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Distribution of epigean Malacostraca in the middle and upper Danube (Hungary, Austria, Germany)

by
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Abstract: The Danube between Harta (rkm 1549) and Kehlheim (rkm 2410) was sampled qualitatively in 1985-1995 at all seasons. Eighteen epigean species of Malacostraca (Janiridae, Asellidae, Gammaridae, Talitridae, Corophiidae, Mysidae, Astacidae, Cambaridae) were recorded. The malacostracan fauna shows a distinct longitudinal zonation in the River Danube. At least nine species are of Ponto-Caspian origin. The actual distribution patterns were analyzed with respect to former studies. At least six species were strongly expansive during the last few decades. Navigation appears to be among the crucial factors for this dispersion.
Keywords: Danube, Malacostraca, zoogeography, distribution, immigration

Introduction

During the first half of the present century, investigations on the higher crustaceans (Malacostraca) were mainly restricted to the lower and middle course of Danube River. The scientific interest on the upper Danube arose as late as in the 1950s and culminated in a book edited by Liepolt (1965-1967) and in the foundation of the international I.A.D.-working group of the Societas Internationalis Limnologiae. Recently, important summarizing lists concerning the fauna of the Austrian Danube were published by Moog *et al.* (1994), Moog *et al.* (1995).

For the majority of taxonomic groups in the animal kingdom, including the Malacostraca, the knowledge about distribution in large rivers is still incomplete. The faunistic research of the Danube is very important because of the immense diversity of species which live in this river which is the second largest in Europe.

The aim of the present study goes beyond local faunistic interest, by describing in detail the actual distribution pattern of selected species of the subclass Malacostraca, and how it has been achieved historically. Special attention is directed to the biological zonation of the Danube River and to the question, how and when the present zoogeographic situtation may have established. The dramatic spreading of some species in recent years is included in this context.

An der Lan (1967) correctly arrived at the following conclusion: "Das Studium der Donau-Organismen führt zwangsläufig zu einer tiergeographischen Betrachtungsweise und einer daraus resultierenden Gesamtschau der Geschichte unserer europäischen Süsswasserfauna". The highly significant biological zonation of the Danube (Nesemann 1991) and the Rhine (Kinzelbach 1985, 1990) is marked by distribution limits, which are essentially the result of the geological development in the past (Pécsi 1959).

Materials and methods

A great number of malacostracans were examined from our own samples as well as from the crustacean collection of the Hungarian Natural History Museum, Budapest. The museum material was collected and determined for example by E. Dudich, I. Loksa, E. Unger, and A. Kesselyák. For each species, only those materials are listed that were examined and checked by the present authors. Our material is deposited in the Hungarian Natural History Museum and a smaller part in the Museum of Natural History in Vienna.

The crustaceans were picked up by hand or qualitatively sampled with a pond net. All samples were preserved in a solution of 70% ethanol. The species were determined by comparison with museum specimens and by using published keys, such as listed by Pöckl (1988). The excellent key by Carausu *et al.* (1955) was especially useful.

Results

Family Janiridae

Jaera istri Vieulle, 1979

Material: Danube at Harta, 05. 09. 1991; Danube at Dunaújváros, 05. 09. 1991; Szentendrei Duna at Leányfalu, 04. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Mosoni Duna at Dunaszeg, 23. 10. 1990; Danube between Korneuburg and Hainburg, from samples at rkm 1883, 1886, 1887, 1888, 1896, 1910, 1915, 1940, 02. and 03. 1991; Danube at Zwentendorf, 20. 04. 1991, leg. Nesmann, H.; Danube, from numerous samples between Altenwörth and Krems, 07. 1985 – 07. 1990, leg. Pöckl, M.; Danube at Engelhartszell, on the Jochstein rocks, 14. 11. 1989, leg. Zerz, J. & H. Nesemann; Danube at Winzer, 07. 07. 1991; Danube at Aicha, 07. 07. 1991; Danube at Barbing, 01. 07. 1990; Lake Balaton at Révfülöp, 14. 08. 1991, leg. Nesemann, H.

J. istri is one of the three Ponto-Caspian species of the genus *Jaera* and was described as late as 1979 by Vieulle from the locus typicus Kladovo near the Kazan-pass reach of the Danube. It is distributed along the river from Romania to Bavaria. The older literature is referring to *Jaera sarsi* Valkanov, 1938 and to *Jaera caspica* Kesselyák, 1938. In contrast to these species, which live in brackish waters, *J. istri* is well adapted to freshwater. The distribution of this group of *Jaera*-species in the large Ponto-Caspian rivers (Danube, Bug, Dniepr, Dniestr, Don, Volga, Ural), in the Caspian Sea and the offshore lakes of the Black Sea was regarded as relictary and typical for the ancient Paratethys (Vieulle 1979).

In the Middle and Upper Danube, only *J. istri* was found. This primarily lithophilous species prefers high flow velocities and does not invade tributaries. It was suggested that *J. istri* is endemic for the Danube, however, it was also recorded from Lake Balaton near Révfülöp by H. Nesemann. Kothé (1968) collected specimens for the first time in the Bavarian Danube, and determined the material as *J. sarsi*. He thought to deal with an isolated population, because this species was previously unknown in Upper Austria. Our results show that *J. istri* is distributed throughout the whole section of the upper Danube at least as far upstream as Barbing near Regensburg.

Family Asellidae

Asellus aquaticus (Linnaeus, 1758)

Material: Danube, deadwater reach Rosskopfarm near Stopfenreuth (rkm 1889), 09. 05. 1987; Danube, deadwater reach near Schönau (rkm 1909), 10. 05. 1987; Danube, in a secondary branch "Giessgang" near Tulln (rkm 1963), 11. 07. 1986; Danube near Erlau (rkm 2214), 23. 09. 1993, leg. Wittmann, K. J.

This species is highly tolerant to organic pollution. It is very common in all adjacent waters of the Danube and is distributed widely throughout the whole river basin.

Family Gammaridae

Gammarus pulex (Linnaeus, 1758)

This amphipod is common in the Rhine river basin and the uppermost Danube in Germany. According to Dudich (1947), it does not occur in the Carpathian Basin. It is known from Upper Austrian streams as far eastwards as the Traun River. Several specimens of *G. pulex* were collected by B. Csányi for the first time in the Austrian part of the Danube, 17. 12. 1991, right bank, directly at the confluence with river Enns.

Gammarus fossarum Koch, 1835

Material: Danube near Orth, 20. 04. 1988, 19. 06. 1989; Danube in Vienna, 19. 04. 1988; Danube upstream of Krems, from numerous collections, 11. 12. 1986 – 17. 12. 1987, leg. Pöckl, M.; Danube at Winzer, 07. 07. 1991, leg. Nesemann, H.

G. fossarum is a widely distributed amphipod, especially in the highlands of Central, Eastern and Southeastern Europe. The distribution area includes the Pyrenees, the Alps, the mountaneous and hilly regions of Central Europe, the Danubian valley, the Balkan Peninsula and Asia Minor (Karaman & Pinkster 1977a).

