

Atherfieldastacus magnus (M'Coy, 1849), a widely distributed crustacean during Early Cretaceous (Valanginian-Albian) times

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ABSTRACT

Several specimens of the mecochirid lobster *Atherfieldastacus magnus* (M'Coy, 1849) collected in Mexico and Colombia, represent the oldest record for this species. The Mexican specimens are from the Valanginian-Hauterivian San Juan Raya Formation, in Puebla, central Mexico, and the Colombian specimens were found in Barremian deposits of the Paja Formation, north of Bogotá. Previous reports of *Atherfieldastacus magnus* include numerous specimens from the Aptian of Europe (UK, Spain), Mexico, Colombia and Tibet. The new specimens collected in shales of the San Juan Raya Formation of Mexico, represent diverse sizes and excellent quality of preservation; in some samples the articles of the antennae can be observed, among other morphological characters not reported previously for this species. The association of the Mexican specimens with mollusks, echinoids and cones of an araucaria gymnosperm, suggest a shallow marine environment. The same is observed for the Colombian specimens, where sediments of the Paja Formation are reported as shallow marine. Additionally, sexual dimorphism in *A. magnus* is recognized, based on the analysis of differential morphology of the pleurae. Thus, for the moment, the biostratigraphic range for *A. magnus* ranges from the Valanginian to the Albian (Early Cretaceous), with the oldest occurrence in Mexico, where it persisted until Aptian times.

1. Introduction

The fossil record of the mecochirid lobster *Atherfieldastacus magnus* (M'Coy, 1849) represents an example of a wide distribution during Early Cretaceous, with occurrences in many localities around the world: United Kingdom (M'Coy, 1849; Bell, 1863; Woods, 1928; Simpson and Middleton, 1985; Robin et al., 2016), Spain (Vía-Boada, 1975; Calzada and Urquiola, 1999; López-Horgue, 2009; Bover-Arnal et al., 2010; Najarro et al., 2011; López-Horgue and Bodego, 2017), Colombia (Vega et al., 2008; González-León et al., 2016), China (Wang, 1981; Zhang, 2000; Zhang et al., 2002), and Mexico (Feldmann et al., 1995a, 2007; González-León et al., 2014, 2015, 2018a and b). These contributions clarify the chronostratigraphic and paleobiogeographic distribution of this decapod. For many years, the biostratigraphic range of *Atherfieldastacus magnus* was considered to be restricted to the Aptian. Recent

reports of new localities and re-examination of specimens of this species suggest that its paleobiogeographic and stratigraphic distribution is more extensive (e.g. López-Horgue, 2009 in Spain; Vega et al., 2008; González-León et al., 2016 in Colombia; González-León et al., 2014, 2015, 2018a and b in Mexico, and Robin et al., 2016 in the United Kingdom). Some of these works report new ages and provide additional information about the biota associated with *A. magnus* (e.g. calcareous algae, foraminifera, calcareous nannoplankton and ammonoids), while others have documented symbiotic relationships (Robin et al., 2016).

The present work is based on new occurrences of specimens of *A. magnus*, not previously reported for the San Juan Raya Formation (Puebla, Mexico) and the Paja Formation (Curití, Colombia). The morphological features present in the Mexican and Colombian specimens correspond to the diagnosis and description of *A. magnus* (see Simpson in Robin et al., 2016; González-León et al., 2018a and b) and

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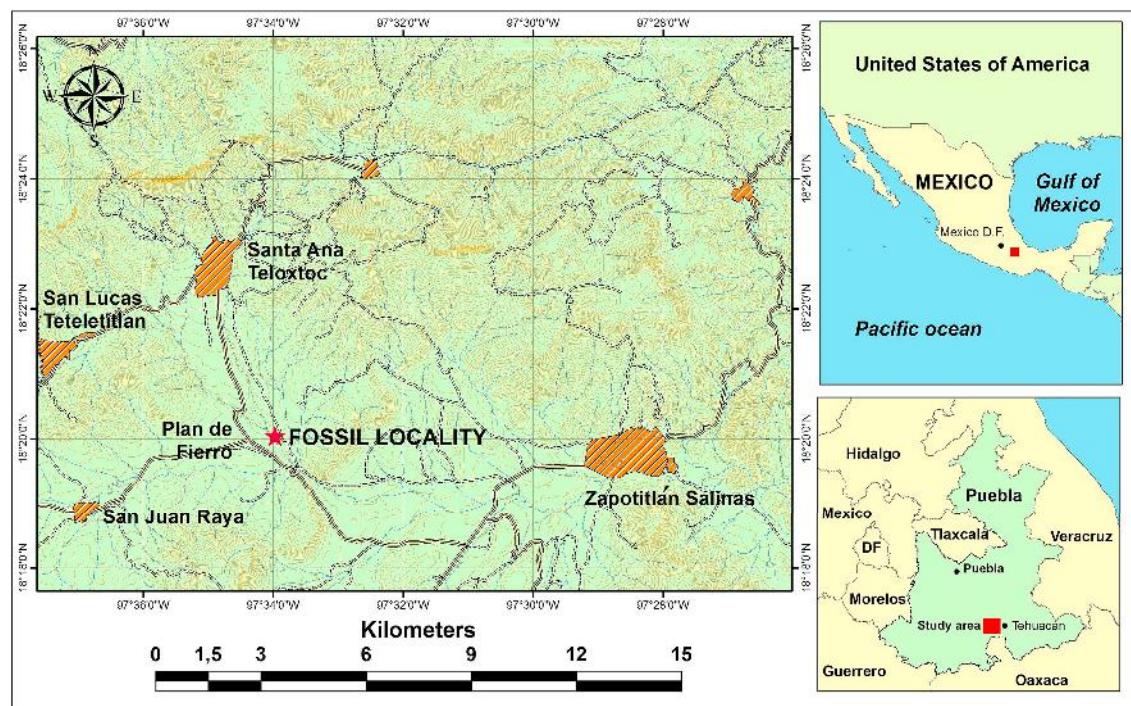


Fig. 1. Topographic map of Central Mexico (Puebla) showing the fossiliferous locality (Barranca El Gavilán) of the Lower Cretaceous (Valanginian-Hauterivian) San Juan Raya Formation.

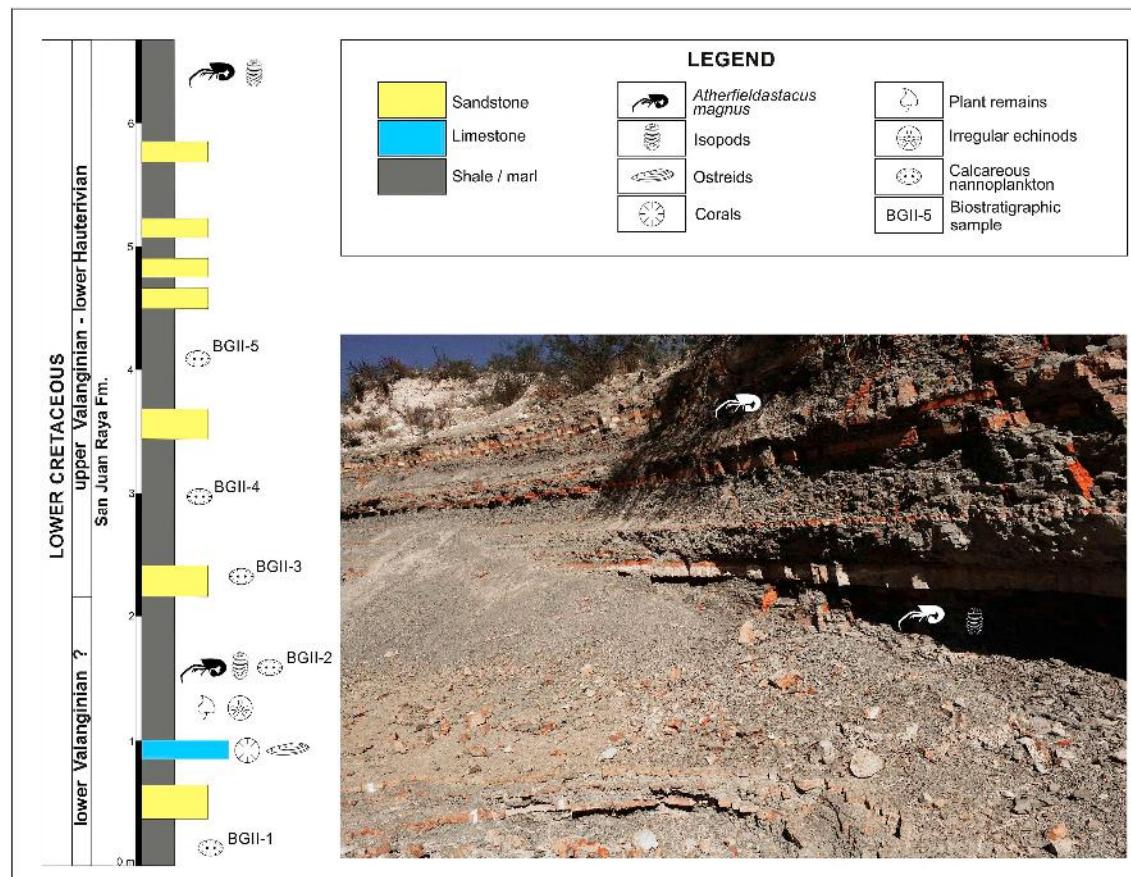


Fig. 2. Stratigraphic section of the Lower Cretaceous (Valanginian-Hauterivian) San Juan Raya Formation at Barranca el Gavilán. Labels indicate position where *Atherfieldia magnus* was collected.

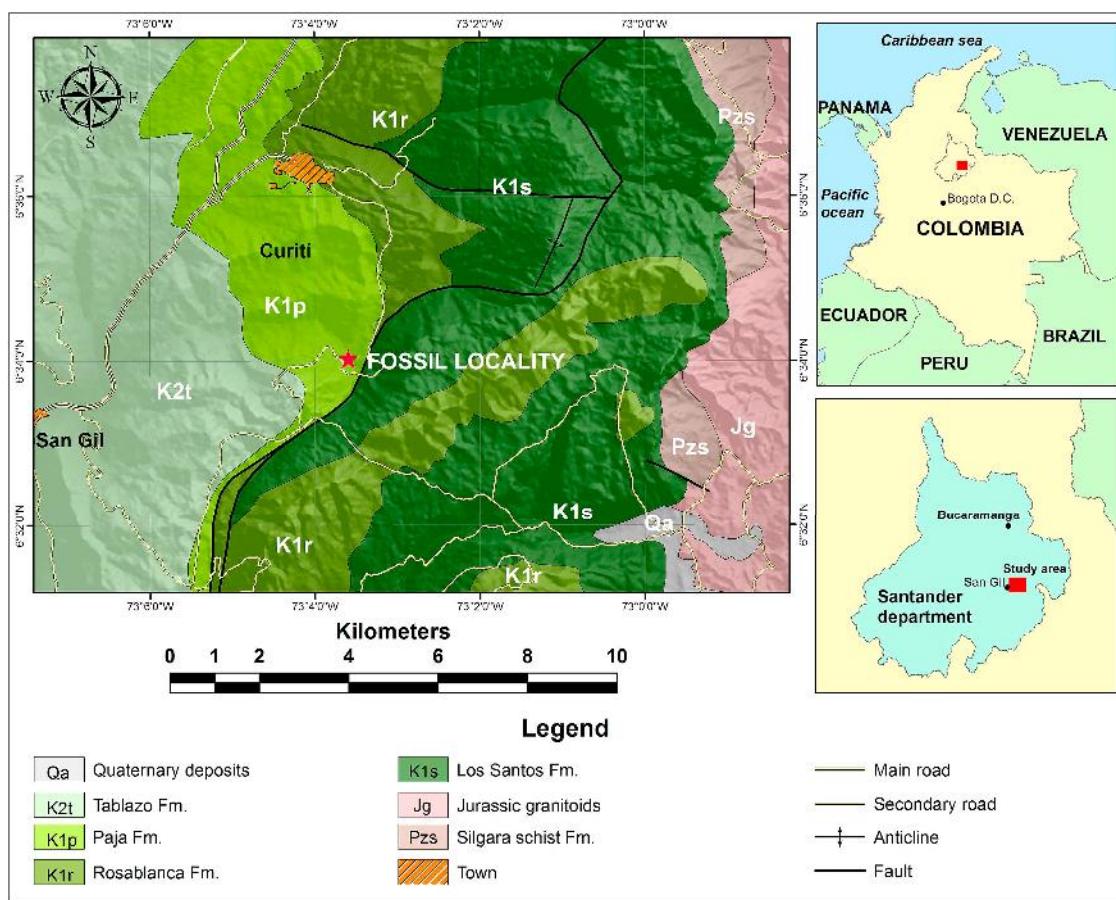


Fig. 3. Geologic map of North Colombia, showing fossiliferous locality (near Curití) of the Lower Cretaceous (Barremian) Paja Formation.

possible sexual dimorphism is discussed, along with the extension of the biostratigraphic and paleogeographic distribution. Deposits from the base of the San Juan Raya Formation where specimens of *A. magnus* were collected, are much older than previously thought, being the oldest record of this species in the world (Valanginian-Hauterivian). The specimens from the Paja Formation represent also the oldest record for the same species for South America (Barremian).

2. Geological and geographical settings

2.1. Mexico

The study area is located in Puebla, southwest of Tehuacán. The outcrop is located 5.5 km northeast from San Juan Raya and 5.6 km southeast from Santa Ana Teloxtoc, over the Barranca el Gavilán canyon, at coordinates 18° 19' 58" N and 97° 33' 56.8" W (Fig. 1). This outcrop was previously reported by Vega et al. (2019), when describing several marine isopod specimens, some of them associated to juvenile stages of *Atherfieldastacus magnus* from the San Juan Raya Formation (Fig. 2). The mecochirid lobsters are abundant and concentrated in approximately 30 cm at the top of the 1-m thick fossiliferous, gray mudstone layer. Mendoza-Rosales (2010) describe the San Juan Raya Formation as 'an alternation of conglomerates, sandstones, siltstones, shales, and boundstones limestones (Agua de Burro member), in layers ranging from thin to thick, often bioturbated; fossils of gastropods, pelecypods, corals, and rudists are abundant in the unit'. For more details of the geological setting from the San Juan Raya Formation see (Mendoza-Rosales, 2010; González-León et al., 2014, 2015; Vega et al., 2019).

