

Two New Species of the Family Hydrobiidae (Mollusca: Caenogastropoda) from Austria

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Abstract. Two new species of the family Hydrobiidae from Austria are described. One belongs to the genus *Belgrandiella* A. J. Wagner, 1928, the second is allocated to *Bythiospeum* Bourguignat, 1882. The crenobiontic *Belgrandiella* species is characterized by one autapomorphic character state of the genital system and by a unique combination of states which are shared with other species. The second species, a stygobiont, is tentatively attributed to *Bythiospeum*, because its description is based only on shell characters. Both species are known from very restricted ranges corresponding to the distributional pattern of their congeners.

In addition, data of 13 abiotic parameters measured over a period of more than 5 years in the springs where the new species were found are presented. The values of these parameters are characteristic for natural, carbonate brooks. Contamination with fecal bacteria suggests influence through agriculture or may be caused by feces of mammals. Chemically, agriculture and forestry appear to have no significant impact on the springs investigated.

INTRODUCTION

Throughout the world, karst systems are known to be inhabited by speciose faunas including many stygobionts (e.g., Illies, 1978; Botosaneanu, 1986; Juberthie & Decu, 1994). Since 1991, the beginning of the karst monitoring projects of the area of the then prospective, now established (25 July 1997) Nationalpark Kalkalpen and its surroundings in the Northern Calcareous Alps of southeastern Upper Austria (Atzwanger, 1993; Haseke, 1993), a number of hydrobioid (*sensu* Davis, 1979) gastropods were found. The species belong to the genera *Belgrandiella* A. J. Wagner, 1928, and *Bythinella* Moquin-Tandon, 1855, both largely crenobiontic genera, and the stygobiontic genera *Bythiospeum* Bourguignat, 1882, and *Hauffenia* Pollonera, 1898. The *Belgrandiella* and *Bythiospeum* species, one species each, turned out to be new to science.

The monitoring not only comprises faunistic recordings but also the collection of physical parameters of the springs. Thus, we are able to present detailed descriptions of the environment of the new hydrobiids, which is an

important step toward understanding the autecology of crenobiontic and stygobiontic organisms.

MATERIALS AND METHODS

All four localities where the snails presented in this study have been collected are in the drainage area of the rivers Steyr or Krumme Steyr, a left tributary of the Steyr, which empties into the Enns shortly before the latter flows into the Danube. This river system is part of the right (southern, Alpine) catchment area of the Danube. More detailed locality data and information about the total number and the number of specimens investigated are given in the systematic descriptions. Physical parameters of the springs measured are listed in Table 3. These data were taken from Haseke (1998). The material is deposited in the Museum of Natural History in Vienna (NHMW). The snails were fixed in Bouin's solution, in 4% formaldehyde or in 70% ethanol, respectively. Anatomical methods were those of Haase (1992). The SEM pictures were partly made on a JEOL JSM 35 Scanning Microscope at the Zoological Institute in Vienna and partly on

a JSM 6300 at the SEM Laboratory of the University of Basel.

SYSTEMATIC DESCRIPTIONS

General Remarks

In the present descriptions of the new species, only characters relevant for the diagnosis of species are presented. The descriptions are based on fixed material. Therefore, several characters whose investigation requires observation of living animals could not be included (cf. Hershler & Ponder, 1998). Whenever possible, we used the terminology of Hershler & Ponder (1998) for the definition of character states. Only the material from the type localities is declared type material in order to avoid taxonomic confusion in case the populations from other localities should turn out not to be conspecific, applying finer methods like molecular techniques.

Belgrandiella A. J. Wagner, 1928

Type species: *Belgrandia kusceri* A. J. Wagner, 1914

Diagnosis: Shell pupiform, rarely turritiform, usually smaller than 2.5 mm; protoconch pitted, teleoconch without sculpture. Stomach without caecum. In females the intestine lies close to the pallial oviduct with only a weakly developed loop to the left; in males this loop is quite distinct. Female genital system characterized by a simple ovary, the presence of a bursa copulatrix, and a receptaculum seminis lying ventral to the bursa; renal oviduct describes a single, wide loop before passing into the pallial oviduct. In males the testis has simple, wide lobes; vas deferens enters and leaves the prostate at its very ends; ejaculatory duct only weakly developed; penis without glands but often a muscular lobe on the left side.

Remarks: This diagnosis is based on Radoman (1983) and Haase (1994). The entire anatomy of a *Belgrandiella* species is presented in Haase (1993a). However, the delimitation of *Belgrandiella* from other, similar nominal genera is ambiguous, and concepts of various authors differ considerably. Lack of knowledge of anatomical data of many species attributed to various nominal genera and nomenclatural problems have prevented a thorough systematic analysis and clear classification of this group of species so far. This problem is outlined in more detail by Haase (1996) in his discussion of the generic allocation of the Austrian radiation attributed to *Belgrandiella*.

Belgrandiella aulaei Haase, Weigand & Haseke, sp. nov.

(Figures 3–7)

Holotype: NHMW 89958.

Paratypes: NHMW 89959 (one series of histological sections, >50 specimens).

Type locality: Rinnende Mauer, a system of springs emerging on the foot of a slightly overhanging wall of conglomerate overgrown with mosses respectively on top of that wall over a length of about 30 m forming a beautiful curtain of drops (Figures 1, 2). This system of springs is close to the left bank of the river Steyr north of Leonstein 405 m above sea level. The snails live in the lower springs and their common discharge.

Additional material: Right spring of the Wunderlucke (Figure 1), a pond, close to the left bank of the river Krumme Steyr in Rabach, 365 m above sea level (NHMW 89960, four series of sections, >25 specimens).

Etymology: *Aulaeum* (Latin, neuter) means splendid curtain and refers to the curtain of drops at the type locality.

Diagnosis: *B. aulaei* is characterized by the position of the receptaculum seminis between albumen gland and bursa copulatrix and by the unique combination of the following characters: capsule gland bipartite, posterior albumen gland asymmetrical, bursa copulatrix behind albumen gland, bursal duct as wide loop.

Description: *Shell.* Pupiform, shallow sutures, transparent, with up to 3.75 moderately convex whorls of which the pitted protoconch comprises about one whorl (Figures 3, 4). Aperture obliquely ovoid; outer lip straight and orthocline. Umbilicus a slit. Measurements are given in Table 1.

