

Synopsis of the fossil freshwater crabs of Europe (Brachyura: Potamoidea: Potamidae)

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With 5 figures

KLAUS, S. & GROSS, M. (2009): Synopsis of the fossil freshwater crabs of Europe (Brachyura: Potamoidea: Potamidae). – N. Jb. Geol. Paläont. Abh., DOI: 10.1127/0077-7749/2009/0032; Stuttgart.

Abstract: The reappraisal of the European Neogene fossil freshwater crabs results in the recognition of eight species, including one new species (*Potamon hegauense* n. sp.) of late Miocene age (c. 10.3 Ma) from Höwenegg (southern Germany). All eight species are assigned to the genus *Potamon* (Potamidae). There is no morphological evidence for a closer relationship with African potamonautids. The oldest known European freshwater crab is *Potamon quenstedti* from Engelswies (early Miocene, c. 17 Ma) in southern Germany. The last occurrence of potamids in Central Europe prior to the Pleistocene is recorded in the Vienna Basin (late Miocene, c. 8 Ma). In Italy (Tuscany) freshwater crabs (*Potamon castellanense*) are documented well before (c. 5.5 Ma) the presumed postglacial invasion of extant *Potamon fluviatile*. The latest Pliocene-Pleistocene species *Potamon antiquum* from northern Hungary probably represents extinct populations of *Potamon ibericum* at the northern limit of its range. The scarce records and the lack of dating of the southwest Asian *Potamon sivalense* hampers considerations about origin, dispersal events and palaeobiogeography of potamids in Europe up to now. However, a slow southward withdrawal of freshwater crabs, induced by climate cooling at the end of the Miocene, is marked by the extinction of *P. hegauense* in the circum-Alpine realm, *P. antiquum* in Hungary, and probably *P. castellanense* in Italy.

Key words: Crustacea, Decapoda, Brachyura, Potamoidea, *Potamon*, freshwater, Neogene, Europe.

1. Introduction

Freshwater crabs comprise about 1300 extant species at present and are one of the most diverse groups of brachyuran crustaceans (NG et al. 2008). They occur in tropical and subtropical climates and are well adapted to life in freshwater both physiologically and by their mode of reproduction with lecithotrophic eggs, direct development, and brood care. Currently, all freshwater crabs of the Old World are assigned to one superfamily Potamoidea (see STERNBERG et al. 1999; KLAUS et al. 2009a, 2009b), subdivided into three families (Potamidae, Potamonautidae and Gecarcinucidae, see KLAUS et al. 2009b).

The first record of a fossil freshwater crab dates back to 1805 when KARG mentioned *Potamon speciosus* (VON MEYER, 1844a) from Öhningen as the cancrid crab *Cancer minutus*. Several decades later, these specimens were recognised as freshwater crabs (VON MEYER 1862; FRAAS 1865). Most of the fossil freshwater crab fragments reported in the following hundred years originated from the German North Alpine Foreland Basin and the Pannonian Basin System, but also from Africa (JOLEAUD & HSU 1935; MORRIS 1976; CARRIOL & SÉCRÉTAN 1992; MARTIN & TRAUTWEIN 2003; FELDMANN et al. 2007) and Asia (GLAESSNER 1933; NARUSE et al. 2003). All fossil freshwater crabs are of Neogene age (for Europe see

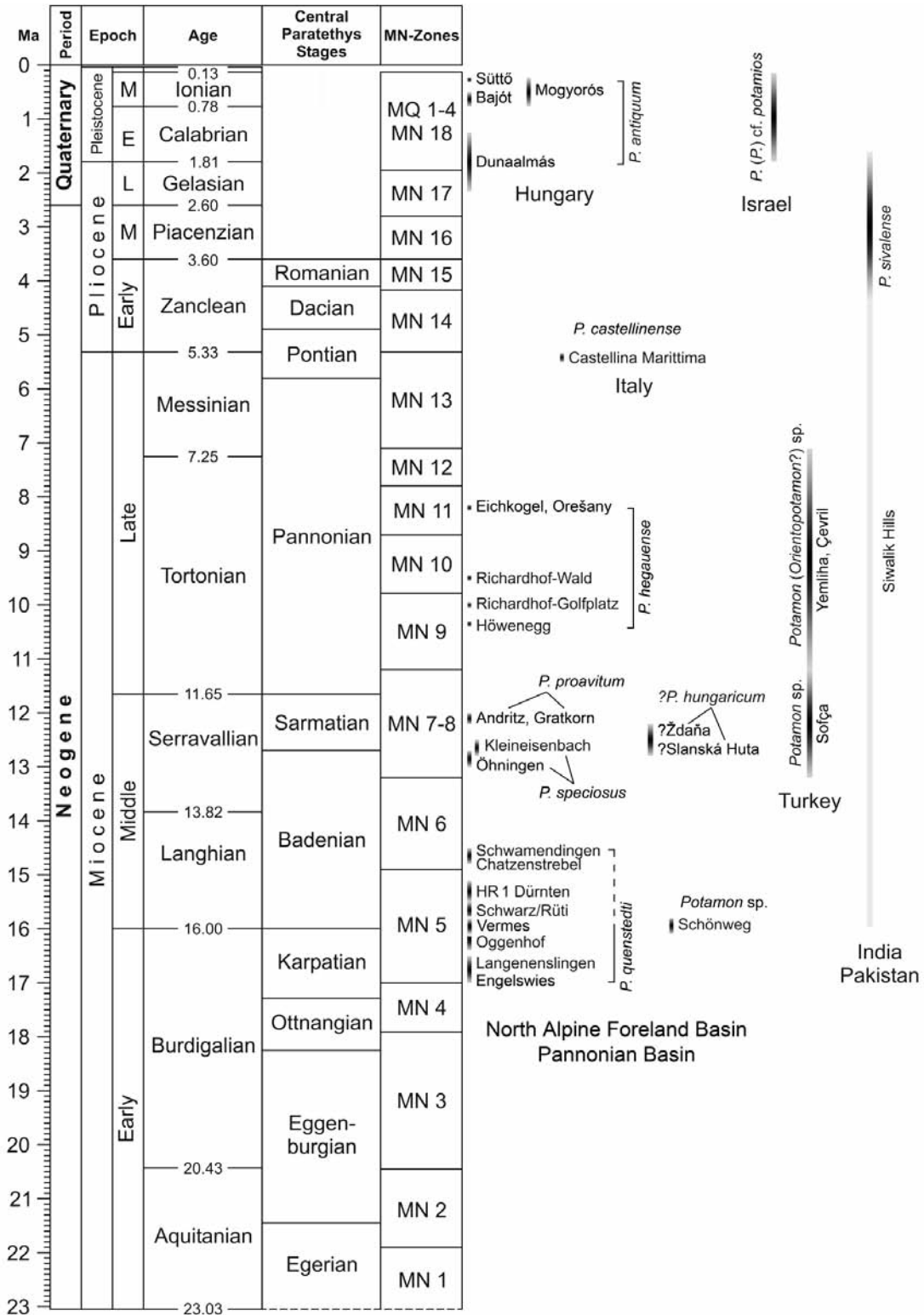


Fig. 1. Stratigraphic chart (adapted from LOURENS et al. 2004, PILLER et al. 2007 and OGG & GRADSTEIN 2008) and records of Eurasian freshwater crabs.

Fig. 1), with exception of *Tanzanonautes tuerkayi* FELDMANN et al., 2007, the oldest known freshwater crab to date, from the Paleogene (Oligocene) of East Africa.

Although scientific interest in extant freshwater crabs was intense during the last century, their fossil record remained poorly known. Their last revisions (GLAESSNER 1928, 1930) are hardly cited. Meanwhile, additional fossil species were described (KÖRÖSSY 1940; GLAESSNER 1933; FELDMANN et al. 2007), freshwater crab taxonomy as a whole changed profoundly (BOTT 1970; YEO & NG 2003; KLAUS et al. 2006, 2009b, CUMBERLIDGE et al. 2008), and the dating of the fossil sites was refined. This makes a revision of the previous taxonomic and chronostratigraphic data necessary. A revised fossil record of freshwater crabs is of significant importance to zoologists, using palaeontological data to constrain biogeographic developments (BRANDIS et al. 2000; BRANDIS 2002; KLAUS et al. 2006) and to calibrate phylogenetic divergence in molecular analyses (DANIELS et al. 2006; SHIH et al. 2008). Herewith we also make the scattered literature record on the fossil freshwater crabs (being mostly from the 19th century) available for future research. The present synopsis is restricted to the speciose European fossil freshwater crabs, including the specimens from the Near and Middle East.

2. Systematics

Phylum Arthropoda VON SIEBOLD, 1845
 Class Malacostraca LATREILLE, 1806
 Order Decapoda LATREILLE, 1802
 Suborder Brachyura LINNAEUS, 1758
 Superfamily Potamoidea ORTMANN, 1896
 Family Potamidae ORTMANN, 1896

 Genus *Potamon* SAVIGNY, 1816

Remarks: The generic status of the fossil freshwater crabs has changed many times, often reflecting postulated affinities to either the Potamidae or the exclusively African Potamonautidae. BOTT (1955) created four new genera (*Propotamonautes*, *Archithelphusa*, *Proballaya*, *Pseudopotamon*) for several of the European fossil crabs. The description and morphological justification of these genera is sparse and based solely on the figures given by the respective taxonomic authorities and does not take into account different states of preservation, especially concerning *Potamon speciosus* (VON MEYER, 1844a). In fact, all available fossil specimens show, where conserved, the typical potamid character state of the postfrontal crest, which is discontinuous with two median postfrontal lobes.

There are also potamonautids with distinct postfrontal lobes, especially within the Madagascan freshwater crabs. However, the Madagascan crabs probably separated from their African relatives during the Cretaceous (based on molecular data, DANIELS et al. 2006) or during the Oligocene (based on biogeographic argumentation, KLAUS et al. 2006). An early dispersal of potamonautids from Africa to Europe is neither morphologically nor biogeographically supported.

