



Redescription of two ghost shrimps (Decapoda: Axiidea: Callianassidae) from the Middle Miocene of the Central Paratethys: systematics, intraspecific variation, and *in situ* preservation

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Abstract

A redescription of two Middle Miocene burrowing ghost shrimps of the Central Paratethys, *Callianassa brocchii* Lörenthey, 1897 and *Callianassa pseudorakosensis* Lörenthey in Lörenthey & Beurlen, 1929, is provided. Material forming the basis of this study comes from the Studienka Formation (lower 'Sarmatian', Serravallian) of the Slovak part of the Vienna Basin and exhibits preservation allowing reassignment of the studied taxa to the genera *Neocallichirus* Sakai, 1988 and *Eucalliax* Manning & Felder, 1991 respectively. The major cheliped of both species exhibits two distinct morphotypes interpreted herein as possible sexual dimorphism. Several specimens of both taxa are preserved within the tube structures and are interpreted as *in situ* preservation within the burrows. Type material of both studied taxa and additional collections from the roughly coeval strata of Hungary and Austria were also studied.

Key words: Ghost shrimp, *Neocallichirus brocchii* **comb. nov.**, *Eucalliax pseudorakosensis* **comb. nov.**, Middle Miocene, Central Paratethys, *in situ* preservation

Introduction

The fossil Callianassidae Dana, 1852 of the Central Paratethys have never received much attention in the literature. The most comprehensive systematic treatments on this topic were published by Lörenthey & Beurlen (1929) and Müller (1984). Since publication of the latter, however, many changes in taxonomy have been proposed, and several major systematic contributions of extant taxa appeared (Manning & Felder 1991; Poore 1994; Sakai 1999, 2005, 2011; Ngoc-Ho 2003 with references therein). Although still inconsistent, the literature on the systematics of extant taxa published in the last 20 years forms the basis for reassignment of fossil material, which has been traditionally classified almost exclusively within the genus *Callianassa* in its widest sense. Recently, a major classification both of extant and fossil decapod crustacean genera summarized the most updated state of systematic arrangement of extant ghost shrimps (De Grave *et al.* 2009). The systematic part of this paper follows the work by De Grave *et al.* (2009) rather than the classification proposed by Sakai (1999, 2005, 2011).

Since the publication of Müller (1984), the Callianassidae of the Central Paratethys have been at least partly discussed by Müller (1996, 1998) and Hyžný & Müller (2010). More recently Hyžný (2011a: table 2) provided a list of Middle Miocene Callianassidae reported from the Central Paratethys and discussed *in situ* preservation of callianassid ghost shrimps.

Hyžný & Müller (2010) were the first to try to apply one of the biological generic concepts on the Miocene ghost shrimps of the Central Paratethys. This research is currently in progress as documented by the present contribution that re-evaluates the fossil record of two Middle Miocene species: "*Callianassa*" *brocchii* Lörenthey, 1897, and "*Callianassa*" *pseudorakosensis* Lörenthey in Lörenthey & Beurlen, 1929. Herein a redescription of both species is provided, including emended diagnoses, generic reassignment, descriptions of intraspecific variations, and *in situ* preservation.

Locality and geological setting

Most material comes from a single locality from the Slovak part of the Vienna Basin – Dúbravská hlavica (Bratislava area) (Fig. 1). At the locality, sands and poorly lithified sandstones of the Sandberg Member (the Studienka Formation) crop out. The sediments have been interpreted as transgressive shelf sands (Baráth *et al.* 1994; Kováč *et al.* 2004). For details on sedimentology and the lithofacies overview of the area see Švagrovský (1981) and Baráth *et al.* (1994).

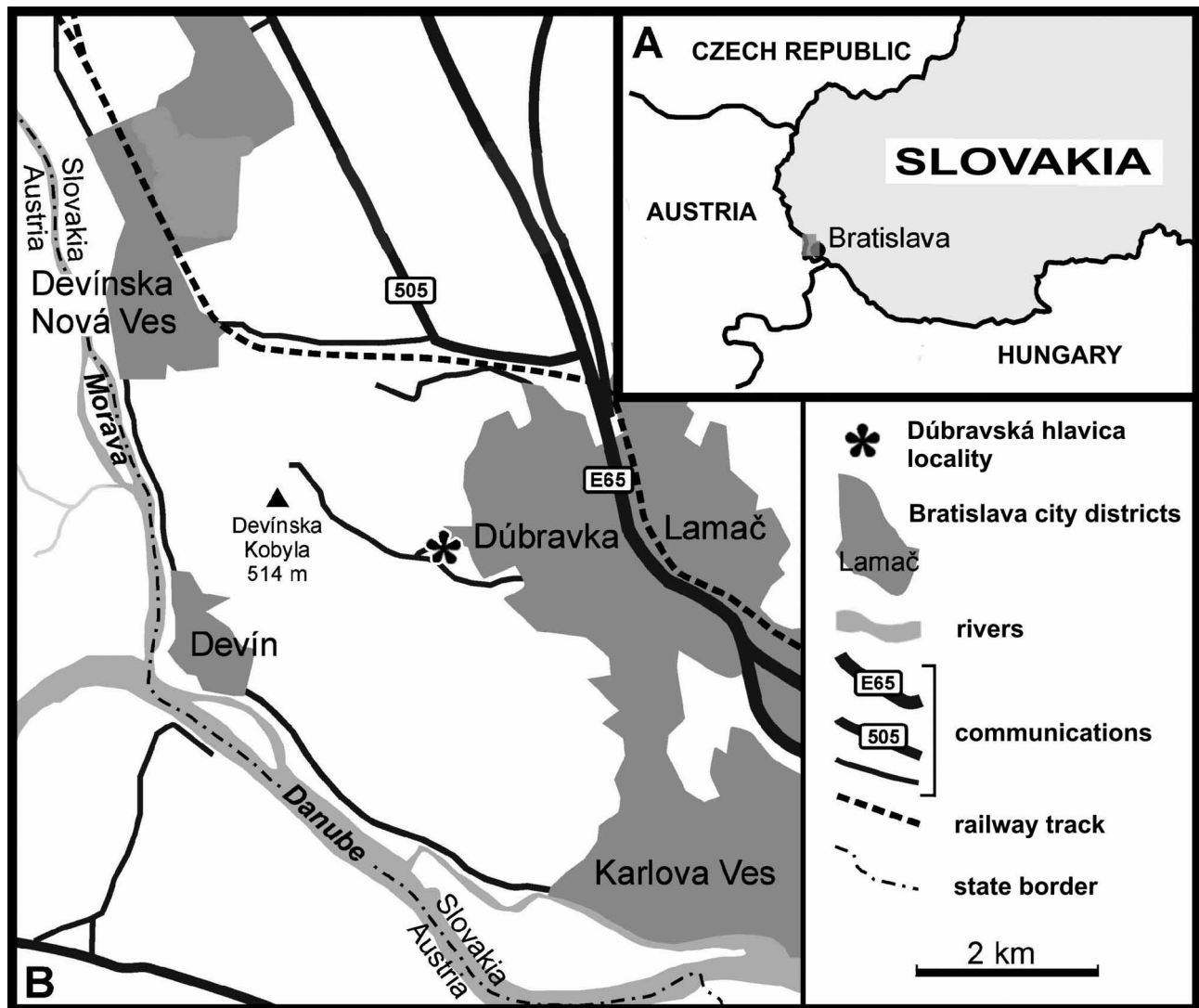


FIGURE 1. Geographical position of the studied locality Dúbravská hlavica.

Following Baráth *et al.* (1994) the age of the sediments at Dúbravská hlavica was first considered to be of late 'Badenian' age (Hyžný 2011a, b); however, analysis of foraminiferal assemblages directly from the sediment containing ghost shrimp remains revealed a slightly younger age. The foraminiferal assemblage points to the early 'Sarmatian' (Serravallian), Large elphidia biozone (Grill 1941) or biozone 10–11 *Cibicides aff. badenensis* – *Elphidium reginum* (Cicha *et al.* 1975). Despite the fact that the assemblage does not contain the main zonal species (*Elphidium reginum* d'Orbigny, 1846), it contains typical 'Sarmatian' genera such as *Nodobaculariella* or *Articulina*. Also, the time span occupied by *Affinetrina voloshinovae* (Bogdanowicz, 1947), identified in the assemblage, is strictly 'Sarmatian' (Cicha *et al.* 1998). Here it should be mentioned that during the Early and Middle Miocene, palaeogeographically the Vienna Basin formed a marginal part of the Central Paratethys Sea (see below). The change in ecological conditions during the late Middle Miocene was significant mainly in such marginal parts. Due to these special contrasts in living conditions for microfaunal assemblages, the lack of planktonic

foraminifera in the Vienna Basin in that time can lead to the inequality in the stratigraphic control (Hudáčkova in Andrejeva-Grigorovich *et al.* 2001).

For the palaeogeographic concept of the Central Paratethys during the Miocene a reference is made to Rögl (1998, 1999), Harzhauser *et al.* (2002) and Harzhauser & Piller (2007). Palaeobiogeographically the Vienna Basin was during the Middle Miocene a part of the Danubian Province of the Central Paratethys *sensu* Harzhauser *et al.* (2002) and Harzhauser & Piller (2007). The current status of the Miocene Central Paratethys stratigraphy was summarized by Piller *et al.* (2007).

Material and methods

The studied locality yielded hundreds of mostly isolated cheliped elements; however, more complete individuals also have been found as documented below. Material is preserved in more-or-less loosened sediment; therefore, the preparation was easy with preparatory needles and a fine pneumatic needle. Specimens were covered with ammonium chloride prior to photography if not stated otherwise.

The type material and also additional material from the roughly coeval localities in Hungary (Great Hungarian Basin) and the Austrian part of the Vienna Basin have also been re-examined, thus allowing comprehensive redescription of both taxa.

Material is deposited in the following institutions: Hungarian Geological Survey, Budapest, Hungary (FI); Department of Geology and Paleontology, Comenius University, Bratislava, Slovakia (KGP MH); Hungarian Natural History Museum, Budapest, Hungary (M – older collections, PAL – acquisitions since 2011); and Natural History Museum of Slovak National Museum, Bratislava, Slovakia (SNM Z). Additional material comes from Radoslav Biskupič (Bratislava, Slovakia) (PCRB) and Miroslav Hornáček (Smolenice, Slovakia) (PCMH) private collections.

Systematics

Order Decapoda Latreille, 1802

Suborder Pleocyemata Burkenroad, 1963

Infraorder Axiidea de Saint Laurent, 1979

Family Callianassidae Dana, 1852

Remarks. The family Callianassidae has a robust fossil record. In view of the delicate nature of the callianassid exoskeleton, however, only chelipeds (which usually are heavily calcified) are likely to be preserved in the fossil record (Bishop & Williams 2005). Nevertheless, in some cases, a complete or near-complete animal is preserved. Features of the carapace, maxillipeds, eyes, pleopods, uropods, and telson are used to assign extant species to the genus; these are very rarely if at all preserved in the fossil record. Systematics based on hard-part morphology is still debated. Discussion on this topic applied to the fossil material can be found in Schweitzer & Feldmann (2002), Schweitzer *et al.* (2006b), and Hyžný & Müller (2010), for example.

Thirty-four extant callianassid genera are currently recognized (De Grave *et al.* 2009; see Sakai 2005, 2011 for a different view). However, as noted by Hyžný & Müller (2010: 37), less than a quarter of these has a fossil record which dates back beyond the Pliocene. This can be ascribed both to preservational and collecting biases. It should also be noted that many extant genera can be differentiated on the basis of soft-part morphology only, so if not re-diagnosed they are bound to remain unrecognized in the fossil record.

Hyžný (2011a: table 2), in his listing of Middle Miocene callianassids of the Central Paratethys, showed that so far, virtually all of them were treated under "*Callianassa*" as a *nomen collectivum* in the widest sense. None of them, however, can be matched with *Callianassa* Leach, 1814 as defined by Manning & Felder (1991) or Ngoc-Ho (2003).

Subfamily Callichirinae Manning & Felder, 1991

Genus *Neocallichirus* Sakai, 1988

Type species. *Neocallichirus horneri* Sakai, 1988 by original designation.

Remarks. The genus was erected by Sakai (1988) to accommodate callianassid forms characterized by the following features: carapace with well-defined dorsal oval, but without rostral carina and cardiac prominence; 3rd maxilliped without exopod, endopod subpediform, propodus expanded, over 3 times broader than dactylus; uropodal endopod broadened posteriorly; telson about as long as broad, about as long as uropods. These characters are, however, of very poor fossilization potential, and as Sakai (1988) stated, the form of the 3rd maxilliped alone is not specific to *Neocallichirus*, but is similar in several other genera, and therefore always a combination of characters has to be used for generic assignment. Later, Manning & Felder (1991) reconsidered the diagnosis of *Neocallichirus* and added also the characters on the chelipeds, which are common in the fossil record and therefore usable for palaeontologists too. They argued for the taxonomic importance of the shape of the merus (e.g. presence/absence of meral hook), which is significant for many callianassid genera. Schweitzer & Feldmann (2002) and Schweitzer *et al.* (2006a) discussed usage of the characters on the major cheliped in the fossil record for assignment to the genus *Neocallichirus*. They noted that the carpus is variable in shape; however, it is not rectangular and typically has a rounded lower margin. The propodus has often serrated distal margin. The fixed finger tends to be edentulous, whereas the dactylus is stout and heavily armed with a triangular or rectangular tooth near the proximal end of the element.

