DIVERSITY OF GROUNDWATER DWELLING CYCLOPOIDA (CRUSTACEA, COPEPODA) IN A DANUBE WETLAND IN AUSTRIA

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DIVERSITY OF GROUNDWATER DWELLING CYCLOPOIDA (CRUSTACEA, COPEPODA) IN A DANUBE WETLAND IN AUSTRIA

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DIVERSITY
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ABSTRACT. – The taxonomic diversity of groundwater dwelling cyclopoid fauna (23 species, 10 hypogean and 13 epigean taxa) occurring within an area of about 0.8 km^2 of the Lobau, a Danube wetland at Vienna, is analysed using several metric scales. These data are compared with those of two other sites, Regelsbrunn and Deutsch-Wagram, located 16 km remote from the Lobau. Laboratory observations on selected cyclopoid species related to their search activity during the election of substrate and potential food items exemplifies aspects of the ecological diversity of groundwater cyclopoids occurring within the Danube wetlands. The origin and the "potential diversity" of the cyclopoids in the investigated area are discussed using statistical, ecological, biogeographic and evolutionary arguments.

DIVERSITÉ
CYCLOPOIDA DES EAUX SOUTERRAI-NES
LOBAU
AQUIFÈRE DU DANUBE

RÉSUMÉ. – La diversité taxinomique de la faune des Cyclopoïdes (23 espèces, 10 hypogées, 13 épigées) habitant la nappe phréatique du Lobau dans un périmètre d'environ 0.8 km^2 de la plaine alluviale du Danube à Vienne, est analysée au niveau de plusieurs échelles métriques. Ces informations sont comparées avec des données obtenues dans deux autres localités, Regelsbrunn et Deutsch-Wagram, situées à 16 km du Lobau. L'activité motrice différente de plusieurs Cyclopoïdes hypogés pendant la recherche du substrat et de la nourriture potentielle documente le problème de la diversité écologique chez les Cyclopoïdes souterrains de la plaine alluviale du Danube. L'origine et la "diversité potentielle" des Cyclopoïdes hypogés de la zone étudiée est discutée à partir d'arguments d'ordre statistique, écologique, biogéographique et de la biologie évolutive.

INTRODUCTION

In a stimulating review Marmonier *et al.* (1993) suggested that it will be important for the future research on the diversity of subterranean fauna to intensify the following activities:

(1) The continuation of faunistic exploration leading to a better understanding of the taxonomic or phylogenetic diversity – Until recently, many parts of the world remained practically unexplored. The unexpectedly rich stygobitic fauna which are continually being discovered in North America (Reid 1997/1998, Strayer & Reid 1999) or in the Western Australia (Humphreys 2000) are excellent examples. This exploration is a necessary activity even in Europe, where the studies on the fauna of subterranean waters (especially those dealing with animals in karstic systems) has a long tradition (Gibert 1992, Stoch 1995). The documentation of the taxonomic diversity should be encouraged because we observe that an ever increasing number of groundwater habitats is endangered by overexploitation or by anthropogenic pollution with fatal consequences for the subterranean fauna, which are becoming endangered or extinct (Sket 1999a, 1999b).

(2) The documentation of the ecological diversity of hypogean fauna – We know very little about the autecology of most of the hypogean aquatic fauna, especially how they exploit subterranean resources (Gibert *et al.* 1994, Stoch 1995).

(3) The study of the genetic diversity of hypogean organisms at infra– or inter-species level – Recent studies, especially those on crustaceans show for instance that the karstic populations display a high genetic diversity (Cobolli Sbordoni *et al.* 1990, Culver *et al.* 1995). Sbordoni *et al.* (1976) and Mathieu *et al.* (1997) documented dif-

Fig. 1. – Geographical location of the main sampling areas in the Danube Valley.

ferences between the genetic diversity of karstic and non-karstic populations of amphipods.

(4) The description of the functional role of groundwater organisms within subterranean ecosystems – Claret *et al.* (1999) showed how one can relate the adaptive traits of subterranean animals to functional aspects of ecosystems.

Moreover, Marmonier *et al.* (1993: p. 394) noted that one of the interesting aspects related to faunistic investigations should be the evaluation of the "potential biodiversity" in a groundwater system corresponding to the potential number of species that can be harboured by that system within its environmental and historical context.

In the present contribution we describe the faunistic and ecological diversity of groundwater dwelling Cyclopoida from a sector of the Danube wetlands in Lower Austria, the Lobau. We compare these data with those obtained from two other sites, the Regelsbrunn wetland and the Deutsch-Wagram area, both sites located at about 16 km remote from the former site (Fig. 1, 2). Long-term ecological investigation on the fauna of this area showed (Danielopol & Pospisil, submitted) that the Cyclopoida is a focal group for the evaluation of groundwater biodiversity at both local and regional scales. Until our investigations, the groundwater copepod fauna in Lower Austria was poorly known as demonstrated by the Austrian copepod checklist (Gaviria 1998). Additionally, we present laboratory observations on selected cyclopoid species related to their activity during the election of substrate and/or food items as well as information on their spatial distribution in the field; this will give us a better idea about the ecological diversity of these crustaceans. Finally, we will discuss the origin of the observed subterranean cyclopoid diversity and estimate the "potential diversity" of this group in the Lobau wetland.

MATERIAL AND METHODS

Study Area and Sampling Programmes: the ecological research was carried out on the Lobau wetland, which is situated on the left side of the Danube in the south-eastern part of the city of Vienna (Fig. 1, 2). The data were collected during various sampling campaigns between 1987 and 1998. Detailed descriptions of this area and the research programmes with their results are presented in Pospisil (1994a, 1994b, 1999), Danielopol *et al.* (1992, 1994, 1997, 1999a, 2000), Dreher *et al.* (1997), and Moesslacher (1994, 1998). Taxonomic descriptions of the fauna are presented in Pospisil (1989, 1994a), Pospisil & Stoch (1997, 1999), Stoch & Pospisil (2000a, b). The present publication deals with the diversity of cyclopoids from two areas called Lobau-B and Lobau-C by Pospisil (1994a). Both sites encompass a total area of about 0.8 km^2, located within the subregion Untere Lobau, which belongs to the former flood plain of the Danube. Since 1987 the Untere Lobau constitutes an UNESCO Biosphere Reserve and was incorporated in the Danube Flood Plain National Park in 1996. From the Lobau-B area (about 600x600 m large, Fig. 2) we present information on 12 widely dispersed groundwater observation wells used originally for hydrologic observations and 12 wells fixed in a regular 3x4 grid within a 27 m^2 area called BLM (details in Pospsil 1994a, b, 1999, Danielopol *et al.* 1999a, see also Fig. 2 and Table II). This small area

