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# Review and additions to the Maastrichtian (Late Cretaceous) crustacea from Chiapas, Mexico

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## ABSTRACT

The Maastrichtian crustacean fauna from Chiapas is illustrated and reviewed with reports of new taxa, including the marine isopod *Palaega* sp., described for the first time from the lower Maastrichtian Ocozocoautla Formation, represented by molted remains of the posterior carapace. New specimens and a neotype of the raninoid *Vegaranina precocia* (Feldmann et al., 1996) are illustrated and compared with specimens of *Vegaranina* sp. from the late Maastrichtian of France. New specimens of *Carcineretes woolacotti* Withers, 1922, from the late Maastrichtian of Chiapas are reported and recognized as the sole species of the genus, distributed in the upper Maastrichtian lithostratigraphic units from the Caribbean; the new specimens are compared with others of the same species and age from the Guinea Corn Formation in Jamaica and the Barton Creek Formation in Belize. *Icriobranchiocarcinus tzutzu* Vega new genus and species, is reported as a new member of the Icriocarcininae Števcic, 2005, a diverse subfamily of lithophylacid crabs, along with illustrations and discussion on *Branchiocarcinus flectus* (Rathbun, 1926) (Maastrichtian, Gulf and Atlantic plains), *Icriocarcinus xestos* Bishop, 1988 (Maastrichtian, Pacific of California and Baja California), and *Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879 (Cenomanian, France), in order to confirm that all of these species belong to the Lithophylacidae Van Straelen, 1936, but to different subfamilies (Lithophylacinae and Icriocarcininae) and genera. *Parazanthopsis meyapaquensis* Vega, Feldmann, García-Barrera, Filkorn, Pimentel & Avendaño, 2001, is compared with *Palaeoxanthopsis cretacea* (Rathbun, 1902) (late Maastrichtian, Brazil), and with *Palaeoxantho libertiensis* Bishop, 1986 (late Maastrichtian, Mississippi), in order to illustrate differences and confirm that these species belong to separate genera. *Megaxantho zoque* Vega, Feldmann, García-Barrera, Filkorn, Pimentel & Avendaño, 2001 is reviewed and compared to *Menippe frescoensis* Remy, 1960 (early Eocene, Senegal) and *Menippe mercenaria* (Say, 1818) (living species, Gulf of Mexico), to confirm the late Maastrichtian species from Chiapas should be recognized as *Menippe zoque* new combination, representing the oldest confirmed species for the genus. The age and lithostratigraphic units for all these Maastrichtian crustaceans from Chiapas is reviewed and corrected, based on recent data reported by other scientists, who defined the litho and biostratigraphy with macro and microfossils reported from the study area, nearby Tuxtla Gutiérrez and Ocozocoautla, Chiapas. A correlation between the late Maastrichtian lithostratigraphic units of Chiapas and those from the Caribbean region is confirmed, and their distribution in turn of the Chicxulub impact area in the Yucatán Peninsula is illustrated.

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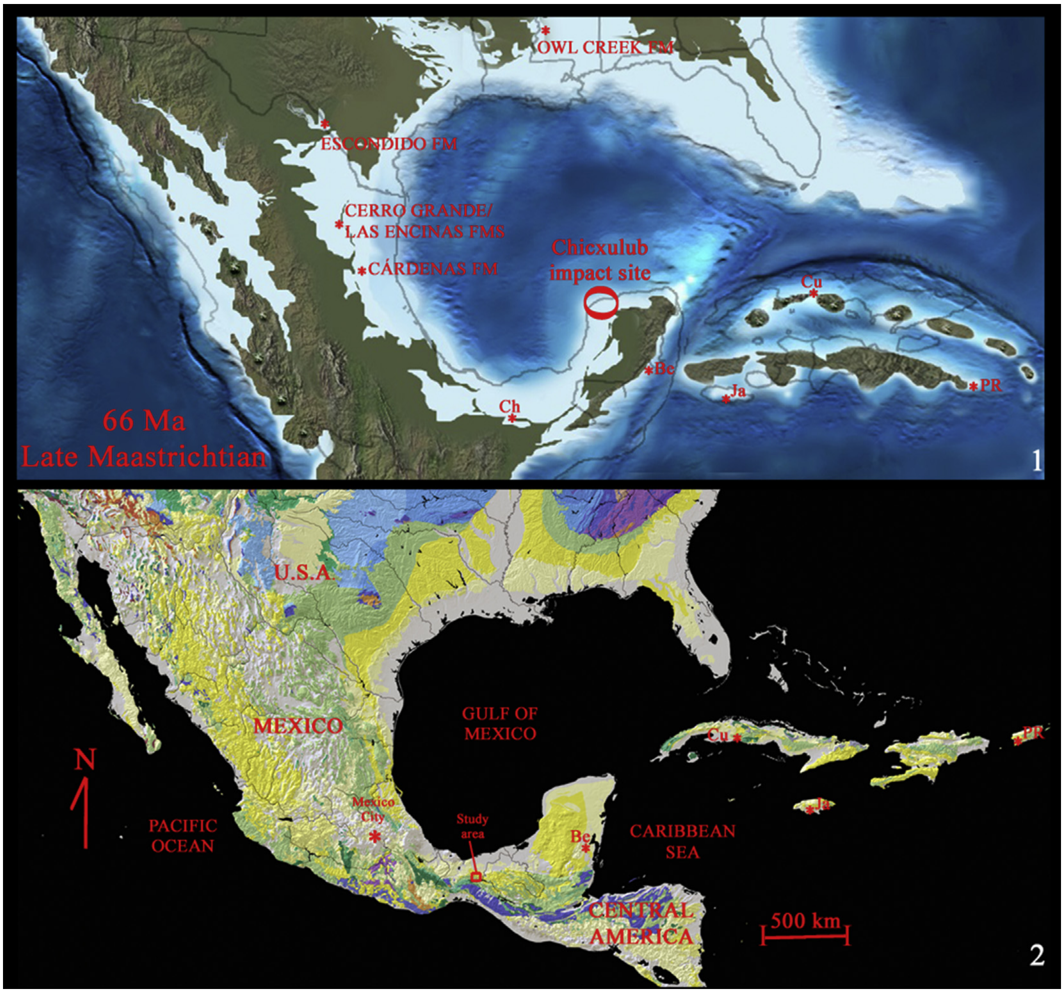


**Fig. 1. 1**, Paleogeographic map for the late Maastrichtian in Southeastern Mexico and the Caribbean, with hypothetical locations of shallow marine environments where decapod species here reported were distributed and probable site of Chicxulub impact at 66 Ma, map courtesy of Ron C. Blakey. **2**, General geologic map indicating fossiliferous location outcrops in Southeastern Mexico, Belize, Cuba, Jamaica and Puerto Rico. Red rectangle corresponds to the studied area (see Fig. 2 present work) (map modified from The North America Tapestry of Time and Terrain, by Kate E. Barton, David G. Howell, José F. Vigil, at https://pubs.usgs.gov/imap/i2781/). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

## 1. Introduction

The fossil crustaceans from Chiapas are the most diverse in Mexico, ranging in age from Albian to Miocene. Recent contributions described an interesting and diverse estuarine crustacean fauna, preserved in early Miocene amber form Chiapas (Serrano-Sánchez et al., 2015a, 2015b; 2016; Huys et al., 2016; Broly et al., 2017; Matzke-Karasz et al., 2017). Late Cretaceous decapod crustaceans from Chiapas were reported for first time by Feldmann et al. (1996), with the description of *Lophoranina precocious* Feldmann et al., 1996, from limestone outcrops at the east side of Tuxtla Gutiérrez, Chiapas. Later, Vega et al. (2001a) described *Carcineretes planetarius* Vega et al., 1997, *Parazanthopsis meyapaquensis* Vega et al. (2001a), and *Megaxantho zoque* Vega et al. (2001a), from Maastrichtian outcrops, west of Tuxtla Gutiérrez. More recently, Hyžný et al. (2013) reported two callianassid species from the Ocozocoautla Formation (these outcrops are now known to belong to the upper Maastrichtian Juan Crispín Formation). Based upon biostratigraphic data for the Ocozocoautla Formation, these crustaceans were assigned to the early Maastrichtian. More recent biostratigraphic data (Pons et al., 2016) places the Juan Crispín and Angostura formations in the upper Maastrichtian, instead of the lower Maastrichtian Ocozocoautla Formation, whose outcrops nearby Ocozocoautla yielded isopod remains and a new genus and species of portunoid crab, both described in this report. Along with a correction of the age, a revision of the systematic position is presented, based upon new material and comparison with specimens of similar age from other localities. Other references include illustrations or mentions of some of the Chiapas specimens here reported (Vega et al., 2005, 2006; Dietl and Vega, 2008; Coutiño-José, 2009; Luque et al., 2017; Vega, 2017).

A new locality nearby the town of Tzu-tzu, includes lower Maastrichtian sandstones of the Ocozocoautla Formation, where specimens of the isopod *Palaega* sp. (Cirolanidae Dana, 1852), and the portunoid crab (Lithophylacidae Van Straelen, 1936: Števčić, 2005) *Icriobranchiocarcinus tzutzu* Vega new genus and species, were collected. The reported specimens of *Palaega* sp. represent the first record for this fossil isopod in Mexico. The description of *I. tzutzu*, offers the opportunity to review a problematic set of species, recently grouped into *Lithophylax* A. Milne-Edwards and Brocchi, 1879, by Kornecki et al. (2017). We compare here specimens of *I. tzutzu*, with *Branchiocarcinus flectus* (Rathbun, 1926) (Maastrichtian: Mississippi, Mexico), *Icriocarcinus xestos* Bishop, 1988 (late Campanian, California, USA; Baja California, Mexico), and *Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879 (Cenomanian: France), to show these species should remain in different genera, but as suggested by Kornecki et al. (2017), included into the Lithophylacidae.

Due to the urbanization of Tuxtla Gutiérrez, some of the type crustacean localities do not exist anymore, while others are now covered by dense vegetation, making it nearly impossible to find new specimens. In the case of *Lophoranina precocious*, now considered as *Vegaranina precocia*, based upon the review of Van Bakel et al. (2012), the holotype is lost and a neotype is here presented. In addition, new specimens from the Juan Crispín and Angostura formations (upper Maastrichtian) are presented and compared with specimens reported from the late Maastrichtian of Cuba and Puerto Rico. *Vegaranina precocia* is also compared with the type and new specimens of the genus from the late Maastrichtian of France.

*Carcineretes planetarius* is here considered as a junior synonym of *C. woolacotti* Withers, 1922, based upon comparison with the holotype from Jamaica, with the two specimens from Belize, and new specimens from the Juan Crispín Formation, Chiapas (upper Maastrichtian).

*Parazanthopsis meyapaquensis* (Juan Crispín Formation, upper Maastrichtian) is here compared with *Palaeoxanthopsis cretacea* (Rathbun, 1902) (late Maastrichtian, Brazil) and with *Paleoxantho libertiensis* Bishop, 1986a,b (upper Maastrichtian, Mississippi), to confirm the specimens from Chiapas belong to a different genus.

*Megaxantho zoque* is here compared with *Menippe frescoensis* Remy, 1960 and *M. mercenaria* (Say, 1818), in order to show that *Megaxantho zoque* should be reassigned to *Menippe* De Haan, 1833.

The paleobiogeographic distribution of the late Maastrichtian decapod species from Chiapas indicates that they were restricted to the Caribbean region (Fig. 1.1), dominated by shallow marine carbonate platforms. When compared with the distribution of other decapod species from the same age in Mexico and southeastern USA, this assemblage (Chiapas-Caribbean) can be considered as nearly autochthonous. The Caribbean was seriously affected by the Chicxulub impact, 66 Ma ago (Ocampo et al., 2006) and thus it is surprising that a genus like *Menippe* was able to survive until now, unless the paleobiogeographic distribution of its species was much wider that it currently known. However, similar genera such as *Carcineretes* Withers, 1922 and *Ophthalmoplax* Rathbun, 1935 also vanished after the K/Pg event, even when *Ophthalmoplax* had a wider paleogeographic distribution during the latest Maastrichtian (Vega et al., 2013).

## 2. Localities and stratigraphy

The studied localities are found near Tuxtla Gutiérrez and Ocozocoautla, Chiapas (Fig. 1.2-2). Specimens of *Palaega* sp. and *Icriobranchiocarcinus tzutzu* Vega new genus and species were found in locality A (Figs. 2 and 3), where lower Maastrichtian sandstones of the Ocozocoautla Formation crop out, near the town of Tzu-tzu, at 16°44′12″N and 93°20′51″W.

*Vegaranina precocia* specimens were found in four localities: locality B (Figs. 2 and 3; upper Maastrichtan Juan Crispín Formation), found in what is now "Colonia El Refugio", SW Tuxtla Guriérrez, at 16°44′36″N and 93°02′12″W, next to the east side of the Sumidero Canyon; locality C (Figs. 2 and 3; upper Maastrichtan Juan Crispín Formation), found in what is now the east side of Ocozocoautla, at 16°45′56″N and 93°22′12″W; locality D (Figs. 2 and 3; lower Maastrichtian Ocozocoautla Formation), a road side section on the Federal Highway 175, between Ocozocoautla and Las Choapas, at 16°52′05″N and 93°24′50″W; and locality E (Figs. 2 and 3; upper Maastrichtian Juan Crispín Formation), a roadcut on the highway between Tuxtla Gutiérrez and Ocozocoautla, at 16°46′41″N and 96°12′36″W.

*Carcineretes woolacotti* specimens were found at three localities: locality F (Figs. 2 and 3; upper Maastrichtian Juan Crispín Formation) reported by Vega et al. (2001a) as locality 1001 at 16°48′58″N and 93°17′25″W, 5 km east of Ocozocoautla; locality G (Figs. 2 and 3; upper Maastrichtian Juan Crispín Formation), reported by Vega et al. (2001a) as locality 1002 at 16°46′32″N and 93°18′30″W, 2 km east of Ocozocoautla and locality H (Figs. 2 and 3; upper Maastrichtian Juan Crispín Formation), reported by Vega et al. (2001a) as locality 1003 at 16°47′21″N and 93°20′00″W, 5 km northeast of Ocozocoautla.

Specimens of *Parazanthopsis meyapaquensis* were found in localities F and H (Figs. 2 and 3), associated to *C. woolacotti*, in outcrops of the upper Maastrichtian Juan Crispín Formation.

Specimens of *Menippe zoque* (Vega et al. (2001a)) new combinaison were found at locality H (Figs. 2 and 3; upper Maastrichtian Juan Crispín Formation).

In a recent review of the stratigraphy of the study area, Pons et al. (2016), based upon the work of Michaud (1987) and Michaud and Fourcade (1989), reported a constrained time for the Upper Cretaceous lithostratigraphic units of the studied area (Fig. 3).

As mentioned by Filkorn et al. (2005) and confirmed by Pons et al. (2016), invertebrate faunas (corals, rudists) are common between Chiapas and Caribbean upper Maastrichtian lithostratigraphic units. The stratigraphic distribution of common crustacean species from Chiapas and the Caribbean region is presented in Fig. 4. Compared with late Maastrichtian diversity of other localities in Mexico and the Caribbean, Chiapas represents the most diverse decapod assemblage. For example, in NE Mexico, the upper Maastrichtian Cerro del Pueblo Formation and the K/Pg Las Encinas Formation include *Ophthalmoplax brasiliana* (Maury, 1930), *Costacopluma grayi* Feldmann and Portell, 2007 and *Linuparus* sp. (Vega et al., 2013; Martínez-Díaz et al., 2017), with *C. grayi* as a survivor species after the K/Pg event (Martínez-Díaz et al., 2016). From the late Maastrichtian assemblage, only *Menippe* persisted after the K/Pg extinction.