2.2. Colombia

Specimens reported herein come from Cordillera Oriental (Colombian Andes), near San Gil and Curití (Santander Department), 220 km northeast Bogotá D.C. The fossil-bearing locality is situated cca 7 km east of San Gil, in the lower portion of the Paja Formation (Fig. 3). The Paja Formation is a typical transgressive formation with occurrences of shallow marine fauna, mostly ammonites, bivalves, fish remains, and gastropods. The lithology includes organic-rich marls, black shales, and micritic limestones (Fig. 4); throughout the unit micritic, and commonly fossiliferous, concretions are very common. The Paja Formation conformably overlies carbonate ramp deposits of the Rosablanca Formation (Hauterivian-lower Barremian), composed mainly by fossiliferous marls and limestones with an abundant fauna of ostracodes, foraminiferous, mollusks, crustaceans and echinoderms (Morales and Colombian Petroleum Industry, 1958; Zamarréno de Julivert, 1963; Patarroyo, 1997; Barrero et al., 2007; Rojas-Briceño and Patarroyo, 2009; Gaona-Narvaez et al., 2013; Gómez-Cruz et al., 2015). The age of the base of the Paja Formation is controversial and apparently heterochronous in central Colombian Andes. According to Patarroyo (1997), in the region of Barichara (about 12 km NW of San Gil), the presence of the ammonites *Nicklesia* sp.; *N. nolani* (Nicklès, 1894); *N. didayana didayana* Bürgl, 1956; *N. didayana multifida* Bürgl, 1956; *N. dumasiana* (d'Orbigny, 1842); *Pseudohaploceras incertum* (Riedel, 1938); *Valde-dorsella* sp. and *Karsteniceras* sp., represents the early Barremian. On the contrary, Gaona-Narvaez et al. (2013) in the Curití area, indicates that the contact between the Paja and Rosablanca formations includes a phosphatic bed, which is characterized by mixed middle and late Barremian and early Aptian faunas, which includes ammonites of the genera *Pulchellia* Uhlig, 1883; *Gerhardtia* Hyatt, 1903; *Toxancyloceras* Delanoy, 2003; *Karsteniceras* Royo and Royo y Gómez, 1945 and

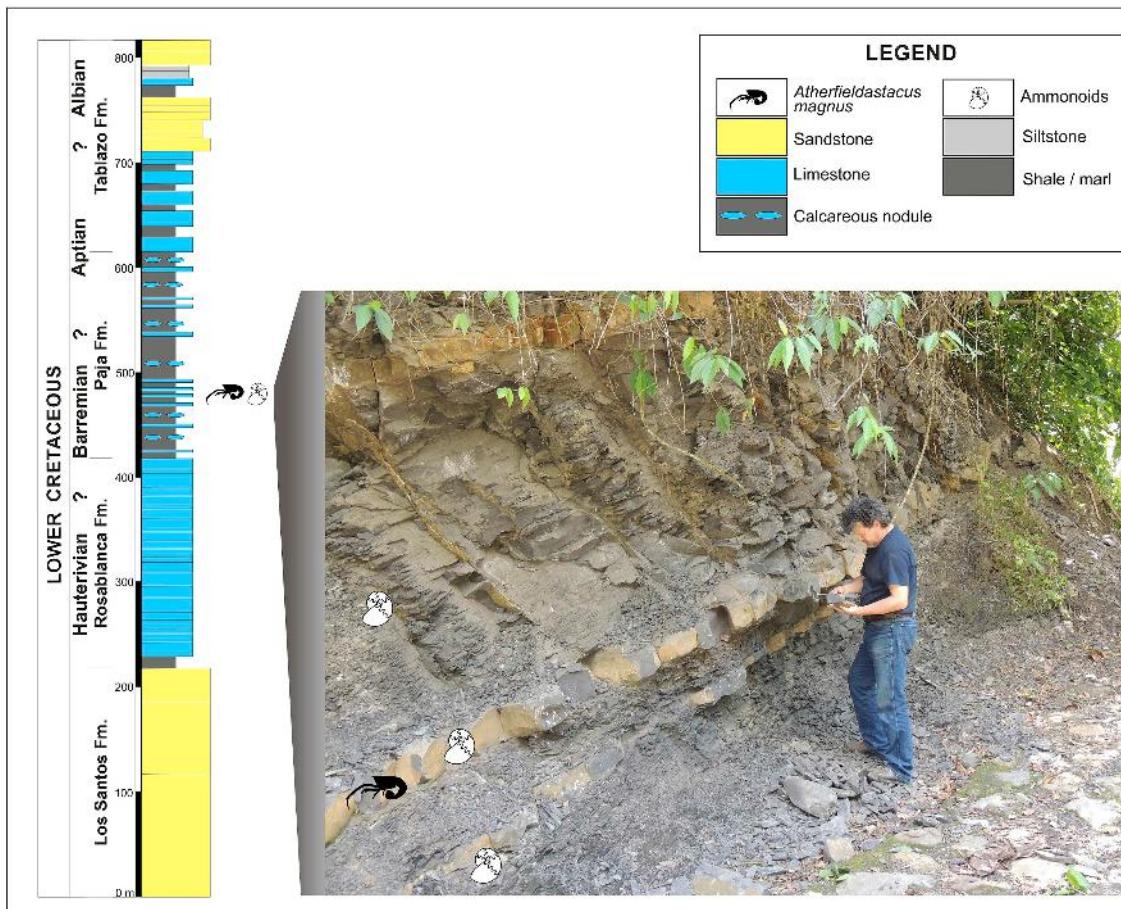


Fig. 4. Stratigraphic section (modified from Patarroyo, 1997) of the San Gil-Curití region (Barremian), and panoramic view of the studied outcrop (marls and mudstones). Labels indicate position where the fossils were collected.

Prodehyesites Casey, 1961.

3. Biostratigraphy

3.1. Mexico, San Juan Raya Formation nannofossil biostratigraphy

San Juan Raya Formation is a well-known locality among Mexican paleontologists. An Aptian age was suggested for the first specimens of *Atherfieldastacus magnus* reported from the lower portion of this lithostratigraphic unit (Feldmann et al., 2007). Nevertheless, González León et al. (2015) and more recently Vega et al. (2019), assigned a Valanginian-Hauterivian age for the San Juan Raya Formation, based on calcareous nannoplankton biostratigraphy (see Vega et al., 2019, p. 122).

3.2. Colombia, Paja Formation ammonoid biostratigraphy

The studied outcrop yields several ammonoids of the Family Pulchelliidae, all of them belong to the genus *Gerhardtia* but even at the generic level, it allows a precise age assignment because of its short generic biostratigraphic range. The majority of the specimens are fragmentary inner casts and this prevents identification at species level. Only in two cases (Fig. 5) it is possible to assign a specific identification as *G. galeatoides* (Karsten, 1856), the type species of the genus *Gerhardtia*. This species is well represented in Colombia but is also present in Europe, according to Vermeulen (2003). In the Americas, this species is represented in Peru and according the conception of the *G. galeatoides* of Vermeulen (2003), this taxon includes several nominal species (see extended synonymy in Vermeulen and Klein, 2006, p. 225–227). Taking

this into account *G. galeatoides* is also present in Mexico, where it was reported using other specific names by several ammonoid specialists (e.g. González-Arreola and Carrillo-Martínez, 1986; Ramírez-Garza, 2007). From a biostratigraphic point of view, *Gerhardtia* and obviously *G. galeatoides* is restricted to the *G. sartousiana* Zone of the standard Mediterranean ammonite zonation for the late Barremian (Reboulet et al., 2018). Patarroyo (2000, 2004) reported a late Barremian age for the Paja Formation, based on the presence of *G. galeatoides* and *Heinzia* (*Gerhardtia*) *veleziensis* (Hyatt, 1903).

Anatomical abbreviations. a = branchio-cardiac groove, a2 = antenna, ac = antennal carina, b = antennal groove, b₁ = hepatic groove, c = post-cervical groove, cp = carpus, cd = cardiac groove, da = dactylus, di = diaeresis, e₁e = cervical groove, en = endopodite, ex = exopodite, gc = gastro-orbital carina, hr = hepatic ridge, i = inferior groove, me = merus, oc = orbital carina, p1-5 = pereiopods, pr = propodus, r1-r3 = branchial ridges, s2-6 = pleonal somites, t = telson.

4. Systematic palaeontology

Order Decapoda Latreille, 1802.

Suborder Pleocyemata Burkenroad, 1963.

Infraorder Glypheidea Zittel, 1885.

Superfamily Glypheoidea Zittel, 1885.

Family Mecochiridae Van Straelen, 1925.

Genus *Atherfieldastacus* Simpson in Robin et al. (2016).

Type species: *Meyeria magna* M'Coy, 1849 by original designation of Robin et al. (2016).

Included species: *Atherfieldastacus magnus* (M'Coy, 1849), *A. rapax*

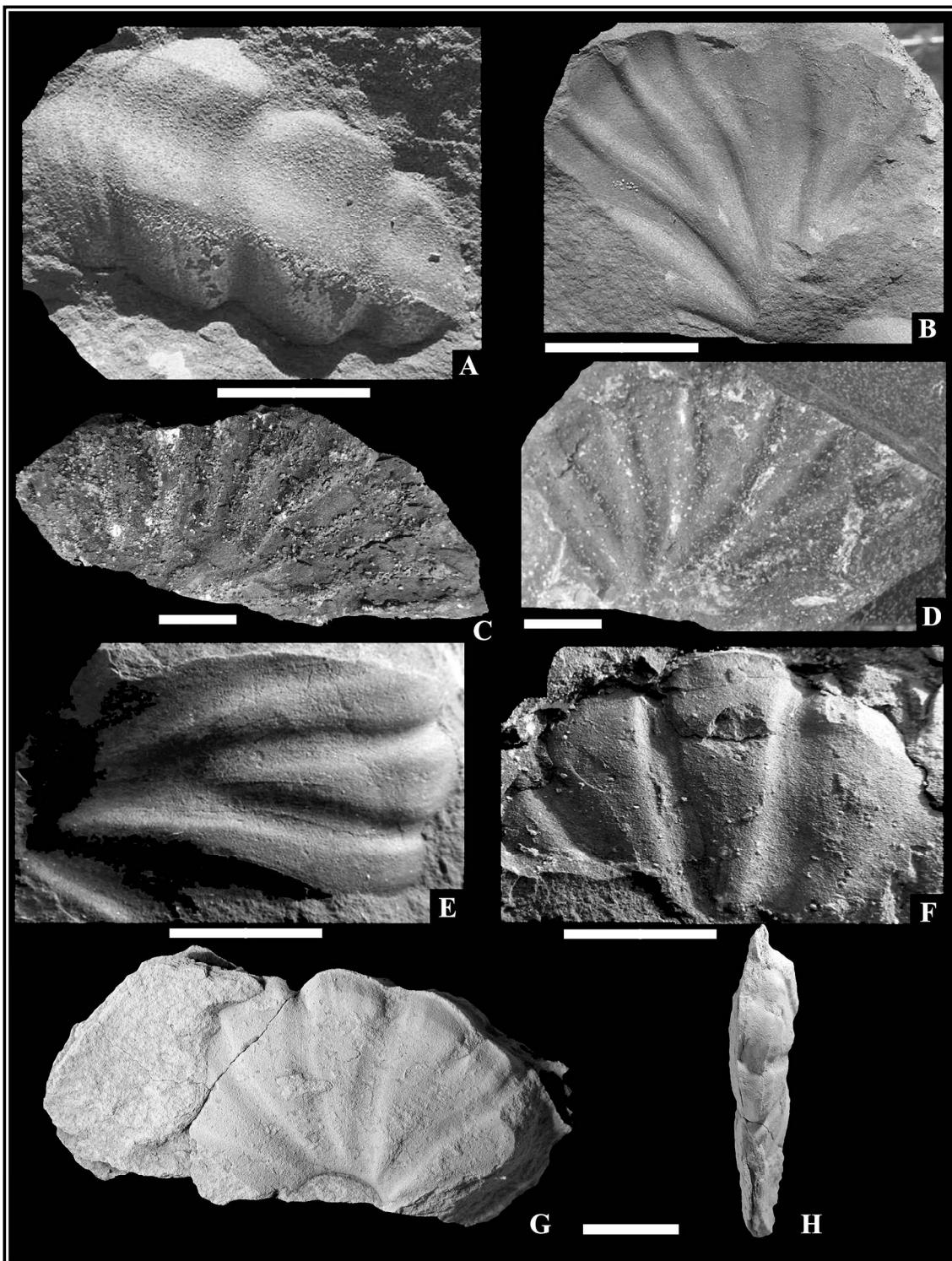


Fig. 5. Ammonites from same outcrop (Barremian) Paja Formation where *Atherfieldastacus magnus* was found. A, *Gerhardia galeatoides* (Karsten, 1856), ventral view (UCAL-289-1). B, *Gerhardia* sp. lateral view (UCAL-289-2). C, *Gerhardia* sp. lateral view (UCAL-289-3). D, *Gerhardia* sp. lateral view (UCAL-289-4). E, *Gerhardia* sp. lateral view (UCAL-289-5). F, *Gerhardia* sp. lateral view (UCAL-289-6). G-H, *G. galeatoides* (Karsten, 1856), lateral and ventral views (IGM-11311). Scale bar = 10 mm.

(Harbort, 1905) and *A. schwartzii* (Kitchin, 1908).