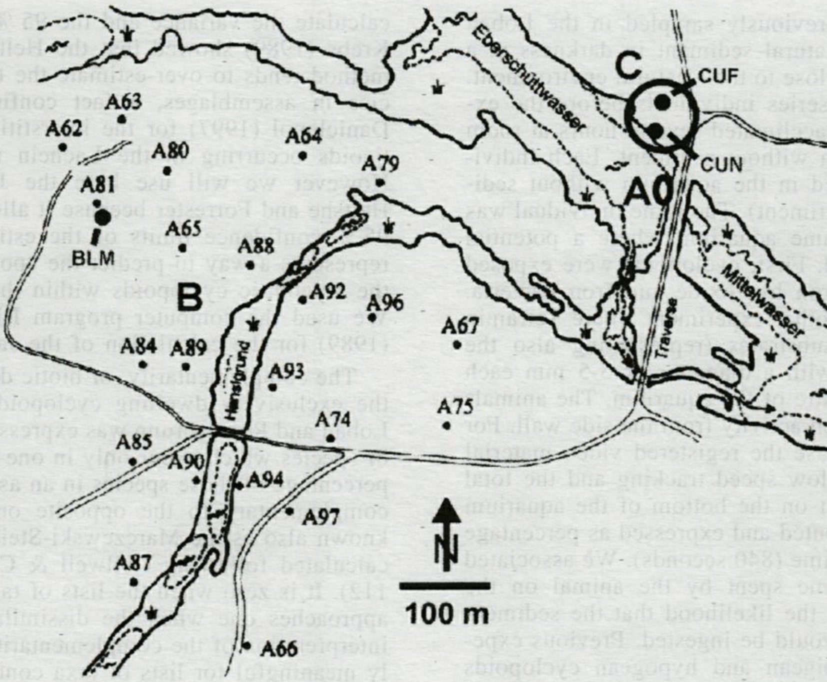

Fig. 2. – The sampling areas A, B, and C in the Lobau wetland (see text for further explanation).

was investigated twice monthly during June 1996 and August 1997, and monthly until January 1998. The groundwater domain of Lobau is part of the Marchfeld aquifer. The Lobau-B area is largely recharged by the Danube river (Danielopol *et al.* 1999a). Lobau-C represents an area of about 900 m^2 forming a mini-groundwater ecosystem that is hydrologically connected to backwaters of the Danube, the Eberschüttwasser and the Mittelwasser (Fig. 2). During 1991 and 1993 we investigated 26 wells seasonally (9 of them were multilevel piezometres sampled at various depths, e.g. 3, 6, 9, 12 m beneath the surface). In this paper we present data for 9 multilevel wells and 4 "simple" piezometres (Table II). In a comparative programme to the BLM we investigated two sites of 27 m^2 each, one located on the banks of the Eberschüttwasser (CUN, in Fig. 2, Table II), the other one some 35 – 40 m further inland (CUF, in Fig. 2, Table II). The CUN and CUF sites had the same 3 × 4 layout of 12 sampling wells as the BLM. At the CUN, CUF and BLM sites, a cluster of 3 wells was randomly chosen at each sampling date and 5 litres of groundwater and sediment from each well using the Bou-Rouch pumpage method were extracted (for more sampling details see Pospisil 1992, 1999, Danielopol *et al.* 1999a).

The cyclopoid fauna is here ecologically classified into two groups: (1) epigean species, which typically occur in surface water habitats but were sampled in various groundwater habitats within the Danube wetlands; (2) exclusively hypogean (or stygobitic) species, which we caught only in subsurface water habitats and never in surface water habitats at the sites investigated by us (for additional information see the Result-section).

Species diversity of the Cyclopoida in the Lobau will be presented at several metric scale levels: (a) metric scale, 1 m – 10 m length, (b) decametric scale, 10 m – 100 m L, (c) hectometric scale, 100 m – 1000 m L and (d) kilometric scale, more than 1 km L. We shall arbitrarily consider the "a" and "b" levels the local scale and "c" and "d" regional scales.

Regelsbrunn (Fig. 1) is a wetland area east of Vienna where old arms of the Danube are being reconnected to the main channel of the river since 1997 in order to revitalise the wetland ecosystems (Schiemer 1999). 10 sampling wells were fixed at 3 stations and different depths (Table II) along a transect of one km L from the Danube inland, crossing distinct types of old arms; they were sampled monthly during 1995 (Wenzl unpubl) and seasonally during 1997 (Steininger in prep). Cyclopoids were found in 7 wells (Table II).

Deutsch-Wagram is located north-east of Vienna (Fig. 1) and the investigated wells are located along the Marchfeld channel. The wells are commonly used for the observation of the local artificial groundwater recharge of the Marchfeld aquifer (Neudorfer 1999). Six wells along a 2 km sector of the Marchfeld channel were investigated by one of us (PP) during 1995 (Table II).

Laboratory observations: Using a SONY CCD video-camera, fixed on a WILD stereo-microscope (60x), we registered in infra-red light (wave length, 950 nm) the movement and the potential feeding behaviour of several species of stygobitic cyclopoids, 3 species of *Diacyclops* and 1 of *Acanthocyclops* (see Results for additional details). This method has been successfully tested during observations on the movement and feeding activity of isopods (Moesslacher 1994).

We used isolated individuals, placed in a cylindrical micro-aquarium with a diameter of 18 mm and a height of 2.5 mm; their activity were recorded for 14-15 minutes. For fully standardised and comparative observations we used only the series of 14 minutes (840 seconds). Copepods previously sampled in the Lobau were maintained on natural sediment in darkness at a constant temperature close to their natural environment. For each experiment series individuals before the experiment started were acclimated several hours at room temperature in aquaria without sediment. Each individual was first recorded in the aquarium without sediment (the control experiment). The same individual was then placed in the same aquarium where a potential food item was offered. First, cyclopoids were exposed to fine sediment of Iron hydroxide and Iron bacteria. It was followed by another experiment where Tetramin was offered. These substrates (representing also the potential food item) with a diameter of 3-5 mm each were placed in the centre of the aquarium. The animals started their exploration activity from the side wall. For each individual and case the registered video material was processed under low speed tracking and the total amount of time at rest on the bottom of the aquarium or substrate was computed and expressed as percentage of the total exposure time (840 seconds). We associated an increase in the time spent by the animal on the offered substrate with the likelihood that the sediment particles we offered would be ingested. Previous experiments with both epigean and hypogean cyclopoids (Pospisil unpubl) showed that these crustaceans generally spend more time on organic substrates than outside the substrate and/or in environments without substrate.