G. fossarum usually inhabits springs and the upper reaches of small streams and rivers. It tolerates high current and low temperatures. When *Gammarus pulex* (Linnaeus, 1758) is absent – most probably in most parts of Austria – *G. fossarum* inhabits the middle and lower reaches of streams and rivers where current velocity is low. There, it coexists and possibly competes with *G. roeseli* Gervais, 1835 (Pöckl 1992, Pöckl & Humpesch 1990). Examples for these types of potamon rivers are the Lajta and Zala, where *G. fossarum* was collected frequently but in low numbers only. In the Danube River, *G. fossarum* was found sporadically, possibly due to passive drift from the prealpine rivers. As the upper Danube typically has a rhithron character, this species may locally find acceptable conditions as far downstreams as Budapest.

Gammarus roeseli Gervais, 1835

Material: Danube at Dunaföldvár, 05. 08. 1991, leg. Ofenböck, T. & H. Nesemann; Danube at the confluence of the river Fischa near Fischamend, 28. 04. 1991, leg. Nesemann, H.; Danube upstream of Vienna, 25. 08. 1987; Danube near Altenwörth, 24. 07. 1986; Danube upstream of Krems, 12. 12. 1986; Danube at the confluence of the river Enns (near rkm 2112), 29. 09. 1993; Danube near Ottensheim (Alte Donau, rkm 2145), 24. 04. 1992, leg. K. J. Wittmann; Danube at the Jochenstein rocks near Engelhartszell, 14. 11. 1989, leg. Zerz, J. & H. Nesemann; Danube at Passau, 28. 08. 1991; Danube at Winzer, 7. 07. 1991; Danube at Aicha, 7. 07. 1991; Lajta near the confluence with the Mosoni Duna at Mosonmagyaróvár, 6. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Rába at Győr, 28. 07. 1990, leg. Nesemann, H.; Main-Danube-Canal near Forchheim (rkm 26), 9. 09. 1994, leg. K. J. Wittmann.

The distribution area of *G. roeseli* includes Asia Minor, the Peloponesos, the western Balkan Peninsula, the Hungarian Great Plain, the Danubian valley and the plains and lower mountains of Central and Western Europe. It was suggested that its evolutionary centre was in Southeastern Europe or Asia Minor (Karaman & Pinkster 1977b). Its penetration in other parts of Europe seems to be a very recent one, or at least postglacial. The present distribution pattern shows rather clearly the network of large and medium sized river valleys as routes of its range extension northwestwards and in particular that of the Danubian system.

The construction of the Ludwigskanal, a waterway which has brought in contact the Rhine and Danube system in 1845, probably facilitated the spreading of *G. roeseli*. However, its invasion of Western Europe had begun earlier, since already in 1835 Gervais had described this species from the vicinity of Paris. In France, *G. roeseli* is still enlarging its distribution area in western (Seine, Loire) and southern (Rhone) direction (Pacaud 1952, Wautier & Roux 1959, Roux 1969).

G. roeseli is found in middle and lower courses of summer-cool runnning waters where current velocities are moderate. There, it coexists with *G. fossarum*. In summer-warm rivers of the lower mountains and plains, where stream velocity is low, *G. roeseli* often is the typical and dominant gammarid species. It is able to reach very high densities and biomass (Pöckl 1992, Pöckl & Humpesch 1990). Examples for potamon rivers where *G. roeseli* was often collected, are the Dyje (Sukop 1990), Morava, Lajta, Rába, Rábca, and Zala.

In the Danube, *G. roeseli* was found sporadically, which is in agreement with Roux (1969), who suggested that *G. roeseli* avoids high current velocities and large rivers, although it may temporally use them as routes of migration. In the Bavarian Danube near Passau and Jochenstein, Kothé (1968) collected numerous *G. roeseli* but did not record *Dikerogammarus haemobaphes*. According to Foeckler (1987), *G. roeseli* and *G. fossarum* seem to avoid the main stream in this section of the Danube, whereas *D. haemobaphes* is very abundant.

Dikerogammarus haemobaphes (Eichenwald, 1841)

Material: Danube at Káposztásmeggyer, 21. 09. 1941, leg. Wiesinger; Danube at Dunakömlőd, 11. 09. 1947, leg. Loksa, I.; Danube at Harta, 05. 09. 1991, leg Ofenböck, T. & H. Nesemann; Danube at Dunaföldvár, 11. 09. 1947, leg. Loksa, I., 31. Jan. 1991, leg. Wimmer, R. & H. Nesemann, 5. 09. 1991; Danube at Dunaújváros, 5. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube near Szalkszentmárton, 31. Jan. 1991, leg. Wimmer, R & H. Nesemann; Danube at Budapest, 30. 09. 1932, leg. Dudich, E.; Danube at Római-fürdő near Budapest, 20. 09. 1947, leg. Wiesinger; Danube at Budafok, 04. 09. 1947, leg. Dudich, E. & I. Loksa; Danube at Újpest, 16. 09. 1926, leg. Dudich, E.; Szentendrei Duna at Leányfalu, 04. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube at Vác, 30. 09. 1930, leg. Dudich, E.; Danube at Nagymaros, 06. 11. 1926, leg. Unger, E. & E. Dudich; Danube at Zebegény, 14. 09. 1946, leg. Dudich, E.; Danube at Esztergom 17. 09. 1947, leg. Loksa, I.; Danube at Dömös, 30. 07. 1927, leg. Dudich, E.; Danube at Nyergesújfalu, 18. 09. 1947; Danube at Komárom, 19. 09. 1947, leg. Loksa, I.; Danube downstream from Gönyü, 03. 04. 1990; Danube near Ásványráró, 11. 09. 1991; Danube near Lipót, 11. 09. 1991; Danube near Dunaremete, 13. 09. 1991; Danube downstream from Hainburg, 22. 02. 1991, 8. 09. 1991; Danube near Stopfenreuth, 21. 02. 1991; Danube upstream from Bad Deutsch-Altenburg, 16. 02. 1991; Danube, in a secondary branch near Regelsbrunn, 14. 03. 1991; Danube at Regelsbrunn, 11. 02. 1991; Danube at the confluence of the river Fischa near Fischamend, 28. 04. 1991; Danube, deadwater reach Kühwörther Wasser between Schönau and Mühlleiten, 20. 10. 1990; Danube near Schönau, 13. 03. 1991; Danube near Mannswörth, 20. 02. 1991, leg. Nesemann, H.; Danube near Korneuburg, 14. 02. 1991, leg. Schay, G. & H. Nesemann; Danube at Zwentendorf, 20. 04. 1991; Danube, from numerous collecting sites between Altenwörth and Krems, 1985-1990, leg. Pöckl, M.; Danube (rkm 2132) near Linz, from the shipping space of two ships and from their hulls 02. 10. 1993; Danube at Linz (rkm 2135), 28. 09. 1994, leg. K. J. Wittmann; Danube at Schlögen, 14. 11. 1989; Danube at Engelhartszell, 14. 11. 1989; Danube upstream from Aschach, 13. 11. 1989, leg. Schwammer, H.; Danube (rkm 2111) at Mauthausen, 29. 09. 1993, leg. K. J. Wittmann; Danube (rkm 2213) near Pyrawang in the confluence of a small stream, 24. 09. 1993; Danube (rkm 2241) at Sandbach, 08. 09. 1994; Danube (rkm 2214) at Erlau, 08. and 23. 09. 1994, leg. K. J. Wittmann; Danube upstream from Passau, 30. 09. 1990, leg. Nesemann, H.; Danube (rkm 2249) at Vilshofen, 23. 09. 1993; Danube (rkm 2301) at Waltendorf, 08. 09. 1994, leg. K. J. Wittmann; Danube near Gaishofen, 30. 09. 1990; Danube at Friesheim, 07. 1990; Danube, in a side-branch near Tegernheim, 30. 09. 1990; Danube at Barbing, 01. 07. 1990, leg. Nesemann, H.; Main-Danube-Canal (rkm 84) near Mittelhembach, 07. 09. 1994, leg. K. J. Wittmann.