Diagnosis. Subcylindrical cephalothorax, laterally compressed, about two-thirds the length and twice the height of pleon; cephalothorax with bevelled, sublanceolate cross section; short pointed rostrum, spineless; branchial region with three lateral branchial ridges broadening the cephalothorax; dorsal branchial ridge (r2) between

postcervical and branchio-cardiac grooves; medial branchial ridge (r3), curved and parallel to posterior margin; ventral branchial ridge (r1), extending hepatic carina; antennal pterygomostomial region with strongly concave ventral margin; cervical groove strongly oblique, ventrally joined to antennal groove, delimiting narrow cephalic region; cephalic region with longitudinal carinae; short gastro-orbital groove originating

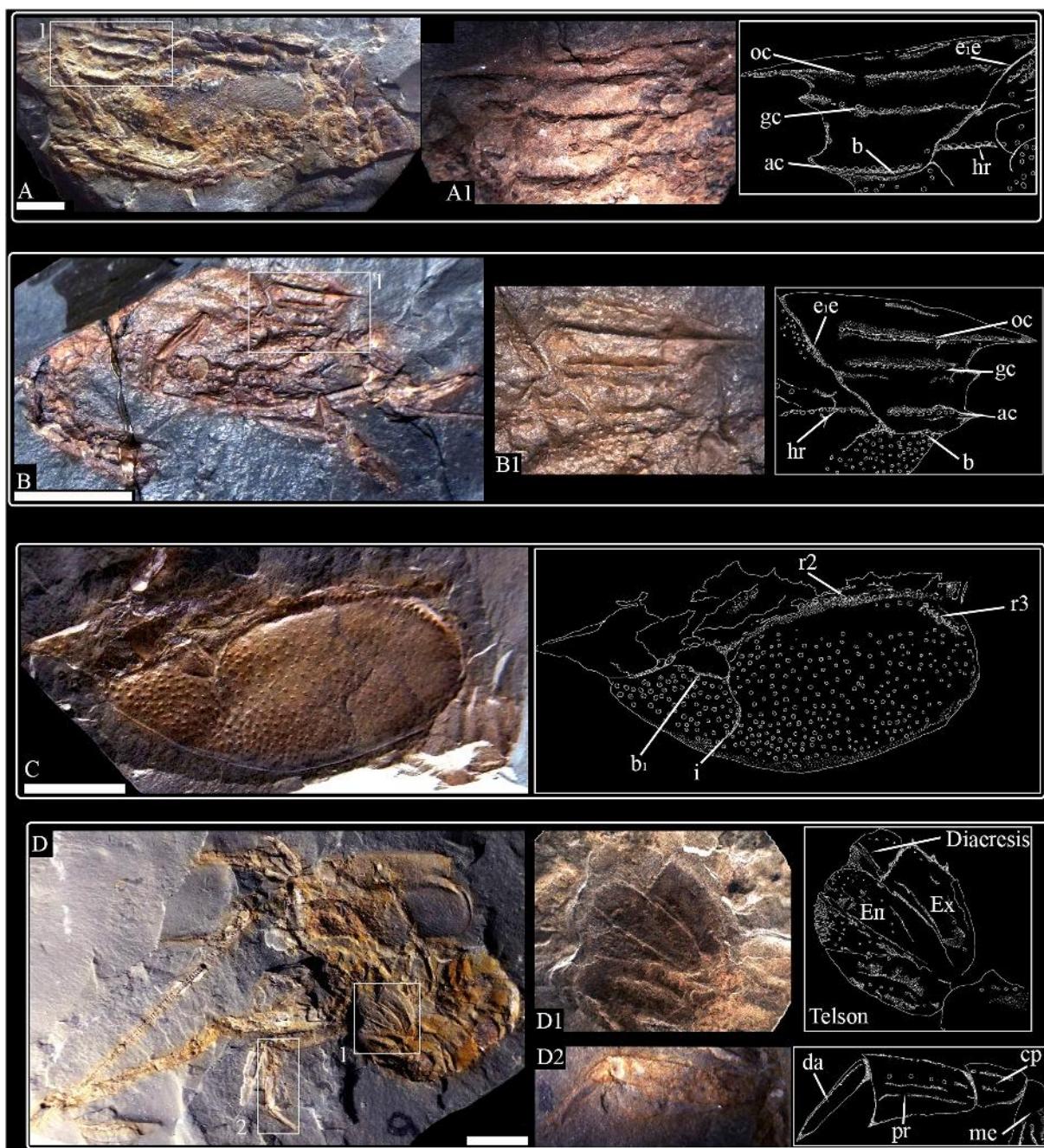


Fig. 6. *Atherfieldastacus magnus* from the Valanginian-Hauterivian, San Juan Raya Formation, Puebla state, Mexico. A, B, Incomplete specimens with longitude of rostral carinae (IGM-11312 and IGM-11313). C, Cephalothorax with granules ornamentation; the inferior groove is evident (IGM-11314). D, Specimen with disarticulated cephalothorax and pleon, possibly a molt; details of diaeresis and second pereiopod can be observed (IGM-11315). Scale bar = 10 mm.

as a slight inflection of the cervical groove at level of gastro-orbital carina; post-cervical and branchio-cardiac grooves parallel, directed toward the posterior margin; post-cervical groove joined ventrally to branchio-cardiac groove, forming one elongated lobe crossed by dorsal branchial ridge (r2); straight cardiac groove, forward-inclined and joined posteriorly to post-cervical groove; cardiac groove joined to dorsal margin; hepatic region with tuberculated longitudinal hepatic carina above hepatic groove, and prolonged by ventral branchial ridge (r1) in branchial region; hepatic groove shallow and curved posteriorly; short inferior groove joined to hepatic groove, and connected to ventral margin; subchelate p1–p2; achelate p3–p5; very elongated p1; uropodal exopod with diaeresis; uropodal endopod with fibrous and flexible distal portion (Robin et al., 2016).

Atherfieldastacus magnus (M'Coy, 1849) Figs. 6–14.

1849 *Meyeria magna* M'Coy, p. 334, Fig. 4; Woods, 1931, p. 71, pl. 19, Figs. 1–4; Vía-Boada, 1975, p. 33, Fig. 1.1–1.9, 2.1–2.6; Vega et al. (2008), p. 5, Figs. 5.1–5.7; 6.1–6.7; 7.1, 7.6; López-Horgue (2009), p. 27, Fig. 2A–J; Astrop (2011), p. 116, Fig. 1B; Klompmaker (2013), app. A-B; González-León et al. (2014), p. 10 Fig. 10A–Q; p. 12, Fig. 11A–M; p. 14 Fig. 12A–J; González-León et al. (2016), p. 4 Fig. 3A–F, 4.

1863 *Meyeria vectensis* Bell, p. 33, pl. 10, Figs. 1–5.

1863 *Oncopareia granulosa* Vilanova, p. 98, pl. 3, Fig. 2; Mallada (1892), p. 157.

1881 *Meyeria pearcei* Spence-Bate in Lee, p. 87, pl. 204, Fig. 14.

1927 *Meyeria bolivari* Van Straelen, p. 80, pl. 1, Fig. 1–2; Glaessner (1929), p. 254; Bataller (1937), p. 617; Bataller (1945), p. 48, 6;

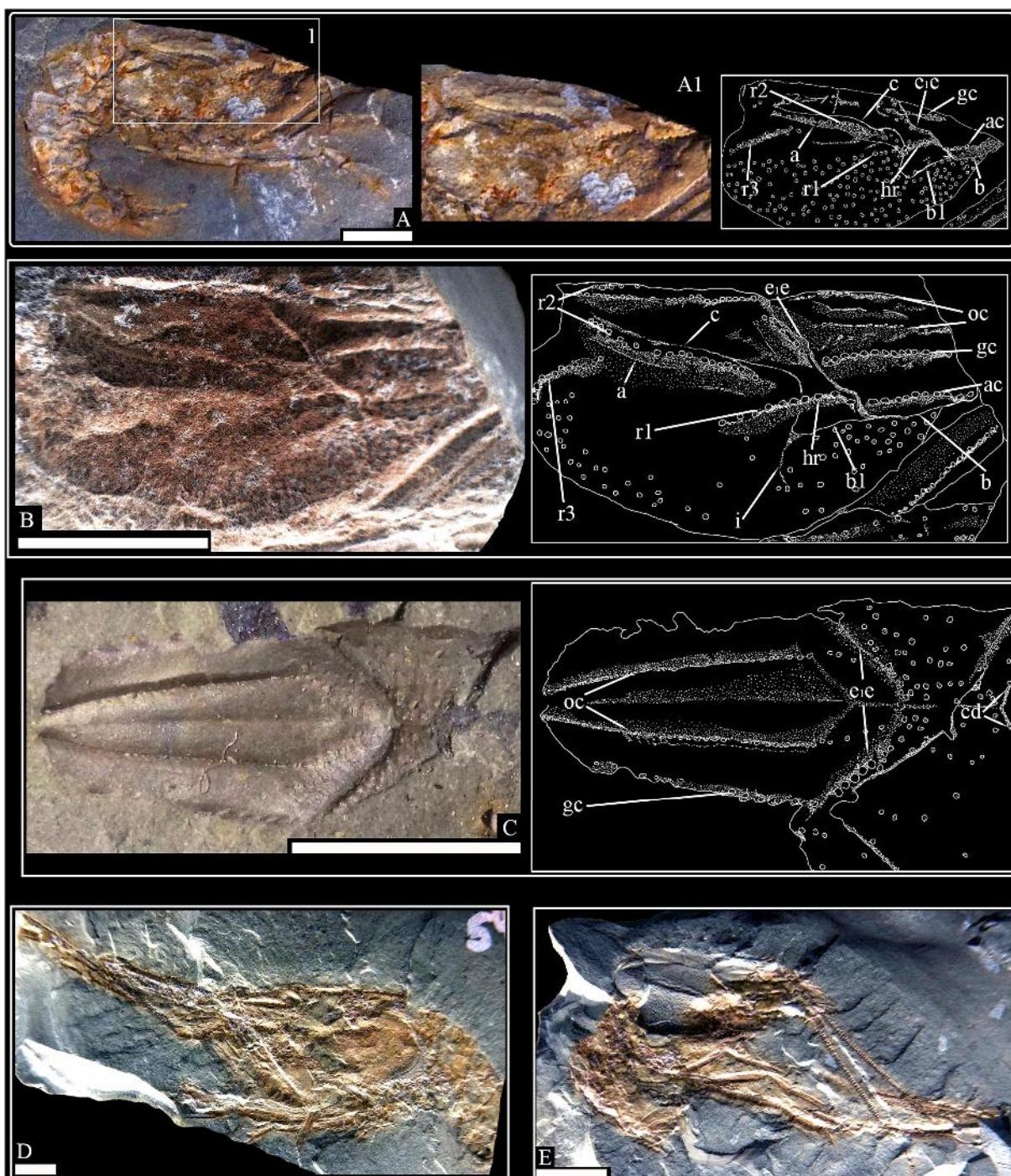


Fig. 7. *Atherfieldastacus magnus* from the Valanginian-Hauterivian of San Juan Raya Formation. A, B, Specimens with details of grooves, rostral carinae and branchial ridges (IGM-11316 and IGM-11317). C, Dorsal view of rostrum (IGM-11318). D, Specimen with articulated cephalothorax, pleon and pereiopods; length of first pair of pereiopods is observed (IGM-11319). E, Possible molt with disarticulated cephalothorax, abdomen and pereiopods; articulated antennal scale and second pair of antennae are observed (IGM-11320). Scale bar = 10 mm.

Bataller (1950), p. 419, Fig. 2; Förster (1971), p. 408, 419.

1935 *Meyeria mexicana* Rathbun, p. 30, pl. 9, Fig. 3.

1951 *Hoploaria granulosa* Vía, p. 154, Fig. 10.

1985 *Meyerella magna* Simpson and Middleton, nomen nudum, p. 203–215.

1995a *Meyeria pueblaensis* Feldmann et al. p. 404, Fig. 2.1–2.4; Feldmann et al. (2007), p. 151, Fig. 6a–g, 7a–g, 8a–c.

2016 *Atherfieldastacus magnus* McCoy, 1849; Robin et al. p. 14, fig. A–F, p. 15, figs. A–J, 4–5; López-Horgue and Bodego (2017), p. 5, Fig. 4F; p. 8, Fig. 7A–C; Ferratges (2017), p. 32, Fig. 15; p. 33, pls. 3A–B;

González-León et al. (2018a), p. 115, Fig. 3A; p. 116, Fig. 4; p. 118, Fig. 5A–H; p. 119, Fig. 6A–F; p. 120, Fig. 7A–E; p. 121, Fig. 8A–D; p. 122, Fig. 9A–I; González-León et al., 2018b, p. 12, Fig. 5; p. 13, Fig. 6; p. 14, Fig. 9; p. 15, Figs. 10–12.

Examined material. Studied specimens are deposited in the Colección Nacional de Paleontología “María del Carmen Perrillat”, Instituto de Geología, Universidad Nacional Autónoma de México, under acronym (IGM) and in the Colección Paleontológica de la Universidad de Caldas, Laboratorio de Estudios Paleontológicos LEP, del Departamento de Ciencias Geológicas, under acronym (UCAL).

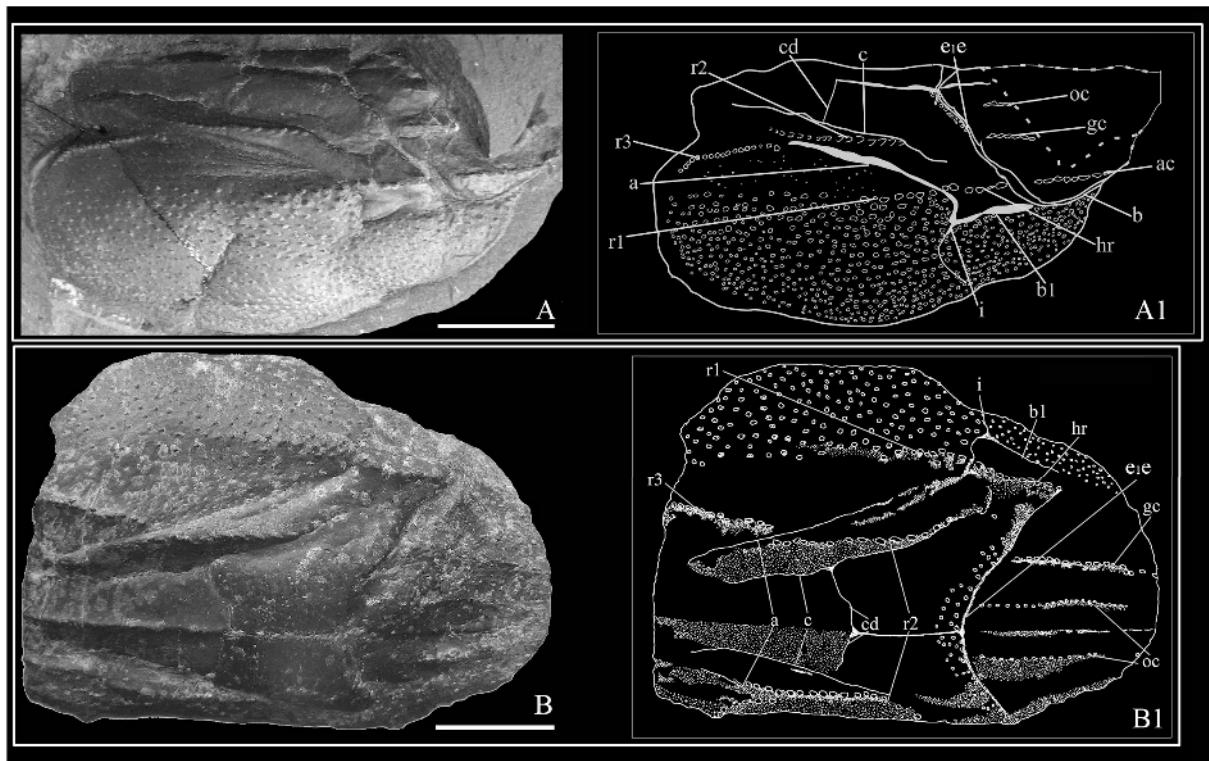


Fig. 8. *Atherfieldastacus magnus* from lower Barremian Paja Formation. A, Complete cephalothorax (UCAL289-7). B, Dorsal cephalothorax with rostrum and branchial region (UCAL289-8). Drawings A1 and B1 indicate morphological features. Scale bar = 10 mm.

Localities and age. San Juan Raya Formation, Valanginian-Hauterivian, Zapotitlán de las Salinas Municipality, Southern Puebla State, Mexico. Paja Formation, Barremian, Curití, Santander Department, Northeast Bogotá, Colombia.

Description of studied specimens. Morphological details of specimens include the presence of grooves, branchial ridges and rostral carinae in the cephalothorax. For the first time, the description includes details of the antennal scale, peduncle and flagellum of the antennae. Pleonal somites with two different shapes and details of the length of the first pair of pereiopods and telson are reported.

