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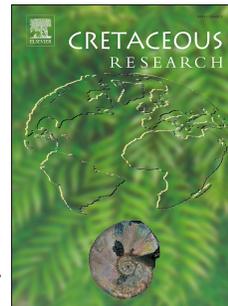
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1 Cenomanian vertebrates from Algora (central Spain): New data on the
2 establishment of the European Upper Cretaceous continental faunas

3

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25

26 ABSTRACT

27 The palaeontological area of Algora (Guadalajara Province, central Spain) provides the
28 largest concentration of vertebrate macroremains for the Cenomanian of south-western
29 Europe. The available faunal list for Algora, based on the analysis of scarce remains
30 collected in geological surveys carried out more than thirty years ago, was never
31 updated. Therefore, and despite the great potential of this site to reveal novel
32 information about the composition of the vertebrate fauna from the base of the Upper
33 Cretaceous in the continent, the previous determination of many of the taxa recognized
34 there is recognized here as inaccurate or erroneous (e.g., the identification of two
35 actinopterygian fishes, a single crocodyliform, the helochelydrid turtle *Helochelys*
36 *danubina* and carcharodontosaurid dinosaurs) . Recent fieldwork campaigns have
37 provided numerous remains, including those of clades poorly represented so far, as well
38 as others hitherto unknown at this site. The new faunal list proposed here included the
39 lepisosteoid *Obaichthys africanus*, the helochelydrid aff. *Plastremys lata*, the
40 pleurodiran *Algorachelus peregrina*, an indeterminate elasmosaurid, a non-eusuchian
41 neosuchian and a eusuchian crocodyliform, a likely abelisaurid theropod and a
42 lithostrotian sauropod. The study of these taxa provides new information about the
43 palaeobiogeography and temporal distributions of some lineages, and increases
44 knowledge about the poorly-known transition between the Lower and the Upper
45 Cretaceous faunas in Europe. This faunal replacement, in which several well-
46 represented lineages in the uppermost Cretaceous were established, is recognized as
47 strongly conditioned by climate changes that took place between the end of the Early
48 Cretaceous and the beginning of the Late Cretaceous.

49

50 *Keywords.* Late Cretaceous; south-western Europe; systematics; faunal replacement;
51 dispersal events.

52

53 **1. Introduction**

54 The palaeontological locality of Algora (Castilian Branch of the Iberian Ranges,
55 Guadalajara Province, Castilla-La Mancha, central Spain; Fig. 1) has yielded the main
56 concentration of Cenomanian vertebrate macroremains identified in south-western
57 Europe (Torices et al., 2012; Pérez-García et al., 2016a; Pérez-García, 2018).
58 Information on the vertebrate fauna from the first stages of the European Upper
59 Cretaceous (i.e. Cenomanian to Coniacian) is extremely limited compared with those of
60 both the Lower Cretaceous and the Santonian-Maastrichtian interval (Vullo and
61 Néraudeau, 2008a; Vullo et al., 2009; Torices et al., 2012; Callapez et al., 2014). The
62 faunas of both time intervals are radically different (Buffetaut and Le Loeuff, 1991;
63 Weishampel et al., 2010; Csiki-Sava et al., 2015; Ortega et al., 2015; Pereda Suberbiola
64 et al., 2015; Pérez-García et al., 2016b; Poyato-Ariza and Buscalioni, 2016). In this
65 sense, the analysis of the taxa represented in the uppermost middle-lowermost upper
66 Cenomanian locality of Algora has great potential to provide new data on how the
67 transition between both faunal assemblages occurred, as well as to identify patterns of
68 dispersal in several of the involved lineages.

69 Although the faunal association of Algora is recognized as exclusive to this region
70 (Torices et al., 2012; Pérez-García et al., 2016a; Mocho et al., 2019), several of the taxa
71 identified there have not been analyzed in detail until now. This is mainly because the
72 palaeontological activity carried out in this area was not initiated until few years ago.
73 Thus, the identification of vertebrate remains in the Cenomanian levels of Algora was
74 reported by Torices et al. (2010) and Segura et al. (2010), based on scarce and

75 fragmentary remains. These specimens had been found in the 1980s, when several
76 geological surveys were conducted. Torices et al. (2012) described these remains and
77 proposed a preliminary faunal list, which has not been updated since then. The same
78 authors described the sediments of these outcrops in the upper part of the Arenas de
79 Utrillas Formation as sandy coastal deposits (bars and channels) with subtidal and
80 intertidal events.

81 Although Torices et al. (2012) indicated that the vertebrate fauna from Algora was
82 composed of fish, turtles, crocodyliforms and dinosaurs, with Laurasian and
83 Gondwanan affinities, scarce information was provided about those taxa. Very few
84 specimens from Algora were known at that time. Thus, these authors recognized: two
85 ganoid scales of actinopterygians, one of them attributable to *Stromerichthys* sp., which
86 was regarded as a probable amiid, and the other to a possible second taxon, that could
87 belong to an indeterminate semionotid or lepisosteid fish; two members of Testudinata,
88 represented by a partial plate of uncertain anatomical position, attributable to an
89 indeterminate helochelydrid turtle (stem Testudines), as well as an indeterminate
90 member of Pan-Pleurodira, identified by scarce disjointed and generally fragmentary
91 plates, and recognized as cf. Eupleurodira; a pair of osteoderms, a cranial element
92 erroneously attributed to a fragment of the fronto-parietal area of the skull (see
93 Discussion), and scarce partial teeth of an indeterminate member of Crocodylomorpha
94 recognized as *Neosuchia* indet.; and three theropod teeth assigned to
95 *Carcharodontosauridae* indet. While the helochelydrid turtles constitute a lineage
96 exclusive to Laurasia, being known in both North America and Europe (Joyce et al.,
97 2011; Scheyer et al., 2015; Pérez-García et al., 2020), the putative identification of
98 *Stromerichthys* sp. and of a carcharodontosaurid theropod (both refuted here, see
99 Systematic discussion), suggested Gondwanan faunal affinities (Torices et al., 2012).

100 Cenomanian outcrops with vertebrate remains are relatively scarce in south-western
101 Europe. Prior to the discovery of the Algora palaeontological locality, the main
102 fossiliferous regions corresponded to those located in the central-western area of
103 Portugal (Buffetaut and Lauerjat, 1978; Jonet, 1981; Callapez et al., 2014), in the
104 vicinity of the Spanish city of Oviedo (La Cabaña Formation, in Asturias; Vullo et al.,
105 2009), and in the French region of Charentes (Vullo, 2007). However, the fossils
106 identified in all these areas corresponded to isolated finds which did not constitute
107 accumulations of macroremains. Algora represents an exception. For this reason,
108 several excavations have been conducted there since 2013 (Pérez-García et al., 2013;
109 2016a). As a result, more than 500 vertebrate macroremains, some of them
110 corresponding to isolated bones or partial bones, but others being articulated elements
111 (see general taphonomic aspects of the site in Torices et al., 2012; and a detailed
112 taphonomic study of the most abundant taxon from Algora, the bothremydid turtle
113 *Algorachelus peregrina*, in Pérez-García, 2018), have been extracted.

114 The most abundant taxon at Algora is a turtle attributable to Pan-Pleurodira. Its
115 belonging to Eupleurodira, previously suggested by Torices et al. (2012), was
116 confirmed (Pérez-García, 2017a). It was attributed to a new taxon, corresponding to a
117 littoral member of Bothremydidae: *Algorachelus peregrina*. The lineage of
118 *Algorachelus* is identified as the oldest pleurodiran clade that reached Laurasia from
119 Gondwana (Pérez-García, 2017a). *Algorachelus peregrina* has recently been recognized
120 in middle Cenomanian levels of Portugal (Pérez-García et al., 2017). In fact, the genus
121 *Algorachelus* is currently not only identified in Europe but also in both the lower-
122 middle Cenomanian of Palestine, being represented by *Algorachelus parva*, and in the
123 uppermost Cenomanian of Utah, where *Algorachelus tibet* is present (Pérez-García,
124 2018). In addition to this coastal form, the remains of a pelagic taxon have been

125 identified at Algora (Bardet et al., 2018). It corresponds to a caudal vertebra and the
126 almost complete pelvic girdle of an elasmosaurid plesiosaur. The only taxa from Algora
127 that have been analyzed in detail are that littoral turtle, this probably pelagic
128 sauropterygian, and a lithostrotian titanosaur taxon recognized by the largest collection
129 of this clade identified in a European Cenomanian site (Mocho et al., 2019). The Algora
130 titanosaur was recovered as sister taxon of the Italian upper Aptian or lower Albian
131 indeterminate form MSNM V7157, a Gondwanan origin having been considered for
132 this lineage (Mocho et al., 2019). However, as a result of the excavations carried out at
133 Algora, new remains of other vertebrate taxa that inhabited fresh and brackish waters
134 (fish and crocodiles), and of terrestrial forms (helochelydrid turtles and theropod
135 dinosaur), have also been found. These fossils have remained unpublished until now.
136 The detailed study of the main remains of each of these four lineages is carried out here.
137 The study of these new specimens allows us to refute some of the systematic
138 attributions performed by Torices et al. (2012). Thus, knowledge about the diversity of
139 vertebrates represented in the main site for the first stages of the Upper Cretaceous in
140 south-western Europe is significantly improved. The more precise characterization of
141 each of the lineages recognized at Algora sheds new light on how the transition between
142 the Lower Cretaceous and the Upper Cretaceous faunas of south-western Europe took
143 place. In fact, several well-represented lineages in the uppermost Cretaceous
144 (Campanian–Maastrichtian) sites of Europe, with a Gondwanan origin, were already
145 represented in this Cenomanian locality. This faunal replacement is related here to the
146 climate change that took place between the Albian and the early Cenomanian in the
147 framework of the major mid-Cretaceous global change that resulted in global warming
148 and finally in a first order eustatic rise at the Cenomanian-Turonian limit.
149

150 *Institutional abbreviations.* ALG, Algora collection, deposited in the Museo de
151 Paleontología de Castilla-La Mancha, Cuenca, Spain; CAMSM, Sedgwick Museum,
152 Department of Geology, University of Cambridge, UK.

153

154 **2. Palaeogeographical framework**

155

156 The Iberian Basin was one of the Mesozoic basins located in the eastern margin of
157 Iberia, at the westernmost region of the Tethys realm. During most of the Mesozoic,
158 Iberia was settled in a peculiar palaeogeographical position between the Atlantic realm,
159 the western Tethys realm and Africa, and remained placed at the northern subtropical
160 latitudinal belt. During the mid-Cretaceous, Iberia experienced drastic
161 palaeogeographical changes in the framework of major large-scale tectonic, climate and
162 eustatic variations. The rift to drift transition in the Atlantic margin of Iberia at the end
163 of the Early Cretaceous, a drastic climate change during the early Albian, and a
164 generalized trend to sea level rise recorded from the late Albian to the Turonian, in turn
165 punctuated by cycles of sea-level fall and rise, outline the palaeogeographical evolution
166 of Iberia during the mid-Cretaceous.

167 Progression of full spreading in the Atlantic Ocean is part of the phenomenon of
168 enhanced production of oceanic crust, and palaeogeographical changes in the
169 distribution of oceans and continents, which induced an overall modification in ocean
170 composition and patterns of oceanic circulation, and affected the interaction ocean-
171 atmosphere thus leading to a major global change (Leckie et al., 2002). That global
172 change resulted in global warming and in a progressive eustatic rise that would
173 culminate in the Cenomanian-Turonian limit, recording the highest absolute eustatic
174 level in the Phanerozoic (Haq et al., 1988).

175 In that framework, the connection of the North and South Atlantic oceans favored the
176 development of an equatorial humid climate belt. As a consequence, arid belts migrated
177 towards higher latitudinal positions, and most of Iberia remained under the influence of
178 a subtropical arid climate from the early Albian onwards (Chumakov et al., 1995;
179 Rodríguez-López et al., 2006, 2008, 2009, 2013). In Iberia, the lower Albian climate
180 change resulted in the development and expansion of sandy desert environments, as
181 recorded by the aeolian successions of the upper part of the Escucha Formation and of
182 the Utrillas Formation at the Iberian Basin (Rodríguez-López et al., 2006, 2008, 2009,
183 2010).

184 The record of the mid-Cretaceous global eustatic rise is diachronic in the Iberian
185 Basin. It progressed from the Tethys Sea, which invaded the basin following a SE-NW
186 direction. The overall transgressive trend was punctuated by repeated second and third
187 order cycles of sea-level rise and fall (Haq et al., 1988; Rodríguez-López et al., 2009,
188 2013). The transgression has been recorded by the progressive replacement of the arid
189 sandy desert environments and the arid siliciclastic coastal environments by shallow
190 carbonate platforms that became widespread during the Turonian (Martín-Chivelet et
191 al., 2019).