D. haemobaphes is a Ponto-Caspian gammarid species of wide distribution. The taxonomic situation of its freshwater form, named *fluviatilis* Martinov, 1919, is not clear. It is especially questionable, whether the use of the third name is justified (Jazdzewski 1980). Therefore, we retained the name *D. haemobaphes* also for the riverine form.

The species advances very high upstream the larger Ponto-Caspian rivers and not so far in the smaller ones. It was also observed in the offshore lakes of the Black and Marmara seas (Brtek & Rothschein 1964, Kaneva-Abadzieva 1972). The invasion of Lake Balaton by *D. haemobaphes* from the Danube via the River Sió can be dated rather precisely to the middle of the 1950s (Ponyi 1956, 1958). According to this author, *Dikerogammarus* spp. appeared simultaneously with the introduction of *Limnomysis benedeni* into the lake (Woynarovich 1955). In the Pannonian lowland, *D. haemobaphes* also entered the lower reaches of some large Danube tributaries, such as the Száva, Dráva, Sió, Rába, Tisza, Kőrös and Sebes-Kőrös (Dudich 1927, Botos *et al.* 1990). In Austria, it was collected in the Danube at Hainburg and Nussdorf near Vienna (Vornatscher 1965). It was, however, not collected by Kothé (1968) in the Bavarian section of the river. In the last two decades it massively expanded its distribution in the upper Danube. Nowadays it is very abundant at least as far upstream as Kehlheim. Since 1992, *D. haemobaphes* invaded the Rhine river basin via the recently constructed Main-Danube-Canal. It is now frequently recorded from the Bavarian section of the Main River (Schleuter *et al.* 1994)

Dikerogammarus villosus (Sovinski, 1894)

Material: Danube at Mohács, 18. 09. 1930, leg. Dudich, E.; Danube at Dunakömlöd, 11. 09. 1947; Danube at Harta, 05. 09. 1991; Danube at Dunaföldvár, 11. 09. 1947, leg. Loksa, I., 05. 09. 1991; Danube at Dunaújváros, 05. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube at Római-fürdő near

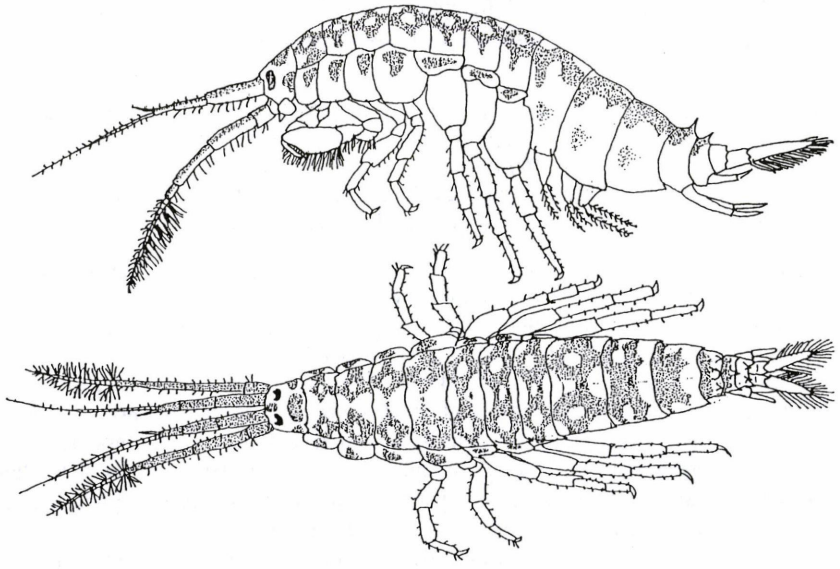

Fig. 1a–b. *Dikerogrammarus. villosus,* different colour variants from dorsal and lateral view, from Danube at Dunaremete

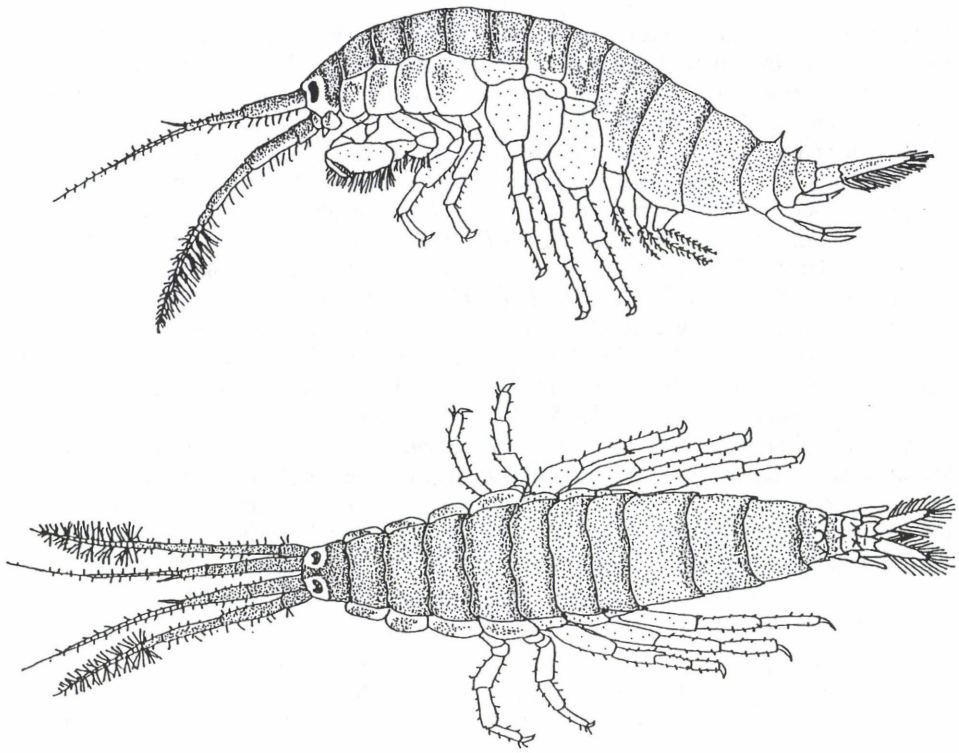

Fig. 2a–b. *Dikerogrammarus villosus,* different colour variants from dorsal and lateral view, from Danube at Dunaremete

Budapest, 20. 09. 1947, leg. Wiesinger; Danube at Budafok, 04. 09. 1947, leg. Dudich, E. & I. Loksa; Danube at Káposztásmegyer, 21. 09. 1947, leg. Wiesinger; Danube at Göd, 21. 05. 1934. leg. Kovács, I.; Szentendrei Duna near Leányfalu, 04. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube at Szob, 12. 10. 1934, leg. Dudich, E.; Danube at Nagymaros, 30. 07. 1927, leg. Dudich, E. & E. Unger; Danube at Zebegény, 06. 05. 1034, leg. Dudich, E.; Danube at Dömös, 30. 07. 1927, leg. Dudich, E. & E. Unger; Danube at Visegrád, 14. 07. 1931, leg. Mödlinger, G.; Danube at Ásványráró, 11. 09. 1991; Danube at Lipót, 11. 09. 1991; Danube at Dunaremete, 13. 09. 1991; Danube downstream from Hainburg, 22. 03. 1991, 08. 09. 1991, leg. Nesemann, H. & M. Pöckl; Danube near Schönau, 13. 02. 1991; Danube at Zwentendorf, 20. 04. 1991; Danube at Linz (rkm 2132) from the shipping space of two ships and from their hulls, 2. 10. 1993, leg. K. J. Wittmann.