Cephalothorax. The rostrum is short pointed spineless, this feature can be seen only in the Mexican specimens (Fig. 6A and B; 11A; 12I; 13H, J; 14D). The rostrum presents three longitudinal carinae, the ocular carinae is small, ends where the rostrum begins; the gastro-orbital and antennal carinae are formed by two rows of forwardly directed spines (Fig. 6A and B; 7A-C; 8A, B; 19A, B; 11A; 12I, J; 13A, F-J; 14A-B). In the branchial region, three lateral branchial ridges are present, one of them is the ventral branchial ridge as continuation of the hepatic carina; the second ridge is the dorsal-branchial, located between post-cervical and branchio-cardiac grooves; the third is the median branchial ridge and is curved and parallel to the posterior margin of the cephalothorax. In Fig. 6C, it is possible to observe the dorsal and median ridges; in Fig. 7A and B, the location of these ridges is indicated for the Mexican specimens; for the Colombian material these features can be observed in Fig. 8A and B; 9A, B. The cervical groove is oblique and is attached to the antennal groove (Fig. 6A and B; 7A, B; 8A; 12A, B, F, H-L; 13A, B, E-J; 14A-B). The branchio-cardiac groove is shallow and inclined to the upper portion of the posterior margin to mid-height of cephalothorax; the post-cervical groove is parallel to the branchio-cardiac groove; both grooves form a lobe crossed by dorsal branchial ridge (Fig. 7A and B; 8A, B; 9A, B). The hepatic groove is shallow and convex ventrally at the junction with the antennal groove (Fig. 6C; 7A, B; 8A, B; 13H; 14B). The hepatic ridge appears tuberculated and is located above the hepatic groove (Fig. 6A

and B; 7A, B, D; 8A, B; 9A-B; 10C; 11A; 12F, I, J, L; 13A, G, H, I; 14B). The inferior groove is connected to the hepatic groove as well as to the ventral margin (Fig. 6C; 7B; 8A, B; 10C; 13H). The forward-inclined cardiac groove joined to the post-cervical groove is only visible partially in two specimens (Fig. 7C; 8A, B).

Antennae. None of the Colombian specimens presented this morphological feature. This anatomical structure is reported for first time in specimens from the San Juan Raya Formation. Several specimens present proximal segment of the antennae articulated, and it is possible to observe details as the antennal scale with spines in the dorsal edge, the peduncle and multiarticulate flagellum (Fig. 11A-C; 12F, G, I, L; 13C, I; 14B, F-G). The length of the antennae appears to be more or less equal to the length of the first pair of pereiopods (Fig. 6D; 7E; 11B; 12L). There is no evidence of presence of the antennule.

Pleon. The tubercles in the pleonal somites are not clearly marked, even so, there are differences in the arrangement of these structures, the same is observed the shape of the abdominal segments, that presents two completely different shapes in the Mexican specimens. One of them present pleonal somites with more rounded edges (Fig. 10A and B; 12A, G, H, L; 14E, H, J, M); others, like the Colombian specimens have anterior and lower margins rounded, while the posterior margin is straight with serrated edges; from the second to fifth, pleonal somites have a similar shape and size, the six pleura is triangular (Fig. 9B and C; 10C; 12I, K; 13C; 14B, D, I).

Pereiopods. Details of the pereiopods can be observed partially in Fig. 6D2, where it is possible to observe details of the achelate second pereiopod, with merus, carpus, propodus and dactylus preserved. The length of the first pair of achelate pereiopods can be seen in Fig. 6D; 7D-E; 10A; 11C; 12A-C, F, I, L; 13C, I; 14F, G. Fragments of other pereiopods are visible in Fig. 6A and B; 7A, B; 10B, C; 11A, C; 12A-D, F, H, K-M; 13C, D, I; 14B-D, F, G, J, K. Preservation of pereiopods in the Colombian specimens is not so evident (Fig. 9A and B).

Telson. This feature is present on several specimens (Fig. 6D1; 11B2; 12B, C, G, I, M; 13D, F, H-J; 14D, I, K, L). The telson displays a

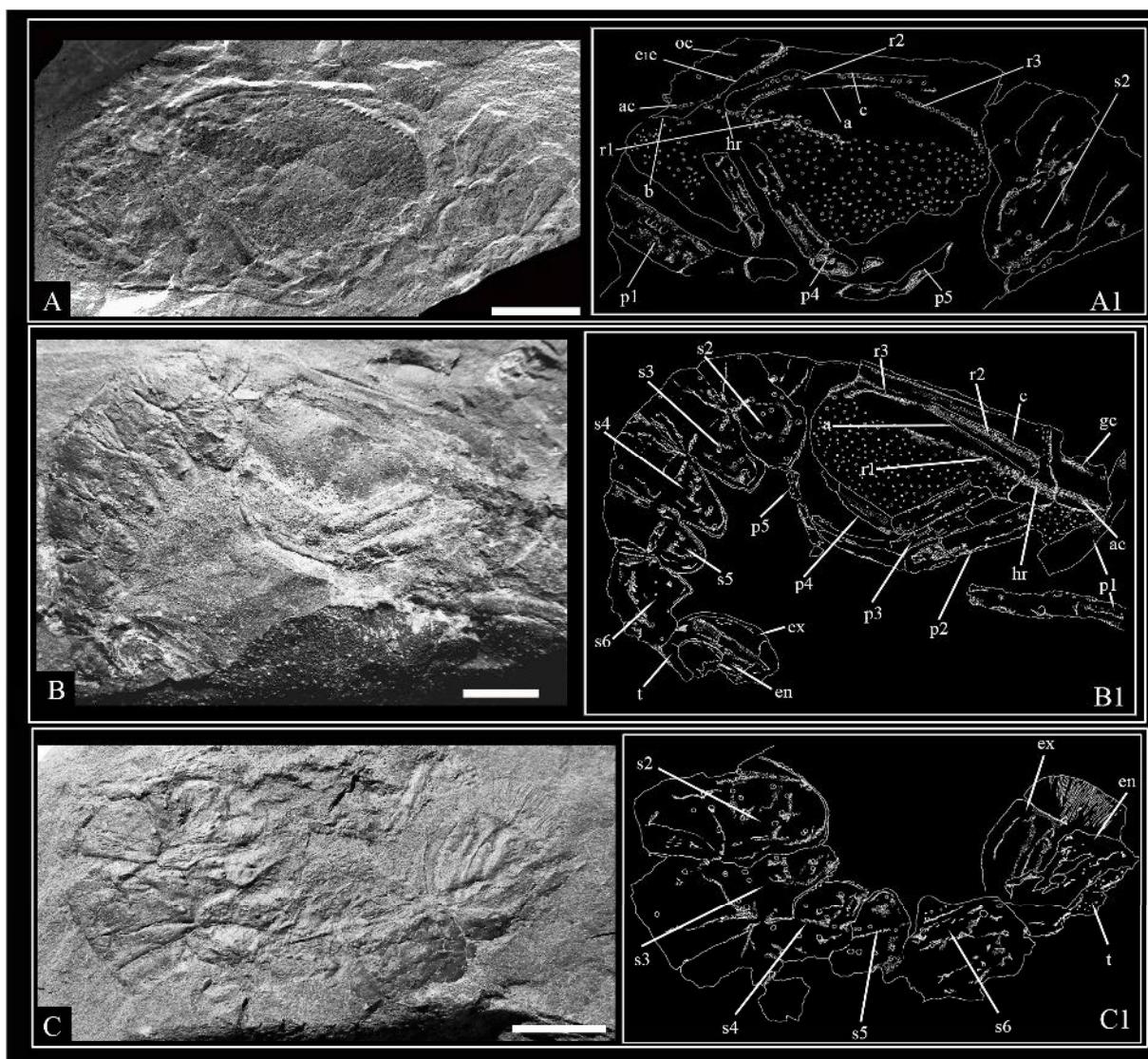


Fig. 9. *Atherfieldastacus magnus* from the lower Barremian Paja Formation. A, Specimen with branchial region and second pleura; image inverted with Adobe Photoshop CC (UCAL289-8). B, Specimen (UCAL289-9) with details of cephalothorax, pleon, telson and pereiopods. C, Specimen with pleon, telson and exopod and endopod (UCAL289-13). Line drawings A1-C1 indicate morphological features. Scale bar = 10 mm.

triangular shape with a sub ovate distal edge; uropod, endopod and exopod with median keel, diaresis present in the uropodal exopod (Fig. 11B2; 12G). For the Colombian specimens, these features can be appreciated in Fig. 9C.

Previously González-León et al. (2017) discusses the difference between *Atherfieldastacus magnus* and *A. rapax* that together with *A. schwartzzi* are part of the genus *Atherfieldastacus* proposed in Robin et al. (2016). In this work they point out that *Atherfieldastacus magnus* has developed three branchial ridges (r_1 = ventral branchial ridge, r_2 = median branchial ridge, and r_3 = dorsal branchial ridge), whereas in *A. rapax* they are only present the median branchial ridge and the dorsal branchial ridge. On the other hand, *A. rapax* present a particular arrangement of the rostral carinae (oc = orbital carinae, gc = gastro orbital carinae and ac = antennal carinae). There is a very short distance between orbital and gastro orbital carinae, at the same time the antennal carinae is separated from the gastro orbital carinae with almost four times the distance than between the orbital and gastro orbital carinae. This feature is very different in *A. magnus*, so it can be easily distinguished (see González-León et al., 2017 p. 64, fig. 8 for more details of these morphological differences). All morphological features included those mentioned above are present in the Mexican and

Colombian specimens, for this, it seems reasonable to assign the Mexican and Colombian lobsters to the species *A. magnus* (aforetime *Meyeria magna*).

5. Discussion

5.1. Sexual dimorphism

The first representative record of sexual dimorphism in *Meyeria* was recognized by (Feldmann et al., 2007) in specimens originally described as *M. pueblaensis* by (Feldmann et al., 1995a) from the San Juan Raya Formation. Feldmann et al. (2007) present a wider range of sizes and variation in details of the pleurae, telson and pereiopods, suggesting sexual dimorphism based mainly in the analysis of the shape of edges of abdominal pleurae, as the main feature used to distinguish between males and females, as observed in modern glypheids and other similar fossil crustaceans (e.g. Étallon, 1859; Forest et al., 1976; Forest and De Saint Laurent, 1989; Feldmann and De Saint Laurent, 2002; Feldmann et al., 2007). These differences in shape of abdominal pleurae are recognized in some Mexican specimens studied in this contribution. We recognize two different forms in the shape of the abdominal pleurae for

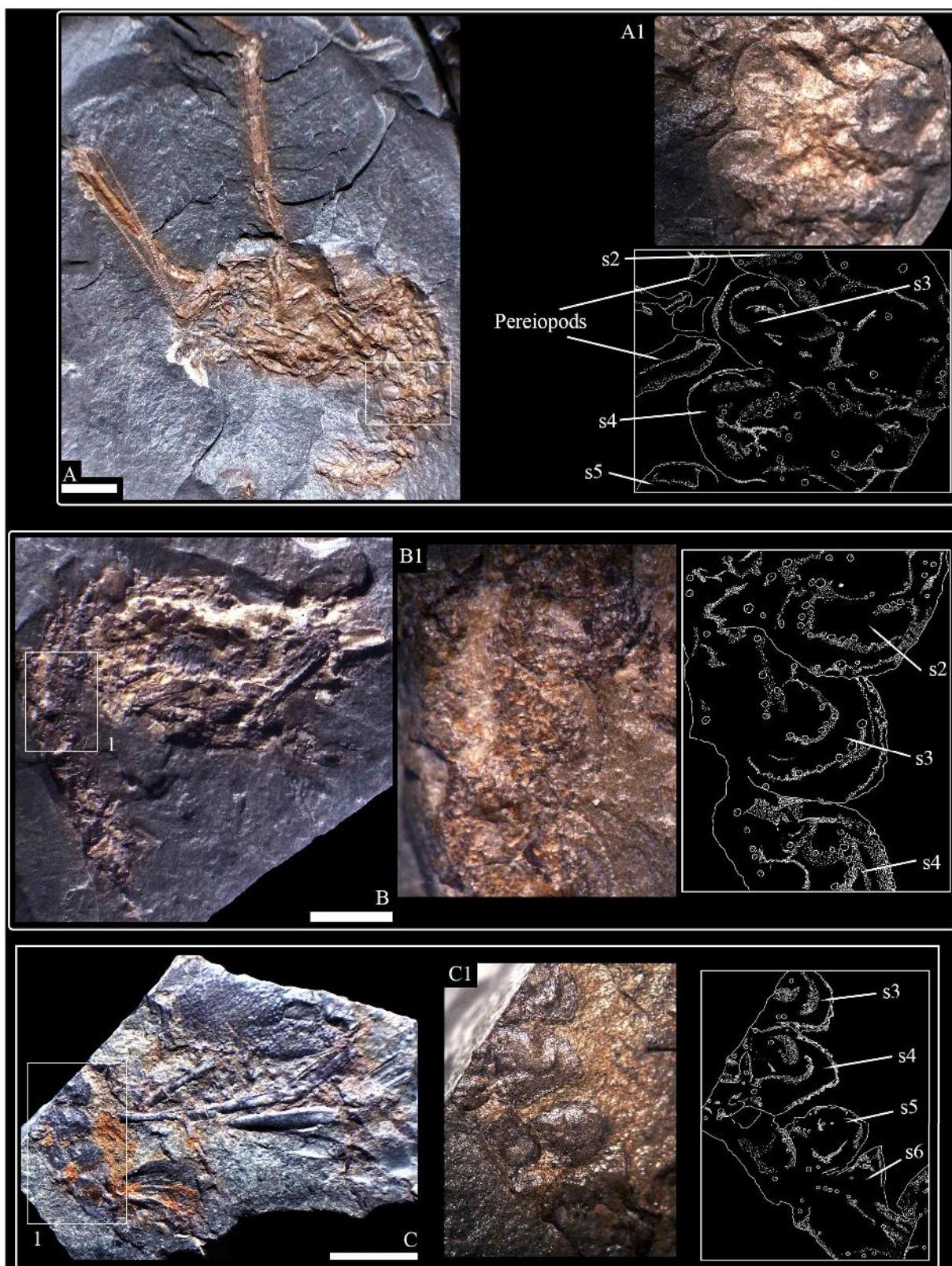


Fig. 10. *Atherfieldastacus magnus* from the Valanginian-Hauterivian of San Juan Raya Formation. A, B, Specimens where redounded edge of pleurae are observed (IGM-11321 and 11322). C, Incomplete specimen (IGM-11323) with straight posterior margin of pleurae. Scale bar = 10 mm.

