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MORPHOLOGICAL AND ALLOZYMIC VARIATION WITHIN AND BETWEEN POPULATIONS OF *BYTHINELLA* MOQUIN-TANDON, 1855 (GASTROPODA: PROSOBRANCHIA). I. MORPHOLOGICAL CHARACTERS

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ABSTRACT: Morphology and anatomy of 20 Central European populations of the spring snail *Bythinella* Moquin-Tandon are described and illustrated. Detailed descriptions, drawings and SEM photographs, as well as measurements of shells, opercula, radulae and soft parts are presented, special attention being paid to the reproductive organs. Intrapopulation and interpopulation differences in 40 biometrical characters in males and 42 in females are analysed, for each sex separately, by means of descriptive statistics and ANOVA. Relations between variables are tested with Kendall's correlation coefficient. Biometrical characters vary widely within and slightly between the studied populations, whose variability ranges overlap. The length ratios: shell/radula, bursa/bursa duct and bursa/receptacle, as well as the length of bursa copulatrix and ctenidium display a statistically significant S-N clinal variation. The wide intrapopulation variation combined with the slight differences between the distinguished morphospecies in almost all the morphological characters examined indicates a limited diagnostic value of these characters in *Bythinella*.

KEY WORDS: spring snail, *Bythinella*, population, variation, morphology, anatomy

INTRODUCTION

Prosobranchs included in the Hydrobiidae sensu lato are minute snails. Since their character states are mostly symplesiomorphies or homoplasies, and all display a wide intraspecific variation, the taxonomy of both specific and supraspecific levels within the family is still obscure. The main problem consists in the estimation of taxonomic value of all the small differences among the hydrobiids (FALNIOWSKI 1987a, HAASE 1993, KABAT & HERSHLER 1993, FALNIOWSKI & SZAROWSKA 1995c). Secondly, this is the most speciose family (or rather a family group) of freshwater snails, distributed worldwide and thus difficult to study as a whole. Moreover, studies by different authors considering local forms may be incompatible (HERSHLER & THOMPSON 1988).

Some progress has been made concerning the Hydrobiidae of Far East, Australia, and North America. It is since quite recently that some workers have tried to coordinate their studies on hydrobiids of various parts of the world, to introduce rigorous phenetic or cladistic analyses, and to seek new taxonomically useful characters. As a result of the hydrobiid workshops at the Eleventh and Twelfth Congresses of Unitas Malacologica in Tübingen (1989) and Siena (1992), respectively, a list of morphological characters to be considered in all the future taxonomical studies on hydrobiids has been compiled (HERSHLER & PONDER 1998). FALNIOWSKI and co-workers (FALNIOWSKI 1989a, 1990a, FALNIOWSKI & SZAROWSKA 1991, 1995a, b, c, FALNIOWSKI et al. 1993, 1996) have demonstrated the usefulness of characters of the internal structure of the shell that had not been previously applied in the hydrobiid taxonomy.

Variation within the European Hydrobiidae, including *Bythinella* Moquin-Tandon, 1855, has not been studied in detail so far. In Poland, such studies concerning *Bythinella* are only those by FALNIOWSKI (1980, 1986, 1987a, b, 1992) who presented wide ranges of morphological variation in populations of *Bythinella* and pointed to the interspecific overlap of these ranges, the absence of conspicuous species-specific characters, and the necessity to consider at least several individuals of one population to identify species. However, he did not apply biometrical analysis.

In the summer of 1994 and 1995, samples of *Bythinella* were collected at 20 localities in Poland, Slovakia, and Hungary (Fig. 1). The aim of the study was an analysis of intra- and interpopulation, morphological and molecular (allozyme electrophoresis) variation, with the use of numerical methods to ensure the objectivity and replicability. The results would contribute to a better understanding of the evolutionary processes that take place in populations of *Bythinella*, and of the systematic position of the morphospecies distinguished previously within the genus. The results of molecular studies on the genus have been partly published elsewhere (FALNIOWSKI et al. 1998, 1999, SZAROWSKA et al. 1998). This paper contains a description of morphological variation, based on descriptive, unidimensional statistics. Results of multidimensional phenetic and phylogenetic analysis of morphological and molecular data and the taxonomical conclusions will be presented in the next paper of this series.

MATERIAL AND METHODS

DESCRIPTION OF LOCALITIES

The distribution of the studied populations of *Bythinella* is presented in Figure 1.

1. Bernecebarati, Oszlopo stream in Nagy volgy valley, Borzsony Mountains, Hungary, ca. 4 km SW of Sahy, a town on the Hungarian-Slovakian border; spring area in mixed deciduous forest (hornbeam, birch, Hungarian oak); in trickling outflow, on decaying leaves.
2. Klenany, Krupinska Vrchovina, Slovakia, ca. 16 km NE of 1; source of Klenansky stream; meadow spring surrounded by bushes, on S slope of Bukovina hill; in trickling outflow, on stones and twigs covered with detritus.
3. Bansky Studenec, mountains Stiavnicke Vrchy, Slovakia, ca. 40 km NW of 2; thin outflow from water intake of spring on NE shore of Kolpazske lake; among fine stones and herbs.
4. Klacno, mountains Mala Fatra, Slovakia, ca. 57 km NW of 3; small brook on swampy meadow; in ooze.
5. Telgart, Nizke Tatry, Slovakia, ca. 115 km E of 4; source of Hron river; in big spring on swampy meadow; on aquatic plants.
6. Zakopane, valley Dolina Strążyska, Tatra Mts, Poland, ca. 50 km NW of 5; permanently waterlogged slope; in ooze.
7. Olszówka, Gorce mountains, Poland, ca. 35 km NE of 6; source of Olszówka stream; in thin, muddy brook, bottom of groove; on dead maple leaves.
8. Krowiarki pass, Beskid Wysoki mountains, Poland, ca. 33 km W of 7, spring in mixed forest of maple and fir; on dead leaves.
9. Zawoja–Składy, Beskid Wysoki mountains, Poland, ca. 7.5 km NW of 8; small, muddy brook on swampy meadow, edge of mixed forest on hill slope; on decaying leaves of maple and burdock.
10. Węglówka, Beskid Wyspowy mountains, Poland, ca. 38 km NE of 9; source of small tributary of Węglówka stream; spring area on swampy slope on right bank of Węglówka stream valley, edge of mixed forest; on small stones and submerged grass blades.
11. Spring Źródło Świętego Eliasza, valley of Eliaszówka stream, Kraków-Częstochowa Upland, Poland, ca. 58 km NW of 10; source of left tributary of the stream; big spring supplying ornamental pond; on limestone substrate, among gravel and on stones and *Fontinalis*.
12. Spring Źródło Bazana, valley of Racławka stream, Kraków-Częstochowa Upland, Poland, 2.75 km NEE of 11; source of left tributary of the stream; big spring in deciduous forest; on limestone substrate, on stones and *Fontinalis*.
13. Spring Źródło pod Grotą, valley Dolina Będkowska, Kraków-Częstochowa Upland, Poland, 5.7 km NEE of 12; source of Będkówka stream; big spring among limestone rocks; on stones and aquatic plants.
14. Valley Dolina Sąspowska, Ojców National Park, Kraków-Częstochowa Upland, Poland, 4.7 km NE of 13; source of right tributary of Sąspówka stream; among herbs.
15. Młynnik spring, Ojców National Park, Kraków-Częstochowa Upland, Poland, 3.8 km NNW of 14; source of left tributary of Prądnik river; big spring; among limestone gravel and on plants.
16. Zimny Dół gorge, Kraków-Częstochowa Upland, Poland, 11.65 km S of 12; source of right tributary of Sanka river; spring with concrete boarding; on small sticks and aquatic mosses growing on concrete.

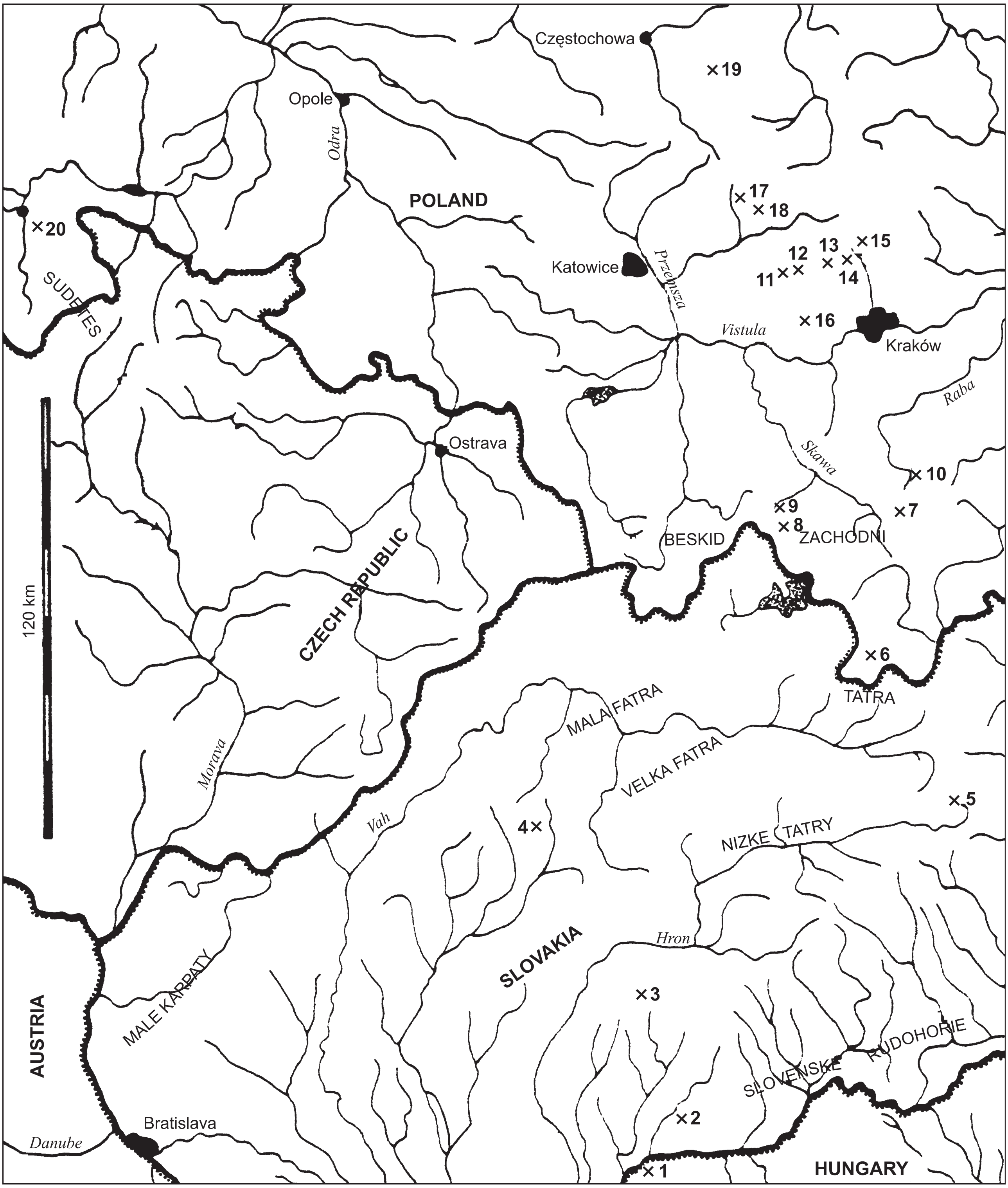


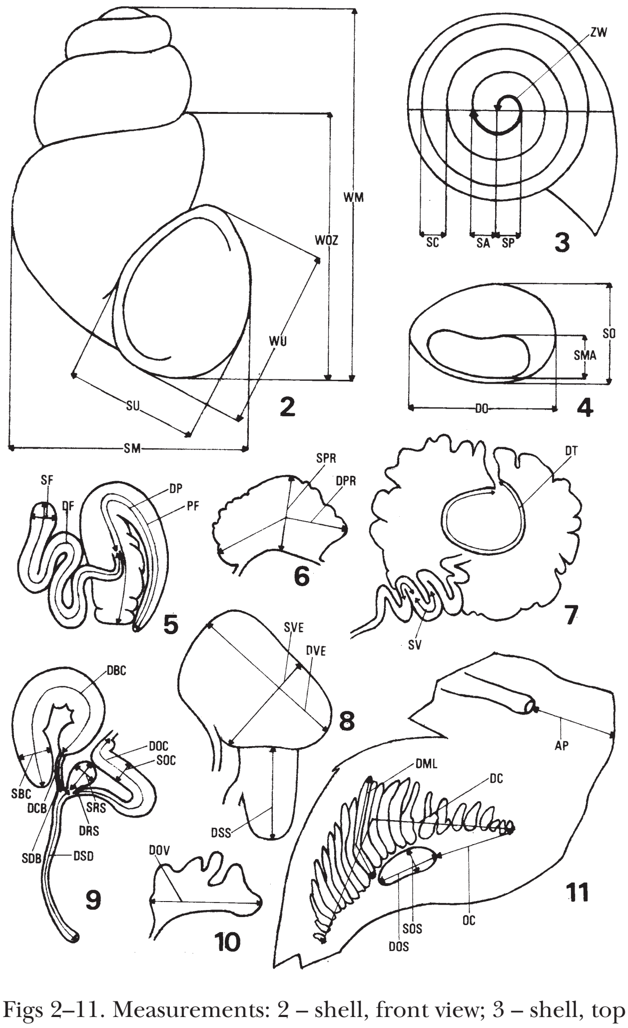
Fig. 1. Distribution of the studied localities of *Bythinella*; after FALNIOWSKI et al. 1998

17. Chechło, Kraków-Częstochowa Upland, Poland, 26.6 km NW of 15; immense outflow of several springs at the foot of steep limestone slope; on borders of the flow, on stones and plants.
18. Kadłubek spring, Kwaśniów, Kraków-Częstochowa Upland, Poland, 5.5 ENE of 17; spring on meadow; on plants.
19. Spring Źródło Zygmunta, stream Potok Złoty, Kraków-Częstochowa Upland, Poland, 37.5 km NW of 18; probably one of the northernmost localities of *Bythinella* in Poland; several big springs in mixed forest of pine and hornbeam; on small stones and sticks.

20. Spring Źródło Romanowskie, Romanowo/Żelazno near Kłodzko, Krowiarki range, Sudetes, Poland, ca. 200 km WSW of 19; the westernmost locality of *Bythinella* in Poland; immense spring at the bottom of gorge in hornbeam wood; on dead hornbeam leaves.

COLLECTION, FIXATION AND DISSECTION

The material was collected by washing small stones, fallen leaves and plants on a sieve of 0.5 mm mesh. The snails were transported alive in a car refrigerator (4°C) or a thermos flask. Of each population which was abundant enough, 60 adults (30 males, 30 females) were taken at random. All the populations were preliminarily classified as the following morphospecies: 1 – *Bythinella* sp. 1 (undescribed); 2 – *Bythinella* sp. 2 (undescribed); 3 – *Bythinella* sp. 3 (undescribed); 4, 11–16, 19, 20 – *Bythinella austriaca* (Frauenfeld, 1856) sensu FALNIOWSKI (1987a); 5 – *Bythinella* sp. 4 (undescribed); 6 – *Bythinella* sp. (5) according to FALNIOWSKI (1987a); 7–10 – *Bythinella cylindrica* (Frauenfeld, 1856), sensu FALNIOWSKI (1987a); 17, 18 – *Bythinella zyvionteki* Falniowski, 1986 (FALNIOWSKI et al. 1999).



Figs 2–11. Measurements: 2 – shell, front view; 3 – shell, top view; 4 – operculum; 5 – penis with flagellum; 6 – prostate; 7 – testis with seminal vesicle; 8 – stomach; 9 – bursa copulatrix, seminal receptacle, coil of oviduct and spermatheca duct; 10 – ovary; 11 – fragment of mantle with ctenidium, osphradium and rectum. For lettering see Appendix I

The snails brought to the laboratory were put in Petri dishes containing tap water with an addition of 1% methylene blue (1:500) and kept for several hours in a refrigerator, to allow the internal organs to be stained in vivo. Next, a camera lucida drawing was made of each shell; measurements were taken from the drawings with a ruler. Each snail was then given a number and put in alcoholic Bouin for 24 hours until the soft tissues fixed and the shell decalcified; following fixation each specimen was transferred to a separate vial labelled with the respective number, containing 70% ethanol.

The snails were placed on a slide and dissected under a CITOVAL stereomicroscope. Measurements were taken with a calibrated eyepiece, or from drawings with a ruler or a curvimeter.

Radulae, removed from the preserved specimens, were immersed in a drop of Clorox and left for a few minutes, then rinsed with water, placed on slides in a drop of Faure's fluid and examined under a ZEISS NFPK light microscope. Cusps were counted, and measurements were taken with a calibrated eyepiece. To avoid erroneous interpretations, several radulae of each population were examined in SEM (JEOL JSM-5400) and photographed. The radulae for SEM examination were cleansed with Clorox, rinsed with 96% ethanol, spread in a drop of ethanol on a stub with double-sided carbon tape, air-dried and gold-coated. Photographs were taken at the midpoint of a radula, to show mature, fully mineralized but not yet worn teeth.

For each population, 40 characters in males and 42 in females were measured or counted, in a total of 1,091 specimens. The measurements are shown in Figures 2–11. Each character was tested for significance of interpopulation differences using ANOVA. Only the characters that differed statistically among populations were further analyzed. For all the variables, descriptive statistics were computed (SOKAL & ROHLF 1987) (Tables 1–8) with the use of SYSTAT for Macintosh v. 5.2.1 and STATISTICA/Mac (StatSoft 1991) packages. Relations between variables were tested with Kendall's correlation coefficient (SOKAL & ROHLF 1987).

RESULTS

EXTERNAL MORPHOLOGY AND ANATOMY OF *BYTHINELLA*

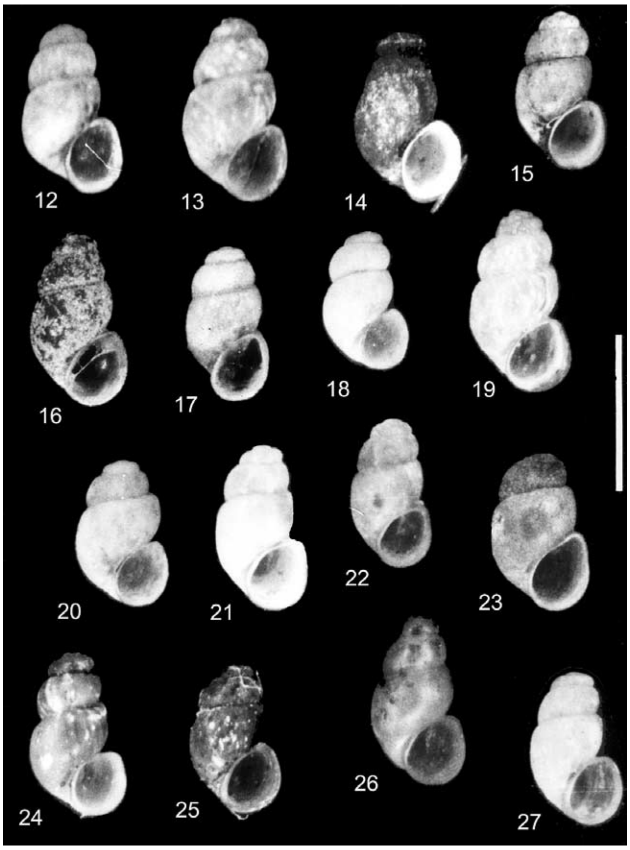
Shell and operculum

The shell of *Bythinella* (Figs 2, 3 and 12–40) is small, usually no more than 3.0 mm in height (mean 2.6 mm), ovate-subquadrate, smooth-surfaced, whitish translucent or creamy. The dark colouring, commonly observed, is due to the pigmented snail body visible through the translucent shell. The shell shows no traces of sexual dimorphism, though the females are usually somewhat larger. The giant specimens found were infected by trematod larvae and had their reproductive organs damaged by the parasites. The regularly increasing whorls, whose number is ca. 4.5, are divided with a deep suture that is almost perpendicular to the columella. The apex is broad, weakly convex or flat. Practically no corrosion of earlier whorls was recorded.

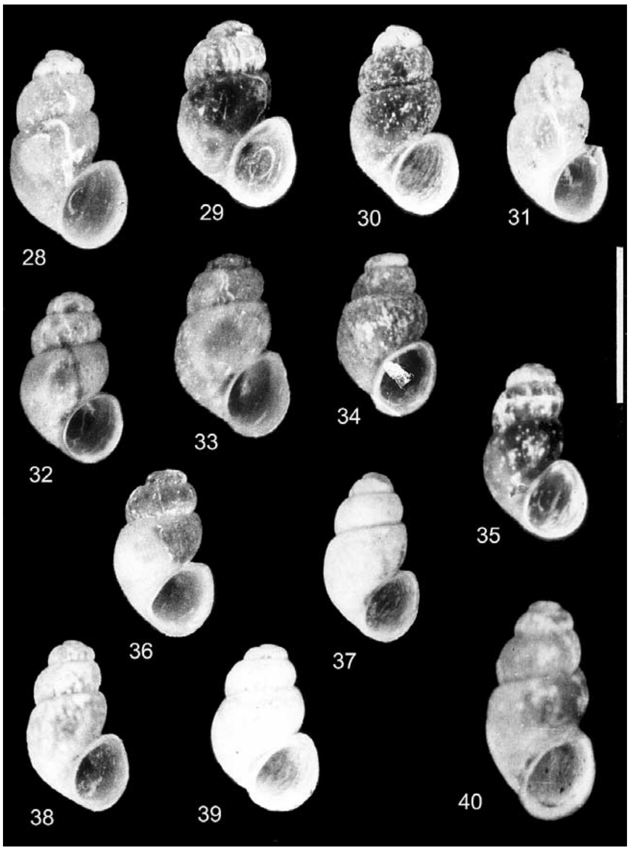
The aperture is broadly oval or oval, or (rarely) ovate-oblong, its outer upper part forms an angle which may be moderately or faintly marked or absent. Like in other Hydrobiidae, the aperture has no incisions, channels or appendages. The peristome is usually continuous; there is no thickened lip. The umbilicus is moderately deep, in the form of a slit located just next to the columellar lip or entirely covered with it. The thin and translucent, conchiolin operculum (Fig. 56) with a conspicuous angle is spiral, has few whorls and an eccentric nucleus.

Body

The head is large, the mouth rather wide, the tentacles long, thin and cylindrical (Figs 41–42). The head pigmentation varies from none (pigmentless head), through a pattern formed by spots of various shape and intensity, to a uniform black. Like in other Hydrobiidae, the eyes in *Bythinella* are situated on



Figs 12–27. Shells: 12, 13 – *Bythinella* sp. 1 (population 1); 14 – *Bythinella* sp. 2 (population 2); 15 – *Bythinella* sp. 3 (population 3); 16, 17 – *B. austriaca* (population 4); 18–20 – *Bythinella* sp. 4 (population 5); 21, 22 – *Bythinella* sp. 5 (population 6); 23–27 – *B. cylindrica*: 23 – population 7; 24, 25 – population 8; 26 – population 9; 27 – population 10. Scale bar 2 mm. For population numbers see: Description of localities



Figs 28–40. Shells: 28–35 – *Bythinella austriaca*: 28 – population 11; 29, 30 – population 12; 31 – population 13; 32, 33 – population 14; 34 – population 15; 35 – population 16; 36–38 – *B. zyvionteki*: 36 – population 17; 37, 38 – population 18; 39–40 – *B. austriaca*: 39 – population 19; 40 – population 20. Scale bar 2 mm. For population numbers see: Description of localities

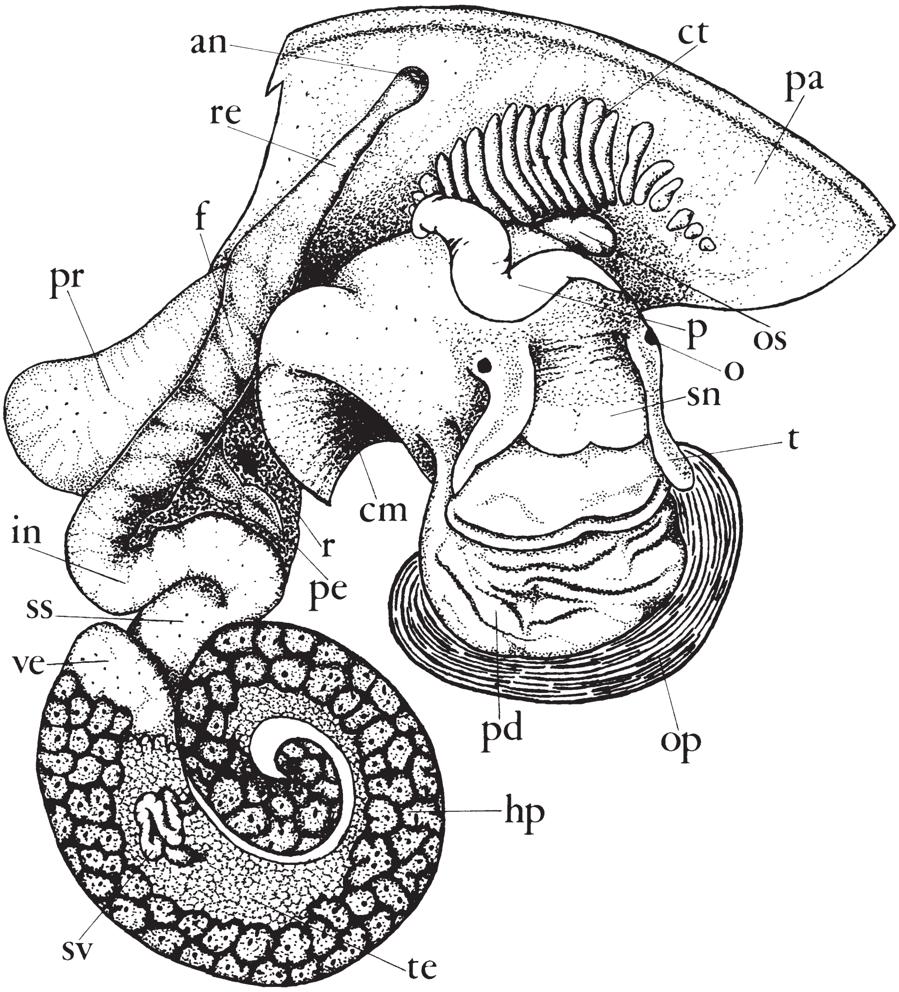


Fig. 41. Anatomy of *Bythinella* male. For lettering see Appendix I

small knobs at the outside of the tentacle bases. The foot is small and narrow, rounded posteriorly.