D. villosus (Figs 1-3) is a widely distributed Ponto-Caspian gammarid species, which is very common in the lower reaches and the delta of the Danube (Mordukhai-Boltowskoi 1969). It advances very high upstream the larger Ponto-Caspian rivers but usually not as far as *D. haemobaphes* (Polischtschuk 1969, Zimbalewskaja 1969). For the Hungarian Great Plain, *D. villosus* is well known since the beginning of systematical investigations in the Danube, where it was collected at Nagymaros by E. Unger & E. Dudich in 1926.

Originally its distribution range was limited by the narrow valley of the Dunakanyar (rkm 1707) near the confluence of the river Ipoly. This species was not listed by Vornatscher (1965) and Dudich (1967) for the Austrian Danube, and was not collected during sampling for the

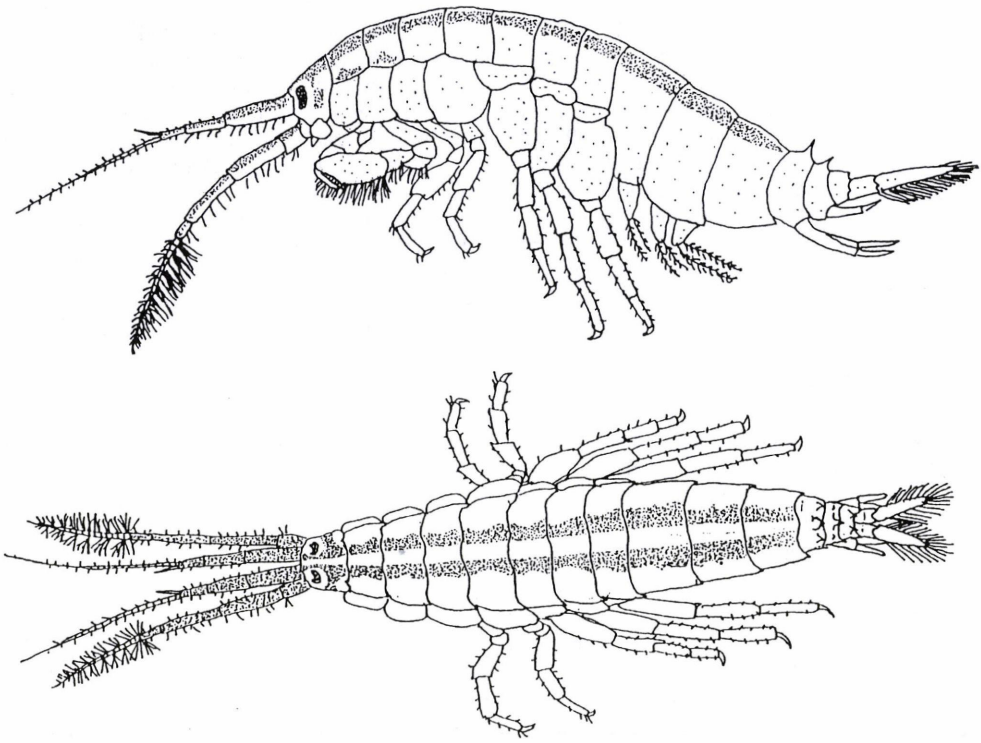

Fig. 3a–b. *Dikerogammarus villosus,* different colour variants from dorsal and lateral view, from Danube at Dunaremete

so-called "Ecosystem Study Altenwörth" (Pöckl 1988). For the first time (1989) in Austria, *D. villosus* was collected by the present authors at several sites, where it was quite abundant.

In September 1992, *D. villosus* was found for the first time abundantly in the Bavarian Danube near Straubing and Regensburg. Recently, *D. villosus* invaded successfully the River Rhine, where it was sampled in the Netherlands (Bij de Vaate & Klink 1995) and in southwestern parts of Germany (leg. M. Spangenberg).

Because of their extreme body dimensions, it seems rather unlikely that specimens of *D. villosus* were overlooked in the past. Adult males reach up to 30 mm total body length. The colouration of living animals is highly variable (Figs 1–3) but spectacular, most frequently showing a light spot or stripe per segment on a dark background. Pale specimens can also be found but it is suggested that they have moulted most recently. In the preserved material the natural colouration disappears within a few days.

D. villosus is found in rockpools and under porous stones, creeping most deeply into the holes where it seems to be rooted, so that it is pulled out only by force. During periods of low water level the rockpools, inhabited by gammarids, may fall dry. Obviously, the abundance of the animals seems to be significantly dependent on water discharge.

Chaetogammarus ischnus (Stebbing, 1898)

Material: Danube at Mohács, 18. 09. 1930, leg. Dudich, E.; Danube at Dunakömlöd, 11. 09. 1947, leg. Loksa, I.; Danube at Harta, 05. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube at Dunafödvár, 11. 09. 1947, leg. Loska, I., 05. 09. 1991; Danube at Dunaújváros, 05. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Ráckevei Duna at Szigethalom, 06. 1991, leg. Nesemann, H.; Danube at Budapest, 30. 09. 1932; Danube at Budafok, 27. 09. 1930, leg. Dudich, E.; Szentendrei Duna near Leányfalu, 04. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube at Vác, 30. 09. 1930, leg. Dudich, E.; Danube at Nagymaros, 04. 06. 1926, leg. Unger & Szabó-Patay; Danube at Dömös, 30. 07. 1927; Danube at Szőny, 17. 09. 1930; Danube at Zebegény, 14. 11. 1946, leg. Dudich, E.; Danube at Esztergom, 17. 09. 1947, leg. Loksa, I.; Danube at Dunaalmás, 29. June 1941, leg. Soós, Á.; Danube at Komárom, 19. 09. 1947, leg. Loksa, I.; Danube at Ásványráró, 11. 09. 1991; Danube at Lipót, 11. 09. 1991; Danube at Dunaremete, 13. 09. 1991; Danube at Hainburg, 08. 09. 1991; Danube at Regelsbrunn, 11. 02. 1991; Danube near Korneuburg, 8. Febr. 1991, leg. Schay, G. & H. Nesemann; Danube at Zwentendorf, 20. 04. 1991; Danube from numerous collecting sites between Altenwörth and Krems, 1985 – 1990, leg. Pöckl, M.

In 1993, Pinkster synonymized the generic name *Chaetogammarus* with *Echinogammarus*. In our opinion, it would have needed a higher degree of necessity to change the name commonly used in literature for many decades. As it is unclear whether the use of the trinominal name for the freshwater- (or inland-) form *sowinskyi* Behning, 1914, is justified (Jazdzweski 1980), the authors retain the name *Chaetogammarus ischnus* for the riverine form.

