

# Characterization of cuticle structure in Late Cretaceous and Early Tertiary decapod Crustacea from Mexico

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## Abstract

Cuticle structure of seven species of Maastrichtian, Paleocene and Eocene crabs from Mexico is reviewed and characterized by examination of thin sections with light (normal and polarized) and cathodoluminescence microscopy, in order to recognize three cuticle layers (endocuticle, exocuticle and epicuticle) and establish possible patterns of mineral replacement during diagenesis. Other cuticle structures such as pore canals, epicuticular cavities and tegumental ducts are also described and illustrated. Most studied species belong to extinct genera and families. Although best preserved in phosphatic concretions, decapod cuticle structure also can be preserved even in coarse-grained sediments. By means of small amounts of iron incorporated during diagenesis, cuticle can be naturally stained and its structures become more evident. As fragile as it is, crustacean cuticle is preserved in many kinds of deposits. However, petrographic atlases usually do not include illustrations of decapod cuticle. This contribution points out the need to consider brachyuran remains as potentially common bioclasts.

*Key words:* Cuticle structure, Decapoda, Late Cretaceous, Early Tertiary, Mexico.

## Introduction

The fossil record of decapod crustaceans is very poor when compared with that of mollusks and other invertebrate groups with heavily calcified skeletons. Inherent diversity of such groups plays an important role, but other parameters such as habitat, size, body structure and depositional history also affect the possibility to be preserved. Different levels of calcification are present on crustacean cuticle and variation even occurs among different parts of the same organism. Certain groups show a delicate cuticle (e. g., anomuran abdomen), while others a very resistant exoskeleton (e. g., cirripedians). Furthermore, diagenetic processes and taphonomy also alter or destroy evidence of decapod remains.

Decapod cuticle has a very distinctive structure when observed in transverse section. Although most atlases and texts on petrography and sedimentology illustrate or describe how to recognize some arthropod bioclasts such as trilobites and ostracods, practically none of them includes decapod cuticle as potentially common remains in Mesozoic and Cenozoic shelf deposits.

Earlier studies of crustacean cuticle focused on parameters that affected preservation of decapod crustaceans, based on taphonomic experiments and direct observations in modern environments (Schäfer, 1951; 1972; Bishop, 1981; 1986; Allison, 1986; 1988; Plotnick, 1986;

Plotnick *et al.*, 1988; 1990; Stempien, 2005, among others). Some of these authors concluded that decapod cuticle begins to deteriorate after a lapse of two weeks (Allison, 1988; Poulicek *et al.*, 1988; Stempien, 2005), but others suggested that it can remain unaltered for nearly a year (Poulicek *et al.*, 1988). It is important to note that many decapod remains are preserved inside concretions and that quality of preservation will depend on their particular taphonomy and early diagenesis.

A few authors have described the structure of the cuticle of fossil decapod crustaceans (Feldmann and Tshudy, 1987; Vega *et al.*, 1994; Feldmann and Gaździcki, 1998; Vega *et al.*, 1998; Haj and Feldmann, 2002), and its possible systematic use (Waugh and Feldmann, 2003).

The purpose of this study is to characterize cuticle structure based on examination of thin sections observed under normal, polarized and cathodoluminescence light microscopy, with emphasis on distinction between layers, unique features, taphonomy and diagenesis.

## Stratigraphy and Paleoenvironment

Specimens used in this study were collected from localities in Maastrichtian, Paleocene and Eocene deposits in northeastern and southeastern Mexico.

The Difunta Group is composed of sediments associated to deltaic deposits (McBride *et al.*, 1974) that crop out in northeastern