## 3. Collections and institutional acronyms

**CM**, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA; **CNCR**, Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México; **DNPM**, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; **GSCM**, Georgia College, Natural History Museum, Milledgeville, Georgia, USA; **IGM**, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City; **IHNFG**, Colección de Paleontología, Museo "Eliseo Palacios Aguilera", Secretaría de Medio Ambiente e Historia Natural, Tuxtla Gutiérrez, Chiapas; **MEP**, Museu Estadual da Paraíba, Brazil; **MMNS**, Mississippi Museum of Natural Science, Jackson, Mississippi; **MNHN.F**, collections de paléontologie, Muséum national d'Histoire naturelle, Paris, France; **MPPM**, Pink Palace Museum, Memphis, Tennessee, USA; **SDSNH**, San Diego Natural History Museum, California, USA; **UCPM**, Museum of Paleontology, University of California, Berkeley, California, USA; **USNM**, United States National Museum, Washington, DC, USA.

## 4. Anatomical abbreviations used in descriptions and figures

**a** = branchiocardiac groove, **as1-6** = abdominal somites 1-6, **als1-4** = anterolateral spines 1-4, **ba** = basis, **bl** = branchial lobe, **br** = branchial ridge, **bu** = bulb, **ca** = carpus, **cas** = carpal spine, **co** = coxa, **cu** = cuticle, **cr** = cardiac region, **crr** = cardiac ridge, **da** = dactylus, **e$_1$e** = cervical groove, **eb** = epibranchial region, **ebl** = epibranchial lobe, **eg/br** = epigastric/branchial ridge; **ebr** = epibranchial ridge, **en** = endopod, **epr** = epigastric ridge, **ex** = exopod, **eys** = eye stalk, **gr** = gastric ridge, **he** = hepatic region, **her** = hepatic ridge, **int** = intestinal region, **intr** = intestinal ridge, **is** = ischium, **lch** = left cheliped, **ls1-4** = lateral spines 1-4, **lur** = left uropod, **max1** = first maxilla, **max2**, second maxilla, **me** = merus, **mes1-3** = meral spines 1-3, **msb** = mesobranchial region, **msbr** = mesobranchial ridge, **msg** = mesogastric region, **msgr** = mesogastric ridge, **mtbr** = metabranchial ridge **mtg** = metagastric region, **mx3** = third maxilliped, **no** = node, **oc** = ocular cavity, **of** = orbital fissure, **ok1-3** = outer keel of carpus 1-3, **or** = orbit, **os** = orbital spine, **os1-3** = orbital spines 1-3, **p2-5** = pereiopods 2-5, **per5-7** = pereonites 5-7, **pl1-pl5** = pleonites 1-5, **plep** = pleura of pereonites, **plt** = pleotelson, **pleu** = pleura of pleonites, **pr** = propodus, **prs** = spine of propodus, **prtp** = protopod, **ps** = posterior spine, **ptg** = protogastric region, **ptgr** = protogastric ridge, **ptp** = protogastric process, **ptpd** = protopod, **pty** = pterygostomial region,

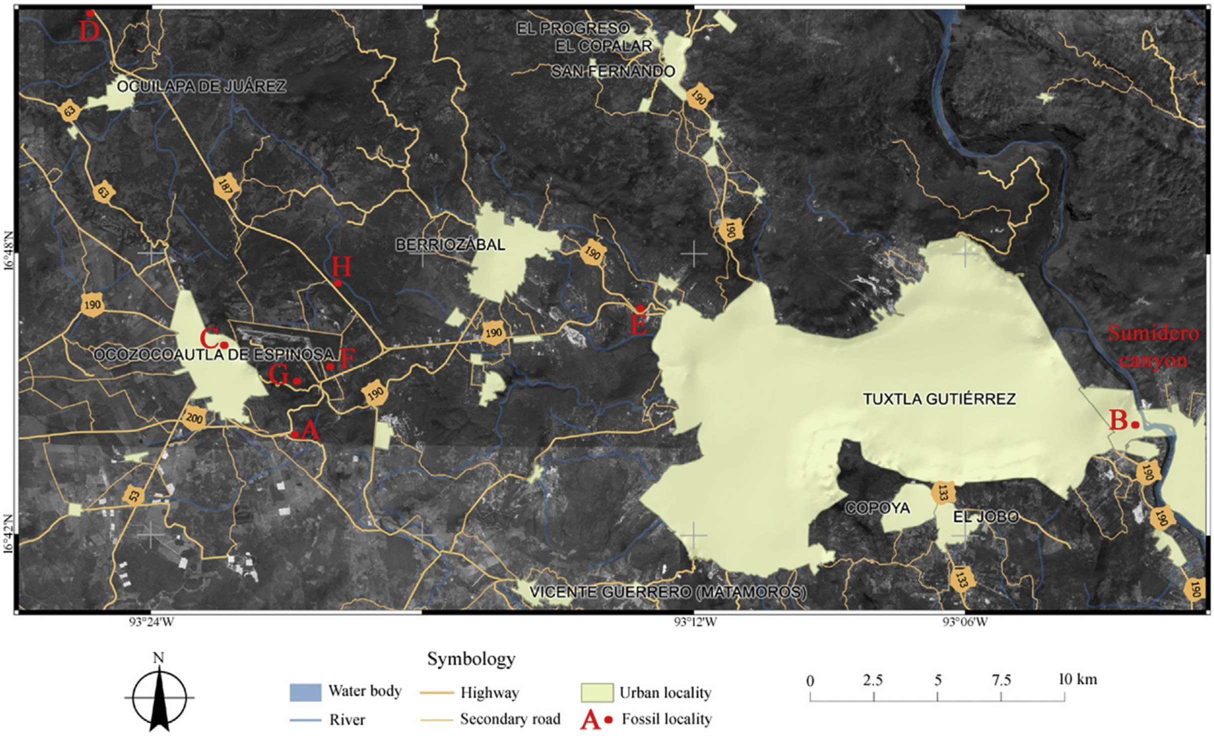


**Fig. 2.** Location map of study area and fossil localities (A–H) near Tuxtla Gutiérrez and Ocozocoautla, Chiapas, Mexico. Map generated from the set of vectorial data of topographic digital information, belonging to the state of Chiapas, Mexico (INEGI, 2015).

**rch** = right cheliped, **ro** = rostrum, **rt1,2** = row of tubercles 1 and 2, **rur** = right uropod, **sob** = suborbital spine, **st1-7** = sternites 1-7, **str** = stridulating organ, **t1-t4** = gastric tubercles 1-4, **tc1-7** = terraces 1-7, **te** = telson, **tu** = tubercle, **ug** = urogastric region, **ugr** = urogastric ridge.

## 5. Systematic palaeontology

Class Malacostraca Latreille, 1802.
Order Isopoda Latreille, 1817.
Suborder Cymothoida Wägele, 1989
Family Cirolanidae Dana, 1852.
Genus *Palaega* Woodward, 1870.

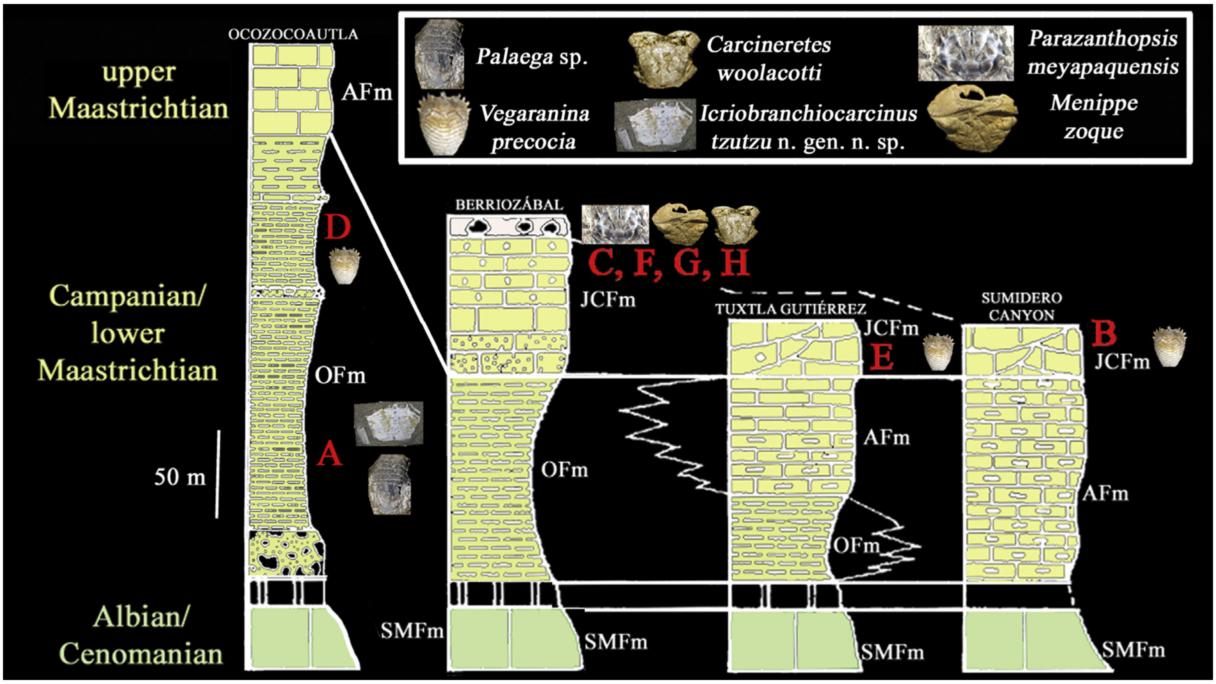
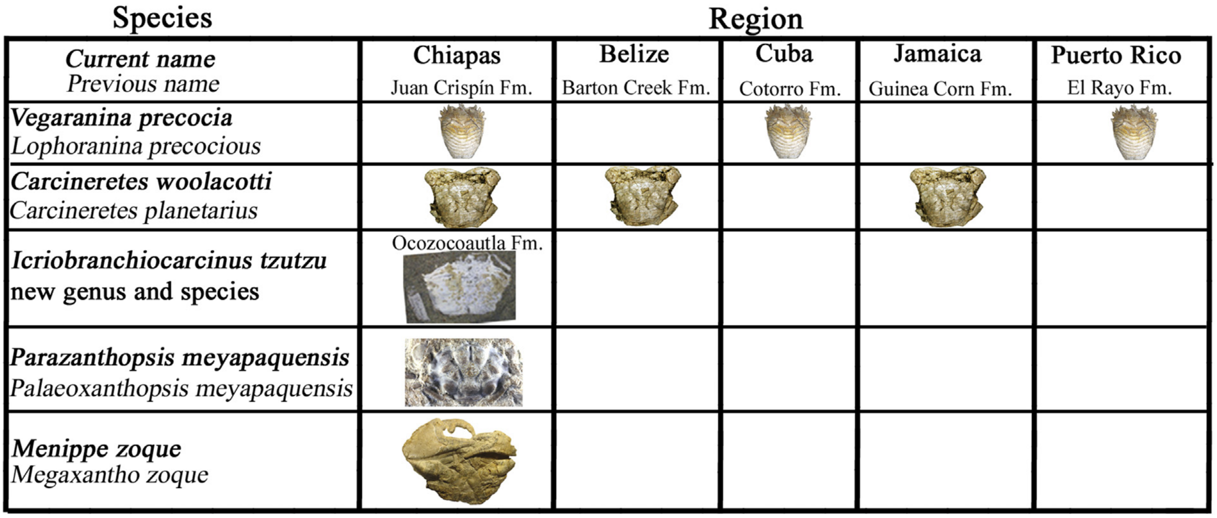


**Fig. 3.** Composed stratigraphic sections at the fossiliferous localities here reported, with relative position of fossil localities, whose geographic positions are found in Fig. 2 (A–H), and occurrence of crustacean species here reported. (Modified from Michaud and Fourcade, 1989).



| Species | Region | | | | |
|---|---|---|---|---|---|
| ***Current name***<br>*Previous name* | **Chiapas**<br>Juan Crispín Fm. | **Belize**<br>Barton Creek Fm. | **Cuba**<br>Cotorro Fm. | **Jamaica**<br>Guinea Corn Fm. | **Puerto Rico**<br>El Rayo Fm. |
| ***Vegaranina precocia***<br>*Lophoranina precocious* | ● | | ● | | ● |
| ***Carcineretes woolacotti***<br>*Carcineretes planetarius* | ● | ● | | ● | |
| ***Icriobranchiocarcinus tzutzu***<br>**new genus and species** | Ocozocoautla Fm.<br>● | | | | |
| ***Parazanthopsis meyapaquensis***<br>*Palaeoxanthopsis meyapaquensis* | ● | | | | |
| ***Menippe zoque***<br>*Megaxantho zoque* | ● | | | | |

**Fig. 4.** Stratigraphic distribution of reported decapod species from the upper Maastrichtian (except for *Icriobranchiocarcinus tzutzu* Vega new genus and species from lower Maastrichtian) lithostratigraphic units of Chiapas, Belize, Cuba, Jamaica and Puerto Rico.

Palaega sp.
Fig. 5.

**Material and locality**.- Four specimens representing posterior carapace exuviae, IHNFG-5335, IHNFG-5336, IHNFG-5490, and IHNFG-5491. Locality A, El Tzu-tzu. Lower Maastrichtian Ocozocoautla Formation.

**Measurements (in mm)**.- Specimens IHNFG-5335, length = 41.2, width = 25.1; IHNFG-5336, length = 37.8, width = 26.6; IHNFG-5490, length = 38.6, width = 29.1, and IHNFG-5491, length = 40.3, width = 27.4.

**Description**.- Medium sized cirolanid, represented only by posterior exuviae preserving: pereonites 5-7, pleonites 1-5, pleotelson and uropods; cuticle reticulated, honeycomb shape; per5-7 rectangular, per5 slightly wider than per6 and per7, all pereonites with acute pleura, directed backwards at an approximate angle of 45°; pl1-pl5 rectangular, pl1-3 narrower than per7, pl1 narrower than pl2-5, pleura of pl2-5 triangular, larger than pleura of pl1, inclined posterolaterally, slightly wider than pleura of pereonites; pleotelson semiovate, twice as long as wide, one third the width of pl5, with median, strong keel, becoming weaker posteriorly from midlength of pleotelson; uropods elongate, two-thirds the length of pleotelson, protopod small, triangular, exopod subovate, as long but twice the width of endopod, endopod filiform.

**Discussion**.- More than 25 species of *Palaega* have been described from Triassic to Pliocene deposits around the world (see Feldmann and Goolaerts, 2005). Specific identification is difficult, especially when only posterior exuviae remains are found. Feldmann and Goolaerts (2005), indicated that all the reported species of *Palaega* should be reviewed in order to establish a more valid generic assignation. They suggested arrangement into three groups, based on morphology of the anterior portion of carapaces.We concur with this suggestion but since all the Chiapas specimens are represented only by posterior molts, we prefer to leave the taxonomic assignation to a generic level, based on morphology of posterior pereonites, pleon, pleotelson and uropods. More recent reports of *Palaega* species include two species from the Kimmeridgian (Jurassic) of Germany (Polz et al., 2006), two species from the Miocene and Pliocene of Italy (Pasini and Garassino, 2012a; b), and one species from the early Eocene of Italy (Vonk, 2014). The early Maastrichtian specimens from the Ocozocoautla Formation represent the first record for the genus in Mexico. They are most similar in age, size and shape to *P. rugosa* Feldmann and Goolaerts, 2005 (Maastrichtian, Tunisia), but we prefer to wait and try to find more complete specimens to suggest a specific identification for the Chiapas specimens. Rathbun (1935) reported *P. williamsonensis* Rathbun, 1935 and *P. guadalupensis* Rathbun, 1935 from the Late Cretaceous of Texas. Both species are also similar to the material from Chiapas, but the median keel of the pleotelson seems to be stronger, although the cuticle of the Texas specimens exhibits the same reticulate ornament of the cuticle.

