



Boletín de la Sociedad Geológica  
Mexicana

ISSN: 1405-3322

[sgm\\_editorial@geociencias.unam.mx](mailto:sgm_editorial@geociencias.unam.mx)

Sociedad Geológica Mexicana, A.C.  
México

Hyžný, Matúš; Vega, Francisco J.; Coutiño, Marco A.  
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Boletín de la Sociedad Geológica Mexicana, vol. 65, núm. 2, 2013, pp. 255-264  
Sociedad Geológica Mexicana, A.C.  
Distrito Federal, México

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## Ghost shrimps (Decapoda: Axiidea: Callianassidae) of the Maastrichtian (Late Cretaceous) Ocozocoautla Formation, Chiapas (Mexico)

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### Abstract

On the basis of newly collected material, two ghost shrimp taxa from the lower Maastrichtian Ocozocoautla Formation in Chiapas (Mexico) are recorded. *Callianassa burckhardti* is reassigned to *Eucalliax*, which extends the known fossil record of this genus to the early Maastrichtian. A new species, *Callianassa* (s.l.) *ocozocoautlaensis*, is described based on a single specimen whose state of preservation does not enable a firm generic assignment, despite the fact that the material exhibits striking similarities to extant *Callianassa modesta*, occasionally treated as a member of the genus *Cheramus*. The fossil record of ghost shrimps from Mexico is briefly reappraised and their survival across the K/Pg boundary is discussed. The conservative body plan of ctenochelid and callianassid taxa is emphasized and it is postulated that virtually all major ghost shrimp clades were already established well before the Cenozoic.

Keywords: Callianassidae, *Eucalliax*, *Callianassa*, Ocozocoautla Formation, Maastrichtian, Mexico.

### Resumen

Con base en material recientemente colectado, se reportan dos taxa de camarones fantasma de la Formación Ocozocoautla del Maastrichtiano inferior de Chiapas (México). *Callianassa burckhardti* es reasignada a *Eucalliax*, por lo que el registro fósil del género respectivo se extiende al Maastrichtiano temprano. Una especie nueva, *Callianassa* (s.l.) *ocozocoautlaensis*, se describe con base en un solo espécimen, cuya preservación no permite la identificación confiable a nivel de género, aunque el material exhibe fuertes afinidades con la especie existente *Callianassa modesta*, que en ocasiones es tratada como un miembro de *Cheramus*. El registro fósil de camarones fantasma de México es brevemente reevaluado, y se discute su supervivencia a través del límite K/P. Se enfatiza el plan conservativo de los taxa de ctenoquélidos y calianásidos, y se postula que virtualmente todos los clados mayores de camarones fantasma se establecieron antes del Cenozoico.

Palabras Clave: Callianassidae, *Eucalliax*, *Callianassa*, Formación Ocozocoautla, Maastrichtiano, México.

## 1. Introduction

Mexican fossil ghost shrimps have previously been recorded by Vega *et al.* (1995a, b, 2001a, b, 2007, 2008, 2009) and Schweitzer *et al.* (2006a, b). These occurrences are briefly summarized in Table 1. The present contribution adds new data on Mexican fossil ghost shrimps by recording *Callianassa burckhardti* Böhm, 1911 for the first time in Mexico, and by transferring it to *Eucalliax* Manning and Felder, 1991. In addition, a new form, *Callianassa* (*s.l.*) *ocozocautlaensis* n. sp., is described from the same strata. The generic placement of the single specimen available to date is obscure, although both chelipeds are preserved, which is usually enough for generic identification (compare Hyžný, 2012; Hyžný and Hudáčková, 2012).

## 2. Localities and geological setting

The specimens recorded herein stem from two localities exposing the Ocozocautla Formation, northeast of Tuxtla Gutiérrez, near the Tuxtla-Veracruz motorway (Figure 1). The ‘Megaxantho locality’ is situated on the east side of that motorway, 25.2 km NW of Tuxtla Gutiérrez, with coordinates 16°48′13.57″N, 93°20′58.35″W. The holotype, and sole specimen known, of *Callianassa* (*s.l.*) *ocozocautlaensis* n. sp. was collected here. Specimens of *Eucalliax burckhardti* (Böhm, 1911) n. comb. originate from the ‘Reptiles locality’, on the west side of the motorway, 39.86 km NW of Tuxtla Gutiérrez, with coordinates 16°54′36.02″N, 93°26′56.26″W.

The type section of the Ocozocautla Formation is situated northwest of the town of the same name. It is 630 m thick, comprising red and brown prodeltaic sandstones, and some conglomerate at the base. Towards the top, the lithology changes to shale, marl and limestone of a beige colour (Gutiérrez-Gil, 1956; Chubb, 1959; Frost and Langenheim, 1974). Channels are exposed at some localities.

