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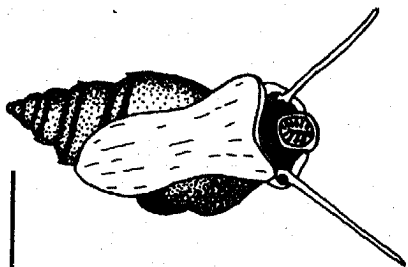
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FOLIA MALACOLOGICA

ZESZYT 1

ANDRZEJ FALNIOWSKI

HYDROBIOIDEA POLSKI
(PROSOBRANCHIA: GASTROPODA)



KRAKÓW

1987

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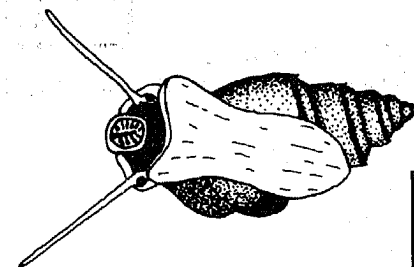
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FOLIA MALACOLOGICA

BULLETIN 1

ANDRZEJ FALNIOWSKI

HYDROBIOIDEA OF POLAND
(PROSOBRANCHIA: GASTROPODA)



CRACOW

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Foreword

Polish malacology has a rich tradition exceeding 100 years of research carried out in a number of scientific centres: at universities and museums of natural history. Researches ranged broadly from subfossil-quaternary to contemporary faunae, and its results have been published in popular and scientific journals of zoology, ecology, geology, paleontology and allied sciences.

In the last decades a vital development of various malacological research on a still broader range of issues has been observed due to a greater number of scientists involved and numerous scientific expeditions made with the participation of Polish scientists. Also we owe the development and progress in malacology to intensified research on the sediments of Quaternary period as well as on the state and changes of natural environment.

Such a brilliant progress led in 1985 to the establishing of the Malacological Section at the Quaternary Research Committee of the Polish Academy of Science. The section is active in all fields of malacological research on the quaternary and contemporarily living molluscs. Its members are 50 scientists of all scientific centres of Poland. An attempt to issue an advanced scientific journal collecting and publishing papers on a broad range of malacological problems has succeeded in the establishing of FOLIA MALACOLOGICA published within the series of The Scientific Revue of the Academy of Mining and Metallurgy of Cracow. The Academy is a scientific centre with illustrious traditions of complex research on geology, and natural resources including the youngest geological period, as well as on the changes and anthropogenous degradation of natural environment. FOLIA MALACOLOGICA is edited by the publishing staff of research workers of 5 universities. The journal is to stimulate a broad interchange of experience, data and information on malacology. Two volumes in the congress languages are going to be published yearly.

FOLIA MALACOLOGICA welcomes the papers of authors from Poland and abroad. All research workers are invited to contribute in the publishing of the journal.

The first volume of FOLIA MALACOLOGICA is issued with the hope of its editors to succeed and evoke resonance among scientists.

Editorial Committee

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Abstract: The paper is devoted to the Polish Hydrobioidea, which have not been studied so far. The vagueness of both systematic position and relationships within the group is presented, as well as their general morphology and anatomy; the taxonomically useful characters are emphasized. Then there follows a comparative discussion of: reproduction, feeding, parasites and abnormalities caused by them, factors determining distribution (salinity, other elements of water chemism, temperature, water movement, environment stability, substratum, vegetation, competition, anthropoppression), ways of expansion, distribution character and inhabited biotopes, origin, and techniques of collection, preservation and study. The key to the genera (Hydrobia, Bythinella, Marstoniopsis, Lithoglyphus and Potamopyrgus) and the keys to the species of Hydrobia and Bythinella are given. The author presents his own concept of speciation and systematics within Bythinella. All the 12 Polish hydrobioid species are described in respect of: shell, forms, pigmentation, ctenidium, osphradium, male reproductive organs, penis, female reproductive organs and distribution.

Andrzej Falniowski
HYDROBIOIDEA OF POLAND
(PROSOBRANCHIA: GASTROPODA)

I. Introduction

The gastropods of the Hydrobioidea superfamily are mostly small, even minute, and show such a high shell variability that for a mere determination it is necessary to study their soft parts morphology and anatomy. The gastropods cover both - brackish- and freshwater forms in Poland. However, among the latter group there are in fact only two species - one occurring commonly and often numerous in a larger part of the country, and the other which is quite common, but hardly findable, whereas all the other species of the group are rare, hard to find with their presently quite limited ranges in Poland. These characteristic features of the group may have made Hydrobioidea seem the most poorly known molluscs of Poland.

All the data on Hydrobia inhabiting the Polish coastal waters of the Baltic can be found in benthos studies of Gdańsk Bay (Demel 1925, 1933, 1935; Jazdzewski 1962 and Żmudziński 1967) which mention Hydrobia ulvae and H. ventrosa (or simply "Hydrobia sp."); however, the correctness of the determinations seem merely doubtful. Feliksiak (1938) describes the radula of the fossil H. ulvae. Falniowski, Dyduch and Smagowicz (1977) describing Hydrobia of Puck Bay take into account the shell forms as well as radulae, but still neglect the soft parts. They record also the occurrence of H. neglecta in the Polish coastal waters.

Potamopyrgus jenkinsi, due to its still uncomplete expansion throughout Poland, has been a popular species for studies amongst field naturalists (Urbański 1938, 1947, 1962; Jackiewicz 1973; Berger and Dzieczkowski 1977; Dyduch and Falniowski 1979) and two papers deal with its ecology (Wolnomiejski and Furyk 1970, Kasprzak 1979). However, nothing has been said on its anatomy; furthermore, some of the records of its occurrence in the Polish coastal waters must have resulted from an erroneous determination of Rissoa membranacea (J. Adams, 1797) occurring numerously there.

Lithoglyphus naticoides and Marstoniopsis scholtzi were only mentioned in faunistic studies. This is Urbański (1947) who wrote on Bythinella in his critical review of the molluscs of Poland: "This genus is quite poorly known in our country. This is to be checked whether there are still more species or only B. austriaca..". Unfortunately, this opinion has still been adequate. In the faunistic papers "Bythinella austriaca" is mentioned with no criticism. Piechocki (1979) regards the observed shell variability as ecophenotypic. The soft parts morphology and anatomy has not been the subject of study in Poland so far.

The aim of this paper which completes my over ten-year studies is, actually, to fill up this gap in the knowledge of Polish molluscs.

The study is based on the material of about 15,000 fixed specimens collected from 138 localities situated over the whole area of Poland. The highest concentration of localities is obviously in northern whereas lower in southern Poland and scarcely were localities situated in the central region. The listing of all the localities seems unjustifiable. All the localities of the uncommon species are given each time. I have also used my own materials collected abroad for a comparison. The list of contributors to whom I owe a large debt of gratitude should include: dr. L. J. M. Butot (Bilthoven, the Netherlands), dr. T. Warwick (Edinburgh, Scotland), dr. F. Giusti (Siena, Italy), dr. L. Berger (Poznań, Poland), and dr. K. Jazdzewski (Łódź, Poland), who have submitted their collections to me. The repository of the whole collection is the Zoological Museum of Jagiellonian University in Cracow.

II. General part

1. Systematic position and relationships within Hydrobioidea

The critical opinion of the knowledge of Polish Hydrobioidea unfortunately seems also applicable to the systematic position and, especially, to the relationships within Hydrobioidea in general. For the present the hydrobioid classification is in chaos which has parallel in no more than a few other molluscan groups. Moreover, various systems question the characters already approved as the basis for systematics and found new distinctive features which again prove soon as justifiable as the previous ones.

Thiele (1931) included the family Hydrobiidae into Rissoacea and this has been acknowledged, however, with some exceptions (Starobogatov 1970; Golikov and Starobogatov 1975). The rank of Rissoacea is defined differently by different authors: either as of a superfamily (Fretter and Graham 1962, 1978a,b; Götting 1974; Davis 1979, 1980; Davis, Mazurkiewicz and Mandracchia 1982) or of a suborder (Nordsieck 1972). The rank of suborder seems justified better if for no other reasons but practical ones, because this enables to grasp in a system all the complex relationships within Rissoacea. For similar reasons I acknowledge, according to Radoman (1973) and Giusti and Pezzoli (1980), the superfamily rank of Hydrobioidea, the question of "the taxonomic rank of differences" within the group leaving out of discussion. Rissoacea, which appears in the Carboniferous, includes over 1,300 species of small gastropods, medium advanced within Mesogastropoda. Hydrobioidea are usually regarded as the most primitive and thus put in the beginning of the rissocean system.

In older systems "Hydrobiidae" constituted a highly differentiated group of numerous species, often not related more closely with one another, characterized however by similar shells and radulae. Bithyniidae, now excluded from Hydrobioidea, may be an example. Basing on the structure of the dens centralis of the radula, the presence or

absence of the spiral caecum on the stomach, the organization of the central nervous system, the female reproductive organs, penis, and the presence or absence of the flagellum; Radoman (1973) divided Hydrobioidea into several families and subfamilies. Later this system was completed by Giusti and Pezzoli (1980). In these systems "Hydrobiidae" consist of two superfamilies: Hydrobioidea and Pyrguloidea. Hydrobioidea contain then the families: Hydrobiidae, Moitessieriidae, Bythinellidae and Lithoglyphidae.

Davis (1979) in the paper on the Pomatiopsidae of the Mekong River excluded Pomatiopsidae from Hydrobiidae and divided the latter into the subfamilies: Benedictinae, Hydrobiinae, and Pyrgulinae, including Littoridininae again into Pomatiopsidae. In the latest paper (Davis, Mazurkiewicz and Mandracchia 1982) he divided Hydrobiidae into Hydrobiinae, Nymphophilinae, Lithoglyphinae and Littoridininae, placing the latter again near Hydrobiinae. Giusti and Pezzoli (1984) abandoned the Radoman's system, suggesting the division of Hydrobiidae into four subfamilies: Hydrobiinae, Littoridininae, Lithoglyphinae and Bythinellinae.

The problem of a systematic position of Potamopyrgus jenkinsi can be a good example of the striking incompleteness of all the newer hydrobioid systems. The gastropod has appeared in Europe recently, and its relatives need to be searched for probably on the Southern haemisphere, in New Zealand or South America. Thiele (1931) and Nordsieck (1972) put it into Littoridininae within Hydrobiidae.

It has been noticed above that Davis included Littoridininae into Pomatiopsidae first, then into Hydrobiidae, and regarded an American genus Meleobia Stimpson, 1865 belonging to Littoridininae, as very closely related to an European genus Semisalsa Radoman, 1974. Potamopyrgus should then belong to the subfamily Semisalsinae, family Moitessieriidae of the Radoman's system. However, it is unjustified because Potamopyrgus shows a variety of features contradicting this position. Boeters (1984) tried to put Potamopyrgus into the system of Davis, Mazurkiewicz and Mandracchia (1982), describing a new subfamily: Potamopyrginae, but his view seems to be doubtful especially because of incomplete, sometimes even erroneous data on the morphology used for the basis. Giusti and Pezzoli (1984) concluded to put Potamopyrgus into Hydrobiinae, however, expressing their serious doubts. Finally, it should be acknowledged that the systematic position of P. jenkinsi has been unclear so far.

The state of the present systematics of Hydrobioidea cannot surprise, anyway, and for the time being it results from a poor knowledge of the group. The range of Hydrobioidea covers nearly the whole world, while

the more recent systems take into account the representatives from small fragments of the whole range: Radoman proposed the system for the Balkans and Asia Minor; Giusti and Pezzoli spread it for neighbouring Italy as well. Davis worked on the materials from Far East and North America. It cannot surprise, therefore, that these merely provisional systems can be hardly applicable enough for all the hydrobioids. There is simply no modern system of Hydrobioidea which could draw their phylogeny at least in outline.