It was proposed that some of the fossil species might have affinities to Southeast Asian Potamidae (SCHWEIGERT 1996; SCHWEIGERT et al. 1997). Within the extant family Potamidae two subfamilies are recognised (YEO & NG 2003; SHIH et al. 2009): the Potaminae with a transverse ridge between 7th and 8th sternal segment, and the Potamiscinae lacking such a transverse ridge (leaving the possibility, that one of the two subfamilies is paraphyletic). The subfamily Potamiscinae has its major diversity in East and Southeast Asia, not extending further west than Assam, with the exception of two isolated occurrences in the central and western Himalaya. The Asian genera of the subfamily Potaminae occur from southern Burma into the Himalaya, and the genus *Socotrapotamon* is endemic to the island of Socotra. The extant genus *Potamon* does not overlap with the other genera of the subfamily Potaminae and ranges from the Hindu Kush to the Maghreb (YEO & NG 2003; BRANDIS et al. 2000; BRANDIS 2005). As many Potamidae have very similar carapace morphologies, a relationship of the fossil crabs with either the Potamiscinae or the Asian Potaminae can theoretically not be ruled out. Only the fossil *Potamon antiquum* from the Pliocene/Pleistocene of Hungary and Slovakia can unequivocally be assigned to the Potaminae, because of the diagnostic transverse ridge (Fig. 2 E, inset).

Although most morphological characters that are diagnostic for the extant potamid genera (e.g., characters of the male copulatory apparatus) are not preserved in the fossil crabs, we follow the taxonomic approach of GLAESSNER (1928, 1929a) and the argumentation of GROSS & KLAUS (2005), assigning all fossil freshwater crab species of Europe to the genus *Potamon*.

Insufficient diagnostic characters directed us to a biogeographic approach. If character-based assignment of a fossil taxon to one of its extant relatives is not properly applicable, the most probable working hypothesis should be the assignment to that related extant taxon with which it shares exclusively its range; and could therefore be considered to be allopatric to the other related extant taxa. The Central European fossil freshwater crab sites are closest to the present distribution of *Potamon* (see Fig. 3), and widely separated from any other recent potamid genus. Also extant *Potamon* does not overlap with other potamid genera (BRANDIS & SHARMA 2005). Thus, we regard the European fossil freshwater crabs and *Potamon* as most probably monophyletic.

Of course, we are aware that this “area-taxon” concept can only be provisional, and is not appropriate if ancient dispersal, associated with faunal replacement, has to be assumed (making the “area-taxon” possibly para- or polyphyletic). Phylogenetic analysis of the Potamidae based on DNA sequences of the ribosomal large subunit was con-

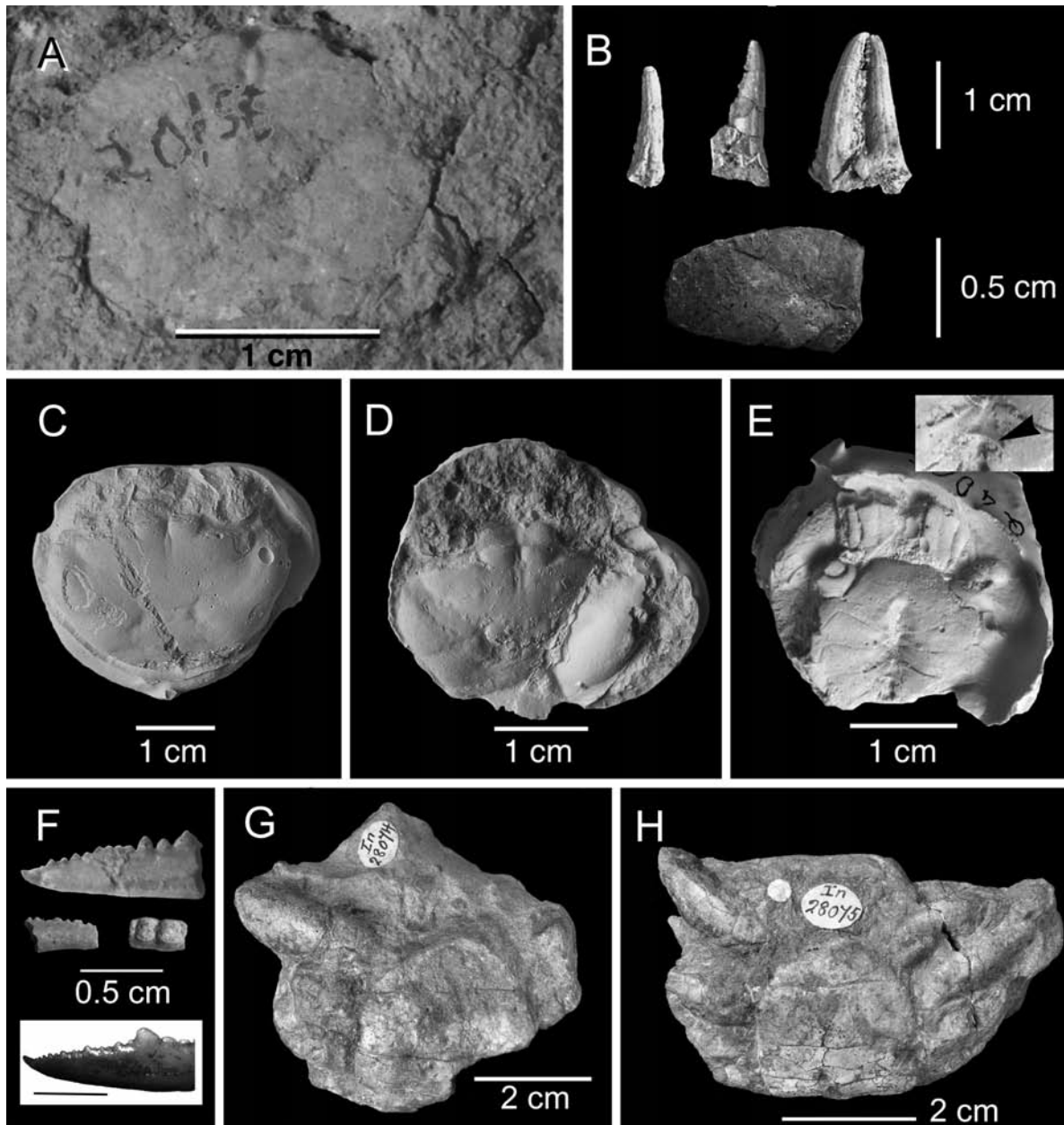


Fig. 2. **A, B** – *Potamon hegauense* n. sp.; **A**: SMNK–PAL 6520, holotype; **B**: Claw fragments (upper row, SMNK–PAL 6522) and right cheliped merus (SMNK–PAL 6523). **C–E** – *Potamon antiquum* SZOMBATHY, 1916; casts of the specimens depicted in SZOMBATHY (1916); **C**: Specimen of pl. 3 fig. 5, syntype; **D**: Specimen of pl. 3 fig. 6; **E**: MTM Q 4066, syntype, ventral side of male specimen; inset: “transverse ridge” (arrowhead). **F** – Claw fragments, Tatrot Formation, India (Coll. R. PATNAIK). Inset: Propodus of extant *Sartoriana spinigera* (WOOD-MASON, 1871), SMF 26057, for comparison (scale bar = 1 cm); **G, H** – *Potamon?* *sivalense* GLAESSNER 1933. **G**: Paratype, female, ventral, NHML 28074; **H**: Holotype, female, ventral, NHML 28075

ducted by SHIH et al. (2009) including estimates of divergence dates by Bayesian relaxed molecular clock calculations. According to these data, *Potamon* and its sister-genus *Parathelphusula* (occurring in the Himalaya) should have diverged during the Middle Miocene (12.5 Ma), after

the earlier divergence of *Himalayapotamon* (14.7 Ma, SHIH et al. 2009), thus making fossil *Potamon* paraphyletic. Although their estimation of the first appearance date of potamid (24 Ma, SHIH et al. 2009) is probably by far too conservative, this could indicate dispersal of *Potamon* to the

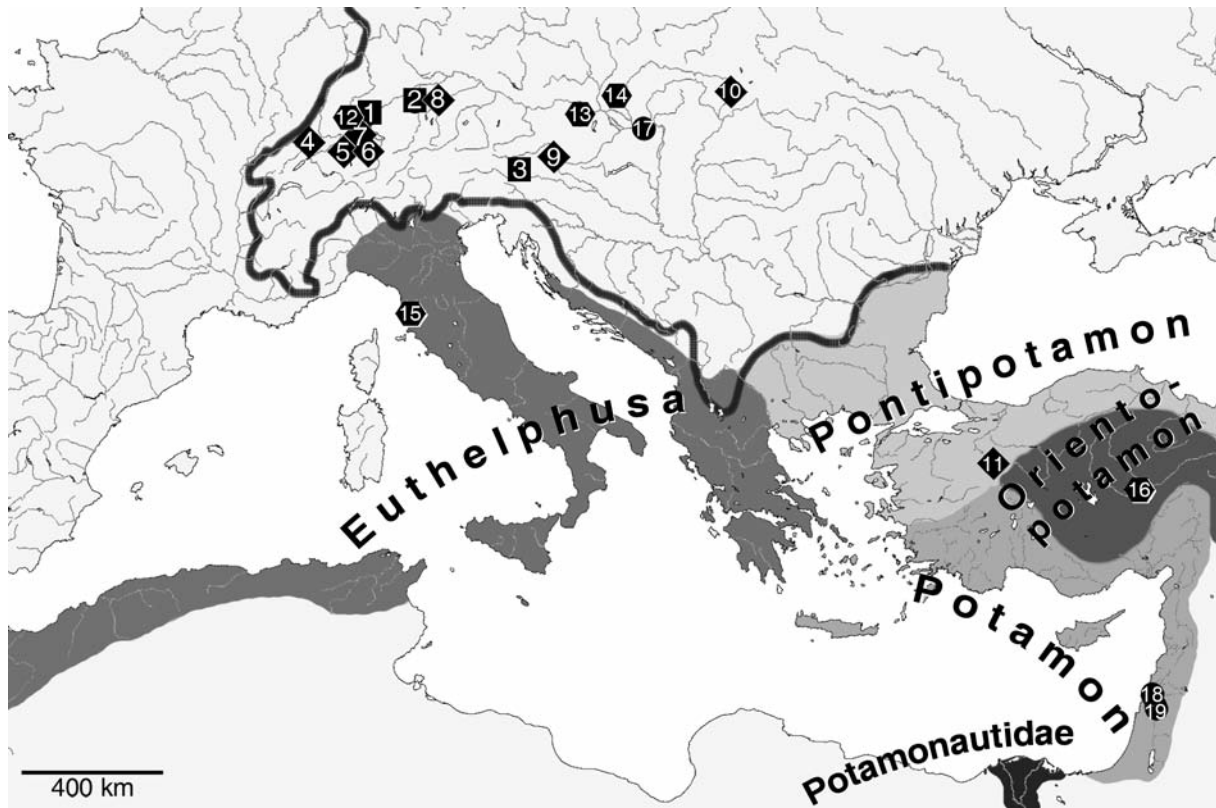


Fig. 3. Approximate distribution of the four extant subgenera of the genus *Potamon* according to BRANDIS et al. 2000) and the sites with fossil freshwater crabs. Squares: early Miocene; diamonds: middle Miocene; hexagons: late Miocene; circles: Pliocene/Pleistocene. Line: Recent 0°C January isotherm. 1: Engelswies and Langenenslingen; 2: Oggenhof; 3: Schönweg; 4: Vermes; 5: Schwarz, Baarburg and Aentlisberg; 6: Chatzenstebel; 7: Öhningen; 8: Kleineisenbach; 9: Andritz and Gratkorn; 10: Ždaňa and Slanská Huta; 11: Sofça; 12: Höwenegg; 13: Eichkogel and Richardhof; 14: Orešany; 15: Castellina Marittima; 16: Yemliha and Çevril; 17: Süttő, Dunaalmás, Bajót and Mužla; 18: Eynan/Ain Mallaha; 19: Geshor Benot Ya'aqov.

east or fragmentation of its eastern range during the middle and late Miocene, resulting in morphological divergence.