The merus of members of *Neocallichirus* is variable in shape but is always serrate along the lower margin. According to Manning & Felder (1991), it lacks a meral spine or hook; according to Sakai (1999, 2005) it is with or without meral hook (mainly due to the synonymisation with the genus *Sergio* Manning & Lemaitre, 1994). Sakai (2011) stated that the merus is with or without ventral convexity.

There are several genera different from *Neocallichirus*, namely *Sergio*, *Podocallichirus* Sakai, 1999, and *Grynaminna* Poore, 2000, which in general share characters on the chelipeds mentioned above. It is typical that such a morphology, i.e. generalized cheliped morphology embracing all above mentioned genera, is in palaeontological literature connected virtually with *Neocallichirus* only. This can be documented by currently recognized fossil taxa assigned to respective genera. According to De Grave *et al.* (2009) and Schweitzer *et al.* (2010) there are 18 fossil species of *Neocallichirus*, but only one fossil species of *Podocallichirus* (known from the Pleistocene strata of Japan; see Karasawa *et al.* 2006) and no fossil *Grynaminna* (see Hyžný & Karasawa in press for a different view). One extant species of *Sergio* is also known from the fossil state (Portell & Agnew 2004).

Much confusion has been created by Sakai (1999, 2005) when he synonymized *Sergio* with *Neocallichirus* and *Grynaminna* with *Podocallichirus* (see also Sakai 2011 for a different view on the taxonomy of these genera). Thus, we can talk about several different taxonomic concepts of *Neocallichirus* presented by Sakai (1988, 1999, 2005, 2011) and Manning & Felder (1991). Identifying the fossil material as a member of any of the above mentioned genera strongly depends on taxonomy adopted. Therefore it is possible that the genus *Neocallichirus* as usually recognized in the fossil record is a mixture of closely allied genera. The issue was recently discussed by Hyžný & Karasawa (in press).

Neocallichirus brocchii (Lörenthey, 1897) new combination

(Figs 2–6)

Calianassa Brocchii Lörenthey, 1897: 161, 168, 169; Lörenthey, 1898a: 106, 114, 115; Lörenthey, 1898b: 132–134, 155, pl. 9, fig. 5; Lörenthey, 1898b: 104–105, pl. 9, fig. 5; Lörenthey in Lörenthey & Beurlen, 1929: 64, pl. 2, fig. 13;

Callianassa Brocchii. — Glaessner, 1929: 77.

?*Calianassa* cf. *Brocchii*. — Lörenthey in Lörenthey & Beurlen, 1929: 69.

Callianassa brocchii. — Müller, 1979: 274; Schweitzer *et al.*, 2010: 34.

'*Callianassa*' *brocchii*. — Müller, 1984: 51, pl. 3 fig.3.

"*Callianassa*" *brocchi* (sic). — Hyžný, 2011a: 41, Table 2.; Hyžný, 2011b: 167, Table 1.

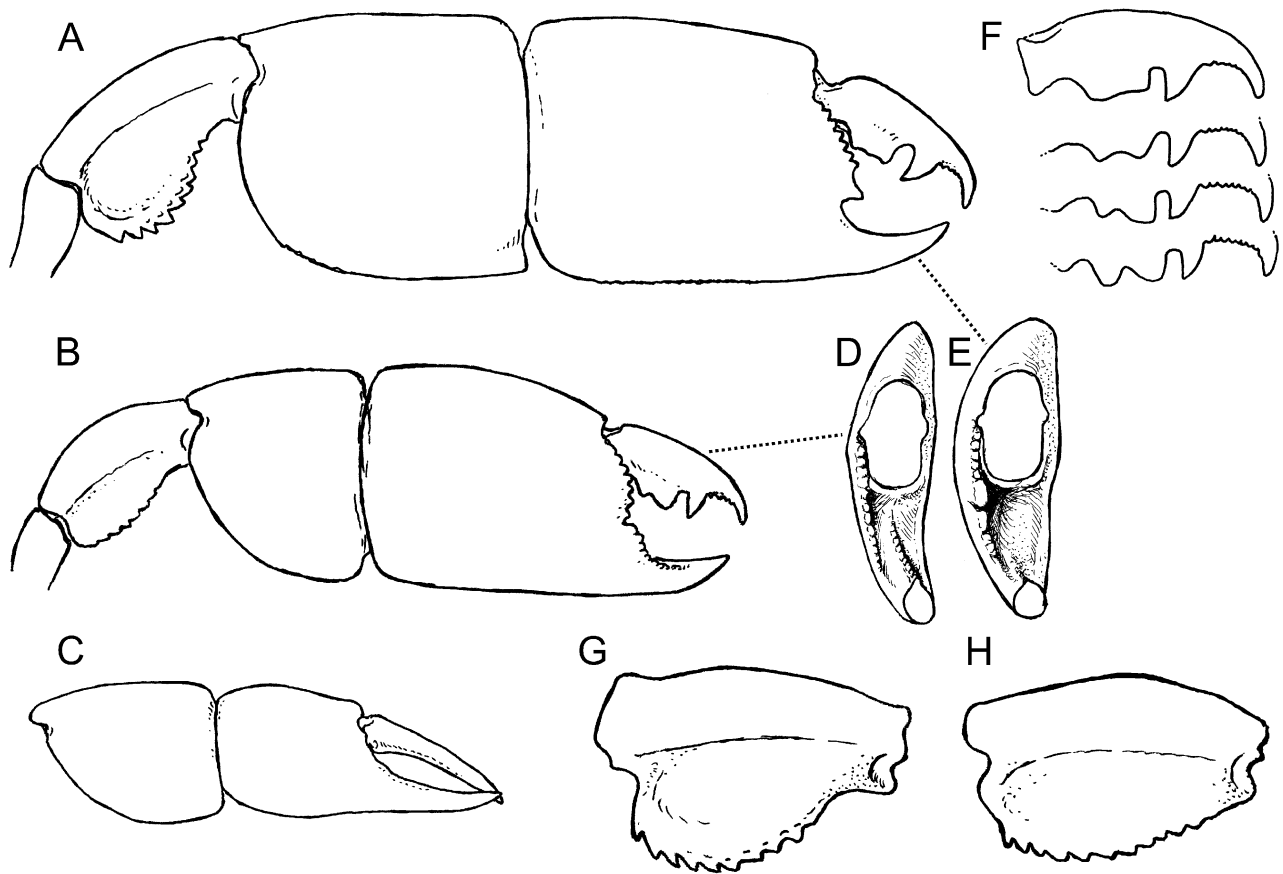


FIGURE 2. *Neocallichirus brocchii* (Lörenthey, 1897) new combination, reconstructions: A, major cheliped of robust morphotype (outer view); B, major cheliped of slender morphotype (outer view); C, minor cheliped (outer view); D–E, distal view of propodus of slender (D) and robust (E) morphotype, note differences in the development of medial keel on the fixed finger; dactyli and fixed finger tips are not depicted; F, variation in the armature of fixed finger; G–H, outer view on merus of robust (G) and slender (H) morphotype. Reconstructions are based on several different specimens; figures A–F are in scale.

Emended diagnosis. Strongly heterochelous callichirine ghost shrimp with chelipeds without pronounced tuberculation. Merus of major cheliped ovoid with lower margin possessing a toothed blade consisting of up to 12 teeth; carpus broad with rounded and serrated lower margin; propodus tapering distally with serrated lower margin, the palm subequal in length and height, distal margin rounded and serrated, occlusal margin of fixed finger armed with small teeth; dactylus long and slender with occlusal margin forming a well developed keel with long, quadrate, blunt tooth proximally and one indented, sharp tooth distally followed with several tiny teeth, tip forming sharp hook. Carpus of minor cheliped slightly higher than propodus; propodus slender, tapering distally, fixed finger about as long as manus; fingers without armature, occlusal margin of dactylus forming weak serrated keel.

Emended description. Major cheliped massive, located on either right or left side of body, smooth, without pronounced tuberculation on lateral surfaces; outer surface usually vaulted. Two different morphotypes were identified in the nature of major cheliped; robust morphotype is relatively larger than slender morphotype. Ischium is slender, longer than high, tapering proximally, not well preserved.

Major chela robust morphotype: Merus ovoid in shape, longer than high ($L/H = 1.5\text{--}1.7$), highest proximally; lower margin with toothed blade (up to 12 teeth present); upper margin slightly convex (Figs 2G, 4F–H, J, K). Carpus broad, massive, approximately as long as high ($L/H = 0.8\text{--}1.1$); upper margin straight; lower margin rounded forming one edge with proximal margin (Figs 4A–E), serrated with tiny denticles (Fig. 4D); upper and lower margin forming prominent keel curved inward. Propodus massive, longer than high, slightly longer than carpus, tapering distally (Figs 2A, 3); palm of the propodus subequal in length and height; upper margin slightly convex; lower margin straight, serrated (Figs 3A, O); upper and lower margins keeled, keel missing on fixed finger; distal margin

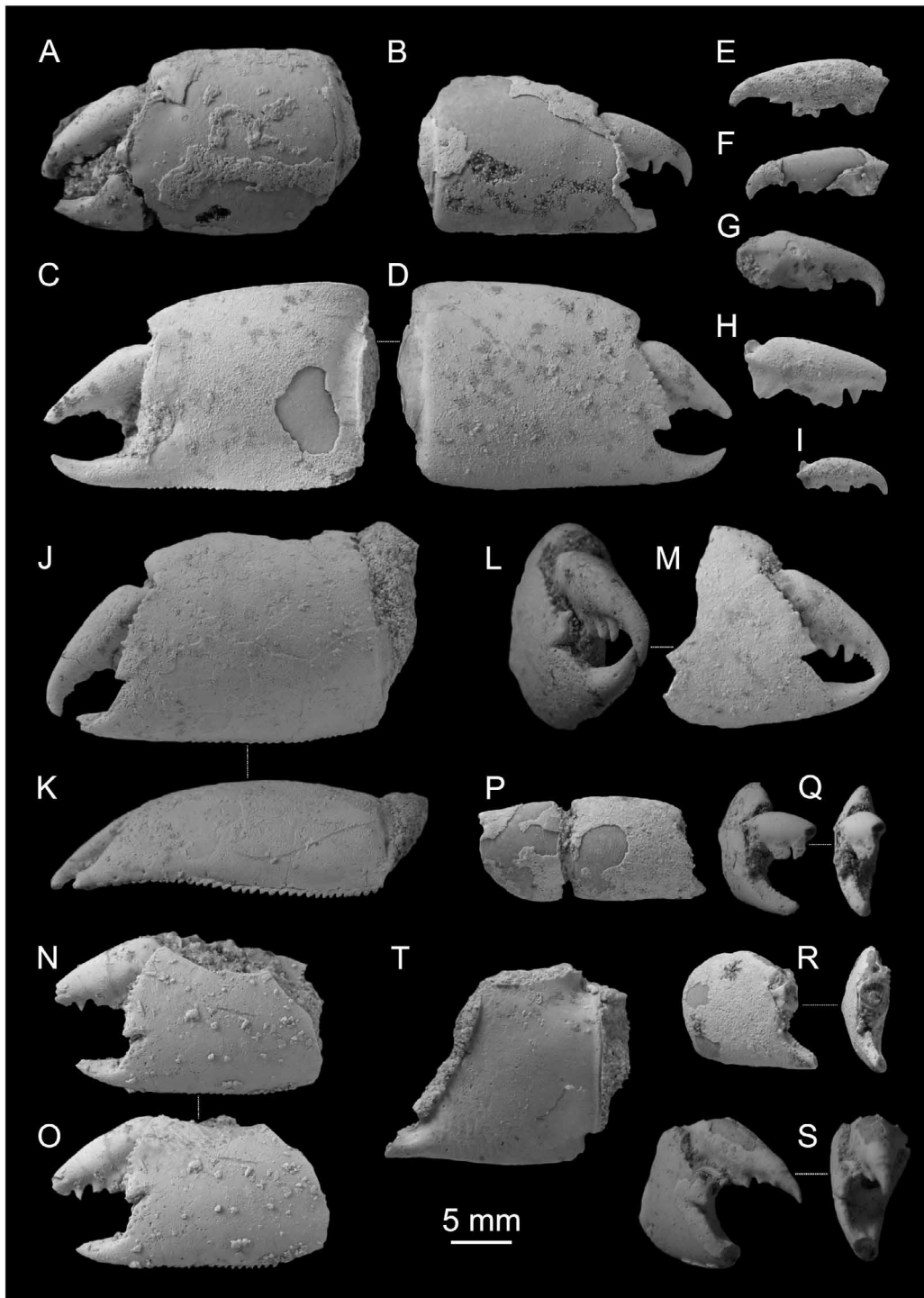


FIGURE 3. *Neocallichirus brocchii* (Lörenthey, 1897) new combination, major chelae (propodi and dactyli): A, left chela (robust morphotype), KGP-MH DH001; B, right chela (slender morphotype), PCMH-001; C–D, right chela from inner and outer view (robust morphotype), PCRB-DH008; E, left dactylus, PCRB-DH001; F, left dactylus, PCRB-DH002; G, right dactylus, KGP-MH DH012; H, right dactylus, PCRB-DH004; I, right dactylus, PCRB-DH003; J, left chela (robust morphotype), KGP-MH DH064, note serration on the lower margin (K); L–M, fragmentary right chela (robust morphotype), PCRB-DH005; N, left chela (robust morphotype), SNM Z-37534, note serration on the lower margin (O); P, right chela (slender morphotype), PCRB-DH010, note short carpus; Q, fragmented right chela (slender morphotype), PCMH-003, note occlusal keel on the fixed finger positioned medially; R, right chela (slender morphotype), PCRB-DH007, note occlusal keel on the fixed finger positioned medially; S, fragmented right chela (robust morphotype), PCMH-002, note occlusal keel on the fixed finger positioned laterally; T, right chela, KGP-MH DH-66, note the unusual length/height ratio. All specimens come from the Dúbravská hlavica locality (Vienna Basin, Slovakia), Middle Miocene. All specimens are to scale and were covered with ammonium chloride prior to photography.

