Inventory of a world hotspot of groundwater fauna biodiversity – the Lobau wetland and the Danube Floodplain National Park (Austria) revisited

Christian Griebler, Clemens Karwautz, Grit Rasch, Lucas Fillinger, Raphael Veits, Rick Junker, Santiago Gaviria, Andreas Fuchs, Florian Scharhauser, Ursula Eisendle, Constanze Englisch, Jan Steger, Matthäus Greilhuber, Fritz Schiemer, Tobias Pfingstl, Peter Pospisil, Dan L. Danielopol

The Danube Floodplain National Park is one of the largest protected floodplain areas in Central Europe. Situated in the east of Austria, it extends from the city of Vienna to the border with Slovakia. This area is not only a hotspot of biodiversity at the surface, but extraordinary species richness extends into the subterranean aquatic environments, i.e. the shallow groundwater habitats. Up to now, 44 species of true groundwater invertebrates (stygobionts) and 93 species of facultatively groundwater-dwelling invertebrates (stygophiles) have been recorded from the shallow aquifer of the Danube Floodplain National Park. The list of animal goups comprises, among others, crustaceans (e.g. Amphipoda, Copepoda, Isopoda, Ostracoda), annelids (Oligochaeta, Aphanoneura, Polychaeta), nematods, turbellarians, mites, and gastropods. In particular, the shallow groundwater habitats of the Lower Lobau, an intensively studied wetland area within the national park, hosts 84 % of the stygobionts and 84 % of the stygophile species discovered in the entire national park. Our compilation of historic and recent data underlines the Danube Floodplain National Park to be among the top-ranked subterranean biodiversity hotspots worldwide. The unique data set from groundwater research over a period of more than 50 years will allow us in the coming years to targeted stress effects of river regulation, floodplain water management, and climate change in relation to biodiversity.

Griebler C, Karwautz C, Rasch G, Fillinger L, Veits R, Junker R, Gaviria S, Fuchs A, Scharhauser F, Eisendle U, Englisch C, Steger J, Greilhuber M, Schiemer F, Pfingstl T, Pospisil P, Danielopol DL (2023) Bestandsaufnahme eines weltweiten Hotspots der Grundwasserfauna-Biodiversität – das Lobau-Feuchtgebiet und der Nationalpark Donau-Auen (Österreich).
Der Nationalpark Donau-Auen ist eines der größten geschützten zusammenhängenden Flussauengebiete in Mitteleuropa. Er liegt im Osten Österreichs und erstreckt sich von Wien bis hin zur slowakischen Grenze. Dieses Gebiet ist nicht nur oberirdisch ein Biodiversitäts-Hotspot mit einem außergewöhnlichen Reichtum an Pflanzen- und Tierarten, sondern beeindruckt auch durch eine enorme Biodiversität innerhalb der Grundwasserfauna. Bis heute konnten 44 echte Grundwasser- (stygobionte) und 93 grundwasseraffine (stygophile) Evertebratenarten (Wirbellose) im Grundwasser des Nationalparks gefunden werden. Die Liste an Tiergruppen umfasst unter anderen Vertreter der Crustaceen (u. a. Amphipoda, Copepoda, Isopoda, Ostracoda), der Anneliden (Oligochaeta, Aphanoneura, Polychaeta), der Fadenwürmer (Nematoda), der Strudelwürmer („Turbellaria"), der Milben (Acari), und der Schnecken (Gastropoda). Hervorzuheben ist die Untere Lobau, ein Teilgebiet des Nationalparks bei Wien. Dieses wurde über Jahrzehnte intensiv beforscht und beherbergt 84 % aller stygobionten und stygophilen Arten, die bislang im Nationalpark gefunden wurden. Diese Zusammenstellung historischer und aktueller Forschungsergebnisse unterstreicht die Position des Nationalparks Donau-Auen als weltweit führender Biodiversitäts-Hotspot der Grundwasserfauna. Der einzigartige Datensatz aus über 50 Jahren Grundwasserforschung erlaubt in naher Zukunft gezielt Effekte der Donauregulierung, des Wassermanagements im Nationalpark und des Klimawandels auf die Grundwasserbiodiversität zu untersuchen.

Keywords: groundwater, biodiversity, Danube Floodplain National Park, Lower Lobau, hotspot.

Introduction

Groundwater systems are, from an ecological perspective, among the least investigated habitats worldwide. Still, groundwater is mainly perceived as a resource for drinking water production, irrigation and many other purposes. However, groundwater systems deliver important ecosystem services, some of which are dependent on active microbial communities and invertebrates (Griebler & Avramov 2015). The more productive an ecosystem is, the more biomass can be sustained. Combined with considerable dynamics in environmental conditions (= intermediate disturbances), highly productive systems likely harbor a high biodiversity. While groundwater ecosystems are often quite stable in environmental conditions (e.g., permanent darkness, constant temperature, low oxygen concentration, little changes in hydrochemistry) when compared to surface waters, shallow aquifers in river floodplains may exhibit a pronounced seasonality with strong dynamics in physico-chemical conditions. In consequence, we assumed that river floodplain aquifers harbour a marked species richness (Ward et al. 1998) and in special cases can be considered hotspots of groundwater biodiversity (Danielopol & Pospisil 2001; Gibert & Culver 2009).

How to define a groundwater biodiversity hotspot? In the year 2000, Culver & Sket (2000) compiled data of 20 cave systems and karst wells that harbored more than 20 species specifically adapted to the life in subterranean environments, i.e. stygobionts (obligatory groundwater dwellers) and troglobionts (obligatory terrestrial cave dwellers) (Culver & Sket 2000). In four cases, sites harbor(ed) more than 30 stygobiont species. Since then, the number of recognized cave and karst biodiversity hotspots and the numbers of species recorded there slightly increased. A recent special issue of the journal *Diversity* contains information on 14 of the currently 22 known global hotspots of subterranean biodiversity (Pipan et al. 2021).

Alluvial aquifers, the shallow, unconsolidated, porous sediment fillings in river valleys and basins, have received considerably less attention with respect to groundwater fauna biodiversity in comparison to karstic environments. While Jack Stanford noted in 1998 that no groundwater biodiversity hotspots have been recorded along riparian and floodplain areas, there are indeed a few examples (Stanford 1998). In fact, the alluvial aquifers and floodplains of the Rhône, the Rhine, and in particular the Danube River are such hotspots of hypogean biodiversity (Dole-Olivier et al. 1994; Pospisil 1994a). One intensively studied site along the Rhône River is the Jons Plain at Lyon. Within a sector of 10×4 km, 38 stygobiont species were discovered (Dole-Olivier et al. 1994). More than 35 stygobionts are recorded for the Rhine River valley, and more than 60 stygobiont species have been identified in samples from the hyporheos and shallow aquifers along the Danube River (Dole-Olivier et al. 1994). Within the Danube alluvial aquifers and floodplains, only the Lobau wetland as part of the Danube Floodplain National Park east of the city of Vienna, Austria, was reported in the year 2001 to harbor 35 taxa of exclusively groundwater dwelling animals (Danielopol & Pospisil 2001).

The Danube Floodplain National Park, with 9,600 ha, is one of the largest protected floodplain areas in Central Europe. Situated in the east of Austria, it extends from the city of Vienna to the border with Slovakia. Historically, selected areas (e.g. the Lobau wetland) were protected as UNESCO biosphere reserve (1977–2016), Nature Protection Areas (1978), and RAMSAR sites (Lower Lobau and Danube-March-Thaya floodplains) in 1983. The status of a National Park (IUCN-Category II) was finally awarded in 1996. Since 2004, parts of the national park are classified as Flora-Fauna-Habitat (FFH) areas. The national park is characterized by a huge diversity of habitats, both aquatic and terrestrial, harboring a vast species richness, e.g. more than 800 vascular plant and 5,000 animal species including about 2,500 insects, 100 brooding birds, 67 fishes, 33 mammals, 13 amphibians and 8 reptiles (Hein et al. 2023).

In the area of the early UNESCO biosphere reserve Lower Lobau (Fig. 1), groundwater ecological research started in 1973. Between 1979 and 1998 the working group of D.L. Danielopol thoroughly studied the groundwater fauna in alluvial sediments of this area (Danielopol 1976a, 1976b, 1984, 1989, 1991; Pospisil 1994a; Danielopol et al. 1999), recording not less than 35 stygobiont invertebrate taxa until the year 2001 (Danielopol & Pospisil 2001). This research was remarkable for the large variety of approaches to groundwater fauna issues at different spatial and temporal scales and for the comparison of natural (e.g., the Lower Lobau) with anthropogenically impacted sites. First, between 1973 and 1976 information on groundwater fauna in the bank sediments of the Danube River upstream and downstream of Vienna, as well as in the city center was collected and its ecological and zoogeographical importance was repeatedly emphasized (e.g., Danielopol 1976a, 1976b, 1976c). Subsequently, work in the Lower Lobau started and natural sites were compared with antrophogenically impacted sites in Vienna (e.g. on the banks of the Donaukanal; see Danielopol 1983). In the later phase of this research period, the focus was laid on the Lower Lobau aquifer. Systematically, ecological drivers of groundwater biodiversity were tackled on different spatial scales, from the decimeter to the >100 m scale (Pospisil 1994a; Danielopol et al. 2000). Unfortunately, in the beginning of the new millennium, research on groundwater fauna in the area of the Danube Floodplain National Park ceased. After a break of 20 years, we recently revived the activities in 2019.

This paper compiles all information available, from historic data to current findings, on groundwater fauna biodiversity in the area of the Danube Floodplain National Park with a special focus on the Lobau wetland. For reasons of comparison, selected sites in the immediate neighborhood of the National Park are considered as well. We report on the species richness of stygobiont and stygophile taxa, including a critical evaluation of single records and the probability to discover new species in the coming years. Finally, current and potential future threats to the groundwater fauna biodiversity hotspot Danube Floodplain National Park are discussed.

Study sites

The Danube Floodplain National Park, established in 1996, extends from the city of Vienna to the Austrian border with Slovakia over an area of 9,600 ha (Fig. 1). It protects one of the largest remaining natural floodplain areas in Central Europe. Focus of the investigations was on the shallow, unconsolidated riverbank sediments, the hyporheic zone and the shallow Quaternary aquifer. The geological structure of this aquifer is formed by Holocene alluvial sediments deposited by the previously strongly meandering and anastomosed Danube. This shallow aquifer along the present-day Danube River and its floodplains mainly consists of gravel, sand, and silt-clay of generally only 5–10 m, and locally more than 30 m thickness.

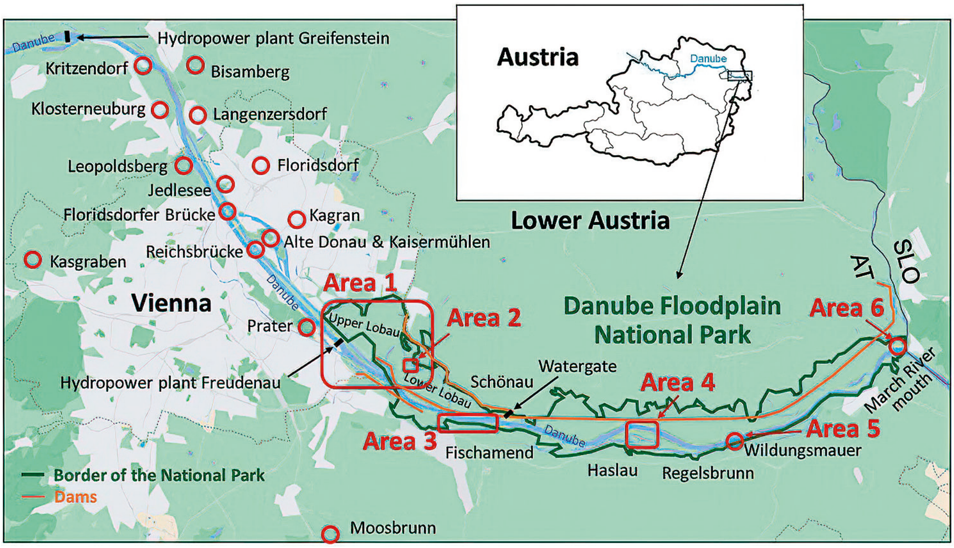

Fig. 1: Location of sampling areas. – Abb. 1: Lage der Untersuchungsstandorte.

The 'Lobau' as part of the national park is located along the Danube River south-east of the city of Vienna (Fig. 1). It is divided into the Upper and Lower Lobau (Fig. 1, Area 1). While the Upper Lobau is located entirely within the city limits of Vienna, the down-gradient Lower Lobau partly extends into the province of Lower Austria. In the Lower Lobau, a small area in the surrounding of the Kreuzgrundtraverse (Area 2 in Fig. 1) belongs to the most intensively studied alluvial aquifers worldwide (Culver & Pipan 2011). After irregular sampling surveys in the 1980s, a period of intense research started there in the mid-1990s. For 20 consecutive years more than 800 samples from about 100 piezometres and wells were collected. Research activities focused on exploring the short-, medium-, and long-term distribution patterns of groundwater fauna at different spatial scales. For this purpose, grids of piezometers and multi-level wells have been installed to tackle questions at micro- and mesohabitat scale, whereas groundwater observation wells of the water works have been used to address macrohabitat issues. A detailed description of the individual sectors and locations of sampling sites is provided in Pospisil (1994a, 1994b). Recent investigations, starting in 2019, targeted individual groundwater observation wells in the Lobau (Fig. 1, Area 1) in a non-systematic way to re-evaluate the former inventory of groundwater fauna. In addition, selected wells in the Lower Lobau, still available from previous campaigns (Fig. 1, Area 2), have been sampled since 2020 in a long-term monitoring approach.

A few more sites within the Danube Floodplain National Park have been in the focus of groundwater ecological research, i.e., the Regelsbrunner Au, and gravel bars as well as river bank sediments at Schönau, Fischamend, Wildungsmauer, and the March River confluence (Fig. 1). The Regelsbrunner Au, a floodplain at the right, southern bank of the Danube River is located between the villages of Haslau and Regelsbrunn (Fig. 1, Area 4). Following the strong regulation of the Danube 150 years ago, backwaters in this wetland system have been successively re-connected with the main river channel in the past three decades to regain hydrological dynamics and prevent siltation (Tockner et al. 1998; Schiemer et al. 1999). Groundwater samples from the Regelsbrunner Au mainly originated from three wells (G1, G2, G3; Fig. 2), described in detail in Steininger (2002). We also integrated data from a study that sampled multiple benthic habitats in the Regelsbrunner Au (Gaviria et al. 1998) which we considered here as a single locality (see RB in Fig. 2). At Fischamend (Fig. 1, Area 3), on the right side of the Danube, one study specifically targeted the nematode fauna in different depths of the riverbank sediments (Eder 1983). At Schönau, on the left side of the Danube (Fig. 1, Area 3), two recently installed groundwater observation wells (Fig. 2, Schönau-A and Schönau-B) have been repeatedly sampled in 2021. At Wildungsmauer (right side of the Danube) and at the confluence of the March River into the Danube (left side of the Danube), invertebrates were collected from different spots and depths of the Danube bank sediments. The sampling stations Fischamend, Wildungsmauer, and March River confluence are described in detail in Danielopol (1976a, 1976b).

