EUCRENON-HYPOCRENON ECOTONE AND SPRING TYPOLOGY IN THE ALPS OF BERCHTESGADEN

(Upper Bavaria, Germany)

A STUDY OF MICROCRUSTACEA (CRUSTACEA: *COPEPODA, OSTRACODA*) AND WATER MITES (ACARI: *HALACARIDAE, HYDRACHNELLAE*)

by

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ABSTRACT

Based on the results of an investigation of 19 springs in the Berchtesgaden National Park (Upper Bavarian Alps), invertebrate species dwelling in springs and springbrooks are classified with regard to their habitat preference. This study focuses on non-insect aquatic arthropods (water mites, ostracod and copepod crustaceans). The ecological valence of spring-dwelling species is characterized by calculating their relative abundance in the eucrenal and hypocrenal. Spring habitats originating from differently shaped outflow horizons are compared with regard to their suitability for investigating the eucrenon/hypocrenon ecotone. The characteristics of crustacean and mite assemblages of rheocrenes and (rheo)helocrenes, and of temporary and permanent springs are presented. The ecological terminology for spring-dwelling organisms is revised and the different share of crenobionts and crenophiles in several taxonomic groups is discussed.

1. Introduction

Springs have long been considered island-like environments with stable communities (Thienemann, 1925; Nielsen, 1950). This paradigm has been replaced by a more complex picture during the last years. The present scenario is somewhat embarassing due to its often contradictary outcomes: the diversity of spring faunas was found to be high (Resh, 1983; Cicolani *et al.,* 1996) or low (Minckley, 1963; Minshall,1968; Ward & Dufford,1979), the sensitivity of the communities to changes in environmental conditions remarkable (Erman & Erman, 1995) or negligible (Minckley, 1968; Thorup, 1970), the long-term changes of faunal composition substantial (Goldschmidt, 1994) or of minor importance (Rasmussen, 1979).

A further handicap for our understanding of spring ecosystems is the persistent confusion regarding the ecological valence of spring-dwelling organisms. The terms "crenobiont", "crenophilous", and "crenoxene" should characterize corresponding specific types of habitat preference, but are mostly used in a rather arbitrary manner (Williams & Williams, 1987). In view of these problems, selected study sites and their communities should be documented as complex individuals, in areas of different climatic and geohistoric setting. As a second step, the individual sites should be compared, elaborating common and differential features, as well as general characteristics of the eucrenal, confronted to the hypocrenal and epirhithral.

In 1993, the Centro di Ecologia Alpina (Viote del Monte Bondone, Trento, Italy) initiated a research of this kind in the Italian and Bavarian Alps. After a first phase, dealing with experimentation of methodology and search for suitable habitats, a detailed faunistic study was undertaken on 11 sites in the Italian region of Trentino-Alto Adige, and 19 sites in the National Park of Berchtesgaden (Upper Bavaria, Germany). The complete results of the study, including detailed descriptions of sampling sites, methods, faunistic and zoogeographic results, are published by Crema *et al.* (1996). The aim of the present paper is to discuss for the 19 Bavarian springs the following aspects:

- criteria for the identification of crenobiont, crenophile and crenoxene species;

- invertebrate assemblages suitable for the discrimination of different spring typologies, and of springs and springbrooks;
- localization of the crenon/epirhithron ecotone in springs of different typology and hydrological regime.

Primarily, this study applies to the local spring typology, but the methodology should be applicable for different geographical areas as well.

2. **Material and Methods**

Each main study locality is labelled by an arabic number (1-19, see Fig. 1), while the single collecting sites are identified by additional letters (lr, lp, le). The physico-chemical water analyses carried out by the Wasserwirtschaftsamt Traunstein followed the DIN-Norm 38410.

2.1. *Sampling techniques*

Due to the mosaique of microhabitats within most spring sites, it is difficult to produce repeatable quantitative data on the composition of their invertebrate fauna. In view of the restricted dimensions of most springs, quantitative sampling in all microhabitats would not be possible without causing heavy damages (Sweeney & Vannote, 1986; Gooch & Glazier, 1991). For this research, we have adopted a rather "mild" technique, collecting a cumulative benthos sample from all types of substrates with a hand net of 100 μm mesh size, removing stones, turning up gravels and sand, squeezing out mosses, and brushing the periphyton. Sampling times in different microhabitats were proportional to the estimated percentage cover of the substratum. Thus, our samples are semiquantitative, allowing for a qualitative analysis and a documentation of the relative abundance of the most important taxa. The material was sieved into two fractions, the large fraction (> 1000 pm) occasionally sorted directly on the spot from living material, the remaining invertebrate fauna in the laboratory. The field work in Bavaria was done in October 1993 by R. Gerecke, and in June 1994 by R. Gerecke and T. Goldschmidt. For more detailed information on techniques see Crema *et al.* (1996).

2.2. *Identification of the taxa*

The investigation concentrates on representatives of the meiofauna: crustaceans were determined by C. Meisch (ostracods) and F. Stoch (copepods), and water mites by R. Gerecke. The study of several other invertebrate groups is still in progress. The identification of insect larvae was difficult in many cases, due to the inadequate knowledge of preimaginal taxonomy, mainly in view of the presence of early instars in large numbers (Crema *et al.*, 1996). For this reason, we will refer to these groups only occasionally. A more accurate study of the distribution and biology of insects in springs of the Berchtesgaden Park is now in progress.

2.3. *Delimitation of eucrenal and hypocrenal*

The lack of seasonal temperature data did not allow to base the distinction between the eucrenal and hypocrenal on the criterion of different temperature amplitudes (Illies & Botosaneanu,1963). Therefore, we are dependent on vegetational and morphological properties: in the eucrenal, a net of branched rivulets and pools is formed (Fig. 3A), with rich moss vegetation and abundant detritus; the hypocrenal springbrook is characterized by a well defined bed without ramifications, little or no submerged vegetation, and substrata containing more stones and gravel. Within our collecting sites, a clearcut morphological difference between eu- and hypocrenal was found only in springs originating from groundwater outflow over horizontal impermeable layers. Such springs are generally associated in numerous spring mouths at about the same elevation along a mountain slope ("spring line", Fig. 3A).

On the contrary, springs 13 and 15 flow from irregularly inclined horizons and are fed by numerous groundwater sources along a vertical line (Fig. 4A). As a consequence, the delimitation of an eucrenal/ hypocrenal limit is impossible. All along the upper springbrook course, groundwater inflow blurs the ecological situation, creating an extended mosaique of eucrenal- and hypocrenal conditions. Spring habitats of this type represent rather complex ecological situations and are not suitable for basic studies on the eucrenal-hypocrenal ecotone. For these reasons we decided to limit the statistical analysis to springs originating from typical spring lines. Furthermore, springs with temporary outflow or linear springs with unclear position of the spring source (Fig. 5A) were excluded as well. For the statistical analysis of crenobiosis, only data from spring sites 1, 5, 7, 16, 17, 18, and 19 were selected.

For each species found in these sites, the frequencies in eucrenal and hypocrenal were calculated, and an X^2 test was used to show the habitat preference of each species within the crenal: probability values of 1% or 0.1% are assumed to indicate a strong preference for the eucrenal or the hypocrenal.

2.4. *Multivariate statistical analysis*

The meiofauna assemblages in all spring mouths of our study sites (including springs originating from oblique groundwater layers and temporary springs) were compared in order to evaluate their significance for spring typology. For this reason, correspondence and principal component analysis were carried out basing on the pooled data of copepoda, ostracoda, and acari, as well as for each of these groups separately. The numbers of individuals were assigned to frequency classes using the method of Verneaux (1973) for correspondence analysis.

A further analysis was conducted using the coefficient of Bray-Curtis (Field *et al.*, 1982) on the basis of presence/absence data. The resulting matrix of similarities between every pair of samples was used to group the samples by hierarchical agglomerative clustering with group-average-linking, and to map the sample interrelationships in an ordination by non metric multidimensional scaling (Clarke,1993). This analysis produced similar, but less clearcut results.

