



Article

urn:lsid:zoobank.org:pub:1AF0BD07-97AB-4018-B973-98AB67951238

***Calliixina chalmasii* (Brocchi, 1883) comb. nov. (Decapoda: Axiidea: Callianassidae: Eucalliicinae), a ghost shrimp from the Middle Miocene of Europe, with reappraisal of the fossil record of Eucalliicinae**

MATÚŠ HYŽNÝ

Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University, Mlynská dolina G1, 842 15 Bratislava, Slovakia, E-mail: hyzny.matus@gmail.com

Abstract

A detailed study of chelipeds of two Middle Miocene burrowing ghost shrimp taxa, *Callianassa chalmasii* Brocchi, 1883, and *Callianassa rakosiensis* Lörenthey, 1897, based on isolated propodi revealed that they are conspecific—the latter species is based on the minor cheliped of the former species. Material coming from several roughly coeval localities of Austria (early 'Badenian'), Hungary (late 'Badenian') and Slovakia (early 'Sarmatian') provided sufficient data for redescription of *C. chalmasii* and its reassignment to the genus *Calliixina* (subfamily Eucalliicinae). As such it is the first recognized representative of the genus in the fossil record. It is argued that for the Eucalliicinae, the following features are diagnostic: a square P1 manus usually converging distally, the presence of a ridge on the lateral surface at the base of fixed finger, and a relatively short fixed finger, often with a triangular tooth. For reliable generic assignment within the Eucalliicinae both chelipeds (propodi), major and minor, should be present.

Key words: Ghost shrimp, Callianassidae, Eucalliicinae, *Calliixina chalmasii* **comb. nov.**, Middle Miocene

Introduction

Callianassidae Dana, 1852 is a distinct family of fossorial heterochelous shrimps predominantly inhabiting shallow intertidal and subtidal marine environments, mainly in the tropics and subtropics (Dworschak 2000, 2005b). Today callianassids represent important components of marine and estuarine environments and are considered as true ecosystem engineers (Berkenbusch & Rowden 2003; Berkenbusch *et al.* 2007). They are among the most commonly found decapods in the fossil record; however, because of the delicate structure of most cuticular surfaces, only chelipeds, which are usually heavily calcified, are likely to be preserved (Bishop & Williams 2005). Many extant callianassid genera currently recognized (see De Grave *et al.* 2009 for comprehensive listing) are based mainly on morphology of weakly calcified parts, which have very poor fossilization potential. Thus, the fossil material usually lacks the diagnostic characters used for extant taxa. The taxonomic importance of chelipeds (first pereopods) in modern taxa was recognized by Manning & Felder (1991). They pointed out that some characters occurring on the merus (usually in combination with other features of hard part morphology) can be used for generic assignment. The present contribution builds on this basis and develops it further by arguing that at least in some genera the morphology of propodi also can be of significant taxonomic importance.

More than 150 fossil species have been described under the collective taxon “*Callianassa*” (Schweitzer *et al.* 2010). No attention has been paid to many callianassid species since their first description, and most of the fossil species of “*Callianassa*” should be considered different from *Callianassa* *sensu* Manning & Felder (1991) or Ngoc-Ho (2003). Rather, fossil “*Callianassa*” represents a heterogeneous mixture of several independent genera.

Callianassa chalmasii Brocchi, 1883 was described by Brocchi (1883) from the upper 'Badenian' (lower Serravallian) strata of Rákos (Budapest area, Hungary). In 1897 Lörenthey described another species as *Callianassa rakosiensis* from the same locality. Veiga Ferreira (1961) described *Callianassa espichelensis* Veiga Ferreira, 1961 from the Miocene (Tortonian) of Portugal. Müller (1984) considered *C. espichelensis* to be a junior

synonym of *C. chalmasii*. However, in the most recent list of fossil decapod crustaceans it is regarded as a distinct species (see Schweitzer *et al.* 2010: 34). The evidence presented herein suggests the synonymisation of all the above-mentioned taxa and their reassignment to the genus *Calliuxina* Ngoc-Ho, 2003 (subfamily Eucalliicinae). Thus, *Calliuxina chalmasii* comb. nov. becomes the first known exclusively fossil member of this genus. Comparison between extant taxa belonging to Eucalliicinae and fossil representatives commonly treated under nomen collectivum “*Callianassa*” (or *Callianassa* sensu lato) reveals possible reassignment of more fossil species to the respective subfamily than previously acknowledged.

Localities and geological settings

Fossil material forming the basis of this work comes from these localities (Fig. 1):

1) Austrian part of the Vienna Basin—the Fenk quarry (Gross Höflein, Lower Austria). The quarry is the type locality of the Leitha Limestone (Papp *et al.* 1978) and consists of two levels, a lower level with a deeper facies and an upper level with the coral facies (Riegl & Piller 2000). The age of strata cropping out at Fenk is middle 'Badenian' (early Serravallian) (T. Wiedl, pers. comm. 2012). Remains of decapod crustaceans are known from the middle sequence of the three sequences recognized in the upper outcrop (Riegl & Piller 2000). For sedimentological details and palaeoecological interpretation reference is made to Dullo (1983) and Riegl & Piller (2000). The latter authors interpreted the palaeoenvironment as coral carpets. The decapod crustacean fauna has been partly described and figured by Bachmayer & Tollmann (1953) and Müller (1984, 1998). Currently, the entire decapod assemblage consisting of several tens taxa is under re-evaluation by the author.

2) Slovak part of the Vienna Basin—Dúbravská hlavica (Bratislava area). At the locality early 'Sarmatian' (Serravallian) sands and poorly lithified sandstones of the Sandberg Member (the Studienka Formation) crop out. For details on sedimentology and the lithofacies overview of the area, see Švagrovský (1981) and Baráth *et al.* (1994). Baráth *et al.* (1994) stated the age of the sediments at Dúbravská hlavica as late 'Badenian', but, analysis of foraminiferal assemblage directly from the sediment containing ghost shrimp remains revealed a slightly younger age, early 'Sarmatian' (Hyžný & Hudáčková 2012). Hyžný & Hudáčková (2012) described in detail two ghost shrimps, *Neocallichirus brocchii* (Lörenthey, 1897), and *Eucalliux pseudorakosensis* (Lörenthey in Lörenthey & Beurlen, 1929), occurring at the locality in high densities. The entire decapod crustacean assemblage consisting of several additional taxa is currently under description by the author.

3) Great Hungarian Basin—several localities in Budapest area: Rákos, Gyakorlo út and Örs vezér tere. At the localities 'Badenian' and 'Sarmatian' limestones with rich marine fauna crop out. The 'Badenian' part of the section at Rákos was chosen as the stratotype of the Rákos Limestone Formation, although using the general term Leithakalk seems to be more practical (Moissette *et al.* 2007). Decapod crustacean material presented herein is of the late 'Badenian' age (Müller 1984). During that time the area around the Rákos locality represented a coral patch reef environment of the carbonate platform (Moissette *et al.* 2007: fig. 7). The decapod crustacean assemblage from the localities has been studied in detail by Müller (1984, 2006).

Material and methods

The fossil material represents mostly isolated distal cheliped elements, in several cases articulated units consisting of carpus and propodus were examined (from the locality Dúbravská hlavica). Preparation was performed with preparatory needles and a fine pneumatic needle. If necessary, specimens were coated with ammonium chloride prior to photography.

Studied fossil material is deposited in the following museums: Hungarian Geological Survey, Budapest, Hungary (FI); Department of Geology and Paleontology, Comenius University, Bratislava, Slovakia (KGP MH); Hungarian Natural History Museum, Budapest, Hungary (M, PAL); Natural History Museum, Wien, Austria (NHMW); and Natural History Museum of Slovak National Museum, Bratislava, Slovakia (SNM-Z). Studied extant material is deposited in Natural History Museum, Wien (NHMW).

Other abbreviations: Mxp3=third maxillipeds; P1=first pereopods (chelipeds).

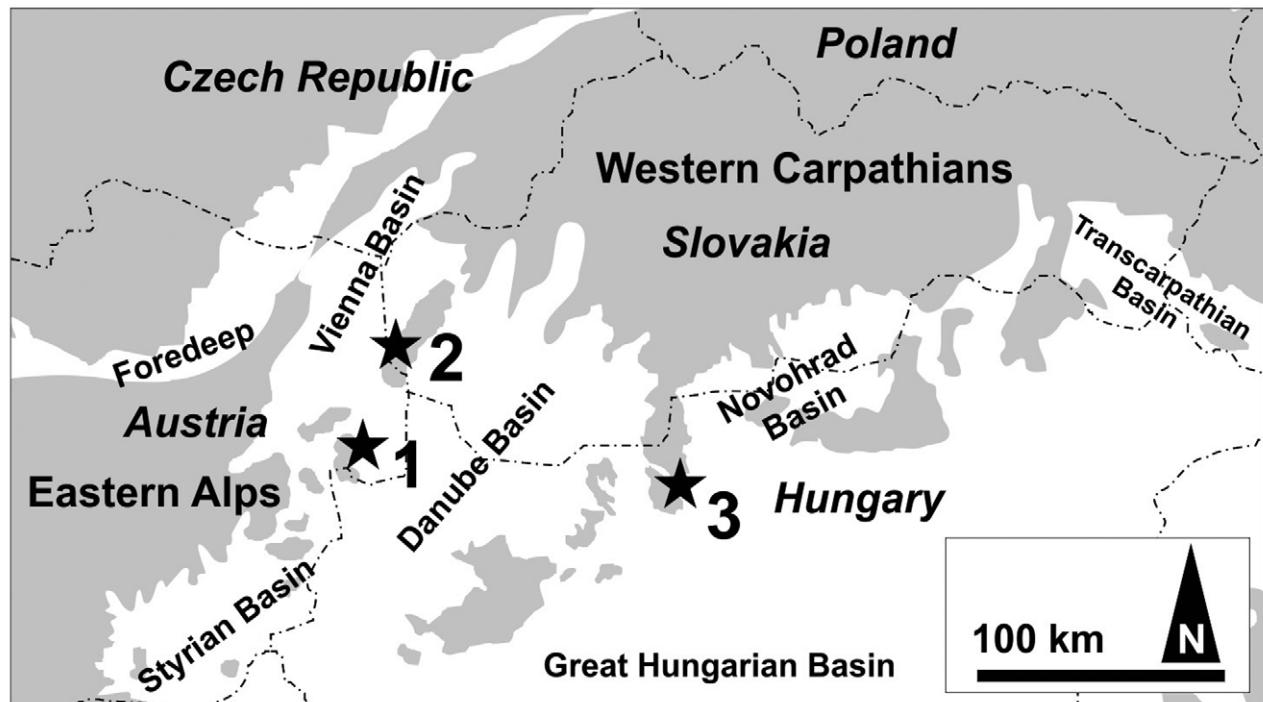


FIGURE 1. Map showing the position of studied localities (modified from Harzhauser *et al.* 2003). In grey are pre-Neogene sediments and basement. 1, the Fenk quarry; 2, Dúbravská hlavica; 3, Budapest city area.