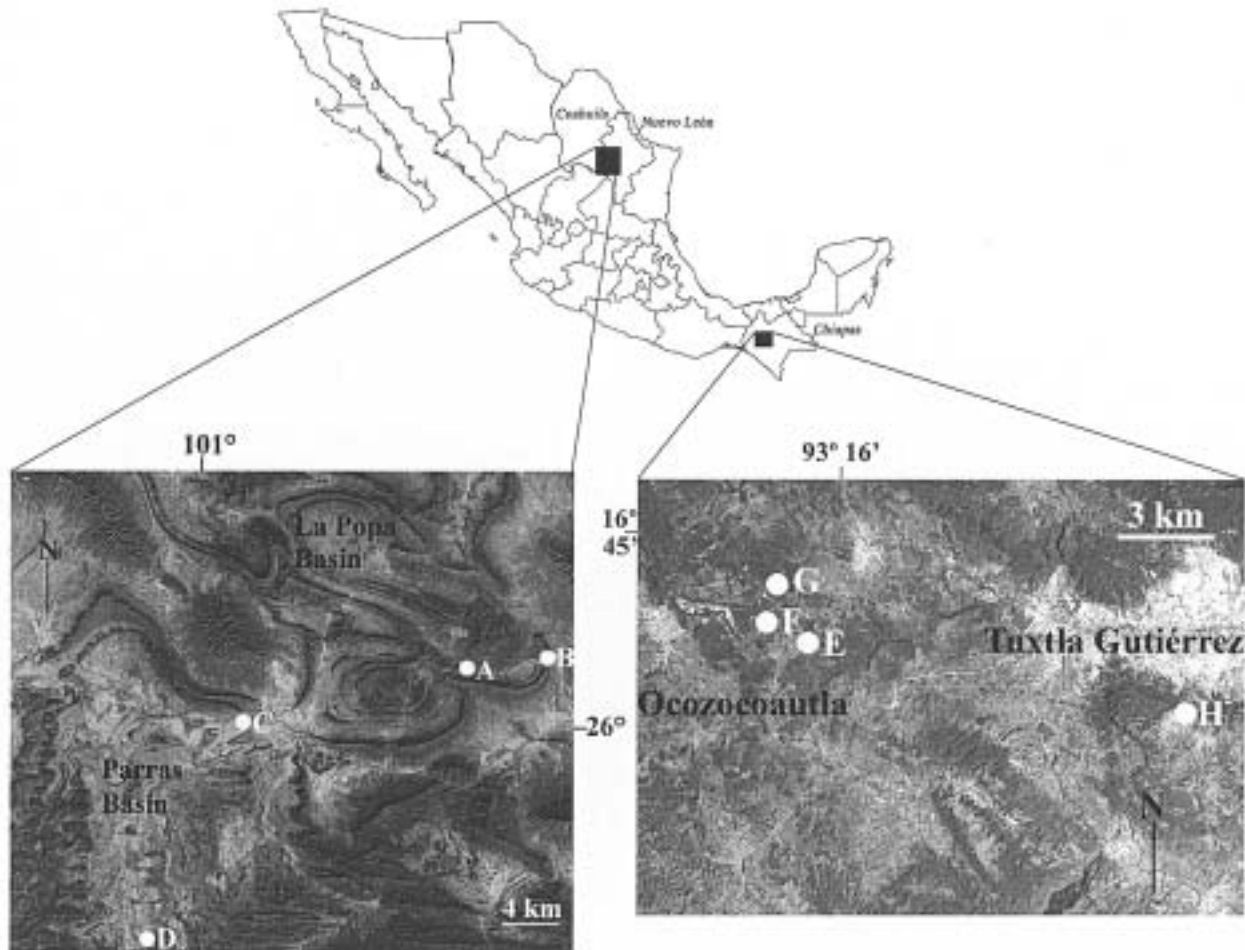


Fig. 1. Location map of Difunta Group (Coahuila and Nuevo León) in northeastern Mexico and the Ocozocoautla Formation in the central part of Chiapas, southeast Mexico, along with satellite images of these areas. A. Localities A (IGM-1571), B, C and D are indicated in La Popa and Parras basins. For more details about localities refer to Vega and Perrilliat, 1989. B. Localities E to H are indicated west of Tuxtla Gutiérrez, Chiapas. For more details about localities refer to Vega *et al.* (2001a, 2001b).

Mexico (Coahuila and Nuevo León states). These strata are 5,400 m thick and range in age from late Campanian to early Eocene (Vega *et al.*, 1989; Eberth *et al.*, 2004). The group was subdivided into two sedimentary basins, known as Parras and La Popa (Fig. 1). Several decapod species have been reported from the Maastrichtian Lower Siltstone and Lower Mudstone members of the Potrerillos Formation (La Popa Basin, Nuevo León), including *Costacopluma mexicana* Vega and Perrilliat, 1989, and *Dakoticancer australis* Rathbun, 1935 (Vega and Feldmann, 1991; Vega *et al.*, 1995). *Dakoticancer australis* occurs in calcareous concretions at the eastern edge of the El Gordo limestone lentil of the Lower Mudstone Member, Potrerillos Formation (locality A, Fig. 1). The lentil is associated with El Gordo diapir, one of the salt tectonic features that affected sedimentation in the La Popa Basin during the Late Cretaceous and Early Tertiary (Lawton *et al.*, 2001). The lentil developed on a topographic promontory created by the diapir, and a biostrome was built due to sediment-free, clear, shallow-water conditions.

*Costacopluma mexicana*, the most abundant and widely distributed decapod crustacean in the Difunta Group, is preserved in dif-

ferent styles with variable quality. Phosphatic concretions from Maastrichtian beds of the Lower Siltstone Member, Potrerillos Formation, at locality B (IGM-1574, Fig. 1), contain the best preserved specimens and these were used to describe the cuticle structure of this species (Vega *et al.*, 1994). This locality is found at the edge of a structural weld and it is possible that the paleoenvironment was affected by fluids associated to the saline feature. Occurrences of red-stained specimens of *C. mexicana* at a newly discovered locality (C, Fig. 1) of the Maastrichtian Las Imágenes Formation (Parras Basin, Coahuila), allow for a comparison of two preservation styles.

Paleocene deposits of the Rancho Nuevo Formation (Parras Basin, Coahuila) contain a diverse crustacean assemblage (Vega *et al.*, 2005). Remains of *Enoploclytia* sp. are found in concretions at locality D (Fig. 1), and this cuticle is preserved with fine detail. Serpulid worms, gastropods, nautiloids, bivalves and echinoderms also found in these beds indicate a shallow marine paleoenvironment. The stratigraphic units of the Difunta Group are presented in Fig. 2.

Maastrichtian deposits of the Ocozocoautla Formation crop out

in Chiapas, southeastern Mexico (Fig. 1). With a thickness of 630 m (Gutiérrez-Gil, 1956), the Ocozocoautla Formation includes deltaic, reefal and lagoonal facies. Three decapod species have been found in the lagoonal deposits at localities E, F, and G (IHN 1001, 1002, and 1003, Fig. 1) along with algae, benthic foraminifera and mollusks (Vega *et al.*, 2001b). *Carcineretes planetarius* Vega, Feldmann, Ocampo and Pope, 1997, is the most abundant decapod here, preserved mostly as molts with articulated appendages. A few specimens of *Palaeoxanthopsis meyapaquensis* (Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001), and of *Megaxantho zoque* Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001, also occur as part of this assemblage. Clear, shallow warm waters are interpreted for this environment.

The Middle Eocene San Juan Formation includes 800 m of fossiliferous limestone, deposited under lagoonal and reefal environments (Licari, 1960; Allison, 1967; Frost and Langenheim, 1974; Aguilar, 1993; Ferrusquía-Villafranca, 1996). Vega *et al.* (2001a) reported four decapod species from locality H (1004, Fig. 3), including fragmentary remains of *Lophoranina cristaspina* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh,

order to obtain transverse cuts of their cuticle. Surfaces were polished and glued with epoxy resin to slides. The sections were reduced by using an abrasive and a glass plate in order to attain the proper thickness to distinguish cuticle structure.

Photomicrographs under normal and polarized light were taken on a Leica petrographic microscope with a 35 mm Leica camera. An EIM 3.1 luminoscope unit adapted to an Olympus Tokyo 214497 microscope was used for cathodoluminescence analysis. Images were taken with an Olympus Camedia C-5060 and manipulated with Paint Shop Pro 8.0.

An X-ray dispersive energy analyzer was used in order to obtain qualitative composition of cuticle in *Enoploclytia* sp., and of red-stained cuticle in *Costacopluma mexicana*.

