

Decapod Crustacea of the Central Paratethyan Otnangian Stage (middle Burdigalian): implications for systematics and biogeography

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Abstract: Decapod crustaceans from the Otnangian (middle Burdigalian, Lower Miocene) of the Western and Central Paratethys remain poorly known. In this study, we review and re-describe mud shrimps (*Jaxea kuemeli*), ghost shrimps (*Gourretia* sp., *Calliax michelottii*) and brachyuran crabs of the families Leucosiidae, Polybiidae and Portunidae. A dorsal carapace of the genus *Calliax* is reported for the first time in the fossil record. Re-examination of the type material of *Randallia strouhali* (Leucosiidae) and *Geryon otnangensis* (Geryonidae) resulted in a transfer of these species into *Palaeomyra* (Leucosiidae) and *Liocarcinus* (Polybiidae), respectively. *Achelous vindobonensis*, originally described as a chela of a portunid crab, probably belongs to a member of Polybiidae and is provisionally treated as *Liocarcinus* sp. Only two species, *J. kuemeli* and *C. michelottii*, are also known from the Karpatian, the succeeding Paratethyan stage. In most cases, the decapod assemblages of the Otnangian consist of rather shallow-water taxa whereas the assemblages of the Karpatian consist of deep-water taxa from the middle and outer shelf. The Central Paratethyan assemblages show similarities in genus composition to the Proto-Mediterranean and recent Indo-Pacific regions. *Gourretia* sp. represents the earliest occurrence of the respective genus in the fossil record. The Oligocene–Early Miocene appearance of *Palaeomyra* and *Liocarcinus* in the circum-Mediterranean implies that sources of present-day diversity hotspots in the Indo-Pacific trace to the Western Tethys (as for other decapod genera), although coeval decapod assemblages in the Indo-Pacific remain poorly known.

Key words: Crustacea, Decapoda, Central Paratethys, Otnangian, Early Miocene.

Introduction

Since the Mesozoic, decapod crustaceans have been increasingly significant components of marine benthic invertebrate associations of the continental shelf and slope (Glaessner 1969; Feldmann 2003; Klompmaker et al. 2013; Noël et al. 2014). Especially brachyuran crabs are among the most successful of all malacostracan crustacean groups in terms of number of ecological niches (Warner 1977; Schram 1986; Taylor & Schram 1999) and sheer number of species (Ng et al. 2008; De Grave et al. 2009; Schweitzer et al. 2010). During the Miocene, one of the major decapod diversification events occurred (Schweitzer 2001; Feldmann & Schweitzer 2006). In the Western Tethys area this was enhanced by the biogeographical differentiation at that time resulting in two different paleogeographical areas, circum-Mediterranean and Paratethys (Rögl 1998, 1999; Harzhauser et al. 2002; Harzhauser & Piller 2007), and leading to complex migration patterns in marine benthic associations (Studencka et al. 1998; Kroh & Harzhauser 1999; Harzhauser et al. 2003, 2007, 2008; Moissette et al. 2006; Kocsis et al. 2012).

In the second half of the 20th century, Miocene decapod crustacean assemblages of the Western and Central Paratethys were studied by Friedrich Bachmayer (Bachmayer

1950, 1953a,b,c, 1954, 1962, 1982; Bachmayer & Tollmann 1953), Reinhard Förster (Förster 1979a,b) and Pál Müller (Müller 1984, 1996, 1998a, 2006). Recently a renewed interest in these faunas provided new data on Ukraine (Radwański et al. 2006; Ossó & Stalennuy 2011), Slovenia (Mikuž 2003, 2010; Mikuž & Pavšič 2003; Gašparič & Hyžný 2014) and Slovakia (Hyžný 2011a,b,c; Hyžný & Schlögl 2011; Hyžný & Hudáčková 2012), as well as new insights into the taxonomy of Central Paratethyan ghost shrimps (Hyžný 2012; Hyžný & Müller 2010, 2012; Hyžný & Gašparič 2014; Hyžný & Dulai 2014). However, most of the work has been done on Badenian material (see Müller 1984 for an overview) because the Middle Miocene Badenian (=Langhian and lower Serravallian) sediments are exposed to a great extent in Austria, Slovakia, Hungary, Poland and Ukraine (Rasser & Harzhauser 2008). In contrast, only a few outcrops exposing good sedimentological record of Otnangian and Karpatian deposits exist. Müller (1998a) described a small Karpatian assemblage from the Korneuburg Basin (Austria) and recently, Hyžný & Schlögl (2011) and Gašparič & Hyžný (2014) described Karpatian deep-water (epibathyal) decapod crustacean assemblages from the Slovak part of the Vienna Basin and the Slovenian part of the Styrian Basin. Decapods from the Otnangian strata were re-

ported by Bachmayer (1953a, 1982) and briefly summarized by Müller (1998b).

The present contribution aims: 1) to provide a systematic overview of all decapods from the Otnangian stage, including the re-examination of older material of Bachmayer (1953a) and report on previously undescribed specimens including new localities with decapod occurrences, and 2) to discuss the paleobiogeographic affinities of the decapod assemblages and implications for their evolutionary patterns.

Geological setting

The material derives largely from the North Alpine Foreland Basin (NAFB) and partly from the Vienna Basin (VB). During the early and middle Otnangian, the NAFB was part of a marine gateway, referred to as the Burdigalian Seaway (Allen et al. 1985). This strait connected the western Proto-Mediterranean Sea with the Central Paratethys and was characterized by extensive shelf areas bordered by the advancing Alpine thrust front. Along the northern shelf, widespread tidal deposits developed under meso- and macrotidal conditions (Pippèrr 2011; Grunert et al. 2012). At that time, the Vienna Basin had not formed yet and the area was part of the junc-

tion between the NAFB and the Carpathian Foreland Basin (Kováč et al. 2004), characterized by offshore deposits of “Schlier”-type. As a result of the uplift of the NAFB, the marine connections ceased and fluvial-lacustrine environments of the Upper Freshwater Molasse were established in the western NAFB (Berger 1996; Reichenbacher et al. 2013) during the late Otnangian. No decapod remains are known from that phase. The decapod crustaceans reviewed here come from several localities (Fig. 1):

Neuhofen bei Tettenweis (Bavaria, Germany) — NAFB, early Otnangian: This is the type locality of the Neuhof Beds (Neuhofener Schichten). It consists of clayey to fine-grained sandy marls (Doppler et al. 2005). The Neuhof Beds in the Eastern Molasse are the equivalent of the Kalkofen Formation in the Western Molasse, and their age is early Otnangian (Heckeberg et al. 2010). Based on foraminifer-assemblages, Pippèrr (2011) assumed deposition on the outer shelf for the Neuhof Beds.

Otnang/Schanze (Upper Austria) — NAFB, early Otnangian: This section has been chosen as the stratotype for the regional Otnangian stage by Rögl et al. (1973). It is part of an abandoned clay pit near a memorial to the Peasant Wars (called “Schanze”) and has been declared a natural heritage site. Recently it was revised by Grunert et al. (2010a,



Fig. 1. Geographic position of the studied localities (triangles). Neogene basins in grey (a) and white (b). Maps modified after Grunert et al. (2010a) and Kroh (2005).

2012), who proposed an age of 17.95–18.056 Ma for the section. The section is about 10 m-thick and exposes clayey silts and clayey-sandy silts with sandy lenses and flaser bedding passing into mollusc-rich and bioturbated pelitic sediments. The analysis by Grunert et al. (2012) revealed a eutrophic environment at the transition from a suboxic outer shelf to upper bathyal towards a better oxygenated middle shelf environment under the influence of storm events and tidal currents.

Allerding (Upper Austria) — NAFB, early Ottnangian: The Allerding locality is situated in the quarry of the Schärddinger Granit Industrie AG close to Schärdding in Upper Austria. At this quarry, the Moldanubian Schärdding Granite is exploited. It is part of the NW-SE trending margin of the Bohemian Massif, which also formed the coast of the western Central Paratethys during most of the Early Miocene. The granite is overlain by a few meters of Ottnangian deposits (Harzhauser et al. 2014). The presence of coastal boulders and the mollusc assemblages suggest a rocky shore, which quickly became sealed by blue-grey pelitic “Schlier” during a major transgression (Harzhauser et al. 2014).

Grosswiesenhart (Upper Austria) — NAFB, early Ottnangian: The material derives from the clays of a claypit at St. Marienkirchen close to Schärdding. Little paleontological information is available for the section aside from a note on the occurrence of the dogfish shark *Isistius* Gill, 1865 in Schultz (2013). According to the geological map (Rupp 2008) the section is part of the lower Ottnangian Ottnang Formation. The depositional environment was most probably shelfal but no details are known to us.