C. ischnus belongs together with *Corophium curvispinum*, to the Ponto-Caspian crustaceans that have advanced farthest northwestwards arriving in the river basins of the North and Baltic seas. In most of the larger Ponto-Caspian rivers *C. ischnus* was found highly upstream. In the River Danube, it advanced as far as the Slovakian reach up to Jarovce (rkm 1856, Brtek 1953, Straskraba 1953, 1959, 1962, Brtek & Rothschein 1964), with recordings along all lower reaches of this river (Dudich 1927, 1967, Carausu *et al.* 1955, Russev 1966, Karaman 1953, Karaman 1974). It also entered the large affluent Tisza upstream to Szeged (Dudich 1927) and Martfű (Botos *et al.* 1990) and lower courses of Dráva and Száva (Karaman 1953). However, it has not been found in Lake Balaton (Muskó 1989) and was not listed by Vornatscher (1965) and Dudich (1967) for the Austrian Danube. Since about 1970, *C. ischnus* must have greatly extended its distribution area in upstream direction. It was first recorded in Austria at Hundsheim near Krems (rkm 2005, Pöckl 1988), where it occurred together with *D. haemobaphes*. *C. ischnus* prefers large potamon rivers where it is chiefly found in the gravel.

Obesogammarus obesus (Sars, 1894)

Material: Danube at Harta, 05. 09. 1991; Danube at Dunaújváros, 05. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube near Szalkszentmárton, 01. 02. 1991, leg. Wimmer, R. & H. Nesemann; Szentendrei Duna near Leányfalu, 4. 09. 1991, leg. Ofenböck, T. & H. Nesemann.

O. obesus (Fig. 4) is a Ponto-Caspian gammarid species of wide distribution in the Caspian, Azov's and Black seas as well as in the lower and middle courses of the large rivers flowing into these basins. However, it does by far not advance as high upstream as the other recorded crustaceans of Ponto-Caspian origin. In the Danube, this species was distributed originally only in the lower parts. It was collected by Carausu (Dudich 1947) and Karaman (1953) in the Kazan-pass, which separates the Eastern Pannonian lowlands from the lower Danube. In the present study, *O. obesus* was found as high upstream as the Szentendrei Duna (rkm 1672), approximately 30 km northwards from Budapest. Downstream the Hungarian capital, at Dunaújváros and Harta, *O. obesus* was collected rather frequently. New records by Csányi (1994) indicate further expansion. Therefore, this species must have intensively extended its distribution in the middle Danube in the last few decades. It also seems to be restricted to the

main course of the middle Danube, because it never has been found in larger tributaries or in Lake Balaton. *O. obesus* prefers large river flows, is most characteristic for the potamon biocoenosis, and is chiefly found in the gravel.

Stygobromus ambulans (Fr. Müller 1846)

Material: see Nesemann (1993), further records: swamps in Carinthia, Burgenland (Strem), 1995.

This gammarid species is an original element of the Pontic fauna. Today, its distributional range includes all drainage systems of the Black Sea. In different large running water systems, *S. ambulans* has advanced very far northwestward, reaching Central Europe (Straskraba 1962). It was at first described for the tributaries of the Elbe River. The Western European populations are isolated from those in the Pannonian lowlands. Along the Danube River, the western distribution limit of the Pontic population is formed by the basins of Lake Fertő (Andrikovics *et al.* 1982), the upper Rába, the lower Lajta and the Morava basin (Nesemann, unpublished). The recently recorded isolated population in the basin of the Lake Ammersee in Bavaria is the westernmost locality in the Danube basin (Hess & Heckes, in prep.). Disjunct populations live in the area of River Po and in the inneralpine basin of Klagenfurt.

S. ambulans is found in different kinds of water bodies, from the lowlands to the lower mountains. The species inhabits puddles, temporary pools, swamps, springs, wells, swampy banks of streams and rivers, and muddy shores of lakes (Dudich 1927). In the present study, *S. ambulans* was collected in many kinds of waters (Fig. 5) which all seem to have one attribute in common: the deficiency of oxygen. Under these conditions no other gammarid species would be able to survive. In large rivers, *S. ambulans* is a typical and locally very abundant component of the fauna, being chiefly restricted to the reed-zones (Ráckevei Duna; Hortobágy in Tisza-system) and swampy meadows of the backwaters (Lajta, Strem). In the Danube, *S. ambulans* is found in adequate habitats of side-branches, where water movement is low. It was mainly found in dense packs of decaying leaf litter of decidous trees, in decaying reed-stems and other plant remains.

Niphargus (*Phaenogammarus*) *hrabei* Karaman, 1932

Material: see Nesemann (1993), additional records: Danube, in a temporary deadwater reach near Klosterneuburg (rkm 1939), 17. 05. 1995, leg. Nesemann, H.; Danube deadwater reach near Schönau (rkm 1909), 10. 05. 1987, leg. Wittmann, K. J.

This amphipod is common in the temporarily flooded deadwater regions of the riverin forests and floodplains along the Danube. It inhabits similar habitats as *S. ambulans*. It seems to be largely restricted on the Danubian valley, whereas *S. ambulans* is common in the floodplains of the Danubian tributaries. It was recently found in the Bavarian section of the Danube (Hess & Heckes, in prep.).

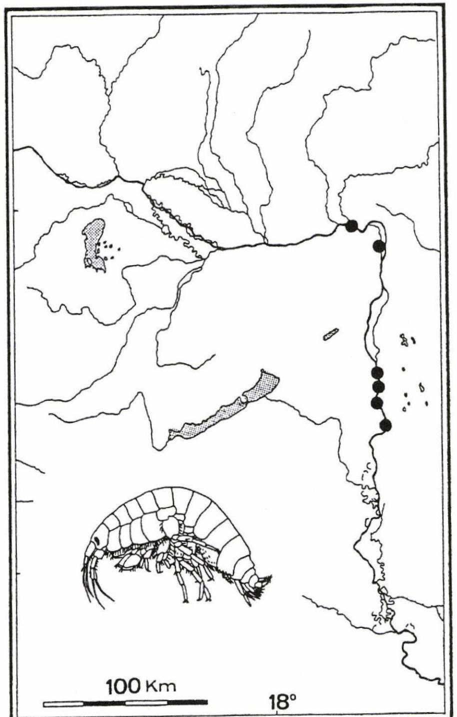

Fig. 4. Distribution of *Obesogammarus obesus* in the Hungarian Danube

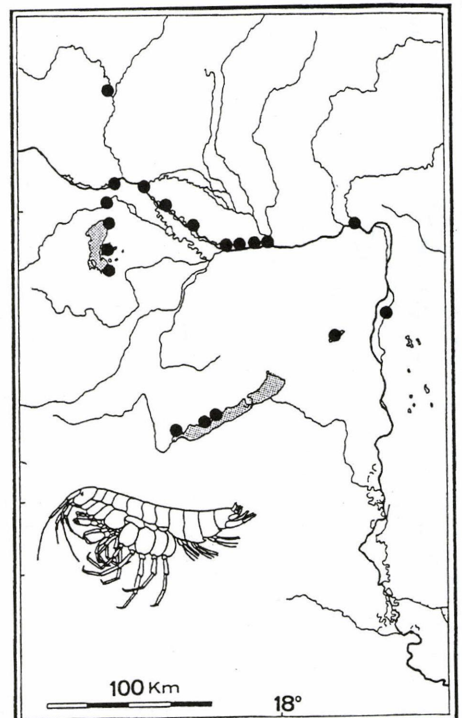

Fig. 5. Distribution of *Stygobromus ambulans* in the Western Pannonian basin.