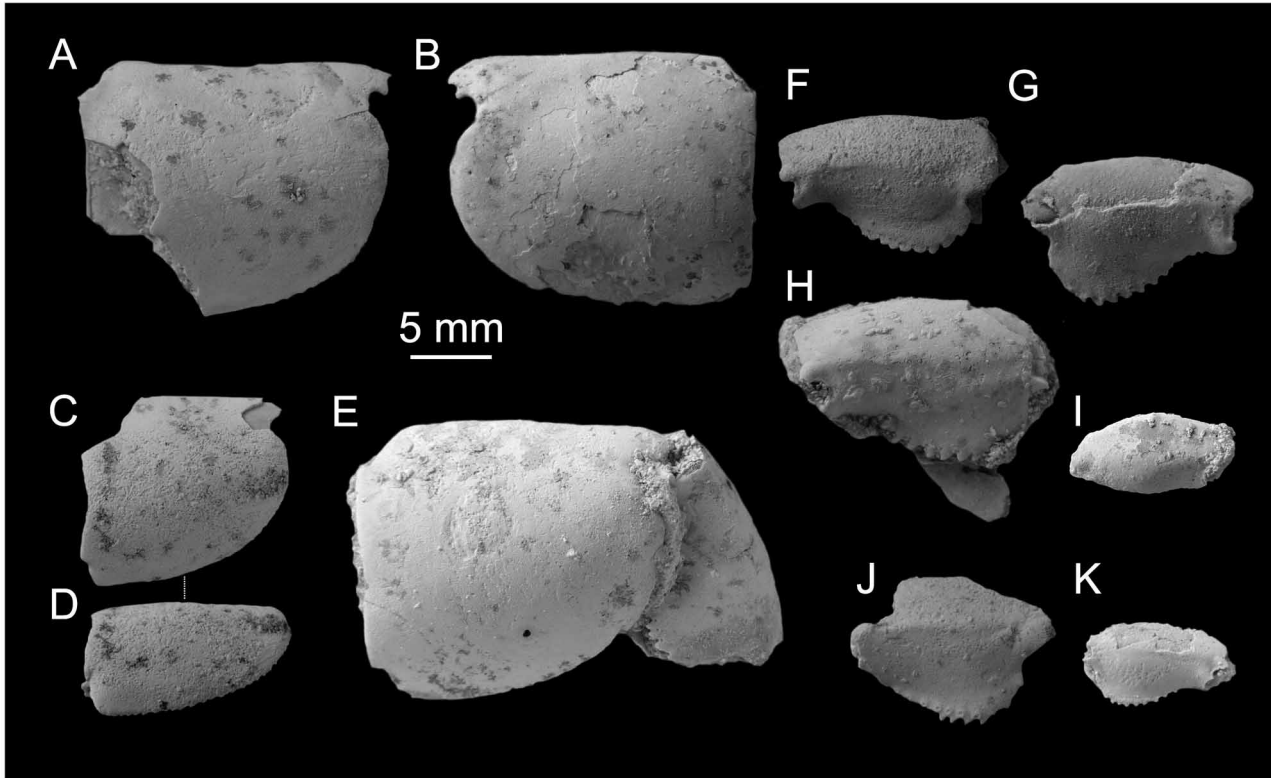


FIGURE 4. *Neocallichirus brocchii* (Lőrentthey, 1897) new combination, major chelae (carpi and meri): A, left carpus, KGP-MH DH065; B, right carpus, KGP-MH DH060; C, left carpus, PCRB-DH009, note serration on the lower margin (D); E, left articulated merus and carpus, SNM Z-37549; F, left merus, PCRB-DH014; G, right merus, KGP-MH DH052; H, left merus, KGP-MH DH010; I, right merus, PCRB-DH016; J, left merus, PCRB-DH015; K, right merus, SNM Z-37542. All specimens belong to robust morphotype, except „I“ being a slender morphotype. All specimens come from the Dúbravská hlavica locality (Vienna Basin, Slovakia), Middle Miocene. All specimens are to scale and were covered with ammonium chloride prior to photography.

rounded and serrated with up to 10 small denticles on each side of articulation with dactylus, serrated incision present just below the articulation with dactylus (Figs 2A, 3D, J, M). Fixed finger slender, triangular in shape; occlusal margin armed with small teeth, forming serrated keel on the outer side of fixed finger from distal view (Figs 2E, 3S); tip curved slightly upward; lower margin serrated. Dactylus long and slender, occlusal margin forming sharp keel with long quadrate blunt tooth proximally and one indented sharp tooth distally followed with several tiny teeth (Figs 2F, 3E–I); tip bent slightly downward or forming sharp hook (Fig. 3G).

Major chela slender morphotype: Merus ovoid in shape, longer than high, highest at midlength; lower margin finely serrated without distinct tooth blade (Figs 2H, 4I). Carpus higher than long ($L/H = 0.70\text{--}0.85$) (Figs 2B, 3P, 6C), keels on upper and lower margins not as pronounced as in robust morphotype; lower margin serrated. Propodus distinctly longer than carpus, general shape much the same as in robust morphotype (Figs 2B, 3B, 6C). Fixed finger with serrated keel on occlusal margin positioned in the middle (Figs 2D, 3Q, R) instead of lateral position of robust morphotype. Dactylus similarly shaped as in robust morphotype (Fig. 3B).

Minor cheliped more slender than major one, smooth (Fig. 2C). Ischium and merus not well preserved. Carpus slightly longer than high, higher than propodus (Figs 2C, 6B); upper and lower margins convex. The palm of the propodus as long as high; distal margin without serration (Figs 5A–D); lower margin of propodus slightly convex at the point where fixed finger begins. Fixed finger about as long as palm, slender, forming sharp tip, occlusal margin not armed. Dactylus long, slender; occlusal margin forming faint finely serrated keel, no bigger teeth present (Fig. 5E).

Variations. The studied material consists of the two morphotypes described above. The overall shape of the propodus and morphology of the dactylus and minor chela clearly demonstrate that both morphs belong to the same species. Both morphotypes occur together in the same strata, so they represent the same population (or sequence of populations). The recognized morphs may mirror sexual dimorphism (slender morphotype being a female one);

however, it is very difficult to determine sex in the fossil state, especially when dealing with *Neocallichirus*. No obvious sexual dimorphism has been observed in several extant species (see Dworschak 2011a, b). Thus, the interpretation of morphs as sexual dimorphism should be considered as a preliminary one. Possible attribution of the slender morphotype to female individuals is based mostly on other callianassid taxa in which mature males usually possess more robust chelipeds than females (e.g., Felder & Lovett 1989 and references therein).

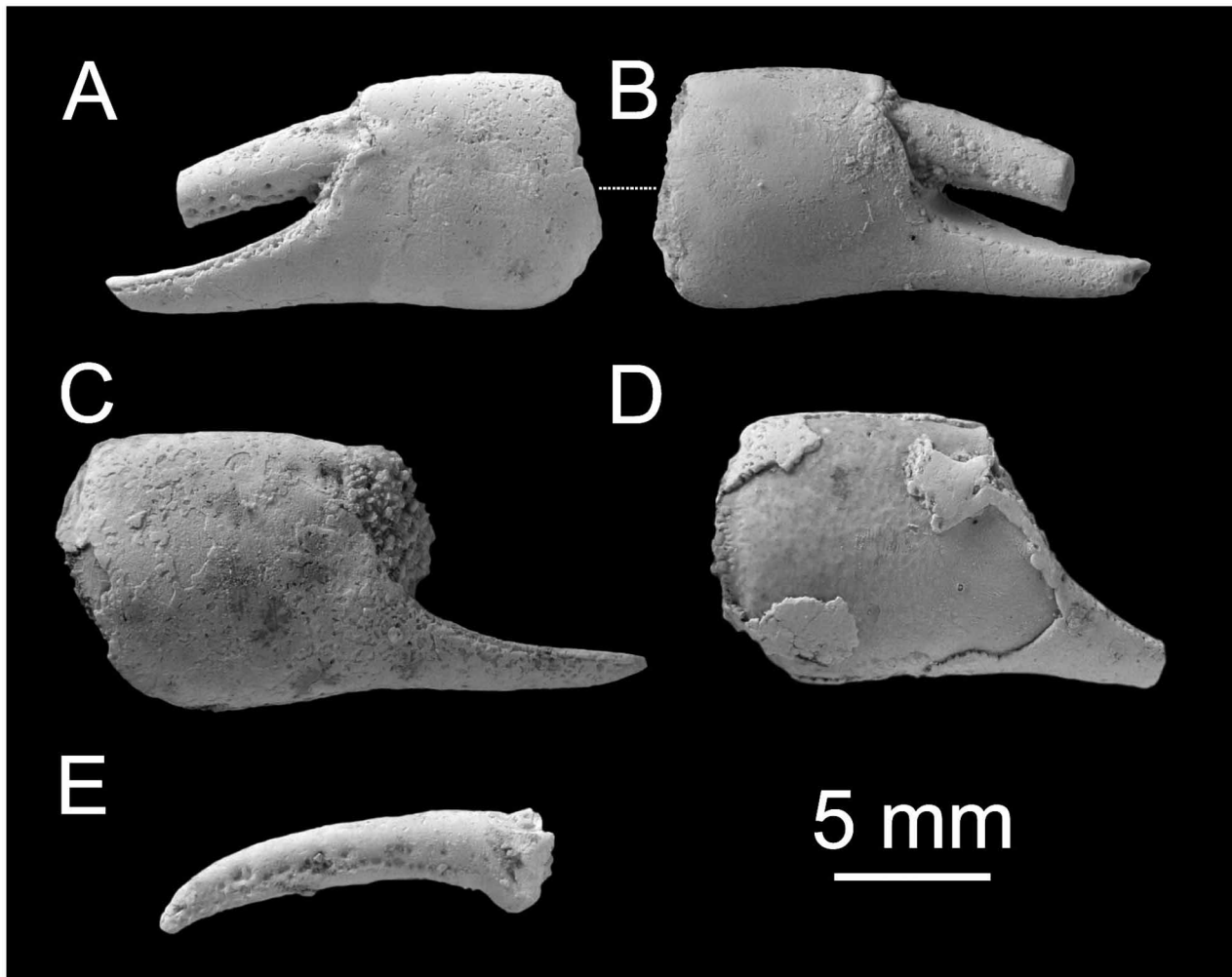


FIGURE 5. *Neocallichirus brocchii* (Lőrentthey, 1897) new combination, minor chelae (propodi and dactyli): A–B, left chela from outer and inner view, KGP-MH DH067; C, right chela, PCRB-DH013; D, fragmented right chela, PCRB-DH011; E, left dactylus, PCRB-DH012. All specimens come from the Dúbravská hlavica locality (Vienna Basin, Slovakia), Middle Miocene. All specimens are to scale and were covered with ammonium chloride prior to photography.

The merus shows variations in the number of teeth on its lower margin which seems to be a consequence of growth (more teeth are present on larger meri) rather than real variability. The variation in meral shape, notably the development of the meral blade, can be documented in several extant *Neocallichirus* species, e.g. in *N. grandimanus* (Gibbes, 1850) (compare e.g. Manning 1987: fig. 2; Lemaitre & Ramos 1992: fig. 5; Blanco-Rambla 2000: fig. 2) and *N. jousseaumei* (Nobili, 1904) (compare e.g. Nobili 1906: fig. 2; Kensley 1976: fig. 2; Dworschak 2011a: figs. 1–4). In this respect the merus of the slender morphotype of *Neocallichirus brocchii* comb. nov., without a pronounced meral blade (Fig. 2H), is similar to the merus of *N. grandimanus* depicted by Lemaitre & Ramos (1992: fig. 5d), whereas the merus of the robust morphotype with a well developed meral blade (Fig. 2G) can be compared with the merus of *N. grandimanus* depicted by Blanco-Rambla (2000: fig. 2c).