For reasons of comparison, groundwater fauna records from several spots inside and outside Vienna (Fig. 1) are discussed. This includes historic data from the Prater (a large park area in Vienna close to the Lobau), Floridsdorf, Kagran, Jedlesee, and Klosterneuburg, among other sites (Spandl 1926; Vornatscher 1938; Strouhal 1958; Kiefer 1964). More recent data from the city of Vienna have been collected at Floridsdorfer Brücke, Reichsbrücke, and from Kritzendorf upstream of the Lobau and the Danube Floodplain National Park. For further locations considered in this study, see Figure 1.

It is worth mentioning that besides the early regulation of the Danube River and the construction of dams, there are two hydropower plants, i.e., Freudenau (constructed 1992–1998) right upstream of the Lobau and Greifenstein (constructed 1981–1985) upstream of Kritzendorf (Fig. 1) which considerably influence both the surface and subsurface hydrology.

Material & Methods

Groundwater fauna collection

Groundwater fauna was sampled using various techniques. The methodology of early studies has often been poorly documented, therefore information on sampling techniques is imprecise. In these early publications, the authors describe net samplers, with and without weight, that have been lowered into large wells, and hand piston pumps of different kind that have been used to withdraw water from wells with subsequent filtration through different nets. In the research period 1973 to 1976, samples were collected from different depths of the bank sediments by means of the Bou-Rouch (Bou & Rouch 1967) and Karaman-Chappuis method (Chappuis 1942). In the Lobau, samples were withdrawn from piezometers (2.5 cm inner diameter) by connecting a piston pump. From the multi-level wells (5 cm inner diameter), samples were withdrawn by means of a double packer system connected to a vacuum pump (Danielopol & Niederreiter 1987). Groundwater samples obtained from piezometers had a volume of 3 L, whereas 5 L were withdrawn from the multilevel wells (Danielopol 1978). From the larger groundwater observation wells (12 cm inner diameter) 50 L of groundwater were pumped. A synthesis of sampling methods is found in Pospisil (1992). In our recent studies, starting 2019, fauna from multi-level groundwater observation wells were collected using a phreatic net sampler, i.e. a miniaturized Cvetkov net (Cvetkov 1968) with a mesh size of 63 µm, lowered to the bottom of groundwater wells (Hahn & Matzke 2005).

Ecological categories for invertebrate taxa sampled in subsurface habitats

For the classification of fauna collected from groundwater, we use the terms stygobiont, stygophile, and stygoxene as defined in Gibert et al. (1994), which mainly refer to life cycles of organisms which can be completed (stygobiont) or partly completed (stygophile) in groundwater. In this sense, stygobionts are species specialized to life in subterranean habitats, i.e. obligatorily hypogean. Stygophiles are considered species that appear to actively exploit resources in the groundwater system, or actively seek protection from unfavorable situations in the surface environment (refugium). In porous aquifers, stygophiles are subdivided, based on their degree of pre-adaptation, into three categories: (1) occasional hyporheobionts (larvae of different insects) (2) amphibionts (e.g. plecopterans, which need the interstitial phase to complete their larval life stage, and cannot survive without this subterranean phase), and (3) permanent hyporheobionts (many species of nematodes, oligochaetes, mites, and crustaceans that may be present at all life stages either in groundwater or benthic habitats) (Gibert et al. 1994). Stygoxenes are organisms that have no affinities with the groundwater system, but occasionally (accidentally) enter subsurface aquatic habitats. Examples are planktonic groups (e.g., calanoid copepods, cladocerans) or benthic crustaceans and insects. The data compilation in this review paper focuses on stygobiont and stygophile species, with the latter ignoring occasional hyporheobionts and amphibionts (the only exception is the marsh beetle *Cyphon palustris*). The authors are aware that a categorization of individual species into stygobiont and stygophile often is difficult. Regularly, species are considered stygobionts if found up to the time point of reporting only in groundwaters. Similarly, the cut-off between amphibionts and permanent hyporheobionts is somehow subjective, excluding clear amphibionts (such as plecopterans) but including oligochaetes and nematodes, where our autecological knowledge is very limited.

Molecular and phylogenetic analyses

For sequencing of barcoding genes, groundwater amphipods and isopods collected in our sampling campaigns were fixed in 96 % ethanol. DNA was extracted from single appendages (legs, antennae) with the QIAamp UCP DNA Micro Kit (QUIAGEN, Hilden, Germany) following the manufacturer's instructions with two modifications. First, digestion with proteinase K was extended to 12–14 hours; second, subsequent DNA elution was achieved with 40 µl of elution buffer.

A ≥ 1000 bp long fragment of the 28S rRNA gene (28S) in amphipods was amplified with primers specific for aquatic malacostracans (Verovnik et al. 2005) see Tab. 1. For the cytochrome c oxidase subunit I gene (COI), inosine primers (Tab. 1) developed by Geller et al. (2013) were used to amplify a 658 bp long fragment in amphipods and isopods. Quality and length of the PCR products were checked with gel electrophoresis and approved products were sequenced externally on a Sanger sequencing platform (MicroSynth, Switzerland). ABI chromatograms of forward and reverse primer products were quality checked, trimmed and aligned in Geneious Prime 2020.1.2 (Biomatters, New Zealand).

Phylogenetic analyses were done using 39 new partial COI sequences (35 new amphipod and 4 new isopod sequences), together with 330 published COI sequences, as well as using 9 new partial 28S sequences of amphipods together with 162 already published 28S rRNA gene sequences from NCBI. COI sequences were aligned with MAFFT v.7 (Katoh & Standley 2013) using the E-insi option (Katoh & Toh 2008), 28S sequences with the L-insi option. Alignments were trimmed and quality checked using Geneious

Tab. 1: Primers for the coding regions of the COI and 28S genes, used for amphipods and isopods. – Tab. 1: Primer für die kodierenden Regionen von COI und 28S, verwendet für Amphipoden und Isopoden..

Coding genes	Primer name	Primer Seq. (5'- 3')	Reference
28S	28_for	CAAGTACCGTGAGGGAAAGTT	Verovnik et al. 2005
28S	28_rev	AGGGAAACTTCGGAGGGAACC	Verovnik et al. 2005
28S (for sequencing)	Niph15i	AGA GTC AAA AGA CCG TGA AAC C	Weber et al. 2021
COI	jgLCO1490	TITCIACIAAYCAYAARGAYATTGG	Geller et al. 2013
COI	jgHCO2198	TAIACYTCIGGRTGICCRAARAAYCA	Geller et al. 2013

Prime 2022.2.2. The optimal substitution model for each alignment was assessed using ModelFinder (Kalyaanamoorthy et al. 2017). The GTR+F+R5 model was the best fit for our 28S alignment, the mtZOA + F + G4 model for the COI dataset. IQTREE (Nguyen et al. 2015) was used for phylogenetic reconstruction using the Ultrafast Bootstrap Approximation UFBoot (Minh et al. 2013) to assess node stability (10,000 bootstrap runs). Additionally, support values were generated using approximate Bayes (aBayes) (Anisimova et al. 2011) and SH-aLRT analyses (Guindon et al. 2010). Final trees were graphically optimized using ITOL v. 6.6 (Letunic & Bork 2021) and Adobe Illustrator CC 22.1 (Adobe Inc.©, San Jose, USA). All sequences have been uploaded to GenBank and accession numbers are included in the trees.

Results

Combining all reliable data from early and recent sampling surveys, the list of stygobiont species for the Lobau comprises 35 stygobiont and 62 stygophile species, with 19 stygobiont and 34 stygophile species found recently, i.e., since the year 2019. Including further records for the Danube Floodplain National Park, this list can be extended to 44 stygobiont and 93 stygophile species in total, with 21 stygobiont and 44 stygophile observed recently (Tab. 2). Another 9 stygobiont and 9 stygophile species recorded from the area of Vienna and its neighborhoods have not yet been found in the shallow aquifers of the national park. Due to current research projects addressing the groundwater fauna in the city of Vienna, there is legitimate hope that several stygobiont and stygophile species new for the region and new to science will be discovered and described in the next years. More than 150 groundwater observation wells have been sampled in 2021 and 2022 in the frame of the project “Heat below the City”, funded by the Vienna Science and Technology Fund (WWTF).

On the other hand, some of the historically recorded taxon names may turn out invalid after molecular analysis. A number of species have already been removed from our list because of synonymy and re-naming. Details are provided in the sections on major animal groups. In Tab. 3 we highlighted in red all species with uncertainties pertaining to their taxonomic position and name, their biogeographic distribution, or their habitat affiliation (stygobiont vs. stygophile vs. stygoxene). In the following, the state of knowledge is compiled for all major invertebrate groups with stygobiont and stygophile representatives in groundwater of the Lobau, the Danube Floodplain National Park, and neighboring sites in the Vienna region.

Tab. 2: List of the major groups of invertebrates found in shallow groundwater of the Danube Floodplain National Park. Numbers of species are distinguished into potentially stygobiont and stygophile taxa. Numbers provided are total species counts, while those in brackets refer to the number of species that were (re)observed recently (2019-2022). The list, in general, ignores groups of animals that are of terrestrial origin (e.g. springtails) or do not live in groundwater (e.g. insects). One exception is the marsh beetle *Cyphon palustris*. For further explanation, see text. – Tab. 2: Liste der Evertebraten-Großgruppen aus dem oberflächennahen Grundwasser des Donau-Auen Nationalparks. Die Artenzahl je Gruppe ist unterschieden in stygobionte und stygophile Arten. Zahlen beinhalten alle bisher beschriebenen Arten. Zahlen in Klammer beziehen sich auf aktuell (2019-2022) nachgewiesene Arten. Die Zusammenfassung ignoriert Tiere terrestrischen Ursprungs (z. B. Springschwänze) und solche, die im Allgemeinen nicht dauerhaft im Grundwasser leben (z. B. Insekten). Die einzige Ausnahme bildet der Sumpfkäfer *Cyphon palustris*. Für weitere Erläuterungen siehe Text.

Phylum	**Subphylum**	**Class**	**Subclass**	**Order**	**stygobiont**	**stygophile**
Platyhelminthes	„Turbellaria“					4 (3)
Rotatoria						1 (0)
Annelida		Clitellata	Oligochaeta		1 (0)	21 (7)
		Aphanoneura			1 (0)	
		Polychaeta			1 (1)	
Mollusca	Gastropoda				2 (2)	
Nematoda					2 (0)	45 (25)
Arthropoda	Crustacea	Ostracoda			7 (3)	7 (2)
		Branchiopoda		Diplostraca		2 (1)
		Malacostraca		Amphipoda	7 (4)	1 (1)
				Isopoda	3 (3)	
		Copepoda		Cyclopoida	14 (6)	3 (0)
				Harpacticoida	5 (1)	4 (1)
	Chelicerata	Arachnida	Acari		1 (1)	4 (3)
	Hexapoda	Insecta				1 (1)
Sum					44 (21)	93 (44)

Major groups of invertebrates

Turbellarians

Turbellarians (formerly class "Turbellaria") are flatworms (Platyhelminthes) excluding the monophyletic, exclusively parasitic Neodermata (Egger et al. 2015). They are predominantly free-living and are therefore often simply referred to as the free-living flatworms. Turbellarians are unsegmented, acoelomate, hermaphroditic animals with a multiciliated epidermis. The term "planarians" is usually reserved for the subgroup Tricladida. Many of the turbellarian species are predators of invertebrates, but some also feed on algae or microorganisms, are fed by symbionts or are parasitic. Freshwater representatives occur in both lentic and lotic surface waters and in groundwater. They are mostly benthic animals, often found below stones and leaves, in sediments, and on water plants. Turbellarians also occur in terrestrial environments that are at least temporarily moist (Houben et al. 2022). There are 738 turbellarian species documented in Europe (de Jong et al. 2014). For Austria, there is an estimate of around 200 species (Geiser 2018).

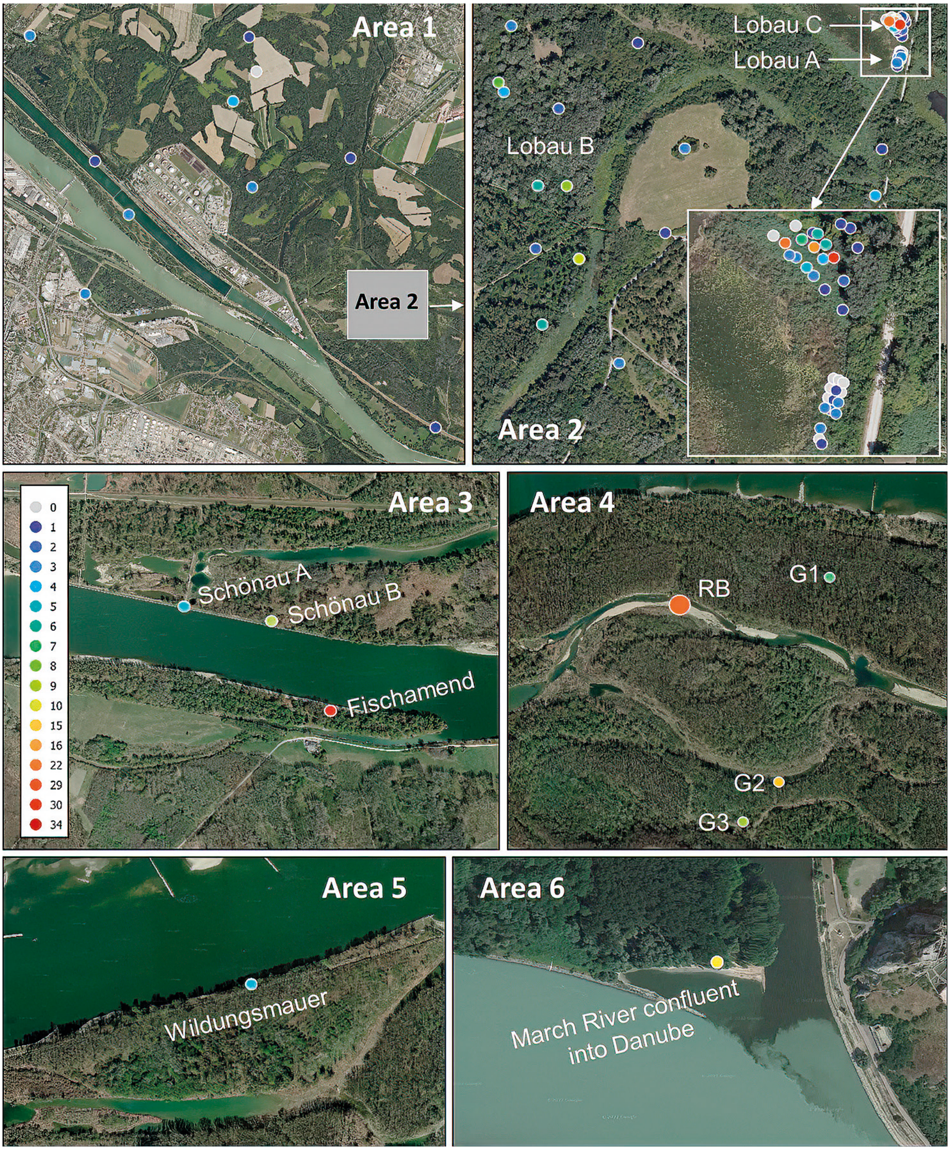

Fig. 2: Location of sampling sites with the total number of stygobiont and stygophile taxa from historical and current sampling campaigns highlighted. – Abb. 2: Lage der Untersuchungsstandorte inklusive der Gesamtzahl an stygobionten und stygophilen Taxa aus historischen und aktuellen Untersuchungen.

