



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE GEOLOGÍA

SISTEMÁTICA

ESTUDIO PALEOECOLÓGICO Y EVOLUTIVO DE LOS CRUSTÁCEOS DECÁPODOS

DEL CRETÁCICO TARDÍO/PALEÓGENO TEMPRANO EN EL NORESTE DE

MÉXICO

TESIS

(POR ARTÍCULO CIENTÍFICO)

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

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MÉXICO, CD. MX. SEPTIEMBRE, 2017



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Lic. Ivonne Ramirez Wence
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted, que el Subcomité de Biología Evolutiva y Sistemática, del Posgrado en Ciencias Biológicas, en su sesión ordinaria del día 24 de abril de 2017, aprobó el jurado para la presentación de su examen para obtener el grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** del alumno **MARTÍNEZ DÍAZ JOSÉ LUIS**, con número de cuenta **301054854**, con la tesis titulada **"ESTUDIO PALEOECOLÓGICO Y EVOLUTIVO DE LOS CRUSTÁCEOS DECÁPODOS DEL CRETÁCICO TARDÍO/PALEÓGENO TEMPRANO EN EL NORESTE DE MÉXICO."**, realizada bajo la dirección del DR. FRANCISCO JAVIER VEGA VERA:

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 04 de septiembre de 2017.


DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA



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1. RESUMEN

El género *Costacopluma* (Brachyura: Decapoda: Retroplumidae) tuvo una amplia distribución durante el Cretácico Tardío y Paleógeno Temprano, siendo representado hasta la fecha por catorce especies fósiles a través de este intervalo de tiempo. Las especies descritas para el Paleógeno Temprano son de una talla promedio menor en comparación con las poblaciones de especies de edad campaniana-maastrichtiana de África, Noreste de México y Sureste de los Estados Unidos. La especie *Costacopluma grayi* Feldmann and Portell, 2007, originalmente descrita para el Paleoceno y Eoceno de Alabama, ahora se documenta para el Maastrichtiano más superior (66.2 Ma) del Noreste de México y Misisipi, así como para el Paleoceno Inferior de Arkansas, todos ellos representando ejemplares de talla mediana. Las características morfológicas de los individuos de edad maastrichtiana tardía (66.2 Ma) son idénticas a las observadas entre las poblaciones de *C. grayi* del Paleógeno de Alabama y Arkansas, los cuales son de un tamaño promedio mucho menor. Esta reducción en talla, o enanismo en *C. grayi* a través del límite K/Pg es un ejemplo del efecto Liliput. El enanismo ha sido documentado en varios grupos de invertebrados como una respuesta al estrés ambiental, pero este es el primer registro del efecto Liliput en crustáceos braquiuros. El alcance geográfico y estratigráfico para *Costacopluma mexicana* Vega and Perrilliat, 1989, es extendido hasta el Campaniano Superior para el Noreste de México y hasta el Maastrichtiano Inferior para Misisipi, siendo también sugerido como un posible ancestro de *C. grayi*. Se discuten los diferentes tipos de preservación para esta especie en el Noreste de México.

3. ABSTRACT

The genus *Costacopluma* (Brachyura: Decapoda: Retroplumidae) had a wide distribution during the early Paleogene and is currently represented by 14 species across the Late Cretaceous and early Paleogene. Described early Paleogene species have a smaller mean body size compared to Campanian-Maastrichtian populations of Africa, northeastern Mexico, and southeastern United States. Originally described from the Paleocene and Eocene of Alabama, *Costacopluma grayi* Feldmann and Portell, 2007, is now documented from the uppermost Maastrichtian (66.2 Ma) of northeastern Mexico and Mississippi and Lower Paleocene of Arkansas, all representing medium size specimens. The morphological features of latest Maastrichtian (66.2 Ma) individuals are identical to those observed among populations of *C. grayi* from the Paleogene of Alabama and Arkansas, which have a smaller mean size. This size reduction, or dwarfism, in *C. grayi* across the K-Pg boundary is an example of the Lilliput effect. Dwarfism has been documented in several invertebrate groups as a response to environmental stress, but this is the first record of the Lilliput effect in brachyuran crustaceans. The stratigraphic and geographic range for *Costacopluma mexicana* Vega and Perrilliat, 1989, is extended to the upper Campanian in northeastern Mexico and lower Maastrichtian in Mississippi and is suggested as a possible ancestor of *C. grayi*. Different preservational modes for this species in northeastern Mexico are discussed.

4. INTRODUCCIÓN

La familia de cangrejos braquiuros Retroplumidae Gill, 1894, consiste principalmente de representantes fósiles, con la inclusión reciente de especies provenientes de África y Europa: *Loerenthopluma danielae* Van Bakel, Artal, Fraaije, y Jagt, 2010; *Gaudipluma bacamortensis* Artal et al., 2013; *Serrablopluma diminuta* Artal et al., 2013; *Retropluma slovenica* Gasparic y Hyžný, 2014, y *Costacopluma mamethioupami* Hyžný et al., 2015. Ésta diversidad es ejemplo de la abundancia relativa y la amplia distribución de los miembros de la familia Retroplumidae durante el Cretácico Tardío y Paleógeno Temprano. Los miembros existentes o actuales, representados por *Retropluma* Gill, 1894, y *Bathypluma* de Saint Laurent, 1989, se encuentran distribuidos en aguas relativamente profundas de la región del Indopacífico (Saint Laurent, 1989; McLay, 2006; Feldmann y Portell, 2007; Brösing, 2008).

El género *Costacopluma* Collins y Morris, 1975, erigido a partir de ejemplares de la especie *Costacopluma concava* Collins y Morris, 1975, es el más diverso y abundante retroplúmido fósil para el Cretácico Superior (Coniaciano?- Maastrichtiano) de Nigeria (Gaetani et al., 1983; Collins y Ward, 2010; Hyžný et al., 2015). *Costacopluma* tiene una amplia distribución geográfica y estratigráfica en los materiales del Cretácico Superior y Paleógeno Inferior, incluyendo 14 especies descritas (Tabla 1) (Feldmann y Portell, 2007; Ossó-Morales et al., 2010; Feldmann et al., 2014; Hyžný et al., 2015). *Costacopluma bishopi* Vega y Feldmann, 1992, representa el registro más antiguo de los Retroplumidae reportados para el Coniaciano de México (Vega y Feldmann, 1992; Fraaije et al., 2006). El alcance estratigráfico para las especies de *Costacopluma* de Norteamérica parte del Coniaciano hasta el Luteciano. Por otra parte, *Costacopluma* forma parte de varios géneros

de crustáceos decápodos (Schweitzer y Feldmann, 2005; Hyžný et al., 2015) que sobrevivieron al evento K/Pg. De hecho, el género parece haber experimentado un incremento en su distribución, diversidad, y abundancia relativa promedio posterior al evento K/Pg, aunque concomitante con un decremento en la talla corporal, posiblemente como resultado de una estrategia de recuperación.

En este trabajo se documentan nuevas ocurrencias geográficas y estratigráficas para *Costacopluma mexicana* Vega y Perrilliat, 1989, y *Costacopluma grayi* Feldmann y Portell, 2007, para el Sureste (SE) de Estados Unidos y Noreste (NE) de México. La reducción en la talla observada en *C. grayi* a través del límite K/Pg se interpreta como una posible respuesta al estrés ambiental.

4. 1. ÁREA DE ESTUDIO

Las localidades del Cretácico Superior y del Paleógeno que documentan los nuevos registros de *C. mexicana* y *C. grayi* en el NE de México y SE de Estados Unidos se ilustran en la Fig. 1. Este estudio reporta la primera ocurrencia para *C. mexicana* en estratos del Campaniano superior de la Formación Cerro del Pueblo, Coahuila, NE de México. Los ejemplares se encuentran preservados en el interior de concreciones y con restos de cutícula.

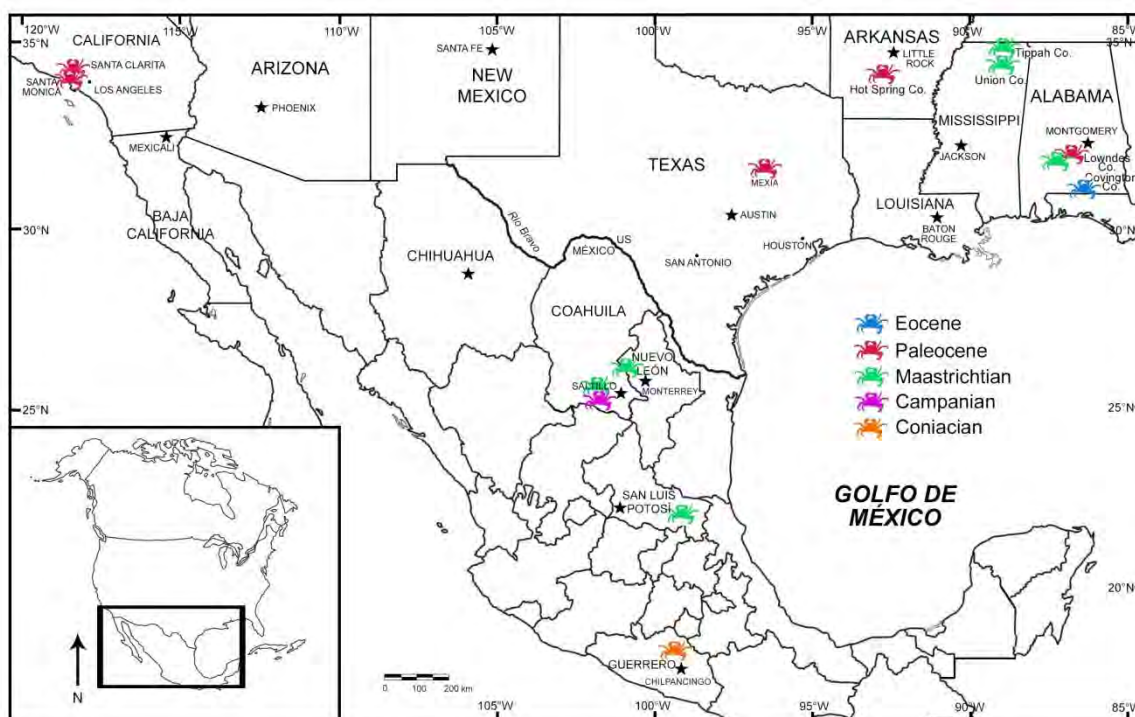


Fig. 1. Localidades del Cretácico Tardío (Coniaciano-Maastrichtiano más Tardío) y del Paleógeno (Daniano-Luteciano) en México y sureste de Estados Unidos donde se han recolectado las especies de *Costacopluma*.

C. mexicana fue originalmente descrita a partir de localidades y afloramientos del Miembro Inferior de limolita (Maastrichtiano inferior) de la Formación Potrerillos, en la Sierra el Antrisco (Cuenca de La Popa), Nuevo León, donde es particularmente abundante en la localidad IGM-1574 (Vega and Perrilliat, 1989), la cual se encuentra situada en el borde de una soldadura de un domo salino expuesto (Giles y Lawton, 1999). En este sitio todos los especímenes han sido reemplazados por hidroxiapatita, resultando una coloración negra brillante (Fig. 2.9, 2.13) con una preservación excepcional de la estructura cuticular (Vega et al., 1994, 2005). Una soldadura salina o “tapón” es una estructura producida por el proceso de diapirismo, el cual depende a la vez de una falla geológica, misma que provee la fuerza tectónica y permite la salida de sal (Mehran, 2012). Algunos minerales asociados a soldaduras como pueden ser apatita, fluyendo a través o alrededor de estas estructuras probablemente favorezcan este tipo de preservación. La acumulación de

materia orgánica en el relieve topográfico relacionado a la soldadura podría ser otra explicación.

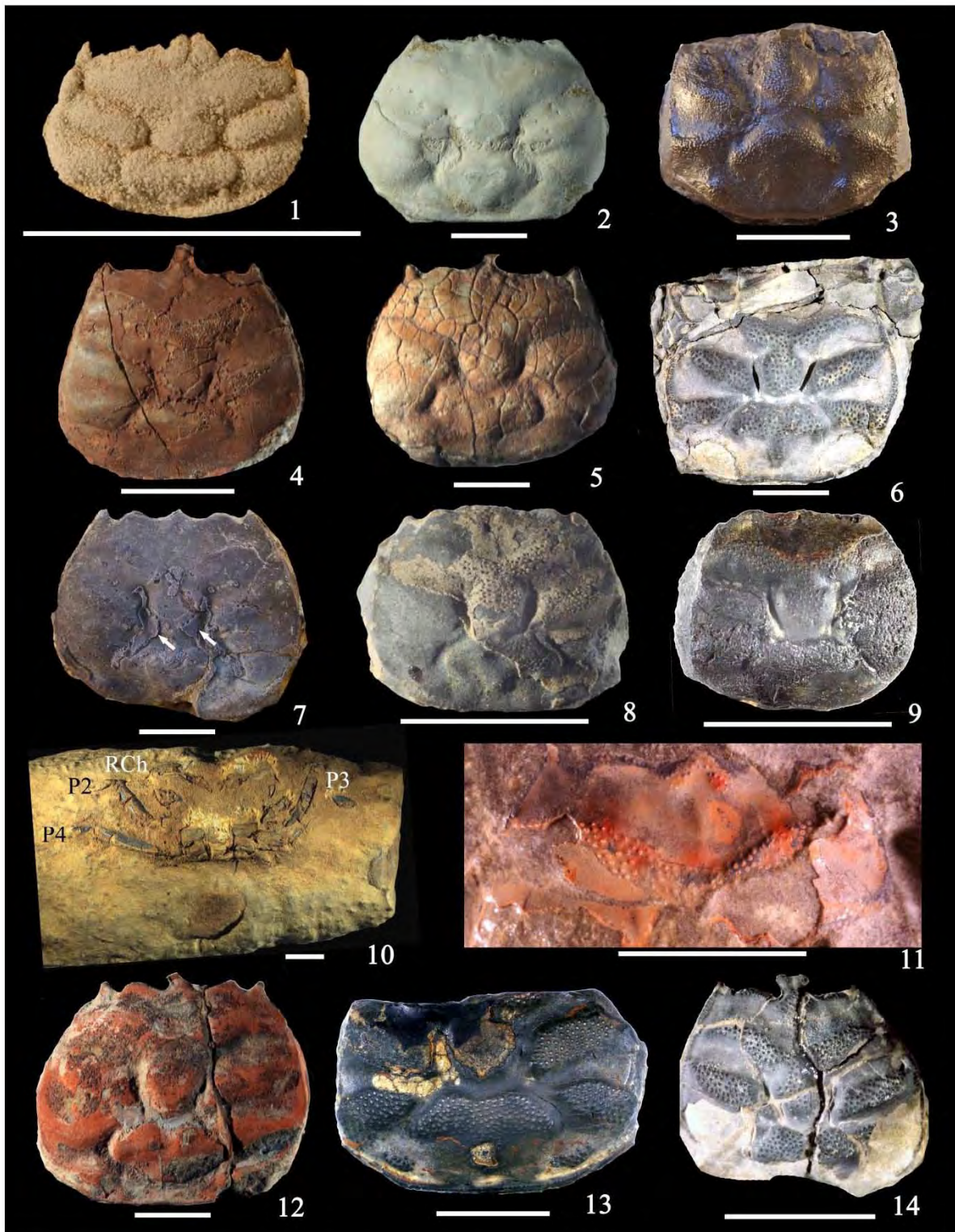


Fig. 2. Especies de *Costacopluma* y estilos de preservación de la cutícula en *C. mexicana*. 1, *Costacopluma bishopi* Vega y Feldmann, 1992, Formación Mexcala, Guerrero, Coniaciano, paratipo IGM-8974. 2, *C. maroccana* Ossó-Morales et al., 2010, Formación Calcaires à slumps de Taghit, Marruecos, Campaniano Superior, CPC-1716. 3, *C. binodosa* Collins y Rasmussen, 1992, Groenlandia, Campaniano Superior, duplicado de MGUH 21.615. 4-14, *C. mexicana* Vega y Perrilliat, 1989; 4, 5, Formación Cerro del Pueblo, Campaniano Superior, Ramos Arizpe, Coahuila, CPC-1693 y 1694. 6, Formación Potrerillos, Miembro Inferior de limolita, Maastrichtiano Inferior, El Antrisco, Nuevo León, paratipo IGM-4130; 7, Formación Ripley, Maastrichtiano Inferior-Superior, Mississippi, espécimen MMNS- 2949, las flechas señalan los restos de cutícula; 8, 9, especímenes juveniles, Formación Potrerillos, Miembro Inferior de limolita, Maastrichtiano Inferior, Paredón, Coahuila y El Antrisco, Nuevo León, CPC-1707 y espécimen perdido; 10, espécimen en una galería, Formación Potrerillos, Miembro Inferior de limolita, Maastrichtiano Inferior, Delgado, Nuevo León, CPC-1715; 11, 12, Formación Potrerillos Miembro Inferior de limolita, Maastrichtiano Inferior, Paredón, Coahuila, CPC-1709 y 1710, nótese el color rojo de la cutícula; 13, 14, caparazón incompleto fosfatizado y espécimen juvenil, Formación Potrerillos Miembro Inferior de limolita, Maastrichtiano Inferior, El Antrisco, Nuevo León, IGM-4131 y espécimen perdido. Escala = 10 mm.

Otra nueva localidad correspondiente al Miembro Inferior de limolita de la Formación Potrerillos ha sido identificado en otro afloramiento cercano a la Falla de San Marcos (ver McBride et al., 1974; Lawton et al., 2009) y próximo al poblado de Paredón, Coahuila. En esta localidad *C. mexicana* también es abundante y la mayoría de los especímenes poseen una particular coloración rojiza (Fig. 2.11 and 2.12), similar al color de la cutícula observado en especímenes de calianasoides del Cretácico Inferior de Japón que está asociados a filtraciones de metano (Karasawa, 2011). Se han identificado fragmentos del calianásido *Glypturus* del Mioceno Medio de Venezuela en ambientes de fisura de metano y quelas reportadas para el Oligoceno de Colombia (Kiel y Hansen, 2015) son parecidas al material estudiado por Karasawa. La influencia de termalismo asociada a la Falla de San Marcos pudo haber afectado la diagénesis y preservación de la cutícula, principalmente porque otros crustáceos de la misma localidad son similarmente rojos. Por otra parte, aquí se identifica a *C. mexicana* a partir de la Formación Cárdenas del Maastrichtiano Inferior de San Luis Potosí, centro-este de México, basada en un ejemplar previamente descrito como *C. bishopi* (Vega et al., 1995). Finalmente, un único caparazón de *C. mexicana* proveniente del Condado Union, Mississippi, fue recolectado del Miembro de arenisca Chiwapa de la Formación Ripley, de edad maastrichtiana tardía temprana. El ejemplar en

cuestión es un clasto retrabajado derivado casi con toda seguridad de capas maastrichtianas más antiguas, más probablemente del Miembro subyacente Coon Creek de la Formación Ripley, la cual es de una edad campaniana tardía y maastrichtiana temprana. *Costacopluma grayi* fue descrita primeramente a partir de materiales del Luteciano (Eoceno Medio) de la Formación Lisbon (sensu Clayton et al., 2013), Alabama (Feldmann y Portell, 2007), más tarde a partir de rocas del Daniano (Paleoceno Inferior) dentro de los estratos Pine Barren de la Formación Clayton, los cuales se ubican justo al norte (Feldmann et al., 2014). Recientemente la especie *C. grayi* fue descubierta en la facies típica (carbonatas) de la Formación Prairie Bluff del Maastrichtiano Superior, inmediatamente subyacente a su ocurrencia en los antes mencionados estratos Clayton del Daniano Inferior. Adicionalmente, se han encontrado caparazones retrabajados de *Costacopluma* provenientes de Prairie Bluff en la base de la Formación Clayton, pero estos son notablemente más grandes (y aún más meteorizados por el retrabajo) que los individuos encontrados más arriba en el Miembro Pine Barren, incluyendo el material reportado por Feldmann et al. (2014). En Misisipi, *C. grayi* se encuentra en las formaciones del Maastrichtiano Superior Owl Creek y Prairie Bluff, y en el lado oeste de la Bahía del Misisipi, la especie es encontrada de nuevo en la Formación Clayton de edad daniana.

Las lodolitas del Maastrichtiano mas Superior (66.2 Ma) de la Formación Las Encinas incluyen *C. grayi* en la sección Amargos en Coahuila, NE México (Fig. 1), donde se han encontrado esférulas de impacto retrabajadas a pocos metros estratigráficamente por encima de la capa que contiene los cangrejos fósiles (Vega et al., 2013).

5. ARTÍCULO

A continuación se anexa el sobretiro del artículo científico ya publicado.



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Lilliput effect in a retroplumid crab (Crustacea: Decapoda) across the K/Pg boundary

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ABSTRACT

The genus *Costacopluma* (Brachyura: Decapoda: Retroplumidae) had a wide distribution during the early Paleogene and is currently represented by 14 species across the Late Cretaceous and early Paleogene. Described early Paleogene species have a smaller mean body size compared to Campanian–Maastrichtian populations of Africa, northeastern Mexico, and southeastern United States. Originally described from the Paleocene and Eocene of Alabama, *Costacopluma grayi* Feldmann and Portell, 2007, is now documented from the uppermost Maastrichtian (66.2 Ma) of northeastern Mexico and Mississippi and Lower Paleocene of Arkansas, all representing medium size specimens. The morphological features of latest Maastrichtian (66.2 Ma) individuals are identical to those observed among populations of *C. grayi* from the Paleogene of Alabama and Arkansas, which have a smaller mean size. This size reduction, or dwarfism, in *C. grayi* across the K–Pg boundary is an example of the Lilliput effect. Dwarfism has been documented in several invertebrate groups as a response to environmental stress, but this is the first record of the Lilliput effect in brachyuran crustaceans. The stratigraphic and geographic range for *Costacopluma mexicana* Vega and Perrillat, 1989, is extended to the upper Campanian in northeastern Mexico and lower Maastrichtian in Mississippi and is suggested as a possible ancestor of *C. grayi*. Different preservational modes for this species in northeastern Mexico are discussed.

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1. Introduction

The brachyuran family Retroplumidae Gill, 1894, consists mainly of fossil representatives, with the recent inclusion of species from Africa and Europe: *Loerenthopluma danielae* Van Bakel, Artal, Fraaije, and Jagt, 2010; *Gaudipluma bacamortensis* Artal et al., 2013; *Serrablopluma diminuta* Artal et al., 2013; *Retropluma slovenica* Gasparić and Hyžný, 2014 and *Costacopluma mamethioupami* Hyžný et al., 2015. This diversity is an example of the relative abundance and widespread distribution of members of the Retroplumidae during the Late Cretaceous and early Paleogene. The

extant members, represented by *Retropluma* Gill, 1894, and *Bathypluma* de Saint Laurent, 1989, are distributed in relatively deep waters of the Indo-Pacific region (de Saint Laurent, 1989; McLay, 2006; Feldmann and Portell, 2007; Brösing, 2008). The genus *Costacopluma* Collins and Morris, 1975, erected from specimens of *Costacopluma concava* Collins and Morris, 1975, is the most diverse and abundant fossil retroplumid from the Upper Cretaceous (Coniacian? to Maastrichtian) of Nigeria (Gaecani et al., 1983; Collins and Ward, 2010; Hyžný et al., 2015). *Costacopluma* has a wide geographic and stratigraphic distribution within the Upper Cretaceous and Lower Paleogene sediments, including 11 described species (Table 1) (Feldmann and Portell, 2007; Ossó-Morales et al., 2010; Feldmann et al., 2014; Hyžný et al., 2015). *Costacopluma bishopi* Vega and Feldmann, 1992, represents the oldest record of

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Table 1

Size range and ridge breadth *Costacopluma* species types. Degrees of relative abundance are indicated by "A" for abundant (40–55 specimens), "S" for scarce (2–10 specimens) and "U" for unique. L = length; W = Width; crabs are for small and medium body size populations; vertical arrows indicate broad or narrow carapace ridges. Measurements in mm. *Small size observed in the single specimen of *C. inodosa* from Campanian shouldn't be seen as a mirror of its body size population, e.g. the type specimen of *C. mexicana* is small in size, but the most of referred material is medium in size.