There are slight variations in the outline of the distal margin of the propodus. Variations exist mainly in the nature of the incision under dactylus articulation. In the robust morphotype the incision is usually deeper and more rounded (e.g. Figs 3D, J, M), whereas in the slender morphotype, it is sometimes completely missing.

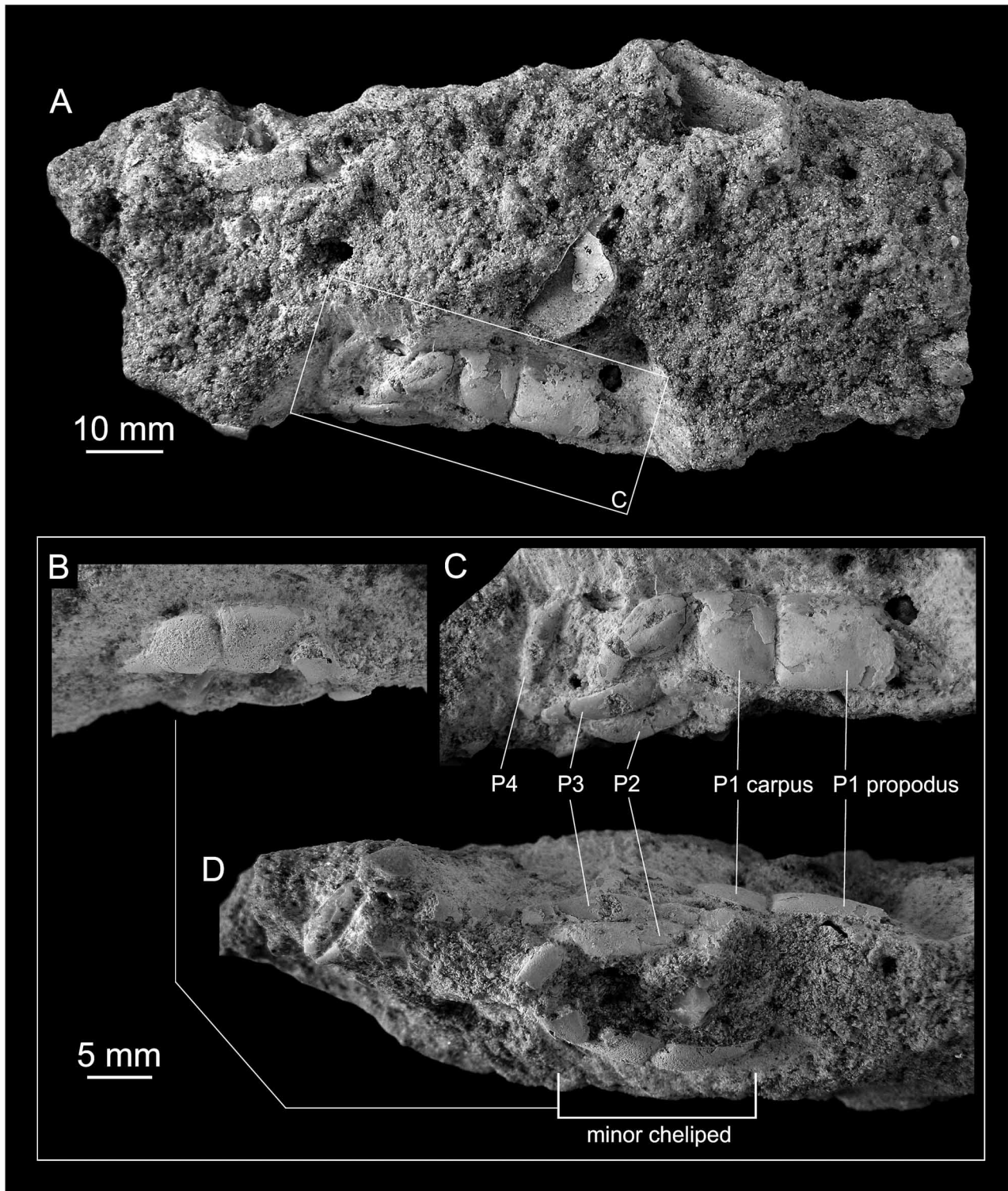


FIGURE 6. *Neocallichirus brocchii* (Lőrentthey, 1897) new combination, *in situ* preservation of the specimen KGP-MH DH-058 (Dúbravská hlavica locality): A, view of the individual (slender morphotype) preserved in a presumed burrow structure; B, minor cheliped; C, major cheliped; D, view from below where both chelipeds can be recognized. Note also the partial preservation of thoracopods P2–P4. All specimens are to scale and were covered with ammonium chloride prior to photography.

Other variations concern the cutting edge of the dactylus. The proximal quadrate tooth is usually divided in two secondary blunt teeth, the distal one being broader. The subdivision is, however, not always distinct and also the shape of the subdivided teeth is variable (Fig. 2F).

No obvious allometric growth in the nature of any cheliped element has been recognized, although there is one isolated propodus in the present collection (KGP-MH DH066; Fig. 3T) which shows a propodus length/height ratio (L/H = 0.6) rather different from all other studied specimens. The nature of the fixed finger (position of serrated keel) resembles that of the slender morphotype. The specimen itself is, however, much bigger than the usual size of the slender morphotype propodus.

Material examined. FI M.2329 (holotype – left propodus of robust morphotype articulated with dactylus); KGP-MH DH-001–KGP-MH DH-015; M.86.249 (1 left and 1 right fragmented propodi; SNM Z-7943 (collective number), SNM Z-16419 (collective number), SNM Z-16433 (collective number), SNM Z-37532–SNM Z-37553; PCMH-001–PCMH-003; PCRB DH-001–PCRB DH-016. For measurements and all the details see Table 1.

TABLE 1. Measurements of selected well preserved specimens of *Neocallichirus brocchii* (Lörenthey, 1897) comb. nov. Handedness: L = left; R = right; measurements: L = max. length; H = max. height; ~ = approximate value; > = "more than" (in case the approximation is not possible due to the state of preservation); values are in mm.

Specimen	morphotype	handedness	merus		carpus		propodus		dactylus
			L	H	L	H	L	H	L
SNM Z-37532	major robust	L	-	-	-	-	14.0	14.4	>9.4
SNM Z-37533	major robust	L	-	-	-	-	10.8	18.3	-
SNM Z-37534	major robust	L	-	-	-	-	~13	>12	9.0
SNM Z-37535	major robust	L	-	-	-	15.7	18.5	17.0	>8.0
SNM Z-37536	major robust	L	-	-	-	-	18.3	17.4	-
SNM Z-37537	major robust	L	-	-	-	-	13.0	13.2	-
SNM Z-37538	major robust	L	-	-	-	-	-	15.0	-
SNM Z-37539	major robust	L	-	-	-	-	11.4	11.4	-
SNM Z-37540	major robust	R	-	-	-	-	14.7	15.0	>8.0
SNM Z-37541	major robust	R	-	-	-	-	14.4	14.0	-
SNM Z-37542	major robust	R	-	-	-	-	17.6	14.2	-
SNM Z-37543	major robust	R	-	-	-	-	13.2	12.2	-
SNM Z-37544	major robust	R	-	-	-	-	17.0	17.2	-
SNM Z-37545	major robust	R	-	-	-	-	18.0	17.0	-
SNM Z-37546	major robust	L	-	-	-	-	-	-	12.6
SNM Z-37547	major robust	L	-	-	11.3	14.1	-	-	-
SNM Z-37548	unknown	R	8.7	5.0	-	-	-	-	-
SNM Z-37549	major robust	L	14	9.6	17.4	15.7	~20	14.0	>10.0
SNM Z-37550	major slender	R	-	-	6.8	8.4	-	-	-
SNM Z-37551	major slender	L	-	-	5.5	8.2	>8.0	8.5	-
SNM Z-37552	major robust	L	-	-	17.5	17.1	-	-	-
SNM Z-37553	minor	R	-	-	-	-	8.6	8.5	-
KGP-MH DH-001	major robust	L	-	-	-	-	15.0	14.2	10.5
KGP-MH DH-002	major robust	R	-	-	-	-	14.3	13.0	-
KGP-MH DH-003	major robust	L	-	-	-	-	>15	15.3	-
KGP-MH DH-004	major robust	R	-	-	-	-	11.3	11.0	-
KGP-MH DH-005	major slender	R	-	-	-	-	8.6	8.6	-
KGP-MH DH-007	major robust	R	-	-	>20.3	15.4	-	-	-
KGP-MH DH-008	major robust	R	-	-	>19.4	14.5	-	-	-
KGP-MH DH-009	major robust	R	-	-	~17	~14	-	-	-
KGP-MH DH-010	major robust	L	13.2	8.5	-	-	-	-	-
KGP-MH DH-011	major robust	R	>15.0	~9	-	-	-	-	-

continued next page

TABLE 1. (continued)

Specimen	morphotype	handedness	merus		carpus		propodus		dactylus
			L	H	L	H	L	H	L
KGP-MH DH-012	major robust	R	-	-	-	-	-	-	12.0
KGP-MH DH-058	minor	L	-	-	7.7	6.5	5.4	5.4	>5.0
KGP-MH DH-058	major slender	R	8.7	5.7	7.6	9.6	11.4	10.5	7.8
KGP-MH DH-064	major robust	L	-	-	-	-	18.0	16.6	-
KGP-MH DH-065	major robust	L	-	-	17.0	>14.3	-	-	-
KGP-MH DH-066	unknown	R	-	-	-	-	8.7	14.7	-
KGP-MH DH-067	minor	L	-	-	-	-	>6.0	6.7	>5.5
PCMH-001	major robust	R	-	-	-	-	12.0	11.8	9.2
PCRB DH-001	major robust	L	-	-	-	-	-	-	12.2
PCRB DH-002	major robust	L	-	-	-	-	-	-	11.1
PCRB DH-003	unknown	R	-	-	-	-	-	-	7.0
PCRB DH-004	major robust	R	-	-	-	-	-	-	>11.0
PCRB DH-005	major robust	R	-	-	-	-	-	14.0	11.2
PCRB DH-007	major slender	R	-	-	-	-	9.0	8.4	-
PCRB DH-008	major robust	R	-	-	-	-	16.1	14.8	>10.0
PCRB DH-009	major robust	L	-	-	>12.0	14.4	-	-	-
PCRB DH-010	major slender	R	-	-	6.2	7.3	8.1	7.6	-
PCRB DH-011	minor	R	-	-	-	-	7.0	7.6	-
PCRB DH-012	minor	L	-	-	-	-	-	-	11.3
PCRB DH-013	minor	R	-	-	-	-	8.0	8.0	-
PCRB DH-014	major robust	L	11.7	7.3	-	-	-	-	-
PCRB DH-015	major robust	L	>11.0	8.0	-	-	-	-	-
PCRB DH-016	major slender	L	11.8	5.5	-	-	-	-	-

Occurrence. The species has been reported only from the Serravallian (Middle Miocene), specifically from the upper 'Badenian' of the Rákos Formation – localities Rákos, Budafok and Gyakorló út in the Budapest City area (Hungary) (Lőrentthey & Beurlen 1929; Müller 1984); and the lower 'Sarmatian' of the Studienka Formation – locality Dúbravská hlavica in the Bratislava district (Slovakia) (Hyžný 2011a, b; this contribution).

Remarks. The species possesses a combination of characters which is quite typical for *Neocallichirus*: serrated lower margins of the merus, carpus and propodus; rounded lower margin of the carpus; upper margin of the propodus converging distally; an edentulous fixed finger (which is only finely denticulated), and an armed dactylus with hooked tip.

In his work, Müller (1984: 51) already noted the morphological similarity of *Callianassa brocchii* to *C. natalensis* Barnard, 1947. Müller (1984) examined only the holotype of *C. brocchii* and five additional propodi from the Budapest City localities (see above). At that time no carpi or meri were known, or at least were not attributed to *C. brocchii*.

Müller (1984: 51) stated that *Callianassa brocchii* can be differentiated from similar extant species (*Callianassa gilchristi* Barnard, 1947, *C. natalensis*) on the basis of "the saw-like lower edge". This is not correct, however, as *C. natalensis* does possess serration on the lower margin of the propodus (see e.g. Dworschak 2011a: fig. 5D, E) as do *Neocallichirus* species.