Lateral lithologic changes within the formation indicate changes in depth of the basin, from shallow, restricted, lagoonal conditions in the East to deeper, outer platform settings in the Northwest. The Ocozocautla Formation is underlain by the Sierra Madre Limestone, which is Early to middle Cretaceous in age (Steele and Waite, 1986), and is conformably overlain by the Paleocene Soyaló Formation (Frost and Langenheim, 1974; López-Ramos,

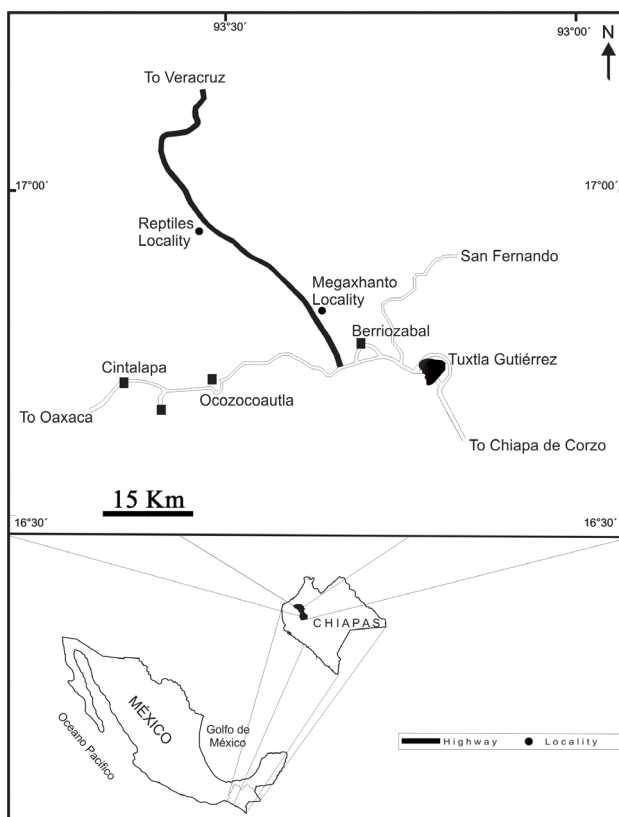


Figure 1. Map showing the two localities of the Ocozocautla Formation from which the specimens studied were collected, near Tuxtla Gutiérrez (Chiapas, Mexico).

Table 1. Synopsis of Mexican callianassid and ctenochelid ghost shrimp occurrences; for details, see the text.

Taxon	Age	Main references	Remarks
<i>Rathbunassa aquilae</i>	Turonian	Vega <i>et al.</i> (2007); Bermúdez <i>et al.</i> (2013)	as <i>Gourretia aquilae</i>
undescribed form	Turonian	Vega <i>et al.</i> (2007)	as <i>Gourretia aquilae</i>
? <i>Eucalliinae</i> gen. et spec. indet.	Maastrichtian	Vega <i>et al.</i> (1995a)	as ? <i>Callianassa</i> sp.
? <i>Cheramus</i> sp.	Maastrichtian	Vega <i>et al.</i> (1995b)	
? <i>Vegarthron</i> sp.	Maastrichtian	Vega <i>et al.</i> (1995b)	
<i>Eucalliax burckhardti</i>	Maastrichtian	herein	
<i>Callianassa</i> ( <i>s.l.</i> ) <i>ocozocautlaensis</i> n. sp.	Maastrichtian	herein	
? <i>Neocallichirus</i> sp.	Eocene	Schweitzer <i>et al.</i> (2005); Vega <i>et al.</i> (2008)	as <i>Neocallichirus</i> cf. <i>rhinos</i>
<i>Callianassidae sensu lato</i> species 1	Eocene	Schweitzer <i>et al.</i> (2005); Vega <i>et al.</i> (2001b, 2008)	
<i>Callianassidae sensu lato</i> species 2	Eocene	Schweitzer <i>et al.</i> (2005)	? <i>Glypturus</i>
<i>Callianassidae sensu lato</i> species 3	Eocene	Schweitzer <i>et al.</i> (2005), Vega <i>et al.</i> (2008)	
<i>Callianassidae sensu lato</i> species 4	Eocene	Schweitzer <i>et al.</i> (2005)	? <i>Callianassa matsoni</i>
<i>Callianassidae sensu lato</i> species 5	Eocene	Schweitzer <i>et al.</i> (2005)	
<i>Callianassa pellucida</i>	Miocene	Collins <i>et al.</i> (2009)	
<i>Ctenocheles</i> sp.	Miocene	Vega <i>et al.</i> (2009)	
<i>Neocallichirus aetodes</i>	Miocene, Pliocene	Vega <i>et al.</i> (2009)	

1981; Quezada-Muñetón, 1987). The latter unit is missing in the area studied. Based upon the presence of calcareous algae, benthic foraminifera and rudists (Gutiérrez-Gil, 1956; Chubb, 1959; Robinson, 1968; Michaud, 1988), a lagoonal environment has been suggested for the upper part of the Ocozocoautla Formation. The early Maastrichtian age for most of the formation is based on foraminiferan biostratigraphy (Omaña-Pulido, 1998, 2006; Alencáster and Omaña-Pulido, 2006). Reference is made to Vega *et al.* (2001a) for more details on biostratigraphy.

