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 especimen, 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 callianassid, 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.) ocozocoautlaensis 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 Ocozocoautla 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.) ocozocoautlaensis 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 Ocozocoautla 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 Ocozocoautla Formation is underlain by the Sierra Madre Limestone, which is Early to middle Cretaceous in age (Steele and Waite, 1986), and is comformably overlain by the Paleocene Soyaló Formation (Frost and Langenheim, 1974; López-Ramos, 2006).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Age</th>
<th>Main references</th>
<th>Remarks</th>
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<tr>
<td>Rathbunassa aquilae</td>
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<td>Vega et al. (2007), Bermúdez et al. (2013)</td>
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<td>undescribed form</td>
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<td>?Cheramus sp.</td>
<td>Maastrichtian</td>
<td>Vega et al. (1995b)</td>
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<td>Vegarbron sp.</td>
<td>Maastrichtian</td>
<td>Vega et al. (1995b)</td>
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<td>Eucalliax burckhardti</td>
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<td>Callianassa (s.l.) ocozocoautlaensis n. sp.</td>
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<td>?Neocallichirus sp.</td>
<td>Eocene</td>
<td>Schweitzer et al. (2005); Vega et al. (2008)</td>
<td>as Neocallichirus cf. rhinos</td>
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<td>Callianassidae sensu lato species 1</td>
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<td>Schweitzer et al. (2005); Vega et al. (2001, 2008)</td>
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<td>Schweitzer et al. (2005)</td>
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<td>Eocene</td>
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<td>Callianassidae sensu lato species 5</td>
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<td>Callianassa pellucida</td>
<td>Miocene</td>
<td>Collins et al. (2009)</td>
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<tr>
<td>Ctenocheles sp.</td>
<td>Miocene</td>
<td>Vega et al. (2009)</td>
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<tr>
<td>Neocallichirus aetodes</td>
<td>Miocene, Pliocene</td>
<td>Vega et al. (2009)</td>
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</tbody>
</table>
Ghost shrimps of the Maastrichtian Ocozocoautla Formation, Chiapas (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 foraminiferal 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", Secretaria 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 Eucalliacinae 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 Eucalliacinae. 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 eucalliacine 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 Eucalliacinae.

*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 Eucalliacinae. 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 Eucalliacinae 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


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.
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 burchardti*. 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, unarmored 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, unarmored 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 Hudačková, 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 Hudačková, 2012). More material is needed to determine the taxonomic
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 *Cheramus* sp. The material preserves a ridge on the fixed finger, which might hint at the Eucalliacinae, 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 *Eucalliax 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,

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 Eucalliacinae (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 Glyptarus 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 Vegarthron. Their Cretaceous records are based on Callichirus waagei Crawford, Feldmann, Waugh, Kelley and Allen, 2006 from the Maastrichtian of South Dakota (USA), Corallianassa acucurvata Swen, Fraaije and van der Zwaan, 2001 from the Maastrichtian of the Netherlands; and Vegarthron sp. from the Maastrichtian of Mexico (Vega et al., 1995b; see Table 1 here), respectively. The present contribution adds also Eucallix with Eucallix burekhardii 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 Eucalliacinae 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 Eucalliacinae 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 Eucalliacinae, 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.

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