Several authors postulated relationships of the fossil freshwater crabs to extant species (SZOMBATHY 1916; GLAESSNER 1928, 1930; SCHWEIGERT et al. 1997). These hypotheses relied on the carapace characters introduced by RATHBUN (1904). Since BOTT (1970) the taxonomy of *Potamon* is based predominantly on characters of the male reproductive organs (the gonopods), which are not preserved in fossil freshwater crabs. The last revision of the genus *Potamon* is exclusively based on characters of the first gonopod (BRANDIS et al. 2000) and recent investigations show that cryptic species that are only diagnosable with molecular genetic techniques are not rare within freshwater crabs (unpublished data). This incongruence between palaeontological and neontologic species definition makes the classification of the fossil specimens extremely difficult and argues for any hypothesis on present-day relationships to be treated cautiously. Concerning species delimitation, we follow a chronological approach. This appears to be the only concept to avoid the use of intra-

specific variable carapace characters (see BRANDIS et al. 2000) at the present state of knowledge. Thereby, we are also able to handle the previous system of species that in large part would not bear up against a strictly typological reappraisal, and to include recently discovered freshwater fragments.

The terminology for the morphological description is based on GLAESSNER (1969), BOTT (1970) and NG (1988), for dentition patterns of chelae see PRETZMANN (1971).

Abbreviations: BSPG = Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; GPIT = Reference collection of the Institut für Geowissenschaften der Universität Tübingen, Germany; LMJ = Landesmuseum Joanneum Graz, Austria; MTM = Magyar Természettudományi Múzeum, Budapest, Hungary; NHM = Natural History Museum London, Great Britain; NHMW = Naturhistorisches Museum Wien, Austria; NMBE = Naturhistorisches Museum Bern, Switzerland; PIMUZ = Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SMF = Senckenbergmuseum, Frankfurt/Main,

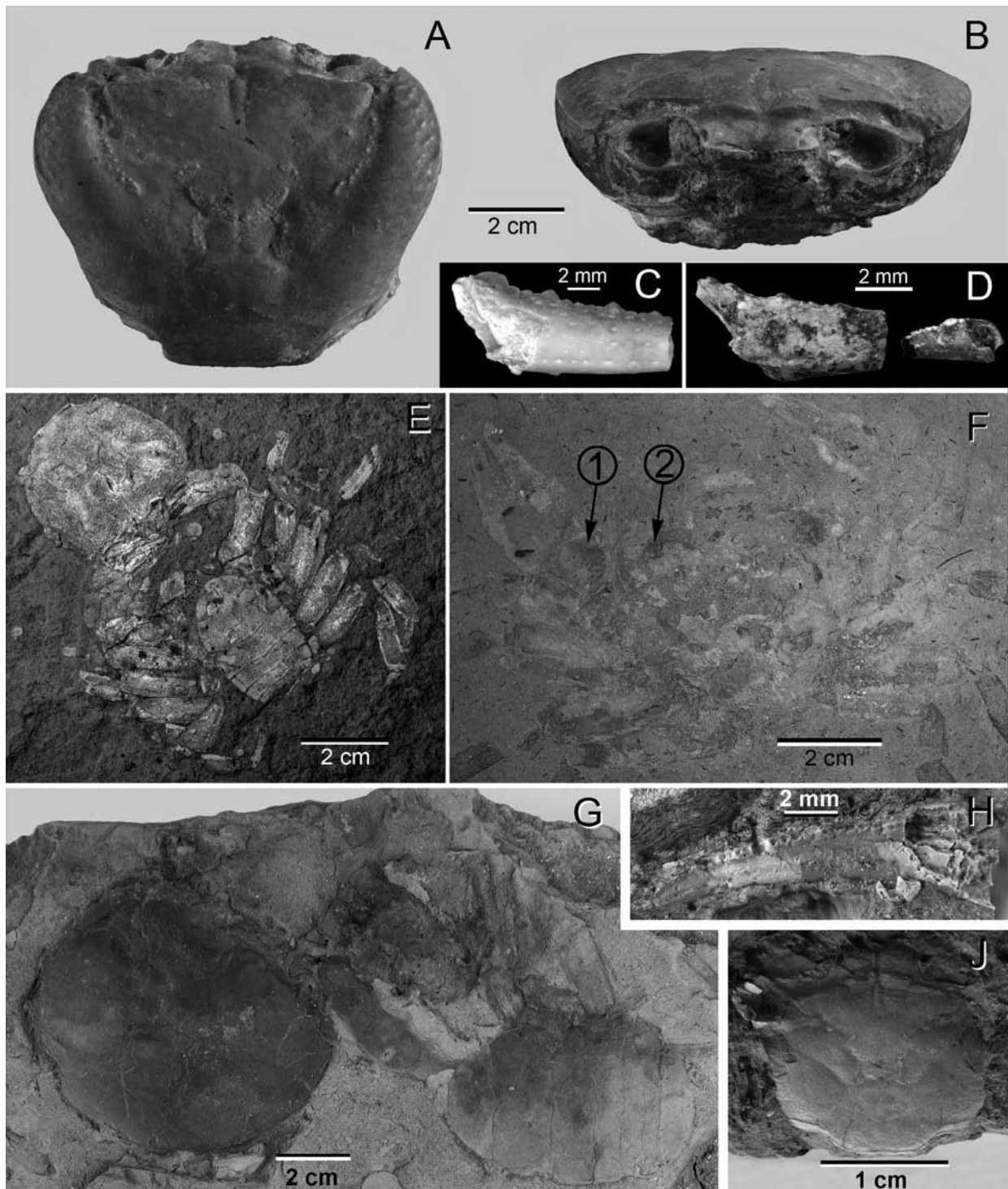


Fig. 4. **A-C** – *Potamon quenstedtii* (ZITTEL, 1885). **A**, **B**: GPIT 15776, lectotype, Engelswies, Germany. **A**: Dorsal view, **B**: Frontal view. **C**: Claw fragment, Oggenhof, Germany, Coll. M. BÖHME. **D** – *Potamon* sp. Claw fragment (LMJ 204339), Schönweg, Austria, Coll. M. BÖHME. **E**, **F** – *Potamon speciosus* (VON MEYER, 1844); Öhningen, Germany. **E**: SMNK-PAL 2626, female, neotype. **F**: SMNS 3795; 1, granulose cheliped merus, 2, granulose branchial region with sharp anterolateral margin. **G-J** – *Potamon provavium* (GLAESSNER, 1928). **G**: Female, holotype, Andritz, Austria LMJ 5828. **H**: Claw fragment, Gratkorn, Austria, LMJ 203390; **G**: Carapace fragment, Gratkorn, Austria, LMJ 203403.

Germany; SMNK-PAL = Staatliches Museum für Naturkunde Karlsruhe (palaeontological collection), Germany; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany.

Potamon quenstedti (ZITTEL, 1885)
Fig. 4A-C

- 1865 *Telphusa speciosa* VON MEYER. – O. FRAAS, p. 278.
v 1885 *Grapsus speciosus*. – QUENSTEDT, p. 400, pl. 31, figs. 5-8.
v* 1885 *Telphusa Quenstedti*. – ZITTEL, p. 715.
1904 *Telphusa Quenstedti* ZITTEL. – RATHBUN, p. 230.
v 1910 *Telphusa speciosa*. – E. FRAAS, p. 222, pl. 67, fig. 27.
v 1916 *Potamonautes quenstedti*. – SZOMBATHY, p. 396, fig. 7 [cop. QUENSTEDT 1885, pl. 31, figs. 6-8].
1928 *Potamonautes quenstedti* ZITTEL. – GLAESSNER, p. 214.
1929 *Potamon quenstedti* (ZITTEL, 1885). – GLAESSNER, p. 338.
v 1929 *Potamon quenstedti*. – GLAESSNER: 54, pl. 6, figs. 4-5.
v 1930 *Potamon quenstedti*. – GLAESSNER, p. 169, pl. 8, fig. 5, pl. 9, fig. 5, pl. 10, fig. 2.
1940 *Potamon quenstedti*. – KŐRÖSSY, p. 106.
1955 *Proballaya quenstedti*. – BOTT, p. 310.
1969 *Proballaya quenstedti*. – BOTT, p. 272.
v 1996 *Proballaya quenstedti* (ZITTEL). – SCHWEIGERT, p. 21, fig. 22.
v 1997 *Proballaya quenstedti* (ZITTEL). – SCHWEIGERT et al., p. 55, fig. 3.
2007 *Proballaya quenstedti* (ZITTEL, 1885). – FELDMANN et al., p. 78, tab. 1.

Lectotype: GPIT 15776 (Fig. 4 A, B).

Type locality: Engelswies (9°7'43"E/48°2'42"N), Baden-Württemberg, Germany.

Type horizon: Calcareous tufas, Upper Freshwater Molasse, early Miocene, Karpatian, 17.0–16.5 Ma, early MN 5 (SCHWEIGERT 1992; ZIEGLER 1995; SCHWEIGERT et al. 1997; HEIZMANN & BEGUN 2001; DAXNER-HÖCK 2003).

Material: SMNS 62534, 4782, 4758, 8578, 8579, 37623, eight uncatalogued specimens; GPIT 1885, 12103, 12755, 12757, 12758, 12759-12761, 12777, 12796, 13408, 13409, 13411, 13412, 14081, 14082, 14272, 14273, 14275, 14664, 15214-15218, 15220, 15692–15694, 15755–15761, 15773, 15776, 15779-15781.