Order Decapoda Latreille, 1802.
Infraorder Brachyura Latreille, 1802.
Section Podotremata Guinot, 1977.
Subsection Gymnopleura Bourne, 1922.
Superfamily Raninoidea De Haan, 1839
Family Raninidae De Haan, 1839
Subfamily Ranininae De Haan, 1839
Genus *Vegaranina* Van Bakel, Guinot, Artal, Fraaije & Jagt, 2012.

**Type species**.- *Lophoranina precocious* Feldmann et al., 1996, by original designation of Van Bakel et al. (2012, p. 95).

*Vegaranina precocia* (Feldmann et al., 1996) Figs. 6.1–6.12, 6.16.

*Lophoranina precocious* Feldmann et al., 1996. — Vega and Perrilliat, 2006, p. 165, 172, Fig. 9.2.b. — Vega et al., 2006, p. 87. — Hernández-Monzón et al., 2007, Fig. 4. — Schweitzer et al., 2008, p. 5. — Varela and Rojas-Consuegra, 2009, p. 119. — García-Barrera et al., 2011, p. 45. — Schweitzer et al., 2010, p. 74.

*Vegaranina precocia* – Van Bakel et al., 2012, p. 95. — Karasawa et al., 2014, 46, table 1. — Vega, 2017, p. 215, Fig. 18.4.2. — Luque et al., 2017, 41.

**Material and localities**.- Neotype IHNFG-1621 herein designated, specimens IHNFG-1702 (ex-paratype), 0030, 4345, 1392 and 5606 from locality B; specimen IHNFG-5600 from locality C; specimen IHNFG-1666 from locality D (see Figs. 2 and 3). After Feldmann et al. (1996), the original type material was composed of three specimens: holotype IHNFG-1703 and two paratypes IHNFG-1702 and 1621. Unfortunately the holotype was lost and it is important to select a neotype. It is specimen IHNFG-1621 from locality B.

**Measurements (in mm)**.- Neotype IHNFG-1621, length = 71.9, width = 57.4; IHNFG-0330, length = 67.5, width = 64.2; IHNFG-1392, length = 55.2, width = 56.5; IHNFG-1666, length = 39.4, width = 53.7; IHNFG-5600, length = 55.8, width = 45.3; IHNFG-4345, length = 54.6, width = 52.2.

**Emended description**.- Carapace large, convex transversely, widest one-quarter from front; surface divided into two distinctly different areas by cervical groove which consists of a smoothly convex forward curve on either side of midline, arising at posterolateral corner and joining groove on opposite side at midline in a broadly V-shaped pattern; rostrum tridentate, well developed, weakly downturned, with

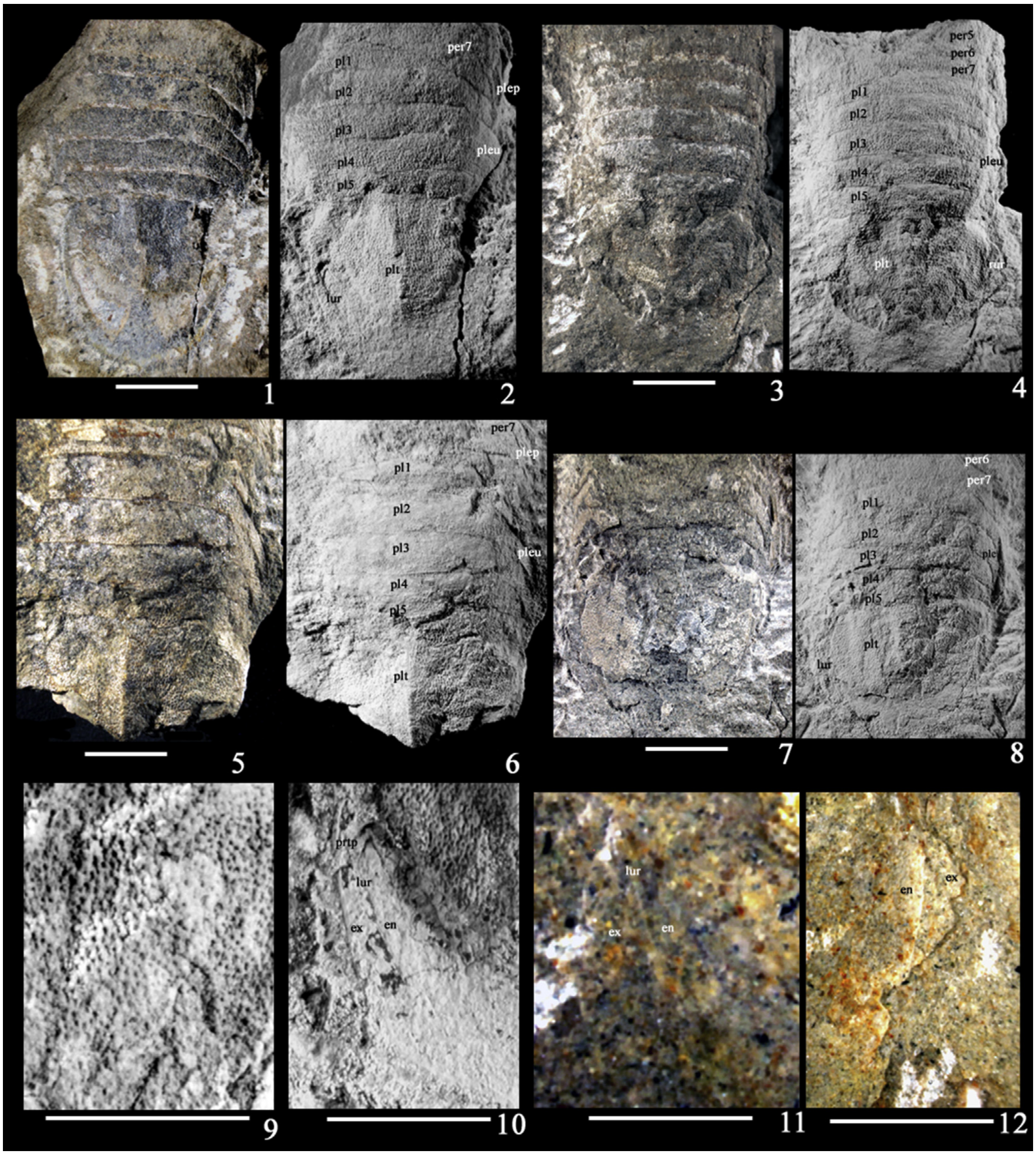
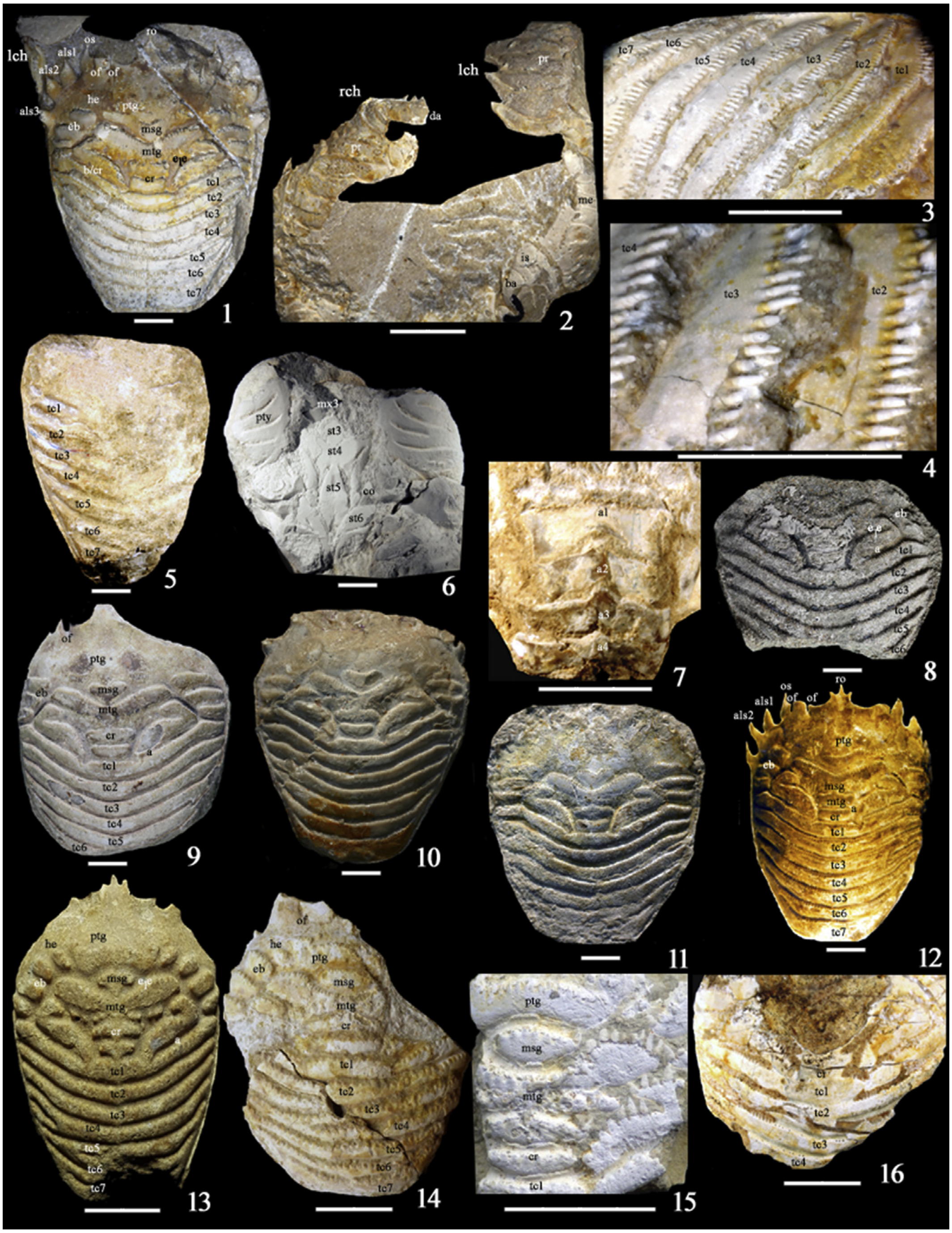


**Fig. 5.** *Palaega* sp. (Crustacea, Isopoda), from the Lower Maastrichtian Ocozocoautla Formation, El Tzu-tzu (locality A), Chiapas, Mexico, dorsal views of posterior exuviae. **1**, **2**, IHNFG-5491; **3**, **4**, IHNFG-5335; **5**, **6**, IHNFG-5336; **7**, **8**, IHNFG-5490; **9**, IHNFG-5491, close-up of reticular cuticle in pleotelson; **10**, IHNFG-5491, close-up of left uropod; **11**, **12**, IHNFG-5335, close-up of left uropod (11) and right uropod (12). Scale bars = 1 cm.

three sharp spines, rostral axis sulcate; fronto-orbital width about half the total carapace width, arcuate, with two deep, open fissures, innermost one situated at about midpoint of orbit and outer one placed between it and postorbital spine which is prominent; anterolateral margin short, with three prominent, sharp spines, excluding orbital spine, longer than basal width, curving toward anterior; posterolateral margin about one-fourth the total length, straight, rimmed, slightly convergent posteriorly; posterior margin nearly straight, half the maximum carapace width; regions anterior to cervical groove produced into gently undulating surface; mesogastric region weakly depressed, protogastric and hepatic regions weakly domed, metagastric region with short, concave forward, spiny terraced ridge, epibranchial region with three sinuous ridges, separated from branchial region by distinct, smooth groove extending from near midpoint on cervical groove posteriorly and laterally to terminate at first terrace which is continuous across entire carapace, extending from posterior end of epibranchial region in concave forward arc, crossing midline posterior to cardiac region as straight axial segment, cardiac region with two short, straight terraces, nonterraced but finely granulated, postfrontal region represented by protogastric regions; eight complete parallel terraces with rows of forward-directed sharp spines (two-three per mm), located posterior to branchiocardiac groove; lobed, spiny terraces anterior of strongly divergent anteriorly branchiocardiac grooves at hepatic regions; deep, posteriorly convergent grooves bound lateral margins of cardiac region, meta-mesobranchial, and intestinal regions not differentiated; crossed by seven terraces; pterygostome with few, closely spaced short, unspiny terraces; sternites 3-6 preserved, fused into nearly flat plate, attaining greatest width about one-fifth the total carapace width, at corner of sternites and at posteriormost corner of st4, tapering to nearly converge at midline at posteriormost corner of st5, axis of sternum with narrow sulcus developed in posterior 1/3 of st4 and across st5. Posterolateral corners of st4 elevated above remainder of sternum, st3 crown shaped, st4 wide anteriorly, with junction sternum/pterygostome, st5 with large lateral expansions, leading to junction sternum-exposed pleurites, st5-6 with medial line, st6 narrow; pleurites 5-7 partially exposed (gymnopleurity), excavated; abdominal somites 1-4 preserved, rectangular, one-sixth the maximum carapace width, with median keel, anterior margin concave, posterior margin of each somite rised at central



**Figs. 6.** 1-12, 16, *Vegaranina precocia* (Feldmann et al., 1996) from the lower Maastrichtian Ocozocoautla and upper Maastrichtian Juan Crispín formations, near Ocozocoautla and Tuxtla Gutiérrez, Chiapas, Mexico. **1-4**, neotype IHNFG-1621 herein selected (locality B), dorsal (**1**) and ventral (**2**) views of carapace and partial right cheliped, close-ups of spines in anterior terraces (**3-4**); **5-7**, IHNFG-5600 (locality C), dorsal (**5**) and ventral (**6**) views of carapace, posterior view of abdomen (**7**); **8**, IHNFG-1666 (locality E), dorsal view of incomplete carapace; **9-11**, IHNFG-1392, 4345 and 0030 (locality B), dorsal views of carapaces; **12**, IHNFG-1703 (lost holotype, locality B), dorsal view of carapace; **16**, IHNFG-5606 (locality B), dorsal view of incomplete carapace. **13-15**, *Vegaranina* sp., upper Maastrichtian yellow-marly limestones near Larcan, Haute-Garonne, France, (**13**), MNHN-.F.R03385, dorsal view of carapace, (**14-16**), specimens in private collection, dorsal views of incomplete carapace and propodus and dactylus of left cheliped. Scale bars = 1 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

portion; third maxillipeds exopod elongated, smooth; left cheliped larger than right cheliped, basis of chelipeds small, triangular, smooth, ischium also triangular, but twice the size of basis, with few smooth terraces, merus longer than wide, outer and inner surfaces bearing five unspiny terraced ridges, many of which bifurcate near upper and lower margins, propodus of both chelipeds bearing at least seven unspiny ridges, right propodus with at least three sharp spines on dorsal surface, three small spines on tubular-shaped dactylus of right cheliped.