Atherfieldastacus magnus (compare Fig. 10A and B with C; a more rounded shape of edges of pleurae can be seen in Fig. 10B; 12A, G, H, L; 14E, J, L, M. Detail of these differences can be seen in Fig. 10A1, B1 and C1, where line drawings indicate the pleura number and represented

form. Feldmann et al. (2007) observed that this difference in abdominal pleurae are also related with size, so pleurae in larger specimens are generally quadrate, whereas those in smaller specimens are more rounded and lack posterolateral spines. In Fig. 10B1, pleurae show

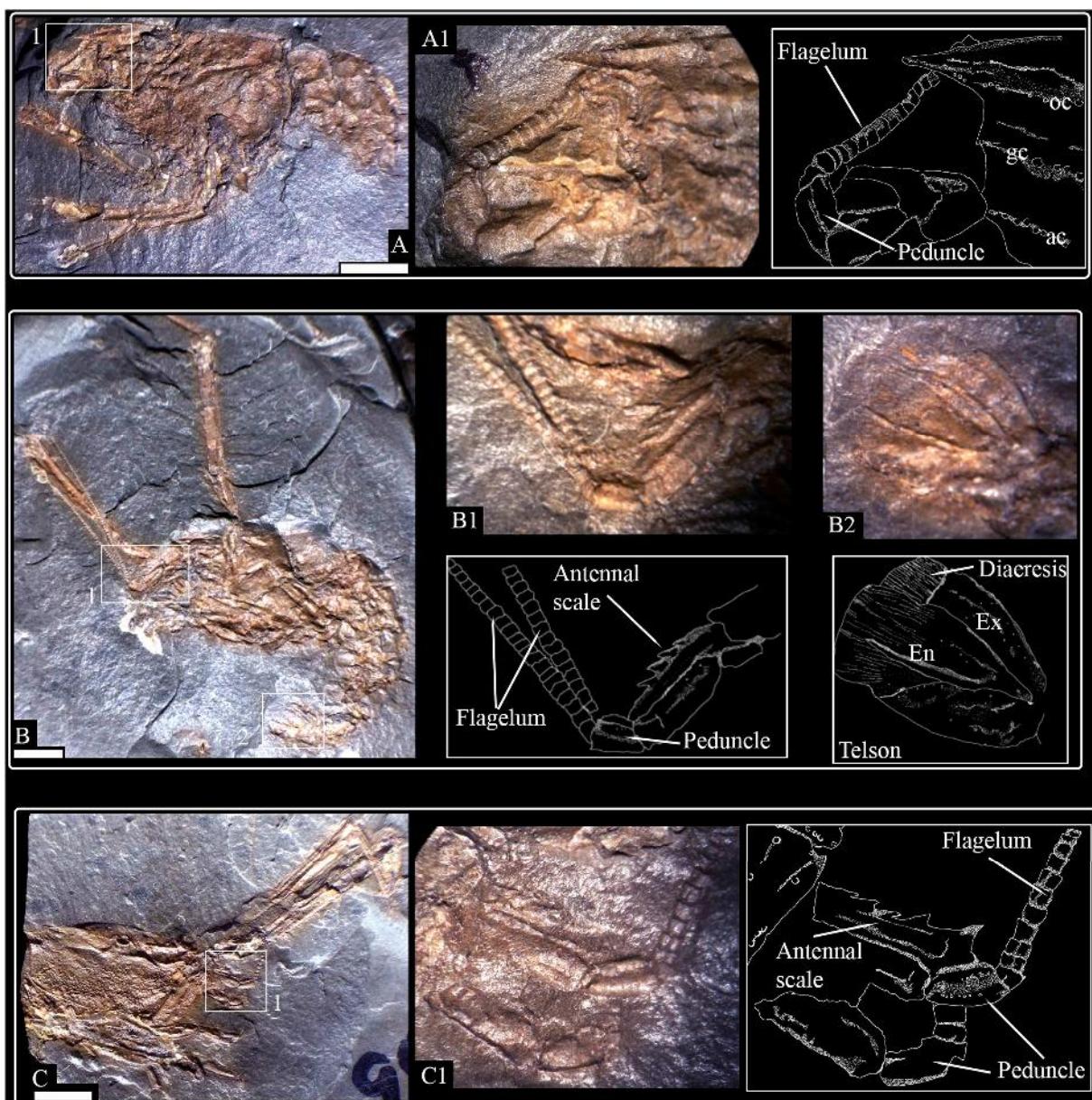


Fig. 11. *Atherfieldastacus magnus* from the Valanginian-Hauterivian of San Juan Raya Formation. A, Presence of the multiarticulate flagellum and peduncle, projected from the frontal part of the rostrum (IGM-11324). A1, Same specimen with multiarticulate flagellum and peduncle. B, Second pair of antennae articulated with peduncle attached to the rostrum; presence of antennal scale is also observed (IGM-11321). B1, Antennal scale, peduncle and flagellum. B2, Uropods are observed. C, Flagellum, peduncle and antennal scale (IGM); length of first pair of pereiopods is appreciated. C1, Antennal scale, peduncle and flagellum (IGM-11325). Scale bar = 10 mm.

serrated edges, feature not observed in the close-up of Fig. 10A1. It is also possible to observe more rounded edges of pleurae of specimen illustrated in Fig. 10C1. Although the recently found Mexican assemblage represents different ontogenetic stages, differences in body size and shape of pleurae seem to indicate that males were larger than females, as suggested by Feldmann et al. (2007). More specimens and more complete specimens are needed in order to confirm that the difference in size can also be used to recognize males and females in juvenile stages.

5.2. Biotic assemblage from San Juan Raya Formation

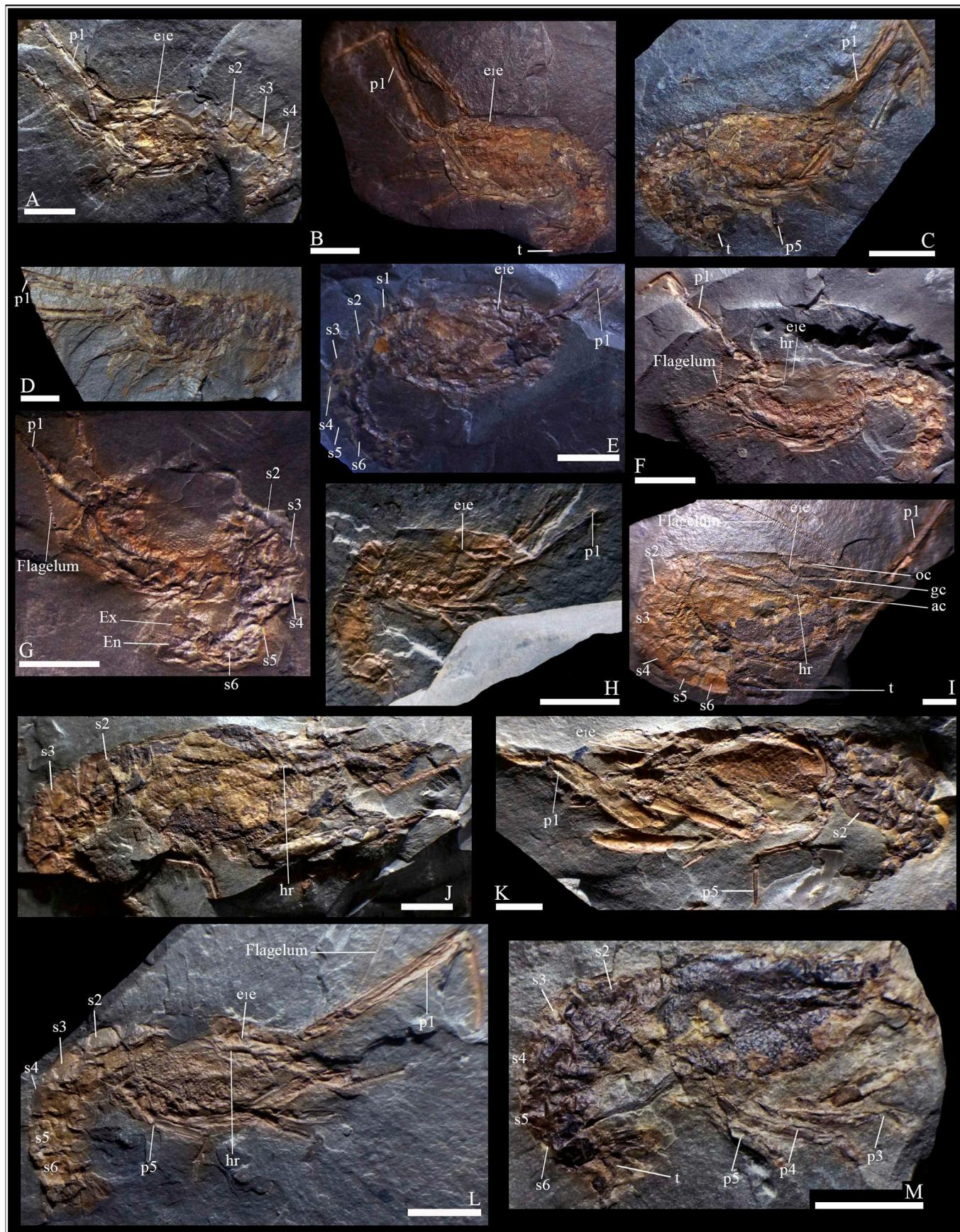
The new assemblage of juvenile stages of *A. magnus* is associated with a delicate isopod exuviae of three species (Vega et al., 2019). The same layer 1 m thick contains also plant remains (a gymnosperm cone),

bivalves, gastropods, ammonites and echinoderms. The echinoderms are found at the base of the layer; the top of the same layer contains the rest of the fossil assemblage. Most of the isopod remains correspond to posterior molts, while others seem to be incomplete corpses. Unlike this, most specimens of *A. magnus* are articulate and only some were found disarticulated. It is possible that the isopod specimens were transported from a different environment (for more details and illustrations see Vega et al., 2019).

5.3. Chronostratigraphic age

5.3.1. United Kingdom

The fossil record associated to *Meyeria magna* (now *Atherfieldastacus magnus*) begins with their description made by McCoy in 1849. This species has long been known from the Atherfield Clay Formation of



(caption on next page)

Fig. 12. *Atherfieldastacus magnus* from Barranca el Gavilán canyon, Valanginian-Hauterivian, San Juan Raya Formation. A, First pereiopod, cervical groove and pleural somites 2–4 (IGM-11326). B, Length of first pair of pereiopods, almost the same as between cephalothorax and pleon; cervical groove and telson also indicated (IGM-11327). C, Length of first pair of pereiopods (IGM-11328). D, Incomplete specimen (IGM-11329). E, First pereiopods, cervical groove and pleural somites (IGM-11330). F, Cervical groove, hepatic ridge and flagellum are indicated (IGM-11331). G, Flagellum, uropods, and pleural somites (IGM-11332). H, Almost complete specimen (IGM-11333). I, Rostrum, three rostral carinae, some pereiopods and part of the flagellum (IGM-11334). J, Granulation in cephalothorax as well as hepatic ridge (IGM-11335). K, Fist pereiopod, cervical groove and pleural somite 2 are indicated (IGM-11336). L, First pereiopod, cervical groove, hepatic ridge, flagellum and pleural somites are indicated (IGM-11337). M, Details of the cuticle (black) and pereiopods (IGM-11338). Scale bar = 10 mm.

Atherfield, Isle of Wight and Yorkshire coast, UK. The sequence in which they were found comprise an early Aptian age assigned by ammonite biostratigraphy (e.g. [Casey, 1961](#); [Simpson and Middleton, 1985](#)). Since then, other localities have been reported with the presence record of this fossil lobster. Apart from Atherfield, *A. magnus* has been reported at Peasmash, Surrey, Petworth, Sussex, Punfield and Dorset ([Simpson and Middleton, 1985](#)).

5.3.2. Spain

[Vía-Boada \(1975\)](#) reported the presence to *Mecochirus magnus* in deposits of “La Tejería de Josa” (Teruel), comparing those specimens with the ones from Torreblanca and Alcalá de Chivert (Spain), and suggested that *Meyeria bolivari* described by [Van Straelen \(1927\)](#), was synonymous with *Mecochirus magnus*, from Lower Aptian of England. Other contributions ([Calzada and Urquiola, 1999](#); [López-Horgue, 2009](#); [López-Horgue and Bodego, 2017](#)) include illustrations of *Meyeria magna* from the Aptian-Albian of Garraf (Catalunya) and Cuchía and Ajo, both being part of the Basque Cantabrian Basin. More recently, two specimens from the Aptian of Teruel were illustrated by [Ferratges \(2017\)](#).

5.3.3. Tibet

[Wang \(1981\)](#) reported the presence of *M. magna* (eight incomplete specimens) found in the Lhasa area, Tibet. Previously ([González-León et al., 2014](#)) considered this attribution as questionable, but a more recent and detailed analyses of those specimens confirm that they belong to *Atherfieldastacus magnus*, from the Aptian-Albian of this region of Tibet ([Wang, 1981](#); [Zhang, 2000](#)).

5.3.4. Colombia

In Colombia, the record of *A. magnus* includes Aptian-Albian ages for two Colombian localities in Tolimá and Santander provinces ([Vega et al., 2008](#); [González-León et al., 2016](#)). The ammonite record associated to this lobster in Colombia allowed the definition of the chronostratigraphic age. The Colombian specimens from Curití studied herein are assigned to the late Barremian, based on the ammonite biostratigraphic range for the study locality, represents the oldest record of *A. magnus* for South America.

5.3.5. Mexico

[Rathbun \(1935\)](#) described one specimen of *Meyeria mexicana* collected from the Abuja Colorado Canyon, Cerro Chino, Chihuahua, Mexico ([Rathbun, 1935](#); [King and Adkins, 1946](#)). More recently [González-León et al. \(2018a\)](#) collected several specimens in concretions from the locality described by [Rathbun \(1935\)](#). According to [González-León et al. \(2018a\)](#), the morphological features of the specimens from Chihuahua correspond to *A. magnus*, representing the northernmost report for the species in the Americas. The ammonites associated to the mecochirid lobsters in this locality of La Peña Formation, confirm the late Aptian age previously indicated by [Rathbun \(1935\)](#).

In the area of San Juan Raya, Puebla, Mexico, the record of *Meyeria* was reported for first time by ([Feldmann et al., 1995a](#)), described as *M. pueblaensis*, based on four nearly complete specimens from two different localities of the San Juan Raya Formation. Later, [González-León et al. \(2014\)](#) found more specimens in two different localities, near the ones reported by [Feldmann et al. \(1995a; 2007\)](#), and noticed there is an important difference in size between the specimens reported by [Feldmann et al. \(1995a; 2007\)](#) and the ones found at the new localities.

[González-León et al. \(2014\)](#) considered that the allometric differences could be related to different ontogenetic stages of *Atherfieldastacus magnus*.