Limberg (Lower Austria) — NAFB, early Ottnangian: The Limberg locality exposes a few meters of finely laminated diatomites and clays of the Limberg Member at the base of the pelitic Zogelsdorf Formation. The section was studied by Roetzel et al. (1996) and Grunert et al. (2010b), who documented upwelling conditions in a distal-shelf environment with nutrient-rich waters established during the early Ottnangian along the steep escarpment of the Bohemian Massif in the eastern NAFB.

Ort im Innkreis (Upper Austria) — NAFB, early Ottnangian: The outcrop exposes “Schlier” deposits, namely clayey silts and clays-sandy silts, which are a part of the lower Ottnangian Ottnang Formation according to the geological map (Krenmayr & Schnabel 2006; Rupp 2008). The depositional environment was most probably shelfal but no details are known to us.

Peterskirchen (Upper Austria) — NAFB, middle Ottnangian: A single specimen in the NHMW collections was found in one of the clay pits at Peterskirchen, which expose light-grey to greenish-grey marly clays and silts (Ćorić 1998). These deposits are part of the middle Ottnangian Ried Formation (Rupp 2008) and formed in an inner shelf environment under low-energy with high abundance of *Ammonia* Brünnich, 1772 (Rupp & van Husen 2007).

Antiesen bluff (Upper Austria) — NAFB, middle Ottnangian: The Ottnang Formation is overlain by mica-rich sand with cross bedding and pelitic intercalations of the middle Ottnangian Reith Formation (Rupp 2008). These are well exposed along the banks of the Antiesen river, 1.7 km SE of

Antiesenhofen. The decapods were collected from these pelitic intercalations. The microfauna is dominated by *Ammonia* and the depositional environment was interpreted by Rupp & van Husen (2007) and Rupp (2008) as a tidal-influenced inner shelf setting.

Pramhof at Schärdding (Upper Austria) — NAFB, early or middle Ottnangian: Little information is available for this locality. According to the geological map (Rupp 2008), the section is part of the lower Ottnangian Ottnang Formation. C. Rupp (pers. comm.), however, pointed out that remnants of the middle Ottnangian Ried Formation also exist in the area. Decapod specimens are preserved in the pelitic “Schlier”, however, it cannot be decided from which formation they actually come.

Grosskrut 3 (Lower Austria) — VB, middle Ottnangian: This is the only locality in the Vienna Basin — the material derives from a core (depth 500 m), which drilled into the Ottnangian Lužice Formation. The sample with a decapod corresponds to the typical lithology of the Lužice Formation, with laminated grey calcareous clays, silt and siltstones with intercalations of sands. The decapod sample was collected from silty clay. The Lužice Formation indicates open marine shelf settings with widespread dysoxic bottom conditions (Kováč et al. 2004).

Material and methods

Studied material comes either from older collections (GBA, KM, NHMW) or was newly collected by one of us (WD). Preparation, if needed, was done with a pneumatic needle. Specimens were photographed either dry and uncoated or covered with ammonium chloride sublimate.

The repositories of specimens illustrated or referred to below are as follows:

GBA — Geological Survey, Vienna (Austria)

NHMW — Natural History Museum, Vienna (Austria)

KM — Krahuletz-Museum, Eggenburg (Austria).

Systematic paleontology

Order: **Decapoda** Latreille, 1802

Infraorder: **Gebiidea** de Saint Laurent, 1979

Family: **Laomediidae** Borradaile, 1903

Genus *Jaxea* Nardo, 1847

Type species: *Jaxea nocturna* Nardo, 1847, by original designation.

Diagnosis: See Ngoc-Ho (2003; p. 501).

Remarks: The fossil record of the genus has recently been revisited by Hyžný (2011c). He showed that the tooth formula and general cheliped shape is more-or-less constant and on its basis the identification to species level can successfully be made. Two extant species, *Jaxea nocturna* Nardo, 1847 from the Mediterranean and adjacent European seas (Ngoc-Ho 2003) and *J. novaezealandiae* Wear & Yaldwyn, 1966 from New Zealand (Wear & Yaldwyn 1966), differ markedly in their tooth formula. The only fossil species,

J. kuemeli Bachmayer, 1954 appears to be much closer to the Mediterranean species (Hyžný 2011c).

Jaxea kuemeli Bachmayer, 1954
Figs. 2–3

- v*1954 *Jaxea kumeli* Bachmayer, 1954, p. 64, pl. 1, figs. 1, 2
1969 *Jaxea kuemeli* Bachmayer — Glaessner, p. R477, fig. 284.4a, 4b
1984 *Jaxea kuemeli* Bachmayer — Müller, p. 49
1998 *Jaxea kumeli* Bachmayer — Mayoral et al., p. 508
2011c *Jaxea kuemeli* Bachmayer — Hyžný, p. 176 figs. 2A–D, 3B, 4A–C, 5A–C, 6A–D
2014 *Jaxea kuemeli* Bachmayer — Gašparič & Hyžný, p. 9, figs. 8–9 (for comprehensive synonymy see Hyžný 2011c, p. 176).

Diagnosis: See Hyžný (2011c; p. 176)

Material examined: Ottngang: 19 specimens (under collective number GBA 2009/014/023), two near-complete specimens (NHMW 2009/0150/0001, NHMW 2010/0090/0001); Pramhof at Schärding: one specimen retaining both chelipeds (NHMW 2009/0160/0001); Grosswiesenhart: one specimen retaining both chelipeds (NHMW 1986/0101/0023). Some specimens, specifically those from Ottngang, possess cuticular surfaces.

Discussion: The studied material fully corresponds to *Jaxea kuemeli* as re-described by Hyžný (2011c). For the

species, the most obvious distinctive character is the position of the large median tooth on the cutting edge of the pollex. In *J. kuemeli* this is located posteriorly relative to the position of the median tooth on the dactylus (Hyžný 2011c; fig. 3B), while it is positioned anteriorly in its close relative, the extant *J. nocturna* (Hyžný 2011c; fig. 3A).

Occurrence: The species has been identified in lower and middle Miocene (upper Burdigalian to Langhian) strata of Austria, Slovenia, Slovakia and Hungary (Bachmayer 1954; Hyžný 2011c; Gašparič & Hyžný 2014).

Infraorder: **Axiidea** de Saint Laurent, 1979

Family: **Ctenochelidae** Manning & Felder, 1991

Genus: *Gourretia* de Saint Laurent, 1973

Type species: *Callianassa denticulata* Lutze, 1937 (= *Callianassa subterranea* var. *minor* Gourret, 1887) by original designation.

Diagnosis: See Ngoc-Ho (2003; p. 498).

Remarks: The fossil record of the genus is poorly known. Vega et al. (2007) re-assigned *Callianassa aquilae* Rathbun, 1935 from the Upper Cretaceous strata of Texas, Louisiana and Mexico to *Gourretia* de Saint Laurent, 1973. Recently, Hyžný in Bermúdez et al. (2013) erected a new genus, *Rathbunassa*, for the species, leaving *Gourretia* without