Another respect is the controversy over the value of basic features of the system. Davis (1982) and Giusti and Pezzoli (1984) questioned the usefulness of the features used in the Radoman's system (1973), as not corresponding to the evolutionary tendencies. The presence or absence of the spiral caecum in the stomach was especially questioned as a criterion above the genus level. In fact, while it is well developed in Hydrobiidae and Potamopyrgus, and absent in Lithoglyphidae, in Bythinellidae cannot be listed among the family characters, since it is absent in Bythinella, and present in Marstoniopsis (Falniowski in press). Also the taxonomical usefulness of both the particular traits of the female reproductive organs (the habitus of the loop of the oviduct, the number and position of receptaculum seminis), and the penis (the presence or absence of elongations, outgrowths, or the second arm) was regarded as unfit for the basis of the hydrobioid system.

The latter opinion is rather controversial. It is a rule, of course, that the peculiarities of the female reproductive organs structure are the more taxonomically useful the more closely related species are concerned. However, it cannot be acknowledged that such traits are of no more than an adaptative character and thus unfit for the families classification. Certainly, one has to be careful, especially regarding small differences as significant. Anyway, the features basic of the recent systems seem to raise not less doubts than the former ones.

Nobody has questioned, for example, the usefulness of the radula even if only the habitus of the central tooth is concerned. Davis (1979) suggested even the positioning of Littoridininae in Pomatiopsidae, basing on the presence of a greater number of basal cusps at the dens centralis in these gastropods than in Hydrobiidae.

In all the Polish Hydrobioidea there are basal cusps in total number: Hydrobiidae: 2 - 4, Bythinellidae: 4 - 6, Lithoglyphidae: 6, and Potamopyrgus: 6 - 8. It is well to add that the radula structure of the Polish Hydrobioidea is little differentiated interspecifically and highly variable infraspecifically, thus it is taxonomically useless

A proposed system of the Polish Hydrobioidea

	<u>Hydrobiidae</u>	<u>Bythinellidae</u>	<u>Lithoglyphidae</u>	<u>Potamopyrgus</u>
1. shell structure	?			
1.1. layer under periostracum	?	+ fine-grained	+/- fine-grained	+/- fine diagonal structures
1.1a its structure				
1.2. layer at inner shell surface	?	+/- gradual	+ sharp	+ sharp
1.2a transition from palisade layer	?	grained-spongy	wide diagonal structures	wide diagonal structures
1.2b its structure	?	- fine	+ -	+ large
1.2c slit spaces	?			
1.2d "cavitai" spaces	?			
2. central nervous system		less long	shortened	?
2.1. pleuro-supraintestinal connectives	relatively long			?
2.2. pleural- with subintestinal ganglia	connected by shortened connectives	usually fused	fused	?
2.3. ganglionated tentacular nerve	-	+	-	?
3. female reproductive organs		loop	loop	loop
3.1. oviduct reaching rs and bc	strongly twisted spiral	strongly	strongly	strongly
3.1a thickened	slightly	-	-	-
3.1b intensively pigmented black	+	-	+	-
3.2 bc and rs imbedded in ga	-	-	+	-
3.3 vagina imbedded in gn	-	+	+	-
4. flagellum	with outgrowths / small 2nd arm	bi-armed	simple	simple
5. penis				
6. genera in Polish fauna	<u>Hydrobia</u>	<u>Bythinella</u> <u>Marstoniopsis</u>	<u>Lithoglyphus</u>	<u>Potamopyrgus</u>

Note: anatomical abbreviations as in figures.

at the level of both: a family and a species. Therefore the radula is ignored in this paper.

According to Davis and also Giusti and Pezzoli (1984) the basic feature for the subfamilies distinction is the separateness of the spermathecal duct (connecting the bursa copulatrix and receptaculum seminis directly with the mantle cavity) from the pallial oviduct. This raises doubts. A good example of this separateness rank as a feature of no taxonomical value even over the species level is that in Valvata naticina Menke, 1845 or Viviparidae and, perhaps, in Potamopyrgus jenkinsi this feature accompanies the ovoviviparity which is a result of adaptation. Such the canal occurs in Potamopyrgus and Bythinellidae, while is absent in Lithoglyphidae and Hydrobiidae.

Hence, there is no system of Hydrobioidea, which could be acknowledged for all the family worldwide. In this paper I limit then the classification drawn to the taxa occurring in Poland. The system is similar, anyway, to those of both Radoman (1973) and Giusti and Pezzoli (1984). I list the main differences only (Table I). I regard Hydrobiidae as the most primitive and Lithoglyphidae as the most advanced, while Potamopyrgus is of an unknown systematic position.

2. General morphology and anatomy of Polish Hydrobioidea

The hydrobioid shells are small, often minute, seldom exceeding 7 mm in height in the Polish representatives (only in Lithoglyphus naticoides - 11 mm) while in Bythinella they even do not exceed 3 mm. They are mostly egg-shaped-conical, seldom barrel-shaped (Bythinella), sometimes almost spherical (Lithoglyphus). The spire is usually high (Lithoglyphus is an exception) while whorls tumidity as well as the outline of the aperture differentiated, the peristome usually continuous, the umbilicus absent or in the form of a narrow slit; the shell surface smooth, only in Potamopyrgus sometimes spiral keel or, exceptionally, bristles; the periostracum thin and translucent, usually olive. The shell surface is often covered with a sediment or periphytic microorganisms, which change the appearance of the shell. It is remarkable that the shells of particular species bear a close resemblance to one another, while the infraspecific variability is very high. Therefore the shell characters are generally insufficient for an exact determination. In the case of Hydrobia and Bythinella the above insufficiency is the rule.

In the shell structure three calcareous layers can be distinguished (Falniowski in press): the one of fine diagonal structures or the fine-grained layer, not always present; the palisade layer with columns

more or less distinguishable and often irregularly arranged; the layer of wide diagonal structures fibrous-spongy in character or the grained-spongy layer. The third one is not always present and in the shell sections parallel to the growth lines shows the elongated cylindrical structures, characteristic for hydrobioids only. The interfamilial differentiation of the shell structure is shown in Table I.

The operculum is thin, horny, elastic and springy, deeply inducted into the shell, spiral with not many whorls, showing no interspecific differentiation.

The head has a straight, short or of medium size snout, a pair of long, filamentous and highly contractile tentacles and the eyes at the external sides of both tentacles, usually on little eye stalks. The head pigmentation varies and often characterizes a particular species. In males the penis is situated posteriorly to the right tentacle. The foot anteriorly with a pair of lobes, posteriorly rounded or sharpened, is relatively broad as for rissoaceans and usually shows a sharp division into pro- meso- and metapodium on its bottom side. In some representatives there is a small pallial tentacle.

The mantle cavity - moderately spacious. The small ctenidium in the form of a single row of laminar lamellae, runs diagonally through the mantle cavity. Its lamellae number is often regarded as characteristic of a species (e.g. Boeters 1973), nevertheless, it is highly variable depending primarily on the gastropod size but also on the habitat character, sex, and seems to be an expression of the genotypic variation as well. Osphradium - straight and short; in connection with the expansion of the gastropods into freshwaters, the kidney is enlarged, but its arm does not extend into the mantle skirt and spreads only between the viscera forming a kind of body cavity. In some species (Marstoniopsis scholtzi) the stores of calcium carbonate are deposited as sphaerulae within the connective tissue, especially of the visceral hump.

The jaws are twin; the radula typical of Taenioglossa, i.e. fulfilling the formula: $2m + 1l + c + 1l + 2m = 5$; the central tooth butterfly-shaped with basal cusps in all the Polish Hydrobioidea. The lateral tooth is axe-shaped, with a relatively long "handle", the inner marginal one relatively broad, with the tip elongated and bent to the side; the outer marginal one proximally broadened, medially narrow, and distally spoon-shaped.

The salivary glands tube-shaped, the pharynx only with short lateral pouches (Thiele 1931), the oesophageal glands absent. The stomach big and sac-shaped, thin-walled in its major part, connected with a big sac of the crystalline style at its pyloric end (Robson 1920; Fretter and

Graham 1962; Radoman 1973). The intestine short. The food varies: detritus, microfauna or microflora, macrophytes.

The central nervous system (Radoman 1973; Giusti and Pezzoli 1980) is characteristically organized. The buccal ganglia located rather forward, the ganglionic thickening on the tentacle nerve often present, the pleural ganglia nearly always connected with the cerebral ones by short connectives. The pleuro-supraintestinal connectives are long, rarely shortened, while the pleuro-subintestinal - short. The sub- and supraintestinal ganglia connected by long connectives with the single abdominal ganglion, the cerebral and pleural ganglia connected with the pedal ganglia by rather long connectives. The propodial ganglia and the metapodial ones connected with the pedal ganglia by shorter and longer connectives respectively. The metapodial ganglia connected with one another by a long commissure. Both zygoneuries (right and left) present. The interfamilial differentiation of the central nervous system is presented in Table I.

The testis dispersed in the first whorl of the visceral hump and is located along the upper side of the hepato-pancreas gland. From the testis a long, intensely coiled and folded, rather thick vas deferens runs and narrows approaching the prostate. The prostate is in the form of a wide sac with the lateral wall thickened by the subepithelial glands and its posterior end submerges in the tissue of the visceral mass (Fretter and Graham 1962). The prostate habitus as well as the position of the outlet of the vas deferens from the gland are sometimes characteristic of the species and in such cases described in this paper. After leaving the prostate the vas deferens branches out the duct (in young specimens broad while in older ones often diminished) running to the mantle cavity; the terminal section of the vas deferens runs to the penis, usually in zigzag. In Bythinellidae there is a flagellum the characters of which are sometimes useful in taxonomy at the species level.

The penis simple or with outgrowths or bi-armed (Table I). In Bythinellidae the right arm includes the outlet of the flagellum.

The folded ovary is situated in the first whorl of the visceral hump, along the upper margin of the hepato-pancreas gland. The thin oviduct runs usually in zigzag. After branching the gonopericardial duct the oviduct becomes broader forming a loop or spiral (Table I). Then it becomes narrower and runs along the accessory gland complex terminating by the gonoporus closely to the mantle border. The vaginal part of the oviduct hardly distinguishable. The bean-shaped accessory gland complex consists of the proximally located albuminoid gland, distally situated nidamental gland and mucous gland as well. This

complex fills closely the space between the rectum and the terminal part of the oviduct, and it communicates broadly with the latter being separated only by a longitudinal fold from the lumen of the oviduct. In viviparous Potamopyrgus jenkinsi instead of the nidamental gland there is a large, thin-walled, undivided brood pouch.

The oviduct receives the bursa copulatrix and 1 - 2 receptaculum seminis, sometimes there is not a receptaculum. In Polish Hydrobioidea there is always 1 receptaculum, in rs_1 position (Radoman 1973). The loop (spiral) of the oviduct narrows reaching the accessory gland complex and joins the duct of the bursa. The receptaculum lies in the angle marked by the loop and that duct. The receptaculum and bursa adhere to the gland complex, and only in Lithoglyphidae they are dipped in it. In the natural position they are covered by the loop (spiral) of the oviduct.

The scheme presented above is common for all the Polish Hydrobioidea (the differences between the families: Table I). The interspecific differences occur within the loop of the oviduct - receptaculum seminis - bursa copulatrix complex, and only this part of the female reproductive organs is described in the systematical part. It is well to add that the loop of the oviduct, due to its glandular functions, shows a great individual variation probably of the physiological character mainly. Therefore, its taxonomical usefulness must be very restricted and then I give up its more detailed description.