192

193 **3. Systematic palaeontology**

194

195 *Actinopterygii* Cope, 1887

196 *Ginglymodi* Cope, 1872

197 *Lepisosteiformes* Hay, 1929 (sensu López-Arbarello, 2012)

198 *Lepisosteioidea* Bonaparte, 1835 (sensu López-Arbarello, 2012)

199 *Obaichthyidae* Grande, 2010

200 *Obaichthys* Wenz and Brito, 1992

201

202 *Obaichthys africanus* Grande, 2010

203 (Fig. 2A–D)

204

205 *Material.* ALG 162 to ALG 165, a selection of four isolated scales.

206

207 *Description.* Specimens ALG 162 (Fig. 2A) and ALG 163 (Fig. 2B) are large,
208 rectangular flank scales much deeper than wide (28 and 22 mm in height, respectively).
209 Both specimens clearly show the typical ornamentation of the species, consisting of one
210 main median ridge flanked by several secondary ridges. The salient main ridge and the
211 smaller secondary ridges are subparallel. A third incomplete scale (ALG 164; Fig. 2C)
212 represents the same morphotype. Its main median ridge typically ends posteriorly in a
213 prominent, well-developed marginal spine. ALG 165 is an incomplete scale with a
214 damaged posterior margin (16 mm in preserved width) (Fig. 2D). This symmetrical
215 scale has a sub-rhombic outline and was probably located in the dorsal midline of the
216 fish. Its ornamentation is similar to that of ALG 162, ALG 163 and ALG 164.

217

218 Testudinata Klein, 1760

219 Helochelydridae Nopcsa, 1928

220

221 aff. *Plastremys lata* Owen in Parkinson, 1881

222 (Fig. 3)

223

224 *Material.* Several isolated elements, including a costal plate, probably corresponding to
225 the fourth on the right side (ALG 167; Fig. 3A–B, M–N); a peripheral plate, probably
226 the eighth on the left side (ALG 168; Fig. 3C–D, O); a second suprapygal (ALG 169;
227 Fig. 3E–F, P); the probably axillary area of a left hyoplastron (ALG 170; Fig. 3G–H,
228 Q); a plastral process, probably corresponding to a right hyoplastron (ALG 171; Fig. 3I–
229 J, R); a right epiplastron (ALG 172, Fig.3K–L); a left femur (ALG 173, Fig. 3T–W);
230 and an osteoderm (ALG 174; Fig. 3X–Y).

231

232 *Description.* The outer surface of the turtle plates presented here (Fig. 3A–L) shows an
233 ornamental pattern consisting of distinct tubercles, both isolated and grouped together
234 forming vermiculations (Fig. 3M–S). Some of these plates are relatively complete: the
235 costal ALG 167 (Fig. 3A–B), the peripheral ALG 168 (Fig. 3C–D), the right epiplastron
236 ALG 172 (Fig.3K–L), and, especially, the second suprapygal ALG 169 (Fig. 3E–F).
237 The width of the latter plate is double its length. The last pair of marginal scutes
238 experience a long overlap on it, equivalent to one third of the length of this plate in the
239 medial plane (Fig. 3E'). The gular scutes are identified as wider than long (Fig. 3K').
240 Other plastral elements are represented by partial plates (Fig. 3G–J). The femur is a
241 relatively robust element, with a slight sigmoidal morphology (Fig. 3T–W). The
242 osteoderm is broken, but it is recognized as subrectangular (Fig. 3X–Y). It displays a
243 well-developed central bulge. As in the case of the plates, the outer surface of this
244 element is covered by distinct tubercles.

245

246 Archosauria Cope, 1869

247 Crocodyliformes Hay, 1930

248 Mesoeucrocodylia Whetstone and Whybrow, 1983

249 Neosuchia Benton and Clark, 1988

250

251 Neosuchia indet.

252 (Figs. 4, 5A–C)

253

254 *Material.* Several isolated elements: ALG 175, a small fragment of the skull table (Fig.
255 4A–B); ALG 176, a complete right ectopterygoid (Fig. 4C–D); ALG 177, an almost
256 complete left exoccipital (Fig. 4E–G); ALG 178, the posterior fragment of a left
257 quadrate ramus (Fig. 4H–K); ALG 179, a fragment of a right angular (Fig. 4L–M);
258 ALG 180, ALG 181, ALG 182 and ALG 183, four isolated teeth (Fig. 4N–Y); ALG
259 184, ALG 185, and ALG 186, three partial osteoderms (Fig. 4Z–AB); ALG 187, the
260 proximal end of a left radius (Fig. 5A–B); and ALG 188, an almost complete left rib
261 (Fig. 5C).

262

263 *Description.* ALG 175 is a small fragment of skull table, corresponding to the region
264 directly anterior to the orbits, formed by the partial frontal and prefrontals (Fig. 4A–B).
265 Part of this piece was described in Torices et al. (2012: fig. 4A–B), but identified as
266 probably corresponding to a fragment of the fronto-parietal area of the skull table. Its
267 dorsal view is densely ornamented with shallow pits. No sutures are observed in that
268 view. A part of the right orbit is preserved in its posterolateral corner. In ventral view, it
269 presents the olfactory passage, corresponding to a longitudinal groove with a sharp
270 ridge in its sagittal axis and which is delimited laterally by two slightly elevated crests
271 (*cristae cranii*, sensu Iordansky, 1973). In addition, the fragment preserves part of the
272 right prefrontal and the anteriormost region of the left one, that contact along their
273 medial edges with the margins of the frontal passage along the *cristae cranii*.

274 ALG 176 is an almost complete isolated right ectopterygoid (Fig. 4C–D), which
275 lacks the posterior part of the jugal process. Thus, is it not possible to know the
276 participation of the ectopterygoid in the postorbital bar. The maxillary branch forms the
277 medial walls of the last three maxillary alveoli, with the most posterior alveolus placed
278 posteriorly to the posteroventral ramus. The anterior process of the ectopterygoid does
279 not form a maxillary shelf. The posteroventral ramus is slender and lacks the posterior
280 margin, so it is not possible to know if it reaches the caudal border of the pterygoid
281 wing.

282 ALG 177 is an almost complete left exoccipital (Fig. 4E–G), which lacks the
283 mediodorsal region and the ventral tip. The exoccipital preserves a slender and short
284 paroccipital process (Fig. 4E). A wide aperture for the cranioquadrate passage is placed
285 ventrally, and continues internally in a tubular groove. The ventral side preserves the
286 suture area with the quadrate, but it is not possible to know if the cranioquadrate groove
287 is laterally open (Fig. 4G). In occipital view, three foramina are located in the medial
288 margin of the exoccipital: a large foramen vagi for the nerves IX–XI, and below, two
289 hypoglossal foramina (XII) (Fig. 4E). The foramen for the carotid artery is not
290 preserved. The exoccipital constitutes the lateral margin of the foramen magnum and
291 part of the lateral wall of the occipital condyle.

292 ALG 178 is a posterior fragment of a left quadrate (Fig. 4H–K) which preserves the
293 lateral hemicondyle. The interalveolar space is not preserved and the foramen aëreum is
294 not observed in the smooth dorsal surface (Fig. 4H). Ventrally, longitudinal ridges
295 cannot be recognized, but a slightly transverse crest appears delimiting a concavity near
296 the lateral margin and close to the articular area (Fig. 4I). The lateral side of this
297 element preserves the sutural area with the quadratojugal (Fig. 4J).

298 ALG 179 is a partial right angular (Fig. 4L–M) which lacks both the anterior and the
299 posterior regions. The dorsal half of the lateral surface is profusely ornamented. A well-
300 marked groove separates longitudinally this region from the smooth ventral half. In the
301 labial surface, the angular region for the insertion of the pterygoid musculature is
302 ventrally exposed. It is not possible to identify any margin either of the external
303 mandibular fenestra or of the foramen intermandibularis caudalis. Medially, part of the
304 mandibular fossa is observed, ventrally bordered by the inner surfaces of the angular.

305 Several isolated teeth are known (Fig. 4N–Y). The crowns are subconical, pointed
306 and have a D-shaped cross-section. The crowns bear a pair of well-marked and smooth
307 carinae, lingually displaced. The labial surface is thus concave, and the apex is lingually
308 directed. The enamel has neither ridges nor ornamentation, but the surface is slightly
309 striated.

310 Some partial osteoderms are recognized (Fig. 4Z–AB). ALG 184 and ALG 185 are
311 flat elements, without projections or ridges, and bear circular pits (Fig. 4Z–AA). ALG
312 186 bears circular pits and displays a slight ridge, separating a flatter region from a
313 more depressed one (Fig. 4AB). All of them are incomplete and it is not possible to
314 determine their anatomical position accurately.

315 ALG 187 is a proximal end of a left radius (Fig. 5A–B). It is a slender element
316 (approximately 38 mm in length), expanded at its proximal end and oval-shaped in
317 cross-section. A soft crest can be observed in the dorsal side, near the proximal facet for
318 the ulna.

319 ALG 188 is an almost complete rib (Fig. 5C), probably a left dorsal rib, preserving
320 the complete capitular process and part of the tubercular process. The shaft is elongated
321 (approximately 140 mm in length from the proximal end of the capitular process to the
322 distal end), oval-shaped in section, lateromedially flattened, and pronouncedly curved.

323

324 *Eusuchia* Huxley, 1875

325

326 *Eusuchia* indet.

327 (Fig. 5D–S)

328

329 *Material.* ALG 189, ALG 190 and ALG 191, three isolated procoelous vertebrae (5D–
330 S).

331

332 *Description.* ALG 189 is an incomplete procoelous vertebra (Fig. 5D–H), preserving the
333 centrum and part of the neural arch, but lacking the neural spine. It is not possible to
334 distinguish the post- and prezygapophyses. The centrum is longer and slightly higher
335 than wide (approximately 20 mm in length, 18 mm in height, and 15 mm in width). The
336 neural canal is wide and there is no evidence of parapophyses, but the specimen
337 preserves the proximal region of the diapophyses in the base of the preserved slender
338 walls of the neural arch. The position of the diapophyses suggests that this vertebra
339 could probably be a cervical.

340 ALG 190 is a procoelous vertebral centrum (Fig. 5I–M), lacking the neural arch. The
341 centrum is similar in height and width (approximately 23 mm) but it is longer than high
342 and wide (approximately 30 mm). The centrum preserves anteriorly the proximal region
343 of the diapophyses, suggesting a cervical position for this vertebra. Ventrally, it bears an
344 anteroposteriorly directed keel, but it is broken anteriorly, and it is not possible to
345 distinguish the presence of hypapophysis. A small foramen is located laterally on each
346 side of the centrum, near the ventral keel.

347 ALG 191 is an almost complete procoelous vertebra of small size (approximately 20
348 mm in length and 36 mm in height) with the neural spine and transverse processes
349 distally broken. Its centrum is similar in height and width, but it is anteroposteriorly
350 twice as long as it is high and wide. Laterally, its body is compressed and bears a
351 shallow and slightly elongated lateral cavity in both sides. In the posterior area of the
352 centrum, the condyle presents a marked convexity. The neural arch is located in the
353 posterior half of the centrum. The parapophysial facets are located on the bases of the
354 transverse processes. Other dorsoventrally oriented depressions are observed between
355 the posteroventral surfaces of the transverse processes and the anteroventral margins of
356 the postzygapophysis. The ventral surface of this vertebral centrum is anteroposteriorly
357 keeled. Anteriorly, it bears a marked hypapophysis. The position of the parapophysial
358 facets above the centrum, at the base of the transverse processes, means it can be
359 classed as a dorsal vertebra, specifically one of the anteriormost ones, considering the
360 presence of the well-developed hypapophyseal keel.

361

362 Dinosauria Owen, 1842

363 Theropoda Marsh, 1881

364

365 Theropoda indet.

366 (Fig. 6A–F)

367

368 *Material.* ALG 192, the centrum of a caudal vertebra (Fig. 6A–F).

369

370 *Description.* The specimen corresponds to the centrum of a distal-middle caudal
371 vertebra assigned to a medium-sized theropod dinosaur. The neural arch has been lost

372 from the neurocentral suture, which does not appear to have been fused. The vertebral
373 centrum is amphicoelus and axially elongated, being more than twice as long as high.
374 Its articular faces are subrectangular and slightly higher than wide (Fig. 6A, D). The
375 posterior articular face is higher than the anterior one. The floor of the neural canal is
376 narrow and deep (Fig. 6F). The lateral surfaces are concave. No pleurocoels are present
377 on the lateral surface (Fig. 6B). A depression just below the neurocentral suture is
378 present on the left side but, since in the same place on the right side only a deformation
379 of the articular area is identified, both are considered as vestigial transverse processes
380 (Fig. 6B-E). The ventral surface is laterally narrow. Well-developed chevron facets are
381 present associated with the anterior and posterior ventral margins. The chevron facets
382 on each side are connected by a ridge that defines a ventral broad and shallow
383 longitudinal groove (Fig. 6C).

384 On the basis of the presence of articular facets for the chevrons and the presence of
385 vestigial transverse processes, the centrum is thought to belong to the distal-middle part
386 of the caudal series.