Systematics

Order Decapoda Latreille, 1802

Suborder Pleocyemata Burkenroad, 1963

Infraorder Axiidea de Saint Laurent, 1979

Family Callianassidae Dana, 1852

Subfamily Eucalliicinae Manning & Felder, 1991

Remarks on taxonomy. De Grave *et al.* (2009) recognized four genera within the subfamily: *Calliax* de Saint Laurent, 1973; *Calliaxina* Ngoc-Ho, 2003; *Eucalliix* Manning & Felder, 1991; and *Paraglypturus* Türkay & Sakai, 1995. Ngoc-Ho (2003) provided an account of morphological differences between the Eucalliicinae genera. Sakai (2005) recognized *Eucalliix* and *Calliaxina* as junior synonyms of *Calliax*; this synonymization was criticized by Dworschak (2007: 159). Later, Sakai (2011) recognized all three genera, *Calliax*, *Eucalliix* and *Calliaxina*, as valid, but his concept of *Eucalliix* and *Calliaxina* differs markedly from that of Ngoc-Ho (2003). Sakai (2011) restricted *Eucalliix* to *Callianassa quadracuta* Biffar, 1970 only (type species of *Eucalliix*), and for *Calliaxina* listed *C. aequimana* (Baker, 1907), *C. bulimba* (Poore & Griffin, 1979), *C. jonesi* (Heard, 1989), *C. mcilhennyi* (Felder & Manning, 1994), *C. panglaoensis* (Dworschak, 2006), *C. novaebritanniae* (Borradaile, 1900), *C. punica* (de Saint Laurent & Manning, 1982) and *C. sakaii* (de Saint Laurent & Le Loeuff, 1979). Sakai (2011) based his concept of the genus *Calliaxina* mostly on the presence of a cardiac sulcus or sulci and the typical forms of Mxp3. The presence of Mxp3 exopod, one of the most important characters used by Ngoc-Ho (2003) to define the genus, together with the morphology of chelipeds (P1) were not considered of great taxonomic importance by Sakai (2011). The original genus concept of Ngoc-Ho (2003) is followed here because of greater stability of diagnostic characters and because it evaluates also cheliped morphology, i.e. body parts commonly preserved in the fossil

record. As a result, only the last three mentioned species from the list above are considered herein as members of *Calliixina*, with the remainder as members of *Eucalliix*. It is also worth mentioning that *Eucalliix kensleyi* Dworschak, 2005a was omitted from the last monograph of Sakai (2011). The taxonomic history of generic assignment of all extant Eucalliicine taxa is summarized in Table 1.

Sakai (2011) raised the Eucalliicinae to family level. Following the classification of De Grave *et al.* (2009) the taxon is here still treated as a subfamily.

Chelipeds of the Eucalliicinae. Manning & Felder (1991) noted that the lower meral margin of the major cheliped bears some important characters for distinguishing genera of the family Callianassidae. There are, in addition, taxonomically important characters also present on the propodus (e.g. in *Glypturus* Stimpson, 1866, see Hyžný & Müller in press). Ngoc-Ho (2003) distinguished genera within the subfamily Eucalliicinae, i.e. *Calliixina*, *Calliix*, *Eucalliix* and *Paraglypturus*, mainly on the basis of 'soft' part morphology (features on dorsal carapace, eye cornea, maxillipeds, pleopods and uropods); however, she also pointed out differences in chelipeds, which are of greatest fossilization potential and therefore useful for palaeontologists. For *Eucalliix* and *Calliixina*, subequal and similar first pereopods are typical. Moreover, *Calliixina* always possesses laterally compressed chelipeds. In *Calliix* they are also laterally compressed, but unequal and dissimilar, whereas in *Paraglypturus* they are unequal, dissimilar and massive.

Many Eucalliicinae species possess a distinct ridge extending obliquely along the fixed finger laterally and may extend to the propodus (as in *Eucalliix panglaoensis*; for details see Dworschak 2006). The presence of the ridge together with its typically square manus, usually converging distally, and relatively short fixed finger often with a triangular tooth at its base can be used to identify members of the Eucalliicinae, although not all of these characters are present in all Eucalliicinae genera. The oblique ridge on the base of the fixed finger is rather typical for Eucalliicinae genera, notably *Eucalliix* and *Calliixina* (Fig. 2). A similar ridge is also present in extant *Callianassa acutirostella* Sakai, 1988; the shape and ratios of cheliped elements (Sakai 2005: fig. 14A, B) are, however, completely dissimilar to any member of the Eucalliicinae. In *Eucalliix* and *Calliixina* there is usually also a depression present in such a position, the ridge forming its lower border. There is a ridge and a deep depression in major cheliped of some *Lepidophthalmus* Holmes, 1904 species too (e.g. *L. rafai* Felder & Manning, 1998, *L. siriboia* Felder & Rodrigues, 1993; *L. richardi* Felder & Manning, 1997). In this genus development of mentioned characters seems to be correlated with sex and size/age (e.g. Felder & Lovett 1989). The shape of propodus is markedly different from any of *Eucalliix* and *Calliixina* species.

Such characters as “robustness” of P1 propodus can be checked on a single fragment, but, to observe the most important characters both chelipeds are usually needed. When working with fossils, the preservation of both chelipeds from the same animal is a quite rare event. Nevertheless there are a few examples when members of the Eucalliicinae were identified on the basis of both chelae (Beschlin *et al.* 2002; Karasawa 1992, 1997). The nature of the minor chela can be diagnostic for *Calliix* sensu Ngoc-Ho (2003), in which the fixed finger is shorter than, and separated from, the dactylus by a wide gap, bearing a large triangular proximal tooth (Fig. 2H). In *Eucalliix*, the minor cheliped seems to be more variable. In *E. aequimana* it is more-or-less identical to the major one (Figs. 2C–D), and in other *Eucalliix* species it is usually slightly smaller (with relatively shorter manus) than the major one. In *Calliixina* the minor cheliped is similarly slightly smaller than the major one and, moreover, a deep depression is present on the minor propodus only (Fig. 2B).

Minor chelipeds in general are usually less calcified and therefore there is a strong bias toward preservation of major chelae in the fossil record, although minor chelipeds should be present in statistically robust samples (e.g. Hyžný & Hudáčková 2012). On the other hand, when dealing with taxa with subequal chelipeds (as some species of *Eucalliix* and *Calliixina* are), identification of minor chelae may be obscure. In such a case, thus when the material consists of isolated elements, a mixture of two (or more) different “species” can be recognized. Precise morphometry and a check of taxonomically important characters can usually resolve this problem as exemplified by this study. Intraspecific variation can be considerable, although some characters are usually consistent within a species.

Eucalliicinae in the fossil record. The fossil record of the Eucalliicinae with the emphasis on the genera *Calliix* and *Eucalliix* was recently briefly discussed by Hyžný & Hudáčková (2012). They commented fossil occurrences assigned at one time to one of respective genera. Here some additional notes on fossil taxa so far treated as members of *Callianassa* (sensu lato) are presented. The combination of characters typical for Eucalliicinae, as discussed above, is present e.g. in *Callianassa atrox* Bittner, 1893 from the Middle Eocene

TABLE 1. Taxonomic history of generic assignment of extant Eucalliaceae taxa.

Taxon	Sakai (1999)	Tudge et al. (2000)	Sakai (2005)	Sakai (2011)	Poore (2012)
<i>Callianassa aequimana</i> Baker, 1907	<i>Calliax</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Eucalliax</i>
<i>Calliax andamanica</i> Sakai, 2002	–	–	<i>Calliax</i>	<i>Andamanacalliiax</i>	<i>Eucalliiax</i>
<i>Callianassa bulimba</i> Poore & Griffin 1979	<i>Calliax</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Eucalliiax</i>
<i>Eucalliiax cearaensis</i> Rodrigues & Manning, 1992	<i>Calliax</i>	<i>Eucalliiax</i>	<i>Calliax</i>	<i>Eucalliiaxiopsis</i>	<i>Eucalliiax</i>
<i>Paraglypturus calderus</i> Türkay & Sakai, 1995	<i>Paraglypturus</i>	<i>Paraglypturus</i>	<i>Paraglypturus</i>	<i>Paraglypturus</i>	<i>Paraglypturus</i>
<i>Calliax doerjesti</i> Sakai, 1999	<i>Calliax</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Eucalliiax</i>
<i>Calliax jonesi</i> Heard, 1989	<i>Calliax</i>	<i>Eucalliiax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Eucalliiax</i>
<i>Eucalliiax kensleyi</i> Dworschak, 2005a	–	–	–	not treated	<i>Eucalliiax</i>
<i>Callianassa lobata</i> De Gaillande & Lagardère, 1966	<i>Calliax</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliax</i>
<i>Eucalliiax mcilhennyi</i> Felder & Manning, 1994	<i>Calliax</i>	<i>Eucalliiax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Eucalliiax</i>
<i>Callianassa novaebritanniae</i> Borradaile, 1900	<i>Paraglypturus</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Calliaxina</i>
<i>Eucalliiax panglaoensis</i> Dworschak, 2006	–	–	–	<i>Calliaxina</i>	<i>Eucalliiax</i>
<i>Calliax punica</i> de Saint Laurent & Manning, 1982	<i>Paraglypturus</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Calliaxina</i>
<i>Callianassa quadracuta</i> Biffar, 1970	<i>Calliax</i>	<i>Eucalliiax</i>	<i>Calliax</i>	<i>Eucalliiax</i>	<i>Eucalliiax</i>
<i>Calliax sakaii</i> de Saint Laurent & Le Loeuff, 1979	<i>Paraglypturus</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Calliaxina</i>
<i>Callianassa tooradin</i> Poore & Griffin, 1979	<i>Paraglypturus</i>	<i>Calliax</i>	<i>Calliax</i>	<i>Calliaxina</i>	<i>Calliaxina</i>
				<i>Pseudocalliiax</i>	<i>Calliax</i>