Operculum. Thin, orange, paucispiral, nucleus submarginal.

Radula (Figure 5): R: 5–7 1 5–7/1 1 L: 3–4 1 5–6 M₁: 24–26 M₂: 24–29. Central tooth trapezoidal; basal tongue of the central tooth as long as lateral margins and V-shaped, with curved edge; basal cusps prominent. Face of lateral teeth taller than wide, with basal projection; lateral wing much longer than cutting edge. Cusps on inner marginal teeth slightly larger than on outer marginal teeth; cutting edge on inner marginal teeth longer than 25% of total tooth length.

Non-genital anatomy. In most specimens mantle entirely black. But the epithelium lying over the distal glands of the genital system (prostate, pallial oviduct) and the stomach may have less pigment. Epidermis of head and foot practically unpigmented. But their connective tissues as well as the radular bolsters and the pharynx contain black granules. Cephalic tentacles bear no cilia. In one female from the Wunderlucke two additional eyes were found on the base of the right tentacle. No crenidium. Hypobranchial gland very short lying in the rear of the mantle cavity. Endothelium of the stomach may contain some granules of black pigment. The stomach and intestine of one individual from the Wunderlucke were full with diatoms.

Male reproductive system. Base of the penis broadened on the left side. A round to elongate lobe is more or less well separated from this base (Figure 6). Behind the tip,

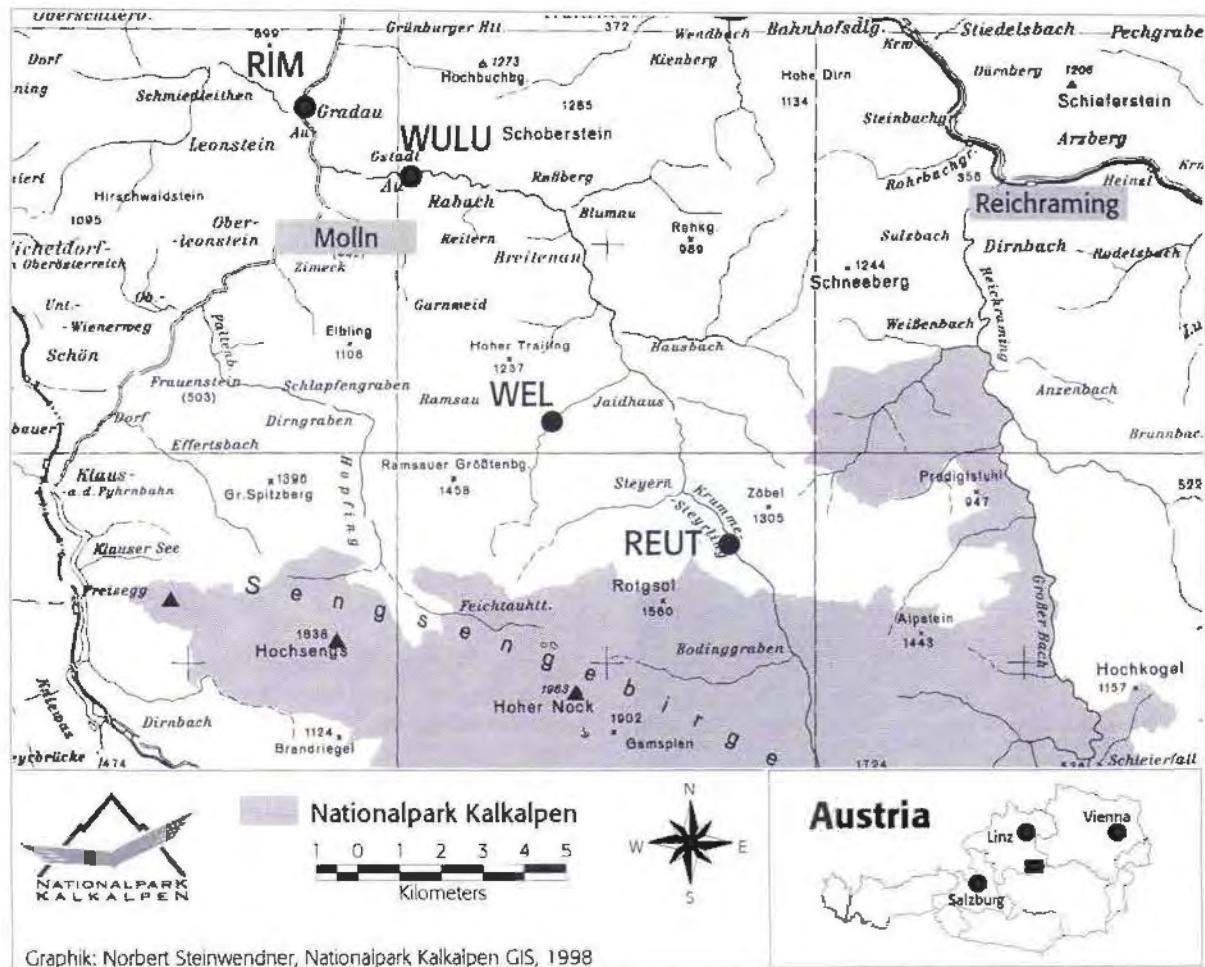


Figure 1

Localities of *Belgrandiella aulaei* Haase, Weigand & Haseke, sp. nov. and *Bythiospeum nocki* Haase, Weigand & Haseke, sp. nov. REUT = Reutersteinquelle, RIM = Rinnende Mauer, WEL = spring Welchau, WULU = Wunderlucke.

black granules forming a spot are deposited in the musculature.

Female reproductive system. Capsule gland divided into two portions of which the smaller, anterior one stains darker in histological sections than the posterior part. Posterior albumen gland asymmetrical in that it is longer on the right ventro-lateral side. Tip of the receptaculum seminis between posterior albumen gland and bursa copulatrix. Bursa copulatrix lies behind albumen gland. Its duct describes a wide loop (Figure 7).