### Cuticle structure

Crustacean decapod cuticle is typically composed of four discrete layers: a non-calcified membranous layer; a thick laminar, heavily calcified endocuticle; a thinner, calcified and laminated exocuticle; and an external, thin bilaminar epicuticle (Travis, 1955a; 1955b; Dennell, 1960; Passagno, 1960; Skinner, 1962; Glaessner, 1969; Neville *et al.*, 1969; Aiken, 1980; Roer and Dillaman, 1984; 1993; Hadley, 1986). These layers have been recognized in fossil decapod crustaceans by several authors (Neville and Berg, 1971; Taylor, 1973; Dalingwater, 1977; Feldmann and Tshudy, 1987; Vega *et al.*, 1994; 1998; Feldmann and Gaździcki, 1998; Haj and Feldmann, 2002).

The typical laminar structure observed in the endocuticle and exocuticle has been interpreted as the result of optical interference by sectioning helicoidal fibers of chitin (Roer and Dillaman, 1984; Hadley, 1986). This arrangement was also interpreted in fossil decapods (Neville and Berg, 1971; Taylor, 1973).

Other structures observed here include a membranous layer, tegumental ducts and balls, and pore canals.

The studied species are grouped by family and presented in phylogenetic order, including data on locality, stratigraphic unit and age. Descriptions of cuticle structures are included, as well as remarks on diagenetic interpretations. Results from different microscopy techniques are also discussed.

Specimens with IHNCH numbers are deposited in the Colección de Paleontología, Instituto de Historia Natural de Chiapas. Other specimens are held in research collections at the UNAM in Mexico City (F. Vega).

Order Decapoda Latreille, 1802  
 Infraorder Astacidea Latreille, 1802  
 Superfamily Erymoidea Van Straelen, 1924  
 Family Erymidae Van Straelen, 1924  
 Genus *Enoploclytia* McCoy, 1849

### *Enoploclytia* sp.

(Pl. 1, Figs. 1–4; Pl. 4, Fig. 3)

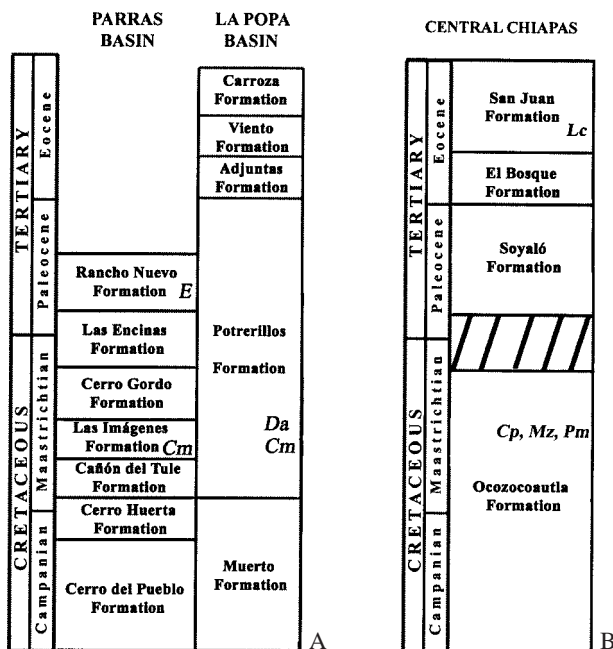


Fig. 2. Stratigraphic units of the Difunta Group (Parras and La Popa basins), northeastern Mexico (A) and coeval strata in central Chiapas, southern Mexico (B). Abbreviations: Cm = *Costacopluma mexicana*, Cp = *Carcineretes planetarius*, Da = *Dakoticancer australis*, E = *Enoploclytia* sp., Lc = *Lophoranina cristaspina*, Mz = *Megaxantho zoque*, Pm = *Palaeoxanthopsis meyapaquensis*.

2001. The stratigraphic units of central Chiapas are presented in Fig. 2.

### Material and Methods

Fragmentary carapaces of 47 specimens were thin sectioned in

**Material:** One incomplete cephalothorax with partial meri preserved on both sides (Pl. 1, Fig. 1). Specimen preserved in concretion, with evidence of lateral compression. Thin sections were obtained from the anterior part of cephalothorax. Locality B, Paleocene, Rancho Nuevo Formation, Parras Basin, Coahuila.

**Cuticle:** Endocuticle very thick, three-fourths the total cuticle thickness, finely laminated toward the base and top, central lamellae separated by spaces twice as wide as themselves. Exocuticle thin, finely laminated, one-sixth as thick as endocuticle. Epicuticle very thin, about one-thirteenth as thick as endocuticle, no lamellae nor epicuticular cavities observed. Lamellae of endo- and exocuticle become more evident under polarized light as black lines (Pl. 1, Fig. 2). Epicuticle colorless. Specimen cuticle shows fractures (Pl. 1, Fig. 3; Pl. 4, Fig. 3), due to lateral compression (Pl. 1, Fig. 1). Pore canals evident under polarized and normal light on endocuticle (Pl. 1, Figs. 2 and 4).

Pore canals were also observed in *Eryma stricklandi* (Woods, 1929) from the Jurassic Oxford Clay of England (Neville and Berg, 1971). However, in *Hoploparia longimana* (Sowerby, 1826) (Upper Cretaceous Cambridge Greensand), and in *H. stokesi* (Weller, 1903) (Cretaceous of Antarctica), pore canals do not reach exocuticle (Dalingwater, 1977; Taylor, 1973).

Feldmann and Tsudy (1987) illustrated scanning electron microscope images of *Hoploparia stokesi*. Here, endocuticle is also the thickest layer, and lamellae are also evident.

X ray dispersive energy analysis revealed a high content of Ca, P and Si, and minor amounts of Al, K and Fe. Most of these elements (except K) were reported as part of modern Crustacea exoskeletons (Clarke and Wheeler, 1922).

Infraorder Brachyura Latreille, 1802  
Superfamily Raninoidea de Haan, 1839  
Family Raninidae de Haan, 1839  
Genus *Lophoranina* Fabiani, 1910

***Lophoranina cristaspina* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001**

(Pl. 1, Figs. 5–7)

**Material:** Eight carapace fragments preserving spiny terraces (Pl. 1, Fig. 5). Thin sections were made in order to observe dorsal cuticular terraces in longitudinal section. Locality H (1004), Middle Eocene, San Juan Formation, Chiapas.