The material studied is deposited in the Museo de Paleontología "Eliseo Palacios Aguilera", Secretaría de Medio Ambiente e Historia Natural/Dirección de Paleontología, Calzada de los Hombres Ilustres s/n, Colonia Antiguo Parque Madero, Tuxtla Gutiérrez, 29000, Chiapas, México (abbreviation: IHNFG).

### 3. Systematic palaeontology

Order Decapoda Latreille, 1802

Infraorder Axiidea de Saint Laurent, 1979

Family Callianassidae Dana, 1852

Subfamily Eucalliinae Manning and Felder, 1991

**Discussion.** The fossil record of the subfamily and the assignment of the extinct material to its respective genera have recently been discussed by Hyžný (2012) and Hyžný and Hudáčková (2012). As pointed out by the former, numerous fossil taxa originally described under the collective name of *Callianassa* may actually represent members of the subfamily Eucalliinae. As documented here (*i.e.*, transfer of *Callianassa burckhardti* to *Eucalliax*), the genus, and hence the subfamily, was already established during the Late Cretaceous.

Genus *Eucalliax* Manning and Felder, 1991

**Type species.** *Callianassa quadracuta* Biffar, 1970

**Discussion.** The complex taxonomy of the genus has lately been reviewed by Hyžný and Hudáčková (2012) and need not be repeated here. Fossil taxa assigned to *Eucalliax* were listed by Schweitzer *et al.* (2010) and briefly reviewed by Hyžný and Hudáčková (2012). In distinguishing eucalliinae genera, we follow Ngoc-Ho (2003) and Hyžný (2012) rather than Sakai (2011). Hyžný (2012) argued that a square major cheliped manus with distally converging margins, the presence of a ridge on the lateral surface at the base of the fixed finger and a relatively short fixed finger, often with a triangular tooth, are of taxonomic importance for the assignment of material to the subfamily Eucalliinae.

*Callianassa burckhardti* virtually possesses all of the above-mentioned characters. It also clearly shows a propodus/carpus articulation which varies between 90° and 130° (contrary to descriptions by Aguirre-Urreta, 1989

and Feldmann *et al.*, 1995), which is not uncommon within the Eucalliinae. This character was once considered of taxonomic importance for identification of *Protocallianassa* Beurlen, 1930; on this basis alone, numerous callianassid taxa have been assigned to this genus. Hyžný (2012) argued that an oblique carpus/propodus articulation also occurs in members of the subfamily Eucalliinae and that this character in itself could not be considered to be of taxonomic importance on the generic level. Recently, Schweitzer and Feldmann (2012) re-examined the type material of *Callianassa archiaci* A. Milne-Edwards, 1860, the type species of *Protocallianassa*, and documented that the carpus/propodus articulation was in fact straight in that species.

*Eucalliax burckhardti* (Böhm, 1911) **new combination**

Figures 2.1–2.8

1911 *Callianassa burckhardti* Böhm, p. 39, text-fig; Glaessner, 1929, p. 77; Aguirre-Urreta, 1989, p. 540, pl. 60, figs. 12–17; Feldmann, Casadío, Chirino-Galvez and Aguirre-Urreta, 1995, p. 4, figs. 4.2–4.3; Schweitzer, Feldmann, Garassino, Karasawa and Schweigert, 2010, p. 34; Hyžný, 2012, p. 55.

*Protocallianassa* (*Callianassa*) *burckhardti* Böhm: Taylor, 1979, p. 22.

?*Protocallianassa* sp.; Feldmann, Casadío, Chirino-Galvez and Aguirre-Urreta, 1995, p. 6, fig. 4.4.

**Diagnosis.** Callianassid with chelipeds of subequal size and dissimilar in shape.

Major propodus usually square, minor propodus subrectangular, external surface densely beset with tubercles, fixed finger with oblique ridge extending onto the manus, the ridge more pronounced in the minor chela.

**Description.** Major cheliped carpus/propodus articulation at angle 90–100°, carpus/propodus articulation in minor chela at 100–130°. Major propodus usually square with slightly converging upper and lower margins, minor propodus usually subrectangular with subparallel upper and lower margins; external surface rounded, ornamented with tubercles, occasionally evenly distributed over the entire surface; internal surface smoother; fixed finger with an oblique ridge extending onto the manus; the ridge more pronounced on the minor chela.

**Material examined.** One major right propodus (IHNFG-4660), one major left propodus (IHNFG-4661) and two minor right propodi (IHNFG-4662, IHNFG-4663); all the material is fragmentary, *i.e.*, lacking the fixed finger.

**Measurements (in mm).** right minor propodus (IHNFG-4662), length 13.3, height 11.4; left major propodus (IHNFG-4661), length 14.5, height 11.1; right minor propodus (IHNFG-4663), length 13.8, height 9.5; right major propodus (IHNFG-4660), length 12.8, height 12.5.