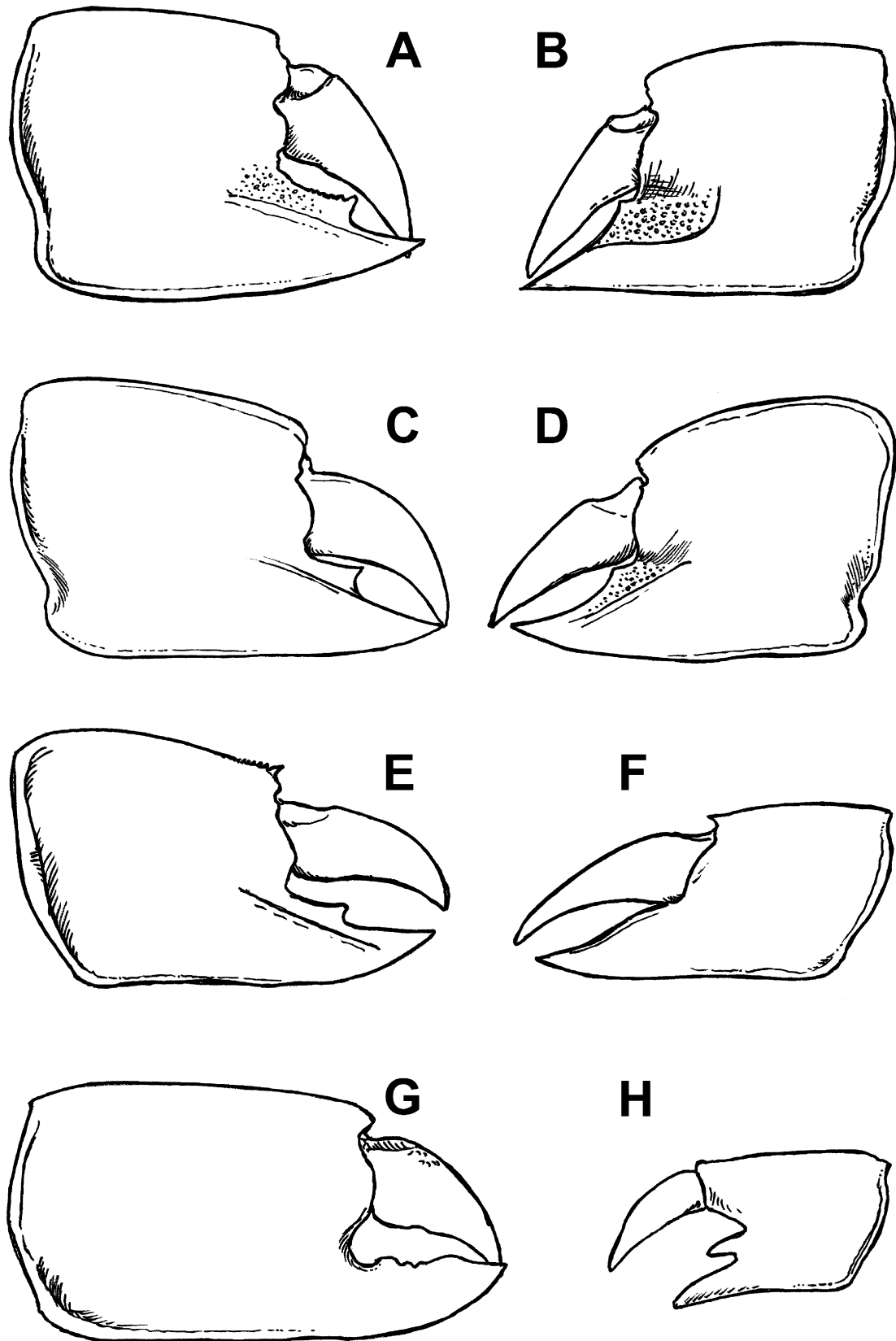


FIGURE 2. Generalized chelae (two distal elements) of Eucalliaceine ghost shrimps. Left column: major chela; right column: minor chela, lateral view. A–B, *Calliaxina novaebritanniae* (Borradaile, 1900); C–D, *Eucalliax aequimana* (Baker, 1907); E–F, *Eucalliax quadracuta* (Biffar, 1970); G–H, *Calliax doerjesti* Sakai, 1999. Sketches after Biffar (1970) (F), Sakai (1999) (G–H), and personal observation. Note that the figures do not consider the presence of setae and intraspecific variations.

(Lutetian) of Romania; *C. beberibae* Beurlen, 1962 from the Turonian of Brazil; *C. burckhardti* Böhm, 1911 from the Maastrichtian and Lower Paleocene (Danian) of Argentina (see also Aguirre Urreta 1989 and Feldmann *et al.* 1995); *C. rovasendae* Crema, 1895 from the Middle Miocene of Italy; and *C. saetosa* Förster & Stinnesbeck, 1987 from the Maastrichtian of Chile. The latter species was already suggested to be placed within the Eucalliinae by Swen *et al.* (2001). Contrary to that, Schweitzer *et al.* (2006) considered the species to be a member of the extinct genus *Protocallianassa* Beurlen, 1930 and as such it also appeared in the list of fossil decapod species (Schweitzer *et al.* 2010). In this case the assignment to *Protocallianassa* was based virtually on a single character, the angle of the carpus/propodus articulation being more than 90°, and typically 120°. *Callianassa saetosa*, however, has very little in common with *Callianassa archiaci* A. Milne-Edwards, 1860, the type species of *Protocallianassa*. Moreover, the angle of the carpus/propodus articulation is a rather subjective and variable character. For instance, in extant *E. panglaoensis* the carpus/propodus articulation is clearly more than 90° (although definitely not 120°; see Dworschak 2006), although the same can not be said for all *Eucalliix* species.

Protocallianassa klofi Bishop, 1983 from the Albian of Texas (USA) was described on the basis of mostly isolated propodi; no articulated carpus with propodus has been found (Bishop 1983: 40). The species exhibits several characters very typical for members of Eucalliinae (as short triangular fixed finger with ridge on its outer surface, square manus with keeled lower margin) and this species is morphologically very close to *Calliixina chalmasii* comb. nov. as recognized herein.

Another interesting case is the co-occurrence of *Callianassa burckhardti* and *Protocallianassa* sp. in the Maastrichtian and Danian strata of the Neuquén Basin (Argentina) reported by Feldmann *et al.* (1995). Possible affinity of *C. burckhardti* to Eucalliinae has already been mentioned above. The material of *Protocallianassa* sp. consists of several isolated chelae which are morphologically very close to minor chelipeds of several extant species of the genus *Eucalliix*. The figure published by Feldmann *et al.* (1995: fig. 4.4) shows a large manus with rather oblique proximal margin and elongated fixed finger with distinctly developed ridge. Such a morphotype corresponds e.g. to the minor chela of *E. quadracuta*. In fact, both minor and major chela of *E. quadracuta* figured by Biffar (1970: fig. 2h) show an oblique angle of propodus/carpus articulation. As a result *C. burckhardti* might represent a member of the genus *Eucalliix*.

Recent re-examination of the type material of *C. archiaci*, the type species of *Protocallianassa*, by Schweitzer & Feldmann (2012) shows that the carpus/propodus articulation is at 90° angle, whereas the carpus/propodus articulation at 100–110° angle is typical for another species, *Protocallianassa faujasi* (Desmarest, 1822), currently classified within the genus *Mesostylus* Bronn and Roemer, 1852. *Mesostylus* was once considered a senior synonym of *Protocallianassa* and simultaneously a nomen oblitum by Karasawa (2003). After resurrection of *Mesostylus* the composition of *Protocallianassa* as listed in Schweitzer *et al.* (2010) needs to be reevaluated.

Genus *Calliixina* Ngoc-Ho, 2003

Type species. *Calliix punica* de Saint Laurent & Manning, 1982.

Extant species included. From the reasons stated above, Ngoc-Ho (2003) rather than Sakai (2011) is followed here in recognizing three species of the genus: *C. novaebritanniae*; *C. punica*; and *C. sakaii*.

Fossil species included. *C. chalmasii* (Brocchi, 1883) comb. nov. More fossil taxa might be accommodated within the genus (see above).

Diagnosis. Chelae on first pereopods subequal, similar, and laterally compressed. Carpus triangular, rounded at corners. Major propodus with well developed ridge running along the fixed finger, fixed finger with tooth on the occlusal margin. Minor propodus with deep depression on the lateral surface at the articulation of dactylus, depression elongate with lower border straight distally and distinctly rounded proximally. Fixed finger of both chelipeds rather short and roughly triangular in outline. Dactylus of both chelipeds unarmed. For diagnostic characters of soft part morphology see Ngoc-Ho (2003: 493).

Remarks. Concerning the shape of P1 chelipeds, *Calliixina* mostly resembles *Eucalliix* which also possesses subequal and similar first pereopods. The distinction between these two genera proposed herein concerns the nature of the minor cheliped, specifically the presence of a well-developed elongate depression on the lateral surface near the base of the fixed finger in *Calliixina* with an often granulated lower border (parallel to lower margin of propodus), which is straight distally and distinctly rounded proximally. The depression was clearly

depicted and mentioned in descriptions by several authors (in *C. novaebritanniae* by de Man 1928: fig. 20d; in *C. punica* by de Saint Laurent & Manning 1982: 219, fig. 4d, and Ngoc-Ho 2003: 496, fig. 19C; and in *C. sakaii* by Sakai 1966: 166, fig. 3b). Concerning the handedness, Sakai (1966) identified a cheliped with a depression as a minor one in *C. sakaii*, but, de Saint Laurent & Manning (1982) identified it as a major one in *C. punica*. Ngoc-Ho (2003) did not state whether the larger depression is present on only one cheliped and if so, on which one. *Calliixina* possesses almost equal chelipeds with slight size differences between them. Cheliped measurements of two extant specimens of *Calliixina novaebritanniae* (NHMW 25399, 25400) clearly show that the cheliped with the larger propodal depression is a minor one (pers. observation). The depression is much less if developed at all on the major cheliped, which usually possesses a ridge (sometimes termed „keel“) at the base of the fixed finger (Fig. 2A). Moreover, the lower margin of the minor propodus in *Calliixina* is virtually always straight along its entire length including the fixed finger (Fig. 2B).