Neocallichirus brocchii comb. nov. is morphologically very similar to the extant *Neocallichirus lemaîtrei* Manning, 1993, and allied species (see also comparison with *N. grandimanus* and *N. jousseaumei* above). The armature of the dactylus is similar to extant *N. cacahuatense* Felder & Manning, 1995, *N. jousseaumei*, *N. lemaîtrei*, *N. monodi* (de Saint Laurent & Le Loeuff, 1979) and *N. natalensis*. In fossil taxa the variation in the shape of the dac-

tylus is not very well known; however, none of those described can be fully compared to *Neocallichirus brocchii* comb. nov. The combination of characters as presented in the diagnosis and description is unique for this species, although some similarities can be found with *Neocallichirus aetodes* Schweitzer, Iturralde-Vinent, Hetler & Velez-Juarbe, 2006 from the Lower Oligocene of Puerto Rico and *N. hattai* Karasawa & Nakagawa, 2010 from the Lower to Middle Miocene of Japan.

The original description of *Callianassa brocchii* is based on a single specimen of left major propodus articulated with dactylus; Lörenthey (1898a) and Lörenthey & Beurlen (1929) erroneously treated it as a right one, although the accompanying figures clearly show it as being left, as re-examination of the type material also confirmed. Lörenthey in Lörenthey & Beurlen (1929: 65) mentioned another two specimens, which may probably be assigned to this species, although no figures of them were added. Another specimen was reported by Beurlen in Lörenthey & Beurlen (1929: 69). He classified the material as *Callianassa* cf. *brocchii*, however, he stated that it morphologically conforms with the description of *C. brocchii*. As no figure of the material was added, we are hesitant to assign the material to the species with certainty. Interestingly in the description it is mentioned that "Form des Carpus, die Grösse, der Index, soweit es das abgebrochene Stück erkennen lässt, stimmen vollkommen mit dieser Art überein" (As far as the broken specimen can be identified, the form of carpus, its size, and the fixed finger correspond precisely to this species). As *C. brocchii* has been described on the basis of an articulated propodus and dactylus only, and no carpus was described in the original description, we assume that Beurlen made a mistake and meant, in fact, propodus instead of carpus.

There is much confusion in citing Lörenthey's works. As stated by Müller (1984: 32): "Lörenthey's first papers were published in parallel Hungarian and German versions with identical contents. He presented the same data in preliminary publications without figures (Lörenthey 1897, 1898a), and in definite papers with excellent figures and detailed descriptions (Lörenthey 1898b, c)". *Callianassa brocchii* was first described as a new species in such a preliminary publication in 1897. In this paper a short description with comparison with similar taxa can be found which satisfies the ICZN rules for a new species designation. Later the description of *C. brocchii* was refined and figures were added (Lörenthey 1898b, c). Thus, the year 1897 is considered as the year of description of *Callianassa brocchii* contrary to Glaessner (1929) and Schweitzer *et al.* (2010) where the species appeared as described in 1898 (see also discussion in Müller 1984: 32).

Müller (1984: 50) erroneously assumed that the handedness is quite typical for every callianassid species: "Most of recent *Callianassids* (sic!) are strongly heterochelous. Surprisingly, in the diverse 'Badenian' material no evidence of heterochely was observed, as right and left chelae are found in same proportion and in same size as well, with the exception of *C. brocchii*". It should be noted here that Müller (1984) examined only six specimens of *C. brocchii* comparing to often tens and hundreds of specimens in other "*Callianassa*" species. Therefore, it seemed to him that *C. brocchii* was the only heterochelous species among 'Badenian' callianassid forms.

Subfamily Eucalliinae Manning & Felder, 1991

Remarks. Recently, Sakai (2011) raised the Eucalliinae to family level. Following the classification of De Grave *et al.* (2009), we still treat it as a subfamily.

Genus *Eucalliix* Manning & Felder, 1991

Type species. *Callianassa quadracuta* Biffar, 1970.

Remarks on taxonomy. The taxonomy of *Eucalliix* is rather complex. The genus was established by Manning & Felder (1991) for several species previously assigned to the genus *Calliax* de Saint Laurent, 1973. They noted that chelipeds are equal and similar in *Eucalliix*, whereas *Calliax* possesses unequal chelipeds. Ngoc-Ho (2003) provided a detailed account on the differences between the two genera both in soft-part and hard-part morphology. She considered chelipeds in *Eucalliix* subequal and similar, whereas in *Calliax*, chelipeds are unequal, and the minor has "fixed finger shorter than and separated from the dactylus by a wide gap, bearing a large triangular proximal tooth" (Ngoc-Ho 2003: 490). She also erected a new genus *Calliixina* Ngoc-Ho, 2003 for three species previously treated as *Calliax*: *C. novaebritanniae* (Borradaile, 1900), *C. punica* (de Saint Laurent & Manning, 1982) and *C.*

sakaii (de Saint Laurent & Le Loeuff, 1979). For *Calliaxina*, subequal, similar and laterally compressed first pereopods are typical, whereas in *Calliax*, they are also laterally compressed, but unequal and dissimilar (Ngoc-Ho 2003). Sakai (1999, 2005) recognized *Eucalliax* and *Calliaxina* as junior synonyms of *Calliax*. Later, he (Sakai 2011) recognized all of them as valid, but his concept of *Eucalliax* and *Calliaxina* differs markedly from that of Ngoc-Ho (2003). He restricted *Eucalliax* to *Callianassa quadracuta* Biffar, 1970 only, and for *Calliaxina* listed *C. aequimana* (Baker, 1907), *C. bulimba* (Poore & Griffin, 1979), *C. jonesi* (Heard, 1989), *C. mcilhennyi* (Felder & Manning, 1994) and *C. panglaoensis* (Dworschak, 2006) besides *C. novaebritanniae*, *C. punica* and *C. sakaii*. We follow Ngoc-Ho (2003) rather than Sakai (2011) in recognizing only three species of *Calliaxina*. We consider the rest of above mentioned species as members of *Eucalliax*, thus following works of Manning & Felder (1991), Felder & Manning (1994) and Dworschak (2005, 2006). In this respect the material presented herein with its subequal and similar chelipeds falls within the range of the genus *Eucalliax*. It possesses massive chelipeds which is in contrast to *Calliaxina* sensu Ngoc-Ho (2003) with laterally compressed chelipeds.

Remarks on the fossil record. All three Eucalliinae genera discussed above have been identified in the fossil record. Concerning distinguishing *Calliax* and *Eucalliax* from each other in the fossil state, Schweitzer *et al.* (2003: 12) mentioned the nature of the lower margin of merus, which is serrated in *Calliax* and without serration in *Eucalliax*. Unfortunately, this does not seem to be consistent. For instance Biffar (1970: 42) mentioned presence of denticulation in *C. quadracuta* which is the type species of *Eucalliax*. In *E. pseudorakosensis* comb. nov. as recognized herein, the denticulation is also present, although only in large specimens (Fig. 10E).

The fossil record of *Calliax* is obscure. *Callianassa whiteavesi* Woodward, 1896 from the Campanian of British Columbia and Alberta, Canada was reassigned to *Calliax* by Schweitzer *et al.* (2003).

Recently Feldmann *et al.* (2011) reported a few claw fragments as "Cheliped Form B" of indeterminate callianassoid. The material shows remarkable similarities to the genus *Calliax* as defined by Ngoc-Ho (2003). Interestingly, a minor chela is also preserved (Feldmann *et al.* 2011: fig. 5E) exhibiting fixed finger shorter than dactylus and separated from it by a wide gap with a proximal tooth, a combination of characters which has been so far documented in *Calliax* only (Ngoc-Ho 2003).

Swen *et al.* (2001) reported a single fragmentary right propodus from the Maastrichtian of the Netherlands classified as *Calliax?* sp. It is very difficult to assign this specimen to any genus of the subfamily Eucalliinae without evidence of both chelipeds.

Van Bakel *et al.* (2006) listed in a table of Cenozoic decapods from Belgium the presence of *Calliax* nov. sp. in the Miocene strata. The systematic placement of the material has recently been reconsidered to represent a new member of the family Axiidae (Fraaije *et al.* 2011).

Eucalliax was reported from the Eocene, Miocene and Pliocene of Japan: *E. yoshihiroii* Karasawa, 1992; *E. yatsuoensis* (Karasawa, 1993); and *E. miyazakiensis* Karasawa, 1993 respectively. Kato (1996) reported several specimens classified as *Eucalliax* sp. from the Miocene of Japan. These specimens, however, possess tubercles on the lateral surface of propodus, which is highly unusual for the genus. Moreover, they were associated with *Callianopsis* spp., for which such tuberculation is quite typical. Kato (1996: 507) stated that *Eucalliax* sp. is distinguishable from *Callianopsis* spp. "by the absence of a large, triangular tooth on the proximal part of the fixed finger, and having a remarkably small fixed finger on the left chela". These characters can not be considered as important for generic assignment (see Hyžný & Schlögl 2011: 326). In fact, the presence and absence of a triangular tooth on the fixed finger may mirror sexual dimorphism in *Callianopsis* de Saint Laurent, 1973 as already documented by Schweitzer Hopkins & Feldmann (1997) and Hyžný & Schlögl (2011). Kato (1996) did not state why he had placed the specimens in *Eucalliax*.

Several occurrences of the genus have been reported also from the Eocene of Italy. Beschin *et al.* (2002) described *Eucalliax vicetina* Beschin, Busulini, De Angeli & Tessier, 2002, based on virtually entire major and minor chelipeds. Finally Beschin *et al.* (2009) reported a single incomplete propodus referred to *Eucalliax* sp. from the Lower Eocene of Italy. Its morphology, however, strongly suggests the assignment to ctenochelid genus *Ctenocheles* Kishinouye, 1926. The presence of *Ctenocheles sereaensis* Beschin, De Angeli & Zorzin, 2009 in the same strata reported in the same paper may confirm the here presented opinion.

It should be noted that virtually none of the above mentioned *Calliax* and *Eucalliax* occurrences have been reexamined with respect to the work by Ngoc-Ho (2003). If following the genus concept of Eucalliinae taxa presented by Ngoc-Ho (2003), all the fossil material assigned at one time to these genera should be revised to confirm or reject their current generic assignment.

Calliuxina has been identified in the fossil record only recently (Hyžný, in prep.). Exhaustive treatment on the distinction between *Eucalliux* and *Calliuxina* in the fossil record is beyond the scope of the paper and will be published elsewhere (Hyžný, in prep.).

***Eucalliux pseudorakosensis* (Lörenthey in Lörenthey & Beurlen, 1929) new combination**

(Figs 7–11)

Callianassa pseudorakosensis Lörenthey in Lörenthey & Beurlen, 1929: 69, pl. 2 figs. 16–18.

Callianassa pseudorakosensis. — Glaessner, 1929: 88; Schweitzer *et al.*, 2010: 36.

Callianassa cf. *pseudorakosensis*. — Bachmayer, 1953: 241; Müller, 1998: 10.

Callianassa cf. *jahringensis* Glaessner, 1928: 166, pl. 3 figs. 2, 2a; Glaessner, 1929: 83; Müller, 1984: 53.

"*Callianassa*" *pseudorakosensis*. — Müller, 1976: 507; Hyžný, 2011a: 41, fig. 4A, B, Table 1, 2.; Hyžný, 2011b: 167, Table 1.

'*Callianassa*' *pseudorakosensis*. — Müller, 1984: 52, pl. 3 figs. 4–5, pl. 4 figs. 1–6, pl. 5 figs. 1–4.

Non *Callianassa pseudorakosensis*. — Radwański & Wysocka, 2004: 390, pl. 9 fig. 2.

Emended diagnosis. Heterochelous eucalliucine ghost shrimp with chelipeds without pronounced tuberculation. Merus of major cheliped ovoid with lower margin possessing faint denticles; carpus about as long as high, squarish or rhomboidal in shape, unarmed with keeled upper and lower margins. Palm massive, subequal in length and height with keeled upper and lower margins; fixed finger with or without triangular blunt tooth; distal margin of propodus finely serrated; weak unarmed excavation extending from below the articulation with the dactylus forming a weak keel. Dactylus heavy, curved, quadrate on the cross section proximally, armed on cutting edge with blunt tooth proximally and keel forming a distal tooth. Minor cheliped smaller in size than major, dissimilar in shape, carpus longer than high, triangular in shape, upper margin keeled and arcuate; propodus higher than long, upper and lower margins distinctly keeled; fixed finger high, cutting edge slightly convex distally, dactylus slender, curved, unarmed.

Emended description. First pereopods with major and minor cheliped strongly developed, slightly unequal in size, dissimilar in shape of propodus and dentition of fingers; major cheliped located on either right or left side of body. Two different morphotypes were identified in the nature of major propodus; morphotype with triangular tooth positioned at the base of fixed finger (Fig. 7A) and morphotype without tooth (Fig. 7B).

