

**A contribution to the glacial refugia hypothesis for *Bythinella*
Moquin-Tandon, 1856:
Bythinella schmidtii (Küster, 1852) and related species**

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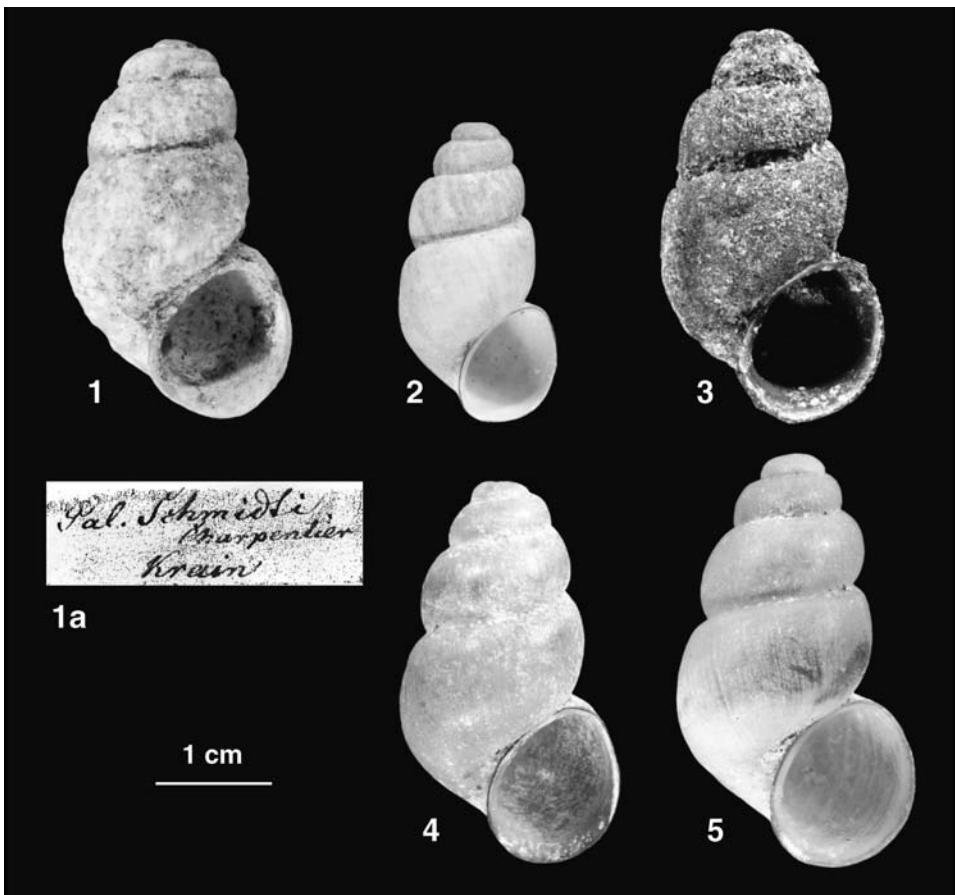
Bythinella bavarica Clessin, 1877, *B. austriaca* (Frauenfeld, 1857) and *B. schmidtii* (Küster, 1852) live in springs of tributaries of the Donau. Tributaries with springs inhabited by *B. austriaca* flow into the Donau, roughly between the more upstream situated drainage area with *B. bavarica* and the more downstream situated drainage area with *B. schmidtii*. A *Bythinella* living within the distribution area of *B. austriaca* and as yet attributed to this species, however, is related, at least conchologically, to the two other species, i.e. *B. schmidtii* and *B. bavarica*. This finding might contribute to the glacial refugia hypothesis for *Bythinella* as discussed by Benke et al. (2007).

Key words: Gastropoda, Caenogastropoda, Hydrobiidae, *Bythinella*, glacial refugia hypothesis, Austria.

Bythinella austriaca (Frauenfeld, 1857) can be found in springs of tributaries of the Donau (Danube) in Austria (Reischütz, 1988: 84, fig. 7) up to the eastern section of said river in Germany (Glöer & Meier-Brook, 2003: 39), whereas *Bythinella bavarica* Clessin, 1877, inhabits essentially more western situated springs of tributaries of the Donau in Austria (Steinmann, 1908: 123; Riezler, 1929: 191) and Germany (Glöer & Meier-Brook, 2003: 39). As regards Große Ache, Inn, Mangfall (Tegernsee tributaries included) and Isar as Donau tributaries, remarkably *B. austriaca* inhabits springs of their lower catchment areas; however, *B. bavarica* lives in springs of the upper areas of these tributaries; see fig. 7.

Since at least *B. austriaca* has been found also in Pleistocene deposits within the glacial boundary cutting across the recent distribution area of this species (Schröder, 1915: 122), it can be assumed that the recent distribution pattern of *B. austriaca* and analogically that of *B. bavarica* are at least partially the result of a secondary invasion after the last glacial period.

