

***In situ* mud shrimps (Decapoda: Axiidea: Callianassidae) preserved within their burrows from the middle Miocene of the Central Paratethys**

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Abstract

In situ preservation of mud shrimps of the family Callianassidae (Decapoda: Axiidea) has rarely been noted in the fossil record. The present contribution reports body fossils of four members of the family (“*Callianassa*” *almerai*, “*C.*” *pseudorakosensis*, “*C.*” sp. 1 and “*C.*” sp. 2) which are apparently preserved within their burrows, all from middle Miocene deposits of Austria, Slovakia and Hungary (Central Paratethys). Description, with detailed figures for each reported occurrence, is given, followed by a review of fossil “thalassinideans”, mainly Callianassidae, preserved within burrow structures or associated with burrows. Occurrences of all middle Miocene callianassids of the Central Paratethys currently known are also summarized.

Key words: Decapoda, Callianassidae, *in situ* preservation, middle Miocene, Central Paratethys

Introduction

The family Callianassidae has a robust fossil record. Unfortunately, systematics based on hard-part morphology are still debated. However, following publication of a paper by Manning and Felder (1991), which highlighted, besides other “traditional” characters, the taxonomic significance of major cheliped morphology, many workers have attempted to assign fossil callianassids more naturally to extant genera or, alternatively, have erected new ones. In view of the delicate nature of the callianassid exoskeleton, only chelipeds (which usually are heavily calcified) are likely to be preserved in the fossil record (Bishop and Williams, 2005).

Thirty-four extant callianassid genera are currently known (De Grave *et al.*, 2009). However, fewer 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 they are bound to remain unrecognized in the fossil record.

Contrary to the rather robust fossil record of callianassid chelipeds, remains of animals preserved inside their burrows are relatively rare. However, Bishop and Williams (2005) noted that the preservation of major and minor chelipeds in close proximity might represent the remains of burrow-dwelling individuals, because the chelipeds would have been dispersed if not protected within a burrow.

The aim of the present contribution is to focus on the *in situ* preservation of Callianassidae in the fossil record. For that reason,

no systematic and taxonomic issues relating to the nature of the body fossils presented herein, are discussed. Detailed re-descriptions of “*Callianassa*” *almerai* Müller, 1993 and “*C.*” *pseudorakosensis* Lörenthey *in* Lörenthey and Beurlen, 1929 with emended diagnoses and a discussion of their systematic affinities are currently being prepared by the author and will be published elsewhere.

Decapods as producers of burrows in the fossil record

There are several higher taxa of decapod crustaceans which independently evolved the construction of permanent burrows or burrow systems. Unfortunately, identifying decapods as producers of burrows without direct evidence of *in situ* preservation is rather difficult. However, ichnofossils commonly attributed to decapod crustaceans are very common, yet usually do not contain any body fossils. Such associations are very rare, as a literature survey shows.

Species that produce permanent burrows have been identified in six decapod infraorders *sensu* De Grave *et al.* (2009). Among carideans the family Alpheidae is known to build rather complex burrow systems. Although no undisputed member of the family has been reported from the fossil record (Schweitzer *et al.*, 2010), Radwański *et al.* (2006) recorded burrow systems from the middle Miocene of Ukraine and interpreted them as having been constructed by alpheid shrimps, although no body fossil evidence had been recovered.

Among astacideans, a burrowing behaviour is quite common (e.g. families Nephropidae, Cambaridae and Parastacidae).

Bedatou *et al.* (2008) described the ichnogenus *Loloichmus* from Jurassic and Cretaceous strata of Argentina and interpreted it as the remains of crayfish burrows. They regarded their possible maker to have been a member of the family Parastacidae, again without any body fossil preserved.

In the Glypheidea, a burrowing behaviour was identified in extinct members of the Erymidae (Monaco and Garassino, 2001), Glypheidae (Sellwood, 1971), and Mecochiridae (Neto de Carvalho and Viegas, 2007; Neto de Carvalho *et al.* 2010). All these reports described body fossils preserved *in situ*.

There are several brachyuran families whose members construct rather simple burrows (e.g. Gecarcinucidae, Goneplacidae, Portunidae, Panopeidae, Gecarcinidae, Sesarmidae, Varunidae, Dotiliidae, Macrophthalmidae, Mictyridae and Ocypodidae). Reports of fossil brachyurans preserved *in situ* within their burrows are limited to goneplacids *Ommatocarcinus corioensis* (Creswell, 1886) from the lower Miocene–Pliocene of Australia (Jenkins, 1975), and *Icriocarcinus xestos* Bishop, 1988 from the upper Campanian or lower Maastrichtian of California, USA (Bishop, 1988; Schweitzer *et al.*, 2007) and longusorbiid *Longusorbis cuniculosus* Richards, 1975 from the upper Campanian to lower Maastrichtian of British Columbia, Canada (Richards, 1975).

The most complex burrow systems are constructed by members of the former Thalassinidea which was subdivided into two independent infraorders, Axiidea and Gebiidea (Robles *et al.*, 2009). Extant members of the Laomedidae, Thalassinidae and Upogebiidae (Gebiidea), and of Axianassidae and Callianassidae (Axiidea) are known to construct very complex burrow systems which can reach more than 1 metre in depth.