Groundwater representatives are found in various turbellarian groups. The identification of turbellarians is notoriously difficult and requires live observation and the interpretation of histological serial sections. Because samples are often preserved in a fixative before analysis, the morphological-taxonomic analysis of limnological samples is biased against the documentation of turbellarians (as with nematodes). This is one reason why we hardly know anything about the turbellarian fauna in groundwater ecosystems. Another reason is the lack of taxonomic experts. For groundwater of the Lobau and the Danube Floodplain National Park around 11 species are recorded so far, four of which (*Bothrioplana semperi*, Fig. 3, *Prorhynchus stagnalis*, a yet unindentified species of the genus *Prorhynchus,* Fig. 3, and *Rhynchomesostoma* cf. *rostratum*) are classified stygophile (Tab. 3). Due to the high degree of endemism in groundwater ecosystems, the relatively late start of relevant studies, and the generally poor knowledge of the group, it is likely that some of the resident species have not been discovered yet. Current initiatives to establish molecular and morphological know-how are on the way.

Rotatoria

Rotatoria predominantly live in freshwaters. For Austria alone, more than 750 species are described. Only a small portion of species (<10 %) inhabits benthic habitats. In groundwater, so far only a few species are known. Due to their small size, rotatorians are usually missed in groundwater fauna samples taken with nets of 60 µm mesh size or larger. Targeted investigations are required to explore rotatorian biodiversity in groundwaters. The record of *Dissotrocha hertzogi* within the Lobau study area (Tab. 3) represents the first finding of this species since its description 60 years ago from wetlands at the Rhine River near Strasbourg (Hauer 1939). This elusive bdelloid species is one of the few rotatorians living exclusively in groundwater, though its ecology remains poorly known.

Annelida

Among Annelida, representatives of oligochaetes, aphanoneurans (family Aeolosomatidae) and polychaetes are regularly found in groundwater habitats. Oligochaetes commonly occur in litter and soils, as well as in sediments of surface aquatic environments. Most of the oligochaetes found in the water-saturated subsurface are stygophiles; only a few species, mainly from the families Lumbriculidae and Dorydrilidae, are stygobiont.

In the shallow aquifer and benthic environments of the national park (hyporheic zone and bank sediments of the Danube River and its backwaters) 41 species of oligochaetes have been reported (Gaviria et al. 1998), 21 of which can be classified as stygophile and one stygobiont based on information from several authors (Gad 2007; Timm 2009; Van Haaren & Soors 2013; S. Gaviria pers. obs.) (Tab. 3).

An impressive species regularly found in groundwater is *Haplotaxis gordioides* (fam. Haplotaxidae) which can reach a length of 40 cm at a width of only 1 mm (Fig. 3) (Van Haaren & Soors 2013). *H. gordioides*, so far not collected in the Lobau area, was found in the Regelsbrunner Au, part of the Danube Floodplain National Park (Gaviria et al. 1998), and in the Danube Riverbank sediments at Kritzendorf, west of Vienna (C. Griebler pers. obs.).

Some oligochaete species of our list are cosmopolitans, *i.e.*, *Limnodrilus hoffmeisteri, Nais communis, N. eliguis, N. variabilis, Pristina longiseta* and *Eiseniella tetraedra*. The enchytraeid *Globolidrilus riparius* (formerly *Marionina riparia*) (Fig. 3) has a Palaearctic distribution while *Marionina argentea* is limited to Europe (Nielsen & Christensen 1959). Among the tubificines, *Potamothrix moldaviensis* is a common European species, while *Rhyacodrilus falciformis* is quite rare. The later is present in groundwater, springs, clean lakes, but also in soil (Timm 2009; Timm & Martin 2019). The two species of *Vejdovskiella* as well as *Uncinais uncinais* have a Holarctic distribution; the latter species has been reported also from Japan and Guyana (Timm 2009). *Pristina bilobata* is mostly found in

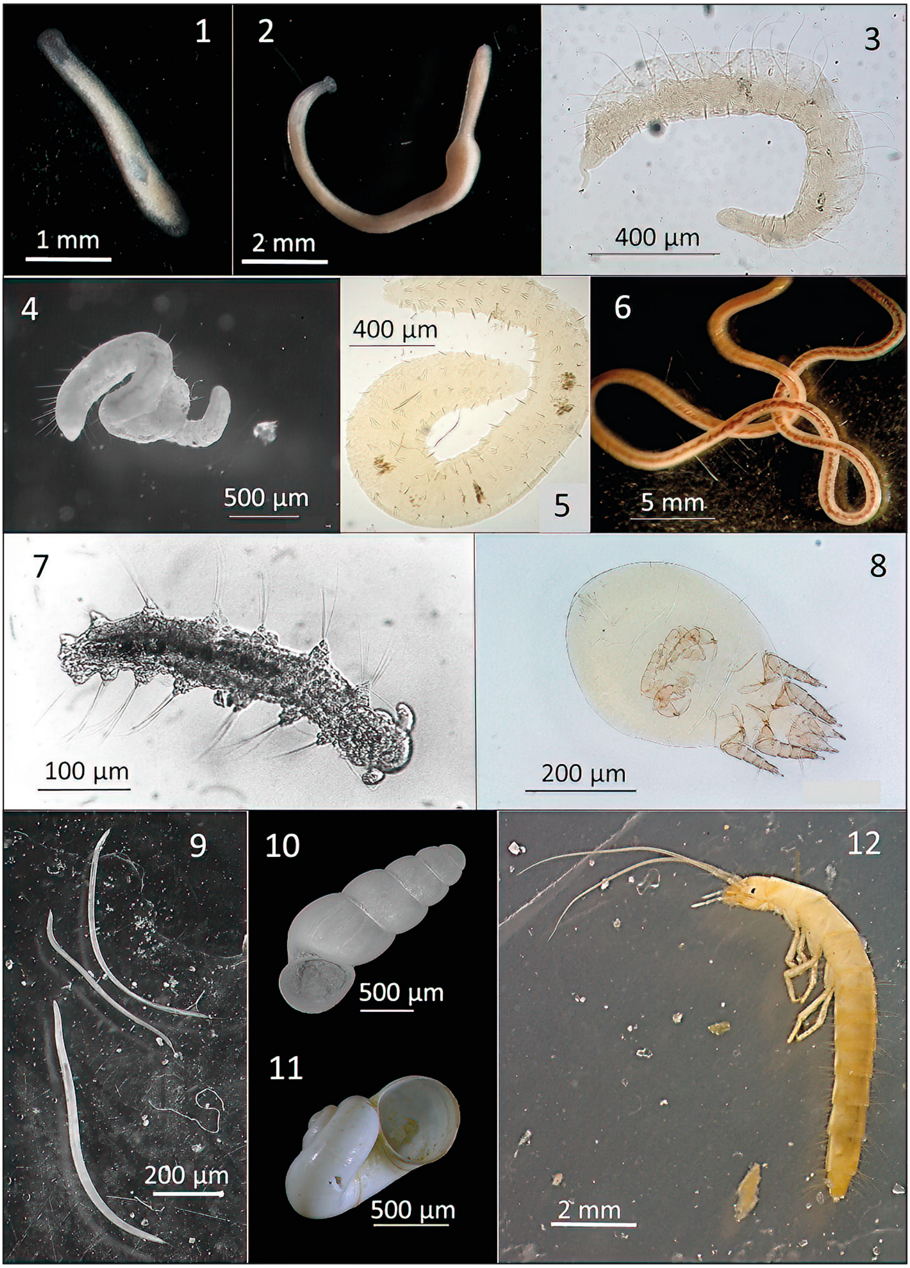

Fig. 3, Abb. 3: 1. *Bothrioplana semperi* ("Turbellaria"; Photo: M. Greilhuber), 2. *Prorhynchus* sp. ("Turbellaria"; Photo: M. Greilhuber), 3. *Pristina proboscidea* (Oligochaeta; Photo: S. Gaviria), 4. *Pristina* sp. (Oligochaeta; Photo: C. Englisch), 5. *Globulidrilus riparius* (Oligochaeta; Photo: S. Gaviria), 6. *Haplotaxis gordioides* (Oligochaeta; Photo: C. Griebler), 7. *Troglochaetus beranecki* (Polychaeta; Photo: P. Rumm), 8. *Schwiebea* sp. (Acari; Photo: T. Pfingstl), 9. (Nematoda), 10. *Bythiospeum* cf. *geyeri* (Gastropoda; Photo: J. Steger), 11. *Hauffenia danubialis* (Gastropoda; Photo: J. Steger), 12. Larvae of *Cyphon palustris* (Insecta, Coleoptera; Photo: C. Englisch).

Europe with single reports from Asia, Africa and the Americas. *Pristina sima* has a Mediterranean distribution and is also know from the Nearctic and Neotropical regions and Japan (Timm & Martin 2019). *Pristina proboscidea* (Fig. 3) is distributed in South America, South and East Asia, Zanzibar and Madagascar, with single reports from Europe. *Nais pseudobtusa* is found in Europe, Africa and Afghanistan (Brinkhurst & Jamieson 1971). Some members of the genus *Cernosvitoviella* are semiterrestrial, others live in surface water bodies and some in groundwater. As the species of the genus found in groundwater of the Danube floodplain have not been identified yet, no more information can be given about its biogeography and ecology.

Up to now only one species of the family Lumbriculidae has been observed in groundwater of the region, i.e. *Rhynchelmis limosella*. This species has a western Palaearctic distribution (Timm & Martin 2019). A second lumbriculid, *Stylodrilus heringianus*, was recorded in benthic habitats of the floodplain; the species is common elsewhere in interstitial habitats (Van Haaren & Soors 2013). If the taxon tentatively assigned to *Dorydrilus/Trichodrilus* (Tab. 3) turns out to be *Trichodrilus*, it would be the second member of the Lumbriculidae in groundwater of the Lobau. Nine *Trichodrilus* species are known from Germany where they are regularly found in groundwater (Gad 2007). Oligochaetes are often recorded as cocoons and juveniles which are difficult or even impossible to determine to species level by morphology. Future molecular analyses shall elucidate the real Oligochaeta biodiversity in groundwater ecosystems.

While oligochaetes are abundant inhabitants of freshwater environments, polychaetes are almost exclusively found in marine habitats; just a few groups colonized freshwater environments. To date only two stygobionts are described for Europe, one of them being *Troglochaetus beranecki* (fam. Nerillidae) (Fig. 3). *T. beranecki* is widely distributed throughout Europe and beyond. It generally lives in shallow porous aquifers accompanying rivers such as the Rhône, Rhine, Weser, Elbe, Oder and Danube (Tilzer 1973). The archiannelid has been recorded also in North America (Strayer et al. 1995; Särkkä & Mäkelä 1998). Specimens of *T. beranecki* were repeatedly collected from groundwater of the Danube Floodplain National Park (Tab. 3). In the past, the family Aeolosomatidae was classified among the Polychaeta. Now it constitutes the subclass Aphanoneura (Thorp & Lovell 2019). *Aeolosoma* is the only genus of the family that has been found in groundwater. Nine species are known from groundwater in Germany (Gad 2007).

Except the stygobiont polychaete *Troglochaetus beranecki*, all other Annelida in groundwater of our study area are stygophile. No endemic annelids are known for the Lobau. It is expected to find additional lumbriculid species in the groundwater of the floodplain, as well as members of Tubificinae.

Gastropoda

Among European freshwater gastropods inhabiting subterranean habitats, Moitessieriidae and Hydrobiidae are important families in terms of species richness. According to the checklist by Bank & Neubert (2017), the moitessieriid genus *Bythiospeum* alone is represented by about 100 species and subspecies in European groundwaters, though species delimitation is still considered problematic (e.g., Haase 1995; Richling et al. 2017). Shells of *Bythiospeum* spp., like those of many other hydrobioid taxa, tend to be rather poor in features, often very similar among species, and exhibit intraspecific morphological plasticity (e.g., Haase 1995; Hofman et al. 2018; Haase et al. 2021). Consequently, it is likely that the number of available species names considerably exceeds that of true biological species (e.g., Richling et al. 2017). Future molecular studies are expected to improve the situation but are limited by the lack of live-collected specimens for many taxa (cf. Hofman et al. 2018). In groundwater of the Lobau and the Danube Floodplain National Park so far only one moitessieriid species, *Bythiospeum* cf. *geyeri* (Fig. 3, Tab. 3), has been recorded (Haase 1995; own samples). Another stygobiont gastropod genus morphologically very different from *Bythiospeum* is *Hauffenia* (fam. Hydrobiidae), characterized by valvatiform shells (Fig. 3). In the Lobau, but also at other sites along the Danube near Vienna (e.g., Kritzendorf, west of Vienna), *Hauffenia danubialis* (formerly *Lobaunia danubialis*) is regularly found (Tab. 3). This species likely feeds on detritus and bacteria (Reischütz & Reischütz 2009). With its large gill lamellae, *H. danubialis* is well adapted to the life in poorly oxygenated groundwater (Haase 1993). In contrast, *B.* cf. *geyeri* – living in the same habitat – has reduced gills, suggesting that physiological adaptations may enable its survival in this temporarily oxygen-deficient environment (Haase 1995). Both *B.* cf. *geyeri* and *H. danubialis* are described as endemic to Vienna and Lower Austria (Haase 1993, 1995; Glöer 2002; Reischütz & Reischütz 2009). However, a recent study focusing on groundwater habitats of the river Mur valley in Styria, Austria, revealed specimens morphologically similar to the two species recorded in Vienna and Lower Austria. These samples still await detailed analysis.