3. **Study area and collecting sites**

The Berchtesgaden National Park is situated in the Triassic mountain range that builds up the northern margin of the Eastern Alps between Vienna and the upper Rhine valley. The basic layer of Permian clay evaporites (with considerable salt deposits) surfaces only occasionally at low elevations. The mountain chains (with the maximum elevation at the Watzmann peak, 2713 m, see Fig. 2) are built up by sedimentary and reef limestones, mainly of Triassic, locally also of Jurassic and Cretaceous origin (Lebling *et al.*, 1935). The present-day geomorphology bears the stamp of the Quaternary glaciations. In that period, valleys were deepened (*e.g.* when the Königssee glacier reached a thickness of more than 1000 m) and prominent mountain peaks were formed. During the postglacial warming, the geomorphology was changed – deep gorges and dumps of boulder and gravel were created at the feet of eroding mountain slopes (Langenscheidt, 1994).

The altimetric distribution of springs in the Berchtesgaden National Park is very irregular (Tab. 1). Due to the karstic phenomena in the nearly exclusively calcareous bedrock, no permanent springs do exist at elevations above 2000 m. At middle elevations, about 1500 m, groundwater outflows are found mainly in areas with impermeable deposits of moraine and slightly siliceous Anisic mass limestone, locally also above Quaternary lake clam. At lower elevations, the highest density of springs is found in the Permian Haselgebirge strata. In most cases, surface water streams flow along dislocations and run dry as soon as they reach permeable bedrock substrata. Only below 1000 m large permanent streams are formed; here, moraine embankments, and Triassic and Permian clay layers are of main importance as ground water barrages.

The highest permanent springs considered (station 12/13, 1900 m) are located near the upper limit of forest vegetation, in an area of transition between alpine meadows with outcropping bedrock and scattered pines. The dominant tree species in the subalpine forests between 1800 and 1400 m are spruce, larch and pines, in mountain forests between 1400 and 800 m beech, fir and spruce, and in the forests at elevations below 800 m beech with maple, oak, yew, elm, and lime trees.

Fig. 1 illustrates the location of the investigated sites; a detailed description of the habitats is given by Crema *et al.* (1996). No limnocrenes were found. Five spring sources are of the helocrenic type (3c, 8c, 16c, 17rh, 18c). They form detritus-rich habitats with an extended net of stagnant water puddles and slowly flowing rills, mostly in cleared areas ("rheo-

Tab. 1: The distribution of springs in 9 geological units in the Berchtesgaden Alps (from data stored in the Geographical Information System, Nationalparkdirektion Berchtesgaden). This table pools geological units with the most extended relative surface (> 5% of the total Park surface) and units with the highest density of springs (>0.1 springs/ha).

Geological unit	rel. surface [% total Park surface]	absolute number of springs	springs/ha	mean elevation [m NN]
Dachstein limestone	50.33	24	0.002	1651
declivity detritus	8.74	18	0.01	1600
moraine	5.00	192	0.18	1530
marl (Fleckenmergel)	1.31	13	0.05	1530
anisic mass limestone	0.02	15	4.23	1480
Ramsau dolomite	4.71	74	0.08	1450
Werfener strata	0.24	27	0.54	1430
Gutensteiner strata	0.25	18	0.34	1280
Haselgebirge	0.06	35	2.74	1280

Tab. 2: Physical and chemical parameters in selected springs in the Berchtesgaden National Park. Date of measurements: X-10-1995. NO_2 values were < 0.005 mg/l, Cl < 5 mg/l.

Station	near 1 (Koppenwand)	15c	Klauswand (conduit)	18
time	10:10	11:30	8:20	17:00
discharge [l/s]	1	3	10	0.5
temperature [°C]	6.1	4.9	4.0	7.0
pH	7.7	7.9	8.0	7.7
conductivity [µS/cm]	310	250	150	240
0_2 [% saturation]	95	92	93	82
phosphate [mg $P0_4$ /l]	0.027	0.031	0.069	0.07
ammonium [mg NH_4/l]	0.05	0.05	0.04	0.04
nitrate [mg NO_3/l]	4.2	3.1	1.7	0.29
calcium [mg Ca/l]	44.9	51.0	25.0	55.7
kalium [mg K/l]	0.2	0.2	0.1	0.3

helocrenes" *sensu* Schwoerbel,1959). The banks are overgrown with pads of a diversified hygrophilous macrophyte vegetation while submerged vegetation is dominated by filamentous algae. In the riparian ecotone, characteristic hygropetric microhabitats are formed by semiaquatic mosses. Station 8 is a special case as the water emerges near the border of lake Königssee; therefore, no spring brook is formed, and the spring can be submerged by lake waters during high water periods. Station 10 is a temporary spring of intermediate helocrene/rheocrene typology. 13 spring sources are rheocrenes (lr, lp, 5c, 6c, 7c, 9c, llc, 12c, 13c, 14c, 15c, 17c, 19c). Among them, stations 6c, 9c, and llc are typical "conduit flow" springs with strong outflow, but subject to summer (and probably also winter) drought. The structure of the remaining springs is more diversified, with patterns of brooklets, small pools, and cascades. They are often found in wooded, but also in cleared areas. Finally, two spring complexes (2, 4) can be considered "linear springs" in the sense of Zollhöfer (1996). Water flows out from the bottom of an eroded channel, but the exact position of the spring mouth cannot be defined as it changes in a seasonal cycle, being at higher elevation during rainy periods, and at lower elevation during summer drought (and winter frost?). In spring 4, the high faunal diversity at site c probably indicates the location of continuous year-round discharge (Fig. 5).

In 11 stations, a first order brook originates from the spring and hypocrenal samples were taken (sites le, 5e, 6e, 7e, 9e, 13e, 15e, 16e, 17e, 18e, 19e). In the "linear springs" of station 2 and 4, due to the irregular hydraulic regime no hypocrenal could be defined. The mean (in brackets: minimum-maximum) temperature measured near the spring source was 6.7 (5.3-8.5)°C at elevations from 600-1000 m, 5.2 (2.9-8.5)°C at 1000-1500 m, and 3.8 (1.9-7.0)°C at 1500-1900 m; the respective measurements in the hypocrenal were: 8.4 (5.7-10.0)°C at 600-1000 m, 7.6 (5.2-10.9)°C at 1000-1500 m, and 9.2 (6.0-12.0)° C at 1500-1900 m. All measurements were taken in summer (June-September). On several occasions, the relatively low spring water temperature at low elevations indicates that the groundwater discharge is influenced by a fast sinking subterranean flow of high altitude snow melt water. A spring water temperature considerably lower than the mean annual temperature near the spring source may indicate strong seasonal changes in discharge including temporary flow (Brehm,1973).

Tab. 2 shows physico-chemical data from several spring habitats in the study area. Calcium concentrations are always high, their inverse proportion to discharge is explainable by the different solution conditions in seeping (low discharge) and conduit (high discharge) groundwater flows (Wilhelm, 1956). Inorganic nutrient levels are mostly low or negligible. As all catchment areas are included in the Natural Park, anthropogenic disturbance of groundwater quality is rare. Organic input from pasturing cattle or herds of game can be only of very local importance, mainly in helocrenes. A reason for elevated nitrogen contents (*e.g.* at station 15) is probably decomposition of organic matter in the immediate surroundings of the spring source. Presently such processes could be enhanced by the destruction of *Picea abies* trees by scolytid beetles. Near Berchtesgaden, extended forest areas have been cleared by the activity of these beetles during the last years. The deeply soaked soils of spring areas are poorly suitable for rooting, and thus often form "cristallization points" of deforestation. A long term study of these aspects is now in course.