Taxa	Reference	Locality	Age	Catalog number	Relative abundance	L	W	Size	Ridges
<i>C. bishopi</i>	Vega and Feldman, 1992	SE Mexico	Coniacian	IGM 5225	S	3.70	4.70		↕
<i>C. marocana</i>	Dissó-Morales et al., 2010	Morocco	Campanian	MGSB 74544	S	19.0	23.0		↕
<i>C. inodosa</i> *	Collins and Barmissen, 1992	Greenland	Campanian	MGUH 21 515	U	—	16.6		↕
<i>C. macrasi</i>	Collins & Morels, 1975	Nigeria–India	Camp-7Maas	NIHMIB In. 44642	A	25.6	44.7		↕
<i>C. mexicana</i>	Vega and Perilliati, 1989	NE Mexico-SE USA	Camp-Maas	IGM 4128	A	14.7	17.6		↕
<i>C. mamothoupani</i>	Hyzný et al., 2015	Senegal	Lt Maas	SENCN 053	U	8.80	9.50		↕
<i>C. grayi</i>	Feldman and Portell, 2007	SE USA (AL, Ark.)	Paleogene	UH 113/49	A	8.40	9.40		↕
		SE USA (AL, Miss.)-NE Mexico	Lt Maas	MMNS 6521	A	23.0	25.5		↕
<i>C. senegaensis</i>	Gorodiski and Rémy, 1959	Senegal	Paleocene	MNHNF R09785	U	6.70	9.53		↕
<i>C. bifida</i>	Collins et al., 1994	Venezuela	Paleocene	MBLUZ P 1242	U	3.80	7.90		↕
<i>C. australis</i>	Feldmann et al., 1995	Argentina	Paleocene	GHUNLPam 7001	S	13.0	15.0		↕
<i>C. sulanica</i>	Feldmann et al., 1997	Argentina	Paleocene	CPBA 17376	S	14.8	17.3		↕
<i>C. nordesina</i>	Feldman and Martinez Neto, 1995	Brazil	Paleocene	MN 8005	A	14.5	15.7		↕
<i>C. squarsi</i>	Nyborg et al., 2005	California	Paleocene	LAQMIP 13560	S	11.2	11.5		↕
<i>C. texana</i>	Armstrong et al., 2009	Texas	Paleocene	NPL 311/2	A	9.70	10.1		↕

retroplumids reported from the Coniacian of Mexico (Vega and Feldmann, 1992; Fraaije et al., 2006). *Costacopluma* species from North America range from Coniacian to Lutetian (Fig. 1).

Costacopluma is among several decapod genera (Schweitzer and Feldmann, 2005; Hyzný et al., 2015) that survived the K/Pg event. In fact, the genus seems to have experienced an increase in distribution, diversity, and overall abundance post-K/Pg, although concomitant with a decrease in body size, possibly as a result of a recovery strategy.

The purpose of this contribution is to document new geographic and stratigraphic occurrences of *Costacopluma mexicana* Vega and Perilliati, 1989, and *Costacopluma grayi* Feldmann and Portell, 2007, from the southeastern (SE) United States and northeastern (NE) Mexico and present an interpretation for the size reduction of the latter across the K/Pg boundary as a possible response to environmental stress. Tables 1–3 summarize information on the known species of *Costacopluma*, from the Coniacian to the Lutetian

as detailed below.

2. Study localities

Upper Cretaceous and Paleogene localities documenting new occurrences of *C. mexicana* and *C. grayi* in NE Mexico and SE United States are illustrated in Figs. 1 and 2. This study reports the first occurrence for *C. mexicana* from upper Campanian strata in the Cerro del Pueblo Formation, Coahuila, NE Mexico. The specimens are preserved in weathered concretions with traces of cuticle. Originally described from localities on outcrops of the Lower Siltstone Member (lower Maastrichtian) of the Potrerillos Formation, in Sierra El Antrisco (La Popa Basin), Nuevo León, *C. mexicana* is particularly abundant at locality IGM-1574 (Vega and Perilliati, 1989), where it is situated on the edge of an exhumed salt weld (Giles and Lawton, 1999). Here, all specimens have been replaced by hydroxyapatite, resulting in a shiny, black color appearance

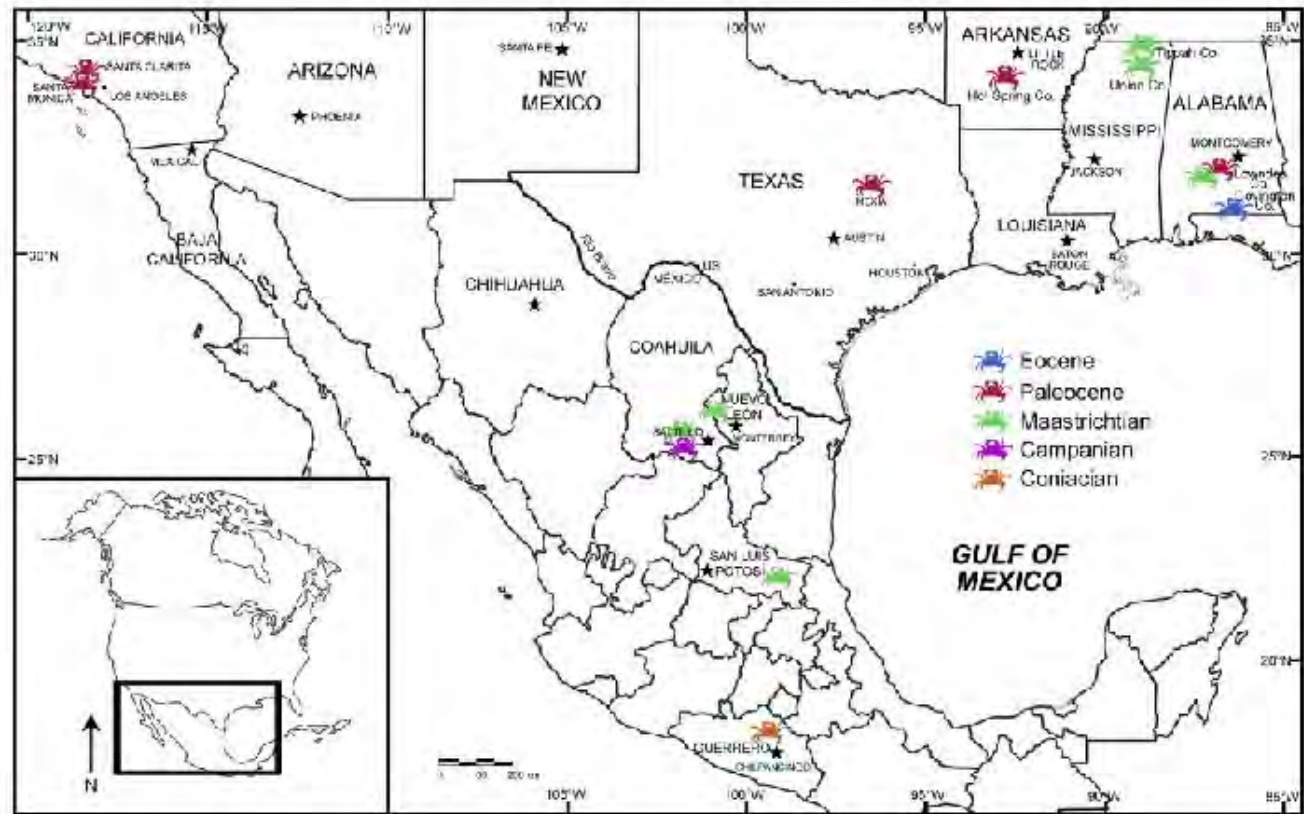


Fig. 1. Late Cretaceous (Coniacian-latest Maastrichtian) and Paleogene (Danian–Lutetian) *Costacopluma* spp. localities in Mexico and southern United States.

Table 2

Measurements (mm) for Late Campanian–Lower Maastrichtian *Costacopluma mexicana* specimens from NE Mexico and SE USA.

System/Series	Stage	Formation, locality		Catalog number	L	W	L/W		
Upper Cretaceous	Lower Maastrichtian	Fotrerillos Fm. Nuevo León and Coahuila, MX	Paredón	CPC-1707	6.40	7.20	0.88		
				CPC-1708	21.1	27.7	0.74		
				CPC-1710	20.3	25.2	0.80		
				CPC-1711	15.0	18.9	0.79		
				CPC-1713	17.5	24.1	0.72		
			CPC-1714	22.6	32.2	0.70			
			El Antirisco	CPC-1726	12.0	13.8	0.18		
				CPC-1715	15.4	20.8	0.54		
			Lower Maastrichtian Upper Campanian	Kipley Fm. Union Co. Miss., US Cerro del Pueblo Fm. Coahuila, MX.	Ramos Arizpe	CPC-1727	8.80	18.7	0.79
						MMNS 2949	25.0	30.0	0.83
	CPC-1692	14.3				15.6	0.85		
	CPC-1693	13.9				17.9	0.40		
	CPC-1694	19.7				24.0	0.43		
	CPC-1695	17.6			22.3	0.47			
	CPC-1696	16.6			21.3	0.47			
	CPC-1697	17.6			22.3	0.51			
	CPC-1698	18.0			21.7	0.82			
	CPC-1700	16.9			20.9	0.80			
	CPC-1701	14.3	19.5	0.52					
	CPC-1702	18.6	23.3	0.47					
CPC-1703	19.3	25.5	0.62						
CPC-1704	20.0	23.9	0.48						
CPC-1705	18.6	25.1	0.67						
CPC-1706	20.2	25.1	0.80						
Mean (*juvenile excluded)				17.6	22.5	0.67			

(Fig. 3.9, 3.13) with an exceptional preservation of the cuticular structure (Vega et al., 1994, 2005). A salt weld or “plug” is a structure produced by diapirism process, which depends in turn of a geologic fault that provide tectonic force and enables the salt uplifting (Mehran, 2012). Associated minerals with salt plugs as can

be a patite flowing through or around the salt weld probably lead to this kind of preservation. Organic matter accumulation in a topographic relief related to the salt weld topography could be another explanation. In an outcrop near the San Marcos Fault (see McBride et al., 1974; Lawton et al., 2009) and close to the town of Paredón,

Table 3
Measurements (mm) for Late Cretaceous–Early Paleogene *Costacoptima grayi* specimens from NE Mexico and SE USA.

<i>C. grayi</i>								
System/Series	Stage	Formation, locality	Catalog number	L	W	L/W		
Middle Eocene	Lutetian	Lisbon Fm. Covington Co. Alabama, US	UF 113749	8.40	9.40	0.89		
			UF 113750	13.7	13.8	0.99		
			MMNS 6491-1	6.20	10.6	0.58		
			MMNS 6491-2	7.50	11.2	0.66		
			MMNS 6491-3	5.50	7.70	0.71		
			MMNS 6492	5.00	7.60	0.65		
			MMNS 6478	7.50	10.5	0.71		
			MMNS 6479	6.20	9.00	0.68		
			MMNS 6481	7.90	11.0	0.71		
			MMNS 5672	12.7	16.8	0.75		
			MMNS 5673	6.00	8.50	0.70		
			MMNS 5674-12	5.60	9.50	0.58		
			MMNS 5737	5.50	9.70	0.56		
			MMNS 6319	9.00	13.6	0.66		
Lower Paleocene	Lower Danian	Clayton Fm. Lowndes Co. Alabama, US	MMNS 6483	4.30	6.90	0.62		
			MMNS 6485	6.90	10.9	0.63		
			MMNS 6487	4.50	6.00	0.75		
			MMNS 5942	7.30	10.4	0.70		
			MMNS 6482	5.70	9.50	0.60		
			MMNS 5674	5.60	9.50	0.58		
			MMNS 5737	5.50	9.70	0.56		
			MMNS 6319	9.00	13.6	0.66		
			MMNS 6483	4.30	6.90	0.62		
			MMNS 6485	6.90	10.9	0.63		
			MMNS 6487	4.50	6.00	0.75		
			MMNS 5942	7.30	10.4	0.70		
			MMNS 6482	5.70	9.50	0.60		
			Mean			7.17	10.1	0.69
K-Pg Boundary Upper Cretaceous	Upper Maastrichtian	Las Encinas Fm. Coahuila, MX	CPC 1717	20.7	31.2	0.66		
			CPC 1718	21.5	31.9	0.69		
			CPC 1720	15.4	23.9	0.64		
			CPC 1721	25.3	36.5	0.69		
			CPC 1722	23.9	35.3	0.67		
			CPC 1723	22.0	30.1	0.73		
			CPC 1724	21.0	29.5	0.71		
			MMNS 6519	21.8	35.8	0.60		
			MMNS 7435	17.9	24.3	0.73		
			MMNS 7436	21.9	30.0	0.73		
			MMNS 7437	19.6	27.4	0.71		
			MMNS 7438	22.0	29.9	0.73		
			MMNS 7439	19.4	26.0	0.74		
			MMNS 7440	16.2	21.7	0.74		
			MMNS 7441	16.5	21.5	0.76		
			MMNS 7442	18.3	25.8	0.70		
		MMNS 7443	19.1	25.1	0.76			
		MMNS 7445	19.3	25.2	0.76			
		MMNS 7447	20.5	27.0	0.75			
		MMNS 7448	16.6	21.4	0.77			
		MMNS 7449	13.4	17.4	0.77			
		USNM 215705	21.1	30.7	0.68			
		MMNS 5259-1	20.0	30.5	0.65			
		Mean			19.8	27.3	0.71	
			Lower Maastrichtian	Prairie Bluff Fm. Union Co. Miss., US	USNM 215705	21.1	30.7	0.68
					MMNS 5259-1	20.0	30.5	0.65

Coahuila, a new locality of the Lower Siltstone Member of the Potrerillos Formation is identified. At this location *C. mexicana* is also abundant and most specimens have a peculiar red color (Fig. 3.11 and 3.12), similar to the cuticle color observed in callianassoid specimens from the Lower Cretaceous of Japan that are associated with a cold-seep (Karasawa, 2011). Fragments of the callianassid *Glypturus* from the Middle Miocene of Venezuela have been identified in methane-seep environments and claws reported from the Oligocene of Colombia (Kiel and Hansen, 2015) resemble the material studied by Karasawa. Influence of thermal fluids linked with the San Marcos Fault may have affected the diagenesis and preservation of the crustacean cuticle, especially since other crustaceans from the same locality are similarly red. Moreover, *C. mexicana* is identified herein from the lower Maastrichtian Cárdenas Formation, San Luis Potosí, East-Central México, based on a specimen previously described as *C. bishopi* (Vega et al., 1995).

Lastly, a single carapace of *C. mexicana* from Union County, Mississippi, was recovered from the Chiwapa Sandstone Member of the Ripley Formation, which is early late Maastrichtian in age. The specimen in question is a reworked clast almost certainly derived

from older Maastrichtian beds, most likely the immediately subjacent Coon Creek Member of the Ripley Formation, which dates to the late Campanian and early Maastrichtian.

C. grayi was first described from Lutetian (Middle Eocene) beds of the Lisbon Formation (sensu Clayton et al., 2013), Alabama (Feldmann and Fortell, 2007), then later from Danian (Lower Paleocene) clays within the Pine Barren beds of the Clayton Formation, which lie just to the north (Feldmann et al., 2014). Recently, the species *C. grayi* was discovered in the typical ('chalk') facies of the upper Maastrichtian Prairie Bluff Formation, immediately subjacent to its occurrence in the aforementioned lower Danian Clayton beds. Additionally, reworked Prairie Bluff *Costacoptima* carapaces have been found in the base of the Clayton Formation, but these are notably larger (and more eroded from reworking) than the individuals found higher in the Pine Barren Member, including the material reported by Feldmann et al. (2014). In Mississippi, *C. grayi* occurs in the upper Maastrichtian Owl Creek and Prairie Bluff formations, and, on the west side of the Mississippi Embayment, the species is found again in the Danian Clayton Formation. Uppermost Maastrichtian (66.2 Ma) mudstones of the Las

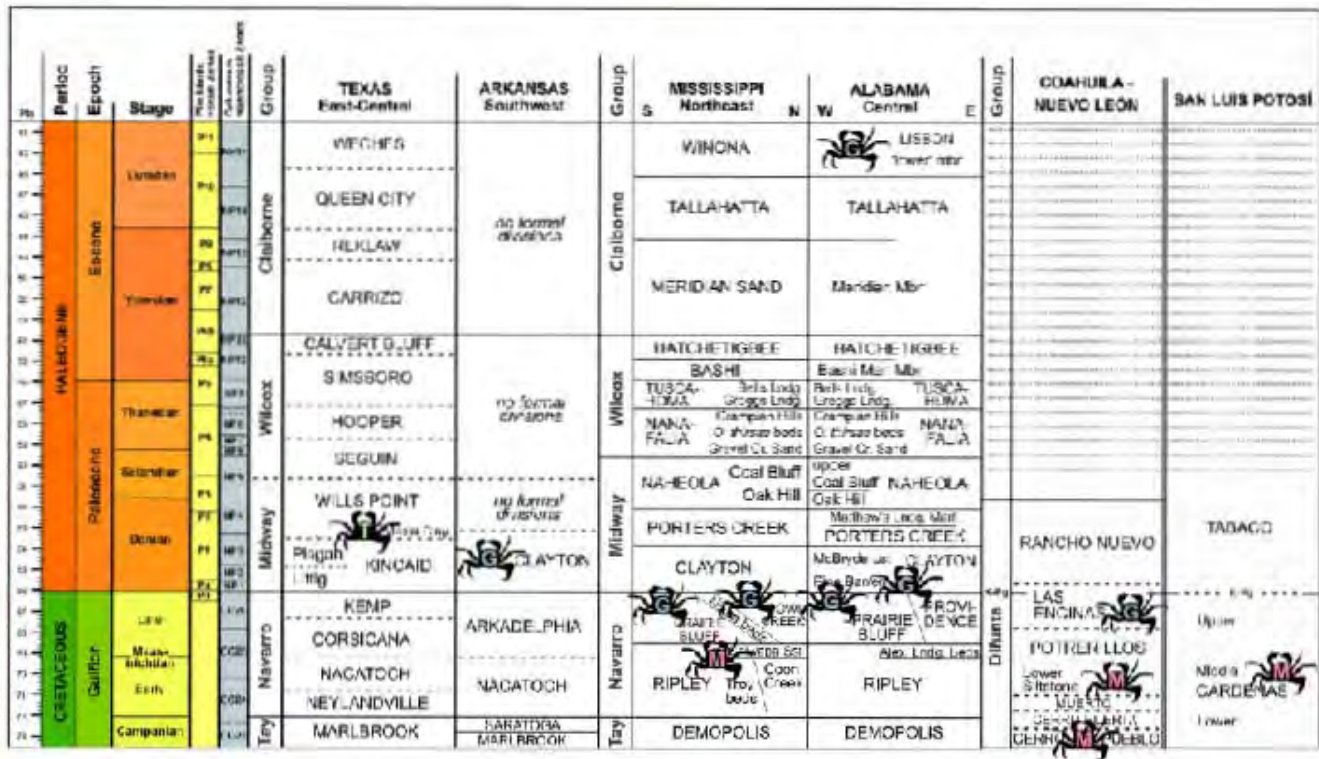


Fig. 2. Late Cretaceous and early Paleogene correlation chart for the Gulf Coastal Plain. The temporal intervals (absolute and named) and the accompanying synchronized planktonic forams and calcareous nannoplankton zones were generated using Time Scale Creator 6.4, which is based on Gradstein et al. (2012). Texas–Arkansas groups and unit boundaries are synchronized to biochronozones (primarily nannoplankton; secondarily planktonic forams) based on Peisango (1969), Oldani (1988), Davidoff and Yancey (1993), Lawless et al. (1997), Dockrey (1998), Schulte et al. (2006), and Garvie (2013). Mississippi–Alabama groups and unit boundaries are synchronized to biochronozones based on Mancini and Tew (1991, 1995), Mancini et al. (1995), Dockrey (1998) and Sosa et al. (2015). Temporal and unit correlations for northeastern Mexico are based largely on the reviews of Lawton et al. (2009) and Heim et al. (2010). Formations are in capitals and member units in lower case. Crab icons indicate stratigraphic and geographic distribution of species of *Costacopluma*: *C. texana* (T), *C. grayi* (G), and *C. mexicana* (M). Gt = Group.

Encinas Formation include *C. grayi* at the Amargos section in Coahuila, NE Mexico (Fig. 1), where reworked impact ejecta are found a few meters stratigraphically above the bed that contains fossil crabs (Vega et al., 2013).

3. Cretaceous species of *Costacopluma*

C. bishopi Vega and Feldmann, 1992 (Fig. 3.1), was described from the Conician of the Mexcala Formation, Guerrero, southern Mexico. The type specimens of *C. bishopi* were at first interpreted as juveniles due to their small size (Vega and Feldmann, 1992). Later, Fraaije et al. (2006) interpreted this as dwarfism for *C. bishopi* as well as associated specimens of similarly small *Longisorbis* Richards, 1975, found at the same locality. According to Fraaije et al. (2006), the dwarfism may have been triggered by a number of different factors, such as scarcity of food, size-related predation, and/or strong influence of brackish water conditions.

Costacopluma marroccana Ossó-Morales et al., 2010 (Fig. 3.2) from the upper Campanian of Morocco has a medium-sized carapace with smooth cuticle (fine granules can be observed on crests in some specimens) and relatively narrow dorsal ridges. Although this species was described based on only four specimens, informal reports suggest it to be locally very abundant (Table 1 for abundances ranges).

Costacopluma binodosa Collins and Rasmussen, 1992 (Fig. 3.3), from the upper Campanian of Greenland is represented by an incomplete, medium sized carapace, whose dorsal regions exhibit relatively fine granulations.

C. concava Collins and Morris, 1975, was reported from the upper Campanian–?Maastrichtian of Nigeria and the upper Maastrichtian of India (Gaetani et al., 1983), but this report may be of an specimen from lower Paleocene sediments, similar to *C. grayi* (see below). *C. concava* is characterized by an ovate, medium-sized carapace with very narrow, granulose dorsal crests. Additional collections increased the sample to 42 specimens (see also Collins and Ward, 2010).