3. Reproduction

Like a majority of Prosobranchia, the hydrobioids reproduce bisexually. The exception is Potamopyrgus jenkinsi, whose males are extremely rare (Patil 1958; Falniowski 1979). The absence of males was stated first by Taylor (1900) and Boycott (1917), and the parthenogenetic reproduction by Boycott (1919), Quick (1921) and Robson (1923, 1926). Krull (1935) and Thorson (1946) regarded P. jenkinsi as a hermaphrodite, however, it has not been confirmed so far. Rhein (1935) and Sanderson (1939) found that there is only one maturation division in oogenesis and that it is non-reductional. The males of the other species comprise averagely a half of the population. However, my observations show that, especially in Bythinella, a strongly marked domination of one sex can often be observed. The sexual dimorphism of the shell is, excluding Lithoglyphus naticoides, poorly and inconsistently marked. The females are in general slightly bigger and their shells are somewhat higher, slimmer, with a slightly higher spire, more convex whorls divided by

the suture marked better. However, the sex determination by the shell is hardly possible.

There is always a veliger stage in the embryonal development, but inside the capsule and with the velum reduced. The free swimming veliger can be observed in the life history of only one species: Hydrobia ulvae whose eggs are small, 3 - 25 per capsule (Quick 1920; Lebour 1937; Smidt 1951; Fretter and Graham 1962; Muus 1967). In the other species there is always only one big egg in a capsule, only in H. neglecta sometimes two instead of one (Muus 1967).

The dispute about the existence of a free swimming veliger, the length of this phase and the velum development level in H. ulvae continued for many years (Henking 1894; Quick 1920; Lebour 1937; Linke 1939; Thorson 1946; Smidt 1951; Fretter and Graham 1962; Milejkovskij 1962; Fretter and Pilkington 1971). Many authors suggested that the pelagic stage is strongly shortened in time or even suppressed; these controversies made McMillan (1948) suggest that in the British Isles distinct biological races of H. ulvae can be distinguished, which differ in the life history and salinity tolerance. However, it seems that the majority of the contradictions resulted from the confusion in the distinction between the larvae of H. ulvae and Littorina littorea (Linnaeus, 1758) (Fish and Fish 1977).

The latter authors estimated that the pelagic phase is of about 3 - 4 weeks duration when the shell grows about 1 1/2 whorls. When the veliger is settling down it has 2 1/2 whorls. They described a newly hatched veliger with a single whorled shell covered here and there with groups of pores, typical for Hydrobioidea (Falniowski in press). The velum small, slightly bilobed and with long preoral cilia enabling the larva to swim freely.

According to Smidt (1951) about 10% of eggs complete their development as young creeping gastropods, which is a very high proportion as for marine organisms with a pelagic larva stage. Smidt (1944) reported that in Potamopyrgus jenkinsi inhabiting brackish waters a short pelagic stage could be observed, but this needs verification.

Eggs are laid in capsules attached to a hard substratum, mostly shells of other specimens of the same species (Hydrobia, Lithoglyphus), only in Bythinella these are generally weeds (Jungbluth 1975). The exception - Potamopyrgus jenkinsi - is viviparous and the young leave the brood pouch one by one as creeping gastropods with their shells about 0.5 mm long. A large brood pouch contains 35 - 40 or even 45 embryos at various development stages (Fretter and Graham 1962; Purchon 1977; Frenzel 1979).

Egg capsules are hemispherical, attached along their flattened base to the substratum. In Marstoniopsis scholtzi they are slightly elongate, with a high keel at the upper side along which the capsule breaks off when the young escapes. In Hydrobia the capsule walls are incrustated with grains of sand and debris. Marstoniopsis scholtzi lays single capsules proportionally large to the size of the animal. The fertility of Lithoglyphus, Bythinella and Hydrobia neglecta remains unknown. H. ulvae lays about 300 eggs per female per breeding period (Linke 1939) so in some populations up to 92% of gastropods bear 4 capsules on each shell averagely but sometimes even 22. In H. ventrosa a mature female manufactures 90 eggs per summer.

Only Potamopyrgus jenkinsi breeds the whole year (Fretter and Graham 1962), while Lithoglyphus naticoides from April till June, Marstoniopsis scholtzi from the end of April to the end of May. The reproduction in Bythinella is still unknown; I have collected the young specimens during the whole vegetation period. In winter due to their high mortality the populations of Bythinella are extremely reduced generally even to no more than a few specimens per spring, while in late spring they are already very numerous, so an intensive reproduction must take place in early spring.

Hydrobia neglecta breeds in spring and summer (Muus 1967), similarly H. ventrosa: in the British Isles in May - July (Fretter and Graham 1962), in Denmark in April - May (Muus 1967). It is noteworthy what Lappalainen (1978) observed that when H. ventrosa occurs sympatrically with H. ulvae, the spawning period of the first starts earlier and is extended in time. Both the modifications together with an altering growth rate enable H. ventrosa to shorten to their minimum the periods of sharp food competition with H. ulvae which is more prolific and usually winning.

A good example of the variation of the life history characters can be Hydrobia ulvae, a popular subject of studies. The recent studies (Anderson 1971; Chatfield 1972; Fish and Fish 1974) show that in the British Isles the gastropod reproduces all the year round with a varying intensity, however, in the main spawning periods different at different places. Thorson (1946) reports of the summer months for Copenhagen, Muus (1967): March - December (maximum intensity: April - June) for the Danish waters, Lappalainen (1978): April - September (maximum: July) for the Finnish Baltic; he also observed that at the rather shallower stations (less than 1 m in depth) the spawning begins earlier. In the southern Baltic all the specimens reach maturity already in the first year of life, while in the British waters only a part of

them, and in the White Sea the gastropods need two years to become mature (Kondratenkov 1972, 1978).

It is a general rule applying to all the gastropods described that in better conditions the life cycles are shorter while in worse become longer. The length of the life of H. ulvae in the Danish waters rarely surpasses 18 months, while in the southern Baltic equals approximately 21 months (at shallow stations surpassing 2 years: Lappalainen 1978); in the laboratory conditions it survives over 5 years (Quick 1924). For H. ventrosa Muus (1967) records 18 months (Danish waters), Lappalainen (1978) - 15 months (Baltic East), and 24 - 30 months in the White Sea (Čuččin 1976a). H. neglecta in the Danish waters also survives about 18 months. The data on the life length of the freshwater Hydrobioidea are scarce. Potamopyrgus jenkinsi survives 6 - 7 months, but the full dimensions reaches in its 4 - 5th month of living (Frömming 1956). The life length of Bythinella and Marstoniopsis probably also does not surpass 1 year. Only Lithoglyphus naticoides survives 3 - 4 years reaching maturity in the second year of living.

4. Feeding

Detritus is known as at least one of the food compounds common for all the Polish Hydrobioidea representatives. The gastropods, as detritus feeders, would be of a high significance in biocenoses, intensifying the processes of organic matter reduction. However, a feeding on detritus is not a uniform, simple and clearly recognized phenomenon which the studies on Hydrobia feeding illustrate well. Detritus being a very poor food itself, consists of an organic matter partly decomposed often unassimilable by the gastropod. This matter inhabit microorganisms: bacteria and fungi. The microorganisms grow well using some assimilable compounds from substratum and the nitrogen oxides from air. According to Newell (1965) these are the microorganisms that are digested by a gastropod (H. ulvae) while the partly decomposed organic matter constituting a major part of detritus is not digested at all and unprocessed deposited in fecal pellets. On the other hand Hylleberg (1976) suggests that the hydrolytic enzymes found in H. ulvae enable it to digest detritus itself, being a poor food source anyway. Kofoed (1975) showed 34% assimilation of sterile detritus in H. ventrosa. Therefore it seems that detritus itself can be used as food to various extent by different species, but it is a supplementary food only.

The food of Polish Hydrobioidea (so far as known) is given in the following list:

Hydrobia ulvae: Enteromorpha, Conferva, other delicate algae (Jeffreys 1867); blue-green algae, green algae (Ulva), detritus (Nordsieck 1972); Ulva, diatoms, blue-green algae, detritus (Ankel 1936; Fretter and Graham 1962); mucous with planctonic microorganisms glued together during the periods of drifting, hanging on the outer side of the water film (Newell 1962).

Hydrobia ventrosa: microflora and microfauna of brackishwaters, often taken from weeds (Robson 1922; Nordsieck 1972); detritus (Kofoed 1975); diatoms, fungi, bacteria gram negative (Hylleberg 1976).

Hydrobia neglecta: diatoms (Muus 1967); detritus (Hylleberg 1976); bacteria gram positive, some diatoms, blue-green algae, detritus (Jensen and Sicko 1971).

Bythinella spp.: little is known on food, combined probably as well as of periphytic diatoms (which I have found numerously in the stomachs) as phragments of macrophytes perhaps, and detritus; Jungbluth (1972) records detritus and diatoms, and Pezzoli (1978) not-green microorganisms living on microsediments when the Bythinella inhabiting underground waters are concerned.

Marstoniopsis scholtzi: detritus, diatoms (Fretter and Graham 1962).

Lithoglyphus naticoides: diatoms, filamentous algae (Jaeckel 1976); Copepoda, Cladocera, Ostracoda, Spongillidae, diatoms, filamentous algae, detritus (Piechocki 1979).

Potamopyrgus jenkinsi: detritus, minute green algae, bacteria of the water film, decaying relics of animals and plants (Fretter and Graham 1962); periphyton, diatoms (Frenzel 1979).

The data above suggest that the food of all the Polish Hydrobioidea is similar. In reality, however, as the results of Hydrobia diet studies suggest, at least a sympatrical occurrence is accompanied by a feeding specialization preventing if not limiting a sharp, "Darwinian" competition. Hylleberg (1976) found the same digestive enzymes in each of three species but in various proportions. The highest proportional quantities of some enzymes accompanying the lowest quantities of the others, which means the highest specialization he found in H. neglecta, being a specialized detritus feeder selecting for the organic matter and some organisms in the sediments (Jensen and Sicko 1971). However, this does not refrain it to feed on diatoms in aquarium, while the competition does not exist (Muus 1967).

H. ventrosa takes from the sediments different organisms than H. neglecta does and also feeds on periphytic diatoms. H. ulvae can feed on the fibres of a green alga Cladophora geometrata without diatoms

attached to them, although a culture of diatoms supports a larger growth (Newell 1965; Jansson 1967). Muus (1967) and Fenchel, Kofoed and Lappalainen (1975) observed that H. ulvae selects for diatoms but only certain diatom species are selected for (Jansson 1969, 1970). In case of the sympatric occurrence with H. ventrosa, H. ulvae grows more rapidly and then feeds on bigger organisms: green algae and some diatoms.

5. Parasites and the resulting abnormalities

The Polish Hydrobioidea are the hosts of many parasites, excluding Potamopyrgus jenkinsi in which no parasite has been found. This confirms a short presence of this species in the European fauna. The list of the hydrobioid parasites includes among others: protozoans, nematodes, trematodes and oligochaetes.

The most frequent is the infection with larval trematodes. Bird faeces containing eggs of a trematode are eaten by snails and cercariae having left the snail body can live in water for 8 hours. In this time they penetrate the skin of fish. Fish are eaten by birds. This kind of a cycle is the most common in Hydrobia, which may be the only one intermediate host, and the final host can be any vertebrate. The trematodes parasite on all the species but both the number of the species of Trematoda found and the rate of infection are different in different representatives. The most advantageous hosts are the gregarious prosobranchs occurring in the habitats frequented by the final hosts. Such species is Hydrobia ulvae which was found infected with 28 trematode species (Fretter and Graham 1962). Noteworthy is that the infection rate in this species is markedly higher in males than in females: the proportion sometimes reached 16 : 1 respectively.

Also the gregarious Bythinella are the hosts of many parasite species (Jungbluth 1972). Although in the less gregarious H. ventrosa only 4 trematode species were found (Fretter and Graham 1962) sometimes 90% specimens of its populations were infected. In Marstoniopsis and Lithoglyphus usually the infection rate is not high and only few trematode species were found.

