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The Ponto-Caspian mysid *Paramysis lacustris* (Czerniavsky, 1882) has colonized the Middle Danube

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Abstract – In 2017, the mysid *Paramysis lacustris* (Czerniavsky, 1882) was found for the first time in the Hungarian Danube section, representing the first psammo-pelophilous Ponto-Caspian peracarid colonizing the Middle Danube. In 2018, a brief survey focusing on this species revealed its presence in a more than 500-km-long river section spanning from Austria (Vienna, river km 1926) to Croatia (Batina, river km 1425). The largest populations of *P. lacustris* might be formed in reservoirs and slow-flowing stretches, where the appearance of the species might imply a considerable impact in connection with its zooplanktivorous feeding and important role in the diet of fish. Similar to all the other Ponto-Caspian peracarids that have crossed the Middle Danube, *P. lacustris* can reasonably be expected to continue its spread toward Western Europe in the future.

Keywords: range expansion / Crustacea / Mysida / psammo-pelophilous / jump dispersal

In recent decades, several Ponto-Caspian peracarid crustaceans (*i.e.*, amphipods, isopods, and mysids) have expanded their ranges in Central and Western Europe, in which the River Danube has played a pivotal role as part of the "southern invasion corridor" (the Danube-Main-Rhine system; Bij de Vaate *et al.*, 2002). Crossing the comparatively unregulated Middle Danube has been identified as the key step of the invasion process; all species that have appeared in the German or Austrian section (Upper Danube) so far have been able to colonize additional Western European catchments (Borza *et al.*, 2015). All these species show affinity to hard substrates (lithophilous), although the majority of the Ponto-Caspian peracarid fauna prefer sandy-muddy habitats (psammo-pelophilous; Borza *et al.*, 2017). In the present publication we report on the range expansion of *P. lacustris* (Fig. 1), the first psammo-pelophilous Ponto-Caspian peracarid colonizing the Middle Danube.

P. lacustris is native to the Black, Azov, and Caspian Seas as well as to the lower sections of rivers draining into them (Audzijonyte *et al.*, 2015). In the Soviet era, it was introduced into several waters outside its native range, including lakes and reservoirs in Lithuania, which allowed its expansion in the Baltic Sea basin (Zettler, 2015; Audzijonyte *et al.*, 2017). In the River Danube, the native range of the species was restricted to the lower ~ 600 river km (Wittmann, 2007); however, during the latest international survey on the river ("Joint Danube Survey 3," 2013), its upstream distributional limit corresponded approximately to the confluence with the River Tisza (river km ~1200, Fig. 2; Borza *et al.*, 2015) in accordance with its previous range expansion in this tributary (Borza and Boda, 2013).

P. lacustris was first detected in the Hungarian Danube section in the summer of 2017. By that time it had already colonized a large area, since it was found in the most upstream part (Szigetköz, river km 1850) during the regular biomonitoring, as well as in Budapest in the course of an ongoing thesis project (river km 1642; Tab. 1, Fig. 2). In 2018, a brief survey focusing on this species (daytime sampling using a hand net with 500 μm mesh size) revealed its presence in a more than 500 km-long river section spanning from Austria to Croatia. The most upstream occurrence was recorded in the impounded river section of the Freudenau dam in Vienna (river km 1926). The species has already entered the major flood-protected sidearms of the Middle Danube (the Slovakian Malý Dunaj, and the Hungarian Mosoni and Ráckevei-Sorokári Danube-arms; Tab. 1). Our records represent the first occurrence of the species for the Slovakian and Croatian fauna, as well as the first indication of a self-sustaining population in Austria (cf. Wittmann, 2007).

Although the species is capable of active upstream spread under certain conditions, as indicated by records in Lithuanian rivers (Arbačiauskas *et al.*, 2011), we consider this mechanism

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Fig. 1. Adult female specimen of *P. lacustris*.