The two potential food items used here were chosen because of previous observations in the field and laboratory. We noted that in many cases samples from the Lobau contained large amounts of fine Iron hydroxide sediment and Iron bacteria. In many residues of sieved samples we found a high number of crustacean faeces (including cyclopoid faeces too) containing this type of sediment. Tetramin is a smelly product used as fish food. One of us (PP) observed large cyclopoids, like *Cyclops strenuus,* in aquarium conditions feeding on this solid medium.

For each of the 3 series of experiments (control without sediment, series with fine sediment and series with Tetramin) we calculated the arithmetic mean and the standard error of the mean.

On batch cyclopoid samples of *Diacyclops* species and *Acanthocyclops gmeineri* several series of observation were done in order to see the potential predatory activity of these cyclopoids.

Estimation of Species Richness: the amount of change in species richness of exclusively hypogean cyclopoids will be determined from the plot of the cumulative number of local species occurring at the main investigated sites, in the Lobau (CUN, Lobau-C, BLM, Lobau-B), Regelsbrunn, and Deutsch-Wagram, as discussed by Collwell & Coddington (1995).

The 1st order Jackknife model (Jack 1) of Heltshe and Forrester (Krebs 1989) was used to estimate the species richness which potentially exist in the Lobau. According to Baltanas (1992) the Jack 1 estimator, based on unique species occurring in various sample units, is the least biased one as compared to other estimators and is suited to assemblages with low number of species. Other specialists, e.g. Walther & Morand (1998), also found the Jack 1 as the least biased and the most precise estimator for the number of species in an assemblage. Using this metric, one is also able to calculate the variance and the 95 % confidence limits. Krebs (1989) showed that the Heltshe and Forrester's method tends to over-estimate the true number of species in assemblages, a fact confirmed by Rouch & Danielopol (1997) for the interstitial dwelling harpacticoids occurring in the Lachein riverbed sediments. However we will use here the Jacknife method of Heltshe and Forrester because it allows to calculate the 95 % confidence limits of the estimated value which represents a way to predict the "potential diversity" of the stygobitic cyclopoids within the investigated area. We used the computer program RICHNESS of Krebs (1989) for the calculation of the Jack1 estimator.

The complementarity, or biotic distinctness, between the exclusively dwelling cyclopoid taxa found in the Lobau and Regelsbrunn was expressed as the proportion of species which occur only in one assemblage, i.e. the percentage of those species in an assemblage which are complementary to the opposite one. The "C index", known also as the Marczewski-Steinhaus distance, was calculated following Collwell & Coddington (1995: p 112). It is zero when the lists of taxa are identical and approaches one when the dissimilarity increases. The interpretation of the complementarity index is especially meaningful for lists of taxa containing more or less equal numbers, as in our case with Lobau (10 stygobitic taxa in Lobau and 8 stygobites in Regelsbrunn). Note that one obtains a similar result using the Jaccard index for association in its special expression $Jd = 1 - J$, which represents the degree of dissimilarity.

RESULTS

Cyclopoida diversity and spatial distribution

During our long-term groundwater ecological research in the Lobau-B and Lobau-C areas we sampled 23 species: 10 exclusively hypogeans and 13 epigeans. Two additional stygobitic and one epigean species were discovered at the sampling sites Regelsbrunn and Deutsch-Wagram (Tables I and II).

From the total of 26 Cyclopidae species, 21 belong to the subfamily Cyclopinae and 5 to the Eucyclopinae (*Eucyclops graeteri* (Chappuis), *E. serrulatus* (Fischer), *E. speratus* (Lilljeborg), *Macrocyclops albidus* (Jurine), and *Austriocyclops vindobonae* Kiefer).

Considering the Cyclopoida of the Lobau area (Table I), one can recognise 2 types of species assemblages (Pospisil 1999): (1) an ecotonal assemblage, located at site Lobau-C, represented by both hypogean and epigean species and (2) a hypogean assemblage located within the Lobau-B area with exclusively dwelling hypogean taxa, (one exception is *D. disjunctus*).

D. disjunctus was repeatedly found at groundwater sites closely located to the Eberschüttwasser, hence we consider this species an hypogean

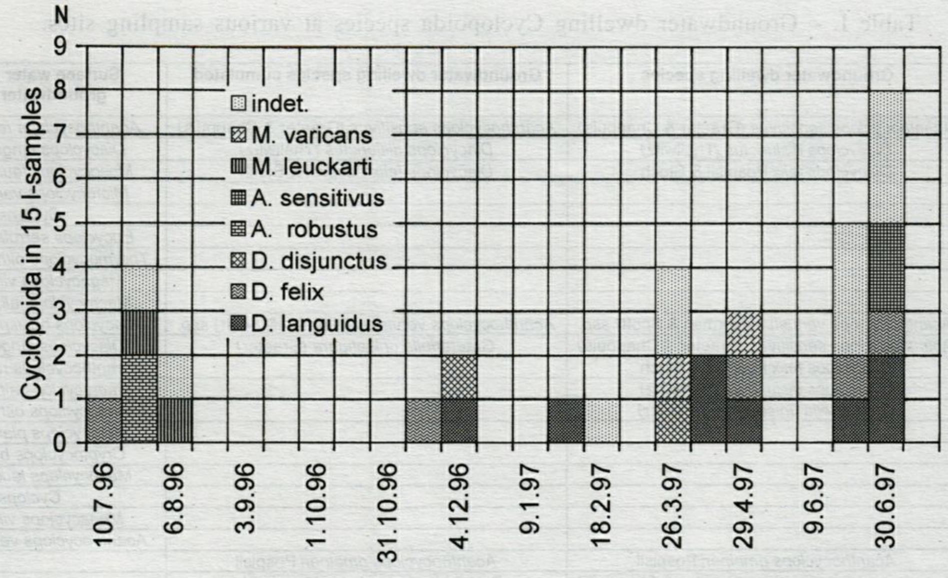

Fig. 3. – Quantitative distribution of cyclopoid species at the CUN site during 12 months; for each date, data cumulated from 3 sampling units.

ecotonal taxon (Pospisil 1999). *Acanthocyclops venustus venustus* (Norman & Scott) was recorded in surface water habitats (e.g. Fryer 1993) but several other subspecies are stygobitic taxa. *A. venustus* (Norman & Scott) *ssp.* from our sampling sites occurred exclusively in groundwater habitats, hence it is here considered a hypogean taxon. Following F. Stoch (pers comm), our populations represent a subspecies with affinities to *A. venustus italicus* Pesce & Maggi, a stygobitic taxon (Lescher Moutoué 1986).