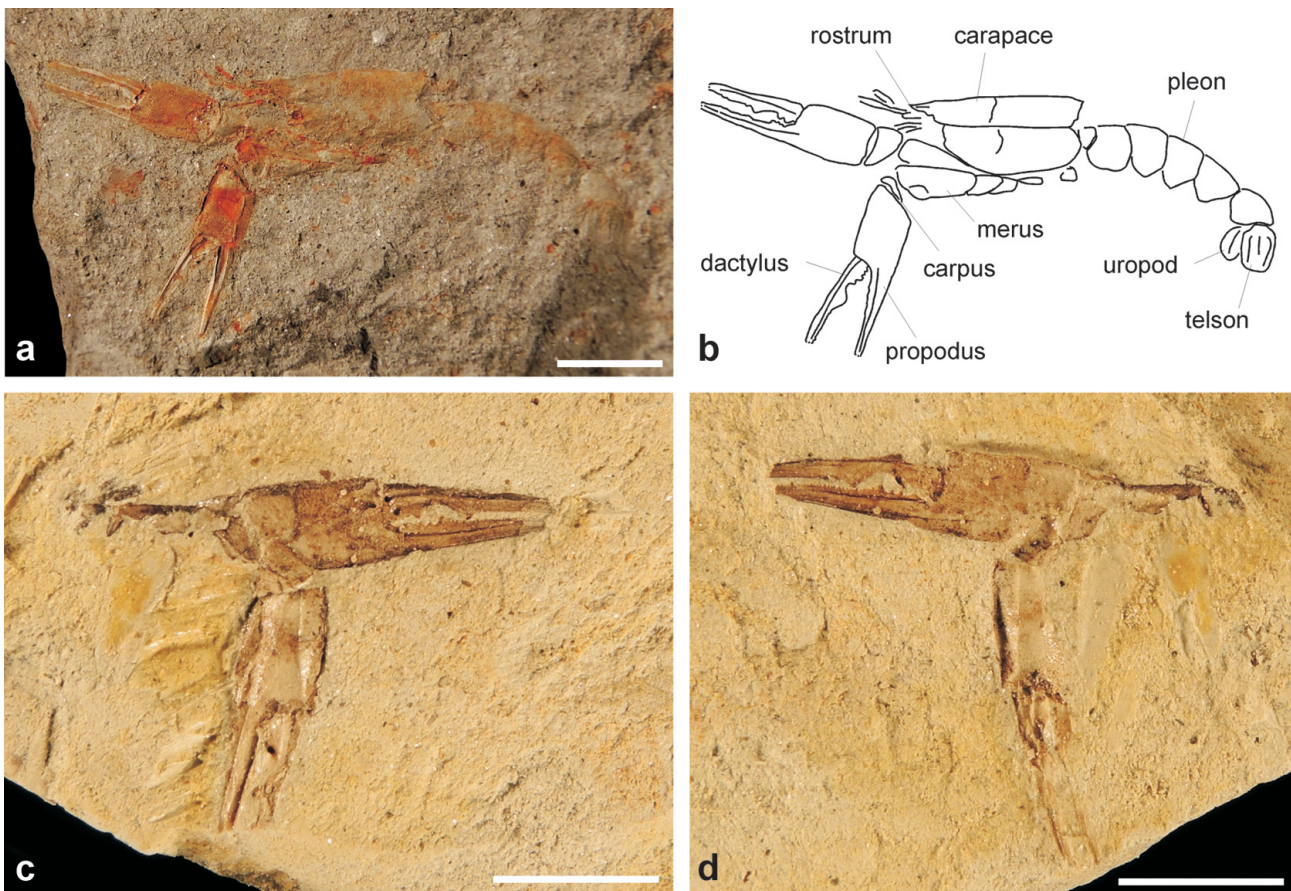


Fig. 2. *Jaxea kuemeli* Bachmayer, 1954. **a–b** — near-complete specimen from Ottngang (NHMW 2009/0150/0001), **c–d** — isolated chelipeds from Grosswiesenhart (NHMW 1986/0101/0023). Scale bar equals 5 mm.

fossil record. Material from Ottnang exhibits striking similarity to the major propodus of *Callianassa denticulata* Lutze, 1937, the type species of *Gourretia* (compare with López de la Rosa et al. 1998, fig. 1B; Ngoc-Ho 2003, fig. 21L; Sakai & Türkay 2005, fig. 2A). It is assigned to this genus based on a number of characters: upper margin is slightly converging distally, the fingers are shorter than manus (palm), dactylus has no prominent teeth on its occlusal margin and is hooked distally. These features alone can hardly be considered of taxonomic importance, however, their combination has affinities to *Gourretia*. The generic assignment, though, should be considered preliminary until more complete material is revealed. If confirmed its attribution to *Gourretia*, the occurrence from Ottnang discussed below is the only known report of the genus in the fossil record.

Gourretia sp.
Fig. 4

Material examined: Ottnang: major left propodus articulated with dactylus plus two isolated dactyli, all with preserved cuticle (collective number GBA 2009/014/0024).

Measurements: Propodus max. length incl. fixed finger=25 mm; propodus max height=13 mm; propodus min. height=11.2 mm; dactylus length=9 mm (measurements taken on articulated specimen).

Description: Propodus longer than high, converging distally; upper and lower margins smooth, without any apparent serration; fixed finger two times shorter than manus, occlusal surface with one prominent tooth at its base; tip of the fixed finger pointed and bent slightly upward; dactylus robust and edentulous.

Discussion: Many Miocene decapod species that are congeneric with the extant ones represent distinct taxa (e.g. Müller 1984; Hyžný 2011c; Hyžný & Müller 2012), thus it is fairly possible that the material studied here represents a new species. Propodus and dactylus, however, cannot be consid-

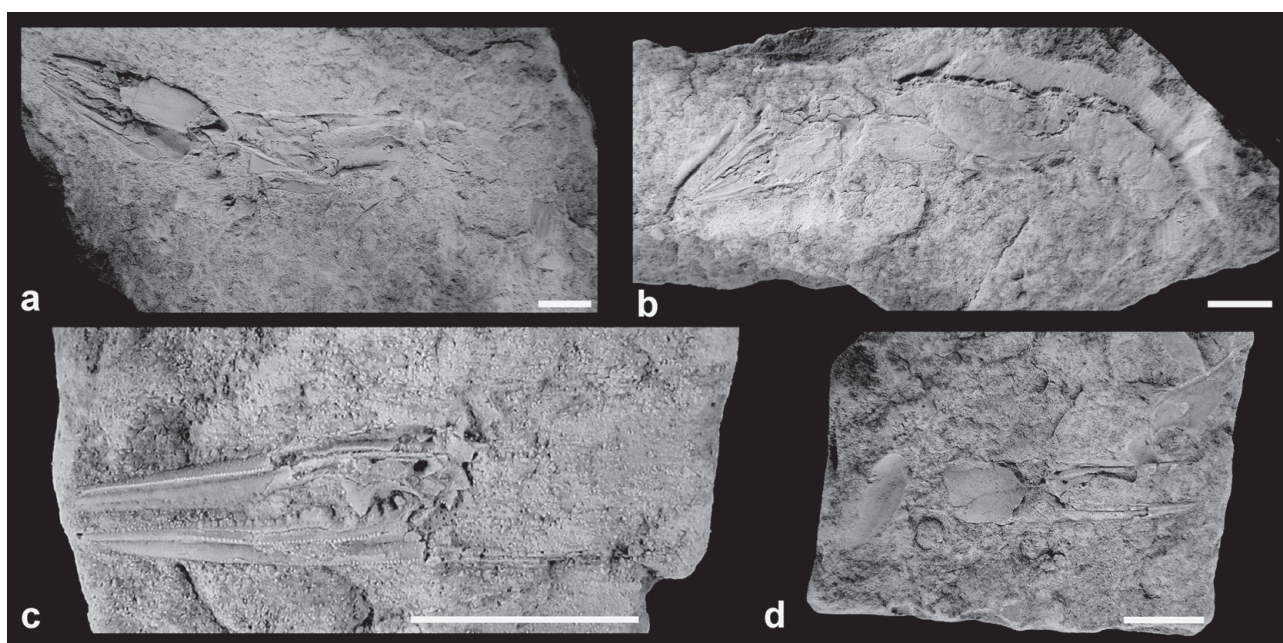


Fig. 3. *Jaxea kuemeli* Bachmayer, 1954. **a** — near-complete specimen (NHMW 2010/0090/0001), **b** — near-complete specimen (GBA 2009/014/023 coll. number), **c-d** — isolated chelae (GBA 2009/014/023 coll. number). All specimens are from Ottnang and were covered with ammonium chloride prior to photography. Scale bar equals 5 mm.



Fig. 4. *Gourretia* sp. from Ottnang (GBA 2009/014/0024). **a** — covered with ammonium chloride, **b** — uncoated, **c** — reconstruction of the chela outline. Scale bar equals 5 mm.

ered of taxonomic importance as these elements are often subject to intraspecific variation. The studied specimens are treated in open nomenclature until more complete material is found.

Occurrence: The species is restricted to the Lower Ottangian of Ottang beds, Austria.

Family: **Callianassidae** Dana, 1852

Subfamily: **Eucalliicinae** Manning & Felder, 1991

Genus *Calliax* de Saint Laurent, 1973

Type species: *Callianassa (Callichirus) lobata* de Gailande & Lagardère, 1966 by original designation.

Diagnosis: See Hyžný & Gašparič (2014; p. 42).

Remarks: *Calliax* de Saint Laurent, 1973 has a complex taxonomic history. It has been discussed in detail by Hyžný (2012) and Hyžný & Gašparič (2014) and there is no need to repeat it here. Discussion on distinguishing *Calliax* from related taxa based on soft-part morphology was provided by Ngoc-Ho (2003). Recently, Hyžný & Gašparič (2014) discussed in detail the identification of the genus in the fossil record: rectangular major cheliped propodus with two ridges on the base of the fixed finger extending onto manus with combination of relatively short fingers is typical for the genus.

Calliax michelottii (A. Milne-Edwards, 1860)

Fig. 5

1860 *Callianassa Michelotti* n. sp. — A. Milne-Edwards, p. 341, pl. 14, fig. 3

1928 *Callianassa Michelottii* A. Milne-Edwards, 1860 — Glaessner, p. 167-168

1984 *Callianassa szobensis* n. sp. — Müller, p. 53, pl. 7, figs. 3-4

2014 *Calliax michelottii* Hyžný & Gašparič, p. 45, figs. 5-10

2014 *Calliax michelottii* Gašparič & Hyžný, p. 5, figs. 4-5

(for comprehensive synonymy see Hyžný & Gašparič 2014, p. 45).