**Discussion**.- The known paleobiogeographic distribution of *Vegaranina precocia* includes upper Maastrichtian outcrops in Chiapas, Cuba and Puerto Rico. Varela and Rojas-Consuegra (2009, 2011) reported a large, complete carapace from the Campanian to Maastrichtian sandstones of the Cotorro Formation (Furrazola-Bermúdez et al., 2001). Schweitzer et al. (2008) described an incomplete carapace, tentatively assigned to *Vegaranina precocia*, from the upper part of the upper Maastrichtian El Rayo Formation (Martinez, 2003). Van Bakel et al. (2012) erected the genus *Vegaranina*, to include *Vegaranina precocia* and an undetermined species from an unknown locality in France (Figs. 6.13-6.15). Although there are clear differences in carapace size, carapace shape on the anterior portion, and ornament, number, and strength of terrace spines between the specimen from France and those from the Caribbean region assigned to *V. precocia*, we concur with the suggestion of Van Bakel et al. (2012) to include the reported specimens from the Caribbean into *Vegaranina*. Based upon a few specimens from a private collection, we suggest that the specimens of *Vegaranina* sp. from France, belong to the upper Maastrichtian yellow-marly limestones near Larcan, Haute-Garonne (D. Téodori, pers. comm.) (see also Téodori et al., 2013). Specimens of *Vegaranina* sp. from the late Maastrichtian of France have a narrow anterior margin, and although presence of the characteristic anterolateral spines, the lateral view of specimen MNHN.F.R03385 in Van Bakel et al. (2012, Fig. 28.C) seems to show scars of at least three anterolateral spines; the sternum of that specimen is also similar to sterna of *V. precocia* illustrated here (Fig. 6.6) and in Feldmann et al. (1996, Fig. 3.2, ex-paratype IHNFG-1702). Therefore, it is clear that during Maastrichtian times, at least two species of *Vegaranina* lived in calcareous platforms of the Caribbean and Tethys regions.

The biostratigraphic range for *V. precocia* in Chiapas, includes the early and upper Maastrichtian, since carapace remains have been recovered from the Ocozocoautla (lower Maastrichtian), Juan Crispín and Angostura formations (upper Maastrichtian). The most complete specimens were found in locality B (“Colonia El Refugio”), in Juan Crispín Formation limestones. Incomplete specimens were found in lower Maastrichtian outcrops of the Ocozocoautla Formation, at locality D, as well as in upper Maastrichtian outcrops of the Juan Crispín Formation in localities C and E.

*Lophoranina cristaspina* Vega et al., 2001a, was described for the middle Eocene San Juan Formation, in outcrops found nearby Tuxtla Gutiérrez, and thus, stratigraphically above the Juan Crispín Formation. Hernández-Monzón et al. (2007) suggested *L. cristaspina* to be direct descendant of *V. precocia*, based upon the wide anterior margin and presence of three anterolateral spines.

Section Eubrachyura Saint Laurent and de, 1980.

Subsection Heterotremata Guinot, 1977.

Superfamily Portunoidea Rafinesque, 1815.

Family Carcineretidae Beurlen, 1930.

Genus *Carcineretes* Withers, 1922.

**Type species**.- *Carcineretes woolacotti* Withers, 1922, by original description.

Carcineretes woolacotti Withers, 1922.

Fig. 7.

*Carcineretes woolacotti* Withers, 1922. — Glaessner, 1969, p. R514, Fig. 34.3. — Morris, 1993, p. 116, Fig. 1.1–1.3. — Vega et al., 1997, Figs. 4.3, 4.4. — Karasawa et al., 2008, p. 122, 125. — Donovan, 2010, p. 41. — Schweitzer and Feldmann, 2010, Fig. 6C. — Schweitzer et al., 2010, p. 105. — Jagt et al., 2015, Figs. 71–15.2.C.

*Carcineretes planetarius* Vega et al., 1997, p. 617, Figs. 4.1, 4.2, 5. new synonym.

*Carcineretes planetarius* — Vega et al., 2005, p. 41, pl.2, Figs. 6–13, pl. 4, Figs. 4, 5. — Vega and Perrilliat, 2006, p. 173, Fig. 9.3.a. — Vega et al., 2006, p. 88, Fig. 2.4. — Karasawa et al., 2008, p. 122, 125. Schweitzer et al., 2007, p. 19. — Schweitzer et al., 2010, p. 105. — García-Barrera et al., 2011, p. 45, Fig. 6.4. — Vega, 2017, p. 217, Fig. 18.4.5.

**Material and localities**.- Specimens IHNFG-0075, 1407, 1418, 1419, 1477, 1492, 5601a, 5601b, from localities F and G; specimen from private collection found at locality H (upper Maastrichtian Juan Crispín Formation). In addition to the specimens here studied, we also reviewed: paratypes IHNFG-3412 to IHNFG-3416, from localities F and G; specimens CM-36050 and CM-36051, as well as holotype NHMUK In.20780 from the upper Maastrichtian Guinea Corn Formation (Donovan, 2010; Mitchell, 1999; Mitchell et al., 2011).

**Measurements (in mm)**.- Specimens IHNFG-0075, length = 41.9, width = 47.4; IHNFG-1418, length = 37.5, width = 44.2; IHNFG-1492, length = 35.5, width = 40.3; IHNFG-5601a, length = 42.1, width = 45.0; IHNFG-5601b, length = 38.7, width = 42.2; IHNFG-1419, length = 40.9, width = 43.8; IHNFG-1407, length = 41.7, width = 43.9; IHNFG-1477, length = 45.1, width = 42.9; specimen in private collection, length = 39.1, width = 42.3.

**Emended description**.- Carapace large, quadrate, wider than long, flattened transversely and longitudinally; regions well defined by broad, distinct grooves; cervical groove separates hepatic from epibranchial regions, and these are separated from meso and metabranchial regions by shallow groove, parallel to cervical groove; rostrum projected in advance of orbital region, broad, downturned, with elevated axial region widening anteriorly between two divergent sulci forming U-shaped depression; base of antenna subrectangular; anterior margin inclined, raised; long orbital margins, concave-forward directed anteriorly or slightly anterolaterally, with two distinct, open fissures, one near mid-length, and one near strong, acute, triangular, forward-directed orbital spine; anterolateral margins slightly curved, with two short, acute, forward directed spines; one arises at level of epibranchial lobe; smaller spine arises at level of mesobranchial region; posterolateral margin curved toward relatively short, straight posterior margin, one half the maximum carapace width; mesogastric region connected to parallel-sided protogastric process, pointed toward rostrum, narrow, but becoming obscure posterior to ridges of protogastric region; mesogastric region broadens abruptly at level of epibranchial region to become 25 percent total carapace width, narrowing posteriorly to distinct, ovate, swollen urogastric region which is about 20 percent carapace width; protogastric regions represent 50 percent carapace width, bordered by curved cervical and hepatic grooves, widest at mid-length, tapering uniformly to intersection with widest part of mesogastric region; protogastric region with distinct, concave forward transverse ridge extending across region just in advance of point of maximum carapace width; metagastric region fused with mesogastric at posterior slope of ovate lobe; cervical groove 33 percent carapace width, convergent posteriorly to urogastric region, to complete general V-shape; curved posterolaterally at level of hepatic regions; hepatic regions swollen with subtle medial protuberance; epibranchial lobes swollen, twice as wide as long, slightly inclined toward posterolateral margin, where small, anteriorly-directed spine is present; metabranchial region slightly elevated, parallel to posterior margin; branchial lobe distinct, forming small boss at level of urogastric lobe; short, curved, deep grooves separate cardiac region from branchial lobes; cardiac region with two small tubercles, indistinctly defined posteriorly; intestinal region indistinct; sternum subquadrate, smooth, sternites 1-4 fused into subtrapezoidal anterior unit with straight posterior margins, st5-7 rectangular, distal portion posteriorly curved, forming a sharp, inverted triangle; st8 subtrapezoidal, slightly narrower and longer than the rest; anterolateral margin directed forward, posterior margin broadly curved; male abdomen pointed, first abdominal somite subdorsal, transversely elongated and slightly wider than posterior margin, second abdominal somite slightly longer than first, abdominal somites 3-5 rectangular, becoming progressively slightly wider and longer, abdominal st6 subquadrate, anterior margin slightly concave, about 20 percent of plastron length, telson triangular, shorter than somite 6, base convex and about 17 percent length of plastrón; female abdomen broadly triangular, first three abdominal somites subdorsal, of equal size and narrower than posterior margin, fourth and fifth somites rectangular, 75 percent width of plastron, sixth somite subtrapezoidal, twice as long as fifth somite, telson broadly triangular, with straight posterior margin as long as sixth somite; buccal cavity quadrate, third maxilliped with subtrapezoidal protopod, endopodite long, rectangular, slightly concave on external surface and convex on internal margin, with at least 12 small, strong teeth, merus subquadrate, exopodite

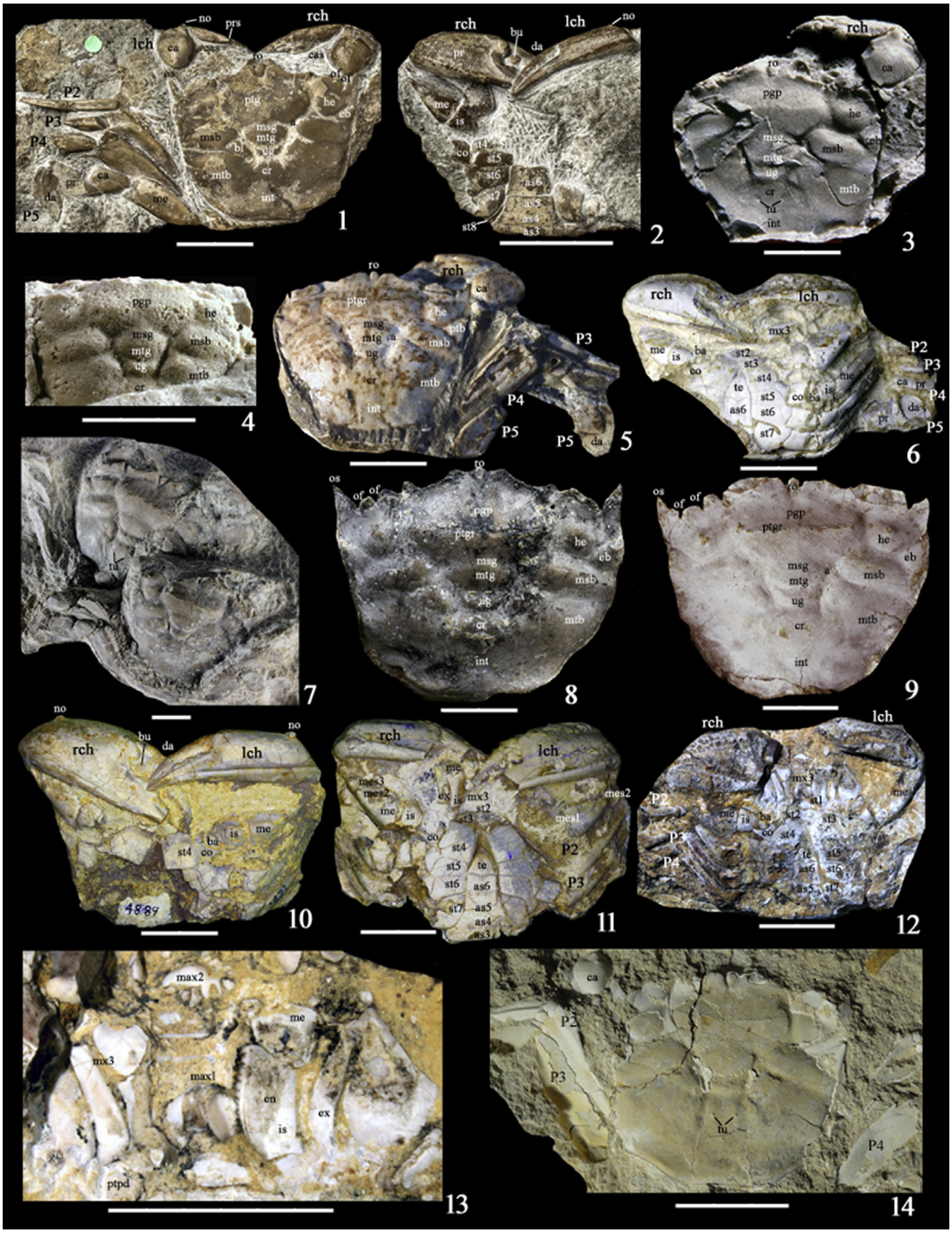


**Fig. 7.** *Carcineretes woolacotti* Withers, 1922 from the late Maastrichtian of Jamaica, Belize, and Mexico. **1-2**, holotype NHMUK In.20780 (Guinea Corn Formation, Río Minho, Clarendon, Jamaica), dorsal and ventral views of carapace; **3**, **4**, CM-36050 and CM-36051 (Barton Creek Formation, Albion Island, Belize), dorsal views; **5-13**, specimens from Juan Crispín Formation (localities F and G, Chiapas, Mexico); dorsal view of carapace IHNFG-1492 (**5**); ventral view of carapace IHNFG-0075 (**6**); dorsal views of carapaces IHNFG-5601a and IHNFG-5601b (**7**); dorsal view of carapace IHNFG-0075 (**8**); dorsal view of carapace IHNFG-1419 (**9**); ventral view of carapace IHNFG-1418 (**10**); ventral view of carapace IHNFG-1407 (**11**); ventral view of carapace IHNFG-1477 (**12**) and close-up of mouth parts (**13**); specimen in private collection (Juan Crispín Formation, locality H, Chiapas, Mexico) dorsal view of carapace. Scale bars = 1 cm. Photographs 1-2 by Kevin Webb (©NHM, London).

acute, elongate, pointed, first maxillae subcylindrical, second maxillae transversely elongate; chelipeds strong and acute, in males, right cheliped larger than left cheliped; chelipeds about equal size in females; coxa strongly concave, basis small, embraced by distal portion of coxa, ischium conical, merus long and robust, quadrate upper surface with small but distinct spine on interior proximal corner, lower surface acute, with three sharp, aligned meral spines directed outwards, proximal two spines of equal size, placed at mid-length, third spine larger; carpus strong, inflated, subquadrate, with sharp inner spine directed anteriorly; propodus inflated, strong, attains maximum thickness below mid-length, strong node present on proximal third of upper, outer surface, sharp spine at midlength on upper surface, directed inwards, strong longitudinal ridge at outer edge on lower surface; left fixed finger acutely triangular, slightly longer than right fixed finger, curved upwards at its tip, forming acute hook, upper surface dentate, with several sharp teeth; dactylus more acute than fixed finger, dentate lower surface with fine, sharp teeth, right strong fixed finger curved at tip with few, blunt strong teeth on upper margin, excavated surface at proximal portion holds massive, rounded tooth of dactylus, dactylus sharp, curved downward, teeth strong and blunt; P2-P4 with subtrapezoidal coxa; basis short, rectangular; ischium subtriangular with elongate anterolateral corner; merus long, smooth, flattened dorsoventrally, anterior edge acute; carpus short, inflated; propodus long, flattened dorsoventrally, half length of merus; dactylus acute, 50 percent length of merus; coxa of P5 inflated, subtrapezoidal, with strong, concave surface toward subtrapezoidal smaller basis, with V-shaped surface toward small, subhexagonal ischium; merus flattened, relatively long; carpus ovate, with excavated concave surface at articulation with propodus largest element of P5, subquadrate in shape, with triangular projection and broadly rounded outer proximal margin; one small fissure at upper portion of outer margin, where it articulates with oval, flat dactylus.