Nematoda

Free-living nematodes can basically be classified into marine and continental forms, the latter separated into terrestrial and aquatic ones. However, this subdivision is not as clear as it seems. Since all nematodes in soil and sediments depend on at least a thin water film, all are basically freshwater/aquatic forms (Andrassy 1978; Abebe et al. 2008). Free-living nematodes (Fig. 3) are recorded from all types of freshwater habitats (including springs, the hyporheic zone and groundwater) (e.g., Eder 1983; Beier & Traunspurger 2003a, b; Eisendle et al. 2013; Eisendle & Battegazzore 2018). Their systemic importance is indicated by their regular high abundances together with a variety of feeding habits and their high adaptability. However, to date they have received distinctly less attention than their terrestrial and marine relatives (Decreamer et al. 2019).

Species lists and numbers from freshwaters specified for certain regions and environments are scarce. This is particularly true for groundwaters (for more details see Eisendle & Hilberg 2015, Hilberg & Eisendle 2016). Overall, species numbers of free-living freshwater nematodes account for about 2,370 worldwide (Abebe et al. 2008; Eisendle et al. 2017), with 1,120 species recorded for the Palaearctic (Eisendle et al. 2017) and about 600 for Europe (Andrassy 1978). Andrassy (1978) marked 76 of the European freshwater species to be recorded also from groundwater, but whether these species are stygophile or even stygobiont is, based on our current state-of-knowledge, impossible to judge. We thus pragmatically term all species that have been repeatedly found in groundwater stygophile, and those found so far exclusively in groundwater stygobiont.

In Austria, 252 out of 420 species have been recorded from freshwater environments (Eisendle unpubl.). Data for nematodes occuring in groundwater, however, are widely scattered and incomplete (Hilberg & Eisendle 2016). All species recorded from the Lobau and the Danube Floodplain National Park represent species typically and sporadically found in different types of freshwater, e.g. streams and rivers, as well as in standing water bodies. Due to the frequent occurrence and permanence in the hyporheic zone and shallow aquifers, about 50 % of these species may be considered stygophiles (Tab. 3).

Our literature search and own current investigations revealed 2 stygobiont and 45 stygophile nematode species in groundwater of the Danube Floodplain National Park, with 19 stygophile species recorded for the Lobau wetland (Tab. 3). This includes representatives of the genera *Eumonhystera*, *Mononchus* and *Tripyla*. *Stenonchulus troglodytes* is a true groundwater species, exclusively recorded from groundwater so far. Not far from the national park another stygobiont species, the nematode *Theristus franzbergeri*, was collected 1975 from a Danube River gravel bar in the city of Vienna (Danielopol 1976a) and was later described as a new species in 1984 (Schiemer 1984). Due to the construction of the hydropower plant Freudenau in Vienna, the *locus typicus* disappeared. The species could not be discovered at any other place, so far, though it likely occurs in the Danube Floodplain National Park. However, Eder (1983) and Schiemer (unpubl.) detected two more *Theristus* species, i.e *T. ruffoi* (stygobiont) at Fischamend (inside the national park) and *T. agilis* (stygophile) near the Floridsdorfer Brücke (outside the national park). Another stygobiont species is *Butlerius micans* (fam. Diploscapteridae), that have been recorded to date only from outside the national park.

Ostracoda

Ostracods are the most species-rich group within the crustaceans (Cohen et al. 1998). More than 700 freshwater ostracod species are known from the Palaearctic region (Horne et al. 2019). Until today, several hundreds of stygobiont species have been described. The inventory of Ostracoda from Austria lists 93 recent species and subspecies (Gaviria 2017). However, there is no recent evaluation on Austrian groundwater ostracod species available. Vornatscher (1938) reported on the stygophile species *Candona candida* from a limnocrene in the Lusthauswasser in the Prater (Fig. 1). Taking the early research and current findings together, the list of groundwater dwelling species in the area of the Lobau and the Danube Floodplain National Park comprises 7 stygobiont and 7 stygophile species (Tab. 2, Tab. 4). These species belong to the families Candonidae, Cyprididae, Darwinulidae and Limnocytheridae. A species of the cytheroid genus *Kovalevskiella* (Limnocytheridae, Timiriaseviinae), known as an unnamed species for several decades, was described very recently (Gaviria 2022) under the name *K. elisabethae* (Fig. 4).

Among the species of stygophile ostracods found in groundwater of the Lobau, one species *i.e. Darwinula stevensoni* has a cosmopolitic distribution and can be found in every type of water body. It has been collected even at high altitudes (3000 m a.s.l.) in an Andean Lake of Colombia (Gaviria pers. obs.). Another species, *i.e., Cyclopypris ovum*, is also a cosmopolitan and common in almost all types of surface waters, but has occasionally been found also in subterranean environments (Meisch 2000). *Candona candida* and *C. neglecta* have a holarctic distribution, although the former is rare in the southern regions. *Candonopsis kingsleii* is holarctic as well, rare in some countries and very common in others. *Pseudocandona albicans* has also a holarctic distribution, while *Pseudocandona lobipes* is restricted to Europe. The stygobiont species *Typhlocypris szoecsi*, formerly *Pseudocandona szoecsi* (Namiokto et al. 2014), was described from Hungary and is also known from Poland and countries of the former Yugoslavia. For *Typhlocypris eremita*, formerly *Pseudocandona eremita* (Namiotko et al. 2014), which is extremely difficult to be identified morphologically, Iepure et al. (2007) proposed for morphotypes of different extant populations belonging to the phylogenetic lineage of *T. eremita* to name them *T. eremita* s.l.. *Limnocythere inopinata* is rather common in the Holarctic region and has been reported also from Africa south of the Sahara, where it has been probably introduced. Another stygobiont species found

Tab. 3: List of stygobiont (-biont) and stygophile (-phile) turbellarians, rotifers, annelids, gastropods, and nematodes in groundwater of the Lobau (Lob) and the Danube Floodplain National Park (DFNP), divided into records prior to the year 2000 (<2000) and recent findings (>2019). Taxa recorded from Vienna and its surrounding areas outside the national park are listed in column 'out'. For more detailed information, see text. – Tab. 3: Zusammenstellung aller stygobionten (-biont) und stygophilen (-phile) Vertreter aus den Großgruppen „Turbellaria", Rotatoria, Annelida, Gastropoda, und Nematoda im Grundwasser der Lobau und des Donau-Auen Nationalparks (DFNP), untergliedert in Nachweise vor dem Jahr 2000 (<2000) und aktuelle Nachweise (>2019). Nachweise von Taxa in Wien und Umgebung, aber außerhalb des Nationalparks, sind in der Spalte 'out' vermerkt. Für detailiertere Informationen siehe Text.

Classification	**Family**	**Species**	**stygo-**	**<2000**	**>2019**	**Lob**	**DFNP**	**out**
„Turbellaria"	Bothrioplanidae	*Bothrioplana semperi* (Braun, 1881)	phile	+	+	+	+	
	Prorhynchidae	*Prorhynchus stagnalis* (Schultze, 1851)	phile	+		+	+	
		Prorhynchus sp.	phile		+	+	+	
	Typhloplanidae	*Rhynchomesostoma* cf. *rostratum* (Müller, 1774; Luther, 1904)	phile		+	+	+	
Rotatoria	Phileodinidae	*Dissotrocha hertzogi* (Hauer, 1939)	phile	+		+	+	
Oligochaeta	Dorydrillidae	*Dorydrilus michaelseni* (Piguet, 1913)	phile	+		+	+	
	Dorydrillidae/Lumbricidae	*Dorydrilus/Trichodrilus* sp.	phile		+	+	+	
	Enchytraeidae	*Globulidrilus riparius* (Bretscher, 1889)	phile		+	+	+	
		Marionina argentea (Michaelsen, 1889)	phile	+			+	
	Haplotaxidae	*Haplotaxis gordioides* (Hartmann, 1821)	biont	+			+	
	Lumbricidae	*Eiseniella tetraedra* (Savigny, 1826)	phile		+	+	+	
	Lumbriculidae	*Stylodrilus heringianus* (Claparède, 1862)	phile	+			+	
		Rhynchlemis limosella (Hoffmeister, 1843)	phile		+	+	+	
	Naididae, Naidinae	*Nais comunis* (Piguet, 1906)	phile	+			+	
		Nais elinguis (Müller, 1774)	phile	+		+	+	
		Nais pseudobtusa (Piguet, 1906)	phile	+			+	
		Nais variabilis (Piguet, 1906)	phile	+			+	
		Pristina bilobata (Bretscher, 1903)	phile	+			+	
		Pristina longiseta (Ehrenberg, 1828)	phile	+			+	
		Pristina proboscidea (Beddard, 1896)	phile		+	+	+	
		Pristina sima (Marcus, 1944)	phile		+	+	+	
		Uncinais uncinata (Oersted, 1842)	phile	+			+	
		Vejdovskiella comata (Vejdovsky, 1884)	phile	+			+	

Classification	Family	Species	stygo-	<2000	>2019	Lob	DFNP	out
		Vejdovskiella intermedia (Bretscher, 1896)	phile	+			+	
	Naididae, Tubificinae	*Limnodrilus hoffmeisteri* (Claparéde, 1862)	phile		+	+	+	+
		Potamothrix moldaviensis (Vejdovsky & Mrázek, 1903)	phile	+			+	
		Rhyacodrilus falciformis (Bretscher, 1901)	phile	+			+	
Aphanoneura	Aelosomatidae	*Aelosoma quaternarium* (Ehrenberg, 1828)	biont	+			+	
Polychaeta	Nerillidae	*Troglochaetus beranecki* (Delachaux, 1921)	biont	+	+	+	+	+
Gastropoda	Hydrobiidae	*Hauffenia danubialis* (Haase 1993)	biont	+	+	+	+	
	Moitessieriidae	*Bythiospeum* cf. *geyeri* (Fuchs 1925)	biont	+	+	+	+	
Nematoda	Achromadoridae	*Achromadora terricola* (de Man, 1880)	phile	+	+	+	+	
		Achromadora dubia (Bütschli, 1873)	phile	+			+	
	Alaimidae	*Paramphidelus uniformis* (Thorne, 1939)	phile	+			+	
		Alaimus sp.	phile		+		+	
	Aphanolaimidae	*Aphanolaimus* sp.	phile		+		+	
	Aporcelaimidae	*Aporcelaimellus obtusicaudatus* (Bastian, 1865)	phile	+			+	
	Bastianiidae	*Bastiania gracilis* (de Man, 1876)	phile	+			+	
	Belondiridae	*Oxydirus oxycephaloides* (de Man, 1921)	phile	+	+	+	+	
	Chromadoridae	*Chromadorina bioculata* (Schulze in Carus, 1857)	phile	+	+	+	+	+
		Chromadorita leuckarti (de Man, 1876)	phile	+		+	+	
	Chronogastridae	*Chronogaster* cf. *typica* (de Man, 1921)	phile		+	+	+	
	Diploscapteridae	*Butlerius micans* (Pillai & Taylor, 1968)	biont		+			+
	Dorylaimidae	*Dorylaimus stagnalis* (Dujardin, 1845)	phile	+	+		+	
	Ethmolaimidae	*Ethmolaimus pratensis* (de Man, 1880)	phile	+			+	
	Hemicyclophoridae	*Hemicycliophora thienemanni* (Schneider, 1925)	phile	+			+	
		Hemicycliophora typica (de Man, 1921)	phile	+	+	+	+	
	Ironidae	*Ironus longicaudatus* (de Man, 1884)	phile	+		+	+	
		Ironus tenuicaudatus (de Man, 1876)	phile	+			+	
	Monhysteridae	*Eumonhystera* cf. *barbata* (Andrássy, 1981)	phile		+	+	+	
		Eumonhystera dispar (Bastian, 1865)	phile	+	+	+	+	
		Eumonhystera cf. *dispar*	phile		+		+	+
		Eumonhystera filiformis (Bastian, 1865)	phile	+	+	+	+	

Classification	Family	Species	stygo-	<2000	>2019	Lob	DFNP	out
		Eumonhystera cf. *filiformis*	phile		+		+	+
		Eumonhystera longicaudatula (Gerlach & Riemann, 1973)	phile	+			+	
		Eumonhystera similis (Bütschli, 1873)	phile	+			+	
		Eumonhystera simplex (de Man, 1880)	phile	+			+	
		Eumonhystera vulgaris (de Man, 1880)	phile	+	+		+	+
		Monhystera paludicola (de Man, 1880)	phile	+	+		+	+
	Mononchidae	*Mononchus truncatus* (Bastian, 1865)	phile	+	+	+	+	+
	Odontolaimidae	*Odontolaimus chlorurus* (de Man, 1880)	phile	+			+	
	Onchulidae	*Stenonchulus troglodytes* (W. Schneider, 1940)	biont	+			+	
	Plectidae	*Plectus cirratus* (Bastian, 1865)	phile	+		+	+	
	Prismatolaimidae	*Prismatolaimus dolichurus* (de Man, 1880)	phile	+	+	+	+	
		Prismatolaimus intermedius (Bütschli, 1873)	phile	+	+		+	+
	Qudsianematidae	*Eudorylaimus carteri* (Bastian, 1865)	phile	+			+	
	Tobrilidae	*Brevitobrilus stefanski* (Micoletzky, 1925)	phile		+		+	
		Epitobrilus allophysis (Steiner, 1919)	phile		+	+	+	
		Epitobrilus husmanni (Altherr, 1958)	phile	+	+		+	
		Neotobrilus diversipapillatus (Daday, 1905)	phile	+			+	
		Neotobrilus breviductus (Loof & Riemann, 1976)	phile	+			+	
		Semitobrilus pellucidus (Bastian, 1865)	phile	+		+	+	
		Tobrilus gracilis (Bastian, 1865)	phile	+	+	+	+	+
	Trichodoridae	*Trichodorus primitivus* (de Man, 1880)	phile	+			+	
	Tripylidae	*Tripyla filicaudata* (de Man, 1880)	phile	+	+	+	+	+
		Tripyla glomerans (Bastian, 1865)	phile	+	+	+	+	+
		Trischistoma monohystera (de Man, 1880)	phile	+			+	
	Tylenchidae	*Malenchus* cf. *neosculus* (Geraert & Raski, 1986)	phile		+	+	+	
	Xyalidae	*Theristus agilis* (de Man, 1880)	phile		+			+
		Theristus franzbergeri (Schiemer, 1984)	biont	+	+			+
		Theristus ruffoi (Andrássy, 1959)	biont	+			+	

in the Lobau, i.e., *Fabaeformiscandona wegelini*, has been recorded also in North America (Marmonier & Ward 1990; Danielopol et al. 1994).