The infection with larval trematodes causes a regression of the reproductive organs in the snail even to their complete reduction but first the destruction of the gonade itself occurs. In males the penis is reduced, sometimes completely. On the other hand there are some data on the occurrence of a small, always functionless penis in more seriously infected females (Krull 1935; Rothschild 1938), however, this needs confirmation.

Wessenberg-Lund (1934), Rothschild (1936, 1938, 1941) and Čučhčín (1976b) described caused by trematodes shell abnormalities like gigantism, ballooning of certain whorls, thinning and corrosion of shells, colour changes and, sometimes, the presence of a keel on last whorls. It cannot be ignored, however, that all these "effects" are not specific and some environmental factors may contribute in cause of these defects. Even the gigantism need not be an effect of parasitism (Ankel 1962; Muus 1967).

The parasitic gigantism was often considered to be caused by the destruction of the gonade by the parasite. This implies that nutrients instead of being used in the production of sex cells, are available for the general growth of the body. However, such an explanation is rather doubtful. The gonade destruction must cause serious hormonal disorders and this is rather a reason for abnormal growth; since nothing is known on the endocrinology of these molluscs, it is only a hypothesis. It is noteworthy that while in H. ulvae the whorl number in giants is the same as in evidently smaller uninfected specimens, in H. ventrosa the gigantism is observed along with a higher whorl number.

In the mantle cavity of Bythinella I found often an oligochaete Chaetogaster limnaei limnaei von Baer, 1827. Its relation with the host is not clear and is usually regarded as commensalism, but parasitism if not a facultative one cannot be excluded. Several authors observed that the occurrence of Ch. limnaei limnaei decreases the level of the trematode infection. My observations seem to support the opinion since Ch. limnaei limnaei feeds probably on trematodes, thus its relation with Bythinella would be rather of a symbiotic character.

6. Distribution factors

A. Salinity

Hydrobioidea in general include predominantly brackishwater but also marine and freshwater gastropods. On the basis of a salinity tolerance four groups of Polish representatives can be distinguished. A gastropod may show different tolerances at different stations or in laboratory, so the data in the literature are likely to be different.

1. Typical freshwater gastropods.

Bythinella spp., Marstoniopsis scholtzi, and Lithoglyphus naticoides. They all but Bythinella can stand temporarily a very low salinity (M. scholtzi to 0.5‰, and L. naticoides to 3‰: that occurs in the outlet of the River Rega), but in general they avoid even slightly brackish habitats (Zilch and Jaeckel 1962; Janssen and Vogel 1965; Macan 1969; Dyduch and Falniowski 1979).

2. B r a c k i s h w a t e r. Hydrobia ventrosa and H. neglecta. The species never occur either in quite fresh or in truly marine waters. In some particular conditions H. ventrosa can occur in 1‰ salinity but usually needs at least 6‰, while the upper limit is of 10 - 29‰ depending on the station (Johansen 1918; Žadin 1952; Mars 1961; Muus 1963, 1967; Bishop 1976; Čučhčín 1976b). H. neglecta prefers higher salinities: from the lowest found in Puck Bay (7‰) through a usual one varying between 10 and 19‰, up to the highest 24 - 31‰ (Muus 1963, 1967; Hylleberg 1975; Bishop 1976). Both the species are sensitive to salinity changes.

3. B r a c k i s h w a t e r - m a r i n e. Only Hydrobia ulvae. The lower limit of salinity between 7 and 22‰ depending on the station. The range covers also truly marine waters (Johansen 1918; Quick 1921; Ehrmann 1956; Frömming 1956; Fretter and Graham 1962; Muus 1963, 1967; Bishop 1976). H. ulvae stands also changes in salinity, occurring in habitats where the salinity oscillates between 13 and 34.7‰.

4. B r a c k i s h - f r e s h w a t e r. Only Potamopyrgus jenkinsi. It is noteworthy that in the British Isles until 1893 it occurred only in brackish waters (Macan 1969); its expansion into freshwater has been observed quite recently. The upper limit of salinities it stands lies between 15 and 23‰ (Johansen 1918; Ellis 1932; Nicol 1936; Adam 1942; Fretter and Graham 1962; Berner 1971; Nordsieck 1972). However, P. jenkinsi occurs very often only in freshwater: several observations in Western Europe as well as practically all, more recent, from Poland prove its absence in brackishwater, once assumed as typical of it (e.g. Puck Bay, Polish rivers estuaries). The earlier reports to some extent can be the result of erroneous determinations but it seems that we observe rather the further rapid evolution: the complete change of a former habitat for a freshwater one by a part of P. jenkinsi - the most probably, a complex taxon.

B. Water chemism: other factors

Almost all the Polish prosobranchs are sensitive to oxygen depletion. The exception is Hydrobia ventrosa which can withstand even a long period of the complete lack of oxygen and creep vigorously over putrid mud (Lambert 1930; Fretter and Graham 1962; Čučhčín 1976b). Potamopyrgus jenkinsi and Marstoniopsis scholtzi can inhabit less oxygenated water while Hydrobia ulvae, H. neglecta and Lithoglyphus naticoides need a good oxygenation. Bythinella demand very well oxygenated water.

In freshwaters significant factors are pH and water hardness. Potamopyrgus jenkinsi can endure a wide range of pH values: from 6.5

(sometimes even 5.4) to 8.5. In the case of Bythinella the range is somewhat less wide: 5.0 - 8.0 (Jungbluth 1972; Giusti and Pezzoli 1977a), while Lithoglyphus naticoides favours slightly alkaline water and its range of pH is narrow: 7.5 - 8.0 (Piechocki 1979).

Potamopyrgus jenkinsi besides Valvatidae, is one of scarce Prosobranchia which can live in soft waters, for instance Lough Leane at Killarney where the calcium content of the water is 7 - 11 mg/dm³ (Boycott 1936; Macan 1950, 1969; Fretter and Graham 1962). The other Polish prosobranchs need hard waters rich in calcium. Many authors emphasize extra-high demands of Bythinella, which never inhabit the areas of magmatic rocks (Wiktor 1964; Pezzoli and Girod 1971; Giusti and Pezzoli 1980). However, Jungbluth (1972) ascertained their occurrence in waters where the hardness was as low as slightly above 1.0°dH, so their demands for this factor do not depart from those typical of the majority of the prosobranchs. All the Polish hydrobioids but Bythinella do not avoid, and Marstoniopsis scholtzi even prefers eutrophic waters.

C. Temperature

Water temperature is not the factor determining the occurrence of Hydrobioidea except those oligostenothermic Bythinella which inhabit springs (Stock 1961; Girod and Pezzoli 1966; Jungbluth 1971a, b, 1972; Pezzoli and Girod 1971; Pezzoli 1975; Radoman 1976; Giusti and Pezzoli 1977a, 1980). Usually 8 - 10°C is regarded as the upper limit of the temperature endurance but for instance in Italy Bythinella inhabit even the waters of the temperature of 14.8°C. Hence, Jungbluth's opinion that temperature is the most important factor determining the distribution of Bythinella could be hardly acknowledged. My observations show also that Bythinella can endure alive except for breeding in about 20°C for several months. The temperature increase is observed along with a high mortality but about the half of the specimens can fit for this temperature.

Potamopyrgus jenkinsi is an actually eurythermic species, which can inhabit (except for Poland) cold springs, and also warm waters e.g. thermal springs. Berner (1971) used to find it in the temperatures from -1 to +33°C: it could creep in 9 - 31°C. The other Polish hydrobioids are more or less markedly eurythermic.

Certainly, the range of bearable temperatures is not the optimum: a good example can be the study of Hylleberg (1975) on the intensity of the metabolism of Hydrobia (species occurring also in Poland) in different temperatures and salinities. In natural conditions the influence of the thermic alteration on the distribution pattern can be

hardly observed. All the species withstand the same temperature range. H. ventrosa, however, is the least specialized species: its metabolism level does not change within a wide range of temperatures (10 - 30°C), while H. neglecta shows the high specialization within a sharply marked optimum: 20 - 25°C. However, the both species are sensitive to changes of temperature and salinity, especially rapid ones. The eurythermic H. ulvae withstands these changes, but the maximum of its metabolism level (30°C) is marked much clearer than in H. ventrosa and less than in H. neglecta. Another interesting observation is that in H. ulvae and H. ventrosa the metabolism level in low salinities is much higher when the temperature is low; thus low temperatures improve their adaptation to freshwater.

D. Water movement

The presence or absence of water movement and exchange seems to be the most important factor determining the distribution of some Hydrobioidea. Potamopyrgus jenkinsi seems the least sensitive to this factor. It prefers a moderate flow (Fretter and Graham 1962; Janssen and Vogel 1965; Macan 1969) but avoids only the waters of either strong current or truly stagnating.

The only Polish species preferring stagnating habitats is Marstoniopsis scholtzi which in slowly flowing rivers, if at all present, inhabits sheltered banks or meanders. The other species are rheophilic. Lithoglyphus naticoides favours water flow but avoids a rather stronger current (Žadin 1952; Janssen and Vogel 1965; Negrea and Negrea 1975), for instance in the River Bug at Serpelice it is present only close to the water edge far from rapids, or in puddles. However, it is a probable result of a lack of food washed out in more exposed places. Bythinella, though rheophilic and favouring torrential habitats (Urbański 1957; Jungbluth 1971a, b, 1972; Radoman 1976), seem to differ interspecifically in this respect.

In marine habitats there is usually no current similar to that of a river, but only a better or worse water exchange occurs. It appears that this factor determines the Hydrobia species distribution (Muus 1967; my observations in Puck Bay). In the habitats with continuous or regular water exchange, also in these exposed to rough waves, there is H. ulvae alone or along with the other 2 Polish Hydrobia species, however, represented very scarcely. On the contrary, the stagnating habitats: backwaters etc. are avoided by H. ulvae and preferred by H. ventrosa which can withstand more rapid water movement only with a salinity close to the lower limit of its endurable values (4 - 5‰; Muus 1967), may be because such a low salinity eliminates H. ulvae.

H. neglecta inhabits intermediate habitats favouring localities with limited water exchange.

E. Habitat stability

Collecting the gastropods in their habitat one usually studies and describes the characteristic conditions of the habitat. Furthermore, the absence of a species in the habitat typical of this species is often observed. Frequently the gastropod is absent simply because the conditions, although still within its limits of tolerance, are too unstable. The alterations in temperature, current, water level or salinity may cause the environmental stress, variously responded by different species.

A good illustration of the importance of the environmental changes are the Baltic Hydrobia. The most sensitive to them is H. neglecta, but also H. ventrosa can be eliminated from its typical habitat by H. ulvae, withstanding then even the extremes of the salinity and temperature and practically the lack of water movement (e.g. shallow pools periodically dried) only because, unlike H. ventrosa, H. ulvae is rather insensitive to the environmental stress.

Bythinella are an example of the gastropods demanding very stable habitats, such as springs, and often not farther than some meters below only very scarce specimens are found (Jungbluth 1971a, b, 1972; Pezzoli and Girod 1971; Berger 1973; Pezzoli 1975; Radoman 1976; my observations in Siedem Żródeł). Furthermore, inhabited springs are mostly located in deciduous forests while those of the open areas are inhabited very rarely; in the Tatra Mountains the upper limit of their distribution covers the upper limit of forest. This is also due to the more stable conditions characteristic of the forest habitat. However, it has to be pointed out, that not each of the Polish Bythinella species is so rigorous in its demands for the stability of the habitat.

F. Substratum

Only Hydrobia ventrosa can inhabit, but does not favour putrid mud. Pure sand, as containing no food, is not inhabited by gastropods either. Bythinella inhabit plants or fallen leaves, then the kind of substrate is not of an implicit importance for them (Pezzoli and Girod 1971; Jungbluth 1972) but with the absence of vegetation they need a substrate fitting for periphyton (stones or gravel).