C. mexicana Vega and Pernilia, 1988 (Fig. 3.4–3.11), represented by abundant carapaces and fragments, was originally described from the lower Maastrichtian Lower Siltstone Member of the Potrerillos Formation in Nuevo León (NE Mexico) and is here reported from the upper Campanian Cerro del Pueblo Formation in Coahuila (NE Mexico) (Fig. 3.4 and 3.5), extending the temporal range for the species. Unconfirmed reports indicate that the species is also found in the upper Maastrichtian (66.8 Ma) Cerro Grande Formation (J. Flores-Ventura, pers. comm., 2015). *C. mexicana* is characterized by its medium size and strong tuberculate dorsal crests. *C. bishopi* from the lower Maastrichtian Cardenas Formation of San Luis Potosí (eastern Mexico) (Fig. 1) is a singular specimen lacking cuticle that possesses a dorsal region identical to *C. mexicana* (Vega et al., 1995). Another single occurrence of *C. mexicana* from the lower Maastrichtian Ripley Formation in Mississippi is also documented as new for the United States (Fig. 3.7). Juvenile specimens of *C. mexicana* (Fig. 3.8 and 3.9) (see also Vega and Feldmann, 1992, Fig. 6) indicate that adult carapace features are present in early stages. Different preservational modes are observed in *C. mexicana* from NE Mexico including one specimen

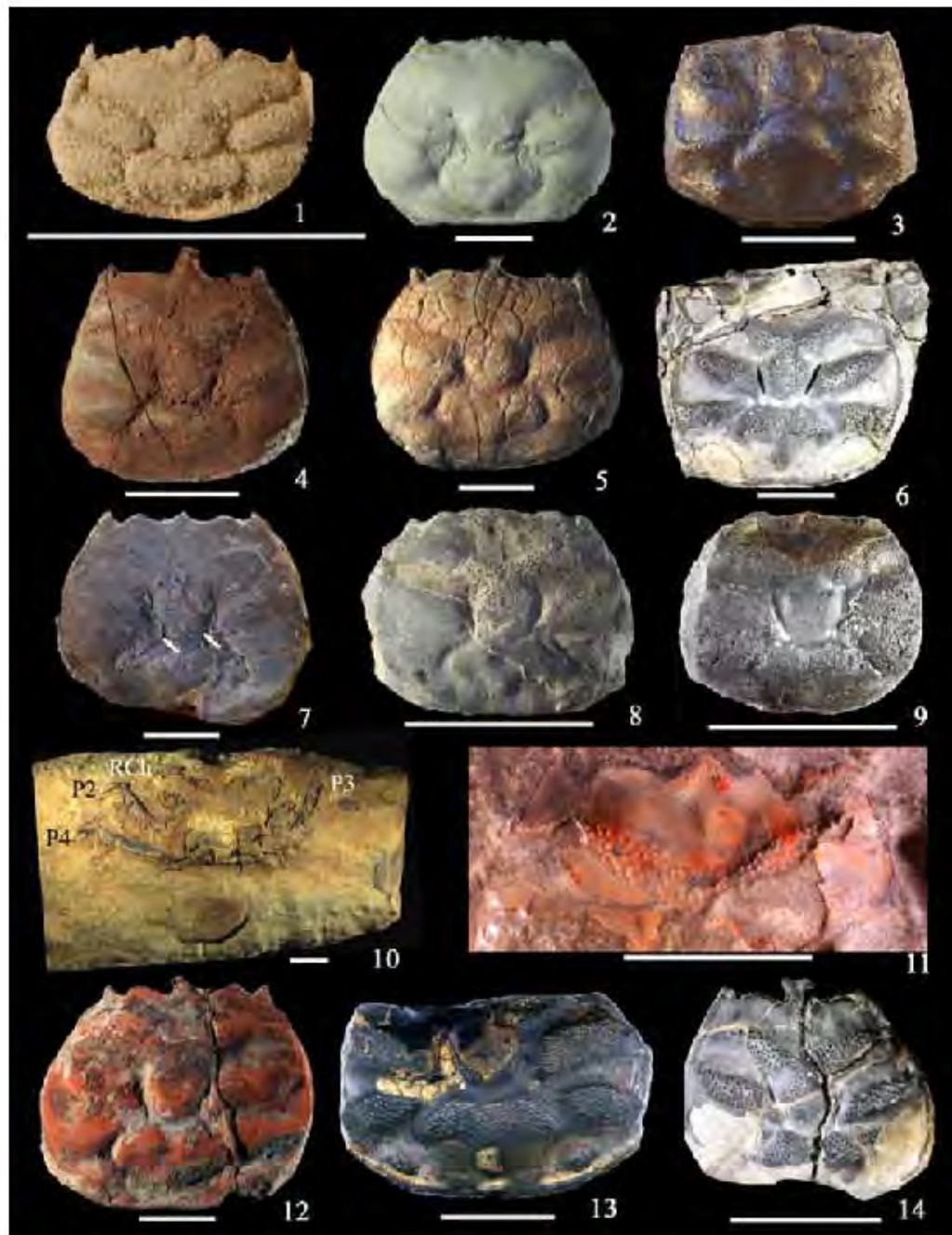


Fig. 3. 1. *Cosmocopluma bohapi* Vega and Feldmann, 1992, Coniacian, Mexcala Formation, Guerrero, paratype IGM-8974; 2. *C. murucanu* Ossó-Morales et al., 2010, upper Campanian, Calcaires à slumps de Taghit Formation, Morocco, CPC-1715; 3. *C. binodosa* Collins and Rasmussen, 1992, upper Campanian, Greenland, cast of MGH 21.615; 4–14. *C. mexicana* Vega and Perrillat, 1989; 4, 5, upper Campanian Cerro del Pueblo Formation, Ramos Arizpe County, Coahuila, CPC-1693 and 1694; 6, lower Maastrichtian Lower Siltstone Member, Potrerillos Formation, El Antrisco, Nuevo Leon, paratype IGM-4130; 7, lower-upper Maastrichtian Ripley formation, Mississippi, specimen MMNS-2949, note arrows point to the circle remains; 8, 9, juvenile specimens, lower Maastrichtian Lower Siltstone Member, Potrerillos Formation, Paredón, Coahuila and El Antrisco, Nuevo León, CPC-1707 and lost specimen; 10, specimen in a burrow, lower Maastrichtian lower Siltstone Member, Potrerillos Formation, Delgado, Nuevo Leon, CPC-1710; 11, 12, lower Maastrichtian Lower Siltstone Member, Potrerillos Formation, Paredón, Coahuila, CPC-1709 and 1710, note red color of cuticle; 13, 14, phosphatized incomplete carapace and juvenile specimen, lower Maastrichtian Lower Siltstone Member, Potrerillos Formation, El Antrisco, Nuevo Leon, lost specimen and IGM-4131. Scale bars = 10 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

found inside a burrow showing articulated appendages (Fig. 3.10). However, since this kind of preservation is the exception and not the rule, we cannot confirm that *C. mexicana* used burrows for protection.

C. mammothipanni Hyžný et al., 2015, from the mid to upper

Maastrichtian of Senegal is the latest species described for *Cosmocopluma*, represented by a single small-sized incomplete carapace that possesses sharp granulate dorsal crests.

C. grayi, Feldmann and Portell, 2007, described from the Paleogene of Alabama, is here reported from the uppermost

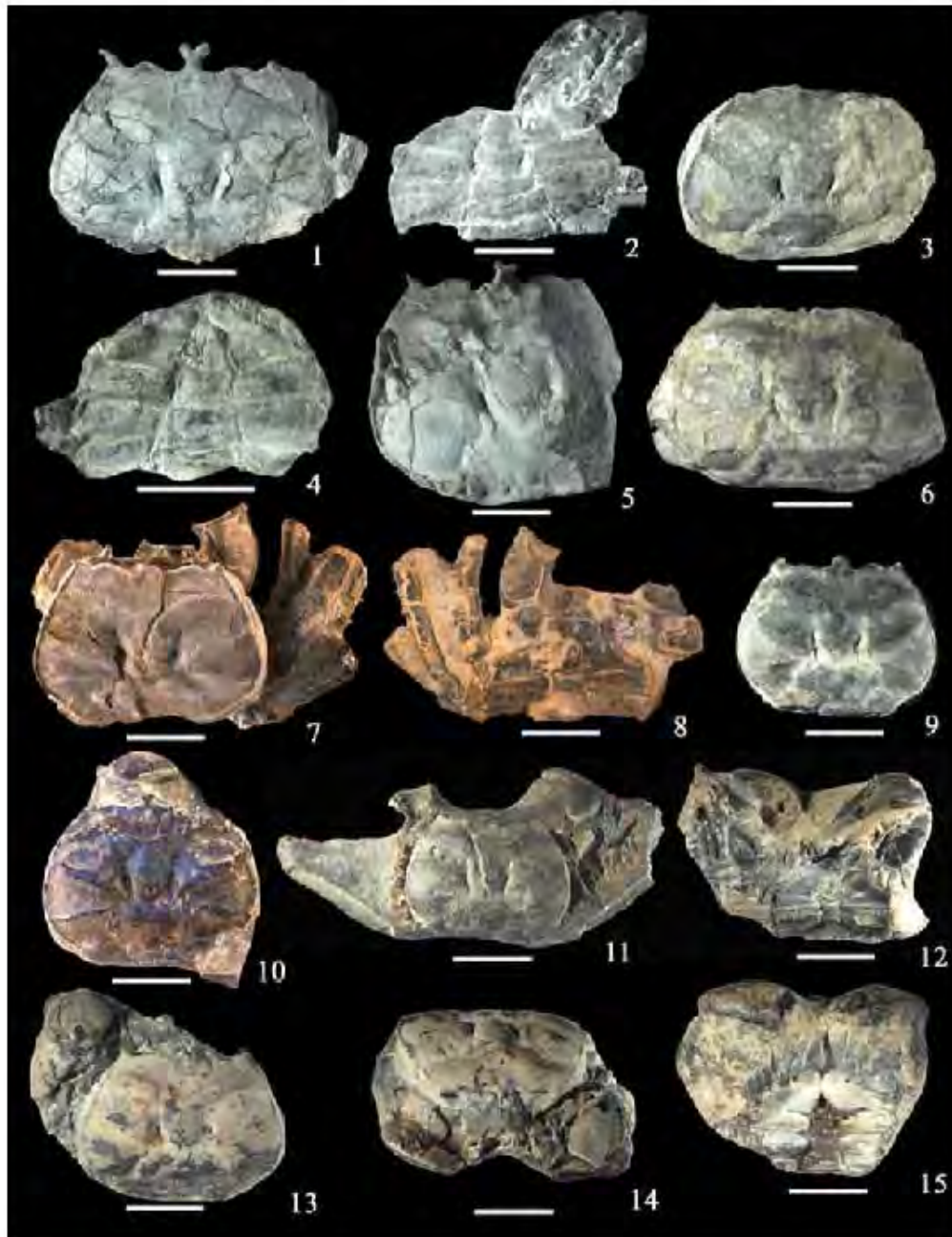


Fig. 4. *Costacopluma grayi* Feldmann and Portell, 2007; 1–6, uppermost Maastrichtian Las Encinas Formation, Arroyo Amargos, Coahuila; 1, 2, dorsal and ventral views, note sharp left chela. CPC-1717; 3, 4, dorsal and ventral views. CPC-1715; 5, 6, dorsal views, CPC-1719 and 1720. 7–15, uppermost Maastrichtian Owl Creek Formation, Tippah County, Mississippi; 7, 8, dorsal and ventral views, USNM-215705; 9, 10, dorsal views. MMNS-7435 and 6519; 11, 12, dorsal and ventral views, MMNS-7436 and 7437; 13–15, dorsal, front and ventral views of carapace, MMNS-7437. Scale bars = 10 mm.

Maastrichtian of NE Mexico (Las Encinas Formation), Mississippi (Owl Creek Formation), and Alabama (Prairie Bluff Formation) with an approximate age of 66.2 Ma (Phillips et al., 2013; Vega et al., 2013). The material encompasses 21 carapaces of medium size exhibiting narrow and finely granulated crests (Fig. 4).

4. Paleogene species of *Costacopluma*

The first reported Paleogene species of *Costacopluma* was *C.*

senegalensis (Remy in Gorodiski and Remy, 1959) (Fig. 5.11), represented by a unique specimen possessing finely granulated, sharp ridges.

Costacopluma bifida Collins et al., 1994, from the Paleocene of Venezuela is known only by a small specimen found as a steinkern in a core. The dorsal carapace has narrow ridges.

Costacopluma australis Feldmann et al., 1995, and *Costacopluma salamanca* Feldmann et al., 1997, are the Paleocene representatives of the genus in Argentina. Both species have narrow ridges.

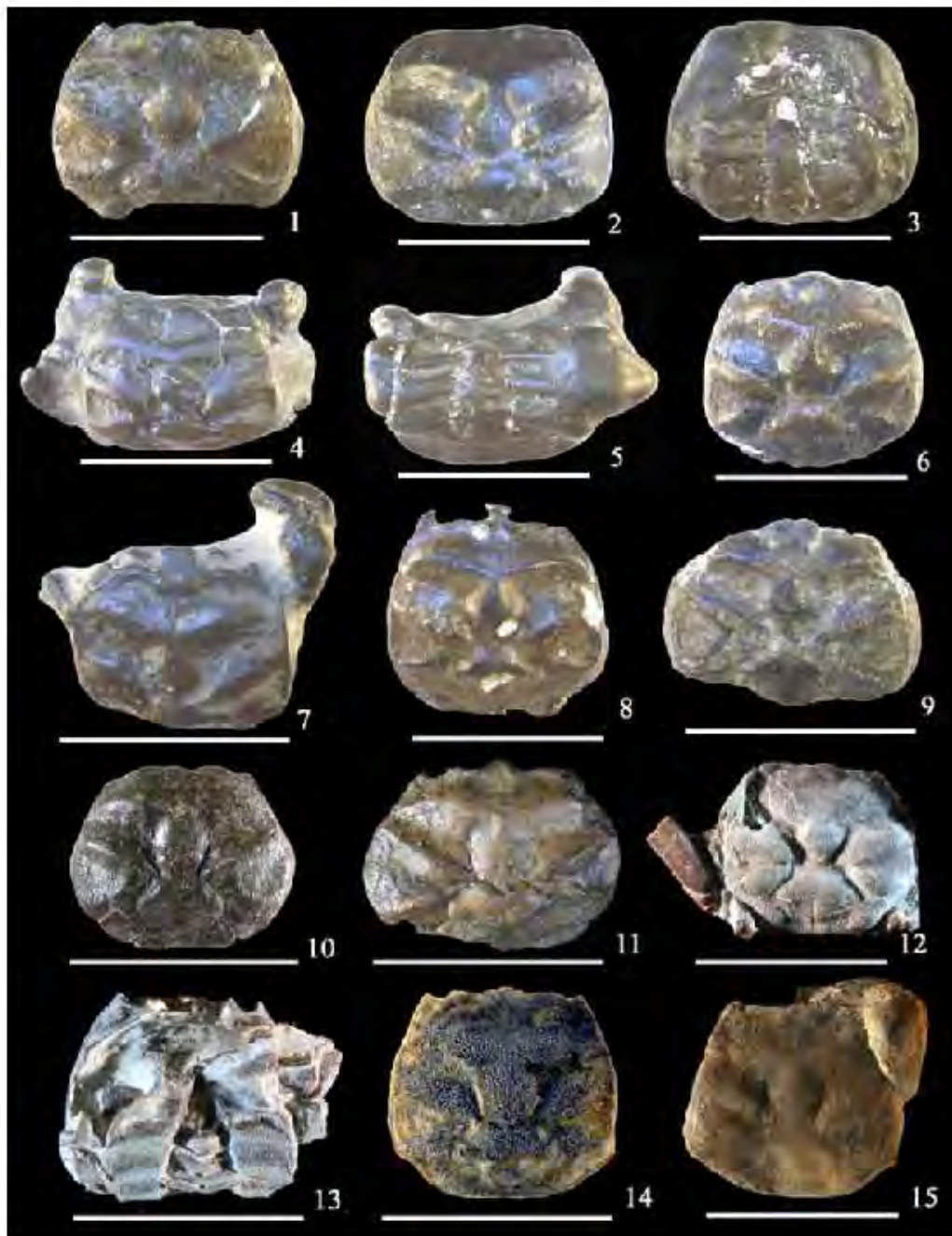


Fig. 5. 1–10, *Costacopluma grayi* Feldmann and Portell, 2007, Paleogene of Arkansas and Alabama; 1–8, Lower Paleocene (Danian), Clayton Formation, Malvern, Arkansas; 1, dorsal view, MMNS 6482; 2, 3, dorsal and ventral views, MMNS 6319; 4, 5, dorsal and ventral views, MMNS 6485; 5, dorsal view, MMNS 6319; 7, dorsal view and right cheliped, MMNS-5737; 8, dorsal view, MMNS-5672; 9, 10, Middle Eocene (Luteftian) Lisbon Formation, Covington County, Alabama, dorsal view of carapace, MMNS-6491, UF-113750. 11, *C. senegalensis* (Remy in Gorodiski and Remy, 1959), Paleocene, Senegal, dorsal view, MNHNF R03785. 12, 13, *C. nordestina* Feldmann and Martins-Neto, 1995, Paleocene, Maria Farinha Formation, Pernambuco, Brazil, dorsal and ventral view, MN-8039-1 and MN-8009-L14, *C. texana* Armstrong et al., 2009, Paleocene Mexia Clay Member of the Wills Point Formation, Texas, dorsal view, NPL3117415. *C. apicalis* Nyberg et al., 2006, Paleocene, San Francisco and Santa Susana formations, southern California, dorsal view of holotype, LACMIP-13590. Scale bars = 10 mm.

Costacopluma nordestina Feldmann and Martins-Neto, 1995, from the Paleocene of Brazil (Fig. 5.12 and 5.13) was originally described based on a single, small specimen. Later, Távora and Miranda (2004) reported 51 specimens of *C. nordestina* (mean carapace width ~15 mm). The dorsal ridges are broad with relatively strong granules, resembling those observed in *C. mexicana*; however, *C. nordestina* bears more similarities with *Costacopluma* (NPL), Paleontological Collection, Kent State University, Kent, Ohio, USA (KSI) and Geological Museum of Copenhagen University, Denmark (MGUH).

texana Armstrong et al., 2009.

C. grayi is known from the Paleocene and Middle Eocene of Alabama (Feldmann et al., 2014; sensu Clayton et al., 2013; Feldmann and Portell, 2007); and is represented by 16 specimens with a carapace width of ~10 mm (Figs. 4.1–4.15, 5.1–5.10). The dorsal carapace ridges are narrow with fine granules. It is also here reported from the Lower Paleocene of Arkansas with a total of 40 branchial ridges inclined 45° with respect to posterior margin, wider at contact with deep cervical groove, narrow at distal contact

with anterolateral margin; metabranchial region transverse, wider at contact with posterolateral margin, narrow towards distal portion of cervical groove; cardiac region a wide “M” shaped; a pair of posterolateral, granulose bumps at level of P5 coxae; sternum subpentagonal; sternites narrow, subtriangular; sternite 4 subtrapezoidal, with granulated outer margins and sharp episternal projection; sternite 5 with sharp granulated transverse crest on posterior third, same for sternite 6, being slightly narrower; sternite 7 subrectangular, half the width of sternite 6, with posterior transverse granulose ridge; abdomen triangular; telson sharp; somite 6 subquadrate, narrow, with ridge on anterior portion; somite 5 subrectangular, as long but slightly wider than somite 6, also with median transverse ridge; somites 4 and 3 subrectangular, with median transverse ridge; somite 2 subdorsal, slightly wider than somites 4 and 3; chelae of variable size, strong and robust in some specimens but slender and thin in others, no clear relation to sexual dimorphism has yet been found; chelae fingers sharp; pereopods 2 to 4 long, slender, with granulose lower margins.

Material examined. Fifteen complete specimens from the Upper Campanian beds of the Cerro del Pueblo Formation, Coahuila, Mexico (CPC-1892 to 1706); one complete specimen from the late Maastrichtian Chiwapa Sandstone (upper Ripley Formation) of Union County, Mississippi, US (MMNS-2949); seven carapaces (one juvenile) from Lower Maastrichtian Potrerillos Formation near Paredón, Coahuila, Mexico (CPC-1707 to 1714); one specimen with articulated appendages inside a burrow from the lower Maastrichtian Potrerillos Formation, Nuevo León, Mexico (CPC-1715); three complete specimens (one juvenile) from the Lower Maastrichtian Potrerillos Formation at Sierra El Antisico, Nuevo León, Mexico (IGM-4128, 4130 and KSU-4).

Discussion. *C. mexicana* is distinguished by the broad, granulose, flat crests on the dorsal carapace ridges, which has also been observed on the two juvenile specimens examined in this study (Fig. 3.8 and 3.9). This observation is a constant feature along the ontogenic development for the species. Specimens lacking cuticle show broad, rounded crests, making them distinguishable from the other *Costacopluma* species, with the exception of small-sized Paleocene species *C. nordestina* and *C. texana*; however, in these two species the crests are not as wide and the metabranchial crests are more inclined.

The presence of *C. mexicana* and *C. grayi* in the same sedimentary basin (Parras Basin) of NE Mexico offers the opportunity to suggest a possible speciation process. *C. mexicana* was distributed in NE Mexico and SE United States from the late Campanian to early late Maastrichtian (74–66.8 Ma) in prodelta and lagoon facies (McBride et al., 1974). Based upon the different facies and preservation types it seems it was a tolerant species to different environmental conditions. *C. grayi* is documented a few meters below the K/Pg boundary in the same region, with an age of 66.2 Ma (Vega et al., 2013). Many similarities can be seen between these two species, with the following observed “trends” in morphological changes: a) width reduction of dorsal ridges; b) granules on crests become finer; c) metabranchial ridges become slightly inclined; and d) the consistently smaller size of *C. grayi* bodies in Paleogene populations. A discussion on the possible causes for this size reduction is given below.

C. grayi Feldmann and Portell, 2007.

Figs. 4.1–4.5; 5.1–5.10; 6.3, 6.4.

C. grayi Feldman and Portell, 2007, p. 92, Figs. 2A–E, 3A–D; Armstrong et al., 2009, Figs. 6.2, 6.3; Feldmann et al., 2014, p. 137, pls. 1, 2.

Emended description. Carapace small to medium-sized, subovate, 1.5x wider than long, wider at mid-length, flat in transverse section and longitudinally curved; anterior margin sinuous, rimmed, finely granulated; outer orbital spine sharp; rostrum spatulate, wider at

distal portion; lateral and posterior margins rimmed, with fine granules; anterolateral margin rounded, posterolateral margin short, inclined; posterior margin straight, one-third the maximum carapace width; dorsal carapace with distinct transverse ridges with sharp crests, covered by scarce but coarse granules and smooth surface between crests; anterior crest arcuate, continuous across protogastric and metagastric regions; mesogastric region subtrapezoidal; mesobranchial ridges inclined 45° with respect to posterior margin, slightly wider near contact with deep cervical groove, narrow at distal contact with anterolateral margin; metabranchial region slightly inclined towards posterolateral margin, slightly wider at midlength; cardiac region shaped as wide “M” shaped; a pair of posterolateral, granulose bumps at level of P5 coxae; sternum subpentagonal; sternite 4 subtrapezoidal, with granulated outer margins and sharp episternal projection; sternite 5 with sharp granulated transverse crest on posterior third, same for sternites 6, being slightly narrower; sternite 7 subrectangular, half the width of sternite 6, with posterior transverse granulose ridge; abdomen triangular; telson sharp; somite 6 subquadrate, narrow, with ridge on anterior portion; somite 5 subrectangular, as long but slightly wider than somite 6, also with median transverse ridge; somites 4 and 3 subrectangular, with median transverse ridge; somite 2 subdorsal, slightly wider than somites 4 and 3; right chela robust, with inflated palm and short, curved dactylus; left chela sharp, with acute dactylus; pereopods 2 to 4 long, slender, meri with regularly spaced, short spines on lower margins.

Material examined. One complete carapace (MMNS 5269) from Lower Maastrichtian Prairie Bluff Formation from Union County, Mississippi; sixteen complete carapaces (MMNS 6519, MMNS 7435–7449, USNM 215705) from uppermost Maastrichtian Owl Creek Formation from Tippah County, Mississippi; nine complete carapaces (CPC-1717 to 1725) from uppermost Maastrichtian Las Encinas Formation of Coahuila; fourteen complete carapaces (MMNS 5942, 6482, 5672–5674, 5737, 6319, 6483, 6485, 6487, 6478–6481) from Lower Paleocene (Danian), Clayton Formation from Arkansas (Hot Spring County) and Alabama (Lowndes County); six carapaces (MMNS-6491, 6491-1, 6491-3, 6492; UF 113749, 113750) from the Middle Eocene (Lutetian) lower member of the Lisbon Formation (Clayton et al., 2013) from Covington County, Alabama.

Discussion. Feldmann and Portell (2007), followed by Feldmann et al. (2014), reported *C. grayi* from the Paleogene of Alabama and mentioned several useful characters to separate *Costacopluma* species, including shape of carapace and rostrum width/length ratios and granules on transverse ridges.