The paucity of remains of “thalassinideans” found within their

burrows was already emphasized by Feldmann and Zinsmeister (1984), Stilwell *et al.* (1997), and Bishop and Williams (2005).

There are several reports of *Upogebia* body fossils associated with burrow structures (Karasawa and Inoue, 1992; Kato and Koizumi, 1992; Ando and Karasawa, 2010). Fraaije *et al.* (2006) reported two species of *Upogebia* preserved in nodules interpreted as parts of burrows. The only unequivocal record of body fossils of *Upogebia* in burrows is that from the Miocene of Japan (Kato, 1996).

Murray and Hanley (1986) gave an account of the famous Australian subfossil mudlobster of the genus *Thalassina* which is preserved in great numbers. They interpreted them as moults which underwent rapid carbonate permineralization within the burrows.

The families Ctenochelidae and Callianassidae are sometimes very difficult to distinguish one from another, especially when exclusively dealing with fragmented chelipeds.

Of the family Ctenochelidae, Glaessner (1947) described *Ctenocheles bakeri* (Glaessner, 1947) from the Eocene of Australia associated with burrows. Later Rasmussen (1971) reported *Ctenocheles* sp. from the lowermost Paleocene of Denmark associated with burrows and Kato (1996) similarly described an assemblage of *Callianopsis* spp. from the Miocene of Japan. Shinn (1968, Pl. 111, Fig. 3) figured a complete specimen of “a shrimp, the presumed architect, preserved in the burrow”, from Texas. It is remarkably similar to *Gourretia aquilae* (Rathbun, 1935) from the Turonian of Mexico (Vega *et al.*, 2007). Both occurrences are from the same lithostratigraphic unit (Eagle Ford Group), and may therefore be conspecific.

There are several reports of callianassids preserved within their burrow structures. *Protocallianassa faujasi* (Desmarest, 1822)

Table 1. Occurrences of fossil callianassid remains preserved within burrow structures or associated with burrows.

Taxon	Age	Country	Remarks	Major reference
<i>Protocallianassa antiqua</i>	Turonian	Czech Republic	associated with burrows	Kříž and Čech, 1974
<i>Protocallianassa</i> ex aff. <i>antiqua</i>	Senonian	Germany	in a burrow	Mertin, 1941
<i>Protocallianassa faujasi</i>	Maastrichtian	Netherlands	in burrows	Swen <i>et al.</i> , 2001
<i>Protocallianassa faujasi</i>	Campanian	Germany	in burrows	Mourik <i>et al.</i> , 2005
<i>Protocallianassa faujasi</i>	Santonian	Germany	associated with burrows	Förster, 1973
<i>Protocallianassa faujasi</i>	Cenomanian	Czech Republic	claw fragment in a burrow	Veselská, 2009
<i>Protocallianassa faujasi</i>	Cenomanian	Czech Republic	associated with burrows	Veselská, 2009
<i>Protocallianassa mortoni</i>	Campanian	Delaware (USA)	associated with burrows	Picket <i>et al.</i> , 1971
<i>Callichirus waagei</i>	Maastrichtian	South Dakota (USA)	cheliped in a burrow	Crawford <i>et al.</i> , 2006
<i>Callichirus symmetricus</i>	Eocene	Antarctica	in burrows	Schweitzer and Feldmann, 2000
<i>Neocallichirus rhinos</i>	Eocene	Mexico	in a burrow	Schweitzer and Feldmann, 2002
<i>Vegarhron santiago</i>	Eocene	Mexico	in a presumed burrow	Schweitzer and Feldmann, 2002
<i>Podocallichirus grandis</i>	Pleistocene	Japan	in burrows	Karasawa <i>et al.</i> , 2006
“ <i>Callianassa</i> ” <i>almerai</i>	Miocene	Austria	in burrows	this paper
“ <i>Callianassa</i> ” <i>burckhardtii</i>	Maastrichtian–Danian	Argentina	associated with burrows	Feldmann <i>et al.</i> , 1995
“ <i>Callianassa</i> ” <i>pseudorakosensis</i>	Miocene	Slovakia	in supposed burrows	this paper
“ <i>Callianassa</i> ” <i>?pseudorakosensis</i>	Miocene	Poland	associated with burrows	Radwański and Wysocka, 2004
“ <i>Callianassa</i> ” sp.	Campanian	Texas (USA)	claw fragment in a burrow	Beikirch and Feldmann, 1980
“ <i>Callianassa</i> ” sp.	Eocene	USA	in burrows	Bishop and Whitmore, 1986
“ <i>Callianassa</i> ” sp. 1	Miocene	Hungary	in a burrow	this paper
“ <i>Callianassa</i> ” sp. 2	Miocene	Hungary	in a burrow	this paper
“ <i>Callianassa</i> ” sp.	Miocene	Austria	claw fragment in a burrow	Ehrenberg, 1938