Remarks: The generic allocation of the new species is justified through shell shape, formation of the digestive system, and genital morphology. The data for the following comparisons are taken from Haase (1993a, 1994, 1996). With the Austrian radiation of *Belgrandiella* species *B. aulaei* shares the lack of the ctenidium, the course

of the bursal duct, and the formation of the penis. Conchologically it is identical with *B. ganslmayri* Haase, 1993, from Weyer/Enns. With this species it also shares the asymmetrical posterior albumen gland (Haase, 1993a). *B. ganslmayri* is geographically the closest of the known *Belgrandiella* species. The course of the bursal duct and the position of the bursa copulatrix of the new species are similar to those in *B. wawrai* Haase, 1996, which is endemic in the valley of the Further Bach. *B. fuchsi*, *B. ganslmayri*, and *B. wawrai* share the orange operculum with *B. aulaei*. The bipartite capsule gland is also found in the three species from the Vienna Basin, *B. parreyssii* (L. Pfeiffer, 1841), *B. pelerei* Haase, 1994, and *B. mimula* Haase, 1996. The penial lobe, finally, can be similar to that found in *B. austriana* (Radoman, 1975) from Graz in the southeast of Austria. *B. aulaei* is after



Figure 2

Rinnende Mauer, type locality of *Belgrandiella aulaei* Haase, Weigand & Haseke, sp. nov.

B. fuchsi (Boeters, 1970), and *B. wawrai*, only the third species of Austrian *Belgrandiella* found in more than one spring.

Bythiospeum Bourguignat, 1882

Type species: *Hydrobia quenstedti* Wiedersheim, 1873

Diagnosis: Shell conical to turritiform, smaller than 5 mm; aperture with an adapical sinus. Epidermis without pigment (stygo-biont). Stomach without caecum. Gonads simple, sac-shaped. Female genital system with one receptaculum seminis and a transverse bursa with bursal duct entering ventrally. In males the prostate may be connected with the pallial cavity through a small duct; penis simple, i.e., it bears no appendages.

Remarks: This diagnosis is based on Bernasconi (1990) and Haase (1995). Haase (1995) gives a detailed description of the whole anatomy of *Bythiospeum* cf. *geyeri*

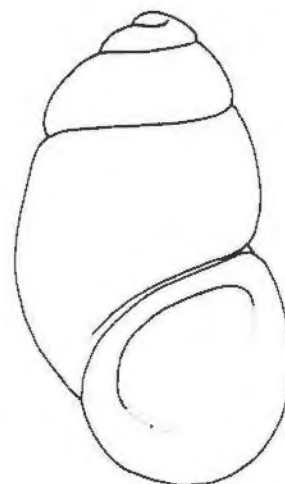


Figure 3

Holotype of *Belgrandiella aulaei* Haase, Weigand & Haseke, sp. nov. (NHMW 89958). Shell height = 1.55 mm.

(Fuchs, 1925). In *Bythiospeum* the situation is similar as for *Belgrandiella*. Different authors have more or less inclusive definitions (cf. Giusti & Pezzoli, 1982; Bernasconi, 1990; Haase, 1995) and a systematic analysis of the species attributed to *Bythiospeum* or a (nominal) genus considered to be closely related to *Bythiospeum* is lacking for the same reasons as for *Belgrandiella* (see above).

Bythiospeum nocki Haase, Weigand & Haseke, sp. nov.

(Figure 8)

Holotype: NHMW 89961 (empty shell).

Paratypes: NHMW 89962 (4 shells: 3 intact, 1 damaged).

Type locality: Reutersteinquelle (Quelle = spring), which is feeding a brook that drains into the river Krumme Steyerling, 570 m above sea level (Figure 1).

Additional material: Wunderlucke (NHMW 89963, 1 specimen, live collected); Welchau, a spring feeding the brook Hilgerbach, which drains into the Krumme Steyerling, 540 m above sea level (NHMW 89964, 1 live collected but damaged specimen, shell dissolved) (Figure 1).

Etymology: The Hohe Nock is the highest mountain (1963 m) of the Sengengebirge and thus of the Nationalpark Kalkalpen.

Diagnosis: *B. nocki* is characterized by its small size, the short spire and the detached peristome.

Description: *Shell.* The empty turritiform shells are opaque white with up to four convex whorls. Under the