The other Polish hydrobioids favour sandy-muddy or muddy substrate rich in detritus. However, while Marstoniopsis scholtzi likely inhabits decaying leaves and stems of weeds, the other species seem to avoid places in which thick layers of detritus are accumulated. Some species,

as for instance Lithoglyphus naticoides, can penetrate rather deep layers of the substrate, and Potamopyrgus jenkinsi in autumn can penetrate down to 15 cm deep (Wolnomiejski and Furyk 1970). Hydrobia ulvae, H. ventrosa, Potamopyrgus jenkinsi and Lithoglyphus naticoides can be found on stones and piles (Nicol 1936; Ehrmann 1956; Janssen and Vogel 1965). Both silt and gravel may be inhabited by Hydrobia ulvae, H. ventrosa and Potamopyrgus jenkinsi. In general, each species can be found on practically any kind of substrate.

The inhabiting of a sandy-muddy or sandy substrate is due to feeding on both the particles of detritus and microorganisms inhabiting it. Of course, bigger particles are rather difficult to feed on so they limit the occurrence of a detritus feeder. Hence its numbers reflecting the suitability of the habitat would depend on an average particle size of the substrate. This interdependence of Hydrobia ulvae was shown by Newell (1965). With the particle diameter below 0.05 mm the density reached 12,000 individuals per sq m, with the diameter of about 0.25 mm - only 800 individuals per sq m, and with the diameter of 0.30 H. ulvae was absent.

G. Vegetation

A component of the food of all the Polish hydrobioids are periphytic algae, the occurrence of which is, therefore, more or less advantageous for certain species. Macrophytes growth alters environmental conditions. Macrophytes can be a food (which is an exception in minute hydrobioids) but also they constitute favourable conditions for the periphyton growth and serve as shelter. The relations between a gastropod and macrophytes are usually not simple: that seems to be a source of several controversies in the literature. The only species which undoubtedly avoids macrophytes is Lithoglyphus naticoides. The others occur among macrophytes; the plant-gastropod correlations reported most frequently are listed below:

Hydrobia ulvae - Ulva, Enteromorpha, Chaetomorpha, Chara, Fucus, Zostera, Potamogeton (Fretter and Graham 1962; Muus 1967; Jaekel 1976).

H. ventrosa - Ulva, Enteromorpha, Chara, Zostera, Potamogeton (Fretter and Graham 1962; Muus 1967; Falniowski, Dyduch and Smagowicz 1977).

H. neglecta - filamentous algae, Ulva, Chaetomorpha, Zostera, Potamogeton (Muus 1967; Falniowski, Dyduch and Smagowicz 1977).

Bythinella spp. - mosses (Fontinalis, Mnium), Nasturtium, the immersed parts of terrestrial plants surrounding a spring, fallen leaves mainly of a beech (Urbański 1957; Wiktor 1964; Janssen and Vogel 1965; Jungbluth 1972; Piechocki 1979).

Marstoniopsis scholtzi - algae (Urbański 1957; Jaeckel 1976), stems of half-immersed and (often) decaying macrophytes (Fretter and Graham 1962; numerous Polish localities), Elodea canadensis (Adamowicz 1939; also gregariously on Elodea in the Lake Śniardwy at the depth of 5 - 6 m while absent inshore).

Potamopyrgus jenkinsi - algae (Dyduch and Falniowski 1979), Typha and Potamogeton (Knipper 1958).

Bythinella are strongly associated with plants, however, they can be satisfied with gravel or stones overgrown with periphytic algae. Marstoniopsis scholtzi seems to avoid bottoms devoid of vegetation. Among the Hydrobia species the most strongly associated with plants is H. ventrosa, but even though it can live on the bottom devoid of plants. In the habitat comparative analysis of the plant-gastropod interrelations one should be aware that the conclusions depend a lot on the kind of vegetationless bottom when compared to plants. H. ulvae, H. neglecta or Potamopyrgus jenkinsi are, in fact, more numerous on plants than on poor in food bottoms devoid of weeds. However, on fine-grained and rich in detritus substrate abundances are usually considerably greater than on plants.

H. Competition

The previous part of this chapter suggests that many of the Polish hydrobioids show in general a great environmental tolerance. The factors presented above often do not determine the occurrence of particular species. In case of freshwater fauna the history of a given locality is also important: whether a species was able to reach this habitat or not. Another important but hardly recognized factor seems to be a competition with other ecologically similar species, also with gastropod species. This has been studied so far only in some Hydrobia that also happen to inhabit the Polish Baltic Sea.

According to Muus (1967) the distribution of Hydrobia is a result of the combination of salinity, water movement, instability of a habitat, drifting on the water film and competition. The sharp "Darwinian" competition is not often observed in nature and if at all it occurs is strictly limited in time. The Gause's principle states that two species cannot coexist at the same locality if their niches overlap each other and its exemplifications have been given (e.g. different growth rate for food niches not to overlap one another, slight differences in preferred food and salinity) or one of the competitors is to be eliminated if not considerably limited by the other as it was observed in Hydrobia (Fenchel 1975a,b; Hylleberg 1975, 1976; Lappalainen 1978).

All the three Polish Hydrobia species in laboratory can stand a wide range of salinity, temperature, substrate and even a water flow and unstable conditions. In nature they show specialization, though differently expressed in different habitats. The reason is that in the habitat good enough for both competitors the winner will be this species for which the given conditions are closer to its optimum.

The evolution strategies of the Baltic Hydrobia are different. H. neglecta is the most specialized: it favours a narrow salinity range, stable conditions, fine-grained muddy substrate and limited water movement. In such conditions it will dominate and can even be a mass species (to 50,000 individuals per sq m) although it is noteworthy that it has never been found as the only Hydrobia at any locality: it has always been accompanied with H. ulvae and/or H. ventrosa. Then it did not eliminate them even in the optimal conditions for itself. On the other hand, only a slight difference from the optimum enable the other Hydrobia competitors to limit H. neglecta in number considerably, even to its complete elimination.

H. ventrosa represents the opposite evolutionary strategy to that of H. neglecta. Besides its high sensitivity to environmental stress, similar to that of H. neglecta, H. ventrosa is extremely eurybiotic and can withstand a wide range of salinity, temperature, substrate, etc. Furthermore, it is hard to indicate a more sharply marked optimum: its metabolism level is practically the same within a wide range of, for instance, salinity or temperature. Such a species has to loose the competition with a specialized one in the conditions approximate to the optimum for another. H. ventrosa "searches" then for the habitats which are not good enough for the other Hydrobia. For instance, it inhabits brackish lakes in Germany and Greece and close the Black Sea. A salinity there is extremely low (1‰) and the lakes frequently dry out but there are neither the other Hydrobia, nor more than a few other animal species so no competition occurs, and H. ventrosa can be very abundant there. Similarly, with the lowest salinities which eliminate H. ulvae, H. ventrosa can endure even intensive water movements.

H. ulvae represents a medium level of specialization: narrower than H. ventrosa but wider than H. neglecta. In general, it favours a higher salinity than those two and its optimum is marked more sharply than that of H. ventrosa. However, it differs from the other Hydrobia in favouring the habitats with an intensive, constant or regular water exchange, also those desiccating. Hence, it eliminates the other two from such habitats. In habitats with a higher salinity it always wins the competition with H. ventrosa, too, although the latter can bear a high salinity in the laboratory conditions.

I. Hydrobioidea under anthropopression

The increasing pollution of the Baltic Sea, especially of the littoral zone, cannot have been of no significance for Hydrobia. It had not been until 1973 that the rich associations of bottom weeds of Puck Bay became overgrown with brown seaweeds Ectocarpus spp. probably because of the pollution with superphosphates. This changed the local conditions resulting in a limited occurrence of Hydrobia. In the following years the situation became worse. It is most likely that H. ventrosa will be the last "surviver" in this organically polluted water but subsequently it must also withdraw from the Polish Baltic.

Well drilling, forest fells, water intakes built on springs, and other actions of this kind destroy the habitats of Bythinella as well as drainage, which had highly unfavourable influence on many spring areas. If a spring has not a considerably substantial outflow the conditions in such a habitat can be seriously affected by fertilizing, cattle grazing, dust fall, etc.

Lithoglyphus naticoides, Potamopyrgus jenkinsi and probably Marstoniopsis scholtzi can withstand a moderate pollution occurring also in the β -mesosaprobic zone (Berner 1971; Piechocki 1979, Kasp-rzak 1982) but are also eliminated by stronger pollution. The river regulation destroying the microhabitats favoured by Lithoglyphus or Marstoniopsis has not a less impact. Marstoniopsis as well as Pota-mopyrgus will probably survive for a long time in lakes or small water bodies. Lithoglyphus, however, which inhabits only big lowland rivers, has become a very rare species in Poland, since most of its localities once recorded in the literature do not exist (Drozdowski 1979; my own observations).

7. Ways of expansion

The hydrobioids are small, slowly creeping gastropods occurring in fresh- or brackishwater, i.e. habitats often more or less isolated. However, it turns out that their abilities to expand into new habitats are quite high. The colonization of new, also distant habitats is easier with the pelagic larva which, among the Polish hydrobioids, is typical for only Hydrobia ulvae. On the other hand the adult Hydrobia can be transported by water currents.

Newell (1965) described the tidal rhythm of activity in H. ulvae. At ebb the gastropods protect themselves by burrowing, while earlier they often crept actively on the surface. With the flood approaching them they come out from the substrate, crawl to the water film and keep hanging on the under side of the water film on a clot of mucous of

the diameter up to 5 mm. They hang for a few hours until with the beginning of the ebb they are let drop on the bottom. With the salinity lower than a favoured one but still endurable the gastropods intract themselves into the shells and drop on the bottom; this protects them against being transported too far from the sea. The mechanism of these changes in activity (creeping on the bottom - hanging on the water film) in H. ulvae need not have an endogenous tidal character. Several outer factors as: low oxygenation or too high density can also induce hanging on the water film. This kind of drift, caused never by tides was observed in H. ventrosa and H. neglecta rather rarely, however also (Muus 1967; Bishop 1976), and quite rarely in H. neglecta.

Fish can enable the expansion of Hydrobia as well, because all the three Baltic species are observed to come through the guts of fish and remain alive and apparently unharmed (Muus 1967). The gastropods use also the passive way, when they get transported attached to the hulls of boats and ships. A proof might be both the rapidity of the expansion of Lithoglyphus naticoides and Potamopyrgus jenkinsi, as well as its extreme reduction since the wooden hulls had been replaced by the steel ones less convenient for the gastropods.

Several species are characterized by a considerable resistance to desiccation. Hydrobia ulvae survives unharmed even long periods of desiccation, whereas the other Hydrobia though less resistant can survive some hours of exposition (Quick 1920; Fretter and Graham 1962; Muus 1967; Berner 1976; Kondratenkov 1978). Potamopyrgus can survive for over a month in a slightly wet tissue-paper; it can be transferred by birds adhered to their bills and legs (Coates 1922); this probably may occur in the other hydrobioids, too. In the case of P. jenkinsi the active passing of small distances of dry land must not be excluded. This is confirmed by their numerous occurrence not less than 1 m above the water level due to active creeping in autumn (Wolnomiejski and Furyk 1970).

Many authors stressed the complete isolation of the populations of Bythinella inhabiting different localities. However, the observed distribution of the species of this genus does not confirm this at all. At first, Bythinella as the only Polish gastropod can inhabit also underground waters (Stock 1961; Jungbluth 1972; Pezzoli and Girod 1971; Pezzoli 1975, 1978; Giusti and Pezzoli 1980), usually as facultative inhabitants but sometimes as populations of numerous, typically troglotic individuals, lacking the eyes. It means that at least the springs supplied by a one reservoir of underground water are reciprocally approachable for Bythinella.