**Discussion**.- Detailed comparison with the holotype NHMUK In.20780 reveal that all late Maastrichtian *Carcineretes* specimens reported from Jamaica, Belize and Mexico, belong to the original species, *C. woolacotti*. Vega et al. (1997, p. 617, Figs. 4.1, 4.2, 5) named a new species – *Carcineretes planetarius* – from the upper Maastrichtian Barton Creek Formation from Albion Island, Belize, based on subtle differences of the lateral margin shape and presence of two small nodes on the cardiac region. However, comparison of the specimens identified as *C. planetarius* reveal that they belong to *C. woolacotti*, and that the observations of Vega et al. (1997, p. 619) were based on a dorso-ventrally crushed carapace, which affected its original shape. Presence of the two small tubercles on the cardiac region can be also seen in at least two specimens from Chiapas (Figs. 7.7 and 7.14). The dorsal and ventral morphology observed in the holotype from Jamaica is identical to the shape and size of the specimens from Belize and Chiapas, and so, we consider *C. planetarius* to be a junior synonym of *C. woolacotti*. In conclusion, we suggest that *C. woolacotti* is the only species for the genus known to live during latest Cretaceous times in the Caribbean region.

Correlation of rudist faunas between the Angostura Formation (equivalent in age to the Juan Crispín Formation) was mentioned by Pons et al. (2016, p. 219). A correlation with the upper Maastrichtian Barton Creek Formation from Belize can also be suggested, not only by the presence of *C. woolacotti* and other invertebrates, but comparing also the age from isotopic data (Ocampo et al., 1996; Pope et al., 1999; Vega et al., 2001b; Keller et al., 2003; King and Petruny, 2003; King et al., 2002, 2004).

*Ophthalmoplax brasiliana* was also an abundant portunoid in late Maastrichtian shallow marine environments, from Brazil to southeastern USA, and it shares with *C. woolacotti* the same shape of mouth parts, morphology of flattened P5 and a right chelae with strong bulb on the proximal side of dactylus, as well as a more sharp left chela (Vega et al., 2013). Both genera became extinct by the end of the Cretaceous, and the paleogeographic distribution of these species near the Chicxulub impact site influenced their extinction.

Family Lithophylacidae Van Straelen, 1936.

**Original diagnosis by Van Straelen (1936, p. 44)**.- Lithophylacidae, characterized by a carapace with subhexagonal outline, a rectilinear frontal margin and the grooves of the branchial regions (literal translation in modern terms). See also Kornecki et al. (2017, p. 315).

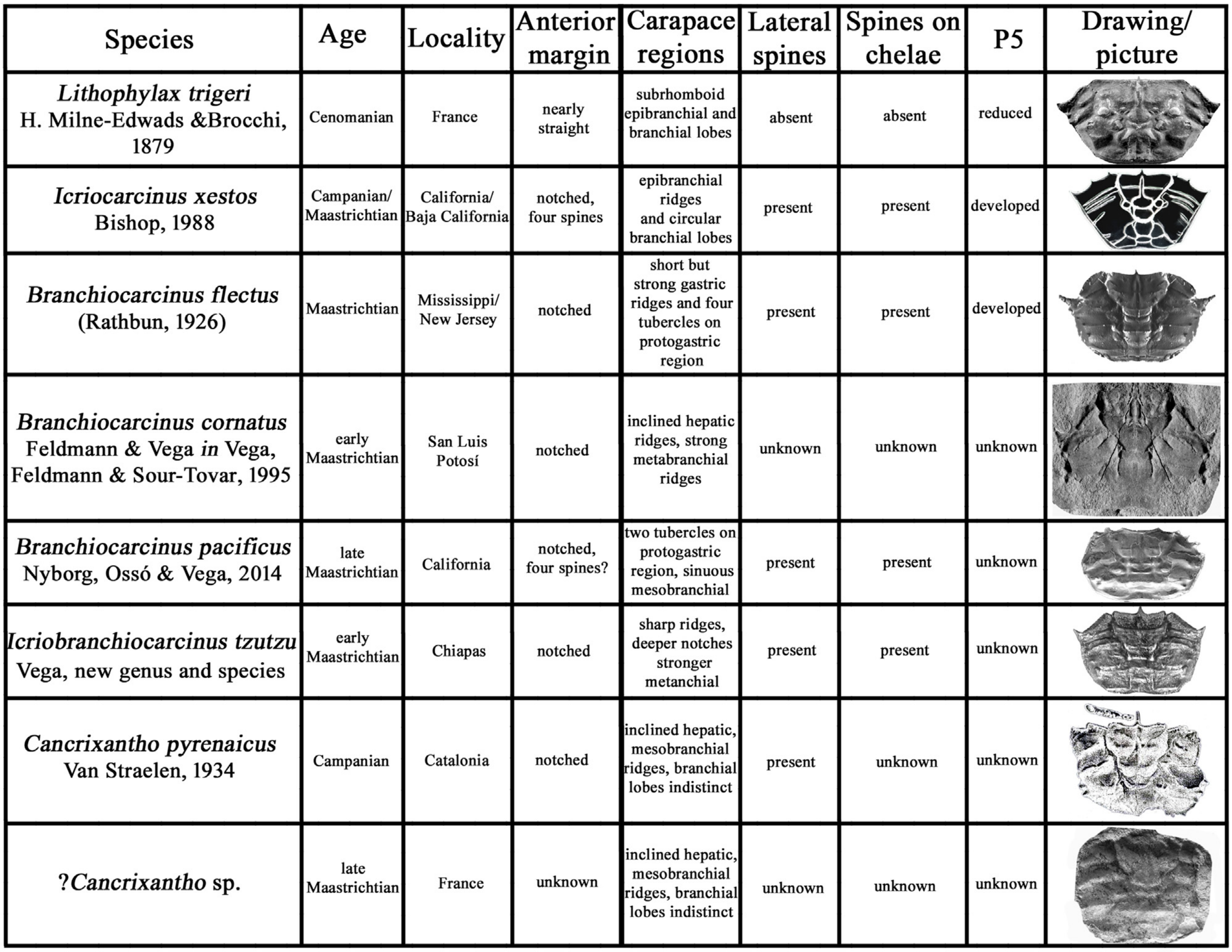
**Discussion**.- Kornecki et al. (2017, p. 315) presented a diagnosis for the Lithophylacidae and suggested inclusion of the genera *Lithophylax* A. Milne-Edwards and Brocchi, 1879, *Icriocarcinus* Bishop, 1988 and *Branchiocarcinus* Feldmann and Vega *in* Vega et al. (1995), based upon common sternal morphology. Kornecki et al. (2017, p. 315) wrote: “this link of common sternal morphology between *Lithophylax*, *Branchiocarcinus* and *Icriocarcinus* provides the foundation for relating these three genera to *Lithophylax*”. Here, we agree with their suggestion to include all of the mentioned genera into the Lithophylacidae, but would like to make emphasis on important differences in carapace shape, dorsal carapace regions, lateral spines, dorsal rows of spines/tubercles on both chelae, as well as development of P5, which are important features to be considered beyond the generic level. Concerning the differences between *Lithophylax*, *Icriocarcinus* and *Branchiocarcinus*, Phillips et al. (2013, p. 149) wrote: “*Lithophylax* bears many similarities with *Icriocarcinus* and *Branchiocarcinus*: inverted subtrapezoidal carapace; sharp anterolateral spines; slender, projected pseudorostrum; ridges and grooves on the dorsal carapace; elongate, subrectangular third maxillipeds; and transverse keels on the abdominal somites. However, the differences between *Lithophylax* and the icriocarcinids are notable. *Lithophylax* has more rounded ridges and bosses on the dorsal carapace. Its anterior margin is straight, whereas that of icriocarcinids has a small notch that breaks the frontal line. The posterolateral margin is smooth whereas in the icriocarcinids it bears small spines. In *Lithophylax*, st6 is more reduced than st5 whereas these same sternites have a similar shape and size in *Branchiocarcinus*. *Lithophylax* has a reduced P5 (according to Guinot and Breton, 2006) and has chelipeds that are not spiny on the dorsal surface, with weak median transverse keel on the anterior surface of the palm (Breton, 2006; Guinot and Breton, 2006). Our examination of new specimens of *Lithophylax* confirms that P5 is very reduced (see Fig. 9.20). The main differences between these genera are presented in Fig. 8, so here we suggest to subdivide the Lithophylacidae into two subfamilies, the Lithophylacinae, to include *Lithophylax trigeri* (Figs. 9.11-9.20) and the Icriocarcininae, to include *Icriocarcinus xestos* (Figs. 9.1-9.10), *Branchiocarcinus flectus* (Figs. 10.8-10.16), *B. cornatus* Feldmann and Vega ***in*** Vega et al. (1995) (Fig. 10.17), *B. pacificus* Nyborg et al., 2014 (see Fig. 8), *Icriobranchiocarcinus tzutzu* Vega new genus and species (Figs. 10.1-10.7) and possibly, *Cancrixantho pyrenaicus* Van Straelen, 1934 (see Fig. 8). Although *B. pacificus* needs a more careful review, beyond the main scope of the present paper, we suggest that this species should be assigned to *Icriocarcinus* based on the general morphology of the carapace.

Subfamily Lithophylacinae Van Straelen, 1936.

**Genus included**.- *Lithophylax* A. Milne-Edwards and Brocchi, 1879.

**Diagnosis**.- Modified from Guinot and Breton (2006, p. 600): carapace broad, hexagonal to inverted trapezoidal, widest at outer-orbital angles, each marked by strong spine; lateral margins diverging anteriorly, markedly slanted; dorsal surface lobulated throughout surface; cervical, gastro-cardiac, branchio-cardiac grooves deep, resulting in H-shaped depression on each side; gastric pits deep; front long, straight, not toothed, rostrum long and narrow; frontal and orbital margins forming same line; orbits extremely broad (long orbital margins posteriorly sloping), deep, obliquely directed towards the axis of carapace, divided into two fosase: eyes with stout stalks, basophthalmite thick; podophthalmite presumably much developed, presumably with inflated cornea; well-defined area (“shutter”) beneath suborbital region; endostome wide; mandibles strong; Mx3 clearly diverging, directed obliquely, with large gap between; sternum wide, sternites 1 and 2 narrow, not fused, sternites 4-6 widened, most of sternite 7 covered by male abdomen, sternite 8 subdorsal, reduced, narrow, covered by abdomen in both sexes, not, visible dorsally; wide sterno-abdominal cavity; male and female abdomens, only weakly dimorphic; male abdomen with all segments free, covering most part of sternite 4, widely triangular; first segments (1-3) completely filling space between coxae of pereopods, telson triangular; sexual openings typically heterotreme, vulvae on sternites 6, male gonopores located on P5 coxae; G1 long, slender, with simple apex, G2 relatively long, only slightly shorter than G1; configuration of press-button type for abdominal maintaining; chelae massive, clear heterochely, weak homodonty, palm not carinated; P2-P4 markedly long, elongated, merus thick, enlarged, compressed, P5 subdorsal, markedly reduced, merus narrow, slender, other articles not preserved; specialized stridulatory apparatus may be present, pars stridens on merus of P1 consisting of well defined, elongated area bearing several prominent striae; plectrum consisting of row of spaced tubercles on the suborbital region.

**Discussion**.- Similarities between the Lithophylacinae and the



| Species | Age | Locality | Anterior margin | Carapace regions | Lateral spines | Spines on chelae | P5 | Drawing/ picture |
|---|---|---|---|---|---|---|---|---|
| *Lithophylax trigeri* H. Milne-Edwads &Brocchi, 1879 | Cenomanian | France | nearly straight | subrhomboid epibranchial and branchial lobes | absent | absent | reduced | |
| *Icriocarcinus xestos* Bishop, 1988 | Campanian/ Maastrichtian | California/ Baja California | notched, four spines | epibranchial ridges and circular branchial lobes | present | present | developed | |
| *Branchiocarcinus flectus* (Rathbun, 1926) | Maastrichtian | Mississippi/ New Jersey | notched | short but strong gastric ridges and four tubercles on protogastric region | present | present | developed | |
| *Branchiocarcinus cornatus* Feldmann & Vega *in* Vega, Feldmann & Sour-Tovar, 1995 | early Maastrichtian | San Luis Potosí | notched | inclined hepatic ridges, strong metabranchial ridges | unknown | unknown | unknown | |
| *Branchiocarcinus pacificus* Nyborg, Ossó & Vega, 2014 | late Maastrichtian | California | notched, four spines? | two tubercles on protogastric region, sinuous mesobranchial | present | present | unknown | |
| *Icriobranchiocarcinus tzutzu* Vega, new genus and species | early Maastrichtian | Chiapas | notched | sharp ridges, deeper notches stronger metanchial | present | present | unknown | |
| *Cancrixantho pyrenaicus* Van Straelen, 1934 | Campanian | Catalonia | notched | inclined hepatic, mesobranchial ridges, branchial lobes indistinct | present | unknown | unknown | |
| ?*Cancrixantho* sp. | late Maastrichtian | France | unknown | inclined hepatic, mesobranchial ridges, branchial lobes indistinct | unknown | unknown | unknown | |

**Fig. 8.** Comparative table between species of the Lithophylacidae, including age, locality, carapace, and chelae features as well as image or drawing.

Icriocarcininae reveal a close relationship, but morphological differences are enough to keep them as separate subfamilies. A reduced P5 in *Lithophylax* is here confirmed and constitutes an important feature to separate the subfamilies Lithophylacinae and Icriocarcininae.

Subfamily Icriocarcininae Števčić, 2005.

**Genera included**.- *Icriocarcinus* Bishop, 1988; *Branchiocarcinus* Feldmann and Vega, *in* Vega et al. (1995); *Icriobranchiocarcinus* Vega new genus, and possibly *Cancrixantho* Van Straelen, 1934.

