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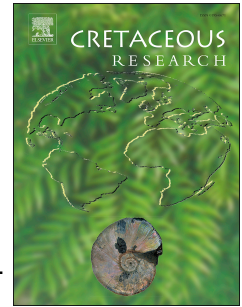
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Cenomanian vertebrates from Algora (central Spain): New data on the establishment of the European Upper Cretaceous continental faunas

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ABSTRACT

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

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

1. Introduction

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

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

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

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

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

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

2. Palaeogeographical framework

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

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

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

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

3. Systematic palaeontology

Actinopterygii Cope, 1887

Ginglymodi Cope, 1872

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

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

Obaichthyidae Grande, 2010

Obaichthys Wenz and Brito, 1992

Obaichthys africanus Grande, 2010

(Fig. 2A–D)

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

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

Testudinata Klein, 1760

Helochelydridae Nopcsa, 1928

aff. *Plastremys lata* Owen in Parkinson, 1881

(Fig. 3)

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

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

Archosauria Cope, 1869

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Neosuchia Benton and Clark, 1988

Neosuchia indet.

(Figs. 4, 5A–C)

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

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

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

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

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

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

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

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

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

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

Eusuchia Huxley, 1875

Eusuchia indet.

(Fig. 5D–S)

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

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

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

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

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Theropoda indet.

(Fig. 6A–F)

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

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

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

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

Tetanurae Gauthier, 1986

Ceratosauria Marsh, 1884

cf Abelisauridae

(Figs. 6G–P)

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

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

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

4. Discussion

4.1. Systematic discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4.2. Faunal implications

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4.3. Climatic changes and faunal replacements

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

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

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

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

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

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

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

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

5. Conclusions

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

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

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

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

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

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Figure captions

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

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

column fitting image

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

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

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 fitting image**

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

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

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

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

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

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).

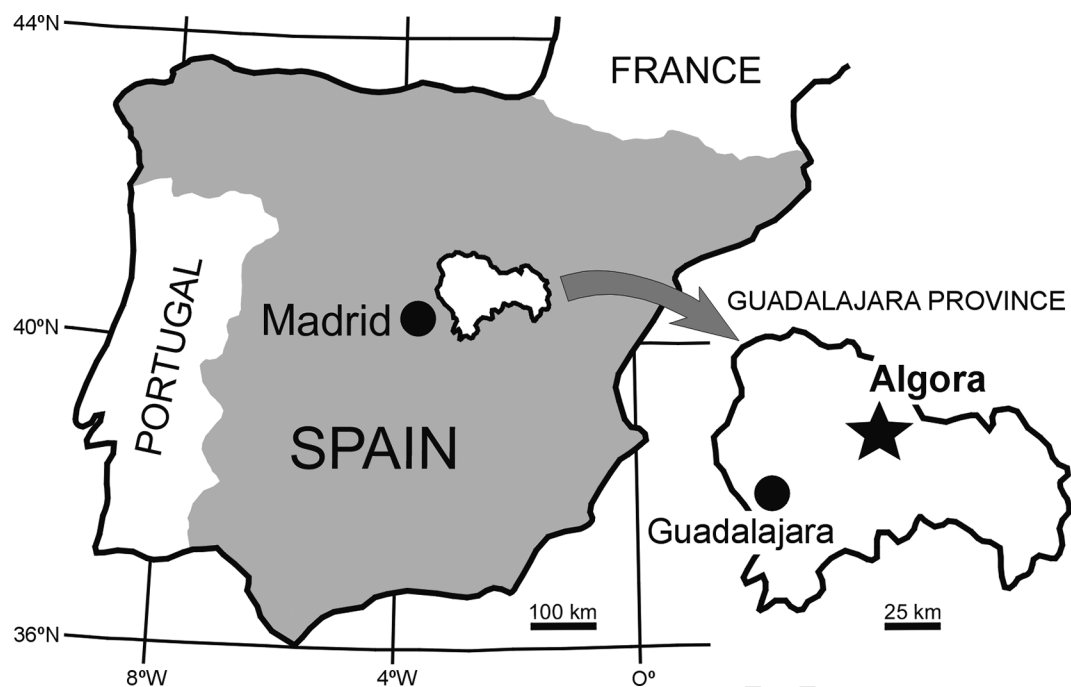
Taxa			Predicted groups					Total	
			Allosaurus	Acrocanthosaurus	Carcharodontosaurus	Abelisaurids	Chenanisaurus		Dromeosaurids
Original		Allosaurus	29	0	0	0	0	0	29
		Acrocanthosaurus	0	15	0	0	0	0	15
		Carcharodontosaurus	0	1	44	2	0	0	47
		Abelisaurids	2	0	0	22	0	0	24
		Chenanisaurus	1	0	0	0	0	0	1
		Dromeosaurids	0	0	0	0	0	3	3
		Not gruped cases (Algora)	1	0	0	4	0	0	5
	%	Allosaurus	100,0	0,0	0,0	0,0	0,0	0,0	100,0
		Acrocanthosaurus	0,0	100,0	0,0	0,0	0,0	0,0	100,0
		Carcharodontosaurus	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
		Chenanisaurus	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									