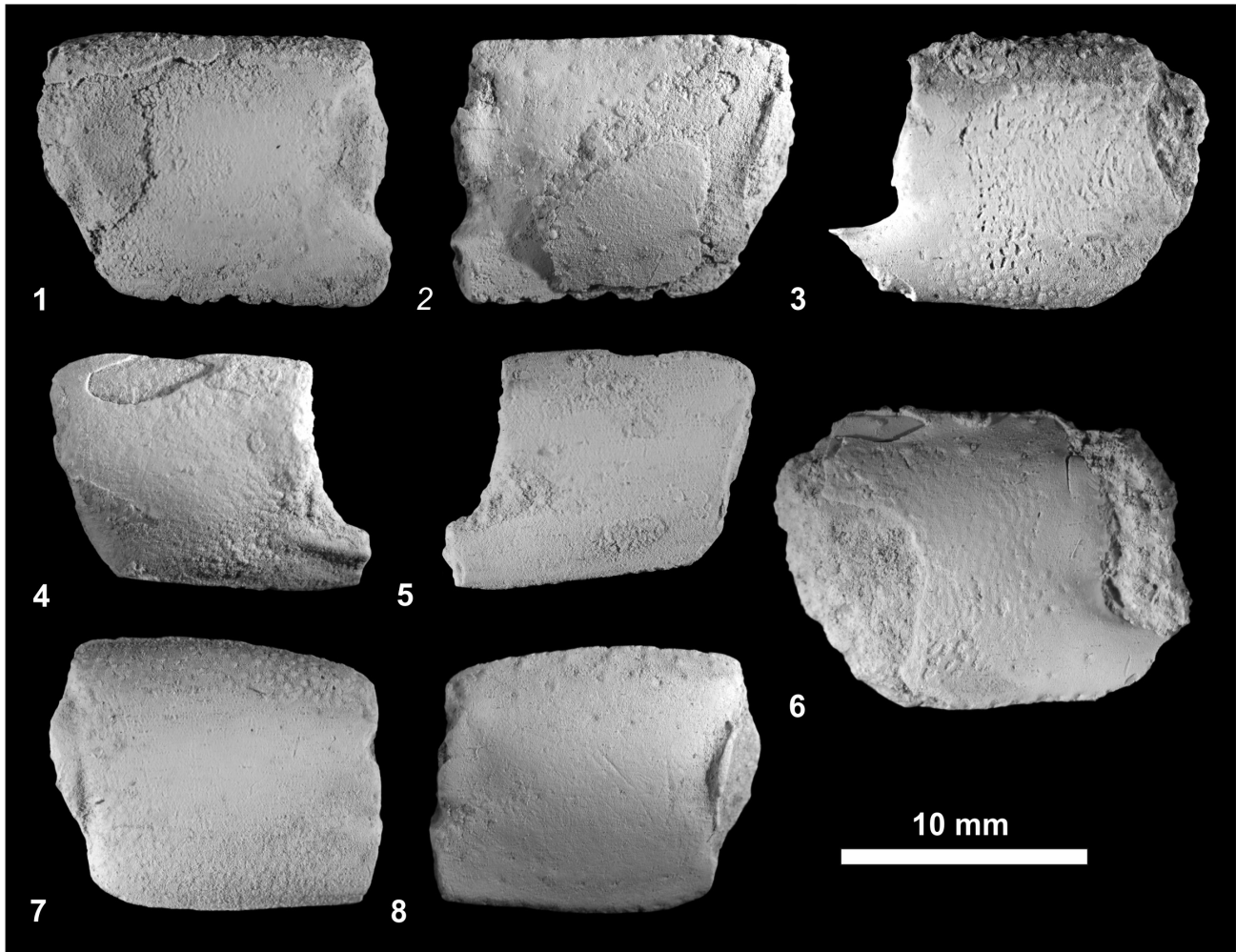


Figure 2. *Eucalliax burckhardti* (Böhm, 1911) **new comb.**, Lower Maastrichtian Ocozocoautla Formation. 1–2: right minor propodus (IHNFG-4662), outer (1) and inner (2) surface; 3, 6: left major propodus (IHNFG-4661), outer (3) and inner (6) surface; 4–5: right minor propodus (IHNFG-4663), outer (4) and inner (5) surface; 7–8: right major propodus (IHNFG-4660), outer (7) and inner (8) surface. All specimens are to scale and coated with ammonium chloride prior to photography.

**Occurrence.** To date, this species is known from the Maastrichtian and Danian (lower Paleocene) of the Neuquén Basin, Argentina (Böhm, 1911; Aguirre-Urreta, 1989; Feldmann *et al.*, 1995). The present record extends its geographic range into Mexico. *Eucalliax burckhardti* is considered the oldest current record of the genus.

**Discussion.** *Eucalliax burckhardti* has massive chelipeds (compare Böhm, 1911; Aguirre-Urreta, 1989), in contrast to *Calliaxina* Ngoc-Ho, 2003 (*non sensu* Sakai, 2011) which has laterally compressed ones. The major cheliped of *Calliax* de Saint Laurent, 1973 is distinctly different from that of *Eucalliax* (Hyžný, 2012) and from the material presented herein. Aguirre-Urreta (1989) described the carpus of *C. burckhardti* as subrectangular and with parallel margins; this matches the morphological variability of carpus in species of *Eucalliax* (compare Hyžný and Hudáčková, 2012). The reassignment of *C. burckhardti* to *Eucalliax* was already hinted at by Hyžný (2012).