Tab. 3: Statistical analysis (X^2) of the habitat preference within the crenal of acari and microcrustacean species represented by at least 5 specimens in stations originating from horizontal groundwater outflow. The species in bold display a particular eucrenal preference in this analysis. The following additional species were found in these springs as single specimens: Acari - *Atractides franciscanus* Bader & Gerecke, *Feltria zschokkei* Koenike, *Lebertia bracteata* K. Viets, *Lebertia lineata* Thor, *Sperchon squamosus* Kramer, *Sperchonopsis verrucosa* (Protz), *Torrenticola elliptica* Maglio; Ostracoda - *Potamocypris fulva* (Müller), *Potamocypris pallida* (Alm), *Psychrodromus olivaceus* (Brady); Copepoda - *Attheyella crassa* (Sars). + = positive correlation with eucrenal.

	total indiv. numb.	frequ.	X^2	probability	
ACARI					
Atractides loricatus Piersig	8	3	7.088	0.01	-
Atractides panniculatus (K.Viets)	33	6	2.634	n.s.	+
Atractides vaginalis (Koenike)	43	4	18.04	0.001	+
Atractides walteri (K.Viets)	38	4	7.38	0.001	+
Bandakia concreta Thor	5	1	4.2	n.s.	+
Feltria minuta Koenike	72	4	43.83	0.001	+
Feltria setigera Koenike	7	4	4.9	n.s.	+
Hydrovolzia placophora (Monti)	76	4	46.62	0.001	+
Hygrobates norvegicus (Thor)	71	5	11.78	0.001	+
Lebertia cuneifera Walter	23	4	1.096	n.s.+	+
Lebertia lativentris K. Viets	17	3	11.9	0.001	+
Lebertia tuberosa Thor	23	4	7.516	0.01	+
Ljania bipapillata Thor	6	2	0.152	n.s.	+
Panisus michaeli Koenike	8	3	5.6	n.s.	+
Partnunia steinmanni Walter	85	6	40.85	0.001	+
Protzia eximia (Protz)	85	3	46.68	0.001	+
Pseudofeltria scourfieldi Soar	15	1	10.5	0.01	+
Soldanellonyx chappuisi Walter	128	6	24.76	0.001	+
Sperchon mutilus Koenike	26	6	12.04	0.001	+
Sperchon thienemanni Koenike	29	4	2.211	n.s.	+
Sperchon violaceus Walter	7	1	4.9	n.s.	+
Tartarothyas romanica Husiatinschi	5	2	3.5	n.s.	+
Thyas palustris Koenike	20	3	14	0.001	+
OSTRACODA					
Candona candida (O.F.Müller)	24	3	14.3	0.001	-
Candona neglecta Sars	348	4	208.9	0.001	-
Cavernocypris subterranea (Wolf)	20	2	3.703	0.01	+
Cryptocandona vavrai Kaufmann	9	1	12.86	0.001	-
Cyclocypris helocrenica Fuhrm. & Pietr.	53	5	1.671	0.01	-
Cypria ophtalmica (Jurine)	31	2	21.7	0.001	+
Eucypris pigra (Fischer)	261	6	22.28	0.001	-
Potamocypris fallax Fox	13	2	10.13	0.05	-
Potamocypris zschokkei (Kaufmann)	7	2	10	0.05	-
Pseudocandona albicans (Brady)	88	2	16.52	0.001	-
Psychrodromus fontinalis (Wolf)	912	5	47.59	0.001	+
COPEPODA					
Acanthocyclops vernalis (Fischer)	53	3	37.1	0.001	+
Attheyella wierzejskii (Mrázek)	462	5	44.08	0.001	+
Bryocamptus cuspidatus (Schmeil)	22	3	9.351	0.01	+
Bryocamptus echinatus s.l. (Mrázek)	48	5	0.05	n.s.	+
Bryocamptus tatrensis Minkiewicz	23	4	2.162	n.s.	+
Paracyclops fimbriatus (Fischer)	198	4	141.7	0.001	+

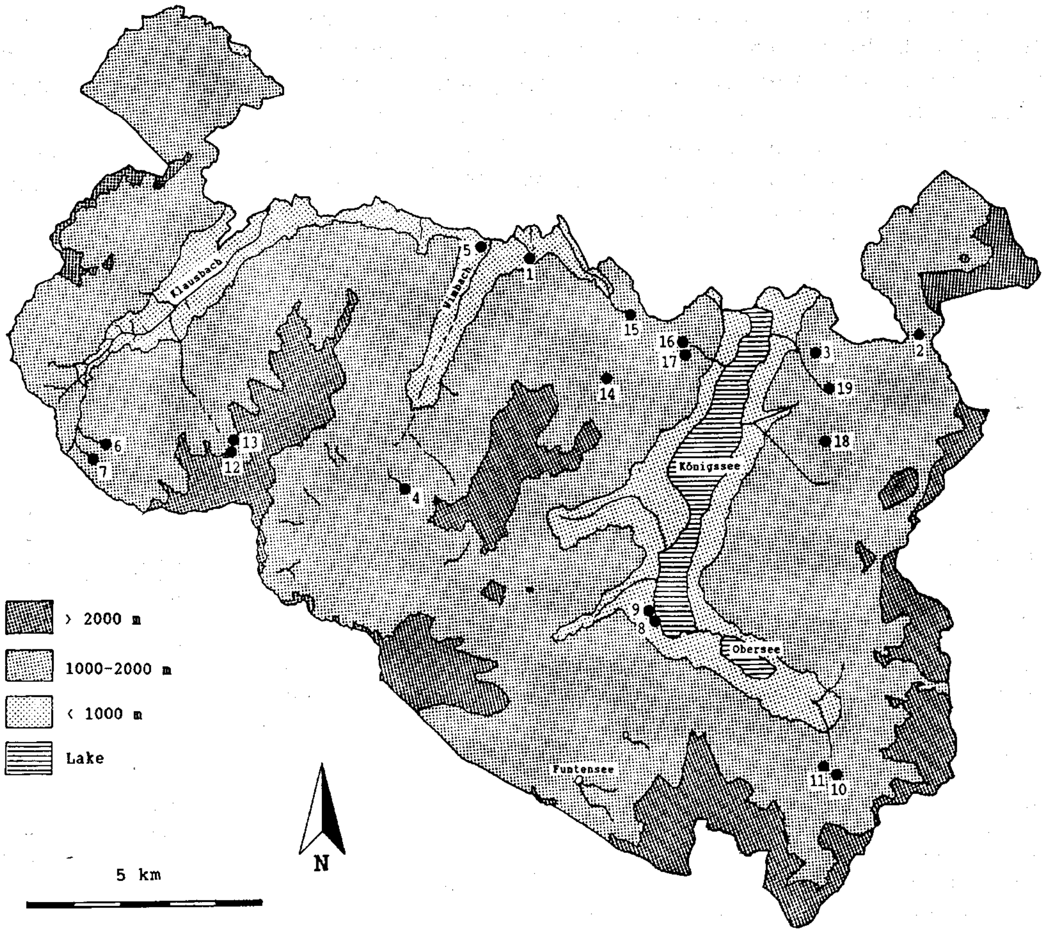

Fig. 1: Geographical map of the Berchtesgaden National Park, indicating the location of the sampling sites (from Crema *et al.*, 1996, modified).

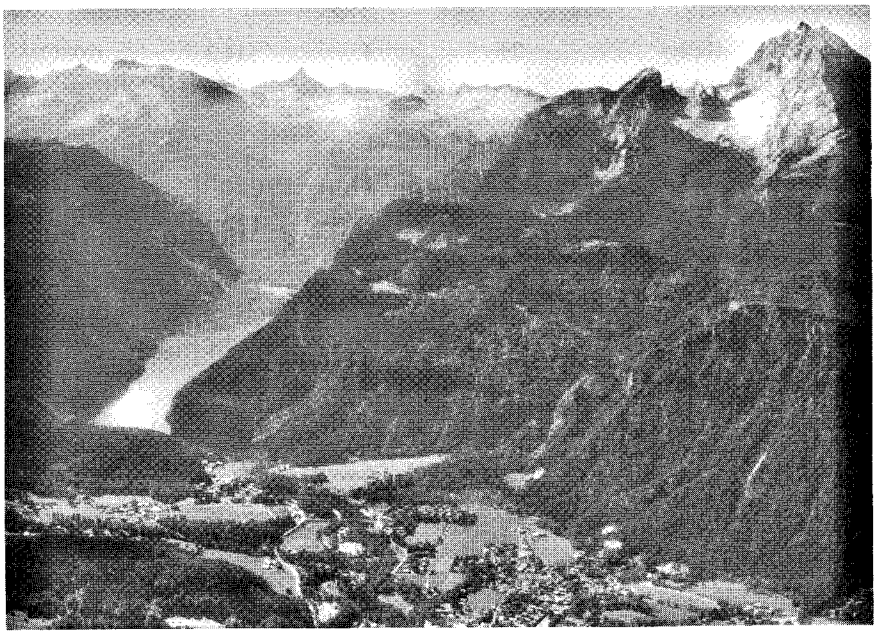

Fig. 2: Aerial view of the Königsee area in N-S direction (archives of the Nationalparkverwaltung Berchtesgaden). At the right, Mt. Watzmann, in the background the "Steinernes Meer". High (> 1800 m) and low elevations (800-1100 m) are mostly impermeable karstic layers, while on the terrace at middle elevation (Herrenroint and Kühroint, NE slopes of Mt. Watzmann) numerous permanently-flowing springs are found (*e.g.* the stations 16 and 17 of this investigation).

