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Well-preserved cuticle of *Atherfieldastacus magnus* (Decapoda, Glypheida) from the Aptian of Mexico

Dobro ohranjena kutikula raka *Atherfieldastacus magnus* (Decapoda, Glypheida) iz aptijskih plasti v Mehiki

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Ključne besede: Pleocyemata, Mecochiridae, kutikula, spodnja kreda, Chihuahua, Mehika

Abstract

The cuticle structure of fossil decapod crustaceans is an important tool, not only for palaeocological and taphonomic interpretations, but also as a potential way to characterise systematically genera and even species the cuticle of which has not been severely altered by diagenetic processes. Localities with abundant decapod crustacean remains can be interpreted either as reflecting mass mortality events or just simple accumulations of exuviae, on the basis of completeness and comparison of cuticle structures between specimens of the same species from different localities. Association with anoxic events by microfacies analyses can offer clues to explain the unusual abundance of decapod crustacean remains. This is the case for the Early Cretaceous lobster *Atherfieldastacus magnus* (M'Coy, 1849), which is found in large numbers in different Lower Cretaceous (mainly Aptian) lithostratigraphic units across the globe. In this case, we document the well-preserved cuticle structure of specimens from the upper Aptian of Chihuahua (Mexico), preserved three-dimensionally, mainly in concretions, which were studied in different transverse sections showing the cuticle in diverse portions of the lobster body. Thin cuticle layers show the typical crustacean cuticular structure that suggest these are corpses preserved in an anoxic environment.

Izvleček

Analiza strukture kutikule fosilnih deseteronožcev je pomembno orodje ne le za paleoekološke in tafonomske interpretacije, ampak tudi kot možen način za sistematsko opredelitev rodov in celo vrst, v kolikor kutikula ni diagenetsko spremenjena. Na podlagi ohranjenosti in primerjave strukture kutikule med primerki iste vrste z različnih nahajališč razlikujemo nahajališča s pogostimi ostanki rakov. Ta lahko kažejo na množičen pogin ali zgolj na akumulacije levov deseteronožcev. V povezavi s prepoznanimi anoksičnimi dogodki v mikrofacialnih analizah nam lahko metoda služi za razlago množičnih nakopičenj fosilnih deseteronožcev na nekaterih lokacijah. Tak primer je zgodnjekredni jastog *Atherfieldastacus magnus* (M'Coy, 1849), katerega številne ostanke najdemo v različnih litostratigrafskih enotah spodnje krede (predvsem v aptiju) po vsem svetu. V prispevku predstavljamo dobro ohranjeno strukturo kutikule osebkov iz zgornjega aptija iz nahajališča Chihuahua (Mehika). Vzorce tridimenzionalno ohranjene kutikule primerkov iz konkrecij smo pregledali na različnih prečnih presekih z različnih delov telesa jastoga. Tanke plasti kutikule z značilno strukturo kažejo, da gre v našem primeru za trupla, ki so se ohranila v anoksičnem okolju.

Introduction

An interesting factor of the study of decapod crustaceans is the review and examination of their cuticule structure. At most localities, cuticle structure is obscured by mineral replacement of the original carbonate, but modified by diagenetic processes as well (Vega et al., 2005). In previous studies (e.g., Dennell, 1960; Hegdahl et al., 1977a, b; Roer & Dillaman, 1984), cuticle structure of Recent taxa has been studied, while other authors have demonstrated the presence of cuticle in the fossil record (e.g., Neville & Berg, 1971; Feldmann & Tshudy, 1987; Vega et al., 1994, 2005; Feldmann & Gaździcki, 1998; Guinot & Breton; 2006; González-León et al., 2016, 2018, among others). Studies of the functional morphology and taphonomic implications have been addressed by various authors (Schäfer, 1951; Guinot, 1979; Plotnick et al., 1988; Savazzi, 1988; Haj & Feldmann, 2002; Waugh et al., 2004). The use of this structure for taxonomic purposes is complicated because there are only few well-established characters. With this in mind, Waugh et al. (2009) analysed the morphological characters of some decapod crustaceans for possible future phylogenetic analysis.