**Cuticle:** Typical terraced cuticle of *Lophoranina* is evident under low magnification (Pl. 1, Fig. 6). Endocuticle laminated, half as thick as exocuticle, distinct contact with exocuticle evident by change of color under polarized light (Pl. 1, Fig. 7). Exocuticle heavily laminated, represents two-thirds of total cuticle thickness. Epicuticle bilaminar, one-ninth total cuticle thickness. Pore canals extended through entire cuticle, being less evident on endocuticle.

The peculiar terraced spiny morphology of dorsal carapace cuticle in *Lophoranina* was described by Savazzi (1981) as an adaptation to burrow on sandy sediments (Beschin *et al.*, 1988).

Superfamily Dakoticancroidea Rathbun, 1917

Family Dakoticancridae Rathbun, 1917

Genus *Dakoticancer* Rathbun, 1917

***Dakoticancer australis* Rathbun, 1935**

(Pl. 1, Figs. 8–12; Pl. 4, Figs. 1, 2)

**Material:** Five specimens preserved in concretions with articulated appendages (Pl. 1, Fig. 8). Locality A, Maastrichtian, Lower Mudstone Member of the Potrerillos Formation, Nuevo León.

**Cuticle:** Endocuticle laminated, three fourths the total thickness of cuticle, lamellae separated by spaces wider than lamellae. Exocuticle very thin, one-sixth the thickness of endocuticle, finely laminaed (Pl. 1, Figs. 9, 10 and 12). Epicuticle well defined, one tenth total cuticle thickness; epicuticular cavities evident (Pl. 1, Figs. 9, 10 and 12). Halcrow (1993) illustrated very similar structures in modern amphipods. Pore canals reach top of exocuticle (Pl. 1, Fig. 12), not evident on endocuticle. Granules of cuticle include folding of epicuticle and upper part of exocuticle (Pl. 1, Fig. 9).

Superfamily Xanthoidea MacLeay, 1838

Family Palaeoxanthopsidae Schweitzer, 2003

Genus *Palaeoxanthopsis* Beurlen, 1958

***Palaeoxanthopsis meyoapaquensis* (Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001)**

(Pl. 2, Figs. 1–4; Pl. 4, Figs. 7, 8)

**Material:** Two specimens (Pl. 2, Fig. 1). Localities 1002 and 1003 (F, G), Maastrichtian, Ocozocoautla Formation, Chiapas.

**Cuticle:** Endocuticle three fourths of cuticle thickness, lamellae uniformly spaced except at the top, where they become finer and closely spaced (Pl. 2, Figs. 3 and 4). Exocuticle one-fourth total cuticle thickness, finely laminated with few lamellae (Pl. 2, Fig. 2). Epicuticle very thin, about one-twentieth the total thickness, with distinct epicuticular cavities (Pl. 2, Fig. 4). Tegumental ducts regularly spaced across exocuticle (Pl. 2, Fig. 2), form a pore on epicuticle (Pl. 2, Fig. 3). No pore canals observed.

Superfamily Goneplacoidea MacLeay, 1838

Family Megaxanthidae Števíč, 2005

Genus *Megaxantho* Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001

***Megaxantho zoque* Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001**

(Pl. 2, Figs. 5–7)

**Material:** One specimen (Pl. 2, Fig. 5; holotype IHNCH-3421 as illustration of the species). Locality 1003 (G), Maastrichtian, Ocozocoautla Formation, Chiapas.

**Cuticle:** Endocuticle very thick, two-thirds total cuticle thickness, heavily laminated. Exocuticle laminated, one-third the total

cuticle thickness, lamellae become finer toward the top (Pl. 2, Figs. 6, 7). Epicuticle thin. No epicuticular cavities, tegumental structures or pore canals observed.

Superfamily Portunoidea Rafinesque, 1815

Family Carcineretidae Beurlen, 1930

Genus *Carcineretes* Withers, 1922

***Carcineretes planetarius* Vega, Feldmann,**

**Ocampo and Pope, 1997**

(Pl. 2, Figs. 8–13; Pl. 4, Figs. 4, 5)

*Material:* Seven specimens (Pl. 2, Fig. 8; specimen IHNCH-3412 as illustration of the species). Localities 1001 and 1003 (E, G), Maastrichtian, Ocozocoautla Formation, Chiapas.

*Cuticle:* Endocuticle thick, lamellae not evident. Exocuticle one third of total cuticle thickness, lamellae evident under polarized light (Pl. 2, Fig. 12). Epicuticle one-seventh the total thickness of cuticle, with epicuticular cavities evident (Pl. 2, Fig. 11). No tegumental structures or pore canals observed. Cuticle thickness changes noticeably on sternites (Pl. 2, Fig. 9).

Superfamily Retroplumoidea Gill, 1894

Family Retroplumidae Gill, 1894

Genus *Costacopluma* Collins and Morris, 1975

***Costacopluma mexicana* Vega and Perrilliat, 1989**

(Pl. 3, Figs. 1–11; Pl. 4, Fig. 6)

*Material:* Nine specimens in phosphatic concretions (Pl. 3, Fig. 1). Locality IGM-1574 (B), Maastrichtian, Lower Siltstone Member of the Potrerillos Formation, Nuevo León. Four specimens with red stained cuticle (Pl. 3, Fig. 7). Locality C, Maastrichtian, Las Imágenes Formation, Parras Basin, Coahuila.

*Cuticle:* Equivalent to membranous layer preserved at the base of endocuticle in phosphatized specimens, visible under polarized light (Pl. 3, Fig. 2); one-fifth the thickness of the cuticle. Endocuticle laminated, two thirds the thickness of cuticle; lamellae separated by spaces wider than themselves (Pl. 3, Figs. 2, 4 and 10). Exocuticle one-fourth the total thickness of cuticle, finely laminated, lamellae become finer to the top (Pl. 3, Figs. 3, 8–10). Epicuticle one-fifth of total thickness, epicuticular cavities subrectangular (Pl. 3, Figs. 5, 6, 8–11). Pore canals through endocuticle and exocuticle (Pl. 3, Figs. 3, 5 and 6). Tegumental ducts through endocuticle and exocuticle, open as tegumental balls in epicuticle (Pl. 3, Figs. 5 and 6).