Ctenidium

The ctenidium (Figs 11, 41–42, 58) has a small number (ca. 28) of short lamellae that are usually weakly bent and arranged loosely in a row. The osphradium (Figs 41–42, 58) is small, usually oval, straight or arched, or may be irregular in shape.

Alimentary tract

The radula, like in all hydrobiids, is taenioglossate. Each transverse row includes seven teeth (Figs 43–55). On either side of the rhachidian there are one lateral and two marginal teeth: the inner and outer ones. The tooth plates bear numerous small cusps (20–36), those on the marginals being uniform. The rhachidian and lateral have one dominant cusp with the smaller ones lying on either side of it, their total number being 15. On the butterfly-shaped rhachidian, besides the cusps located along the cutting edge, like in all Polish hydrobiids, there are 2–3 cusps at the tooth base (Figs 44–55). The stomach (Fig. 57) is little variable; its anterior and posterior parts are well defined, divided by the major typhlosole (typhlosolis maior), the style sac being marked off from the rest of the stomach. A part of the stomach is covered with the hepatopancreas that opens to the gut at the posterior part of the stomach (Figs 41–42). The rectum is straight and terminated with the anus situated on the right side of the mantle cavity, in its anterior part, at the mantle border.

Reproductive system

The female reproductive organs are very much variable (Figs 42, 60–61, 74–86, 98–109, 120–132, 138–143, 150–156, 162–167, 173–178, 185–190, 195–200, 206–211, 217–220, 227–233, 239–243, 248–253, 259–265, 271–275, 281–285, 291–295, 301–305, 312–317). The ovary is sac-shaped, with more or less discernible, lobular convexities situated opposite to the columella. The oviduct is thin anteriorly, then broadens and makes a U-shaped coil lying on the ventral side of the bursa copulatrix. The sac-shaped receptaculum seminis opens to the oviduct at the end of the coil. Next, the oviduct receives

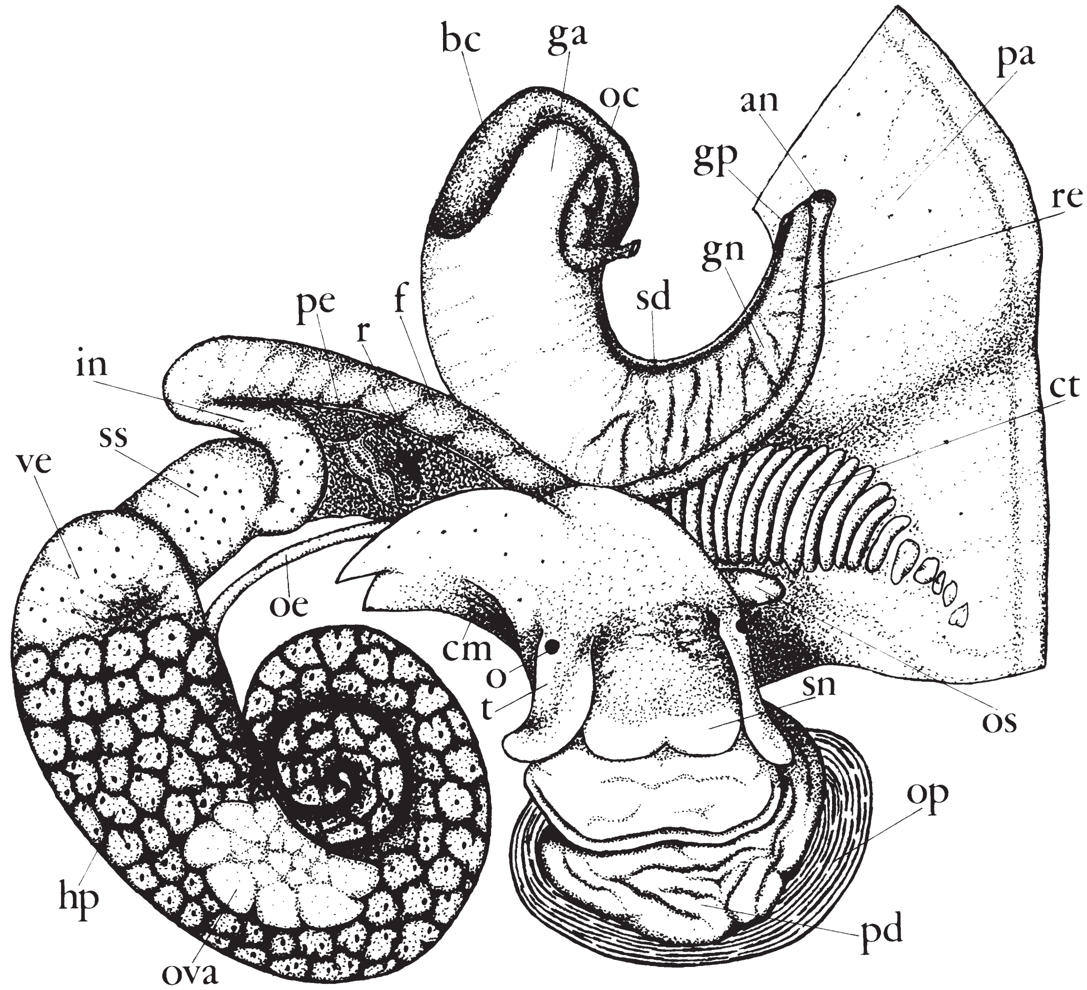


Fig. 42. Anatomy of *Bythinella* female. For lettering see Appendix I

the outlet of the albumen gland and opens to the spermatheca duct, a canal that runs along the pallial section of the oviduct and opens to the mantle cavity in its anterior part. The bursa duct also opens to the spermatheca duct at this point. The bursa, which may be U-shaped, J-shaped, arched or straight in outline, is situated on the ventral side of the albumen gland. The capsule gland is not clearly delimited from the albumen gland and both extend along the spermathecal duct.

The male reproductive organs are shown in Figures 41, 59, 62–73, 87–97, 110–119, 133–137, 144–149, 157–161, 168–172, 179–184, 191–194, 201–205, 212–216, 221–226, 234–238, 244–247, 254–258, 266–270, 276–280, 286–290, 296–300, 306–311. The testis, in the form of branching lobes, is embedded in the hepatopancreas and they both overlap the stomach. The folded seminal vesicle emerges from the testis and, forming several to about a dozen coils, runs along the gonad. Then the vas deferens opens to the prostate gland and next, narrowing gradually, enters the penis which is situated on the back of the head. The prostate gland is well developed and well discernible; it is usually kidney-shaped and lies in the pallial section of the reproductive organs (Fig. 41). The bifid penis is very much variable in shape and size. The vas deferens opens at the end of the left, usually narrower, arm of the penis; in the right arm flagellum runs. The latter is coiled and immersed in the cephalic haemocoel; its proximal end may be

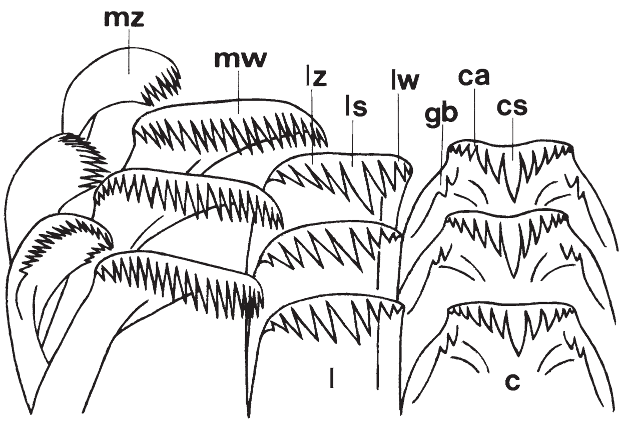
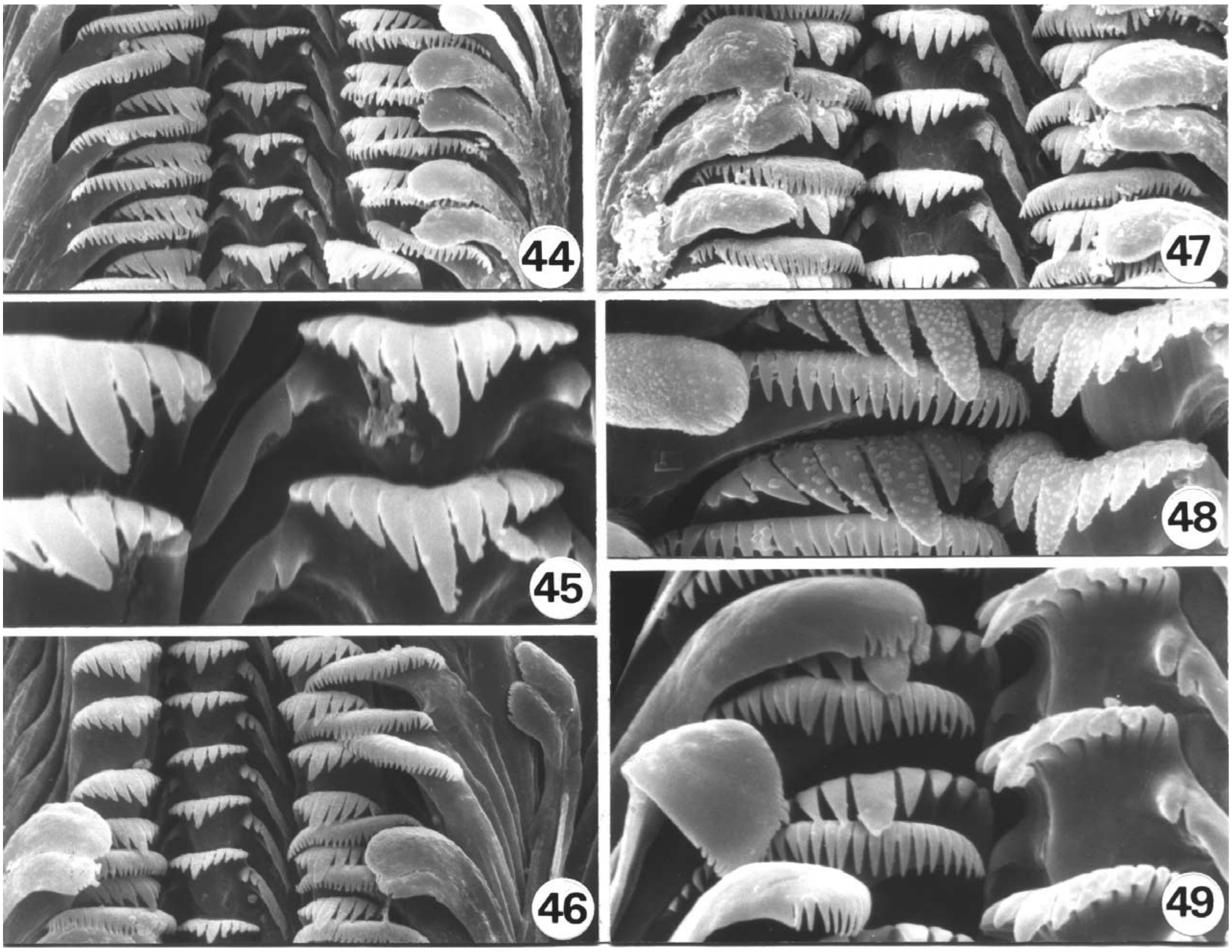


Fig. 43. Transverse radular row in *Bythinella*, diagrammatic. For lettering see Appendix I



Figs 44–49. Radulae: 44 – *Bythinella* sp. 1 (population 1), general view (1,000 ×); 45 – *Bythinella* sp. 1 (population 1), central and lateral teeth (3,000 ×); 46 – *Bythinella* sp. 4 (population 5), general view (1,000 ×); 47 – *Bythinella* sp. 5 (population 6), general view (1,500 ×); 48 – *B. cylindrica* (population 7), left side of radula (2,600 ×); 49 – *B. cylindrica* (population 8), left side of radula (2,400 ×). For population numbers see: Description of localities

broadened and it is usually longer than the penis. The distal end of the flagellum can be everted.

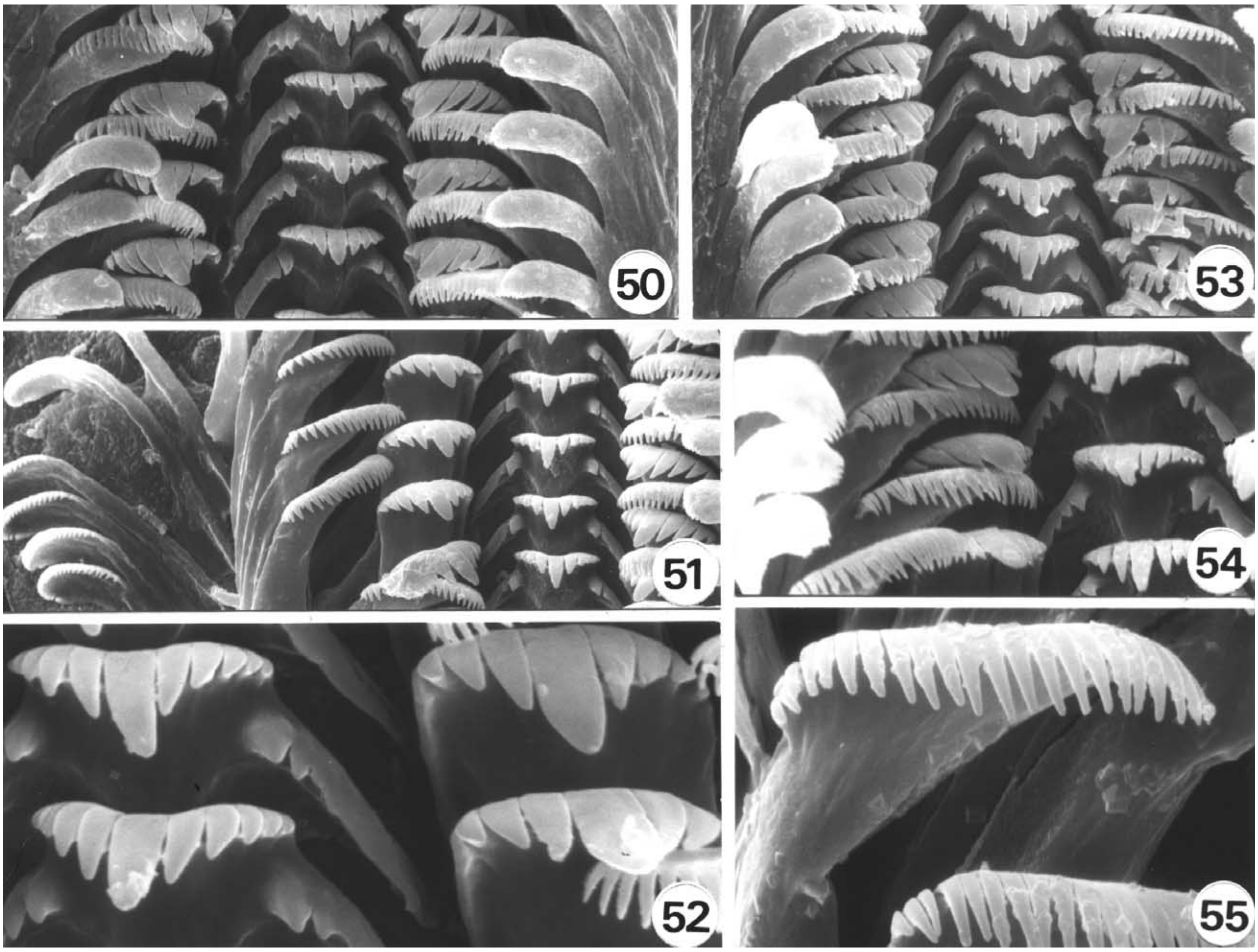
VARIATION OF MORPHOLOGICAL CHARACTERS

Shell and operculum

In the males, the shell varied in height from 1.95 to 3.25 mm; the mean ranging from 2.31 and 2.40 mm in populations 10 and 9 to 2.82 and 2.88 mm in populations 20 and 11, respectively. The widest variability of shell height was recorded in populations 3 and 9, the lowest in population 15 (Tables 1, 2). The females were somewhat larger, their shell height varying from 2.04 to 3.35 mm; the mean value ranged from 2.34 mm in population 10 to 2.84 and 2.89 mm in populations 11 and 20, respectively (Tables 3, 4). The highest values of variability coefficient were recorded for populations 3 and 8, the lowest for populations 17, 18 and 19.

The width of the male shell varied from 1.23 to 2.00 mm; the mean ranging from 1.43 mm in populations 2 and 10 to 1.74 mm in 11; the character was the most variable in populations 2 and 9, the least so in populations 8, 15 and 19. In the females, the shell width ranged from 1.21 to 2.00 mm, while the mean value varied from 1.46 to 1.72 mm in 10 and 11, respectively. The female shell width was the most variable in populations 4, 8, 9, the least variable in populations 17, 18 and 19. The interpopulation variation in shell height/width ratio is shown in Figure 318. The slimmest shells were found in populations 2 and 20 (Figs 14, 40), the stoutest in 5 and 19 (Figs 18–20, 39).

The number of whorls in the male shell was 3.65–5.20; the mean ranging from 4.22 to 4.67 in populations 3 and 20, respectively; the number of whorls was the most variable in populations 3 and 4, the least so in 1 and 2 (Tables 1, 2). In the females, the range was narrower: 3.80–5.00, the mean varying from 4.22 in population 3 to 4.66 in 20. The variation in this character being lower than in the males (Tables 3, 4), it was the highest in populations 3, 12, 15, the lowest in 17, 18, 20. The protoconch diameter varied within



Figs 50–55. Radulae: 50 – *B. austriaca* (population 11), general view (1,000 ×); 51 – *B. austriaca* (population 14), general view (1,000 ×); 52 – *B. zyvionteki* (population 17), central and lateral teeth (2,600 ×); 53 – *B. zyvionteki* (population 17), general view (1,000 ×); 54 – *B. austriaca* (population 20), left side of radula (1,500 ×); 55 – *B. austriaca* (population 20), inner marginal tooth (3,000 ×). For population numbers see: Description of localities

populations, but there was little difference in its mean value among populations (Tables 1–4); it ranged from 0.17 mm to 0.19 mm. It was only in population 3 that its value exceeded the upper limit to reach 0.22 mm in both sexes. On the other hand, population 15 differed from the remaining ones in having the smallest protoconch in both sexes, the diameter being only 0.13 mm, which was accompanied by the widest variability range.

The width of the first and third whorls describe the shape of the spire. The first whorl had the widest variability range in the males of population 5. In that population, and also in 3 and 15 (and 20, females) the variability coefficient of this character reached the highest value, while it varied the least in populations 4, 6 and 10. The variation in the third whorl width was similar in all the populations and in both sexes (Tables 1–4). In general, most shell characters in the males were the most variable in populations 3 and 9, and in the females – in populations 3 and 8. In both sexes the least variable shells were those of the snails of populations 17, 18 and 19. For the little varied operculum measurements, the highest values of variability coefficient were found in the males of population 15 (Table 2) and females of populations 3 and 8 (Table 3).

Radula

SEM photographs of radulae (Figs 44–55) show variation in the radular morphology of the studied snails, manifest mainly in the size and number of cusps in particular tooth types. On the rhachidian tooth, the number of cusps on either side of the central cusp was usually 5 or 6 (Tables 1–4, Fig. 319). It was only in two populations (1 and 6) that the maximum (7), mean and most frequent numbers were biased towards the higher value, whereas in populations 12 and 15 there were usually 4 cusps on the rhachidian. On the lateral tooth, the cusp number was low in populations 15, 17 and 18 (Fig. 319) while the least numerous cusps on the two marginals were found in population 20 (Fig. 320).

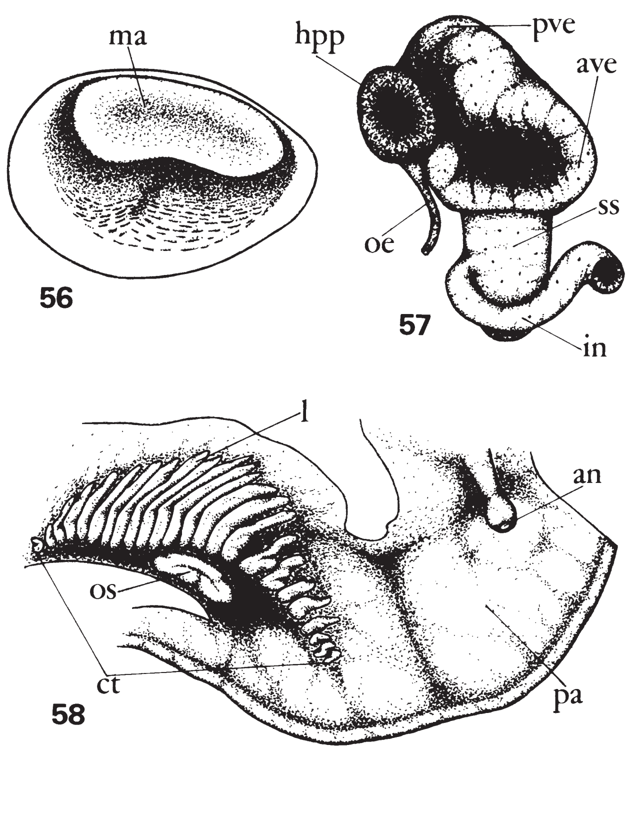
The length of the radula in individuals of both sexes ranged from 0.64 to 1.17 mm, but in the males there was less intrapopulation variation and the mean

(*text is continued on p. 129*)

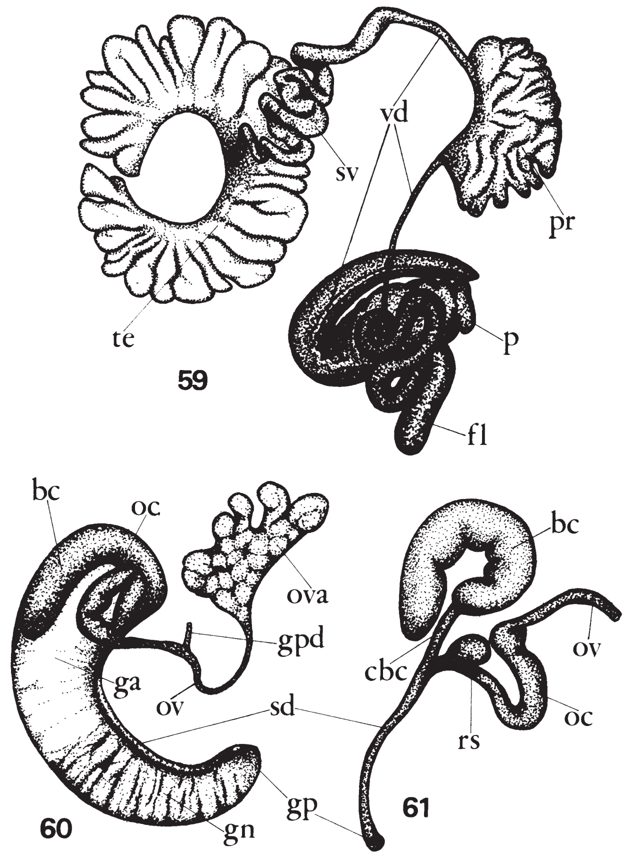
Table 1. Descriptive statistics of shell, operculum and radula: males. Measurements in [mm]. For population numbers see: Description of localities