Aguirre-Urreta (1989) noted that large propodi were

usually square, whereas smaller specimens were slightly subrectangular. She argued that this was a consequence of allometric growth; this is not unlikely, but it is more plausible that smaller specimens represent minor chela. Thus, we interpret the square morphotype as the major chela (Figs. 2.3, 2.6–2.8), whereas the subrectangular morphotype is seen as the minor chela (Figs. 2.1–2.2, 2.4–2.5) of the same taxon.

From the Danian of Argentina, Feldmann *et al.* (1995) recorded two propodi which were attributed to *Protocallianassa* sp.; these originated from the same locality as *Callianassa burckhardti*. These specimens are similar to the minor chelae of some extant species of *Eucalliax*, and thus might belong to *Callianassa burckhardti*. However, they are quite large and their shape does not really fit the supposed minor chelae of *C. burckhardti*. Thus, their affinities remain questionable.

The oblique carpus/propodus articulation is visible in the holotype of *C. burckhardti*; illustrated both by Böhm

(1911) and Aguirre-Urreta (1989), although the latter author described it as “straight” (*i.e.*, at right angle). In the supposed minor chela (subrectangular morphotype), the angle is larger.

*Eucalliax burckhardti* is easily distinguished from congeners as there is no other extant or fossil species of *Eucalliax* known with a similar tuberculation; in this respect, *E. burckhardti* is unique.

Interestingly, Ramos (1981) and Aguirre-Urreta (1989) recorded *C. burckhardti* to be associated with *Thalassinoides*-type ichnofossils. Although no specimen was recovered from inside such burrows, the abundance of chelipeds and their close proximity to fossil burrows leave little room for doubt - *C. burckhardti* was the tracemaker. The association of burrows together with ghost shrimp body fossils is rather rare in the fossil record (*e.g.* Bishop and Williams, 2005; Hyžný, 2011), and thus deserves attention.

#### Subfamily Callianassinae Dana, 1852

**Discussion.** The subfamily currently comprises 13 genera (but see Sakai, 2011) and numerous species, most of them assigned to *Callianassa*. The group apparently encompasses several clades (Felder and Robles, 2009), the interrelationships of which are currently under study (P.C. Dworschak, personal communication, 2011).

The material studied exhibits close similarities to *Callianassa modesta* De Man, 1905 (see below), which has been treated as a member of *Cheramus* Bate, 1888 (*e.g.*, Biffar, 1973; Sakai, 2011) or *Callianassa* (Poore, 2012). De Grave *et al.* (2009) assigned *Cheramus* to its own subfamily, but the phylogenetic analysis of Felder and Robles (2009) resolved the genus inside the subfamily Callianassinae. In this respect, we follow Felder and Robles (2009) and Sakai (2011) in abandoning the Cheraminae as a distinct subfamily.

#### Genus *Callianassa* Leach, 1814

**Type species.** *Cancer (Astacus) subterraneus* Montagu, 1808

**Discussion.** *Callianassa sensu lato* should be treated as a polyphyletic group (compare Ngoc-Ho, 2003). Thus, the new form described below cannot be placed in *Callianassa* as defined by Manning and Felder (1991) or Ngoc-Ho (2003). However, the generic concept of *Cheramus* is in flux (compare Manning and Felder, 1991; Poore, 1994; Sakai, 1999, 2005, 2011), and therefore, despite the close affinities to *C. modesta* (sometimes treated as *Cheramus*, see above), we here do not refer the new material to *Cheramus*. Additional studies of the morphological variability of the chelipeds in this genus are needed in order to apply its concept also to the fossil record. For the time being, we refer the new taxon to *Callianassa sensu lato*.

#### *Callianassa (s.l.) ocozocoautlaensis* new species Figures 3.1–3.3

**Diagnosis.** Callianassid with chelipeds of unequal size and dissimilar shape. Major cheliped manus upper margin arcuate, lower margin straight, fixed finger shorter than manus, lateral surface with longitudinal depression, fingers of approximately the same length, occlusal margins armed. Minor cheliped carpus subtriangular, propodus long and slender, both fingers slender, unarmed and pointed.

**Description.** Cheliped unequal in size and dissimilar in shape. Carpus/propodus articulation at about 90°. Major cheliped merus poorly preserved, upper margin smooth, lower margin damaged. Carpus length approximately equal to height, proximo-lower margin damaged, no spines observed. Manus length slightly exceeding height; upper margin arcuate, smooth; lower margin straight, smooth. Fixed finger shorter than manus, triangular in shape, lateral surface with longitudinal depression (furrow), occlusal margin armed with small teeth, the dentition of the distal half poorly preserved. Dactylus approximately as long as fixed finger, occlusal margin armed with several blunt teeth.

Minor cheliped carpus subtriangular. Propodus long and slender, manus length approximately equal to height, distinctly shorter than fixed finger. Both fingers slender, unarmed and pointed.