X ray dispersive energy analysis revealed a small content of Fe on red-stained specimens, giving the peculiar color to their cuticle. The main difference in composition between red-stained and black concretions of *C. mexicana* is the content of phosphate. Specimens in phosphatic concretions from locality B (IGM-1574) are composed of carbonate-hydroxyapatite (Vega *et al.*, 1994), while red specimens from locality C revealed a high content of calcite.

## Cathodoluminescence results

Cathodoluminescence was used in order to recognize diagenetic events that affected the crustacean cuticle. Petrographic characterization of cuticle was done before thin sections were observed under cathodoluminescence. Cuticle can be affected by early or late diagenetic changes, and for this reason it is important to detect primary features of studied specimens. Cathodoluminescence allows detection of weathering surfaces, as seen in *Dakoticancer australis* epicuticle covered by a thin FeO layer which contrasts with the reddish color of carbonate on the matrix and interior part of cuticle (Pl. 4 Fig. 1). Slight recrystallization on both sides (internal and external) of exocuticle is expressed in cathodoluminescence as thin threads of more intense color. Endocuticle seems to be more affected by recrystallization, as relatively non-luminescent large crystals cut across this layer (Pl. 4, Fig. 2). Different fracture events are observed on the cuticle of *Enoplocyrtia* sp., possibly due to rapid burial. Calcite filled fractures, and the non-calcareous nature of most cuticle layers is observed. An interesting feature is noted on the curved areas of cuticle in this specimen, where lamellae are separated by parallel calcite veins, creating a false lamination detected by composition, continuity and thickness (Pl. 4, Fig. 3). Cuticle laminar nature and surrounding bioclasts are detected in *Carcineretes planetarius* thin sections (Pl. 4, Figs. 4 and 5). Tegumental ducts are detected also by tone changes, as seen in *Costacopluma mexicana* (Pl. 4, Fig. 6) and in *Palaioxanthopsis meyapaquensis* (Pl. 4, Figs. 7 and 8).

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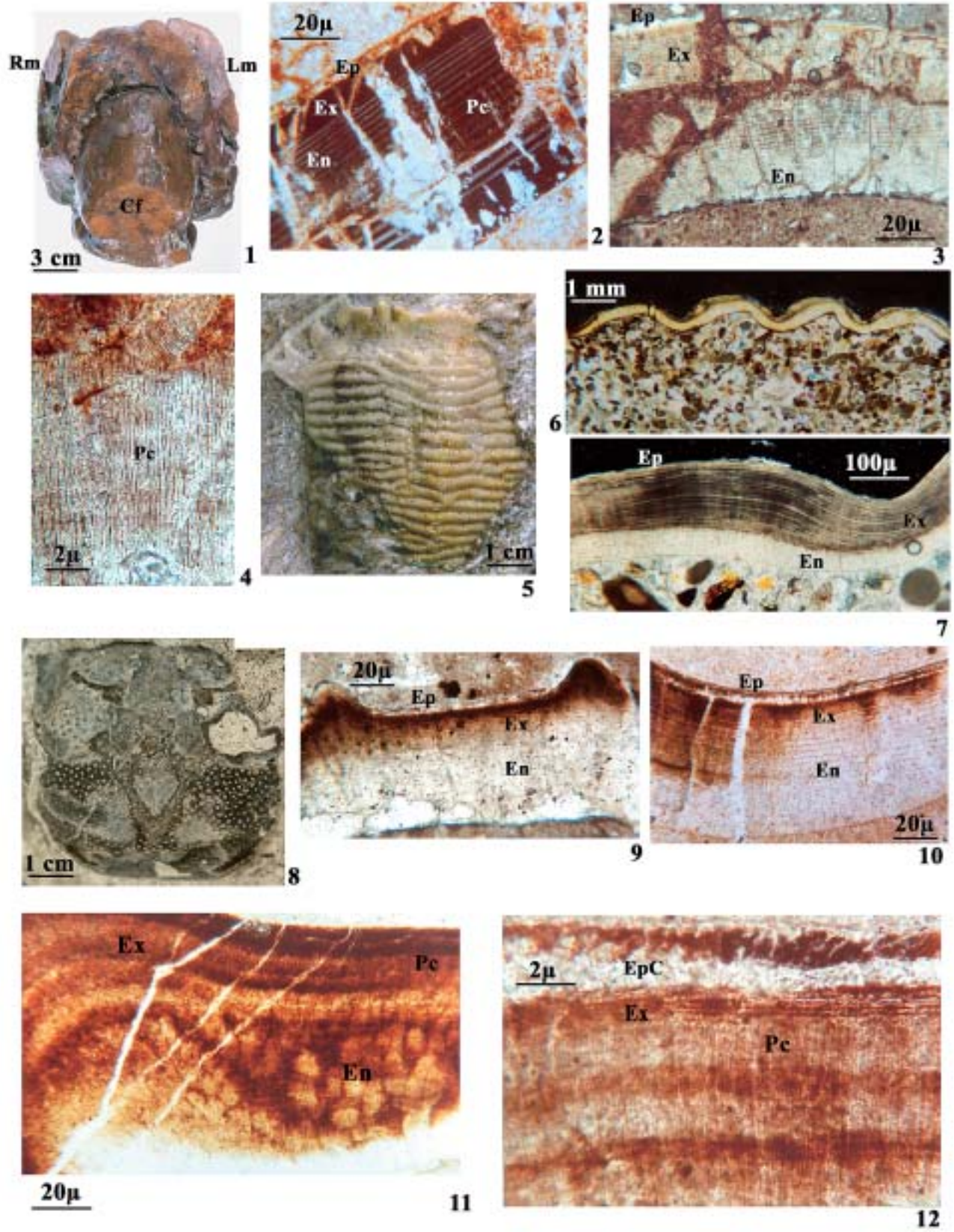
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## Plate 1