387

388 Tetanurae Gauthier, 1986

389 Ceratosauria Marsh, 1884

390

391 cf Abelisauridae

392 (Figs. 6G–P)

393

394 *Material.* Seven isolated teeth, ALG 193 to ALG 199 (Fig. 6G–P).

395 *Description.* Three of the new theropod teeth from Algora presented in this paper (ALG
396 195, ALG 196 and ALG 199; Fig. 6K–L, M, P) have a blade-like general shape. ALG

397 193 is more elongated and triangular and resembles an anterior/premaxillary tooth (Fig.
398 6G–H). ALG 197 is broken although its general shape seems to tend to blade-like and
399 its cross-section is more similar to ALG 194, ALG 196 and ALG 199 (Fig. 6N). ALG
400 198 maintains a blade-like shape but its cross-section is more flattened, probably
401 because it corresponds to a more distal position in the jaw (Fig. 6O). Although the tip of
402 ALG 194 is broken, its shape is clearly blade-like and its cross-section more similar to
403 ALG 195, ALG 196 and ALG 199 (Fig. 6I–J). These teeth have a height that varies
404 between 17.3 and 27.6 mm; a FABL (fore-aft basal length) that varies between 11.2 and
405 16.1 mm; and a width that varies between 4.7 and 8.4 mm. These teeth possess denticles
406 on both carinae although in two of them, the anterior denticles are not visible due to
407 breakage and erosion. Posterior denticle density varies between 2 and 3 denticles per
408 mm and the anterior denticle density varies between 2.5 and 3. Denticle shape is
409 rectangular in all cases. In ALG 193, ALG 194, ALG 195 and ALG 199 it is possible to
410 identify some wrinkle enamels although they are faint and difficult to see. These
411 structures cannot be observed in the other teeth because of the lack of preserved enamel
412 or the presence of iron crusts on the tooth surface.

413

414 **4. Discussion**

415

416 *4.1. Systematic discussion*

417

418 *Fishes.* The kind of isolated fish scales identified at Algora (e.g., Fig. 2A–D) has long
419 been described as *Stromerichthys aethiopicus* (e.g., Jonet, 1971; Vullo and Néraudeau,
420 2008a; Torices et al., 2012), an enigmatic taxon originally erected on the basis of a
421 mixture of elements from different taxa (Weiler, 1935; Cavin et al., 2015). Recent

422 studies have shown that these ornamented scales actually belong to the Cenomanian
423 lepisosteoid *Obaichthys africanus* (Grande, 2010; Cavin et al., 2015).

424 Most of the scales found at Algora are abraded, as indicated by the worn, non-shiny
425 ganoin enamel surface and the posterior margin devoid of spines. However, the new
426 scales presented here (Fig. 2A–D), as well as similar ones found in the site, are better
427 preserved and more diagnostic than those previously described (Torices et al., 2012),
428 and allow us to confirm the presence of *Obaichthys africanus* at the Algora site. The
429 second scale morphotype reported by Torices et al. (2012: fig. 3D) is reinterpreted here
430 as a smaller scale of *Obaichthys africanus* devoid of the primary ridge because it was
431 located in a region of the body not corresponding to the flank (as observed in
432 *Obaichthys decoratus*; Grande, 2010: fig. 479h). Therefore, *Obaichthys africanus*
433 represents the only fish taxon identified so far in the locality. Outside Spain, this gar is
434 known in the Cenomanian of Morocco (Grande, 2010; Cavin et al., 2015), Algeria
435 (Benyoucef et al., 2015), Egypt (Weiler, 1935), Portugal (Sauvage, 1897-1898; Jonet,
436 1971, 1981) and France (Vullo and Néraudeau, 2008a).

437

438 *Helochelydrid turtles*. The presence of an ornamental pattern formed by tubercles on the
439 outer surfaces of the plates (Fig. 3A–S) has been recognized as exclusive of the lineage
440 of basal turtles (i.e. stem Testudines) Helochelydridae (Lapparent de Broin and
441 Murelaga 1996, 1999; Scheyer et al., 2015). A partial plate of this group of turtles, with
442 an indeterminate anatomical position, showing a morphology and disposition of the
443 tubercles compatible with those of the plates presented here, was previously identified
444 at Algora (see fig. 3J in Torices et al., 2012). It was attributed to an indeterminate
445 member of Helochelydridae (a clade at that moment designated as Solemydidae)
446 (Torices et al., 2012). The differential diagnosis among the members of Helochelydridae

447 is mainly based on the ornamental pattern (Lapparent de Broin and Murelaga 1996,
448 1999; Joyce et al., 2011; Joyce, 2017; Pérez-García et al., 2020). Thus, all the plates
449 attributable to this lineage from Algora suggest the presence of a single form.

450 Helochelydridae is a group of terrestrial forms (Scheyer et al., 2015). Like other
451 terrestrial turtles (see Pérez-García, 2020), they possess osteoderms. The osteoderm
452 ALG 174 (Fig. 3X–Y) is attributable to Helochelydridae because its outer surface is
453 also covered by granulations. The morphology of the osteoderms varies depending on
454 their anatomical position (Barrett et al., 2002; Joyce et al., 2014). ALG 174 is very
455 similar to those of some osteoderms previously recognized for representatives of this
456 clade (e.g., fig. 20.3 in Joyce et al., 2014). The morphology and robustness of the femur
457 presented here (Fig. 3T–W) is also similar to that of the members of this lineage (e.g.,
458 fig. 16 in Joyce et al., 2014; fig. 11W-AB in Pérez-García et al., 2020).

459 Fragmentary material attributable to two indeterminate helochelydrid taxa, with a
460 different ornamental pattern, was identified in some Cenomanian outcrops in south-
461 western Europe, in the French region of Charentes (Vullo et al., 2010). In fact, the
462 ornamental pattern of each helochelydrid species has been recognized as one of the
463 main aspects to characterize the different representatives of this clade (see information
464 and figures of each taxa in: Meyer, 1855; Andrews, 1920; Bergounioux, 1957;
465 Lapparent de Broin and Murelaga 1996, 1999; Joyce et al., 2011; Joyce, 2017; Pérez-
466 García et al., 2020). Torices et al. (2012) recognized the only fragment of plate of a
467 helochelydrid from Algora which was found, at that time, as different from the
468 morphotype A of Vullo et al. (2010) (see fig. 3J in Torices et al., 2012; and fig. 4 in
469 Vullo et al., 2010), because the relative distance between each granulation or group of
470 granulations was greater in the Algora specimen. Torices et al. (2012) indicated that the
471 distance between its granulations was similar to that of the second morphotype from

472 Charentes (see fig. 6.1 in Vullo et al, 2010), but differed from this French form because
473 some tubercles were fused. Joyce (2017) recently performed a review of several clades
474 of basal turtles, including Helochelydridae. Considering the limited information on the
475 helochelydrids from Algora published by Torices et al. (2012), exclusively based on
476 that fragmentary plate, Joyce (2017) recognized the presence of *Helochelys danubina* in
477 this locality. This species corresponds to a form defined in the Cenomanian of Germany
478 by scarce material, currently lost (Meyer, 1855). Joyce (2017) proposed the presence of
479 this form in the Albian of the Cambridge Greensand Formation in England, to which he
480 attributed the entoplastron CAMSM B56424. Personal observation (A.P.-G.) of this
481 specimen, as well as of many others from the same Formation with an ornamental
482 pattern supporting their attribution to the same taxon, allows us to refute the
483 identification of this plate from the Cambridge Greensand Formation to *Helochelys*
484 *danubina*. In fact, its ornamental pattern is like that of the British form *Plastremys lata*
485 or very similar to that of this species. Joyce (2017) characterized the ornamental pattern
486 of *Helochelys danubina* as indistinguishable from that of the British Lower Cretaceous
487 *Helochelydra nopcsai*, with sharply delineated high tubercles, which dislocate and
488 never coalesce (Joyce et al., 2011). However, the tubercles of the taxon from Algora are
489 notably lower than wide, they do not dislocate easily, and they usually converge,
490 forming vermiculations consisting of two or more tubers. Other characters, as it is the
491 case of the area occupied by the tubercles in relation to the surface between them, allow
492 us to recognize clear differences between *Helochelydra nopcsai* and the forms from the
493 Cambridge Greensand Formation and Algora. Thus, this area is much higher in the
494 taxon from Algora than in *Helochelydra nopcsai*, being similar to that of the taxon from
495 the Cambridge Greensand Formation. Therefore, the taxon from Algora clearly differs

496 from *Helochelydra nopcsai*, but it also differs from the form present in the Cambridge
497 Greensand Formation, whose attribution to *Helochelys danubina* cannot be sustained.

498 A form recognized as aff. *Helochelydra* is currently identified in the Lower
499 Cretaceous record (Hauterivian to Barremian) in Spain (see Pérez-García, 2017b and
500 references therein). Its ornamental pattern is similar to that of *Helochelydra nopcsai*, so
501 it clearly differs from the Algora taxon. A second helochelydrid was identified in the
502 Spanish Lower Cretaceous record, the recently described Albian *Aragochersis*
503 *lignitesta*, with an ornamental pattern that also differs radically from that of the taxon
504 from Algora (Pérez-García et al., 2020). A third taxon has also been recognized. It
505 corresponded to ‘*Trachyaspis turbulensis*’, defined by several peripheral plates, and
506 currently recognized as a *nomen dubium* (see Pérez-García, 2017b and references
507 therein). The size, the distribution in relation to the spacing between them, and the
508 height of the tubercles of the type material of ‘*Trachyaspis turbulensis*’, are compatible
509 with those from Algora. However, poor knowledge about this species, referred by some
510 authors to the Aptian-Cenomanian *Plastremys lata* (Joyce, 2017), means that its
511 attribution to this British form cannot be confirmed. In fact, abundant unpublished
512 Spanish material, currently under study and which will allow an assessment of the
513 validity of ‘*Trachyaspis turbulensis*’, shows that the vermiculations were probably
514 absent or very limited in that Lower Cretaceous form, as in *Plastremys lata*. However,
515 the ornamental pattern of the taxon from Algora is much closer to that of the Lower
516 Cretaceous forms *Plastremys lata* and ‘*Trachyaspis turbulensis*’ than to that of the
517 Spanish and French Campanian-Maastrichtian genus *Solemys*, which is markedly
518 vermiculated (Lapparent de Broin and Murelaga 1996, 1999; Pérez-García et al.,
519 2016b).

520

521 *Crocodyliforms*. Currently available specimens from Algora are represented by isolated
522 cranial and postcranial elements, belonging to an indeterminate number of individuals.
523 The information provided by most of the specimens (e.g., frontal, ectopterygoid,
524 exoccipital, radius, rib, teeth, osteoderms) confirms their attribution to Neosuchia, but
525 lacks sufficient details to assess whether they belong to a more exclusive group or to
526 know the number of species represented.

527 The angular shows a well-marked ventral exposition of the region for the insertion of
528 the pterygoid musculature. This is a condition of non-eusuchian neosuchians, while
529 more derived forms, such as eusuchians, have a more lateral orientation of this area
530 (Ortega, 2004).

531 In the case of the ectopterygoid, this element closely borders the posterior maxillary
532 tooth-row, a common feature in Eusuchia. However, this character does not appear in
533 alligatoroids or in some non-eusuchian neosuchians such as *Bernissartia* and
534 *Pachycheilosuchus*, where the ectopterygoid is separated from the tooth-row by a
535 maxillary shelf (Brochu, 1997; Rogers, 2003).

536 The tooth morphology is common among Neosuchia and identified as compatible
537 with members of this clade (Groh et al., 2019). Some teeth are slender (Fig. 4W–Y),
538 and could resemble those of longirostrine crocodylians.

539 The osteoderms recovered at Algora are very incomplete, but their morphology is
540 compatible with that of neosuchian crocodiles. The ridge observed in ALG 186 is
541 interpreted as the lateral keel of a non-eusuchian neosuchian osteoderm. The
542 identification of a non-eusuchian form can also be confirmed by the presence of a lateral
543 flap.

544 Procoelous vertebrae are characteristic of the representatives of Eusuchia (*sensu*
545 Clark and Norell, 1992), although this character is shared by caudal vertebrae of some
546 advanced neosuchians such as *Bernissartia* (Norell and Clark, 1990).

547 Both ALG 189 and ALG 190 have a stout centrum with a wide neural canal,
548 resembling the morphology of a procoelous caudal vertebra previously assigned to a
549 titanosaur from La Cabaña Formation, near Oviedo (Vullo et al., 2009), and
550 subsequently reinterpreted as belonging to a crocodyliform (Narváez et al., 2014). With
551 a similar size to the specimens from Algora, this vertebra preserves part of the slender
552 wall of its neural arch, like that in ALG 189, but there is no evidence of diapophysis,
553 and it is not possible to assign it to a cervical vertebra. In addition, the centrum of the
554 vertebra from La Cabaña is higher than wide, differing from the Algora specimens,
555 more rounded than oval-shaped. Despite the similarities with ALG 189 and ALG 190,
556 we conclude here that it is not possible to confirm its assignment to crocodyliforms due
557 to its poor preservation.