The specimens of *C. grayi* from the upper Maastrichtian of NE Mexico and SE United States show identical morphological features to those from the Paleogene of Alabama and Arkansas. In both groups, the crests are sharp with scarce but relatively coarse granules and the anterior ridge as well as mid and posterior ridges are equally sinuous, which show identical shape and inclination. The width/length ratio is not here applied because the specimens show some deformation, which may affect the result of this feature. *C. bishopi*, from the Coniacian of Southern Mexico is very small, ovate and the dorsal crests are very inflated. *C. concava*, from the Campanian–Maastrichtian of Nigeria has a wider carapace with much narrower ridges and metabranchial ridges more inclined. The specimen identified by Gastani et al. (1983) as *C. concava* is in need of re-evaluation as the morphology resembles that of *C. grayi* in that it has a small size (length = 22 mm, width = 12 mm) and was reportedly found in lower Paleocene sediments (Nicora et al., 1987; Fuchs and Willems, 1990). *C. maroccana* from the late Campanian of Morocco has a smoother carapace with very fine tubercles on the transverse crests. The only known specimen of *C. binodosa* is an incomplete carapace, whose posterior ridges are relatively narrow

but with strong tubercles on their crests. *C. mexicana*, from the late Campanian–late Maastrichtian of NE Mexico exhibits similar features with respect to carapace shape, size (latest Maastrichtian *C. grayi*), sinuous anterior ridge, and inclined median ridge; however, the metabranchial ridges are slightly more inclined in *C. grayi*. Noteworthy are the larger conspicuous terraces and stronger granules on the crests. Additional specimens collected in the basal Clayton beds (Paleocene) of the K/Pg section of Alabama are possibly reworked from the underlying Prairie Bluff Fm are likely *C. grayi*, but the age is needed to be corroborated therefore they are not listed in this work. *C. mamethioupani* from the middle-upper Maastrichtian of Senegal is represented by a small carapace with sharp tuberculous crests, a strong protogastric process, a transversely subtrapezoidal mesogastric lobe and transverse metabranchial ridges, which differentiates it from any known species of *Costacopluma* (Hyžný et al., 2015). The latter along with *C. bishopi* are the only Cretaceous members of the genus whose known populations exhibit a small mean body size. *C. senegalensis* from the Paleocene of Senegal resembles *C. grayi* in carapace shape and dorsal ridges. *C. squiresi* from the Paleocene of California has sharp dorsal ridges with very fine granulations and a subtrapezoidal carapace. South American Paleocene *Costacopluma* species are represented by small specimens with narrow, finely granulated ridges, with the exception of *C. nordestina* from Brazil, where the broader crests and strong granules resemble specimens of *C. texana* (Paleocene of Texas). A similarity between these relatively abundant species of the early Paleogene seems to suggest that they may be the same; however, detailed revision and comparison of specimens is necessary.

6. Dwarfism and lilliput effect

Although long-term increase in body size is typically characteristic for decapod crustaceans since their origin in the Mesozoic (Klompaker et al., 2015), there are a few reports suggesting dwarfism in crabs (Fraaije et al., 2006; Guzmán et al., 2016).

With the exception of *C. bishopi* and *C. mamethioupani*, there is a noticeable change in carapace size between Cretaceous and Paleogene species of *Costacopluma* (Ossó-Morales et al., 2010). In comparison with Paleogene populations of the same species, *C. grayi* carapaces from the upper Maastrichtian of NE Mexico, Mississippi, and Alabama average nearly three-times larger and with identical dorsal and ventral morphologies, including the general shape of carapace and arrangement of narrow transverse crests with scarce fine granules. As observed in *C. mexicana* by Vega and Feldmann (1992), juvenile specimens show the same morphology as adults, therefore one possible interpretation for the reduced mean size observed in *C. grayi* is that Paleogene specimens correspond to juveniles, but this seems unlikely. Dwarfism or phyletic nanism was previously reported for *C. bishopi* from the Coniacian of southern Mexico (Vega and Feldmann, 1992; Fraaije et al., 2006). Dwarfism is a type of corporal size evolution (Gould and MacFadden, 2004) and has been previously linked with a variety of causes, including a rise in ocean temperature (Price, 1982; Roy et al., 2001), oxygen and sea level changes (Keller et al., 2009), global warming and anoxia (Chu et al., 2015), as well as extremely dry conditions (Bowen et al., 2004; Smith et al., 2009), all potentially related to the K/Pg mass extinction (Smit et al., 1992; Erwin, 1998; Keller et al., 2009). Despite of the extensive literature around the K/Pg event, detailed information on the recovery processes after the biotic crisis remains scarce. An exception, consist in the identified patterns involved with the escalate of diversity during the K/Pg transition (Alroy, 2010; Sessa et al., 2012), which reflect changes in ecology after extinction. Preservational causes also have been involved, especially the grade of lithification

of the geological units with respect to alteration and selecting against the small taxa (Sessa et al., 2009). Dwarfism, as a selective evolutionary process, favors individuals of small size (Hanken and Wake, 1993; Roy, 2008; Donovan, 2009; Smith et al., 2009). In the aftermath of mass extinction, the Lilliput effect has been observed (Kalje, 1996; Harries and Knorr, 2009; Keller and Abramovich, 2009) in foraminifera (Macleod et al., 1990; Keller and Abramovich, 2009; Panekar et al., 2016), bivalves (Roy et al., 2001), ostracods (Roy, 2008; Chu et al., 2015), echinoderms (Price, 1982), and ichnofossils (Smith et al., 2009), but, to our knowledge, it has only been documented for *C. bishopi* in decapod crustaceans, as a possible result of food limitations, increased predation, and/or decreased salinity (Fraaije et al., 2006). The ecologic and physiologic consequences of dwarfism have been discussed by Hanken and Wake (1993). In the case of *C. grayi*, a reduction in size may be the result of declining sea level in the oceans (Keller et al., 2009), decreased ability to synthesize skeletal calcium carbonate due to ocean acidification (Friba et al., 2010; Panekar et al., 2016), significant fluctuations in salinity (Price, 1982), food shortage (Kiel and Hansen, 2015; Woelders and Speijer, 2015), and/or progenesis (Macleod et al., 1990; Haye et al., 2010; Hsueh, 2015; Ríos-Elósegui and Hendrickx, 2015). In this framework, the eurytopic detritus feeders seem to have had the great potential for surviving such extinction events (Sheehan et al., 1996; Erwin, 1998; Solé et al., 2010). Phenotypic plasticity has been observed as a mechanism to enhance larval survival under high salinity fluctuations in the grapsid crab *Chasmagnathus granulata* (Charmantier et al., 2002), but also, as an adaptation to living in a fluctuating environment by developing different size morphotypes (Haye et al., 2010). There is a peculiar trend that link high levels of phenotypic plasticity with high dispersal potential in long-lived larvae (Hollander, 2008), which may explain the dispersal ability and latitudinal occurrence in the species of *Costacopluma* of the Paleocene. Thus, the reduced size in *C. grayi* across the K/Pg boundary may be a result of any of the above factors or even some combination thereof. The upper Maastrichtian shallow marine/lagoonal sediments (66.2 Ma, see Larina et al., 2011; Vega et al., 2013) of the Las Encinas (Coahuila, NE Mexico) and Owl Creek formations (Mississippi) (McBride et al., 1974; Maurini et al., 1995; Sessa et al., 2015) are often equivalent to the shallow marine deposits of the succeeding Paleogene facies in which small specimens of *C. grayi* have been reported (Feldmann and Portell, 2007; Feldmann et al., 2014). Thus, in some instances, it is possible that the species could remain in the same environment before, during, and after the K/Pg event. In NE Mexico, *C. grayi* (Latest Maastrichtian) is found associated with callianassoid remains and *Ophthalmoplax brasiliana* Maury, 1930, the latter probably a carnivorous swimming portunoid. In the Owl Creek Formation of Mississippi, *C. grayi* is found with callianassoid remains, the lobster *Linuparus* sp., the raninoid *Cretacorantina* sp., and the portunoids *Branchiocarcinus fictus* (Rachbun, 1935) and *O. brasiliana* (see Phillips et al., 2013; Vega et al., 2013). By the beginning of the Paleogene, only few associated taxa from the Cretaceous like callianassoids and *Linuparus* White, 1847, persisted alongside *Costacopluma* in the Paleocene of Texas (Armstrong et al., 2009); all of which are of small body size.

According to Schweitzer and Feldmann (2005) decapod crustaceans were not severely affected by the K/Pg event. It seems that *C. grayi*, as an adaptable eurytopic species was not only able to survive, but experienced a relatively rapid dispersion, if *C. senegalensis* and *C. concava* from India are assumed to be phylogenetically close to *C. grayi*. However, additional specimens and comparisons are needed in order to test this theory. At minimum, *Costacopluma* was an origin point for several species in the relatively short recovery interval subsequent to K/Pg mass extinction (Sessa et al., 2009). At present, the best numerically

represented Paleogene species are *C. grayi*, *C. nordestina*, and *C. texana*, thus our knowledge of their intra-specific population variation exceeds that of described species represented by unique and scarce specimens (Table 1). This is not to say the latter species are not valid, but additional specimens would help confirm their distinctiveness and variability.

Based on similarities in carapace shape, width of dorsal ridges, and finely granulate ornamentation, we observe two possible schemes for phyletic relationships among the best represented species in North and South America (Fig. 6). In scheme A, *C. mexicana* (Fig. 6.1 and 6.2), before its extinction, gave rise to *C. grayi* (Fig. 6.3), which remained in NE Mexico and SE United States; then, crossing the K/Pg boundary, *C. grayi* became smaller due to the Lilliput effect (Fig. 6.4). In scheme B, *C. mexicana* gave rise to *C. grayi* and did not become extinct, instead giving rise also to *C. nordestina* and/or *C. texana* (Fig. 6.6) as both species show similar morphology. The first seems to be a more likely evolutive path, since there are no records of *C. mexicana* in latest Maastrichtian deposits anywhere.

7. Conclusions

The K/Pg event influenced the structure of all ecosystems, affecting several animal groups, particularly some dominant families of decapod crustaceans of shallow marine environments that disappeared during the extinction event. *Costacopluma* is one of the few decapod genera that survived the extinction, but all Paleogene species are significantly smaller compared to their Campanian–Maastrichtian relatives. The presence of *C. grayi* in upper Maastrichtian sediments of NE Mexico and SE United States, heretofore unreported, offers the opportunity to document a phenomenon that could explain how and why some genera were able to persist. Fortunately, the fossil record for *Costacopluma* is becoming more robust, which allows the comparison of size and morphology among a greater number of populations, leading to the proposition that size reduction in *C. grayi* is an example of the Lilliput effect. The temporal distribution of *C. grayi*, from 66.2 Ma (latest Maastrichtian) to 47.76 Ma (Middle Eocene), indicates that the species developed under favorable conditions for nearly 20 Ma. New occurrences of *C. mexicana* in upper Campanian and lower Maastrichtian localities in NE Mexico, as well as a new record in SE United States are documented, suggesting that the species was tolerant of different environmental conditions, an advantage for prevailing under adverse conditions. Finally, it is proposed that *C. mexicana* is a possible ancestor of *C. grayi* and also likely of *C. nordestina* and *C. texana*, two species that may represent the same taxon. However, additional material is required in order to assess variability in carapace shape and dorsal ornamentation for the Paleogene species of *Costacopluma*.

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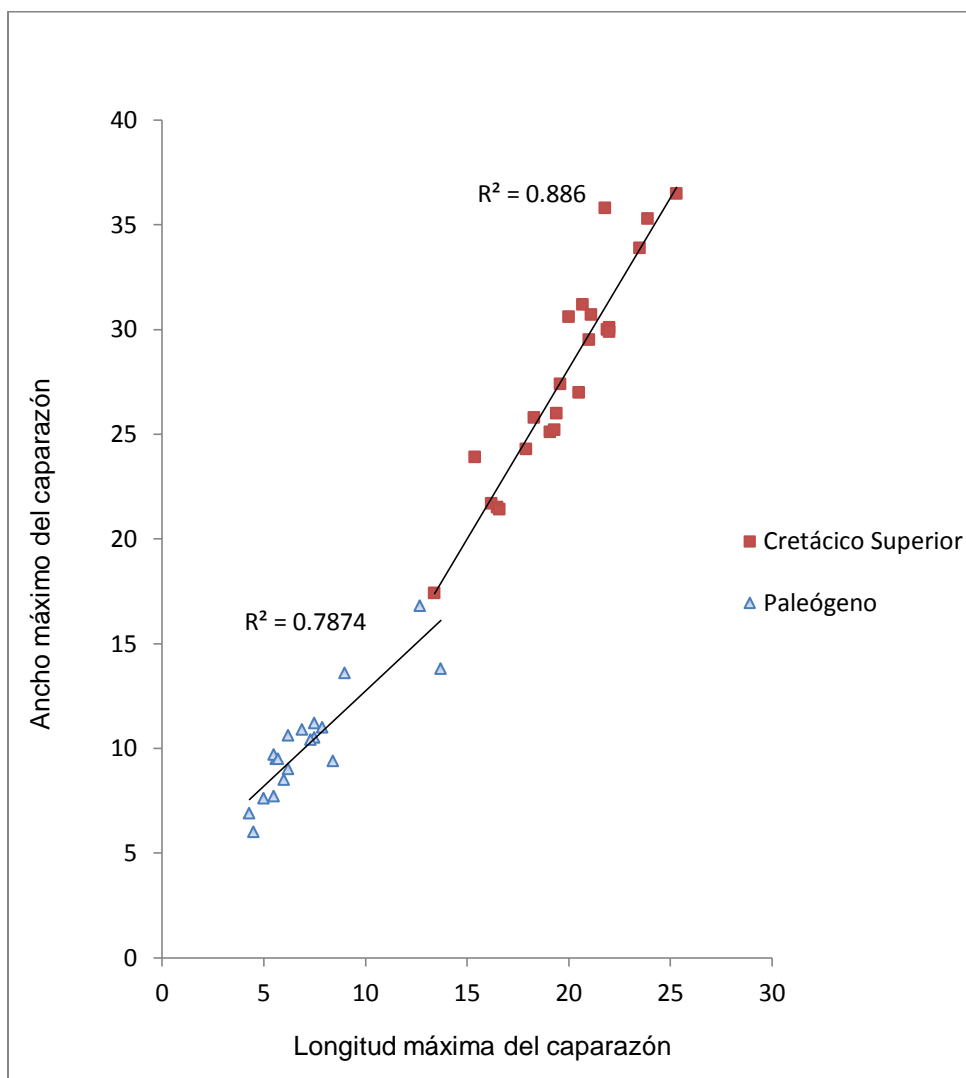
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6. DISCUSIÓN GENERAL

Entre los principales patrones de evolución del tamaño corporal el fenómeno del enanismo ha sido ampliamente documentado a través del registro fósil (Bell, 2014), con ejemplos que incluyen tanto a los individuos fósiles como a las evidencias indirectas de su actividad o icnofósiles (Wiest et al., 2015). La reducción de la talla asociada a los efectos inmediatos de un evento de extinción constituyen un ejemplo del Efecto Liliput (Twitchett, 2007), el cual a pesar de ser un fenómeno cuyo estudio va en aumento, los mecanismos por los cuales opera aún no son del todo comprendidos (Bell, 2014). El estudio de las extinciones masivas ha mejorado el conocimiento de estos eventos aunque los procesos de recuperación posteriores no menos complejos, han recibido menos atención (Erwin, 2001). Particularmente, la magnitud del evento K/Pg junto con las secciones abundantes del Paleógeno Temprano han aportado un registro vasto en cuanto a la recuperación biótica (Erwin, 2001).

La reducción de talla corporal observada en los ejemplares de *Costacopluma grayi* del Paleoceno Inferior-Eoceno Medio de varias Formaciones del SE de Estados Unidos a partir de ejemplares de la misma especie de talla mayor provenientes de estratos del Maastrichtiano más Tardío de formaciones del NE de México y SE de Estados Unidos es interpretada como un ejemplo del Efecto Liliput. La proporción longitud/ancho entre los ejemplares de *C. grayi* del Cretácico más Tardío ($n = 19.8, 27.8, ds = 2.90, 5.02$) y del Paleógeno ($n = 7.12, 10.1, ds = 2.43, 2.56$) muestra una correlación similar (Gráfica 1) sin traslape de variación entre ambos grupos. Las abundancias relativas en los ejemplares de *C. grayi* de las unidades paleógenas del SE de Estados Unidos, así como las abundancias de otras especies de *Costacopluma* del Paleógeno en Sudamérica, apuntan más a reflejar una tendencia conservativa por la talla pequeña en lugar de evidenciar un estadio juvenil.

Es posible que *C. grayi* al igual que *C. mexicana* fuera una especie euritópica, lo cual representaría una ventaja para sobrevivir al evento K/Pg y conformar las faunas iniciales posteriores a la extinción, caracterizadas por tener baja diversidad así como abundantes taxa euritópicos (Erwin, 2001). Por otra parte, la reducción abrupta de la talla en *C. grayi* ocurre dentro de un intervalo de recuperación postextinción, sin embargo establecer una duración para este intervalo es más complejo debido a que se ha observado que diferentes clados pueden recuperarse a distinta tasa durante un mismo evento, o un mismo clado puede recuperarse a distintas tasas en diferentes regiones (Erwin, 2001). El intervalo temporal de *C. grayi* que va de los 66.2 Ma (Maastrichtiano más Tardío) a los 47.76 Ma (Eoceno Medio), indica que la especie prosperó durante casi 20 Ma. Sin embargo, el periodo de recuperación a partir del evento K/Pg en el cual se presenta *C. grayi* de talla pequeña pudo ser de una duración mucho menor, abarcando un rango estimado de 2.6 Ma hasta la aparición de otras especies como *C. texana*.



Gráfica 1. Líneas de regresión para las medidas de longitud/ancho del caparazón en ejemplares de *Costacopluma grayi* del Cretácico Superior (Maastrichtiano) del NE de México y SE de Estados Unidos y del Paleógeno (Paleoceno-Eoceno) del SE de Estados Unidos.

6.1 Tipos de preservación en *C. mexicana*

Los distintos estilos de preservación observados en los crustáceos decápodos fósiles de diversas localidades de las cuencas de Parras y de La Popa en el NE de México (Vega et al., 2016) sugieren condiciones particulares del ambiente en que vivían. Son de especial interés las localidades en Sierra el Antrisco (Cuenca de La Popa) y Paredón (Cuenca de Parras). La preservación excepcional de los numerosos ejemplares fosfatizados de *Costacopluma mexicana* en Sierra el Antrisco, Nuevo León, podría explicarse por la

influencia de precipitación de minerales en la soldadura exhumada de un diapiro (Vega et al., 2016) o acumulación de materia orgánica relacionada a la topografía de la soldadura. En la Cuenca de La Popa ocurrieron eventos de evacuación de sal que dieron origen a los diapiros El Gordo y El Papalote (Tamez et al., 2011) por lo cual el diapirismo de la región podría haber aportado minerales que afectaran la diagénesis y preservación de la cutícula. En la Cuenca de Parras, una nueva localidad cercana a La Falla de San Marcos y al poblado de Paredón, Coahuila, otro tipo de factores como son el hidrotermalismo, filtraciones de metano, y/o acumulación de materia orgánica podrían haber afectado la preservación de la cutícula roja observada en los ejemplares de *C. mexicana*, así como de otros crustáceos recolectados en esta localidad como son: *Dakoticancer australis*, *Bournelyreidus oaheensis* y *Sodakus mexicanus* (Vega et al., 2016), los cuales representan una asociación diversa. El hidrotermalismo se expresa en la actualidad en al menos dos localidades (Espinazo e Icamole) en las cuales la Falla de San Marcos ejerce influencia. Asociado al hidrotermalismo se encuentran los ambientes de fisura de metano (cold seep), caracterizados por la presencia de hidrocarburos atrapados bajo el piso oceánico y que eventualmente escapan hacia la columna de agua (Cordes et al., 2016). En la localidad de Paredón es posible que ocurrieran condiciones similares, ya que otros ejemplares rojos han sido reportados a partir de depósitos similares para el Cretácico de Japón (Karasawa, 2011).

Los hidrocarburos atrapados con frecuencia se encuentran asociados a fallas inducidas por depósitos de sal (Acosta et al., 2003) a través de las cuales los hidrocarburos se filtran al piso oceánico manifestándose como un fluido hipersalino que al acumularse forma grandes cuerpos de agua de una densidad mayor que la del agua suprayacente, constituyendo así una “trampa” en la cual se ha observado la preservación inusual de cangrejos y crustáceos isópodos (Cordes et al., 2016). Otras estructuras formadas bajo

condiciones de fisura de metano son los montículos de carbonatos (Levin et al., 2016) caracterizados por su elevada actividad de oxidación microbiana de metano y sulfuro, así como su fuerte colonización por peces, poliquetos, y cangrejos (estos últimos exhibiendo una coloración roja). Los montículos constituyen un hábitat favorable para la colonización en el cual el escape de hidrocarburos puede representar un aporte nutricional para la red trófica (Wheeler et al., 2007). Finalmente, depresiones formadas por los gases de la materia orgánica en descomposición representan también un ambiente rico en nutrientes aprovechados por bacterias simbiotas e invertebrados (Acosta et al., 2003). Cualquiera de las condiciones anteriores o una combinación de ellas pudo haber permitido la preservación de cutícula roja en los especímenes de Paredón, siendo los montículos de carbonatos uno de los más plausibles. La actividad hidrotermal y un ambiente rico en hidrocarburos como metano o sulfuro podrían haber sustentado una comunidad quimiosintética que podría explicar la abundancia y diversidad de crustáceos decápodos observadas en la localidad de Paredón.

7. CONCLUSIONES

Se documentan nuevos hallazgos de *C. mexicana* en localidades de edad campaniana superior y maastrichtiana superior, así como un nuevo registro en el SE de Estados Unidos, sugiriendo que la especie fue tolerante a diferentes condiciones ambientales, posiblemente ampliando también su distribución geográfica.

Por vez primera, se reporta la presencia de *C. grayi* en rocas del Maastrichtiano Superior del NE de México y SE de Estados Unidos. Este nuevo registro fósil nos permite entender cómo y por qué algunos géneros fueron capaces de sobrevivir tras un evento de extinción catastrófico como fue el K/Pg. El evento alteró la estructura de todos los ecosistemas, afectando varios grupos animales, particularmente de algunas familias de

crustáceos decápodos de ambientes marinos someros que desaparecieron durante el evento de extinción. *Costacopluma* es uno de los pocos géneros que sobrevivieron a la extinción, pero todas las especies del Paleógeno son significativamente más pequeñas en comparación con las especies del Campaniano-Maastrichtiano.

La mejora en el conocimiento del registro fósil de *Costacopluma* ha permitido comparar la morfología y talla de las poblaciones. La aquí documentada disminución abrupta de la talla corporal para *C. grayi* conduce a señalar la ocurrencia de un efecto Liliput. Este fenómeno aunque cada vez más estudiado, ha sido pobremente documentado para crustáceos decápodos. Se propone también a *C. mexicana* como posible ancestro de *C. grayi* y probablemente de *C. nordestina* y *C. texana*, dos especies que podrían representar el mismo taxón. Los próximos estudios apoyados con material adicional permitirán evaluar el grado de variabilidad de la forma y ornamentación dorsal del caparazón a fin de dilucidar las relaciones entre las especies paleógenas de *Costacopluma*.

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9. ANEXOS

A continuación se anexan tres artículos publicados durante la realización del proyecto de maestría.

Occurrence of *Retrocypoda almelai* Via Boada, 1959 (Decapoda: Retroplumidae) in the Eocene of Central Iran

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Abstract

The decapod crustacean *Retrocypoda almelai* Via Boada, 1959 is reported from Bartonian (middle Eocene) strata of Soh (North of Isfahan, Iran) and represents the most oriental record for the species, hitherto considered endemic and restricted to the western margin of Tethys. This finding is important to understand the paleobiogeographic distribution of retroplumid crabs, which were abundant during Late Cretaceous in America and Africa, but today their representatives are restricted to the Indopacific region.