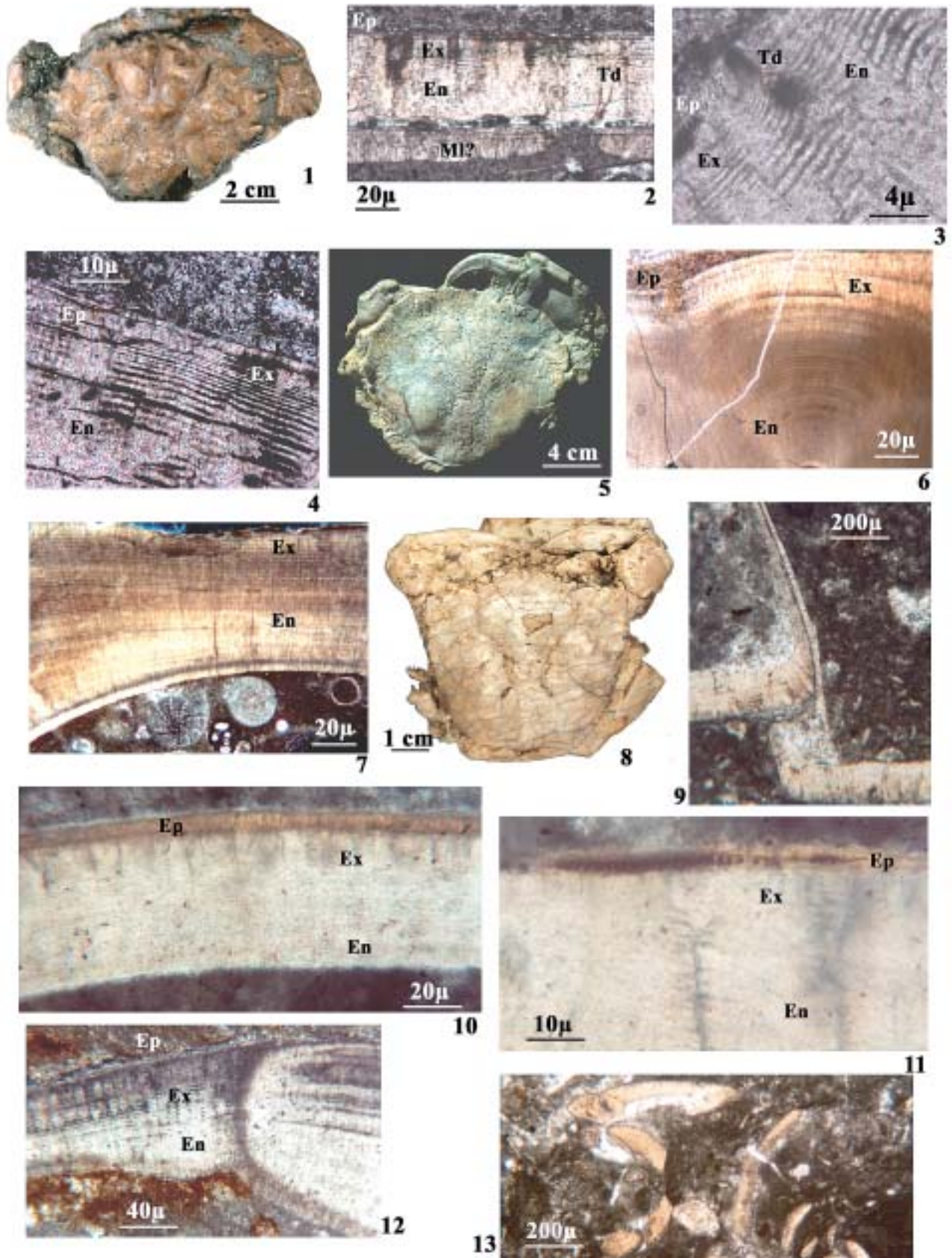
- Figs. 1–4. *Enoploclytia* sp. Locality D, Paleocene, Rancho Nuevo Formation, Parras Basin, Coahuila. Abbreviations for cuticle structures: Cf = cephalothorax, En = endocuticle, Ep = epicuticle, Ex = exocuticle, Lm = left merus, Pc = pore canals, Rm = right merus.
- Fig. 1. Frontal view of concretion, with incomplete cephalothorax and both meri.
- Fig. 2. Section of lateral cephalothorax cuticle. Note thick laminated exocuticle. Polarized light.
- Fig. 3. Section of lateral cephalothorax cuticle. Note cuticle broken by lateral compression. Normal light.
- Fig. 4. Detail of pore canals in exocuticle. Normal light.
- Figs. 5–7. *Lophoranina cristaspina* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer and Waugh, 2001. Locality H, Middle Eocene, San Juan Formation, Chiapas.
- Fig. 5. Dorsal view of incomplete specimen.
- Fig. 6. Longitudinal section showing terraces of dorsal carapace. Polarized light.
- Fig. 7. Cuticle structure between two terraces. Polarized light.
- Figs. 8–12. *Dakoticancer australis* Rathbun, 1935. Locality A, Maastrichtian, Lower Mudstone Member, Potrerillos Formation, La Popa Basin, Nuevo León.
- Fig. 8. Dorsal view of specimen in calcareous concretion.
- Fig. 9. Section of dorsal carapace cuticle including two granules. Normal light.
- Fig. 10. Section of dorsal carapace cuticle. Normal light.
- Fig. 11. Perpendicular section of dorsal carapace cuticle. Normal light.
- Fig. 12. Detail of dorsal carapace exocuticle and epicuticle. Note pore canals in exocuticle and epicuticular cavities. Normal light.





## Plate 2

- Figs. 1–4. *Palaeoxanthopsis meyapaquensis* (Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001). Locality F, Maastrichtian, Ocozocoautla Formation, Chiapas. Abbreviations for cuticle structures: En = endocuticle, Ep = epicuticle, Ex = exocuticle, MI = membranous layer, Pc = pore canals, Td = tegumental duct.
- Fig. 1. Dorsal view of specimen with both chelae articulated.
- Fig. 2. Section of dorsal carapace cuticle. Note tegumental ducts. Polarized light.
- Fig. 3. Detail of opening of tegumental duct. Polarized light.
- Fig. 4. Section of dorsal carapace cuticle. Note epicuticular cavities. Polarized light.
- Figs. 5–7. *Megaxantho zoque* Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001. Locality G, Maastrichtian, Ocozocoautla Formation, Chiapas.
- Fig. 5. Dorsal view of holotype IHNCH-3421.
- Fig. 6. Section of movable finger cuticle. Polarized light.
- Fig. 7. Section of dorsal carapace cuticle. Polarized light.
- Figs. 8–13. *Carcineretes planetarius* Vega, Feldmann, Ocampo and Pope, 1997. Locality E, Maastrichtian, Ocozocoautla Formation, Chiapas.
- Fig. 8. Dorsal view of holotype IHNCH-3412.
- Fig. 9. Section of sternites in ventral carapace cuticle. Normal light.
- Fig. 10. Section of dorsal carapace cuticle. Normal light.
- Fig. 11. Section of dorsal carapace cuticle. Note epicuticular cavities. Normal light.
- Fig. 12. Section of carpus cuticle. Polarized light.
- Fig. 13. Endophragmal cuticle. Normal light.