Decapod crustaceans rank amongst the most common animals inhabiting a number of different environments, both at the present day (Abele, 1974) and in the past (Klompmaker et al., 2013; Schweitzer & Feldmann, 2014). The calcified cuticle of decapod crustaceans comprises the hard exoskeleton of the animal and is composed of three layers (Haj & Feldmann, 2002); these layers have been documented in some fossil decapod crustaceans as well (Neville & Berg, 1971; Taylor, 1973; Dalingwater, 1977; Vega et al., 1994, 1998; Feldmann & Gaździcki, 1998; Haj & Feldmann, 2002; Waugh & Feldmann, 2003; Vega et al., 2005; Waugh et al., 2006; Amato et al., 2008; Waugh et al., 2009; González-León et al., 2016, 2018). The decapod cuticle has a very distinctive structure when observed in cross section. In spite of the fact that decapod crustacean cuticle is frequently preserved in material from Mesozoic and Cenozoic shelf deposits (Vega et al., 2005), very few efforts have been made as to how to distinguish corpses from exuviae. For this reason, it is important to recognise and characterise the microstructure as a potential tool in preliminary identification of, at least, major decapod crustacean groups and taphonomic interpretations (Feldmann & Tshudy, 1987; Vega et al., 1994; Klompmaker et al., 2015). The present paper analyses and complements information on cuticule structure of numerous specimens of *Atherfieldastacus magnus* that are preserved in concretions from the upper Aptian La Peña Formation in Chihuahua State (northern Mexico).

Locality and stratigraphy

The main locality is in the Cerro Chino region (Chihuahua State), close to the towns of Coyame del Sotol and Cuchillo Parado (Fig. 1). Specimens were collected from upper Aptian strata assigned to the La Peña Formation (Fig. 2); for details on these localities and local stratigraphy, reference is made to Ovando-Figueroa et al. (2017) and González-León et al. (2018).