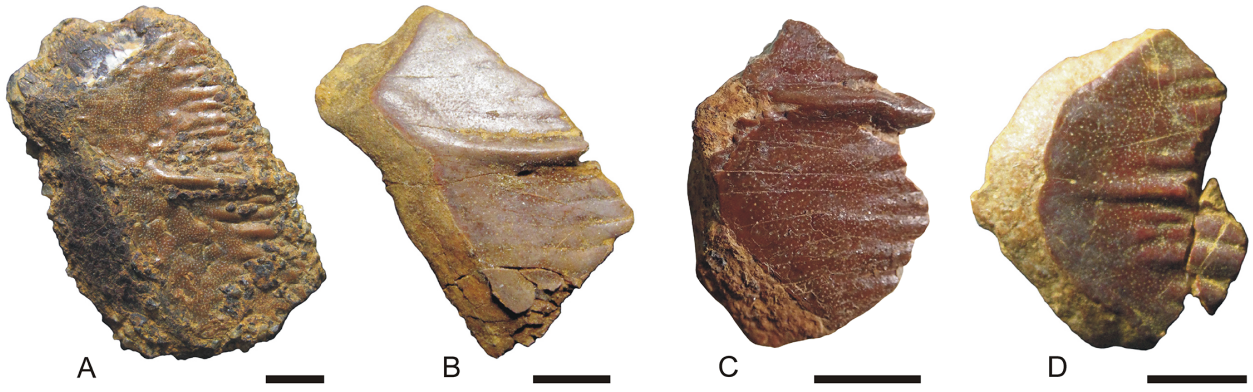
[illegible]