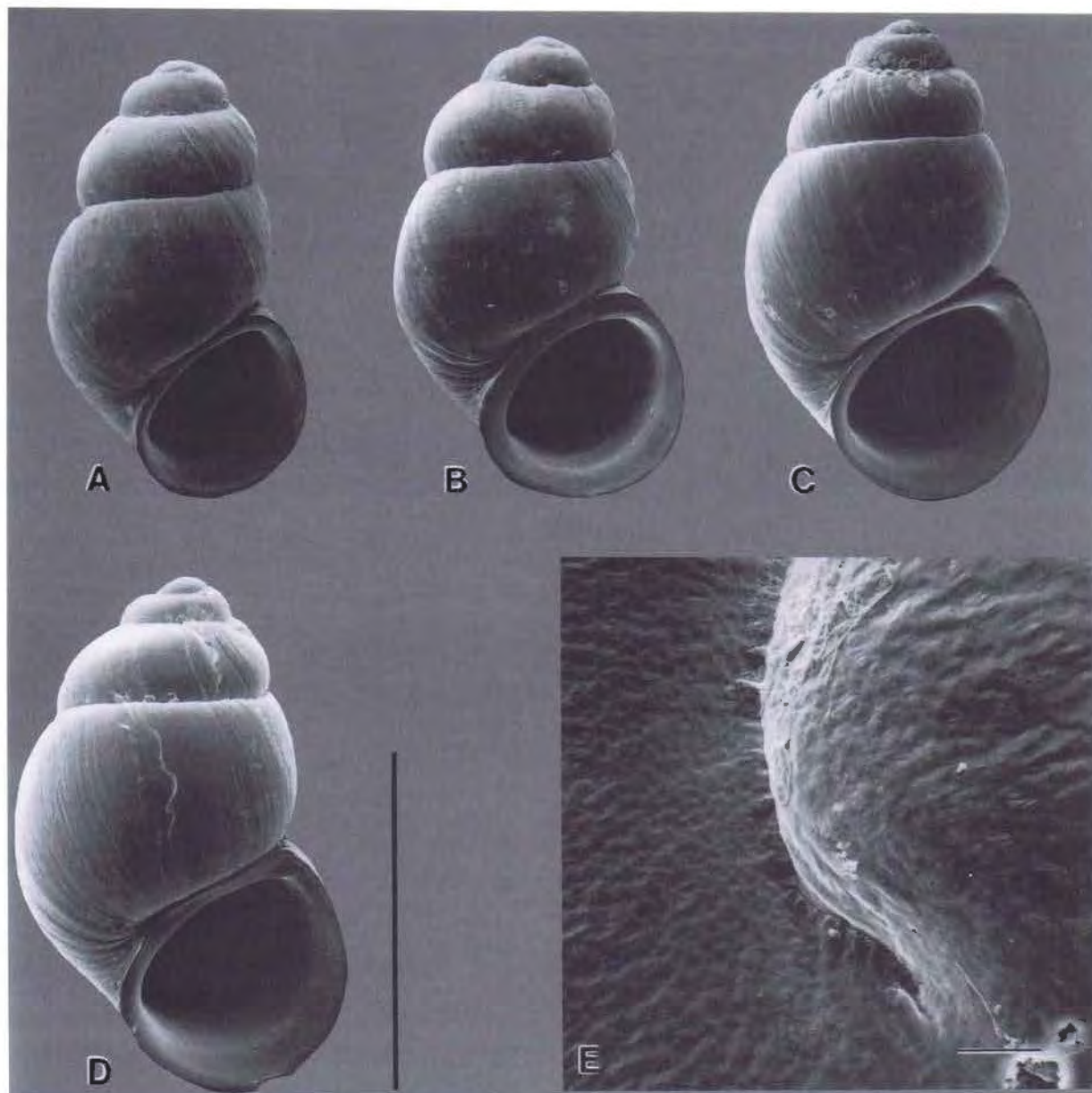


Figure 4

Shells of *Belgrandiella aulacae* Haase, Weigand & Haseke, sp. nov. A, B, Rinnende Mauer, paratypes (NHMW 89959); C, D, Wunderlucke (NHMW 89960); E, Structure of protoconch, Wunderlucke. Scale bars = 1 mm in A–D, 10 μ m in E.

dissection microscope no distinct surface structure could be detected. Spire rather short. Aperture slightly higher than wide, orthocone, sinuate apically; lip slightly reflected; peristome detached from body whorl (Figure 8). Measurements are given in Table 2.

Operculum. Thin, light orange, paucispiral, nucleus submarginal.

Non-genital anatomy. No eye-spots visible.

Remarks. The generic allocation of *B. nocki* is tentative due to the lack of anatomical data. But that holds for the vast majority of the nominal species and subspecies ascribed to the genus *Bythiospeum* (cf. Bernasconi, 1990; Haase, 1995).

B. nocki is by far the smallest *Bythiospeum* known so far (cf. Bernasconi, 1990). The next larger species from Austria is *B. elseri* (Fuchs, 1929) (shell height: $P < 0.01$,



Figure 5

Radula of *Belgrandiella aulaei* Haase, Weigand & Haseke, sp. nov. from the Rinnende Mauer. A. Ten rows; B. Central teeth. Scale bars = 10 μ m in A, 5 μ m in B.

t-test), but this is much more slender (shell height/shell width: $P < 0.001$, t-test; data for *B. elseri* from Haase, 1995). It is the 11th [nominal (cf. Haase, 1995)] species that is described from Austrian ground waters [In his review, Haase (1995) mentions only eight taxa. But he has overlooked Mahler's (1950) species, *B. excelsior* (Mahler, 1950) and *B. excessa* (Mahler, 1950). However, the syntype series of these two species are lost.].

B. nocki is, as far as we know today, restricted to the drainage area of the Krumme Steyerling. The single spec-

Table 1

Shell morphometry of *Belgrandiella aulaei*. Measurements in mm, $s*100/\bar{x}$ in %. Abbreviations: ah = aperture height, aw = aperture width, max = maximum, min = minimum, N = number of specimens, s = standard deviation, $s*100/\bar{x}$ = coefficient of variation, sh = shell height, sw = shell width, W = number of whorls, \bar{x} = mean.

Locality		sh	sw	ah	aw	sh/sw
Rinnende Mauer	holotype	1.55	0.97	0.78	0.70	1.60
N = 21	min	1.28	0.81	0.54	0.56	1.49
W _{max} = 3.6	max	1.58	1.00	0.78	0.73	1.71
	\bar{x}	1.43	0.91	0.67	0.64	1.58
	s	0.09	0.06	0.05	0.04	0.06
	$s*100/\bar{x}$	5.95	6.04	8.12	6.43	3.76
Wunderlucke	min	1.16	0.72	0.55	0.57	1.37
N = 19	max	1.58	1.00	0.76	0.69	1.74
W _{max} = 3.75	\bar{x}	1.34	0.86	0.63	0.62	1.57
	s	1.13	0.07	0.06	0.04	0.10
	$s*100/\bar{x}$	9.27	7.76	9.54	6.35	6.45

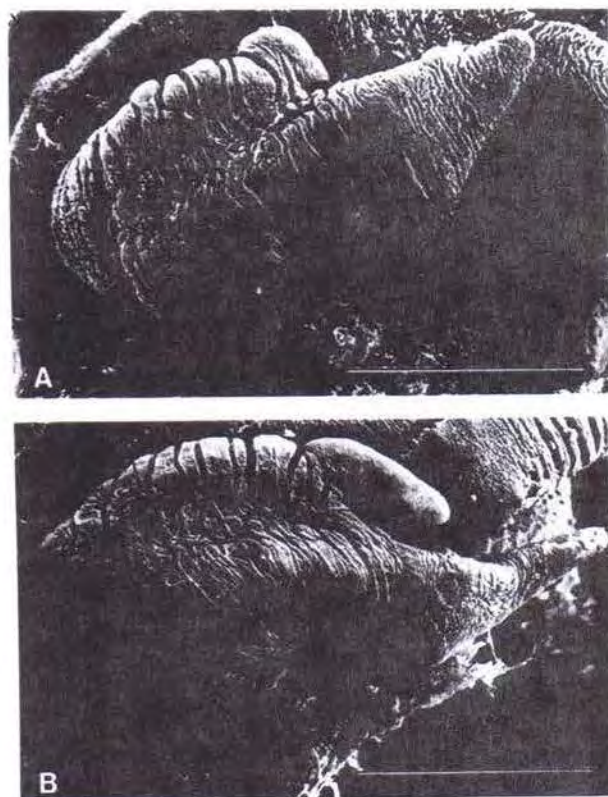


Figure 6

Penes of *Belgrandiella aulaei* Haase, Weigand & Haseke, sp. nov. from the Wunderlucke. Scale bars = 100 μ m.