Some species found in the Lobau are regional endemics, as they occur only at other sites within the national park (e.g., at Regelsbrunn, see Fig. 1) or along the Danube Valley in Vienna and Lower Austria. The ostracods *Mixtacandona spandli* (Löffler 1963; Rogulj & Danielopol 1993; Roguli et al. 1993; Danielopol & Pospisil 2001) and *Cryptocandona kieferi danubialis* (Fig. 4) (Namiotko et al. 2005) are such examples. *Mixtacandona laisi vindobonensis* (Löffler 1963) is a subspecies of *Mixtacandona laisi* present in the area and regionally endemic (Tab. 4).

Diplostraca (Cladocera)

Diplostraca, also called Cladocera, are typical members of zooplankton living in surface waters. A considerable number of species are found in open cave waters and may be termed stygophiles. However, stygophile cave Cladocera are not known from Austria. Moreover, a significant fraction of cladocerans are indeed members of benthic communities (Bledzki & Ryba 2016), with a few species that may penetrate into the unconsolidated sediments of the hyporheic zone of streams and rivers as well as into shallow aquifers. The number of cladocerans is estimated to reach 700 worldwide (Smirnov 2014). Negrea & Pospisil (1995) indicated that 20 % of the species described could also live in subterranean waters. In groundwater of the Lobau aquifer and the Danube Floodplain National Park, five species were reported from shallow groundwater, i.e., *Acroperus harpae*, *Alona guttata* (Fig. 4), *Alonella nana*, *Biapertura affinis*, and *Chydorus sphaericus* (Negrea & Pospisil 1995). Following the ecological definition of Gibert et al. (1994), these species may be termed 'stygophile', as representatives of occasional or even permanent hyporheobionts. Taking the morphological adaptations of the different species into account (see eyeless specimen of *A. guttata*, Fig. 4.) as well as the frequency of its detection in shallow aquifers, we decided to carry the two species *A. guttata* und *C. sphaericus* into Tab. 4. These two species have also regularly been reported from shallow groundwater and spring waters in other regions (Hrbácek et al. 1978; Schminke 2007c). In addition, in the direct vicinity of surface waters, stygoxene species inhabiting the surface water bodies of the floodplain are regularly found in groundwater samples. Negrea & Pospisil (1995) documented 11 stygoxene species occuring in the Lobau groundwater in low numbers, 4 of them typical planktonic and 7 benthic. None of the stygophile species are endemic to the Danube floodplain. Due to the high number of samples and the different periods of intensive sampling (1971–1980 and 1991–1993), it is very unlikely to find additional stygophile species of Cladocera in groundwater of this area. So far, none of the stygophile cladoceran taxa have been observed in our recent investigations, *i.e.*, starting in the year 2019.

Amphipoda

Already Spandl (1926) regularly collected specimens of *Niphargus* sp. in the area of Vienna from springs at Leopoldsberg and from several wells in Klosterneuburg and Kritzendorf (Fig. 1). Unfortunately, he did not provide species-level identifications. Vornatscher (1938) first mentioned three species of *Niphargus*, *i.e., Niphargus aquilex aquilex*, *N. foreli vornatscheri* and *N. leopoliensis molnari* collected from springs (limnocrenes) in the Lusthauswasser (old backwater of the Danube) in the Prater (Fig. 1). In 1972, Vornatscher presented an extended list of stygobiont amphipods found in Vienna, including *N. aquilex aquilex*,

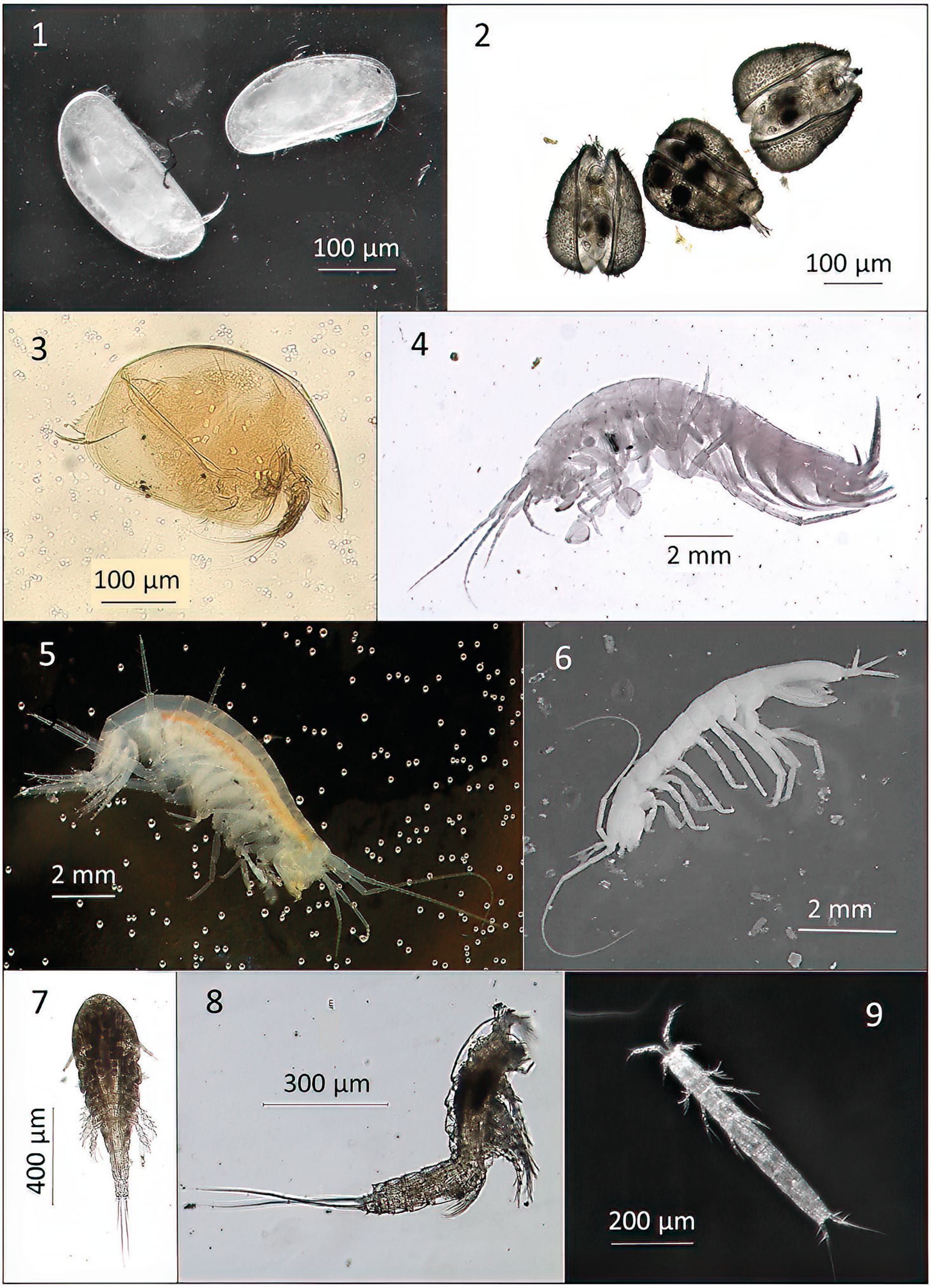

Fig. 4, Abb. 4: 1. *Cryptocandona kieferi danubialis* (Ostracoda; Photo: C. Englisch), 2. *Kovalevskiella elisabethae* (Ostracoda; Photo: S. Gaviria), 3. *Alona guttata* (Cladocera; Photo: S. Gaviria), 4. *Niphargus inopinatus* (Amphipoda; Photo: C. Englisch), 5. *Niphargus caspary* (Amphipoda; Photo: C. Englisch), 6. *Proasellus cavaticus* (Isopoda; Photo: C. Englisch), 7. *Diacyclops danielopoli* (Cyclopoida, Copepoda; Photo: S. Gaviria), 8. *Bryocamptus pygmaeus* (Harpacticoida, Copepoda; Photo: S. Gaviria), 9. *Parastenocaris* sp. (Harpacticoida, Copepoda; Photo: C. Englisch).

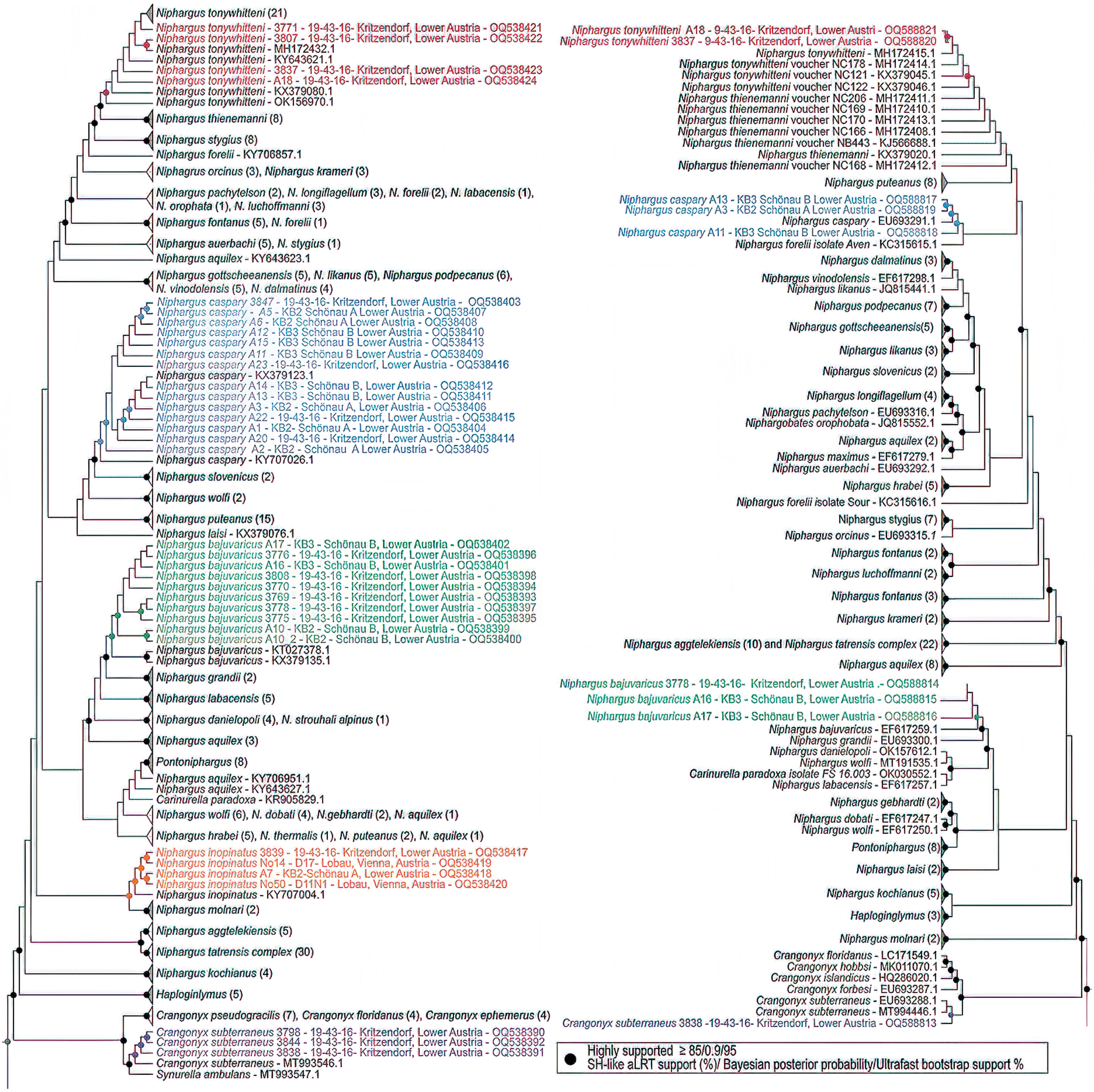

Fig. 5: Phylogenetic tree based on COI (left) and 28S (right) genes for amphipods in groundwater. In color, sequences of specimens collected in the study area are highlighted. – Abb. 5: Phylogenetischer Baum für Grundwasser-Amphipoden basierend auf den Genen für COI (links) und 28S (rechts). Sequenzen aus dem Untersuchungsgebiet sind farblich hervorgehoben.

N. fontanus, *N. inopinatus*, *N. jovanovici bajuvaricus*, *Niphargopsis caspary*, *Crangonyx subterraneus*, *Bogidiella albertimagni*, and a *Niphargellus* species not further determined. New localities herein included the Bisamberg, Prater, Jedlesee, Kagran, Klosterneuburg, and Langenzersdorf (Fig. 1). *N. foreli vornatscheri* and *N. leopoliensis molnari*, mentioned by him earlier, are replaced in Vornatscher's more recent review by *N. fontanus* and *N. inopinatus*. The author also mentioned four stygobiont amphipods from the floodplains, without providing detailed localities: *N. inopinatus*, *N. jovanovici bajuvaricus*, *N. caspary*, and *Crangonyx subterraneus*. Very recently, a record of *N. puteanus* (Weber et al. 2020) in the west of Vienna (a spring in Kasgraben, Fig. 1) added another amphipod species to the regional species inventory.

To date, six and seven species, respectively, of amphipods of the family Niphargidae (all in the genus *Niphargus*) have been reported for the area of the Lobau wetland and the Danube Floodplain National Park (Tab. 4). Based on our recent investigations and first molecular analyses, we see clear evidence for the presence of *N. bajuvaricus* (formerly *N. jovanovici bajuvaricus*), *N. caspary* (formerly *Niphargopsis caspary*), and *N. inopinatus* (Fig. 4). These three species are widely distributed in the Danube catchment. *N. caspary* and *N. inopinatus* are found all along the Danube River down to Romania (Schellenberg 1932; Dancău & Căpuşe 1959; Karaman 1989; Brad 1999; Andreev 2001). Further records come from the Rhône catchment (Straškraba 1972; Karaman 1982; Dole-Olivier et al. 1994), the upper Rhine valley and the Main catchment (Fuchs 2007), as well as from Switzerland (Altermatt 2019). Their present-day distribution still reflects the extent of the Pleistocene Danube catchment (Fink 1966). Similarly, *N. bajuvaricus* occurs from Bavaria to Romania (Schellenberg 1932; Straškraba 1972; Karaman 1980). There are no records west of Bavaria. If these species are part of a species-complex awaits a molecular evaluation.