Keywords: Crustacea, Decapoda, Retroplumidae, Eocene, Isfahan, central Iran

Resumen

El crustáceo decápodo *Retrocypoda almelai* Via Boada, 1959 es reportado en estratos del Bartoniano (Eoceno medio) de la región de Soh (Norte de Isfahan, Iran), y representa el registro más oriental de la especie, considerada previamente como endémica y restringida al margen occidental del Tethys. Este hallazgo es importante para comprender la distribución paleobiogeográfica de los cangrejos retroplumidos, que fueron abundantes durante el Cretácico Tardío en América y África, pero actualmente sus representantes están restringidos a la región Indopacífica.

Palabras clave: Crustacea, Decapoda, Retroplumidae, Eoceno, Isfahan, central Irán.

1. Introduction

The discovery of one specimen of *Retrocypoda almelai* Via Boada, 1959 on Bartonian (middle Eocene) strata of Soh (North of Isfahan, Iran) (Fig. 4.1), represents the most oriental record for the species, hitherto considered endemic and restricted to the western margin of Tethys. The genus *Retrocypoda* was created by Via Boada (1959) to accommodate the sole species *R. almelai* Via Boada, 1959, based upon samples recovered in the Bartonian (middle Eocene) outcrops of Central Catalonia (NE Iberian Peninsula), but he also reported and figured the presence of *R. almelai* in Lutetian (middle Eocene) outcrops of

other localities of Central Catalonia (see also Via, 1969, p. 330–331). Beschin *et al.* (1996, 2012) reported the presence of specimens of *R. almelai* in the Lutetian outcrops of the Vicenza area (northern Italy). In addition, *R. almelai* is also recorded in the Lutetian outcrops of Alicante Province (south-eastern Spain) (AO pers. obs.), and also in the Priabonian (middle Eocene) outcrops of the Central Pyrenees in Huesca Province (northern Spain), where the species migrated westward during the Bartonian transgression (Ossó *et al.*, 2014). Likewise, the genus is recorded lately also in Ilerdian (early Ypresian) outcrops of Aude (south-eastern France) (AO pers. obs.). Therefore, we can observe that until now the genus *Retrocypoda* seemed

confined to the Mediterranean margin of the western Tethys during the early to late Eocene. The new Iranian specimen demonstrates that *Retrocypoda* also inhabited the oriental part of the Tethys during Eocene times.

The systematic position of *Retrocypoda almelai* has been the object of different placements and proposals of phylogenies through time. Originally, it was placed by Via (1969, 1988) and Via Boada (1959, 1980, 1982) as Retroplumidae Gill, 1894, within Ocyropodoidea Rafinesque, 1815 with possible relationship with the Macropluminae Dana, 1851. Glaessner (1969) placed it within Palicidae Bourvier, 1898, albeit with a query. It was not until 1989 that de Saint Laurent clarified the systematics of *Retrocypoda*, and included it within the Retroplumoidae Gill, 1894, pointing out its possible relationship with *Costacopluma* Collins and Mortis, 1975.

The Iranian specimen of *Retrocypoda almelai* expands eastward the distribution of this species during the Eocene and by extension the paleobiogeographical distribution of the family Retroplumoidae. The paleobiogeography of this family has been discussed formerly by many authors (for instance: Via and Cals, 1979; Via, 1980; Vega and Feldmann, 1992; McLay, 2006; Fraaije et al., 2006; Hyžný and Müller, 2010; Feldmann et al., 2014), who also hypothesized about the origins of the group and its apparent subsequent expansion eastward from both sides of the Atlantic, whether from Central America or from the west coast of Africa, where it is assumed that the group arose during the Late Cretaceous (Hyžný et al., 2016).

2. Geological setting

Outcrops in the Soh area include the widely distributed Paleozoic (Zahedi, 1973; Adhamian, 2003; Wendt et al., 2005; Ghobadipour et al., 2013; Bahrami et al., 2015) and Mesozoic deposits (Mannani and Yazdi, 2009; Yazdi et al., 2010), as well as the Paleocene to Oligo-Miocene deposits, the youngest marine sequences, which start with terrigenous red to white sequence of Paleocene conglomerate and sandstone, continued by Eocene fossiliferous carbonates and marls. The Sabkha deposits at the top of the Oligo-Miocene Qom Formation terminates the depositional cycle of the marine sequence.

A thick Eocene succession is widely exposed in the studied region (Sadri, 2011; Janssen et al., 2013). The studied section is located near the village of Soh (70 km northwest of Isfahan) (Fig. 1) and is accessible by a 35 km unpaved road off the Isfahan – Tehran highway. The section is situated on the right side of a seasonal river valley that is observable from a distance in the plain. Coordinates for the fossil locality are: N 33°28'36", E 51°27'6". Structurally, the locality belongs to the Central Iran microplate, which is restricted by the NW-SE Sanandaj-Sirjan metamorphic belt to the West, and by the Great Kavir fault to the East. The studied profile (Figs. 2, 3) is about 354 meters thick. Based

on field observation, sedimentological features and fossil contents, 11 lithological packages are discriminated. The details of each package are given from the top to the base:

- Alternation of light brown to grey sandstone and conglomerate with reworked clasts including *Heterastridium* spp. of late Triassic due to movements of Alpine orogeny, 33 m (package 11)
- Alternation of thin bedded sandstone with green to white marly subminors including two igneous levels (trachy-andesite and basalt), 20 m (package 10)
- Alternation of white to light brown limestone, sandy limestone, thin layers of marly limestone with abundant silicified bivalves and gastropods (*Pinna* sp., *Glycymeris* sp., *Velates* sp., *Conus* sp., *Oliva* sp., *Natica* sp.), solitary corals, condensed ostreoid layers and the *Retrocypoda almelai* specimen here reported, 68 m (package 9).
- Pink to brown trachy-andesite, 10 m (package 8).
- White to yellow green marl with sandy limestone including foraminifers, echinoids, bivalves and gastropods, 35 m (package 7)
- Alternation of dark brown to grey siliceous conglomerate and sandstone, 35 m (package 6).
- Yellow to grey medium to thick bedded sandy limestone including micro and macrofauna (*Ostrea* sp., *Natica* sp., *Velates* sp., *Cardium* sp., bivalve coquina and bryozoan remains), 30 m (package 5).
- Alternation of sandstone and marl, two green to grey tuffaceous silty horizons, and purple fossiliferous marl with abundant bivalves, 60 m (package 4).
- Green to gray loose marl including, pteropods (marine pelagic gastropods), *Helioconoides* sp., crinoids, ostracods, tiny layers of siliceous sandy limestone with foraminifera (*Nodosaria catesbi*, *Nodosaria scalaris*, *Elphidium* sp., *Marginulina* sp., *Nummulites globulus*, *Coskinolina* sp., *Spirolina cylindracea*, *Textularia* sp.), and bivalves (*Ostrea* sp., *Pinna* sp.), 30 m (package 3).
- Brown fine grained cross bedded marly sandstone, 15 m (package 2).
- Grey marls with thin layer of brown to yellow limestone including abundant *Rotularia* sp. (polychaete worm), charophyte algae, ostracods, oysters and foraminifera (*Nodosaria catesbi*, *N. scalaris*, *Elphidium* sp., *Marginulina* sp., *Nummulites globulus*, *Coskinolina* sp.), fine sandy carbonate bed rich in crustacean remains, mainly Callinassidae at the base of the package, 18 m (package 1 – Eocene).
- Discontinuity (Paleocene-Eocene boundary)
- Alternation of red to dark brown conglomerate, sandstone and siltstones including siliceous *Orbitolina* and mollusk debris, reworked from the Cretaceous due to the post Laramidian orogenic movements, 60 m, (Paleocene).

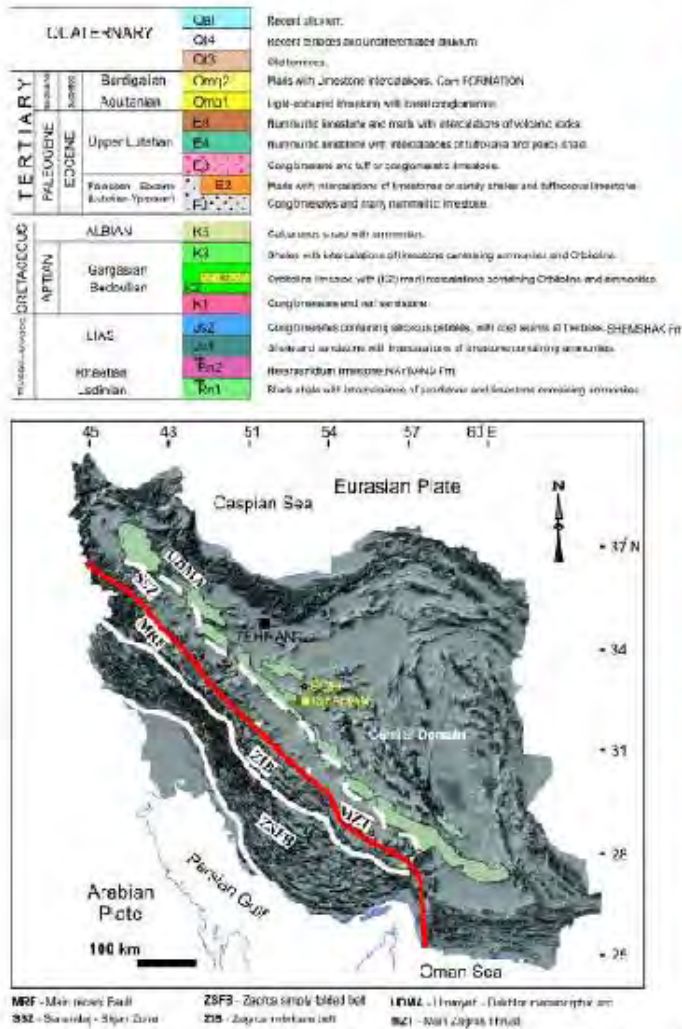


Figure 1. Location and geologic maps of study area with position of fossil locality (arrow), north of Isfahan, Iran.

3. Repository

Department of Geology, Faculty of Science, University of Isfahan, Iran; EUIC, Museo del Desierto, Saltillo, Coahuila, Mexico; MUDE, Museu de Geologia de Barcelona (Barcelona, Catalonia); MGD, Museo Civico "G Zannato" di Montecchio Maggiore (Vicenza, Italy); MCZ.

4. Systematic Paleontology

Order Decapoda Latreille, 1802
 Infraorder Brachyura Latreille, 1802
 Section Eubranchyura de Saint Laurent, 1980
 Subsection Heterotremata Guinot, 1977
 Superfamily Retroplumoidea Gill, 1894
 Family Retroplumidae Gill, 1894

Genus *Retrocypoda* Via Boda, 1959 Type species. *Retrocypoda almelai* Via Boda, 1959

Retrocypoda almelai Via Boda, 1959 (Fig. 4)

- 1943 Fragmentos de crustáceos: Ríos *et al.*, p. 360
 1949 "especie completamente inédita"; Via, p. 1/1
 1950 *Macrophthalmus almela* n. sp.; Bataillier, p. 224
 (*nomen nudum*).
 1952 *Ocyrodidae* n. sp.; Via, p. 86.
 1959 *Retrocypoda almela* Via Boda, 1959; p. 394,
 f. 20
 1961 *Retrocypoda almela* Via Boda, 1959; Farrés,
 p. 21
 1969 *Retrocypoda almela* Via Boda, 1959; Glaessner
 in Moore, p. 532, f. 339.1
 1969 *Retrocypoda almela* Via Boda, 1959; Via, p.

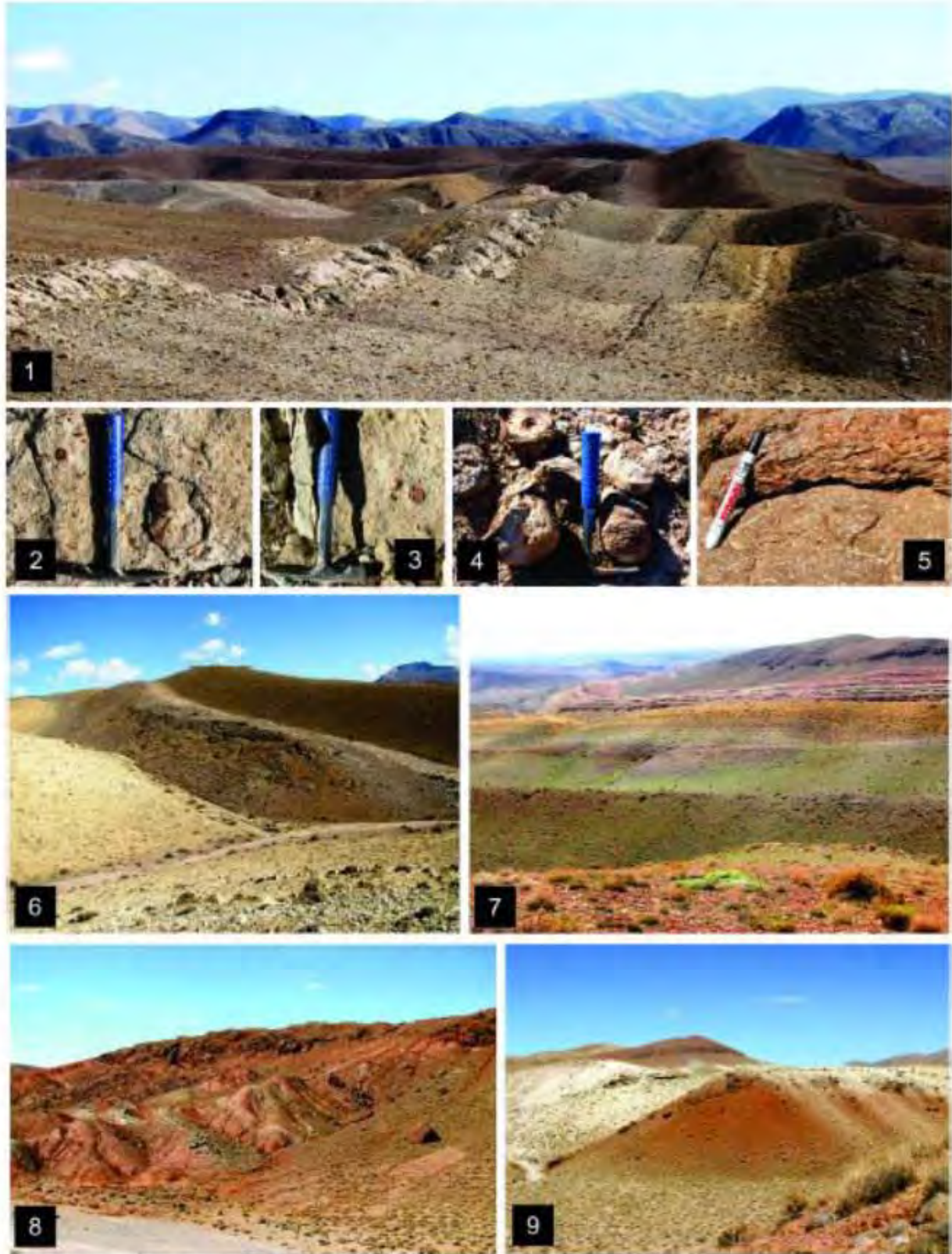


Figure 2.1. General view of the Sarakab syncline with indication of the crustacean horizon in studied carbonate level. 2, 3, Silicified echinoids, bivalve and foraminifers found below and within the studied carbonate horizon. 4, Oyster rich level at the top of the carbonate horizon. 5, Silicified foraminifer horizon 2 m above the Oyster rich level. 6, Igneous (trachy-andesite) below the carbonate level. 7, General view of the Sarakab syncline with indication of conglomerate levels at the base and top of the carbonate horizon. 7, Paleocene red clastic and continental deposits at base of studied profile. 9, Paleocene Eocene boundary (red to white) transitional level.

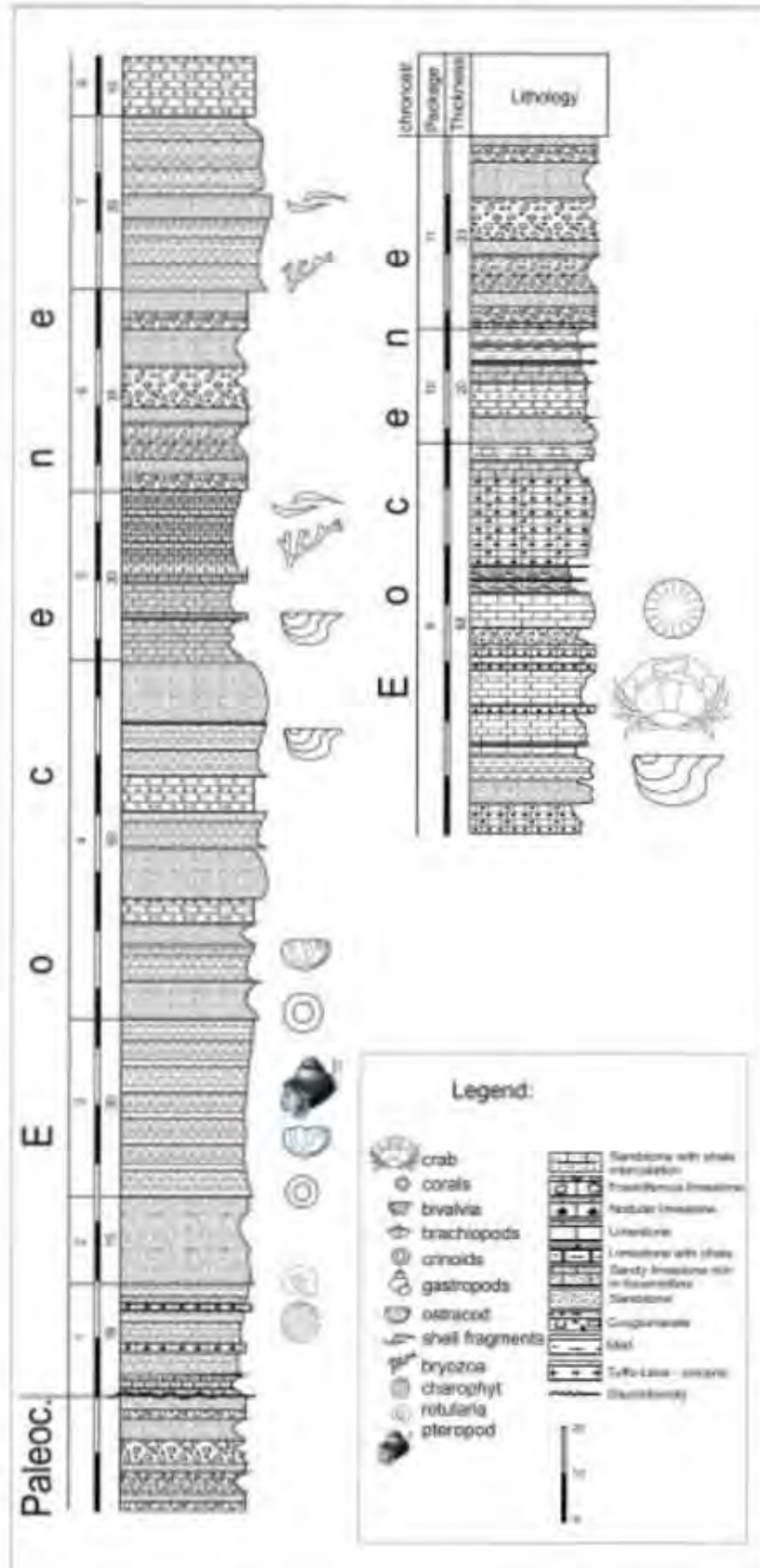


Figure 3. Stratigraphic profile of study section.



Figure 4. *Retrocypoda almelus* Via Bouda, 1939: 1: EUC 2238, Bartonian (middle Eocene) of Soh (Tafahan, Iran). 2: MGB 70438, Priabonian (late Eocene) of Yebrá de Basa (Huesca, Spain). 3: CPC-1840, Bartonian (middle Eocene) of La Pobla de Claramunt (Añoia, Catalonia). 4: MCZ 2727, Lutetian of Grola, (Vicenza, Italy). 5: AO C-023/6, Priabonian (late Eocene) of Yebrá de Basa (Huesca, Spain). Scale bar equal to 10 mm.

- 330, fig. 41, t. 38, f. 4, t. 39, ff. 1–5.
- 1980 *Retrocypoda almelai* Via Boada, 1959; Via Boada, p. 58, t. 1, f. 5.
- 1982 *Retrocypoda almelai* Via Boada, 1959; Via Boada, p. 18, f. 1.
- 1985 *Retrocypoda almelai* Via Boada, 1959; Vela, p. 22.
- 1988 *Retrocypoda almelai* Via Boada, 1959; Via, p. 351, f. 343.G.
- 1989 *Retrocypoda almelai* Via Boada, 1959; Solé and Via, p. 31.
- 1989 *Retrocypoda almelai* Via Boada, 1959; de Saint Laurent, p. 143–150, t. 6, ff. A–E, t. 7, ff. A–G.
- 1996 *Retrocypoda almelai* Via Boada, 1959; Beschin *et al.*, p. 96, fig. 5, t. 2, f. 1.
- 2001 *Retrocypoda almelai* Via Boada, 1959; De Angeli and Beschin, p. 28, f. 21.3.
- 2006 *Retrocypoda almelai* Via Boada, 1959; De Angeli and Garassino, p. 52.
- 2007 *Retrocypoda almela* Via Boada, 1959; Feldmann and Portell, p. 91.
- 2010 *Retrocypoda almelai* Via Boada, 1959; Schweitzer *et al.*, p. 100.
- 2011 *Retrocypoda almelai* Via Boada, 1959; De Angeli *et al.*, p. 41, T1.
- 2013 *Retrocypoda* Via Boada, 1959; Guinot *et al.*, p. 140, 216.
- 2015 *Retrocypoda almelai* Via Boada, 1959; Jagt *et al.*, p. 887, 880, f. 71–15.6, B–C.

Description. Carapace medium sized; subrectangular, wider than long (ratio 0.80), maximum width at midlength of carapace; sculptured, finely granulated; crossed by four more or less marked transverse ridges. Frontal margin long; front very narrow, not present; supraorbital margin long, sinuous; strong outer orbital tooth broken. Lateral margins convex; laterally stepped, inward directed anteriorly, finely spiny; anterolateral margins gently arched toward the anterior corner, posterolateral margins convex, posteriorly convergent; posterior margin long, slightly convex, rimmed. Anterior first ridge straight medially, and downward oblique laterally crossing the protogastric and hepatic regions; second ridge sinuous, with rounded edge, acute in mesogastric lobe, crossing mesogastric and epibranchial regions; third ridge acute, downward oblique, short, traverses from epi- and mesobranchial regions to branchicardiac groove; posterior fourth ridge upward oblique, short, crossing mesobranchial and cardiac regions, interrupted by branchicardiac groove. Epigastric lobes slightly inflated; protogastric lobes slightly swollen; mesogastric lobe well marked, bounded and separated from narrow metagastric lobes by deep cervical groove; urogastric region depressed; cardiac lobe rhomboidal, slightly swollen; intestinal region depressed. Gastric pits present between meso- and metagastric lobes.

Material. One specimen, EUIC 2238.

Measurements (in mm). Length = 39.9 Width =

51.6, Fronto-orbital width = 32.3. Ratio L/W = 0.77; ratio FOW/W = 0.62.

Discussion. The Iranian specimen of *Retrocypoda almelai*, dorsally well preserved (Fig. 4.1), fits perfectly with the Iberian and Italian specimens of this species (Fig. 4.2 – 4.5), being noteworthy in its unusual larger size (51 mm width). This discovery expands the paleobiogeographic range of this species, so far considered endemic of the Western Tethys. It was recovered in a sandy limestone level attributed to the Bartonian. Accompanying fauna such as bivalves, gastropods and oyster layers, indicates a nearshore environment (Janssen *et al.*, 2013).