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	16	3	30	27	30	30	21	30
shell height	min./max.	2.27–3.01	2.27–2.79	2.24–2.98	2.51–2.86	2.31–2.89	2.38–2.81	2.16–2.84	2.24–3.07	1.95–2.87	2.03–2.58
	mean/med.	2.60/2.61	2.51/2.51	2.54/2.53	2.68/2.66	2.49/2.46	2.56/2.53	2.50/2.50	2.57/2.56	2.40/2.39	2.31/2.33
	sd/C.V.	0.15/5.90	0.15/6.06	0.21/8.29	0.17/6.52	0.12/4.73	0.12/4.77	0.16/6.31	0.17/6.51	0.22/9.21	0.13/5.54
shell width	min./max.	1.25–1.70	1.26–1.84	1.36–1.76	1.48–1.66	1.47–1.93	1.27–1.59	1.34–1.65	1.40–1.67	1.23–1.80	1.27–1.63
	mean/med.	1.54/1.55	1.43/1.41	1.52/1.50	1.58/1.59	1.61/1.60	1.48/1.47	1.50/1.50	1.55/1.55	1.47/1.47	1.43/1.41
	sd/C.V.	0.11/7.14	0.16/10.90	0.11/7.38	0.09/5.79	1.93/6.20	0.09/5.80	0.07/5.86	0.07/4.37	0.14/9.55	0.08/5.56
aperture height	min./max.	1.03–1.32	0.92–1.30	1.06–1.36	1.21–1.38	1.13–1.35	1.08–1.32	1.11–1.30	1.10–1.45	1.03–1.36	1.05–1.26
	mean/med.	1.16/1.17	1.16/1.14	1.21/1.20	1.29/1.27	1.24/1.23	1.20/1.19	1.20/1.20	1.23/1.21	1.17/1.17	1.15/1.14
	sd/C.V.	0.07/5.84	0.10/8.52	0.09/7.05	0.08/6.41	0.05/4.34	0.06/5.12	0.05/4.16	0.07/5.76	0.09/7.45	0.05/4.69
aperture width	min./max.	0.70–0.94	0.71–0.99	0.79–1.09	0.86–1.05	0.82–0.99	0.66–0.96	0.76–0.92	0.75–1.00	0.62–1.00	0.74–0.92
	mean/med.	0.84/0.84	0.81/0.79	0.88/0.87	0.96/0.97	0.90/0.90	0.88/0.89	0.85/0.86	0.88/0.89	0.83/0.84	0.83/0.83
	sd/C.V.	0.06/7.17	0.08/9.76	0.07/8.02	0.09/9.85	0.04/4.61	0.07/7.62	0.04/5.08	0.05/6.27	0.10/11.63	0.04/5.11
number of whorls	min./max.	4.25–4.65	4.05–4.45	3.65–4.60	4.45–4.50	4.05–4.75	4.25–5.00	4.05–4.75	4.20–4.90	4.00–4.60	4.00–4.50
	mean/med.	4.40/4.40	4.27/4.25	4.22/4.25	4.47/4.45	4.27/4.25	4.47/4.45	4.33/4.30	4.45/4.45	4.31/4.30	4.24/4.25
	sd/C.V.	0.12/2.33	0.10/2.32	0.24/5.62	0.03/6.46	0.14/3.38	0.15/3.34	0.14/3.33	0.18/4.00	0.15/3.37	0.15/3.50
body whorl height	min./max.	1.66–2.13	1.64–2.06	1.72–2.22	1.84–2.08	1.72–2.07	1.72–2.02	1.67–2.01	1.71–2.20	1.50–2.14	1.62–1.92
	mean/med.	1.87/1.87	1.84/1.84	1.92/1.92	1.96/1.97	1.88/1.87	1.85/1.84	1.84/1.85	1.87/1.86	1.82/1.81	1.76/1.75
	sd/C.V.	0.11/5.79	0.10/5.68	0.13/7.02	0.12/6.33	0.08/4.01	0.08/4.57	0.08/4.32	0.11/6.00	0.15/8.20	0.09/4.87
protoconch diameter	min./max.	0.13–0.26	0.13–0.24	0.17–0.27	0.16–0.19	0.15–0.32	0.13–0.22	0.11–0.26	0.13–0.24	0.14–0.25	0.11–0.23
	mean/med.	0.20/0.21	0.19/0.19	0.22/0.22	0.18/0.18	0.20/0.20	0.17/0.18	0.17/0.17	0.18/0.18	0.17/0.16	0.17/0.17
	sd/C.V.	0.03/15.13	0.03/14.14	0.03/14.29	0.01/6.90	0.03/16.28	0.02/13.76	0.03/19.53	0.02/12.81	0.03/15.38	0.04/21.62
first whorl width	min./max.	0.17–0.27	0.14–0.23	0.14–0.26	0.18–0.19	0.07–0.28	0.18–0.22	0.14–0.24	0.15–0.24	0.16–0.24	0.17–0.23
	mean/med.	0.21/0.21	0.20/0.20	0.20/0.20	0.19/0.19	0.20/0.20	0.19/0.19	0.20/0.20	0.20/0.20	0.19/0.18	0.19/0.19
	sd/C.V.	0.02/10.82	0.02/11.57	0.03/16.29	0.00/1.67	0.03/16.85	0.01/5.90	0.02/11.25	0.02/10.76	0.02/9.46	0.02/6.43
third whorl width	min./max.	0.10–0.18	0.10–0.17	0.09–0.18	0.11–0.15	0.09–0.18	0.10–0.16	0.11–0.18	0.11–0.18	0.10–0.18	0.09-0.19
	mean/med.	0.14/0.13	0.13/0.13	0.13/0.13	0.13/0.15	0.14/0.15	0.13/0.13	0.14/0.14	0.14/0.14	0.14/0.13	0.14/0.13
	sd/C.V.	0.02/12.72	0.02/15.00	0.02/17.33	0.02/15.62	0.02/14.57	0.02/12.21	0.02/17.06	0.02/14.21	0.02/17.27	0.02/17.1
operculum length	min./max.	0.77–1.05	0.81–1.06	0.77–1.05	0.85–0.96	0.80–1.06	0.87–1.04	0.87–1.06	0.82–1.05	0.85–1.06	0.86-0.97
	mean/med.	0.91/0.90	0.90/0.89	0.93/0.92	0.92/0.94	0.94/0.94	0.94/0.94	0.93/0.91	0.95/0.95	0.94/0.94	0.91/0.91
	sd/C.V.	0.06/6.51	0.07/8.02	0.08/8.21	0.06/6.44	0.05/5.74	0.05/4.99	0.05/5.70	0.05/5.41	0.06/6.30	0.03/3.65
operculum width	min./max.	0.52–0.71	0.54–0.70	0.56–0.71	0.55–0.62	0.54–0.69	0.56–0.70	0.56–0.67	0.51–0.72	0.52–0.74	0.56–0.70
	mean/med.	0.62/0.62	0.61/0.61	0.62/0.62	0.60/0.61	0.62/0.62	0.62/0.60	0.60/0.59	0.64/0.65	0.64/0.64	0.61–0.61
	sd/C.V.	0.05/7.44	0.05/7.39	0.04/7.17	0.04/6.74	0.04/7.02	0.04/6.98	0.03/4.86	0.05/7.13	0.05/7.80	0.03/4.76
width of operculum attachment area	min./max.	0.20–0.37	0.21–0.29	0.25–0.44	0.24–0.26	0.22–0.32	0.19–0.31	0.21–0.37	0.21–0.32	0.22–0.29	0.21–0.30
	mean/med.	0.28/0.29	0.25/0.26	0.34/0.32	0.25/0.25	0.27/0.26	0.25/0.25	0.27/0.26	0.27/0.27	0.25/0.25	0.25/0.25
	sd/C.V.	0.04/14.99	0.02/7.86	0.06/16.25	0.01/5.00	0.03/11.18	0.03/13.19	0.04/15.04	0.03/9.54	0.02/6.27	0.02/8.04
radula length	min./max.	0.64–0.89	0.71–0.90	0.84–1.09	0.87–0.94	0.67–0.94	0.75–0.88	0.74–0.92	0.71–0.91	0.76–0.96	0.72–0.91
	mean/med.	0.78/0.77	0.76/0.75	0.93/0.92	0.90/0.90	0.79/0.78	0.82/0.82	0.82/0.81	0.82/0.82	0.84/0.84	0.81/0.81
	sd/C.V.	0.06/7.64	0.05/6.07	0.06/6.48	0.03/3.48	0.07/9.07	0.04/4.32	0.05/6.06	0.06/6.94	0.05/5.45	0.05/6.12
radula width	min./max.	0.07–0.09	0.06–0.09	0.07–0.09	0.08–0.09	0.07–0.09	0.06–0.09	0.07–0.09	0.07–0.09	0.07–0.09	0.07–0.09
	mean/med.	0.08/0.07	0.08/0.08	0.08–0.07	0.09/0.09	0.08/0.09	0.08/0.07	0.08/0.08	0.08/0.08	0.08/0.07	0.08/0.08
	sd/C.V.	0.00/6.17	0.01/8.19	0.01/6.55	0.00/4.22	0.01/8.26	0.01/7.11	0.01/7.29	0.01/7.01	0.00/6.15	0.01/6.46
number of transverse rows	min./max.	87–137	85–112	105–145	95–103	82–138	98–130	93–127	88–122	98–171	87–117
	mean/med.	103.60/102	100.58/100	122.69/117	99.33/100	110.13/107	111.70/112	109.20/109	103.60/102	112.67/108	101.33/101
	sd/C.V.	11.36/10.97	7.14/7.10	13.32/10.86	4.04/4.07	13.31/12.09	7.22/6.46	8.93/8.17	7.99/7.72	15.74/13.97	8.28/8.17
half number of rhachis lateral cusps	min./max.	5.00–6.00	5.00–6.00	5.00–6.00	5.00–5.00	5.00–6.00	5.00–6.50	4.50–6.00	5.00–6.00	5.00–6.00	5.00–6.00
	mean/med.	5.73/6.00	5.45/5.00	5.18/5.00	5.00/5.00	5.68/6.00	5.89/6.00	5.02/5.00	5.62/6.00	5.14/5.00	5.62/6.00
	sd/C.V.	0.43/7.50	0.50/9.12	0.31/5.97	0.00/0.00	0.43/12.09	0.32/5.44	0.28/5.54	0.45/7.99	0.36/6.97	0.47/8.33

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	16	3	30	27	30	30	21	30
half number of rhachis basal cusps	min./max.	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	3.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00
	mean/med.	2.70/3.00	2.58/3.00	2.50/2.50	2.33/2.00	2.30/2.00	3.00/3.00	2.53/3.00	2.37/2.00	2.62/3.00	2.43/2.00
	sd/C.V.	0.47/17.26	0.51/19.67	0.52/20.66	0.58/24.74	0.47/20.26	0.00/0.00	0.50/20.03	0.49/20.71	0.50/19.00	0.50/20.71
number of cusps on inner edge of lateral tooth	min./max.	3.00–6.00	4.00–5.00	4.00–5.00	4.00–4.00	4.00–5.00	4.00–5.00	3.00–4.00	3.00–5.00	4.00–5.00	3.00–5.00
	mean/med.	4.87/5.00	4.58/5.00	4.37/4.00	4.00/4.00	4.63/5.00	4.56/5.00	3.87/4.00	4.23/4.00	4.24/4.00	3.87/4.00
	sd/C.V.	0.57/11.74	0.51/11.08	0.50/11.43	0.00/0.00	0.49/10.58	0.51/11.11	0.35/8.94	0.50/11.91	0.44/10.30	0.51/13.12
number of cusps on outer edge of lateral tooth	min./max.	4.00–6.00	4.00–5.00	4.00–6.00	4.00–4.00	4.00–6.00	5.00–7.00	3.00–5.00	4.00–6.00	4.00–5.00	4.00–6.00
	mean/med.	4.93/5.00	4.84/5.00	5.06/5.00	4.00/4.00	4.87/5.00	5.74/6.00	4.20/4.00	5.07/5.00	4.81/5.00	4.50/4.00
	sd/C.V.	0.58/11.82	0.37/7.74	0.44/8.74	0.00/0.00	0.51/10.43	0.71/12.40	0.48/11.53	0.53/10.28	0.40/8.37	0.63/13.99
number of cusps on inner marginal tooth	min./max.	24.00–33.00	23.00–28.00	21.00–27.00	22.00–25.00	24.00–30.00	24.00–28.00	20.00–29.00	22.00–28.00	20.00–27.00	22.00–27.00
	mean/med.	26.80/27.00	25.74/26.00	23.56/23.50	23.67/24.00	26.63/26.00	25.67/26.00	23.97/23.00	23.83/24.00	24.86/25.00	23.87/24.00
	sd/C.V.	1.99/7.42	1.28/4.99	1.90/8.05	1.53/6.45	1.45/5.44	1.41/5.51	2.13/8.87	1.66/6.98	1.53/6.14	1.31/5.47
number of cusps on outer marginal tooth	min./max.	25.00–33.00	26.00–31.00	25.00–32.00	27.00–28.00	25.00–31.00	27.00–32.00	26.00–31.00	22.00–29.00	26.00–30.00	25.00–31.00
	mean/med.	28.87/28.50	28.58/29.00	27.69/27.50	27.67/28.00	27.93/28.00	29.37/29.00	28.13/28.00	26.00/26.00	27.33/27.00	27.53/28.00
	sd/C.V.	2.05/7.09	1.26/4.41	2.12/7.66	0.58/2.09	1.26/4.50	1.50/5.10	1.31/4.64	2.05/7.89	1.28/4.68	1.63/5.94
rhachis width	min./max.	0.01–0.02	0.01–0.01	0.01–0.02	0.01–0.02	0.01–0.01	0.01–0.01	0.01–0.01	0.01–0.02	0.01–0.01	0.01–0.01
	mean/med.	0.01/0.01	0.01/0.01	0.01/0.01	0.02/0.02	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01
	sd/C.V.	0.00/4.97	0.00/6.79	0.00/7.68	0.00/7.78	0.00/6.81	0.00/4.66	0.00/6.15	0.00/3.29	0.00/4.31	0.00/5.94



Figs 56–58. Operculum and soft parts of *Bythinella*: 56 – operculum; 57 – stomach; 58 – mantle fragment with ctenidium, osphradium and rectum. For lettering see Appendix I

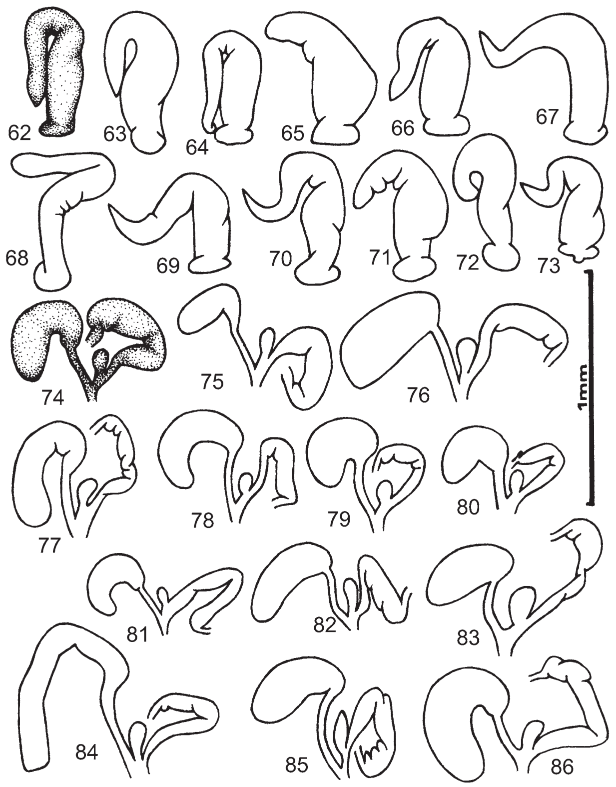


Figs 59–61. Reproductive organs of *Bythinella*: 59 – male, 60 – female, 61 – female with albumen and nidamental glands removed to show seminal receptacle. For lettering see Appendix I

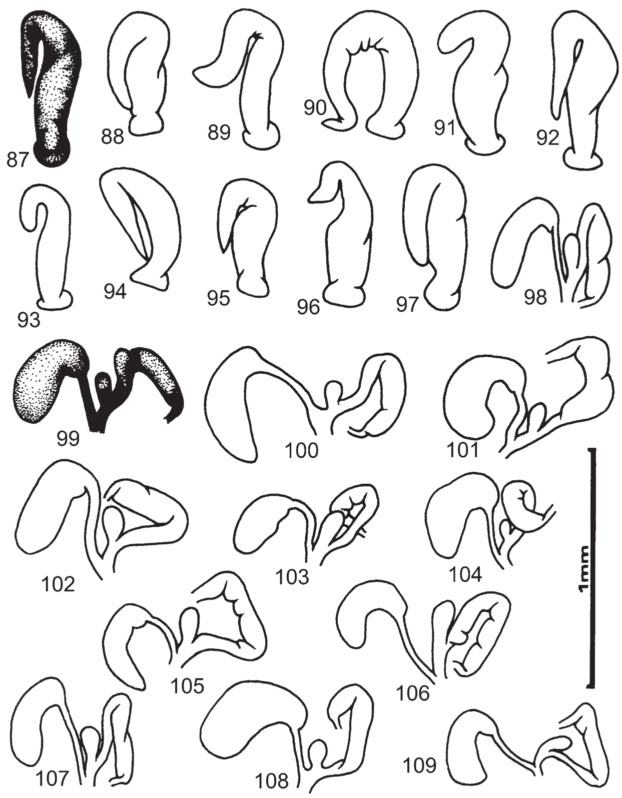
Table 2. Descriptive statistics of shell, operculum and radulae: males. Measurements in [mm]. For population numbers see: Description of localities

Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	21
shell height	min./max.	2.39–3.25	2.51–3.15	2.29–2.85	2.36–2.98	2.23–2.71	2.38–3.00	2.24–2.94	2.30–2.83	2.47–2.90	2.43–3.19
	mean/med.	2.88/2.87	2.78/2.75	2.55/2.55	2.68/2.68	2.51/2.50	2.62/2.62	2.51/2.50	2.54/2.53	2.67/2.66	2.82/2.82
	sd/C.V.	0.19/6.74	0.15/5.52	0.15/5.95	0.16/6.04	0.10/3.98	0.17/6.39	0.15/6.11	0.12/4.54	0.12/4.41	0.20/7.14
shell width	min./max.	1.43–2.00	1.46–1.87	1.33–1.84	1.47–1.91	1.47–1.81	1.36–1.80	1.38–1.77	1.43–1.80	1.54–1.81	1.40–1.88
	mean/med.	1.74/1.74	1.69/1.70	1.57/1.57	1.67/1.65	1.58/1.59	1.61/1.60	1.56/1.54	1.55/1.55	1.69/1.69	1.58/1.57
	sd/C.V.	0.11/6.32	0.11/6.29	0.12/7.69	0.11/6.82	0.08/5.05	0.11/6.68	0.08/5.27	0.09/5.64	0.08/4.65	0.13/8.03
aperture height	min./max.	1.21–1.54	1.15–1.53	1.09–1.43	1.14–1.40	1.14–1.39	1.09–1.40	1.09–1.38	1.13–1.34	1.21–1.41	1.13–1.40
	mean/med.	1.37/1.36	1.31/1.31	1.24/1.24	1.27/1.27	1.25/1.25	1.27/1.27	1.23/1.22	1.23/1.24	1.31/1.29	1.23/1.21
	sd/C.V.	0.08/5.76	0.08/5.90	0.08/6.58	0.08/5.97	0.06/4.95	0.07/5.72	0.07/5.64	0.05/4.39	0.05/4.20	0.08/6.14
aperture width	min./max.	0.76–1.14	0.76–1.08	0.72–1.07	0.78–1.04	0.70–0.99	0.77–1.03	0.76–1.03	0.79–1.00	0.84–1.06	0.70–1.08
	mean/med.	0.99–1.00	0.93/0.93	0.88/0.87	0.93/0.93	0.87/0.88	0.92/0.92	0.90/0.90	0.90/0.92	0.96/0.97	0.89/0.89
	sd/C.V.	0.08/8.09	0.07/7.82	0.07/7.73	0.06/6.95	0.06/7.26	0.07/7.17	0.07/7.42	0.05/6.04	0.05/5.12	0.10/10.91
number of whorls	min./max.	4.25–4.75	4.25–4.98	4.20–4.65	4.15–4.85	4.00–4.65	4.25–4.70	4.10–4.55	4.10–4.55	4.05–4.80	4.35–5.20
	mean/med.	4.52/4.50	4.52/4.55	4.41/4.40	4.44/4.45	4.39/4.45	4.43/4.45	4.30/4.30	4.33/4.30	4.39/4.40	4.67/4.70
	sd/C.V.	0.14/3.16	0.19/4.19	0.12/2.65	0.17/3.93	0.13/2.98	0.11/2.59	0.12/2.89	0.11/2.52	0.15/3.36	0.21/4.40
body whorl height	min./max.	1.84–2.26	1.80–2.27	1.72–2.14	1.78–2.15	1.75–2.08	1.71–2.14	1.69–2.13	1.78–2.04	1.84–2.06	1.75–2.24
	mean/med.	2.09/2.09	2.01/2.01	1.87/1.87	1.97/1.95	1.91/1.89	1.93/1.93	1.89/1.88	1.90/1.90	1.96/1.98	1.96/1.94
	sd/C.V.	0.11/5.20	0.11/5.42	0.10/5.12	0.10/4.85	0.08/3.94	0.09/4.82	0.10/5.39	0.06/3.32	0.06/3.17	0.12/6.15
protoconch diameter	min./max.	0.15–0.22	0.11–0.26	0.14–0.24	0.13–0.24	0.09–0.22	0.13–0.22	0.13–0.24	0.13–0.23	0.13–0.24	0.15–0.23
	mean/med.	0.18/0.18	0.18/0.18	0.19/0.19	0.18/0.19	0.13/0.13	0.17/0.17	0.18/0.18	0.17/0.17	0.19/0.19	0.19/0.19
	sd/C.V.	0.02/10.23	0.03/18.95	0.03/14.09	0.03/16.46	0.03/20.83	0.02/13.39	0.02/13.81	0.03/14.69	0.02/11.86	0.02/11.19
first whorl width	min./max.	0.16–0.23	0.13–0.24	0.15–0.22	0.16–0.23	0.12–0.25	0.16–0.22	0.16–0.22	0.16–0.23	0.16–0.24	0.16–0.23
	mean/med.	0.19/0.19	0.19/0.19	0.18/0.18	0.20/0.19	0.19/0.20	0.19/0.19	0.19/0.19	0.19/0.19	0.19/0.18	0.20/0.21
	sd/C.V.	0.02/8.39	0.03/13.67	0.02/8.59	0.02/8.70	0.03/16.04	0.01/7.57	0.02/8.36	0.02/9.97	0.02/9.45	0.02/8.79
third whorl width	min./max.	0.12–0.20	0.13–0.18	0.11–0.22	0.13–0.22	0.11–0.20	0.13–0.22	0.12–0.19	0.12–0.19	0.13–0.20	0.11–0.20
	mean/med.	0.16/0.16	0.15/0.15	0.16/0.16	0.17/0.16	0.15/0.14	0.17/0.16	0.16/0.16	0.14/0.13	0.16/0.15	0.15/0.15
	sd/C.V.	0.02/14.55	0.02/10.52	0.02/14.34	0.02/12.25	0.02/15.82	0.02/13.58	0.02/14.21	0.02/14.16	0.02/10.46	0.02/14.81
operculum length	min./max.	0.81–1.16	0.82–1.02	0.86–1.05	0.84–1.06	0.76–1.09	0.84–1.07	0.84–1.01	0.77–1.05	0.91–1.05	0.89–1.04
	mean/med.	1.03/1.02	0.96/0.95	0.95/0.95	0.97/0.97	0.94/0.95	1.00/1.00	0.92/0.93	0.93/0.94	0.98/0.97	0.96/0.95
	sd/C.V.	0.07/6.98	0.06/5.82	0.05/5.11	0.05/5.49	0.08/8.72	0.05/5.28	0.05/4.94	0.06/6.10	0.04/3.60	0.05/4.99
operculum width	min./max.	0.60–0.77	0.52–0.71	0.56–0.70	0.59–0.72	0.50–0.82	0.60–0.74	0.56–0.70	0.55–0.70	0.56–0.74	0.55–0.69
	mean/med.	0.71/0.71	0.64/0.65	0.63/0.62	0.64/0.65	0.64/0.63	0.66/0.66	0.63/0.62	0.63/0.62	0.64/0.63	0.61/0.61
	sd/C.V.	0.04/5.88	0.05/7.53	0.03/4.30	0.04/5.66	0.06/9.54	0.03/5.03	0.04/6.54	0.04/5.71	0.04/5.93	0.04/6.38
width of operculum attachment area	min./max.	0.22–0.36	0.22–0.49	0.20–0.30	0.20–0.31	0.19–0.39	0.22–0.32	0.22–0.32	0.21–0.26	0.22–0.31	0.25–0.31
	mean/med.	0.29/0.29	0.29/0.28	0.25/0.25	0.27/0.27	0.29/0.29	0.28/0.27	0.27/0.26	0.24/0.25	0.28/0.27	0.27/0.26
	sd/C.V.	0.03/11.11	0.05/18.22	0.02/9.16	0.02/8.99	0.05/15.86	0.02/9.29	0.02/8.96	0.01/5.14	0.02/8.51	0.02/8.04
radula length	min./max.	0.85–1.02	0.85–1.17	0.72–0.95	0.80–0.96	0.86–1.04	0.79–1.00	0.76–0.89	0.90–1.07	0.92–1.04	0.78–0.99
	mean/med.	0.93/0.92	0.98/0.99	0.83/0.82	0.87/0.87	0.92/0.91	0.90/0.90	0.83/0.84	0.97/0.97	0.85/0.85	0.87/0.86
	sd/C.V.	0.05/4.90	0.07/7.48	0.06/6.83	0.04/4.24	0.04/4.68	0.05/5.29	0.04/4.52	0.04/4.60	0.04/4.26	0.05/5.68
radula width	min./max.	0.07–0.10	0.07–0.10	0.07–0.09	0.07–0.10	0.07–0.09	0.07–0.09	0.07–0.10	0.08–0.10	0.07–0.10	0.08–0.10
	mean/med.	0.09/0.09	0.09/0.09	0.08/0.08	0.09/0.09	0.08/0.08	0.08/0.08	0.09/0.09	0.09/0.09	0.09/0.09	0.09/0.09
	sd/C.V.	0.01/7.40	0.01/8.72	0.01/7.01	0.00/5.48	0.01/7.28	0.01/6.93	0.01/7.26	0.01/6.48	0.01/6.64	0.00/4.24
number of transverse rows	min./max.	80–150	86–120	86–117	94–128	84–111	95–122	86–102	102–143	96–124	82–119
	mean/med.	104.10/104	103.63/101	98.33/97	105.73/103	99.73/101	109.37/109	96.67/97	121.80/121	108.20/108	101.48/100
	sd/C.V.	14.43/13.86	8.09/7.81	8.05/8.18	7.89/7.46	6.92/6.94	7.05/6.45	4.14/4.28	10.44/8.57	5.79/5.35	9.49/9.35
half number of rhachis lateral cusps	min./max.	4.50–5.50	3.00–5.00	5.00–5.50	5.00–6.00	3.00–5.00	5.00–6.00	4.00–5.50	4.00–5.00	5.00–6.00	5.00–6.00
	mean/med.	4.98/5.00	4.25/4.00	5.03/5.00	5.58/5.50	3.80/4.00	5.62/5.50	4.92/5.00	4.92/5.00	5.25/5.00	5.67/6.00
	sd/C.V.	0.16/3.21	0.45/10.59	0.13/2.52	0.44/7.83	0.47/12.27	0.41/7.27	0.26/5.40	0.27/5.40	0.31/6.00	0.40/7.02

Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	21
half number of rhachis basal cusps	min./max.	3.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00
	mean/med.	3.00/3.00	2.53/3.00	2.90/3.00	2.37/2.00	2.63/3.00	2.60/3.00	2.67/2.00	2.63/3.00	2.63/3.00	2.90/3.00
	sd/C.V.	0.00/0.00	0.51/20.03	0.31/10.52	0.49/20.71	0.49/18.61	0.50/19.16	0.50/19.84	0.49/18.61	0.49/18.61	0.30/10.35
number of cusps on inner edge of lateral tooth	min./max.	3.00–5.00	3.00–5.00	3.00–5.00	4.00–5.00	3.00–4.00	3.00–5.00	3.00–4.00	3.00–4.00	3.00–5.00	3.00–4.00
	mean/med.	4.00/4.00	3.63/4.00	4.10/4.00	4.27/4.00	3.50/3.50	4.03/4.00	3.50/3.50	3.13/3.00	4.00/4.00	3.62/4.00
	sd/C.V.	0.37/9.28	0.56/15.30	0.40/9.82	0.45/10.54	0.51/14.53	0.41/10.26	0.51/14.53	0.35/11.03	0.26/6.56	0.50/13.75
number of cusps on outer edge of lateral tooth	min./max.	4.00–5.00	3.00–5.00	4.00–6.00	4.00–6.00	3.00–4.00	3.00–5.00	3.00–4.00	4.00–6.00	4.00–5.00	4.00–5.00
	mean/med.	4.40/4.00	4.10/4.00	4.60/5.00	4.53/4.00	3.70/4.00	4.03/4.00	3.97/4.00	4.10/4.00	4.30/4.00	4.14/4.00
	sd/C.V.	0.50/11.32	0.40/9.82	0.62/13.51	0.63/13.87	0.47/12.60	0.32/7.93	0.18/4.60	0.40/9.82	0.47/10.84	0.36/8.65
number of cusps on inner marginal tooth	min./max.	20.00–25.00	21.00–27.00	23.00–28.00	22.00–26.00	20.00–27.00	21.00–26.00	24.00–28.00	21.00–27.00	23.00–29.00	21.00–25.00
	mean/med.	22.53/23.00	23.60/23.00	24.77/25.00	23.47/23.00	23.47/24.00	23.80/24.00	26.00/26.00	24.00/24.00	24.83/24.00	22.86/23.00
	sd/C.V.	1.28/5.68	1.65/7.00	1.30/5.27	1.07/4.58	1.66/7.05	1.35/5.67	1.17/4.52	1.14/4.77	1.46/5.90	1.06/4.65
number of cusps on outer marginal tooth	min./max.	26.00–34.00	25.00–34.00	25.00–30.00	24.00–32.00	23.00–29.00	23.00–32.00	27.00–33.00	27.00–33.00	28.00–33.00	24.00–28.00
	mean/med.	29.27/29.00	28.6/28.00	27.70/28.00	28.23/28.00	25.57/26.00	28.40/28.00	29.73/30.00	29.63/29.00	30.23/30.00	25.71/26.00
	sd/C.V.	1.62/5.53	2.33/8.14	1.37/4.94	1.55/5.48	1.61/6.30	2.19/7.71	1.44/4.83	1.61/5.43	1.43/4.73	1.19/4.62
rhachis width	min./max.	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02
	mean/med.	0.02/0.02	0.02/0.02	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.02/0.02
	sd/C.V.	0.00/6.43	0.00/5.33	0.00/4.68	0.00/6.18	0.00/7.40	0.00/5.83	0.00/4.49	0.00/4.40	0.00/4.92	0.00/6.04



Figs 62–86. Variation in reproductive organs of *Bythinella* sp. 1 (population 1): 62–73 – penis, 74–86 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

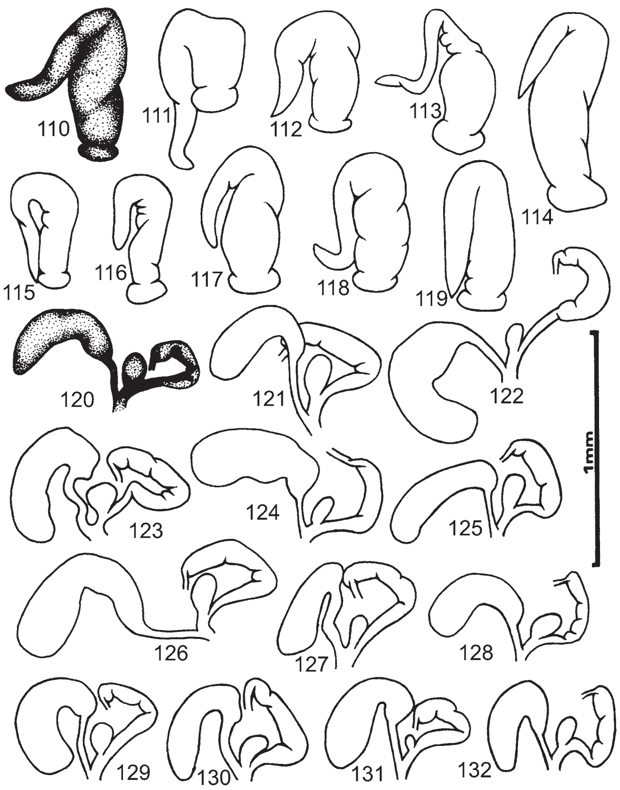


Figs 87–109. Variation in reproductive organs of *Bythinella* sp. 2 (population 2): 87–97 – penis, 98–109 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

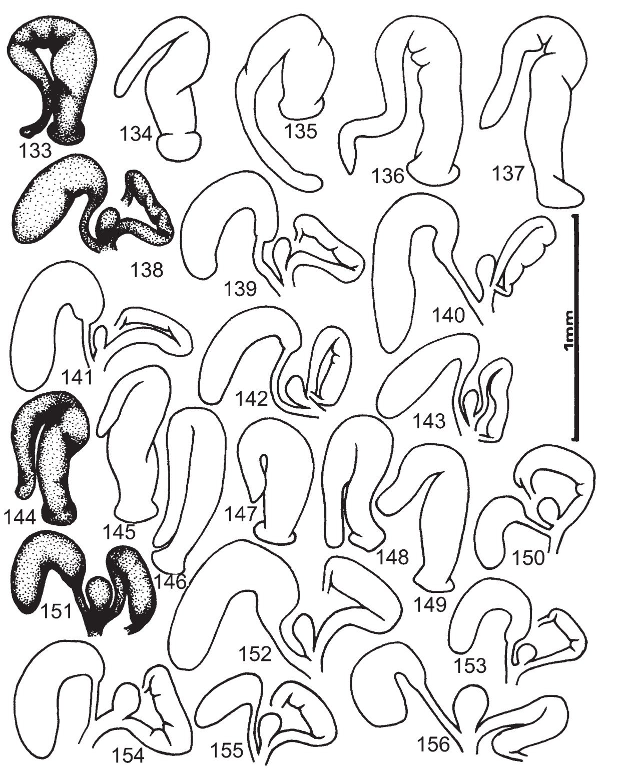
Table 3. Descriptive statistics of shell, operculum and radulae: females. Measurements in [mm]. For population numbers see: Description of localities

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	20	15	30	30	30	30	30	30
shell height	min./max.	2.39–2.99	2.37–2.97	2.27–3.26	2.27–2.96	2.35–3.01	2.31–2.91	2.44–3.08	2.24–3.35	2.18–2.84	2.04–2.73
	mean/med.	2.71/2.71	2.63/2.65	2.56/2.51	2.55/2.49	2.56/2.51	2.60/2.62	2.68/2.63	2.61/2.56	2.57/2.60	2.34/2.32
	sd/C.V.	0.15/5.53	0.16/5.90	0.21/8.26	0.20/7.93	0.17/6.62	0.13/4.99	0.16/6.05	0.25/9.64	0.16/6.30	0.14/6.15
shell width	min./max.	1.36–1.84	1.32–1.69	1.25–1.74	1.35–1.80	1.39–1.84	1.33–1.82	1.33–1.77	1.29–1.79	1.21–1.78	1.31–1.61
	mean/med.	1.58/1.57	1.48/1.48	1.53/1.52	1.55/1.50	1.56/1.54	1.51/1.51	1.56/1.56	1.54/1.50	1.57/1.56	1.46/1.46
	sd/C.V.	0.12/7.67	0.10/6.54	0.12/7.85	0.13/8.55	0.11/7.35	0.10/6.65	0.10/6.31	0.13/8.61	0.13/8.62	0.09/6.03
aperture height	min./max.	1.09–1.40	1.06–1.36	1.09–1.40	1.16–1.41	1.12–1.39	1.16–1.34	1.14–1.33	1.10–1.47	1.05–1.43	1.10–1.43
	mean/med.	1.24/1.24	1.21/1.21	1.22/1.20	1.26/1.25	1.25/1.25	1.24/1.25	1.24/1.22	1.24/1.23	1.23/1.23	1.18/1.16
	sd/C.V.	0.07/5.36	0.07/6.18	0.08/6.46	0.08/6.16	0.07/5.73	0.05/3.97	0.05/3.74	0.07/6.05	0.08/6.74	0.07/5.98
aperture width	min./max.	0.75–1.05	0.69–1.00	0.60–0.97	0.81–1.09	0.40–1.01	0.82–1.00	0.80–1.10	0.66–1.04	0.68–1.02	0.74–0.94
	mean/med.	0.89/0.87	0.85/0.84	0.89/0.90	0.92/0.90	0.88/0.89	0.91/0.90	0.88/0.86	0.87/0.86	0.89/0.89	0.85/0.84
	sd/C.V.	0.06/7.21	0.07/8.21	0.08/8.78	0.08/8.76	0.06/7.24	0.05/5.01	0.06/6.54	0.08/9.22	0.08/8.59	0.05/5.48
number of whorls	min./max.	4.25–4.65	4.05–4.60	3.80–4.55	4.05–4.55	4.00–4.65	4.20–5.00	4.25–4.85	4.05–4.75	4.20–4.75	4.00–4.50
	mean/med.	4.42/4.42	4.30/4.30	4.22/4.25	4.35/4.35	4.30/4.25	4.46/4.45	4.42/4.45	4.39/4.35	4.40/4.35	4.25/4.25
	sd/C.V.	0.12/2.73	0.13/3.02	0.19/4.56	0.15/3.52	0.15/3.53	0.16/3.60	0.16/3.62	0.17/3.97	0.17/3.81	0.13/2.95
body whorl height	min./max.	1.73–2.11	1.76–2.14	1.73–2.23	1.70–2.12	1.78–2.20	1.76–2.08	1.79–2.09	1.73–2.33	1.65–2.15	1.59–2.07
	mean/med.	1.97/1.96	1.93/1.92	1.93/1.91	1.90/1.89	1.92/1.90	1.91/1.91	1.93/1.93	1.91/1.87	1.92/1.90	1.78/1.76
	sd/C.V.	0.09/4.62	0.11/5.58	0.11/5.82	0.12/6.40	0.10/5.06	0.08/4.40	0.08/4.06	0.15/7.72	0.11/5.86	0.10/5.48
protoconch diameter	min./max.	0.15–0.33	0.13–0.27	0.17–0.30	0.15–0.25	0.14–0.26	0.11–0.21	0.13–0.24	0.11–0.24	0.12–0.25	0.10–0.21
	mean/med.	0.21/0.21	0.19/0.19	0.22/0.21	0.19/0.19	0.19/0.19	0.16/0.17	0.17/0.18	0.18/0.18	0.17/0.17	0.17/0.17
	sd/C.V.	0.04/17.81	0.03/16.41	0.04/18.14	0.03/14.76	0.03/15.14	0.03/18.41	0.03/16.09	0.04/19.97	0.03/16.94	0.03/15.93
first whorl width	min./max.	0.16–0.24	0.15–0.26	0.13–0.27	0.14–0.21	0.14–0.24	0.16–0.22	0.18–0.28	0.15–0.24	0.14–0.22	0.16–0.22
	mean/med.	0.20/0.20	0.21/0.21	0.19/0.18	0.18/0.17	0.19/0.19	0.19/0.19	0.22/0.21	0.19/0.19	0.19/0.19	0.19/0.19
	sd/C.V.	0.02/9.70	0.03/13.99	0.03/17.26	0.02/7.54	0.02/14.49	0.02/7.88	0.03/12.37	0.02/11.90	0.02/9.53	0.02/7.95
third whorl width	min./max.	0.11–0.19	0.11–0.17	0.11–0.16	0.11–0.18	0.09–0.22	0.09–0.18	0.11–0.15	0.08–0.18	0.11–0.18	0.10–0.18
	mean/med.	0.15/0.15	0.13/0.13	0.13/0.13	0.14/0.14	0.14/0.13	0.14/0.13	0.12/0.12	0.14/0.13	0.15/0.15	0.14/0.14
	sd/C.V.	0.02/12.93	0.02/14.65	0.02/11.95	0.02/13.12	0.03/18.48	0.02/17.42	0.01/8.84	0.03/18.56	0.02/13.32	0.03/17.92
operculum length	min./max.	0.81–1.12	0.85–0.99	0.82–1.07	0.80–1.02	0.84–1.05	0.86–1.04	0.89–1.06	0.71–1.14	0.91–1.12	0.81–1.05
	mean/med.	0.97–0.96	0.91/0.90	0.94/0.94	0.88/0.86	0.95/0.94	0.95/0.95	1.00/1.00	0.97/0.98	1.01/1.00	0.93/0.94
	sd/C.V.	0.07/6.89	0.04/4.36	0.06/6.36	0.06/7.08	0.06/5.82	0.04/4.62	0.04/4.21	0.08/8.02	0.05/4.83	0.06/6.47
operculum width	min./max.	0.56–0.72	0.52–0.66	0.54-0.74	0.55–0.66	0.52–0.70	0.57–0.71	0.56–0.72	0.42–0.72	0.61–0.72	0.51–0.70
	mean/med.	0.63–0.62	0.60/0.60	0.62/0.62	0.59/0.57	0.61/0.61	0.63/0.62	0.64/0.63	0.63/0.64	0.67/0.67	0.61/0.61
	sd/C.V.	0.03/5.50	0.04/6.49	0.05/8.75	0.03/5.90	0.03/5.72	0.03/5.35	0.04/5.80	0.05/8.47	0.04/5.26	0.04/7.20
width of operculum attachment area	min./max.	0.25–0.44	0.24–0.39	0.19–0.45	0.22–0.30	0.22–0.31	0.19–0.31	0.22–0.31	0.16–0.37	0.20–0.32	0.22–0.36
	mean/med.	0.33/0.31	0.28–0.26	0.31/0.29	0.25/0.25	0.26/0.26	0.26/0.26	0.26/0.25	0.28/0.27	0.26/0.25	0.26/0.26
	sd/C.V.	0.04/12.13	0.04/16.01	0.08/25.03	0.02/8.02	0.02/8.84	0.02/10.92	0.02/8.07	0.04/15.56	0.03/11.76	0.03/10.90
radula length	min./max.	0.71–1.09	0.72–0.95	0.82–1.12	0.77–0.99	0.72–1.09	0.75–0.97	0.81–1.15	0.75–1.05	0.80–1.10	0.64–0.95
	mean/med.	0.82/0.79	0.84/0.85	0.91/0.90	0.88/0.87	0.84–0.81	0.85/0.85	0.91/0.89	0.85/0.84	0.90/0.89	0.82/0.82
	sd/C.V.	0.09/10.63	0.06/6.71	0.08/8.70	0.05/6.19	0.10/12.21	0.04/5.16	0.06/6.73	0.07/8.53	0.07/8.14	0.06/7.78
radula width	min./max.	0.07–0.09	0.06–0.09	0.07–0.09	0.07–0.09	0.07–0.10	0.07–0.09	0.07–0.09	0.07–0.10	0.06–0.09	0.07–0.09
	mean/med.	0.08/0.09	0.08/0.07	0.08/0.07	0.09/0.09	0.08/0.09	0.08/0.07	0.08/0.08	0.09/0.09	0.08/0.08	0.08/0.08
	sd/C.V.	0.01/6.64	0.01/8.60	0.01/8.22	0.01/6.01	0.01/8.83	0.01/6.66	0.01/6.96	0.01/6.88	0.01/7.84	0.01/7.12
number of transverse rows	min./max.	70–142	98–130	100–146	94–126	90–146	97–124	102–161	89–128	103–166	87–116
	mean/med.	109.67/108	112.95/113	119.30/118	101.73/101	113.07/108	113.60/116	117.93/117	109.97/110	121.00/118	100.77/100
	sd/C.V.	13.57/12.37	7.46/6.61	12.74/10.68	8.16/6.02	16.12/14.26	7.80/6.86	10.54/8.94	10.38/9.44	13.79/11.39	7.83/7.77
half number of rhachis lateral cusps	min./max.	5.00–7.00	5.00–6.00	4.00–6.00	5.00–6.00	5.00–6.00	5.00–7.00	4.00–6.00	4.00–6.00	4.00–6.00	5.00–6.50
	mean/med.	5.88/6.00	5.32/5.00	5.02/5.00	5.06/5.00	5.60/6.00	5.95/6.00	5.12/5.00	5.50/5.50	5.13/5.00	5.62/5.00
	sd/C.V.	0.54/9.12	0.45/8.42	0.47/9.40	0.26/5.10	0.46/8.26	0.33/5.56	0.36/7.11	0.54/9.84	0.43/8.46	0.47/8.33

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	20	15	30	30	30	30	30	30
half number of rhachis basal cusps	min./max.	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	3.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00
	mean/med.	2.73/3.00	2.53/3.00	2.55/3.00	2.20/2.00	2.60/3.00	3.00/3.00	2.93/3.00	2.50/2.50	2.57/3.00	2.57/3.00
	sd/C.V.	0.45/16.45	0.51/20.31	0.51/20.02	0.41/18.82	0.50/19.16	0.00/0.00	0.25/8.65	0.51/20.34	0.50/19.64	0.50/19.64
number of cusps on inner edge of lateral tooth	min./max.	4.00–6.00	4.00–5.00	3.00–5.00	3.00–4.00	4.00–5.00	4.00–5.00	3.00–5.00	3.00–5.00	4.00–5.00	3.00–5.00
	mean/med.	4.97/5.00	4.63/5.00	4.15/4.00	3.67/4.00	4.47/4.00	4.50/4.50	4.03/4.00	4.07/4.00	4.33/4.00	3.93/4.00
	sd/C.V.	0.49/9.87	0.50/10.70	0.59/14.15	0.49/13.31	0.51/11.36	0.51/11.30	0.32/7.93	0.52/12.81	0.48/11.06	0.45/11.44
number of cusps on outer edge of lateral tooth	min./max.	4.00–6.00	4.00–6.00	4.00–6.00	3.00–5.00	4.00–6.00	5.00–6.00	4.00–5.00	4.00–5.00	4.00–5.00	4.00–6.00
	mean/med.	4.97/5.00	4.79/5.00	4.80/5.00	4.00/4.00	4.79/5.00	5.67/6.00	4.73/5.00	4.67/5.00	4.77/5.00	4.40/4.00
	sd/C.V.	0.49/9.87	0.54/11.18	0.52/10.90	0.38/9.45	0.49/9.87	0.48/8.46	0.45/9.50	0.48/10.27	0.43/9.02	0.56/12.80
number of cusps on inner marginal tooth	min./max.	23.00–28.00	24.00–30.00	21.00–27.00	22.00–24.00	22.00–31.00	24.00–28.00	20.00–26.00	21.00–27.00	20.00–28.00	21.00–27.00
	mean/med.	25.57/25.50	25.74/25.00	23.10/23.00	23.13/23.00	26.43/27.00	25.70/26.00	23.37/23.50	23.40/23.00	24.30/24.00	23.97/24.00
	sd/C.V.	1.33/5.20	1.73/6.71	1.33/5.77	0.83/3.60	2.34/8.87	1.47/5.70	1.47/6.31	1.45/6.21	1.86/7.65	1.40/5.85
number of cusps on outer marginal tooth	min./max.	26.00–36.00	25.00–32.00	25.00–31.00	27.00–30.00	26.00–33.00	26.00–34.00	24.00–30.00	24.00–33.00	23.00–33.00	25.00–34.00
	mean/med.	29.37/29.0	28.16/28.00	27.35/27.00	28.27/28.00	29.07/29.00	29.77/30.00	27.37/28.00	26.77/26.00	27.43/27.50	28.60/28.00
	sd/C.V.	2.24/7.61	1.57/5.59	1.42/5.21	1.10/3.89	1.96/6.76	2.16/7.26	1.50/5.47	1.96/7.32	2.33/8.49	1.99/6.97
rhachis width	min./max.	0.01–0.02	0.01–0.01	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.01	0.01–0.02	0.01–0.02	0.01–0.01	0.01–0.02
	mean/med.	0.01/0.01	0.01/0.01	0.01/0.01	0.02–0.02	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01	0.01/0.01
	sd/C.V.	0.00/3.93	0.01/6.68	0.00/7.50	0.00/5.78	0.00/7.21	0.00/3.93	0.00/6.98	0.00/5.79	0.00/8.07	0.00/5.86



Figs 110–132. Variation in reproductive organs of *Bythinella* sp. 3 (population 3): 110–119 – penis, 120–132 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

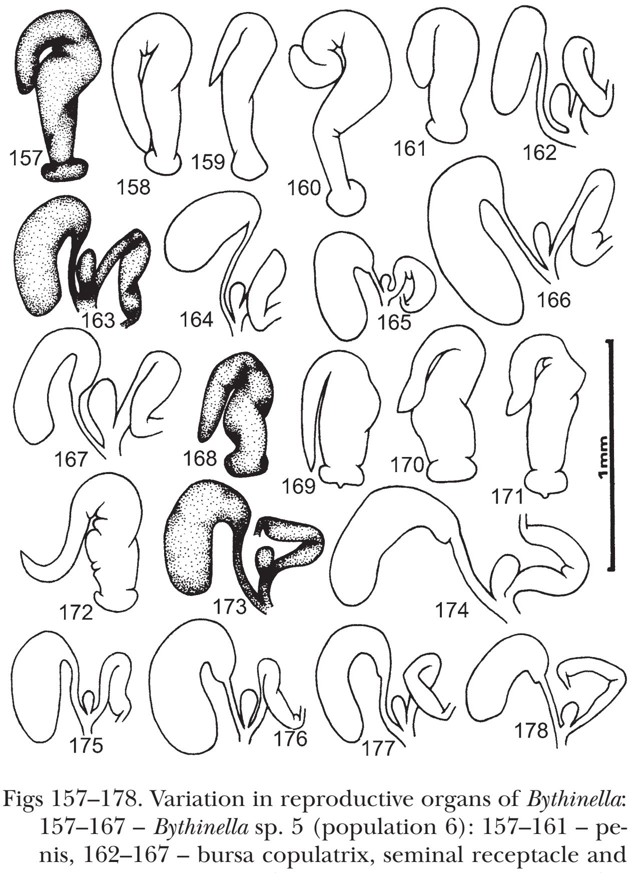


Figs 133–156. Variation in reproductive organs of *Bythinella*: 133–143 – *B. austriaca* (population 4): 133–137 – penis, 138–143 – bursa copulatrix, seminal receptacle and coil of oviduct; 144–156 – *Bythinella* sp. 4 (population 5): 144–149 – penis, 150–156 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

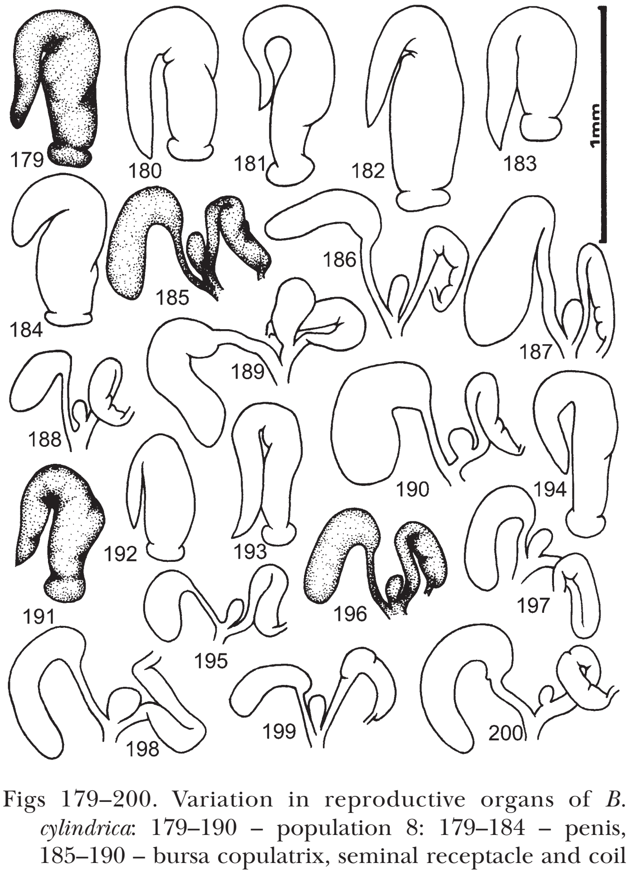
Table 4. Descriptive statistics of shell, operculum and radulae: females. Measurements in [mm]. For population numbers see: Description of localities

Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	30
shell height	min./max.	2.48–3.09	2.43–3.18	2.29–2.97	2.27–3.05	2.35–2.86	2.36–3.08	2.32–2.82	2.38–2.68	2.43–2.84	2.50–3.29
	mean/med.	2.84/2.83	2.76/2.75	2.53/2.49	2.68/2.68	2.57/2.57	2.62/2.59	2.53/2.54	2.54/2.54	2.61/2.62	2.89/2.88
	sd/C.V.	0.14/5.11	0.15/5.61	0.15/6.01	0.18/6.72	0.14/5.58	0.16/6.28	0.12/4.58	0.09/3.53	0.11/4.37	0.19/6.62
shell width	min./max.	1.48–1.97	1.43–2.00	1.35–1.74	1.43–1.86	1.43–1.96	1.48–1.97	1.42–1.69	1.38–1.67	1.55–1.81	1.38–1.86
	mean/med.	1.72/1.73	1.70/1.69	1.55/1.54	1.67/1.67	1.60/1.56	1.62/1.62	1.56/1.55	1.55/1.55	1.67/1.67	1.64/1.63
	sd/C.V.	0.10/5.63	0.14/8.12	0.10/6.18	0.11/6.69	0.13/7.90	0.10/6.21	0.08/4.87	0.07/4.49	0.08/4.61	0.12/7.55
aperture height	min./max.	1.13–1.51	1.16–1.51	1.08–1.34	1.09–1.48	1.14–1.41	1.13–1.51	1.17–1.34	1.16–1.33	1.19–1.43	1.17–1.46
	mean/med.	1.36/1.38	1.32/1.31	1.21/1.21	1.26/1.25	1.27/1.26	1.29/1.28	1.24/1.24	1.24/1.24	1.29/1.29	1.29/1.30
	sd/C.V.	0.08/6.23	0.08/6.13	0.05/4.43	0.09/6.80	0.06/5.05	0.07/5.76	0.04/3.29	0.04/3.59	0.06/4.48	0.06/4.77
aperture width	min./max.	0.84–1.08	0.74–1.07	0.74–0.97	0.76–1.11	0.71–1.07	0.86–1.16	0.80–0.99	0.77–0.97	0.84–1.08	0.74–1.07
	mean/med.	0.99/1.00	0.94/0.93	0.87/0.88	0.93/0.94	0.87/0.86	0.93/0.93	0.88/0.88	0.88/0.87	0.94/0.94	0.94/0.96
	sd/C.V.	0.05/5.16	0.08/8.61	0.05/6.02	0.07/7.57	0.08/8.78	0.06/6.31	0.05/5.70	0.05/5.82	0.05/5.18	0.09/9.11
number of whorls	min./max.	4.30–4.85	4.15–4.95	4.25–4.70	4.25–4.90	3.85–4.95	4.05–4.55	4.15–4.45	4.05–4.55	4.15–4.65	4.30–5.00
	mean/med.	4.51/4.50	4.48/4.45	4.43/4.42	4.42/4.40	4.42/4.42	4.36/4.37	4.30/4.25	4.32/4.30	4.34/4.30	4.66/4.70
	sd/C.V.	0.15/3.28	0.20/4.55	0.14/3.15	0.15/3.34	0.22/4.93	0.14/3.28	0.09/2.06	0.10/2.20	0.13/2.90	0.17/2.74
body whorl height	min./max.	1.82–2.25	1.87–2.34	1.67–2.02	1.70–2.20	1.79–2.20	1.73–2.22	1.77–2.11	1.78–2.05	1.79–2.11	1.86–2.27
	mean/med.	2.09/2.09	2.05/2.07	1.87/1.87	1.99/2.00	1.95/1.96	1.97/1.95	1.92/1.92	1.92/1.92	1.95/1.94	2.03/2.02
	sd/C.V.	0.09/4.52	0.10/4.91	0.08/4.08	0.11/5.76	0.10/4.88	0.10/5.28	0.08/4.12	0.06/3.22	0.08/4.34	0.10/4.99
protoconch diameter	min./max.	0.14–0.26	0.12–0.29	0.12–0.22	0.13–0.24	0.09–0.22	0.13–0.22	0.13–0.22	0.11–0.21	0.14–0.25	0.13–0.24
	mean/med.	0.18/0.18	0.19/0.19	0.18/0.18	0.18/0.18	0.13/0.13	0.18/0.19	0.18/0.18	0.17/0.16	0.18/0.18	0.19/0.19
	sd/C.V.	0.03/15.09	0.04/19.02	0.03/16.31	0.03/14.22	0.04/24.32	0.02/13.34	0.02/13.51	0.02/13.52	0.03/15.97	0.03/13.42
first whorl width	min./max.	0.16–0.24	0.15–0.25	0.16–0.22	0.16–0.22	0.15–0.24	0.16–0.22	0.16/0.22	0.15–0.25	0.13–0.22	0.16–0.24
	mean/med.	0.20/0.19	0.20/0.20	0.18/0.19	0.19/0.19	0.19/0.20	0.19/0.19	0.19/0.19	0.20/0.19	0.18/0.19	0.20/0.20
	sd/C.V.	0.02/9.01	0.02/10.47	0.02/8.35	0.02/9.15	0.02/14.75	0.02/8.50	0.02/8.89	0.02/11.85	0.02/10.09	0.02/17.33
third whorl width	min./max.	0.12–0.20	0.11–0.20	0.09–0.22	0.11–0.24	0.10–0.22	0.11–0.23	0.11–0.19	0.10–0.22	0.13–0.22	0.11–0.22
	mean/med.	0.16/0.16	0.15/0.15	0.15/0.15	0.16/0.16	0.16/0.16	0.17/0.16	0.15/0.15	0.16/0.16	0.17/0.17	0.16/0.16
	sd/C.V.	0.02/11.43	0.02/14.51	0.03/18.16	0.03/16.00	0.03/16.54	0.02/14.52	0.02/14.13	0.03/17.45	0.02/13.56	0.03/17.33
operculum length	min./max.	0.85–1.11	0.84–1.07	0.86–1.07	0.87–1.09	0.79–1.10	0.87–1.09	0.85–0.99	0.86–1.00	0.92–1.07	0.89–1.05
	mean/med.	1.05/1.05	0.97/0.96	0.95/0.94	0.98/0.98	0.96/0.96	1.00/1.00	0.92/0.92	0.94/0.94	1.00/1.00	0.97/0.96
	sd/C.V.	0.05/4.91	0.06/5.92	0.05/5.37	0.05/5.33	0.06/6.51	0.05/4.88	0.04/3.84	0.04/4.17	0.04/3.62	0.04/4.00
operculum width	min./max.	0.60–0.82	0.57–0.70	0.56–0.71	0.54–0.72	0.56–0.79	0.60–0.75	0.57–0.75	0.54–0.72	0.57–0.72	0.56–0.71
	mean/med.	0.71/0.71	0.65/0.65	0.65/0.64	0.64/0.64	0.65/0.65	0.67/0.67	0.62/0.62	0.63/0.64	0.65/0.65	0.61/0.61
	sd/C.V.	0.06/7.98	0.04/6.02	0.04/6.11	0.05/7.41	0.04/6.72	0.04/5.94	0.03/5.04	0.04/6.25	0.04/5.77	0.03/5.36
width of operculum attachment area	min./max.	0.24–0.37	0.25–0.40	0.22–0.35	0.22–0.31	0.20–0.40	0.25–0.34	0.24–0.40	0.22–0.31	0.22–0.34	0.25–0.31
	mean/med.	0.28/0.27	0.31/0.31	0.26/0.26	0.27/0.26	0.30/0.30	0.29/0.29	0.27/0.27	0.26/0.26	0.27/0.27	0.27/0.27
	sd/C.V.	0.03/11.72	0.04/12.17	0.02/9.52	0.02/8.90	0.04/14.16	0.03/8.79	0.03/10.92	0.02/8.07	0.03/9.28	0.02/7.37
radula length	min./max.	0.90–1.11	0.84–1.17	0.82–1.05	0.71–1.00	0.85–1.06	0.77–1.05	0.76–0.96	0.87–1.07	0.76–0.96	0.70–0.99
	mean/med.	1.00/1.00	0.97/0.94	0.91/0.89	0.87/0.87	0.95/0.95	0.93/0.94	0.86/0.85	0.95/0.95	0.87/0.87	0.89/0.90
	sd/C.V.	0.05/5.19	0.08/7.95	0.05/6.04	0.07/7.77	0.05/5.73	0.07/7.84	0.04/4.71	0.05/5.42	0.04/5.11	0.06/6.41
radula width	min./max.	0.07–0.10	0.07–0.10	0.07–0.10	0.07–0.10	0.07–0.09	0.07–0.09	0.07–0.10	0.07–0.10	0.08–0.10	0.07–0.10
	mean/med.	0.09/0.09	0.09/0.09	0.09/0.09	0.09/0.09	0.08/0.09	0.08/0.09	0.09/0.09	0.09/0.09	0.09/0.09	0.09/0.09
	sd/C.V.	0.01/7.74	0.01/7.21	0.01/8.34	0.01/6.78	0.01/6.92	0.01/5.99	0.01/7.92	0.01/6.32	0.01/5.67	0.01/6.72
number of transverse rows	min./max.	70–136	83–127	88–131	84–130	89–121	95–131	90–114	105–155	97–123	87–121
	mean/med.	110.13/109	105.97/107	108.13/108	105.27/106	99.40/97	112.57/115	97.43/97	120.07/119	109.13/108	103.37/101
	sd/C.V.	13.65/12.39	11.87/10.20	9.84/9.10	9.40/8.93	6.69/6.73	10.55/9.37	5.41/5.55	9.33/7.77	7.05/6.46	8.50/8.22
half number of rhachis lateral cusps	min./max.	4.00–6.00	3.00–5.00	5.00–5.50	5.00–6.00	3.00–5.00	5.00–6.00	4.00–6.00	4.50–5.50	4.50–6.00	5.00–6.50
	mean/med.	4.95/5.00	4.33/4.50	5.08/5.00	5.57/5.50	3.83/4.00	5.68/6.00	4.87/5.00	4.88/5.00	5.27/5.00	5.70/5.75
	sd/C.V.	0.36/7.19	0.48/11.06	0.19/3.73	0.43/7.73	0.42/11.01	0.40/7.11	0.37/7.60	0.28/5.82	0.41/7.78	0.39/6.76

Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	30
half number of rhachis basal cusps	min./max.	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00	2.00–3.00
	mean/med.	2.97/3.00	2.70/3.00	2.93/3.00	2.63/3.00	2.33/2.00	2.53/3.00	2.17/2.00	2.63/3.00	2.60/3.00	2.93/3.00
	sd/C.V.	0.18/6.15	0.47/17.26	0.25/8.65	0.49/18.61	0.48/20.55	0.51/20.03	0.38/17.49	0.49/18.61	0.50/19.16	0.25/8.65
number of cusps on inner edge of lateral tooth	min./max.	4.00–5.00	3.00–4.00	4.00–5.00	3.00–5.00	3.00–5.00	3.00–5.00	3.00–4.00	3.00–4.00	3.00–5.00	3.00–4.00
	mean/med.	4.10/4.00	3.53/4.00	4.33/4.00	4.17/4.00	3.57/4.00	4.03/4.00	3.33/3.00	3.20/3.00	4.00/4.00	3.57/4.00
	sd/C.V.	0.31/7.44	0.51/14.36	0.48/11.06	0.53/12.74	0.57/15.93	0.41/10.26	0.48/14.38	0.41/12.71	0.26/6.56	0.50/14.13
number of cusps on outer edge of lateral tooth	min./max.	4.00–5.00	3.00–5.00	4.00–6.00	4.00–5.00	3.00–5.00	3.00–5.00	3.00–5.00	4.00–5.00	4.00–5.00	4.00–5.00
	mean/med.	4.53/5.00	3.93/4.00	4.80/5.00	4.40/4.00	3.73/4.00	4.13/4.00	4.03/4.00	4.17/4.00	4.70/5.00	4.33/4.00
	sd/C.V.	0.51/11.19	0.52/13.24	0.48/10.09	0.50/11.32	0.52/13.95	0.43/10.50	0.49/12.15	0.38/9.10	0.47/9.92	0.48/11.06
number of cusps on inner marginal tooth	min./max.	20.00–26.00	21.00–26.00	22.00–27.00	22.00–26.00	20.00–27.00	22.00–26.00	22.00–28.00	21.00–28.00	23.00–27.00	20.00–25.00
	mean/med.	23.27/23.00	23.23/23.00	24.73/25.00	23.73/24.00	23.93/24.00	24.13/24.00	25.93/26.00	23.40/23.00	24.50/24.00	22.67/23.00
	sd/C.V.	1.26/5.40	1.25/5.38	1.14/4.62	1.11/4.69	1.74/7.27	1.28/5.30	1.26/4.84	1.40/6.00	1.31/5.33	1.37/6.06
number of cusps on outer marginal tooth	min./max.	25.00–34.00	25.00–34.00	27.00–30.00	25.00–32.00	21.00–31.00	25.00–32.00	27.00–34.00	26.00–34.00	28.00–34.00	23.00–32.00
	mean/med.	29.70/30.00	28.50/28.00	28.50–28.00	28.40/28.50	26.27/27.00	28.53/28.00	29.77/30.00	29.40/29.50	30.23/30.00	26.27/26.00
	sd/C.V.	1.86/6.26	2.52/8.83	0.86/3.02	1.73/6.11	2.29/8.71	1.81/6.36	1.74/5.83	1.65/5.62	1.38/4.57	1.76/6.70
rhachis width	min./max.	0.01–0.01	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02	0.01–0.02
	mean/med.	0.01/0.01	0.02/0.02	0.01/0.01	0.01/0.01	0.01/0.01	0.02/0.02	0.01/0.01	0.01/0.01	0.01/0.01	0.02/0.02
	sd/C.V.	0.00/5.67	0.00/6.56	0.00/6.84	0.00/5.90	0.00/9.35	0.00/3.93	0.00/5.40	0.00/5.38	0.00/4.98	0.00/6.33



Figs 157–178. Variation in reproductive organs of *Bythinella*: 157–167 – *Bythinella* sp. 5 (population 6): 157–161 – penis, 162–167 – bursa copulatrix, seminal receptacle and coil of oviduct; 168–178 – *B. cylindrica* (population 7): 168–172 – penis, 173–178 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

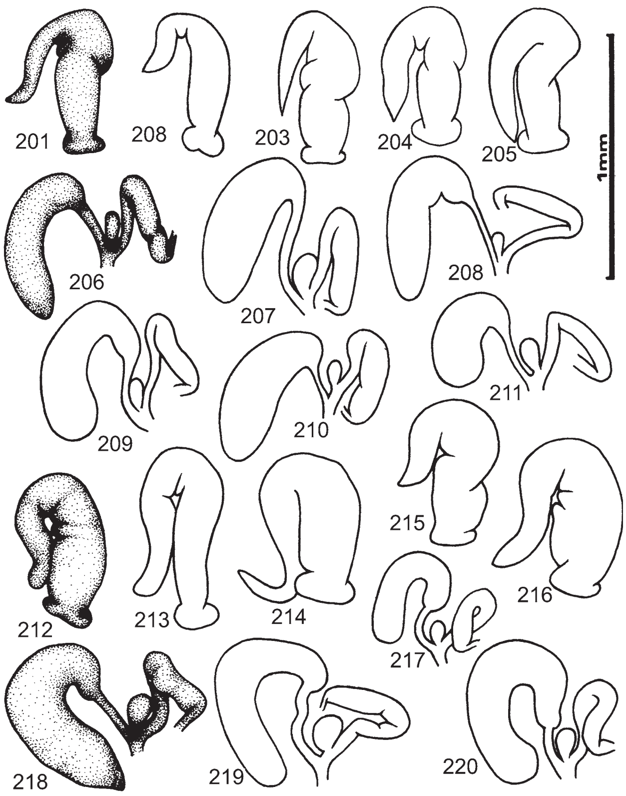


Figs 179–200. Variation in reproductive organs of *B. cylindrica*: 179–190 – population 8: 179–184 – penis, 185–190 – bursa copulatrix, seminal receptacle and coil of oviduct; 191–200 – population 9: 191–194 – penis, 195–200 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

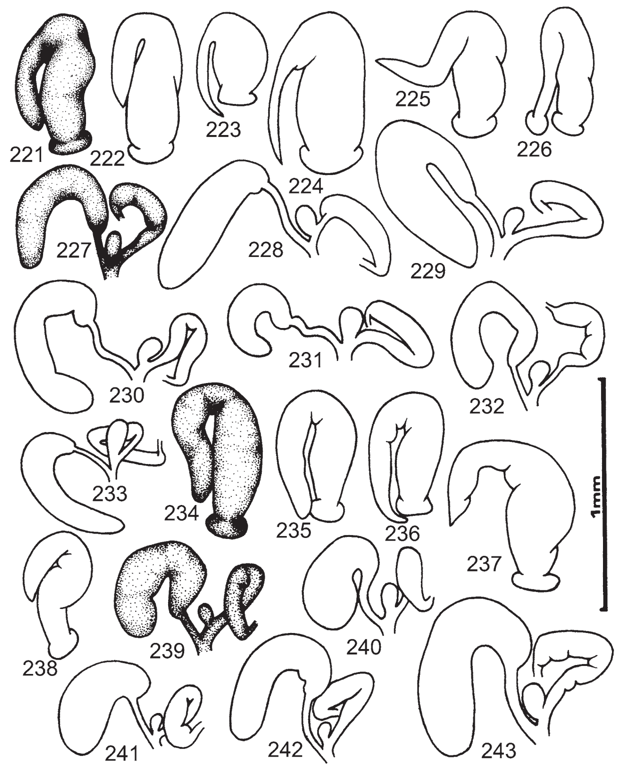
Table 5. Descriptive statistics of anatomy: females. Measurements in [mm]. For population numbers see: Description of localities

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	20	15	30	30	30	30	30	30
ctenidium length	min./max.	0.64–1.25	0.85–1.27	0.75–1.32	0.94–1.26	0.81–1.19	0.89–1.32	0.87–1.26	0.82–1.50	0.90–1.39	0.79–1.25
	mean/med.	0.97/0.98	0.99/0.97	1.03/1.04	1.08/1.05	0.99/0.98	1.06/1.06	1.09/1.09	1.10/1.07	1.15/1.17	0.98/0.96
	sd/C.V.	0.12/12.61	0.13/12.70	0.13/13.03	0.11/10.64	0.10/9.79	0.11/9.95	0.10/9.09	0.17/15.56	0.12/10.47	0.10/10.67
number of ctenidium lamellae	min./max.	19.00–24.00	19.00–24.00	16.00–24.00	19.00–24.00	17.00–23.00	17.00–22.00	20.00–25.00	17.00–24.00	19.00–25.00	16.00–22.00
	mean/med.	21.57/21.00	21.11/21.00	20.05/20.00	21.93/22.00	19.73/20.00	18.93/19.00	22.57/22.50	20.87/21.00	21.80/22.00	18.53/18.00
	sd/C.V.	1.45/6.74	1.20/5.67	2.19/10.91	1.53/6.99	1.62/8.20	1.31/6.93	1.55/6.85	1.46/6.98	1.32/6.07	1.41/7.60
maximum length of ctenidium lamella	min./max.	0.20–0.38	0.22–0.39	0.19–0.39	0.21–0.35	0.21–0.32	0.22–0.34	0.21–0.32	0.19–0.32	0.21–0.32	0.20–0.30
	mean/med.	0.28/0.27	0.30/0.30	0.29/0.29	0.27/0.26	0.28/0.29	0.28/0.27	0.28/0.27	0.27/0.27	0.27/0.26	0.25/0.25
	sd/C.V.	0.05/17.22	0.04/13.06	0.04/14.72	0.04/16.10	0.03/9.57	0.03/10.54	0.02/8.66	0.03/12.52	0.03/10.23	0.03/11.07
osphradium length	min./max.	0.19–0.33	0.17–0.31	0.24–0.35	0.26–0.37	0.24–0.35	0.13–0.35	0.18–0.35	0.19–0.43	0.22–0.37	0.21–0.37
	mean/med.	0.26/0.27	0.25/0.25	0.29/0.27	0.31/0.31	0.29/0.29	0.27/0.27	0.28/0.27	0.32/0.32	0.30/0.30	0.29/0.29
	sd/C.V.	0.03/12.87	0.04/16.07	0.03/12.21	0.03/10.90	0.03/9.92	0.04/15.09	0.04/13.01	0.05/17.27	0.04/12.87	0.05/15.82
osphradium width	min./max.	0.07–0.13	0.07–0.12	0.07–0.13	0.08–0.12	0.08–0.14	0.07–0.13	0.06–0.13	0.08–0.16	0.09–0.15	0.08–0.13
	mean/med.	0.10/0.10	0.10/0.09	0.10/0.10	0.09/0.09	0.10/0.10	0.10/0.10	0.09/0.09	0.11/0.11	0.10/0.10	0.10/0.10
	sd/C.V.	0.01/13.64	0.01/14.74	0.02/17.87	0.01/11.66	0.01/11.98	0.01/14.35	0.01/16.35	0.02/18.00	0.02/14.91	0.01/13.21
anterior cten. to anterior osphr. distance	min./max.	0.20–0.44	0.20–0.37	0.15–0.51	0.25–0.44	0.19–0.47	0.26–0.47	0.26–0.41	0.22–0.50	0.24–0.44	0.29–0.24
	mean/med.	0.30/0.29	0.27/0.26	0.33/0.34	0.33/0.31	0.31/0.30	0.37/0.37	0.32/0.32	0.35/0.35	0.35/0.34	0.30/0.29
	sd/C.V.	0.06/19.19	0.05/16.53	0.08/23.75	0.05/16.08	0.07/22.72	0.05/14.46	0.04/13.01	0.07/20.22	0.06/16.23	0.05/16.85
anus to mantle border distance	min./max.	0.22–0.39	0.17–0.35	0.24–0.45	0.25–0.42	0.29–0.45	0.26–0.45	0.26–0.40	0.25–0.47	0.26–0.39	0.24–0.41
	mean/med.	0.32/0.31	0.28/0.30	0.34/0.32	0.35/0.37	0.37/0.38	0.37/0.37	0.32/0.32	0.36/0.36	0.32/0.32	0.31/0.30
	sd/C.V.	0.05/15.76	0.04/15.57	0.06/17.57	0.05/15.67	0.04/12.02	0.05/12.73	0.03/10.52	0.06/15.88	0.03/10.79	0.05/15.60
stomach length	min./max.	0.62–0.93	0.59–0.85	0.55–0.86	0.57–0.76	0.62–0.93	0.58–0.89	0.68–0.92	0.63–0.95	0.47–0.94	0.48–0.84
	mean/med.	0.75/0.75	0.71/0.70	0.69/0.68	0.66/0.67	0.76/0.75	0.73/0.72	0.77/0.77	0.78/0.77	0.74/0.74	0.74/0.75
	sd/C.V.	0.08/10.68	0.07/10.53	0.08/12.26	0.07/10.28	0.08/10.55	0.06/8.75	0.05/6.96	0.09/10.92	0.11/15.26	0.07/9.39
stomach width	min./max.	0.36–0.55	0.35–0.52	0.28–0.47	0.35–0.48	0.37–0.56	0.37–0.55	0.39–0.58	0.37–0.63	0.33–0.63	0.32–0.57
	mean/med.	0.45/0.44	0.44/0.44	0.39/0.38	0.40/0.40	0.47/0.47	0.45/0.44	0.48/0.47	0.48/0.49	0.46/0.45	0.46/0.47
	sd/C.V.	0.05/12.13	0.05/10.32	0.05/13.06	0.04/9.35	0.05/11.54	0.04/9.22	0.05/10.19	0.06/13.21	0.07/14.70	0.06/12.37
style sac length	min./max.	0.26–0.46	0.25–0.41	0.20–0.42	0.24–0.43	0.29–0.55	0.27–0.53	0.29–0.48	0.28–0.48	0.24–0.46	0.28–0.48
	mean/med.	0.36/0.36	0.35/0.35	0.31/0.30	0.34/0.33	0.36/0.36	0.37/0.38	0.40/0.40	0.38/0.38	0.36/0.36	0.37/0.36
	sd/C.V.	0.04/12.17	0.04/10.82	0.05/16.94	0.06/16.81	0.06/15.20	0.06/15.01	0.05/11.48	0.05/14.40	0.06/15.34	0.05/12.99
spermatheca duct length	min./max.	0.44–0.88	0.52–0.84	0.42–0.88	0.57–0.79	0.48–0.93	0.62–0.91	0.58–1.04	0.46–1.06	0.53–0.97	0.53–1.10
	mean/med.	0.70/0.71	0.71/0.74	0.58/0.58	0.69/0.68	0.72/0.67	0.76/0.74	0.80/0.81	0.78/0.79	0.77/0.76	0.74/0.73
	sd/C.V.	0.11/15.22	0.09/12.77	0.12/19.95	0.06/9.32	0.12/17.24	0.08/10.78	0.12/14.55	0.14/18.27	0.11/13.71	0.13/16.94
bursa copulatrix length	min./max.	0.31–0.99	0.31–0.59	0.42–0.90	0.57–0.98	0.27–1.01	0.44–0.85	0.44–0.90	0.34–0.96	0.25–0.82	0.54–1.03
	mean/med.	0.53/0.52	0.47/0.48	0.64/0.64	0.76/0.79	0.57/0.56	0.59/0.56	0.68/0.68	0.63/0.64	0.51/0.51	0.74/0.73
	sd/C.V.	0.13/25.38	0.07/15.84	0.13/20.56	0.10/12.97	0.17/30.25	0.09/14.52	0.12/17.48	0.14/22.40	0.13/25.69	0.11/15.43
bursa copulatrix width	min./max.	0.11–0.25	0.10–0.21	0.11–0.22	0.13–0.24	0.10–0.26	0.15–0.28	0.12–0.25	0.11–0.31	0.09–0.19	0.13/0.26
	mean/med.	0.16/0.16	0.16/0.15	0.17/0.16	0.17/0.15	0.16/0.15	0.20/0.20	0.19/0.20	0.19/0.17	0.14/0.15	0.20/0.20
	sd/C.V.	0.03/18.93	0.03/20.93	0.03/17.55	0.03/19.92	0.04/25.99	0.03/16.69	0.04/19.49	0.05/21.86	0.03/18.21	0.03/16.37
bursa duct length	min./max.	0.22–0.42	0.20–0.37	0.13–0.33	0.18–0.35	0.11–0.37	0.11–0.56	0.20–0.44	0.21–0.53	0.18–0.33	0.15–0.42
	mean/med.	0.28/0.27	0.27/0.26	0.22/0.22	0.26/0.26	0.22/0.22	0.36/0.35	0.29/0.29	0.32/0.31	0.24/0.23	0.25/0.24
	sd/C.V.	0.05/17.52	0.06/20.49	0.06/25.13	0.06/21.90	0.05/23.23	0.09/24.47	0.06/20.27	0.07/21.86	0.03/14.49	0.06/22.18
bursa duct width	min./max.	0.02–0.05	0.02–0.04	0.02–0.05	0.02–0.04	0.02–0.33	0.01–0.04	0.02–0.04	0.02–0.06	0.02–0.04	0.02–0.04
	mean/med.	0.04/0.04	0.03/0.03	0.03/0.03	0.03/0.04	0.04/0.03	0.03/0.03	0.03/0.03	0.04/0.04	0.03/0.04	0.03/0.03
	sd/C.V.	0.01/20.60	0.01/23.57	0.01/26.14	0.01/20.49	0.06/131.65	0.01/31.37	0.01/23.51	0.01/31.06	0.01/25.35	0.01/18.64