558 ALG 191 exhibits a pronounced hypapophysis. The presence of hypapophysis is
559 common on the cervical and first dorsal vertebrae of Eusuchia. In derived neosuchians
560 like *Bernissartia*, the hypapophyseal keels are present on the tenth vertebra behind the
561 atlas, while in Crocodylia this structure reaches the eleventh or twelfth vertebrae behind
562 the atlas (*sensu* Brochu, 1997). The parapophysial facets of this specimen from Algora
563 have migrated with respect to the vertebral centrum, as occurs in the tenth or eleventh
564 postaxial vertebrae in Eusuchia, which belongs to the first dorsal vertebra.

565 On the other hand, a peculiar character in ALG 191 is the presence of depressions on
566 the lateral sides of the vertebral centrum. This feature is common in the eusuchian
567 presacral vertebrae (i.e., posteriormost dorsal vertebrae), but it is unusual for the first
568 dorsal vertebrae (Mook, 1921; Erickson, 1976; Frey, 1988; Brochu, 1992). In addition,

569 these depressions in eusuchian crocodiles are never as evident as in the specimen from
570 Algora, despite being shallow. Similarly, the presence of posterior depressions between
571 the posteroventral surfaces of the transverse processes and the anteroventral margins of
572 the postzygapophysis could be observed in some dorsal vertebrae, in which the
573 parapophysis is on the transverse process. The presence of this kind of depression is
574 commonly interpreted as a feature with pneumatic origin (e.g. pneumatic fossae; see
575 O'Connor, 2006), but this character is not present in the eusuchian first dorsal vertebrae.
576 On the other hand, these depressions in the Algora specimen are not as deep as the
577 pneumatic fossae observed in these vertebrate clades. These structures are absent in the
578 dorsal vertebra of an indeterminate member of Eusuchia from the middle Cenomanian
579 at the Portuguese locality of Nazaré (see fig. 4F in Callapez et al., 2014).

580

581 *Theropods.* Most of the described features of the centrum ALG 192 are common in the
582 vertebral centra of the posterior caudals of theropods. The elongation of the centrum is a
583 widespread feature of the theropod distal caudal vertebrae, present in most
584 neotheropods. A longitudinal groove, ventrally flanked by two longitudinal ridges, is
585 reported in most theropods (Carrano et al., 2002; Rauhut, 2003). Therefore, considering
586 the relatively limited information provided by this element, it is attributed to Theropoda
587 indet.

588 A previous study of the theropod teeth from Algora classified them as belonging to
589 Carcharodontosauridae (Torices et al., 2012). The two theropod teeth previously
590 described in Torices et al. (2012) are perfectly compatible in measurements and
591 morphometric characteristics with all the new teeth described here. Both sets of teeth
592 are blade-like in shape and the cross-section is basically the same in all of them. They
593 share some qualitative features. Enamel wrinkles can be recognized in all teeth in which

594 that region is preserved. Principal component and discriminant analyses were performed
595 for the first time for the teeth from this locality in order to confirm or refute the previous
596 systematic assignment. The data sample was built using databases that included
597 carcharodontosaurids like *Acrocanthosaurus*, abelisaurids including data from
598 *Arcovenator escotae* (Tortosa et al., 2016), cf. *Arcovenator escotae* (Pérez-García et al.,
599 2016b) and *Allosaurus* from Smith et al. (2005), Fanti et al. (2014), Richter et al.
600 (2013), Hendrickx et al. (2015, 2020), and Longrich et al. (2017).

601 In the Principal Component Analysis, the total variance is explained at 90.75% by
602 two components. In the first component the variables that weigh more are the ones
603 describing the general size of the tooth, while in the second component the denticle
604 variables are the ones that weigh more.

605 In Figure 7 it is possible to observe how the Algora teeth group together and slightly
606 overlap with the *Allosaurus* teeth although they are also near to some abelisaurid
607 specimens, including *Arcovenator* and cf. *Arcovenator* teeth. It can be observed that the
608 carcharodontosaurid and abelisaurid teeth overlap. *Allosaurus* teeth also overlap partly
609 with the *Acrocanthosaurus* teeth as well as with some abelisaurid teeth.

610 Four discriminant analyses have been performed to analyze the possible assignment
611 of the Algora teeth. In the first analysis, without *Arcovenator* teeth, the Algora teeth
612 were not assigned to any group and the analysis assigned one tooth to *Allosaurus* (ALG
613 195) and four of them to an abelisaurid (ALG 193, ALG 194, ALG 197 and ALG 199).
614 In this discriminant analyses the sample correctly classified is 95% (Table 1). We have
615 to consider how the different groups of teeth behave in the analysis. None of the
616 *Allosaurus* teeth are reclassified and the same happens with the dromaeosaurid,
617 *Acrocanthosaurus* and *Chenisauros barbaricus* teeth. One tooth of carcharodontosaurid
618 dinosaur is reassigned to *Acrocanthosaurus* and two teeth are assigned to abelisaurids,

619 and two abelisaurid teeth are reassigned to *Allosaurus*. This shows that there is some
620 overlapping between these groups as observed in Figure 7.

621 In the second discriminant analysis (90.3% of correctly classified sample, Table 2),
622 Algora teeth were assigned to its own group and the results were that only one of
623 Algora teeth (ALG 195) was reassigned to *Allosaurus*. This suggests that the variation
624 between these seven teeth could be caused by individual or intraspecific variation and
625 all the samples could belong to the same taxon.

626 In the third and fourth analyses *Arcovenator* teeth were included as this European
627 abelisaurid is the only one that has teeth associated to postcranial material (Tortosa et
628 al., 2016) and other teeth from the Iberian Peninsula assigned to cf. *Arcovenator* (Perez-
629 Garcia et al., 2016b) are also considered. Although *Arcovenator* and cf. *Arcovenator*
630 teeth come from upper Campanian deposits, we found interesting to compare these teeth
631 with our sample in order to better discriminate their assignment and test the hypothesis
632 if they could belong to the same lineage. In the third analysis, Algora teeth were not
633 assigned to any group and two teeth were assigned to abelisaurids (ALG 194 and 197),
634 two teeth to *Arcovenator* (ALG 193 and 199) and one tooth to *Allosaurus* (ALG 195).
635 In this analysis the sample was correctly classified at 93.2% (Table 3). In the analysis
636 only one tooth of *Arcovenator* is reassigned to *Allosaurus*. In abelisaurids, two teeth are
637 reassigned to *Allosaurus* and one tooth to *Arcovenator*. In carcharodontosaurids, two
638 teeth are reassigned to *Acrocanthosaurus* and one tooth to abelisaurids. Only one
639 *Allosaurus* tooth is reassigned to *Arcovenator*. This is a result of the overlapping
640 between the different theropod groups.

641 In the fourth analysis where Algora teeth are assigned to its own group and the
642 sample is correctly classified at 93.4%, the Algora teeth are correctly classified in its

643 own group and the rest of the groups behave in the same way as the third analysis
644 (Table 4).

645 However, it is interesting to analyze how, in the first and third analyses, the Algora
646 group is divided between *Allosaurus* and abelisaurid teeth (including *Arcovenator* in the
647 third). The teeth are quite separate from the carcharodontosaurid teeth. The main factor
648 of separation between the groups is tooth size. It could be argued that these teeth might
649 belong to a juvenile but the whole sample of theropod teeth from Algora comes from
650 different levels and parts of the site so it is highly improbable that all of them could
651 belong to juvenile individuals. In this new theropod teeth sample being analyzed, as
652 well as in the two theropod teeth from Algora described before (Torices et al., 2012), we
653 do not observe characters that are cited as exclusive of Carcharodontosauridae (Canudo
654 et al., 2010). Bilobate denticles are absent and the anterior denticles extend through the
655 anterior carina while in carcharodontosaurids they are absent in the lower half of the
656 anterior carina. We could not observe, due to the preservation of the enamel in the teeth
657 and the iron crust covering the surface, the presence of enamel wrinkles in some of the
658 teeth but they were present faintly in four of them and the ones described by Torices et
659 al. (2012). Although enamel wrinkles have been considered in the past as exclusive to
660 the carcharodontosaurids, they are now regarded as a synapomorphy observed in several
661 basal tetanurans, and they are also present in abelisaurids (Brusatte et al., 2007; Canudo
662 et al., 2010; Hendrickx et al., 2020).

663 In Figure 7, the Algora teeth are quite near the abelisaurid teeth from the Moroccan
664 Cenomanian Kem Kem beds described by Richter et al. (2013). The crowns from Kem
665 Kem and Algora show some characteristics in common, such as the profile of the tooth
666 with the mesial carina strongly curved and the distal one straight. In addition, the
667 crowns are small in comparison with other abelisaur or carcharodontosaurid teeth.

668 However, it is not possible to see, in the Algora teeth, the presence of a flat or concave
669 area along each carina in the lateral teeth, which is considered a synapomorphy of the
670 ceratosaurians (Rauhut, 2004, Richter et al., 2013). A distinct size difference between
671 mesial and distal denticles was also recognized as present in abelisaurids according to
672 Richter et al. (2013), but Hendrickx et al. (2020) indicated that mesial and distal
673 denticles are similar in size. Mesial and distal denticles have the same size in the Algora
674 teeth.

675 In Algora teeth the mesial carina reaches the cervix, which is a character shown in
676 abelisauroids, with the exception of *Masiakasaurus* (Hendrickx, 2015) and *Arcovenator*
677 (Tortosa et al., 2014), where it is twisted in its lateral teeth (Hendrickx, 2015). The
678 distal carina is centrally positioned or slightly labially displaced in abelisauroids, which
679 is in agreement with Algora teeth, where is centrally positioned (Hendrickx, 2015).

680 Regarding cross section, it varies in abelisaurids depending the position they have in
681 the jaw. Abelisaurids present a salinon to J-shaped cross section in the anterior teeth
682 (Fanti and Therrien, 2007; Smith, 2007, Hendrickx and Mateus, 2014) and D-shaped to
683 lanceolate (Gianechini et al., 2015; Novas et al., 2010) cross-section in lateral teeth
684 (Hendrickx et al., 2020). Algora teeth present a cross section between lanceolate and D-
685 shaped (this last condition being present in a single tooth). Therefore, taking into
686 account the results of the statistical analyses performed here, and the qualitative
687 characteristics, it is reasonable to assign these Algora teeth to cf. Abelisauridae.

688

689 *4.2. Faunal implications*

690

691 *Fishes.* As mentioned above, *Obaichthys africanus* is compatible with the Cenomanian
692 age of Algora, whereas the closely related Brazilian species *Obaichthys decoratus* is

693 known in Albian deposits (Grande, 2010). From a palaeobiogeographical point of view,
694 *Obaichthys africanus* is one of the better-known forms of evidence for the dispersal of
695 Gondwanan taxa to the European archipelago during the Cenomanian. Other taxa that
696 clearly support this dispersal event are the hybodont shark *Tribodus* and the basal snake
697 *Simoliophis*, identified in France (Vullo and Néraudeau, 2008b; Rage et al., 2016); but
698 also the lineage of the turtle *Algorachelus*, whose type locality is Algora (Pérez-García,
699 2017a, 2018). Obaichthyid gars were small to medium-sized piscivorous predators that
700 inhabited fresh and brackish waters of fluvial–deltaic and lacustrine–lagoonal
701 environments (Grande, 2010; Cavin et al., 2015; Brito et al., 2016). However, the
702 apparent dispersal of *Obaichthys africanus* from northern Africa to south-western
703 Europe suggests that this form may have been able to live temporarily in marine
704 environments, as observed in some other species of extinct and extant gars (see
705 Alvarado-Ortega et al., 2016).

706

707 *Helochelydrid turtles*. Solemydidae is a clade of basal turtles exclusive to the
708 Laurasiatic record; being known in North America and Europe (Lapparent de Broin and
709 Murelaga 1996, 1999; Scheyer et al., 2015; Joyce, 2017; Pérez-García, 2017b; Pérez-
710 García et al., 2020). This terrestrial clade is poorly represented in the uppermost
711 Jurassic, but it is well-known throughout the Cretaceous up to the Maastrichtian.

712 Helochelydridae is a well-represented clade in the uppermost Cretaceous of south-
713 western Europe and, especially, in the Iberian Peninsula and in Southern France, where
714 *Solemys* is recognized (Lapparent de Broin and Murelaga, 1999; Pérez-García, 2017b).
715 That latest Cretaceous form displays a vermiculated pattern, which clearly differs from
716 the one recognized at Algora. The attribution of the taxon from Algora to the German
717 and putatively British Lower Cretaceous form *Helochelys danubina* is here refuted. It is

718 identified as a closely related form to the European Lower Cretaceous taxa '*Trachyaspis*
719 *turbulensis*', from the upper Aptian-lower Albian in Teruel (Spain), and *Plastremys*
720 *lata*, defined in the Albian-Cenomanian on the Isle of Wight (United Kingdom). Thus,
721 the survival of the lineage of Helochelydridae to which *Plastremys lata* belongs at the
722 beginning of the Late Cretaceous is supported by the findings at Algora.