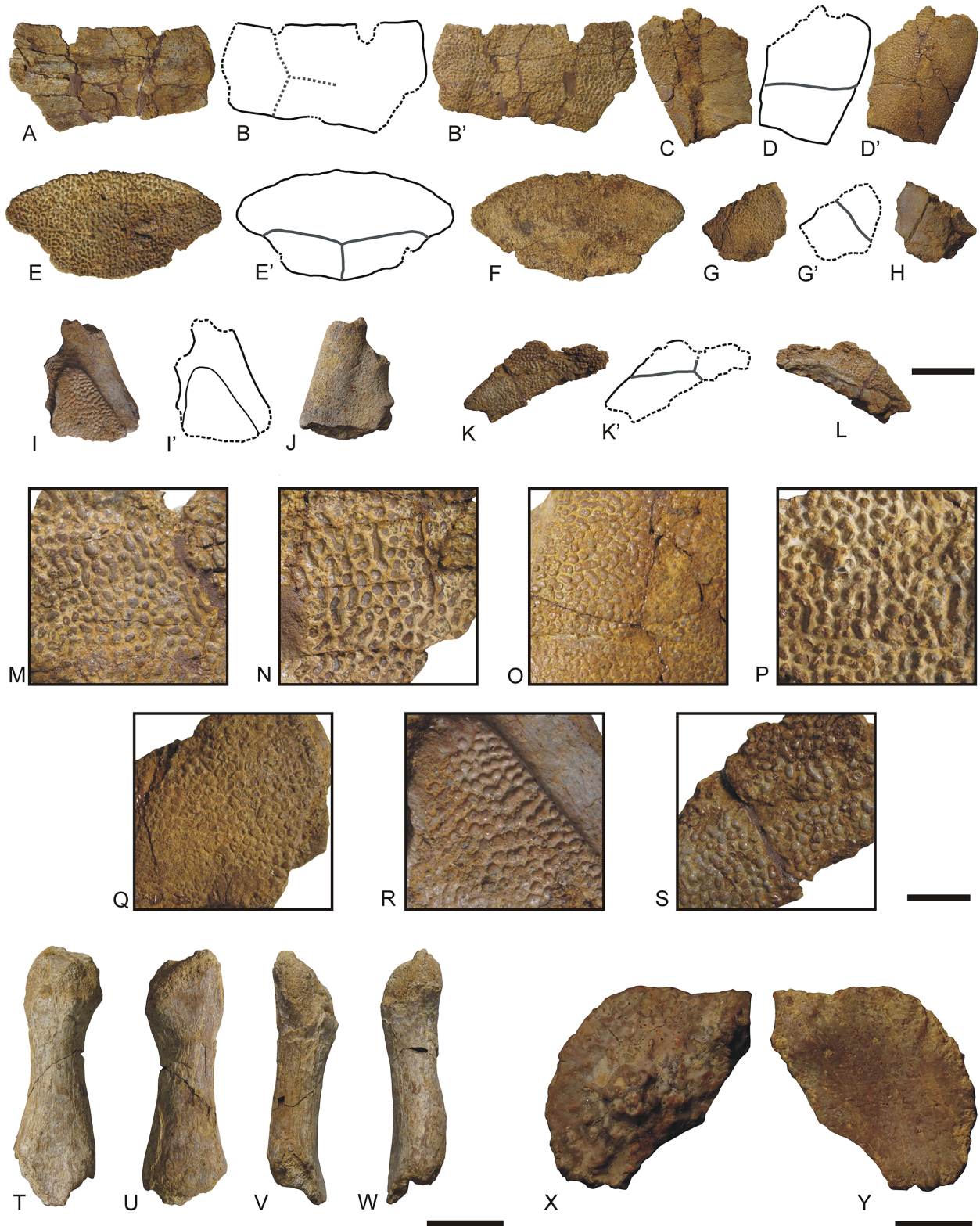
Taxa		Predicted group							Total	
		<i>Allosaurus</i>	<i>Acrocanthosaurus</i>	<i>Carcharodontosaurus</i>	Abelisaurids	<i>Chenanisaurus</i>	Dromeosaurids	<i>Arcovenator</i>		
Original		<i>Allosaurus</i>	28	0	0	0	0	0	1	29
		<i>Acrocanthosaurus</i>	0	15	0	0	0	0	0	15
		<i>Carcharodontosaurus</i>	0	1	44	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										