Diagnosis: See Hyžný & Gašparič (2014; p. 45).

Material examined: Neuhofen bei Tettenweis: left major chela (NHMW 2010/0089/0001); Peterskirchen: major left chela associated with dorsal carapace consisting of part and counterpart (NHMW 2014/0412/0001); Ort: major right propodus associated with carpus (NHMW 2014/0405/0001);

Antiesen: isolated major left propodus (NHMW 1985/0067/0026). Only specimens from Ort and Antiesen retain cuticular surfaces.

Description: Carapace without dorsal oval and with cardiac prominence; major cheliped merus longer than high and keeled along its midline, upper margin straight, lower margin poorly preserved; carpus higher than long, upper margin concave, proximo-lower margin rounded; propodus distinctly longer than high, upper and lower margins parallel to each other; fixed finger with double ridge running onto manus; outer lateral surface of propodus covered with several tubercles near the base of the fixed finger; dactylus deep and robust; occlusal surface of both fingers armed with a row of tiny teeth.

Discussion: The species was originally described as *Callianassa* Leach, 1814. Recently, Hyžný & Gašparič (2014) redescribed the species and transferred it to *Calliax*. The re-description is based on the chelae, as these are often the only fossil remains known from ghost shrimps (Bishop & Williams 2005). In this respect, the material from Peterskirchen is exceptional because it also exhibits features of the dorsal carapace which is usually not preserved in ghost shrimps because of its weak calcification (but see e.g. Hyžný & Schlögl 2011, text-fig. 2C for the opposite). Dorsal carapace of the Peterskirchen specimen possesses cardiac prominence which is also present in extant *Calliax doerjesti* Sakai, 1999. Features of the major chela fully conform to the description made by Hyžný & Gašparič (2014).

Occurrence: Late Oligocene–Middle Miocene of Germany, Italy, Austria, Slovenia, Slovakia and Hungary (Hyžný & Gašparič 2014; Gašparič & Hyžný 2014).

Infraorder: **Brachyura** Linnaeus, 1758

Section: **Eubrachyura** de Saint Laurent, 1980

Subsection: **Heterotremata** Guinot, 1977

Superfamily: **Leucosioidea** Samouelle, 1819

Family: **Leucosiidae** Samouelle, 1819

Subfamily: **Eballinae** Stimpson, 1871

Genus *Palaemyra* A. Milne Edwards in Sismonda, 1861

= *Ebalites* Müller, 1978

? = *Tanaoa* Galil, 2003

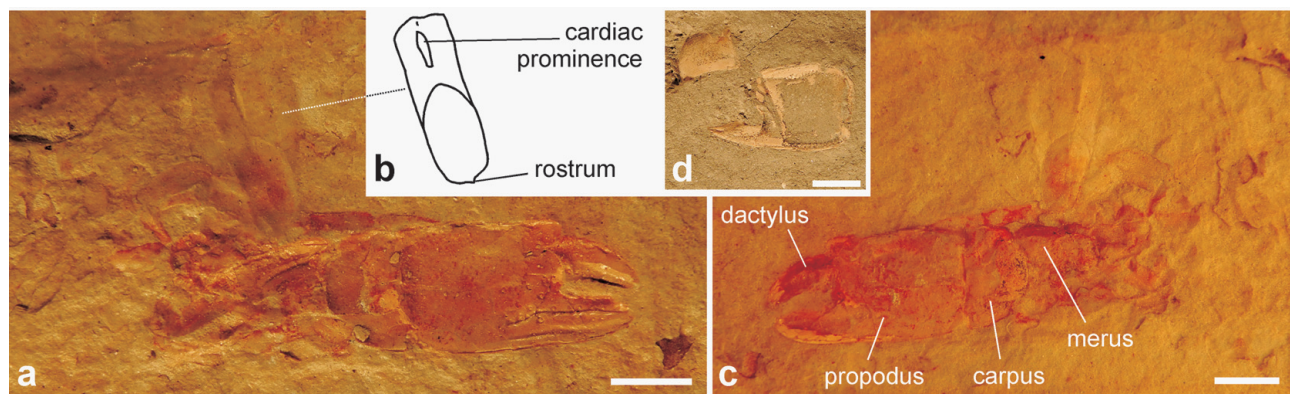


Fig. 5. *Calliax michelottii* (A. Milne-Edwards, 1860). **a–c** — specimen from Peterskirchen (NHMW 2014/0412/0001) in moulting position with preserved chelae and dorsal carapace; interpretative drawing in **(b)**. **d** — isolated carpus and propodus from Ort (NHMW 2014/0405/0001). Scale bar equals 5 mm.

Type species: *Palaeomyra bispinosa* A. Milne Edwards in Sismonda, 1861 by original designation and monotypy.

Diagnosis: Carapace subcircular, globose, covered with granules. Front narrow, bilobed. Outer orbital margin with three sutures. Branchial and intestinal regions swollen, demarcated by grooves, 2 pairs of pits along cardiobranchial grooves. Posterior margin narrow and bidentate.

Remarks: *Palaeomyra* was erected by A. Milne Edwards in Sismonda (1861) to accommodate a single species, *P. bispinosa* A. Milne Edwards in Sismonda, 1861 from the Miocene of Torino, Italy. Although the original material, a single specimen (holotype), has been lost (De Angeli & Garassino 2006), Garassino et al. (2004) reported six additional and more complete specimens from the Oligocene of Morbello, Alessandria and the Upper Miocene of Cocconato, Asti, both in Italy, which helped the re-evaluation of the species.

Müller (1978) erected *Ebalites* for *Ebalia globulosa* Müller, 1975 from the Middle Miocene of Hungary. Later, he (Müller 1984) recognized the genus to be synonymous with *Palaeomyra* and reassigned *E. globulosa* once more, this time to *Palaeomyra*. Until now, *P. bispinosa* and *P. globulosa* have been considered the only known species of the genus (Schweitzer et al. 2010). Based on the major similarities in the carapace outline, swollen branchial and intestinal regions demarcated by grooves, 2 pairs of pits along cardiobranchial grooves, posterior margin with 2 prominent spines and distinct granulation covering the surface of the carapace, the specimen from Ottnang, originally described as *Randallia strouhali* Bachmayer, 1953a is transferred here into *Palaeomyra*.

Since no generic diagnosis of *Palaeomyra* was given by Glaessner (1969) or any subsequent author, it is provided here based on the description and figure of A. Milne Edwards in Sismonda (1861; p. 14, figs. 18–20) and additional material reported by Garassino et al. (2004).

Galil (2003) revised selected species of *Randallia* Stimpson, 1857 and erected four new genera, including *Tanaoa* Galil, 2003. Interestingly, Bachmayer (1953a) noted similarities between *Randallia strouhali* and extant *R. pustulosa*

Wood-Mason in Wood-Mason & Alcock, 1891, the type species of *Tanaoa*. The dorsal carapace morphology of *Palaeomyra* (Müller 1984; pl. 47, figs. 1–6) corresponds to the variation of *Tanaoa* as expressed in Galil (2003; fig. 1B–D). In fact, swollen branchial and intestinal regions demarcated by grooves and 2 pairs of pits along cardiobranchial grooves are the characters typical not only for *Palaeomyra* but also for *Tanaoa* and *Toru* Galil, 2003 (Galil 2003), whereas strong granulation on the entire surface of the dorsal carapace of *Palaeomyra* is closer to *Tanaoa*. These two genera may well be considered synonymous, but we are reluctant to synonymize them without direct comparison with some extant material of *Tanaoa*.

Based on the supposed close relationship between *Palaeomyra* and *Tanaoa*, former taxon, previously unplaced at subfamily level, they are assigned here to the subfamily Eballiinae.

Palaeomyra strouhali (Bachmayer, 1953a) n. comb.

Fig. 6

1953a *Randallia strouhali* Bachmayer, p. 137, pl. 5, figs. 1–2

1998b *Randallia strouhali* Bachmayer — Müller, p. 24, pl. 2, fig. 1

Emended diagnosis: Almost circular carapace with nearly straight posterolateral margins and bidentate posterior margin; dorsal surface covered with densely packed granules of two sizes; cardiac and intestinal regions without any tubercles or spines.

Material examined: Holotype NHMW 1953/0051/0001 showing incomplete dorsal carapace with preserved cuticle.

Measurements: Maximum length of the fragmentary carapace = 7 mm; greatest width = 8.5 mm.