Species diversity at the metric scale

The sites CUN and BLM (with a surface of 4.5 × 6 m each) differ from both the qualitative and quantitative point of view (Fig. 3, 5 and Tables I, II).

The CUN species assemblage (12 species) is represented by hypogeans (3) and epigeans (9) species (Tables I, II), occurring at low frequencies (Fig. 3).

The most frequent species is the epigean *D. languidus* (Sars) (Fig. 3). Besides this latter two other *Diacyclops* species occur (*D. felix* Pospisil & Stoch and *D. disjunctus*).

The BLM site displays 6 taxa (Tables I, II) which occur exclusively in groundwater. Figure 4 shows that their abundance is higher than those of the CUN sites, it appears however low as compared to the abundance of Cyclopoida at the site Lobau-A were several hundreds of individuals occurred in volumetrically equivalent samples (Danielopol 1983, Fig. 53, 55). One should note that from the 24 wells at the CUN and CUF sites, three of them (CUN-A2, CUF-B2, CUF-B4) remained completely barren during the whole investigation period.

Species diversity at decametric and hectometric scales

The sites Lobau-C (approx. 23 × 40 m L) and Lobau-B (approx. 600 × 600 m L) display generally the same pattern of qualitative diversity like the CUN and BLM sites, respectively, but with a slight difference in the species composition (Tables I, II). For instance, another epigean species, *Diacyclops bicuspidatus* (Claus), and the stygobitic species *Greateriella unisetigera* (Graeter) were caught in the Lobau-C area (Tables I, II). The stygobitic species *Eucyclops graeteri* and *Austriocyclops vindobonae* and the epigean *Diacyclops bicuspidatus* appeared rarely in the wells of Lobau-B and Lobau-C areas respectively (Table II).

No cyclopoids were found despite repeated investigations in several wells of Lobau-B (B-A67, B-A79, B-A80, B-A96).

The diversity of the Deutsch-Wagram and the Regelsbrunn cyclopoid assemblages follows the pattern of Lobau-B and Lobau-C (Tables I, II). One has to note the occurrence of additional taxa as compared to the Lobau fauna, i.e. the hypogean *Acanthocyclops kieferi* and the epigean *E. speratus* (Lilljeborg) in Regelsbrunn and the hypogean *Paragraeteriella* sp. in Deutsch-Wagram (Tables I, II). From the investigated 10 wells in Regelsbrunn wetland only in 7 we found cyclopoids. The piezometres RGB-SW 7m, RGB-M 3 m and RGB-D 2 m remained barren.

Table I. – Groundwater dwelling Cyclopoida species at various sampling sites.

Sampling Station	Groundwater dwelling species	Groundwater dwelling species cumulated	Surface water species in groundwater habitats
Lobau CUN	*Acanthocyclops sensitivus* (Graeter & Chappuis)	*Acanthocyclops sensitivus* (Graeter & Chappuis)	*Acanthocyclops robustus* (Sars)
	Diacyclops disjunctus (Thallwitz)	*Diacyclops disjunctus* (Thallwitz)	*Diacyclops languidus* (Sars)
	Diacyclops felix Pospisil & Stoch	*Diacyclops felix* Pospisil & Stoch	*Mesocyclops leuckarti* (Claus)
			Microcyclops varicans (Sars)
			Cyclops sp.
			Eucyclops serrulatus (Fischer)
			Thermocyclops oithonoides (Sars)
			Megacyclops viridis (Jurine)
			Macrocyclops albidus (Jurine)
Lobau-C	*Acanthocyclops venustus* (Norman & Scott) *ssp.*	*Acanthocyclops venustus* (Norman & Scott) *ssp.*	*Diacyclops bicuspidatus* (Claus)
	Acanthocyclops sensitivus (Graeter & Chappuis)	*Graeteriella unisetigera* (Graeter)	*Diacyclops languidus* (Sars)
	Diacyclops felix Pospisil & Stoch		*Acanthocyclops robustus* (Sars
	Diacyclops disjunctus (Thallwitz)		*Macrocyclops albidus* (Jurine)
	Graeteriella unisetigera (Graeter)		*Thermocyclops oithonoides* (Sars)
			Metacyclops planus (Gurney)
			Cryptocyclops bicolor (Sars)
			Mesocyclops leuckarti (Claus)
			Cyclops sp.
			Megacyclops viridis (Jurine)
			Acanthocyclops vernalis (Fischer)
Lobau BLM	*Acanthocyclops gmeineri* Pospisil	*Acanthocyclops gmeineri* Pospisil	
	Acanthocyclops sensitivus (Graeter & Chappuis)	*Diacyclops cohabitatus* Monchenko	
	Acanthocyclops venustus (Norman & Scott) *ssp.*	*Diacyclops danielopoli* Pospisil & Stoch	
	Diacyclops felix Pospisil & Stoch		
	Diacyclops cohabitatus Monchenko		
	Diacyclops danielopoli Pospisil & Stoch		
Lobau-B	*Austriocyclops vindobonae* Kiefer	*Austriocyclops vindobonae* Kiefer	*Diacyclops bicuspidatus* (Claus)
	Eucyclops graeteri (Chappuis)	*Eucyclops graeteri* (Chappuis)	
	Acanthocyclops gmeineri Pospisil		
	Acanthocyclops sensitivus (Graeter & Chappuis)		
	Acanthocyclops venustus (Norman & Scott) *ssp.*		
	Diacyclops felix Pospisil & Stoch		
	Diacyclops cohabitatus Monchenko		
	Diacyclops danielopoli Pospisil & Stoch		
Regelsbrunn	*Diacyclops felix* Pospisil & Stoch	*Acanthocyclops kieferi* (Chappuis)	*Eucyclops speratus* (Lilljeborg)
	Diacyclops cohabitatus Monchenko		*Acanthocyclops robustus* (Sars)
	Diacyclops danielopoli Pospisil & Stoch		*Thermocyclops oithonoides* (Sars)
	Acanthocyclops gmeineri Pospisil		
	Acanthocyclops venustus (Norman & Scott) *ssp.*		
	Acanthocyclops kieferi (Chappuis)		
	Acanthocyclops sensitivus (Graeter & Chappuis)		
	Eucyclops graeteri (Chappuis)		
Deutsch-Wagram	*Diacyclops danielopoli* Pospisil & Stoch	*Paragraeteriella sp.*	
	Acanthocyclops gmeineri Pospisil		
	Diacyclops felix Pospisil & Stoch		
	Paragraeteriella sp.		