Description: Straight postorbital cristae, postfrontal lobes and median lobe prominent, anterolateral rim smooth or only slightly serrated, epibranchial teeth short, branchial region strongly convex, anteriorly granular, H-shaped gastric groove present, urogastric and cardiac regions well developed (Fig. 4 A, B).

Occurrence: Engelswies; Langenenslingen near Riedlingen, Baden-Württemberg, Germany (claw fragment, SMNS 62534-2, 9°23'10"E/48°9'3"N), Oggenhof near Augsburg, Bavaria, Germany (claw fragment, BSPG, 10°45'40"E/48°21'29"N; Fig. 4C).

The claw from Langenenslingen was assigned to *Potamon quenstedti* by SCHWEIGERT et al. (1997) and is of the same age and originates from the same lithology as the type specimens of Engelswies (SCHWEIGERT 1996). The site of Oggenhof is younger than Engelswies (latest Karpatian, MN 5, 16.4-16.0 Ma; DE BRUIJN et al. 1992; ABDUL AZIZ et al. 2008, M. BÖHME, pers. comm). Both the age and the relative proximity to Engelswies argue for this claw fragment being conspecific with *Potamon quenstedti*.

Several sites from the Swiss Molasse Basin (Upper Freshwater Molasse = OSM) were reported to yield brachiuran claw fragments: Schwamendingen (8°51'E/47°23'N, see HEER 1865) (early Badenian, MN 6, c. 14.8-?14.5 Ma; REICHENBACHER et al. 1998); Chatzenstrebél (9°22'E/47°26'N, see BOLLIGER & GUBLER 1997: 624, fig. 9; PIMUZ 17374) (early Badenian, MN 6, 14.8-14.6 Ma; REICHENBACHER et al. 1998; DAXNER-HÖCK 2003); HR1 Dürnten (8°51'E/47°16'N, see BOLLIGER 1992) (early Badenian, MN 5, ?15.6-?15.1 Ma; BOLLIGER & GUBLER 1997); Schwarz/Rüti (8°50'E/47°15'N, see BOLLIGER 1992; BOLLIGER & GUBLER 1997: 624, fig. 9; PIMUZ 17373) (early Badenian, MN 5, ?15.9-?15.5 Ma; BOLLIGER 1992; BOLLIGER & GUBLER 1997); Vermes (7°28'N/47°19'N, see ENGESSER et al. 1981) (early Badenian, MN 5, c. 16 Ma; ENGESSER 2005, KEMPF et al. 1999); Aentlisberg (8°31'E/47°19'N, see PAVONI 1952, 1957) (OSM; BOLLIGER & GUBLER 1997), Baarburg (8°33'E/47°12'N, see BOLLIGER & GUBLER 1997) (OSM).

These fragments from the OSM of Switzerland are younger than the chela of Oggenhof, especially concerning the sites of Schwamendingen and Chatzenstrebél from the lower MN 6 (see Fig. 1), and can not unambiguously be assigned to *Potamon quenstedti*. BOLLIGER & GUBLER (1997) also reported ichnofossils (*Diplichnites/Kouphichnium*, PIMUZ 17371; location Hochdorf, Switzerland, 8°16'E/47°10'N, MN 5, OSM) that where proposed to originate from reptantian crustaceans.

Comment: *Potamon quenstedti* was assigned to the African genus *Potamonautes* by SZOMBATHY (1916) based on the erroneous figures given in QUENSTEDT (1885). However, this was disproved by GLAESSNER (1930), as SZOMBATHY's argumentation was based on characters that in fact show the state as in *Potamon* (postfrontal crest discontinuous, external orbital angle not different from *Potamon*, anterolateral margin sharp – but in agreement with SZOMBATHY only slightly serrated). BOTT (1955), apparently unaware of GLAESSNER's work, followed SZOMBATHY assuming an African relationship and established a new genus for *Potamon quenstedti*, *Proballaya*, in allusion to the African species *Potamonautes ballayi*. There are no carapace characters in all investigated specimens of *Potamon quenstedti* that would support the assignment to a different genus or point to African affinities.

Potamon sp.
Fig. 4D

Material: Two claw fragments, LMJ 204339, coll. M. BÖHME (Fig. 4 D).

Location: Schönweg (“Brüchl”, 14°48’01”E/46°44’37”N) in Carinthia (Southern Austria). Limnic, heavily debris-flow influenced layers of late Karpatian/early Badenian age (MN 5, c. 16 Ma; BECK-MANNAGETTA & DRAXLER 1987; WANK 1991; REISCHENBACHER et al. 2007).

Comment: This claw fragment marks the oldest European freshwater crab record south of the Alpine orogene up to now. Although the dentition is not well preserved, in the middle group three interteeth can be recognised.

Potamon speciosus (VON MEYER, 1844)
Figs. 4E, F, 5C

- 1805 *Cancer minutus* LINNÉ. – KARG, p. 43, pl. 1, fig. 2.
*1844a *Grapsus speciosus*. – VON MEYER, p. 331.
1844b *Grapsus speciosus*. – VON MEYER, p. 690.
1862 *Grapsus speciosus* MEYER. – VON MEYER, p. 168, pl. 19, figs. 1-2.
1865 *Telphusa speciosa* VON MEYER, 1863. – HEER, p. 379, fig. 242.
? 1865 *Gecarcinus punctatus*. – HEER, p. 379, fig. 243.
1874 *Pseudotelphusa speciosa*. – CAPELLINI, p. 559 4.
1885 *Grapsus speciosus*. – QUENSTEDT, p. 400.
p 1885 *Pseudotelphusa speciosa*. – MERCANTI, p. 215.
1904 *Potamon speciosus* (VON MEYER). – RATHBUN, p. 230.
1916 *Potamonautes speciosa*. – SZOMATHY, p. 387.
? 1916 *Gecarcinus punctatus*. – SZOMBATHY, p. 395.
1928 *Potamon speciosum* (VON MEYER). – GLAESSNER, p. 214.
1929 *Potamon speciosum* VON MEYER, 1862. – GLAESSNER, p. 338.
1930 *Potamon speciosum*. – GLAESSNER, p. 168, pl. 8 fig. 6.
1955 *Propotamonautes speciosus*. – BOTT, p. 310.
? 1955 *Archithelphusa punctulatus*. – BOTT, p. 310.
1969 *Potamon speciosus*. – GLAESSNER, p. 524, fig. 331.
1969 *Propotamonautes speciosus*. – BOTT, p. 271.
? 1969 *Archithelphusa punctulatus*. – BOTT, p. 272.
? 1997 *Gecarcinus punctatus*. – BOLLIGER & GUBLER, p. 623.
1997 *Potamon* (= *Telphusa*) *gracilis*. – BOLLIGER & GUBLER, p. 623.
? 2007 *Archithelphusa punctata* (HEER, 1865). – FELDMANN et al., p. 78, tab. 1.
2007 *Propotamonautes speciosus* (VON MEYER, 1862). – FELDMANN et al., p. 78, tab. 1.

Neotype: SMNK–PAL 2626 (Fig. 4 E).

Type locality: “Upper quarry” (Oberer Salenhof) and “Lower quarry” (Ziegelhof) near Öhningen, Schiener Berg (8°55’E/47°40’N), Baden-Württemberg, Germany.

Type horizon: Calcareous Öhningen Beds, middle Miocene, late Badenian/early Sarmatian, 13–12.7 Ma, early MN 7 (GEYER et al. 2003; GIERSCH 2004; ZIEGLER et al. 2005).

Material: SMNK–PAL 2624, 2627, 2630, three uncatalogued specimens; SMNK–PAL ex Sammlung Freiburg i. Br. 37/1263, 37/1264, 37/1270; SMNK–PAL ex Sammlung Mannheim 62, one uncatalogued specimen; SMNS 4382, 3795; permanent loan of the SMNK to the Museum Fischerhaus, Wangen am Untersee: one uncatalogued specimen and SMNK–PAL 2628; PIMUZ 018054; loan of the ETH Zurich to the PIMUZ: one specimen; NMBE Oe23.

Description: Except for the specimens SMNK–PAL 2626 (neotype) and SMNS 3795, in all known fossils of *Potamon speciosus* only the sternal side is visible. The lost holotype (depicted by VON MEYER, 1862; Fig. 5C) and the neotype, with the carapaces flipped away to the front, probably represent exuviae. All specimens still have their extremities articulated but are strongly compressed.

The carapace surface appears to be smooth (SMNK–PAL 2626, Fig. 4 E), as most of its sculpture apparently has been eroded away. Traces of postorbital cristae and cervical grooves are observable. SMNS 3795 shows a sharp anterolateral margin and a granular anterior branchial region (Fig. 4F). Both chelae are similar in size and shape, heterochely is not recognisable. The teeth of the chelae are evenly formed. Carpus of chelae with carpal spine; lateral to the carpal spine a row of granules is situated. Ambulatory meri without sharp subterminal spine. The lost type was, according to the image given by VON MEYER, a carapace of a male with prominent epifrontal lobes, a median mesogastric lobe and a granulose frontal area (Fig. 5C). The cervical grooves were deep, the urogastric region divided by an anterior cardiac lobe. The branchial regions were granulose. GLAESSNER (1930) gives descriptions of further characters, which are not visible in the available specimens: front densely covered with coarse granules, granules transversely oriented on the branchial region, an “angular groove on both sides of the large anterior plate” of the sternum. As main difference to *Potamon quenstedti* the ischium of the maxilliped 3 is shorter and wider (width to length 1:1.33) than in *P. quenstedti* (width to length 1:1.66) (GLAESSNER 1930).

Occurrence: Beside the type locality of the Öhningen Beds, a chelae fragment from the site of Kleineisenbach near Munich (Bavaria) is known (11°35’50”E/48°21’52”N, Sarmatian, MN 8, ?12.8–12.5 Ma; PRIETO 2007, 2008), that we assign to *Potamon speciosus* with reservation.