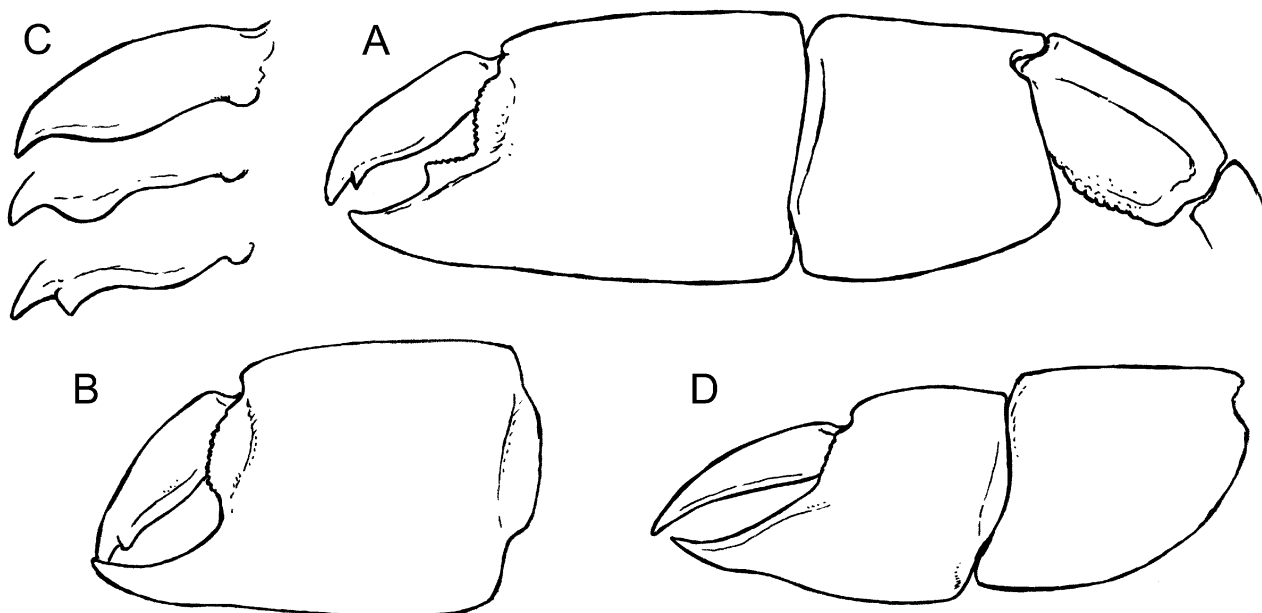


FIGURE 7. *Eucalliux pseudorakosensis* (Lörenthey in Lörenthey & Beurlen, 1929) new combination, reconstructions: A, major cheliped of morphotype with tooth; B, major chela of morphotype without tooth; C, variation in the armature of dactylus; D, minor cheliped. All figures are in outer view. Reconstructions are based on several different specimens and are in scale.

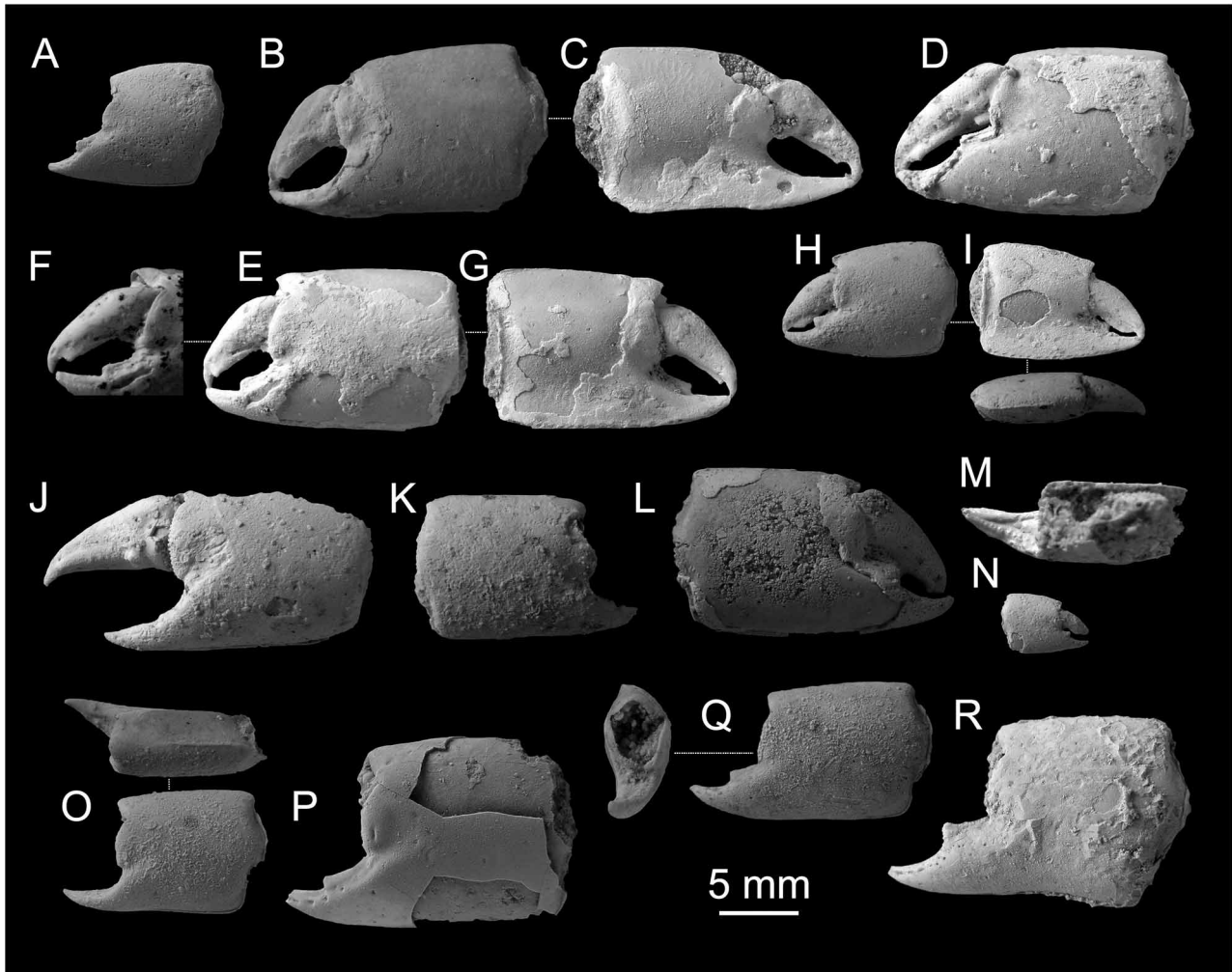


FIGURE 8. *Eucalliax pseudorakosensis* (Lörenthey in Lörenthey & Beurlen, 1929) new combination, major chelae (propodi and dactyli): A, left propodus (morphotype with tooth), KGP-MH DH-026; B–C, left chela from outer and inner view (morphotype without tooth), PCRB-DH019; D, left chela (morphotype with tooth), PCRB-DH020; E–G, left chela (morphotype with tooth) from outer and inner view, KGP-MH DH-069, note distal tooth on dactylus (F); H–I, left chela (morphotype with tooth) from outer, inner and upper view, PCRB-DH021; J, left chela (morphotype without tooth), PCRB-DH022, note the partial rotation of dactylus enabling the view of its proximal blunt tooth; K, right propodus (morphotype without tooth), PCRB-DH018; L, right chela (morphotype with tooth), KGP-MH DH-027; M, fragmented left propodus (morphotype without tooth), PCRB-DH017, note faint denticulation on mesial edge of the fixed finger; N, right chela (morphotype with tooth), PCRB-DH023; O, left propodus (morphotype without tooth), PAL 2011.25, note upper view showing keeled upper margin; P, left propodus (morphotype with tooth), PAL 2011.26; Q, left propodus (morphotype with tooth), PAL 2011.24, note distal view with quadrate opening for dactylus; R, left propodus (morphotype with tooth), PAL 2011.27, note unusually concave lower margin. Specimens A–N come from the Dúbravská hlavica locality (Slovakia); specimens O, Q come from Gyakorló út (Hungary); specimens P, R come from Mátraverebély-Szentkút (Hungary). All specimens are to scale and were covered with ammonium chloride prior to photography.

Major cheliped massive and strongly calcified; ischium slender (Fig. 10C), upper margin sinuous, lower margin with row of tiny denticles; merus ovoid, longer than high ($L/H = 1.8–2.0$), highest at midlength, lower margin straight or slightly convex, with tiny denticles, upper margin slightly convex, smooth, lateral surface with keel positioned around the middle (e.g. Figs 10E, G, H); carpus about as long as high, highest distally, about as long as merus, squarish or rhomboidal in shape (Figs. 7A, 10), unarmed, lower margin arcuate, upper and lower margins keeled (Figs 8I, O), terminating distally in blunt corners, margins of proximo-lower corner forming almost right angle; propodus heavy, palm approximately as long as high, lateral surfaces smooth, upper and lower margins keeled, keel of lower bent slightly inward, becoming ill-defined beyond midlength and absent on fixed finger; fixed finger thick, prehensile margin unarmed (morphotype without tooth) or armed with one well separated tooth in

midlength (morphotype with tooth), serrated with tiny denticles distally, otherwise unarmed, terminating in rounded tip, tip bent slightly upward; distal margin of propodus finely serrated; weak unarmed excavation extending from below the articulation with the dactylus to below the tooth on mesial face, thus forming a faint keel; dactylus heavy, curved, quadrate on the cross section proximally (Fig. 8Q), armed on cutting edge with blunt tooth proximally (Fig. 8J) and keel forming a distal tooth distally pointing downward near the tip of dactylus (e.g. Figs 7C, 8F), tip sharp and slightly hooked.

Minor cheliped smaller in size than major, dissimilar in shape, carpus longer than high, triangular in shape (Figs 7D, 9E, F), upper margin keeled and arcuate; articulation between carpus and propodus more than 90°; propodus higher than long (Fig. 9), upper and lower margins distinctly keeled; fixed finger high, cutting edge slightly convex distally, the tip narrowing abruptly, pointed and bent slightly upward; dactylus slender, curved, unarmed.

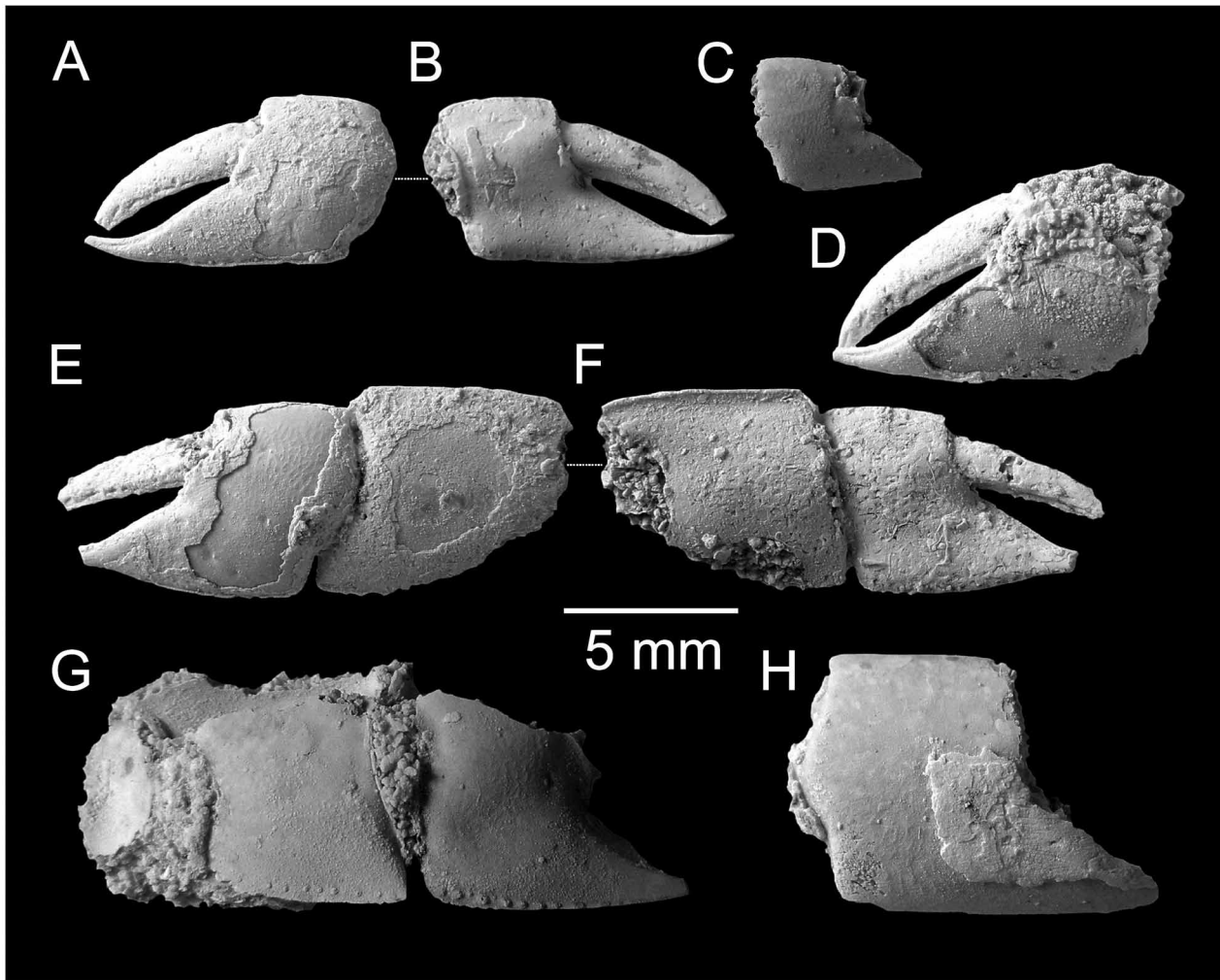


FIGURE 9. *Eucalliax pseudorakosensis* (Lörenthey in Lörenthey & Beurlen, 1929) new combination, minor chelae: A–B, left chela, PCRB-DH025; C, right propodus, PCRB-DH26; D, left chela, PCRB-DH024; E–F, left chela (with articulated carpus), KGP-MH DH070; G, left chela (with articulated carpus), PCRB-DH027; H, right propodus, PCRB-DH028. All specimens come from the Dúbravská hlavica locality (Vienna Basin, Slovakia), Middle Miocene. All specimens are to scale and were covered with ammonium chloride prior to photography.