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	20	15	30	30	30	30	30	30
seminal receptacle length	min./max.	0.08–0.15	0.08–0.18	0.06–0.18	0.11–0.17	0.09–0.22	0.08–0.25	0.09–0.20	0.11–0.29	0.08–0.16	0.09–0.16
	mean/med.	0.11/0.11	0.13/0.13	0.14/0.14	0.13/0.13	0.15/0.15	0.15/0.15	0.13/0.12	0.16/0.15	0.12/0.11	0.13/0.13
	sd/C.V.	0.02/18.05	0.02/17.15	0.03/20.95	0.02/14.74	0.03/19.15	0.03/20.50	0.02/17.99	0.04/24.02	0.03/21.81	0.02/15.36
seminal receptacle width	min./max.	0.04–0.11	0.04–0.09	0.04–0.13	0.05–0.09	0.05–0.14	0.04–0.14	0.04–0.10	0.05–0.14	0.04–0.11	0.05–0.10
	mean/med.	0.07/0.07	0.07/0.07	0.08/0.08	0.07/0.07	0.10/0.09	0.08/0.08	0.07/0.07	0.09/0.09	0.07/0.07	0.07/0.07
	sd/C.V.	0.01/22.24	0.01/16.08	0.02/23.60	0.01/11.89	0.02/21.42	0.02/24.51	0.01/20.24	0.02/24.12	0.02/21.62	0.01/18.17
oviduct coil length	min./max.	0.37–0.73	0.53–0.77	0.35–0.92	0.44–0.84	0.47–0.86	0.45–0.77	0.48–0.78	0.42–1.10	0.44–0.87	0.54–0.79
	mean/med.	0.59/0.58	0.63/0.62	0.62/0.58	0.66/0.65	0.67/0.66	0.65/0.66	0.64/0.64	0.73/0.71	0.66/0.68	0.64/0.63
	sd/C.V.	0.09/14.69	0.06/9.85	0.12/19.79	0.10/15.64	0.10/15.56	0.08/12.80	0.08/13.30	0.16/22.21	0.11/16.87	0.07/11.14
oviduct coil width	min./max.	0.05–0.13	0.06–0.13	0.04–0.10	0.06–0.10	0.07–0.17	0.08–0.15	0.06–0.12	0.05–0.13	0.05–0.13	0.06–0.12
	mean/med.	0.09/0.09	0.10/0.09	0.07/0.08	0.08/0.08	0.11/0.11	0.11/0.11	0.09/0.09	0.10/0.10	0.10/0.10	0.10/0.10
	sd/C.V.	0.02/21.75	0.02/22.76	0.02/23.27	0.01/14.86	0.02/18.79	0.02/16.48	0.02/19.29	0.02/17.09	0.02/18.12	0.01/15.24
ovary length	min./max.	0.34–0.84	0.35–0.66	0.26–0.86	0.35–0.62	0.42–0.70	0.26–0.66	0.35–0.88	0.29–0.72	0.29–0.60	0.34–0.64
	mean/med.	0.60/0.59	0.44/0.42	0.45/0.46	0.46/0.44	0.52/0.52	0.51/0.52	0.58/0.56	0.52/0.53	0.45/0.47	0.47/0.45
	sd/C.V.	0.11/19.12	0.08/17.83	0.14/32.12	0.07/15.11	0.08/15.81	0.09/17.03	0.11/18.49	0.10/19.42	0.08/17.66	0.08/16.58



Figs 201–220. Variation in reproductive organs of *Bythinella*: 201–211 – *B. cylindrica* (population 10): 201–205 – penis, 206–211 – bursa copulatrix, seminal receptacle and coil of oviduct; 212–220 – *B. austriaca* (population 11): 212–216 – penis, 217–220 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

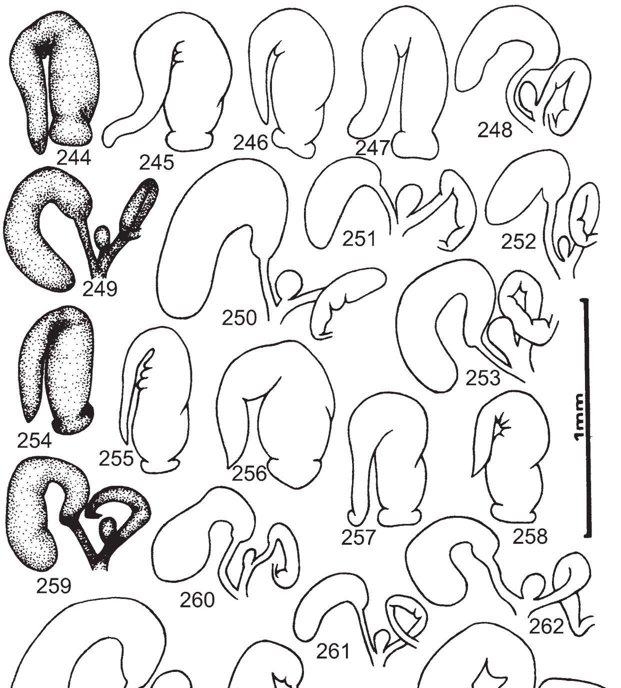


Figs 221–243. Variation in reproductive organs of *B. austriaca*: 221–233 – population 12: 221–226 – penis, 227–233 – bursa copulatrix, seminal receptacle and coil of oviduct; 234–243 – population 13: 234–238 – penis, 239–243 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

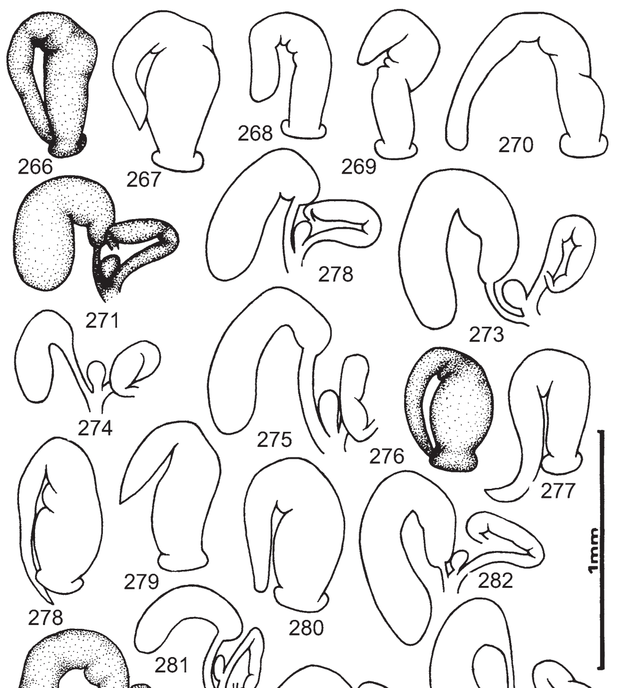
Table 6. Descriptive statistics of anatomy: females. Measurements in [mm]. For population numbers see: Description of localities

Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	30
ctenidium length	min./max.	1.00–1.27	0.71–1.20	0.84–1.31	0.89–1.37	0.84–1.18	0.82–1.46	0.92–1.34	0.90–1.52	0.75–1.46	1.04–1.44
	mean/med.	1.13/1.13	0.98/0.97	1.00/0.99	1.13/1.16	0.99/0.98	1.16/1.15	1.10/1.11	1.13/1.12	1.12/1.12	1.22/1.21
	sd/C.V.	0.08/6.63	0.12/12.57	0.13/13.00	0.15/13.02	0.09/8.59	0.15/12.58	0.09/8.63	0.12/10.47	0.16/13.99	0.11/9.18
number of ctenidium lamellae	min./max.	21.00–25.00	19.00–25.00	16.00–22.00	20.00–27.00	19.00–24.00	19.00–25.00	16.00–23.00	19.00–24.00	19.00–25.00	21.00–26.00
	mean/med.	22.73/23.00	21.17/21.50	19.53/19.00	22.57/22.00	21.10/21.00	21.87/22.00	19.27/19.00	21.17/21.00	21.40/21.00	23.37/23.00
	sd/C.V.	1.17/5.16	1.46/6.92	1.41/7.21	1.52/6.75	1.63/7.71	1.43/6.55	1.53/7.94	1.02/4.82	1.48/6.90	1.33/5.67
maximum length of ctenidium lamella	min./max.	0.25–0.37	0.21–0.42	0.22–0.37	0.21–0.37	0.24–0.44	0.22–0.32	0.24–0.32	0.24–0.31	0.20–0.31	0.24–0.35
	mean/med.	0.32/0.32	0.32/0.32	0.28/0.26	0.31/0.31	0.32/0.32	0.28/0.27	0.28/0.27	0.28/0.27	0.26/0.26	0.28/0.27
	sd/C.V.	0.03/10.69	0.05/15.72	0.04/12.65	0.04/11.67	0.05/16.95	0.03/10.24	0.02/8.23	0.02/8.58	0.02/9.52	0.03/11.13
osphradium length	min./max.	0.24–0.41	0.20–0.34	0.20–0.33	0.18–0.35	0.21–0.38	0.22–0.40	0.25–0.33	0.23–0.34	0.22–0.33	0.27–0.42
	mean/med.	0.30/0.29	0.27/0.27	0.27/0.27	0.28/0.28	0.27/0.26	0.30/0.30	0.30/0.30	0.28/0.28	0.27/0.26	0.36/0.35
	sd/C.V.	0.04/13.88	0.03/13.10	0.04/13.19	0.04/14.03	0.04/16.00	0.04/12.39	0.02/7.42	0.03/10.06	0.03/10.03	0.04/10.25
osphradium width	min./max.	0.09–0.15	0.05–0.11	0.07–0.13	0.08–0.13	0.07–0.14	0.09–0.14	0.09–0.14	0.07–0.12	0.09–0.14	0.09–0.18
	mean/med.	0.12/0.11	0.08/0.09	0.11/0.11	0.11/0.11	0.10/0.10	0.11/0.11	0.12/0.11	0.10/0.10	0.11/0.11	0.13/0.13
	sd/C.V.	0.02/15.89	0.01/15.95	0.01/13.80	0.01/12.26	0.02/16.73	0.01/13.07	0.01/11.41	0.01/11.24	0.01/12.01	0.02/14.40
anterior cten. to anterior osphr. distance	min./max.	0.26–0.47	0.20–0.46	0.22–0.40	0.26–0.46	0.25–0.45	0.26–0.44	0.24–0.46	0.25–0.47	0.20–0.44	0.26–0.45
	mean/med.	0.38/0.38	0.33/0.32	0.30/0.29	0.36/0.37	0.34/0.34	0.35/0.36	0.33/0.33	0.36/0.36	0.34/0.31	0.36/0.37
	sd/C.V.	0.06/16.24	0.06/19.15	0.04/14.64	0.06/15.66	0.06/17.75	0.04/12.82	0.06/17.54	0.06/15.85	0.06/17.48	0.05/12.85
anus to mantle border distance	min./max.	0.29–0.50	0.19–0.45	0.25–0.37	0.25–0.46	0.24–0.44	0.22–0.45	0.30–0.44	0.27–0.45	0.25–0.44	0.25–0.52
	mean/med.	0.37/0.36	0.31/0.31	0.33/0.34	0.36/0.37	0.33/0.33	0.36/0.36	0.37/0.36	0.36/0.35	0.37/0.37	0.40/0.39
	sd/C.V.	0.05/13.87	0.07/23.37	0.03/10.55	0.05/14.40	0.06/16.92	0.05/14.13	0.04/10.38	0.04/12.39	0.04/11.03	0.07/17.85
stomach length	min./max.	0.69–1.00	0.58–0.99	0.62–1.04	0.51–0.96	0.59–0.92	0.64–0.92	0.73–0.95	0.60–0.92	0.62–0.86	0.77–1.01
	mean/med.	0.83/0.83	0.79/0.77	0.76/0.75	0.79/0.79	0.72/0.72	0.76/0.76	0.80/0.80	0.75/0.75	0.74/0.75	0.89/0.89
	sd/C.V.	0.08/9.96	0.09/11.60	0.09/11.27	0.10/12.95	0.08/11.41	0.07/8.85	0.05/6.11	0.08/10.27	0.07/9.18	0.06/6.97
stomach width	min./max.	0.45–0.67	0.34–0.66	0.40–0.64	0.33–0.60	0.29–0.49	0.37–0.57	0.42–0.57	0.35–0.61	0.33–0.56	0.46–0.69
	mean/med.	0.53/0.53	0.45/0.44	0.50/0.49	0.49/0.49	0.39/0.39	0.48/0.48	0.49/0.48	0.47/0.46	0.46/0.46	0.58/0.59
	sd/C.V.	0.05/9.60	0.07/16.02	0.06/12.24	0.06/11.61	0.05/12.07	0.05/10.70	0.04/8.26	0.05/10.40	0.05/11.94	0.06/9.94
style sac length	min./max.	0.31–0.51	0.28–0.51	0.27–0.44	0.24–0.47	0.29–0.42	0.31–0.46	0.25–0.53	0.27–0.45	0.24–0.42	0.33–0.55
	mean/med.	0.41/0.42	0.38/0.37	0.36/0.35	0.37/0.37	0.35/0.36	0.38/0.38	0.38/0.38	0.36/0.35	0.34/0.33	0.42/0.42
	sd/C.V.	0.04/10.78	0.05/14.42	0.04/12.13	0.04/11.58	0.04/10.52	0.03/8.96	0.05/13.31	0.05/14.34	0.04/12.50	0.05/11.36
spermatheca duct length	min./max.	0.55–0.84	0.40–0.88	0.55–1.14	0.54–0.99	0.38–0.95	0.66–1.04	0.65–0.98	0.48–1.13	0.65–0.88	0.64–1.14
	mean/med.	0.69/0.68	0.58/0.58	0.74/0.69	0.79/0.80	0.57/0.55	0.78/0.77	0.77/0.77	0.79/0.78	0.77/0.77	0.84/0.86
	sd/C.V.	0.07/10.40	0.11/18.30	0.14/19.49	0.10/12.89	0.11/20.14	0.09/11.36	0.08/9.93	0.14/17.30	0.08/10.53	0.14/16.62
bursa copulatrix length	min./max.	0.57–1.09	0.46–1.10	0.51–1.22	0.47–1.15	0.44–0.99	0.53–1.17	0.33–1.10	0.44–1.31	0.54–1.20	0.36–1.10
	mean/med.	0.90/0.90	0.81/0.81	0.78/0.77	0.82/0.82	0.70/0.71	0.80/0.80	0.78/0.87	0.96/0.98	0.88/0.91	0.82/0.88
	sd/C.V.	0.10/10.67	0.15/18.36	0.16/19.91	0.18/22.50	0.15/21.16	0.14/18.01	0.20/25.32	0.17/17.37	0.16/17.83	0.16/19.99
bursa copulatrix width	min./max.	0.11–0.35	0.10–0.22	0.14–0.24	0.13–0.25	0.07–0.24	0.13–0.29	0.10–0.26	0.13–0.29	0.13–0.25	0.13–0.38
	mean/med.	0.21/0.21	0.15/0.15	0.20/0.20	0.18/0.18	0.17/0.17	0.21/0.21	0.17/0.17	0.21/0.21	0.19/0.20	0.24/0.24
	sd/C.V.	0.05/24.22	0.03/21.34	0.03/14.52	0.03/18.41	0.04/23.03	0.04/19.35	0.04/21.44	0.04/17.16	0.03/16.87	0.07/30.81
bursa duct length	min./max.	0.09–0.35	0.15–0.35	0.12–0.33	0.14–0.34	0.13–0.33	0.19–0.35	0.09–0.33	0.15–0.31	0.21–0.41	0.24–0.56
	mean/med.	0.23/0.22	0.24/0.22	0.20/0.20	0.22/0.21	0.23/0.23	0.24/0.23	0.23/0.22	0.22/0.22	0.27/0.27	0.38/0.38
	sd/C.V.	0.06/27.09	0.05/21.58	0.06/27.52	0.04/20.17	0.05/20.06	0.04/17.63	0.05/22.74	0.04/17.35	0.05/16.89	0.07/18.84
bursa duct width	min./max.	0.03–0.06	0.02–0.06	0.03–0.05	0.02–0.04	0.02–0.06	0.03–0.06	0.02–0.04	0.02–0.04	0.03–0.05	0.02–0.05
	mean/med.	0.05/0.04	0.03/0.03	0.04/0.04	0.04/0.04	0.04/0.04	0.04/0.04	0.03/0.03	0.03/0.03	0.04/0.04	0.04/0.04
	sd/C.V.	0.01/18.60	0.01/31.13	0.00/11.18	0.01/17.64	0.01/33.62	0.01/15.03	0.01/21.97	0.01/19.34	0.00/12.47	0.01/15.53

Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	30
seminal receptacle length	min./max.	0.10–0.18	0.07–0.16	0.07–0.14	0.10–0.18	0.06–0.16	0.11–0.20	0.08–0.14	0.09–0.15	0.11–0.18	0.09–0.24
	mean/med.	0.14/0.15	0.12/0.12	0.10/0.10	0.13/0.12	0.10/0.09	0.13/0.12	0.12/0.12	0.12/0.11	0.13/0.13	0.17/0.18
	sd/C.V.	0.02/15.08	0.02/19.54	0.02/18.90	0.02/17.01	0.03/26.30	0.02/14.60	0.02/15.63	0.02/16.08	0.02/13.19	0.03/19.19
seminal receptacle width	min./max.	0.05–0.14	0.02–0.10	0.04–0.10	0.04–0.13	0.04–0.10	0.05–0.11	0.04–0.09	0.04–0.13	0.06–0.11	0.06–0.13
	mean/med.	0.09/0.09	0.07/0.08	0.06/0.06	0.08/0.08	0.06/0.06	0.08/0.08	0.07/0.07	0.08/0.07	0.08/0.07	0.09/0.09
	sd/C.V.	0.02/19.31	0.02/27.15	0.01/23.49	0.02/24.52	0.01/23.89	0.01/18.46	0.01/16.61	0.02/24.35	0.01/14.50	0.02/18.20
oviduct coil length	min./max.	0.46–0.76	0.44–0.79	0.44–0.75	0.53–0.89	0.33–0.88	0.44–0.77	0.44–0.78	0.44–0.82	0.54–0.88	0.64–1.10
	mean/med.	0.62/0.63	0.68/0.70	0.62/0.62	0.68/0.66	0.61/0.60	0.63/0.63	0.61/0.59	0.64/0.66	0.72/0.74	0.88/0.90
	sd/C.V.	0.07/11.57	0.10/15.00	0.08/13.50	0.09/13.42	0.14/22.72	0.08/11.99	0.09/15.24	0.09/13.51	0.09/12.45	0.12/13.50
oviduct coil width	min./max.	0.07–0.13	0.07–0.15	0.06–0.13	0.06–0.11	0.04–0.11	0.07–0.14	0.05–0.12	0.07–0.13	0.08–0.16	0.06–0.13
	mean/med.	0.09/0.09	0.09/0.09	0.10/0.10	0.09/0.09	0.08/0.09	0.10/0.11	0.09/0.09	0.10/0.10	0.12/0.11	0.10/0.10
	sd/C.V.	0.02/17.81	0.02/21.75	0.02/16.16	0.01/14.81	0.02/22.85	0.02/14.98	0.01/16.57	0.01/14.85	0.02/15.28	0.02/18.08
ovary length	min./max.	0.34–0.64	0.22–0.57	0.34–0.75	0.34–0.60	0.24–0.57	0.42–0.78	0.31–0.59	0.33–0.66	0.40–0.75	0.40–0.73
	mean/med.	0.48/0.47	0.42/0.44	0.52/0.51	0.50/0.50	0.42/0.42	0.60/0.59	0.44/0.44	0.51/0.50	0.56/0.56	0.55/0.54
	sd/C.V.	0.08/15.95	0.07/17.17	0.11/22.01	0.06/12.10	0.08/18.98	0.09/15.04	0.07/15.89	0.08/15.20	0.09/15.40	0.08/15.48



Figs 244–265. Variation in reproductive organs of *B. austriaca*: 244–253 – population 14: 244–247 – penis, 248–253 – bursa copulatrix, seminal receptacle and coil of oviduct; 254–265 – population 15: 254–258 – penis, 259–265 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape



Figs 266–285. Variation in reproductive organs of *Bythinella*: 266–275 – *B. austriaca* (population 16): 266–270 – penis, 271–275 – bursa copulatrix, seminal receptacle and coil of oviduct; 276–285 – *B. zyvionteki* (population 17): 276–280 – penis, 281–285 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

Table 7. Descriptive statistics of anatomy: males. Measurements in [mm]. For population numbers see: Description of localities