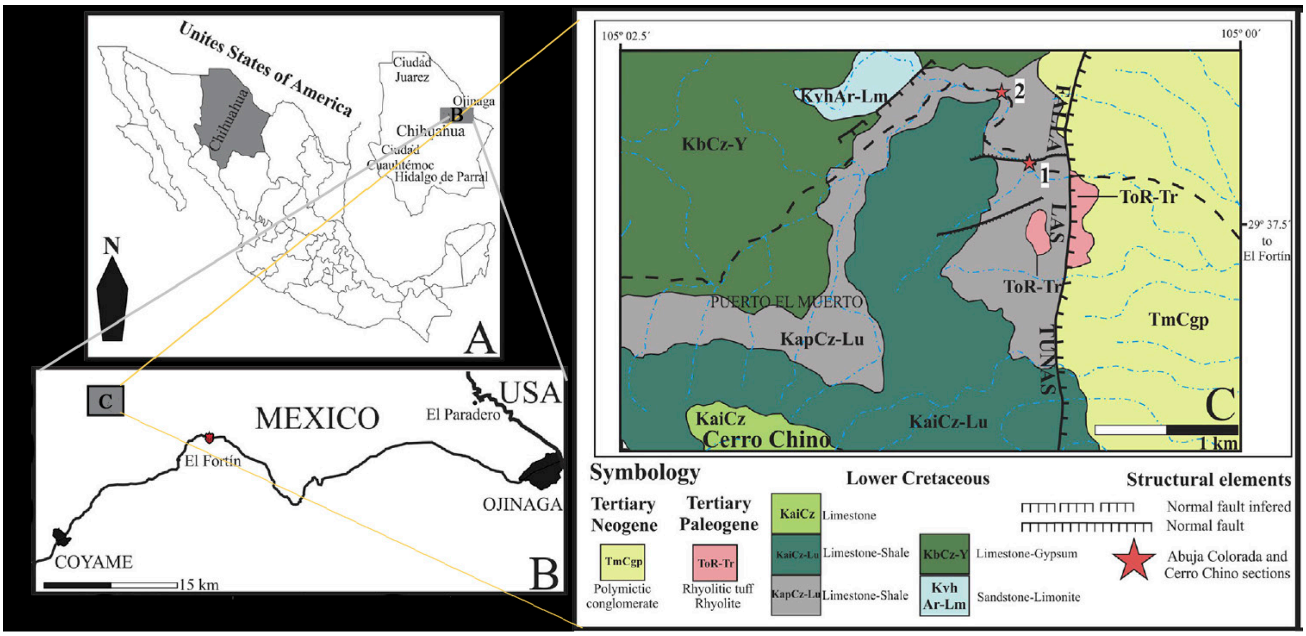

Fig. 1. Locality map showing the fossil site in northern Mexico (Chihuahua State) (modified from González-León et al., 2018).

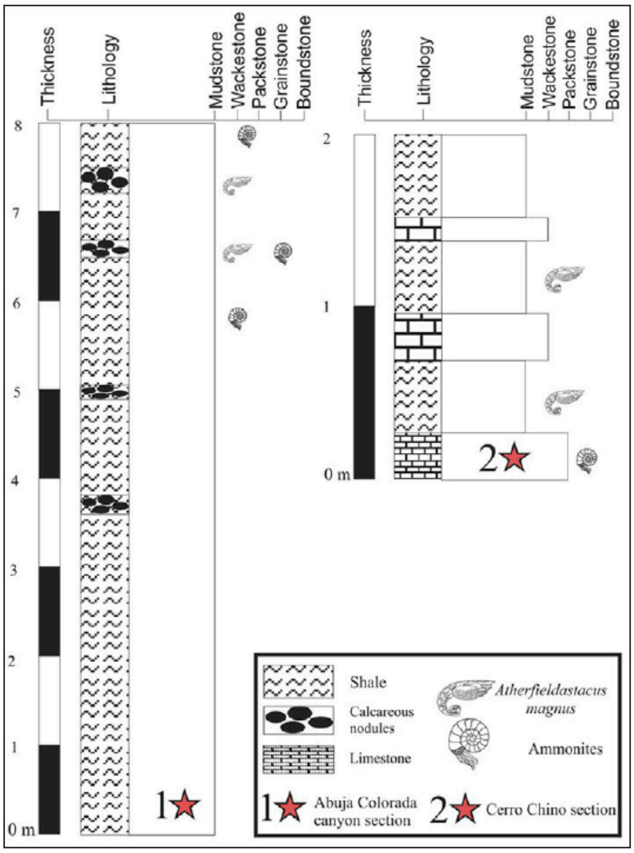

Fig. 2. Stratigraphical sections of outcrops of upper Aptian strata in Chihuahua State, showing fossiliferous beds (modified from González-León et al., 2018).

Material and methods

About 20 calcareous concretions were collected near Abuja Colorada, in a fossiliferous section dominated by shale. Specimens recorded herein were recovered from concretions of varying size, between 3 and 12 cm in length (Fig. 3) and were prepared with a Paleotools ME-9100 pneumatic percutor and subsequently sectioned transversely with a diamond saw blade and glued to microscopic slides with resin, which were then polished by hand, using Kemet polishing abrasive. A Zeiss polarising microscope, with an adapted Canon EOS Mark I camera, was used to take numerous images of cuticule structure. Thin sections and complete specimens are deposited in the Colección Nacional de Paleontología "María del Carmen Perrilliat", Instituto de Geología, Universidad Nacional Autónoma México (abbreviation: IGM).