According to Benke et al. (2007: 21) "Network and gene flow analyses indicated three distinct recolonization routes: one from the Pyrenees ..., one from northern Italy and Croatia (*B. bavarica*), and one from areas east of the Alps (*B. austriaca*)."
Based on their genetic investigations they postulated a closer relationship between *B. bavarica* and *B. schmidtii* (Küster, 1852) than between both of them and *B. austriaca*. Their sample of *B. schmidtii* was collected in Croatia but not in Kranjska [Krain], i.e. western Slovenia, where the type locality is located. In any case, *B. schmidtii* has its northwestern limits in springs of Donau tributaries in Slovenia (Radoman, 1976: 132, fig. 1 and 139). As mentioned above, in general, *B. austriaca* inhabits springs of Donau tributaries upstream of tributaries with springs inhabited by *B. schmidtii* and downstream of tributaries with springs inhabited by *B. bavarica*. As regards the area inhabited by *B. austriaca*, however, species closely related to *B. bavarica* and *B. schmidtii* have not yet been reported. Only *B. cylindrica* (Frauenfeld, 1857) with its small distribution area in Niederösterreich (Reischütz, 1988: 84, fig. 8) and *B. intermedia* Mahler, 1950, as yet known only from its type locality in Upper



Figs 1-5. *Bythinella* shells and label. 1. *Bythinella schmidtii* (Küster, 1852), lectotype of *Paludina schmidtii* Küster, 1852 (SMF 244716); label (fig. 1a) in Küster's handwriting "Pal. Schmidti Charpentier Krain" [Kranjska, Slovenia]. 2. *Bythinella austriaca* (Frauenfeld, 1857). Boeters leg., 13.iv.2005 (BOE 2572); Lower Austria, Weidlingbach at Weidling, captured spring with basin of Dambachgraben at Rosskopfwiese, 450 m, 3.46.150/7.43.900. 3. *Bythinella lunensis* spec. nov., holotype (SMF 188707); label "Bythinella austriaca Frfld. Lunz, Untersee 17 m Nov. 1966 lg. Hadl det. Hadl". 4-5. *Bythinella bavarica* Clessin, 1877. 4, Boeters leg., 29.x.1980 (BOE 1006), Partenkirchen, Loisachauen, 400 m SE railway and road bridge over river Loisach, ditch in meadow outside spring mouth 5 m beside brook running down from Schafkopf, 52.64.400/44.33.350; 5, Boeters leg., 09.xi.2006 (BOE 2767), Mindelheimer Stadtwald 2.3 km E of Mindelheim (ancient market place), 10 m N Landsberger Strasse at transformer house, spring with brook, 53.24.050/43.89.750.

Austria, can be mentioned, which – at least as regards conchological and anatomical features – must be grouped with *B. austriaca* and not with *B. bavarica* and *B. schmidtii*.

Following Benke et al. that *B. bavarica* invaded from northern Italy and Croatia, the question arises whether the remarkably large geographical gap between the recent distribution areas of *B. bavarica* and *B. schmidtii* is really free of any species more closely relat-

ed to them than to *B. austriaca*. An examination of shells of a *Bythinella*, which were not collected in a spring but on the bottom of a lake, the Untersee at Lunz in Lower Austria, within the distribution area of *B. austriaca*, surprisingly showed a striking similarity with *B. bavarica* and *B. schmidtii* in comparison with *B. austriaca*. This lacustric *Bythinella* will now be described.

By the way, since as mentioned the sample of *B. schmidtii* examined by Benke et al. was collected in Croatia instead of Slovenia, not to mention at the type locality, a typification seems to be reasonable; see fig. 1.

Bythinella lunzensis spec. nov.

Bythinella austriaca; Brehm, 1942: 298, 311.

Bythinella austriaca; Hadl, 1967: 167-168, figs 1-2.

Material. – Lower Austria, Lunz, Untersee, depth 17 m, G. Hadl leg. xi.1966; holotype and 4 ad. and 1 juv. paratypes SMF 188707/6.

Description. – Shell of cylindric conical shape with 4.0 to 4.5 fairly convex whorls, which are separated by a deep suture, the last one being slightly flattened; apex flattened; last whorl in front of the aperture moderately broadened and ascending on the shell wall; border of the aperture slightly broadened at its basis and beneath the slit-like opened umbilicus; aperture slanted ovoid and touching the shell wall; edge of the aperture sharp.

Measurements. Height 3.50-3.65-3.80 mm and width 1.95-2.08-2.20 mm [n = 5].

Animal. – Not examined. Drawings of the operculum and the radula were given by Hadl (1967: 167, figs 1-2).