Other genera of Eucalliicinae may have a similar propodal depression at the base of the fixed finger of the minor chela. However, these are never developed so strongly and the transition between the depression and the rest of the lateral propodal surface is not as abrupt as in *Calliixina*. The most similar genus, *Eucalliix*, usually has the manus of the minor cheliped shorter than that of the major cheliped (e.g. Biffar 1970: figs. 2h–i; Heard 1989: figs 1, 4A–B; Felder & Manning 1994: figs 2b–d). Thus, the shape of the depression as stated above is considered of taxonomic significance at the genus level.

The Middle Miocene species, *Callianassa chalmasii*, is reassigned to *Calliixina* on the basis of 1) the general shape of P1 propodus, which is slightly tapering distally, with keeled upper and lower margins, a rather short fixed finger, and being laterally compressed; 2) the presence of a deep depression on the outer lateral surface of the minor propodus at the base of fixed finger; 3) the shape of the depression being straight (parallel to the lower margin of the propodus) at its lower margin and rounded proximally; 4) the presence of a well developed ridge extending along the base of the fixed finger of the major propodus; and 5) the shape of P1 carpus, which is triangular, rounded at the corners, and keeled on the upper and lower margins. The combination of these characters is considered to be of taxonomic significance for assignment of callianassid material to the genus *Calliixina*.

***Calliixina chalmasii* (Brocchi, 1883) comb. nov.**

(Figs. 3A–B, 4A–R, 5A–E, 6A–E)

Callianassa Chalmasii Brocchi, 1883: 6, 7, pl. 5, figs. 7, 8.

Callianassa Chalmasi.—Glaessner, 1929: 77.

Callianassa chalmasii.—Müller, 1979: 274, pl. 1, fig. 5; Schweitzer *et al.*, 2010: 34.

Callianassa chalmasii.—Lörenthey, 1897: 150, 160, 168; Lörenthey, 1898a: 93, 105, 114; Lörenthey, 1898b: 9, 129, 130, 155; Lörenthey, 1898c: 102; Lörenthey, 1904: 161; Lörenthey, 1913: 332; Lörenthey in Lörenthey & Beurlen, 1929: 33, 65, pl. 2, figs. 15a, 15b.

‘*Callianassa chalmasii*.—Müller, 1984: 50, pl. 2, figs. 3–7.

Callianassa espichelensis Veiga Ferreira, 1961: 479–481, pl. 1, figs. 1–11; Schweitzer *et al.*, 2010: 34.

Callianassa rákosiensis Lörenthey, 1897: 160, 161, 168, 169 (new synonym); Lörenthey, 1898a: 105, 114, 115; Lörenthey, 1898b: 131, 132, pl. 9, fig. 4; Lörenthey, 1898c: 103, 104, pl. 9, fig. 4;

Callianassa rákosensis.—Lörenthey in Lörenthey & Beurlen, 1929: 33, 66, 67, pl. 2, fig. 14.

Callianassa rákosensis.—Müller, 1979: 274, 276, pl. 1, fig. 4.

Callianassa rakosiensis.—Glaessner, 1929: 89; Schweitzer *et al.*, 2010: 36.

‘*Callianassa rakosiensis*.—Müller, 1984: 51, pl. 3, figs. 1, 2.

Callianassa cf. *rákosensis*.—Bachmayer, 1953: 242; Bachmayer & Tollmann, 1953: 312.

?, ‘*Callianassa*“ sp. 2.—Hyžný, 2011: 42, fig. 4E, F.

non *Callianassa chalmasii*.—De Angeli *et al.*, 2009: 168, figs. 2C, D; Garassino *et al.*, 2012: 18. (= *Calliixina punica*)

Diagnosis. *Calliixina* with both P1 propodi quadrate, upper and lower margins keeled; fixed finger of major propodus with diagonally oriented ridge, occlusal margin toothed; minor propodus with well developed tuberculated depression on the base of fixed finger.

Description. First pereopods (chelipeds) with major and minor cheliped strongly developed, subequal in size, similar, laterally compressed.

Carpus unarmed, slightly higher than long, triangular in shape, upper and lower margin keeled, terminating in blunt corner at articulation with propodus, lower margin together with proximal margin forming a single rounded edge.

Both major and minor propodus quadrate, about as high as long, sometimes longer or shorter than high, converging distally; upper and lower margins keeled, terminating in blunt corners at articulation with carpus; keel on the upper margin forming sharp extension distally; keel on the lower margin distinctly broader proximally, forming flat edge; inner surface of propodi smooth with distinct setal pores; setal pores on the upper margin large, elongated in vertical aspect, i.e. perpendicular to the longitudinal axis of the limb.

In major propodus (previously described as *Callianassa chalmasii*), area at the articulation with dactylus covered with fine tubercles; fixed finger short, triangular, with distinct obliquely oriented ridge on the lateral surface; occlusal margin of fixed finger with distinct tooth followed by serrated edge; lower margin of propodus slightly convex proximally.

In minor propodus (previously described as *C. rakosiensis*), area at the articulation with dactylus distinctly depressed, covered with tubercles; depression forming sharp edge at its lower margin, which is parallel to the lower margin of propodus distally and distinctly rounded proximally; lower margin of propodus usually distinctly straight.

Dactylus slightly curved, unarmed.

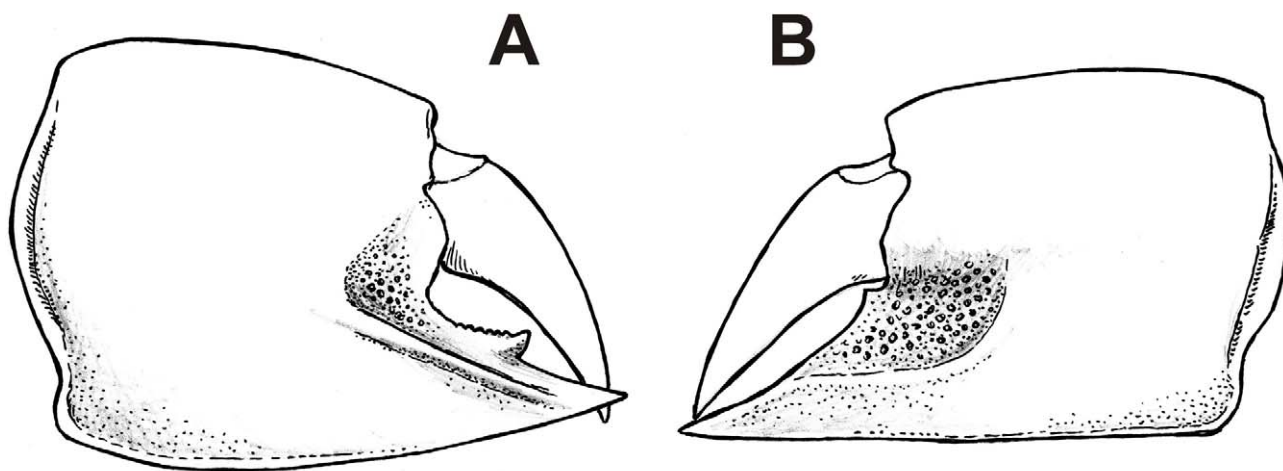


FIGURE 3. Reconstruction of major (A) and minor (B) chelae of *Callianassa chalmasii* (Brocchi, 1883) comb. nov.

Variations. The material shows a degree of variation in certain characters present on propodus. The length/height ratio is variable; both forms with distinctly longer (Figs. 4E, I) or shorter propodus (Fig. 4K) are present, although the majority of material exhibits more-less equal ratio (e.i. quadrate manus) (Table 2). Short morphotype has already been depicted, but not commented upon by Müller (1984: pl. 2, fig. 3).

Lower margin of minor propodus is sometimes concave at its distal end (Figs. 4M, P). In such cases the fixed finger bears a distinct tooth on its occlusal margin.

Material examined. Holotype of *Callianassa rakosiensis* representing right propodus (FI 29); Müller (1984: 51) stated that it had been probably lost, however, it was found during a visit of the Hungarian Geological Institute. The holotype of *C. chalmasii* has not been found and at present it should be considered to be lost as already stated by Müller (1984: 51). Material from Rákos collected by P. Müller and deposited at the Hungarian Natural History Museum comprises the right propodus of *C. rakosiensis* (M.86.244, illustrated also by Müller 1984: pl. 3, figs 1–2.) and several isolated propodi of *C. chalmasii* (M.86.275). Newer material collected by P. Müller is deposited under numbers PAL 2011.29, PAL 2011.32–37 (locality Rákos), PAL 2011.30 (Örs vezér tere), and PAL 2011.31 (Gyakorló út) (Fig. 4). Material from Rákos collected by the author is deposited under numbers KGP-MH RA020–037 (Fig. 4). Additional material comprises five specimens from the Fenk quarry (NHMW-2011-0167–0116–0120) (Fig. 5) and several propodal fragments (one articulated with carpus) from Dúbravská hlavica (SNM-Z 37570, 37571); KGP-MH DH074–076) (Fig. 6).

Measurements and details about the specimens are summarized in Table 2.

Other material. For comparative purposes, the extant material of several Eucalliinae taxa have been examined (all deposited in NHMW), namely *Callianassa novaebritanniae* (NHMW 25399, 25400); *Eucalliix aequimana* (NHMW 19365); and *E. kensleyi* (NHMW 16779).

TABLE 2. Measurements (mm) of *Calliaxina chalmasii* (Brocchi, 1883) comb. nov. Abbreviations: M = major, m = minor, ? = unknown; handedness: L = left; R = right; max.L = maximum length of the element, max.H. = maximum height of the element; measurements: ~ = approximate value.