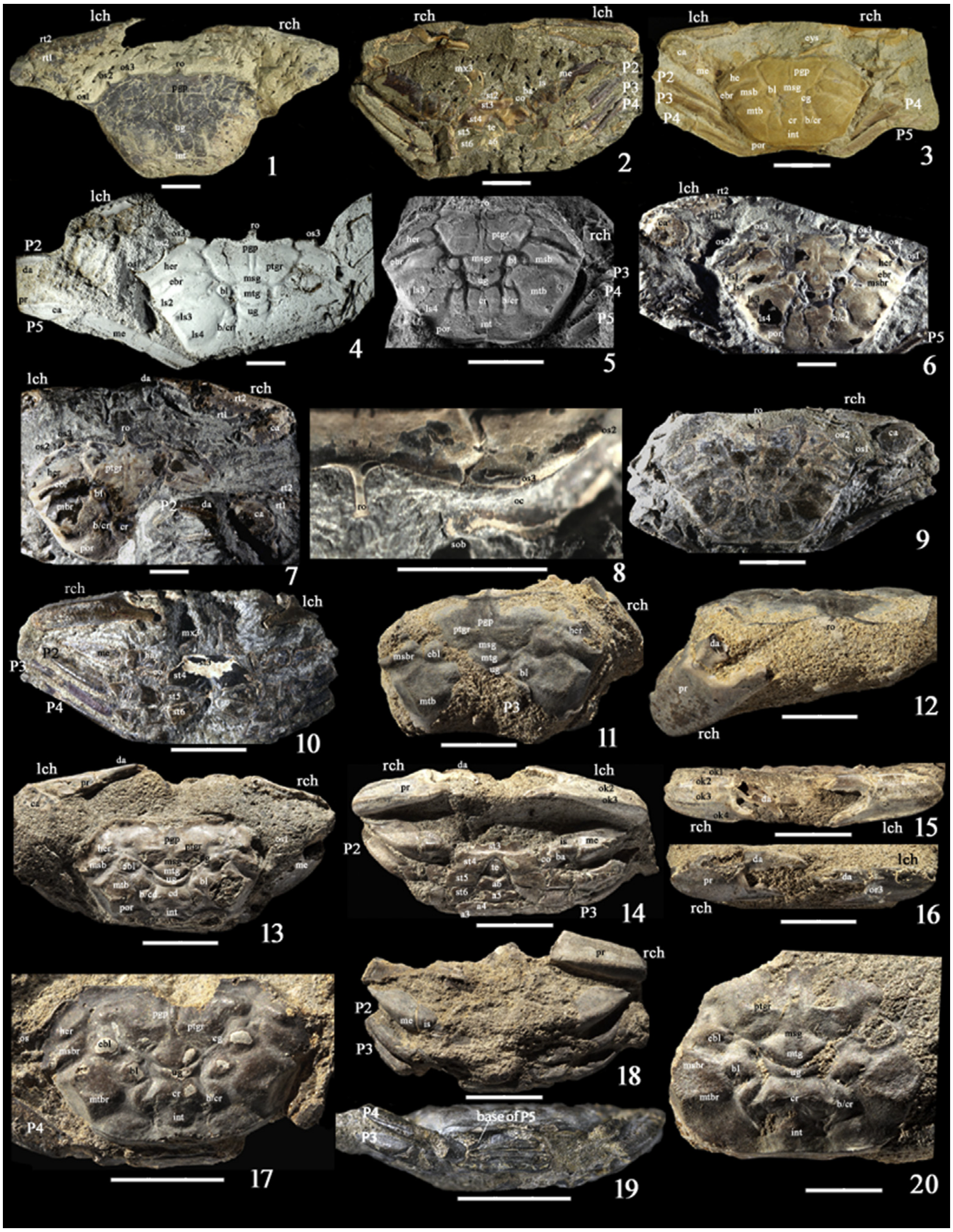
**Diagnosis**.- Carapace small to medium, inverted subtrapezoidal, twice as wide as long, widest at level of sharp, front-directed orbital spines; anterior margin represents the widest portion of carapace, central portion of anterior margin straight, with relatively deep fissures at level of epigastric-branchial groove, anterior margin curves toward orbital spine, rostrum narrow, long, downturned, t-shaped at tip, eyestalks long and slender, distal portion reaches orbital spine; orbits wide, ovate; lateral margin straight, inclined, slightly arched with four lateral spines, posterior one being stronger; posterior margin slightly convex, rimmed, one-third the maximum carapace width; dorsal carapace regions marked by strong transverse ridges and relatively deep grooves; sharp transverse ridges on protogastric, mesogastric, urogastric, cardiac, intestinal, hepatic, epibranchial, branchial, mesobranchial, metabranchial regions; sternum wide, transversely subovate, widest at midlength, st3 transversely subtrapezoidal, st4 subtrapezoidal, st5 transversely subrectangular, st6 similar to st5, st7 rectangular, st8 small and subquadrate, episternal process of st4-6 inverted, triangular; male abdomen triangular, telson triangular, somite 6 subtrapezoidal, somite 5 subrectangular, somites 4 and 3 similar to somite 5; endopodite of third maxilliped inverted subtrapezoidal; chelipeds slightly unequal, right chela slightly larger than left, coxa concave, basis subtrapezoidal inverted, ischium conical, merus robust, with three meral spines on ventral surface, carpus also robust, but one-third the length of merus, with strong spine on inner distal margin, propodus robust, subrectangular elongated, with four strong transverse outer keels that run from base of propodus to distal margin, dorsal surface of propodus with two rows of tubercles, ventral margin with fine tubercles; dorsal surface of dactylus with row of longitudinal spines; P2-P5 long, slender, P3 and P4 the longest and stronger, P5 well developed, nearly subdorsal, P2-P5 meri with median longitudinal sulcus, become stronger at distal portion, dactili unciform, with two lateral rows of fine tubercles.

**Discussion**.- In talking about the genus *Cancrixantho*, Phillips et al. (2013, p. 151) wrote: "The sole known specimen of the carcineretid *Cancrixantho* Van Straelen, 1934, from the Campanian of Spain, is similar to the Icriocarcinidae in its anterior margin, pseudorostrum, and dorsal carapace. It also has spines on the posterolateral margin, but the original shape of the carapace has been lost … more complete specimens may reveal that *Cancrixantho* (currently in the Carcineretidae) may instead belong to the Icriocarcinidae, thus extending the paleobiogeographic and biostratigraphic range of the family". Possibly derived from the Lithophylacinae, the Icriocarcininae had a wide distribution and diversification during Late Cretaceous times.

Genus *Icriobranchiocarcinus* Vega, new genus.

**Type species**.- *Icriobranchiocarcinus tzutzu* Vega, new genus and species.

**Diagnosis**.- As for the species.



**Figs. 9. 1–10**, *Icriocarcinus xestos* Bishop, 1988 from the lower Maastrichtian Point Loma Formation, Carlsbad Research Center, California (**1-3**) and lower Maastrichtian El Rosario Formation, Punta Santo Tomás, Baja California (**4-10**): paratype SDSNH 26113, dorsal (**1**) and ventral (**2**) views of carapace; holotype SDSNH 26038 dorsal view of carapace (**3**); IGM-7957 dorsal view of incomplete carapace (**4**); unregistered specimen UCMP dorsal view of carapace (**5**); IGM-6625-2 dorsal view of carapace (**6**); IGM-6625-1 dorsal view of carapace and close-up of rostrum and left orbit (**7, 8**); IGM-7722 dorsal (**9**) and ventral (**10**) views of carapace. **11-20**, *Lithophylax trigeri* A. Milne-Edwards and Brocchi, 1879, Cenomanian, Sables du Perche Formation, Le Mans, France: MNHN.F.A68061 dorsal (**11**) and anterior (**12**) views of carapace; MNHN.F.A68058 dorsal (**13**), ventral (**14**) and anterior (**15**) views of carapace; MNHN.F.A68060 anterior view of carapace (**16**); **17-19**, MNHN.F.A68057 dorsal (**17**), ventral (**18**) and posterior (**19**) views of carapace; MNHN.F.A68059, dorsal view of carapace (**20**). Scale bars = 1 cm. Photographs 11-20 by Peter Massicard.

**Description**.- As for the species.

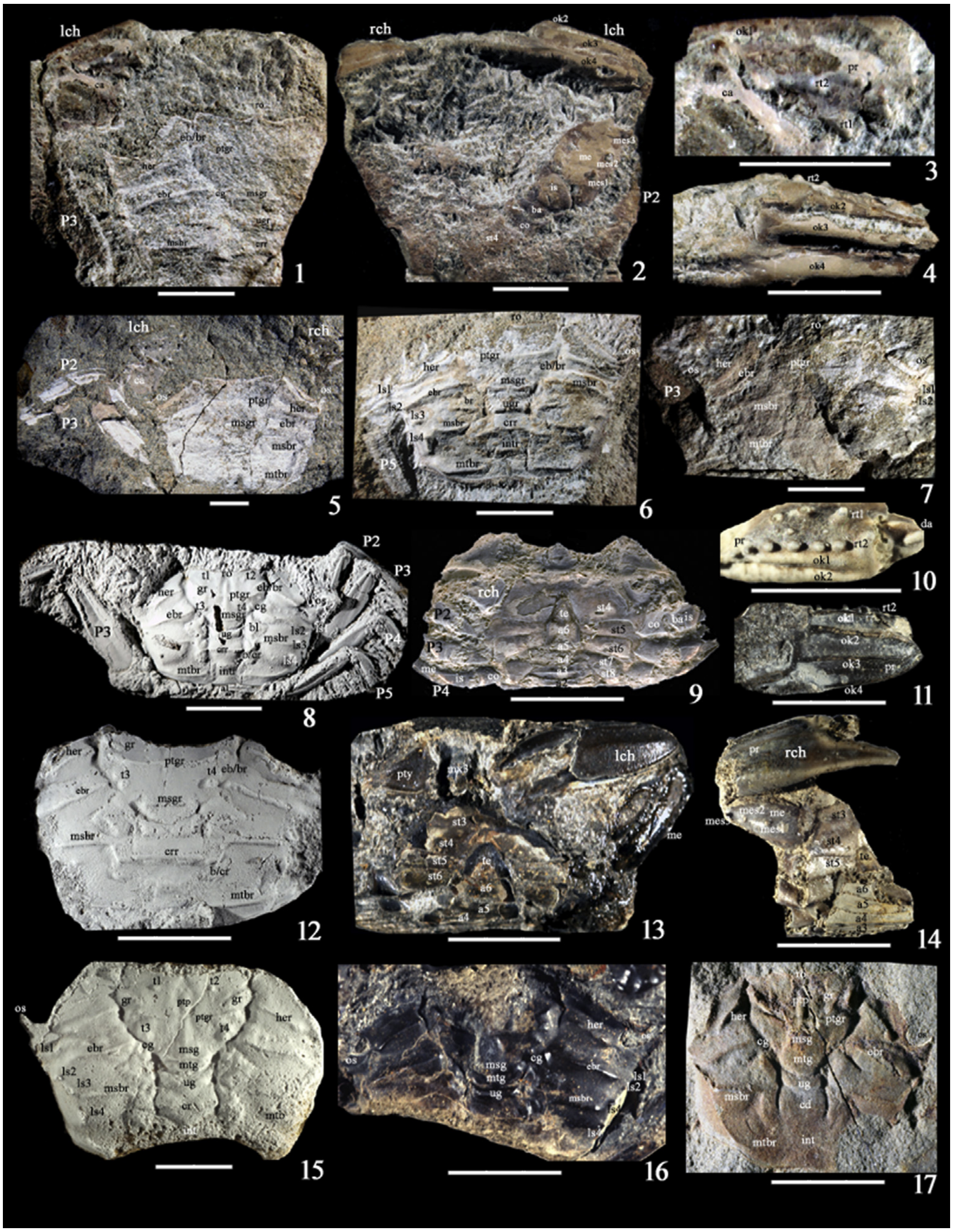
**Etymology**.- Fused name from *Icriocarcinus* and *Branchiocarcinus*, as the new genus includes features of both genera.

**Discussion**.- The morphology of the carapace, dorsal carapace regions, lateral spines of carapace, shape of chelae and presence of dorsal rows of spines are common features bewteen *Icriocarcinus*, *Branchiocarcinus* and *Icriobranchiocarcinus* new genus. The stratigraphic distributions of these genera correspond to the latest Cretaceous, both in the Pacific Realm and the Mississippi Embayment. In Europe, Téodori et al. (2013) reported a specimen of ?*Cancrixantho* sp. with features of the Icriocarcininae from the upper Maastrichtian of the Gensac yellow-marly Limestone Formation in Larcan, Haute-Geronne, France, and suggested that this portunoid group had a wide distribution during that time, in the Americas and Europe, and compared that specimen with *Cancrixantho pyrenaicus* from the Campanian of Catalonia (Van Straelen, 1934). Until more and more complete specimens of *Cancrixantho* spp. are found, we can only suggest that this genus is related to the Icriocarcininae, since the carapace regions, rostrum and lateral spines preserved in the type specimen are different to those observed in *Lithophylax*. *Icriobranchiocarinus* shares features of both *Icriocarcinus* and *Branchiocarcinus*; for the first, it includes more numerous and strong transverse carapace ridges, as well as stronger orbital spines; and for the second, in has less but stronger spines on the dorsal rows of the left chela and a carapace not as wide when compared with *Icriocarcinus*. The occurrence of: *Branchiocarcinus cornatus* in the lower Maastrichtian of San Luis Potosí, Mexico, *B. flectus* in the Maastrichtian of Mississippi and New Jersey, USA (Phillips et al., 2013; Landman et al., 2007), *B. pacificus* Nyborg et al., 2014, from the latest Maastrichtian of California (USA) (Nyborg et al., 2014), *Icriocarcinus xestos* in the Campanian-Maastrichtian of Baja California (Mexico) and California (USA), suggest that the Icriocarcininae, possibly derived from the Lithophilacinae, has a major radiation at the end of the Cretaceous Period, and was probably affected by the K/Pg event.

Icriobranchiocarcinus tzutzu Vega new genus and species.

Figs. 10.1-10.7.

**Etymology**.- The specific epithet refers to the small town of Tzu-tzu,



**Figs. 10. 1–7**, *Icriobranchiocarcinus tzutzu* Vega, new genus and species, from the lower Maastrichtian Ocozocoautla Formation, near Tzu-tzu (locality A), Chiapas, Mexico; **1-5**, holotype IHNFG-5502a/b: dorsal (**1**) and ventral (**2**) views of incomplete carapace; dorsal (**3**) and anterior (**4**) views of left chela; steinkern of dorsal carapace with some pereiopods (**5**); paratype IHNFG-5333 dorsal view of carapace (**6**); paratype IHNFG-5334, dorsal view of carapace (**7**). **8-16**, *Branchiocarcinus flectus* (Rathbun, 1923) from the upper Maastrichtian Owl Creek Formation, Tippah County, Mississippi (**8, 9, 16**); upper Maastrichtian Nixon Sand, Pontotoc County, Mississippi (**10, 14**); lower Maastrichtian Ripley Formation, Coon Creek Member, Union County, Mississippi (**11-13, 15**): MMNS IP-4388 dorsal view of carapace (**8**); USNM 543041 ventral view of carapace (**9**); MMNS IP-2868 dorsal view of right chela (**10**); MPPM 1972.46.452 anterior view of left chela (**11**); dorsal carapace, same specimen (**12**); MMNS IP-2813 ventral view of carapace (**13**); MMNS IP-2868 ventral view of incomplete carapace (**14**); MMNS IP-2813 dorsal view of carapace (**15**); MMNS IP-4390 dorsal view of carapace (**16**). **17**, *Branchiocarcinus cornatus* Feldmann and Vega, *in* Vega et al. (1995), holotype IGM-6244, lower Maastrichtian Cárdenas Formation, Montebello, San Luis Potosí, Mexico, dorsal view of carapace. Scale bars = 1 cm.

near Ocozocoautla, Chiapas.

**Material and locality**.- Holotype IHNFG-5502a, b and two paratypes IHNFG-5333, 5334 from locality A, lower Maastrichtian Ocozocoautla Formation. All were found associated with *Palaega* sp. and represent the third record of icriocarcinids in the Maastrichtian of Mexico.

**Measurements (in mm)**.- Holotype IHNFG-5502, length = 31.1, width = 34.2; paratypes IHNFG-5333, length = 32.2, width = 35.7; IHNFG-5334, length = 28.3, width = 35.5.

**Diagnosis**.- Carapace of medium size, inverted subtrapezoidal, twice as wide as long, widest at level of sharp, front-directed orbital spines; central portion of anterior margin straight, deep fissures mark division with curved anterior margin towards strong, orbital spine, rostrum narrow; lateral margin straight, inclined, slightly arched with four lateral spines, posterior margin slightly convex; dorsal carapace regions marked by strong transverse ridges and relatively deep grooves; st4 subtrapezoidal; left chela robust, with three meral spines on ventral surface, carpus robust, propodus robust, subrectangular elongated, with strong transverse outer keels, dorsal surface of propodus with two rows of tubercles; P2 and P3 long, slender.