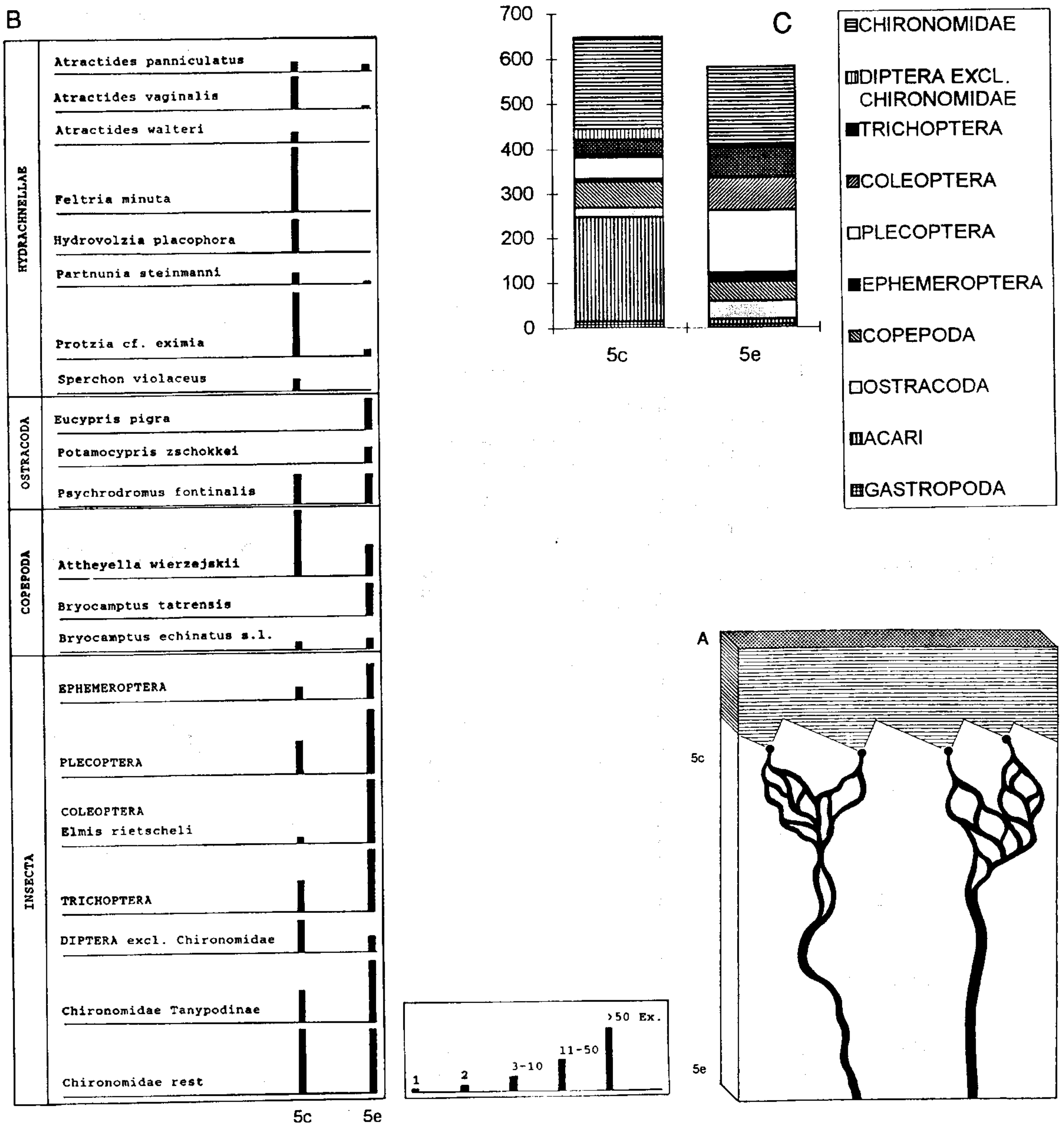

Fig. 3: A: Sketch of the morphology of a spring originating from horizontal impermeable layers (groundwater-bearing sediments slashed, groundwater banking layers white; black circles and lines: permanent springs and channels). B: distribution of the frequent species (> 5 specimens) of crustacea, acari, and of the main insect groups in the eucrenal and hypocrenal of a spring of this type (station 5 - eu- and hypocrenal are at a distance of ca. 100 m). C: General composition of the fauna at sites 5c and 5e. A clear eucrenon/ hypocrenon ecotone is marked by the presence/absence of crenobionts and rhithrobionts, and by the relative abundance of major taxonomic groups (C from Crema *et al.*, 1996, modified).

4. **Results**

4.1. *Differences between eucrenal and hypocrenal*

The ecological valence of less motile spring dwelling organisms should be reflected in their statistical distribution along spring brooks: truly crenobiontic species should be restricted to the surroundings of the spring source (eucrenal, Fig. 8.5), while crenophilous species may be equally distributed all over the crenal or more abundant in the hypocrenal (Fig. 8.2). Species only occasionally present in springs are defined as crenoxenes. In most cases they are present only as scattered, randomly distributed individuals, but capable to build up larger populations under favourable conditions. Therefore, a simple approach to the question if a species can be considered a crenobiont, is the comparison of its presence and frequency in the eucrenal and hypocrenal reaches.