Although an Aptian age has been proposed by many authors for the San Juan Raya Formation ([Feldmann et al., 2007](#), [González León et al., 2014, 2015](#), among many others), a re-examination of the age of calcareous nannoplankton from the same layers that contain *A. magnus* allow to establish an older (late Valanginian-Hauterivian) age for the studied localities of the San Juan Raya Formation ([González-León et al., 2015](#)). A different age was confirmed for a different locality of the same level of the San Juan Raya Formation, found in Santa Isabel Atenayuca, Puebla, Mexico ([González-León et al., 2014](#)). Calcareous nannoplankton species found in the same stratigraphic interval where specimens of *A. magnus* were found, indicate a late Valanginian-early Hauterivian age (see [Vega et al., 2019](#) for details of the calcareous nannoplankton analysis). This age was also previously suggested by [González-León et al. \(2015\)](#), based on data obtained from calcareous nannoplankton from two locations of the San Juan Raya Formation, as indicated by the presence of *Speetonia colligata* ([Black, 1971](#)), *Cruciliopsis cuvillieri* ([Thierstein, 1971](#)), *Rhagodus dekaenelli* ([Bergen, 1994](#)), *Zeughrabdatus fluxus* ([Casellato, 2010](#)), *Tubodiscus verenae* ([Thierstein, 1973](#)), *Helenea quadrata* (Bown and Rutledge, in [Bown et al., 1998](#)) and the relative high abundance of *Cyclagelosphaera marginella* ([Noël, 1965](#)). The above-mentioned species, along with new calcareous nannoplankton analyses reported by [Vega et al. \(2019\)](#), confirm that the record of *A. magnus* found in the lower part of the San Juan Raya Formation represents the oldest occurrence known worldwide for this mecochirid species. The stratigraphic range assigned to *A. magnus* (aforetime *Meyeria magna*) worldwide as well as, the works that we consider contain specimens that should be considered as *Atherfieldastacus magnus* is presented in [Fig. 15](#).

To compare the differences in size between locations worldwide, we apply a simple morphometric model comparing the height versus length of the cephalothorax. Apart from showing the morphometric relationship between the data, this model allows recognizing the record of juvenile stages for the San Juan Raya Formation for *A. magnus*. The morphometric data were obtained from previously published specimens in which the cephalothorax was complete and well preserved (e.g. [Wang, 1981](#); [Vega et al., 2008](#); [López-Horgue, 2009](#); [González-León et al., 2014, 2016; 2018](#); [Robin et al., 2016](#)). The size range between the length and the height of the cephalothorax of different specimens of *A. magnus* from China, Colombia, Spain, United Kingdom, and Mexico are represented by a linear model ([Fig. 16](#)). Morphological and morphometric data obtained from specimens here reported from the San Juan Raya Formation, compared with other occurrences around the world, allow to conclude that we deal with the three different ontogenetic stages suggested by [González-León et al. \(2014\)](#), being the majority juveniles and juveniles/sub-adult with sizes that do not exceed 4 cm, and a few specimens larger than 4 cm, so they were considered as a sub-adult/adult stage.

5.4. Paleobiogeography

The fossil record of *A. magnus* has a wide distribution during Early Cretaceous times. Its occurrence in different localities around the world (United Kingdom, Spain, Tibet, Colombia and Mexico) includes records from the Valanginian to the Albian. A paleogeographical map ([Fig. 17](#))

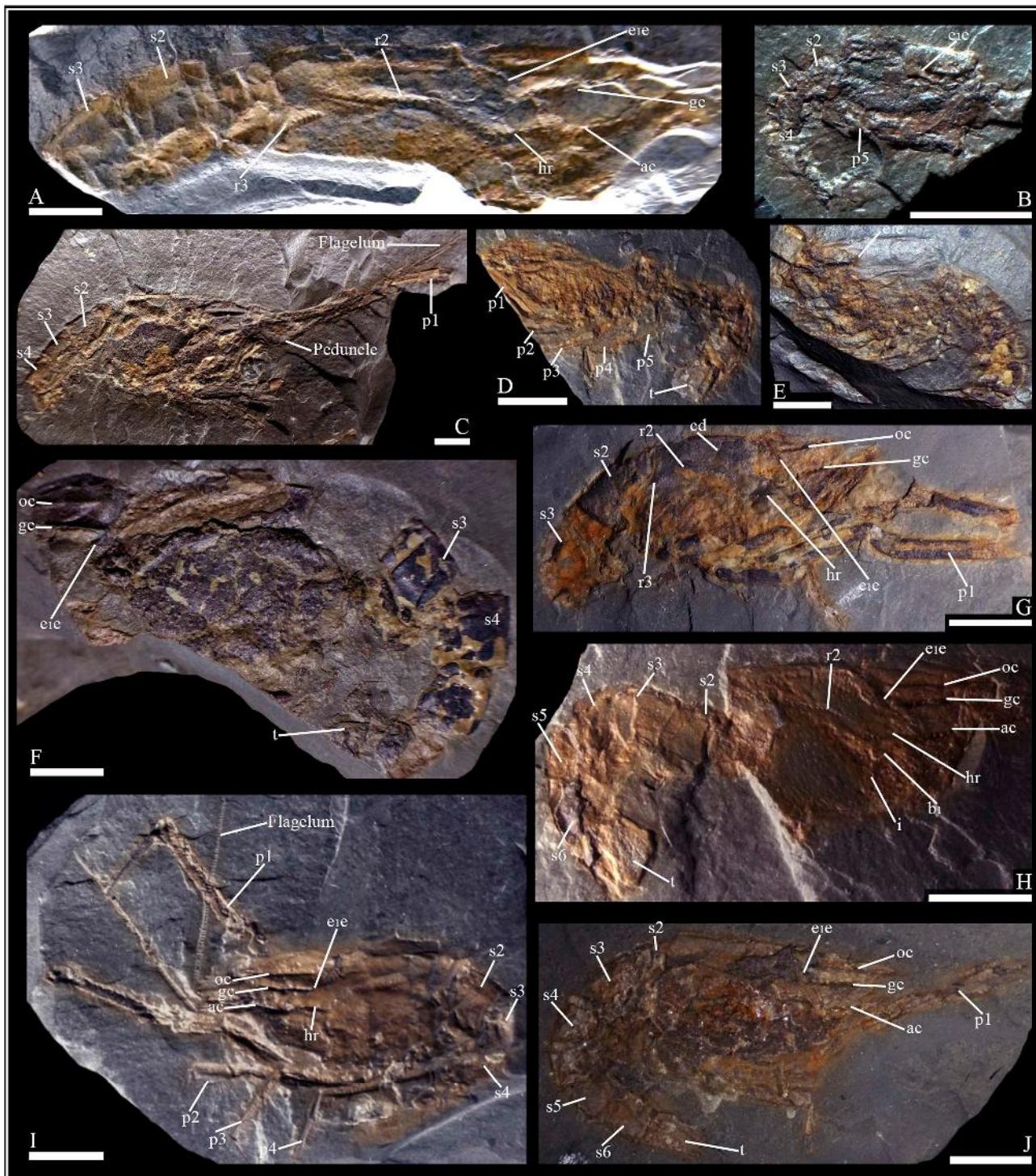


Fig. 13. *Atherfieldastacus magnus* from Barranca el Gavilán canyon, Valanginian-Hauterivian, San Juan Raya Formation. A, Cervical groove, rostral carinae and branchial ridges (IGM-11339). B, Small specimen (IGM-11340), some morphological features are observed. C, First pair of pereiopods, peduncle and flagellum of antennae, and pleural somites 2–3 (IGM-11341). D, Details of pereiopods, pleon, and telson (IGM-11342). E, Small specimen with cervical groove (IGM-11343). F, Cervical groove, rostral carinas, pleural somites and uropods (IGM-11344). G, Morphological details of the cephalothorax are indicated (IGM-11345). H, Pleon separated from the cephalothorax, position of pleural somites and telson are indicated (IGM-11346). I, Details of pereiopods 1–4, flagellum of antennae, cervical groove, rostral carinae, hepatic ridge and pleural somites 2–4 (IGM-11347). J, Cephalothorax and pleon (IGM-11348). Scale bar = 10 mm.

indicates the possible position of the localities during the Early Cretaceous, in paleoenvironments interpreted as shallow marine carbonate platforms with deltaic influence (López-Horgue, 2009) in Spain; shallow lagoon (Feldmann et al., 1995a, 2007) in Mexico; supratidal (Zhang et al., 2002) in Tibet; offshore deposits (González-León et al., 2016) in Colombia; shallow and low energy subtidal platform and outer

platform and shallow seaway (González-León et al., 2015; Vega et al., 2019) in Mexico. This distribution in the northern hemisphere mainly could have been related with the planktonic nature of the larval stages, associated with the paleocurrents that predominated during the Early Cretaceous.

The paleobiogeographic patterns previously recognized within

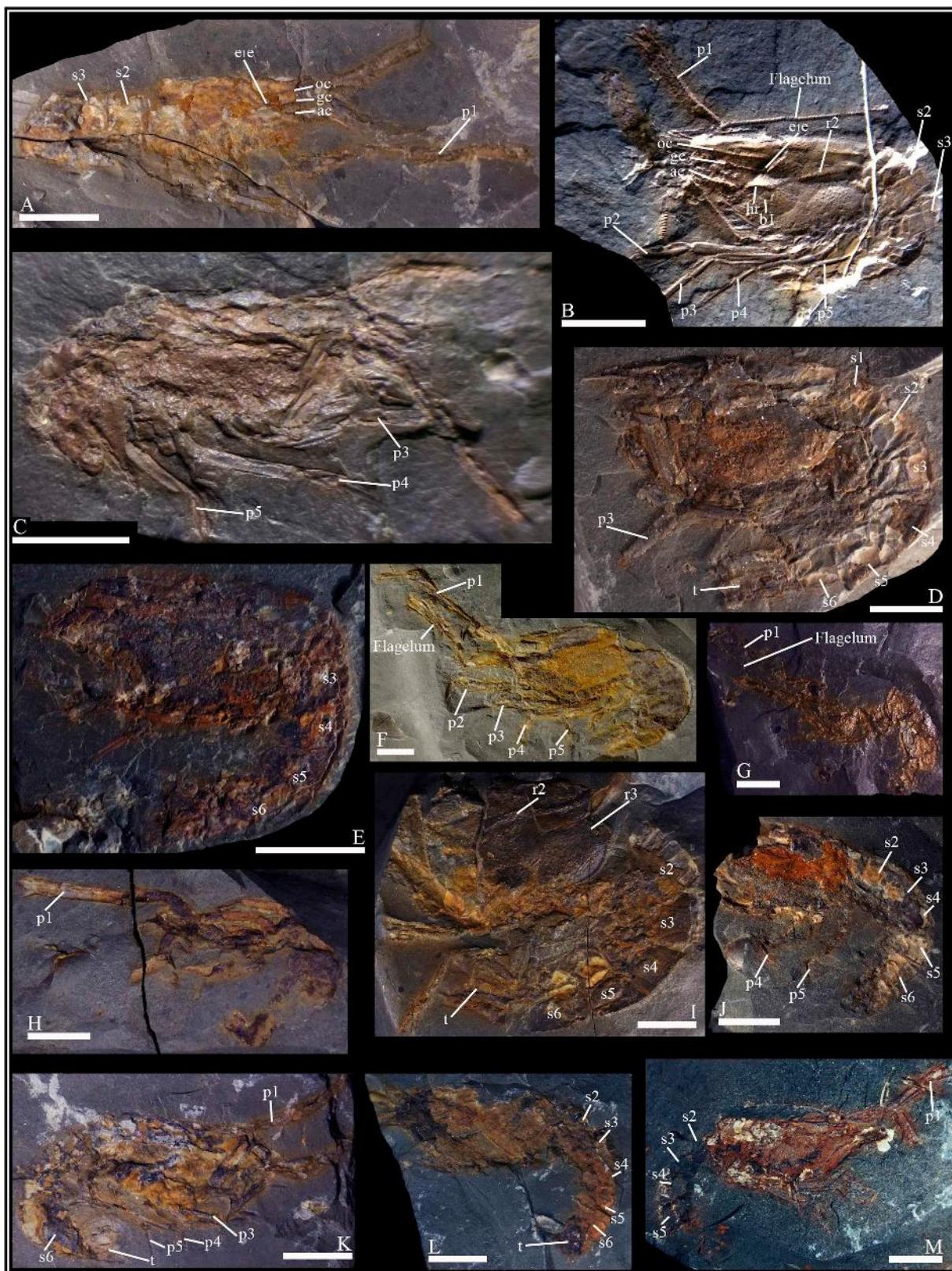


Fig. 14. *Atherfieldastacus magnus* from Barranca el Gavilán canyon, Valanginian-Hauterivian, San Juan Raya Formation. A, Rostral carinae and cervical groove (IGM-11349). B, Well-preserved details of cephalothorax and pereiopods (IGM-11350). C, Details of pereiopods (IGM-11351). D, Short-pointed rostrum, pleural somites and some pereiopods (IGM-11352). E, Rounded form of pleural somites 4 and 5 (IGM-11353). F, Details of pereiopods including length of first pair and some details of the flagellum of antennae (IGM-11354). G, Length of first pair of pereiopods as well as of the flagellum of the antennae in small specimen (IGM-11355). H, Part of the first pereiopod preserved (IGM-11356). I, Details of branchial ridges, pleural somites and telson (IGM-11357). J, Pleural somites and pereiopods 4 and 5 (IGM-11358). K, Some pereiopods are preserved (IGM-11359). L, Poorly preserved specimen (IGM-11360). M, Rounded form of the pleural somites 2–5 (IGM-11361). Scale bar = 10 mm.

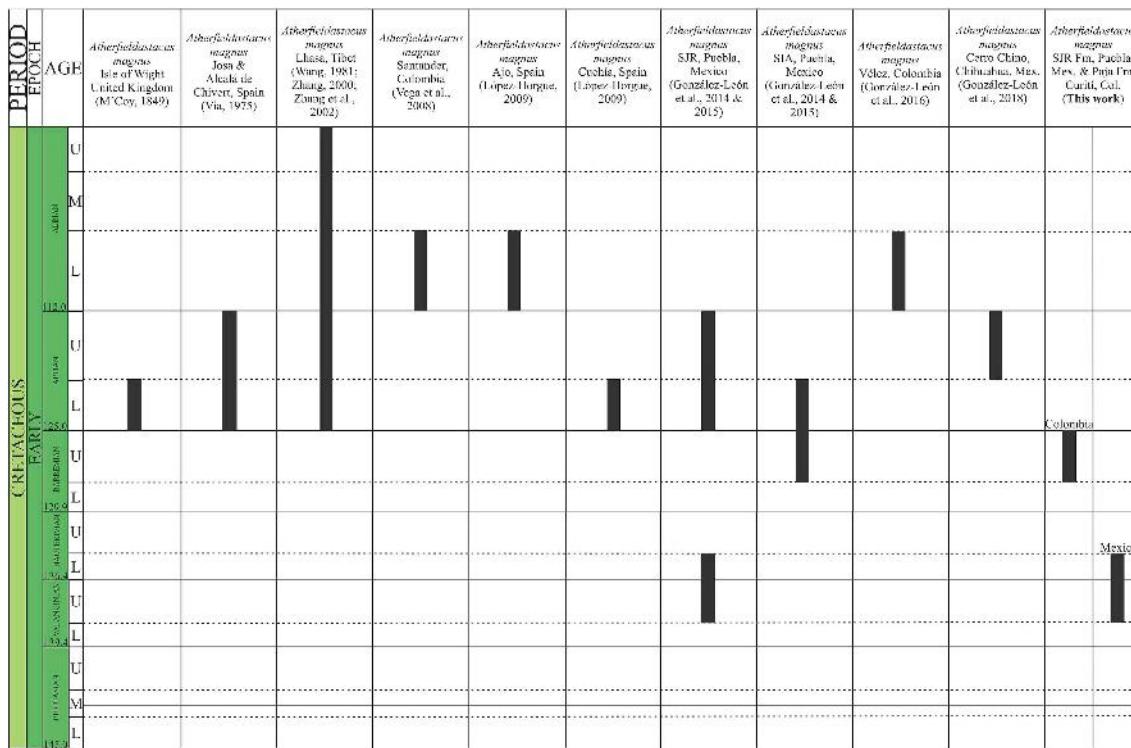


Fig. 15. Chronostratigraphic age assigned to *Atherfieldastacus magnus* in the United Kingdom, Spain, China, Colombia and Mexico. An interval from the upper Valanginian to the Albian is established as the biostratigraphic range for this species.