preserved *in situ* was noted by several authors from the Upper Cretaceous of Germany, the Netherlands and the Czech Republic (Förster, 1973; Swen *et al.*, 2001; Mourik *et al.*, 2005; Veselská, 2009). Two species of *Callichirus* were described from *in situ* occurrences in the Maastrichtian of South Dakota (Crawford *et al.*, 2006) and the Eocene of Antarctica (Stilwell *et al.*, 1997; Schweitzer and Feldmann, 2000). One more *in situ* Eocene occurrence is known (*Neocallichirus rhinos* Schweitzer and Feldmann, 2002) from Mexico. Schweitzer and Feldmann (2002) also recorded *Vegarthon santiago* Schweitzer and Feldmann, 2002 from the Eocene of Mexico preserved in a presumed burrow structure. So far, from Miocene strata there has been a single record of *in situ* callianassid remains by Ehrenberg (1938). He reported a claw fragment preserved at the blind end of a tunnel, which was a part of a burrow system from the lower Miocene of Austria. The present paper describes several additional examples from Austria, Hungary, and Slovakia.

All occurrences of Callianassidae preserved within burrow structures or associated with burrows known to the author, inclusive of the ones reported herein are summarized in Table 1.

Geological and geographical settings

The material presented herein comes from several localities (Fig. 1):

1. Styrian Basin – Retznei quarry in Austria (Steiermark), where strata of the Weissen-egg Formation are exposed. The age is early “Badenian” (Langhian). For sedimentological details see Friebe (1990). Decapod remains of several species were reported by Schoupe (1949) and Flügel (1986); however, a large portion of the decapod fauna present has not yet been described.
2. Vienna Basin – the Dúbravská hlavica locality in Slovakia (vicinity of Bratislava), where strata of the Sandberg Member (Studienka Formation) crop out, their age being late “Badenian” (early Serravallian). For details on sedimentology see Baráth *et al.* (1994).

3. Danube Basin – the Gyakorló and Rákos localities in Hungary (Budapest area), where strata of the Rákos Formation are exposed, whose age is late “Badenian” (early Serravallian). For sedimentological data and details on the associated decapod fauna, see Müller (1984) and references cited therein.

Palaeogeographically, all localities were situated within the Central Paratethyan Sea during the middle Miocene. For details of the current status of Miocene Central Paratethys stratigraphy reference is made to paper by Piller *et al.* (2007). For details of the palaeogeography and palaeobiogeography of the Central Paratethys see Harzhauser and Piller (2007) and references cited therein.

Middle Miocene Callianassidae of the Central Paratethys

To date, some thirteen species of Callianassidae have been identified in middle Miocene strata of the Central Paratethys (see Table 2). Some species have also been reported from other European regions; however, these are not included here. The list shows the relative diversity of Callianassidae within the same palaeogeographical area during roughly the same time (i.e., middle Miocene). The list should be considered preliminary because it includes only occurrences mentioned in the literature or examined personally.

According to personal observation it can also be stated that many of the species listed can be accommodated within genera other than *Callianassa* Leach, 1814 (*sensu* Ngoc-Ho, 2003), thus, representing a mixture of several independent genera in several subfamilies of the Callianassidae. However, such reassignment is beyond the scope of the present contribution and will be considered elsewhere. Therefore, the material presented herein is treated under “*Callianassa*” as a *nomen collectivum* in the broadest sense.

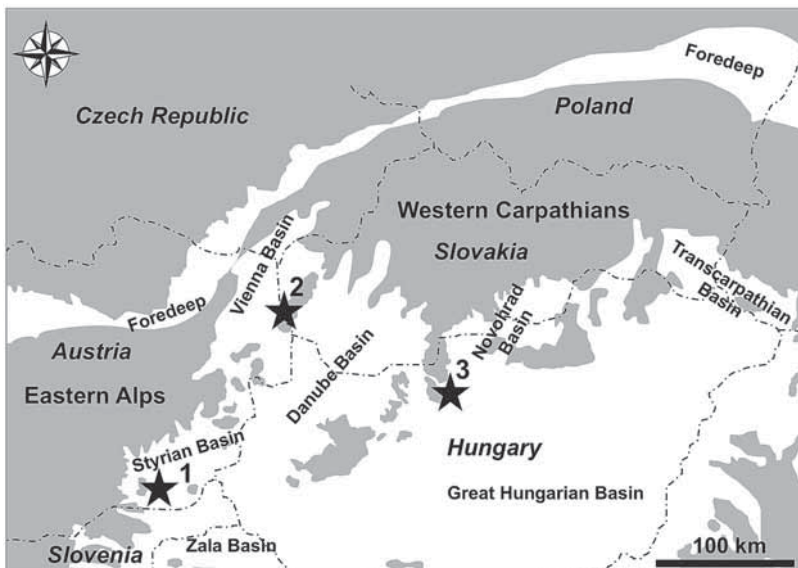


Fig. 1. Map showing the position of the study area in the Carpathian–Pannonian Basin complex of the Central Paratethys (modified from Harzhauser *et al.*, 2003). In grey are pre-Neogene sediments and basement. Localities studied: 1 – Retznei (Styrian Basin), 2 – Dúbravská hlavica (vicinity of Bratislava), 3 – Rákos and Gyakorló (Budapest area).