Systematic palaeontology

Order Decapoda Latreille, 1802
Suborder Pleocyemata Burkenroad, 1963
Infraorder Glypheida Zittel, 1885
Superfamily Glypheoidea von Zittel, 1885
Family Mecochiridae Van Straelen, 1925
Genus *Atherfieldastacus* Simpson *in* Robin, Charbonnier, Merle, Simpson, Petit & Fernandez, 2016

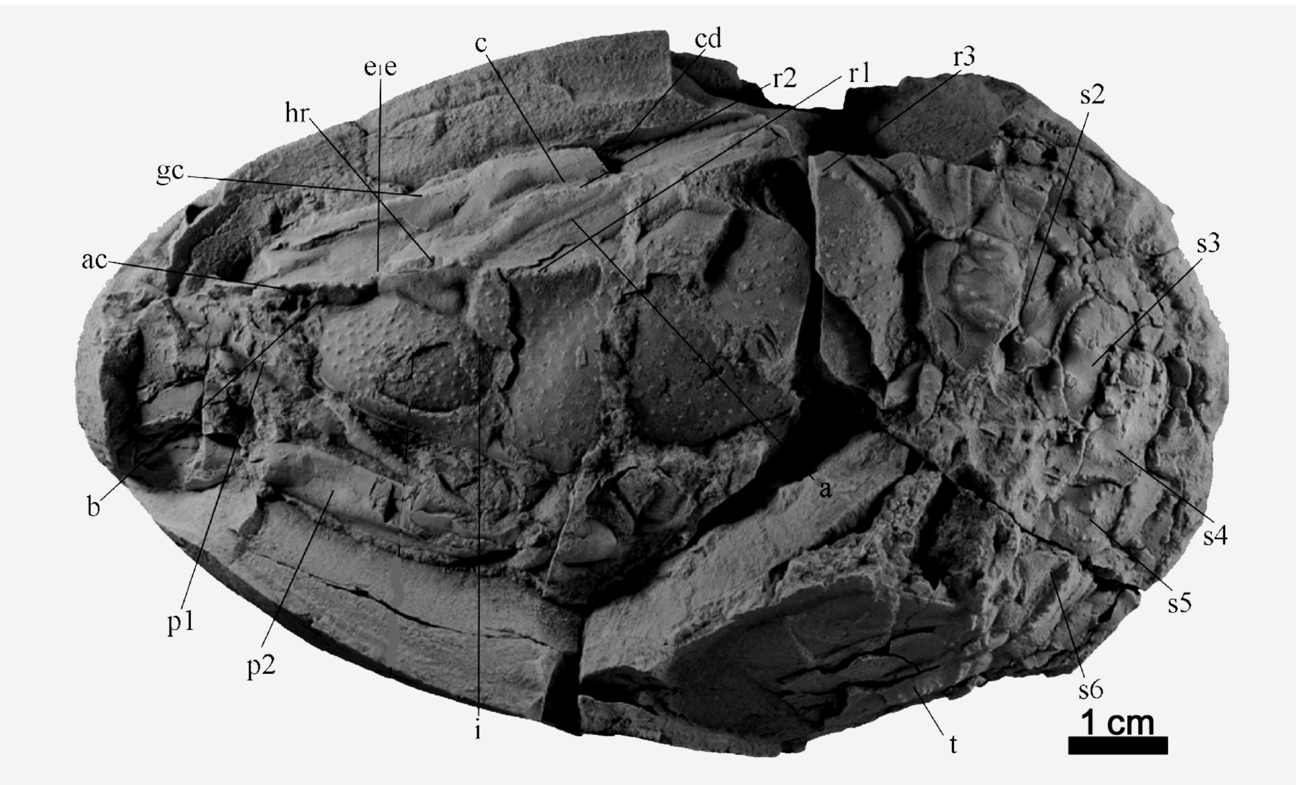

Fig. 3. *Atherfieldastacus magnus* (M'Coy, 1849), Abuja Colorada Canyon section (locality 1), Chihuahua State, northern Mexico; a near-complete specimen (IGM 9478) preserved in a calcareous nodule. Anatomical abbreviations are as follows: a = branchiocardiac groove; ac =antennal carina; b = antennal groove; c = post-cervical groove; cd = cardiac groove; e1e = cervical groove; gc = gastro-orbital carina; hr = hepatic ridge; i = inferior groove; p1-2 = pereiopods; r1-r3 = branchial ridges; s2-6 = pleonal somites; t = telson. Scale bar in cm. Photograph: Josep A. Moreno-Bedmar (modified from González-León et al., 2018).