Tab. 3 collects the data from a statistical analysis of

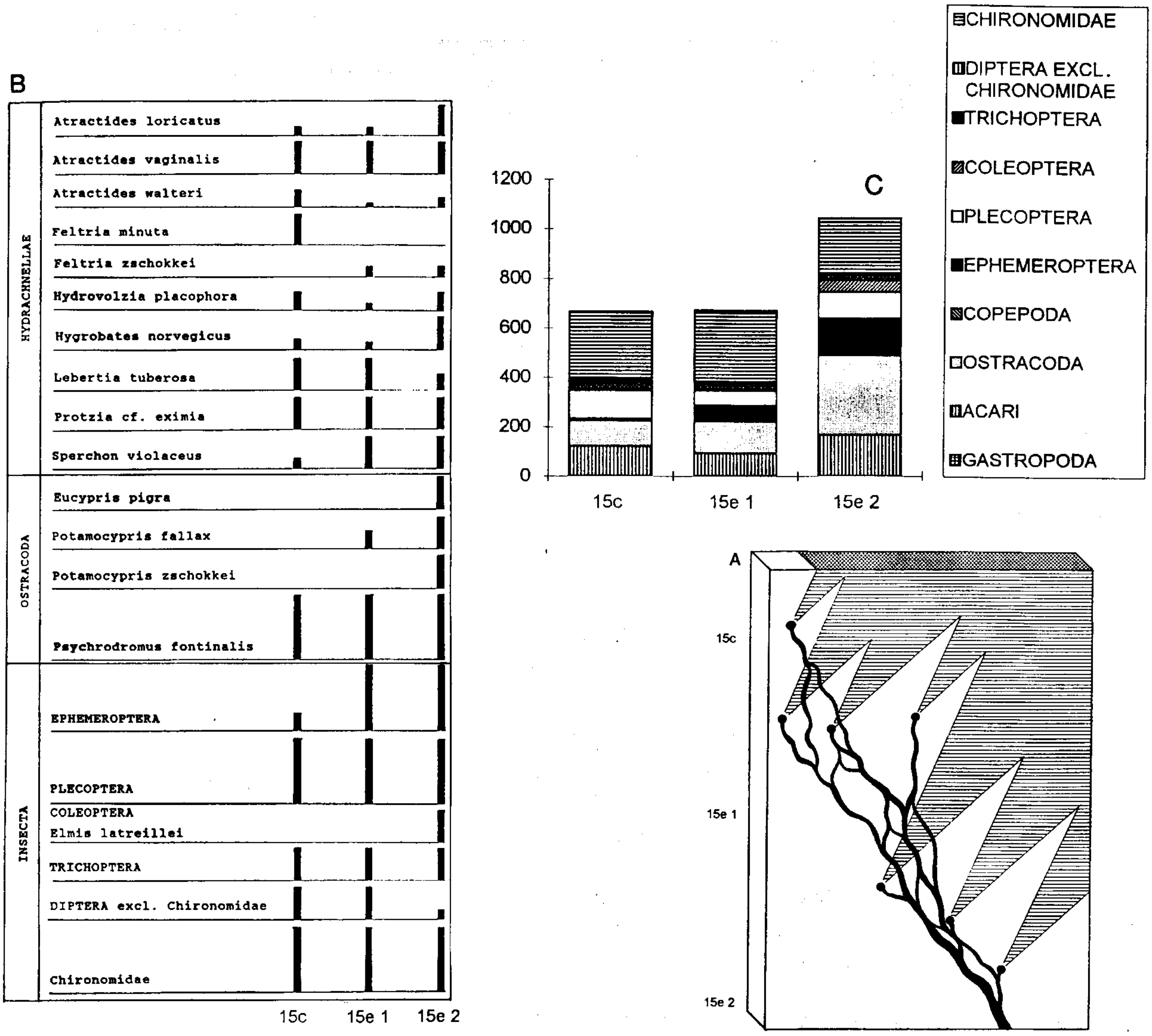

Fig. 4: A: Sketch of the morphology of spring sources originating from irregular, vertically folded impermeable layers (See caption for Fig. 3). B: distribution of the frequent species (> 10 specimens) of crustacea, acari, and of the main insect groups in the eucrenal and hypocrenal of a spring of this type (station 15 – the distance between 15c and 15e2 is about 300 m). C: General composition of the fauna at sites 15c, 15el and 15e2. The eucrenon/hypocrenon ecotone is blurred by the presence of numerous spring mouths at different elevations, resulting in an intermingled fauna of crenobionts and rhithrobionts in the lower part of the spring (C from Crema *et al.*, 1996, modified).

7 permanent springs originating from horizontal groundwater layers. All species with a probability value of 0.1% or 1% can be considered as possible crenobionts, while crenophiles and crenoxenes are characterized by a probability of 0.05% or less.

Our data confirm a strong preference for the eucrenal for a high number of water mite species (11 species, 47%). *Protzia eximia* is known from different types of mountain and lowland running waters in Central Europe, but the identity of the alpine populations belonging to the *eximia* group is not yet clear (Gerecke, 1996). For all other species, bibliographic data corroborate the hypothesis that they are strictly bound to crenal habitats. An additional 8 water mite species, in our material not represented by sufficient specimens for a clear assessment, are reported as well known crenobionts in the literature: *Atractides panniculatus, Bandakia concreta, Lebertia cuneifera, L. tuberosa, Panisus michaeli, Pseudofeltria scourfieldi, Sperchon violaceus* and *Tartarothyas romanica* (Schwoerbel,1959; Gerecke & Di Sabatino, 1996). *Sperchon thienemanni* is strictly crenobiontic in peninsular southern Italy (Gerecke & Di Sabatino, 1996), but in the North German lowlands and Sardinia it was found also in running water habitats far from springs (Gerecke & Di Sabati-no, in

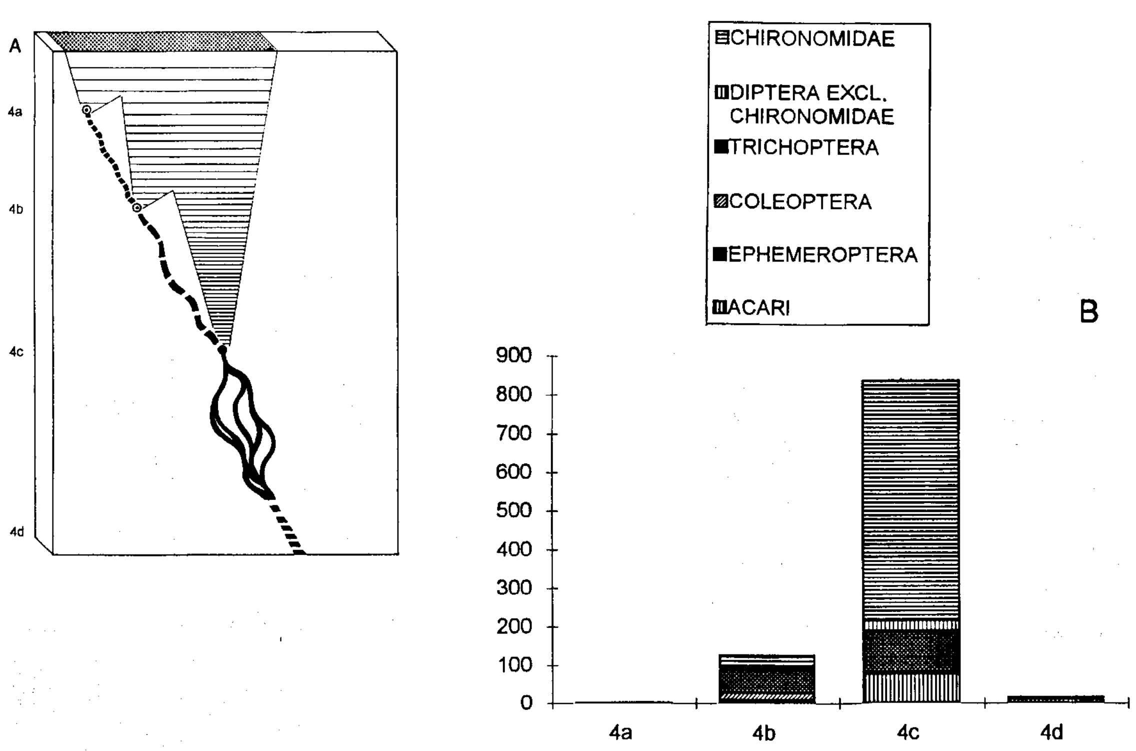

Fig. 5: A: Sketch of the morphology of a "linear spring" (See caption for fig. 3; white circles and interrupted lines: springs and channels with temporary flow). B: distribution of the fauna in a spring of this type (Station 4). The increased faunal diversity at site 4c reflects the more stable discharge conditions as compared to upstream (4b) and downstream (4d) (B from Crema *et al.*, 1996, modified).

press; Martin, in press); *Ljania bipapillata* and *Atractides loricatus* are crenophilous rhithrobionts. Most ostracods are present indifferently in the eucrenal and hypocrenal sectors or reach their highest density in the hypocrenal. A preference for the eucrenal is found only in *Psychrodromus fontinalis, Cavernocypris subterranea,* and *Cypria ophtalmica. P. fontinalis* and *C. subterranea* are cold stenothermic, inhabiting springs and subterranean waters, mainly interstitial habitats of streams; *C. subterranea* shows a preference for the temperature range of 6-12°C (Marmonier *et al.*,1989). The presence of *C. ophtalmica* in the group of species showing preference for the eucrenal is at first surprising (see below): this species is one of the most common and euryoecious ostracod species of the central European fauna and can be very abundant in temporary pools (Klie, 1938; Meisch, in prep.).

Four out of six copepods prefer the eucrenal of our study sites. Among them, populations of *Attheyella wierzejskii* extend the furthest downstream into the hypocrenal. From our present state of knowledge (Einsle,1993), *Paracyclops fimbriatus* colonizes both streams and springs, and *Acanthocyclops vernalis* is common in the zooplankton communities of lakes and ponds, but regularly present in lentic reaches of helocrenes. All other species listed in Tab. 3 are recorded also from shores of alpine lakes and streams, and from ground-water habitats (Einsle,1993; Janetzky *et al.*,1996).