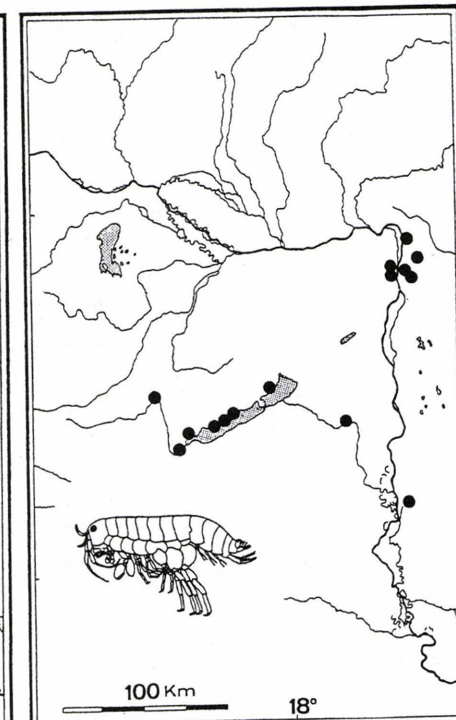

Fig. 6. Distribution of *Orchestia Cavimana* in the Western Pannonian basin

Family Corophiidae

Corophium curvispinum Sars, 1895

Material: see Wittmann (1995); further records: Danube at Harta, 05. 09. 1991; Szentendrei Duna near Leányfalu, 04. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube downstream from Hainburg, on rocky slopes, 22. 02. 1991; Danube near Stopfenreuth, 21. 02. 1991; Danube at Bad Deutsch-Altenburg, 16. 02. 1991; Danube near Regelsbrunn, 11. 02. 1991; Danube, in a side-branch at Regelsbrunn, 14. 03. 1991; Danube at Schönau, 13. 02. 1991; Danube at Mannswörth, 20. 02. 1991; Danube, in a deadwater reach Kühwörther Wasser between Schönau and Mühlleiten, 20. 10. 1990; Danube near Korneuburg, 14. 02. 1991, leg. Schay, G. & H. Nesemann; Danube at Zwentendorf, 20. 04. 1991; Danube, from numerous collecting sites between Altenwörth and Krems, 1985-1990, leg. Pöckl, M.; Danube (rkm 2111) at Mauthausen, 29. 09. 1993, leg. K. J. Wittmann; Danube upstream from Aschach, 13. 11. 1989, leg. Schwammer, H.; Danube at Schlögen, 13. 11. 1989; Danube at Engelhartszell, 14. 11. 1991; Danube on the Jochstein rocks near Engelhartszell, 14. 11. 1991, leg. Zerz, J. & H. Nesemann; Danube near Gaishofen, 30. 09. 1990; Danube at Aicha, 08. 1991, Danube at Wörth, 08. 1991; Danube downstream from Barbing, 01. 07. 1990; Danube, in a side-branch near Tegernheim, 30. 09. 1990; Rába at Győr, 28. 07. 1990, leg. Nesemann, H.

C. curvispinum is the most widely distributed Ponto-Caspian corophiid species, which has – probably since the beginning of this century – rapidly expanded its initial area to the north and northwest. It has reached the basin of the Baltic and North Sea. At first it was found beyond the Ponto-Caspian basin and was described under the name *Corophium devium* Wundsch, 1912 in the vicinity of Berlin. In Belgium (Wouters 1985, D'Udekem *et al.* 1988) and the Netherlands (Van Der Brink *et al.* 1989) *C. curvispinum* is still spreading in a southern (Meuse) and western direction (Rhine, Schöll 1990). The occurrence of the species in England (Crawford 1937, Gledhill *et al.* 1976) is somewhat isolated from the populations on the continent.

The population of *C. curvispinum* in the Danube was early noted (Unger 1918, Kothé 1968). The species was recorded as far as the German section (Vornatscher 1965, Dudich 1967) upstream to the narrow valley "Weltenburger Enge" (rkm 2415) near Kehlheim. It has been noted along all downstream sections. In the lower parts of the large Danubian tributaries Tisza, Körös (Botos *et al.* 1990), and Rába. Its arrival in Lake Balaton via the River Sió and its quick spreading in this basin was dated rather precisely to the early 1930s (Moon 1934, Sebestyén 1934, 1937).

In our material from the middle and upper Danube, *C. curvispinum* was the only *Corophium* species, showing a very high intraspecific morphological variation. *Corophium sowinskyi* Martinov, which was discriminated from *C. curvispinum* by Straskraba (1962), has not been found in the samples, nor in the museum collections examined. In contrast to Straskraba's description, we assume that *C. sowinskyi* from the Slovakian section of the river Danube is only an ecological form of *C. curvispinum.*

The species prefers large, slowly flowing and stagnant waters such as the lower reaches of the potamon rivers. It lives on the bottom and in the littoral zone on stones, wooden piles, aquatic macrophytes, algae, silt and sponge debris on the brickwork of locks and bridges. On these substrates it builds U-shaped tunnels made of grains of sand and excretion fluids. Under optimal conditions, densities of several hundreds or even thousands of specimens per square meter were recorded, covering the whole surface with their tubes (Schellenberg 1942, D'Udekem *et al.* 1988).

Family Talitridae

Orchestia cavimana Heller, 1865

Material: Sükösd, near the Danubian floodplain at the Molaván-hegy, 11. 05. 1933, leg. Dudich, E.; Római-fürdő near Budapest, in the drainage ditch of a thermal spring, 25. 02. 1934, leg. Balogh; Csillaghegy near Budapest, 14. 10. 1928, leg. Kesselyák, A.; Alsórákos near Budapest, 25. 06. 1926, leg. Vasváry, M.; Rákos near Budapest, 1927, leg. Mödlinger, G.; Vác, in a spring, 06. 10. 1934, leg. Kesselyák, A.

The distribution pattern of this talitrid amphipod (Fig. 6) is best characterized as Ponto-Mediterranean and its ecological requirement as semi-aquatic (or semi-terrestric) because it is generally found just above the water's edge. It is very common and widespread in the area of the Mediterranean and Black Sea. Following French river systems, it extended its range from the western Mediterranean area far to the north and northeast in this century (Kinzelbach 1965).

In the drainage system of the River Danube its distribution is restricted to the middle and lower reaches. It was never recorded beyond the mountain ridge (Bakony, Visegrádi hegység), that separates the larger Hungarian Plain (Alföld) in the east from the smaller plain (Kisalföld) in the west. *O. cavimana* does not inhabit the main course of the Danube, but is restricted to tributaries and lakes with approximately stable water levels, where it is found just above the water's edge. Dead plant matter washed ashore is a preferably inhabited substrate. Specimens of *O. cavimana* were collected in the humid edge of springs, on swampy lake shores and on the banks of lowland streams (Rákos-patak) and smaller rivers (Zala, Zagyva). Some of the Hungarian populations were examined in the 1920ies (Dudich 1927, Abonyi 1928). Until nowadays, they show no tendency to extend their range in a westward direction, although acceptable conditions would also be available in the Kisalföld plain.