Variations. There are two distinct forms, occurring on both right and left chelae, most probably due to a dimorphism. One morphotype has a triangular tooth at the base of the fixed finger, the other one has no such tooth; this dimorphism was already recognized by Lörenthey & Beurlen (1929) and Müller (1984). A quick scan of published figures showed that at least in some taxa, such dimorphism may mirror sex. A toothed fixed finger seems to be present mostly in females, whereas a morphotype without the tooth is more typical for males as can be documented in the following examples: a distinctly toothed fixed finger has been figured in female specimens of *E. aequimana* (Poore & Griffin 1979: fig. 12d), *E. kensleyi* Dworschak, 2005 (Dworschak 2005: figs. 3, 4), and *E.*

mcilhennyi (Felder & Manning 1994: fig. 1); a morphotype without a toothed fixed finger has been figured in male specimens of *E. aequimana* (Poore & Griffin 1979: fig. 121), *E. bulimba* (Poore & Griffin 1979: figs. 21d, e), *E. jonesi* (Heard 1989: figs. 1, 4b; Felder & Manning 1994: fig. 5e) and *E. mcilhennyi* (Felder & Manning 1994: figs. 2b, c). On the other hand, no such pattern has been observed in *E. cearaensis* Rodrigues & Manning, 1992, and *E. panglaoensis*. Interestingly, sexual dimorphism has been observed in *E. panglaoensis*, although in different pattern. In this species chelipeds of females and small males are almost equal in size, whereas in large males they become slightly unequal (Dworschak 2006: 356, fig. 7); the triangular tooth is present in major chelae in both sexes. Concerning *E. cearaensis*, it is questionable whether it is representative for the genus; Sakai (2011) erected for this species a new genus *Eucalliixiopsis*.

We do not explain unequivocally the variability in the nature of major propodus of *E. pseudorakosensis* comb. nov. as a consequence of sexual dimorphism. It should, however, be mentioned that the same pattern of dimorphs have been recognized in the ctenochelid genus *Callianopsis* as mirroring sexual dimorphism; thus, the presence of a tooth at the base of the fixed finger is indicative of females, whereas males have no such tooth (Schweitzer Hopkins & Feldmann 1997; Hyžný & Schlögl 2011). In this context it is worth mentioning that recent molecular analysis by Felder & Robles (2009) has shown a rather close phylogenetic relationship between Ctenochelidae Manning & Felder, 1991 and Eucalliicinae.

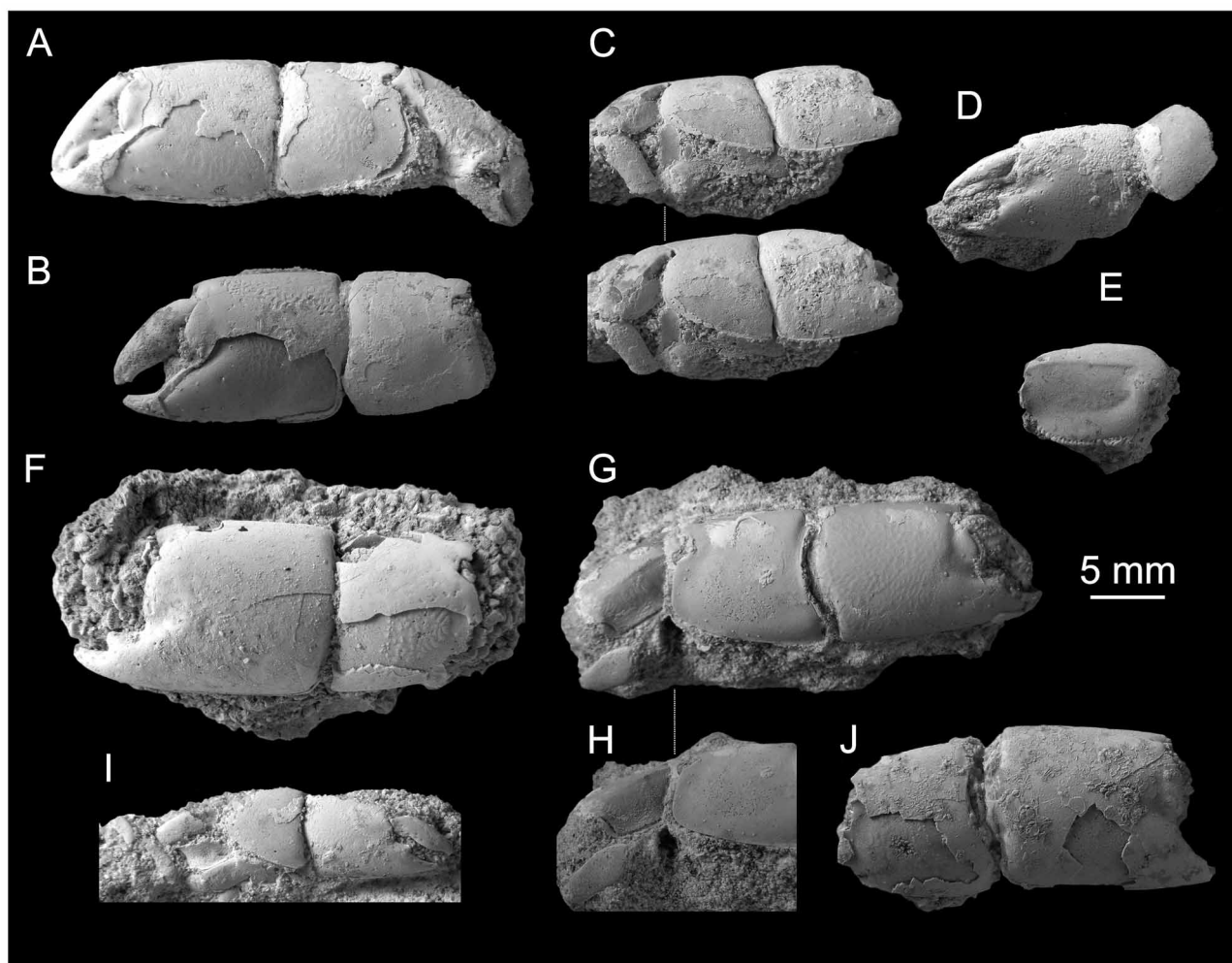


FIGURE 10. *Eucalliix pseudorakosensis* (Lőrenthey in Lőrenthey & Beurlen, 1929) new combination, articulated major chelae: A, left cheliped (morphotype with tooth), PCMH-005; B, left cheliped (morphotype without tooth), SNM Z-37565; C, right cheliped (morphotype with tooth), KGP-MH DH-034, note partially preserved ischium; D, left cheliped (morphotype with tooth), KGP-MH DH033; E, right merus, PAL 2011.23; F, left cheliped (morphotype with tooth), PAL 2011.28; G–H, right cheliped (morphotype with tooth), KGP-MH DH-039, note serration on the lower margin of merus (H); I, right cheliped (morphotype with tooth), SNM Z-37568; J, right cheliped (morphotype without tooth), SNM Z-37563. All specimens except E and F come from the Dúbravská hlavica locality (Slovakia); E and F come from Mátraverebély-Szentkút (Hungary). All specimens are to scale and were covered with ammonium chloride prior to photography.

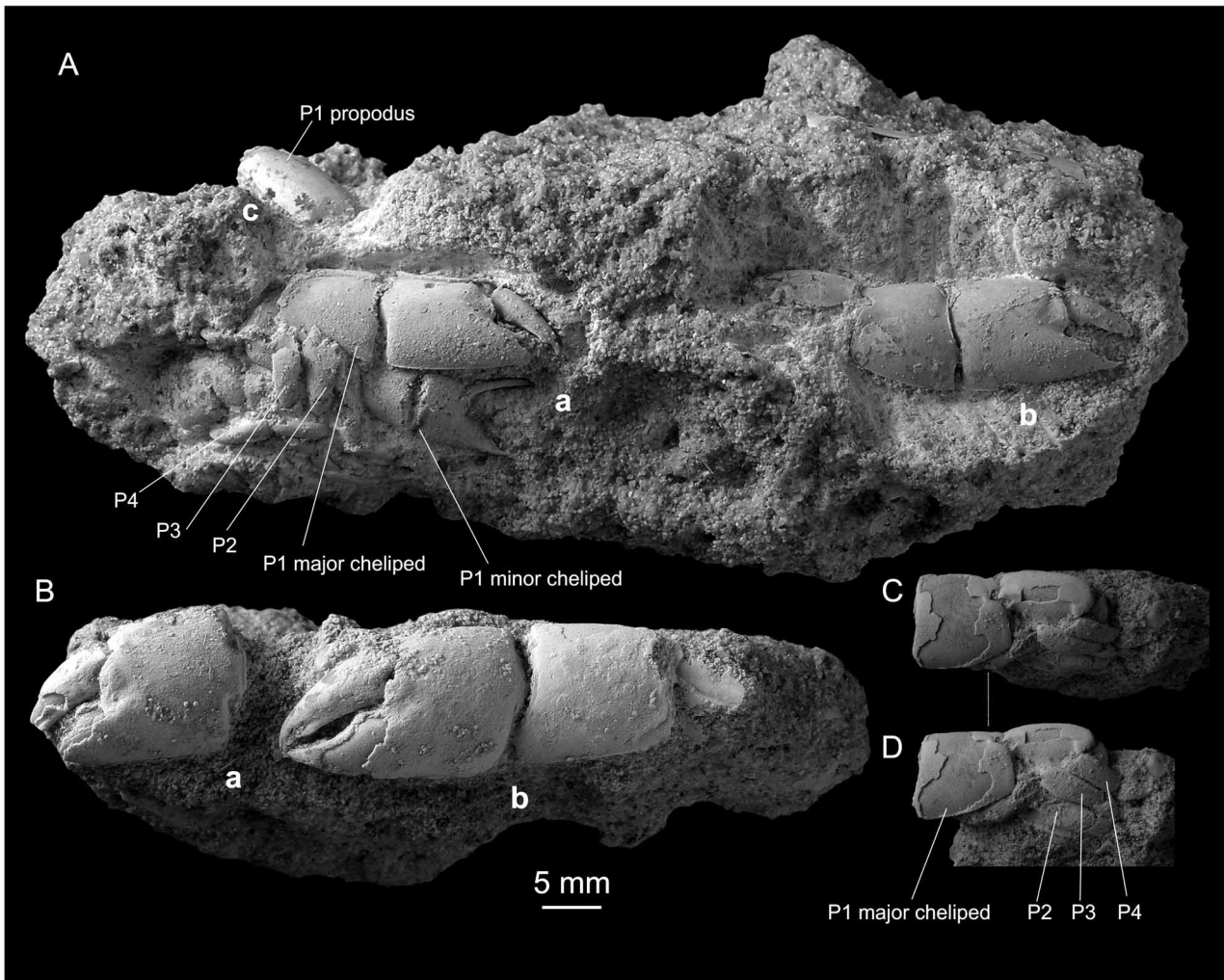


FIGURE 11. *Eucalliax pseudorakosensis* (Lörenthey in Lörenthey & Beurlen, 1929) new combination, *in situ* preservation: A, specimen SNM Z-21373 representing a burrow structure with remains of three individuals; B, specimen PCMH-006 with remains of two individuals in a horizontal burrow structure; C–D, specimen PCMH-004 representing cheliped and thoracopod association preserved in a burrow button *sensu* Bishop & Williams (2005). All specimens come from the Dúbravská hlavica locality (Vienna Basin, Slovakia), Middle Miocene. Symbols "a–c" denote specimens as appearing in Table 1 and Table 2 with measurements. All specimens are to scale and were covered with ammonium chloride prior to photography.

Variations in the nature of the dactylus have also been observed. Usually smaller specimens have the distal tooth on the occlusal margin of dactylus rather blunt, or even not developed at all, however, in that case a swollen area in the place is present. In larger specimens the tooth becomes sharper and more distinct (Fig. 7C). The same can be said about the keel on the occlusal margin of dactylus itself, which is very well pronounced in larger specimens. This type of variation can be correlated with size/age of the individual.