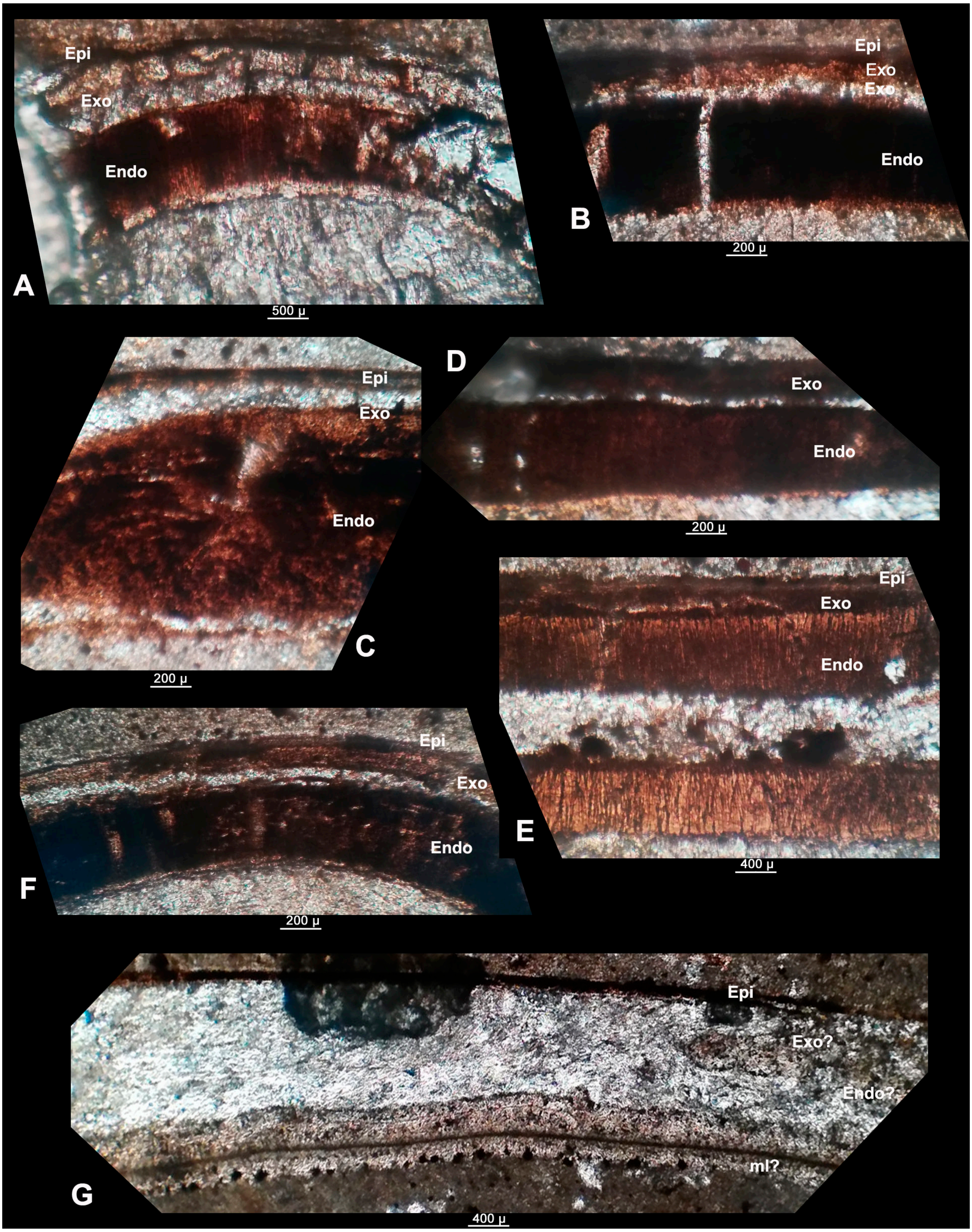

Fig. 4. A-G, Several views of thin sections of *Atherfieldastacus magnus* (M'Coy, 1849) from the upper Aptian of Chihuahua State, northern Mexico. Abbreviations: Endo = endocuticle; Epi = epicuticle; Exo = exocuticle.