### Plate 3

Figs. 1–11. *Costacopluma mexicana* Vega and Perrilliat, 1989. Locality B, Maastrichtian, Lower Siltstone Member, Potrerillos Formation, La Popa Basin, Nuevo León. Locality C, Maastrichtian, Las Imágenes Formation, Parras Basin, Coahuila. Abbreviations for cuticle structures: En = endocuticle, Ep = epicuticle, EpC = epicuticular cavities, Ex = exocuticle, MI = membranous layer, Pc = pore canals, Tb = tegumental ball, Td = tegumental duct.

Fig. 1. Dorsal view of phosphatized specimen from locality B.

Fig. 2. Section of dorsal carapace cuticle. Polarized light.

Fig. 3. Section of dorsal carapace cuticle. Note tegumental ducts and balls distributed at regular distances and epicuticular cavities. Normal light.

Fig. 4. Section of dorsal carapace cuticle. Normal light.

Fig. 5. Perpendicular section of dorsal carapace cuticle. Note tegumental ducts and balls distributed at regular distances and epicuticular cavities. Polarized light.

Fig. 6. Detail of upper part of exocuticle and epicuticle on dorsal carapace. Note pore canals and epicuticular cavities. Normal light.

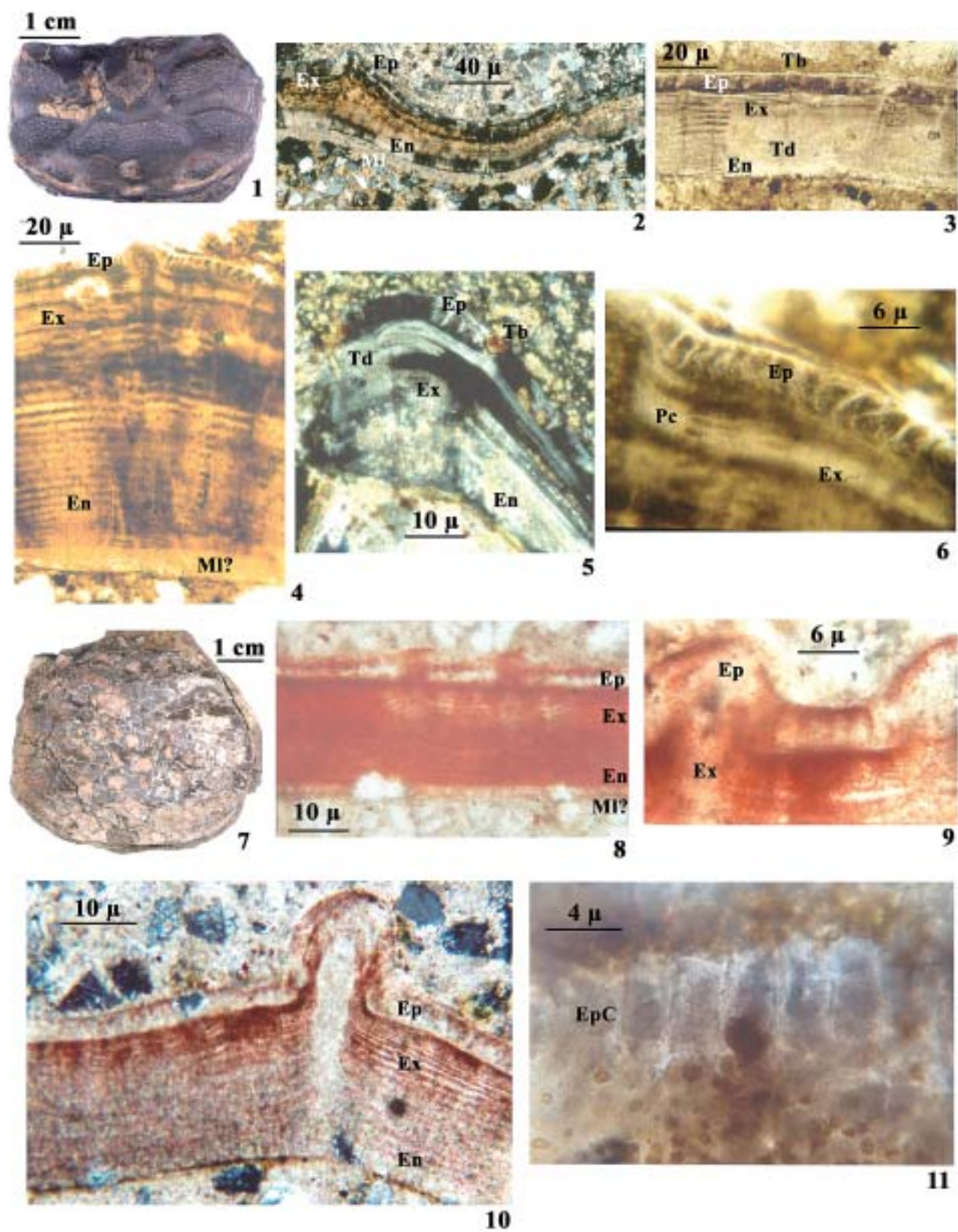
Fig. 7. Dorsal view of red stained specimen from locality C.

Fig. 8. Section of dorsal carapace cuticle. Normal light.

Fig. 9. Detail of upper part of exocuticle, epicuticle and granules on dorsal carapace. Note epicuticular cavities. Normal light.

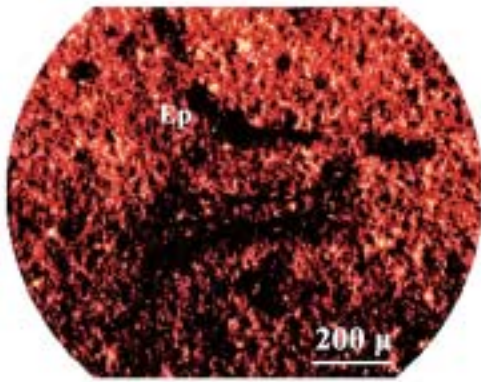
Fig. 10. Section of dorsal carapace cuticle. Note granule. Polarized light.