The apparent confinement of *Retrocypoda* to the Mediterranean margin of Western Tethys might not be such, in light of this new discovery in Iran, and to attribute this apparent confinement to the lack of fossil record in other Tethyan areas. However, the fossil record shows that Europe and especially the area of the western end of Tethys (comprised between northern and eastern of Iberian Peninsula and northern Italy), comprises the highest stock of retroplumids genera during the Eocene, higher than any other geological epochs, including the present time, namely: *Gaudipluma* Artal, Van Bakel *et al.*, 2013, *Loerenthopluma* Beschin *et al.*, 1996, *Loerenthoplumopsa* Schweitzer *et al.*, 2011 (see *Loerenthaya* Beurlen in Lörenthey and Beurlen, 1929), *Retrocypoda* Via Boada, 1959, *Retropluma* Gill, 1894 (2 species) and *Serrabiopluma* Artal *et al.*, 2013, which have their first occurrences mainly in the mentioned area since the early Eocene. This fact might support in part, the hypothesis of Hyžný *et al.* (2016) according to which, ancestors of these Tethyan retroplumids, would have to be found among the African lineage of *Costacopluma* Collins and Morris, 1975, for instance *C. senegalensis* (Rémy in Gorodiski and Rémy, 1959) from the Paleocene of Senegal, which is geographically and temporally closest to the aforementioned area of the Western Tethys (Hyžný *et al.*, 2016, p. 153). We concur, at least regarding *Retrocypoda* which is *Costacopluma*'s closest genus, differing from it in their spiny lateral margins medially convex, carapace sculpture and by its supplementary fourth transverse ridge, instead of the three in *Costacopluma*.

Since de Saint Laurent (1989) clarified the retroplumid condition of *Retrocypoda almelai*, subsequent authors, with some exceptions, accepted this systematic placement (e.g. Beschin *et al.*, 1996; De Angeli and Beschin, 2001; De Angeli and Garassino, 2006; Feldmann *et al.*, 2006; McLay, 2006; Feldmann and Portell, 2007; Hyžný and Müller, 2010; Schweitzer *et al.*, 2010; De Angeli *et al.*, 2011 and Hyžný *et al.*, 2016). We can add in support of the retroplumid condition of *Retrocypoda*, that besides the contrasted presence of modified and reduced sternite 8 and reduced coxa of P5 (Via, 1969, p. 335; de Saint Laurent, 1989, T7, fig. A–B), some samples preserved in matrix of *Retrocypoda almelai* from outcrops of Central Catalonia, preserved remains of the reduced subcylindrical P5 (See appendix). However, *Retrocypoda* possesses stronger and

more developed chelipeds, markedly heterochelic, mainly in males, characterised by long palms with acute upper margin, with short and stout dactily, unlike most of other retroplumid genera whose chelipeds are usually slender and thin with elongate and sharp tipped dactily (Via, 1969, p. 329; de Saint Laurent, 1989, p. 113-114, f.7; McLay, 2006, p. 389). These cheliped features can be observed also in some samples of *Costacopluma nordestina* Feldmann and Martins-Neto, 1995 (cfr. Távoras and Miranda, 2004, fig. 5), thus arguing in favor of the close relationship of *Retrocypoda* with *Costacopluma*.

Extant and Miocene-Pleistocene retroplumids prefer deep water with muddy or muddy sand bottoms, in contrast to the Paleogene fossil record (de Saint Laurent, 1989; Collins et al., 2003; De Angeli et al., 2011; Baldanza et al., 2013; Gásparič and Hyžný, 2014). *Retrocypoda* dwelt in muddy sandy or sandy bottoms, in shallower waters from inner to outer continental platform. Occurrences of *Retrocypoda* during Ypresian to Bartonian indicates a nearshore environment, whereas the Priabonian occurrences are on muddy soft bottom of an offshore environment (see Abad, 2001; Beschin et al., 2012; Ossó et al., 2014 and herein).

5. Discussion and conclusions

Extant members of Retroplumidae, *Retropluma* and *Bathypluma* are reported only in Indo-West Pacific waters. The Iranian *Retrocypoda aimelai* documents the presence of the family in the Middle East during the Eocene (Fig. 5), as does *Costacopluma cf. concava* Collins and Morris, 1975, recorded in the uppermost Maastrichtian of northern India (Gaetani et al., 1983) and *Retropluma laurentae* Collins et al., 2003 in the Miocene of Indonesia. Therefore, albeit being represented by very scarce taxa, Retroplumidae is documented in the Middle and Eastern Tethys during the Late Cretaceous and Cenozoic. This means either that Retroplumidae inhabited simultaneously from the Atlantic coast of America to the coast of Africa and the eastern Tethys, though the fossil record is scarce in those eastern areas, or rather, that the eastward migratory trend, widely discussed by the majority of works above mentioned, was real (Fig. 6). Given the abundant retroplumid stock of Atlantic, represented by *Costacopluma* in the Late Cretaceous and the varied Cenozoic retroplumid stock of the West Tethys, the second hypothesis seems more plausible for the time being. It is noteworthy that unlike other retroplumid genera, which generated different species through time, *Retrocypoda* remains monotypic during the whole Eocene.

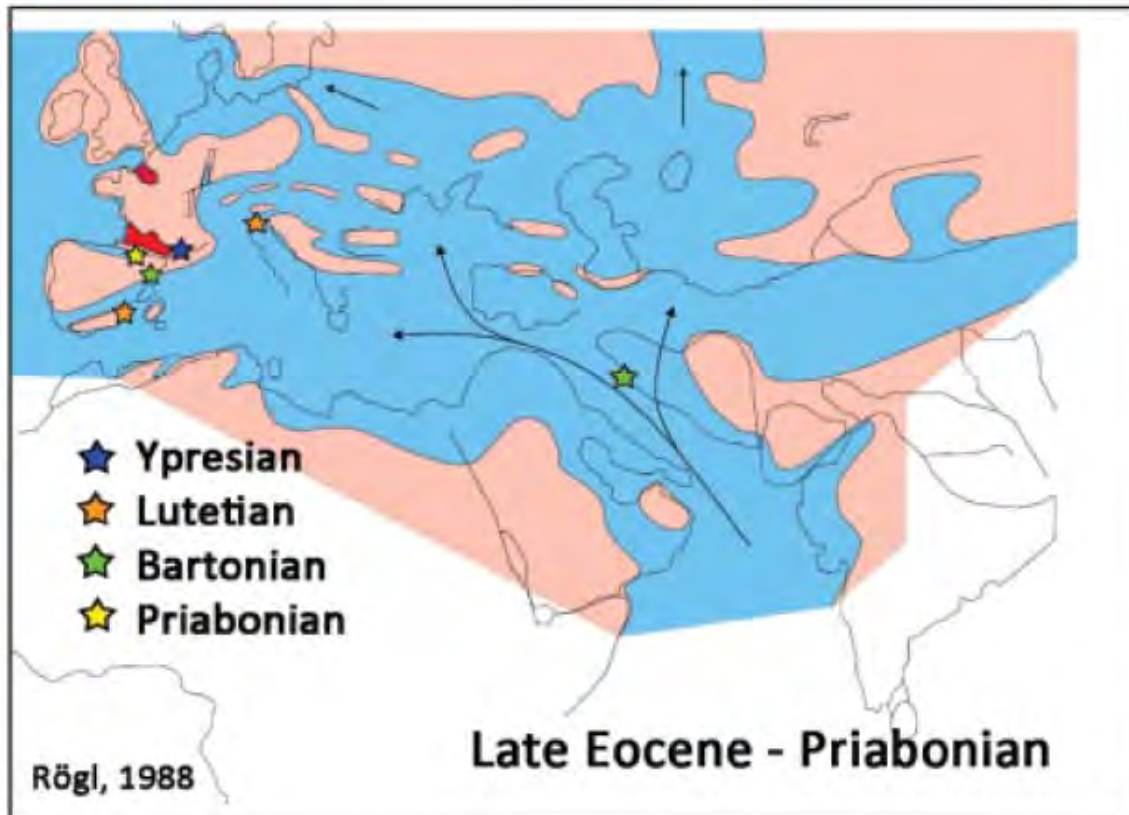


Figure 5. Approximate distribution of *Retrocypoda* during the Eocene (modified from Rögl, 1998).

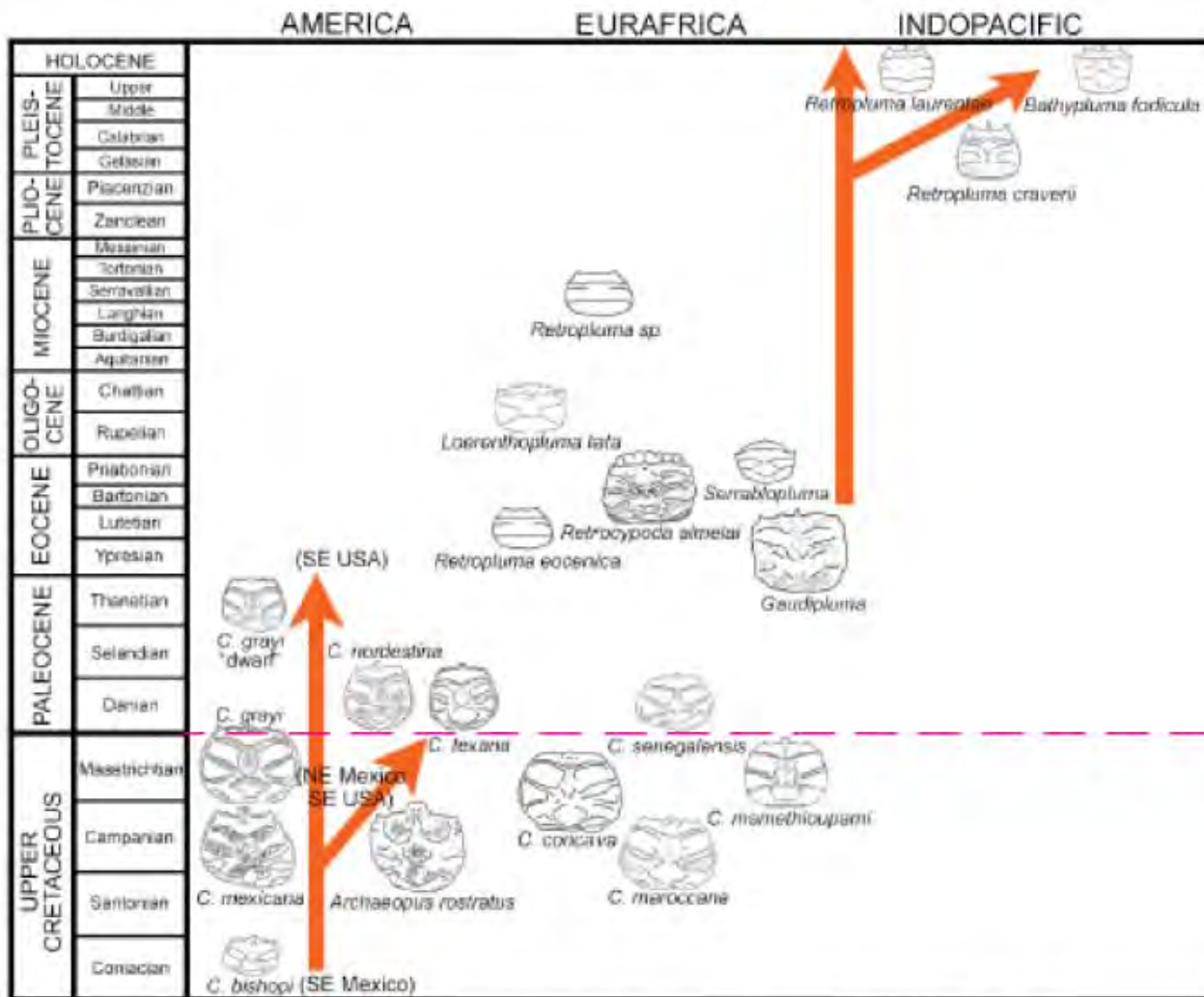


Figure 6. Paleobiogeographic distribution of Retroplumidae since Late Cretaceous (modified from Via, 1969).

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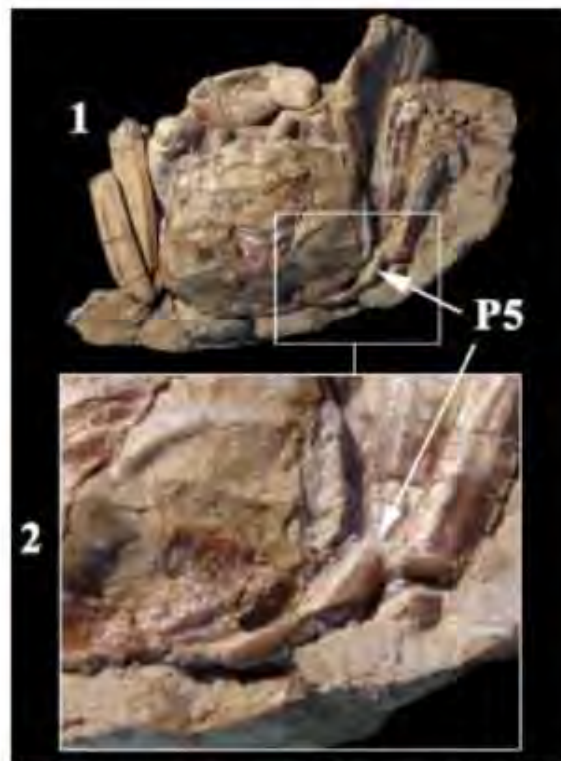
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Appendix. *Retrocypoda aimelai* Via Boada, 1959. AO C-023/4, Bartonian (middle Eocene) of La Pobla de Claramunt (Anoia, Catalonia). 1: Dorsal view; 2: close-up showing the reduced P5. Abbreviations: P5 = fifth pereopod. Scale bar equal to 10 mm.

LATE CRETACEOUS BRACHYURAN CRUSTACEANS FROM NORTHEASTERN MEXICO

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Abstract—Late Cretaceous (Campanian-Maastrichtian) brachyuran crustaceans from NE Mexico represent an interesting assemblage of species preserved in different environments, revealing their potential to fit to extreme conditions, such as marine hydrothermalism or hypersaline water affected by salt tectonics. Here we present a preliminary interpretation of the paleoecology, distribution and extinction of the decapod species with a fossil record from this region of the ancient Gulf of Mexico, including unpublished and undescribed specimens, some of which may represent new taxa. Although some previous works have considered that decapod crustaceans were not severely affected by the K/Pg event, our data reveal that in NE Mexico only one species seemed to be able to survive, through a strategy known as the Lilliput effect.

INTRODUCTION

Shallow marine lithostratigraphic units of NE Mexico include an interesting assemblage of Campanian-Maastrichtian (Late Cretaceous) crustaceans (Decapoda: Brachyura). Beyond the systematic importance of these crustaceans, they represent an opportunity to study the evolution and ecological features of the different groups that inhabited the ancient Gulf Coast of Mexico. Since the most abundant species and genera became extinct during the K/Pg event, it is important to try to understand their ecological role, habitat and distribution in order to offer possible explanations for their extinction.

The first fossil decapod crustaceans from Mexico were reported by Rathbun (1930, 1935), who described a few species from Cretaceous, Paleogene and Neogene deposits. Other reports include a few Cretaceous species (Stenzel, 1944; Alencaster, 1977). Today, more than 50 fossil crustacean species are known from Cretaceous (Barremian) to Miocene (Aquitainian) deposits in Mexico (Vega et al., 2009). Several Maastrichtian species are known from Coahuila, Nuevo Leon, San Luis Potosí (NE Mexico) and Chiapas (SE Mexico), but most of them are found in Campanian-Maastrichtian deposits of the Difunta Group and the Cárdenas Formation in NE Mexico (Fig. 1).

We offer a review and discussion of the regional distribution and habitat of the decapod crustacean species reported from the Campanian-Maastrichtian shallow marine deposits of NE Mexico, including some preliminary new records. The detailed position of fossiliferous localities at La Popa and in the Parras Basin is given in Figure 2.

DECAPOD SPECIES, LOCALITIES AND PALEOENVIRONMENT

Zygostrocarinus carolinaensis Klompmaker,
Flores-Ventura and Vega, 2013

Fig. 3A

The small, molted carapace of this species allows us to illustrate the oldest figured example of a fossil humulid sternum for the genus and also of the entire section of a fossil homoloid. It also represents the southernmost occurrence of the genus in the Americas. The specimen was collected in shallow marine to deltaic plain facies of the Late Campanian Cerro del Pueblo Formation, Parras Basin, Coahuila, NE Mexico.

Dakoticancer australis Rathbun, 1935

Fig. 3B-F

The second crustacean species to be reported from the Difunta Group and the Cárdenas Formation (NE Mexico) is *Dakoticancer australis*, a robust, medium-sized crab, previously reported from the early to middle Maastrichtian of Mississippi and Texas (Rathbun, 1935; Bishop, 1986), in localities where it is very abundant. The species is found in the Cerro del Tale Formation and Lower Mudstone Member of the Potrerillos Formation (both formations of the Difunta Group), where it occurs mostly as molts, although a few corpses of juveniles were found (Fig. 3B), one in the Paredón locality (Fig. 2), associated

with other species with red cuticle. The specimens are numerous and represented by corpses with attached appendages in black, calcareous concretions (Fig. 3C-D) found at the base of the El Gordo limestone lentil (Fig. 2), developed as a rudist-corals-calcareous-algae biostrome at the top of the El Gordo diapir during middle Maastrichtian time (Lawton, 1984, 1996; Lawton et al., 2001; Giles and Lawton, 2002). In the Cárdenas Formation, it is also found as corpses, some with attached appendages in shallow marine sandstones (Vega et al., 1995), and a few wider specimens that may represent sexual dimorphism (Fig. 3E). Dakoticancerid crabs became extinct by the late Maastrichtian (but before the K/Pg event), perhaps as a result of the cooling of sea waters, since the carapace of *Dakoticancer* is more calcified in comparison to the other Late Cretaceous crabs. The short fingers of the dakoticancerid crabs suggest that they were scavengers.

Sodakus mexicanus Vega, Feldmann and Villalobos-Hiriart, 1995
Fig. 3F-I

Schweitzer and Feldmann (2011) and Karasawa et al. (2011) considered *Sodakus* as a dakoticanceroid, likely closer to Ibericanceridae based on its sternal configuration, which in turn differs mainly from Dorippoidea in that the latter has much broader sternites. We think



FIGURE 1. Location map of the Difunta Group and Cárdenas Formation in NE Mexico (Campanian-Maastrichtian), where all of the Late Cretaceous decapod species are found.

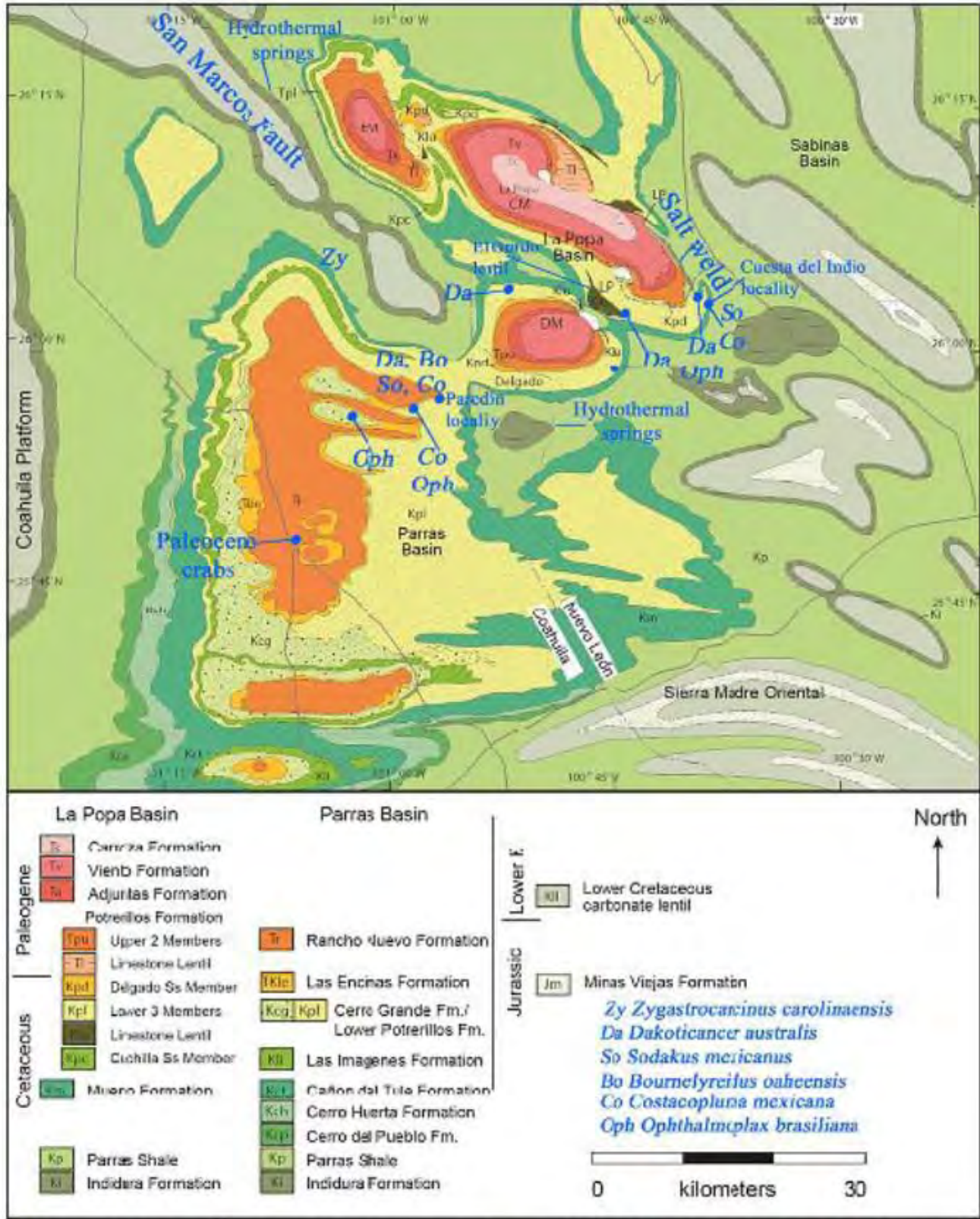


FIGURE 2. Detailed position of Maastrichtian fossiliferous localities at Parras and La Popa basins, with distribution of studied crustacean species. Modified from Lawton et al. (2009).