723

724 *Crocodyliforms*. Until recently, the Cenomanian record of crocodyliforms from the
725 Iberian Peninsula was limited to undescribed, isolated and scarce remains of uncertain
726 systematic attribution from several outcrops near Lisbon (Portugal) (Jonet, 1981), and to
727 a jaw fragment belonging to a longirostrine crocodile found in the Portuguese locality of
728 Nazaré, which was preliminarily assigned to Dyrosauridae by Buffetaut and Laverjaut
729 (1978), but reinterpreted as not attributable to a particular group of Mesoeucrocodylia
730 because of its lack of diagnostic characters (Buffetaut, 1979). Callapez et al. (2014)
731 supported this hypothesis and reported the discovery of new vertebrate remains in
732 Nazaré, including some osteoderms of Mesoeucrocodylia indet. and a relatively
733 complete dorsal vertebra of an indeterminate member of Eusuchia.

734 Vullo et al. (2009) recognized the presence of some isolated elements of this group
735 of reptiles near Oviedo (Asturias). These authors presented a poorly preserved caudal
736 procoelous vertebra, referred to as an indeterminate eusuchian taxon, and also several
737 teeth with different morphologies and a small fragment of dentary, all of them
738 recognized as taxonomically congruent with the presence of a form which may
739 correspond to one of the earliest alligatoroids.

740 Although scarce remains of crocodyliform from Algora were previously recognized
741 (see introduction), they allowed the identification of indeterminate advanced
742 neosuchians, based on the pitted ornamental patterns, the conical-shaped teeth with

743 smooth ridges and mesial and distal carinae, and the morphology of the osteoderms
744 (Torices et al., 2012). As indicated by Callapez et al. (2014), the evidence of western
745 European crocodyliforms from the lower Upper Cretaceous to the Campanian-
746 Maastrichtian is relatively rare and therefore, the process of replacement of non-
747 eusuchian Neosuchia by eusuchian crocodyliforms is poorly known. Recently,
748 *Portugalosuchus azenhae* has been described based on a partial skull and lower jaw
749 material from the Cenomanian in the Tentugal Formation in west-central Portugal
750 (Mateus et al., 2018). *Portugalosuchus* is proposed as a member of Eusuchia and
751 discussed as a possible Crocodylia.

752 The available information from the Algora crocodyliforms allows the determination
753 of at least a non-eusuchian neosuchian and an indeterminate member of Eusuchia.
754 Currently available material does not allow the relationships among the Portuguese and
755 Spanish Cenomanian crocodyliforms to be established.

756
757 *Theropods*. Previously described theropod teeth from Algora were assigned to
758 carcharodontosaurids, suggesting a connection between Gondwana and Laurasia during
759 the mid-Cretaceous (Torices et al., 2012). The skeletal remains of Theropoda from
760 Algora joined the scarce theropod skeletal record from the Cenomanian of Europe.
761 From southern France, there is the description of an isolated tooth from the Gard
762 department attributed to '*Megalosaurus*' (Buffetaut et al., 1991) and the teeth from
763 Charentes assigned to dromaeosaurids, troodontids and carcharodontosaurids (Vullo et
764 al., 2007; Vullo and Néraudeau, 2010). Teeth from Charentes so far identified as
765 belonging to carcharodontosaurid are from the earliest Cenomanian to lower-mid
766 Cenomanian sites (Vullo and Néraudeau, 2008a). An isolated tooth from northern Spain
767 was also assigned to a carcharodontosaurid. It was found in the lower Cenomanian

768 levels of Limanes (Asturias) (Ruiz-Omeñaca et al., 2009). Based on the current
769 discussion on the dental theropod features (Brusatte, 2007; Hendrick et al., 2015, 2020),
770 all these specimens should be revised in order to re-evaluate their relationships with
771 carcharodontosaurids.

772 Despite the archipelago condition of Europe in the Cenomanian, it seems that the
773 same kind of theropod dinosaur faunas at broad taxonomic level could be found across
774 Europe. These Cenomanian faunas also seems to be a continuation of the Lower
775 Cretaceous (or even older) faunas in this continent (Csiki-Sava et al., 2015). In addition
776 to these older European theropod faunas, which were the result of the evolution of
777 isolated members of tetanurans (Csiki-Sava et al., 2015), we find a few additions that
778 suggest Laurasian connections, such as dromaeosaurids and troodontids (Vullo et al.,
779 2007; Vullo and Néraudeau, 2010). The previous identification of carcharodontosaurids
780 in the above indicated Spanish and French Cenomanian sites suggested putative
781 Gondwana influences (Vullo et al., 2007; Torices et al., 2012). Although the Algora
782 teeth initially resembled to those of the carcharodontosaurids (Torices et al., 2012), the
783 results of our statistical analyses show that their assignment could agree most closely to
784 an abelisaurid. The fact that two teeth in the third analyses were assigned to
785 *Arcovenator*, and another two to abelisaurids, is quite interesting. These teeth could
786 belong to the abelisaurid lineage that would be present at the end of the Upper
787 Cretaceous of Europe (Campanian–Maastrichtian). Abelisaurid dinosaurs are present in
788 the Cenomanian of Gondwana in Kem Kem beds (Smith and Lamanna, 2006, D’orazi
789 Porchetti et al., 2011, Richter et al., 2013, Longrich et al., 2017). The Algora specimens
790 resemble abelisaurid teeth in the general shape of the tooth and size but there are also
791 features that are not in agreement with that assignment, such as the presence of a flat or
792 concave surface near the carina. In contrast, large theropods in the Upper Cretaceous

793 (Campanian–Maastrichtian) of Europe are represented by abelisaurid theropods, this
794 Gondwanan clade having reached Europe during the Upper Cretaceous (Csiki-Sava et
795 al., 2015; Pérez-García et al., 2016b; Tortosa et al., 2014). Carcharodontosauria
796 theropods are known in Europe from the Upper Jurassic, their record in Lower
797 Cretaceous levels of this continent being relatively abundant (Brusatte et al., 2008;
798 Ortega et al., 2010; Malafaia et al., 2019). The presence of enamel wrinkles and the
799 similar size of mesial and distal denticles in the Algora is shared by both
800 carcharodontosaurids and abelisaurids (Hendrickx et al., 2020). For this reason, we
801 cannot assign these teeth definitely to Abelisauridae and their assignment to this group
802 must be left as tentative until more material is found.

803

804 *4.3. Climatic changes and faunal replacements*

805

806 The replacement identified when the Lower Cretaceous faunas of the Iberian Peninsula
807 are compared with those of the uppermost Cretaceous might have been induced or, at
808 least, strongly conditioned by the climate change that took place between the end of the
809 Early Cretaceous and the beginning of the Late Cretaceous, during the Albian and early
810 Cenomanian, before the Algora sediments were deposited. Thus, as above explained,
811 during the early Albian, the connection of the North and South Atlantic resulted in the
812 migration of arid belts towards higher latitudinal positions. As a consequence, Iberia
813 remained under the influence of a subtropical arid climate during much of the Albian
814 and the Cenomanian (Chumakov et al., 1995; Rodríguez-López et al., 2006, 2008,
815 2009).

816 The lower Albian climate change resulted in the development of sandy desert
817 environments in the Iberian Basin, as recorded by the thick sedimentary successions in

818 the upper part of the Escucha Formation and in the Utrillas Formation (Rodríguez-
819 López et al., 2006, 2008, 2009, 2010). The Albian climate change coincides with the
820 Iberian disappearance or loss of diversity of several vertebrate lineages well represented
821 in the Lower Cretaceous faunas (e.g., the disappearance of the freshwater basal
822 cryptodiran and the pleurosternid turtles, the neosuchian bernissartiid and goniopholidid
823 crocodyliforms, the basal styracostern ornithopod and the non-titanosaurian
824 somphospondylan dinosaurs; Schwarz-Wings et al., 2009; McDonald et al., 2012;
825 Buscalioni et al., 2013; Pérez-García et al., 2015; Gorscak and O'Connor, 2016; Pérez-
826 García, 2017b). The expansion of desert systems was also favored by a second order
827 eustatic fall (Rodríguez-López et al., 2008, 2009), by which the low level of the Tethys
828 Sea could have facilitated potential faunal exchanges with Gondwana due to the
829 elimination of biogeographical barriers. This desert system remained active until the late
830 Cenomanian, when a major transgression of the Tethys invaded the whole Iberian Basin
831 and the well-known Upper Cretaceous carbonate platforms developed (Rodríguez-
832 López et al., 2006, 2008, 2009; Martín-Chivelet et al., 2019). As the transgression
833 progressed the siliciclastic aeolian and associated ephemeral alluvial sediments were
834 reworked into coastal and shallow marine environments and gradually mixed with
835 carbonate sediments. The extensive depositional system would comprise a complex
836 array of environments ranging from back-erg environments in the more inner and
837 proximal positions in the western and north-western areas of the basin, to central erg,
838 and finally to fore-erg environments in the distal reaches of the system at its encounter
839 with the Tethys Sea in the eastern and southeastern regions of the Basin (Rodríguez-
840 López et al., 2006, 2008, 2009, 2010).

841 The Algora succession had occupied an inner and proximal palaeogeographical
842 position, probably corresponding to back-erg environments (i.e., interaction of aeolian

843 and ephemeral fluvial environments, resulting in such structures as dunes, wadis, mud
844 playas, deflation plains) that were progressively invaded by the sea from the early
845 Cenomanian, thus developing coastal siliciclastic environments where the faunal
846 association studied here has been found.

847 The development of desert environments could allow the the disappearance or loss of
848 abundance and diversity of some clades of vertebrates and the subsequent establishment
849 of other lineages, including those that migrated from Africa to Europe (e.g., gar fishes,
850 bothremydid turtles). The location of Algora in the coastal transgressive fringe had
851 favored the growth of large vegetable masses, which is compatible with the presence of
852 large herbivorous animals (i.e. titanosaur sauropods). In fact, the remains of large plants
853 are abundant in the Algora site (see Torices et al., 2012).

854 The studied faunal replacement as a response to climate change is part of the long-
855 term process of global change that took place during the mid-Cretaceous and ended up
856 in the Cenomanian-Turonian limit coinciding with the maximum sea-level recorded in
857 the Phanerozoic (Haq et al., 1988). This global change had a strong biotic impact in
858 marine environments and, for instance, during the limit Cenomanian-Turonian a mass
859 extinction event and a faunal turnover occurred (Kauffman, 1995; Harris and Little,
860 1999; Hallam and Wignall, 1999; Leckie et al., 2002). However, the continental biota
861 did not undergo any event of extinction (Benton, 1989; Eaton et al., 1997; Benson et al.,
862 2013), although displacement of brackish taxa, and appearances and disappearances of
863 certain taxa occurred locally and regionally (Eaton et al., 1997). Undoubtedly, the mid-
864 Cretaceous global change affected the continental biota, but the impact and changes
865 might have been strongly dependent on the specific regional patterns of change in time
866 and space, all along a complex process that lasted almost twenty millions of years, as
867 the results of this study support. This scenario variable and palaeogeographically

868 distributed impacts, and some problems of sampling bias of the continental record of
869 tetrapods, might explain the staggered patterns of the Cretaceous continental faunal
870 turnover described by Benson et al. (2013).

871

872 **5. Conclusions**

873

874 Knowledge about the vertebrate fauna from Algora, a site that represents the main
875 concentration of Cenomanian vertebrate macroremains identified in south-western
876 Europe, has increased remarkably as a result of the study of the specimens found in
877 recent palaeontological excavations there. Thus, the previous identification of fish
878 scales as corresponding to two actinopterygian taxa, one of them attributable to
879 *Stromerichthys* sp., and the second one to an indeterminate semionotid or lepisosteid, is
880 refuted. All scales previously found at this site, as well as the new ones, are compatible
881 with a single form, corresponding to *Obaichthys africanus*. The attribution of the
882 helochelydrid turtle from Algora to *Helochelys danubina* is refuted. In contrast, aff.
883 *Plastremys lata* is recognized. The identification of carcharodontosaurid theropods at
884 Algora cannot be supported. The revision of the specimens previously attributed to this
885 clade, and the study of the new theropod teeth presented here, allow us to identify a
886 single theropod representative, corresponding to a possible abelisaurid. The new
887 crocodile remains allow to justify, for the first time, the presence of Eusuchia in this
888 locality; at least two crocodyliforms being identified for the first time at the site, with
889 the other form represented by a non-eusuchian neosuchian.

890 As a result of this study, the faunal list of vertebrates currently recognized at Algora
891 is formed by at least eight taxa: the lepisosteoid fish *Obaichthys africanus*; the
892 helochelydrid turtle aff. *Plastremys lata*; the bothremydid turtle *Algorachelus*

893 *peregrina*; an indeterminate elasmosaurid plesiosaur; a non-eusuchian neosuchian and a
894 eusuchian crocodyliform; an indeterminate lithostrotian titanosaur; and an indeterminate
895 theropod that could belong to Abelisauridae (Table 3).