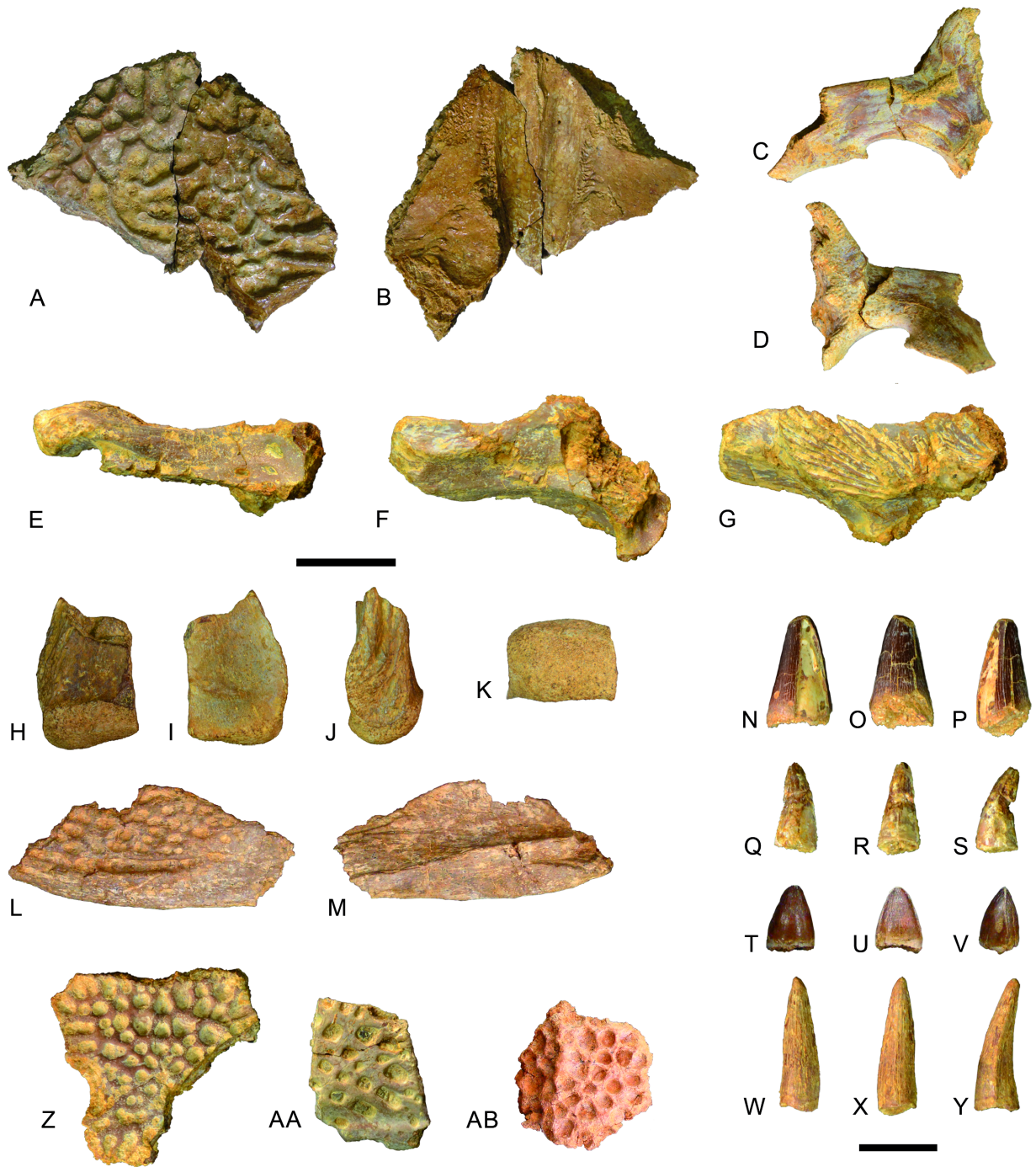
Taxa			Predicted group							Total	
			<i>Allosaurus</i>	<i>Acrocanthosaurus</i>	<i>Carcharodontosaurus</i>	Abelisaurids	Algora teeth	<i>Chenanisaurus</i>	Dromeosaurids		<i>Arcovenator</i>
Original		<i>Allosaurus</i>	28	0	0	0	0	0	0	1	29
		<i>Acrocanthosaurus</i>	0	15	0	0	0	0	0	0	15
		<i>Carcharodontosaurus</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											