Material examined. FI M.20 (holotype, right major propodus, morphotype with tooth, figured in Lörenthey & Beurlen 1929: pl. 2, fig. 16), FI M.2347 (right major propodus, morphotype with tooth); KGP-MH DH-016–KGP-MH DH-040, KGP-MH DH-040, KGP-MH DH-043, KGP-MH DH-044, KGP-MH DH-047, KGP-MH DH-051, KGP-MH DH-053, KGP-MH DH-054, KGP-MH DH-057, KGP-MH DH-059, KGP-MH DH-062, KGP-MH DH-063, KGP-MH DH-069, KGP-MH DH-069; M.86.530 (collective number); SNM Z-7943 (collective number), SNM Z-16419 (collective number), SNM Z-16433 (collective number), SNM Z-21373; SNM Z-37554–SNM Z-37569; PAL 2011.22–PAL 2011.28; PCMH-004–PCMH-007, PCRB DH-017–PCRB DH-028. For measurements and all the details see Table 2.

TABLE 2. Measurements of selected well preserved specimens of *Eucalliax pseudorakosensis* (Lörenthey in Lörenthey & Beurlen, 1929) comb. nov. Handedness: L = left; R = right; measurements: L = max. length; H = max. height; ~ = approximate value; > = "more than" (in case the approximation is not possible due to the state of preservation); values are in mm.

Specimen	morphotype	handedness	merus		carpus		propodus		dactylus
			L	H	L	H	L	H	L
SNM Z-21273a	with tooth	R	-	-	~6.1	~6.1	8.0	8.2	6.7
SNM Z-21273b	with tooth	R	8.3	4.2	7.2	8.4	8.0	8.8	6.4
SNM Z-21273c	with tooth	R	-	-	-	-	8.7	8.4	6.8
SNM Z-37554	without tooth	L	-	-	-	-	7.1	8.2	-
SNM Z-37555	without tooth	L	-	-	-	-	8.2	7.9	8.0
SNM Z-37556	with tooth	R	-	-	-	-	9.0	8.3	6.0
SNM Z-37558	with tooth	R	-	-	-	-	11.2	9.0	-
SNM Z-37559	with tooth	L	-	-	-	-	7.6	7.8	~5.0
SNM Z-37560	with tooth	L	-	-	-	-	6.0	5.4	>3.3
SNM Z-37561	minor	R	-	-	-	-	6.0	8.1	-
SNM Z-37562	without tooth	R	-	-	-	-	8.5	8.6	-
SNM Z-37563	without tooth	R	-	-	>7	9.5	10.7	10.0	-
SNM Z-37564	without tooth	L	7.1	-	7.7	8.5	7.6	9.2	-
SNM Z-37565	without tooth	L	-	-	7.3	9.1	9.0	9.4	-
SNM Z-37566	with tooth	L	-	-	-	9.5	-	10.1	-
SNM Z-37567	unknown	R	-	-	5.0	7.5	7.5	-	-
SNM Z-37568	with tooth	R	-	-	>3.8	5.7	5.4	5.3	5.3
SNM Z-37569	without tooth	R	7.0	4.4	-	-	9.0	>8.0	>8.4
KGP-MH DH-016	without tooth	L	-	-	-	-	>8.0	10.1	-
KGP-MH DH-018	without tooth	R	-	-	-	-	11.1	10.0	-
KGP-MH DH-019	without tooth	R	-	-	-	-	10.7	10.2	-
KGP-MH DH-020	unknown	R	-	-	-	-	8.4	7.7	-
KGP-MH DH-021	with tooth	L	-	-	-	-	>7.5	7.5	-
KGP-MH DH-022	with tooth	L	-	-	-	-	>10.5	9.4	-
KGP-MH DH-023	with tooth	L	-	-	-	-	9.0	8.8	-
KGP-MH DH-024	with tooth	L	-	-	-	-	5.7	8.2	-
KGP-MH DH-025	with tooth	L	-	-	-	-	8.2	7.5	-
KGP-MH DH-026	with tooth	L	-	-	-	-	6.2	7.3	-
KGP-MH DH-027	with tooth	R	-	-	-	-	10.4	10.1	9.2
KGP-MH DH-028	without tooth	R	-	-	-	-	9.5	10.3	-
KGP-MH DH-029	without tooth	R	-	-	-	-	7.0	7.2	-
KGP-MH DH-030	with tooth	R	-	-	-	-	>9.0	>7.5	-
KGP-MH DH-033	with tooth	L	-	-	-	-	7.1	7.1	6.0
KGP-MH DH-034	unknown	R	6.2	5.2	5.5	7.2	~6.0	7.3	-
KGP-MH DH-036	unknown	R	-	-	8.2	8.7	-	-	-
KGP-MH DH-037	unknown	R	-	-	8.0	10.0	-	-	-
KGP-MH DH-039	with tooth	R	9.5	5.1	9.6	9.4	10.0	9.3	~8.0
KGP-MH DH-040	without tooth	R	-	-	-	-	10.9	10.0	>7.5
KGP-MH DH-043	without tooth	L	-	-	-	-	10.7	9.5	-
KGP-MH DH-051	with tooth	L	-	-	-	-	8.2	8.0	-

continued next page

TABLE 2. (continued)

Specimen	morphotype	handedness	merus		carpus		propodus		dactylus
			L	H	L	H	L	H	L
KGP-MH DH-069	with tooth	L	-	-	-	-	10.4	9.5	8.0
KGP-MH DH-070	minor	L	-	-	6.1	5.8	3.7	5.2	>4.5
PAL 2011.22	with tooth	L	-	-	-	-	10.4	10.2	-
PAL 2011.23	unknown	R	8.7	6.4	-	-	-	-	-
PAL 2011.24	with tooth	L	-	-	-	-	8.7	8.3	-
PAL 2011.25	withou tooth	L	-	-	-	-	7.6	7.0	-
PAL 2011.26	with tooth	L	-	-	-	-	9.4	8.7	-
PAL 2011.27	with tooth	L	-	-	-	-	10.3	11.1	-
PAL 2011.28	with tooth	L	-	-	8.6	10.1	11.3	11.1	-
PCMH-004	unknown	L	7.7	4.7	7.0	8.5	-	-	-
PCMH-005	with tooth	L	8.4	5.5	7.8	9.2	10.1	10.1	9.3
PCMH-006a	with tooth	R	-	-	-	-	9.6	11.1	>9.0
PCMH-006b	with tooth	R	-	-	9.0	10.4	9.5	11.0	10.6
PCRB DH-018	without tooth	R	-	-	-	-	9.6	11.1	-
PCRB DH-019	without tooth	L	-	-	-	-	8.0	8.2	7.0
PCRB DH-020	with tooth	L	-	-	-	-	9.4	9.7	9.3
PCRB DH-021	with tooth	L	-	-	-	-	7.0	7.2	5.5
PCRB DH-022	without tooth	L	-	-	-	-	~11.5	-	9.5
PCRB DH-023	with tooth	R	-	-	-	-	3.2	3.4	2.6
PCRB DH-024	minor	L	-	-	-	-	~3.7	5.1	6.1
PCRB DH-025	minor	L	-	-	-	-	3.0	4.2	>4.5
PCRB DH-026	minor	R	-	-	-	-	3.4	4.4	-
PCRB DH-027	minor	L	-	-	-	-	~4.5	>4.2	-
PCRB DH-028	minor	R	-	-	-	-	5.2	7.5	-

Occurrence. The species is very common in the sediments of the Middle Miocene age of the countries once forming an area of the Central Paratethys Sea. Up to now it has been reported from the late Early ('Karpatian') and Middle Miocene ('Badenian') of Hungary (Lörenthey & Beurlen 1929; Müller 1984), Romania (Lörenthey & Beurlen 1929; Müller 1984), Austria (Glaessner 1928; Müller 1984, 1998), and Slovakia (Hyžný 2011a, b, this contribution).

The species often occurs in large numbers as exemplified in studied material from Dúbravská hlavica and published material from Hungarian localities Rákos and Mátraverebély-Szentkút (Müller 1984), and from the Romanian locality Minișu de Sus (Felménes) (Lörenthey & Beurlen 1929; Müller 1984).

Remarks. *Eucalliax pseudorakosensis* comb. nov. is very easily distinguishable from all similar fossil forms. Its propodus is heavy and when viewed distally, it is very robust in its upper half (in place of articulation with dactylus), whereas the lower part is more depressed, partly also due to the arcuate and keeled lower margin curved inward. Moreover, it has a rounded cross section of the fixed finger, whereas similar Middle Miocene forms, as "*Callianassa*" *chalmasii* Brocchi, 1883 and "*Callianassa*" *rakosiensis* Lörenthey, 1897, are oval (Lörenthey in Lörenthey & Beurlen 1929: 68). When dealing with more complete chelipeds, *E. pseudorakosensis* comb. nov. can be characterized by a squarish or rhomboidal carpus, and a dactylus armed with a distal tooth. These characters distinguish the species from all extant members of the genus, as well as from all relative fossil taxa.

Radwański & Wysocka (2004) reported from the Middle Miocene of Poland a single chela attributed to *Callianassa pseudorakosensis* associated with trace fossils of the ichnogenus *Ophiomorpha* Lundgren, 1891. The morphology of the specimen is, however, distinctly different from *E. pseudorakosensis* comb. nov. The preserved propodus with articulated dactylus is somewhat fractured and slightly deformed (Radwański & Wysocka 2004: fig.

1.2); however, the general morphology can be inferred. The upper margin seems to taper proximally unlike *Eucalliax pseudorakosensis* comb. nov. for which the opposite is true. The keel on the fixed finger is strongly developed; in *E. pseudorakosensis* comb. nov., it is developed only weakly. The dactylus is completely unlike that of *E. pseudorakosensis* comb. nov. in being very high and lacking the distinctive tooth positioned distally on the occlusal margin. Moreover, the specimen seems to be rather flat (laterally compressed *sensu* Ngoc-Ho, 2003) and not massive which is quite typical for *E. pseudorakosensis* comb. nov., and therefore it resembles members of the genus *Calliixina* Ngoc-Ho, 2003. As the specimen has been examined only via photographs, we are hesitant to discuss its affinities further, although it is clear that it is not conspecific and possibly even not congeneric with *E. pseudorakosensis* comb. nov. Personal observation is needed to definitely state its systematic affinity.

***In situ* preservation**

Ghost shrimp body fossils found within burrow structures interpreted as *in situ* preservation are very rarely to be found. This issue was discussed by Bishop & Williams (2005) and Hyžný (2011a). The latter author also provided a short review of the Callianassidae preserved within or in direct association with trace fossils representing remains of burrows.

At the studied localities, the majority of specimens represent isolated cheliped elements (often fragmented). However, at the locality of Dúbravská hlavica several ghost shrimp specimens preserved within tube structures interpreted as parts of the ghost shrimp burrow system have been collected. Trace fossils exhibiting Y-branching attributed to the ichnogenus *Thalassinoides* Ehrenberg, 1944, have also been identified. Unfortunately, no vertical shafts connected with horizontal tunnels have been found. The burrow structures themselves are preserved in a poorly consolidated sandstone; thus, their cross section is difficult to determine (cf. Hyžný 2011a). However, the mode of preservation of the individuals suggests preservation within the burrow (cf. Bishop & Williams 2005).

A single specimen of *Neocallichirus brocchii* comb. nov. apparently preserved within a burrow structure has been found (KGP-MH DH-058; Fig. 6). The sample exhibits an individual of slender morphotype with both chelipeds and remains of thoracopods. Contrary to the case of *E. pseudorakosensis* comb. nov., preserved as more or less lying on the side (see below), the specimen of *N. brocchii* comb. nov. is preserved in the position similar to that of the famous Australian subfossil mudlobster of the genus *Thalassinina* Latreille, 1806 discussed at length by Murray & Hanley (1986).

One sample (SNM Z-21373; Fig. 11A) represents articulated remains of three individuals of *Eucalliax pseudorakosensis* comb. nov. preserved in a single horizontal burrow structure as already discussed in Hyžný (2011a). In one individual, both chelipeds together with scattered remains of other pereopods are preserved, which can be characterized as cheliped and thoracopod disassociation units *sensu* Bishop & Williams (2005). Another sample (PCMH-006; Fig. 11B) shows two individuals in a burrow structure. Interestingly, in both samples individuals are oriented in the same direction. Although the burrow walls are not discernible, from the arrangement of the individuals it may be assumed they were preserved lying on one side (possibly on the bottom of a burrow). Similar *in situ* preservation was reported in *Protocallianassa fujasi* (Desmarest, 1822) from the Lower Campanian of Germany (Mourik *et al.* 2005) and "*Callianassa*" *almerai* Müller, 1993 from the Middle Miocene of Austria (Hyžný 2011a).

At Dúbravská hlavica many more specimens of *Eucalliax pseudorakosensis* comb. nov. are preserved with scattered remains of pereopods in close association with chelipeds as burrow buttons *sensu* Bishop & Williams (2005) (Figs 11C–D).

Discussion on the taphonomy of Dúbravská hlavica specimens was provided by Hyžný (2011a).

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