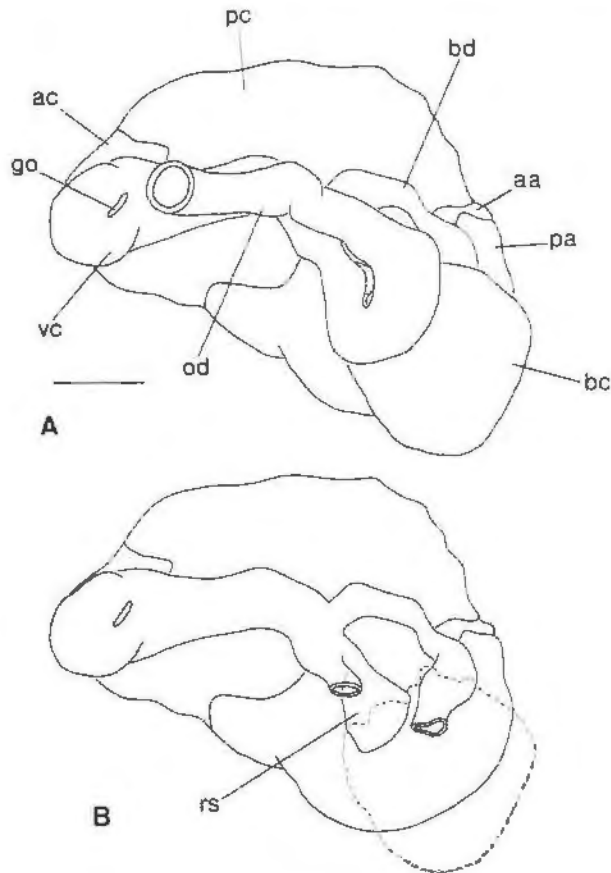


Figure 7

Distal female genitalia of *Belgrandiella aulaei* Haase, Weigand & Haseke, sp. nov. from the Rinnende Mauer. Abbreviations: aa = anterior albumen gland, ac = anterior capsule gland, bc = bursa copulatrix, bd = bursal duct, go = genital opening, od = oviduct, pa = posterior albumen gland, pc = posterior capsule gland, rs = receptaculum seminis, vc = ventral channel. Scale bar = 100 μ m.

Table 2

Shell morphometry of *Bythiospeum nocki*. Abbreviations as in Table 1.

Locality		sh	sw	ah	aw	sh/sw
Reuterstein	holotype	1.47	0.78	0.58	0.53	1.89
N = 4	min	1.10	0.57	0.40	0.41	1.84
W _{reut} = 4.0	max	1.47	0.78	0.58	0.54	1.93
	\bar{x}	1.33	0.70	0.52	0.50	1.89
	s	0.16	0.09	0.08	0.06	0.04
	s*100/ \bar{x}	11.98	13.22	15.81	11.99	2.10
Wunderlucke		1.17	0.62	0.43	0.43	1.89
W = 3.6						

imens from the springs Welchau and Wunderlucke are not enough material for anatomical investigations, therefore we left them intact.

Abiotic characterization of the springs: Table 3 lists 13 parameters measured. Only ranges are given because the data were collected unevenly distributed over the seasons during up to 6 years, so that means and any other statistics would be biased toward the overrepresented season.

The Rinnende Mauer and Wunderlucke are permanently water-bearing with moderate discharge, whereas the Reutersteinquelle and the spring Welchau may dry up, especially the former, but occasionally show very high discharge of 200 L/sec and more. All four springs are quite cold and vary only little in temperature with the exception of the Wunderlucke, which had an amplitude of 10.1°C during the period of observation. Temperature maxima and minima fall naturally in summer and winter, respectively. All four springs are alkaline with pH values >7.3. The Rinnende Mauer and the Reutersteinquelle are well oxygenated with relative concentrations of over 90%. The spring Welchau, which may even be oversaturated with oxygen as the preceding two springs, shows quite large fluctuations in oxygen concentration, whereas



Figure 8

Shells of *Bythiospeum nocki* Haase, Weigand & Haseke, sp. nov. from the Reutersteinquelle. A, Holotype (NHMW 89961); B–E, Paratypes (NHMW 89962). Shell height of the holotype = 1.47 mm.

Table 3

Physical parameters of the springs. Abbreviations: C = electrical conductivity ($\mu\text{S}/\text{cm}$), min = minimum, max = maximum, N = number of measurements, Q = discharge (L/s), relO_2 = relative concentration of oxygen (%), T = temperature ($^{\circ}\text{C}$). All concentrations are given in mg/L.

Spring, period		Q	T	pH	O ₂	relO ₂	C	Mg ²⁺	Ca ²⁺	Na ⁺	K ⁺	NO ₃ ⁻	SO ₄ ²⁻	Cl ⁻
Rinnende Mauer	N	20	19	18	7	6	19	20	20	15	15	20	18	17
5/22/92–20/8/97	min	7.0	6.8	7.39	8.90	95.0	228	4.03	35.19	0.18	0.20	7.70	6.67	0.55
	max	25.0	10.7	8.25	11.55	102.0	343	31.96	70.07	1.14	0.89	14.07	15.85	1.77
Wunderlucke	N	22	22	19	7	6	22	22	22	11	1	22	18	16
7/18/91–20/8/97	min	0.5	3.6	7.36	5.30	79.0	348	0.02	38.77	0.25	0.23	1.52	4.35	0.15
	max	30.0	13.7	8.26	9.80	89.0	571	22.97	126.0	1.07	0.54	11.87	84.74	0.73
Reutersteinquelle	N	20	10	9	5	5	10	10	10	5	5	10	7	7
7/18/91–15/5/97	min	0	6.1	7.53	10.70	92.0	213	6.56	27.37	0.15	0.18	3.97	3.90	0.12
	max	200.0	6.7	8.30	13.50	116.0	265	13.19	43.30	0.34	0.24	13.79	5.47	0.52
Welchau	N	19	18	17	6	5	18	18	18	9	9	18	16	14
7/18/91–20/8/97	min	0.0	6.8	7.35	7.50	66.0	313	15.85	32.78	0.19	0.28	2.75	4.24	0.24
	max	295.0	8.0	8.15	11.62	102.4	380	23.60	51.00	0.73	0.42	8.16	15.70	0.63

the Wunderlucke fluctuates in a quite small range but never reaches saturation. Ion concentrations and hence electrical conductivity vary most strongly in the Wunderlucke. Especially remarkable are the minimum concentration of 0.02 mg/L of magnesium and the peak at 84.74 mg/L of sulfate.

