).

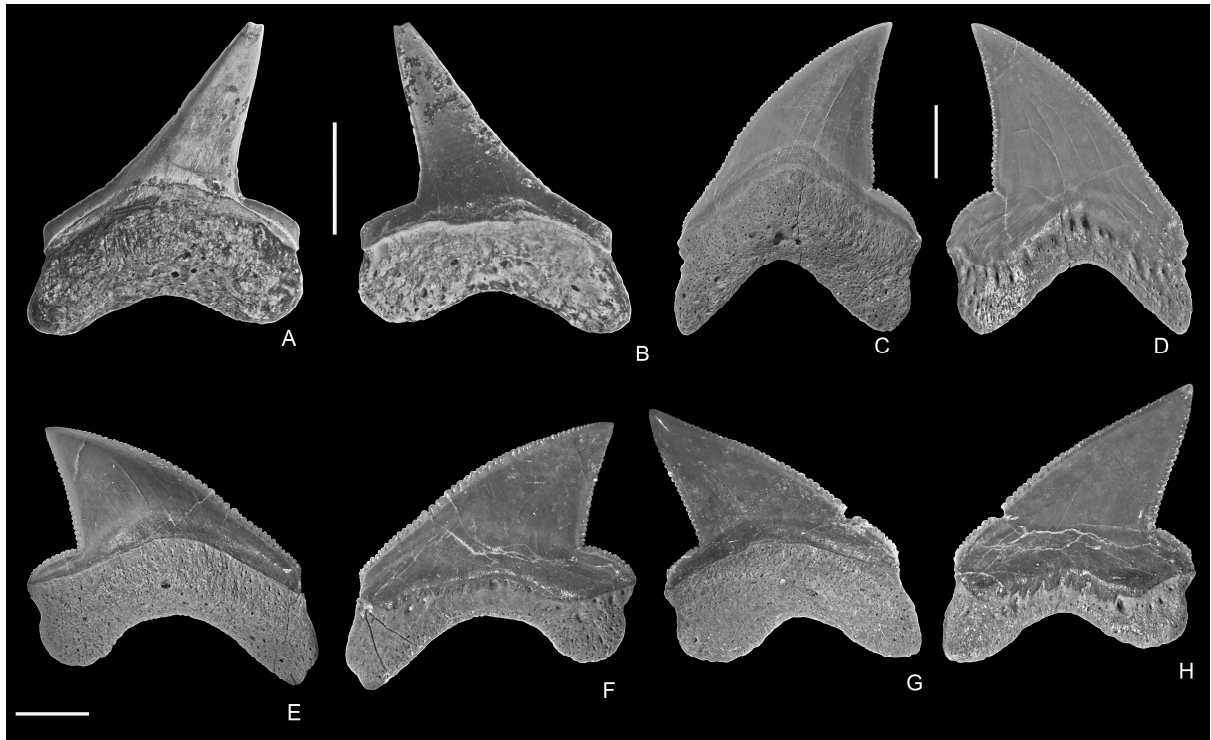
1353  
1354 Figure 7. **A-M**, *Acutalamna karsteni* gen. et sp. nov. **A-C**, anterior tooth (AMU-CURS-908) in **A**, lingual,  
1355 **B**, profile and **C**, labial views, **holotype**. **D-E**, anterolateral tooth (AMU-CURS-909) in **D**, lingual and **E**,  
1356 labial views. **F-J**, lateral tooth (AMU-CURS-910) in **F**, lingual, **G**, basal, **H**, labial/occlusal, **I**, profile and  
1357 **J**, labial views. **K-L**, anterolateral tooth (AMU-CURS-911) in **K**, lingual and **L**, labial views. **M**, anterior  
1358 tooth (MBLUZ P-431) embedded in sediment, in lingual view. All scale bars equal 2 mm.







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