Emended description: Carapace almost circular in outline, widest approximately at midlength; anterior portion not preserved. Posterolateral margins nearly straight. Posterior carapace margin straight and narrow, with two stubby protrusions. Dorsal surface of carapace covered with many large, densely packed granules, nearly identical in size (dia-

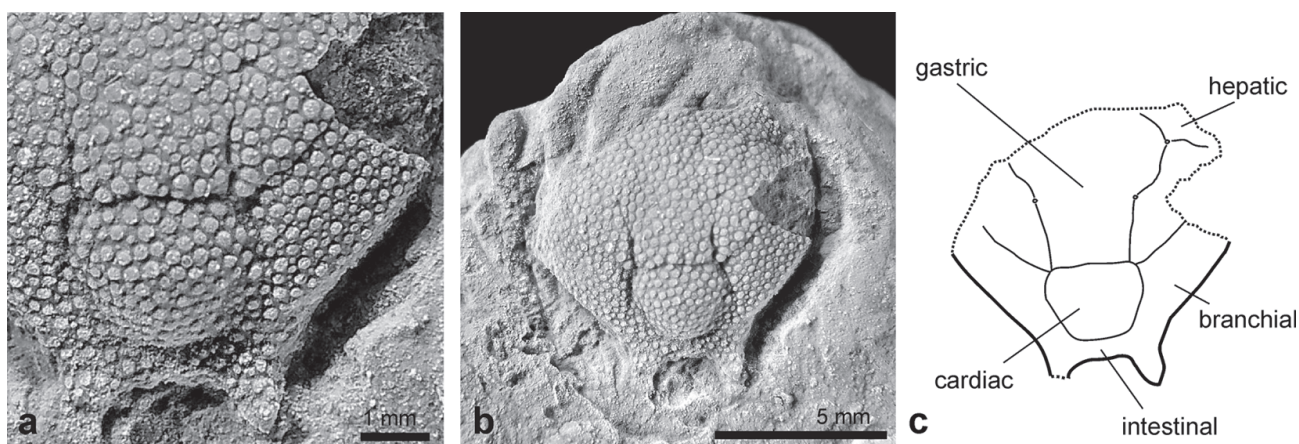


Fig. 6. *Palaeomyra strouhali* (Bachmayer, 1953a). Holotype (NHMW 1953/0051/0001) from Ottnang. **a** — detail of the posterior portion of the carapace; note the tuberculation, **b** — entire specimen, whitened with ammonium chloride prior to photography, **c** — interpretative drawing with carapace regions indicated.

meter 0.3 mm), interspaced with smaller ones (diameter 0.1 mm). Two pairs of pits present along cardiobranchial grooves. Hepatic, gastric, cardiac and branchial regions demarcated with grooves; grooves deepest in posterior carapace portion. Gastric region large and only indistinctly demarcated with grooves. Cardiac region circular in outline and strongly arched. Branchial regions broad and ovate. Intestinal region narrow, without any tubercles.

Discussion: Bachmayer (1953a) described the species based on a single incomplete specimen. The description is emended here as a result of re-examination of the holotype; some characters (pits along cardiobranchial grooves) were omitted in the original description.

The most-anterior portion of the holotype is missing, so the frontal margin cannot be described. Nevertheless, the cuticular surface and distinct groove pattern in the posterior portion of the carapace allow distinguishing of *P. strouhali* from its two congeners. Garassino et al. (2004; p. 267) noted the variation in dorsal tuberculation of *P. bispinosa* and the same is apparent from the figures of *P. globulosa* published by Müller (1984; pl. 47, figs. 3–6). However, none of these species has tubercles as flattened and densely packed as *P. strouhali*.

Palaeomyra strouhali also differs from six extant species of *Tanaoa*. Most of the extant species, including *Tanaoa distinctus* (Rathbun, 1894), *T. nanus* Galil, 2003, *T. pustulosus* and

T. serenei (Richer de Forges, 1983) possess a cardiac spine (Galil 2003; Ng & Richer de Forges 2007), which is lacking in *P. strouhali*. Granulation of the carapace seems to be distinct in different species of *Tanaoa*. In this respect, *P. strouhali* is closest to *T. serenei* (Ng & Richer de Forges 2007, fig. 1D).

Occurrence: The species is known only from the early Ottnangian of Ottnang, Austria.

Superfamily: **Portunoidea** Rafinesque, 1815

Family: **Polybiidae** Ortmann, 1893

Genus: *Liocarcinus* Stimpson, 1871

Type species: *Portunus holsatus* Fabricius, 1798, by original designation.

Diagnosis: See Manning & Holthuis (1991; p. 83).

Remarks: Recent analyses (Schubart & Reuschel 2009; Spiridonov et al. 2014) resolved the paraphyletic nature of the genus. Revision of all extant species is currently in progress (Schubart & Reuschel 2009). Considering rather high morphological differences among fossil taxa attributed to *Liocarcinus* so far (Schweitzer et al. 2010), the revision of the fossil record of the genus is needed as well.

Liocarcinus ottnangensis (Bachmayer, 1953a) n. comb.

Figs. 7–9

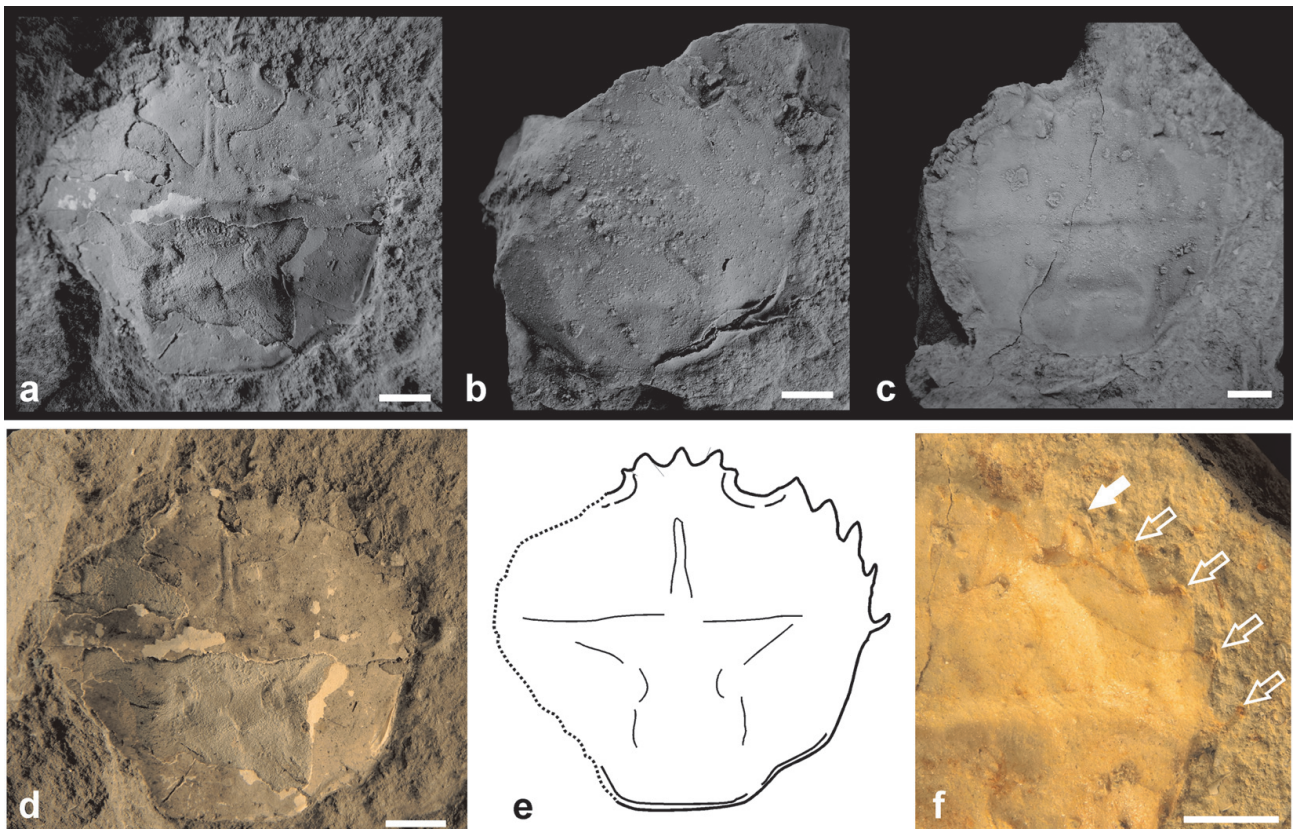


Fig. 7. *Liocarcinus ottnangensis* (Bachmayer, 1953a). **a, d** — holotype (NHMW 1953/0052/0001) from Ottnang, **b, c, f** — specimen from Allerding (NHMW 2014/0402/0001), part (b) and counterpart (c), **e** — line drawing of the holotype showing the number of frontal and anterolateral teeth, **f** — detail of the anterolateral margin with four anterolateral teeth (empty arrows) and outer orbital tooth (filled arrow). Specimens in a–c were covered with ammonium chloride prior to photography. Scale bar equals 5 mm.