Table 2. Middle Miocene occurrences of Callianassidae reported from the Central Paratethys (occurrences reported in open nomenclature as “*Callianassa*” sp. are not included).

Taxon	Geographic distribution within the CP area	Major reference
“ <i>Callianassa</i> ” <i>almerai</i> Müller, 1993	Austria (Styrian Basin)	Müller, 1993
“ <i>C.</i> ” <i>brocchi</i> Lörenthey, 1898	Hungary (Budapest area), Slovakia (Vienna Basin)	Müller, 1984
“ <i>C.</i> ” <i>chalmasii</i> Brocchi, 1883	Hungary (Budapest area)	Müller, 1984
“ <i>C.</i> ” <i>floriana</i> Glaessner, 1928	Austria (Styrian Basin)	Glaessner, 1928
“ <i>C.</i> ” <i>kerepesiensis</i> Müller, 1976	Hungary (Budapest area, Novohrad Basin)	Müller, 1984
“ <i>C.</i> ” cf. <i>kerepesiensis</i> Müller, 1976	Hungary (Budapest area), Poland (Carpathian Foredeep)	Müller, 1984
“ <i>C.</i> ” <i>munieri</i> Brocchi, 1883	Hungary (Budapest area), Austria (Vienna Basin., Styrian Basin)	Müller, 1984
“ <i>C.</i> ” <i>norica</i> Glaessner, 1928	Austria (Styrian Basin)	Glaessner, 1928
“ <i>C.</i> ” <i>pseudorakosensis</i> Lörenthey in Lörenthey & Beurlen, 1929	Hungary (Budapest area, Novohrad B.), Romania (Gr. Hungarian B.), Slovakia (Vienna Basin), Poland (Carpathian Foredeep)	Müller 1984
“ <i>C.</i> ” cf. <i>pseudorakosensis</i> Lörenthey in Lörenthey & Beurlen, 1929	Austria (Styrian Basin)	Glaessner, 1928; Müller, 1998
“ <i>C.</i> ” <i>roztoczensis</i> Müller, 1996	Poland (Lublin Upland), Hungary (Budapest area)	Müller, 1996
“ <i>C.</i> ” <i>sismondai</i> A. Milne-Edwards, 1860	Austria (Styrian Basin)	Glaessner, 1928
“ <i>C.</i> ” <i>szobensis</i> Müller, 1984	Hungary (Börzsöny Mts.)	Müller, 1984
<i>Callichirus bertalani</i> Hyžný and Müller, 2010	Hungary (Bakony Mts.)	Hyžný and Müller, 2010

In situ preservation

The material presented herein is deposited in the collections of the Natural History Museum of Slovak National Museum in Bratislava, Slovakia (SNM Z) and of the Hungarian Natural History Museum at Budapest, Hungary (M), as well as in the private collections of Miroslav Hornáček at Smolenice, Slovakia (MH), Pál Müller at Budapest (PM) and Gerhard Wanzenböck at Bad Vöslau, Austria (GW).

Bishop and Williams (2005), in their review on taphonomy of “thalassinidean” shrimps, used several terms which mirrored the nature of their body fossil preservation. Body fossils preserved as parts of burrows in the form of button-like disks were referred to as burrow buttons (Bishop and Williams, 2005: 219). The material presented herein is, however, preserved within these parts of the burrows which can clearly be identified as trace fossils. Their shape is not button-like, it rather corresponds with the real shape of a burrow. Therefore, in such cases I use the term “burrow structure”, and intentionally avoided using ichnotaxonomic determination as nearly all the material was not collected by myself and in most specimens the position of the burrow structure in the section can no longer be precisely determined.

“*Callianassa*” *almerai* Müller, 1993 (Figs. 2A–G, 3A–D)

The material comprises at least five individuals apparently preserved within their burrow structures and several other fragmentary specimens from the Retznei quarry (Styrian Basin). Specimens preserved inside the burrows are represented by articulated chelipeds (cheliped disassociation unit *sensu* Bishop and Williams, 2005), so the characters of ischium, merus, carpus, propodus and dactylus can be observed (Figs. 2, 3). Remains of both major and minor chelipeds are preserved in two cases (GW RET04-010, GW RET01-014, Figs. 2E, 3B). In a single case, two specimens are preserved within one and the same burrow structure

(Fig. 3B). Both of them are oriented in the same direction. In three cases (GW RET93-021, GW RET04-010, GW RET01-014; Figs. 2B–F, 3A–B) individuals are preserved on one side of the burrow structure, so probably the fossils are seen from the underside. A similar preservation style was reported by Mourik *et al.* (2005). One specimen (GW RET05-011, Fig. 2G) represents a propodus positioned at right angle with the burrow structure. Another one (GW RET96-009, Fig. 3D) is preserved in the middle of the burrow tube. For this specimen it is clear that the cheliped of an individual did not lie on its side during the process of fossilization, suggesting that rather might be a live animal that was buried. Similarly, in one propodus a geopetal texture (sparite) can be observed (GW RETXX-017, Fig. 3C) documenting that the specimen did not lie on its side either when fossilized.