Comment: VON MEYER (1844a) described *Potamon speciosus* based on a specimen that originated from the “Collection Meersburg” and was housed in the “Collection Carlsruhe”, now SMNK. According to VON MEYER (1844a) this was the same specimen that KARG (1805) mentioned earlier. A second specimen from the “Collection LAVATER” in Zurich was already known at that time. It was initially thought to be the counterplate of the specimen from the

“Collection Carlsruhe”, however, this was falsified by VON MEYER (1844b). Both specimens were depicted by VON MEYER (1862, pl. 19 fig. 1 and 2). Here, we reprinted the figure of the specimen from the “Collection Carlsruhe” (Fig. 5C). As the description of *P. speciosus* is based solely on the specimen from the “Collection Carlsruhe” (VON MEYER 1844a), this specimen implicitly represents the holotype of *P. speciosus* and the specimen of the “Collection LAVATER” consequently does not represent a syntype. Unfortunately the holotype can not be retrieved from the SMNK. GLAESSNER (1930) examined twelve specimens of *Potamon speciosus* both from the SMNK and the SMNS and described characters that are not detectable in the available specimens. This indicates that further specimens housed in the SMNK were lost due to war damages. However, the holotype was probably lost earlier, as already GLAESSNER (1930) depicted SMNK-PAL 2626 instead of VON MEYER’s type specimen.

The discussion on the occurrence of a second species of freshwater crab in the Öhningen beds makes the designation of a neotype necessary. The specimen from the “Collection LAVATER” can not unequivocally be identified. The male specimen PIMUZ 018054 shows a very similar position and shape of the chelae and first walking legs compared to the figure of VON MEYER (1862, pl. 19, fig. 2), but the posterior legs differ in shape and preservation. We designate the female SMNK-PAL 2626 as neotype, because it is the best preserved specimen of *Potamon speciosus* with both sternal side, carapace and extremities being visible.

All investigated specimens are not very well preserved due to the dorso-ventral compression. This makes a morphological comparison with the other species of the Northalpine Foreland Basin (the older *Potamon quenstedti* and the younger *Potamon proavitum* and *Potamon hegauense* n. sp.) or an evaluation of the relationship between these species impossible. However, as with *Potamon quenstedti*, SZOMBATHY assigned *Potamon speciosus* to the African genus *Potamonantes*. Again, this was falsified by GLAESSNER (1930) and irrespective of this, BOTT (1955) assigned *P. speciosus* to a new genus *Propotamonantes* to affirm its potamonautid relationship. Neither the assignment of SZOMBATHY nor that of BOTT is based on a convincing morphological argumentation (see comments to *Potamon quenstedti*). The absence of heterochely could reflect a closer relationship to the subgenera *Pontipotamon* or *Euthelphusa* than to the subgenus *Potamon*.

HEER (1865) described a second species from the Öhningen beds, *Gecarcinus punctatus*. He gives two rather schematic figures of both species, showing *Potamon speciosus* with a straight, potamonautid-like postfrontal crest (Fig. 5A) while the carapace of *Gecarcinus punctatus* resembles more closely the genus *Potamon* (Fig. 5B). GLAESSNER (1929a) already doubted the existence of a second species and later synonymised it with *Potamon speciosus* arguing that differences depicted by HEER are due to different states of preservation (1930). BOTT (1955), unaware of GLAESSNER’s synonymisation, assigned *Gecarcinus punctatus* to a new genus, *Archithelphusa*. The neotype gives only rudimentary evidence of a postorbital crest, while SMNS 3795 shows a left branchial region similar to *Potamon quenstedti* (granules, sharp anterolateral margin,

Fig. 4F). Given the poor illustration of HEER, compared to the figure given by VON MEYER (1862) (Fig. 5C), we follow GLAESSNER in synonymising *G. punctatus* with *Potamon speciosus*, although the existence of a second species can not definitely be ruled out.

Potamon proavitum GLAESSNER, 1928

Fig. 4G

- v *1928 *Potamon proavitum*. – GLAESSNER, p. 212, pl. 4 (lower fig. & carbon copy).
- v 1929 *Potamon proavitum* GLAESSNER, 1928. – GLAESSNER, p. 338.
- v 1930 *Potamon proavitum*. – GLAESSNER, p. 170.
- v 1940 *Potamon proavitum* – KÖRÖSSY, p. 106.
- v 1955 *Pseudopotamon proavitum* – BOTT: 310.
- v 1998 *Potamon proavitum* GLAESSNER, 1928. – MÜLLER: 39.
- v 2005 *Potamon proavitum* GLAESSNER, 1928. – GROSS & KLAUS, p. 21.
- v 2005 *Potamon proavitum* GLAESSNER, 1928. – KLAUS & GROSS, p. 6.
- v 2007 *Potamon proavitum* GLAESSNER, 1928. – FELDMANN et al., p. 78, tab. 1.

Holotype: LMJ 5828, (Fig. 4G).

Type locality: Clay pit “Wolf“/Andritz (15°26’5”E/47°5’57”N, near Graz, Styria, Austria).

Type horizon: Pelitic sediments of the Gleisdorf Formation, isochronous with the site of Gratkorn (middle Miocene, early late Sarmatian, MN 7-8, 12.2-12 Ma; GROSS et al. 2007; HARZHAUSER et al. 2008; GROSS 2008).

Description: GLAESSNER (1928) gives an extensive description of the well-preserved female type specimen. With more material available from the site of Gratkorn, we can identify the following characters that distinguish *Potamon proavitum* from *Potamon quenstedti*: the postfrontal crest being rather transverse than straight in *P. proavitum* (median anterior to lateral posterior, see Fig. 4J; less significant in the type specimen), the branchial granules covering the whole lateral branchial region from anterior to posterior with the granules being more transversely oriented, in some specimens appearing as transverse ridges.

Occurrence: Beside the type specimen, numerous carapace and claw fragments (LMJ 203389-203418, 203726-203728) were found in the clay pit “St. Stefan“/Gratkorn (15°20’55”E/47°8’17”N, Styria, Austria; Figs. 4H, J; GROSS & KLAUS 2005; KLAUS & GROSS 2005).

Comment: GLAESSNER (1928) proposed that *Potamon proavitum* might be closely related to the extant *Potamon ibericum*. He based his hypothesis on a character of the mesogastric region. The mesogastric region continuously broadens from anterior to posterior in *P. proavitum* and *P. ibericum* while it shows anteriorly a narrower zone in the fossil *Potamon antiquum* and in extant *Potamon fluviatile*

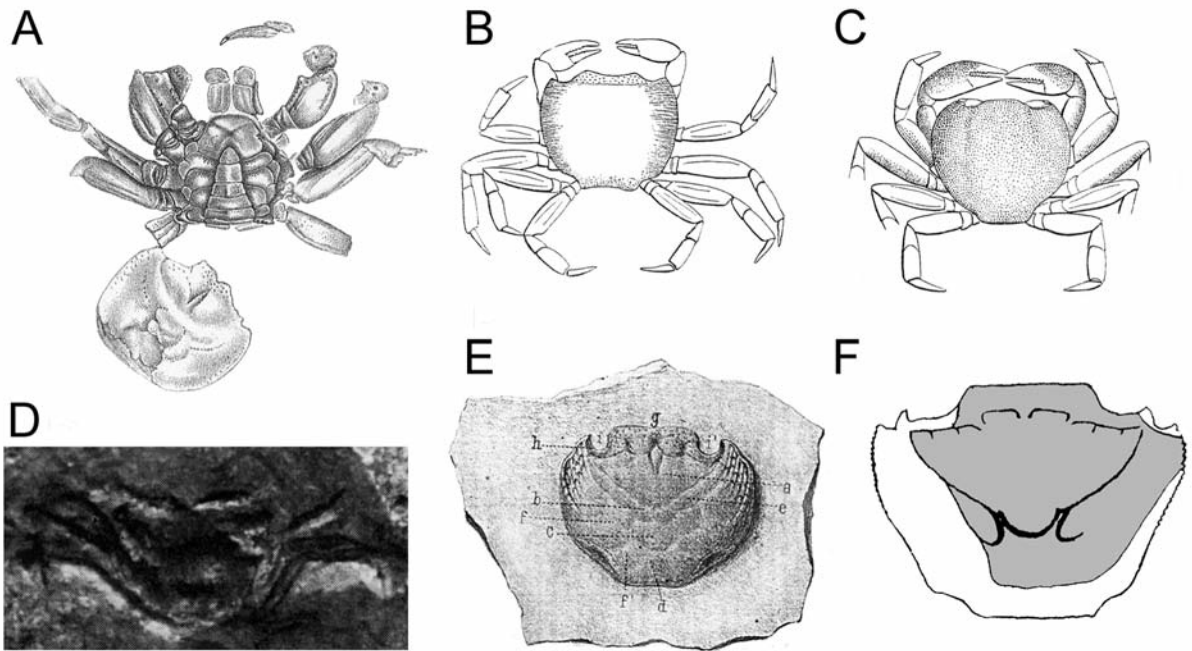


Fig. 5. Reprints of illustrations. **A** – VON MEYER (1862, pl. 19 fig. 1), *Potamon speciosus*, lost holotype; **B** – HEER (1865, fig. 242), *Potamon speciosus*; **C** – HEER (1865), fig. 243, *Gecarcinus punctatus*; **D** – KÖRÖSSY (1940, fig. 9), *Potamon hungaricum*; **E** – CAPELLINI (1874, pl. 7 fig. 2) *Potamon castellanense*; **F** – GLAESSNER (1933, text-fig. p. 12), *Potamon sivalense*, holotype NHML 28075, dorsal, with reconstructed parts.

and *Potamon potamios*. We examined the fossil material, the figures of *Potamon antiquum* given by SZOMBATHY (1916) and LÖRENTHEY (1898), and specimens of the extant species. However, what GLAESSNER meant remains cryptic. The anterior part of the mesogastric area is, posterior to the median mesogastric lobe, not distinctly defined and is similar among all crabs of the genus *Potamon*.

Potamon? hungaricum KÖRÖSSY, 1940

Fig: 5D

- *1940 *Potamon hungaricum*. – KÖRÖSSY, p. fig. 9.
- 1955 *Pseudopotamon hungaricum*. – BOTT, p. 310.
- 1969 *Pseudopotamon hungaricum*. – BOTT, p. 272.

Holotype: Specimen lost (P. MÜLLER, pers. comm.). KÖRÖSSY designated the specimen with the whole outline of the carapace and the five right extremities visible as holotype (Fig. 5D).

Paratype: Specimen lost (P. MÜLLER, pers. comm.). According to KÖRÖSSY, the specimen with the posterior carapace margin, the left chelae and four right pereiopods visible, is the paratype.

Type locality: Clay deposits of Ždaňa (21°22' 26"E/48°35' 12"N, Hernádzsadány in KÖRÖSSY 1940, Slovakia).