Species Richness and Complementarity

The values of the species richness of Cyclopoida depend largely on the spatial scales we consider (Tables I, II). In the Lobau, the CUN area has 9 epigean and 3 hypogean species, while BLM displays 6 species at a metric scale. Several wells, like CUN-B2, CUN-B3 and CUN-C2, display a rich cyclopoid fauna, both epigeans and hypogeans (6-7 taxa). The highest number of species in the BLM wells is 4 (i.e. in the wells BLM-A1, BLM-A3, BLM-A4, BLM-C1 and BLM-C2).

Considering the decametric and hectometric scales, i. e. the cyclopoid fauna occurring within the Lobau-B and Lobau-C areas, one notices an increase in the species richness especially with regard to stygobites (Table I, Fig. 5). There are 5 hypogean taxa in Lobau-C and 8 in Lobau-B (Fig. 5). We recorded 13 epigean species in the whole Lobau-C area, including the CUN species too (Tables I, II). In several isolated wells of the Lobau-B area (B-A81, B-A84, B-A89), we caught between 5 and 7 stygobitic taxa while in Lobau-C the well D3 displayed 9 species (Table II).

The total number of the groundwater dwelling cyclopoids in Regelsbrunn (Tables I, II) is 11 (8 hypogeans, 3 epigeans), while in the Deutsch-Wagram wells only 4 hypogean dwelling species were sampled (Tables I, II).

The species richness of the exclusively hypogean taxa living in groundwater of the sites CUN, Lobau-C and Lobau-B approximately doubles (3 – 5 – 8) with the increase of the metric scales (Table I, Fig. 5).

The contribution to the total hypogean species richness by taxa found at the comparative areas, Regelsbrunn and Deutsch-Wagram, is reduced. It represents an increase of only 10 % per site as compared to the Lobau area (Table I, Fig. 5).

Table II. – Presence (1) absence (0) data of 26 Cyclopoida taxa found in 71 wells, within the Lobau, Regelsbrunn and the Deutsch-Wagram areas. The wells are named with the code we have in our original data-basis.

WELLS	*A. gmeineri* Pospisil	*A. venustus* (Norman & Scott) *ssp.*	*A. sensitivus* (Graeter & Chappuis)	*D. cohabitatus* Monchenko	*D. felix* Pospisil & Stoch	*D. danielopoli* Pospisil & Stoch	*D. disjunctus* (Thallwitz)	*E. graeteri* (Chappuis)	*A. vindobonae* Kiefer	*Paragraeteriella sp.*	*A. kieferi* (Chappuis)	*G. unisetigera* (Graeter)	*D. languidus* (Sars)	*M. varicans* (Sars)	*M. leuckarti* (Claus)	*A. robustus* (Sars)	*A. vernalis* (Fischer)	*Cyclops. sp.*	*D. bicuspidatus* (Claus)	*M. albidus* (Jurine)	*E. serrulatus* (Fischer)	*E. speratus* (Lilljeborg)	*T. oithonoides* (Sars)	*M. viridis* (Jurine)	*M. planus* (Gurney)	*C. bicolor* (Sars)
Lobau C																										
D3	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	1
D4	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
D5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
D9	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
D10	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
D11	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D15	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0
D17	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T3	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
R2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
R3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
R4a-g	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
R6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
R8	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
R17	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
R18	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
R26	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUN-A1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUN-A3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
CUN-A4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
CUN-B1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
CUN-B2	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0
CUN-B3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0
CUN-B4	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
CUN-C1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
CUN-C2	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0
CUN-C3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
CUN-C4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-A1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-A2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-A3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
CUF-A4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
CUF-B1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-B3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C3	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C4	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobau B																										
B-A63	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A66	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
B-A81	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A84	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A85	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A87	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A89	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A90	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A3	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A4	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B2	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B3	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B4	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C2	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C3	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C4	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Regelsbrunn																										
RGB-SW 3m	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
RGB-SW 6-7m	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RGB-SW 8m	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RGB-M 5m	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
RGB-M 6-7m	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
RGB-D 4m	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RGB-D 6m	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deutsch-Wagram																										
MF-EM4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM61	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM56	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM57	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM58	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-GW-Br.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

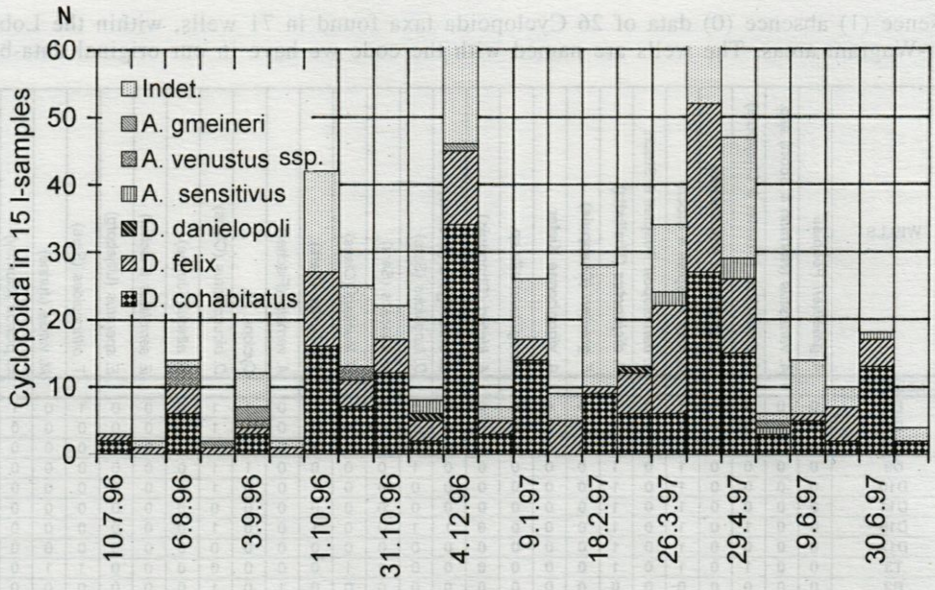

Fig. 4. – Quantitative distribution of cyclopoid species at the BLM site during 12 months; for each date, data cumulated from 3 sampling units.