The burrow structures are preserved in carbonate facies. Their cross section is rounded (Fig. 2), although in one specimen it is rather elliptical (GW RET01-014, Fig. 3A).

The species “*Callianassa*” *almerai* was until recently known only from the middle Miocene of Spain (Müller, 1993). The present report extends its geographic distribution to Austria, i.e., to the Central Paratethys.

Material described by Müller (1993) comprises a dozen or so specimens represented by isolated propodi only. He reported remains of both right and left major chelae and erroneously interpreted the species to be isochelous. However, in axiideans both right- and left-handed individuals occur and “*C.*” *almerai* is no exception. Material from Retznei documents specimens with both chelipeds preserved and, indeed, minor chelae are also present (Figs. 2E, 3B). This also allows assignment of two propodi which were described and figured by Müller (1993) as “*Callianassa*” sp. and which come from the same locality as “*C.*” *almerai*. Their morphology corresponds with that of minor chelipeds of “*C.*” *almerai* reported herein.

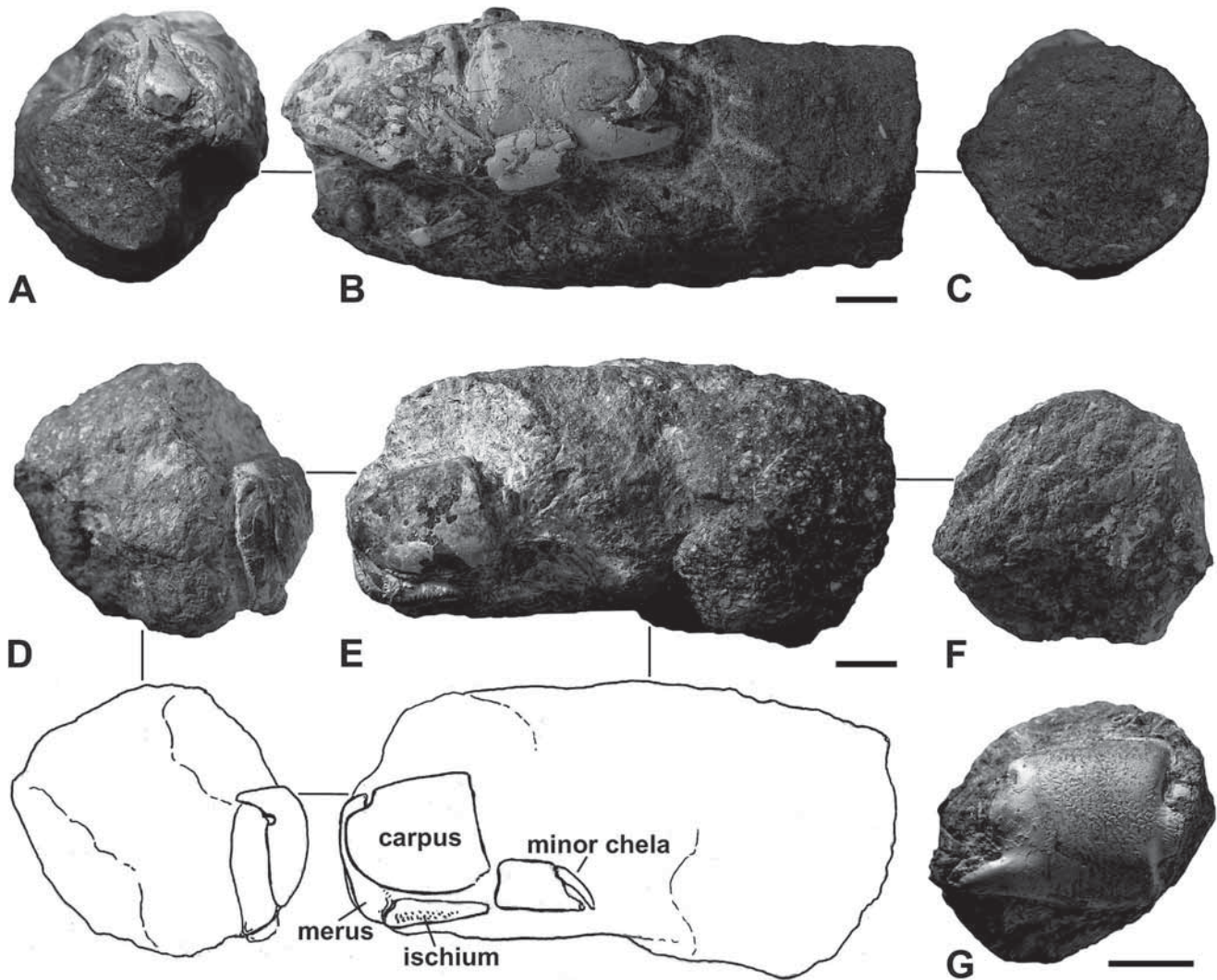


Fig. 2. “*Callianassa*” *almerai* Müller, 1993: A–C – a near-complete right major cheliped with the remains of the minor one within the burrow structure (GW RET93-021); D–F – remains of the right major (ischium, merus and carpus preserved) and left minor cheliped within a burrow structure (GW RET04-010); G – an isolated left major propodus preserved perpendicular to the burrow structure (GW RET05-011). Note the rounded cross section of the burrows. All specimens come from the Retznei quarry (Styrian Basin, Austria). All scale bars represent 10 mm.