From our preliminary results on other invertebrate groups it is clear that most insect groups show a high diversity, but are represented by only low numbers of true spring specialists (Crema *et al.*, 1996). Obviously, spring mouths are important egg-deposition sites for many stream-dwelling species of plecopterans (enormous amounts of first instar larvae were found), but no crenon specialist is present. Ephemeropterans are absent from most eucrenal habitats, colonizing running waters only from the hypocrenal downstream. Ongoing studies for a more complete documentation of trichopterans and dipterans demonstrate that these orders are represented in the study area by several species with distinct preference for the crenal. However, the taxonomic group richest in species in alpine springs, the dipteran family Chironomidae, is representated nearly exclusively by euryoecious elements dwelling also in running waters, swamps, or montane lakes (Crema *et al.*, 1996; see also Lindegaard, 1995).

Among Coleoptera, several dytiscids of the genus *Hydroporus* (*Hydroporus ferrugineus* Stephens and the members of the subgenus *Sternoporus*) are restricted to the eucrenal. *Elmis latreillei* (Bedel), *E.*

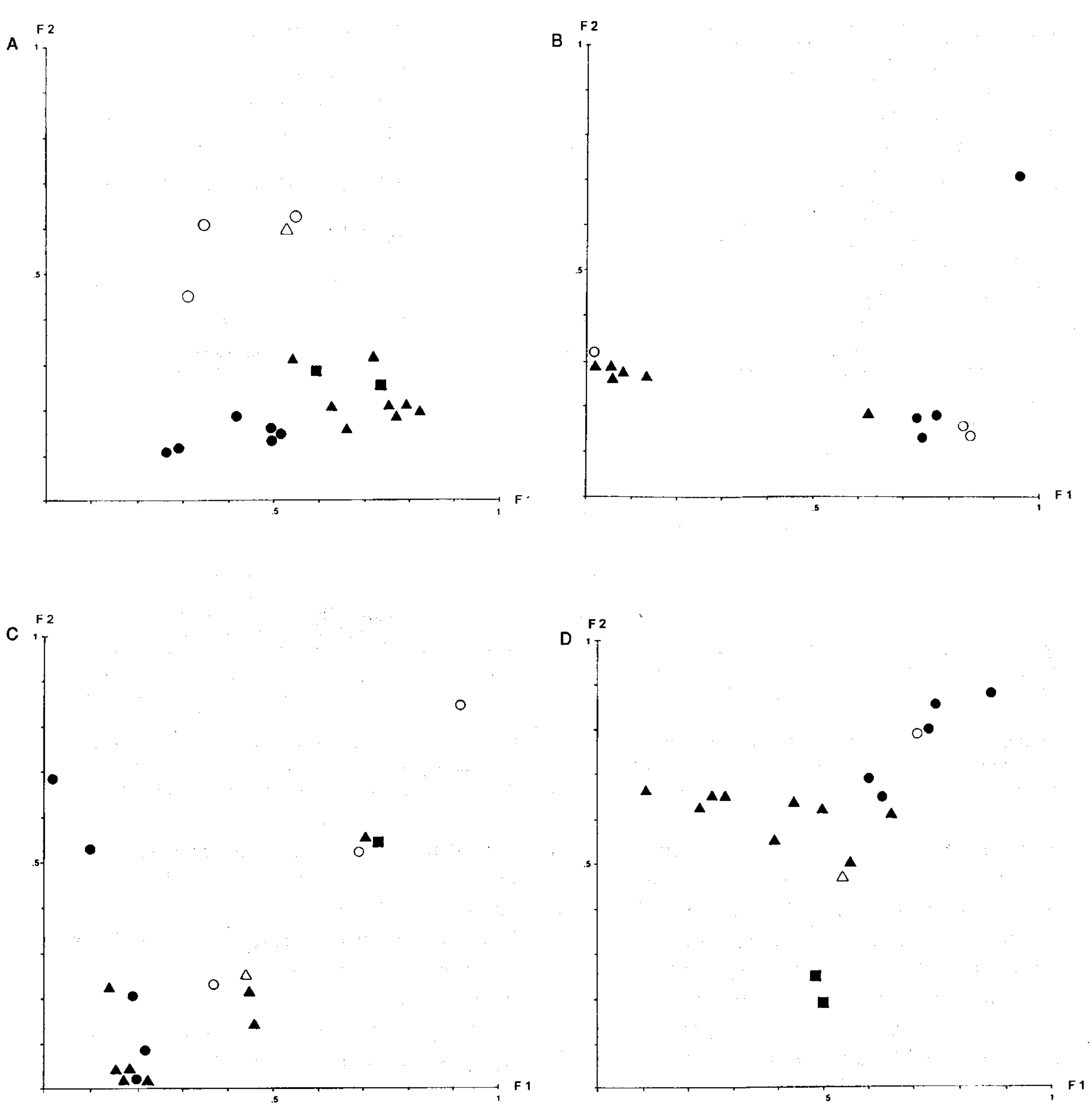

Fig. 6: Ordination of 24 spring sources belonging to 19 springs in the Alps of Berchtesgaden, using the first two axes of correspondence analysis. Black/white symbols = permanent/temporary springs; circles = helocrenes; quadrates = linear springs; triangles = rheocrenes A. Based on the complete arthropod meiofauna (water mites, copepods, ostracods) B. Based on ostracods C. Based on copepods D. Based on water mites.

rietscheli Steffan (Elmidae) and the more rarely found hydraenids (mainly *Hydraena saga alpicola* D'Orchymont) clearly prefer the hypocrenal and only rarely reach the immediate surroundings of the spring source. The larvae of *Elodes hausmanni* Gredler and *E. sp. gr. minuta* (Scirtidae) are found in high numbers in the crenal, but are also found in the epirhithral and in various types of standing or slowly running waters.

4.2. *Spring typology*

Fig. 6A gives an ordination of our spring sources as based on a principal component analysis of the raw data of crustaceans and mites. Temporary and permanent springs are clearly recognized as two separate groups; the F2-axis represents a gradient from year-round stable to seasonal flow. Within both groups, helocrenes are concentrated on the left, and rheocrenes on the right side; thus, the F1-axis represents a gradient from lentic to lotic flow conditions. A separate ordination for each of the three taxonomic

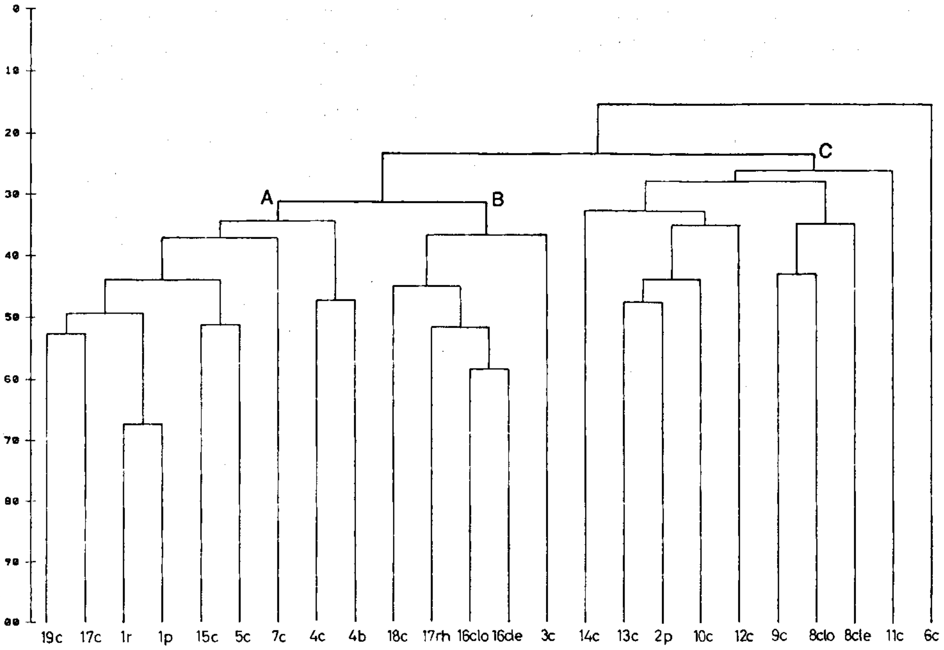

Fig. 7: Dendrogram showing the classification (Bray-Curtis-coefficient) of 24 spring sources belonging to 19 different springs in the Alps of Berchtesgaden, based on the composition of the mite fauna. A: Rheocrenes; B: Helocrenes; C: Temporary springs, one spring with very low discharge (14c) and a high altitude spring (13c). At sites 6, 11 and 12 only terrestrial mites were found. Further explanations in the text.