The way of spreading and the habitat requirements of the Eastern European populations in the Danube system seem to be quite different from those of the Western European populations. In the Rhine River, *O. cavimana* inhabits gravel banks and seems to be better adapted to highly variable water levels, tolerating droughts and floods of considerable duration. On the contrary, the populations of the Hungarian Danube valley are restricted to sheltered and shaded parts of banks and shores, semi-aquatic microhabitats of high atmospheric humidity. The size of the Danubian animals (up to 14 mm total body length) is considerably smaller than that of their Western European relatives (20 mm).

Family Mysidae

Limnomysis benedeni Czerniavsky, 1882

Material: see Wittmann (1995); further records: Danube at Dunaújváros, 05. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube, in a secondary branch Rosskopfarm near Stopfenreuth, 15. 03. 1991; Danube, in a side-branch at Regelsbrunn, 14. 03. 1991; Danube, upstream from Regelsbrunn, 17. 03. 1991; Danube, in a deadwater reach near Fischamend, 16. 03. 1991, leg. Nesemann, H.; Danube upstream from Krems, 1987, leg. Zoufal, W. & E. Weigand; Lake Balaton at Keszthely, 21. 06. 1990, leg. Forró, L. & H. Nesemann.

L. benedeni is a widely distributed Ponto-Caspian mysid species which prefers fresh or oligohaline waters. It lives in slow-flowing and stagnant waters where it lives mainly in the hyperbenthic zone among aquatic macrophytes, at flooded banksides, or associated with artificial hard substrate (Wittmann 1995).

L. benedeni was found in most rivers flowing to the Black and Caspian Sea (Danube, Ural, Volga, Don, Dniepr, Bug, Dniestr). In the majority of the Ponto-Caspian river systems, it was not found very far upstream from the mouth (e.g. km 200 in the Ural, Woynarovich 1955). In the Danube, it has been recorded continously from the delta as far upstream as rkm 400 in Romania (Bácescu 1940). The next records were made between Mohács and Budapest (Bácescu 1954, Woynarovich 1955), near Bratislava (rkm 1800, Bacescu 1954), from nine localities between Hainburg and the Kühwörther Wasser near Vienna (Weish & Türkay 1975) and in the main course of the Danube at rkm 1989 (Pöckl 1988). Wittmann (1995) documented the areal expansion, which proceeded in several steps from Vienna (rkm 1920) in 1982/83 to Passau (rkm 2228) in 1994. In the upper Danube the species is mainly known from waters, that are in connection with the main river at least in times of flood, whereas it is still rare in permanently isolated waters.

Longterm monitoring in waters of Vienna revealed that *Limnomysis* may be distributed through tubes used for pumping water into the deadarms. By this way it entered the backwater Schillerwasser a few years before 1992, and the backwater Alte Donau in summer 1992. In both waters, the species was not found during thorough investigations in 1983-1986, whereas it is present in large quantities since 1993.

Family Astacidae

Austropotamobius torrentium (Schrank, 1805)

Occasionally, the stone crayfish is found in the Danube (Jansky 1987), whereas it is very abundant in small cold creeks.

Astacus astacus (Linnaeus,1758)

Rarely, the noble crayfish is found in stagnant waters near the Danube (Gemenc-section of the Danube, 1993, leg. Csányi, B.; Stopfenreuth, 1983, leg. Kinzelbach, R.; records published in Csányi *et al.* 1994, and Nesemann 1994).

Astacus leptodactylus Eschscholz, 1823

Material: Danube at Harta, 05. 09. 1991; Danube at Dunaújváros, 05. 09.; Szentendrei Duna near Leányfalu, 04. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube, in a deadwater lake Kühwörther Wasser between Schönau and Mühlleiten, 02. 1989; deadwater Alte Donau in Vienna, 31. 05. 1992, leg. Wittmann, K. J.; pond Rosenteich in Vienna, 06. 08. 1992, leg. Storch, C. & M. Rössler.

The distribution area of the Pontian crayfish *A. leptodactylus* includes the northwestern part of Asia Minor (Roth & Kinzelbach 1986), the Balkan Peninsula, the Pannonian lowlands, the middle and lower Danube valley, the basin of the Black, Caspian and Aral seas and their drainage systems, the Northeastern European lowlands and rivers flowing into the Baltic Sea and the adjacent regions of Asia. The description of a series of subspecies and species has brought some confusion in the nomenclature. Some relatives of the nominal species are also found in more or less brackish waters of the Caspian and the northwestern Black Sea. It is extending its range into Western Europe and – because of some economic importance as culinary delicacy – was introduced into all kinds of lakes and fishponds outside its original distribution area. In Central and Western Europe it is said to replace the noble crayfish *Astacus astacus* (Cukerzis 1968).

The lower and middle Danube belongs to the original area of *A. leptodactylus* (Entz 1909,

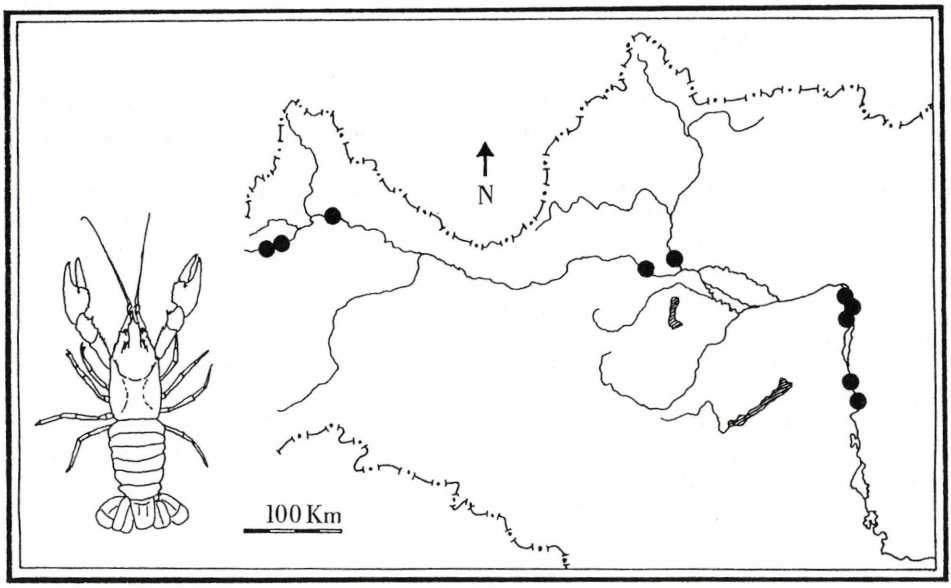

Fig. 7. Distribution of *Orconectes limosus* in the middle and upper Danube (with watershed)

1914). It was found in stagnant backwaters of Vienna, which seem to be the westernmost record. In Hungary, the species is widespread and locally of high abundance, especially in the rivers Danube and Tisza (Thuránszky & Forró 1987). *A. leptodactylus* was collected in the river Tisza near Sarud and its alluvial floodplain (Hortobágy: Németéri főcsatorna near Nagyiván) in 1991. Surprisingly, even in the main course of the Danube, specimens of this crayfish were caught as high upstream as Leányfalu (rkm 1672). South of Budapest it appears to be more numerous, e. g. at Harta.

In contrast to *Orconectes limosus*, which inhabits the shallow waters along the stony banks of the river, *A. leptodactylus* prefers the more precipitous parts of the bank and bottom, which never fall dry, even at low water levels. The species is a typical member of the potamon biocoenosis and is restricted to running and stagnant waters of the lowlands.