DISCUSSION

The Austrian species of both genera *Belgrandiella* and *Bythiospeum* have been the subject of recent revisions (Haase, 1995, 1996). The finding of the new *Belgrandiella* species extends the known range of this genus toward the west, and brings the range of the extant species closer to the extinct *B. intermedia* Boeters (1970) from the Tiefsteinschlucht near Salzburg, whose generic allocation is presumptive due to the lack of anatomical data (cf. Haase, 1996). In their distributional pattern both new species correspond to their congeners (Haase, 1995, 1996) in that their ranges are very narrow being, as far as we know today, restricted to two springs and the drainage area of the Krumme Steyr.

The type locality of *B. aulaei*, Rinnende Mauer, has been threatened through a gravel mining project and plans to build an incinerating plant and a waste disposal site in its drainage area. Protests of the local population have stopped these projects, at least for the time being. The company involved has already announced plans to seek approval of a modified project (Maier & Maier, 1997). We hope that the discovery of the new species will strengthen arguments for protection of this area, which has been the aim of local organizations since 1983 (Maier & Maier, 1997). Furthermore, the finding of two new, presumably highly endemic species in the surroundings of the Nationalpark Kalkalpen, demonstrates that also this surrounding area is faunistically peculiar, suggesting an extension of the borders of the national park.

To those species ascribed to *Belgrandiella* tentatively because of lack of anatomical data listed in Haase (1996), viz. *B. intermedia* and *B. styriaca* Stojaspal, 1978, two more species, *B. multiformis* Fischer & Reischütz, 1995, and *B. kreisslorum* Reischütz, 1997, both from the south-east of Austria, were added recently (Fischer & Reischütz, 1995; Reischütz, 1997). But these species are not identical to those represented by samples deposited in the NHMW mentioned in Haase (1996). These two undescribed species, as well as that mentioned in Haase (1993a), have still not been rediscovered in the field and therefore we refrained from a formal description. Whether the fossil *B. dehmi* Boeters, 1995, from Oberfranken in Germany is a true *Belgrandiella* will remain subject to speculation, although its shell shape and occurrence suggest a close relationship to the Austrian species (Boeters, 1995).

In general, very little is known about the biology of freshwater hydrobiids in contrast to their brackish water relatives of the genus *Hydrobia* Hartmann, 1821 (e.g., Fretter & Graham, 1978; Lassen & Clark, 1979; Davis et al., 1989; and literature cited therein), and *Potamopyrgus antipodarum* Gray, 1843 (e.g., Duncan & Klekowski, 1967; Winterbourn, 1969; Ponder, 1988; Jacobsen & Forbes, 1997; Jokela et al., 1997; and literature cited therein), which tolerates a wide range of salinities from brackish to freshwater. *Bythinella dunkeri* (Frauenfeld, 1856) is the only species of hydrobioid spring snails in which feeding was systematically investigated (Oswald et al., 1991; Brendelberger, 1992, 1995). Diatoms were among the preferred food sources beside cyanobacteria, bacteria, hyphomycetes, and certain algae. Diatoms appear to be an important component of the diet also of *Belgrandiella aulaei* as may be judged by the contents of the stomach and intestine of one specimen.

The values of the 13 parameters measured in all four

springs are characteristic for natural carbonate brooks and groundwaters (e.g., Drever, 1982; Otto & Braukmann, 1983; Braukmann, 1987; Kummert & Stumm, 1989). However, in all springs, fecal bacteria such as *Escherichia coli*, other coliform bacteria, and enterococci were detected (Schmidt, personal communication). This contamination may be due to agricultural influences in the drainage areas of the Rinnende Mauer and the Wunderlucke, or, in case of the Reutersteinquelle and the spring Welchau, caused by feces of deer and other mammals. Chemically, agriculture and forestry appear to have no significant impact on the springs investigated, at least not on the parameters measured. The relatively high fluctuations of the various concentrations measured in the Wunderlucke may be due to the influence of the nearby Krumme Steyring at highwater. That holds also for the occasionally low concentrations of magnesium. The high peaks of sulfate in this spring may indicate that part of the water drains from rock strata containing gypsum (Tollmann, 1985) at times.

Because of the extreme fluctuations of the discharge ranging from 0 to 200 and more L/sec, crenobiontic species cannot establish permanent populations in the Reutersteinquelle and the spring Welchau. In the Reutersteinquelle only a second stygobiontic species of the genus *Hauffenia* was found. *Hauffenia* sp. was also washed out of its habitat in the spring Welchau. Nevertheless, some specimens of a *Bythinella* species were also found here probably indicating recent recolonization from a nearby source population. At the Rinnende Mauer and in the Wunderlucke, both with moderate and permanent discharge, *B. aulaei* was accompanied by a *Bythinella*.

Since there is, to our knowledge, no comparable study as to the number of physical parameters measured in a spring inhabited by hydrobioids and as to the continuity of the data collection over a period of more than 5 years, we are not able to bring these data into a wider context of general ecology of crenobiontic hydrobioids. Occasionally, temperature data, pH values, and/or electrical conductivity are given (e.g., Bregenzer, 1915; Girod & Pezzoli, 1967; Boeters, 1969, 1970, 1977; Jungbluth, 1972; Ponder, 1989; Hershler, 1998). The majority of those species for which this kind of information is available live in similarly cool waters as the two species dealt with in this paper. However, a number of species inhabit constantly warm or even thermal springs with temperatures of 19°C and more (e.g., *Neohoratia ateni* [Boeters, 1969]; 33°C [Boeters, 1969]; *Belgrandiella parreyssii* [L. Pfeiffer, 1841]; 23.5°C [Boeters, 1970]; *B. mimula*: 19.5°C [Boeters, 1970], cf. Haase [1996] for the identity of this species]; *Heleobia aponensis* [Martens, 1858]: ca. 30°C [Boeters, 1977]; several unnamed Australian species: up to 46°C [Ponder, 1989]; several species of *Pyrgulopsis* Call & Pilsbry, 1886: up to 36°C [Hershler, 1998]). Oswald et al. (1991) observed that the hydrobioid *Bythinella dunkeri* reproduced also at room temperature although the