Specimen	M/m	handedness	element	max.L	max.H
KGP-MH DH-074	M	L	propodus	8.0	7.1
KGP-MH DH-075	M	L	propodus	6.2	6.7
KGP-MH RA-020	M	L	propodus	10.0	8.5
KGP-MH RA-021	M	L	propodus	~7.5	7.3
KGP-MH RA-022	M	L	propodus	6.0	5.5
KGP-MH RA-023	M	R	propodus	4.4	3.6
KGP-MH RA-024	M	L	propodus	6.0	4.3
KGP-MH RA-025	M	R	propodus	4.0	3.4
KGP-MH RA-026	M	R	propodus	4.6	4.5
KGP-MH RA-027	m	R	propodus	7.2	7.0
KGP-MH RA-028	?	R	carpus	5.3	5.8
KGP-MH RA-029	?	L	propodus	~6.0	~6.3
KGP-MH RA-030	?	R	carpus	5.0	5.7
KGP-MH RA-031	?	R	carpus	5.5	6.0
KGP-MH RA-032	?	L	carpus	3.2	3.7
KGP-MH RA-033	M	R	propodus	6.0	6.3
KGP-MH RA-034	M	L	propodus	5.6	5.7
KGP-MH RA-035	m	L	propodus	7.6	7.7
KGP-MH RA-036	m	L	propodus	5.0	6.0
KGP-MH RA-037	m	R	propodus	6.8	6.2
NHMW-2011-0167-0116	?	R	carpus	5.7	5.6
NHMW-2011-0167-0117	m	R	propodus	5.1	5.0
NHMW-2011-0167-0118	m	L	propodus	7.3	7.3
NHMW-2011-0167-0120a	M	R	propodus	7.0	6.7
NHMW-2011-0167-0120b	M	L	propodus	3.2	3.0
PAL 2011.29	m	L	propodus	6.3	6.4
PAL 2011.30	m	L	propodus	~4.5	4.2
PAL 2011.31	m	L	propodus	8.6	8.3
PAL 2011.32	m	L	propodus	5.0	4.5
PAL 2011.33	M	L	propodus	5.6	5.4
PAL 2011.34	M	R	propodus	6.5	7.0
PAL 2011.35	M	R	propodus	6.4	7.0
PAL 2011.36	M	R	propodus	7.0	7.4
PAL 2011.37	M	L	propodus	6.4	5.7
SNM Z-37570	m	R	propodus	6.6	6.4
SNM Z-37570	m	R	carpus	4.5	6.3
SNM Z-375701	M	L	propodus	8.5	8.8

Occurrence. The oldest occurrence of *Calliaxina chalmasii* comb. nov., as reported herein, is that from the Fenk quarry, Gross Höflein, Austria, which is middle 'Badenian' (upper Langhian) in age. From the upper 'Badenian' (lower Serravallian), the species is known from the surroundings of the Budapest area, Hungary (Müller 1984). It was reported also from the Middle Miocene of Portugal (Veiga Ferreira 1961). Thus, it appears that during

Miocene the species was widespread in the Central Paratethys. Since, the Late Miocene, when the seaways between these two palaeogeographic areas were closed and the Central Paratethys became Lake Pannon (Rögl 1998, 1999; Harzhauser *et al.* 2002; Harzhauser & Piller 2007), the species might have migrated into the Mediterranean where it gave rise to extant *Calliaxina punica*. Following the chronological approach (see below) the material of *Callianassa chalmasii* reported from the Early Pliocene of Italy (De Angeli *et al.* 2009; Garassino *et al.* 2012) may in fact represent *C. punica*, as numerous extant decapod species are known from their Pliocene occurrences. This conclusion may be supported by the reported co-occurrence of presumed *C. chalmasii* and *Calliaxina* cf. *C. punica* at one of the Italian localities (Garassino *et al.* 2012).

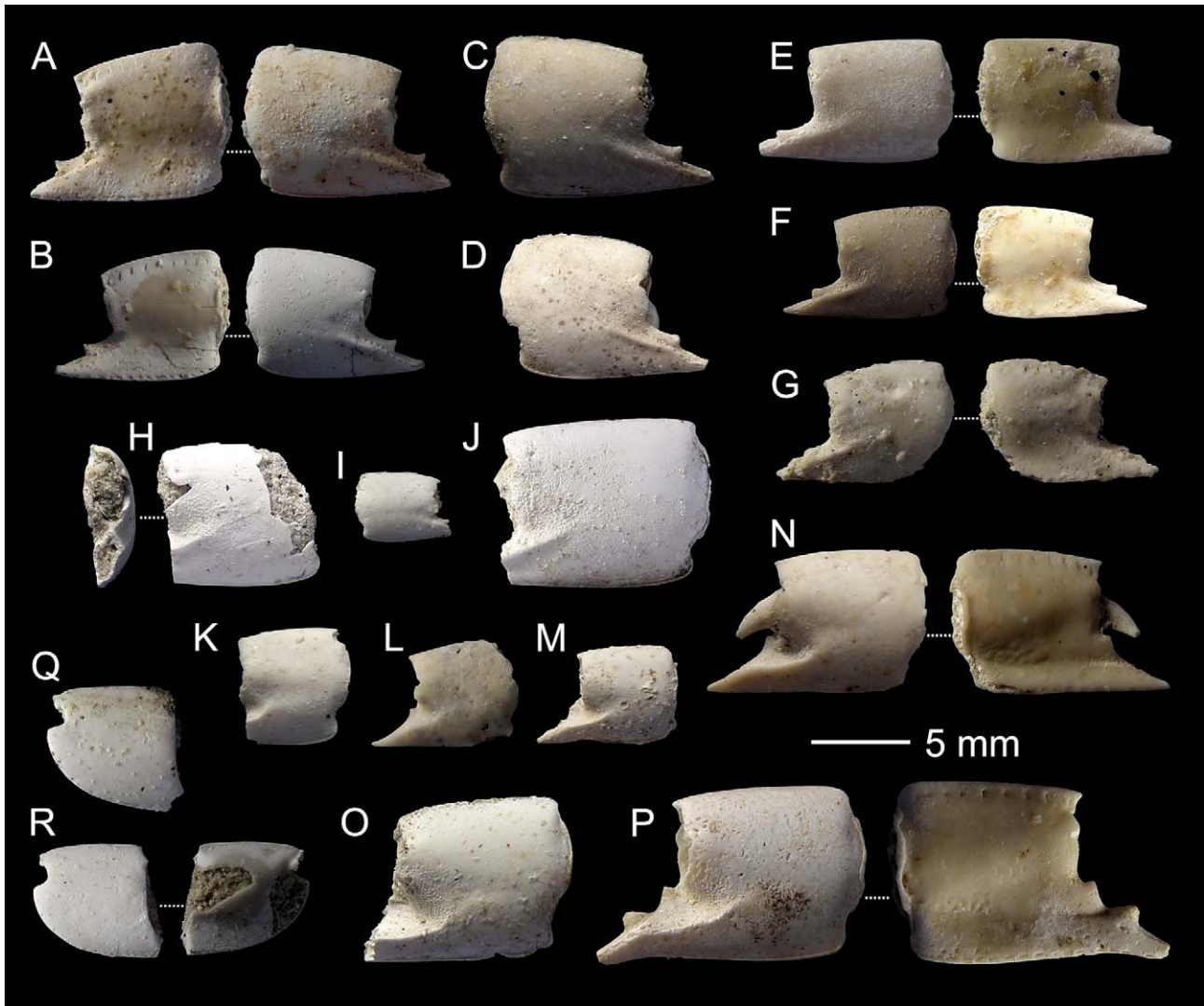


FIGURE 4. *Calliaxina chalmasii* (Brocchi, 1883) new combination, Budapest area (Great Hungarian Basin, Hungary): A, right major propodus (inner and outer view), PAL 2011.36; B, right major propodus (inner and outer view), KGP-MH RA-033; C, right major propodus, PAL 2011.34; D, right major propodus, PAL 2011.35; E, left major propodus (outer and inner view), PAL 2011.37; F, left major propodus (outer and inner view), PAL 2011.33; G, left major propodus (outer and inner view), KGP-MH RA-034; H, left major propodus, KGP-MH RA-021; I, right major propodus, KGP-MH RA-023; J, left major propodus, KGP-MH RA-020; K, left minor propodus (“short” morphotype), KGP-MH RA-036; L, left minor propodus, PAL 2011.30; M, left minor propodus, PAL 2011.32; N, left minor propodus articulated with dactylus (outer and inner view), PAL 2011.29; O, left minor propodus, KGP-MH RA-035; P, left minor propodus (outer and inner view), PAL 2011.31; Q, right carpus, KGP-MH RA-031; R, right carpus (outer and inner view), KGP-MH RA-028. All specimens are to scale.

Remarks. In description of *Callianassa rakosiensis* from the Middle Miocene of Hungary Müller (1984: 51) stated: “The species is remarkably similar to *C. chalmasii* in its general form, size and the distribution of pores. The form of the ridge on the finger and the position of the tooth is completely different in the two species and no trend was observed toward a transitional form. Thus their independence seems highly probable though a close

relation is likely.” What Müller (1984) recognized as two separate species in fact represents minor (*C. rakosiensis*) and major chelae (*C. chalmasii*) of a single species. Müller's observation of no transitional form and simultaneously the presence of both morphotypes at the same localities (Rákos, Gyakorlo út and Örs vezér tere) support the synonymisation proposed here.