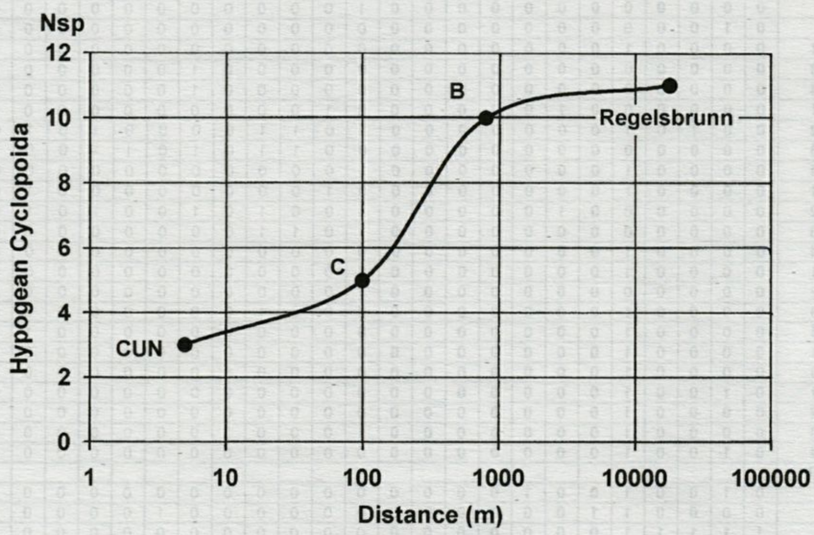

Fig. 5. – Cumulative number of stygobitic Cyclopoida species as a function of the linear distance between the sampling sites Lobau (Lobau-CUN, Lobau-C, Lobau-B) and Regelsbrunn.

Within the whole Lobau area we investigated, two cyclopoid genera display a high number of species (Table I), i.e. *Diacyclops* (6 species) and *Acanthocyclops* (5 taxa). Nine other genera (Table I) are represented by unique species and one genus (*Eucyclops*) by 2 species.

The frequency of the occurrence of various cyclopoid taxa for the whole Lobau area (Table II) is variable. One notes that the number of the exclusively hypogean taxa which were caught only once is 3 (*G. unisetigera, A. vindobonae, E. graeteri*), while there is only one species (*D. felix*) which occurs in 70 % of the wells containing cyclopoids (i.e. 43 cases from 58 wells). This latter species also appears as the most frequent species in all three areas, Lobau, Regelsbrunn and Deutsch-Wagram, i.e. it occurs in 52 wells from a total 71 containing cyclopoids (Table II). *Acanthocyclops kieferi* and *Paragreteriella* sp. are rare species, they occur only 2 and 5 times, respectively, in Regelsbrunn and Deutsch-Wagram. The other exclusively hypogean taxa display intermediary frequencies (they occur in 12-17 cases). Therefore, considering the exclusively hypogean dwelling cyclopids, there are more rare species than frequent ones.

When calculated with the non-parametric Jackknife method, the estimated diversity for the ob-

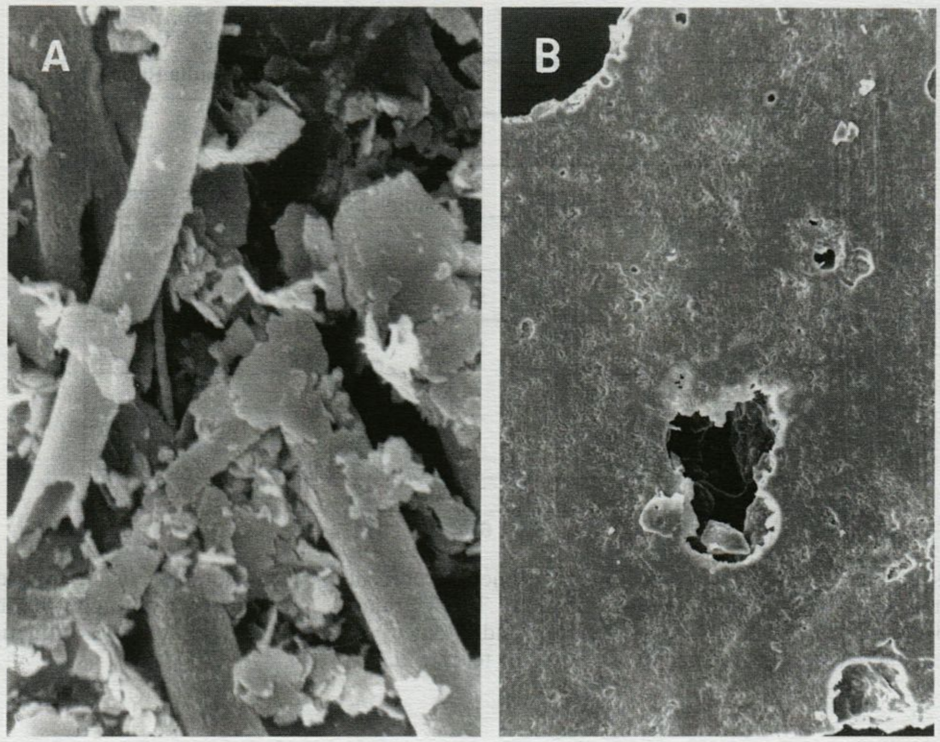

Fig. 6. – Sediment types used for movement and feeding experiments (Micrographs by T. Loser with a JEOL scanning electron microscope at the University of Vienna, Department of Marine Biology). A, fine Iron hydroxide sediment and filamentous rests of Iron bacteria (5000×); B, fragment of Tetramin (1000×).

served exclusively hypogean cyclopoid fauna of the Lobau gave a value of 12.9 (i.e. 13 species) with 95 % confidence limits between 9.6 (10 species) and 16.3 (16 species). The most frequent epigean species in our groundwater sites are *D. languidus* and *A. robustus,* they occurred in 13 wells (Table II). There are 9 epigean species which were rarely found, i.e. they occurred in 1-5 wells (Table II).

The complementarity, or species distinctness *sensu* Colwell & Coddington (1995), between the stygobitic fraction of the cyclopoid assemblages found in the groundwater of the Lobau and Regelsbrunn wetlands (Table I) has a C value of 0.36. The Jaccard Jd value is 0.38.

Movement and Feeding Behaviour of Selected Species

Figure 6 shows the type of substrate on which cyclopoids were successively exposed. One notices on Figure 6A that the fine sediment is composed by minute particles (approx. 1-3 µm length) of Iron hydroxide and filamentous Iron bacteria (3-4 µm diameter). The total content in organic Carbon and respectively Nitrogen of this sediment is low (TOC, 2.7 mg/g and TON 3.45 mg/g). Figure 6B shows the structure of a piece of Tetramin. This has a compact solid structure with slightly rugous surfaces. Tetramin is a standard fish food containing a high amount of proteins extracted from fish, mussels and/or crustaceans. Hence it has an important energetic value (TOC, 43.5 mg/g and TON 47.6 mg/g) and is able to act as a chemical attractor for the crustaceans used in these experiments.