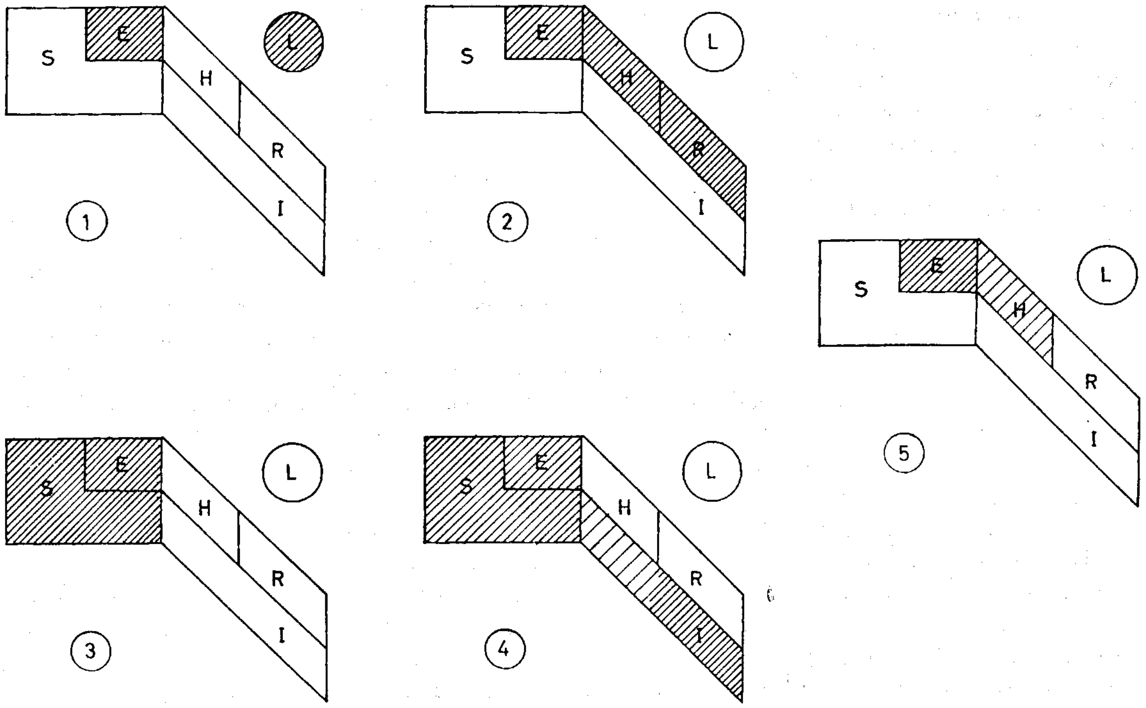

Fig. 8: Schematic illustration of the distribution of spring-dwelling organisms with different habitat-preference patterns. Abbreviations: E = eucrenal, H = hypocrenal, I = interstitial, L = lentic habitats, R = rhithral, S = stygal. 1. lentobiontic crenophiles; 2. rhithrobiontic crenophiles; 3. stygobiontic crenophiles; 4. stygo- and hyporheobiontic crenophiles; 5. crenobionts.

groups reveals more detailed information: In ostracods (Fig. 6B), no clear separation is found between temporary and permanent springs, but the x-axis represents a gradient from high to low flow velocity, with the only exception of the rheocrene source 19 shifted towards the helocrene group. Within our study sites, 19 is the only spring disturbed by human impact (partially captured). We propose that disturbance by hydraulic intervention and/or livestock might be responsible for the unusual composition of the fauna, characterized also by an extraordinary immigration of *Elmis latreillei* (Coleoptera Elmidae) into the eucrenal (Crema *et al.*, 1996).

The copepod fauna (Fig. 6C) does not allow for a separation of rheocrenes and helocrenes, and also the temporary springs do not form a distinct cluster. Obviously, the main factors influencing the composition of copepod assemblages are others than substratum and flow conditions in the spring source.

In mites (Fig. 6D), the F1-axis represents a lotic-lentic gradient, with rheocrenes grouped in the left, and helocrenes in the right part of the graph. The two linear springs with seasonally shifting spring source are recognized as a separate cluster in the lower part of the graph, while no separation is found between permanent and temporary springs.

In the following brief presentation of the spring types, we indicate the characteristic species of mites and crustaceans (found to at least 95% of the total individual number in habitats of this type, and represented by at least 5 individuals).

11 species were found exclusively in rheocrenic springs: Acari-*Lebertia tuberosa, Atractides panniculatus, A. vaginalis, Hydrovolzia placophora, Protzia eximia, Sperchon violaceus*; Ostracoda - *Cavernocypris subterranea, Potamocypris pallida, P. zschokkei, Psychrodromus fontinalis*; Copepoda - *Bryocamptus vandouwei.* Most of the water mite species listed here were also found restricted to rheocrenes in other studies (Schwoerbel, 1959; Bader, 1975; Gerecke & Di Sabatino, 1996), with the exception of *Hydrovolzia placophora* (occasionally found in rheohelocrenes) and *Protzia* cf. *eximia* (revision of taxonomic status necessary). The four ostracod species are known as characteristic inhabitants of springs and springbrooks (Klie, 1938: Meisch, in prep.). *Bryocamptus vandouwei* is a poorly-known, rare species of springs and shores of alpine lakes (Janetzky *et al.*, 1996).

Four species were found exclusively in helocrenic springs: Acari - *Bandakia concreta, Thyas palustris, Panisus michaeli* (except for one deutonymph in a rheocrene); Copepoda - *Attheyella crassa.* Also the ostracod *Cryptocandona vavrai* was found in large numbers only in a helocrene, but restricted to the hypocrenal. All three water mite species are well-known character species of helocrenic springs in Central and Southern Europe (Gerecke & Di Sabatino, 1996), but were found to be more euryoecious in Scandinavia (Lundblad, 1962). The ostracod *Cryptocandona vavrai* is tolerant to a wide range of environmental conditions. It is commonly found in springs (rheo-, limno- and especially helocrenic springs) and waters connected to springs (Klie, 1938; Meisch, in prep.). *Attheyella crassa* has been found in springs, running waters and cave waters.

Helocrenes are the most suitable habitat for aquatic and semiaquatic oribatid mites. *Mucronothrus nasalis* (Willmann), a species adapted to submerged life (Norton *et al.,* 1988), was found as one of the most frequent mite species in helocrenes (mean number/site 34 specimens, representing 62% of the total oribatid fauna: Schatz & Gerecke, 1996). Among Coleoptera, *Elodes* sp. gr. *minuta* and *Hydroporus ferrugineus* were restricted to helocrenes (Crema *et al.*, 1996).

Temporary springs have varied typological and substratum characteristics, but are mostly rheocrenes with strong flow during the high discharge season. The only water mite population found in springs of this type was of the halacarid *Soldanellonyx chappuisi*; hydrachnellae were occasionally present as single individuals. Two copepod species were found in relevant individual numbers exclusively in temporary springs: *Bryocamptus pygmaeus* and *Eucyclops* cf. *serrulatus*, both known as inhabitants of a wide variety of freshwater habitats. The following species were dominant in at least one temporary spring: *Potamocypris fallax* (Ostracoda), *Bryocamptus pygmaeus, B. tatrensis* (Copepoda); among other invertebrate groups (Crema *et al.*,1996): *Nemoura cinerea* (Retzius), *N. marginata* (Pictet) (Plecoptera), *Diamesa* sp. gr. *czernyi, Paratrichocladius skirwithensis* (Edwards), and *Pseudodiamesa branickii* (Nowicki) (Diptera Chironomidae). Linear springs are always of the rheocrenic type. They are not colonized by own character species, but in the ordination of the acari a typical assemblage of the spring-dwelling *Sperchon thienemanni* and the rheobiont *Atractides loricatus* is recognized. In sections with instable hydraulic regime they are similar to temporary springbrooks, in reaches with continuous flow, their fauna is diversified and similar to that of rheocrenes (Fig. 5).