Fig. 11. Detail of epicuticle. Note epicuticular cavities. Normal light.

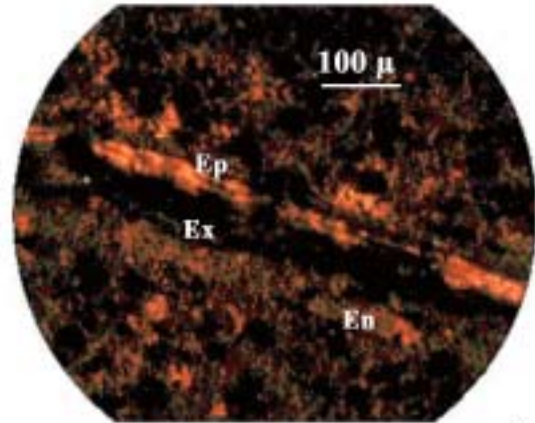


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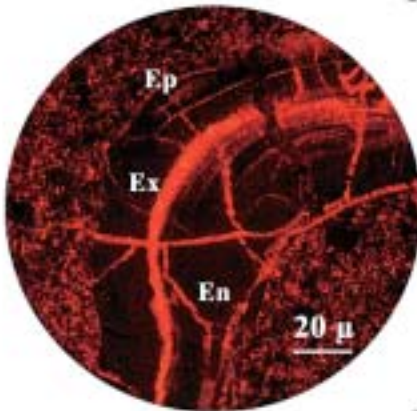
- Figs. 1–6. Cathodoluminescence images (except Fig. 8) of cuticle sections from different species. Abbreviations for cuticle structures: Bioc = bioclast, En = endocuticle, Ep = epicuticle, Ex = exocuticle, Td = tegumental duct.
- Fig. 1. *Dakoticancer australis* Rathbun, 1935. Weathering surfaces (black) of ventral carapace cuticle (contact between sternites) , covered by thin FeO layer.
- Fig. 2. *D. australis*. Exocuticle in red bright color produced by slight recrystallization. Note presence of epicuticle in the external limit of tubercle.
- Fig. 3. *Enoploclytia* sp. At least two events of fracture (red and black) are shown in this specimen. Fractures parallel to lamination are observed in the upper right section.
- Fig. 4. *Carcineretes planetarius* Vega, Feldmann, Ocampo and Pope, 1997. Note laminar nature of endocuticle and exocuticle.
- Fig. 5. *C. planetarius* Vega, Feldmann, Ocampo and Pope, 1997. Lamellae of endocuticle and exocuticle. Note bioclast in the lower part.
- Fig. 6. *Costacopluma mexicana* Vega and Perrilliat, 1989. Granule of cuticle showing void of tegumental duct.
- Fig. 7. *Palaeoxanthopsis meyapaquensis* Vega, Feldmann, García-Barrera, Filkorn, Pimentel and Avendaño, 2001. Note tegumental ducts and compare lamination of endocuticle and exocuticle with next figure. Normal light.
- Fig. 8. *P. meyapaquensis*. Same image as previous figure under cathodoluminescence.



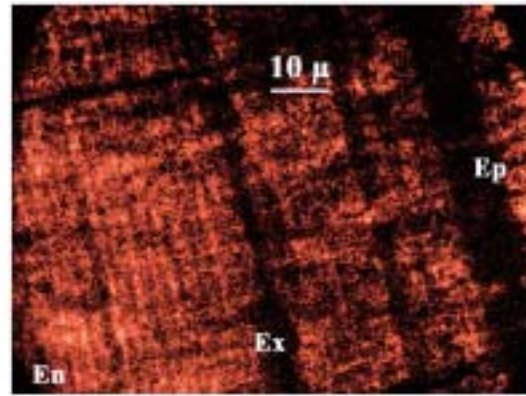
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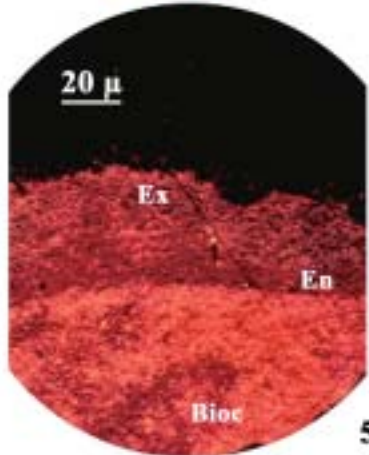
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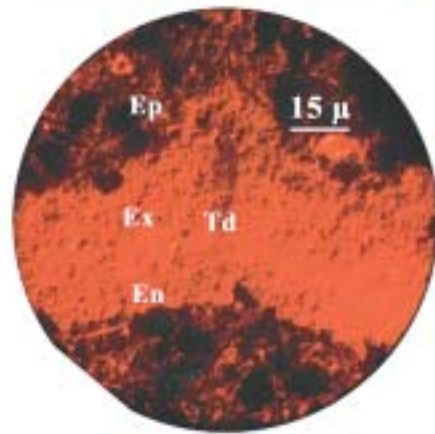
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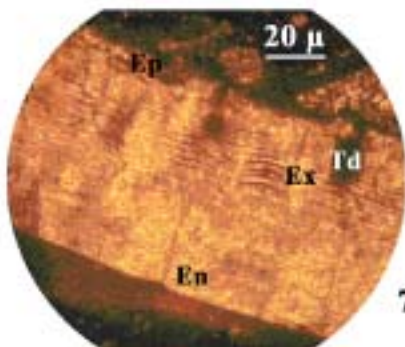
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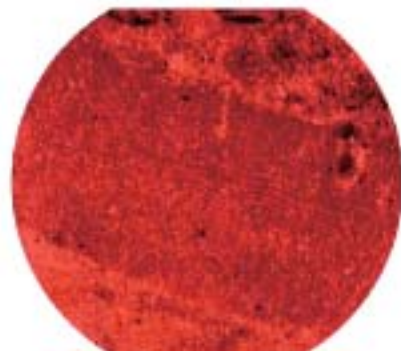
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