“*Callianassa*” *pseudorakosensis* Lörenthey in Lörenthey and Beurlen, 1929 (Figs. 4A, B)

The material consists of several burrow structures with preserved animal remains from the Dúbravská hlavica locality in the vicinity of Bratislava. In one case the articulated remains of three individuals are preserved (SNM-Z-21.373, Fig. 4A), in the other case two individuals are present (MH specimen, Fig. 4B). Both chelipeds together with scattered remains of other pereiopods are preserved of one individual (Fig. 4A), which can be characterized as cheliped and thoracopod disassociation units *sensu* Bishop and Williams (2005). Interestingly, individuals are oriented in the same direction in both depicted specimens. 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).

Many more specimens of this species preserved with scattered remains of pereiopods in close association with chelipeds as

burrow buttons *sensu* Bishop and Williams (2005) were collected from the locality.

The burrow structures are preserved in a poorly consolidated sandstone. Their cross section is difficult to determine; however, the mode of preservation of the individuals suggests preservation within the burrow (Bishop and Williams, 2005).

At the locality very abundant remains of “*Callianassa*” *brocchi* Lörenthey, 1898 co-occur with very rare *Calappa heberti* Brocchi, 1883.

“*Callianassa*” *pseudorakosensis* is very common in the area of the Central Paratethys. Up to now it has been reported from Hungary (Lörenthey and Beurlen, 1929; Müller, 1984), Romania (Müller, 1984), Austria (Müller, 1998), and Slovakia (the present contribution). Recently, Radwański and Wysocka (2004) reported a single chela associated with *Ophiomorpha* from the middle Miocene of Poland. However, the morphology of that specimen is rather unusual for “*C.*” *pseudorakosensis*, so it might represent