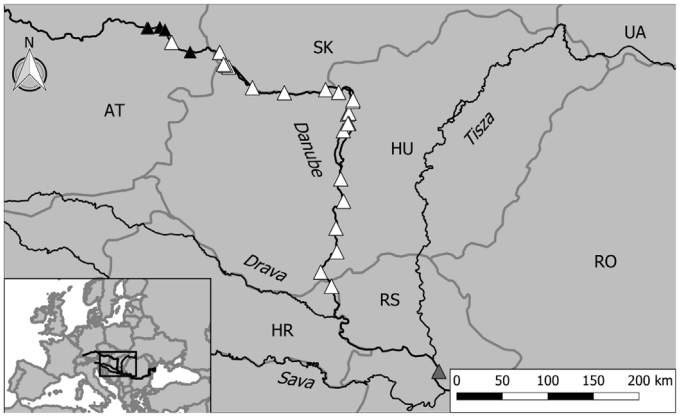

Fig. 2. Sampling sites in the Middle Danube. White triangles: *P. lacustris* present; black triangles: *P. lacustris* absent; grey triangle: the most upstream occurrence of *P. lacustris* during the Joint Danube Survey 3 (Borza *et al.*, 2015). Country codes in addition to Table 1: RO: Romania, UA: Ukraine, RS: Serbia.

Table 1. Records of mysids in the Middle Danube (ordered by river km-s). PL: *Paramysis lacustris* (Czerniavsky, 1882), KW: *Katamysis warpachowskyi* G.O. Sars, 1893, LB: *Limnomysis benedeni* Czerniavsky, 1882. River km-s of sampling points in sidearms represent the nearest point in the main channel. Country codes: AT: Austria, SK: Slovakia, HU: Hungary, HR: Croatia. Since the samples were collected during the day, they cannot be regarded as representative for the nocturnally active *Hemimysis anomala* (G.O. Sars, 1907). The sampling was not quantitative; therefore, the numbers of collected specimens serve as only a rough indication of the relative densities of the three mysid species.

Date	River km	Country	Location	Geographic coordinates	Habitat	PL	KW	LB
17.09.2018	1963	AT	Tulln 1	48°20′13.30″ N 16°03′34.70″ E	Rip-rap		6	14
17.09.2018	1962	AT	Tulln 2	48°20′15.53″ N 16°04′42.07″ E	Mud, gravel, algae		9	
17.09.2018	1949	AT	Greifenstein	48°21′01.15″ N 16°14′59.97″ E	Mud		49	5
17.09.2018	1942	AT	Klosterneuburg	48°19′41.88″ N 16°19′43.43″ E	Sand, gravel		13	1
17.09.2018	1926	AT	Vienna, Alte Donau	48°12′49.30″ N 16°26′15.45″ E	Stones, macrophytes		2	22
17.09.2018	1926	AT	Vienna, Danube main arm	48°12′29.01″ N 16°26′10.52″ E	Rip-rap, mud	47	5	4
17.09.2018	1902	AT	Haslau	48°07′18.57″ N 16°42′55.58″ E	Gravel			8
17.09.2018	1866	SK	Bratislava, Danube inlet	48°07′39.24″ N 17°09′02.26″ E	Mud	23	1	
17.09.2018	1866	SK	Bratislava, Malý Dunaj	48°07′43.43″ N 17°09′07.31″ E	Mud, riparian vegetation	9	3	12
22.08.2017	1850	HU	Rajka, Mosoni-Danube	48°00′45.84″ N 17°12′59.47″ E	Gravel	2		2
22.08.2017	1848	HU	Rajka	48°00′14.88″ N 17°14′53.62″ E	Gravel, mud	6		19
22.08.2017	1845	HU	Dunakiliti, Helenai-Danube arm	47°59′16.34″ N 17°17′35.44″ E	Rip-rap, mud	6		16
04.04.2018	1806	HU	Vámosszabadi (Győrzámoly)	47°47′30.92″ N 17°39′03.69″ E	Gravel	3		7
15.05.2018	1806	HU	Vámosszabadi (Győrzámoly)	47°47′30.92″ N 17°39′03.69″ E	Gravel	49	9	10
31.08.2017	1768	HU	Komárom	47°45′03.93″ N 18°07′14.93″ E	Gravel, mud	8		1
30.09.2018	1719	SK	Štúrovo	47°47′25.65″ N 18°43′25.98″ E	Mud, algae	15		10
15.09.2018	1699	HU	Dömös	47°45′59.05″ N 18°55′02.18″ E	Mud	14		1
28.08.2018	1670	HU	Göd 1	47°41′40.02″ N 19°07′45.00″ E	Sand, mud	7		
28.08.2018	1668	HU	Göd 2	47°40′38.92″ N 19°07′29.08″ E	Clay, shells	13		1
28.08.2018	1655	HU	Budapest, Újpest	47°33′44.86″ N 19°04′15.45″ E	Sand, mud	5		
28.08.2018	1653	HU	Budapest, Óbudai-sziget	47°33′06.99″ N 19°02′53.90″ E	Sand, mud	11		
29.08.2018	1642	HU	Budapest, Ráckevei-Soroksári Danube arm	47°27′39.49″ N 19°04′20.90″ E	Rip-rap, mud	5	1	10
04.07.2017	1642	HU	Budapest, Lágymányosi-öböl	47°27′33.90″ N 19°03′30.50″ E	Mud	1	8	
29.08.2018	1631	HU	Budapest, Nagytétény	47°23′19.70″ N 18°59′32.16″ E	Sand, gravel	5		
19.09.2018	1572	HU	Dunavecse	46°54′43.32″ N 18°57′53.50″ E	Sand, mud	45		
19.09.2018	1545	HU	Harta	46°41′33.58″ N 19°00′34.35″ E	Sand, gravel	49		
19.09.2018	1507	HU	Fajsz	46°25′35.06″ N 18°54′22.90″ E	Mud	20		
19.09.2018	1480	HU	Baja	46°11′36.28″ N 18°55′27.05″ E	Sand, mud	54		
19.09.2018	1446	HU	Mohács	45°59′21.37″ N 18°41′52.03″ E	Mud, clay	35		
19.09.2018	1425	HR	Batina	45°51′05.35″ N 18°51′16.09″ E	Mud, clay	25		