Differentiating features. – (1) *B. austriaca*. It should not be overlooked that already Hadl (1967: 168) drew attention to the fact that the lacustric *Bythinella*, i.e. *Bythinella lunzensis* spec. nov. and a *Bythinella* found in springs of the surrounding area, certainly *B. austriaca*, differ conchologically when stating: "Auffallend war die Größe der Tiere. ... In umliegenden Quellen gefundene *Bythinella austriaca* erreichten diese Maße niemals." Neighbouring springs with *Bythinella* had already been mentioned by Mahler & Sperling (1955: 14-15, localities 15-16). (2) *B. bavarica* inhabits springs and their drainage. Shells show strongly rounded whorls and correspondingly a rounded angle of the aperture; see Boeters, 1981 (p. 202, figs 96-97) and 1998 (p. 62, pl. P fig. 10) supplemented in 2000 (p. 40). However, in *B. lunzensis* spec. nov. at least the body whorl forms a slight shoulder beneath the suture and the vaulted contour of the last whorl beneath said shoulder is slightly flattened. (3) As regards *B. schmidtii*, Küster (1852: 40, pl. 8 figs 26-30) describes the shell of *Paludina schmidtii* with "Höhe 1 1/3 ", Breite fast 3/4 " ..." corresponding to 2.71 and 1.52 mm, respectively (1 bayerische Duodecimallinie = 2.03 mm; see Anonymus, 1871: 80). However, Radoman (1976: 139) citing the type locality correctly, i.e. "in Krain, in der Umgebung von Laibach" [Ljubljana], mentioning, for example, a "spring by the motel in Medvode by Ljubljana", describes remarkably larger shell heights from the "locus typicus", viz. 2.90-3.28 mm (1976: 141, table 1). These measurements are close to those of four examined syntypes (SMF 244716/4) with a shell height of 2.85-3.14-3.30 mm, the diameter being 1.80-1.95-2.10 mm [n = 4]. Further, from Radoman (1976: 145, pl. 2 fig. 2, "locus typicus", combined with 1983: pl. 12 fig. 204) even a shell height of 3.33-3.45 mm can be concluded. In any case, *B. schmidtii* is restricted to springs and their drainage. Its shell is less elongated and more conical and at least slightly smaller than that of *B. lunzensis* spec. nov.

Habitat and distribution. – Known only as living on the bottom of a lake at a depth of 17 to 25 m in Lower Austria at Lunz, viz. Untersee (Brehm, 1942: 298, 311; Hadl, 1967)

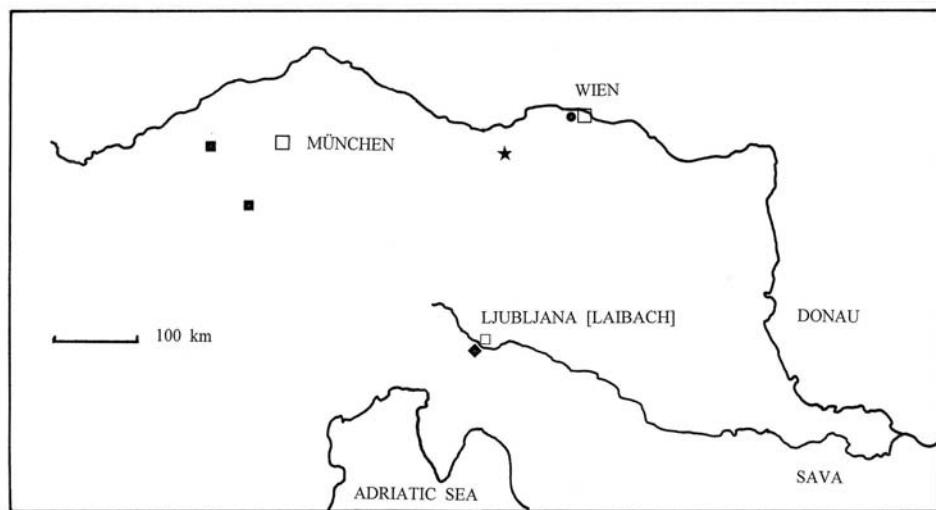


Fig. 6. Geographic position of the localities where the shells of *B. bavarica* (squares), *B. lunzensis* spec. nov. (star), *B. austriaca* (dot) and *B. schmidti* (rhombus) illustrated in figs 1-5 have been collected.

draining into the river Ybbs flowing into the Donau at Ybbs. Hadl (1967: 167) reports from a depth of 17 m a colonization density of about 1780 animals per square meter.