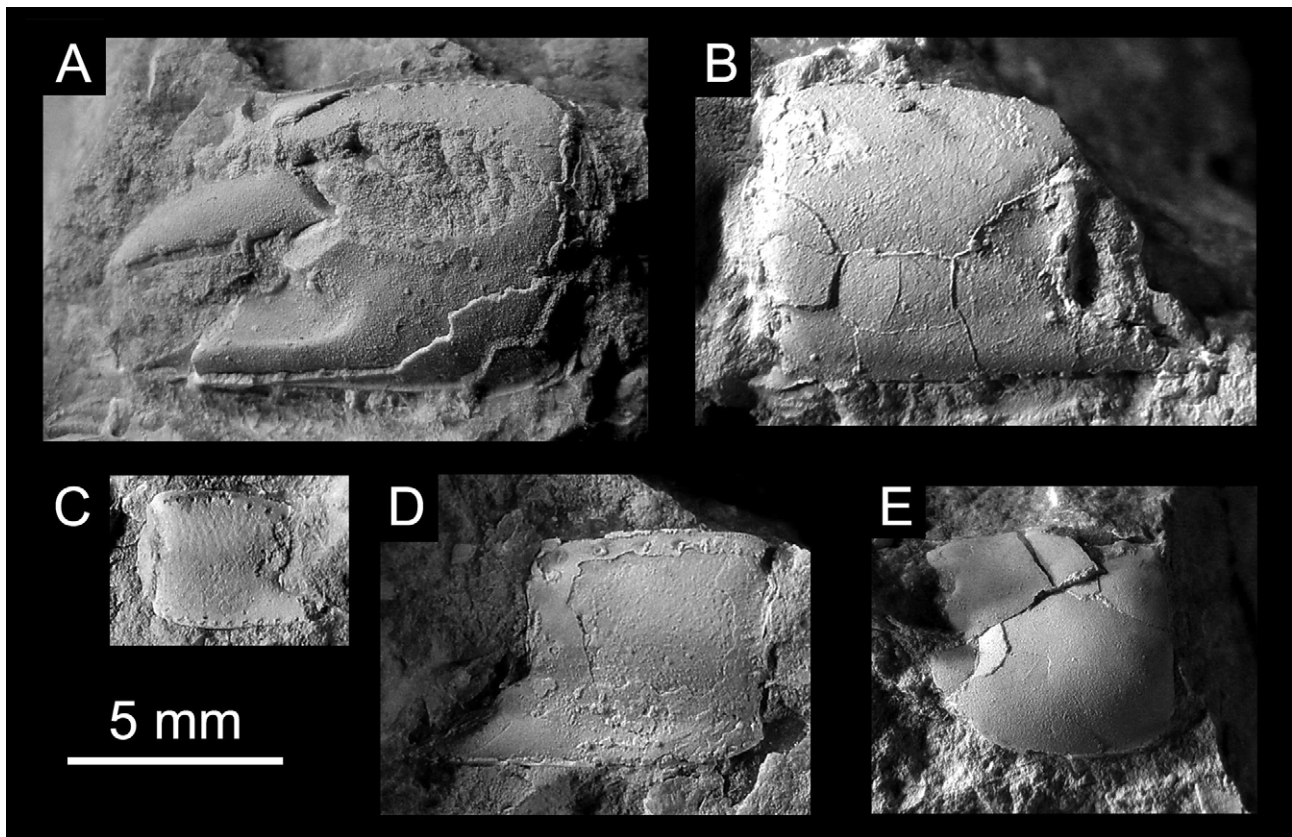


FIGURE 5. *Callianassa chalmasii* (Brocchi, 1883) new combination, Fenk quarry (Vienna Basin, Austria): A, left minor propodus articulated with dactylus, NHMW-2011-0167-0118; B, right major propodus, NHMW-2011-0167-0120a; C, left major propodus, NHMW-2011-0167-0120b; D, right minor propodus, NHMW-2011-0167-0117; E, right carpus, NHMW-2011-0167-0116. All specimens are to scale and were coated with ammonium chloride prior to photography.

Callianassa espichelensis described by Veiga Ferreira (1961) has already been considered as a junior synonym of *C. chalmasii* (Müller 1984). Figures (Veiga Ferreira 1961: fig. 1) clearly show the same morphotype. Most illustrated specimens represent major chelae (*C. chalmasii* morphotype); however, one specimen (fig. 1.4) seems to represent the minor chela (*C. rakosiensis* morphotype). It is illustrated from the inner side, so, the depression present on the outer lateral surface is not visible. Veiga Ferreira (1961: 480), however, mentioned the presence of a ridge, depression, and also faint tuberculation at the base of the fixed finger. I concur with Müller (1984), contrary to Schweitzer *et al.* (2010), and consider *C. espichelensis* as a junior subjective synonym of *C. chalmasii*.

Hyžný (2011: 42) reported a burrow structure with the cheliped remains of two individuals identified as “*Callianassa*” sp. 2 from the Gyakorló út locality. Although the material is insufficiently preserved, one individual clearly possesses equal or subequal chelipeds. Thus, it might represent *C. chalmasii* comb. nov., which has already been reported from that locality (Müller 1984; this paper). The material itself is, however, fragmentary and poorly preserved. As taxonomically important characters are discussed herein are not readily visible, I am hesitant to consider it to be conspecific with *C. chalmasii* comb. nov.

Callianassa chalmasii comb. nov. can be easily distinguished from all other Middle Miocene callianassid forms (for a review see Hyžný 2011: table 2); none of them has a well developed tuberculated depression on minor propodus at the base of the fixed finger. Moreover, *C. chalmasii* comb. nov. has laterally compressed chelipeds, a character that is uncommon in callianassid taxa co-occurring at the same localities. On the other hand, *C. chalmasii* comb. nov. is virtually indistinguishable from the extant forms, notably *C. punica* and *C. novaebritanniae*, on the basis of propodus and carpus alone. Characters on merus might resolve this issue. I concur with Müller (1984: 48)

that: “identification of 12–15 million year old species with extant ones should be done with caution”. Thus, a chronological approach (which operates with chronospecies rather than morphospecies) is followed here (see also Klaus & Gross 2010) and *Calliaxina chalmasii* comb. nov. is considered a separate species distinct from all extant congeners.

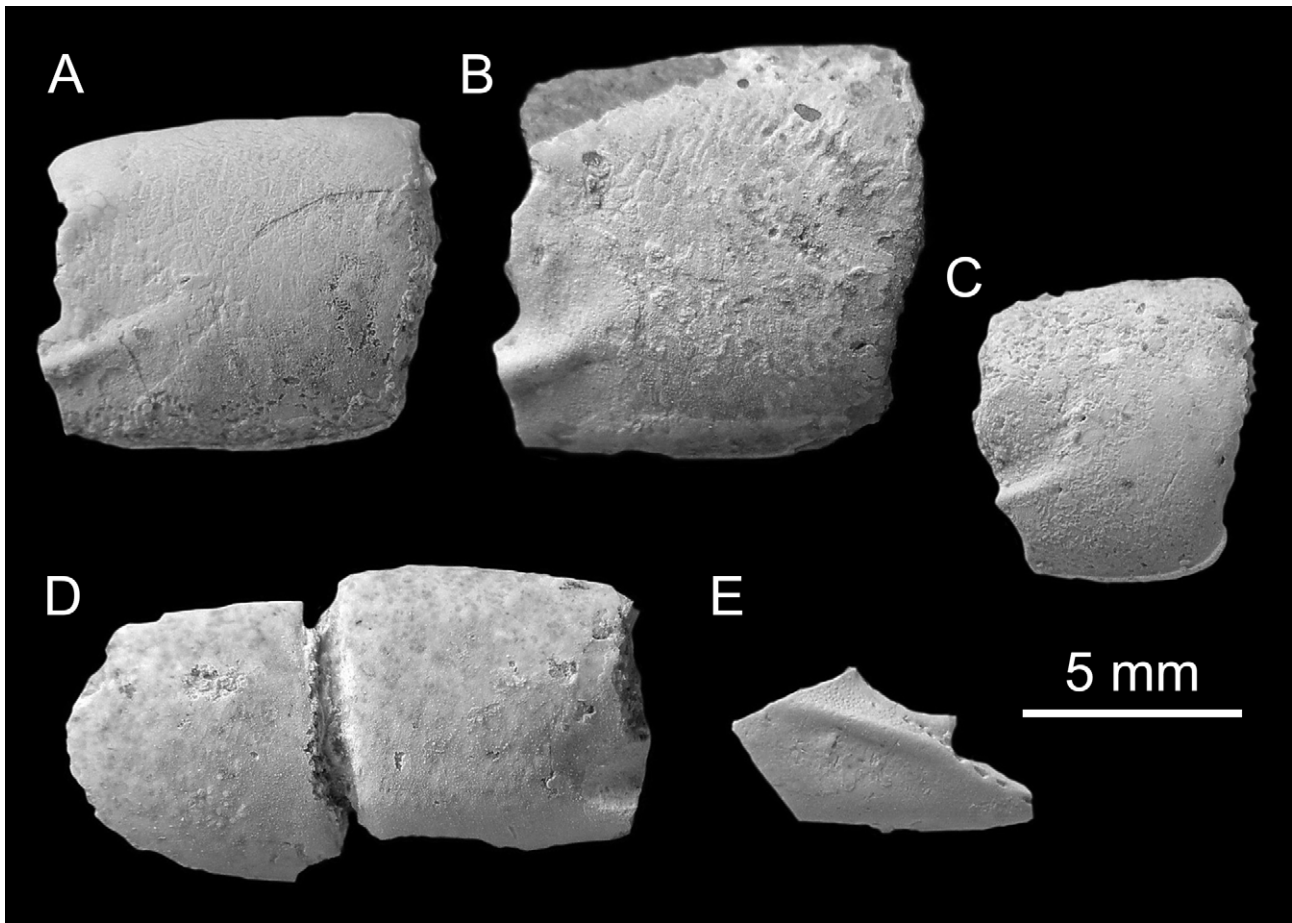


FIGURE 6. *Calliaxina chalmasii* (Brocchi, 1883) new combination, Dúbravská hlavica (Vienna Basin, Slovakia): A, left major propodus, KGP-MH DH-074; B, left major propodus, SNM-Z 37570; C, left minor propodus, KGP-MH DH-075; D, right minor propodus articulated with carpus, SNM-Z 37571 ; E, fragmented right pollex (from right chela). All specimens are to scale and were coated with ammonium chloride prior to photography.