Family Cambaridae

Orconectes limosus (Rafinesque, 1817)

Material: Danube at Dunaföldvár, 05. 09. 1991; Danube at Dunaújváros, 05. 09. 1991; Danube at Csillaghegy near Budapest, 04. 09. 1991; Szentendrei Duna at Leányfalu, 4. 09. 1991, leg. Ofenböck, T. & H. Nesemann; Danube near Újpest at the Népsziget, 20. 10. 1988, leg. Forró, L. & H. Nesemann; Danube port Ölhafen near Vienna (rkm 1918), 09. 1991, leg. Nesemann, H., Dorninger, C. & K. J. Wittmann, 9. 07. 1992; Danube in a side-branch near Tegernheim, 30. 09. 1990; Danube at Menning, 3. 11. 1985; Danube at Marching, 3. 11. 1985; Morava (March) near Schlosshof, 08. 1990, leg. Nesemann, H..

A species introduced from eastern North-America into Germany and France at the end of the 19th century (1894 in the Oder system) to support fisheries, as native crayfish were decimated by the parasitic fungus *Aphanomyces astaci*. North of the Pyrenees and Alps, *O. limosus* is a common and widespread crayfish in most of the river systems flowing into the Baltic and North seas as well as into the Atlantic Ocean (Holthuis 1979). Living stocks were also transferred to localities in Bavaria and the vicinity of Budapest (Thuránszky 1960). Up to 1985, free living populations of *O. limosus* in the Danube system were not known. It was first recorded in a large secondary branch of the Hungarian Danube, called Téli kikötő, near Újpest at the Népsziget (rkm 1654; Thuránszky & Forró 1987) and in the Bavarian Danube near Ingolstadt (Nesemann 1987).

Hence, in the 1980s two disjunct populations in the upper and middle course of the Danube could be distinguished. In the Bavarian Danube near Ingolstadt, *O. limosus* was the only decapod crustacean species and was found infrequently and sparsely. Since that time it spread downstream as far as Donaustauf. The second Danubian population of *O. limosus* in Hungary and in the river Morava is denser and is associated with a further decapod crustacean, *A. leptodactylus*. In 1991, *O. limosus* was caught frequently in the main course of the Danube River between Leányfalu (rkm 1673) and Dunaföldvár (rkm 1562), indicating a progressive spreading in the last six years. From the Rhine River an advance of five km per year was reported (Schweng 1968). Under optimal conditions, this species may reach high population densities, e.g. 20 individuals per square meter in the Rhine. In the Danube, 1-2 specimens were caught per square meter at Csillaghegy. In September 1991, the first population of *O. limosus* in the Austrian part of the Danube was observed. The crayfishes live abundantly in the port Ölhafen near Vienna (rkm 1918). This isolated locality may be the effect of an unknown importation by ship (Fig. 7).

O. limosus prefers the shallow water of the stony banks of large lowland rivers and seems to be perfectly adapted to these types of running waters with periodical floods and droughts, always strictly following the water's edge.

Discussion and conclusions

The number of species of higher crustaceans tends to increase discontinously in downstream direction. The Bavarian section of the Danube River, which is a typical lowland river with meanders, is inhabited by six Ponto-Caspian species: *J. istri* (Janiridae), *D. villosus, D. haemobaphes*, *N. hrabei* (Gammaridae), *C. curvispinum* (Corophiidae) and the recently immigrated *L. benedeni* (Mysidae). Locally, some of these are of high abundance, density and biomass. In the eastern part of Lower Austria, three species are added to the previously named ones: *C. ischnus*, *S. ambulans* (Gammaridae) and *A. leptodactylus* (Astacidae). Downstream of the Dunakanyar (rkm 1700), the structure of the community is completely changed and the diversity of the fauna increases markedly. Three further species are frequently found, *O. obesus* (Gammaridae), *O. cavimana* (Talitridae) and the introduced crayfish *O. limosus* (Cambaridae).

Corresponding to important geological and hydrological changes, the following distribution limits can be distinguished: the Dunakanyar at rkm 1700, the "Wiener Pforte" (rkm 1940), the narrow valley of the "Wachau" (rkm 2006), and the "Weltenburger Enge" (rkm 2420).

Correspondingly, several species show approximately the same distribution pattern. *D. haemobaphes* and *C. curvispinum* are frequently collected throughout the whole upper reach of the Danube as far upstream as Kehlheim, or even further. Before the explosive upstream

expansion, in 1989-90 the western limit of D. *villosus* and *C. ischnus* was located a few km upstream from Krems. *S. ambulans* and *A. leptodactylus* did not expand beyond the basin of Vienna in western direction. Here *L. benedeni* had its western limit in 1982-83. *O. obesus* and *O. limosus* are restricted to the Great Hungarian Plain in the Eastern part of Hungary.

Records of *J. istri* and *C. curvispinum* in early investigations in Hungary and in Germany show, that these Ponto-Caspian elements did not largely extend their Danubian range (unlike in other riverine systems) in the present century. *N. hrabei*, *S. ambulans* and *A. leptodactylus* show a stable distribution pattern (Nesemann 1991).

Since the beginning of the present century, some Malacostraca have significantly extended their range in upstream direction. This fact, however, did not basically change the biological zonation of the Danube River. The precise informations about the distribution of these species given in the 1930s, chiefly by Dudich (1927) and by museum material for the Hungarian Danube, extended in the 50s and 60s for the Austrian and German Danube by Vornatscher (1965) and Kothé (1968), respectively, are most suitable for a comparison with the current situation. The following species have extended their previously wide distribution for several 100 km: *O. obesus* in the Hungarian section of the Danube, *L. benedeni*, *C. ischnus*, and *D. villosus* in Austria and Germany (Weish & Türkay 1975, Wittmann 1995). In addition *D. haemobaphes*, *D. villosus*, and *C. ischnus* are currently invading even the Rhine (Bij de Vaate & Klink 1995).

D. haemobaphes (before 1987), and later also *D. villosus* (1992), and *L. benedeni* (1993) explosively invaded the Bavarian Danube (compare Kothé 1968, Foeckler 1987, Wittmann 1995). Also the American crayfish, *O. limosus*, significantly extended its previously very limited distributional range and is rapidly expanding lately in the Danube.

In the Danube at Linz, three ships were examined for the presence of Malacostraca (Wittmann 1995). This material was now examined also for gammarids and so we can give the following species list: inside ships: *D. villosus, D. haemobaphes,* and *C. curvispinum.* Outside attached to hulls we found the same three species plus *L. benedeni*. So there is no doubt that navigation is among the crucial factors for dispersion of Malacostraca.

The decapod *Atyaephyra desmaresti* (Millet, 1831) was recently found in the Main-Danube-Canal, but records from the Danube itself are still lacking (Wittmann 1995). The record by Pretzmann & Pauler (1981) for backwaters in the Lobau near Vienna was questioned by Wittmann (1995).

Among the mysid species, *Paramysis intermedia* (Czerniavsky 1882) was introduced by fishery biologists into Lake Balaton and other Hungarian waters in about 1955 (Prof. M. Bácescu, pers. comm.). So we may expect this species also in the middle Danube, but so far we have no positive records. In the lower Danube, we found it together with *L. benedeni* and *Paramysis lacustris tanaitica* (Martinov 1924) on several locations between the delta and as far upstream as the confluence with river Iskar (leg. B. Csányi, 01. 12. 1991).

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