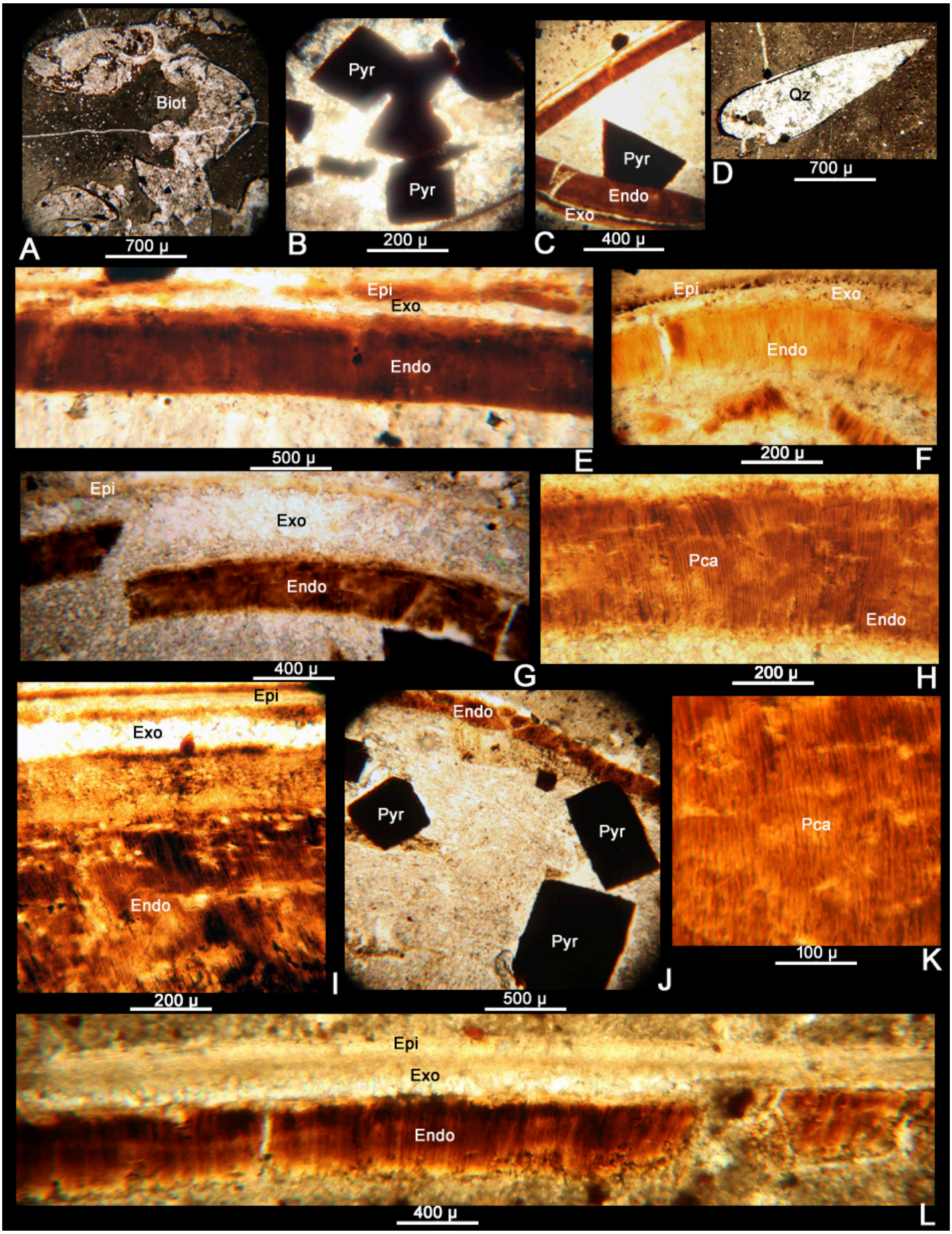

Fig. 5. Several views of thin sections of *Atherfieldastacus magnus* (M'Coy, 1849) from the upper Aptian of Chihuahua State, northern Mexico. Abbreviations: Biot = bioturbation; Endo = endocuticle; Epi = epicuticle; Exo = exocuticle; Pca = pore channels; Pyr = pyrite; Qz = quartz. Scale bars in µm.

Type species: *Meyeria magna* M'Coy, 1849, by original designation.

Other included species: *Atherfieldastacus rapax* (Harbort, 1905) and *A. schwartzi* (Kitchin, 1908).

Atherfieldastacus magnus (M'Coy, 1849)
(Fig. 3)

Diagnosis: See González-León et al. (2018).

Material examined: Specimens in 22 calcareous concretions, of which eight were sectioned for analysis of cuticular structure; in total, 30 thin sections of different portions of the lobster body were obtained.

Cuticle structure

Analysis and discussion: In our analysis of cuticule structure, it was possible to recognise clearly the three cuticle layers. In some cases, only a single layer was discernible. Elements of cuticule microstructure, such as pore canals, were also observed (Figs. 4, 5). Previously, such features had been recorded by Feldmann & Tshudy (1987), Vega et al. (1994) and González-León et al. (2016, 2018), both for other species and for *Atherfieldastacus magnus*, but recrystallised cuticles do not show clear layers (González-León et al., 2016).

The newly collected specimens clearly present three discrete layers of cuticle. The first layer observed is the epicuticle (epi), which normally has a thin bilaminar structure; this could not be observed. Below the epicuticle is the second layer or exocuticle (exo), composed of chitin protein fibres, stacked in layers with variable orientations (Green & Neff, 1972; Haj & Feldmann, 2002). This layer is altered, but still discernible in almost all specimens studied (Fig. 4). The microstructure is replaced by sparry calcite, as seen in Figures 4A-C and G, although some fibres can still be noted (Fig. 4E). The