**Etymology.** After the Ocozocoautla Formation.

**Material examined.** Holotype, and sole, specimen is IHNFG-4664.

**Measurements (in mm).** Major chela: carpus length 5.2, carpus height 5.4, manus length 6.0, manus height 5.6, dactylus length 4 (preserved portion); minor chela: carpus length 3.1, carpus height 2.6, manus length 2.3, manus height 2.3, dactylus length 4.5.

**Occurrence.** To date, this species is exclusively known from the lower Maastrichtian Ocozocoautla Formation, Chiapas (Mexico).

**Discussion.** Although the specimen possesses both chelae, it is difficult to assign it to any callianassid genus. The merus of the major cheliped usually is crucial in assigning fossil ghost shrimps to a particular genus (*e.g.*, Schweitzer *et al.*, 2003, 2006a; Hyžný and Hudáčková, 2012). In the material studied the merus is damaged and the lower margin is not discernible. The shape of the elements that are preserved, *i.e.* three distalmost elements (dactylus, propodus, carpus) of both chelae, exhibit similarities to extant *Callianassa modesta* as illustrated by De Man (1928; see Fig. 3.4 here). Both species share the general shape of the major manus and the fixed finger possessing a furrow over its full length. The differences mainly concern with the shape of the fingers: minor cheliped fingers of *C. modesta* are comparatively longer and the dentition on the major cheliped fingers is slightly different in both taxa. The dentition of cheliped fingers, however, is often subject to intraspecific variation (*e.g.*, Hyžný and Hudáčková, 2012). More material is needed to determine the taxonomic