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	16	3	30	27	30	30	21	30
ctenidium length	min./max.	0.62–1.20	0.74–1.19	0.85–1.34	1.07–1.19	0.75–1.17	0.90–1.42	0.90–1.29	0.85–1.45	0.71–1.25	0.75–1.14
	mean/med.	0.87/0.85	0.97/0.96	1.05/1.00	1.14/1.16	0.93/0.94	1.09/1.07	1.03/1.01	1.16/1.19	1.05/1.04	0.92/0.89
	sd/C.V.	0.14/15.63	0.13/13.34	0.16/15.38	0.06/5.17	0.11/12.17	0.12/11.29	0.11/10.95	0.13/11.13	0.12/11.34	0.13/13.96
number of ctenidium lamellae	min./max.	18.00–25.00	19.00–23.00	16.00–23.00	21.00–22.00	16.00–21.00	17.00–22.00	19.00–23.00	17.00–24.00	19.00–23.00	15.00–21.00
	mean/med.	20.73/20.00	21.00/21.00	18.94/19.00	21.33/21.00	18.97/19.00	19.07/19.00	21.37/22.00	20.40/20.00	20.38/20.00	17.93/18.00
	sd/C.V.	1.95/9.39	1.33/6.35	2.02/10.64	0.58/2.71	1.35/7.12	1.33/6.96	1.16/5.42	1.73/8.50	1.16/5.70	1.46/8.14
maximum length of ctenidium lamella	min./max.	0.17–0.32	0.22–0.36	0.24–0.41	0.25–0.37	0.20–0.34	0.22–0.32	0.24–0.35	0.25–0.35	0.22–0.31	0.19–0.29
	mean/med.	0.25/0.25	0.29/0.29	0.31/0.30	0.32/0.32	0.28/0.29	0.28/0.27	0.28/0.29	0.28/.27	0.26/0.26	0.25/0.25
	sd/C.V.	0.04/15.76	0.04/13.34	0.05/16.53	0.06/19.87	0.04/13.52	0.03/9.93	0.03/8.91	0.03/9.80	0.02/8.77	0.02/9.19
osphradium length	min./max.	0.18–0.34	0.16–0.32	0.22–0.57	0.26–0.33	0.18–0.40	0.22–0.32	0.23–0.38	0.23–0.44	0.22–0.33	0.20–0.37
	mean/med.	0.26/0.26	0.26/0.26	0.32/0.30	0.30/0.31	0.30/0.30	0.28/0.27	0.30/0.30	0.34/0.33	0.28/0.27	0.29/0.28
	sd/C.V.	0.04/16.68	0.05/17.85	0.08/26.60	0.03/11.18	0.05/17.66	0.03/10.80	0.00/13.02	0.05/13.98	0.04/13.89	0.04/12.43
osphradium width	min./max.	0.06–0.15	0.06–0.14	0.08–0.14	0.08/0.11	0.08–0.15	0.08–0.15	0.08–0.15	0.08–0.18	0.08–0.15	0.06–0.13
	mean/med.	0.11/0.11	0.10/0.11	0.10/0.10	0.09/0.09	0.10/0.10	0.11/0.11	0.11/0.11	0.12/0.12	0.11/0.11	0.11–0.11
	sd/C.V.	0.02/17.59	0.02/20.07	0.02/17.56	0.02/16.28	0.01/14.84	0.02/14.44	0.02/17.65	0.02/19.12	0.02/17.21	0.01/13.92
anterior cten. to anterior osphr. distance	min./max.	0.17–0.44	0.19–0.37	0.21–0.45	0.29–0.39	0.20–0.40	0.25–0.45	0.19–0.45	0.21–0.44	0.22–0.44	0.19–0.37
	mean/med.	0.25/0.22	0.29/0.29	0.33/0.32	0.33/0.31	0.29/0.27	0.33/0.32	0.30/0.31	0.34/0.34	0.32/0.32	0.26/0.25
	sd/C.V.	0.07/27.26	0.06/19.05	0.08/24.30	0.05/15.81	0.05/18.27	0.04/13.38	0.06/18.72	0.07/20.13	0.05/16.78	0.05/20.01
anus to mantle border distance	min./max.	0.22–0.41	0.19–0.36	0.25–0.46	0.26–0.39	0.31–0.44	0.26–0.47	0.27–0.56	0.29–0.49	0.19–0.36	0.24–0.37
	mean/med.	0.30/0.29	0.29/0.30	0.36/0.37	0.33/0.35	0.37/0.37	0.35/0.35	0.37/0.35	0.37/0.38	0.29/0.29	0.30/0.30
	sd/C.V.	0.05/17.05	0.05/18.04	0.07/20.28	0.06/19.24	0.04/9.55	0.05/14.92	0.07/18.12	0.06/14.70	0.04/14.29	0.04/12.99
stomach length	min./max.	0.53–0.86	0.58–0.81	0.46–0.85	0.62–0.66	0.50–0.95	0.47–0.88	0.64–0.78	0.68–0.95	0.53–0.81	0.60–0.79
	mean/med.	0.66/0.65	0.70/0.71	0.71/0.71	0.65/0.66	0.70/0.70	0.70/0.70	0.72/0.73	0.79/0.77	0.67/0.67	0.70/0.70
	sd/C.V.	0.08/12.20	0.07/10.55	0.09/12.91	0.06/3.94	0.09/13.05	0.08/11.98	0.04/5.35	0.07/8.64	0.09/13.16	0.05/6.50
stomach width	min./max.	0.32–0.51	0.33–0.51	0.27–0.64	0.35–0.44	0.29–0.66	0.37–0.53	0.36–0.58	0.42–0.59	0.31–0.52	0.38–0.55
	mean/med.	0.41/0.39	0.43/0.43	0.43/0.41	0.40/0.42	0.45/0.44	0.45/0.44	0.44/0.44	0.50/0.50	0.41/0.41	0.46/0.45
	sd/C.V.	0.06/14.40	0.05/11.92	0.09/20.72	0.05/12.34	0.08/18.56	0.04/8.44	0.05/10.95	0.04/8.06	0.06/13.74	0.04/9.75
style sac length	min./max.	0.22–0.42	0.24–0.37	0.20–0.44	0.29–0.35	0.22–0.53	0.27–0.40	0.31–0.53	0.29–0.51	0.24–0.48	0.29–0.40
	mean/med.	0.41/0.39	0.31/0.32	0.33/0.32	0.32/0.33	0.32/0.32	0.36/0.37	0.40/0.40	0.39/0.39	0.35/0.34	0.36/0.36
	sd/C.V.	0.06/14.40	0.04/13.92	0.06/17.45	0.03/10.41	0.06/18.72	0.04/9.97	0.05/11.72	0.05/13.04	0.06/17.78	0.03/8.95
penis length	min./max.	0.66–1.19	0.73–1.12	0.86–1.32	1.20–1.36	0.89–1.42	0.66–1.42	0.81–1.32	0.92–1.30	0.73–1.40	0.79–1.23
	mean/med.	0.90/0.88	0.88/0.87	1.08/1.10	1.26/1.22	1.12/1.12	1.05–1.01	1.06/1.05	1.12/1.12	1.03/1.01	1.02/1.04
	sd/C.V.	0.13/14.46	0.11/12.97	0.12/10.79	0.09/7.10	0.13/11.99	0.17/15.79	0.11/10.27	0.10/9.01	0.18/17.54	0.10/9.30
flagellum outlet to vas deferens outlet distance	min./max.	0.37–0.87	0.42–0.75	0.48–0.88	0.77–0.93	0.48–0.91	0.43–1.01	0.56–0.95	0.56–0.88	0.44–0.93	0.07–0.81
	mean/med.	0.56/0.55	0.57/0.55	0.71/0.75	0.83/0.79	0.73/0.73	0.66/0.64	0.73/0.74	0.75/0.76	0.69/0.68	0.65/0.66
	sd/C.V.	0.11/18.94	0.10/17.09	0.11/14.90	0.09/10.76	0.11/17.69	0.13/19.25	0.10/13.15	0.07/9.43	0.10/16.90	0.14/20.84
flagellum length	min./max.	0.55–2.10	0.66–2.38	1.01–2.70	1.09–1.81	0.75–2.14	0.68–2.00	0.89–1.58	0.90–1.89	0.59–1.44	0.80–1.68
	mean/med.	1.23/1.20	1.35/1.36	1.69/1.76	1.51/1.64	1.40/1.40	1.45/1.55	1.23/1.25	1.33/1.27	1.00/1.01	1.18–1.14
	sd/C.V.	0.34/27.38	0.43/32.21	0.43/25.55	0.38/25.01	0.29/20.58	0.37/25.59	0.17/13.72	0.24/18.12	0.25/25.34	0.22/18.51
flagellum width	min./max.	0.07–0.16	0.05–0.12	0.09–0.16	0.11–0.13	0.08–0.18	0.04–0.16	0.08–0.15	0.09–0.14	0.06–0.16	0.06–0.15
	mean/med.	0.10–0.10	0.09/0.09	0.12/0.12	0.12/0.13	0.12/0.12	0.11/0.11	0.12/0.12	0.11–0.11	0.10/0.11	0.12/0.12
	sd/C.V.	0.02/21.38	0.02/24.28	0.16/18.65	0.01/7.35	0.02/17.69	0.03/25.28	0.02/14.28	0.01/12.10	0.03/27.13	0.02/17.20
prostate length	min./max.	0.49–0.86	0.26–0.70	0.52–1.17	0.62–0.76	0.37–1.01	0.44–0.87	0.46–0.90	0.54–0.94	0.37–0.82	0.42–0.87
	mean/med.	0.66/0.67	0.48–0.45	0.75/0.71	0.71/0.74	0.62/0.60	0.66/0.65	0.70/0.74	0.75/0.77	0.58/0.57	0.72/0.74
	sd/C.V.	0.09/13.89	0.12/25.01	0.15/20.28	0.07/10.34	0.14/23.22	0.11/16.82	0.11/15.89	0.10/13.90	0.12/20.26	0.09/12.90
prostate width	min./max.	0.24–0.41	0.19–0.42	0.30–0.55	0.27–0.44	0.19–0.45	0.16–0.42	0.24–0.43	0.19–0.47	0.17–0.42	0.19–0.39
	mean/med.	0.33/0.35	0.30/0.30	0.38/0.36	0.35/0.35	0.33–0.31	0.33/0.32	0.36/0.37	0.35/0.36	0.29/0.30	0.30/0.30
	sd/C.V.	0.05/14.40	0.06/21.38	0.08/19.90	0.08/22.96	0.06/18.92	0.06/17.64	0.05/14.89	0.05/12.66	0.06/22.17	0.04/14.42

Population		1	2	3	4	5	6	7	8	9	10
N		30	19	16	3	30	27	30	30	21	30
number of seminal vesicle coils	min./max.	11.00–19.00	9.00–16.00	10.00–23.00	13.00–15.00	7.00–18.00	9.00–20.00	9.00–21.00	8.00–17.00	7.00–20.00	7.00–15.00
	mean/med.	15.4/15.5	12.68/13.00	15.12/14.00	14.00/14.00	12.67/12.00	15.48/15.00	12.97/12.50	12.67/13.00	12.33/11.00	10.77/11.00
	sd/C.V.	2.25/14.63	2.21/17.44	3.98/26.32	1.00/7.14	2.63/20.77	2.71/17.49	2.68/20.70	2.40/18.93	3.43/27.77	2.46/22.84
testis length	min./max.	0.78–1.25	0.59–1.25	0.70–1.17	0.97–1.13	0.74–1.22	0.76–1.29	0.81–1.23	0.74–1.65	0.68–1.22	0.73–1.30
	mean/med.	0.96/0.95	0.87/0.88	1.00/1.00	1.06/1.07	0.97/0.97	0.98/0.99	1.02/1.00	1.13/1.15	0.88/0.81	1.03/1.03
	sd/C.V.	0.14/14.01	0.16/18.95	0.15/15.81	0.08/7.86	0.12/12.20	0.13/13.35	0.12/11.66	0.18/16.22	0.15/17.16	0.13/12.37

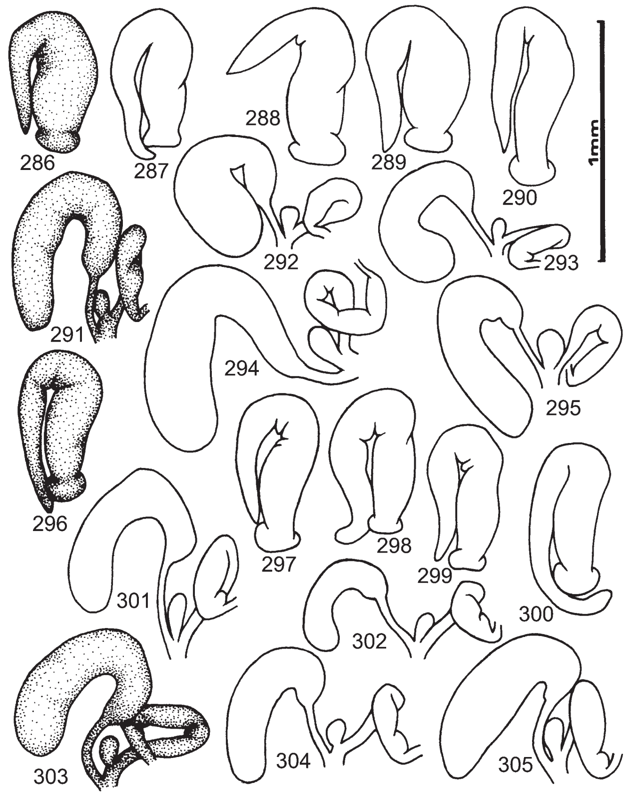
value was lower (except populations 3, 4, 12, 18), not exceeding 1.00 mm (Tables 1–4). The number of transverse rows, not correlated with the length of radula, was similar in both sexes, ranging from 70 to 171 (Tables 1–4); mean values below 100 were recorded only for populations 15 and 17 (in the males also 4 and 13), the highest mean values were those in populations 3, 9 and 18. The most varied number of rows was found in populations 1, 3, 5, 9 and 11, the least varied – in populations 4 and 17. For most of the radular characters the variability coefficient assumed the highest value in population 12 in the males and population 15 in the females (Tables 1–4). The exceptionally low variation of radulae in the snails of population 4 was probably due to the small sample size.

A statistically significant, clinal variation in the shell height/radula length proportion was recorded. The cline was S-N directed (Fig. 321); Kendall's rank correlation coefficient between this proportion and the S-N situation of a population was tau = 0.337, P = 0.05.

Ctenidium, osphradium and stomach

An S-N directed clinal variation was recorded in the length of the ctenidium (tau = 0.311, P = 0.05), the length increasing northward (Tables 5–8, Fig. 322). The mean length was the lowest in population 1 (0.87 mm in the males, 0.97 mm in the females), but most frequently it exceeded 1.00 mm, the highest value being observed in population 20 (1.19 in the males, 1.22 in the females).

The number of ctenidium lamellae was not correlated with the ctenidium length and varied from 16 to 27 in both sexes. The mean number of ctenidium lamellae (Tables 5–8) assumed its lowest value in population 10 (17.93 in the males, 18.53 in the females) and the highest value in population 20 (22.95 in the males, 23.37 in the females). For both sexes, the number of lamellae was the most varied in population 3 and the least so in population 18 (for the males, also 4 and 16). The length of the longest lamella ranged from 0.17 mm to 0.52 mm and its variability coefficient was little differentiated among the populations. The measurements of the osphradium and stomach displayed no significant interpopulation variation (Tables 5–8). With respect to most of the above soft part anatomy characters, population 3 (both sexes) was the most varied and population 17 (males) the least so.



Figs 286–305. Variation in reproductive organs of *Bythinella*: 286–295 – *B. zyvionteki* (population 18): 286–290 – penis, 291–295 – bursa copulatrix, seminal receptacle and coil of oviduct; 296–305 – *B. austriaca* (population 19): 296–300 – penis, 301–305 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

Female reproductive organs

Of the female reproductive organs, the most varied characters were the shape and size of bursa copulatrix and receptaculum seminis (Tables 5, 6, Figs 74–86, 98–109, 120–132, 138–143, 150–156, 162–167, 173–178, 185–190, 195–200, 206–211, 217–220, 227–233, 239–243, 248–253, 259–265, 271–275, 281–285, 291–295, 301–305, 312–317). The length of spermatheca duct, the length and width of oviduct loop and the length of gonad turned out to be

Table 8. Descriptive statistics of anatomy: males. Measurements in [mm]. For population numbers see: Description of localities

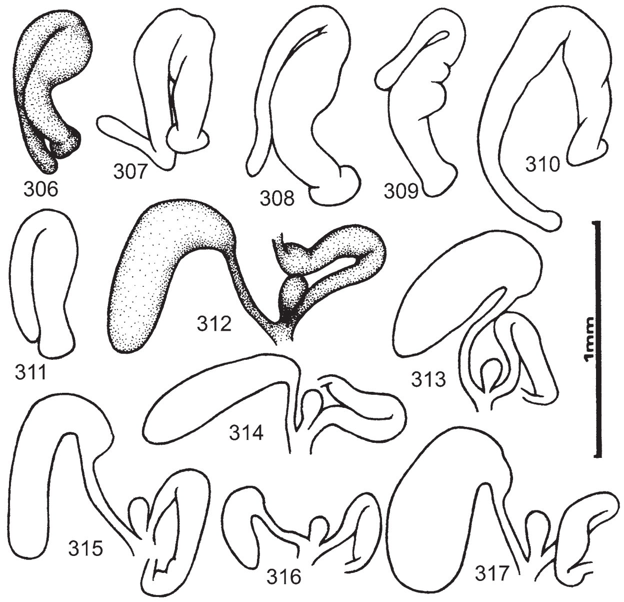
Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	21
ctenidium length	min./max.	0.90–1.52	0.74–1.08	0.81–1.35	0.96–1.46	0.76–1.11	0.90–1.32	0.75–1.30	0.87–1.29	0.81–1.29	0.97–1.51
	mean/med.	1.18/1.15	0.92/0.91	1.01/0.97	1.18/1.19	0.95/0.95	1.09/1.08	1.06/1.05	1.09/1.11	1.05/1.03	1.19/1.19
	sd/C.V.	0.18/14.74	0.09/9.88	0.14/13.82	0.15/12.50	0.09/9.08	0.09/7.84	0.13/12.67	0.11/9.69	0.12/11.64	0.14/11.82
number of ctenidium lamellae	min./max.	20.00–25.00	19.00–23.00	16.00–20.00	20.00–25.00	19.00–24.00	19.00–24.00	16.00–21.00	18.00–23.00	19.00–24.00	20.00–27.00
	mean/med.	22.10/22.00	20.83/21.00	18.03/18.00	22.70/22.50	20.37/20.00	21.70/22.00	18.70/19.00	20.57/20.00	21.00/21.00	22.95/23.00
	sd/C.V.	1.32/5.98	1.51/7.25	1.10/6.09	1.24/5.44	1.38/6.76	1.12/5.16	1.51/8.09	1.10/5.37	1.36/6.50	1.69/7.35
maximum length of ctenidium lamella	min./max.	0.24–0.41	0.24–0.52	0.22–0.36	0.26–0.44	0.24–0.42	0.22–0.37	0.24–0.32	0.24–0.35	0.25–0.32	0.22–0.37
	mean/med.	0.33/0.32	0.32/0.32	0.29/0.29	0.32/0.32	0.32/0.32	0.28/0.27	0.28/0.27	0.30/0.30	0.29/0.29	0.27/0.25
	sd/C.V.	0.05/15.02	0.06/18.60	0.04/12.79	0.03/10.19	0.04/12.53	0.03/12.25	0.02/8.67	0.03/9.53	0.02/6.87	0.04/15.27
osphradium length	min./max.	0.22–0.44	0.17–0.35	0.22–0.35	0.22–0.40	0.22–0.37	0.24–0.37	0.26–0.33	0.24–0.34	0.22–0.33	0.24–0.40
	mean/med.	0.31/0.31	0.26/0.26	0.28/0.29	0.31/0.31	0.28/0.29	0.31/0.31	0.30/0.30	0.29/0.28	0.27/0.27	0.34/0.33
	sd/C.V.	0.05/16.34	0.04/16.05	0.04/13.54	0.04/13.08	0.03/12.04	0.03/9.17	0.02/6.35	0.03/12.19	0.03/9.85	0.05/14.46
osphradium width	min./max.	0.10–0.18	0.05–0.13	0.09–0.15	0.09–0.15	0.08–0.14	0.09–0.15	0.11–0.15	0.09–0.15	0.09–0.18	0.09–0.16
	mean/med.	0.13/0.13	0.09/0.09	0.12/0.11	0.12/0.11	0.11/0.11	0.12/0.12	0.13/0.13	0.11/0.11	0.13/0.12	0.12/0.13
	sd/C.V.	0.02/16.92	0.02/21.09	0.02/16.91	0.02/13.82	0.02/17.44	0.01/11.23	0.01/11.19	0.02/14.27	0.02/15.31	0.02/15.62
anterior cten. to anterior osphr. distance	min./max.	0.25–0.50	0.21–0.44	0.24–0.45	0.27–0.50	0.24–0.42	0.25–0.44	0.24–0.43	0.22–0.46	0.31–0.22	0.29–0.44
	mean/med.	0.38/0.37	0.30/0.30	0.31/0.30	0.38/0.37	0.31/0.31	0.34/0.34	0.31/0.30	0.33/0.31	0.31/0.31	0.35/0.35
	sd/C.V.	0.08/19.92	0.06/19.03	0.06/18.81	0.06/15.16	0.04/13.72	0.05/14.39	0.06/18.44	0.06/18.70	0.06/19.70	0.04/11.90
anus to mantle border distance	min./max.	0.32–0.55	0.19–0.40	0.26–0.45	0.25–0.52	0.21–0.45	0.30–0.45	0.25–0.43	0.25–0.45	0.29–0.47	0.29–0.51
	mean/med.	0.41/0.39	0.29/0.27	0.36/0.36	0.38/0.39	0.32/0.31	0.37/0.36	0.35/0.35	0.35/0.35	0.36/0.35	0.39/0.39
	sd/C.V.	0.07/16.07	0.05/17.10	0.04/11.77	0.06/16.79	0.06/17.79	0.04/10.67	0.05/13.03	0.04/12.44	0.04/11.56	0.07/16.94
stomach length	min./max.	0.64–1.01	0.59–0.89	0.57–0.89	0.70–0.99	0.57–0.91	0.62–0.88	0.70–0.88	0.60–0.81	0.46–0.86	0.67–0.97
	mean/med.	0.81/0.82	0.75/0.74	0.74/0.74	0.80/0.79	0.70/0.69	0.72/0.71	0.76/0.75	0.73/0.73	0.68/0.68	0.84/0.84
	sd/C.V.	0.01/12.33	0.06/8.52	0.08/11.38	0.07/8.89	0.06/9.09	0.07/9.37	0.05/5.91	0.05/7.07	0.07/10.23	0.08/8.95
stomach width	min./max.	0.34–0.77	0.33–0.55	0.37–0.62	0.41–0.59	0.31–0.54	0.42–0.80	0.40–0.57	0.37–0.71	0.33–0.53	0.46–0.69
	mean/med.	0.53/0.52	0.42/0.41	0.49/0.48	0.51/0.51	0.41/0.40	0.50/0.49	0.47/0.46	0.47/0.46	0.44/0.44	0.55/0.53
	sd/C.V.	0.08/15.59	0.06/13.48	0.06/11.90	0.04/8.64	0.05/12.13	0.07/14.70	0.05/10.64	0.07/15.27	0.05/11.42	0.06/10.71
style sac length	min./max.	0.35–0.55	0.26–0.46	0.24–0.48	0.32–0.44	0.26–0.41	0.30–0.46	0.29–0.51	0.26–0.46	0.27–0.41	0.29–0.53
	mean/med.	0.43–0.43	0.36/0.36	0.36/0.35	0.38/0.38	0.36/0.36	0.35/0.35	0.38/0.38	0.34/0.35	0.32/0.32	0.39/0.40
	sd/C.V.	0.06/13.69	0.06/15.46	0.05/13.56	0.03/7.61	0.04/10.36	0.04/10.15	0.05/12.77	0.04/12.95	0.03/10.75	0.06/16.20
penis length	min./max.	0.79–1.34	0.77–1.25	0.88–1.32	0.86–1.36	0.75–1.23	0.90–1.40	0.85–1.32	0.97–1.30	1.00–1.55	0.97–1.88
	mean/med.	1.15/1.17	1.01/1.00	1.10/1.09	1.14/1.15	1.06/1.08	1.14/1.15	1.11/1.12	1.11/1.12	1.22/1.23	1.41/1.40
	sd/C.V.	0.12/10.56	0.11/11.19	0.12/10.81	0.13/11.03	0.11/10.49	0.12/10.89	0.11/9.62	0.09/7.90	0.12/9.97	0.27/18.97
flagellum outlet to vas deferens outlet distance	min./max.	0.54–1.04	0.51–0.88	0.57–0.87	0.57–1.08	0.51–1.08	0.56–0.93	0.65–0.92	0.62–0.89	0.73–1.09	0.60–1.23
	mean/med.	0.80/0.79	0.71/0.70	0.73/0.72	0.83/0.83	0.74/0.75	0.76/0.75	0.77/0.76	0.76/0.76	0.84/0.85	0.93/0.88
	sd/C.V.	0.10/12.98	0.11/14.92	0.09/11.91	0.11/13.35	0.13/17.79	0.11/13.95	0.08/10.66	0.07/9.03	0.09/10.23	0.19/20.85
flagellum length	min./max.	0.66–2.90	0.88–2.20	0.70–1.67	0.87–2.05	0.70–1.76	0.87–1.97	0.76–1.69	1.11–2.31	0.84–2.13	0.93–3.68
	mean/med.	1.43/1.44	1.25/1.17	1.24/1.31	1.39/1.36	1.20/1.19	1.36/1.33	1.28/1.29	1.68/1.69	1.41/1.39	2.03/1.85
	sd/C.V.	0.40/27.90	0.28/22.81	0.25/20.47	0.24/18.78	0.26/21.87	0.28/20.49	0.22/17.48	0.27/16.11	0.25/18.04	0.71/34.72
flagellum width	min./max.	0.07–0.13	0.05–0.13	0.06–0.15	0.07–0.14	0.07–0.15	0.09–0.17	0.08–0.14	0.09–0.14	0.07–0.13	0.04–0.13
	mean/med.	0.11/0.11	0.09/0.09	0.10/0.10	0.11/0.11	0.74/0.75	0.12/0.12	0.11/0.11	0.11/0.11	0.10/0.11	0.08/0.09
	sd/C.V.	0.01/13.51	0.02/24.65	0.02/16.32	0.02/16.25	0.02/21.13	0.02/18.20	0.02/14.11	0.01/12.99	0.01/13.00	0.02/24.63
prostate length	min./max.	0.37–1.04	0.55–0.91	0.56–1.19	0.57–0.99	0.44–1.00	0.50–0.99	0.54–0.96	0.59–1.06	0.69–1.06	0.37–0.95
	mean/med.	0.79/0.80	0.75/0.75	0.81/0.82	0.79/0.81	0.72/0.71	0.79/0.77	0.76/0.75	0.78/0.76	0.89/0.90	0.69/0.69
	sd/C.V.	0.13/16.79	0.09/11.82	0.14/17.39	0.13/15.98	0.10/14.58	0.11/13.69	0.10/12.75	0.10/12.76	0.11/12.21	0.17/24.14
prostate width	min./max.	0.25–0.51	0.30–0.50	0.26–0.56	0.29–0.47	0.27–0.49	0.31–0.50	0.24–0.39	0.29–0.45	0.37–0.50	0.22–0.52
	mean/med.	0.38/0.39	0.39/0.39	0.37/0.37	0.38/0.37	0.40/0.40	0.41/0.41	0.34/0.35	0.36/0.36	0.44/0.43	0.38/0.39
	sd/C.V.	0.05/14.12	0.06/14.26	0.07/19.01	0.05/13.74	0.05/12.47	0.05/12.82	0.03/9.72	0.04/11.10	0.03/7.38	0.06/17.04

Population		11	12	13	14	15	16	17	18	19	20
N		30	30	30	30	30	30	30	30	30	21
number of seminal vesicle coils	min./max.	9.00–18.00	14.00–19.00	9.00–19.00	9.00–21.00	11.00–17.00	12.00–19.00	7.00–15.00	12.00–18.00	10.00–18.00	9.00–21.00
	mean/med.	13.33/13.00	16.23/16.00	12.97/13.00	15.03/15.00	13.70/13.50	15.03/15.00	10.33/10.50	14.60/15.00	15.47/16.00	12.90/12.00
	sd/C.V.	2.07/15.55	1.63/10.06	2.54/19.58	3.17/21.07	1.76/14.88	1.96/15.01	2.19/21.16	2.03/13.89	1.93/12.45	3.75/29.09
testis length	min./max.	0.73–1.32	0.68–1.25	0.85–1.46	0.86–1.65	0.75–1.34	0.84–1.43	0.75–1.41	0.80–1.37	1.06–1.66	0.79–1.25
	mean/med.	0.95/0.91	0.97/0.93	1.12/1.13	1.07/1.04	0.97/0.93	1.06/1.06	1.02/1.00	1.04/1.04	1.31/1.30	0.99/0.99
	sd/C.V.	0.15/16.10	0.14/14.18	0.16/14.50	0.16/15.30	0.14/14.61	0.15/14.10	0.14/13.28	0.15/14.47	0.16/12.57	0.13/13.43

little varied among populations (Tables 5, 6). For all these characters, the variability coefficient assumed the highest values in populations 3, 8 and 15 (Figs 120–132, 185–190, 259–265) and the lowest in populations 14 and 16 (Figs 248–253, 271–275). Population 2 (Figs 98–109) was characterised by a low variation in the length of oviduct loop accompanied by a wide variation in its breadth (Table 5).