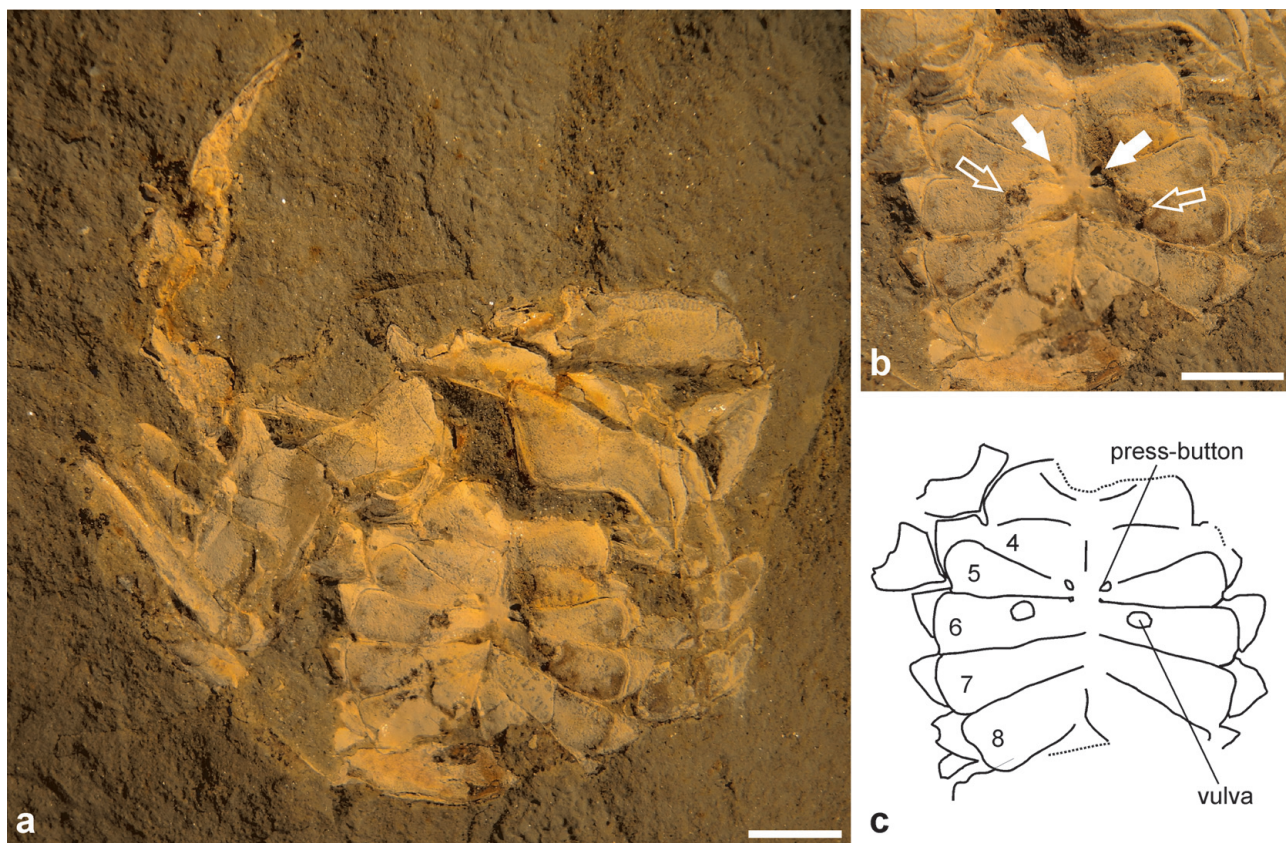


Fig. 8. *Liocarcinus ott nangensis* (Bachmayer, 1953a). **a-c** — female specimen in ventral aspect from Pranhof (NHMW 1971/1486 A), **b-c** — detail of the sternum with indicated press-button structures (filled arrows) and vulvae (empty arrows). Scale bar equals 5 mm.

1953a *Geryon ott nangensis* Bachmayer, p. 138, pl. 5, figs. 3–4
 1998b *Geryon ott nangensis* Bachmayer — Müller, p. 37
 2010 *Chaceon ott nangensis* (Bachmayer); Schweitzer et al., p. 106

Emended diagnosis: Carapace hexagonal, 1.1 times wider than long; front with three prominent teeth, orbits deep and rounded; anterolateral margin with four large teeth (excluding outer orbital tooth), third smallest but distinct; first three anterolateral teeth equally spaced from each other, distance between the third and fourth somewhat greater. Cardiac region wide and elevated, bearing two swellings at widest points; epibranchial regions with prominent transverse ridge running across the mesogastric region.

Material examined: Ottnang: holotype of *Geryon ott nangensis* NHMW 1953/0052/0001; Allerding: dorsal carapace NHMW 2014/0402/0001, fragmentary cheliped NHMW 2014/0402/0003, sixteen cheliped fragments NHMW 2014/0402/0004–0007, 2014/0402/0008 (collective number); Pranhof at Schärding: carapace with chelipeds in ventral aspect exposing female sternum NHMW 1971/1486 A. Cuticle is entirely or partly preserved in all studied specimens.

Measurements: Holotype NHMW 1953/0052/0001: max. carapace width = 32.5 mm, max. carapace length = 30.4 mm; NHMW 2014/0402/0001: max. carapace width = 31.5 mm, max. carapace length = 29.0 mm (preserved part).

Emended description: Carapace hexagonal, 1.1 times wider than long, strongly convex from front to posterior

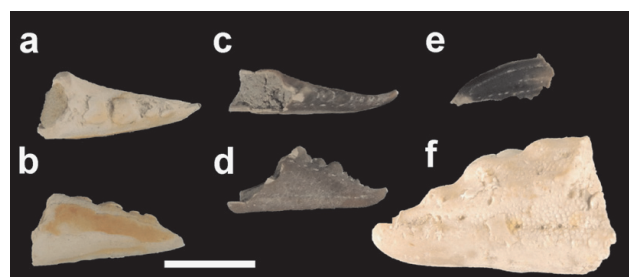


Fig. 9. *Liocarcinus ott nangensis* (Bachmayer, 1953a). **a-b** — fragmentary fixed finger (NHMW 2014/0402/0004) in occlusal and lateral view, **c-d** — fragmentary fixed finger (NHMW 2014/0402/0005) in occlusal and lateral view, **e** — fragmentary dactylus (NHMW 2014/0402/0006) in lateral view, **f** — fragmentary fixed finger (NHMW 2014/0402/0007) in lateral view. All specimens are from Allerding. Scale bar equals 5 mm.

margin; carapace surface covered with very fine granules and pits. Frontal margin with three prominent teeth, orbits relatively deep and rounded; anterolateral margin with four large teeth (excluding outer orbital tooth), all sharp, third smallest but distinct; first three anterolateral teeth equally spaced from each other, distance between the third and fourth somewhat greater. Regions well developed; mesogastric region with a long anterior process ending in a frontal sulcus, urogastric region depressed; cardiac region wide and

elevated, bearing two swellings at widest points; epibranchial regions with prominent transverse ridge running across the mesogastric region; branchial regions swollen, with prominent ridge longitudinally along the midline of the branchial region.

Female sternum ovoid, slightly longer than wide, greatest width at sternite 6, lateral margins forming a series of arcs defined by smoothly curved lateral somite margins and narrow episternal projections; sternites 1–4 (supposedly) fused completely, elements 1–3 not preserved. Axial depression prominent, narrow. Vulvae positioned near the anterior margin of sternite 6, the genital opening ovate and slightly oblique; press-button structure positioned on sternite 5.

First pereiopods (chelipeds) strong. Both fingers bearing dome-shaped denticles on occlusal surface.

Discussion: The original description of *Geryon ottnangensis* is based on a single carapace. Bachmayer (1953a; pl. 5, fig. 4) interpreted the frontal margin as having a single tooth. Thorough re-examination of the holotype revealed the presence of three teeth (excluding inner orbital teeth), a character typical of *Liocarcinus* and *Benthochascon* Alcock & Anderson, 1899. Anterolateral margin of *Geryon ottnangensis* possesses five teeth (including outer orbital tooth), a character typical for *Liocarcinus* (Manning & Holthuis 1981; Froggia & Manning 1982) whereas *Benthochascon* has only four anterolateral teeth (including outer orbital tooth) (Ng 2000). As a result, *Geryon ottnangensis* is transferred to *Liocarcinus* here. Interestingly, all five teeth can be distinguished on the holotype, although Bachmayer (1953a) did not recognize their number. *Geryon ottnangensis* Bachmayer, 1953a is listed as *Chaceon* Manning & Holthuis, 1989 by Schweitzer et al.

(2010), although no arguments for this act were stated. *Chaceon*, however, always has four frontal teeth (Manning & Holthuis 1989; Schweitzer & Feldmann 2000), which is in contrast with the three frontal teeth of *Geryon ottnangensis*.