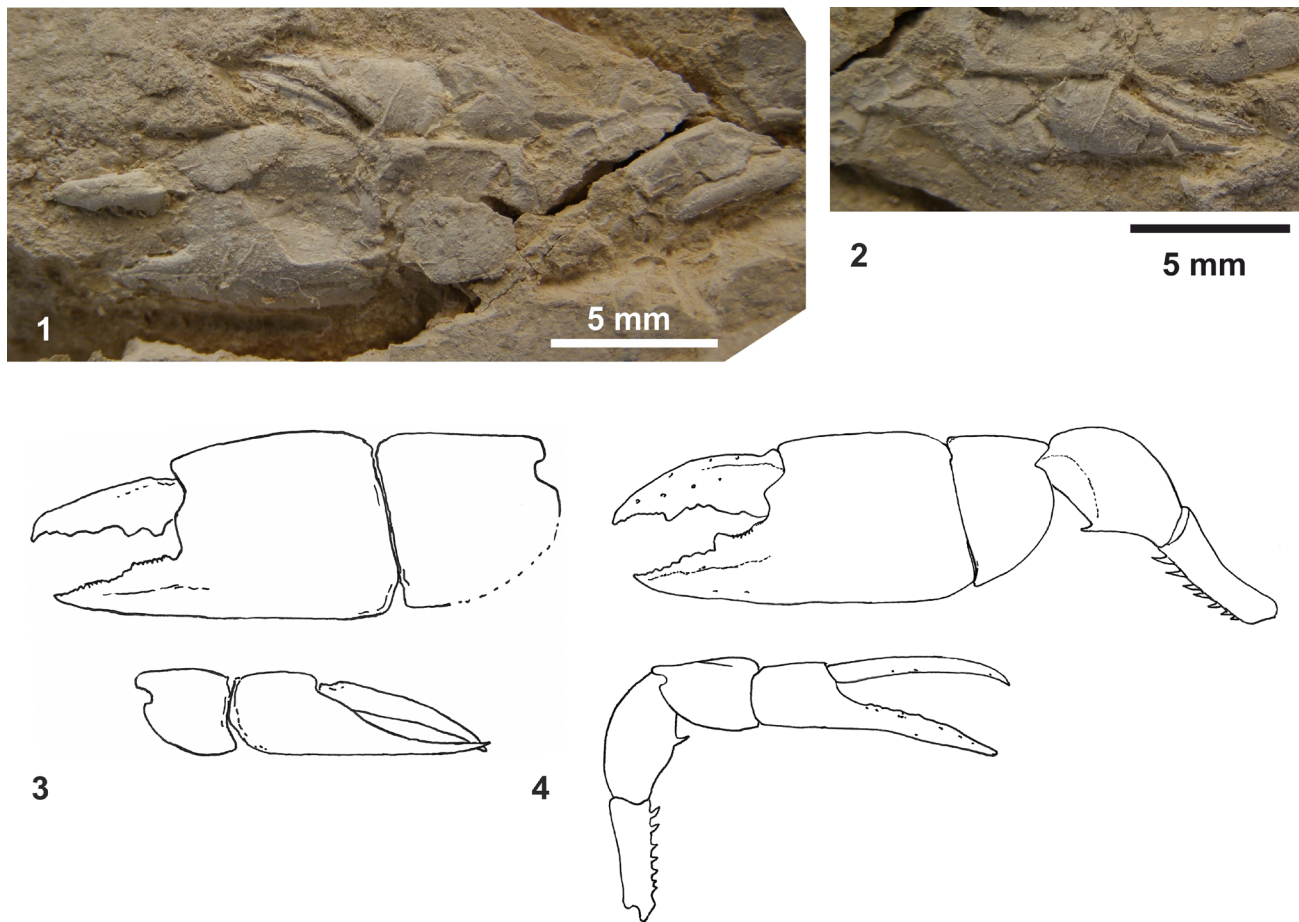


Figure 3. *Callianassa* (s.l.) *ocozocoautlaensis* **new species** from the Lower Maastrichtian Ocozocoautla Formation, in comparison to extant *Callianassa modesta* De Man, 1905. 1: holotype of *Callianassa* (s.l.) *ocozocoautlaensis*, IHNFG-4664, with major and minor cheliped preserved; 2: same as 1, minor chela photographed under different light angle; 3: reconstruction of chelipeds of *Callianassa* (s.l.) *ocozocoautlaensis* (meri of both chelipeds are not sufficiently preserved), major chela (above) and minor chela (below). 4: *Callianassa modesta*, redrawn and modified (setae omitted) from De Man (1928; fig. 16b, c).

importance of these differences, but because *Callianassa* (s.l.) *ocozocoautlaensis* is of Maastrichtian age, we treat it as a separate species.

#### 4. Discussion

##### 4.1. Mexican fossil ghost shrimps

The ghost shrimp fossil record of Mexico is relatively rich (Table 1), but given its fragmentary nature, it is difficult to document the true diversity. Only a limited number of taxa were identified at the generic level. A revision of Mexican ghost shrimp fossil record is desirable so as to understand the real diversity of their forms. Herein, a brief discussion is provided for each occurrence.

##### 4.1.1. Upper Cretaceous

The oldest ghost shrimp record is *Callianassa aquilae* Rathbun, 1935 from the Turonian of the Eagle Ford Group

of Múzquiz. Vega *et al.* (2007) transferred this species to *Gourretia* de Saint Laurent, 1973, but Bermúdez *et al.* (2013) have recently noted that the material illustrated as *Gourretia aquilae* by Vega *et al.* (2007) in fact comprised two different taxa. One proved to be conspecific with the type material of *Callianassa aquilae* and formed the basis for a new genus, *Rathbunassa* Hyžný in Bermúdez *et al.* (2013). The second taxon awaits formal description.

Vega *et al.* (1995a) recorded three incomplete chelae from the Maastrichtian Portrerillos Formation as ?*Callianassa* sp. The material preserves a ridge on the fixed finger, which might hint at the Eucalliinae, but due to poor preservation a more detailed identification is impossible. The lateral surface of the propodus, however, is not ornamented with tubercles; thus, the species seems to differ from contemporaneous *Eucalliix burckhardti* (see above).

Vega *et al.* (1995b) noted several callianassid remains from the Maastrichtian Cárdenas Formation which they identified as *Cheramus* sp. and *Protocallianassa* sp. The material assigned to *Cheramus* does not preserve the merus,

making identification doubtful. Schweitzer and Feldmann (2002) reassigned the material reported as *Protocallianassa* sp. to a new extinct genus, *Vegarthon* Schweitzer and Feldmann, 2002.

#### 4.1.2. Eocene

Schweitzer *et al.* (2006a) described numerous callianassid remains from the Eocene Bateque and Tepetate formations of Baja California Sur, Mexico. Two specimens showing incomplete chelae were attributed to *Neocallichirus* Sakai, 1988, one as *Neocallichirus* cf. *N. rhinos* Schweitzer and Feldmann, 2002, the second as *Neocallichirus* sp. Despite the fact that both specimens come from the same locality, Schweitzer *et al.* (2006a) stated that, because one possesses the reentrant in the distal margin of the manus and the other does not, they in fact represent two distinct species. However, we argue that the shape of the manus and carpus as depicted in Schweitzer *et al.* (2006a) clearly speaks for the conspecificity of these specimens. The presence of a reentrant often is subject to intraspecific variation and may also mirror sexual dimorphism (*e.g.*, Sakai, 1969; Hyžný and Hudáčková, 2012) and therefore cannot be successfully used in species delimitation. Later, Vega *et al.* (2008) recorded a single articulated specimen from the lower Eocene El Bosque Formation and referred it to *Neocallichirus* cf. *N. rhinos*. The specimen seems to be conspecific with the material from the Tepetate Formation (Schweitzer *et al.*, 2006a), but differs significantly from *N. rhinos* as originally described from the Eocene of California (Schweitzer and Feldmann, 2002). The shape of merus of *N. cf. rhinos* has a strongly arcuate upper margin and the same can be said about the meral keel, while in *N. rhinos* these are straighter. We do acknowledge *N. cf. rhinos* as a separate taxon, but refrain from discussing its affinities further because this is beyond the scope of the present contribution. A re-examination of the original material is needed to establish its true affinities.