Diacyclops disjunctus, D. felix and D. danielopoli

The individuals used for the experiments were all non-ovigerous female adults. Their body length varied between 0.5 mm and 0.7 mm.

Figure 7 shows that when placed in micro-aquaria without substrate (the control series), all individuals spend very little time at rest on the bottom, on the average only five percentage of the total exposure time (14 minutes).

In aquaria with Iron hydroxide substrate one sees that *D. disjunctus,* after discovering the substrate, spends long periods of time on it, on the average 26.2 % ± 11.34 of the exposure time. The number of visits of the substrate followed by longer stops is on the average 3.6 ± 1.4.

D. felix and *D. danielopoli* spend less time on the fine substrate, the former 11.1 % ± 4.21, the latter 3.54 % ± 1.2. On the average, *D. felix* visited the substrate 7.45 ± 1.1 times, which is more than the number of visits of *D. disjunctus* and *D. danielopoli* (4.0 ± 1.0 times).

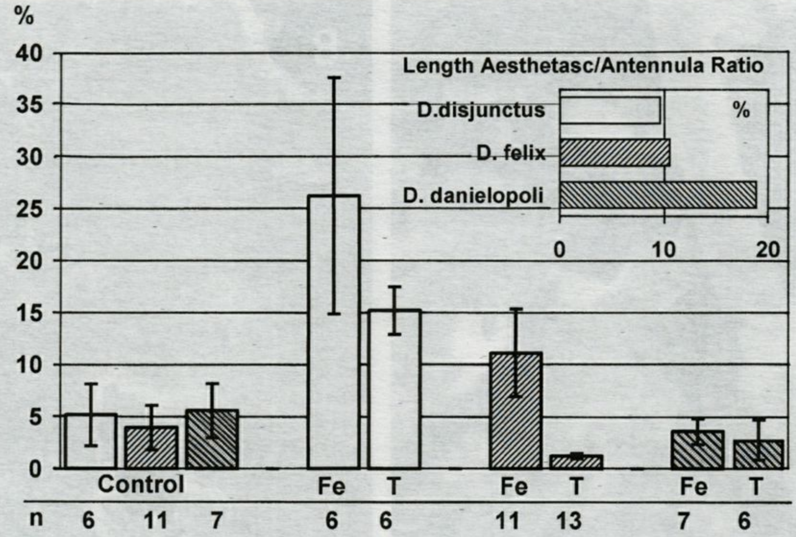

Fig. 7 – Results of the movement and feeding experiments; percentage (of a total exposure time of 840 seconds) spent on substrates (Fe – fine Iron hydroxide sediment, T – Tetramin) as compared to the control (no substrate); n – number of specimens recorded for each situation and species; bar and vertical line – arithmetic mean from n individual data ± standard error (further explanation in text).

When exposed to Tetramin again, *D. disjunctus* (Fig. 6) spends significantly more time on the substrate (15.2 % ± 2.3) as compared to *D. felix* (1.2 % ± 0.24) and *D. danielopoli* (2.76 ± 1.9). The number of stops on the Tetramin substrate is similar for *D. disjunctus* and *D. felix* (6.8 ± 1.2), while *D. danielopoli* visits this substrate only rarely, i. e. 2.8 ± 0.65 times on the average.

None of these species were observed to prey on living animals.

Acanthocyclops gmeineri

This species is much larger (1.2-1.3 mm body length) as compared to the previous *Diacyclops*. The observed specimen showed a highly significant (G-test for 2 × 2 contingency table, $p = 3.3 \times 10^{-9}$) preference for the Iron hydroxide substrate as compared to the Tetramin, i.e. 97.5 % from the total cumulated time spent on both substrates were used on Iron hydroxide substrate. Beside this, we observed one individual preying on a small *Diacyclops*. The large *A. gmeineri* reacted to the movement of the prey swimming by at a close range. The engulfing of the *Diacyclops* happened instantaneously.

DISCUSSION

Hotspots of Cyclopoida Diversity

The diversity of the exclusively dwelling hypogean species of different animal groups from the Danube wetlands is high (Danielopol & Pospisil submitted) as compared to other data sets at equivalent scales (Dole-Olivier *et al.* 1994, Rouch & Danielopol 1997, Culver & Sket 2000). This peculiarity applies also to the Cyclopoida as one can see from the following comparative data:

Within the Lobau area, the stygobitic cyclopoid taxa form the most diverse group of Crustacea; there are twice as many hypogean Cyclopoida species than stygobitic Harpacticoida (Danielopol & Pospisil submitted).

Considering the comparative species richness of hypogean Cyclopoida in Europe, we note that Rouch & Lescher-Moutoué (1992) found seven stygobitic cyclopoid species within an area of 70 m^2 in the Lachein, in the French Pyreneans, while we found six species within a 27 m^2 area (BLM) and seven species in one single well (B-A89). For the karstic system Postojna-Planina Caves (approximately 25 km passages explored) in Slovenia, Brancelj (1987) recorded six troglobitic species. Rouch & Danielopol (1987) documented that only 1–3 stygobitic cyclopoid species were registered at other groundwater sites.

The high number of *Diacyclops* taxa from Lobau (six species) can be compared with the data of Boxshall & Evstigneeva (1994) from Lake Baikal. They found 12 species in this lake which is about 600 km long. Stoch (in press) found between two and seven *Diacyclops* species in the subterranean water habitats of northern Italy and Slovenia, within areas of approximately 100 km^2. It is noteworthy that in several wells we found up to three stygobitic *Diacyclops* species (wells BLM-A3, BLM-C4, B-A84 and A89) or even four species of both hypogean and epigean taxa (the well D3). A similar species richness (four stygobitic *Speocyclops* taxa) was mentioned for the Baget karstic system by Lescher-Moutoué (1973).

Origin of the Diversity of Hypogean Dwelling Cyclopoida

The surface dwelling cyclopoids encountered by us in the subsurface waters at both the Eberschüttwasser (the Lobau–C area) and the Regelsbrunn sites point out to the ability of these crustaceans to repeatedly colonise the alluvial sediments closely located to open water habitats. This supports the ecotonal model of Gibert *et al.* (1990).