The mean length of the bursa (Tables 5–6, Fig. 322) was statistically significantly higher in the northern populations (Kendall's rank correlation coefficient tau = 0.621, P = 0.01); the same, S-N directed clinal variation was detected in the bursa/bursa duct length ratio (tau = 0.516, P = 0.01) and bursa/receptaculum seminis length ratio (tau = 0.379, P = 0.05) (Fig. 323). The considerable variation of the bursa copulatrix and receptaculum seminis concerned not only their size, but also shape and, in the case of the receptaculum, position. Measurements cannot fully reflect the shape and topography of particular components of the female reproductive organs, hence variation in these components in particular populations is shown in Figures 74–86, 98–109, 120–132, 138–143, 150–156, 162–167, 173–178, 185–190, 195–200, 206–211, 217–220, 227–233, 239–243, 248–253, 259–265, 271–275, 281–285, 291–295, 301–305, 312–317. In respect of its outline, the bursa copulatrix can be described as straight (as in Fig. 210), J-shaped (as in Fig. 185) or U-shaped (as in Fig. 249), and in respect of proportions, it can be described as bulging (as in Fig. 99) or slim (as in Fig. 227). In almost all the populations, all kinds of bursae were represented and in each population one of the types was found to be the most common. In the figures, these typical bursae are dotted. The straight bursa was the most common in population 10 (Figs 206–211), the J-shaped one in populations 1, 3, 4, 6, 8, 9, 11 and 20 (Figs 74–86, 120–132, 138–143, 162–167, 185–190, 195–200, 217–220, 312–317); in the remaining populations, the U-shaped bursa prevailed (Figs 98–109, 150–156, 173–178, 227–233, 239–243, 248–253, 259–265, 271–275, 281–285, 291–295, 301–305). In all the populations except 1, 2, 5 and 6, the slim bursa predominated (Figs 74–86, 98–109, 150–156, 162–167).

The receptaculum seminis was also varied in shape. The predominant type was oval, of various size, but in populations 5 and 8, numerous specimens had



Figs 306–317. Variation in reproductive organs of *B. austriaca* (population 20): 306–311 – penis, 312–317 – bursa copulatrix, seminal receptacle and coil of oviduct. For population numbers see: Description of localities. Dotted figures – most common shape

irregular, sac-shaped receptacula, many of which were also big (Figs 150–156, 185–190). The receptaculum was mostly small in populations 1, 13 and 15 (Tables 5, 6, Figs 74–86, 239–243, 259–265). The receptaculum was most often situated close to the oviduct loop, but in populations 4–6, 9–11, 16 and 20 most individuals had it situated at the outlet of the bursa copulatrix duct (Figs 138–143, 150–156, 162–167, 195–200, 206–211, 217–220, 271–275, 312–317). The most varied bursa and receptaculum were found in population 5 (Table 5, Figs 150–156), but also in populations 3, 6, 8, 12 and 15 (Figs 120–132, 162–167, 185–190, 227–233, 259–265); they were the least varied in populations 4 and 19 (Figs 138–143, 301–305). Populations 1, 9 and 17 (Figs 74–86, 195–200, 281–285) were distinguished by the most, while population 11 by the least varied length of the bursa copulatrix (Table 6, Figs. 312–317).

Male reproductive organs

Of all the male soft parts examined, the reproductive organs (Tables 7, 8) were the most varied. The penis length ranged from 0.66 to 1.88 mm. The mean

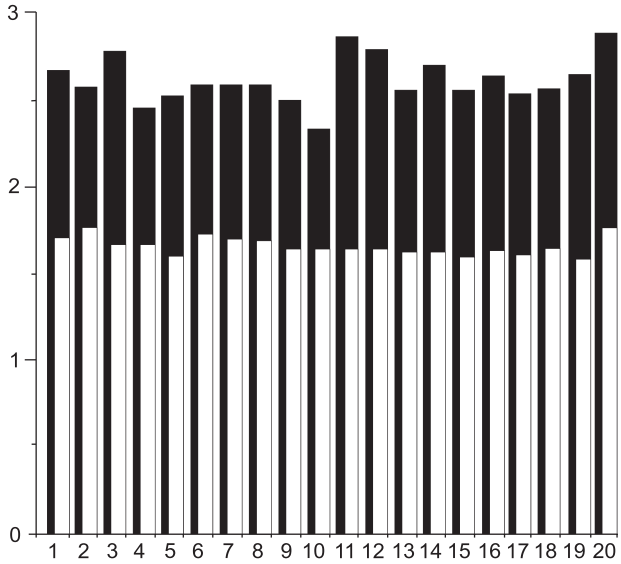


Fig. 318. Mean values of shell height (solid bars) and shell height/width ratio (hollow bars) in *Bythinella* populations. For population numbers see: Description of localities

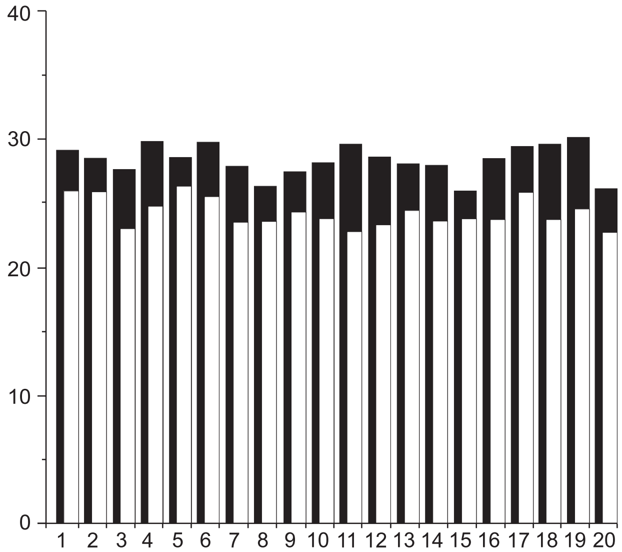


Fig. 320. Mean number of cusps on outer (solid bars) and inner (hollow bars) marginal radular teeth in *Bythinella* populations. For population numbers see: Description of localities

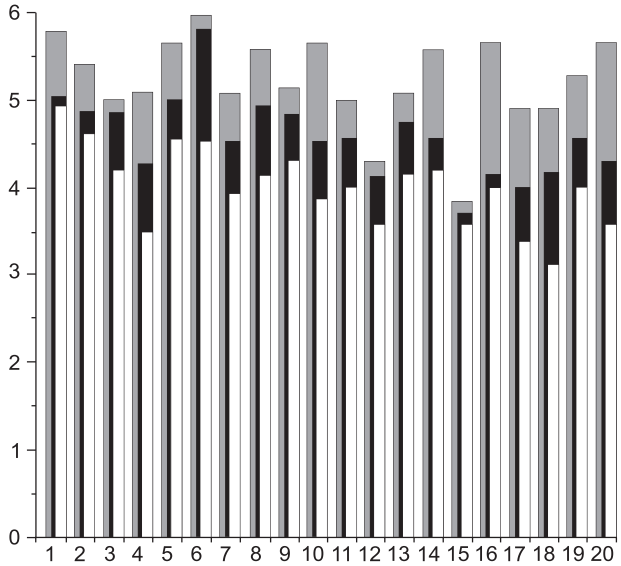


Fig. 319. Mean number of lateral cusps on rhachidian (shaded bars), outer lateral (solid bars) and inner lateral (hollow bars) radular teeth in *Bythinella* populations. For population numbers see: Description of localities

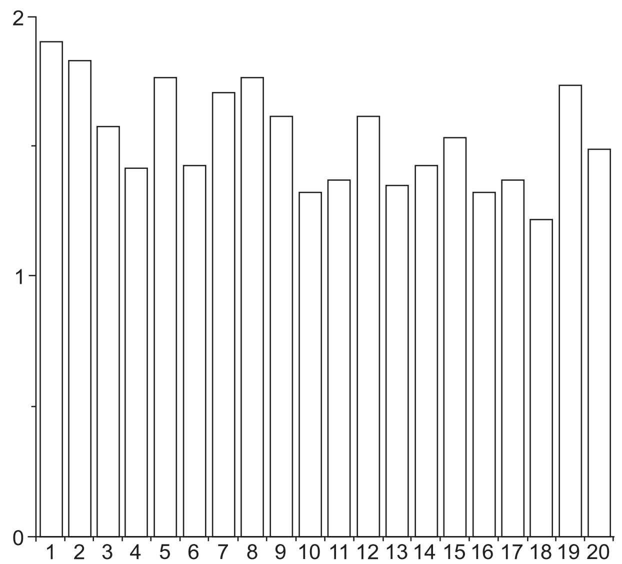


Fig. 321. Radula length/shell height ratio in *Bythinella* populations. For population numbers see: Description of localities

length was the lowest in populations 2 and 1 (Figs 62–73, 87–97), the highest in 20 (Figs 306–311), and also in 4 and 19 (Figs 133–137, 296–300). The character was the most variable in populations 6, 9 and 20 (Figs 157–161, 191–194, 306–311) and the least so in 4 and 18 (Figs 133–137, 286–290). The distance between the flagellum opening and the end of the left penis arm varied the most in populations 1, 2, 5, 6, 9, 10, 15 and 20, and the least in populations 8 and 18.

Like in the case of the female reproductive organs, measurements do not fully describe the shape of the penis, whose variability is shown in the figures (Figs 62–73, 87–97, 110–119, 133–137, 144–149, 157–161, 168–172, 179–184, 191–194, 201–205, 212–216, 221–226, 234–238, 244–247, 254–258, 266–270, 276–280, 286–290, 296–300, 306–311). Like with the bursa copulatrix, the following population-specific shapes were distinguished: massive (as in Fig. 184), slim (as in Fig. 310) and intermediate (as in Fig. 234); the left arm of the penis relative to the right arm was described as of similar width (e.g. Fig. 235) or much slimmer (e.g. 276). The massive penis was the most common type in population 8 (Figs 179–184) and also in 7, 9, 17 and 18 (Figs 168–172, 191–194, 276–280, 286–290); the slim penis predominated in populations 1, 4 and 20 (Figs 62–73, 133–137, 306–311) and was less common in 14 and 15 (Figs 244–247, 254–258); in the remaining populations the most frequently observed width of the penis was described as intermediate. The biggest width difference between the two arms of penis was recorded in populations 17 and 18 (Figs 276–280, 286–290) but also in part of the populations 3, 5, 7, 8, 9 and 10 (Figs 110–119, 144–149, 168–172, 179–184, 191–194, 201–205).

The flagellum length varied much among the populations (Tables 7, 8). Its range was 0.55–3.68 mm, the highest mean value was recorded in population 20 (2.03 mm), as well as in 3 and 18, and the lowest value was found in population 9 (1.00 mm). The highest variation was recorded in populations 2 and 20, the lowest in populations 7, 17, 18 and 19. The flagellum diameter was the most varied in populations 2, 6, 9, 12 and 20, the least variation in this character being observed in 4, 18 and 19. The most varied length and width of the prostate were recorded in populations 2, 5, 8 and 20, the least varied – in 8, 17, 18 and 19. The number of loops of the seminal vesicle, ranging from 7 to 23, was the most varied in populations 3, 9 and 20, and the least so in populations 4, 12, 17 and 19. Considering all the characters, the male reproductive organs were the most varied in populations 2, 9 and 20, and the most uniform in 4, 8, 18 and 19.

The variation in one morphological character did not have to be necessarily correlated with that in the other characters: snails of the same population could vary much in some characters and be homogeneous with respect to others. In almost any population, some character states could be found that were specific exclusively for this population. The reproductive organs were found to be the most variable. For both sexes, most of the studied characters were highly varied in populations 1 and 3, and for the females also in 8 and 12 (Tables 1–8).

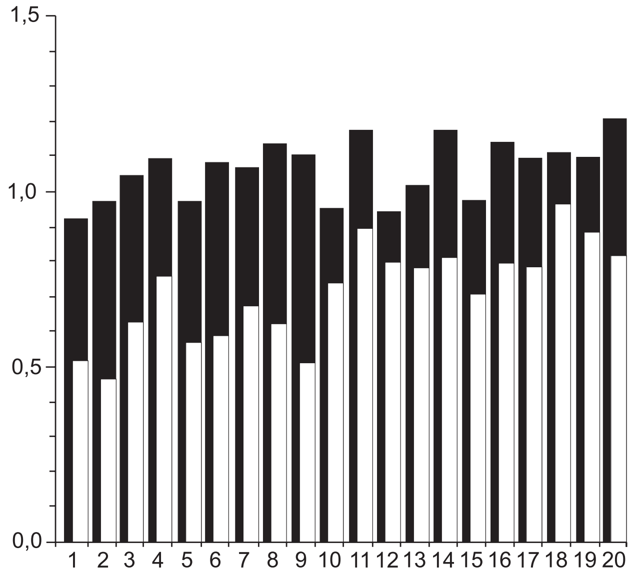


Fig. 322. Mean length of ctenidium (solid bars) and bursa copulatrix (hollow bars) in *Bythinella* populations. For population numbers see: Description of localities

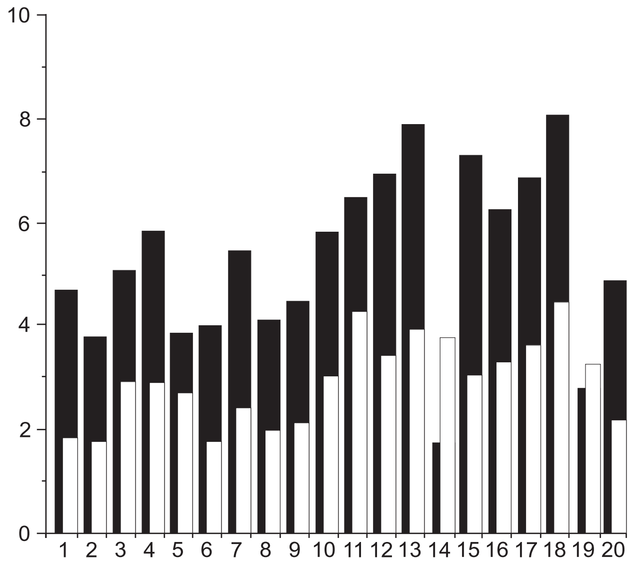


Fig. 323. Length ratios of bursa copulatrix/seminal receptacle (solid bars) and bursa/bursa duct (hollow bars) in *Bythinella* populations. For population numbers see: Description of localities

DISCUSSION

The external morphology and anatomy of soft parts in *Bythinella* do not deviate from the hydrobiid pattern described by numerous authors (RADOMAN 1973, 1983, DAVIS et al. 1985, HERSHLER 1985, FALNIOWSKI 1987a, DAVIS et al. 1988, PONDER et al. 1991, HAASE 1994). The tube-shaped spermatheca duct and bifid penis of *Bythinella* are rare among hydrobiids and regarded as apomorphic within the family (DAVIS et al. 1982, 1985, HERSHLER 1985). The sexual dimorphism, in *Bythinella*, manifest in the shell height, is in accordance with the common records of larger sizes of gastropod females (DAVIS & PONS DA

SILVA 1984, DAVIS & MAZURKIEWICZ 1985, HERSHLER 1985, FALNIOWSKI 1987a, 1989b, WILLIAMS 1994, PONDER et al. 1996).

The low variation in the protoconch diameter indicates that, like in *Heleobops* (Hydrobiidae: DAVIS & MCKEE 1989), the studied populations did not differ in the duration of intracapsullar development. Differences in this character may occur in closely related prosobranch gastropods (REHFELDT 1968, VAN AARTSEN & VERDUIN 1978, COLOGNOLA et al. 1986, VERDUIN 1986). In most cases, the protoconch diameter and shape are not useful in species-level taxonomy, and many authors have instead focused their attention on the microsculpture of this region of the shell (PONDER 1982, DAVIS et al. 1985, HERSHLER & THOMPSON 1988, FALNIOWSKI 1990a, PONDER et al. 1993, HERSHLER 1995). In some snail taxa, the shell microsculpture has turned out to be an important diagnostic character (MARSHALL 1983) but in most cases it does not convey much information. In his SEM study of the protoconch surface of 14 prosobranch species, FALNIOWSKI (1990a) found that the character was very useful within the Valvatidae, less so in the Bithyniidae, while in the Hydrobiidae its usefulness was very much restricted. The protoconchs of two members of *Bythinella* examined in his study (*B. micherdzinskii* Falniowski, 1980; *B. zyvionteki* Falniowski, 1986) did not differ much. The same pertains to the embryonic shell of *B. austriaca* (Fraunfeld, 1859) (SZAROWSKA 1996), and consequently this character is not dealt with in the present study.

The biometrical analysis of the shell in *Bythinella* indicates a high intrapopulation and a low interpopulation variation, these combined with the overlapping variability ranges of the taxa. Such a situation is typical of hydrobiids (KRULL 1935, MUUS 1963, GIUSTI & PEZZOLI 1977, HERSHLER 1985, FALNIOWSKI 1987a, PONDER & CLARK 1988, PONDER et al. 1996) and frequent in other snails. In his studies on deep-water *Lymnaea* from the lake Leman, ROSZKOWSKI (1914) found that shell characters alone were not sufficient to distinguish between species. DAVIS (1979) pointed out that numerous shell characters were convergences and parallelisms which would limit the taxonomic value of the shell. Nonetheless, descriptions of many species are based on shell alone (ANGELOV 1976, VAN AARTSEN & VERDUIN 1978, BECH & FERNANDEZ 1986, VERDUIN 1986, 1988) or, at most, both shell and radula are considered (MARSHALL 1983, 1987, PONDER 1984). In some taxa, including the Hydrobiidae, the scarcity of shell characters necessitates considering anatomical characters in taxonomy (JUNGBLUTH & BOETERS 1977, PONDER 1982, RADOMAN 1983, FALNIOWSKI 1987a).

Some of the examined populations of *Bythinella* differ from the others in their radular characters. Of internal structures, the radula is the most commonly applied in prosobranch taxonomy (DYBOWSKI 1884, ROSZKOWSKI 1914, 1929). Once thought to be an important gastropod character (e.g. DYBOWSKI 1884), its structure soon turned out to be very much variable (ROSZKOWSKI 1929, KRULL 1935) and show numerous homoplasies (DAVIS 1979, DAVIS et al. 1985, FALNIOWSKI 1990b). The form of radula undoubtedly reflects the kind of food consumed; on one hand, many snail species feed on the same kind of food, on the other most radulae are universal inasmuch as they can take various kinds of food. Hence, there seems to be little stabilizing selection to maintain a certain form of radula and the taxonomic value of the latter is most often limited and questionable (FALNIOWSKI 1983, 1989a, 1990a, b). In some cases, however, statistical analysis of quantitative radular characters may reveal differences that can be applied to phylogeny reconstruction (FALNIOWSKI et al. 1996).

According to the ontogenetic criterion, teeth with a higher number of cusps represent a plesiomorphic condition of the radula. Observations on the embryonic development of radula in the Lymnaeidae (ROSZKOWSKI 1927, FELIKSIAK 1938, 1939, FALNIOWSKI 1983) and Viviparidae (FALNIOWSKI et al. 1996) revealed a gradual reduction in the number of cusps on particular teeth, and thus it is most likely that such a reduction took place also in the phylogeny of these snails. Apart from the observed wide variarion, from among the studied populations of *Bythinella*, a high number of cusps on the laterals was most frequently noted in populations 1 and 6 that represented two distinct morphospecies. In respect of their radular structure, these two are probably primitive, and the smallest number of cusps on the laterals in populations 12, 15 (*B. austriaca*) 17, 18 (*B. zyvionteki*) and 20 (*B. austriaca ehrmanni*) suggests that these five populations are more derived.

The observed clinal variation (MAYR 1974) in shell height/radula length ratio may reflect an adaptation to a different kind of food or a substrate from which the food is scraped off. The heavier the radula is loaded at feeding, the longer it must be, and in snails feeding on soft food the radula length will decrease (FRETTER & GRAHAM 1962, PURCHON 1977). *Bythinella* is a typical spring inhabitant and, however short the distance from the spring, it often becomes very scarce downstream (JUNGBLUTH 1971a, b, PEZZOLI & GIROD 1971, BERGER 1973, RADOMAN 1976, FALNIOWSKI 1987a and own, unpublished, observations). It is usually found crawling on submerged remnants of terrestrial plants, aquatic mosses, fallen leaves (URBAŃSKI 1957, WIKTOR 1964, JUNGBLUTH 1972, PIECHOCKI 1979, FALNIOWSKI 1987a), as well as on stones and gravel overgrown with periphytic algae (FALNIOWSKI 1987a and own unpublished results). In spite of some differences between the springs inhabited by the examined populations, it is difficult to specify what kind of difference is concerned: the type, quantity or availability of food. Stomachs of *Bythinella* contain diatoms, fragments of macrophytes and detritus particles (JUNGBLUTH 1972, FALNIOWSKI 1987a). It could not be ascertained if the reason for the observed clinal variation in shell height/radula length ratio was the adaptation of the radulae to different kinds of food, or another factor. The variation may as well reflect interspecific differences. Similar observations concern the clinal variation of the ctenidium length.

Some authors regard the shape of bursa copulatrix as the crucial character in distinguishing species of *Bythinella* (BOETERS 1988). Many others, however, stress the wide variation of both the bursa and the rest of the female reproductive organs (GIUSTI & PEZZOLI 1977, FALNIOWSKI 1980, 1986, 1987a, b, 1992), found also in this study. Despite their variation, the female reproductive organs are commonly applied in the hydrobiid taxonomy (RADOMAN 1973, 1976, GIUSTI & PEZZOLI 1980, 1982, BOETERS 1981, PONDER 1982, BANK & BUTOT 1984, FALNIOWSKI 1987a). FALNIOWSKI (1987a) considered these characters to be of primary importance when distinguishing species of *Bythinella* and at the same time pointed to the weak interspecific differentiation and the overlapping variability ranges that would in some cases preclude species identification, unless character states were recognized in at least a few individuals of the examined population. His opinion is confirmed by the present biometrical study.

Another observation that agrees with earlier data (FALNIOWSKI 1987a, 1992) is the statistically significant, S-N clinal variation in the length of bursa copulatrix, bursa/bursa duct and bursa/receptacle length ratios. What has not been fully confirmed, is the remark that the baggy shape and the large size of seminal receptacle are distinctive characters of *B. cylindrica*. On the other hand, the receptacle length/width ratio actually assumed the highest value in three out of the four studied populations (except population 9) of this morphospecies, whereas the lowest values were noted in the populations of *B. austriaca*.

The structure of the male reproductive organs is regarded as the chief diagnostic character in some taxa, e.g. insects (the key-and-lock model: MAYR 1974). Though in some gastropod taxa the penis is widely variable, some authors tried to ascribe to it the same importance (MUUS 1963, RADOMAN 1978, FREYER et al. 1987, BOETERS 1988). The snail penis has no hard element whose close fitting would enable copulation. Moreover, it changes with season or the physiological condition of the animal and is prone to artifacts. All this raises doubts as to its taxonomic value (FALNIOWSKI 1990a). Likewise, the wide variation of penis, presented in this paper, renders its diagnostic value doubtful. The interspecific differences in flagellum/penis length ratio observed by FALNIOWSKI (1987a) in *Bythinella* have not been confirmed.

The high intrapopulation variation combined with the slight differences between the distinguished morphospecies in almost all the morphological characters examined, conforms with FALNIOWSKI'S (1987a) observations and points to the limited usefulness of these characters for the taxonomy of *Bythinella*. To draw any taxonomic conclusions, both phenetic and phylogenetic multidimensional analysis of all morphological characters is needed, combined with molecular data analysis which will be presented in separate papers.

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APPENDIX I: Lettering to figures and abbreviations of measured characters

A. ABBREVIATIONS:

an – anus;
ave – anterior part of stomach (ventriculus anterior);
bc – bursa copulatrix;
c – central (rhachidian) tooth (rhachis);
ca – lateral cusps of central tooth;
cbc – duct of bursa copulatrix (canalis bursae copulatricis);
cm – columellar muscle (musculus columellaris);
cs – central cusp of rhachidian tooth;
ct – ctenidium;
f – faecal pellets;
fl – penial gland (flagellum);
ga – albumen gland (glandula albuminalis);
gb – basal cusps (of central tooth);
gn – nidamental gland (glandula nidamentalis);
gp – gonopore (gonoporus);
gpd – gono–pericardial duct (ductus gonopericardialis)
hp – hepatopancreas;
hpp – hepatopancreas outlet;
in – posterior intestine (intestinum posterior)
l – ctenidium lamella,
ls – central cusp of lateral tooth;
lt – lateral tooth;
lw – inner cusps of lateral tooth;
lz – outer cusps of lateral tooth;
ma – attachment area of operculum;
mw – inner marginal tooth;
mz – outer marginal tooth;
o – eye (oculum);
oc – coil of oviduct;
oe – oesophagus;
op – operculum;
os – osphradium;
ov – oviduct (oviductus);
ova – ovary (ovarium);
p – penis;
pa – mantle (pallium);
pd – foot (pes);
pe – pericardium;
pr – prostate (prostata);
pve – posterior part of stomach (ventriculus posterior);
r – kidney (ren);
re – rectum;
rs – seminal receptacle (receptaculum seminis);
sd – spermatheca duct (ductus spermathecae);
sn – snout;
ss – style sac;
sv – seminal vesicle (vesicula seminalis);
t – cephalic tentacle;
te – testis;
vd – vas deferens;
ve – stomach (ventriculus).

B. MEASURED CHARACTERS:

AP – distance from anus to mantle border;

DBC – bursa copulatrix length;
DC – ctenidium length;
DCB – bursa duct length;
DF – flagellum length;
DML – maximum length of ctenidium lamella;
DO – operculum length;
DOC – oviduct coil length;
DOS – osphradium length;
DOV – ovary length;
DP – penis length;
DPR – prostate length;
DRS – seminal receptacle length;
DSD – spermatheca duct length;
DSS – slyle sac length;
DT – testis length;
DVE – stomach length;
OC – distance from anterior ctenidium to anterior osphradium;
PF – distance from flagellum outlet to vas deferens outlet on second arm of penis;
SA – first whorl width;
SBC – bursa copulatrix width;
SC – third whorl width;
SDB – bursa duct width;
SF – flagellum width;
SM – shell width;
SMA – width of operculum attachment area;
SO – operculum width;
SOC – oviduct coil width;
SOS – osphradium width;
SP – protoconch diameter;
SPR – prostate width;
SRS – seminal receptacle width;
SU – aperture width;
SV – coil of seminal vesicle;
SVE – stomach width;
WM – shell height;
WOZ – body whorl height;
WU – aperture height;
ZW – whole whorl (360°).

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