original habitat had a mean temperature of only 8.8°C. This finding contrasts with frequent statements that *Bythinella* species are cold stenothermic (e.g., Bregenzer, 1915; Jungbluth, 1972) and suggests that low temperatures might not necessarily be a prerequisite for hydrobioid crenobionts for the colonization of a spring. We rather assume that the current of a spring may not exceed a certain velocity so that both the food sources of the snails and the snails can establish populations and are not swept away. In addition, competition and predation pressure may also play an important role for the restriction of certain hydrobioids to the crenal region of a brook (Oswald et al., 1991).

The only stygobiontic hydrobioid species we are aware of for which measurements of temperature and oxygen concentration were made directly in their habitat, i.e., in the groundwater, are *Lobaunia danubialis* Haase, 1993, and *Bythiospeum* cf. *geyeri* from the groundwaters of the river Danube in Vienna (Pospisil, 1989, who referred to these species as *Horatia* sp. and *Paladilhopsis geyeri*, respectively; as to the identity of these species see Haase, 1993b, 1995). The temperatures of 8.6 to 12.4°C in the Danube groundwater are well in the range measured for the majority of European crenobiontic hydrobioids. But the oxygen concentrations of 0.042 to 0.7 mg/L are remarkably low and in strong contrast to the oxygen situation in springs. It can be assumed that the oxygen concentration in the real habitats of *B. nocki* is much lower than measured in the springs where it has been found, while the measurements of the other parameters may well reflect the actual conditions in the groundwaters draining to the Krumme Steyring.

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LITERATURE CITED

- ATZWANGER, M. 1993. Geplanter Nationalpark Kalkalpen. Unterschutzstellung und vernetztes Forschungsprogramm. Wissenschaftliche Beihefte zur Zeitschrift Die Höhle 42:109–116.
- BERNASCONI, R. 1990. Revision of the Genus *Bythiospeum* (Mollusca Prosobranchia Hydrobiidae) of France, Switzerland and Germany. Privately published: Münchenbuchsee. 44 pp., 19 figs.
- BOETERS, H. D. 1969. *Pseudamnicola klemmi* n. sp. aus Südf Frankreich und *Microna ateni* n. sp. aus den spanischen Pyr-