One species recently collected in the groundwater of the Lower Lobau, *N. hrabei*, belongs to a group of Niphargidae predominantly found epigeic in surface waters, although they also regularly dwell in groundwater (e.g., Dudich 1941; Karaman 1950; Sket 1981; Meijering et al. 1995; Nesemann 1993; Nesemann et al. 1995). *N. hrabei* is widely distributed in the Danube catchment, ranging from the Black Sea westwards to Austria (Karaman 1932; Dudich 1941; Straškraba 1972; Karaman 1973; Sket 1981; Nesemann 1993; Nesemann et al. 1995; Brad 1999; Balázs et al. 2015). There are recent records from several surface water bodies in the Lower Lobau at Mühleiten, Schönau, Eckartsau, and Witzelsdorf (Nesemann 1993), as well as from a backwater near Klosterneuburg (Nesemann et al. 1995). Our observation from groundwater (A. Fuchs pers. obs.) is based on the morphological determination of only one specimen. It awaits confirmation by the collection of further individuals and molecular analysis.

Some of the records from the past, i.e., *N. aquilex aquilex*, *N. foreli vornatscheri* (now *N. foreli* and *N. vornatscheri*), *N.* cf. *kochianus*, *N. leopoliensis molnari* (now *N. leopoliensis* and *N. molnari)*, *N. stygius*, and *N. tatrensis* (Vornatscher 1972; Pospisil 1994a; Danielopol & Pospisil 2001) are in need of confirmation (Tab. 4). Although none of these species could be collected in the past three years of research in the Lobau area, we cannot exclude the occurrence of at least some of them. For example, records for *N. aquilex* come from Burgenland, Lower Austria, Salzburg, and Styria (Vornatscher 1965). Moreover, as it happened with *N. tatrensis*, which was found to be a large complex of closely related species (Fišer et al. 2010; Stoch et al. 2020), we expect some major changes to the list of stygobiont amphipod species after a molecular re-examination. For *N. fontanus*, records are known from the Danube floodplains of Lower Austria, and the provinces of Upper Austria, Salzburg, and Vorarlberg (Priesel-Dichtl 1959; Vornatscher 1965). Recently, evidence was provided that specimens classified as *N. fontanus* may be *N. tonywhitteni* (Weber 2023). This is interesting because our molecular analysis of two specimens from Kritzendorf that could not be determined with certainty based on morphological criteria clustered to sequences of *N. tonywhitteni* (Fig. 5). This species was described as new to science only recently, and was found in Lower Austria, Upper Austria, and Tyrol (Fišer et al. 2018). It has been also recorded several times in the northern half of Switzerland (Alther & Altermatt 2021) and southern Bavaria (Fišer et al. 2018, Weber et al. 2023).

Besides representatives of the Niphargidae, one species of the family Crangonyctidae, i.e. *Crangonyx subterraneus*, is regularly collected in the area of the national park and is also found in the shallow aquifer of the Danube west of Vienna (e.g. in Kritzendorf) (Tab. 4). The genus *Crangonyx* shows a holarctic distribution with the core area in North America that harbors most *Crangonyx* species (Zhang & Holsinger 2003). For the palaearctic, only a few species are currently known. *C. subterraneus* – reported from Great Britain, France, Germany, Switzerland, Poland, and the Czech Republic – is the most widely distributed species (Schellenberg 1942; Dole-Olivier et al. 1994; Schminke 2007a; Altermatt et al. 2019; Weber et al. 2021).

A very recent sample from the bank sediments of the River Danube at Kritzendorf contained one specimen of *Bogidiella* cf. *albertimagni*, family Bogidiellidae (Tab. 4). As mentioned above, this species was already found by Vornatscher (1972) in a well in the Prater (Fig. 1). *B. albertimagni* is widely distributed in Europe, but always rare. Records are currently known from France (Hertzog 1933), Germany (Fuchs 2007), Italy and the Balkans. For the latter region, a number of new congeneric species have been described in recent decades (Karaman 1989, Koenemann et al. 1998). Considering the early records at different sites in Vienna (Vornatscher 1972), the species may also be expected to occur in the shallow aquifer of the Danube Floodplain National Park. The recent record of *B.* cf. *albertimagni* is so far based on a single specimen. Further collection and molecular examination could lead to a reliable determination of the the species.

Isopoda

The majority of freshwater isopod species in Europe are stygobiont. As with the amphipods, their core distribution area encompasses the Mediterranean karst and the Balkans. For Austria, to date only taxa of the families Asellidae and Microparasellidae are known. This latter group is represented by the stygobiont taxon *Microcharon* sp. which was recorded only once in groudwater of the river Piesting alluvial aquifer, at Moosbrunn (Fig. 1) in Lower Austria (Danielopol 1976b). All other stygobiont species belong to the genus *Proasellus* (Asellidae), formerly included in the genus *Asellus*. An early investigation within the Vienna city limits (Vornatscher 1938) yielded *Asellus cavaticus*, collected in limnocrenes of the Lusthauswasser in the Prater (Fig. 1). On the basis of this material Karaman (1955) described *Asellus cavaticus strouhali*. Henry (1976) elevated this taxon to a full species, *Proasellus strouhali*. In the meantime, the status of *P. strouhali* was confirmed by genetic analysis (Eme et al. 2013). In his review of groundwater ecological research in Vienna, Vornatscher (1972) mentioned another stygobiont isopod, *Asellus slavus vindobonensis*, observed at different spots in Vienna including Floridsdorf, Jedlesee, Kaisermühlen, Kagran, and the Prater (Fig. 1). Also in this case, the generic affiliation of the stygobiont species was later changed to *Proasellus*. Karaman (1955) and Strouhal (1958) had decribed two subspecies of *Proasellus slavus*, *i.e., P. slavus salisburgensis* (occurring in the eastern part of Austria) and *P. slavus salisburgensis* (occurring in the western part). The morphological discrimination of these two subspecies and *P. slavus slavus* is very difficult (Strouhal 1958).

For the Danube floodplains of the national park, besides the epigeic species *Asellus aquaticus*, so far three species of *Proasellus* have been reported, *i.e., Proasellus cavaticus*, *P. slavus vindobonensis* and *P. strouhali* (Tab. 4). While the review of Pospisil (1994a) lists *P. slavus* and *P. strouhali* for the Lower Lobau area, the compilation of Danielopol & Pospisil (2001) lists the two subspecies mentioned above, *i.e., P. slavus vindobonensis* (Fig. 4) and *P. strouhali strouhali* for the Danube Floodplain National Park. The presence of *P. cavaticus* is unclear. Based on morphological analysis, our recent investigations provided evidence for the frequent occurrence of *P. cavaticus* in the Danube floodplains. Unfortunatly, our first attempt of a molecular analysis of a few putative specimens of *P. cavaticus* failed. On the other hand, our analyses provided further evidence for the occurrence of *P. slavus vin-*

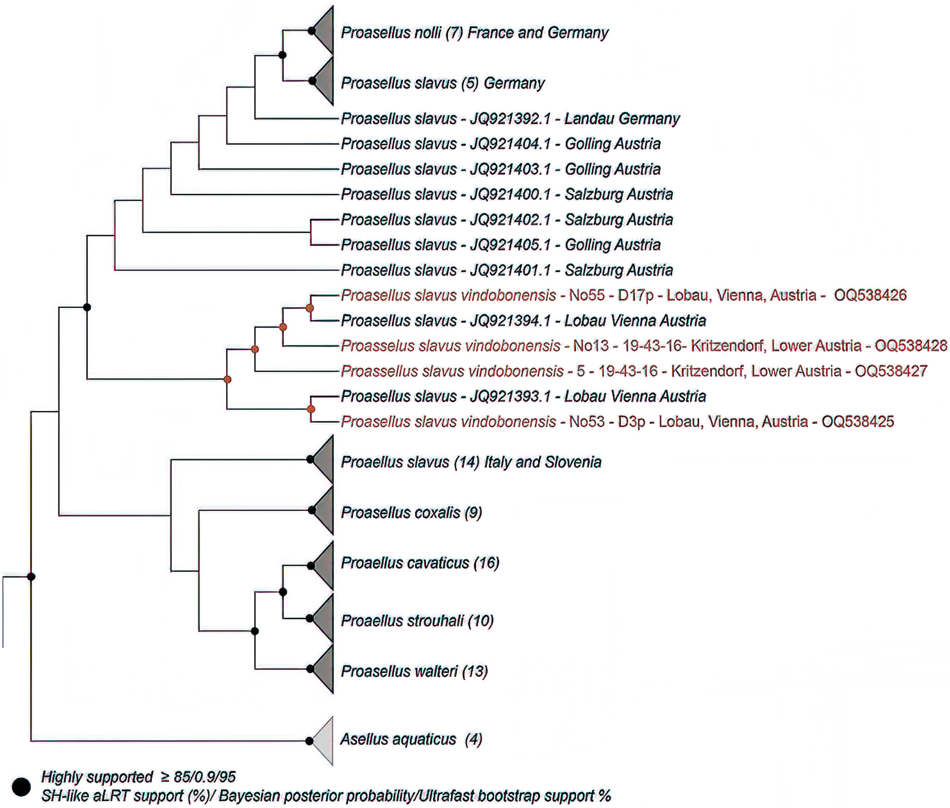

Fig. 6: Phylogenetic tree based on the COI genes for groundwater isopods. In red, sequences of specimens collected in the Lower Lobau and Kritzendorf are highlighted. The epigean species *Asellus aquaticus* is used as outgroup. – Abb. 6: Phylogenetischer Baum für Grundwasser-Isopoden basierend auf COI. Sequenzen aus dem Untersuchungsgebiet sind farblich hervorgehoben. Die epigäische Art *Asellus aquaticus* dient als als Außengruppe.

dobonensis. The extremely limited number of sequences, i.e., 4*COI (Fig. 6), does not allow a final conclusion. However, in the near future, a systematic evaluation will shed light on the species richness of stygobiont isopods in Vienna, the Lobau and the entire Danube Floodplain National Park.

Syncarida

Syncarids are a phylogenetically ancient group of crustaceans known since the Carboniferous. In Europe, two families of the order Bathynellacea, namely Bathynellidae and Parabathynellidae, have been recorded (Camacho et al. 2018). This group of stygobionts is hardly studied. With the exception of Spain, its species richness and geographic distribution in Europe are insufficiently understood due to a lack of taxonomic expertise.

Three species are so far scientifically recorded for Austria, i.e., *Bathynella vindobonesis* and *Bathynella natans*, as well as *Antrobathynella stammeri*. *Antrobathynella stammeri* is recorded from sediments of a tributary of the river Ötztaler Ache (Husmann 1973) und in sediments of the Mur River near the city of Murau (Kirchengast 1981). Based on only 2 males and 3 females collected from a large well near the Alte Donau (a Danube backwater in the city of Vienna) in 1973, the new species *B. vindobonensis* was described by Serban (1989). This *locus typicus* is very close to the Danube Floodplain National Park. We may therefore expect *B. vindobonensis* to occur also within the area of the national park. Since the original species description of *B. natans* (Vejdovsky 1882) was not very detailed, early records of bathynellids in Austria were all classified as *B. natans* (Husmann 1964; Schminke 2007b), as is true for the specimens collected in the Prater (e.g., Vornatscher 1972). Looking at the records of other genera, we may expect more than one bathynellid species for Austria and the Danube Floodplain National Park. For example, *Antrobathynella stammeri* is reported from the British Isles as well as from Romania (Sterba 1963; Serban & Geldhill 1965; Husmann 1973). Three species of the genus *Parabathynella* (Parabathynellidae) are known from the Rhine and Danube catchment in Southern Germany (Fuchs et al. 2012; Cho unpupl.). Further species of this genus have been reported from Slovakia (Juberthie & Decu, 2001), Serbia (Chappuis 1926), and Romania (Serban & Dancau 1963). Danielopol (1976b) reported specimen of Parabathynellidae from the cities Moosbrunn (Fig. 1) and Baden in Lower Austria, close to Vienna. A current project ('Heat below the city') exploring the shallow groundwater in the city of Vienna revealed bathynellids from several wells. Moreover, recent investigations in the river Mur valley, Styria, indicated that Bathynellacea might be not uncommon in shallow alluvial aquifers. The collected specimens are awaiting a closer determination.

Copepoda

Of more than 2,800 species of freshwater copepods known worldwide (Boxshall & Defaye 2008), 500 species are recorded for Europe (WoRMS 2022). Copepods are the most abundant groundwater invertebrates and are represented by around 1,000 species and subspecies worldwide (Galassi et al. 2009). More than half of the European species are stygobiont and many others are stygophile. The majority belong to the orders Cyclopoida and Harpacticoida. Early records of stygobiont and stygophile copepods from groundwater in the area of Vienna are published in Kiefer (1964) and Vornatscher (1972). *Acanthocyclops venustus*, *A. sensitivus*, *Austriocyclops vindobonae*, and *Diacyclops* cf. *languidoides* are reported from several sites within the city limits of Vienna, i.e., the Prater and Kagran. To date, 13 stygobiont and 3 stygophile cyclopoid species as well as 4 stygobiont and 4 stygophile harpacticoid species are recorded for groundwater of the Lobau wetland. For the area of the Danube Floodplain National Park one stygobiont cyclopoid and one harpacticoid species can be added (Tab. 2, Tab. 4).

Among the stygobiont species recorded in groundwater of the Lobau, *Diacyclops languidoides* has an holarctic distribution, *Diacyclops disjunctus* is palaearctic, and *Eucyclops graeteri* is known from Europe (Gaviria 1998). Prior to 1999, *D. languidoides* was referred as *D.* aff. *languidoides* or *D.* sp. gr. *languidoides*. In 1999, two species, i.e., *D. danielopoli* and *D. felix,* belonging to the *D. languidoides* species complex, were described (Pospisil & Stoch 1999). Still, it is assumed that the *D. languidoides* species complex may consist of different cryptic species that await detailed examination. *D. languidoides goticus* is known from the basin of the Triesting river (Stoch & Pospisil, 2000), but has so far not been found in groundwater of the Lobau. *D. cohabitatus* has also been reported from Ukraine and the eastern Carpathian range (Gaviria et al. 2002; Dussart & Defaye 2006; Defaye & Dussart 2011).

Within the genus *Acanthocyclops*, the species *A. gmeineri, A. kieferi, A. rhenanus* and *A. sensitivus* are stygobiont, while *A. venustu*s is stygophile. The stygophile species *Acanthocyclops venustus* is widespread throughout Europe and Russia (Dussart & Defaye 2006). *A. sensitivus* (Austria, Belgium, France, Germany, Great Britain, Switzerland, former Yugoslavia) and *A. kieferi* (Germany, Austria, Italy, Spain, Northern Macedonia) are widely distributed in Europe, while *A. rhenanus* was known until 1998 only from Germany and the Seewinkel in Austria (Gaviria 1998). *Acanthocyclops gmeineri* is endemic to the Lobau and the adjacent Marchfeld. Other endemic species of the region are *Diacyclops danielopoli* and *D. felix* (Lobau and Haslau) (Danielopol et al. 2006; Pospisil 1989; Pospisil & Stoch 1999). *Austriocyclops vindobonae* is a regional endemic species known from Traismauer (Lower Austria), a well in Kagran, and from the Lobau (Kiefer 1964; Vornatscher 1972; Pospisil & Stoch 1997; Gaviria 1998). The stygophile species *Paracyclops fimbriatus* and *Epactophanes richardi* found in the Lobau have a cosmopolitan distribution (Gaviria 1998).