896 The Algora fauna consists of some vertebrate lineages that were present in the
897 European Lower Cretaceous record (e.g., helochelydrid turtles closely related to the
898 Aptian-Cenomanian *Plastremys lata*, lithostrotian titanosaurs), as well as by others not
899 recognized in the Lower Cretaceous fossil record in Europe, such as gar fishes,
900 bothremydids turtles and likely abelisaurid theropods, representing Gondwanan clades.
901 Both the gar fishes and the bothremydids turtles are known to be very abundant in the
902 uppermost Cretaceous (Campanian–Maastrichtian) levels in Europe, and the
903 abelisaurids represent the largest terrestrial predators in these ecosystems. Another of
904 the most abundant clades of reptiles in the uppermost Cretaceous levels in the continent
905 is that of the lithostrotian titanosaurs, which are very scarce in European pre-Campanian
906 levels. Algora fossil locality provides valuable information about this group of
907 sauropods for the European Cenomanian, based on several osteological remains. The
908 detailed study of the lithostrotian titanosaur of Algora revealed a Gondwanan origin for
909 some lithostrotians from Europe. The presence of members of Eusuchia is also shared
910 with the European uppermost Cretaceous faunas, while more primitive forms are
911 frequent in Lower Cretaceous sites. Therefore, the faunal composition of Algora differs
912 markedly from that recorded in the Lower Cretaceous levels in Europe, but shows some
913 affinities with that of the uppermost Cretaceous. Thus, the faunal replacement identified
914 when the European Lower and uppermost Cretaceous continental vertebrate faunas are
915 compared had already occurred, for some lineages, before or during the middle
916 Cenomanian. The climate change that took place between the end of the Early

917 Cretaceous and the early Cenomanian is here identified as one of the factors that
918 conditioned this faunal replacement.

919

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921

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934

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1323

1324 **Figure captions**

1325

- 1326 **Fig. 1.** Geographic position of the palaeontological area at Algora, located in uppermost
1327 middle-lowermost upper Cenomanian levels (Arenas de Utrillas Formation) in the
1328 vicinity of the homonymous town (Guadalajara Province, central Spain). **1.5 column**
1329 **fitting image**

1330

1331 **Fig. 2.** Fish remains from the Cenomanian (Late Cretaceous) of Algora (Guadalajara
1332 Province, central Spain). A–D, ALG 162 to 165, scales of *Obaichthys africanus*. Scale
1333 bars equal 5 mm. **2 column fitting image**

1334

1335 **Fig. 3.** Helochelydrid remains from the Cenomanian (Late Cretaceous) of Algora
1336 (Guadalajara Province, central Spain), belonging to aff. *Plastremys lata*. A–L, carapace
1337 and plastral plates. A–B, ALG 167, probably fourth right costal, in ventral (A) and
1338 dorsal (B) views. C–D, ALG 168, probably eight left peripheral, in dorsal (C) and
1339 ventral (D) views. E–F, ALG 169, second suprapygal, in dorsal (E) and ventral (F)
1340 views. G–H, ALG 170, probably axillary area of the left hyoplastron, in ventral (G) and
1341 dorsal (H) views. I–J, ALG 171, plastral process, probably corresponding to the right
1342 hyoplastron, in ventral (I) and dorsal (J) views. K–L, ALG 172, right epiplastron, in
1343 ventral (K) and dorsal (L) views. M–S, details of the external surface of these plates. M,
1344 proximal region of ALG 167. N, distal region of ALG 167. O, ventral area of ALG 168.
1345 P, ALG 169. Q, ALG 170. R, ALG 171. S, ALG 172. T–W, ALG 173, left femur in
1346 ventral (T), dorsal (U), posterior (V) and anterior (W) views. X–Y, ALG 174,
1347 osteoderm, in external (X) and visceral (Y) views. Scale bars equal 30 mm for A–L, 10
1348 mm for M–S, 20 mm for T–W, and 5 mm for X–Y. **2 column fitting image**

1349

1350 **Fig. 4.** Crocodyliform remains from the Cenomanian (Late Cretaceous) of Algora
1351 (Guadalajara Province, central Spain). A–B, ALG 175, fragment of frontal, in dorsal
1352 (A) and ventral (B) views. C–D, ALG 176, right ectopterygoid, in dorsal (C) and ventral
1353 (D) views. E–G, ALG 177, fragment of left exoccipital, in occipital (E), dorsal (F) and
1354 ventral (G) views; H–K, ALG 178, posterior fragment of left quadrate, in dorsal (H),

1355 ventral (I), lateral (J) and occipital (K) views. L–M, ALG 179, fragment of right
1356 angular, in labial (L) and lingual (M) views. N–P, ALG 180, isolated tooth, in labial
1357 (N), lingual (O) and lateral (P) views. Q–S, ALG 181, isolated tooth, in labial (Q),
1358 lingual (R) and lateral (S) views. T–V, ALG 182, isolated tooth, in labial (T), lingual
1359 (U) and lateral (V) views. W–Y, ALG 183, isolated tooth, in labial (W), lingual (X) and
1360 lateral (Y) views. Z–AB, ALG 184, ALG 185, and ALG 186, three partial osteoderms,
1361 in dorsal view. Scale bars equal 20 mm for A–M and Z–AB, and 10 mm for N–Y. **2**

1362 **column fitting image**

1363

1364 **Fig. 5.** Crocodyliform remains from the Cenomanian (Late Cretaceous) of Algora
1365 (Guadalajara Province, central Spain). A–B, ALG 187, proximal end of left radius, in
1366 dorsal (A) and ventral (B) views. C, ALG 188, a dorsal left rib, in anterior view. D–H,
1367 ALG 189, probably cervical vertebra, in anterior (D), posterior (E), right lateral (F),
1368 dorsal (G) and ventral (H) views. I–M, ALG 190, probably cervical vertebra, in anterior
1369 (I), posterior (J), right lateral (K), dorsal (L) and ventral (M) views. N–S, ALG 191,
1370 dorsal vertebra, in anterior (N), posterior (O), dorsal (P), left lateral (Q), right lateral (R)
1371 and ventral (S) views. Scale bar equals 20 mm. **2 column fitting image**

1372

1373 **Fig. 6.** Theropod remains from the Cenomanian (Late Cretaceous) of Algora
1374 (Guadalajara Province, central Spain). A–F, ALG 192, caudal vertebra, in anterior (A),
1375 right lateral (B), ventral (C), posterior (D), left lateral (E) and dorsal (F) views. G–P, cf.
1376 Abelisauridae teeth. G, ALG 193. H, Detail of anterior denticles of ALG 193. I, ALG
1377 194. J, Detail of posterior denticles of ALG 194. K, ALG 195. L, Detail of posterior
1378 denticles of ALG 195. M, ALG 196. N, ALG 197. O, ALG 198. P, ALG 199. Scale bars

1379 equal 10 mm for A–F, 5 mm for G, I, K and M–P, and 1 mm for H, J, and L. **2 column**

1380 **fitting image**

1381

1382 **Fig. 7.** Discriminant function analysis of the Algora (Cenomanian; Guadalajara
1383 Province, central Spain) theropod teeth including carcharodontosaurids such as
1384 *Acrocanthosaurus*, abelisaurids such as *Arcovenator escotae* (Tortosa et al., 2016) and
1385 cf. *Arcovenator escotae* (Pérez-García et al., 2016b), and *Allosaurus* from Smith et al.
1386 (2005), Fanti et al. (2014), Richter et al. (2013), Hendrickx et al. (2015, 2020), and
1387 Longrich et al. (2017). **1.5 column fitting image**

1388

1389 **Table 1.** Discriminant analysis of the Algora (Cenomanian; Guadalajara Province,
1390 central Spain) theropod teeth where they have not been assigned to any group. 95% of
1391 the sample is correctly classified.

1392

1393 **Table 2.** Discriminant analysis of the Algora (Cenomanian; Guadalajara Province,
1394 central Spain) theropod teeth assigned to its own group.

1395

1396 **Table 3.** Discriminant analysis of the Algora (Cenomanian; Guadalajara Province,
1397 central Spain) theropod teeth where they have not been assigned to any group and
1398 *Arcovenator* teeth have been included. 93.2% of the sample is correctly classified.

1399

1400 **Table 4.** Discriminant analysis of the Algora (Cenomanian; Guadalajara Province,
1401 central Spain) theropod teeth where they have been assigned to its own group and
1402 *Arcovenator* teeth have been included. 93.4% of the sample is correctly classified.

1403

1404 **Table 5.** New faunal list for the Cenomanian (Late Cretaceous) site of Algora
1405 (Guadalajara Province, central Spain) proposed in this paper, based on the studies
1406 reported here and on the information provided by recent papers, and comparison with
1407 that previously proposed (Torices et al., 2012).

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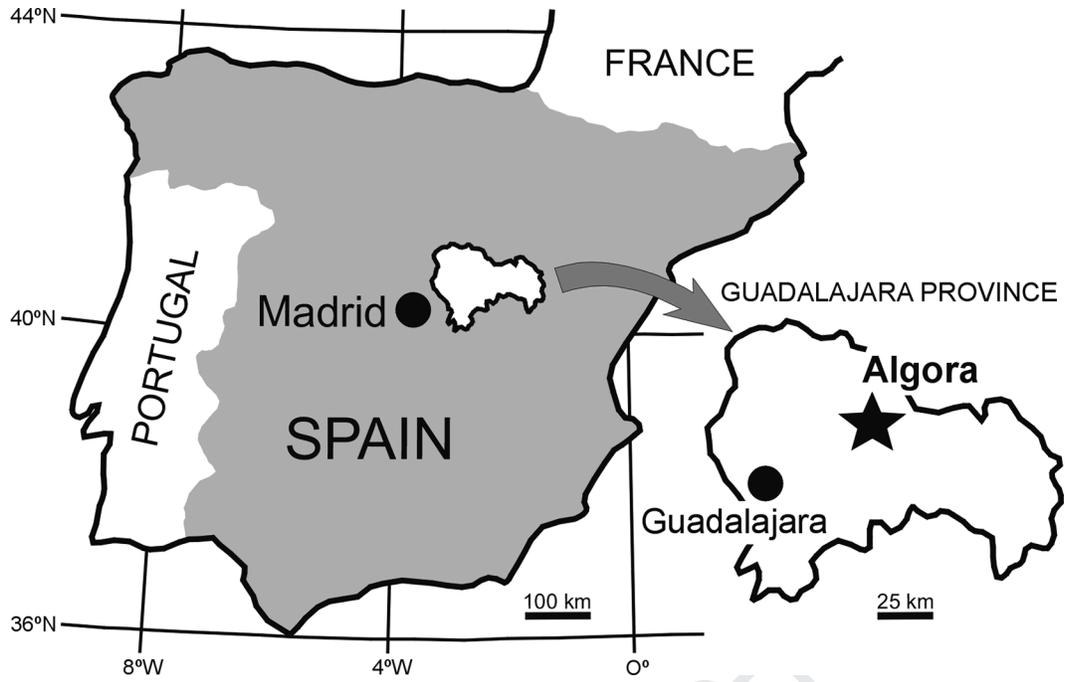
Taxa		Predicted groups						Total
		<i>Allosaurus</i>	<i>Acrocanthosaurus</i>	<i>Carcharodontosaurus</i>	Abelisaurids	<i>Chenanisaurus</i>	Dromeosaurids	
Original	<i>Allosaurus</i>	29	0	0	0	0	0	29
	<i>Acrocanthosaurus</i>	0	15	0	0	0	0	15
	<i>Carcharodontosaurus</i>	0	1	44	2	0	0	47
	Abelisaurids	2	0	0	22	0	0	24
	<i>Chenanisaurus</i>	1	0	0	0	0	0	1
	Dromeosaurids	0	0	0	0	0	3	3
	Not gruped cases (Algora)	1	0	0	4	0	0	5
%	<i>Allosaurus</i>	100,0	0,0	0,0	0,0	0,0	0,0	100,0
	<i>Acrocanthosaurus</i>	0,0	100,0	0,0	0,0	0,0	0,0	100,0
	<i>Carcharodontosaurus</i>	0,0	2,1	93,6	4,3	0,0	0,0	100,0
	Abelisaurids	8,3	0,0	0,0	91,7	0,0	0,0	100,0
	<i>Chenanisaurus</i>	100,0	0,0	0,0	0,0	0,0	0,0	100,0
	Dromeosaurids	0,0	0,0	0,0	0,0	0,0	100,0	100,0
	Not gruped cases (Algora)	20,0	0,0	0,0	80,0	0,0	0,0	100,0
95,0% correctly classified								