**Description**.- Carapace of medium size, inverted subtrapezoidal, twice as wide as long, widest at level of sharp, front-directed orbital spines; anterior margin represents the widest portion of carapace, central portion of anterior margin straight, with relatively deep fissures at level of epigastric-branchial groove, separating lateral curved margin ending in a sharp orbital spine, narrow rostrum; lateral margin straight, inclined, with four lateral spines, posterior one being stronger; posterior margin slightly convex, rimmed, one-third the maximum carapace width; dorsal carapace regions marked by strong transverse ridges and relatively deep grooves; sharp transverse ridges on protogastric, mesogastric, urogastric, cardiac, intestinal, hepatic, epibranchial, branchial, mesobranchial, metabranchial regions; st4 subtrapezoidal; left cheliped with coxa concave, basis subtrapezoidal inverted, ischium conical, merus robust, with three meral spines on ventral surface, carpus also robust, but one-third the length of merus, with strong spine on inner distal margin, propodus robust, subrectangular elongated, with at least three strong transverse outer keels that run from base of propodus to distal margin, dorsal surface of propodus with two rows of tubercles; P2 and P3 long, slender, P2 and P3 meri with median longitudinal sulcus, become stronger at distal portion.

**Discussion**.- As mentioned above, *Icriobranchiocarcinus tzutzu* Vega new genus and species represents a possible link between the genera *Icriocarcinus* and *Branchiocarcinus*, due to its paleobiogeographic distribution, right at the ancient junction between the Pacific Realm and the Mississippi Embayment.

Superfamily Carpilioidea Ortmann, 1893.

Family Palaeoxanthopsidae Schweitzer, 2003.

Genus *Parazanthopsis* Vega et al., 2001a

**Type species**.- *Parazanthopsis meyapaquensis* Vega et al., 2001a, by original designation (not *Xanthopsis cretacea* Rathbun, 1902, by subsequent designation of Beurlen, 1958, as indicated by Schweitzer, 2003, p. 1122).

**Diagnosis**.- Carapace medium size, subhexagonal, wider than long; anterolateral and posterolateral margins of equal length, anterolateral margins with four short, slightly raised spines of approximately equal size; fronto-orbital margin narrow, orbits small; rostrum narrow, sulcate, with two small spines at margin of sulcus; regions of carapace well defined by bluntly rounded elevations, posterior part of carapace with steep slope, posterior margin short; chelae massive, right chela larger than left, dactulus and fixed finger pigmented in both chelae; sternum relatively narrow, st2-4 with median, longitudinal sulcus, st4 subtrapezoidal, with inclined lateral sulci; abdomen narrow.

**Discussion**.- Vega et al. (2001a, p. 323) wrote: "*Palaeoxanthopsis* Beurlen, 1958, described from the Maastrichtian of Brazil is also similar to this new genus. However, *Palaeoxanthopsis* has much shorter posterolateral margins, its anterolateral margins have fissures instead of spines, and there is a long lateral spine which separates the anterolateral and posterolateral margins". Despite these clear differences between these late Maastrichtian genera, Schweitzer et al. (2002, p. 36) synonymized *Parazanthopsis* with "*Palaeozanthopsis*", in clear mistake of spelling the correct name *Palaeoxanthopsis*. Later, Schweitzer (2003, p. 1123) wrote: "Schweitzer et al. (2002) synonymized *Parazanthopsis* with *Palaeoxanthopsis*; that discussion need not be repeated here. The type species is known from Maastrichtian rocks of Brazil, and *P. meyapaquensis* has been reported from Maastrichtian rocks of Chiapas, Mexico". There was no discussion at all in Schweitzer et al. (2002) and the synonymy was made arbitrarily. Another mistake in Schweitzer (2003: table 1) is found, since she cited *Zanthopsis cretacea* as *Zanthopsis brasiliana* Maury, 1930.

Morphologic differences bewteen *Palaeoxanthopsis* and *Parazanthopsis* are clear enough to support existence of two separate genera, distributed in the Atlantic Coast of Brazil and the Caribbean region. From a direct comparison between specimens of *Palaeoxanthopsis cretacea* (Rathbun, 1902) from the upper Maastrichtian Grammame Formation of Brazil and specimens of *Parazanthopsis meyapaquensis* from the upper Maastrichtian of the Juan Crispín Formation in Chiapas, we can add the following differences, to the ones cited by Vega et al. (2001a) at generic level: for *Palaeoxanthopsis*, extremeley long, sharp anterolateral spine 4, the length of each equals half of the maximum carapace width, anterolateral margin with other three, much smaller anterolateral spines, separated each by deep, short grooves; posterior margin strongly concave, bounded by sharp posterolateral spines and carapace bosses more prominent.

*Palaeoxantho* Bishop, 1986a,b (late Maastrichtian, Mississippi) is most similar to *Parazanthopsis*, but the carapace is much smaller (maximum carapace width about 1 cm), anterolateral spines are weaker and the cuticle is finely pustulose, and thus it should remain as a separate genera within the Palaeoxanthopsidae.

*Parazanthopsis meyapaquensis* Vega et al., 2001a

Figs. 11.1-11.7.

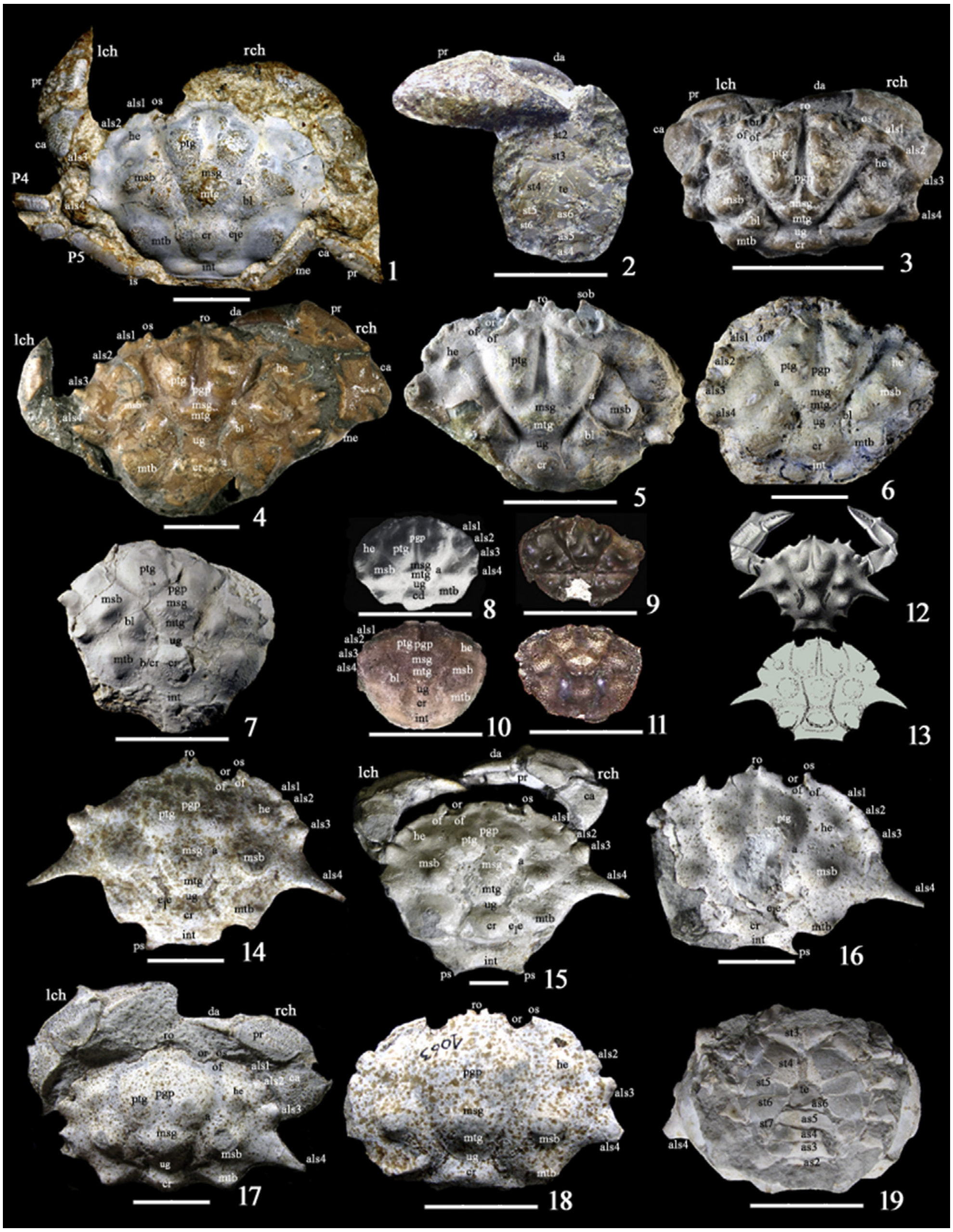
*Parazanthopsis meyapaquensis* Vega et al. (2001a); Vega and Perrilliat, 2006, p. 173, Fig. 9.3.d; García-Barrera et al., 2011, p. 45, Figs. 6.5, 6.6.

*Palaeoxanthopsis meyapaquensis* – Schweitzer et al., 2002, p. 36. — Schweitzer, 2003, p. 1122, 1123. — Vega et al., 2005, pl. 2, Figs. 1-4; pl. 4, Figs. 7 and 8. — Schweitzer et al., 2010, p. 115.

**Material and locality**.- Holotype IHNGF-3418, from locality F, two paratypes IHNFG-3419, 3420 and specimens IHNFG-2060, 5602, 5604 from locality H, upper Maastrichtian Juan Crispín Formation.

**Measurements (in mm)**.- Holotype IHNFG-3418, length = 34.8, width = 47.2; paratypes IHNFG-3419, length = 14.8, width = 21.1; IHNFG-3419, length = 27.2, width = 33.9; specimens IHNFG-5602, length = 34.7, width = 20.8; IHNFG-2060, length = 34.3, width = 18.2; IHNFG-unregistered, length = 22.8, width = 13.4.

**Emended description**.- Carapace of medium size, subhexagonal to ovate, strongly convex in longitudinal section, one-third percent wider than long; anterolateral and posterolateral margins of equal length; anterior margin short, slightly raised, less than half the máximum width, orbits small and circular, their diameter 12 percent maximum width, orbital margin weakly rimmed, two small orbital fissures, strong, projected suborbital spines, rostrum small, bifid, with two short, forward-projected divergent spines; anterolateral margins a broadly rounded, undulate surface with four upturned anterolateral spines of small to médium size, become slightly longer toward midlength of carapace, fourth anterolateral spine perpendicular to longitudinal axis of carapace; posterolateral margin straight, 66 percent maximum length, inclined about 45° to long axis, reaching the short, straight, slightly raised posterior margin, which is about 25 percent maximum width; carapace regions with rounded bosses and well defined grooves, mesogastric region lowest elevation on carapace, subpentagonal, with subparallel axial sulci directed forward, converges before reaching frontal margin, fused epigastric and protogastric lobes form tricuspate boss, of inverted triangular shape, delimited by cervical groove, with a small projection toward the frontal margin, parallel to furrow of mesogastric region; cervical groove deeply impressed, convergent behind mesogastric lobe, one-third maximum length, hepatic lobes small, elongated and inclined, almost parallel to anterolateral margin, with sharp, centrally-located spine, epibranchial lobe ovate, inclined toward fourth anterolateral spine, 17 percent maximum width, mesobranchial lobe elongate, smaller than epibranchial and perpedicular to it, situated at mid-length of carapace, at level of maximum width, metabranchial (mtb) lobes relatively large and prominent, located near mid-length of posterolateral margin, bearing low spine near lateral margin, cardiac lobe subtrapezoidal, with transverse ridge at midlength, width 25 percent maximum carapace width, separated from short posterior margin by steep slope, intestinal region small, depressed; buccal frame quadrate, endopodite of third maxilliped rectangular, straight-sided; sternum relatively small, subovate in longitudinal section, fused st1-3 forming a triangle, with deep longitudinal groove in middle part, fourth sternite rectangular, longer than wide, with deep groove slightly inclined in middle part, sharp, episternal process at posterolateral corner overlaps fifth sternite, fifth sternite subquadrate, much smaller than fourth, with episternal process at lower part of lateral margin, which overlaps sixth sternite, sixth sternite smaller than fifth and subquadrate, remaining sternites not preserved; abdomen partially preserved, sixth abdominal somite large, subrectangular, length equivalent to st4 and st5, telson triangular, with curved posterior margin, two-thirds length of st6; ischium of cheliped small, subtriangular, merus strong, subrectangular, with sharp, ventral longitudinal keel, carpus subquadrate, massive, with short, sharp spine projecting from anterolateral dorsal surface, right cheliped larger than left one, propodus massive, surface ventricose, keel on dorsal surface, distal external surface with rounded boss at insertion of dactylus, propodus strongly pigmented on distal two thirds, relatively short, triangular, with three rounded teeth on occlusal surface, dactylus completely pigmented, slightly curved toward carapace, triangular and with five rounded teeth on occlusal surface; P4 and P5 very long, ischium of P5 short, subquadrate; merus very long, ovate in transverse section, carpus short, subtriangular, carpus of P4