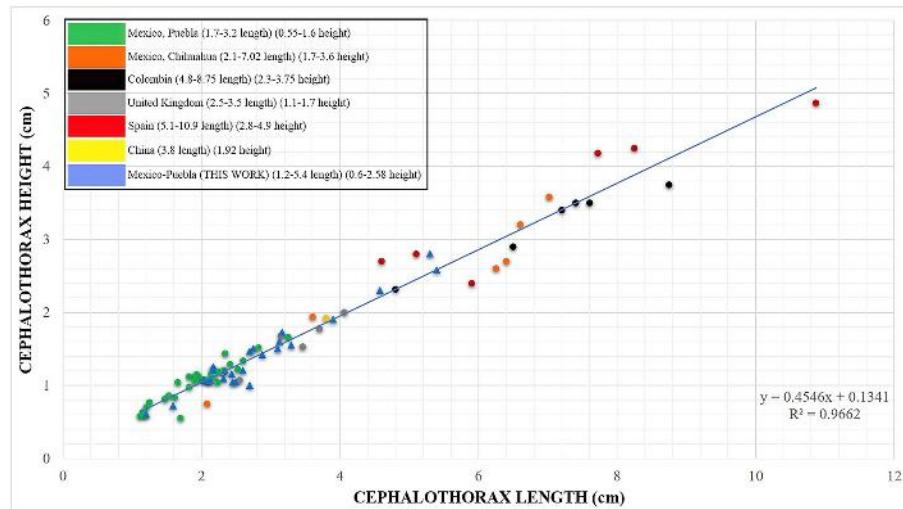


Fig. 16. Biometric analysis showing L/H relationship of the cephalothorax of 81 specimens of *Atherfieldastacus magnus*. Ranges between length and height by country are indicated.

Decapoda during Cretaceous times include mainly brachyurans (Feldmann et al., 1995b, 1997; 1998; Schweitzer, 2001; Feldmann and Schweitzer, 2006). Some of the maps in these works show dispersal routes they have been inferred based upon timing of appearance of generic taxa worldwide and the interaction with the paleocurrent data (Feldmann and Schweitzer, 2006). The record of macruran decapods has been less explored and there are few examples where a broad distribution has been confirmed. The genus *Hoploparia* (M'Coy, 1849) has been found in deposits belonging to the Hauterivian of Europe and North America. Additionally, it has been found in Cretaceous rocks of Japan (Schweitzer, 2001). A similar distribution pattern to that of *Atherfieldastacus magnus* was presented by Vega et al. (2007) for the raninoid *Cenomanocarcinus vanstraeleni* Stenzel (1945) during late

Cenomanian and early Turonian times. In this case, the wide distribution is supported by occurrences in Germany, Texas, Mexico and Colombia, inferring a semi-pelagic habit to explain this ample distribution. An additional example of wide distribution in the past and subject of much discussion is marked by the presence first in Nigeria and recently in Texas of *Costacopluma concava* Collins and Morris, 1975. The recent record of this species in Texas (Collins et al., 2018) extend the paleobiogeographic and chronostratigraphic range for this species Cenomanian-Coniacian). This species become to the oldest known member of the genus and suggest that the origin of *Costacopluma* could be in the Americas (see Fraaije et al., 2006).

For some Cretaceous decapods, different authors reported paleobiogeographic routes that indicate dispersal patterns from Europe to

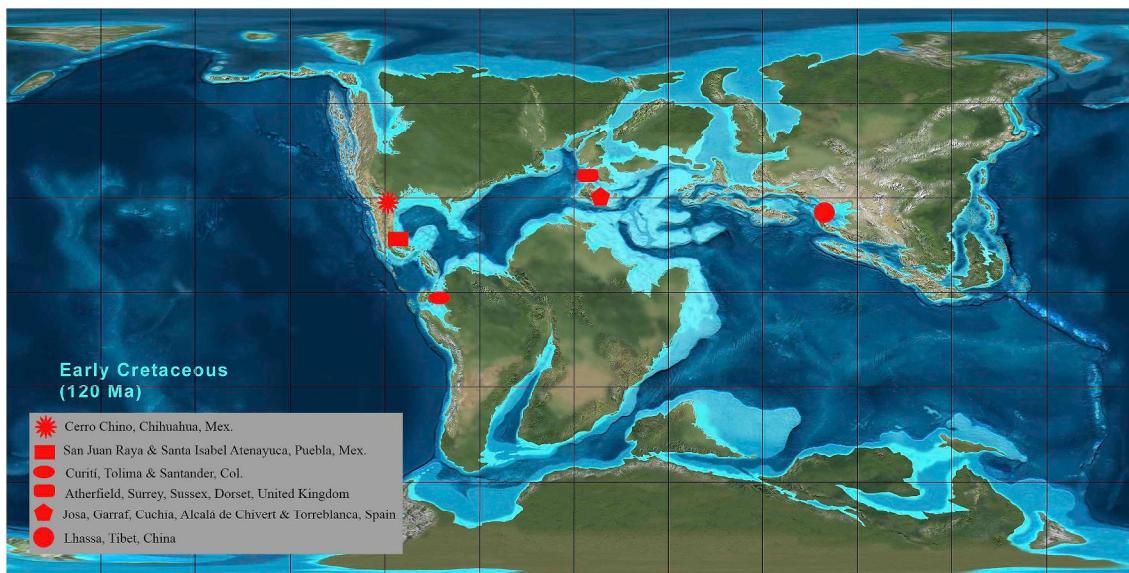


Fig. 17. Aptian paleogeographic map with inferred configuration of continental mass and oceans, with distribution of *Atherfieldastacus magnus*. With exception of Tibet, United Kingdom and Spain, the species has been reported from at least two localities with different ages. Red symbols indicate approximate locations of fossiliferous outcrops. Image modified courtesy of Ron Blakey. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

America (Feldmann et al., 1995b, 1997; 1998; Schweitzer, 2001; Feldmann and Schweitzer, 2006). In the particular case of *Atherfieldastacus magnus*, the paleobiogeographic routes indicate a distribution and dispersal pattern from the Americas to Europe (Vega et al., 2008; González-León et al., 2014, 2015, 2018 and the present report). According to the available data *A. magnus* may had its origin in Mexico during the late Valanginian, then disperse to South America in Barremian times, and finally migrated to Europe and Asia during the early Aptian, to become extinct during the Albian.

6. Conclusions

The current work synthetizes all the current taxonomic, ontogenetic, paleobiogeographic and chronostratigraphic knowledge of the mechiocirid lobster *A. magnus*. At the same time, two new records of this species are reported from Mexico and Colombia. The new Mexican record is reported as a part of a fossil assemblage that is analyzed of a paleoenvironmental point of view. In addition, sexual dimorphism is also studied in *A. magnus* and is suggested by the presence of two different morphologies of the abdominal pleurae, a character previously recognized for other glypheids and for this species. This Mexican record also contains uncommonly preserved structures like the antennae that are described and depicted. All this information constitutes a strong framework that allows us to analyze the paleobiogeographic distribution of this lobster.

The presence of *A. magnus* in the Valanginian-Hauterivian of Mexico and Barremian of Colombia, allow to conclude that the oldest records of this species are found in the Americas, being Mexico the country with the oldest record of this species.

According the current available data, *A. magnus* could have migrate to Europe during Aptian times and this species disappears everywhere during the early Albian.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jsames.2019.102261>.

References

- Astrop, T.I., 2011. Phylogeny and evolution of Mecochiridae (Decapoda: reptantia: Glypheoidea): an integrated morphometric and cladistic approach. *J. Crustac Biol.* 31 (1), 114–125.
- Barrera, D., Pardo, A., Vargas, C.A., Martínez, J.F., 2007. Colombian Sedimentary Basins: Nomenclature, Boundaries and Petroleum Geology, a New Proposal. Agencia Nacional de Hidrocarburos, Bogotá D.C., pp. 91.
- Bataller, J.R., 1937. Catàleg de les espècies fòssils noves del cretaci de Catalunya i d'altres regions. *Arxiu d'Escola Superior d'Agricultura (n.s.)* 3 (1), 581–619.
- Bataller, J.R., 1945. Enumeración de las especies nuevas del Cretácico de España. *Mem. R. Acad. Cienc. Artes Barc.* 27 (11), 373–441 (3a ed.), n. 571, t.
- Bataller, J.R., 1950. Sinopsis de las especies nuevas del Cretácico de España. Pars. IX, Arthropoda. *Anales de la Escuela de Agricultura de Barcelona* 9, 418–428.
- Bell, T., 1863. A Monograph of the Fossils Malacostraceous Crustacea of Great Britain. Part II. Crustacea of the Gault and Greensand. *Palaeontographical Society Monographs, The Palaeontographical Society, London*, pp. 21.
- Bergen, I.A., 1994. Berriasian to Early Aptian calcareous nannofossils from the Vocontian Trough (S.E. France) and deep sea drilling site 534: new nannofossil taxa and a summary of low-latitude biostratigraphic events. *J. Nannoplankt. Res.* 16 (2), 59–69.
- Black, M., 1971. Coccoliths of the speeton Clay and sutterby marl. *Proc. Yorks. Geol. Soc.* 38 (3), 381–424.
- Bover-Arnal, T., Moreno-Bedmar, J.A., Salas, R., Skelton, P.W., Bitzer, K., Gili, E., 2010. Sedimentary evolution of an Aptian syn-rift carbonate system (Maestrat Basin, E Spain): effects of accommodation and environmental change. *Geol. Acta* 8 (3), 249–280.
- Bown, P.R., Rutledge, D.C., Crux, J.A., Gallagher, L.T., 1998. Early cretaceous. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. British Micropalaeontological Society Publication Series, Chapman & Hall, pp. 86–131.
- Bürgl, H., 1956. Catálogo de las ammonitas de Colombia. Parte I. Pulchelliidae. *Bol. Geol.* 4 (1), 1–119.
- Burkenroad, M.D., 1963. The evolution of the Eucarida (Crustacea, Eumalacostraca), in relation to the fossil record. *Tulane Stud. Geol.* 2, 3–17.