The stygobitic genus *Austriocyclops* Kiefer, represented by a unique species, *A. vindobonae* in Vienna and Lower Austria, could represent an old phylogenetic lineage, relict of a once widely distributed group. Pospisil & Stoch (1997) noted that *A. vindobonae* displays closer morphological affinities with *Ochridacyclops brevicaudatus* Shen & Tai, from surface lotic habitats in Southern China.

Considering the present day geographical distribution of stygobitic species like *Acanthocyclops sensitivus, Eucyclops graeteri* or *Graeteriella unisetigera* in Europe, they could have migrated to the Lobau area along the subsurface alluvial sediments bordering the Danube Valley. These species are widely distributed in Western Europe within the Rhine and the Rhône drainage systems (Dole-Olivier *et al.* 1994, Pospisil 1994a). Due to repeated connections of the river systems of Rhine, Rhône and Danube during the Upper Pliocene and the Pleistocene, they may have migrated downstream along alluvial aquifers, reaching the Danube flood plain here investigated. Thienemann (1950) proposed a similar scenario when discussing the geographical distribution of the stygobitic amphipod *Niphargopsis casparyi* (Pratz).

Other species like *Acanthocyclops gmeineri, Diacyclops felix* and *D. danielopoli* could have originated locally in this area.

The high number of exclusively hypogean dwelling cyclopoid species reported here could also have its origin in the inter-specific ecological differences and in their diverse micro-geographical distribution.

In the field *D. disjunctus* occurs in habitats closely located to surface waters, whereas in the laboratory this cyclopoid spent the highest amount of time on the fine sediment representing an apparently palatable food item. It is interesting that *D. danielopoli,* which has very well developed antennary aesthetascs as compared to *D. disjunctus* and *D. felix* (Fig. 7), spent the least time on both substrates and it did not discover or elect the Tetramin substrate (supposed to be more attractive) faster than the fine Iron hydroxide sediment. The difference in the election of the substrate by *D. danielopoli* as compared to *D. disjunctus* is much similar with the differences observed for the search behaviour of the asellids (Isopoda) *Proasellus slavus,* a stygobitic species, and *Asellus aquaticus,* an epigean crustacean. *P. slavus* moved frequently and spent little time on the substrate (a dead leaf offered as food), while *A. aquaticus,* being very voracious, spent long periods of time on the leaf on which he fed (Moesslacher 1994, Danielopol *et al.* 1994).

D. felix, equipped with moderately developed aesthetascs (Fig. 7) and an intermediary behaviour between those of the two other *Diacyclops* species, displayed in our research area a very wide spatial distribution.

One should also observe the difference between the feeding preferences of *A. gmeineri* electing both fine sediment and living prey, and the *Diacyclops* species which were exclusively detritivores.

The subtle ecological differences displayed by the three *Diacyclops* species observed under laboratory conditions and their field distribution call to attention the data presented by de Bovée *et al.* (1995). These authors showed that three hypogean *Metacrangonyx* species from the High Atlas, in Morocco, display spatial ecological and micro-geographical distributions which could be related to different habitat preferences, i.e. different granulometric characteristics of the alluvial sediments.

One has to note that the data discussed here are partly in line with the "Collection storage model" of Culver *et al.* (1995), further refined by Danielopol *et al.* (1999b), and partly with the "Adaptive zone model" of Stoch (1995). This latter model postulates that the co-occurrence of closely related species at one groundwater site is due to their small non-overlapping niches. This is apparently the case with our *Diacyclops* species-group.

The «Potential Diversity» of Hypogean Dwelling Cyclopoida in the Lobau

The "potential diversity" of the exclusively hypogean cyclopoids to be found within our Danube wetland sector can be discussed using several types of arguments i.e. ecological and biogeographical ones, inferences from statistical data and evolutionary considerations of the potential speciation of selected cyclopoid groups.

Given the diversity of backwater systems in the wetlands of the Danube east of Vienna, it is to be foreseen that at a regional scale the epigean species richness of Cyclopoida is high. Hence one has to expect the occurrence of other surface dwelling species in the peripheral alluvial groundwater systems connected hydrologicaly to the Danube backwaters.

Considering the exclusively hypogean cyclopoid species at a local and/or regional scale, within the Lobau sector of the alluvial Danube aquifer we expect to find additional species, especially taxa belonging to the genera *Acanthocyclops* and *Diacyclops*. These groups display minute morphological traits (i. e. useful for species identification) as shown by various publications (Pospisil 1994a, Reid 1997/1998, Stoch in press) or diverse behavioural reactions, as documented here. We already know that other *Diacyclops* and *Acanthocyclops* taxa exist around our Danube wetlands area, e.g. *Diacyclops languidoides goticus* (Kiefer), at Bad Vöslau, south of Vienna (Stoch & Pospisil 2000b) or *Acanthocyclops rhenanus* Kiefer, mentioned in Lobau-A (det. G. Pfaffenwimmer, in Danielopol 1983) and rediscovered by one of us in the province of Burgenland (Pospisil in prep) as well as the two species, *A. kieferi* and *Paragreteriella* sp., found in Regelsbrunn and Deutsch-Wagram. However, for the Lobau area investigated a dramatic increase in the diversity value for the exclusively groundwater dwelling cyclopoid species is not expected for the near future. The statistical estimation of the potential species richness lays not far away from the observed species richness, the degree of complementarity between the stygobitic assemblages of Lobau and Regelsbrunn is low (i.e. the two lists of taxa are rather similar) and the accumulation species curve presented for the stygobitic assemblages approaches an asymptotic trajectory.

CONCLUSION

The present contribution on the diversity on groundwater dwelling Cyclopoida in the Danube wetlands constitutes an excellent reference database for similar ecological studies in the future. We hope that this information will enable a better evaluation of the diversity state of other cyclopoid assemblages occurring in groundwater areas under environmental conditions which are different from those we studied, e.g. at sites variously impacted by anthropogenic activities.

Future studies on this topic have to consider that in addition to environmental constraints of a groundwater aquifer, which strongly influence the species richness of a given animal group, the organismic constraints displayed by the animals during the various colonisation events may also play a considerable role in the evolutionary process. Therefore in the future one needs thorough investigations of the ways animals perceive the subterranean environment and on their ability to develop adaptive responses to the various groundwater conditions. It appears now that from the multitude of colonists and colonisation events only few succeeded in the evolution of stable and durable stygobiontic solutions.

Finally, the high diversity of groundwater dwelling Cyclopoida we documented in the Danube wetlands, especially in the Lobau, supports Strayer's idea (1994: p. 289) that "groundwater invertebrates are not distributed randomly around the world, but are concentrated in regions that support very diverse communities. These areas are the underground equivalents of the tropical rain forests."

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