Type horizon: Marine to brackish pelites of the Stretava Formation, middle Miocene, early Sarmatian (*Mohrensternia*-lower *Ervilia* Zone), MN 7–8, 12.8–12.2 Ma; KÖRÖSSY 1940; ZLINSKÁ & FORDINÁL 1995; KALIČAK 1996; KOVÁČ 2008).

Description: The better preserved specimen described by KÖRÖSSY, most probably a juvenile, has a maximum width of 14 mm and maximum length of 11 mm. According to KÖRÖSSY the frontal lobe is straight, in contrast to *Potamon antiquum*. *Potamon? hungaricum* differs from *Potamon proavitum* in having more slender and longer legs and more robust chelae, and from *Potamon quenstedti* in its smaller size and different carapace proportions.

Occurrence: ZLINSKÁ & FORDINÁL (1995) mentioned claws of crabs from the same formation a few kilometres to the east at Slanská Huta (21°28' 11"E/48°35' 40"N) that probably belong to *Potamon hungaricum*.

Comment: KÖRÖSSY (1940) discovered this species in pelitic layers in association with a reduced marine biota. Also the findings at Slanská Huta are associated with lower Sarmatian marine taxa (ZLINSKÁ & FORDINÁL 1995). Thus the possibility arises that the specimens described by KÖRÖSSY represent marine crabs rather than potamids. Especially the very long and narrow legs (see Fig. 5E) argue strongly against the assignment to the genus *Potamon*.

Potamon hegauense n. sp.

Fig. 2A, B

- v 1971 *Potamon (Pontipotamon) ibericum* BIEBERSTEIN n. subsp.? – BACHMAYER & PRETZMANN, p. 284.
 v 1972 *Potamon (Pontipotamon) ibericum*. – PRETZMANN, p. 71.
 1994 *Potamon (Pontipotamon) ibericum* BIEBERSTEIN. – FORDINÁL, p. 72, pl. 11, fig. 4.
 v 1998 *Potamon (Pontipotamon) ibericum* BIEBERSTEIN, 1971 n. subsp.? – MÜLLER, p. 39.
 v 2003 *Brachyuridea* indet. – HEIZMANN et al., p. 12.

Etymology: The species name *hegauense* refers to the geographic region of the type locality, the Hegau, situated north of the Lake Constance in SW Germany.

Holotype: SMNK–PAL 6520 (Fig. 2A).

Paratypes: Four claw fragments (SMNK–PAL 6522) and one right cheliped merus (SMNK–PAL 6523a, b) (Figs. 2B), one carapace fragment (SMNK–PAL 6521).

Type locality: Höwenegg (8°44'35"E/47°54'43"N, near Immendingen, Baden-Württemberg, SW Germany).

Type horizon: Calcareous marl layers, Höwenegg Beds, Upper Freshwater Molasse, late Miocene, MN 9, 10.3–10.4 Ma (SWISHER 1996; HEIZMANN et al. 2003, S. GIERSCH, pers. comm.).

Diagnosis: Transverse postfrontal crista, carapace granules/ridges absent, ventral side of cheliped merus without granules.

Description: The holotype specimen is rather small (max. width: 1.9 cm; max. length: 1.4 cm), probably belonging to a juvenile. With exception of few carapace fragments at the posterior it represents a mold of the interior. The left postfrontal crista is preserved, indicating its slightly transverse orientation from median anterior to lateral posterior. The epibranchial lobes are prominent, not extending far beyond the (preserved left) postfrontal crista. The median mesogastric lobe is present, and shorter than the neighbouring epigastric lobes. All structures in front of the postfrontal crest are not preserved, nor are both anterolateral margins. The cervical groove is discontinuous, urogastric and cardiac regions are well defined. The urogastric region is divided by a median lobe, extending anteriorly from the cardiac region. There are no remains of any carapace granules, neither on SMNK–PAL 6520 nor on SMNK–PAL 6521. The size of the chelae fragments argues for the existence of much larger specimens. The claw teeth are small and conical, a crushing cusp is absent. Both dactylus and pollex show laterally shallow longitudinal grooves. The preserved right cheliped merus is covered on its lateral side with small ridges. Contrary to extant species, the ventral side of the merus shows no teeth or granules. On its dorsal margin small and low granules are situated.

Occurrence: Beside the type locality of the Höwenegg, freshwater crab fragments of Pannonian origin were described from four sites in the Vienna and the Danube Basin, for which we propose an assignment to *Potamon hegauense*:

Eichkogel (374 claw fragments, NHMW 1971–1440 A, 16°17'42"E/48°3'60", near Mödling, Lower Austria, Austria; freshwater marls, late Pannonian, Papp-Zone "H", MN 11, c. 8.2 Ma; BACHMAYER & PRETZMANN 1971; DAXNERHÖCK 1996; HARZHAUSER & BINDER 2004; HARZHAUSER & TEMPFER 2004; HARZHAUSER et al. 2004).

Orešany (claw fragments, 17°53'41"E/48°30'29"N, Považsky Mts., Slovakia; alm, late Pannonian, Papp-Zone "H", MN 11, c. 8.2 Ma; FORDINÁL 1994; FORDINÁL & NAGY 1997).

Richardhof–Wald (claws, 16°16'12"E/48°3'39"N, close to the locality Eichkogel; freshwater marls/marly limestones, late Pannonian, Papp-Zone "G", MN 10, c. 9.6 Ma; DAXNER-HÖCK 1996; HARZHAUSER & BINDER 2004; HARZHAUSER & TEMPFER 2004; HARZHAUSER et al. 2004).

Richardhof-Golfplatz (claws, 16°16'8"E/48°3'23"N, close to the locality Eichkogel; freshwater marls/marly limestones, middle Pannonian, Papp-Zone "E", late MN 9, c. 10.1 Ma; DAXNER-HÖCK 1996; HARZHAUSER & BINDER 2004; HARZHAUSER & TEMPFER 2004; HARZHAUSER et al. 2004).

Comment: *Potamon hegauense* differs from the spatially closest species *Potamon quenstedti* in having a transverse postfrontal crest and from the chronologically closest, *Potamon proavitum*, by the absence of any carapace granules. The lack of carapace granules of the fragment SMNK–PAL 6521 might be due to poor preservation and *P. hegauense* and *P. proavitum* are rather similar in respect of their transverse postfrontal cristae (at least in juvenile specimens). The Pannonian *P. hegauense* marks the last occurrence of true freshwater crabs at the northern/eastern fringe of the Alps.

BACHMAYER & PRETZMANN (1971) investigated the claw fragments of the Eichkogel site in Austria and extrapolated from the basal width of the largest dactylus fragment (7 mm) to a dactylus length of 25 mm and further to a carapace length of 40 mm. They also examined number and alignment of the claw teeth. The dactyli show 20–27 teeth and the pollices 21–26. Based on both carapace-length estimation and number of teeth they eliminated a close relationship to the subgenera *Euthelphusa*, *Potamon*, and *Orientopotamon* (their *Centropotamon*) and assigned it to *Potamon (Pontipotamon) ibericum* BIEBERSTEIN, 1809. Unfortunately they conceal how they calculated the carapace-length exactly, and refrain from giving a statistical comparison with dentition patterns of extant *Potamon fluviatile*, *Potamon ibericum* and *Potamon potamios*. The use of dentition patterns in general was criticised by BOTT (in PRETZMANN 1972), especially concerning genus assignments (but see ASHKENAZI et al. 2005 for a thorough morphometric comparison of fossil and extant chelae). However, by qualitative examination of several specimens, we can confirm that *Potamon fluviatile* does not seem to exceed 20 teeth per claw finger.

Potamon castellanense (SZOMBATHY, 1916)

Fig. 5D

- 1874 *Pseudotelphusa speciosa*. – CAPELLINI, p. 559, pl. 7, figs. 1-2.
 1885 *Pseudotelphusa speciosa*. – MERCANTI, p. 215, pl. 2 fig. 15 [cop. CAPELLINI 1874, pl. 7, fig. 2].
 1904 *Potamon speciosus*. – RATHBUN, p. 231.
 *1916 *Pseudotelphusa castellanensis*. – SZOMBATHY, p. 399, pl. 8, fig. a, b [cop. CAPELLINI 1874, pl. 7, figs. 1-2].
 1928 “*Pseudotelphusa*” *castellanensis* SZOMBATHY. – GLAESSNER, p. 214.
 1929 *Potamon? castellanense* (SZOMBATHY), 1916. – GLAESSNER, p. 337.
 1930 *Potamon castellanensis*. – GLAESSNER, p. 170.
 1955 *Pseudopotamon speciosus*. – BOTT, p. 310.
 1969 *Pseudopotamon speciosus*. – BOTT, p. 272.
 2007 *Potamon? castellanense* (SZOMBATHY, 1916). – FELDMANN et al., p. 78, tab. 1.

Holotype: Specimen lost, figure given by CAPELLINI (1874) (Fig. 5D).

Type locality: “Cerretello” near Castellina Marittima, Marmolaio valley (10°36' E/43°24'), Tuscany, Italy.

Type horizon: “Strati a Congerie”, “Lago-Mare” facies, latest Miocene, late Messinian, MN 13, 5.5-5.3 Ma (CAPELLINI 1874; ESU 2007, S. DOMINICI, pers. comm.).

Description: The image given by CAPELLINI, and refigured by SZOMBATHY (1916), shows a carapace with a very wide frontal margin and very narrow orbits (Fig. 5D). The frontal area seems to be covered with small granules, while on the anterolateral region, more coarse and transversely oriented granules are situated. If the drawing is accurate, several characters would be unique to freshwater crabs: external orbital angles and epibranchial teeth seem to be merged, a mesogastric lobe is present, but the flanking epigastric lobes are absent; instead, each postorbital crista forms an anomalous sharp lobe. The remaining carapace sculpture is depicted more potamid-like, cervical grooves are prominent, urogastric and cardiac regions are distinct with the urogastric region divided by a cardiac lobe. It seems very probable, that this image is not adequate and shows a distorted potamid postfrontal crest. Thus, we endorse, unless new findings support the morphology as depicted by CAPELLINI, that *Potamon castellanense* belongs to the genus *Potamon*, and definitely not to the Potamonautidae.