Schweitzer *et al.* (2006a) further listed fragmentary material of five other distinct morphotypes from the Eocene Bateque and Tepetate formations. Callianassidae *sensu lato* species 1 possesses a fixed finger with a longitudinal ridge which could underscore identification as a member of the Eucalliinae (Hyžný, 2012). Vega *et al.* (2001b, 2008) recorded several specimens (as *Callianassa sensu lato* sp. and Callianassidae 2, respectively) from the El Bosque Formation that seem to be conspecific with Callianassidae *sensu lato* species 1 as described by Schweitzer *et al.* (2006a).

Callianassidae *sensu lato* species 2 of Schweitzer *et al.* (2006a) has affinities to *Glypturus* Stimpson, 1866; this material was discussed by Hyžný and Müller (2012).

Callianassidae *sensu lato* species 3 from the Eocene Bateque Formation, as described by Schweitzer *et al.* (2006a), clearly corresponds to Callianassidae 1 from the Middle Eocene San Juan Formation as reported by Vega *et al.* (2008). The material shows an elongated propodus

which is somewhat similar to that of *e.g. Gourretia*. For a proper generic assignment, however, better-preserved material is needed.

Callianassidae *sensu lato* species 4 from the Eocene Bateque Formation, recorded by Schweitzer *et al.* (2006a), shows affinities to *Callianassa matsoni* Rathbun, 1935. This species, from the Miocene of Florida (USA), was reassigned to *Neocallichirus* by Schweitzer and Feldmann (2002). Hyžný and Karasawa (2012) expressed doubts over the assignment of *C. matsoni* to *Neocallichirus*.

Callianassidae *sensu lato* species 5 from the Eocene Bateque and Tepetate formations (Schweitzer *et al.*, 2006a) may represent the minor chelae of some of the other taxa listed above. A re-examination of the material is called for to either confirm or reject this assumption.

#### 4.1.3. Neogene

Rathbun (1919) described *Callianassa pellucida* from the Oligocene of Anguilla. Collins *et al.* (2009) noted its presence also in the middle Miocene Tuxpan Formation in Mexico.

Vega *et al.* (2009) recorded *Neocallichirus aetodes* Schweitzer, Iturralde-Vinent, Hetler and Vélez-Juarbe, 2006b from the Miocene of Chiapas and the Pliocene of Veracruz, as well as *Ctenocheles* sp. from the Miocene of Chiapas.

#### 4.2. Survival across the K/Pg boundary

Schweitzer and Feldmann (2005) studied the survivorship of the decapod crustaceans across the K/Pg boundary and concluded that this catastrophic event did not have a severe impact on this group. They also listed several ghost shrimp genera which survived the K/Pg boundary perturbations, namely *Calliax*, *Neocallichirus*, *Protocallianassa* and *Ctenocheles* Kishinouye, 1926. However, recently doubts (although without detailed discussion) were expressed by Hyžný and Karasawa (2012) over the true status of Cretaceous occurrences of *Neocallichirus*. Several additional genera can now be added to the list, namely *Callichirus* Stimpson, 1866, *Corallianassa* Manning, 1987 and *Vegarthon*. Their Cretaceous records are based on *Callichirus waagei* Crawford, Feldmann, Waugh, Kelley and Allen, 2006 from the Maastrichtian of South Dakota (USA), *Corallianassa acuruvata* Swen, Fraaije and van der Zwaan, 2001 from the Maastrichtian of the Netherlands; and *Vegarthon* sp. from the Maastrichtian of Mexico (Vega *et al.*, 1995b; see Table 1 here), respectively. The present contribution adds also *Eucalliix* with *Eucalliix burckhardti* as the oldest record of the genus. This species, known both from Maastrichtian and Danian of Argentina (Böhm, 1911; Aguirre-Urreta, 1989; Feldmann *et al.*, 1995), is the sole known ghost shrimp species and one of the very few decapod crustacean species that straddled the K/Pg boundary (compare Schweitzer and Feldmann, 2005).

Interestingly, only members of the Ctenochelidae and



the callianassid subfamilies Callichirinae and Eucalliinae have so far been recorded to survive the K/Pg boundary. The present paper adds the first record of a confirmed member of the subfamily Callianassinae. The molecular analysis by Felder and Robles (2009) hinted at the paraphyletic nature of the subfamily Eucalliinae and the basal position of its members close to the Ctenochelidae. The subfamilies Callichirinae and Callianassinae are positioned higher in the resulting tree topology (Felder and Robles, 2009), but as shown by the present study, all major ghost shrimp lineages (Ctenochelidae together with Eucalliinae, Callichirinae, Callianassinae) were already established well before the Cenozoic. It seems that ghost shrimps are rather conservative taxa, which is not surprising given their fossorial life style

## Acknowledgements

We thank the reviewers, John W.M. Jagt (Natuurhistorisch Museum, Maastricht, the Netherlands) and Alessandro Garassino (Museo Civico di Storia Naturale, Milan, Italy), for their constructive comments and improvement of the English. MH acknowledges the support of PalSIRP Sepkoski Grant 2011 and APVV-0436-12.

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Manuscript received: October 10, 2012.

Corrected manuscript received: October 29, 2012.

Manuscript accepted: November 4, 2012.