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

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Abstract

A detailed study of chelipeds of two Middle Miocene burrowing ghost shrimp taxa, *Callianassa chalmasii* Brocchi, 1883, and *Callianassa rakosiensis* Lőrenthey, 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 *Calliaxina* (subfamily Eucalliacinae). As such it is the first recognized representative of the genus in the fossil record. It is argued that for the Eucalliacinae, 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 Eucalliacinae both chelipeds (propodi), major and minor, should be present.

**Key words:** Ghost shrimp, Callianassidae, Eucalliacinae, *Calliaxina 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 pereiopods) 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 Lőrenthey 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 *Calliaxina* Ngoc-Ho, 2003 (subfamily Eucalliacinae).

Thus, *Calliaxina chalmasii* comb. nov. becomes the first known exclusively fossil member of this genus. Comparison between extant taxa belonging to Eucalliacinae 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 *Eucalliax 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 pereiopods (chelipeds).
Systematics

Order Decapoda Latreille, 1802

Suborder Pleocyemata Burkenroad, 1963

Infraorder Axiidea de Saint Laurent, 1979

Family Callianassidae Dana, 1852

Subfamily Eucalliacinae 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; Eucalliax Manning & Felder, 1991; and Paraglypturus Türkay & Sakai, 1995. Ngoc-Ho (2003) provided an account of morphological differences between the Eucalliacinae genera. Sakai (2005) recognized Eucalliax and Calliaxina as junior synonyms of Calliax; this synonymization was criticized by Dworschak (2007: 159). Later, Sakai (2011) recognized all three genera, Calliax, Eucalliax and Calliaxina, as valid, but his concept of Eucalliax and Calliaxina differs markedly from that of Ngoc-Ho (2003). Sakai (2011) restricted Eucalliax to Callianassa quadracuta Biffar, 1970 only (type species of Eucalliax), and for Calliaxina listed C. aequimana (Baker, 1907), C. bulimba (Poore & Griffin, 1979), C. jonesi (Heard, 1989), C. mcilhennyi (Felder & Manning, 1994), C. panglaeoensis (Dworschak, 2006), C. novaebritanniae (Borredaile, 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 chelipep morphology, i.e. body parts commonly preserved in the fossil.
Calliaxina record. As a result, only the last three mentioned species from the list above are considered herein as members of Calliaxina, with the remainder as members of Eucalliax. It is also worth mentioning that Eucalliax kensleyi Dworschak, 2005a was omitted from the last monograph of Sakai (2011). The taxonomic history of generic assignment of all extant Eucalliacine taxa is summarized in Table 1.

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

**Chelipeds of the Eucalliacinae.** 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 Eucalliacinae, i.e. Calliaxina, Calliax, Eucalliax 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 Eucalliax and Calliaxina, subequal and similar first pereiopods are typical. Moreover, Calliaxina always possesses laterally compressed chelipeds. In Calliax they are also laterally compressed, but unequal and dissimilar, whereas in Paraglypturus they are unequal, dissimilar and massive.

Many Eucalliacinae species possess a distinct ridge extending obliquely along the fixed finger laterally and may extend to the propodus (as in Eucalliax panglaeomensis; 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 Eucalliacinae, although not all of these characters are present in all Eucalliacinae genera. The oblique ridge on the base of the fixed finger is rather typical for Eucalliacinae genera, notably Eucalliax and Calliaxina (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 Eucalliacinae. In Eucalliax and Calliaxina 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 Eucalliax and Calliaxina 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 Eucalliacinae were identified on the basis of both chelae (Beschin et al. 2002; Karasawa 1992, 1997). The nature of the minor chela can be diagnostic for Calliax 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 Eucalliax, 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 Eucalliax species it is usually slightly smaller (with relatively shorter manus) than the major one. In Calliaxina 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 chela 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 Eucalliax and Calliaxina 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.

**Eucalliacinae in the fossil record.** The fossil record of the Eucalliacinae with the emphasis on the genera Calliax and Eucalliax 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 Eucalliacinae, 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 Eucalliacline taxa.