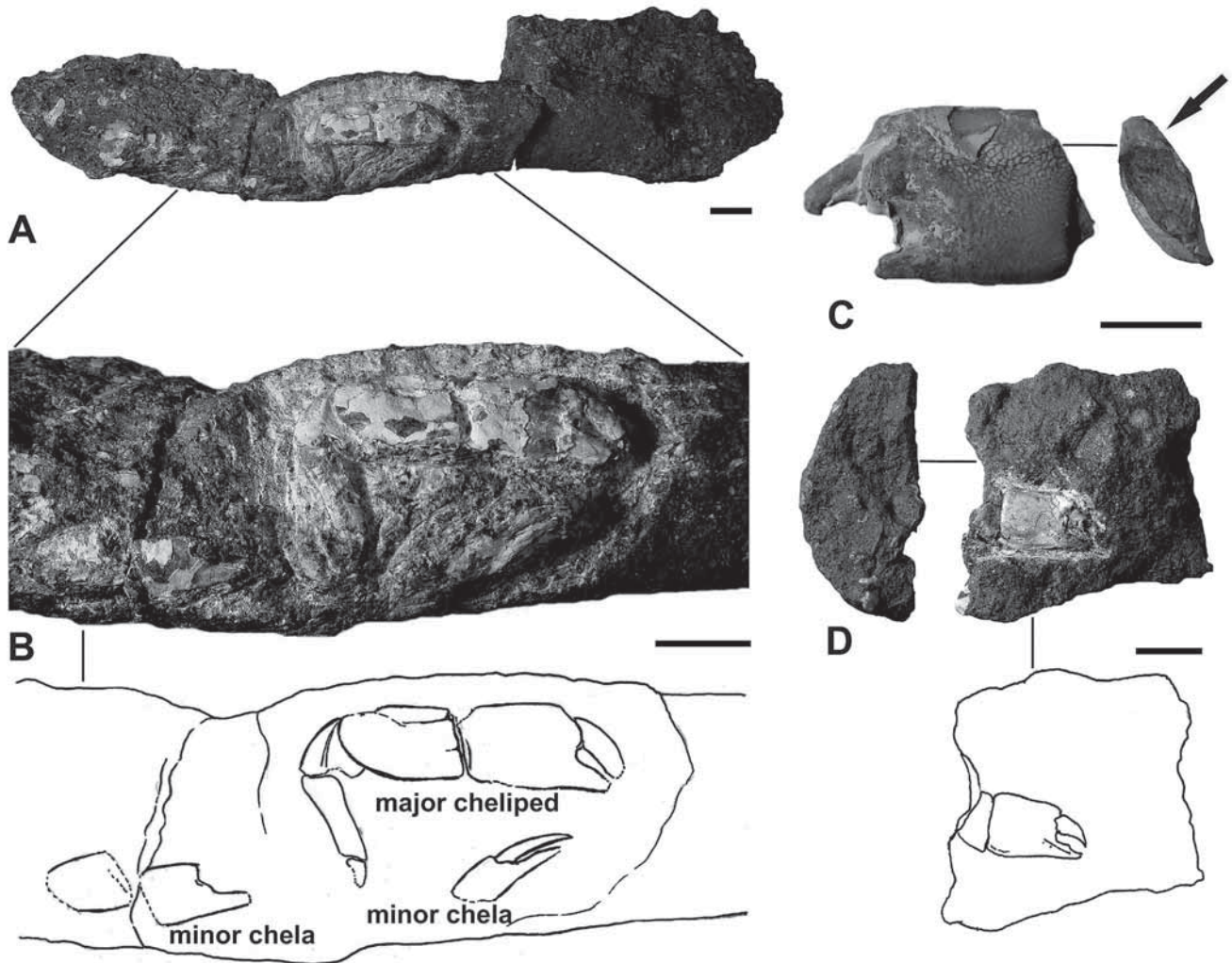


Fig. 3. “*Callianassa*” *almerai* Müller, 1993: A–B – two individuals preserved within the same burrow structure (GW RET01-014), note propodi of minor chelipeds as indicated in the interpretive drawing; C – an isolated left major propodus (GW RETXX-017) with geopetal texture (sparite) in its upper part (black arrow); D – remains of a left major cheliped preserved within a burrow structure (GW RET96-009). All specimens come from the Retznei quarry (Styrian Basin, Austria). All scale bars represent 10 mm.

another species.

“*Callianassa*” sp. 1 (Figs. 4C, D)

The material from the locality Rákos MR8 (sensu Müller, 1984) represents one burrow structure with a preserved fragment of propodus inside it (M 2010.511.1.1; Figs. 4C, D). The cross section of the burrow is elliptical. The same shape was also observed in other burrow structures (without any fossilized inhabitants) collected from the same locality (pers. observation).

Because of the fragmentary nature of the specimen, specific identification is impossible.

“*Callianassa*” sp. 2 (Figs. 4E, F)

The material from the locality Gyakorl6 (in the Budapest area) represents one burrow structure with the remains of two individuals (PM specimen, Figs. 4E, F). The burrow structure is preserved in a sandstone. Its cross section is elliptical (Fig. 4F); however, compaction cannot be ruled out.

The material is too fragmentary for specific identification, although it should be mentioned that one individual possessed equal or subequal chelipeds (not visible on figures). Such chelipeds are known for instance in the genera *Eucalliax* Manning and Felder, 1991 or *Calliaxina* Ngoc-Ho, 2003 of the subfamily Eucalliinae. However, without more complete material a generic assignment is impossible.

At both Hungarian localities mentioned herein several species of Callianassidae have been recorded (for details see Müller, 1984).

Discussion and conclusions

The material presented herein represents very rare occurrences of fossil callianassids preserved *in situ* within their burrows. As stated by Bishop and Williams (2005), callianassids might enter the preservation process as corpses, moults or disassociation units. They regarded most mortality of these animals as “resulting from drastic causes such as voluminous shifting sediments, poisoning by