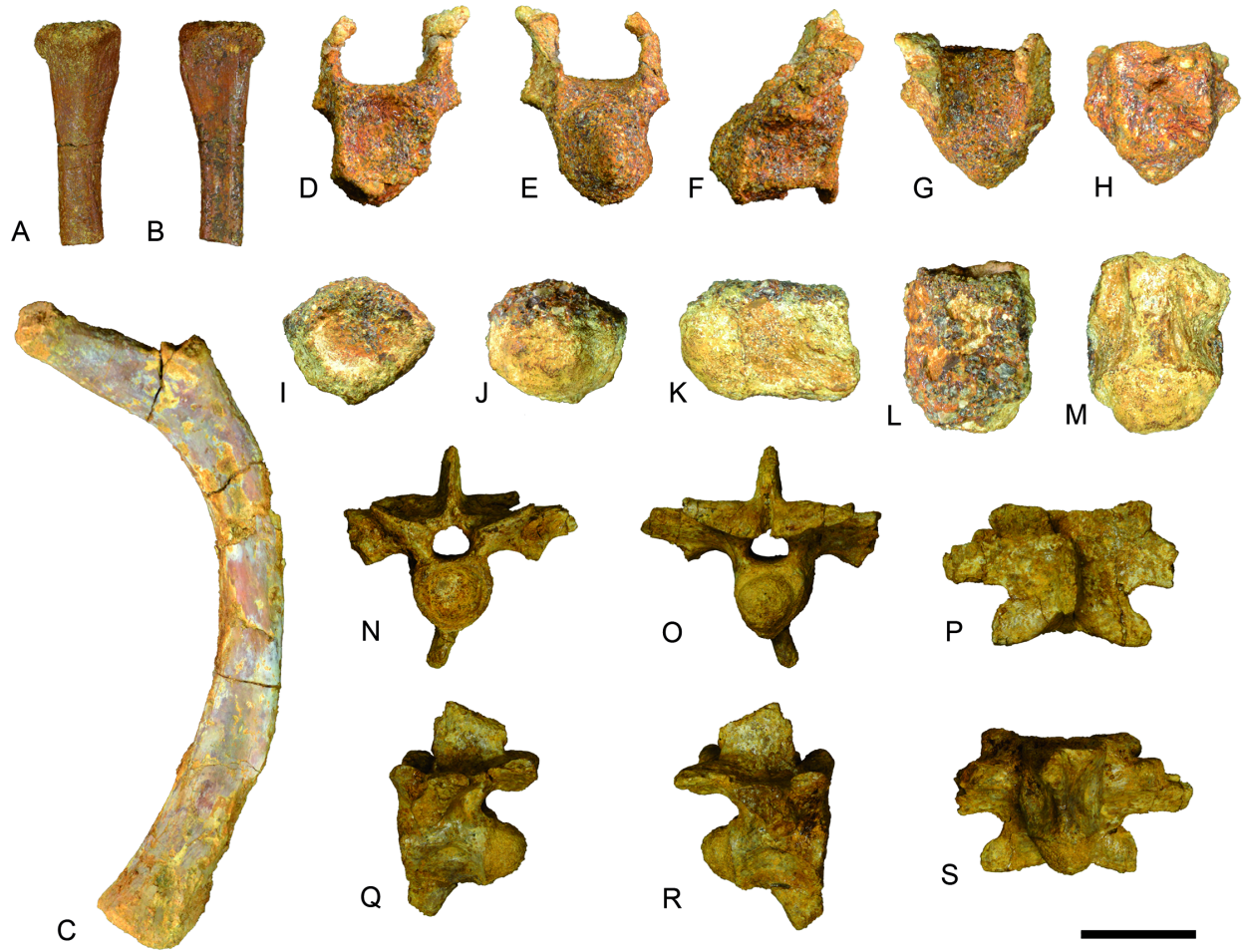
			Faunal list in Torices et al. (2012)	New determinations in subsequent papers	New faunal list proposed in this paper
Osteichthyes			Amiidae?: <i>Stromerichthys</i> sp.		A single taxon: <i>Obaichthys africanus</i>
			Semionotidae or Lepisosteidae indet.		
Reptilia	Testudinata	Stem Testudines	Solemydidae 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.