Acknowledgements

I would like to express the deepest thank to following individuals for their help in my research: Alfréd Dulai (Hungarian Natural History Museum, Budapest, Hungary); Mathias Harzhauser, Andreas Kroh and Oleg Mandić (Natural History Museum, Wien, Austria); Peter Klepsatel and Barbara Chalupová (Slovak National Museum, Bratislava, Slovakia); and Pál Müller (Hungarian Geological Survey, Budapest, Hungary) provided access to the fossil material deposited in respective institutions. Pál Müller provided guidance on the fieldtrip at Rákos locality. Peter C. Dworschak (Natural History Museum, Wien, Austria) provided access to the collection of extant ghost shrimps deposited in NHMW, helped with a lot of fruitful discussion on systematics and biology of callianassids and commented earlier version of the manuscript. Rodney M. Feldmann (Kent State University, Ohio, USA) improved English of the manuscript. The papers benefited from the constructive criticism of two anonymous reviewers. The work has been supported by research grants APVV 0280-07 to Daniela Reháková (Comenius University, Bratislava, Slovakia), KEGA K-09-009-00 to Natália Hudáčková (Comenius University, Bratislava, Slovakia), and Comenius University Grant UK/168/2011 and PalSIRP Sepkoski Grant 2011 to the author.

References

- Aguirre-Urreta, M. (1989) The Cretaceous decapod Crustacea of Argentina and the Antarctic Peninsula. *Palaeontology*, 32, 499–552.
- Bachmayer, F. (1953) Die Dekapodenfauna des tortonischen Leithakalkes von Deutsch-Altenburg (Niederösterreich). *Mitteilungen der Geologischen Gesellschaft in Wien*, 44 [for 1951], 237–262.
- Bachmayer, F. & Tollmann (1953) Die Crustaceen-Fauna aus dem tortonischen Leithakalk (Steinbrüche der Firma Fenk) bei Groß-Höflein im Burgenland. *Kober-Festschrift 1953, Skizzen zum Antlitz der Erde. Geologische Arbeiten, herausgegeben aus Anlaß des 70. Geburtstages von Prof. Dr. L. Kober, Universität Wien*, Gesellschaftsbuchdruckerei Brüder Hollinek, Wien, 308–314.
- Baker, W.H. (1907) Notes on South Australian decapod Crustacea. Part V. *Transactions of the Royal Society of South Australia*, 31, 173–191.
- Baráth, I., Nagy, A. & Kováč, M. (1994) Sandberg Member – Late Badenian Marginal Sediments on the Eastern Margin of the Vienna Basin. *Geologické práce, Správy*, 99, 59–66. [In Slovak with English Summary]
- Berkenbusch, K. & Rowden, A.A. (2003) Ecosystem engineering - moving away from 'just-so' stories. *New Zealand Journal of Ecology*, 27, 67–73.
- Berkenbusch, K., Rowden, A.A. & Myers, T.E. (2007) Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. *Journal of Experimental Marine Biology and Ecology*, 341, 70–84.
- Beurlen, K. (1930) Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. *Fortschritte in der Geologie und Paläontologie*, 8, 317–586.
- Beurlen, K. (1962) O género *Callianassa* nas formações Cretácicas de Pernambuco. *Arquivos de Geologia, Universidad do Recife*, 2, 1–10.
- Biffar, T.A. (1970) Three new species of callianassid shrimp (Decapoda, Thalassinidea) from the western Atlantic. *Proceedings of the Biological Society of Washington*, 83(3), 35–50.
- Bishop, G.A. (1983) Fossil decapod crustaceans from the Lower Cretaceous Glen Rose Limestone of Central Texas. *Transactions of the San Diego Society of Natural History*, 20, 27–55.
- Bishop, G.A. & Williams, A.B. (2005) Taphonomy and preservation of burrowing thalassinidean shrimps. *Proceedings of the Biological Society of Washington*, 118(1), 218–236.
- Bittner, A. (1893) Decapoden des pannonischen Tertiärs. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften in Wien*, 102, 10–37.
- Borradaile, L.A. (1900) On the Stomatopoda and Macrura brought by Dr. Willey from the South Seas. In: Willey, A., *Zoological results based on material from in New Britain, New Guinea, Loyalty Islands and elsewhere collected during the years 1895, 1896 and 1897*. Vol. 4. Cambridge, University Press. 395–428.
- Böhm, J. (1911) *Callianassa burckhardti* n. sp. nebst einer Zusammenstellung der fossilen Arten der Gattung *Callianassa*. *Zeitschrift der deutschen geologischen Gesellschaft, Monatsberichte*, 63, 37–46.
- Brocchi, P. (1883) Notes sur les Crustacés fossiles des terres tertiaires de la Hongrie. *Annales des Sciences Géologiques*, (2)14, 1–8.
- Bronn, H.G. & Roemer, F. (1852) *Lethaea geognostica, oder Abbildung und Beschreibung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen*, 2(5). Stuttgart, E. Schweizerbart. 1–124.
- Burkenroad, M.D. (1963) The evolution of the Eucarida, (Crustacea, Eumalacostraca), in relation to the fossil record. *Tulane Studies in Geology*, 2(1), 2–17.
- Dana, J.D. (1852) *Conspectus Crustaceorum, &c. Conspectus of the Crustacea of the Exploring Expedition under Capt. Wilkes, U.S.N. Macroura. Proceedings of the Academy of Natural Sciences of Philadelphia*, 6, 10–28.
- De Angeli, A., Garassino, A. & Pasini, G. (2009) New reports of anomurans and brachyurans from the Cenozoic of Tuscany (Italy). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 150(2), 163–196.
- De Gaillande, D. & Lagardère, J.-P. (1966) Description de *Callianassa (Callichirus) lobta* nov. sp. (Crustacea Decapoda Callianassidae). *Recueil des Travaux de la Station Marine d'Endoume*, 40, 259–265.
- De Grave, S., Pentcheff, N.D., Ah Yong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Tshudy, D. & Wetzer, R. (2009) A classification of living and fossil genera of decapod crustaceans. *The Raffles Bulletin of Zoology Supplement*, 21, 1–109.
- Desmarest, A.G. (1822) *Histoire naturelle des Crustacés fossiles. Les Crustacés proprement dits*, Paris, F.G. Levrault. 67–154, pls. 5–11.
- Dullo, W.C. (1983) Fossilidiagenese im miozänen Leitha-Kalk der Paratethys von Österreich: Ein Beispiel für Faunenverschiebung durch Diageneseunterschiede. *Facies*, 8, 1–112.
- Dworschak, P.C. (2000) Global diversity in the Thalassinidea (Decapoda). *Journal of Crustacean Biology*, 20(Special Number 2), 238–245.
- Dworschak, P.C. (2005a) A new species of *Eucalliax* Manning & Felder, 1991 (Decapoda: Callianassidae) from the Red Sea. *Proceedings of the Biological Society of Washington*, 118, 209–217.
- Dworschak, P.C. (2005b) Global diversity in the Thalassinidea (Decapoda): an update (1998–2004). *Nauplius*, 13(1), 57–63.
- Dworschak, P.C. (2006) A new species of *Eucalliax* Manning & Felder, 1991 (Decapoda: Callianassidae) from the Philippines. *The Raffles Bulletin of Zoology*, 54(2), 349–359.
- Dworschak, P.C. (2007) Book review. Sakai, K. 2005. Callianassoidea of the world (Decapoda: Thalassinidea). *Crustaceana Monographs 4. Journal of Crustacean Biology*, 27(1), 158–169.