unlikely in the range expansion reported here for the following reasons: (1) Based on the considerable research and monitoring activity on the river in recent decades (including several samples taken and/or identified by mysid specialists; *e.g.*, Wittmann, 2002, 2007; Borza, 2007; Borza *et al.*, 2015), it is not likely that the species has been overlooked in this river section for a long time. (2) The more than 700 km-long river section upstream of the last reported range limit of the species (river km ~1200 in 2013, Fig. 2; Borza *et al.*, 2015) is blocked by two dams (at Freudenau and Gabčíkovo), and most of it can be characterized by relatively strong currents and coarse substrates (Fig. 2 in Borza *et al.*, 2015), offering only small and isolated patches of suitable habitat for *P. lacustris*.

Rather, we assume that the species reached Vienna by jump dispersal (*e.g.*, by ships) and colonized the intermediate river section rapidly by downstream drift, similar to all the other Ponto-Caspian peracarid species expanding in the river after the opening of the Main-Danube canal in 1992 (Borza *et al.*, 2015). The establishment of the species in Vienna might be in connection with a previous record of a single specimen in 2004 (Wittmann, 2007). Such long lag-periods are often reported in terrestrial invasions where small "bridgehead" populations are more likely to be detected (Crooks and Soulé, 1999).

The species prefers fine sediments (sand, mud, or clay) with standing water or slow to moderate currents (Băcescu, 1954); therefore, the largest populations in the recently colonized river section might be formed in reservoirs. In fast-flowing stretches with coarse sediments, the presence of the species might be restricted to isolated lentic patches (*e.g.*, around groynes), whereas in slow-flowing sections of the river, it might inhabit the entire littoral zone. Revealing whether the species can also inhabit the offshore zone in such stretches would require further investigations.

The overall impact of the species is hard to predict. Stable isotope analyses have identified *P. lacustris* as omnivorous with larger specimens relying primarily on zooplankton (Lesutienė *et al.*, 2007, 2008). The species also serves as an important food source for fish; however, long-term positive effects on fish production have not been proved (Arbačiauskas *et al.*, 2010). Considerable negative consequences on the other mysids cannot be expected, since their habitat preferences (Borza *et al.*, 2017) as well as their diets (Rothhaupt *et al.*, 2014) are markedly different.

Based on the fact that all Ponto-Caspian peracarids that have crossed the Middle Danube have been able to continue their spread, *P. lacustris* can reasonably be expected to colonize the Upper Danube as well as other catchments in Western Europe in the future. As most of these waters can be characterized as a more-or-less continuous chain of reservoirs, the species might become an important member of their biota.

Borza *et al.* (2017) discussed the possibility of a new invasion wave consisting of psammo-pelophilous Ponto-Caspian peracarids in case substantial hydromorphological modifications (*e.g.*, establishment of reservoirs, or deepening of the shipping channel) were carried out in the Middle Danube. We assume that *P. lacustris* is not the harbinger of a new wave but a late representative of the previous one. Its invasion success indicates that the large-scale spread of psammo-pelophilous species is possible even under the present conditions; however, drastic anthropogenic disturbances might considerably accelerate the process.

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