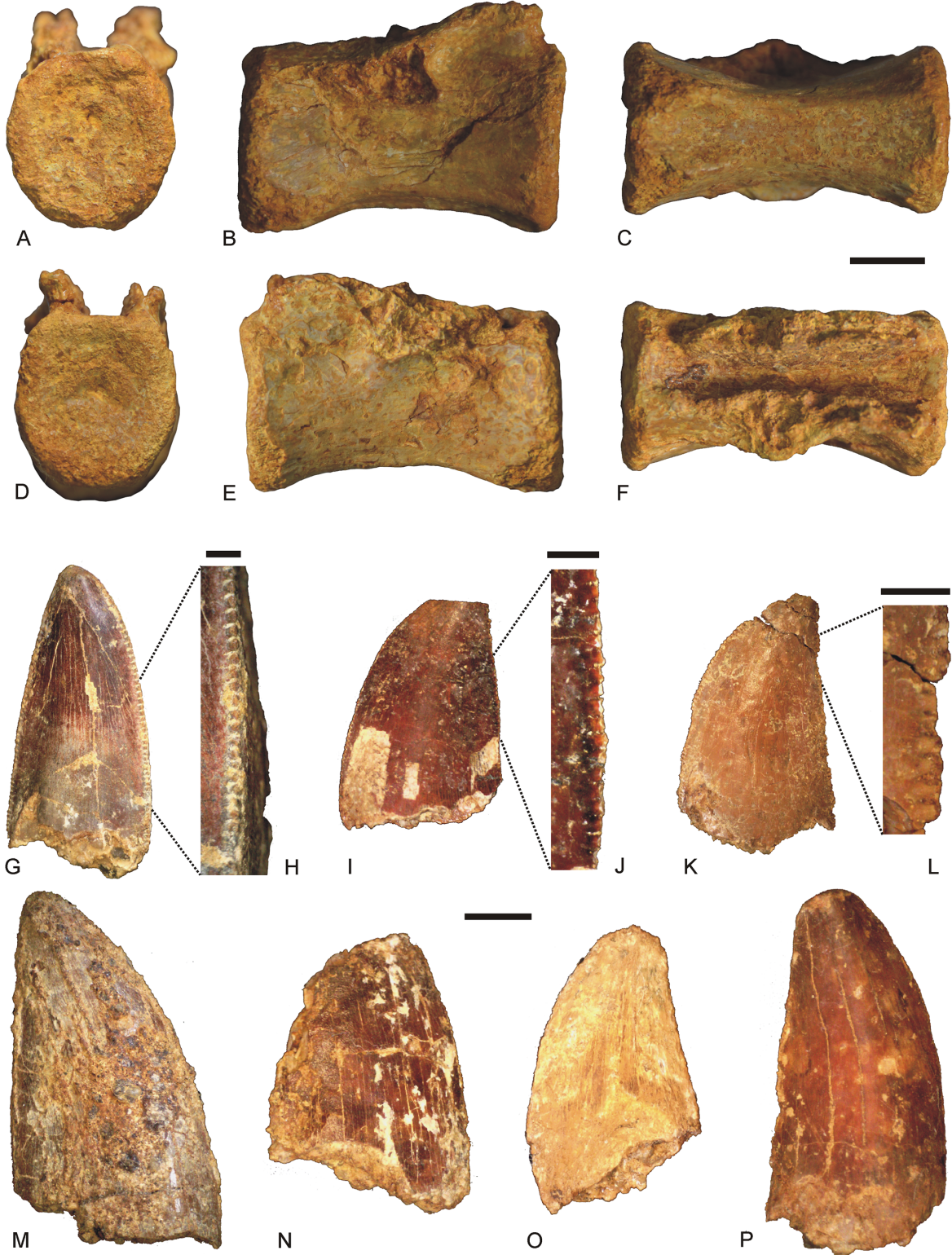


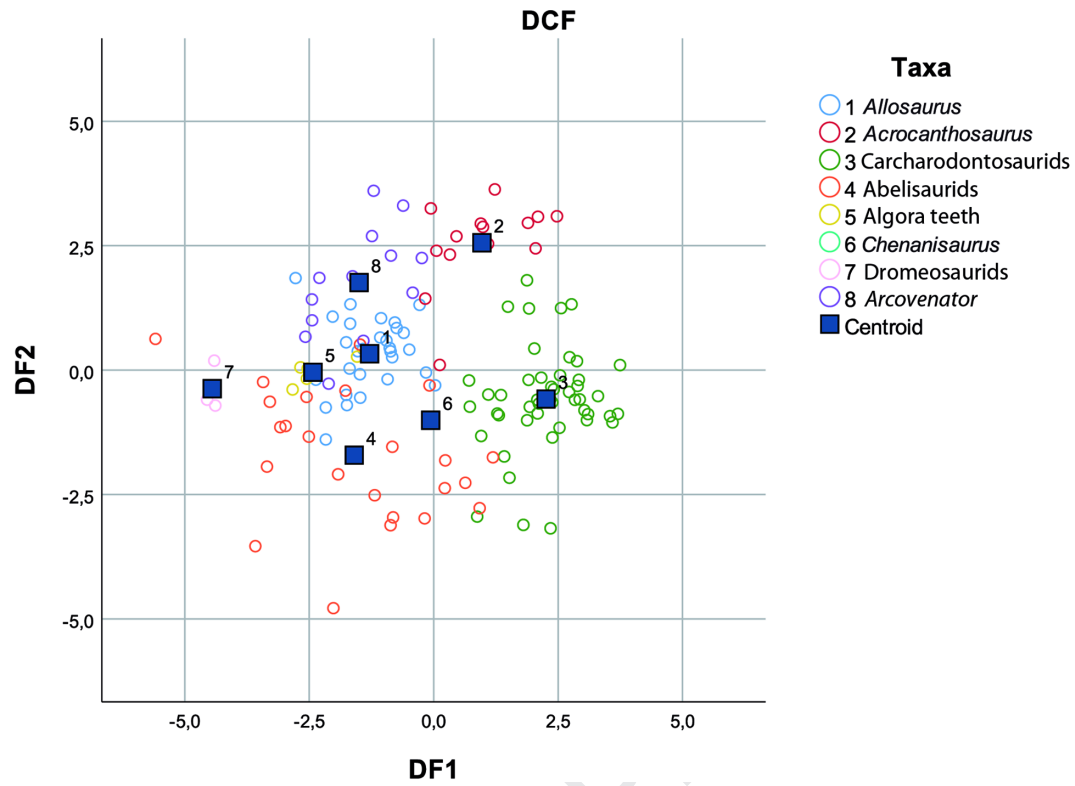












The largest Europe Cenomanian concentration of macrovertebrates comes from Algora.

>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.

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: