Late Cretaceous dwarf decapods from Guerrero, southern Mexico and their migration patterns

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Abstract

Two new brachyuran species are described for the Upper Cretaceous Mexcala Formation, Guerrero State, Mexico. *Longusorbis quadratus* new species (Coniacian, Temalac region) is the oldest and southernmost record for the genus. *Xanthosia zoquiapensis* new species (Campanian, Zoquiapa region) is the first record for the genus in Mexico. In addition, the age for *Costacopluma bishopi* Vega and Feldmann is discussed (Coniacian, Temalac region) and represents the oldest and southernmost record for Cretaceous representatives of this genus in North America. All specimens are considerably smaller compared to other species of the same genera and are interpreted as the first example of brachyuran dwarfism in the geological record. These species add new insight into possible migratory routes during the Late Cretaceous. Within *Longusorbis*, a northwestern migratory route is documented from the Coniacian in Mexico to the Campanian - Maastrichtian of the west coast of North America (Canada), whereas within the genus *Xanthosia*, a western migratory route from the Albian of Europe to the Campanian of Mexico is indicated. *Costacopluma* migrated east and north to the west coast of Africa, southeast North America and Greenland.

Introduction

The Mexcala Formation crops out in southern Mexico. It is reported from the states of Puebla, Morelos and Guerrero. This lithostratigraphic unit is a complex sedimentary sequence, as it includes deep-water facies as well as very shallow marine sediments, with lateral and vertical changes, overlying Lower Cretaceous limestones of the Morelos Formation. Defined by Fries (1960) as a 1,220 m flysh-like sequence of pelagic limestones and marls at its base, the Mexcala Formation grades upward to shales, siltstones, sandstones, and conglomeratic lenses. An early Coniacian age was proposed by Bohnenberg-Thomas (1955) for the Mexcala Formation. Cserna (1965) named, described, and interpreted the lithological units in the area. More recent stratigraphic reports have detailed facies distribution, sedimentology, diagenesis, and subdivided the formation into members (Ontiveros-Tarango, 1973; Cserna *et al.*, 1980; Ortega-Gutierrez, 1980; González-Pacheco, 1988; Hernández-Romano *et al.*, 1998; Hernández-Romano, 1999, among others). Most authors agree that deposition of the first sediments of the Mexcala Formation occurred in Turonian times, while the last marine deposits are found in late Maastrichtian siltstones and sandstones of the study area (Alencáster, 1980; Perrilliat *et al.*, 2000).

Fossil content of the Mexcala Formation includes foraminifera (Hernández-Romano *et al.*, 1997; Lang...
The brachyuran decapods described herein were collected at two localities of the Mexcala Formation in Guerrero. Locality IGM-2448 is found 5 km north of Temalac, a small village located 35 km southeast of Iguala, Guerrero. Locality IGM-3557 is found near the town of Zoquiapa, northeast Guerrero (Fig. 1).

Vega and Feldmann (1992) described *Costacopluma bishopi* based on very small specimens found on light-brown siltstones of locality IGM-2448. They proposed a Maastrichtian age for these sediments, but from recent studies on foraminifera and rudists it is now clear that the age is Coniacian. Although no complete section was measured due to intense folding and covered outcrops, a composite column of 25 m of limestones, siltstones and sandstones has been constructed (Fig. 2). The base of this sequence is represented by an alternation of dark-brown limestones and light-brown siltstones and mudstones, with a rich content of fossils (fo-
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Fig. 2. Composite stratigraphic section at localities IGM-2448 and IGM-3557, showing lithology and thickness of Morelos and Mexcala formations.

The study area is characterized by the presence of Lang and Frerichs (1998), who proposed a Coniacian age for the first Laramide pulses in the study area, marking as a change in the sedimentary regime from carbonates to fine siliciclastic sediments. Based on identification of the *Dicarinella concavata* biozone, Lang and Frerichs (1998) placed the first strata of the Mexcala Formation in the Coniacian just above what they called the Cuautla Formation limestones. An interesting fact is that one of the species here reported, *Longusorbis quadratus* new sp-

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from the Coniacian-early Santonian Pacific Ocean. However, occurrence of the other representative species of Longusorbid, L. cuniculosus Richards, 1975 in upper Campanian – lower Maastrichtian sediments of the Shelter Point locality at Vancouver Island, Canada (Richards, 1975; Schweitzer et al. 2003), clearly indicates a northwest migration of this genus during the Late Cretaceous. The uppermost part of the Mexcala Formation is represented by siltstones and sandstones of early to late Maastrichtian age in the Temalac – Mitepec area (Perrilliat et al., 2000).

The Mexcala Formation is represented by shallow marine light brown siltstones nearby Zoquiapa town, northeastern Guerrero, where a composite section of 25 m (Fig. 2) contains several species of gastropods and bivalves of Campanian age.

The material studied is deposited in the Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México. Types are included in the Type Collection and classified under the acronym IGM.

Systematic palaeontology

Order Decapoda Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Carcineretidae Beurlen, 1930
Genus Longusorbid Richards, 1975

Type species. Longusorbid cuniculosus Richards, 1975 by monotypy.

Longusorbid quadratus new species
Figures 3.1, 3.2, 4.1

Diagnosis. Relatively small Longusorbid, with quadratce carapace, ornamented margins and narrow urogastric region.

Description. Relatively small carapace, quadratce in outline, widest across the anterior third located at the outer orbital spines, weakly convex transversely and longitudinally. Rostrum medially sulcate and downturned, broadly rimmed and bicornate base. Wide orbits cut by two fissures, inner third concave, outer two-thirds first sinuous ending in a forwardly and outwardly directed, massive outer orbital spine. Including the outer orbital spine, the lateral margin is armed with 4 equally outwardly directed spines decreasing in size posteriorly. Regions are distinct and demarcated by furrows. The anterior process of the relatively small mesogastric region extends almost to the frontal, the distinct top fading into the downturned sulcus of the rostrum. The most prominent furrow is the cervical furrow extending sinu	ously from the base of the mesogastric lobe ending below the outer orbital spine defining the posterior margin of the swollen protogastric and hepatic regions. The forwardly-directed hepatic furrow separates the protogastric and hepatic regions. The width of the urogastric region is smaller than the maximum width of the mesogastric region. The broad shield shaped cardiac region is separated from the branchial regions by broad shallow furrows. The mesobranchial lobes bear three tubercles forming a triangle. The posterolateral margins are long and converging posteriorly, slightly concave at the probable point of attachment of the fifth pereiopods.


Measurements. Holotype IGM-8969 length ca. 5.0 mm, width ca. 5.0 mm. Paratype IGM-8970 length ca. 13.0 mm, width ca. 13.8 mm.

Etymology. Refers to carapace outline.

Remarks. This new species differs from L. cuniculosus in having a quadratce outline, a spinose poste-ror-lateral margin, a significantly narrower urogastric region and a more robust front.

This genus migrated at the end of the Cretaceous to the north where, in the late Campanian-early Maastrichtian, the closely related L. cuniculosus reaches up to 5 cm in carapace width (4 times larger than L. quadratus n. sp.) in the Shelter Point locality at Vancouver Island, Canada (Richards, 1975; Schweitzer et al. 2003).

An eastward migration has also to be taken in account considering the close evolutionary relationship with the genus Carcineretes known from the Maastrichtian of SE Mexico, Belize and Jamaica (Vega et al. 1997; 2001). Longusorbid and Carcineretes have
a very similar quadratic outline, bicornate and downturned rostrum, orbital incisions, carapace groove-arrangement and posterior margin morphology.

The genera *Withersella*, *Torynoma* and *Binkhorstia*, all belonging to the Torynommidae (van Bakel *et al.*, 2003), also have very similar to almost identical dorsal carapace morphologies as seen in the carcineretids. Distinction often can only be made on the ventral characters. Torynommidae differ only from the Carcineretidae in having a dorsally orientated, strongly reduced fourth and/or fifth pair of pereiopods, and being much smaller in overall size. Either the Carcineretidae and the Torynommidae are evolutionary very closely related or the dorsal similarities are a matter of convergence. In the first case the Torynommidae should also be placed in the Superfamily Portunoidea. To solve this matter more study and material is needed.

The carcineretids and torynommids, although relatively successful during the Cretaceous, finally didn’t cross the K/T boundary. It seems that they couldn’t cope with the thinner, more spinose and hexagonal carapaces (better swimming morphology) and much larger orbits (better predatory morphology) of the Late Cretaceous radiating genera like *Xanthosia* and *Cretachlorodius* (Fraaye, 1996).

Distribution of the two known species of *Longusorbis* is given in Figure 5.

Section Podotremata Guinot, 1977
Family Etyidae Guinot and Tavares, 2001
Genus *Xanthosia* Bell, 1863

Type species. *Xanthosia gibbosa* Bell, 1863 (= *Podophthalmus buchii* Reuss, 1845) by subsequent designation of Glaessner (1929).

*Xanthosia zoquiapensis* new species
Figures 3.3, 3.4, 4.2

Diagnosis. Very small etyid; carapace sub-hexagonal in outline, wider than long; anterolateral margin scalloped and posterior margin convex; front sulcate; orbits very large; orbitofrontal margin more than half total width; prominent sinuous cervical furrow, several branchial furrows.

Description. The carapace is subhexagonal in outline, almost flat longitudinally and gently inclined at the margins transversely, length about two-thirds the width. The frontal area is bilobed and slightly extended beyond the orbits; a deep median sulcus divides around the anterior part of the mesogastric process. The orbits are extremely large, elliptical and outward facing. The rimmed orbital margin bears two short notches. Orbitofrontal margin covers about 70% the total carapace width. The anterolateral margin is straight starting at the large, blunt outer orbital spine, and regularly divided by four notches. The widest part of the carapace is at the epibranchial angle. The posterolateral margin is clearly convex and indented by a relatively long, frontally directed mesobranchial notch. Carapace separated into distinct regions by shallow groove system. Cervical furrow strongly sinuous. Posterior margin concave, bordered with distinct ridge and about half the total carapace width.


Measurements. Holotype IGM-8971 length ca. 9.0 mm, width ca. 6.0 mm. Paratype IGM-8972 length ca. 9.0 mm, width ca. 7.0 mm.

Etymology. Named after Zoquiapa town, nearby locality IGM-3557.

Remarks. *Xanthosia zoquiapensis* n. sp. differs clearly from the American Gulf Coast Plain species (Schweitzer Hopkins *et al.*, 1999) in having a much wider orbitofrontal area, a strongly convex posterolateral margin and the absence of granular ornamentation. Concerning groove arrangement, orbit and margin morphologies, *X. zoquiapensis* n. sp. is most closely related to *X. buchi* (Reus, 1845) (Albian-Cenomanian), *X. socialis* Bakel, Fraaije & Jagt, 2005 (Campionian) and *X. semiornata* Jagt, Collins & Fraaye, 1991 (Maastrichtian) all known from NW Europe.

It differs from *X. buchi* and *X. socialis* in having a much more convex posterolateral margin and a shorter and interrupted mesobranchial furrow and from *X. semiornata* in lacking a strong anterior ornamentation. In addition, the new species is stockier than most species of *Xanthosia*.

Van Bakel *et al.* (2005) drew attention to a possible westward migration from the possible ancestor...
Fig. 3. 1, 2, *Longusorbis quadratus* new species. 1. Holotype IGM-8969. 2. Paratype IGM-8970. 3, 4, *Xanthosia zoquiapensis* new species. 3. Holotype IGM-8971. 4. Paratype IGM-8972. 5, 6, *Costacopluma bishopi* Vega and Feldmann. 5. Paratype IGM-8973. 6. Paratype IGM-8974. Scale bars equals 5.0 mm.

Fig. 4. 1. Reconstruction of *Longusorbis quadratus* new species. 2. Reconstruction of *Xanthosia zoquiapensis* new species. 3. Reconstruction of *Costacopluma bishopi* Vega and Feldmann.

Fig. 5. Coniacian–Paleocene paleobiogeographic distribution of brachyuran species of genera present in Temalac and Zoquiapa study areas, Guerrero. Base map modified from Barron, 1981; Dhondt, 1992 and Smith, 1994. Data based on: Collins and Morris, 1975; Richards, 1975; Vega and Perrilliat, 1989; Collins and Rasmussen, 1992; Collins et al., 1994; Feldmann and Matins-Neto, 1995; Vega et al., 1995; Feldmann et al., 1997; Schweitzer et al., 1999; Guinot and Tavares, 2001; Schweitzer et al., 2003; Nyborg et al., 2003; Araujo-Távora and Da Cruz-Miranda, 2004; van Bakel et al., 2005.
X. buchi towards the Campanian species from the American Western Interior and Atlantic Coastal Plain. The occurrence of X. zoquiapensis n. sp. in the Campanian of Mexico perfectly fits into this paleomigratory model. Figure 5 illustrates distribution of species of Xanthosia during the Late Cretaceous.

Superfamily Retroplumoidea Gill, 1894
Family Retroplumidae Gill, 1894
Genus Costacopluma Collins and Morris, 1975

Type species. Costacopluma concava Collins and Morris, 1975 by original designation.

Costacopluma bishopi Vega and Feldmann, 1992
Figures 3.5, 3.6, 4.3

Description. Carapace small, ovate in transverse section, widest at level of mesobranchial areas, with three prominent, rounded transverse ridges. Anterolateral margins straight, with a small spine at level of cervical groove; posterolateral margins rounded; posterior margin straight; anterior margin nearly straight, slightly concave above orbits, bordered by two prominent, forward directed spines. Orbits large, rounded. Rostrum prominent, bilobulate. Fused protogastric and mesogastric lobes form anterior transverse ridge, slightly inclined backwards in central part to ovate mesogastric lobe. Cervical groove deep, parallel to protogastric lobes, curved at level of mesobranchial lobes. Second ridge formed by fusion of epibranchial and mesobranchial lobes, of nearly uniform width, inclined posteriorly to base of mesogastric lobe where they become narrower. Posterior ridge formed by metabranchial lobes and cardiac/intestinal regions. Metabranchial lobes perpendicular to carapace length, half as long as epibranchial/mesobranchial lobes. Cardiac region subtrapezoidal, intestinal region narrow at base of cardiac region.

Material. Hypotypes IGM-8973 to IGM-8974.

Measurements. Hypotype IGM-8973 length ca. 6.5 mm, width ca. 7.5 mm. Hypotype IGM-8974 length ca. 6.3 mm, width ca. 9.0 mm.

Remarks. In documenting Costacopluma concava from the Upper Cretaceous of Nigeria, Collins and Morris (1975) mentioned presence of two paratypes from the Coniacian of the Awgu Limestone, Abakiliki Province. However, none of these paratypes is illustrated and although their morphology may resemble Costacopluma, it is not clear if these specimens do belong to this genus. Thus, C. bishopi is the first well-documented report for Costacopluma in Coniacian beds and may represent the oldest occurrence of a widely distributed genus during Late Cretaceous – Northeastern Mexico, Greenland, Nigeria, Northern India – (Collins and Morris, 1975; Gaetani et al., 1983; Vega and Perrilliat, 1989; Collins and Rasmussen, 1992; Vega and Feldmann, 1992;), and the Paleocene – California, Venezuela, Senegal, Brazil, Argentina – (Collins et al., 1994; Feldmann and Martins-Neto, 1995; Feldmann et al., 1995; 1997; De Araújo-Távora and Da Cruz-Miranda, 2004; Nyborg et al. 2003) (Fig. 5).

C. binodosa from the upper Campanian of Greenland was described by Collins and Rasmussen, 1992 on the basis of one incomplete specimen. It is larger than C. bishopi and bears straight lateral margins.

If the genus raised in America, it must have migrated eastwards to Africa, and northwards to Greenland. African retroplumids also migrated to the east, to reach the north part of India, and by Paleocene times, Costacopluma prevailed in the Paleocene seas of Senegal (Fig. 5). Although abundant in northeastern Mexico during Maastrichtian times, the genus vanished in this area by Paleocene times, and dispersed west to California and south to the north and central parts of South America (Fig. 5).

During Eocene times in Europe, Costacopluma may have given rise to the extant genus Retropluma Gill, 1894 (see Via, 1982), known from deep-water settings of the modern Indopacific sea (Saint Laurent, 1989).

Discussion

Vega and Feldmann (1992) described Costacopluma bishopi on the basis of eight carapaces. Because of the extremely small size (average width: 4.9 mm) of their material, these authors interpreted them as juveniles, yet, at the same time, they also noted overall carapace morphology to be closely similar to adults of the related taxa, Costacopluma mexicana
and *C. concava*. Comparing the mean carapace width of *C. bishopi* (ten specimens and four fragmentary carapaces known to date), with that of *C. mexicana* (numerous specimens known) and *C. concava* (four known specimens) yields ratios of 1:3.5 and ca. 1:4, respectively.

A comparison of average carapace width in *Longo-surbinus quadratus* n. sp. and *Xanthosia zoquiaper-sis* n. sp. with their closest relatives reveals a striking similarity; that of the former species (two specimens known) is approximately 3.5 times less than of *L. cuniculosus* (numerous specimens available) and that of the latter (two specimens at hand) equals around 30% of that of *X. buchi*, around 30% of that of *X. socialis* (a single specimen known) and around 25% of that of *X. semiornata* (six specimens).

The above-mentioned consistency in width ratios in all three species described, i.e. all being about 3.5 times smaller than their closest relatives, and overall adult carapace morphology (Fig. 6) suggests interpretation of this decapod assemblage as the first example of brachyuran dwarfism in the geological record. The environmental selection to favour this type of dwarfism in this tectonically active basin are still unknown, and further study is needed. Factors such as limited food supply, size-correlated predators and/or strong fluviatile input/admixture inducing brackish waters might be worthwhile pursuing in detail to understand the observed size abnormality.

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