Among the harpacticoid copepods recorded, the distribution of seven species (*Fontinalicaris fontinalis fontinalis, Horstkurtcaris nolli*, *Graeteriella laisi*, *G. unisetigera*, *Nitocrella hirta hirta*, *Parastenocaris germanica*, and *Proserpinicaris phyllura*) is limited to Europe.

The ameirid *Nitocrella hirta hirta* collected in Regelsbrunn and *N. hofmilleri* collected in Schönau are both stygobionts. The latter find was the second record of *N. hofmilleri* in Austria and worldwide. The species was previously known only from a well in the province of Salzburg (Janetzky et al. 1996). *Bryocamptus pygmaeus* has a palearctic distribution, and is present in surface and groundwaters (Dussart 1967). After a report of the species in a brook near Lunz am See (Kowarc pers. comm.), this is the second report of the species in Lower Austria.

We may expect the discovery of further copepod species in the coming years. For example, a species of the harpacticoid genus *Moraria* was recently found in the interstitial sediments of the river Danube at Kritzendorf, upstream of Vienna (Gaviria pers. obs. 2019). The species *Moraria glitzae* was described few years ago from groundwater near the Salzach river, a tributary of the Inn River, which is itself a tributary of the Danube (Gaviria & Defaye 2017). Most species of the genus *Moraria* known from Central Europe live in mosses and semiterrestrial habitats, but some have been reported from subterranean habitats, i.e., *M. brevipes*, *M. poppei*, *M. mrázeki* and *M. fontinalis* (Schminke 2007d). Schminke further argues that *M. varica* has being found almost exclusively in groundwater. The species from Kritzendorf still awaits identification or description.

Important to mention, some ... changes have occurred in the nomenclature. Within the parastenocaridids, three species originally placed into the genus *Parastenocaris* have been assigned to different genera: *Horstkurtcaris nolli*, *Fontinalicaris fontinalis fontinalis,* and *Proserpinicaris phyllura* (Schminke 2010; Karanovic & Lee 2012).

Acari

Among the Arachnida, mites have made their way into surface freshwaters but also into subsurface waters. The water mites worldwide comprise more than 6,000 species, i.e. 5,000 species of Hydrachnidia and 1,000 species of Halacaroidea (Gerecke 2007). Within the 1,000 species of water mites described for Europe, there are more than 100 species that dwell in groundwater. If there are strictly stygobiont species among these is under discussion. Some experts assume that all mites in groundwater are merely stygophile. Indeed, many species sampled from groundwater are also regularly found in surface waters or soils. Among the mites found in freshwater environments, some are ectoparasitic while others are predatory (Martin 2008). However, hardly anything is known about their autecology. For groundwater of the Lobau and the Danube Floodplain National Park four species of the family Halacaridae are documented, i.e., *Lobohalacarus weberi*, *Parasoldanellonyx parviscutatus*, *Soldanellonyx monardi*, all three classified as stygophile, and *Soldanellonyx chappuisi*, a stygobiont species (Tab. 4). Of *Lobohalacarus weberi*, the species list by Pospisil (1994) contains two subspecies, i.e., *L. weberi weberi* and *L. weberi quadriporus*.

During the construction of the subway tunnel at Stephansplatz in Vienna, in 1976 D.L. Danielopol collected mites in temporarily accessible groundwater outcrops in excavation pits. The samples contained five species of the genus *Schwiebea*, with two known species (*S. ruiensenis* and *S. talpa*) and three new species later described by Fain (1982), i.e., *Schwiebea aquatilis*, *S. danielopoli* and *S. subterranean*. According to Wurst (2006), these 'new' species are synonyms of already known species recorded from both phreatic and moist terrestrial habitats, i.e., *S. cavernicola*, *S. eurynympha*, and a species of the *Schwiebea nova* complex. Moreover, *Schwiebea ruiensenis* is synonym to *S. schmuttereri* (Wurst 2006). Specimen of *Schwiebea* collected from groundwater in the national park have unfortunately never been determined to species level. The samples of D.L. Danielopol also included a trombidiform mite, viz. the hyporheobiont, Central European *Stygothrombium chappuisi* (Fig. 5).

In general, mites collected in groundwater are rarely examined by taxonomists nor sequenced. There is a clear lack of experts in this field of research and therefore the real diversity of water mites dwelling in groundwater remains largely unknown.

Insecta

In subsurface waters insect larvae are regularly found in shallow aquifers. Among these there are typical representatives of the macrozoobenthos, i.e., larvae of Diptera, Plecoptera, and Ephemeroptera. However, these animals cannot complete their entire life cycle in groundwater, however, some can be considered stygophile (e.g. Stanford et al. 1994). There are also stygobiont representatives among the Coleoptera. For Europe, five stygobiont beetles from the family Dytiscidae have been described from France, Spain, Italy, and Portugal. On other continents, especially in Australia, stygobiont beetles (Coleoptera) are regular members of groundwater fauna and exhibit an extraordinarily high diversity (Leys

Tab. 4: List of stygobiont (biont), stygophile (phile), stygoxene (xene) crustaceans, Acari, and Insecta in groundwater of the Lobau (Lob) and the Danube Floodplain National Park (DFNP), divided into records prior to the year 2000 (<2000) and recent findings (>2019). Taxa recorded from Vienna and areas adjacent to the national park are listed in column 'out'. Uncertain taxonomic status and/or occurrence of taxa recorded in the past are indicated in red. For more detailed information, see text. – Tab. 4: Zusammenstellung aller stygobionten (-biont) und stygophilen (-phile) Vertreter aus den Großgruppen Crustacea, Acari, und Insecta im Grundwasser der Lobau und des Donau-Auen Nationalparks (DFNP), untergliedert in Nachweise vor dem Jahr 2000 (<2000) und aktuelle Nachweise (>2019). Nachweise von Taxa in Wien und Umgebung, aber außerhalb des Nationalparks, sind in der Spalte 'out' vermerkt. Für detailiertere Informationen siehe Text.

Classification	**Family**	**Species**	**stygo-**	**<2000**	**>2019**	**Lob**	**DFNP**	**out**
Ostracoda	Candonidae	*Candona candida* (O.F. Müller, 1776)	phile	+		+	+	+
		Candona neglecta (Sars, 1887)	phile	+		+	+	
		Candonopsis kingsleii (Brady & Robertson, 1870)	phile	+		+	+	
		Cryptocandona kieferi danubialis (Namiotko et al., 2005)	biont	+	+	+	+	+
		Fabaeformiscandona wegelini (Petkovski, 1962)	biont	+	+	+	+	
		Mixtacandona laisi vindobonensis (Löffler, 1963)	biont	+		+	+	+
		Mixtacandona spandli (Rogulj & Danielopol, 1993)	biont	+		+	+	
		Pseudocandona albicans (Brady, 1864)	phile	+	+	+	+	+
		Pseudocandona lobipes (Hartwig, 1900)	phile	+	+	+	+	
		Thyphlocypris eremita s.l. (Vejdovsky, 1882)	biont	+		+	+	
		Thyphlocypris szoecsi (Farkas, 1958)	biont	+		+	+	
	Cyprididae	*Psychrodromus fontinalis* (Wolf, 1920)	phile	+				+
	Darwinulidae	*Darwinula stevensoni* (Brady & Robertson, 1870)	phile	+		+	+	
	Lymnocytheridae	*Kovalevskiella elisabethae* (Gaviria, 2022)	biont	+	+	+	+	+
		Lymnocythere inopinata (Baird, 1843)	phile	+		+	+	
Diplostraca	Chydoridae	*Alona guttata* (Sars, 1862)	phile	+		+	+	
		Chydorus sphaericus (O.F. Müller, 1776)	phile	+		+	+	
Amphipoda	Bogidiellidae	*Bogidiella* cf. *albertimagni* (Hertzog, 1933)	biont		+		+	
	Crangonyctidae	*Crangonyx subterranus* (Spence Bate, 1859)	biont	+	+	+	+	
	Niphargidae	*Niphargus aquilex* s.l. (Schiödte, 1855)	biont	+				+
		Niphargus bajuvaricus (Schellenberg, 1932)	biont	+	+	+	+	

Classification	Family	Species	stygo-	< 2000	> 2019	Lob	DFNP	out
		Niphargus caspary (Pratz, 1866)	biont	+		+	+	
		Niphargus hrabei (S. Karaman, 1932)	phile	+	+	+	+	
		Niphargus inopinatus (Schellenberg, 1932)	biont	+	+	+	+	+
		Niphargus jovanovici (S. Karaman, 1931)	biont	+				+
		Niphargus cf. *kochianus* (Spence Bate, 1859)	biont	+		+	+	
		Niphargus puteanus (Koch, 1836)	biont		+			+
		Niphargus tatrensis s.l. (Wrzesniovsky, 1888)	biont	+		+	+	
		Niphargus vornatscheri (Schellenberg, 1934)	biont	+				+
Isopoda	Asellidae	*Proasellus cavaticus* (Leydig, 1871)	biont	+	+	+	+	+
		Proasellus slavus vindobonensis (Karaman, 1955)	biont	+	+	+	+	
		Proasellus strouhali strouhali (Karaman, 1955)	biont	+	+	+	+	
	Microparasellidae	*Microcharon* sp. (Karaman, 1934)	biont	+				+
Cyclopoida	Cyclopidae	*Acanthocyclops gmeineri* (Pospisil,, 1989)	biont	+	+	+	+	
		Acanthocyclops kieferi (Chappuis, 1925)	biont	+			+	
		Acanthocyclops rhenanus (Kiefer, 1936)	biont	+		+	+	
		Acanthocyclops sensitivus (Graeter & Chappuis, 1914)	biont	+		+	+	+
		Acanthocyclops venustus (Norman & Scott, 1906)	phile	+		+	+	+
		Austriocyclops vindobonae (Kiefer, 1964)	biont	+		+	+	+
		Diacyclops cohabitatus (Monchenko, 1980)	biont	+	+	+	+	
		Diacyclops danielopoli (Pospisl& Stoch, 1999)	biont	+	+	+	+	
		Diacyclops disjunctus (Thallwitz, 1927)	phile	+		+	+	
		Diacyclops felix (Pospisl & Stoch,1999)	biont	+		+	+	
		Diacyclops languidoides (Lilljeborg, 1901)	biont	+		+	+	+
		Diacyclops languidoides goticus (Kiefer, 1931)	biont	+		+	+	+
		Diacyclops sp. gr. *languidoides*	biont	+	+	+	+	+
		Eucyclops graeteri (Chappuis, 1927)	biont	+	+	+	+	
		Graeteriella laisi (Kiefer, 1936)	biont		+	+	+	
		Graeteriella unisetigera (Graeter, 1908)	biont	+		+	+	

Classification	Family	Species	stygo-	<2000	>2019	Lob	DFNP	out
		Paracyclops fimbriatus (Fischer, 1853)	phile	+		+	+	
Harpacticoida	Ameiridae	*Nitocrella hirta hirta* (Chappuis, 1924)	biont	+		+	+	+
		Nitocrella hofmilleri (Brehm, 1953)	biont		+		+	
	Canthocamptidae	*Elaphoidella gracilis* (Sars, 1863)	phile	+		+	+	
		Bryocamptus cf. *rhaeticus*	phile		+	+	+	
		Epactophanes richardi (Mrázek, 1893)	phile	+		+	+	
		Moraria sp.	phile/biont		+			+
	Parastenocarididae	*Fontinalicaris fontinalis fontinalis* (Schnitter & Chappuis, 1915)	biont	+		+	+	
		Horstkurtcaris nolli nolli (Kiefer, 1960)	biont	+		+	+	
		Parastenocaris germanica Kiefer, 1936	biont	+		+	+	
		Proserpinicaris phyllura (Kiefer, 1938)	phile	+		+	+	
Syncarida	Bathynellacea	*Bathynella vindobonensis* (Serban, 1989)	biont	+				+
	Parabathynellacea	*Parabathynella* sp. (Noodt, 1965)	biont	+				+
Acari	Acaridae	*Schwiebea cavernicola (*Vitzthum, 1932)	phile	+				+
		Schwiebea eurynympha (Oudemans, 1911)	phile	+				+
		Schwiebea sp. gr. *nova* (Oudemans, 1906)	phile	+				+
		Schwiebea schmuttereri (Türk & Türk, 1957)	phile	+				+
		Schwiebea talpa (Oudemans, 1916)	phile	+				+
		Schwiebea sp.	phile	+	+	+	+	
	Halacaridae	*Lobohalacarus weberi* (Romijn &Viets, 1924)	phile	+		+	+	+
		Parasoldanellonyx parviscutatus (Walter, 1917)	phile	+	+	+	+	
		Soldanellonyx chappuisi (Walter, 1917)	biont	+	+	+	+	+
		Soldanellonyx monardi (Walter, 1919)	phile		+	+	+	
	Stygothrombiidae	*Stygothrombium chappuisi* (Walter, 1947)	phile	+				+
Insecta	Scirtidae	*Cyphon palustris* (Thomson, 1855)	phile	+		+	+	

et al. 2003; Watt & Humphreys 2003; Humphreys 2008; Watts & Humphreys 2009). They belong to the families Dytiscidae, Noteridae, Hydrophilidae and Elmidae.

At investigation Area 1 (site C) in the Lower Lobau, larvae of the marsh beetle *Cyphon palustris* (fam. Scirtidae) are regularly found in the shallow aquifer down to several meters below the groundwater table. It appears that the larvae actively migrate into the sediments and into groundwater at the banks of surface waters (Klausnitzer & Pospisil 1991). It is not yet understood how the larvae, which depend on atmospheric oxygen, can migrate such long distances into the water saturated sediments and stay there for such a long time. Moreover, once every few years these marsh beetles show a mass development with several hundred beetle larvae occasionally collected from one single well, while in the following years they are hardly found (Klausnitzer 2008). The rhythm of these mass developments is unknown. In our inventory, *C. palustris* is classified stygophile.