Some dishes containing Bythinella were allowed to dry out. All the substrate with Bythinella were dried completely. I was keeping such desiccated lots with no water for about 6 weeks and then the dishes were filled with normal, tap water. It appeared that about 10% of the gastropods stayed alive and unharmed. Hence, this means quite not slight possibilities of expansion. Such minute gastropods can be transported by birds or by winds with the inhabited by them foliage fallen away, covering even considerably long distances.

8. Character of occurrence, inhabited biotopes

Three Bythinella species, as well as Hydrobia neglecta, Lithoglyphus naticoides and Marstoniopsis scholtzi should be considered the rare in Poland. Maybe M. scholtzi is not as rare as hard to find, especially because it never occurs in mass. Lithoglyphus naticoides happens to be numerous, but never mass (up to a couple of thousand of individuals per sq m). The other species can occur in mass reaching the numbers of not less than some scores of thousand of individuals per sq m and also tend to aggregate. Of course, the numbers are usually incomparably lower, the most likely mass species are Hydrobia ulvae and Potamopyrgus jenkinsi.

The aggregations of H. ulvae are sometimes of an unexpectedly great size. Linke (1939) described the aggregation of living specimens of this species that was observed along the base of the dam in Jadesbusenwatt. It was 20 m long, 2 m wide and 2 cm thick averagely though locally 20 cm thick; the author estimated the number as 55,000,000. In autumn Potamopyrgus jenkinsi forms the accumulations of more than 100,000 individuals per sq m occurring along the water edge (Wolnomiejski and Furyk 1970).

Hydrobioidea are the gastropods of shallow waters favouring usually the depths not greater than 1 - 2 m, though sometimes they are found at deeper levels. I collected Marstoniopsis scholtzi in the Lake Śniardwy at 6 m, in Plöner See it can reach 13 m (Zilch and Jaeckel 1962). Bythinella inhabit springs, but Hadl (1967) found them at 17 m in the Lunzer Untersee (Oberösterreich, Austria). H. ulvae can reach 130 m (Fretter and Graham 1962), while H. ventrosa 55 m (Grossu 1956; Čučhčín 1976b) but only in the Black Sea where H. ulvae is absent.

The only species able to inhabit waters along open beaches is H. ulvae; it is also one of the dominants of the Macoma balthica community or its Scrobicularia variation (Linke 1939), although it inhabits more abundantly sheltered bays with the regular and intensive water exchange. At more stagnant stations there occur H. ventrosa and, very scarcely, H. neglecta.

Bythinella can be found in springs but also in the spring areas where a small quantity of water infiltrates through the soil, stream edges in the upper course, sometimes small meadow streams (Zawoja-Składny, Mszana Dolna) and, exceptionally, in a muddy ditch with cold water on the edge of a meadow (Lubomir).

Lithoglyphus naticoides inhabits large, less often medium lowland rivers. Its occurrence in some big flow lakes needs confirmation.

Marstoniopsis scholtzi inhabits stagnant water of all kind, even the smallest as ditches or old peat-hags filled with water, while in rivers it can be found only at stagnating sections, in sheltered microhabitats.

Potamopyrgus jenkinsi can be found in freshwaters of all kind but small stagnant water bodies like ditches or small pools. In Poland it is also absent in springs and streams, though in Western Europe those habitats are characteristic of it as well.

9. The origin of Polish Hydrobioidea

The representatives of Hydrobia inhabiting the Polish Baltic are the Atlantic elements which came here in the Littorinid Period.

The reconstruction of the history of the Bythinella distribution seems impossible so far. The Jungbluth's theory (1972) on the probable ways of expansion is not convincing. Bythinella endured the glacial period most probably in the Alpine lakes. Later, with the glacier withdrawing the Bythinella followed it northward and with the climat growing warmer its distribution was restricted to cold springs only. Then, the Bythinella seem to be both the Alpine elements and the glacial relicts.

The recent range of Bythinella covers a part of Europe, Asia Minor and Transcaucasia (Žadiņ 1952; Radoman 1973, 1976). In Europe Bythinella are absent in the northern part of the continent, the genus range border runs more or less parallelly, also across southern Poland: along the northern edge of the Carpathian Chain with the only one exception which is an isolated enclave situated northward (Jura Krakowsko-Częstochowska Upland). In Poland Bythinella inhabit, besides Jura, only the Carpathian Mountains and their highlands as well as the single still existing station in the Polish Sudetes Mountains.

The genus Marstoniopsis in Europe is represented by two species: M. insubrica (Küster, 1853) and M. scholtzi whose reciprocal separateness is questionable (Falniowski 1983). The species inhabit respectively northern Italy (very local range) and the middle Europe from the Netherlands to Ladoga Lake. M. scholtzi seems to be a branch of the Bythinella trunk, anyway, which did not withdraw to the cold

springs as the climate became warmer but adapted themselves to the life in the changed conditions.

The other two Polish hydrobioid species are both unfamiliar to the Polish fauna and they have emerged here only recently due to the man's activity. The original, endemic area of Lithoglyphus naticoides covers the region of the Sea of Azov, the Dnieper basin and a part of the Danube basin (from Regensburg to its delta). It expanded onto the new territory in about 1830 - 1930 inhabiting about 1,000,000 sq km of the area that makes about 33% of the whole present range of this species. This rapid distribution was probably due to the development of the canal system connecting the rivers of the Baltic and Black Sea catchment basins.

In Poland for the first time it was found in the Bug River in 1873. The following observations were: the Vistula River at Toruń in 1882. and at Kostrzyń in 1883, West Pomerania in 1887, the River Warta (Poznań district) in 1910. In 1903 it was found in the Pregoła River (the former East Prussia territory) and in the twenties of the XXth century near the Bay of Riga (Nowak 1974).

In Germany it appeared in 1883 in the vicinities of Berlin and Brandenburg, in 1887 near Hamburg, 1893/94 near Wiesbaden, 1895 near Düsseldorf, while in Gelsenkirchen (Westfallen) not sooner than in 1929. The northern part of Germany was invaded by East European populations of the Dnieper catchment basin, while the southern part of the country by those from the upper Danube. In 1909 it appeared also in Switzerland near Basle. By the canal system connecting the Rhine and Mosel rivers this gastropod got to France and in the beginning of the twenties it colonized the basins of the Seine and Oise rivers. In Belgium it was found in 1910 while in the Netherlands (the region of Rotterdam) it has been known since as early as the seventies of the XIXth century.

While the origin of L. naticoides is quite well recognized, that of Potamopyrgus jenkinsi still remains unclear, especially in the light of the data on the complexity of the taxon. P. jenkinsi was described in 1889 from the specimens taken from the brackish water at Plumstead, in the marshes alongside the Thames. Though Frömming (1956) suggested that it may have been introduced into the British Isles as early as in 1859 and Kennard (1941) concluded that this species was living in England in Roman times, there are no confirmed data on the occurrence of P. jenkinsi in Europe before 1889. Steusloff (1927) regarded it as a mutant of Hydrobia ventrosa, it was thought to have been introduced from the West Indies. Now it is usually acknowledged after Boettger (1951) that it is closely related to P. badia (Gould, 1848) inhabiting the brackish waters of South Island, New Zealand (Butot and Kiauta 1966).

In the British Isles P. jenkinsi inhabited only brackishwaters at first, but as early as in XIXth century it colonized various inland freshwater habitats. It spread most rapidly in the industrial regions where there were canal systems; in about 30 years it spread through the greater part of England and Wales (Boycott 1936; Fretter and Graham 1962) though it is still unrecorded from considerable areas in W and N Scotland, where the first record was 1906 (Hunter and Warwick 1957). Its slow spread in Scotland may be due to the lack of a canal system. Similarly it is still unrecorded from the central Ireland.

In 1897 P. jenkinsi, transported probably from England by birds, appeared in Wismar Bay in Germany (Jaeckel 1976). In NW Europe the first inland records showed it in brackish water (Hubendick 1947, 1950; Bondesen and Kaiser 1949) and later it was reported to have spread to freshwater, though in Sweden the species had not been observed in inland localities up to 1947. In 1899 it was found in the Nord-Ostsee Canal, the following records were: 1908 Breitling, 1933 Suomenlahti, 1945 the northern part of Bottenhavet. The first record in France was 1912, later it spread through the Netherlands and Belgium (the first record 1927). In 1935 it was recorded near Erfurt and in 1958 near Strassburg. Its present distribution in N Europe includes the territory from Flandres to Riga, reaching 61°N. In 1952 this species was recorded in Catalonia, by the end of fifties in the Mediterranean region of France. There is one isolated population of this species, recorded in 1950 in the Danube delta. The rest of its populations are contiguous and the species is still expanding.

The first record in Poland was 1925 from the Bay of Gdańsk, and Puck Bay (Urbański 1938). Later it was recorded from the Vistula, Bydgoszcz Canal, Noteć River and northern Wielkopolska (Lake Trląg at Mała Koźuda).

10. Material collection, preservation and elaboration methods

The hydrobioids can be collected by means of common hydrobiological methods. In the sea and the large inland water bodies a small and light dredge is very useful, while in the smaller flows and ponds the most convenient for the material collection is a net. The specimens of Marstoniopsis often occur at the bases of foliage, e.g. sweet rush, so they should be searched for in there. Bythinella, Hydrobia and other Hydrobioidea are taken from the weeds by washing out on a sieve.

The washed out material should be sorted as quickly as possible to separate it from vegetable detritus and plant particles. 70% alcohol can be used for fixation, but 4% formol is more suitable and more useful. Because of a great variability it is necessary to take from a

locality not single specimens of a particular species but a series of some dozens of specimens per species.

For dissection under stereo-microscope it is optimal to use two micro-tweezers and two needles: the thicker and the thinner (e.g. - the thinnest entomological pin). The tools should be sharpened thoroughly with unglazed china.

Any muscle dissections are best to carry out by lacerating with micro-tweezers. After opening of the body cavity all the structures should be identified at first, and this is sometimes difficult. It is well to do the final dissections of tiny structures in Faure's solution, and for the proper arrangement it is often necessary to cover the structures gently with a cover glass slip.

11. Key to the genera of Polish Hydrobioidea

1. Shell almost spherical, bulgy and thick-walled, over 7 mm high, spire low (its height about 1/3 of shell height); penis uni-armed, simple, stout triangular in shape; big lowland rivers, rare
..... Lithoglyphus (L. naticoides)
- Shell never a spheroid, more slender and less thick-walled, less than 7 mm high, spire high; penis bi-armed or uni-armed with outgrowths, of other outline and proportions 2
2. Apex blunt, rounded and broad, shell rather cylindrical, slowly narrowing towards the apex; penis bi-armed; springs, spring areas, mountain stream edges; southern Poland Bythinella
- Apex sharp, not rounded or rounded slightly, and narrow, shell rather conical, abruptly narrowing towards the apex 3
3. Shell always slender with flat whorls and a sharp apex, mouth protruded, parietal lip narrow but distinct, some specimens with a keel or bristles in the upper part of some last whorls; males absent; well visible brood pouch big and with the embryos visible inside; freshwater or sometimes the Baltic . . . Potamopyrgus (P. jenkinsi)
- Shell not always slender with whorls from flat to rather distinctly convex and the apex from sharp to blunted, mouth not protruded, parietal lip slightly marked or absent, neither keel nor bristles; males numerous 4
4. Shell stout with the apex rather broad and often truncate; penis bi-armed; freshwater Marstoniopsis (M. scholtzi)
- Shell often more slender with the apex frequently narrow and never truncate; penis uni-armed with outgrowths (or the second arm very small); the Baltic Hydrobia

12. Abbreviations in the figures

bc - bursa copulatrix, bp - brood pouch, cbc - canalis bursae copulatrix (duct of bursa), dgp - ductus gono-pericardialis (gono-pericardial duct), fl - flagellum, ga - glandula albuminoidea (albuminoid gland), gac - glandula albuminoidea complex = ga + gn + gm, gm - glandula mucosae (mucous gland), gn - glandula nidamentalia (nidamental gland), gp - gonoporus, hp - hepato-pancreas, osphr - osphradium, ov - oviductus (oviduct), ova - ovarium (ovary), p - penis, pr - prostata (prostate), rec - rectum, rs - receptaculum seminis, sov - spiral of oviduct, te - testis, v - vagina, vd - vas deferens

N o t e: All the dimensions given in the systematical part with no unit are in millimetres.