Several *Liocarcinus* species are known from the Miocene Paratethys; all of them differ from *L. ottnangensis*. *Liocarcinus praeearcuatus* Müller, 1996 and *L. rakosensis* (Lórenthey in Lórenthey & Beurlen, 1929) from the Middle Miocene of Poland and Hungary (Müller 1984, 1996) have complete frontal margins; *L. oroszyi* Bachmayer, 1953b and *L. kuehni* Bachmayer, 1953b from the Middle Miocene of Austria (Bachmayer 1953b; Müller 1984, 1998b) have strongly elevated branchial regions and distinctly ornamented carapaces, respectively. *Liocarcinus lancetidactylus* Smirnov, 1929 from the Lower Miocene of Caucasus has three anterolateral teeth according to Garassino & Novati (2001), but based on their figures the real number may be higher. The preservation (flattened crab bodies within shales) does not allow further comparison with *L. ottnangensis*. *Liocarcinus oligocaenicus* Paucă, 1929 from the Oligocene of Romania (Paucă 1929), Czech Republic (Jaroš 1939) and Poland (Jerzmańska 1967) is preserved in a similar manner and the character of the carapace is obscured.

From the extant congeners, *L. ottnangensis* is closest to the type species *L. holsatus* from Europe (Türkay 2001), which differs in the nature of its anterolateral teeth: in *L. ottnangensis* the distance between the fourth and fifth teeth is proportionately greater than in *L. holsatus*.

Occurrence: The species is known from the early to middle Ottnangian in the North Alpine Foreland Basin.



Fig. 10. *Liocarcinus* sp. **a–b** — holotype of *Achelous vindobonensis* Bachmayer, 1950 (NHMW 2014/0409/0001) from Grosskrut 3, **c–d** — fragmentary chelae from Ottnang (GBA 2009/014/0025 coll. number). Specimens in **b** and **c** were coated with ammonium chloride prior to photography. Scale bar equals 5 mm.

Liocarcinus sp.
Fig. 10

1950 *Achelous vindobonensis* Bachmayer, p. 137, pl. 1, figs. 5, 5a,b
1998b Portunidae ind. sp. — Müller, p. 32

Material examined: Ottnang: several cheliped fragments GBA 2009/014/0025; Grosskrut 3: holotype of *Achelous vindobonensis* NHMW 2014/0409/0001, with preserved cuticle.

Discussion: Bachmayer (1950) described *Achelous vindobonensis* based on a single incomplete chela coming from the Grosskrut 3 drilling. The material was later treated as Portunidae indet. by Müller (1998b). Dentition of chelipeds has been considered of taxonomic significance recently (Spiridonov et al. 2014). The holotype of *A. vindobonensis* possesses fingers with bi- and trilobed serial conical teeth. Comparison with chelipeds of extant portunoid crabs has shown close affinities to *Liocarcinus* (Spiridonov et al. 2014; fig. 3D), but identification on the species-level is not possible. We refrain from referring this taxon to *nomen dubium* so that the name remains available in case better-preserved material becomes available which may justify or refute this species name.

Family: **Portunidae** Rafinesque, 1815
Subfamily: **Necronectinae** Glaessner, 1928

Remarks: Glaessner (1928) created a new family Necronectidae to accommodate an extinct genus *Necronectes* A. Milne-Edwards, 1881 (= *Gatunia* Rathbun, 1919). The phylogenetic analysis of Karasawa et al. (2008a) recognized a clade grouping *Necronectes*, *Scylla* de Haan, 1833 and *Sanquerus* Manning, 1989 within the family Portunidae. As a result, they treated Necronectinae as the subfamily-level group and it also appeared as such in the classifications of De Grave et al. (2009) and Schweitzer et al. (2010), which are followed here. The classification of Brachyura presented by Ng et al. (2008) recognized extant genera *Scylla* and *Sanquerus* as members of Portuninae.

Necronectinae gen. et spec. indet.
Fig. 11

Material examined: Allerding: left propodus articulated with dactylus NHMW 2014/0042/0002.

Description: First pereiopods (chelipeds) strong. Fixed finger of left chela straight with grooves running along its entire length on both lateral surfaces. Dactylus slightly curved, elongate. Both fingers bearing biserial conical teeth on occlusal surface; left dactylus also bearing large molariform tooth proximally.

Discussion: The studied chela bears strong resemblance to claws of *Scylla* as documented in detail by Keenan et al. (1998). We are, however, hesitant to assign the material to this genus, as there is another member of the subfamily known from the Miocene of Europe, namely *Necronectes* (Glaessner 1928, 1933). Therefore, we retain

the fragmentary chela from Allerding in the open nomenclature until more material is recovered.

Portunoidea gen. et sp. indet.
Fig. 12

1982 ?*Geryon* spec. — Bachmayer, p. 22
1998b ?*Geryon* sp. — Müller, p. 38

Material examined: Limberg: two dorsoventrally near-complete flattened specimens deposited in KM (without repository number), without preserved cuticular surfaces.

Discussion: Bachmayer (1982) reported two near-complete specimens of ?*Geryon* sp. preserved in diatomites of Limberg. Due to the extreme flattening their preservation was not sufficient for closer identification. Without a well preserved carapace, no closer identification than Portunoidea gen. et spec. indet. is possible. Unfortunately, the specimens reported and figured by Bachmayer (1982) could not be traced in the NHMW collections where they were supposed to be deposited. Two other specimens from the same locality and presumably of the same taxon are deposited in the

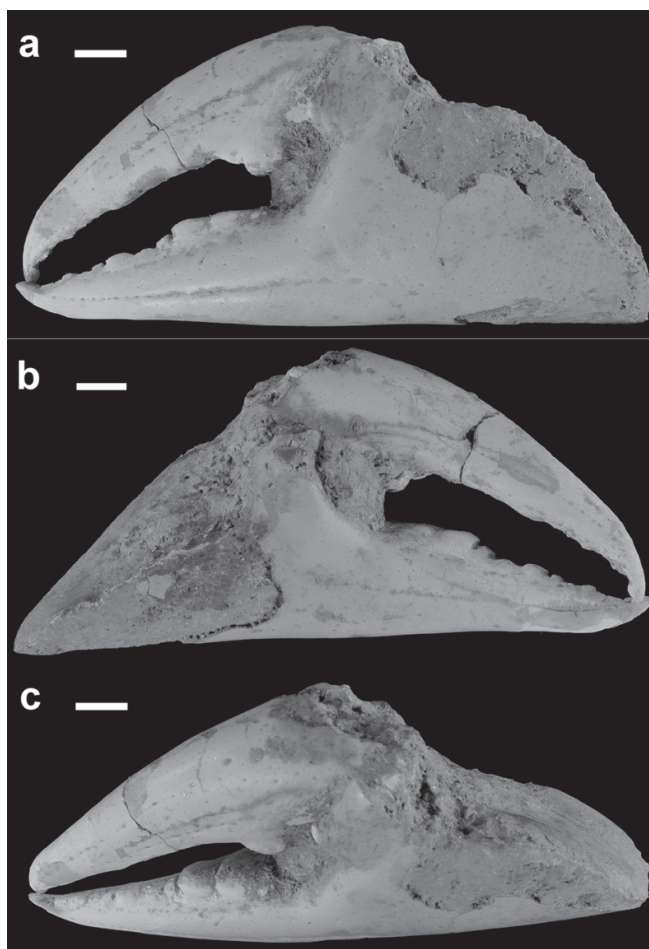


Fig. 11. Necronectinae gen. et spec. indet. a–c — incomplete chela (NHMW 2014/0402/0002) in lateral (a), mesial (b) and dorso-lateral (c) aspects. Scale bar equals 5 mm.

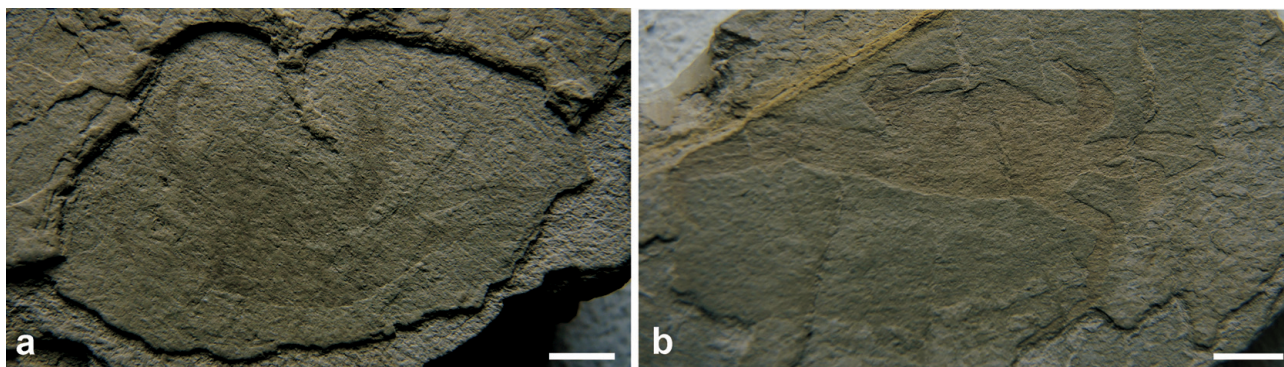


Fig. 12. Portunoidea gen. et spec. indet. Uncatalogued specimens from Limberg deposited in the Krahuletz-Museum at Eggenburg. Scale bar equals 5 mm.