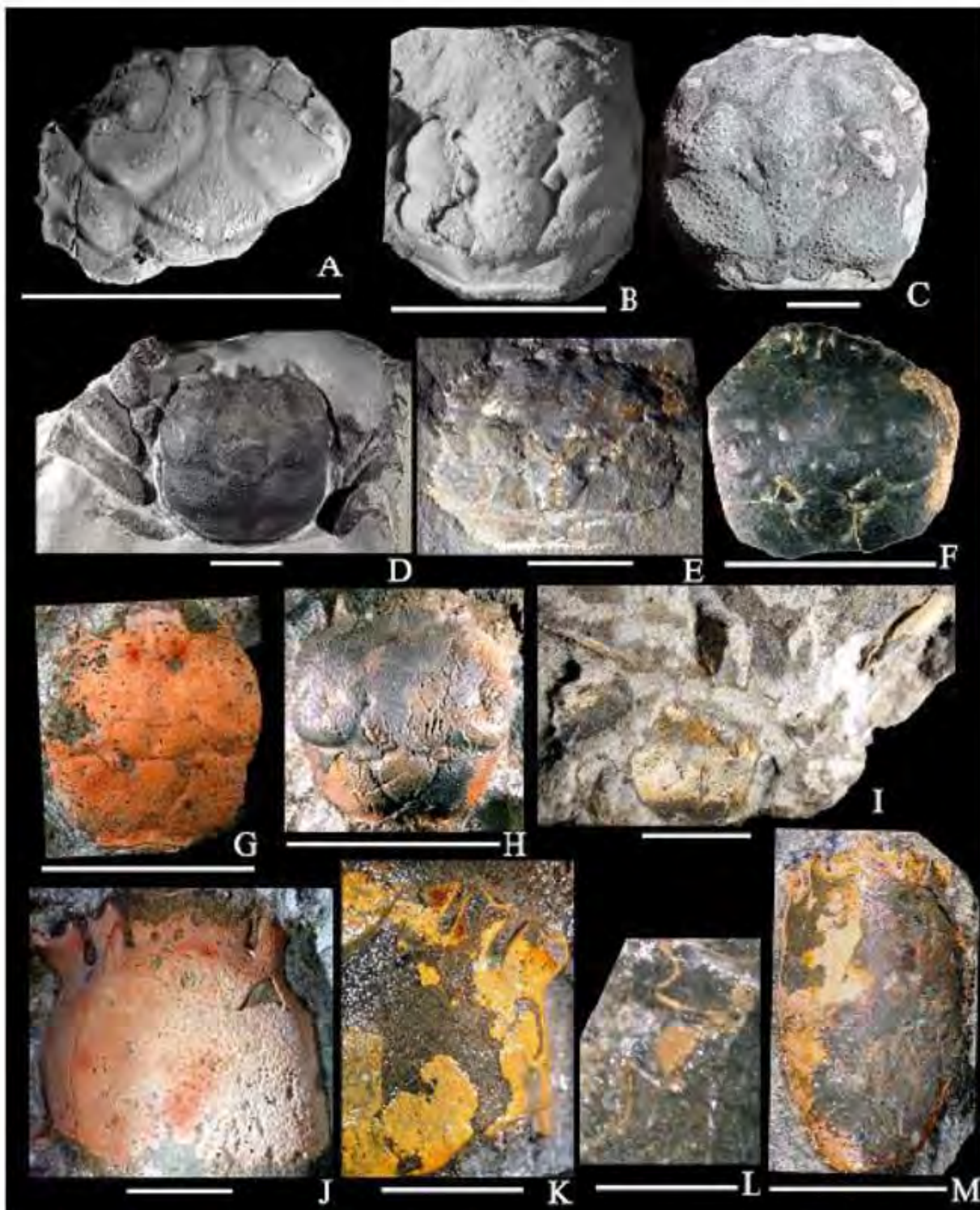


FIGURE 3. A, *Zygastocarcinus carolinaensis* Kloumpnaker, Flores-Ventura and Vega, 2013, Late Campanian Cerro del Pueblo Formation (Parras Basin), Coahuila, NE Mexico. B-E, *Dakoticancer australis* Rathbun, 1935, B, Juvenile specimen, Early Maastrichtian Lower Mudstone Member, Potrerillos Formation (La Popa Basin), Nuevo León, NE Mexico. C, D, Specimens in calcareous concretions, El Gordo Lenti, Early Maastrichtian Lower Mudstone Member, Potrerillos Formation (La Popa Basin), Nuevo León, NE Mexico. E, Possible sexual dimorphism, Early Maastrichtian Cárdenas Formation, San Luis Potosí, NE Mexico. F-I, *Sodakus mexicanus* Vega, Feldmann and Villalobos-Hiriart, 1995. F, Specimen replaced by hydroxyapatite, Cuesta del Indio, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (La Popa Basin), Nuevo León, NE Mexico. G-I, Red cuticle specimens, Paredón, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (Parras Basin), Coahuila, NE Mexico, note long pereopods next to carapace in I. J-M, *Bournefyreidus oahuensis* (Bishop, 1978), Red cuticle specimens, Paredón, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (Parras Basin), Coahuila, NE Mexico. J-L, Details of front with bifid anterior spines. M, Complete carapace. Scale bars = 1 cm.

this is not correct, and a review of the systematic affinities of *Sodakus mexicanus* is in progress.

S. mexicanus was first reported from the early Maastrichtian Lower Siltstone Member of the Potrerillos Formation, represented by only a few molts (Fig. 3F), whose cuticle was replaced by hydroxyapatite as a result of the influence of the salt weld in the La Popa Basin (Fig. 2). It has also been found at the Paredón locality (Parras Basin) (Fig. 2) as numerous, red-cuticle corpses (Fig. 3G, 3H), some with articulated long and slender pereopods (Fig. 3I) and cuticle of carapaces also affected by the hydrothermalism of the San Marcos fault (see *Costacopiluma mexicana* Vega and Perrilliat, 1989, this chapter). Small chelae of these crabs suggest they fed on organic matter. A juvenile of *Dakotancancer australis* was found at the Paredón locality, and it is interesting to note that while in South Dakota the decapod assemblage was dominated by *D. overanus* Rathbun, 1917, at the Paredón locality the dominant species seems to be *C. mexicana*. *Sodakus tatanakoyotankaensis* Bishop, 1978 was reported together with *Dakotancancer overanus* and the raninoid *Bournehyreidus oahensis*, formerly reported from the late Campanian to early Maastrichtian Pierre Shale of South Dakota (Bishop, 1978).

***Bournehyreidus oahensis* (Bishop, 1978)**

Fig. 3J-M, 4E

Bishop (1978) described *Raninella oahensis* based on about 20 small specimens, whose preservation is relatively poor. Although most of the carapaces are complete, the anterolateral spines are broken and do not show the bifid spines that are visible in some specimens from the Paredón locality (Fig. 2). The species was placed questionably into the genus *Bournehyreidus* by van Bakel et al. (2012). Posteriorly, Karasawa et al. (2014) confirmed placement of the species in the genus. The small size and delicate anterolateral spines prevent a complete preservation of the carapaces, and, in fact, only partial red carapaces have been recovered from the Paredón locality (Fig. 3J-M), but among these fragments, complete fronts with four bifid anterolateral spines and carapaces lacking a cervical groove suggest that the small red raninoids from the early Maastrichtian Lower Siltstone Member of the Potrerillos Formation are to be assigned to *B. oahensis*, reported also from the same age strata of Montana, North Dakota and the Fox Hills Formation of South Dakota (Tucker et al., 1987; Crawford et al., 2006). These small raninoids fed probably on organic matter and small invertebrates associated with the hydrothermal environments near the San Marcos fault.

***Costacopiluma mexicana* Vega and Perrilliat, 1989**

Fig. 4A-F

The first crustacean species reported for the Difunta Group (McBride et al., 1974) and the Cárdenas Formation (Myers, 1968) (NE Mexico) is *Costacopiluma mexicana* (Vega and Perrilliat, 1989; Vega et al., 1995a), a relatively abundant retropiumid crab of small to medium size (2 to 6 cm in width), whose distribution during the early Maastrichtian reached Mississippi and central Texas (Martínez-Díaz et al., 2016). Only one specimen was reported from the Cárdenas Formation (Fig. 4A), where this species seems to be scarce. In the Difunta Group, the species is found in late Campanian deposits of the Cerro del Pueblo Formation (Eberth et al., 2004) preserved as concretions with detached cuticle (Fig. 4B).

In early Maastrichtian deposits, *C. mexicana* is found in the Lower Siltstone Member of the Potrerillos Formation, where it occurs in different facies and with different preservation styles. One specimen is found complete and preserved within a gallery, and some other specimens are found in gray siltstone of prodeltaic sediments (Fig. 4C). However, it is represented in higher numbers as silicified remains (Fig. 4D) at a peculiar locality (Cuesta del Indio, Fig. 2), affected regionally by salt tectonics in a feature known as a weld (Giles and Lawton, 1999), which may be topographic ridge in the sea floor, where silica was abundant due to the exsorption of Jurassic evaporites. Here, the population of *C. mexicana* is represented by juveniles (less than 1 cm in width), adults (5 cm in width), corpses and exuviae; preservation of the cuticle is outstanding (Vega et al., 1994). Red specimens (Fig. 4E, 4F) are also found (juveniles and adults) in high numbers at the Paredón locality (Fig. 2) of the Lower Siltstone Member of the Potrerillos Formation, found near the San Marcos fault, which today is still expressed as hydrothermalism in at least two localities of Coahuila (Espinazo and Icamole). The red color of the cuticle is interpreted here as result of the influence of hydrothermalism, as this kind of preservation is also found in decapod crustaceans from the Cretaceous of Japan (Karasawa, 2011). This locality is interesting, since it includes

the most diverse assemblage of crustaceans, including *Dakotancancer australis*, *Bournehyreidus oahensis* (Fig. 4E), *Sodakus mexicanus* and other fragmentary decapods. The red color of the cuticle in *C. mexicana* is related to iron found in layers of the exo and endocuticle (Vega et al., 2005). The high diversity and abundance may be related to organic matter and methane associated with the hydrothermal deposits.

***Costacopiluma grayi* Feldmann and Portell, 2007**

Fig. 4G-H

Costacopiluma is one of the decapod crustacean genera to survive the K/Pg event, and although it became extinct by the Eocene, it seems that a Lilliput effect may have helped the latest Cretaceous species to survive (Martínez-Díaz et al., 2016). *Costacopiluma grayi* was first described from the Paleocene and Eocene of Alabama (Feldmann and Portell, 2007; Feldmann et al., 2014), represented by numerous, small (width = 1 cm) carapaces. According to Martínez-Díaz et al. (in press), the species arose in latest Maastrichtian (66.2 Ma) shallow marine environments of the Las Encinas (NE Mexico) and Owl Creek (Mississippi) formations (Vega et al., 2013; Phillips et al., 2014), represented by middle-sized carapaces (Fig. 4G, 4H), and the species was able to survive across the K/Pg event, through an evolutionary process known as the Lilliput effect (size reduction and increase in number of individuals), reported also for other invertebrate groups (Martínez-Díaz et al., 2016). Modern retropiumids live in deep waters of the Indo-Pacific region, and their main feature is the presence of reduced, plumose fifth pereopods that help the crabs in the collection of organic matter as a food source (Saint Laurent, 1989). If those appendages were present in Cretaceous species of *Costacopiluma*, then this generalist feeding strategy may have helped this crustacean family (retropiumid crabs) to survive.

***Ophthalmoplax brasiliensis* (Maury, 1930)**

Fig. 4I-K

Reported as *Mascaranada difuntaensis* by Vega and Feldmann (1991), *Ophthalmoplax brasiliensis* is found in the early Maastrichtian (70.0 Ma) Lower Siltstone Member of the Potrerillos Formation (middle-size carapaces, Fig. 4I), the late Maastrichtian (66.8 Ma) Cerro Grande Formation (large-size carapaces, Fig. 4J) and the latest Maastrichtian (66.2 Ma) Las Encinas Formation (middle-size carapaces, Fig. 4K). Vega et al. (2013) suggested that this portunoid species was affected by cold, shallow marine water and had a noticeable increase in carapace size 66.8 Ma ago, when sea waters reached an important decrease in temperature. *O. brasiliensis* had fifth pereopods modified as paddle-like structures that helped to swim and hide in the sand. The species was distributed in shallow marine (lagoon) paleoenvironments from Brazil to North Carolina, where it is very abundant in late Maastrichtian lithostratigraphic units. The movable finger of the right chela show a strong, bulbous structure to help crush mollusk shells, while the left chela is sharp and must have been an excellent tool to cut and tear apart soft tissues. This suggests that *O. brasiliensis* was an active predator, which became extinct during the K/Pg event.

***Branchiocarcinus flectus* (Rathbun, 1923)**

Fig. 5A-C

This portunoid crab has a fragile carapace of small to middle size. It is known from the early to latest Maastrichtian of Mississippi, New Jersey and San Luis Potosí (Phillips et al., 2014). The sharp and spiny morphology of the chelae of this species suggest it was an active predator of small invertebrates. Its absence in the Difunta Group may be related to the delicate nature of the carapace and paleoenvironments of high energy, compared with the more stable, lagoon paleoenvironments of San Luis Potosí. The Icriocarcinidae seem to have a wide distribution during the Late Cretaceous (late Campanian-latest Maastrichtian) in France, Spain, the Atlantic and Gulf coasts and the Pacific coast of California and Baja California (Teodori et al., 2013; Nyborg et al., 2014; Phillips et al., 2014).

Mathildellidae Karasawa and Kato, 2003

Fig. 5D-L

A possible new genus of Mathildellidae crab is found in one locality of the late Campanian Cerro del Pueblo Formation (Parras Basin, Coahuila), associated with more abundant specimens of *Costacopiluma mexicana*, in a nearshore paleoenvironment where these crabs are preserved as concretions. The molted carapaces lack cuticle, but a few preserve dorsal and ventral regions of the carapace, with features that suggest affinity with the Mathildellidae. If this affinity is confirmed, this

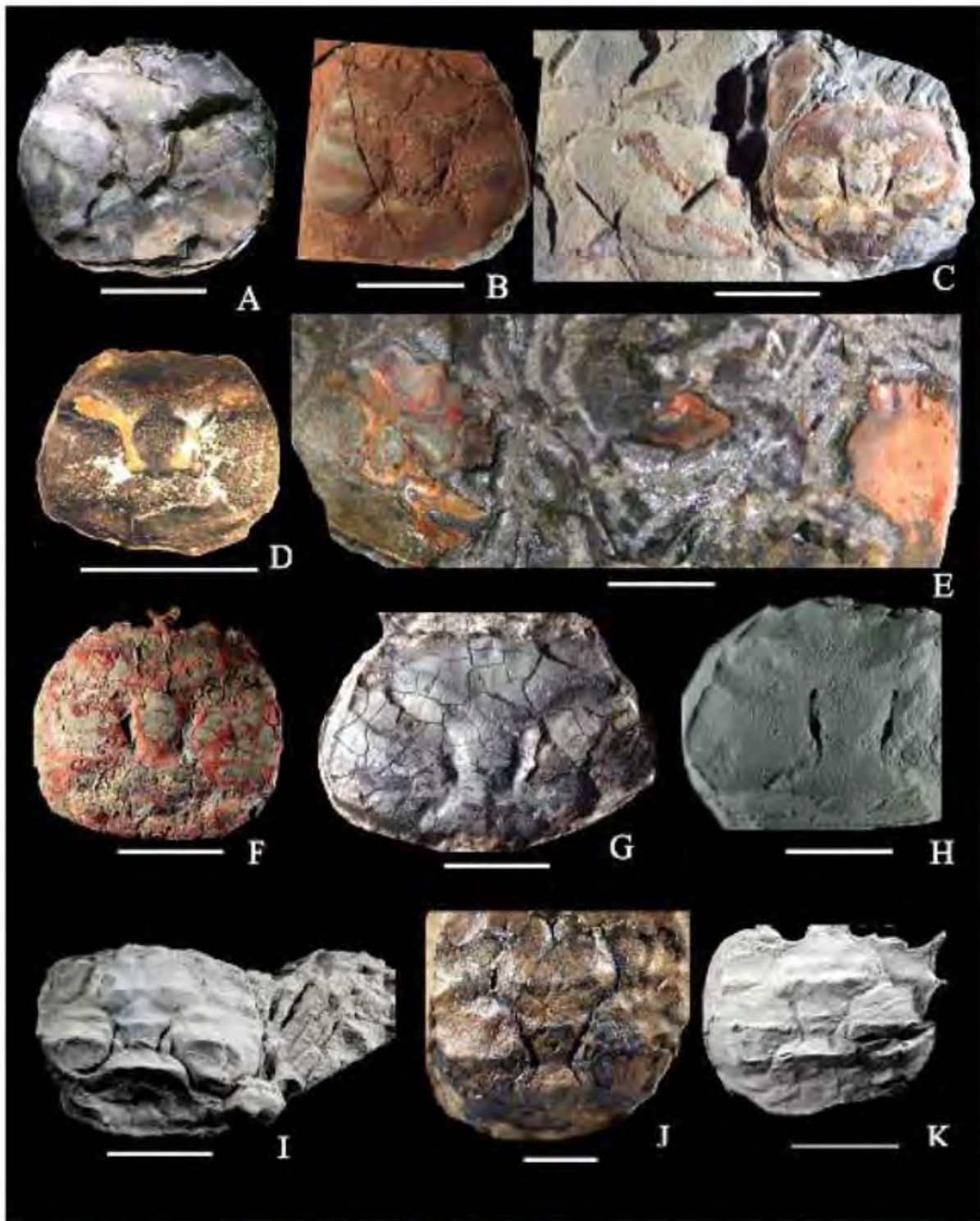


FIGURE 4. A-F, *Costacoplona mexicana* Vega and Perrilliat, 1989. A, Early Maastrichtian Cárdenas Formation, San Luis Potosí, NE Mexico. B, Late Campanian Cerro del Pueblo Formation (Parras Basin), Coahuila, NE Mexico. C, Specimen with articulated pereopods, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (Parras Basin), Coahuila, NE Mexico. D, Juvenile specimen replaced by hydroxycapatite, Cuesta del Indio, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (La Popa Basin), Nuevo León, NE Mexico. E, Red cuticle specimen (left) next to *Bournelyreidus oahoenziz* (Bishop, 1978) (right), Paredón, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (Parras Basin), Coahuila, NE Mexico. F, Red cuticle specimen, Paredón, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (Parras Basin), Coahuila, NE Mexico. G, H, *Costacoplona grayi* Feldmann and Portell, 2007, Arroyo Amargos, Latest Maastrichtian Las Encinas Formation (Parras Basin), Coahuila, NE Mexico. I-K, *Ophthalmoplax brasiliana* Maury, 1930. I, Early Maastrichtian Lower Siltstone Member, Potrerillos Formation (La Popa Basin), Nuevo León, NE Mexico. J, Late Maastrichtian Cerro Grande Formation (Parras Basin), Coahuila, NE Mexico. K, Arroyo Amargos, Latest Maastrichtian Las Encinas Formation (Parras Basin), Coahuila, NE Mexico.

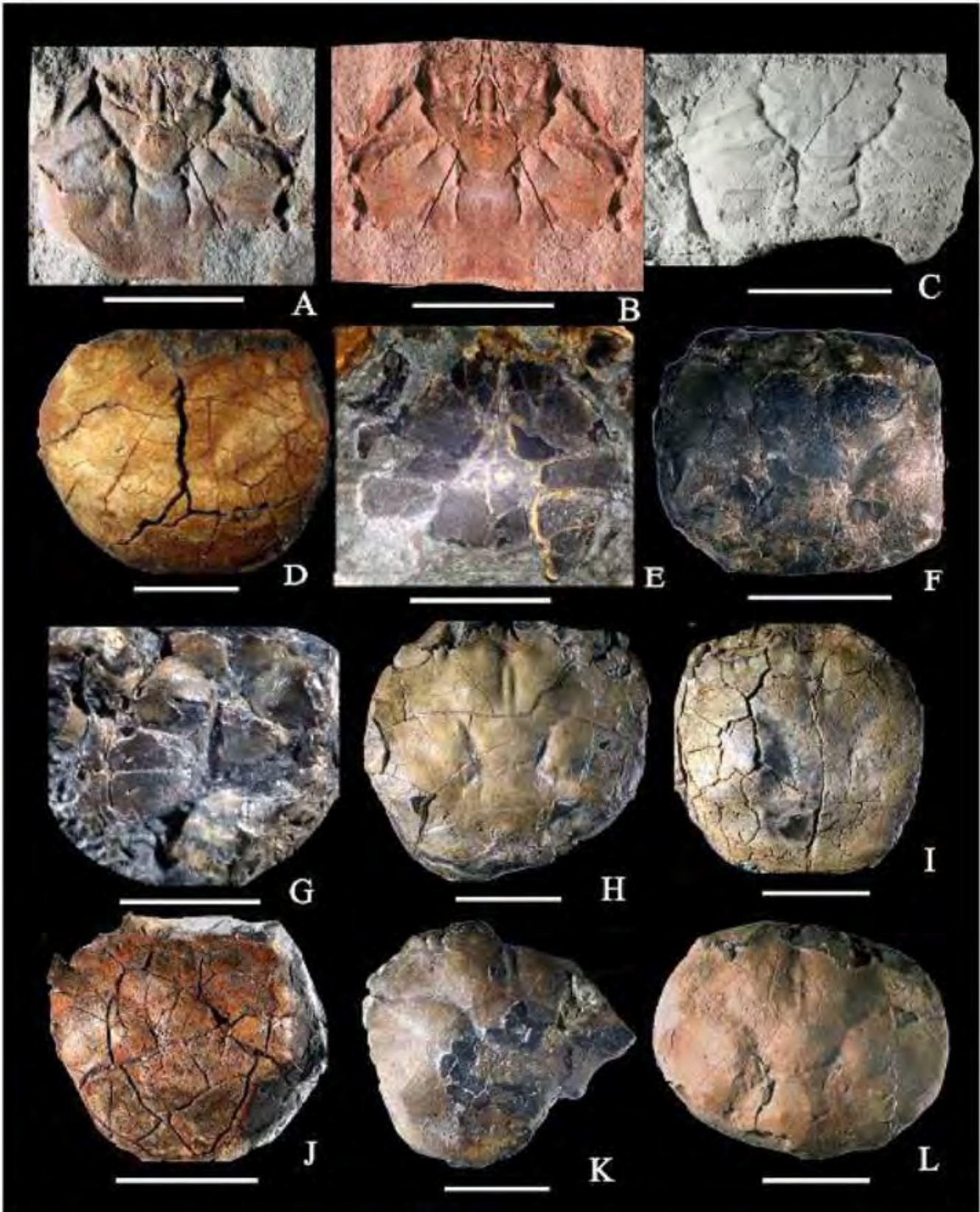


FIGURE 5. A-C, *Branchiocarcinus flectus* (Rathbun, 1926). A, Early Maastrichtian Cárdenas Formation, San Luis Potosí, NE Mexico. B, C, Latest Maastrichtian, Owl Creek Formation, Mississippi. D-L, Mathildellidae, dorsal and ventral views of possible new genus, Late Campanian Cerro de Pueblo Formation (Parras Basin), Coahuila, NE Mexico. Scale bars = 1 cm.

could be the earliest record for the family, which according to Castro (2007) and Ng et al. (2008), belongs to the Goneplacoidea MacLeay, 1838. The formal description of this possible new genus and species is in progress.

CONCLUSION

The study of the Late Cretaceous decapod crustaceans is crucial to understand the evolution and extinction of many groups that were dominant during Maastrichtian time. According to Schweitzer and Feldmann (2005), decapod crustaceans were not severely affected by the K/Pg event. However, Maastrichtian shallow marine decapod assemblages of NE and SE Mexico show that only a few genera were able to continue their presence in Paleocene strata of the same region. A decrease in size of the species that were able to survive the K/Pg event has been recorded for some invertebrate groups, and for the moment, only one species of *Costacopluma* seems to have been able to survive,

due to a strategy known as the Lilliput effect (Martinez-Diaz et al. 2016).

The preservation potential of crab species varies according to the calcification of their carapace and taphonomic features. Most late Maastrichtian assemblages of NE Mexico and SE USA are not very diverse, compared to the diversity found in early Paleocene shallow marine deposits of the same area (see Vega et al., 2007; Armstrong et al., 2009). Although several decapod genera prevail in the early Paleocene, most of the latest Maastrichtian species became extinct, and more diverse assemblages of smaller brachyurans founded the successive evolution of this important crustacean group. Figure 6 indicates the stratigraphic distribution of most of the species mentioned in this chapter, mainly those found in lithostratigraphic units of the Difunta Group (Parras and La Popa basins), where a preliminary scenario of the evolution of Late Cretaceous brachyuran species can be envisioned.