Comment: Currently, no other freshwater crab species than *Potamon fluviatile* is found in Italy, a species occurring both in Italy and Greece. *P. fluviatile* dispersed from Greece to Italy probably at the end of the Pleistocene, as suggested by molecular data (JESSE et al. 2008). Therefore, *Potamon castellanense* is probably not closely related to *P. fluviatile*. Nevertheless, it could belong to the subgenus *Euthelphusa*, linking the ranges of *P. fluviatile* from Greece and *Potamon*

algeriense from Northern Africa, the latter probably reaching Africa during the Messinian event (BRANDIS et al. 2000). The question remains if *P. fluviatile* replaced *P. castellanense*, or if *P. castellanense* became extinct before the arrival of *P. fluviatile* (during the glacial cooling?). No freshwater crab fragments are known so far from the Italian Pliocene and Pleistocene.

Potamon (Pontipotamon?) antiquum SZOMBATHY, 1916

Fig. 2C, D

- v 1898 *Telphusa fluviatilis* LATREILLE. – LÖRENTHEY, p. 107, pl. 8, fig. 7.
 v 1904 *Telphusa fluviatilis*. – RATHBUN, p. 231.
 v *1916 *Potamon antiquum*. – SZOMBATHY, p. 384, figs. 4a, 5, 6a, b; pl. 3, figs. 1-8.
 v 1928 *Potamon antiquum* SZOMBATHY. – GLAESSNER, p. 215.
 v 1929 *Potamon antiquum* SZOMBATHY. – LÖRENTHEY & BEURLEN, p. 230, pl. 15, figs. 9-14, text-figs. 4-6.
 v 1929 *Potamon antiquum* SZOMBATHY, 1916. – GLAESSNER, p. 337.
 v 1930 *Potamon antiquum* SZOMBATHY. – GLAESSNER, p. 170.
 v 1940 *Potamon antiquum*. – KÖRÖSSY, p. 105.
 v 1955 *Pseudopotamon antiquum*. – BOTT, p. 310.
 v 1969 *Pseudopotamon antiquum*. – BOTT, p. 272.
 v 2007 *Potamon antiquum* SZOMBATHY, 1916. – FELDMANN et al., p. 78, tab. 1.

Neotype: MTM 1446-5 (Fig. 2C).

Paratypes: MTM 1446-6 (Fig. 2D), 1446-7. Eight additional carapaces and 44 fragments, Budapest.

Type locality: Süttő (18°24'E/47°42'N, Komitat Komárom-Esztergom, Hungary; Sittelbruck-stock, Haraszti-quarry, quarry in the Diós-valley).

Type horizon: Calcareous tufa/travertine, middle Pleistocene, 310-240 ka (SIERRALTA et al. 2007 and submitted, P. SUMEGI, pers. comm.).

Description: SZOMBATHY (1916) gives a very detailed description of *Potamon antiquum*. Nevertheless, many of the carapace and pereopod characters he described are known to be subject to intraspecific variability (BRANDIS et al. 2000). The frontal area is granulose, the frontal margin is nearly straight (but transverse as in *Potamon proavatum* in the figure of LÖRENTHEY 1898). The epifrontal lobes are prominent and reach beyond the postfrontal crest in some specimens, the median mesogastric lobe reaches the height of the postfrontal crest (Fig. 2C, D). The cervical groove is deep, as are the grooves that separate mesogastric, urogastric, and cardiac areas. The urogastric area is divided by a median cardiac lobe. SZOMBATHY (1916) stated that the ischium of the maxilliped 3 has a ratio width to length of 1:1.5 (Fig. 2E).

Occurrence: The following close sites to the type locality of Süttő were mentioned by SZOMBATHY, all referred more or less to the latest Pliocene and Pleistocene:

Duna-Almás (= Dunaalmás, 5 poorly preserved carapace fragments 18°19'E/47°43'N, Komitat Komárom-Esztergom, Hungary): calcareous tufa, late Pliocene – ?Pleistocene (P. SUMEGI & P. MÜLLER, pers. comm.).

Mogyorós quarry (= Mužla, today in Slovakia, 2 carapaces, 2 carapace fragments, 18°35'E/47°47'N): calcareous tufa, middle Pleistocene, ?780-130 ka (P. SUMEGI, pers. comm.).

Bajót (one carapace, two carapace fragments, 18°33'E/47°43'N, Komitat Komárom-Esztergom, Hungary): calcareous tufa, middle Pleistocene, ?800-500 ka (P. SUMEGI, pers. comm.).

Comment: SZOMBATHY (1916) speculated that *Potamon antiquum* was distributed throughout the present range of *Potamon* and later split into the extant species *Potamon fluviatile*, *Potamon ibericum* and *Sinopotamon denticulatum*. This hypothesis is based upon insufficient knowledge of freshwater crab diversity at that time and the use of highly variable carapace characters. The identification of a transverse ridge between sternites 7 and 8 (Fig. 2E, inset) excludes a closer relationship to Asian species for *P. antiquum* and argues for the assignment to the potamid subfamily Potaminae.

GLAESSNER (1928), in his critic of SZOMBATHY's work, stated that the epifrontal lobes (elongated beyond the postfrontal cristae in *Potamon antiquum*) are the only character that distinguishes this species from both the recent *Potamon ibericum* and from the other Miocene species. This character led GLAESSNER to the assumption that *P. antiquum* is more closely related to *Potamon fluviatile*, also showing more elongated epifrontal lobes. However, these elongated lobes are not present in all studied specimens of *P. antiquum* (e.g., Fig. 2D) and the application of this character remains doubtful, concerning species identification with extant *Potamon* (BRANDIS et al. 2000). The very young age of most sites where *P. antiquum* was found, together with the fact that at present only *Potamon ibericum* occurs in the Danube drainage system, argues against a closer relationship with *Potamon fluviatile*. The young age of *P. antiquum* even raises the question, of whether it could be synonymised with *P. ibericum*. Only a chronospecies approach can differentiate here between recent and fossil freshwater crabs.

Potamon? *sivalense* GLAESSNER, 1933

Fig. 2G, H

- *1933 *Potamon (Potamon) sivalense*. – GLAESSNER, p. 12 (incl. figure in text), pl. 3, fig. 4.
 2004 *Potamon (Potamon) sivalense*. – SCHWEITZER et al., p. 90, tab. 1.
 2007 *Potamon silvalense* GLAESSNER, 1933. – FELDMANN et al., p. 78, tab. 1.

Holotype: NHML 28075 (female); CAUTLEY coll. (Fig. 2H).

Paratype: NHML 28074 (female, sternum only); CAUTLEY coll. (Fig. 2G).

Type locality: Siwalik Hills, India/Pakistan?

Type horizon: "Siwalik Beds" (GLAESSNER 1933), Neogene, c. 16-5 Ma (PILBEAM et al. 1977; GAUTAM et al. 2000).

Description: GLAESSNER (1933) noted that the two specimens are poorly preserved with few specific characters. He illustrated a reconstruction of the dorsal side of the holotype (NHML 28075). Based on this reconstruction, epifrontal lobes are present, the postfrontal cristae are slightly transverse, the right anterolateral margin shows traces of small teeth. Cervical grooves and H-like groove are prominent, and the urogastric and cardiac regions are not distinctly separated.

Occurrence: RHAGAVAN et al. (2007) reported fragments of freshwater crabs ("*Potamon* sp.") from the Upper Siwalik Subgroup of India (Pinjor Formation, Ghaggar River section; "otter horizon": mudstone/siltstone, floodplain deposits, c. 2.14 Ma; locality "G3", above the otter horizon, fluviatile deposits). There are also fragments of older age from the Indian Siwaliks known (Tatrot Formation, c. 2.5 Ma, Kanthro, Himachal Pradesh; R. PATNAIK, pers. comm.). These comprise fragments of chelae, either with many conical teeth of different size or fragments with large proximal crushing cusps (Fig. 2F).

Comment: The locality of *Potamon sivalense* overlaps with the present range of the freshwater crab family Gecarcinucidae. The preservation of the fragments does not allow an unambiguous assignment to the Potamidae and the genus *Potamon*; e.g., the recent gecarcinucid species *Sartoriana spinigera* (WOOD-MASON, 1871) has distinct epifrontal lobes, too. The morphology of one chela fragment (Fig. 2F, upper fragment) with its prominent three proximal teeth in fact closely resembles the character state as in *S. spinigera* (Fig. 2F, inset, SMF 26057). However, in extant *S. spinigera* the two most proximal teeth are always strongly abraded.

Unfortunately the exact type location of *Potamon sivalense* is not documented. As the Siwalik molasse was deposited at least through the entire Miocene, it remains impossible to correlate this Asian fossil potamid with the European specimens. Given the recent discovery of fragments (RHAGAVAN et al. 2007 and R. PATNAIK, pers. comm.) and the high diversity of extant freshwater crabs on the Indian subcontinent, it is likely that the Siwalik Group will yield a rich fossil freshwater crab fauna.

Potamon sp.

- 1972 *Potamon* sp. – PRETZMANN, p. 72.

Material: Two small pollices from juveniles (NHMW).

Location: Sofça (30°10'E/39°38'N, near Kütahya, Turkey; mentioned in BECKER-PLATEN et al. 1975 under locality

no. "65", limnic marls, middle Miocene, MN 7-8, ?13.2-11.2? Ma (BECKER-PLATEN et al. 1975 ; DE BRUIJN et al. 1992 ; SARAÇ 2003, Y. İSLAMOĞLU, pers. comm.).

Comment: PRETZMANN points out that both pollices have a crushing cusp, and thus suggested relationships to either *Potamon potamios*, *Potamon setiger* (both species now occurring more to the south) or *Potamon ibericum meandris* (subspecies not regarded valid any more, see BRANDIS et al. 2000). A closer relationship to the subgenus *Orientopotamon* cannot be excluded.

Potamon (Orientopotamon ?) sp.

1972 *Potamon (Centropotamon) magnum?* – PRETZMANN, p. 71.

Material: Six nightdactyli (NHMW).

Location: Yemliha (35°15'E/38°53'N, near Kayseri, Turkey; mentioned under Himmetdede–Yemliha in PRETZMANN 1972, corresponding to locality no. "76" in BECKER-PLATEN et al. 1975) and Çevril (35°27'E/38°56'N, near Kayseri, Turkey; mentioned under Erkiilet-Cevil in PRETZMANN 1972, corresponding to locality no. "19" in BECKER-PLATEN et al. 1975). Both sites are of the same facies and age: fluvial, late Miocene, Vallesian-early Turolian, MN 9-12, 11.2-7.1 Ma (BECKER-PLATEN et al. 1975, SARAÇ 2003, Y. İSLAMOĞLU, pers. comm.).