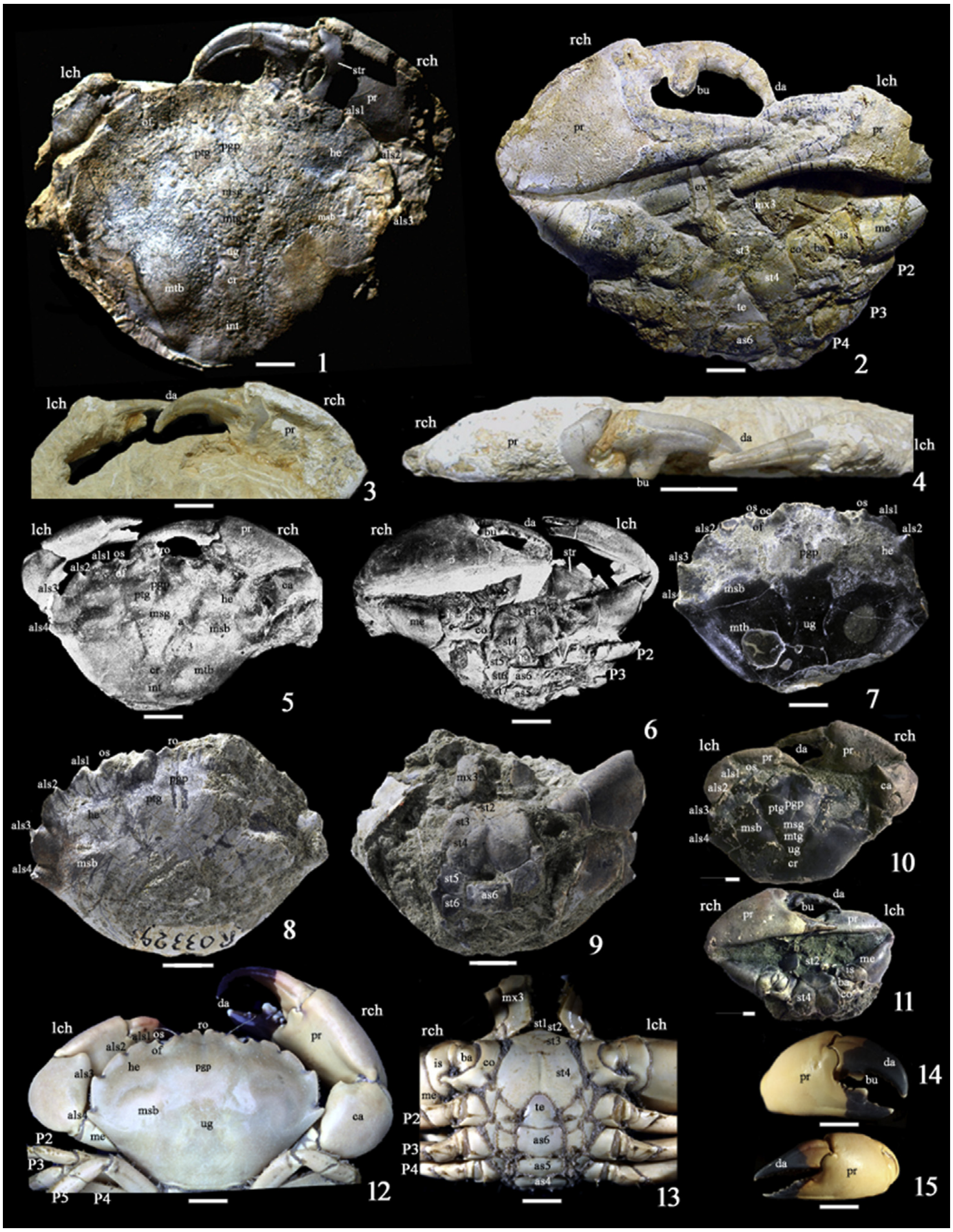


**Figs. 11. 1–7**, *Parazanthopsis meyapaquensis* Vega et al., 2001a, upper Maastrichtian Juan Crispín Formation. **1**, **2**, holotype IHNFG-3418, locality F, dorsal (1) and ventral (2) views of carapace; **3**, paratype IHNFG-3419, locality H, dorsal view of carapace; **4**, IHNFG-5602, locality H, dorsal view of carapace; **5**, paratype IHNFG-3420, locality H, dorsal view of carapace; **6**, **7**, IHNFG-2060 (6) and IHNFG-5604 (7), locality H, dorsal views of carapaces. **8-11**, *Palaeoxantho libertiensis* Bishop, 1986a, upper Maastrichtian Prairie Bluff and Owl Creek formations, Mississippi: **8**, Holotype GSCM-1692, dorsal view of carapace, modified image from Bishop (1986b); **9-11**, MMNS-IP-5270; 4106; 4809, dorsal views of carapaces. **12-19**, *Palaeoxanthopsis cretacea* (Rathbun, 1902), upper Maastrichtian Grammame Formation, Paraíba, Brazil: **12**, **13**, drawings of dorsal carapaces, modified from Maury (1930) and Beurlen (1958), respectively; **14**, dorsal view of carapace DGM-1059; **15**, dorsal view of carapace MEP-PN1; **16**, dorsal view of carapace DGM-1064; **17**, dorsal view of carapace DGM-1063; **18**, **19**, dorsal and ventral views of carapace DGM-1060. Scale bars = 1 cm. Photographs 9-11 courtesy of George E. Phillips.

twice as long as in P5.

**Discussion**.- *Parazanthopsis meyapaquensis* was found associated with *Carcineretes woolacotti* at locality F, in upper Maastrichtian sediments of the Juan Crispín Formation, being much more scarce than the portunoid species. In Brazil, *Palaeoxanthopsis cretacea* (Figs. 11.12-11.19) is relatively abundant in localities of the upper Maastrichtian Grammame Formation. *Palaeoxantho libertiensis* Bishop, 1986a (Figs. 11.8-11.11), is represented by scarce, small carapaces of the upper Maastrichtian Prairie Bluff and Owl Creek Formations in Mississippi (George Phillips, pers. comm.). These three species share a subovoid carapace shape with four anterolateral spines, and dorsal carapace regions well defined by prominent bosses. These features are also observed in some genera within the Palaeoxanthopsidae, such as *Jakobsenius* Schweitzer, 2005, from the late Paleocene of Europe. More detailed studies are needed to explore the possible morphological changes that enabled the species of this family to survive the K/Pg event. Vega et al. (2001c, p. 942) described *Verrucoides stenohedra* Vega et al., 2001c, from the middle Eocene San Juan Formation (later corrected by Perrilliat et al., 2006 and Vega et al., 2008, as the basal Eocene El Bosque Formation, El Veinte, Depresión Central, Chiapas) as a member of the Xanthidae MacLeay, 1838 *sensu lato*. Schweitzer (2003, p. 1120) erected the family Palaeoxanthopsidae to include the genera *Palaeoxanthopsis*, *Paraverrucoides* Schweitzer, 2003, *Remia* Schweitzer, 2003, and *Verrucoides* Vega et al., 2001c. Later, Schweitzer (2005, p. 287) included *Jakobsenius* into the Paleoxanthopsidae. We belive *Parazanthopsis* should also be included into this family, and its similarity to *Verrucoides* suggests the late Maastrichtian genus from Chiapas may had been the precursor of *Verrucoides* (and possibly of other paleoxanthopsids) with a probable ancestor to survive the Chicxulub impact in the earliest Paleogene Chiapas seas. The Paleogene occurrence and wide distribution of most of the Palaeoxanthopsidae suggests a group of crabs that radiated after the Mesozoic extinction.

Schweitzer et al. (2008) reported *Palaeoxanthopsis tylotus* Schweitzer et al., 2008, from two small specimens collected from the upper Maastrichtian El Rayo Formation, Puerto Rico (Volckmann, 1984). Differences between this species and *Parazanthopsis*



**Figs. 12. 1–4**, *Menippe zoque* (Vega et al., 2001a) new combination, upper Maastrichtian Juan Crispín Formation, locality H; **1**, **2**, holotype IHNFG-3421, dorsal and ventral views of carapace; **3**, **4**, hypotype IHNFG-5603, dorsal anterior and frontal view of incomplete carapace. **5-11**, *M. frescoensis* Remy, 1960, Eocene of the Fresco cliffs (Ivory Coast); **5**, **6**, holotype (modified from Remy, 1960, Figs. 4 and 5), dorsal and ventral views of carapace; **7**, paratype MNHN.F.-R03329, dorsal view of carapace; **8**, **9**, paratype MNHN.F.-R03329, dorsal and ventral views of carapace; **10**, **11**, specimen in private collection, dorsal and ventral views of carapace. **12-15**, *M. mercenaria* (Say, 1818), CNCR-2015, Laguna de Tamiahua, Veracruz, Mexico, dorsal, ventral carapace, right and left chelae. Scale bars = 1 cm.

*meyapaquensis* are explained in Schweitzer et al. (2008, p. 8). The species from Puerto Rico is similar to *Palaeoxanthopsis*, but has a short, transverse anterolaretal spine, which is different in strength and shape to the fourth anterolateral spine of *Parazanthopsis*. Therefore we suggest that the small species from Puerto Rico should be kept in *Palaeoxanthopsis*.

Superfamily Xanthoidea MacLeay, 1838.

Family Xanthidae MacLeay, 1838.

Genus *Menippe* De Haan, 1833.

**Type species**.- *Cancer rumphii* Fabricius, 1798, by subsequent designation of Glaessner (1929).

*Menippe zoque* (Vega et al., 2001a) new combination.

Figs. 12.1-12.4.

*Megaxantho zoque* Vega et al., 2001a, p. 325, Figs. 5 and 6. — Vega et al., 2005, p. 40, pl. 2, Figs. 5-7. — Vega and Perrilliat, 2006, p. 173, Fig. 9.3.c. — Dietl and Vega, 2008, p. 290, Fig. 1. — Schweitzer et al., 2010, p. 130. — García-Barrera et al., 2011, p. 45, Fig. 6.7.

**Material and locality**.- Holotype IHNFG-3421, and specimen IHNFG-5603 from locality H, upper Maastrichtian Juan Crispín Formation.

**Measurements (in mm)**.- Holotype IHNFG-3421, length = 109.4, width = 126.7; specimen IHNFG-5603, length = 77.8, width = 115.3.

**Emended diagnosis**.- Carapace large, hexagonal, wider than long; front wide, orbits large, with two orbital fissures; anterolateral margins broadly rounded, with four curved anterolateral broad spines; posterolateral margin inclined toward short, straight posterior margin; dorsal surface apparently flat, pitted, cervical groove and regions weakly defined; heterochelous, chelipeds massive and large, right cheliped much larger than left; sternum subrectangular, relatively small; abdomen triangular, longer than wide.

**Emended description**.- Carapace large, hexagonal, one-fourth wider than long; anterolateral margins broadly rounded and with four anterolateral spines, separated by deep grooves, first anterolateral spine short, second anterolateral spine wider, twice the width of first anterolateral spine, third spine two-thirds the width of second spine, more prominent, fourth spine sharp, triangular, one-fourth the width of third spine; front relatively wide, orbits large, curved inward, 20 percent width of frontal margin, with two parallel fissures situated lateral to orbital midline; posterolateral margins smooth, 66 percent maximum length, inclined toward relatively short posterior margin, which is straight, 33 percent maximum width; regions of carapace weakly marked, surface pitted, mesogastric and metagastric regions subrhombic, with shallow protogastric process projected toward rostrum; protogastric lobes circular, low, rounded protuberances, cervical groove V-shaped, weakly marked, inclined and convergent toward posterior portion of metagastric region, hepatic lobes relatively small, slightly raised and circular, cardiac region subtrapezoidal, branchial regions undifferentiated; posterior slope of carapace gently inclined toward posterolateral and posterior margins; sternum relatively small, elongate and subrectangular, 66 percent maximum length, and 33 percent maximum width of carapace; st1-4 fused with shallow, straight grooves, directed anterolaterally, defining junction of abdominal somites 3 and 4, anterior margin broadly rounded, surface smooth and flat; male abdomen triangular, 33 percent maximum length, and 25 percent maximum width of carapace, fifth abdominal somite subrectangular, much wider than long, sixth somite rectangular, three times longer but slightly narrower than fourth somite, telson triangular; subhepatic regions smooth, rectangular, with straight, slightly raised posterior margin; buccal frame widens anteriorly, longer than wide; third maxillipeds strong, exopodite subrectangular, elongate; chelipeds massive, coxa short, concave, basis wide and short, distal margin concave, ischium subrectangular, short, merus very strong, 66 percent carapace length and 25 percent maximum width, lower surface smooth, with broadly rounded keel, carpus not preserved, chelae strong and massive, heterochelous, right cheliped much larger and morphologically different than left cheliped, propodus of right cheliped pitted, twice as long as high, distal inside surface of right palm shows patches of oblique, parallel striae, possibly some kind of stridulating organ, fixed finger strong, triangular, with short longitudinal keel on inner surface and longitudinal groove on outer surface, curved inward, with five blunt teeth on occlusal surface, dactylus broadly curved, with smooth upper surface, and shallow, curved longitudinal groove on inner surface, four teeth on occlusal surface, large basal bulb, articulates with large subbasal tooth, arising on distal margin of palm; left cheliped half the height of right cheliped, palm surface pitted, fixed finger triangular, curved inward, with longitudinal groove on outer margin, more than five blunt teeth on occlusal surface, dactylus nearly straight, slightly curved inward, dorsal and distal surfaces each with longitudinal grooves; badly preserved meri of P2 to P4.

**Discussion**.- Števčić (2005, p. 69) suggested the erection of the Family Megaxanthidae, with *Megaxantho* as the type genus, within the Superfamily Goneplacoidea, MacLeay, 1838. Later, Schweitzer et al. (2010, p. 130) placed the genus as *incerta sedis* into the Xanthoidea. Based on a large, single carapace (molt) found at locality H, Vega et al. (2001a) described a new genus and species of xanthoid crab, reported as *Megaxantho zoque*. Recently, a second incomplete specimen was found at the same locality; unfortunately, the specimen only preserved the shape of carapace and articulated chelae. In describing the new species, Vega et al. (2001a, p. 325, 327) wrote: "*Menippe* has a transversely oval carapace, smaller orbits, and a narrower distance between orbits than the new genus from Chiapas. *M. mercenaria* (Figs. 12.12-12.15) from the Pleistocene and Recent of the Atlantic Ocean, Gulf of Mexico and Caribbean is similar in shape of the carapace and lack of development of carapace regions (Say, 1818; Rathbun, 1935; Williams, 1984). The anterolateral margins of *M. mercenaria* are similar to *Megaxantho zoque* in having three wide lobes, and a small lateral spine located in the widest portion of carapace. The posterior margin of *Menippe mercenaria* is relatively wider, its orbits are smaller with indistinct fissures, and the distance between them is relatively shorter than in *Megaxantho zoque*. Patches of parallel striae on the inner surface of the chelipeds of the Recent menippid crab *M. mercenaria* can be observed in adult specimens". Detailed review of the holotype and comparison with specimens of *Menippe frescoensis* Remy, 1960 (Figs. 12.5-12.11) from the early Eocene of Ivory Coast and with extant specimens of *Menippe mercenaria* (Say, 1818) (Figs. 12.12-12.15) from the Gulf of Mexico, indicates that *M. zoque* includes the diagnostic features and shape of the extant genus. Rathbun (1935, p. 57) reported *Menippe cretacea* Rathbun, 1935, from the Cenomanian Woodbine Formation of Texas based upon two right cheliped fingers. Schweitzer et al. (2010, p. 131) listed all the known fossil species of *Menippe*, and suggested *M. cretacea* to probably belonged to a different genus. Schweitzer (2005, p. 282) wrote: "*Menippe frescoensis* is the earliest known member of the genus, subfamily, and family, each ranging from Eocene to Recent".

In conclusion, we proposed the new combination *Menippe zoque* and we noted that this species represents the oldest confirmed record for the genus. Another large specimen of *Menippe* sp. from the Miocene of Chiapas was found recently and is to be reported soon.

## 6. Conclusions

The Maastrichtian crustacean fauna from Chiapas represents the most diverse assemblage for its age in the Caribbean region. Species were well adapted to live in calcareous environments in tropical shallow seas, that correspond to the paleoenvironmental interpretation for the Juan Crispín Formation. This unit can be correlated with other lithostratigraphic units of the Caribbean region, such as the Barton Creek Formation (Belize), the Cotorro Formation (Cuba), the Guinea Corn Formation (Jamaica) and the El Rayo Formation (Puerto Rico). The Gramame Formation (Paraíba, Brazil), can also be correlated in age, but not in decapod crustacean fauna, even though *Ophthalmoplax brasiliana* is also found in upper Maastrichtian units of Venezuela, Colombia, northeastern Mexico and southeastern USA (Vega et al., 2013). *Palaeoxanthopsis cretacea* is relatively similar to *Parazanthopsis meyapaquensis*, but they clearly belong to different genera, so endemism of certain species was common during late Maastrichtian times in the Caribbean region. *Vegaranina* sp. from the late Maastrichtian of France is similar to *Vegaranina precocia* from Chiapas, but they represent separate species, and more complete specimens of the species from France are needed to define a possible new species. Form the lower Maastrichtian Ocozocoautla Formation, the isopod *Palaega* sp. represents an extension of the paleobiogeographic range of the genus. The remains reported here are too incomplete to indicate a specific affinity. Presence of *Icriobranchiocarcinus tzutzu* Vega new genus and species confirms the wide distribution of icriocarcinid crabs during the Late Cretaceous, and suggests that the group was very diverse, with other species yet to be reported.

The crustacean paleobiodiversity of Chiapas is the most diverse in Mexico, with crustaceans having been reported from Albian (Cretaceous) to Miocene (Neogene). In the area known as "Depresión Central", Paleogene lithostratigraphic units bear a diverse crustacean fauna across the K/Pg boundary (Vega et al., 2001c, 2008).

Paleobiogeographic affinities suggest: the early Maastrichtian species had a possible influence from the Tethyan fauna; the late Maastrichtian assemblage indicates endemism in the Caribbean region; the early Eocene decapod assemblage indicates influence from the Pacific Realm as well as from the Tethyan region (Vega et al., 2008); and the Neogene assemblage (Vega et al., 2009) suggests influence from the south Atlantic, the Tethys region and the Gulf of Mexico.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jsames.2018.05.017.

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