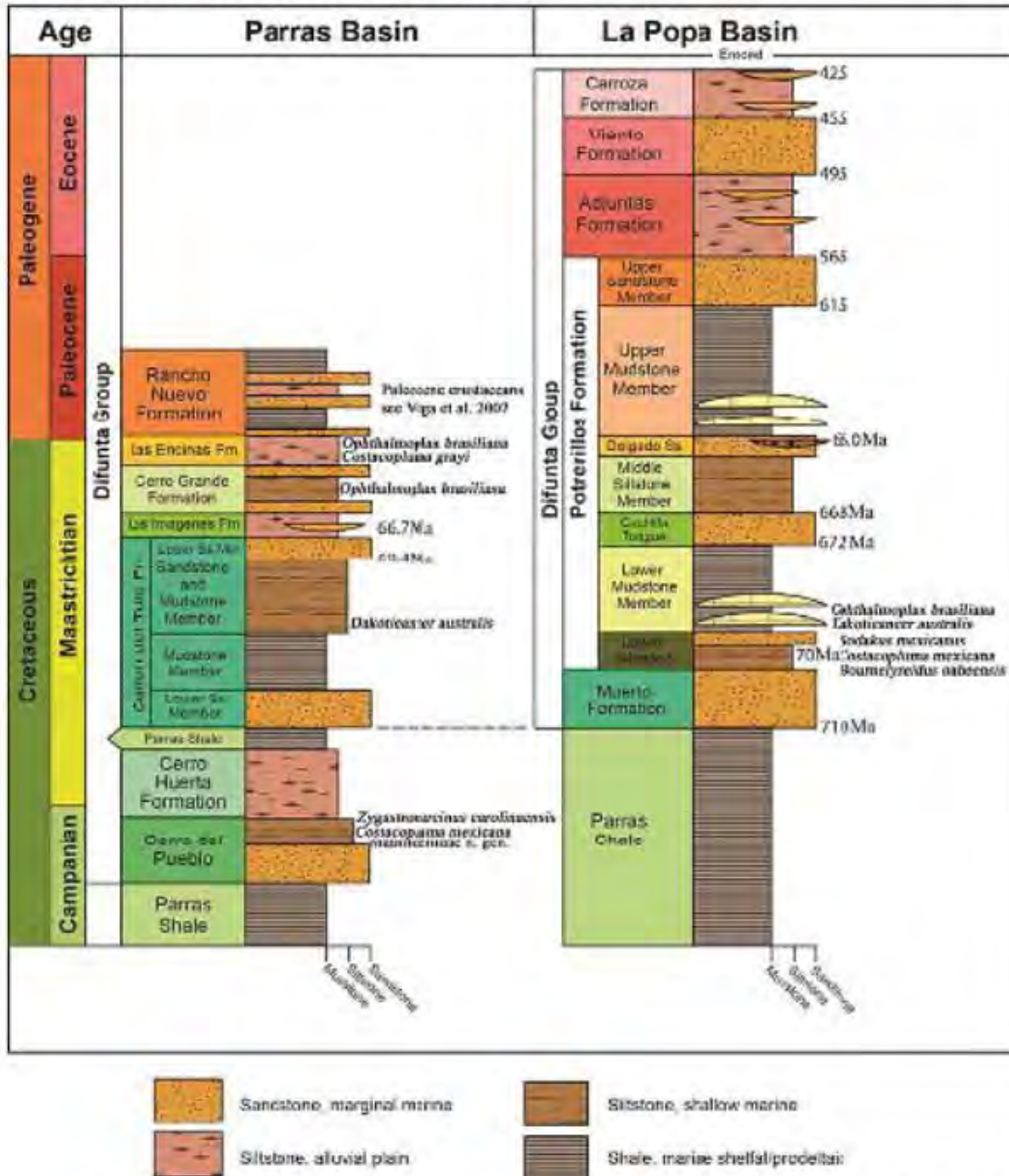


FIGURE 6. Stratigraphic distribution of most of the brachyuran species mentioned in this chapter, mainly those found in lithostratigraphic units of the Difunta Group (Parras and La Popa basins). Modified from Lawton et al. (2009).

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CRUSTÁCEOS FÓSILES DE NUEVO LEÓN Y COAHUILA

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Los estados de Nuevo León y Coahuila incluyen un rico legado fosilífero. En el municipio de Mina afloran rocas del Cretácico y Paleoceno, que fueron estudiadas y caracterizadas por McBride y colaboradores (1974), con base en la secuencia de sedimentos depositados en aguas poco profundas, hace unos 70 millones de años. En el Cañón de Potrerillos se encuentran varios afloramientos, de los cuales se han recuperado fósiles de invertebrados en distintas localidades (Vega y Perilliati, 1989a; 1995). La parte inferior de la Formación Potrerillos (Sierra El Antrisco) (figura 1) es la que ha aportado la mayoría de los hallazgos, principalmente crustáceos fósiles. Por su parte, en las inmediaciones de Paredón (Coahuila), se encuentran también importantes localidades fosilíferas que mencionaremos más adelante.

Los cangrejos representan un grupo de invertebrados sumamente numeroso y abundante en la actualidad, sin embargo, su registro fósil es escaso, comparado con el de otros invertebrados, como los moluscos. Dado que los cangrejos (y artrópodos en general) presentan crecimiento por

ecdisis (mudas), su registro fósil puede estar representado tanto por cuerpos como por exuvias; la cutícula de quitina y el carbonato de calcio son los elementos que se preservan en el registro fósil, en ocasiones, con un excepcional estado (Vega, Jackson y Ossó, 2014). Los primeros trabajos formales en cangrejos fósiles para México fueron realizados por Rathbun (Rathbun, 1930; 1935), quien reportó especies del Cretácico, Paleógeno y Neógeno (Vega, Nyborg y Perilliati, 2006; Vega, *et al.*, 2016). Posteriormente se describirían algunas especies para el Cretácico de San Luis Potosí y Guerrero (Stenzel, 1944; Alencáster, 1977). En 1989

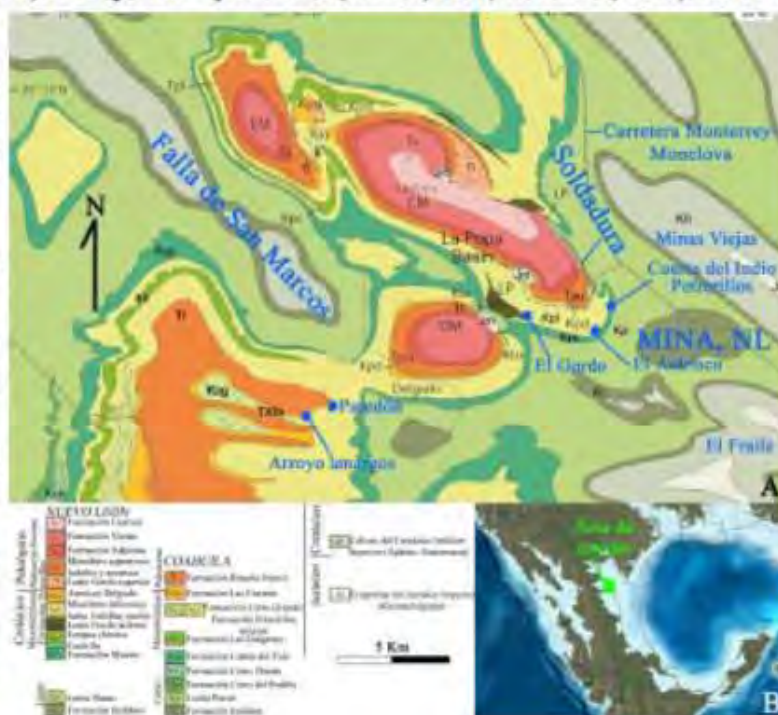


Figura 1. A. Mapa geológico correspondiente a los municipios de Mina y Paredón, con ubicación aproximada de localidades fosilíferas, modificado de Lawton *et al.* (2009). B. Paleogeografía del noreste de México, hace aproximadamente 70 millones de años, se enmarca el área correspondiente al mapa (área de estudio), reproducido con autorización de Ron Blakey.

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se reportó el cangrejo retroplúmido *Costacopluma mexicana* (figura 2 A y B), que representa el primer crustáceo fósil para Nuevo León y el primer reporte del género para América (Vega y Perrilliat, 1989b). Hallazgos posteriores en esta zona del municipio de Mina incluyen *Ophthalmoplax brasiliana* (figura 2C) originalmente descrita como *Mascaranada difimtaensis* (Vega y Feldmann, 1991) y *Sodakus mexicanus* (Vega, Feldmann y Villalobos, 1995; figura 2 D y E). Otro hallazgo importante fue el del cangrejo *Dakoticancer australis* (Vega y Feldmann, 1991; figura 2F), que también se encuentra en rocas de edad similar, en el área de Ciudad del Maiz, San Luis Potosí. A pesar del escaso trabajo inicial sobre paleontología de crustáceos decápodos fósiles, en la actualidad los estudios van en aumento, con más de 50 especies de crustáceos fósiles conocidas para México con edades que van desde el Cretácico Temprano (Barremiano, 127 millones de años) hasta el Mioceno (Aquitaniense, 23 millones de años) (Vega, Nyborg y Perrilliat, 2006; Vega *et al.*, 2016). Aunque se conocen varias especies de otras localidades de los estados de Baja California, San Luis Potosí y Chiapas, la mayor parte corresponde a especies encontradas en la sierra El Antrisco. El número cada vez mayor de ejemplares fósiles recuperados ha permitido interpretar el ambiente en que vivían estas

especies. En particular, resulta interesante la excelente preservación del cangrejo *Costacopluma mexicana*, encontrado en la Cuesta del Indio, y que corresponde a un alto topográfico del fondo marino, en donde hace 70 millones de años existía un ambiente hipersalino, con aporte de sílice, lo que permitió que la cutícula de esta especie se preservara de manera excepcional (Vega, Feldmann, y Dávila, 1994). En esta misma localidad, algunos ejemplares del pequeño cangrejo *Sodakus mexicanus* (Vega, Feldmann y Villalobos, 1995) fueron encontradas con excelente grado de preservación. Ambas especies se encuentran también cerca de los límites entre Nuevo León y Coahuila, en donde la falla de San Marcos pudo afectar el ambiente marino, ya sea a través de zonas de termalismo o surgencia de materia orgánica (metano), que en una localidad de Japón (Karasawa, 2011) permitió la preservación de la cutícula de los crustáceos, con un color rojo peculiar (Vega, *et al.*, 2016; figura 2G). El tipo de roca en el cual se preservan los crustáceos decápodos aporta información crucial sobre el paleoambiente en el que vivían (Vega, *et al.*, 2016). La mayor parte de los sedimentos en los que se han preservado los decápodos fósiles en el NE de México corresponden a ambientes de tipo marino-somero, como pueden ser deltas, lagunas, y arrecifes. En este último caso, llama la atención la preservación

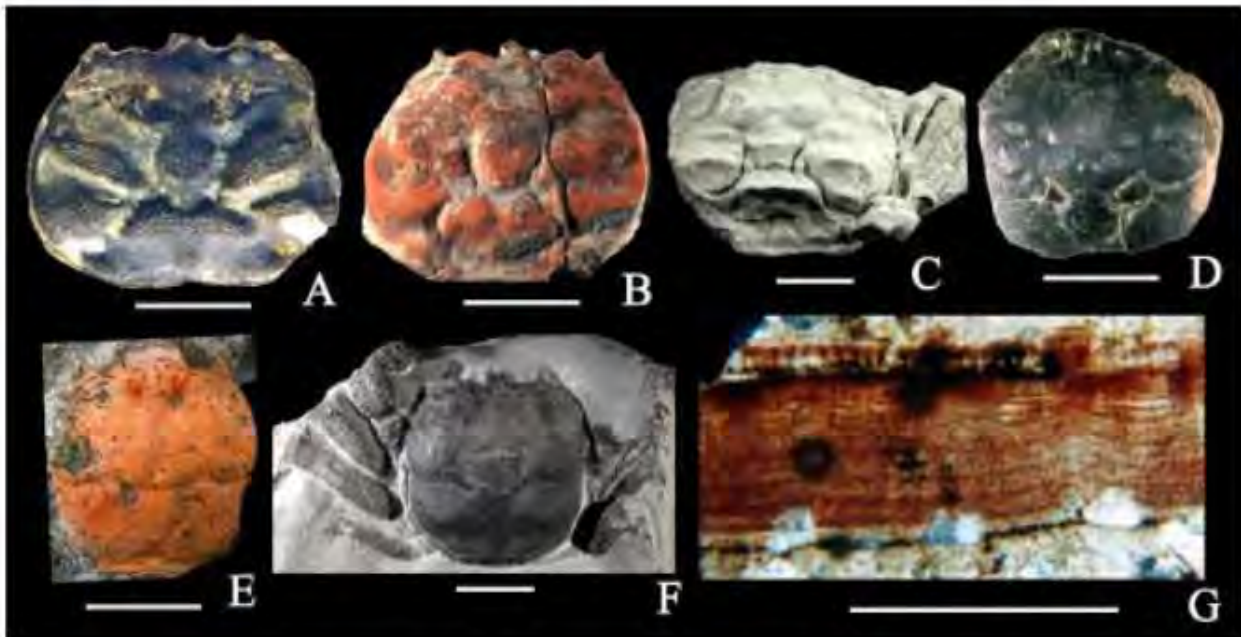


Figura 2. A y B, *Costacopluma mexicana*, ejemplares de la Cuesta del Indio (A, influencia de evaporitas) y de Paredón (B, influencia de surgencia de metano y hidrotermalismo). C, *Ophthalmoplax brasiliana*, Mina, Nuevo León. D y E, *Sodakus mexicanus*, ejemplares de la Cuesta del Indio (D, influencia de evaporitas) y de Paredón (E, influencia de surgencia de metano e hidrotermalismo). F, *Dakoticancer australis*, ejemplar preservado en concreción calcárea, lente El Gordo, sierra El Antrisco, Nuevo León. G, sección microscópica de la cutícula del caparazón de *Costacopluma mexicana*, preservando la estructura original, por influencia de minerales relacionados a surgencia de metano de la falla de San Marcos, Coahuila. Barras de escala = 1 cm, excepto en G = 0.1 cm.

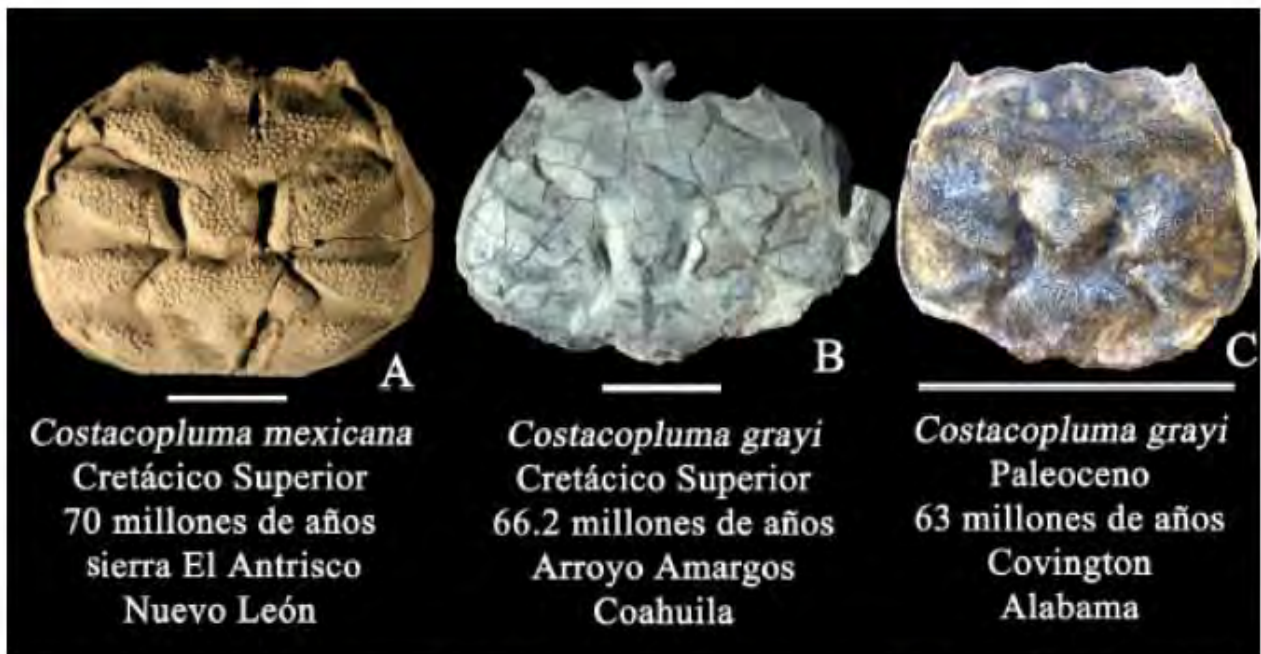


Figura 3. A, *Costacopluma mexicana*, ejemplar de talla mediana, Cretácico Terminal (70 millones de años), sierra El Antrisco, Nuevo León. B, *Costacopluma grayi*, ejemplar de talla mediana, Cretácico Terminal (66.2 millones de años), Arroyo Amargos, Coahuila. C, *Costacopluma grayi*, ejemplar de talla pequeña, Paleoceno (aproximadamente 65 millones de años), Alabama, EUA. Barras de escala = 1 cm.

de *Dakoticancer australis* en la lente El Gordo (parte de la sierra El Antrisco), ya que se encuentra en concreciones calcáreas sumamente duras y difíciles de limpiar, pero el resultado es interesante, considerando las características preservadas del caparazón (Vega *et al.*, 2016).

PALEOECOLOGÍA Y EL EVENTO DE EXTINCIÓN K/Pg

De caparazón robusto y dedos cortos, es posible que *Dakoticancer australis* se alimentara de carroña, aunque se extinguió a finales del Cretácico, antes del evento K/Pg. *Ophthalmoplax brasiliana*, una especie de amplia distribución durante el Maastrichtiano (hace 70 a 66 millones de años), estaba adaptada para el nado activo y poseía quelas apropiadas para la depredación posiblemente de moluscos (Vega *et al.*, 2016). *Costacopluma mexicana* fue una especie dominante hace 70 millones de años. Los miembros actuales de la familia *Retroplumidae* se caracterizan por tener un último par de patas de tipo plumoso, lo que les permite alimentarse recolectando materia orgánica. Es posible que las especies de *Costacopluma* hayan tenido el mismo tipo de alimentación, como parte de una estrategia generalista que permitió la supervivencia de la familia. Un ejemplo de estrategias de supervivencia ha sido docu-

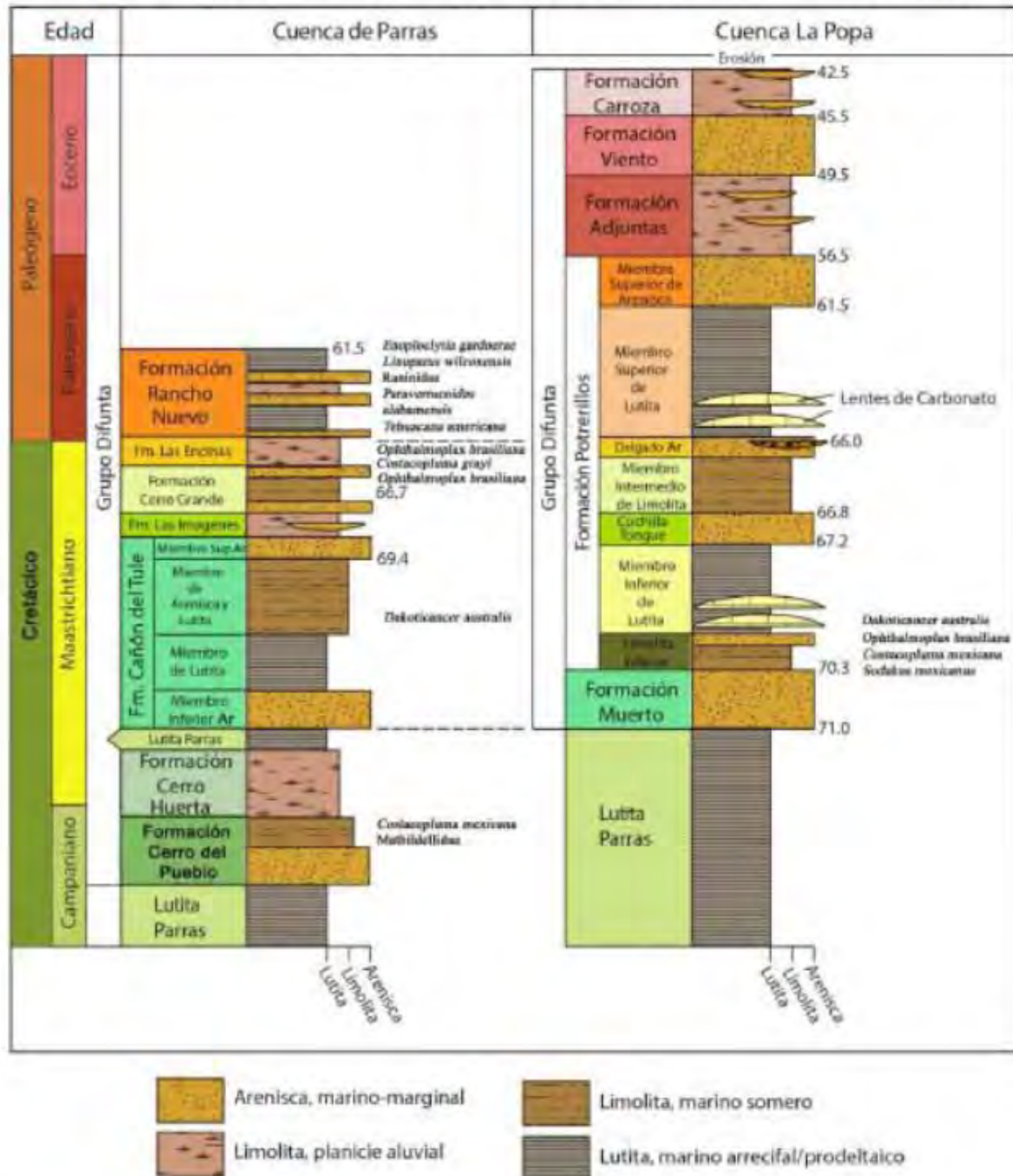
mentado recientemente para la especie *Costacopluma grayi* (Vega *et al.*, 2016; Martínez *et al.* 2016), inicialmente descrita para el Paleoceno y Eoceno de Alabama, a partir de numerosos individuos de talla pequeña. La misma especie fue reportada para una localidad cercana a Paredón, Coahuila, en rocas de una edad cercana a la extinción de los dinosaurios (66.2 millones de años), con individuos de una talla casi tres veces mayor y de tamaño similar a *C. mexicana*, especie de la que pudo derivar *C. grayi* (figura 3). Se ha propuesto que *C. grayi* pudo sobrevivir gracias al desarrollo de la estrategia conocida como efecto Liliput (Martínez *et al.*, 2016), que es la tendencia a la reducción de la talla corporal como respuesta a eventos de extinción masiva, fenómeno también observado en otros grupos de invertebrados. *Costacopluma grayi* ha sido encontrada junto con *Ophthalmoplax brasiliana* en el mismo afloramiento cercano a Paredón, lo que indica que las especies coexistieron seguramente diferenciadas por su nicho ecológico, siendo las especies de *Costacopluma* recolectoras de materia orgánica en suspensión; por su parte, *O. brasiliana* era un depredador con capacidad de nado, semejante a las actuales jaibas. *Costacopluma mexicana* se extinguió 800 mil años antes del evento K/Pg (66 millones de años), aunque se ha propuesto como posible ancestro de *Costacopluma grayi* con base en la presencia de ambas especies en localidades de la misma región. Una vez establecida en el NE de México y SE de Estados Unidos, *C. grayi* sobrevivió a la extinción

del K/Pg, reduciendo su talla a causa del efecto Liliput.

CONCLUSIONES

El estudio de los crustáceos decápodos fósiles en México representa una oportunidad para conocer la distribución, ecología, evolución y extinción de distintos grupos de cangrejos, lo cual requiere de un trabajo sistemático (básicamente, descripción de especies) que

ha crecido en las casi tres décadas de estudio, y que continúa conforme a los nuevos descubrimientos. El análisis de las poblaciones a través de distintos rangos temporales ha permitido observar patrones que ofrecen explicaciones sobre la persistencia o desaparición de grupos durante eventos de extinción, en particular la correspondiente al Cretácico/Paleógeno, que en el noroeste de México está bien documentada, con base en estudios de las faunas de crustáceos del Cretácico Tardío y Paleógeno (figura 4). Los estudios a futuro no sólo



enriquecerán la diversidad de los crustáceos decápodos fósiles, también permitirán una mejor comprensión de los fenómenos biológicos y sus interacciones con el ambiente.

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