Taxa		Predicted group							Total	
		<i>Allosaurus</i>	<i>Acrocanthosaurus</i>	<i>Carcharodontosaurus</i>	Abelisaurids	Algora teeth	<i>Chenanisaurus</i>	Dromeosaurids		
Original	<i>Allosaurus</i>	27	0	0	2	0	0	0	29	
	<i>Acrocanthosaurus</i>	0	15	0	0	0	0	0	15	
	<i>Carcharodontosaurus</i>	0	1	45	1	0	0	0	47	
	Abelisaurids	2	0	1	18	3	0	0	24	
	Algora teeth	1	0	0	0	4	0	0	5	
	<i>Chenanisaurus</i>	1	0	0	0	0	0	0	1	
	Dromeosaurids	0	0	0	0	0	0	3	3	
	%	<i>Allosaurus</i>	93,1	0,0	0,0	6,9	0,0	0,0	0,0	100,0
		<i>Acrocanthosaurus</i>	0,0	100,0	0,0	0,0	0,0	0,0	0,0	100,0
		<i>Carcharodontosaurus</i>	0,0	2,1	95,7	2,1	0,0	0,0	0,0	100,0
		Abelisaurids	8,3	0,0	4,2	75,0	12,5	0,0	0,0	100,0
		Algora teeth	20,0	0,0	0,0	0,0	80,0	0,0	0,0	100,0
		<i>Chenanisaurus</i>	100,0	0,0	0,0	0,0	0,0	0,0	0,0	100,0
	Dromeosaurids	0,0	0,0	0,0	0,0	0,0	0,0	100,0	100,0	
90,3% correctly classified										

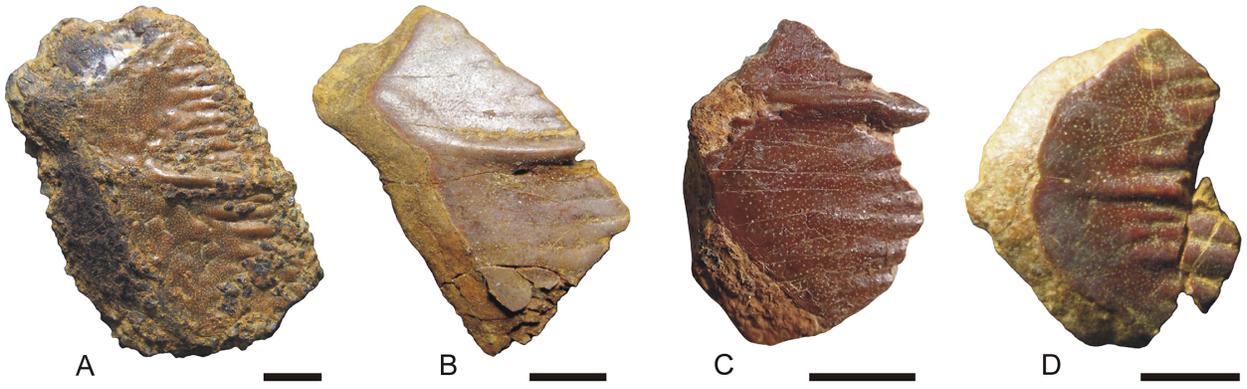
Taxa		Predicted group							Total
		<i>Allosaurus</i>	<i>Acrocanthosaurus</i>	<i>Carcharodontosaurus</i>	Abelisaurids	<i>Chenanisaurus</i>	Dromeosaurids	<i>Arcovenator</i>	
Original	<i>Allosaurus</i>	28	0	0	0	0	0	1	29
	<i>Acrocanthosaurus</i>	0	15	0	0	0	0	0	15
	<i>Carcharodontosaurus</i>	0	1	44	2	0	0	0	47
	Abelisaurids	2	0	0	21	0	0	1	24
	<i>Chenanisaurus</i>	1	0	0	0	0	0	0	1
	Dromeosaurids	0	0	0	0	0	3	0	3
	<i>Arcovenator</i>	1	0	0	0	0	0	12	13
	Not gruped cases (Algora)	1	0	0	2	0	0	2	5
%	<i>Allosaurus</i>	96,6	0,0	0,0	0,0	0,0	0,0	3,4	100,0
	<i>Acrocanthosaurus</i>	0,0	100,0	0,0	0,0	0,0	0,0	0,0	100,0
	<i>Carcharodontosaurus</i>	0,0	2,1	93,6	4,3	0,0	0,0	0,0	100,0
	Abelisaurids	8,3	0,0	0,0	87,5	0,0	0,0	4,2	100,0
	<i>Chenanisaurus</i>	100,0	0,0	0,0	0,0	0,0	0,0	0,0	100,0
	Dromeosaurids	0,0	0,0	0,0	0,0	0,0	100,0	0,0	100,0
	<i>Arcovenator</i>	7,7	0,0	0,0	0,0	0,0	0,0	92,3	100,0
	Not gruped cases (Algora)	20,0	0,0	0,0	40,0	0,0	0,0	40,0	100,0
93,2% correctly classified									

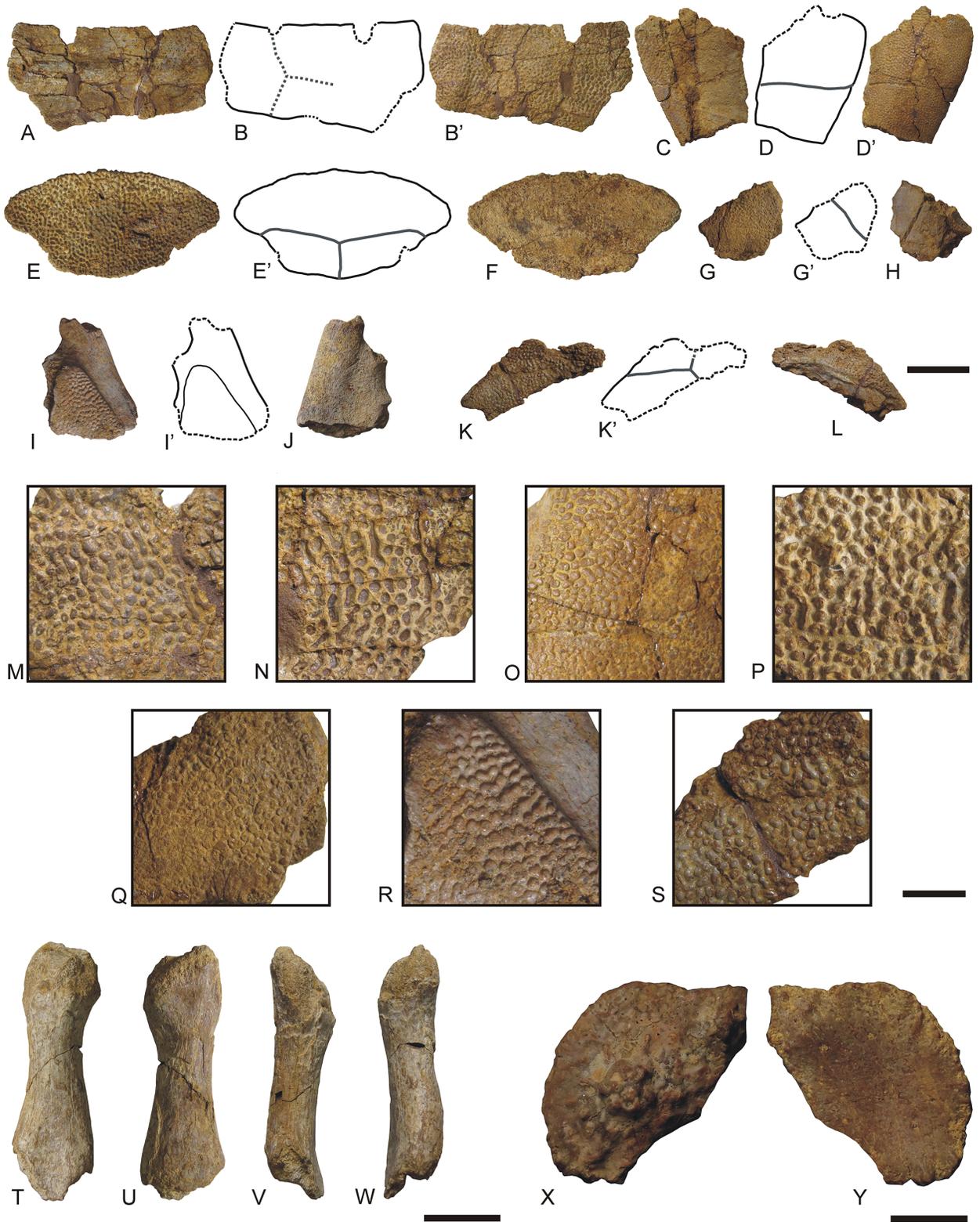
Taxa		Predicted group							Total	
		<i>Allosaurus</i>	<i>Acrocanthosaurus</i>	<i>Carcharodontosaurus</i>	Abelisaurids	Algora teeth	<i>Chenanisaurus</i>	Dromeosaurids		<i>Arcovenator</i>
Original	<i>Allosaurus</i>	28	0	0	0	0	0	0	1	29
	<i>Acrocanthosaurus</i>	0	15	0	0	0	0	0	0	15
	<i>Carcharodontosaurus</i>	0	1	44	2	0	0	0	0	47
	Abelisaurids	2	0	0	21	1	0	0	0	24
	Algora teeth	0	0	0	0	5	0	0	0	5
	<i>Chenanisaurus</i>	1	0	0	0	0	0	0	0	1
	Dromeosaurids	0	0	0	0	0	0	3	0	3
	<i>Arcovenator</i>	1	0	0	0	0	0	0	12	13
%	<i>Allosaurus</i>	96,6	0,0	0,0	0,0	0,0	0,0	0,0	3,4	100,0
	<i>Acrocanthosaurus</i>	0,0	100,0	0,0	0,0	0,0	0,0	0,0	0,0	100,0
	<i>Carcharodontosaurus</i>	0,0	2,1	93,6	4,3	0,0	0,0	0,0	0,0	100,0
	Abelisaurids	8,3	0,0	0,0	87,5	4,2	0,0	0,0	0,0	100,0
	Algora teeth	0,0	0,0	0,0	0,0	100,0	0,0	0,0	0,0	100,0
	<i>Chenanisaurus</i>	100,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	100,0
	Dromeosaurids	0,0	0,0	0,0	0,0	0,0	0,0	100,0	0,0	100,0
	<i>Arcovenator</i>	7,7	0,0	0,0	0,0	0,0	0,0	0,0	92,3	100,0
93,4% correctly classified										

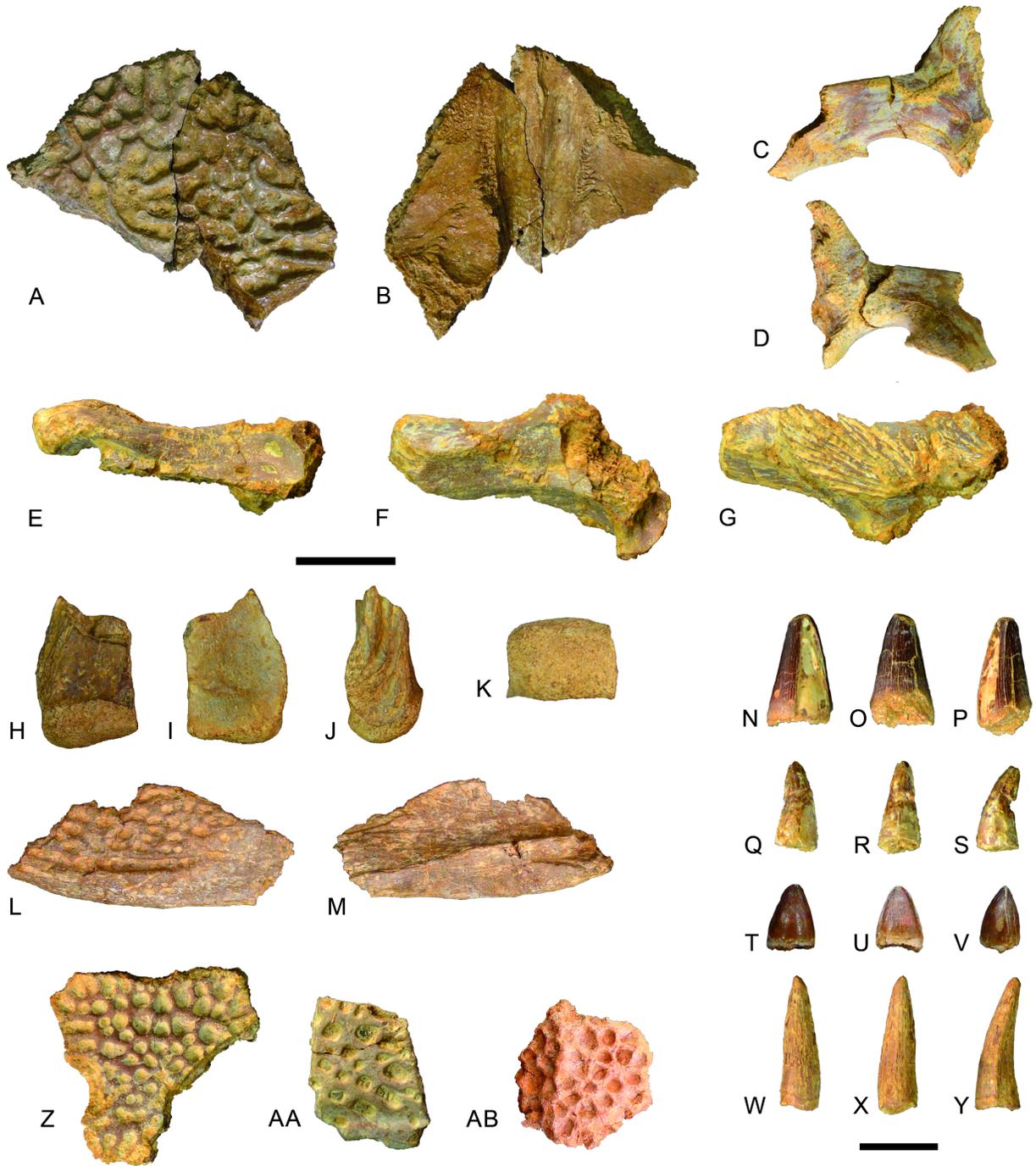
		Faunal list in Torices et al. (2012)	New determinations in subsequent papers	New faunal list proposed in this paper	
Osteichthyes		Amiidae?: <i>Stromerichthys</i> sp.		A single taxon: <i>Obaichthys africanus</i>	
		Semionotidae or Lepisosteidae indet.			
Reptilia	Testudinata	Stem Testudines	Solemydidae indet. (= Helochelydridae indet.)	<i>Helochelys danubina</i> (Joyce, 2017)	aff. <i>Plastremys lata</i>
		Testudines	cf. Eupleurodira indet.	<i>Algorachelus peregrina</i> gen. et sp. nov. (Pérez-García, 2017a)	<i>Algorachelus peregrina</i>
	Sauropterygia		-	Elasmosauridae indet. (Bardet et al., 2018)	Elasmosauridae indet.
	Crocodyliformes		A single taxon: Neosuchia indet.		Neosuchia indet. (non-eusuchian)
					Eusuchia indet.
	Dinosauria	Theropoda	Carcharodontosauridae indet.		cf. Abelisauridae
Sauropoda		-	Lithostrotia indet. (Mocho et al., 2019)	Lithostrotia indet.	