III. Systematical part

GENUS HYDROBIA HARTMANN, 1821

Since numerous attempts to divide the genus into several subgenera seem insufficiently justified, I regard the three species from the Polish Baltic as belonging to the genus Hydrobia.

The species belonging here are characterized by a great shell variability which actually refers to all the characters: habitus, proportions, spire height, whorl convexity and suture depth, mouth shape, peristome form, dimensions, wall thickness and shell colouration. The variability ranges of particular species are overlapping, often in a high degree; furthermore, while in the Danish waters, with the variability range as wide as in the Polish Baltic the shells of about 95% of gastropods could be referred to the main types and untypical specimens are scarce (Muus 1963, 1967), whereas in the Polish Baltic any "typical" specimens can be hardly distinguished and a majority is markedly different from the forms, typical of the non-Baltic populations described in the literature. The determining of Hydrobia basing on the conchological characters is difficult and it can never be ascertained. Due to a low salinity the Polish specimens are smaller.

The limited taxonomical usefulness of the conchological features of Hydrobia was the reason why the pigmentation of soft parts was taken into consideration relatively early (Jeffreys 1867; Seifert 1935; Fretter and Graham 1962; Muus 1963, 1967; Janssen and Vogel 1965; Davis 1966; Graham 1971; Bishop 1976; Čučičin 1976b; Hershler and Davis 1980; Falniowski 1986a). The snout and tentacles pigmentation shows interspecific differentiation and it is one of the best diagnostical features of the Polish Hydrobia species, though its variability is higher than most of the authors suggested (Falniowski 1986a).

The tentacles are filamentous, the left one strongly hyperciliated (Fretter and Graham 1962; Bishop 1976). The eyes imbedded in small

swellings. The penis uni- or bi-armed but never simple, containing glandular structures (Davis 1966; Bishop 1976) characteristic of particular species. The pallial tentacle short, cord-like, ciliated. The opercular lobe big, without the appendix.

1. Snout often unpigmented, if pigment occurs it is never in the form of a distinct transverse belt; tentacles unpigmented, only exceptionally with irregular and diluted spots; penis slender with a long and slender filament, at the left side of the filament a small second arm H. ventrosa
- Snout nearly always pigmented, pigmentation in the form of a distinct (or only rather distinct) transverse belt; tentacles nearly always with undiluted spots of pigment; penis stout with neither filament nor the second arm 2
2. Tentacles with a transverse belt of its breadth smaller than the distance from the belt to the tip of the tentacle; penis big with no distinguishable lobes but with numerous well marked folds, vas deferens well visible running proximally and medially in zigzag and opening at a small papilla distally at the left side, accessory duct absent H. ulvae
- Tentacles with a longitudinal belt of its length bigger than its distance from the tip of the tentacle; penis small with a big, broad and blunt lobe at the left but the folds less numerous and poorly marked, vas deferens hard to distinguish running proximally and distally straight and opening on a broad and weakly distinguishable lobe distally at the right side, accessory duct at the left side....
..... H. neglecta

1. Hydrobia ulvae (Pennant, 1777)

A - Turbo ulvae Pennant, 1777

Peringia ulvae (Pennant, 1777)

B - The shell (Figs 1,1 - 1,16 and 2,1 - 2,21) conical (sometimes turreted, fusiform or ovate), the spire usually elongated but sometimes shortened or extremely elongate. The shell breadth up to 0.5 of its height. Whorls 4 - 6, exceptionally 7, flattened and divided by a shallow suture. The whorls growth regular and slow, the body whorl not swollen and its height equal to $1/2 - 3/5$ of the shell height. The apex blunt, apex angle about 38° . The mouth closely adhering to the columella, upwards with an acute angle sometimes marked less distinctly. The parietal lip broad. The peristome not always continuous: only in no more than 60% of specimens from Puck Bay. The outer lip absent, mouth edge rather thick.

The umbilicus usually absent or in the form of a slit, only exceptionally more conspicuous. Among the specimens from Puck Bay the lack of umbilicus noted in 61%, the umbilicus in the form of a very narrow slit in 22%, small but distinct in 9%, of a medium size in 4%, and very big in 4%. The shell dimensions of the typical form from the waters with the salinity higher than in the Polish Baltic: height: 3 - 5 - 6 - 7, exceptionally in giants: up to 7.8 or even 10; breadth: 2.3 - 3 - 3.5, in giants: up to 5. The shell height of the Polish specimens: males: 3.5 - 4.5, usually: 3.8 - 4.3; females: 3.4 - 5.8, usually: 3.9 - 4.9. Apparently the females slightly bigger; furthermore, the Baltic specimens seemingly less "miniaturized" than usually suggested in the literature.

The shell walls very thick or thick, never thin, from white to glossy-black, the most often yellowbrown, yellowish or brown. The surface of the uncorroded shell smooth and silky. The older whorls frequently corroded, sometimes very strongly.

One of the most constant conchological features of this species is the shape of the aperture. The form of the umbilicus indicates to some degree the age variability (Falniowski, Dyduch and Smagowicz 1977): in young specimens the umbilicus usually open, with the progress in age covered, though not always, with the parietal lip. The shell wall thinner in freshened waters, but the impact of other factors on the shell wall thickness also observable: for instance, Muus (1967) found on some locality a small population significant of the shells about 3.5 times thicker than the normal, characterized also by completely flat whorls and hardly visible suture. Lambert (1930) and Nicol (1936) found the occurrence of colourful forms characteristic of particular habitats. In general the Polish specimens are remarkable for deeper than typical suture and more convex whorls. It confirms the opinion of Nicol and Muus who associate the occurrence of more convex whorls and deeper suture with more sheltered habitats rich in vegetation.

C - In the Polish Baltic the following forms occur out of the numerous ones:

- f. albida Jeffreys - the shell white or whitish; found scarcely on localities of various kind;
- f. barleei Jeffreys - the shell smaller than of the typical form (in Puck Bay max. 3.2×2.0), fusiform, the body whorl contracted at the base, the mouth much smaller than average; Hebrides (Loch Carron and at Stornoway), eastern coasts of the Baltic, also the Polish; a littoral form, though found accidentally in deep water;
- f. tumida Marshall - 4 - 5 swollen whorls divided by a deep suture (especially the body whorl); sheltered localities;

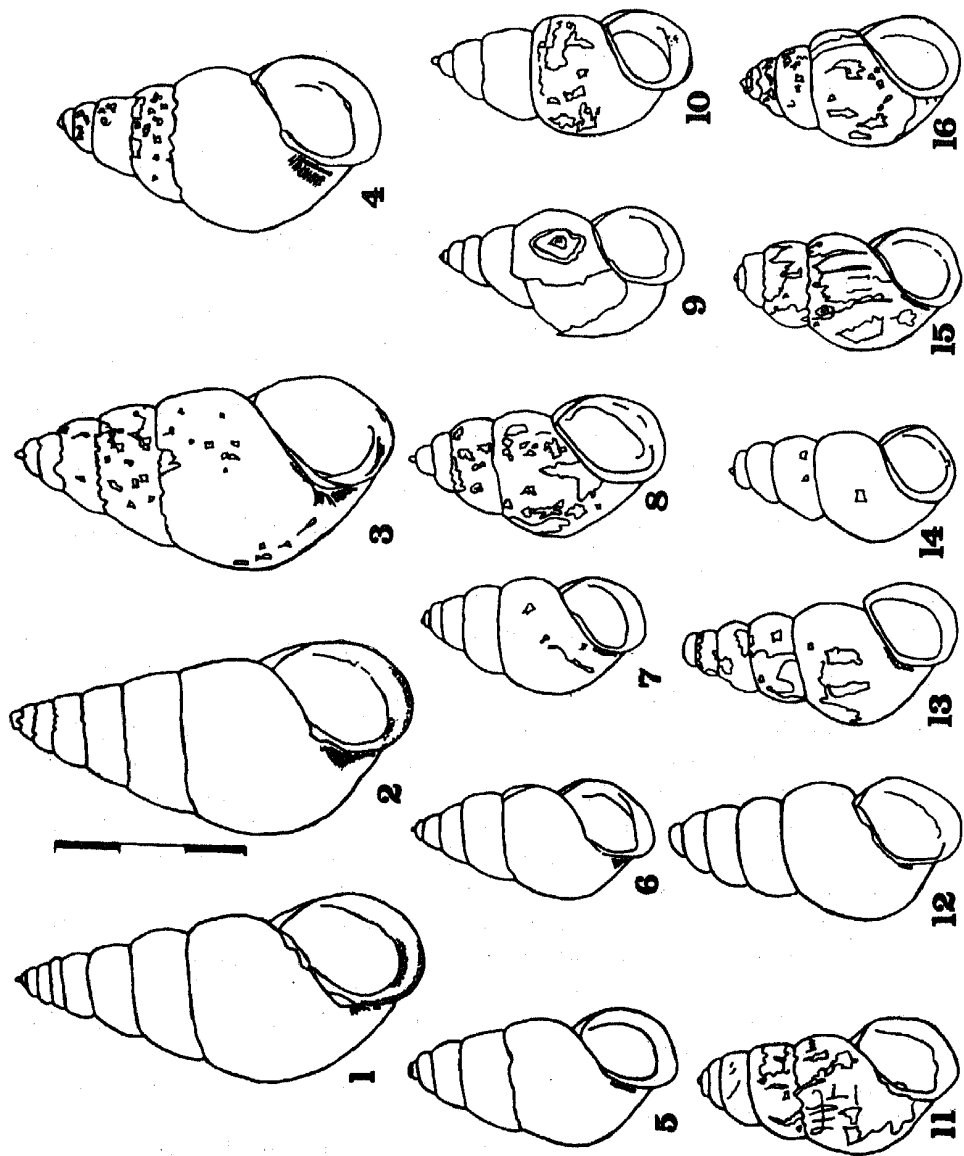


Fig. 1. Shells of *Hydrobia ulvae* males: 1 - 4 - Ooze of Vianen, Island of Schouwen-Duiveland, Prov. of Zeeland, the Netherlands, leg. L. Butot, R.A. Bank; 5 - 16 - Puck Bay, the Baltic (2 - 4 and 9 - infected with larval trematodes)