Krahuletz-Museum in Eggenburg; the opportunity is taken to publish photos of these specimens (Fig. 12). The preservation hinders description of any details.

Discussion

Environmental distribution: During the early and middle Otnangian the Paratethys Sea in the North Alpine Foreland Basin was a shelfal sea with strong tidal currents and distinct upwelling areas (Rupp & van Husen 2007; Grunert et al. 2010b, 2012). The various sections described in the Geological settings chapter represent depositional environments of the upper bathyal to outer shelf (e.g. Otnang Schanze, Limberg) to high energy (e.g. Peterskirchen) and protected (e.g. Antiesen) inner shelf settings. For many localities, however, no detailed paleoecological analysis is available.

Decapod crustaceans may have a rather broad bathymetric distribution on the genus or family level (Abelló et al. 1988; McLay 1999; Ingle & Christiansen 2004; Ateş et al. 2006). However, certain species prefer specific conditions and in some cases can be indicative of unique environmental conditions. For example, many species inhabiting coral reefs do not occur in deeper settings and vice versa: crabs living on muddy substrates usually do not occur in reefal environment (Abele 1976; Poupin & Juncker 2010). This general rule has also been demonstrated for Badenian decapods of Central Paratethys (Müller 1984). There is also a general increase in bathymetric range towards greater depth; since decapod species within the first 50 m display a median range of approximately 150 m, whereas abyssal faunas tend to have far greater ranges (Rosa et al. 2012). This may be connected to seasonal bathymetric differences in bathyal species reaching 500 m (Mura & Cau 1994).

Two taxa are relatively common in the Otnangian deposits, namely *Jaxea* and portunoid crabs. Portunoids have broad bathymetric distribution; however, *Liocarcinus* is usually present at depths of less than 100 m (Manning & Holthuis 1981). The paleobathymetric distribution of mud and ghost shrimps *Jaxea*, *Gourretia* and *Calliax* is less clear. They were reported from a broad range of depths, from the shallow settings to those exceeding 100 m (Ngoc-Ho 2003;

Hyžný 2011c; Hyžný & Gašparič 2014), and even up to 800 m in the case of *Calliax* (Taviani et al. 2013). Similarly, *Tanaoa* (as a possible synonym of *Palaeomyra*) has been reported from depths of a few tens of meters but also from depths exceeding 1–200 m (Galil 2003).

At Otnang/Schanze, the environment has been interpreted as transition from outer neritic to upper bathyal based on a detailed statistical analysis of the microfauna. This is dominated by benthic foraminiferal assemblages with *Laevidentalina* spp., *Oridorsalisum bonatus*, *Gyroidinoides* spp. and *Valvulineria complanata*, characteristic for an outer neritic to bathyal setting (Grunert et al. 2012 and references therein). Numerous individuals of *Jaxea kuemeli* that occur at this locality, frequently with articulated carapace and pleon, suggest minor post-mortem transport. The influence of occasional storm events and tidal currents in the upper part of the succession, which formed in inner shelf settings (Grunert et al. 2012), is a possible cause why brachyurans at this locality are known only from isolated carapaces (*Palaeomyra*, *Liocarcinus*), whereas preservation of articulated specimens of *Jaxea* was most probably promoted by the burrows, in which the animals live (Pervesler & Dworschak 1985). The near-complete body fossils of *J. kuemeli* from Pramhof and Grosswiesenhart may, thus, indicate that they were actually preserved within their burrows.

At Peterskirchen, the Otnangian deposits were formed in a shallow marine low energy environment with high amounts of *Ammonia* (Rupp & van Husen 2007). The specimen of *Calliax michelottii* with both articulated chelipeds, including carapace, is in accordance with this interpretation of low-energy conditions and suggests autochthonous preservation coupled with rapid burial.

At Allerding, coastal boulders and the mollusc assemblages indicate that a rocky shore environment was sealed by pelitic “Schlier” during a transgression event (Harzhauser et al. 2014). The presence of *Liocarcinus* can be connected to the transgressive event of the “Schlier” deposition, as this genus prefers muddy substrates (Rufino et al. 2005).

At Antiesen bluff a tidal-influenced shelf setting was present (Rupp & van Husen 2007; Rupp 2008). The presence of *Calliax*, today known also from very shallow environments (Ngoc-Ho 2003) is in accordance with this interpretation.

Table 1: Occurrences of selected genus-level taxa in space and time. * — denotes the unpublished occurrence (MH pers. obs.)

	Oligocene	Early Miocene	Middle Miocene	Late Miocene	Recent
Boreal region	<i>Calliax</i>				<i>Liocarcinus</i>
Central Paratethys	<i>Liocarcinus</i>	<i>Jaxea</i> <i>Calliax</i> <i>Gourretia</i> <i>Palaeomyra</i> <i>Liocarcinus</i>	<i>Jaxea</i> <i>Calliax</i> <i>Gourretia</i> * <i>Palaeomyra</i> <i>Liocarcinus</i>		
(Proto-)Mediterranean	<i>Palaeomyra</i>		<i>Jaxea</i> <i>Calliax</i>	<i>Jaxea</i> <i>Palaeomyra</i> <i>Liocarcinus</i>	<i>Jaxea</i> <i>Calliax</i> <i>Gourretia</i> <i>Liocarcinus</i>
Indo-Pacific					<i>Jaxea</i> <i>Gourretia</i> <i>Tanaoa</i> <i>Liocarcinus</i>

Most decapod occurrences in the Ottnangian deposits thus represent rather shallow-water components in contrast to deep-water assemblages from the Karpatian deposits documented from the Slovak part of the Vienna Basin (Hyžný & Schlögl 2011) and Slovenian part of the Styrian Basin (Gašparič & Hyžný 2014).

Biogeography: The Ottnangian decapod assemblages of the Central Paratethys exhibit affinities to the (Proto-)Mediterranean, Boreal and Indo-Pacific regions, suggesting faunal exchange among these regions (Table 1). Mud and ghost shrimps *Jaxea*, *Calliax* and *Gourretia* are also known from the modern Mediterranean Sea (Ngoc-Ho 2003). *Jaxea* and *Calliax* occurred in the Proto-Mediterranean Atlantic Region (*sensu* Harzhauser et al. 2002) already during the Miocene (Hyžný 2011c) and Oligocene (Hyžný & Gašparič 2014), respectively. In the Central Paratethys, *Jaxea kuemeli* and *Calliax michelottii* persisted into the latest Early Miocene (Karpatian) (Hyžný 2011c; Hyžný & Gašparič 2014). *Liocarcinus* is today widespread in the Mediterranean (Türkay 2001) and is also known from the Indo-Pacific (Manning & Holthuis 1981). Its oldest occurrence is *Liocarcinus oligocae-nicus* from the Oligocene of Paratethys (Paučá 1929; Jaroš 1939; Jerzmańska 1967). The first occurrence of *Palaeomyra* is from the Oligocene of the (Proto-)Mediterranean (Garassino et al. 2004). In the Miocene, the genus was already spread and is known from the Early and Middle Miocene in Central Paratethys (Müller 1984; this paper) and Late Miocene in the (Proto-)Mediterranean (Sismonda 1861; Garassino et al. 2004). *Tanaoa* as its supposed close relative (see above) is presently restricted to the Indo-Pacific (Galil 2003; Ng & Richer de Forges 2007). Thus, both, *Tanaoa* and *Liocarcinus* may have Tethyan origin. Tethyan ancestry for several decapod taxa inhabiting the Indo-Pacific has already been proposed (for non-decapod taxa see Harzhauser et al. 2007, 2008), including the mud shrimp *Jaxea* (Hyžný 2011c) and the ghost shrimp *Glypturus* Stimpson, 1866 (Hyžný & Müller 2012). Although the Miocene fossil record of decapods in the Indo-Pacific is moderate (Noetling 1901; Böhm 1922; Van Straelen 1938; Morris & Collins 1991; Collins et al. 2003; Karasawa et al. 2008b), the Early Miocene appearance of *Palaeomyra* (? = *Tanaoa*) and *Liocarcinus* in the circum-Mediterranean can also imply that the sources of present-day diversity hotspots trace to the Western Tethys.

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