- Calzada, S., Urquiola, M., 1999. Revisión de "Mytilus vilanovaæ" Lánderer (Bivalvo cretácico). Rev. Esp. Palaontol. 14 (2), 293–295.
- Casellato, C.E., 2010. Calcareous nannofossil biostratigraphy of upper callovian-lower berriasian successions from the southern alps, north Italy. Riv. Ital. Paleontol. Stratigr. 116, 357–404.
- Casey, R., 1961. The stratigraphical palaeontology of the Lower Greensand. Palaeontology 3 (4), 487–621.
- Collins, J.S.H., Garvie, C.L., Mellish, C.J.T., 2018. *Costacopluma concava* Collins and Morris, 1975 (Decapoda, Brachyura) from the woodbine formation (cenomanian) of Texas, USA. Cretac. Res. 87, 145–149.
- Delanoy, G., 2003. *Toxancyloceras* gen. nov. (Ammonoidea, Ancyloceratina) un nouveau genre du Barrémien supérieur. Ann. Mus. Hist. Nat. Nice 18, 1–19.
- Étallon, A., 1859. Description des Crustacés fossiles de la Haute-Saône et du Haut-Jura. Bulletin de la Société Géologique de France, Séries 2 (16), 169–205.
- Feldmann, R.M., De Saint Laurent, M., 2002. *Glypheia foresti* n. sp. (Decapoda) from the cenomanian of northern territory, Australia. Crustaceana 75, 359–373.
- Feldmann, R.M., Schweitzer, C., 2006. Paleobiogeography of southern hemisphere decapod Crustacea. J. Paleontol. 80 (1), 83–103.
- Feldmann, R.M., Vega, F.J., García-Barrera, P., Rico-Montiel, R., Martínez-López, L., 1995a. A new species of *Meyeria* (Decapoda: Mecochiridae) from the san juan Raya Formation (aptian: cretaceous) Puebla state, Mexico. J. Paleontol. 69 (2), 402–406.
- Feldmann, R.M., Casadio, S., Chirino-Gálvez, L., Aguirre-Urreta, M., 1995b. Fossil Decapod Crustaceans from the Jagüel and Roca Formations (Maastrichtian-Danian) of the Neuquén Basin, vol. 43. Paleontological Society Memoir, Argentina, pp. 1–22.
- Feldmann, R.M., Aguirre-Urreta, M., Chirino-Gálvez, L., Casadio, S., 1997. Paleobiogeography of Cretaceous and Tertiary decapod crustaceans from southern South America: the link with Antarctica. In: Ricci, C.A. (Ed.), The Antarctic Region: Geological Evolution and Processes, pp. 1007–1016.
- Feldmann, R.M., Bice, K.L., Schweitzer, C., Hopkins, E.W., Salva, Pickford, K., 1998. Decapod crustaceans from the eocene castle hayne limestone, North Carolina: paleoceanographic implications. Paleontol. Soc. Mem. 48, 1–28.
- Feldmann, R.M., Vega, F.J., Martínez-López, L., González-Rodríguez, K.A., González-León, O., Fernández-Barajas, R.M., 2007. Crustacea from the muhi quarry (Albian-Cenomanian), and a review of aptian Mecochiridae (astacidae) from Mexico. Ann. Carnegie Mus. 76 (4), 135–144.
- Ferratges, F.A., 2017. Los crustáceos fósiles de las cuencas Surpirenaicas. Cuad. Paleontol. Aragón 8, 100.
- Forest, J., De Saint Laurent, M., 1989. Nouvelle contribution à la connaissance de *Neoglypheia inopinata* Forest and de Saint Laurent, à propos de la description de la femelle adulte. Résultats des campagnes MUSORSTOM, 5. Mémoires du Muséum National d'Histoire Naturelle, Paris, (A) 144, 75–92.
- Forest, J., De Saint Laurent, M., Chace, F.A., 1976. *Neoglypheia inopinata*: a crustacean "living fossil" from the Philippines. Science 192, 884.
- Förster, R., 1971. Die Mecochiridae, eine spezialisierte Familie der mesozoischen Glypheoidea (Crustacea, Decapoda). Neues Jahrbuch Geol. Palaontol. Abhand. 137, 396–421.
- Fraaije, R.H.B., Vega, F.J., van Bakel, B.W.M., GaribayRomero, L.M., 2006. Late Cretaceous dwarf decapods from Guerrero, Southern Mexico and their migration patterns. Contrib. Zool. 75 (3/4), 121–132.
- Gaona-Narvaez, T., Maurrasse, F.J.-M.R., Etayo-Serna, F., 2013. Geochemistry, paleoenvironments and timing of aptian organic-rich beds of the Paja Formation (Curití, eastern Cordillera, Colombia). Geological Society, London, Special Publications 382 (1), 31–48.
- Glaessner, M.F., 1929. Crustacea Decapoda. In: Pompeckj, J.F. (Ed.), Fossilium Catalogus I: Animalia. Part 41. W. Junk, Berlin, pp. 1–164.
- Gómez-Cruz, A. de J., Bermúdez, H.D., Vega, F.J., 2015. A new species of *dialulax* Bell, 1863 (Brachyura: dialucidae) in the early cretaceous of the Rosalblanca formation, Colombia. Bol. Soc. Geol. Mex. 67 (1), 103–112.
- González-Arreola, C., Carrillo-Martínez, M., 1986. Amonitas del Jurásico Superior (Titoniano superior) y del Cretácico Inferior (Hauteriviano-Barremiano) del área de San Joaquín-Vizarrón, Estado de Querétaro. Universidad Nacional Autónoma de México, Revista del Instituto de Geología 6 (2), 171–177.
- González-León, O., Moreno-Bedmar, J.A., Vega, F.J., 2014. Morphology and ontogeny of the fossil lobster *Meyeria magna* M'coy, 1849 (astacidae, Mecochiridae) from the lower cretaceous (lower aptian) of Mexico, United Kingdom and Spain. Neues Jahrbuch Geol. Palaontol. Abhand. 271 (1), 49–68.
- González-León, O., Jeremiah, J., Schlagintweit, F., Bover-Arnal, T., Moreno-Bedmar, J.A., Mendoza-Rosales, C., Vega, F.J., 2015. Novel contributions and errata of the work "morphology and ontogeny of the fossil lobster *Meyeria magna* M'coy, 1849 (astacidae, Mecochiridae) from the lower cretaceous (lower aptian) of Mexico, United Kingdom and Spain". Neues Jahrbuch Geol. Palaontol. Abhand. 276 (3), 323–334.
- González-León, O., Patarroyo, P., Moreno-Bedmar, J.A., Nyborg, T., Vega, F.J., 2016. A new record and cuticular structure of *Meyeria magna* (Decapoda, Mecochiridae) from the lower Albian (Lower Cretaceous) of Colombia. Cretac. Res. 57, 342–349.
- González-León, O., Ossó, A., Bover-Arnal, T., Moreno-Bedmar, J.A., Frijia, G., Vega, F.J., 2017. *Atherfieldastacus rapax* (harbort, 1905), (glypheidae, Mecochiridae) from the lower cretaceous of the maestrat basin (NE Spain). Cretac. Res. 77, 56–68.
- González-León, O., Moreno-Bedmar, J.A., Vega, F.J., Oviedo-García, A., Franco-Rubio, M., 2018a. Review of *Meyeria mexicana* Rathbun, 1935 (Glypheidea, Mecochiridae) from the upper aptian (cretaceous) of Chihuahua, northern Mexico. Cretac. Res. 91, 111–125.
- González-León, O., Vega, F.J., Ferratges, F.A., Moreno-Bedmar, J.A., 2018b. La presencia del crustáceo fósil *Atherfieldastacus magnus* en México. Universidad Nacional Autónoma de México, Instituto de Geología, Nuestra Tierra 30, 11–15.
- Harbort, E., 1905. Die fauna der Schaumburg-lippeschen kreidemulde. Abhandlungen der Preussischen geologischen landesanstalt. Neue Folge 14, 10–22.
- Hyatt, A., 1903. *Pseudoceratites* of the cretaceous. United States Geological Survey, Monographs 44, 1–351.
- Karsten, H., 1856. Über die geognostischen Verhältnisse des Westlichen Columbiens, der heutigen Republiken Neu-Granada und Ecuador. Amtlicher Bericht der Versammlung Deutscher Naturforscher und Aerzte 32, 80–117.
- King, R.E., Adkins, W.S., 1946. Geology of a part of the lower conchos valley, Chihuahua, Mexico. Bull. Geol. Soc. Am. 57 (3), 275–294.
- Kitchin, F.L., 1908. The invertebrate fauna and palaeontological relations of the Uttenhage series. Ann. S. Afr. Mus. 7, 212–268.
- Klopmaker, A.A., 2013. Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. Cretac. Res. 41, 150–185.
- Latrelle, P.A., 1802. Histoire naturelle, général et particulière des crustacés et des insectes, vol. 3. F. Dufart, Paris, pp. 468 1803.
- Lee, J.L., 1881. Notebook of an Amateur Geologist. Longmans Green, London, pp. 90.
- López-Horgue, M.A., 2009. New occurrences of *Meyeria magna* M'coy, 1849 (Decapoda: Mecochiridae) in the early aptian and early albian of the Basque cantabrian basin (north Spain). Geocacta 47, 25–28.
- López-Horgue, M.A., Bodego, A., 2017. Mesozoic and Cenozoic decapod crustaceans from the Basque-Cantabrian basin (Western Pyrenees): new occurrences and faunal turnovers in the context of basin evolution. Bull. Soc. Geol. Fr. 188 (14), 1–28.
- Mallada, L., 1892. Catálogo general de las especies fósiles encontradas en España. Boletín de la Comisión del Mapa Geológico de España 18, 1–253.
- Mendoza-Rosales, C.C., 2010. Estratigrafía y facies de las cuencas cretácicas del sur de Puebla y su significado tectónico. PhD dissertation, Posgrado en Ciencias de la Tierra. Universidad Nacional Autónoma de México, pp. 192.
- Morales, L.G., Colombian Petroleum Industry, 1958. general geology and oil occurrences of the middle magdalena valley, Colombia. In: Weeks, L.G. (Ed.), Habitat of Oil: A Symposium: Tulsa. American Association of Petroleum Geologists, Oklahoma, pp. 641–695.
- M'Coy, F., 1849. On the classification of some British fossil Crustacea, with notices of new forms in the University Collection at Cambridge. Ann. Mag. Nat. Hist. 4 (2), 330–335.
- Najarro, M., Rosales, I., Moreno-Bedmar, J.A., de Gea, G.A., Barrón, E., Company, M., Delanoy, G., 2011. High-resolution chemo- and biostratigraphic records of the Early Aptian oceanic anoxic event in Cantabria (N Spain): palaeoceanographic and paleoclimate implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 299, 137–158.
- Nicklès, R., 1894. Contributions à la Paléontologie du Sud-Est de l'Espagne. Terrain crétacé. I. Neocomien. Mémoires de la Société Géologique de France. Paleontologie (Prague) 4, 1–59.
- Noël, D., 1965. Note préliminaire sur des Coccoïthes jurassiques. Cah. Micropaleontol. 1 (1), 1–25.
- Orbigny, A.d', 1842. Voyage Dans l'Amérique Méridionale. Tome 3ème, 4ème Partie: Paléontologie. Société Géologique de France, Paris et Strasbourg, pp. 187.
- Patarroyo, P., 1997. Barremiano Inferior en la Base de la Formación Paja, Barichara, Santander - Colombia. Geol. Colomb. 22, 135–138.
- Patarroyo, P., 2000. Distribución de Amonitas del Barremiano de la Formación Paja en el Sector de Villa de Leyva (Boyacá, Colombia). Bioestratigrafía. Geol. Colomb. 25, 149–162.
- Patarroyo, P., 2004. Die Entwicklung der Ammoniten der Familie Pulchelliidae aus dem Barrème von Zentral-Kolumbien (Südamerika). Rev. Paléobiol. 23 (1), 1–65.
- Ramírez-Garza, B.M., 2007. Bioestratigrafía de la Formación San Lucas con base en el estudio de ammonites del Barremiano inferior y la parte más baja del Barremiano superior, en Huetamo, Michoacán. MS thesis, Posgrado en Ciencias de la Tierra. Universidad Nacional Autónoma de México, pp. 89.
- Rathbun, M.J., 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain. Geological Society of America, Special Paper, 2, pp. 1–160.
- Reboulet, S., Szives, O., Aguirre-Urreta, B., Barragán, R., Company, M., Frau, C., Kakabadze, M.V., Klein, J., Moreno-Bedmar, J.A., Lukeneder, A., Pictet, A., Ploch, I., Raisossadat, S.N., Vaříšek, Z., Baraboshkin, E.J., Mitta, V.V., 2018. Report on the 6th international meeting of the IUGS lower cretaceous ammonite working group, the kilian group (Vienna, Austria, 20th august 2017). Cretac. Res. 91, 100–110.
- Riedel, L., 1938. Amonitas del cretácico inferior de la Cordillera Oriental. In: Scheibe, E.A. (Ed.), Estudios geológicos y paleontológicos sobre la Cordillera Oriental de Colombia, parte 2. Ministerio de Industria y Trabajo, Departamento de Minas y Petróleos, Bogotá, Colombia, pp. 7–78.
- Robin, R., Charbonnier, S., Merle, D., Simpson, M., Petit, G., Fernandez, S., 2016. Bivalves on mecochirid lobsters from the aptian of the Isle of Wight: snapshot on an early cretaceous palaeosymbiosis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 453, 10–19.
- Rojas-Briceño, A., Patarroyo, P., 2009. Occurrence of *Sellityris sella* (brachiopoda) in the Rosalblanca formation, boyacá, Colombia. Bol. Geol. Univ. Ind. Santander 31, 129–132.
- Royo y Gómez, J., 1945. Fósiles del Barremiense Colombiano. Compilación de los Estudios geológicos oficiales en Colombia. Servicio Geológico Nacional, Bogotá 6, 459–494.
- Schweitzer, C.E., 2001. Paleobiogeography of cretaceous and tertiary decapod crustaceans of the north pacific ocean. J. Paleontol. 75 (4), 808–826.
- Simpson, M.I., Middleton, R., 1985. Gross morphology and the mode of life of two species of lobster from the Lower Cretaceous of England: *Meyeria ornata* (Phillips) and *Meyerella magna* (M'Coy). Trans. R. Soc. Edinb. Earth Sci. 76, 203–215.
- Stenzel, H.B., 1945. Decapod crustaceans from the cretaceous of Texas. The University of Texas Publication 4401, 401–477.
- Thierstein, H.R., 1971. Tentative lower cretaceous calcareous nannoplankton zonation. Eclogae Geologicae Helvetiae 64 (3), 459–488.
- Thierstein, H.R., 1973. Lower Cretaceous calcareous nannoplankton biostratigraphy. Abh. Geol. Bundesanst. 29, 1–52.
- Uhlig, V., 1883. Die Cephalopodenfauna der Wernsdorfer Schichten. Denkschriften der

- kaiserlichen Akademie der Wissenschaften. Wien, Mathematisch-Naturwissenschaftliche Klasse 46, 127–290.
- Van Straelen, V., 1925. Contribution à l'étude des crustacés décapodes de la période Jurassique. Mémoires de l'Académie Royale de Belgique, Classe des Sciences, series 2 (7), 1–462.
- Van Straelen, V., 1927. Contribution à l'étude des crustacés décapodes de la Péninsule ibérique. Eos 3, 69–79.
- Vega, F.J., Nyborg, T., Rojas-Briceño, A., Patarroyo, P., Luque, J., Porras-Múzquiz, H., Stinnesbeck, W., 2007. Upper Cretaceous Crustacea from Mexico and Colombia: similar faunas and environments during Turonian times. Rev. Mex. Ciencias Geol. 24, 403–422.
- Vega, F.J., Feldmann, R.M., Etayo-Serna, F., Bermúdez-Aguirre, H.D., Gómez, J., 2008. Occurrence of *Meyeria magna* McCoy, 1849 in Colombia: a widely distributed species during Aptian times. Bol. Soc. Geol. Mex. 60, 1–10.
- Vega, F.J., Bruce, N.L., González-León, O., Jeremiah, J., Serrano-Sánchez, M.L., Alvarado-Ortega, J., Moreno-Bedmar, J.A., 2019. Lower cretaceous marine isopods from the san juan Raya and tlayúa formations; Puebla, Mexico. J. Crustac Biol. 39 (2), 121–135.
- Vermeulen, J., 2003. Étude stratigraphique et paléontologique de la famille des Pulchelliidae (Ammonoidea, Ammonitina, Endemocerataceae). Géologie Alpine. Mémoire Hors Série 42 (2002), 1–333.
- Vermeulen, J., Klein, J., 2006. Lower cretaceous ammonites II, endemocerataceae: pulchelliidae. In: Riegraf, W. (Ed.), Fossilium Catalogus I: Animalia. vol. 141. Backhuys Publishers, Leiden, pp. 187–278.
- Vía, L., 1951. Contribución al estudio de los decápodos del secundario en España. Anales de la Escuela de Peritos Agrícolas y de Especialidades Agropecuarias y de los Servicios Técnicos de Agricultura de España 10, 151–180.
- Vía-Boada, L., 1975. Contribución al estudio de "Mecochirus magnus" (McCoy), crustáceo decápodo del "Lower Greenand" de Inglaterra, abundante en el Cretáceo nororiental Ibérico. In: 1er Symposium sobre el Cretáceo de la Cordillera Ibérica, Cuenca, España, pp. 27–49.
- Vilanova, J., 1863. Ensayo de descripción geognóstica de la provincia de Teruel en sus relaciones con la agricultura de la misma. Junta general de Estadística, Madrid, pp. 312.
- Wang, Y., 1981. In: The Scientific Expedition to the Qinghai-Xizang Plateau, 1981. Palaeontology of Xizang (Book III). Science Press, Beijing, pp. 349–354.
- Woods, H., 1928–1931. A Monograph of the Fossil Macrurous Crustacea of England. Palaeontographical Society Monographs. The Palaeontographical Society, London, pp. 122.
- Zamarreño de Julivert, I., 1963. Estudio petrográfico de las calizas de la Formación Rosablanca de la región de la Mesa de los Santos. Bol. Geol. Univ. Ind. Santander 15, 5–34.
- Zhang, K.J., 2000. Cretaceous palaeogeography of Tibet and adjacent areas (China): tectonic implications. Cretac. Res. 21 (1), 23–33.
- Zhang, K.J., Xia, B., Liang, X., 2002. Mesozoic–Paleogene sedimentary facies and paleogeography of Tibet, western China: tectonic implications. Geol. J. 37, 217–246.
- Zittel, K.A., 1885. Handbuch der Paläontologie, 1. Abtheilung Palaeozoologie, Band 2, Mollusca und Arthropoda: München und Liepzig. R. Oldenbourg, pp. 525–721.