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<td><em>Callianassa aequimana</em> Baker, 1907</td>
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<td>Eucalliæx</td>
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<td><em>Calliæx andamanica</em> Sakai, 2002</td>
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<td>Calliæx</td>
<td>Andamancalliæx</td>
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<td><em>Callianassa bulimba</em> Poore &amp; Griffin 1979</td>
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<td><em>Eucalliæx cearaensis</em> Rodrigues &amp; Manning, 1992</td>
<td>Calliæx</td>
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<td><em>Paraglypturus calderus</em> Türky &amp; Sakai, 1995</td>
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<td><em>Calliæx doerfesti</em> Sakai, 1999</td>
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<td><em>Calliæx jonesi</em> Heard, 1989</td>
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<td><em>Eucalliæx kensleyi</em> Dworschak, 2005a</td>
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<td>Eucalliæx</td>
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<td><em>Callianassa lobata</em> De Gaillande &amp; Lagardère, 1966</td>
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<td><em>Eucalliæx melhennyi</em> Felder &amp; Manning, 1994</td>
<td>Calliæx</td>
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<td>Calliæxina</td>
<td>Eucalliæx</td>
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<td><em>Callianassa novaebritanniae</em> Borradaile, 1900</td>
<td>Paraglypturus</td>
<td>Calliæx</td>
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<td>Calliæxina</td>
<td>Eucalliæx</td>
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<td><em>Eucalliæx panglaeensis</em> Dworschak, 2006</td>
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<td>Calliæxina</td>
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<td><em>Calliæx punica</em> de Saint Laurent &amp; Manning, 1982</td>
<td>Paraglypturus</td>
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<td><em>Callianassa quadracuta</em> Biffar, 1970</td>
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<td><em>Calliæx sakati</em> de Saint Laurent &amp; Le Locuff, 1979</td>
<td>Paraglypturus</td>
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<tr>
<td><em>Callianassa tooradin</em> Poore &amp; Griffin, 1979</td>
<td>Paraglypturus</td>
<td>Calliæx</td>
<td>Calliæx</td>
<td>Pseudocalliæx</td>
<td>Calliæx</td>
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(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. novasendae* 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 Eucalliacinae 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 archiacci* 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. panglaensis* 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 *Eucalliax* 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 Eucalliacinae (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 *Calliaxina 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 Eucalliacinae 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 *Eucalliax*. 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 *Eucalliax*.

Recent re-examination of the type material of *C. archiacci*, 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 ressurection of *Mesostylus* the composition of *Protocallianassa* as listed in Schweitzer *et al.* (2010) needs to be reevaluated.

### Genus *Calliaxina* Ngoc-Ho, 2003

**Type species.** *Calliax 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 accomodated within the genus (see above).

**Diagnosis.** Chelae on first pereiopods 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 unarmored. For diagnostic characters of soft part morphology see Ngoc-Ho (2003: 493).

**Remarks.** Concerning the shape of P1 chelipeds, *Calliaxina* mostly resembles *Eucalliax* which also possesses subequal and similar first pereiopods. 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 *Calliaxina* 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 chelifed 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 chelifed and if so, on which one. *Calliaxina* possesses almost equal chelifeds with slight size differences between them. Chelifed measurements of two extant specimens of *Calliaxina novaebritanniae* (NHMW 25399, 25400) clearly show that the chelifed with the larger propodal depression is a minor one (pers. observation). The depression is much less if developed at all on the major chelifed, 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 *Calliaxina* is virtually always straight along its entire length including the fixed finger (Fig. 2B).

Other genera of Eucalliacinae 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 *Calliaxina*. The most similar genus, *Eucalliax*, 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 for assignment of callianassid material to the genus *Calliaxina*.

The Middle Miocene species, *Callianassa chalmasii*, is reassigned to *Calliaxina* 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 *Calliaxina*.

**Calliaxina 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 esphichelensis* Veiga Ferreira, 1961: 479–481, pl. 1, figs. 1–11; Schweitzer et al., 2010: 34.
*Callianassa rakosiensis* 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 rakosensis.* —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*‘ 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. (= *Calliaxina punica*)

**Diagnosis.** *Calliaxina* 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 pereiopods (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 *Calliaxina 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 Eucalliacinae taxa have been examined (all deposited in NHMW), namely *Calliaxina novaebritanniae* (NHMW 25399, 25400); *Eucalliax aequimana* (NHMW 19365); and *E. kensleyi* (NHMW 16779).
Occurrence. The oldest occurrence of *Callixaina chalmassii* 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

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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).

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

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.
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 Órs vezér tere) support the synonymisation proposed here.

FIGURE 5. Calliaxina 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 chelifeds. 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.

Calliaxina 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.

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