- Felder, D.L. & Lovett, D.L. (1989) Relative Growth and Sexual Maturation in the Estuarine Ghost Shrimp *Callinassa louisianensis* Schmitt, 1935. *Journal of Crustacean Biology*, 9(4), 540–553.
- Felder, D.L. & Manning, R.B. (1994) Description of the ghost shrimp *Eucalliax mcilhennyi*, new species, from south Florida, with reexamination of its known congeners (Crustacea: Decapoda: Callianassidae). *Proceedings of the Biological Society of Washington*, 107, 340–353.
- Felder, D.L. & Manning, R.B. (1997) Ghost shrimps of the genus *Lepidophthalmus* from the Caribbean region, with description of *L. richardi*, new species, from Belize (Decapoda: Thalassinidea: Callianassidae). *Journal of Crustacean Biology*, 17(2), 309–331.
- Felder, D.L. & Manning, R.B. (1998) A new ghost shrimp of the genus *Lepidophthalmus* from the Pacific coast of Columbia (Decapoda: Thalassinidea: Callianassidae). *Proceedings of the Biological Society of Washington*, 111(2), 398–408.
- Felder, D.L. & Rodrigues, S. de A. (1993) Reexamination of the ghost shrimp *Lepidophthalmus louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and comparison to *L. siriboia*, new species, from Brazil (Decapoda: Thalassinidea: Callianassidae). *Journal of Crustacean Biology*, 13, 357–376.
- Feldmann, R.M., Casado, S., Chirino-Gálvez, L. & Aguirre-Urreta, M. (1995) Fossil decapod crustaceans from the Jaguel and Roca Formations (Maastrichtian-Danian) of the Neuquén basin, Argentina. *Paleontological Society Memoir*, 43, 1–22.
- Förster, R., & Stinnesbeck, W. (1987) Zwei neue Krebsse, *Callianassa saetosa* n. sp. und *Homolopsis chilensis* n. sp. (Crustacea, Decapoda) aus der Oberkreide Zentral-Chiles. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 27, 51–65.
- Garassino, A., Pasini, G., De Angeli, A., Charbonnier, A., Famiani, F., Baldanza, A. & Bizzarri, R. (2012) The decapod community from the Early Pliocene (Zanclean) of “La Serra” quarry (San Miniato, Pisa, Toscana, central Italy): sedimentology, systematics, and palaeoenvironmental implications. *Annales de Paléontologie*, 98, 1–61.
- Glaessner, M.F. (1929) Crustacea Decapoda. In: Pompeckj, F.J. (ed.) Fossilium catalogus, 1: Animalium, 41, 1–464. W. Junk, Berlin.
- Harzhauser, M., Mandic, O. & Zuschin, M. (2003) Changes in Paratethyan marine molluscs at the Early/Middle Miocene transition: diversity, palaeogeography and palaeoclimate. *Acta Geologica Polonica*, 53, 323–339.
- Harzhauser, M. & Piller, W.E. (2007) Benchmark data of a changing sea – Palaeogeography, Palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 253, 8–31.
- Harzhauser, M., Piller, W.E. & Steininger, F.F. (2002) Circum-Mediterranean Oligo-Miocene biogeographic evolution – the gastropods' point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183, 103–133.
- Heard, R.W. (1989) *Calliax jonesi*, n. sp. (Decapoda: Thalassinidea: Callianassidae) from the Northwestern Bahamas. *Gulf Research Reports*, 8(2), 129–136.
- Holmes, S. J. (1904) On some new or imperfectly known species of West American Crustacea. *Proceedings of the California Academy of Sciences, series 3*, 3, 307–328
- Hyžný, M. (2011) *In situ* mud shrimps (Decapoda: Axiidea: Callianassidae) preserved within their burrows from the middle Miocene of the Central Paratethys. *Bulletin of the Mizunami Fossil Museum*, 37, 37–46.
- Hyžný, M. & Hudáčková, N. (2012) Redescription of two ghost shrimps (Decapoda: Axiidea: Callianassidae) from the Middle Miocene of the Central Paratethys: systematics, intraspecific variation, and *in situ* preservation. *Zootaxa*, 3210, 1–25.
- Hyžný, M. & Müller, P. (in press) The fossil record of *Glypturus* Stimpson, 1866 (Crustacea, Decapoda, Axiidea, Callianassidae) revisited, with notes on palaeoecology and palaeobiogeography. *Palaeontology*.
- Karasawa, H. (1992) Fossil decapod crustaceans from the Manda Group (middle Eocene), Kyushu, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New series*, 167, 1247–1258.
- Karasawa, H. (1997) A Monograph of Cenozoic stomatopod, decapod, isopod and amphipod Crustacea from West Japan. *Monograph of the Mizunami Fossil Museum*, 8, 1–81.
- Karasawa, H. (2003) Mesostylus Bronn and Roemer, 1852, a senior subjective synonym of Protocallinassa Beurlen, 1930 (Crustacea: Decapoda: Thalassinidea): a reversal of precedence. *Paleontological Research*, 7, 181–182.
- Klaus, S. & Gross, M. (2010) Synopsis of the fossil freshwater crabs of Europe (Brachyura: Potamoidea: Potamidae). *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, 256, 39–59.
- Latreille, P.A. (1802-1803) Histoire naturelle, générale et particulière, des Crustacés et des Insectes, 3, 1–468. (F. Dufart, Paris)
- Lőrenthey, E. (1897) Adatok Magyarország harmadkorú rák faunájához. *Mathematikai és Természettudományi Értesítő*, 15, 149–169.
- Lőrenthey, E. (1898a) Beiträge zur Decapodenfauna des ungarischen Tertiärs. *Mathematischen und Naturwissenschaftlichen Berichte aus Ungarn*, 14, 92–115.
- Lőrenthey, E. (1898b) Adatok Magyarország harmadkorú rák-faunájához. *Mathematikai és Természettudományi Közlemények*, 27(2), 103–271.
- Lőrenthey, E. (1898c) Beiträge zur Decapodenfauna des Ungarischen Tertiärs. *Természettudományi Füzetek*, 21, 1–133.
- Lőrenthey, E. & Beurlen, K. (1929) Die fossilen Dekapoden der Länder der Ungarischen Krone. *Geologica Hungarica, Series Palaeontologica*, 3, 1–421.
- Man, J.G. de (1928) The Decapoda of the Siboga-Expedition. Part 7. The Thalassinidae and Callianassidae collected by the Siboga-Expedition with some remarks on the Laomediidae. *Siboga Expédition*, 39(A6), 1–187.
- Manning, R. B. & D. L. Felder (1991) Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea). *Proceedings of the Biological Society of Washington*, 104, 764–792.
- Milne-Edwards, A. (1860) Monographie des décapodes macroures fossiles de la famille des Thalassiniens. *Annales des Sciences Naturelles, 4e série*, 14, 294–357.
- Moissette, P., Dulai, A., Escarguel, G., Kázmér, M., Müller, P. & Saint Martin, J.-P. (2007) Mosaic of environments recorded by

- bryozoan faunas from the Middle Miocene of Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 252, 530–556.
- Müller, P. (1979) Decapoda (Crustacea) fauna a budapesti miocénból (5). *Földtani Közlöny, Bulletin of the Hungarian Geological Society*, 108, 272–318.
- Müller, P. (1984) Decapod Crustacea of the Badenian. *Geologica Hungarica, Series Palaeontologica*, 42, 3–317.
- Müller, P. (1998) Crustacea Decapoda. In: Flügel, H. W. (Ed.): *Catalogus Fossilium Austriae*, 1–48 Wien (Verlag der Österreichischen Akademie der Wissenschaften).
- Müller, P.M. (2006) New decapods from the Miocene of Hungary – with remarks about their environment. *Földtany Közlöny*, 136(1), 37–49.
- Ngoc-Ho, N. (2003) European and Mediterranean Thalassinidea (Crustacea, Decapoda). *Zoosystema* 25, 439–555.
- Papp, A., Cicha, I., Seneš, J. & Steininger, F. (eds.) (1978) *Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys. Volume VI. M₄ Badenien (Moravien, Wielicien, Kosovien)*. Veda SAV, Bratislava. 594 pp.
- Poore, G.C.B. (2012) Eucalliinae. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=477376> on 2012-02-07.
- Poore, G.C.B. & Griffin, D.J.G. (1979) The Thalassinidea (Crustacea: Decapoda) of Australia. *Records of the Australian Museum*, 32(6), 217–321.
- Riegl, B. & Piller, W.E. (2000) Biostromal Coral Facies – A Miocene Example from the Leitha Limestone (Austria) and its Actualistic Interpretation. *Palaios*, 15, 399–413.
- Rodrigues, S. de A. & Manning, R. B. (1992) Two new callianassid shrimps from Brazil (Crustacea: Decapoda: Thalassinidea). *Proceedings of the Biological Society of Washington*, 105, 324–330.
- Rögl, F. (1998) Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien*, A99, 279–310.
- Rögl, F. (1999) Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geologica Carpathica*, 50, 339–349.
- Saint Laurent, M. de (1973) Sur la systématique et la phylogénie des Thalassinidea: définition des familles des Callianassidae et des Upogebiidae et diagnose de cinq genres nouveaux (Crustacea Decapoda). *Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences, série D*, 277, 513–516.
- Saint Laurent, M. de (1979) Sur la classification et la phylogénie des Thalassinides: définitions de la superfamille des Axioidea, de la sous-famille des Thomassiniinae et de deux genres nouveaux (Crustacea Decapoda). *Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences, Paris*, 288, 1395–1397.
- Saint Laurent, M. de & Le Loeuff, P. (1979) Upogebiidae et Callianassidae. Crustacés Décapodes Thalassinidea, 1. Campagnes de la Calypso au large des cotes Atlantiques africaines (1956 et 1959)(suite), 22. *Résultats scientifiques des campagnes de la Calypso*, 11, 29–101.
- Saint Laurent, M. de & Manning, R.B. (1982) *Calliax punica*, espèce nouvelle de Callianassidae (Crustacea, Decapoda) des eaux méditerranéennes. *Quaderni del Laboratorio di Tecnologia della Pesca*, 3(2–5), 211–224.
- Sakai, K. (1988) A new genus and five new species of Callianassidae (Crustacea: Decapoda: Thalassinidea) from Northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, 5(1), 51–69.
- Sakai, K. (1999) Synopsis of the family Callianassidae, with keys to subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea). *Zoologische Verhandlungen, Leiden*, 326, 1–152.
- Sakai, K. (2002) Callianassidae (Decapoda, Thalassinidea) in the Andaman Sea, Thailand. *Phuket Marine Biological Center Special Publication*, 23(2), 461–532.
- Sakai, K. (2005) Callianassoidea of the world (Decapoda: Thalassinidea). *Crustaceana Monographs*, 4, 1–285.
- Sakai, K. (2011) Axioidea of the World and a Reconsideration of the Callianassoidea (Decapoda, Thalassinidea, Callianassida). *Crustaceana Monographs*, 13, 1–520.
- Schweitzer, C.E. & Feldmann, R.M. (2012) Revision of Decapoda deposited in The Muséum national d'Histoire naturelle, Paris. *Bulletin of the Mizunami Fossil Museum*, 38, 15–27.
- Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H. & Schweigert, G. (2010) Systematic list of fossil decapod crustacean species. *Crustaceana Monographs*, 10, 1–222.
- Schweitzer, C.E., Feldmann, R.M., Encinas, A. & Suárez, M. (2006) New Cretaceous and Eocene Callianassoidea (Thalassinidea, Decapoda) from Algarrobo, Chile. *Journal of Crustacean Biology*, 26(1), 73–81.
- Švagróvský, J. (1981) Lithofazielle Entwicklung und Molluskenfauna des oberen Badeniens (Miozän M_{4d}) in dem Gebiet Bratislava – Devínska Nová Ves. *Západné Karpaty, séria paleontológia*, 7, 5–204.
- Stimpson, W. (1866) Descriptions of new genera and species of Macrurous Crustacea from the coasts of North America. *Proceedings of the Chicago Academy of Sciences*, 1, 46–48.
- Swen, K., Fraaije, R.H.B., & Zwaan, G.J. van der (2001) Polymorphy and extinction of the Late Cretaceous burrowing shrimp *Protocallianassa faujasi* and first record of *Corallianassa* and *Calliax* (Crustacea, Decapoda, Thalassinidea) from the Cretaceous. *Contributions to Zoology*, 70, 85–98.
- Tudge, C.C., Poore, G.C.B. & Lemaitre, R. (2000) Preliminary phylogenetic analysis of generic relationships within the Callianassidae and Ctenochelidae (Decapoda: Thalassinidea: Callianassoidea). *Journal of Crustacean Biology*, 20 (Special Issue 2), 129–149.
- Türkay, M. & Sakai, K. (1995) Decapod Crustaceans from a Volcanic Hot Spring in the Marianas. *Senckenbergiana maritima*, 26(1/2), 25–35.
- Veiga Ferreira, O. da (1961) Nove espécie de Callianassa no Miocénico da Bacia do Tejo. *Comunicações dos Serviços Geológicos de Portugal*, 45, 479–481.