most strongly calcified layer is the third one; this is the endocuticle (endo) which presents broad lamellae in the outer portion and thin laminations on the inner part (Feldmann & Tshudy, 1987). Vertical laminations within the endocuticle were noted in specimens from Chihuahua and interpreted as pore channels (Figs. 4A, E; 5H, K). A pigmented layer at the top of the endocuticle could also be observed (Fig. 4D-F). This might be associated with the original pigment (quinona), as previously recognised by Taylor (1973) and Vega et al. (1994). An example of how the microstructure and boundaries between layers can be altered by diagenetic processes was observed as well (Fig. 4G). The epicuticle can be clearly recognised (Figs. 4B, E; 5F, G, I, L), but only as a single layer, not as a double layer, which is typical. The membranous layer was not preserved, similar to what has been recorded for other extinct species (Roer & Dillaman, 1984; Vega et al., 1994, 2005; Haj & Feldmann, 2002).

Conclusions

The completeness of cuticule structure (especially the basis of the endocuticle) and the 3-D preservation and articulation of carapaces with appendages suggest that the Chihuahua specimens represent corpses that were accumulated during anoxic events. The presence of small pyrite crystals in the matrix and larger ones in appendages (Fig. 5B, C, J) supports such an interpretation, along with bioturbations observed in some thin sections; these were possibly caused by scavengers that were feeding on cuticle remains and other organic matter (Fig. 5A). Abundant pyrite has also been observed in specimens of *Atherfieldastacus magnus* from the Aptian of Colombia (González-León et al., 2016). This suggests that localities around the world, where *A. magnus* is abundant, may represent anoxic events that either killed the lobster populations and/or preserved the remains of this globally distributed species during the Early Cretaceous.

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