Comment: PRETZMANN (1972) assumes identity with the extant species *Potamon (Orientopotamon) magnum* based on dentition patterns (23 teeth in total, basal groups 2-3 interteeth, middle groups 4-5 interteeth, see PRETZMANN 1971 for terminology). As stated above, it is questionable to identify species merely by dentition patterns. Especially the assignment to an extant species seems to be disputable.

Potamon (Potamon) cf. potamios (OLIVIER, 1804)

1991 *Potamon fluviatilis*. – HORWITZ & GARFINKEL, p. 70.

2005 *Potamon* sp. – ASHKENAZI et al., p. 675, fig. 4.

2006 *Potamon cf. potamios*. – HORWITZ & ASHKENAZI, p. 168.

Material: 5033 freshwater crab fragments of 1-40 mm size from the site of Gesher Benot Ya'aqov; housed in the archaeozoological laboratory, Dep. of Evolution, Systematics and Ecology, Hebrew University, Jerusalem.

Locations: Gesher Benot Ya'aqov (33°1'N/35°38'E, Jordan valley north of the Sea of Galilee, Israel), lacustrine-riparian sediments; early-middle Pleistocene, Acheulean, OIS 20.2–18.2 (ASHKENAZI et al. 2005). ASHKENAZI et al. (2005) also mentioned three other sites in the Upper Jordan Valley, where remains of fossil freshwater crabs were found: 'Ubeidiya (32°41'N/35°33'E; 1.4 Ma), Ohalo II (32°43'N/35°34'E; upper Pleistocene, 23 ka) and Eynan/Ain Mal-

laha (33°18'N/35°31'E; anthropogenic deposit, late Epi-palaeolithic, Natufian, 10.5 ka, ASHKENAZI et al. 2007). The younger neolithic site of Gesher (32°37'N/35°33'E; Jordan Valley, anthropogenic mud/clay deposits, HORWITZ & ASHKENAZI 2006) also yielded plenty of fragments of *Potamon cf. potamios* (HORWITZ & GARFINKEL 1991; HORWITZ & ASHKENAZI 2006).

Comment: Evidence of burned crab fragments at the site of Gesher indicate that freshwater crabs were used as food source by neolithic humans (HORWITZ & GARFINKEL 1991). ASHKENAZI et al. (2007) conducted detailed morphometric studies on the chelae found in Gesher Benot Ya'aqov and Eynan/Ain Mallaha, taking different measurements of dactyli and pollices and compared these data with extant *Potamon potamios*. They found significant differences between fossil and extant claws, both concerning size and shape.

3. Palaeoecology

Application of a nearest living relative approach, using extant species of the genus *Potamon* for comparison, should allow inference on abiotic palaeoecological and palaeoclimatological conditions. Unfortunately, few ecological data for potamid crabs are available (e.g., ERPENBECK 1970; BARBARESI et al. 2007) and present potamid freshwater crabs seem to show high plasticity concerning abiotic factors. Nevertheless, despite these difficulties, we can set at least some limits for ecological parameters correlated with the occurrence of *Potamon*.

Water chemistry. – Experimentally, freshwater crabs can survive in saline water (see MORRIS & VAN AARDT 1998, and references therein), e.g., *Potamonautes warreni* (Potamonautidae) was shown to be able to regulate water and salt balance in up to 40 % seawater, but not in 80 % seawater (MORRIS & VAN AARDT 1998), *Potamon fluviatile* seems to tolerate 80 % seawater but dies at higher concentrations (HARRIS & MICALLEF 1971). However, in the natural environment, *Potamon* is exclusively found in freshwater. On the Peloponnesus, juveniles of *Potamon fluviatile* can be found in streams, a few metres from the estuary mouth, but they never enter the brackish water (pers. observation). Therefore, the occurrence of *Potamon* indicates definitely a freshwater environment. This is in agreement with environmental data of the fossil sites with *Potamon* species. All localities, except Ždaňa and Slanská Huta, with the questionable potamid *Potamon hungaricum*, belong to limnic and/or fluvial facies.

The Mediterranean and Paratethys Sea as well as the brackish Pannonian Lake were a considerable barrier for freshwater crab migration. Changing seaways and landbridges and the uplift of the Alpine mountain chain might have had a significant control for their palaeogeographic distribution as for other biota (see RÖGL 1998; POPOV et al. 2004; PILLER et al. 2007). The still fragmentary knowledge of spatial and temporal freshwater crab distribution makes further palaeobiogeographic considerations arbitrary at the moment.

Remarkably, the fossil records originate mainly from tufaceous limestones or marls. An elevated CaCO_3 concentration was demonstrated for the habitat of *Potamon fluviatile* in Italy, while regions with relatively lower concentrations are dominated by crayfish (74.305 ± 17.99 mg/l for the crab and 66.238 ± 12.61 mg/l for the crayfish area; BARBARESI et al. 2007). Generally, Ca^{2+} is needed for calcification of the crustacean cuticle, at concentrations below 5 mg/l, the complete calcification of the carapace in crayfish was shown to be impossible (RUKKE 2002). Alternatively, the delicate carapaces could be susceptible to dissolution in more acidic settings and thus filtered out from the palaeontological record.

Water depth and velocity. – Recent *Potamon* occurs in fast flowing streams and broad rivers, but also in lakes and isolated, slowly flowing runlets. The predominant habitat of *Potamon* in lakes is the riparian zone, e. g., *Potamon fluviatile* is not expected to occur in greater depths (BARBARESI et al. 2007) and *Potamon rhodium* was never observed below 1.6 m depth (ERPENBECK 1970).

From the preservation of the fossils we can, with reservations, postulate some information on water current and depth. The articulation of the extremities with the thorax, as is always the case in *Potamon speciosus* from Öhningen, indicates that the specimens were not or only slightly moved after death. This can be either due to fast embedding/high sedimentation rate and/or indicate the absence of strong currents. In contrast to the site of Öhningen, the fossils of Höwenegg (*Potamon hegauense* n. sp.) and Gratkorn (*Potamon proavatum*) are only preserved as disarticulated fragments of carapaces and chelae. At both localities crab-bearing strata are deposited in an overall calm limnic environment (WOODBURNE et al. 1996; HEIZMANN et al. 2003; Gross 2008). Nevertheless, the preservation of *Potamon* points to a relocation of the crab fragments into deeper areas of the lake during

floodwaters or storm induced currents. This observation is in agreement with the intercalated mudflows (Höwenegg) and the occurrence of layers with re-located plant fragments (Gratkorn).

Palaeoclimatology. – Extant potamids live an amphibious life, are able to make terrestrial excursions for many days, and can withstand short phases of dryer conditions in deep burrows (GHERARDI et al. 1988a, b). *Potamon ibericum* (see LIGNAU 1928) and *Potamon potamios* (see KINZELBACH 1985) were reported to have burrows several kilometres away from the next lake or watercourse. However, the females carrying hatchlings are dependant on the presence of water, arguing for permanent presence of water (MINEI 1976).

Extant *Potamon* is restricted to subtropical climates. The present-day northern limit of potamids in Europe previously has been used to estimate palaeotemperatures (BACHMAYER & PRETZMANN 1971). In the European potamids (*Potamon fluviatile* and *Potamon ibericum*) the natural northern limit coincides roughly with the 0°C January isotherm (see Fig. 3 and PRETZMANN 1972). The occurrence of fossil *Potamon* north of the Alps is consistent with previous palaeoclimatological assumptions on the Miocene climate of Central Europe (e. g., BRUCH et al. 2004; MOSBRUGGER et al. 2005). Generally it is assumed that temperatures decreased at the end of the middle Miocene (BÖHME 2003; BÖHME et al. 2008; BRUCH et al. 2007).

The occurrence of *Potamon* in the late middle Miocene (*Potamon speciosus* and *Potamon proavatum*) confirms that the CMMT (= coldest month mean temperature) still remained above 0°C in the circum-Alpine realm. The last occurrence date of freshwater crabs north of the Alps around 10 Ma is marked by *Potamon hegauense*. This points to CMMT's above 0°C in the German Molasse Basin and at the eastern fringe of the Alps (Vienna Basin) even during the middle and late Pannonian (MN 9-11), which is in good agreement with palaeobotanic data (BRUCH et al. 2007, ERDEI et al. 2007) At the site of Eichkogel, dated at around 8.2 Ma (MN 11; HARZHAUSER et al. 2004), it remains unclear to what extent the activity of thermal springs (see HARZHAUSER & TEMPFER 2004) could have prolonged their existence in this area. Extant *Potamon algeriense* was reported to inhabit such travertine-forming thermal springs of 39°C water temperature (MASON 1939).

Even during the Pleistocene, freshwater crabs (*Potamon antiquum*) occur in the Pannonian Basin at the Gerecse Mountains. As stated in the taxonomic part, *P. antiquum* probably represents the remains of ancient range expansions and retractions of extant *Potamon ibericum* (that still inhabits the lower part of the Danube), caused by Pleistocene temperature oscillations. As at the Eichkogel section, the formation of travertine in this area is associated with thermal springs (SIERRALTA et al. 2007), which might have given *Potamon* the chance to survive even in glacial times.

Acknowledgements

We are grateful to the following persons, who kindly supplied specimens or images, gave access to collections under their care, or shared information on freshwater crab sites: GÜNTER SCHWEIGERT and MICHAEL RASSER (SMNS); SAMUEL GIERSCH and WOLFGANG MUNK (SMNK); HARTMUT SCHULZ and WOLFGANG GERBER (GPIT); URSULA MENKVELD (NMBE); GERHARD LUDS (Museum Fischerhaus, Wangen); RAJEEV PATNAIK (Panjab University, Chandigarh); ANDREW ROSS and CLAIRE MELLISH (NHML); HEINZ FURRER (PIMUZ); MICHAEL TÜRKAY (SMF); SHOSHONA ASHKENAZI and GABI LAROM (Hebrew University, Jerusalem); PÁL SUMEGI (Szeged University, Szeged); PÁL MÜLLER (MOL, Budapest); YEŞİM İSLAMOĞLU (MTA General Directorate; Ankara) and STEFANO DOMINICI (University of Florence). We like to thank GYÖRGY CSANÁDY (Helmholz Zentrum, Munich) for translation of Hungarian literature. Special thanks goes to MADELAINE BÖHME and JEROME PRIETO (LMU, Munich) for making available data and freshwater crab fragments from several Bavarian sites. GÜNTER SCHWEIGERT (SMNS) and ROD FELDMANN (Kent, Ohio) reviewed and improved our manuscript, and kindly streamlined our English.

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Manuscript received: January 7th, 2009.

Revised version accepted: January 27th, 2009.

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