- enäen (Mollusca, Prosobranchia). Archiv für Molluskenkunde 99:69–72.
- BOETERS, H. D. 1970. Die Gattung *Microna* Clessin, 1890 (Prosobranchia, Hydrobiidae). Archiv für Molluskenkunde 100: 13–145.
- BOETERS, H. D. 1977. Westeuropäische Hydrobiidae. 6. *Hydrobia* (*Semisalsa*) Radoman (Prosobranchia). Archiv für Molluskenkunde 108:45–50.
- BOETERS, H. D. 1995. *Belgrandiella* aus einem holozänen Kalktuff in Oberfranken (Prosobranchia: Hydrobiidae). Heldia 2: 69–72, 1 pl.
- BOTOSANEANU, L. 1986. Stygo fauna mundi. E. J. Brill/Dr. W. Backhuys: Leiden. vi + 740 pp.
- BREGENZER, A. 1915. Anatomie und Histologie von *Bythinella dunkeri*. Zoologische Jahrbücher (Anatomie) 39:237–290.
- BRENDELBERGER, H. 1992. Food selection experiments with two freshwater gastropods. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 25:4260–4272.
- BRENDELBERGER, H. 1995. Dietary preference of three freshwater gastropods for eight natural foods of different energetic content. Malacologia 36:147–153.
- BRAUKMANN, U. 1987. Zoozoologische und saprobiologische Beiträge zu einer allgemeinen regionalen Bachtypologie. Archiv für Hydrobiologie Beiheft. Ergebnisse der Limnologie 26:iv + 355 pp.
- DAVIS, G. M. 1979. The Origin and Evolution of the Gastropod family Pomatiopsidae with Emphasis on the Mekong River Triculinae. Monographs of the Academy of Natural Sciences Philadelphia 20:viii + 120 pp.
- DAVIS, G. M., M. McKEE & G. LOPEZ. 1989. The identity of *Hydrobia truncata* (Gastropoda: Hydrobiidae): comparative anatomy, molecular genetics, ecology. Proceedings of the Academy of Natural Sciences of Philadelphia 141:333–359.
- DREVER, J. I. 1982. The Geochemistry of Natural Waters. Prentice-Hall: Englewood Cliffs, New Jersey. xii + 388 pp.
- DUNCAN, A. & P. K. S. KLEKOWSKI. 1967. The influence of salinity on the survival, respiratory rate and heart beat of young *Potamopyrgus jenkinsi* (Smith) (Prosobranchia). Comparative Biochemistry and Physiology 22:495–505.
- FISCHER, W. & P. L. REISCHUTZ. 1995. Zwei neue Taxa von Quellschnecken aus den Gattungen *Graziana* Radoman 1975 und *Belgrandiella* A. J. Wagner 1927 (Gastropoda: Prosobranchia: Hydrobiidae). Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 3:3–7.
- FRETTER, V. & A. GRAHAM. 1978. The prosobranch molluscs of Britain and Denmark. Part 3—Neritacea, Viviparacea, Valvatacea, terrestrial and freshwater Littorinacea and Rissoacea. Journal of Molluscan Studies, Supplement 5:101–152.
- GIROD, A. & E. PEZZOLI. 1967. Ecologia e distribuzione di *Bythinella lacheineri* (Küster) e di *Bythinella schmidtii* (Küster) in Lombardia. Lavori della Società malacologica italiana 3: 97–139.
- GIUSTI, F. & E. PEZZOLI. 1982. Notes on the small Hydrobioidea in Italian subterranean waters: catalogue, biogeography and some systematic problems. Malacologia 22:463–468.
- HAASE, M. 1992. A new, stygobiont, valvuliform, hydrobiid gastropod from Austria (Caenogastropoda: Hydrobiidae). Journal of Molluscan Studies 58:207–214.
- HAASE, M. 1993a. *Belgrandiella ganslmayri*, a new hydrobiid species from Upper Austria (Caenogastropoda). Annalen des Naturhistorischen Museums Wien 94/95 B:181–186.
- HAASE, M. 1993b. *Hauffenia kerschneri* (Zimmermann 1930): zwei Arten zweier Gattungen (Caenogastropoda: Hydrobiidae). Archiv für Molluskenkunde 121:91–109.
- HAASE, M. 1994. Differentiation of selected species of *Belgrandiella* and the redefined genus *Graziana* (Gastropoda: Hydrobiidae). Zoological Journal of the Linnean Society 111: 219–246.
- HAASE, M. 1995. The stygobiont genus *Bythiospeum* in Austria: a basic revision and anatomical description of *B. cf. geyeri* from Vienna (Caenogastropoda: Hydrobiidae). American Malacological Bulletin 11:123–137.
- HAASE, M. 1996. The radiation of spring snails of the genus *Belgrandiella* in Austria (Mollusca: Caenogastropoda: Hydrobiidae). Hydrobiologia 319:119–129.
- HASEKE, H. 1993. Das Projekt "Karstdynamik" im "Nationalpark Kalkalpen": Schwerpunkte Karstschutz und Karstforschung. Wissenschaftliche Beihefte zur Zeitschrift Die Höhle 42:117–128.
- HASEKE, H. 1998. Nationalpark Karstprogramm, Forschungsprojekt Karstquellen-Monitoring und Ereigniskampagnen 1997. Unpublished report submitted to the Nationalpark Oberösterreichische Kalkalpen GmbH, Salzburg. 82 pp.
- HERSHLER, R. 1998. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part I. Genus *Pyrgulopsis*. The Veliger 41:1–132.
- HERSHLER, R. & W. F. PONDER. 1998. A review of morphological characters of hydrobioid snails. Smithsonian Contributions to Zoology 600: iv + 55 pp.
- ILLIES, J. 1978. Limnofauna Europaea: eine Zusammenstellung aller die europäischen Binnengewässer bewohnenden mehrzelligen Tierarten mit Angaben über ihre Verbreitung und Ökologie. Gustav Fischer: Stuttgart. xvii + 532 pp.
- JACOBSEN, R. & V. E. FORBES. 1997. Clonal variation in life-history traits and feeding rates in the gastropod, *Potamopyrgus antipodarum*: performance across a salinity gradient. Functional Ecology 11:260–267.
- JOKELA, J., C. M. LIVELY, J. A. FOX & M. F. DYBDAL. 1997. Flat reaction norms and "frozen" phenotypic variation in clonal snails (*Potamopyrgus antipodarum*). Evolution 51: 1120–1129.
- JUBERTHIE, C. & V. DECU. 1994. Encyclopaedia Biospeologica, Vol. 1. Société de Biospéologie: Moulis & Bucarest. xii + 834 pp.
- JUNGBLUTH, H. J. 1972. Die Verbreitung und Ökologie des Rasenkreises *Bythinella dunkeri* (Frauenfeld 1856). Archiv für Hydrobiologie 70:230–273.
- KUMMERT, R. & W. STUMM. 1989. Gewässer als Ökosysteme. Grundlagen des Gewässerschutzes. Verlag der Fachvereine. Zürich & B. G. Teubner: Stuttgart. xii + 331 pp.
- LASSEN, H. & M. E. CLARK. 1979. Comparative fecundity in three Danish mud snails (Hydrobiidae). Ophelia 18:171–178.
- MAHLER, F. 1950. Zur Spezialisierung der Salzburger Hydrobiden unter Berücksichtigung der neu entdeckten Arten. Mitteilungen der Naturwissenschaftlichen Arbeitsgemeinschaft am Haus der Natur in Salzburg, zoologische Arbeitsgruppe 1:60–61.
- MAIER, F. & A. MAIER. 1997. Steyrerschluht—Rinnende Mauer. Nationalpark Oberösterreichische Kalkalpen (Molln). Oesterreichischer Alpenverein: Innsbruck. 92 pp.
- OSWALD, D., A. KURECK & D. NEUMANN. 1991. Populationsdynamik, Temperaturtoleranz und Ernährung der Quellschnecke *Bythinella dunkeri* (Frauenfeld 1856). Zoologische Jahrbücher (Systematik) 118:65–78.
- OTTO, A. & U. BRAUKMANN. 1983. Gewässertypologie im land-

- lichen Raum. Schriftenreihe des Bundesministers für Ernährung, Landwirtschaft und Forsten, Reihe A: Angewandte Wissenschaft 288:1–61.
- PONDER, W. F. 1988. *Potamopyrgus antipodarum*: a molluscan coloniser of Europe and Australia. *Journal of Molluscan Studies* 54:271–285.
- PONDER, W. F. 1989. Mollusca. Pp. 71–77 in W. F. Ponder & W. Zeidler (eds.), *The Natural History of Dalhousie Springs*. South Australian Museum: Adelaide.
- POSPISIL, P. 1989. *Acanthocyclops gmeineri* n. sp. (Crustacea, Copepoda) aus dem Grundwasser von Wien (Österreich): Bemerkungen zur Zoogeographie und zur Sauerstoffsituation des Grundwassers am Fundort. *Zoologischer Anzeiger* 223: 220–230.
- RADOMAN, P. 1983. Hydrobioidea, a superfamily of Prosobranchia (Gastropoda). I. Systematics (*sic!*). Serbian Academy of Sciences and Arts, Monographs 547. Department of Sciences 57, Belgrade. ii + 256 pp., 12 pls.
- REISCHUTZ, P. L. 1997. *Belgrandiella kreisslorum* n. sp., eine neue Quellschnecke aus der Steiermark. *Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft* 5:20–22.
- TOLLMANN, A. 1985. *Geologie von Österreich*. Vol. 2. Ausser-zentralalpiner Anteil. Franz Deuticke: Wien. xv + 710 pp.
- WINTERBOURN, M. J. 1969. Water temperature as a factor limiting the distribution of *Potamopyrgus antipodarum* (Gastropoda—Prosobranchia) in the New Zealand thermal region. *New Zealand Journal of Marine and Freshwater Research* 3: 453–458.