Red list species

Difficulties associated with the morphological determination of many groups of stygobiont invertebrates (e.g., amphipods), the lack of reliable determination keys, and the lack of taxonomic experts are reasons for the limited number of groundwater species included in Red Lists. The global red list contains 10 amphipod species (all fam. Niphargidae) considered as 'endangered' (Baillie & Groombridge 1996). None of the species occurring in the Danube Floodplain National Park are in the world red list. The red list of Bavaria, Germany, currently includes three species considered extinct or lost, among them *Cragonyx subterraneus* and *Niphargus caspary*, both occurring in the Danube Floodplain National Park. Moreover, the Bavarian red list ranks *N. inopinatus*, a species abundant in the Danube national park, as close to extinction. A similar status has *N. bajuvaricus*, which is a persistent member of the groundwater amphipod community of the national park. With the status 'at high risk', the Bavarian red list mentions *N. hrabei*. Studies by Nesemann revealed *N. hrabei* to occur in several backwaters of the Danube (Nesemann 1993, Nesemann et al. 1995). A current sample from the Lobau provided evidence for the occurrence of *N. hrabei* also in shallow groundwater. For the German province Saarland, *N. kochianus* is listed as 'extinct' (Weber & Flot 2019), a species that was recorded in the Danube flood plain some time ago (Pospisil 1994a). In France, seven *Niphargus* species are listed at risk, two are potentially at risk, and 14 species are not endangered, among the latter *N. kochianus* (Allanic 2012). No stygobiont or stygophile amphipods, other crustaceans, or worms (annelids, nematodes, turbellarians) are in the red list of Austria so far. As an exception, most hydrobioid gastropods inhabiting springs and groundwater habitats in Austria are threatened to varying degrees; *Hauffenia danubialis* and *Bythiospeum geyeri* are both considered "endangered" according to the Red List of Austrian Molluscs (Reischütz & Reischütz 2007).

Discussion

Knowledge on groundwater biodiversity is growing at an increasing rate. However, it lags behind compared to the state of biodiversity research of surface aquatic ecosystems. This is not surprising. Although studies addressing subterranean aquatic environments started long ago (see Racovitza 1907; Spandl 1926; Chappuis 1927, and references therein), groundwater systems are generally out of sight, often difficult to access, and rarely perceived as habitats hosting a specialized and diverse biota by the general public. Their inhabitants are mostly small-sized and inconspicuous, lacking charismatic flagship species that help raising public awareness on the important contribution of subterranean biological communities to societally relevant ecosystem goods and services (Griebler & Avramov 2015). Finally, within the scientific community, there is a lack of taxonomists for many groups of groundwater fauna and a lack of useful identification keys. It is assumed that groundwater fauna has a significant, yet largely underestimated share in the global freshwater biodiversity (Malard 2022). It is important to keep in mind that a location or region needs to be repeatedly sampled for a reliable assessment of groundwater biodiversity. These efforts have been directed to only a limited number of habitats so far, many of which achieved the status of a 'biodiversity hotspot' (Culver & Sket 2000; Pipan et al. 2021). In other words, the detection of 'biodiversity hotspots' may largely reflect the dedication put into sampling the local groundwater biotas. In the past, single-site species richness (α-diversity) was often considered a minor component of overall species richness (γ-diversity) (Gibert & Deharveng 2002). However, this was mainly shown for karst and cave habitats with extremely small distribution areas of most cave specialists (Culver et al. 2006; Malard et al. 2009; Zagmajster et al. 2014). The current ranking of subterranean biodiversity hotspots (Culver et al. 2021) contains 22 caves distributed all over the world. These authors state: "There may be additional non-cave subterranean sites, particularly in hyporheic habitats, but these data have for the most part not been assembled into species lists for individual sites. In addition, there is the difficulty in deciding what constitutes a single site, is it just one Bou-Rouch pump site or a stream reach (e.g., a riffle)?" We agree that defining a 'site' in an alluvial aquifer is difficult. However, we can describe the local and regional species richness, with α-diversity referring to a single sampling point (i.e., groundwater observation well, piezometer or natural spring), and γ-diversity referring to the region of habitat type (e.g., the Lobau wetland or the Danube Floodplain National Park). With >650 km of surveyed passageways, the Mammoth Cave system (Kenducky, U.S.) is the largest subterranean biodiversity hotspot, home to 17 stygobiont species (Niemiller et al. 2021), listed as a single site in Culver et al. (2021). The Lobau and The Danube Floodplain National Park, in focus of our current groundwater fauna inventory, have a longitudinal extension of about 10 km and 40 km, respectively, thus being considerably smaller in size. When focusing on stygobiont species only, eight sites in the list of Culver et al. (2021), including five anchialine or deep phreatic sites, two sites in the Dinaric karst, and one site in the Cantabrian Mountains of Spain, harbor more than 35 stygobiont species. A richness of such magnitude has been reported for the shallow alluvial aquifer of the Danube Floodplain National Park by Danielopol & Pospisil as early as 2001.

The alluvial sediments of a riverine aquifer are extremely heterogeneous. In floodplain aquifers like those of the Danube in the Vienna Basin, the sandy gravels are interbedded with well sorted gravel and layers or lenses of silt and clay. These reflect the history of fluviatile deposition and form an anisotropic geologic formation that generates spatially and temporally heterotrophic and dynamic environmental conditions. There is evidence that groundwater fauna, and in particular stygobiont species, accumulate along the alluvial valleys of large rivers like 'beads on the string' (Creuzé des Châtelliers 1991; Danielopol et al. 1997; Ward and Voelz 1997; Ward et al. 1998). Groundwater biodiversity in riverine alluvial aquifers has received considerably less attention compared to karstic and cave environments, with a few exceptions. The alluvial aquifers and floodplains of the Rhône, the Rhine, the

Main, and in particular the Danube River are regions of high hypogean biodiversity (Noll & Stammer 1953; Dole-Olivier et al. 1994; Pospisil 1994a; Steenken 1998). Further examples are found in North America, i.e., the Flathead River in Montana (Stanford et al. 1994) and the South Platte River in Colorado (Ward & Voelz 1994).

The area of the Danube Floodplain National Park in eastern Austria holds a transitional position in Central Europe with regard to climatic, geomorphologic, botanical, and zoological factors. This applies also to groundwater: species with their main distribution in western and eastern Europe meet and coexist in this area (Danielopol 1976a; Pospisil 1989). Most studies on groundwater fauna in the Danube Floodplain National Park concentrated on the Lobau wetland, located almost entirely within the city limits of Vienna. With the incisive regulation of the Danube River (1869–1875) in the Vienna region, the Lobau has been truncated to a large extent from the Danube main channel and its hydrological dynamics. In the natural state, alluvial aquifers are highly interactive with contiguous surface waters (Stanford and Ward, 1988; Gibert et al. 1990; Vervier et al. 1992). Today the Upper Lobau is an urban recreation area, artificially donated with surface water to maintain at least partly its wetland character. The Lower Lobau, the more natural part, currently suffers from water shortage and sinking groundwater levels with increasing intermittency of originally perennial surface waters. Danube floods can enter the Lobau floodplain only at high river levels as backflow via a watergate from downstream at Schönau (Fig. 1). Further downstream, the Danube floodplains are in a more natural state, communicating with the river. For more than three decades, projects tackle the re-connection of individual wetland backwaters and floodplain areas with the main river channel (e.g., Tockner et al. 1998; Schiemer et al. 1999). However, groundwater fauna studies in these areas are rare.

Our inventory for the Danube Floodplain National Park, and the Lobau area in particular, revealed 44 stygobiont and 93 stygophile invertebrate species. The higher groundwater fauna richness in the Lower Lobau, as compared to the Upper Lobau and other areas of the national park (Fig. 2), may have several reasons. First, investigations of the past were mainly focused in this area. Second, the Lower Lobau is the more natural and hydrologically dynamic part of the Lobau. We can therefore assume that the more eastern part of the Danube Floodplain National Park has a similar biodiversity. In accordance with the common notion, the groundwater fauna of the national park is mainly composed of crustaceans. Danielopol et al. (2000) found that more than two-thirds of the stygobiont species of the Lobau belonged to the copepods, ostracods, and amphipods. In our current species list, crustaceans have a share of 84 % within the stygobionts and 22 % within the stygophiles. Once other invertebrates such as mites and nematodes receive similar attention, this proportions may change, as is indicated by the large number of nematodes found (Eder 1983). Currently, the list of stygobionts only contains 7 % of worms (turbellarians, Annelida, Nematoda), but with stygophiles they account for 71 %. However, in these animal groups it will always be difficult to distinguish between stybobiont and stygophile species.

Issues worth considering are single species records from the early period of groundwater investigations, improper descriptions and the loss of sampling locations due to human intervention. Since the earliest records of groundwater fauna are not older than the beginning of the last century (e.g., Spandl 1926, Vornatscher 1938), we have no clue how the regulation of the Danube (1869–1875) influenced the richness of stygobiont and stygophile taxa in the area. Within the city of Vienna, the original collecting places of several stygobionts disappeared in the course of urban development (Vornatscher 1972; Danielopol & Pospisil 2001). In addition, an inventory of species richness is challenged by changes in the affiliation and nomenclature of taxa. Our data set contains a number of obsolete species names that we have not listed but mentioned in the text. Moreover, in our species list we have highlighted in red font species with an 'uncertain' taxonomic status or uncertain occurrence within the study area (Tab. 3). The flagging of 'problematic' taxa enables the reader to identify knowledge gaps and promote targeted future investigations with modern methods. In particular, the use of molecular tools, in addition to traditional morphological approaches, will certainly provide novel insights into the diversity and biogeography of the groundwater biota of the Danube Floodplain National Park. The application of sequencing (COI and 28S genes) to stygobiont amphipods and isopods collected from the Lobau, Schönau and Kritzendorf, supported the occurrence of several species reported in earlier publications. Among the amphipods this was the case with *Niphargus bajuvaricus*, *N. caspary*, and *Crangonyx subterraneus*. For *N. inopinatus*, species assignment is based only on COI sequences. Both primer sets provided evidence for the presence of a species new to the study area related to *N. tonywhitteni* (Fig. 4), collected from a groundwater observation well in Kritzendorf, Lower Austria. All isopods tested genetically match known sequences of *Proasellus slavus,* but clearly differ from sequences of *P. slavus* collected in Salzburg, Germany and France (Fig. 5). We thus maintain the subspecies name *P. slavus vindobonensis* established by Strouhal (1964) for the populations of the Vienna region until a systematic revision of the *P. slavus* species complex is available. From the western part of Austria Strouhal (1964) reported *P. slavus s. str.* and the subspecies *P. slavus salisburgensis*.

With the application of molecular analysis and the inclusion of previously disregarded invertebrate groups we expect our species list to grow in the near future. The ability to prospect groundwater fauna in protected areas like the Danube Floodplain National Park is of great advantage as it increases the chances to locate new populations of rare groundwater dwelling species (Danielopol & Pospisil 2001). For example, only a few specimens of the stygobiont cyclopoid *Austriocyclops vindobonae* were found at the periphery of the Lobau at Vienna, in a well at Kagran, as described by Kiefer (1964). 30 years later, a few more specimens were sampled from a single piezometer in the Lobau and a unique locality in Lower Austria (Traismauer) (Pospisil 1994a, 1994b). This peculiar copepod with unique morphological traits that complicate the systematic classification within the Cyclopidae was redescribed by Pospisil & Stoch (1997). It is an example of a rare stygobiont species. Other species such as *Mixtacandona spandli* (Rogulj & Danielopol 1993) exhibit a kind of pseudo-rarity (*sensu* Gaston, 1994). This ostracod has a very patchy distribution within the Lobau area and is always found in low numbers (Rogulj & Danielopol 1993).

As already mentioned, particularly the Lower Lobau currently experiences severe stress due to water shortage caused by inconsequent water management measures, complemented by climate change effects. There is a considerable risk that these habitats of extraordinarily high groundwater fauna richness are impaired or lost. It must be remembered that in many areas the thickness of the porous aquifer is only a few meters, and thus this ecosystem is very vulnerable to direct and indirect anthropogenic pressure, despite its protection status. Some species may be at high risk of extinction. Ongoing investigations will hopefully allow us in a few years to evaluate effects of the altered hydrology and climate change by comparison with the studies of the last century. The Lobau is intended to become a long-term monitoring site for groundwater ecology.

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Addresses:

Christian Griebler, E-Mail: christian.griebler@univie.ac.at (corresponding author)

Clemens Karwautz, E-Mail: clemens.karwautz@univie.ac.at

Grit Rasch, E-Mail: grit.rasch@univie.ac.at

Lucas Fillinger, E-Mail: fillinger.lucas@gmail.com

Raphael Veits, E-Mail: raphael.veits@univie.ac.at

Rick Junker, E-Mail: Rickjunker@outlook.com

Florian Scharhauser, E-Mail: florian.scharhauser@univie.ac.at

Constanze Englisch, E-Mail: constanze.englisch@univie.ac.at

Fritz Schiemer, E-Mail: friedrich.schiemer@univie.ac.at

Peter Pospisil, E-Mail: peter.pospisil@gmx.net

University of Vienna, Department of Functional and Evolutionary Ecology, Djerassiplatz 1, A-1030 Vienna, Austria.

Santiago Gaviria, E-Mail: santiago.gaviria@univie.ac.at
University of Vienna, Department of Functional and Evolutionary Ecology, Djerassiplatz 1, A-1030 Vienna, Austria; Technisches Büro für Biologie Dr. Gaviria Melo, Fred-Raymond-Gasse 19/2/4, A-1220 Vienna, Austria.

Andreas Fuchs, E-Mail: fuchs@groundwaterecology.de
University of Vienna, Department of Functional and Evolutionary Ecology, Djerassiplatz 1, A-1030 Vienna, Austria; Institut für Grundwasserökologie IGÖ GmbH at the Universität Koblenz-Landau, Campus Landau Fortstraße 7, D-76829 Landau, Germany.

Ursula Eisendle, E-Mail: ursula.eisendle@plus.ac.at
Paris Lodron University Salzburg, Working Group Nematology, Hellbrunnerstraße 34, A-5020 Salzburg, Austria.

Jan Steger, E-Mail: jan.steger@univie.ac.at
University of Vienna, Department of Palaeontology, Josef-Holaubek-Platz 2 (UZA II), A-1090 Vienna, Austria.

Matthäus Greilhuber, E-Mail: mgreilhuber@gmail.com
Natural History Museum Vienna, Third Zoological Department & Central Research Laboratories, Burgring 7, A-1010 Vienna, Austria.

Tobias Pfingstl, E-Mail: tobias.pfingstl@uni-graz.at
University of Graz, Institute of Biology, Universitätsplatz 2, A-8010 Graz, Austria.

Dan L. Danielopol, E-Mail: dldanielopol@icloud.com
Karl-Franzens University Graz, Institute of Earth Sciences, NAWI Graz Geocenter, Heinrichstraße 26, A-8010 Graz, Austria.