For the above mentioned reasons, springs with numerous outflows feeding the springbrook along a vertical line (13, 15) were excluded from the crenobiosis analysis. Characteristics of springs discharging from oblique groundwater horizons are here illustrated by a comparison of sites 15 and 5, two springs with considerable similarity regarding the faunal composition at the top source (see their position in Fig. 7). Spring 5 is a rheocrene originating from a horizontal groundwater outflow (Fig. 3A), while spring 15 obviously originates from irregularly folded oblique groundwater-damming layers (Fig. 4A). Therefore, in spring 5 several typical crenobionts are restricted to the immediate surroundings of the spring source (Fig. 3B), whereas in spring 15, they are found for several hundred meters along the springbrook, in the lowest part of the spring complex (15e2) associated with typical immigrating rhithrobionts (Fig. 4B). There is no exclusive species characterizing this type of spring; rather, the biocenotic interlocking of eucrenon and hypocrenon and the lack of a clearly defineable ecotone is the main feature of such springs.

4.3. *Hypocrenon*

Among the species so far identified from our samples, only two water mites seem to be restricted to the hypocrenal: *Feltria zschokkei* Koenike is a moss-dwelling species that obviously replaces the more crenophilous *F. setigera* and *F. minuta* when the moss carpet extends into the springbrook. *Panisopsis curvifrons* (Walter) prefers hygropetric habitats and is found mostly in springbrooks, but also further downstream, if cascades are formed. Additional water mite species found mainly in the hypocrenal (but only in low numbers) are the rhithrobionts *Atractides loricatus, Sperchonopsis verrucosa* (Protz), and *Torrenticola elliptica* Maglio. Following Crema *et al.* (1996) the hypocrenon differs from the eucrenon in high numbers of mayfly larvae (*Baetis alpinus* Pictet, *Baetis muticus* (Linnaeus), *Ecdyonurus helveticus* (Eaton) and *Rhithrogena hybrida* Eaton were identified) and Elmid beetles (*Elmis latreillei* or *Elmis rietscheli*; in no case both species were found together).

5. **Discussion**

A comparison of relative abundance in spring mouth and springbrook assemblages supplies necessary, but not sufficient information concerning the ecological valence of a species.

If attention is restricted to the distribution within the longitudinal pattern of surface running water communities, some of our species would be ranked with the crenobionts (Figs 8.1, 8.3, 8.4). However, they are capable of colonizing a wide range of different lentic or interstitial habitats and should therefore more correctly be considered as crenophiles. *E. g.*, in our comparison of eucrenal and hypocrenal the ostracods *Psychrodromus fontinalis* and *Cypria ophtalmica* are both characterized as restricted to the eucrenal, but they are known to colonize a wide range of different habitats (*P. fontinalis*: cave waters and interstitial groundwater, Fig. 8.4; *C. ophthalmica*: ponds, swamps and lakes, Fig. 8.1). Consequently, *P. fontinalis* is a hyporheobiontic crenophile, and *C. ophtalmica* a lentobiontic crenophile. Similarly, among copepods, *Paracyclops fimbriatus* is a rhithrobiontic crenophile (Fig. 8.2), *Acanthocyclops vernalis* a lentobiontic crenophile (Fig. 8.1), and all other species listed in Tab. 3 are hyporheobiontic crenophiles (Fig. 8.4).

In the case of crenophiles, the colonization of springs is not an exclusive autecological feature of an extremely stenoecious species, but a partial aspect of the habitat preference pattern of a more euryoecious species. By their restriction to the eucrenal within the community structure of a running water course, hypo-rheobionts and stygobionts (such as the ostracods *Psychrodromus fontinalis*, but also the amphipods *Niphargus foreli* Humbert found at site 9, and *N. strouhali* Schellenberg at site 13 - Crema *et al.*, 1996) characterize the spring mouth as a groundwater/surface water ecotone (Figs 8.3, 8.4). Other species, *e.g.* several ostracods as well as beetles of the genus *Elodes* (Crema *et al.*, 1996), are restricted to the spring source area only due to their preference for small shallow water bodies with particular substrate conditions that are rarely found downstream in the running water course. It is particularly interesting that in water mites no faunistic similarity is found between hypogean (hyporheic) and crenal fauna. Not a single representative of the diversified stream-interstitial mite fauna was detected either in spring source waters or in Bou-Rouch digs near springs (Crema *et al.*, 1996). Since we are lacking any information on life cycles of hyporheic mite species in Europe, we can only speculate that their host preferences could be incompatible with the host assortment available in springs. Possibly, the reinstallation of hyporheophilous and subterranean invertebrate assemblages at high elevations has been proceeding slowly since the end of the last glaciations, and crustaceans might be the first pioneers that come back to high altitude subterranean habitats.

The word "crenobiont" means that a species is restricted to spring habitats. It should be reserved for species living exclusively in springs, with a preference for the surroundings of the spring mouth (eucrenal). Therefore, true crenobionts not only should necessarily prove a high eucrenal preference in statistical analyses of longitudinal distribution patterns in streams, but should also be unable of colonizing other habitat types (Fig. 8.5).

This is not true for any of our crustacean species, but for most water mite species with a strong eucrenal preference in Berchtesgaden springs, bibliographic data confirm that they fulfill this condition. We are still far from understanding the reasons of such an extremely restricted ecological valence. A relatively low share of crenobionts in the fauna of remote islands indicates that in continental areas migration and competition during climatic changes may have played an important role in the evolution of preference for spring habitats (Gerecke & Di Sabatino, in press), but this factor should be of equal importance for other invertebrate groups as well. The attempts of former authors to explain crenobiosis of water mites as a result of coldstenothermy and reduction of the parasitic larval stage in the life cycle, is not verified by the results of more recent research (for a discussion, see Gerecke, 1996). On the contrary, springs could be suitable habitats for species with parasitic larval stages due to their particularly rich dipteran fauna, as well as to their attractiveness as egg deposition sites for other insect groups. Feeding behaviour of spring-dwelling mites is still unstudied, but adults and nymphs of species living in different habitat types are known to feed on eggs of the same insect species that they use as phoretic-parasitic hosts during their larval stage (Collins,1975; Davids, 1991; Stevens & Greven, 1994). Mite larvae are often observed accumulating in large numbers on single host individuals, and the flight radius of insects parasitized by water mite larvae decreases with mite load (Davids, 1991). Through their negative influence on the host, crenobiontic water mite larvae have a good chance to return to their preferred habitat even when attached to species which are not generally bound to spring habitats. At the same time, evolutionary maintenance of a parasitic-phoretic larval stage in crenobiontic mite species reflects the (often underestimated) long term instability of spring habitats. Only due to their phoretic stage, crenobiontic water mites are able to survive droughts of their habitat and to colonize springs even in isolated geographic areas. Our data agree with the observations of Biesiadka (1974, 1979) concerning the drastically reduced water mite diversity in the hypocrenal. At least for this taxonomic group, the hypocrenal appears to be an impoverished transition zone. Bibliographic data from different Western Palaearctic mountain ranges (*e.g.* Schwoerbel, 1959; Biesiadka 1974, 1979) exemplify that species found in high numbers in the spring source, but only as scattered specimens in the springbrook, are replaced by other, rheobiontic assemblages further downstream. In this regard, a study of the invertebrate assemblages of epirhithral and metarhithral stream sectors in the Berchtesgaden National Park is desirable.

Our scenario of variously motivated preference for spring habitats may become enriched when data on the eucrenal preference will become available also for species of other invertebrate groups, mainly dipterans and trichopterans (Williams & Williams, 1987). Due to their larger dimensions and considerable mobility, larvae of crenobiontic trichopterans can be found also further downwards from the spring source (Erman,1986). Therefore, we would expect less distinct eucrenal/hypocrenal distribution patterns in crenobiontic species of caddisflies and other groups of larger invertebrates.

To learn more about the reasons for which crenobiontic and crenophilous species are bound to these habitats, a better knowledge of their life cycles is necessary. Our correspondence analyses of spring typology (Figs 6A-D) produced diverse, but in each case informative results depending on the taxonomic group taken into consideration. The coexistence of a highly diversified fauna composed by taxa with completely diverging bionomic and autecologi-cal requirements is the unique and most fascinating aspect of spring habitats.

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