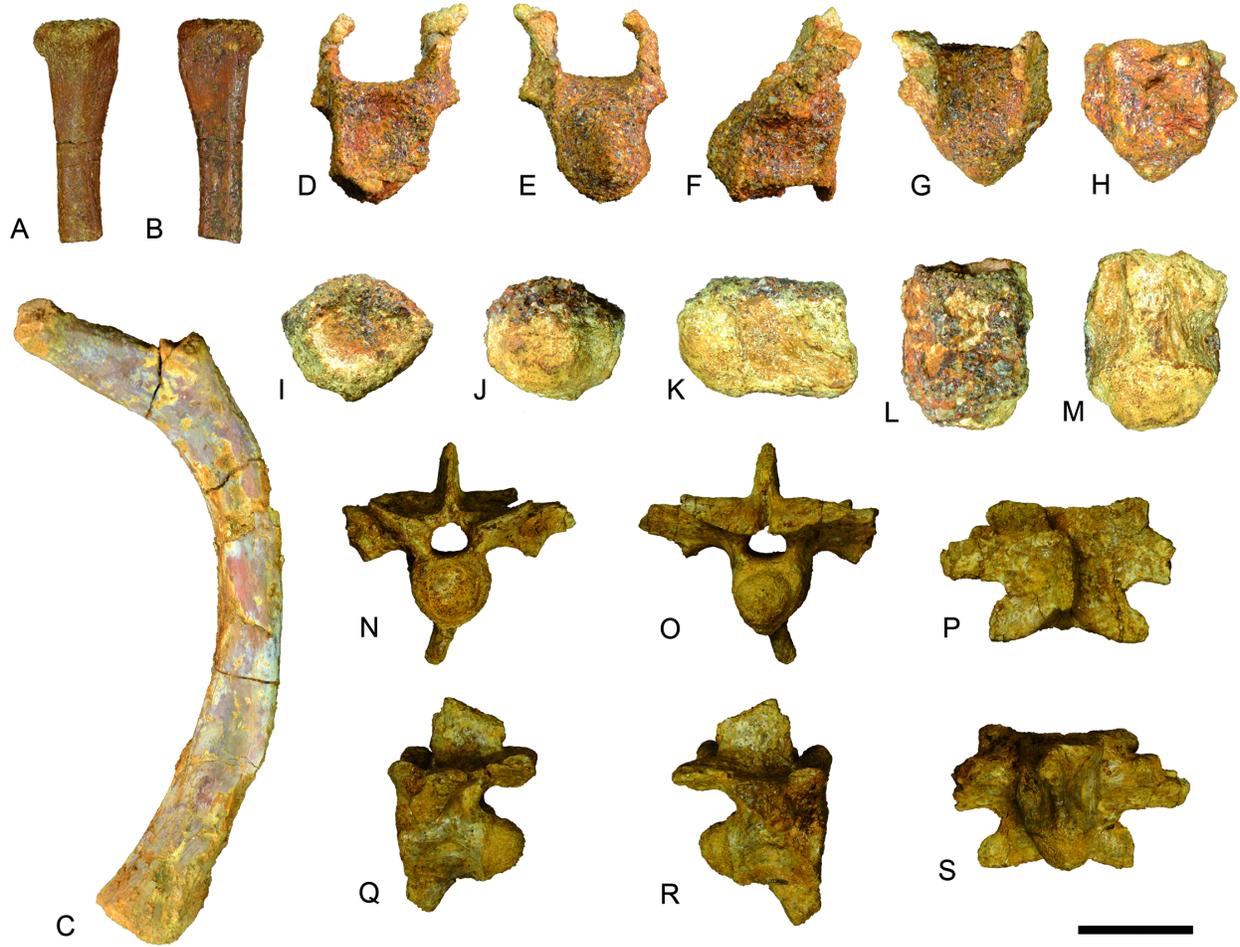


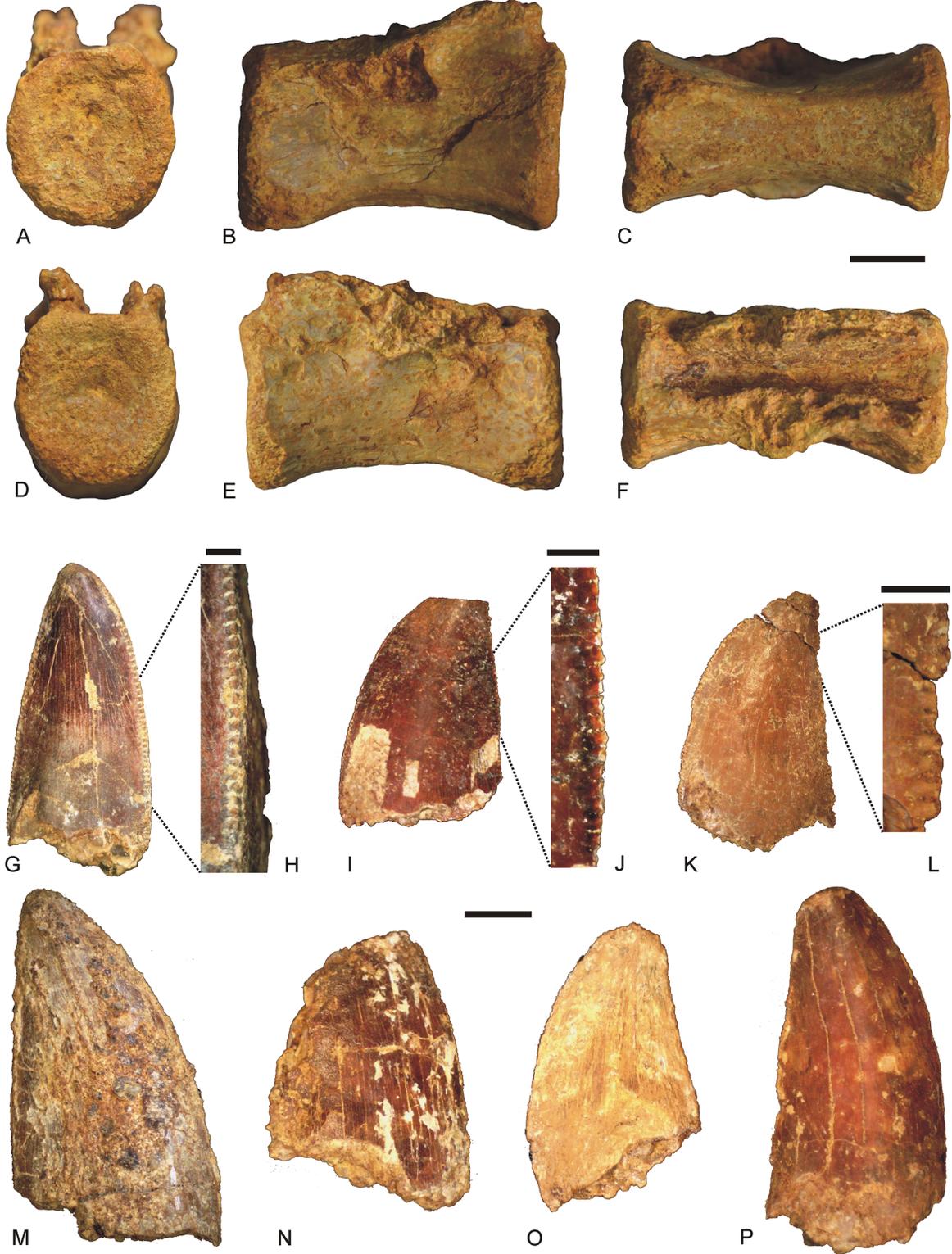
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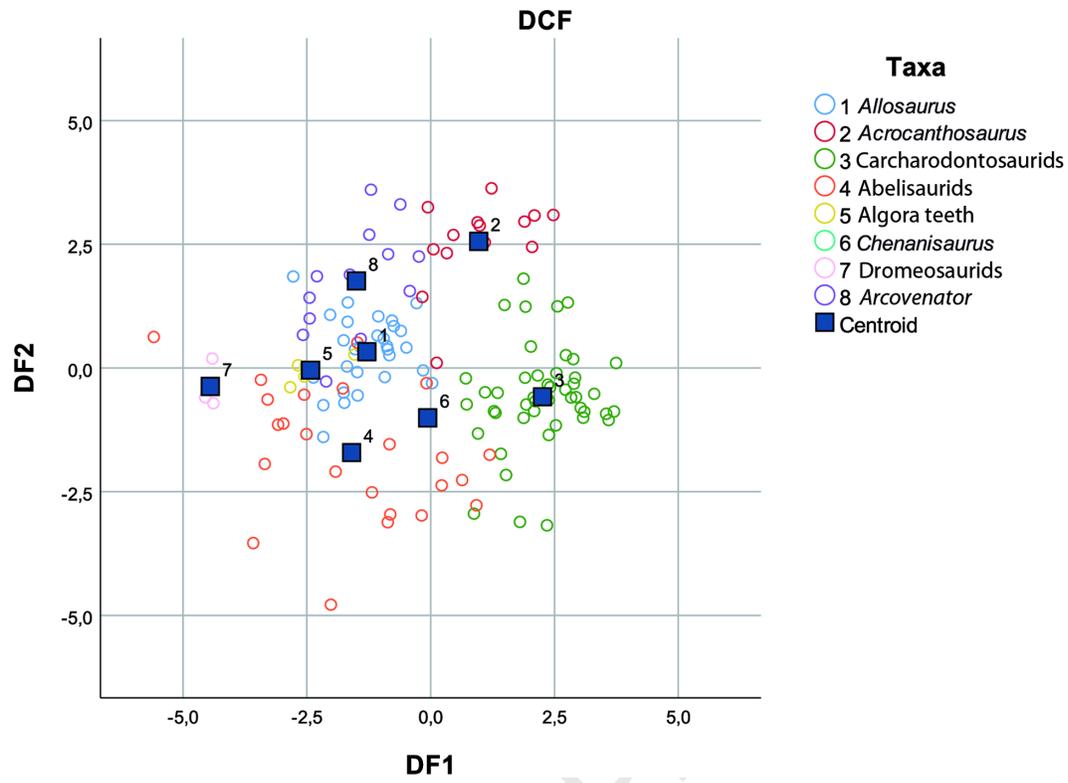












The largest Europe Cenomanian concentration of macrovertebrates comes from Algora.
>Recent fieldwork campaigns in Algora have provided numerous remains. >The faunal list of the site is updated here. > Information about the Early to Late Cretaceous faunal transition is provided. >This replacement is recognized as strongly conditioned by climate changes.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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