Other reports of *Bythinella* on the bottom of lakes in the northern Alps have not yet become known. However, for the sake of completeness it should be added that Colling collected one animal of *B. austriaca* in the littoral of the Chiemsee (Boeters, 1992: 332). Further, Micoletzky (1913: 8-9) mentions *B. alta* Clessin, 1890, i.e. *B. bavarica*, from a lake at Salzburg, the Faistenauer Hintersee, obviously from its littoral, the equisetum and the characetum. This finding needs confirmation. *B. bavarica* has also been reported by Gaschott (1925; 1927: 306-307) from the littoral of another lake, the Starnberger See, but with the following remark (1925: 273): "Beim Pisidiensieben habe ich im Starnbergersee lebende Bythinellen in das Sieb bekommen. Zu ihrer Ehre muß jedoch gesagt werden, daß nicht weit davon ein Quellbach in den See mündete, der *B. alta* in größerer Anzahl enthielt."

Finally, two other records from lakes in the Alps should be mentioned which, however, have never been confirmed. Blanchet (1911: 356-357) reported *Bythinella* from the Lac Léman with the interesting remark: "à de très grandes profondeurs", and Frauenfeld (1863: 201) mentioned *Bythinella* "aus dem Veldeser See in Kärnten" [lake at Bled (formerly Veldes) in Slovenia]. Since this locality is situated in the southern Alps, not only *Bythinella* but also *Marstoniopsis* Regteren-Altena, 1936, should be taken into consideration.

Remark. – The late Adolf Zilch had already selected a lectotype of *Paludina schmidti* Küster, 1852, out of 4 syntypes. This selection is herewith confirmed and published. However, whereas Küster describes the shell of *P. schmidti* with a height of 2.71 mm and a diameter of 1.52 mm, the measurements of the lectotype are 3.30 and 2.00 mm. When comparing the figures given by Küster, first, the syntype selected as lectotype corresponds better to the figures than all of the other syntypes, and second, as mentioned above, the measurements of the lectotype are in conformity with data published by Radoman for material collected at the "locus typicus".

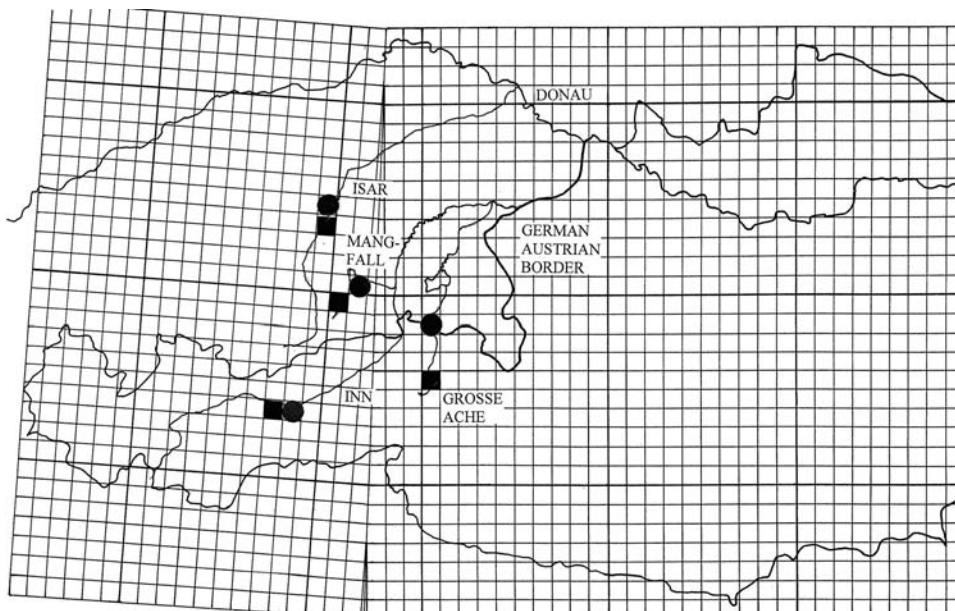


Fig. 7. Illustration of upstream limits of colonization by *B. austriaca* and downstream limits of colonization by *B. bavarica* of Isar, Mangfall, Inn and Grosse Ache Rivers, each by selected localities, viz. - for *B. bavarica* (squares): PU93, Upper Bavaria, München, restaurant Siebenbrunn (BOE 0900); QT08, Upper Bavaria, Bad Wiessee, restaurant Sonnenbichl (BOE 1454); PT73, Northern Tyrol, between Zirl and Innsbruck, Meilbrünnl (BOE 0209) [if one follows Schröder (1913: 46) the limit is further downstream at Kufstein]; UN05, Northern Tyrol, Kitzbühel (Riezler 1929: 191; to be confirmed); - for *B. austriaca* (dots): PU 94, Upper Bavaria, Ismaning (BOE 1100); QU00, Germany, Upper Bavaria, Mangfall bridge of motorway (BOE 1373); PT 83, Northern Tyrol, Weiherburg (BOE 0207); UN08, Northern Tyrol, Kössen (BOE 2674).

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