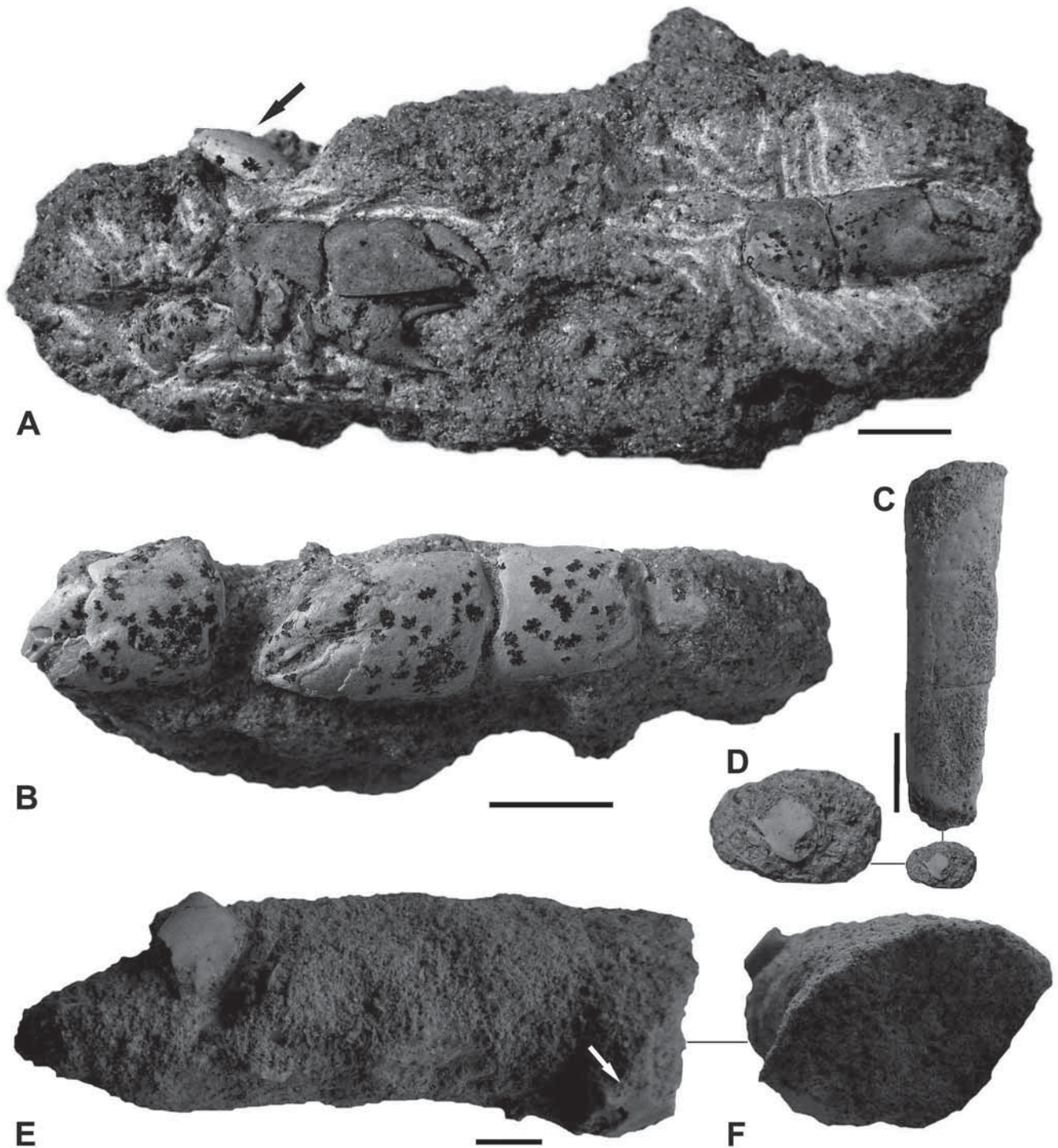


Fig. 4. “*Callianassa*” *pseudorakosensis* Lórenthey in Lórenthey and Beurlen, 1929: A – three individuals within the same burrow structure (SNM-Z-21.373), note the propodus in oblique view indicated by a black arrow; B – remains of major chelipeds of two individuals within the same burrow structure (MH specimen). “*Callianassa*” sp. 1: C–D – a burrow structure with a fragment of propodus preserved inside it (M 2010.511.1.1). “C.” sp. 2: E–F – propodi of two individuals within a burrow structure (PM specimen), note the propodus indicated by a white arrow. Localities: A, B – Dúbravská hlavica (Vienna Basin, Slovakia), C, D – Rákos (Budapest area, Hungary), E, F – Gyakorlói (Budapest area, Hungary). All scale bars represent 10 mm.

red tides, or severe and prolonged changes in oxygen levels, salinity, etc.” (Bishop and Williams, 2005: 224). In general it is assumed that members of the Callianassidae moult and die within their burrow systems, however, often it is virtually impossible to recognize moults from corpses.

It can be assumed that there are two main types of preservation

in the material described and figured herein:

1) preservation of supposedly dead animals or moults lying on their side when entering the fossilization process. They are preserved on one side of the burrow structures, so when observed the underside is seen. The remains sank down with the heaviest exoskeleton part, the large cheliped, to the bottom of the burrow

tunnel, so the large claw is always visible. This is the case in material of “*C.*” *almerai* (Figs. 2A–F; 3A, B) and “*C.*” *pseudorakosensis* as well (4A, B). Roughly the same mode of preservation when the tracemaker is preserved on the side of a burrow (i.e. at its bottom) was reported and figured by Mertin (1941: Fig. 30.1), Shinn (1968: Pl. 111, Fig. 3), Swen *et al.* (2001: Figs. 5.5, 5.6), and Mourik *et al.* (2005: Pl. 2).

2) preservation of animals in the middle of the burrow. Some specimens of “*C.*” *almerai* (Figs. 2G, 3D) and “*Callianassa*” sp. 1 (Figs. 4C, D) represent cheliped fragments which are not preserved on the side of the burrow structure. In one case (Fig. 3D) the cheliped is positioned in the burrow longitudinally in its centre. It may represent an animal which was buried alive, however, the fragmentary nature of the specimen does not allow further speculation. Preservation of cheliped parts positioned at right angles to the burrow tunnel (Figs. 2G, 4C, D) may indicate a vertical or subvertical shaft of a burrow or a horizontal or subhorizontal tunnel filled with debris together with exoskeleton remains. Unless the exact position of a preserved burrow tube within the section which yielded them is known, no further conclusions can be drawn. Unfortunately, this information is unavailable in the case of the specimens presented herein.

The preservation of several *in situ* individuals in the same direction has already been reported in *Protocallianassa faujasi* (Desmarest, 1822) from the lower Campanian of Germany (Mourik *et al.*, 2005). They interpreted them as remains of presumably dead animals, although there are difficulties to explain how such an arrangement can originate. They hypothesized that the dead individuals were carried away and stored in dead-end tunnels by living ones. Such systematic removal of exoskeletal fragments (moulted or corpses) into disposal chambers that subsequently may be closed off was mentioned also by Bishop and Williams (2005); however, this behaviour has never been directly observed in extant species (P. Dworschak, pers. comm., 2010). Unfortunately, the material presented herein cannot shed new light on this issue due to the imperfect preservation and limited samples.

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