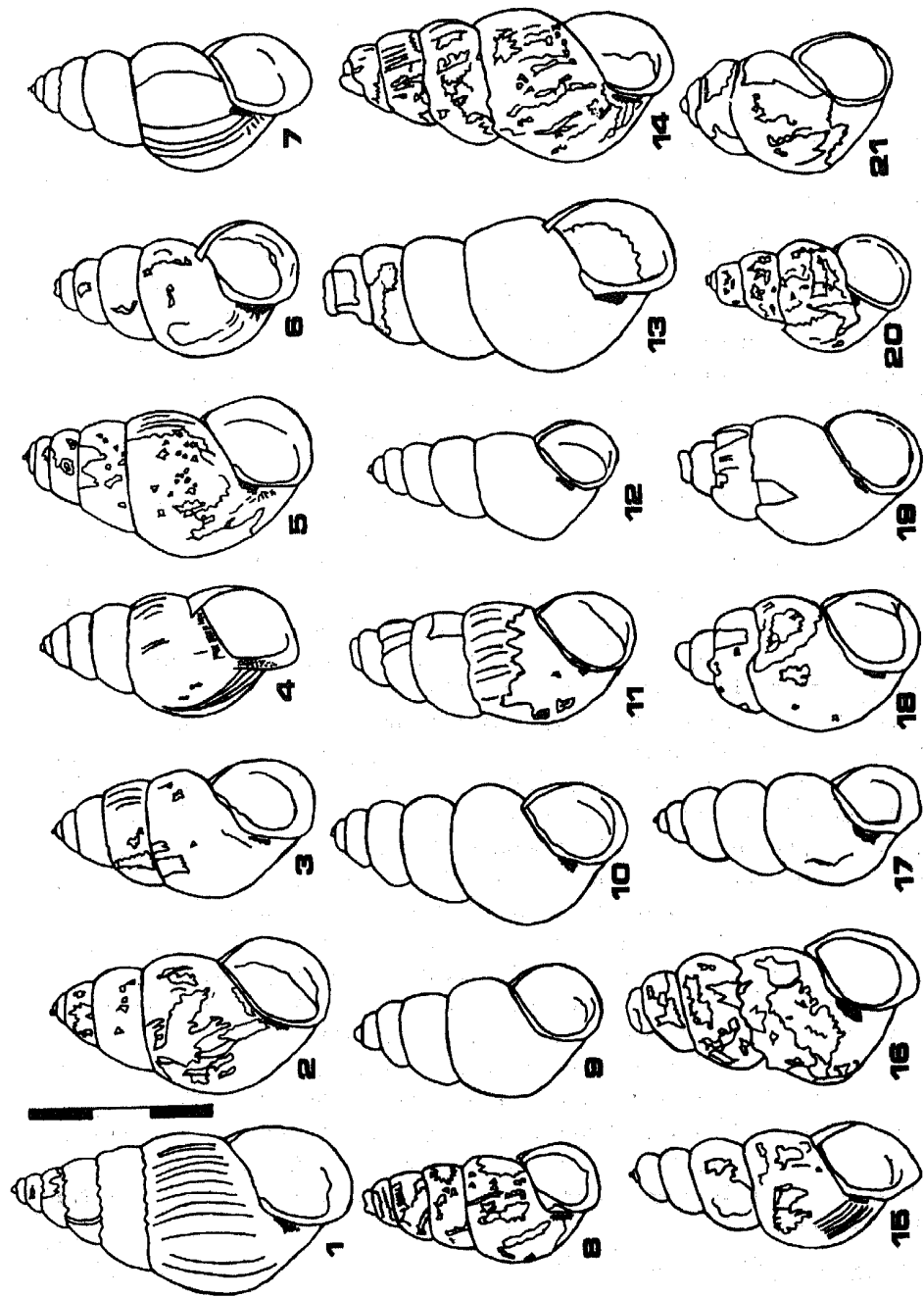


Fig. 2. Shells of *Hydrobia ulvae* females: 1 - Ooze of Vianen, Island of Schouwen-Duiveland, Prov. of Zeeland, the Netherlands, leg. L. Butot, R.A. Bank; 2 - 21 - Puck Bay, the Baltic

- *f. octona* Jeffreys - the shell smaller than average, thin-walled, glossy and horn-colour, with the whorls increasing more slowly, more convex and divided by a deeper suture; a large pool of brackish water called Arnold's Pond (near Grand Havre Bay, Guernsey), Brittany, southern coasts of the Baltic (Jeffreys 1867); this form is rather connected with sheltered, freshened localities, the majority of the specimens from the Polish Baltic approximate to this form.

D - The typical pattern of the snout pigmentation of *H. ulvae* is shown in Fig. 6,1, and the whole variability range in Figs 6,2 - 6,9. The snouts of more than the half of my specimens from the Polish Baltic were pigmented typically, although in numerous cases the pigmented belt was diluted or less distinct. The variability covers the range from the complete lack of pigment which is not frequent (more rare than in *H. ventrosa*) to the entirely black head and tentacles, with very narrow lighter transverse streaks and light lines along the middle of the tentacles (Figs 6,8 - 6,9). The last type of the pigmentation pattern is not rare: the most common among the untypical ones, not only in the Baltic (several specimens from the Netherlands). The other patterns of pigmentation are rarer (Falniowski 1986a: there their descriptions). It is also well to add that the snout pigmentation is a worse taxonomical feature than the tentacle pigmentation and both the characters should be analysed thoroughly.

There may be also the other pigmentation patterns of the tentacles (Figs 6,11 - 6,17) besides the typical of *H. ulvae* (Fig. 6,11) transverse belt of pigment, usually limited to the upper surface of the tentacle out sometimes in the form of a band, its width less than its distance from the tip of the tentacle. Quite untypical and rather common are the specimens with the entirely black snouts (Figs 6,8 - 6,9 and 6,16): the tentacles are also black with a delicate lighter transverse striation and a light, narrow line along the middle of the dorsal side, while ventrally they usually lack pigment. The other patterns of untypical pigmentations are sporadic and usually correspond to the type of a reduced transverse belt (Falniowski 1986a).

E - The number of the ctenidium lamellae: 21 - 32: males: 21 - 32, females: 24 - 32 (Giusti and Pezzoli 1984: 45 - 47).

G - The radula was described by: Meyer and Möbius (1872); Kuhlitz (1898); Krull (1935); Seifert (1935); Feliksiak (1938); Muus (1963, 1967); Falniowski, Dyduch and Smagowicz (1977); Giusti and Pezzoli (1984).

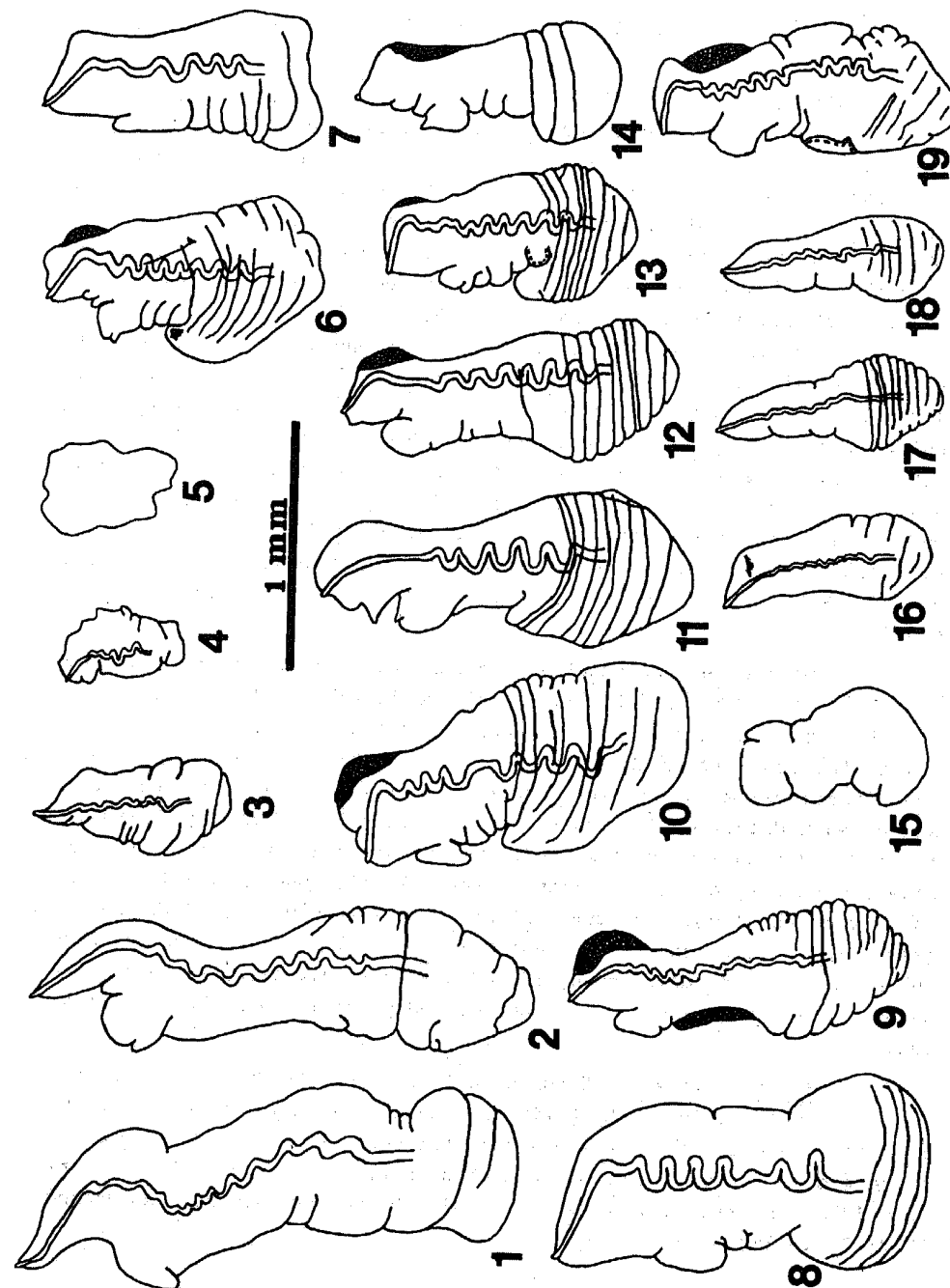


Fig. 3. Penes of *Hydrobia ulvae*: 1 - 5 - Ooze of Vianen, Island of Schouwen-Duiveland, Prov. of Zeeland, the Netherlands, leg. L. Butot, R.A. Bank (3 - 5 - of the specimens of normal size but strongly infected with larval trematodes); 6 - 19 - Puck Bay, the Baltic

H - The vas deferens leaves the big yellowish prostate at its distal end.

I - The penis of *H. ulvae* (Figs 3,1 - 3,19) is big, much bigger than in the other *Hydrobia* species: its length in the specimens from Puck Bay reached 1.2 - 1.6 (Figs 3,6 - 3,19) while in the specimens from the Netherlands as much as 2.2 with the shell height of 6.4 (Figs 3,1 - 3,2). The penis is quite reduced in specimens rather seriously infected with larval trematodes (e.g. in one of the Dutch specimens with the shell 6.4 high the length of the penis did not exceed 0.475) and its habitus is often abnormal (Figs 3,3 - 3,5).

The penis stout, with no filament. The gonoporus at a small papilla situated distally at left. The penis uni-armed with no lobes but with numerous folds, especially at the left side of the proximal part. Noteworthy is the common occurrence of a thin lobate "fold" (Figs 3,6; 3,9 - 3,10; 3,12 - 3,14 and 3,19) distally at the right side. Nearly always easy to distinguish the vas deferens along the proximal and medial part travels in zigzag, while distally straight to the papilla. No accessory duct. The penes of the Polish specimens do not differ from both those described in the literature and the Dutch specimens I have studied.

J - The female reproductive organs were described by: Henking (1894); Krull (1935); Giusti and Pezzoli (1984); Falniowski (1986b). Also in this respect the Polish specimens (Figs 7,1 - 7,4) do not differ from either the Dutch ones (Fig. 7,5) nor those pictured in the literature; moreover, the descriptions in the literature are scarce and often undetailed. The spiral of the oviduct rather big, strongly twisted and intensively pigmented. The bursa copulatrix ovate or oval, always straight, not bent, with a markedly distinguishable duct being usually rather long. The bursa itself small as compared with the accessory gland complex, the receptaculum seminis big as compared with the bursa: its diameter about 1/2 of the bursa diameter. The receptaculum nearly always with a rather markedly distinguishable and long duct.

K - *H. ulvae* inhabits European waters: from the White Sea and Nova Zemla, through the North Sea and the Atlantic also around the British Isles, to the Mediterranean (although from the Mediterranean there are no certain records), and also nearly the entire Baltic (Ehrmann 1956; Fretter and Graham 1962; Zilch and Jaeckel 1962; Nordsieck 1972; Smith 1974).

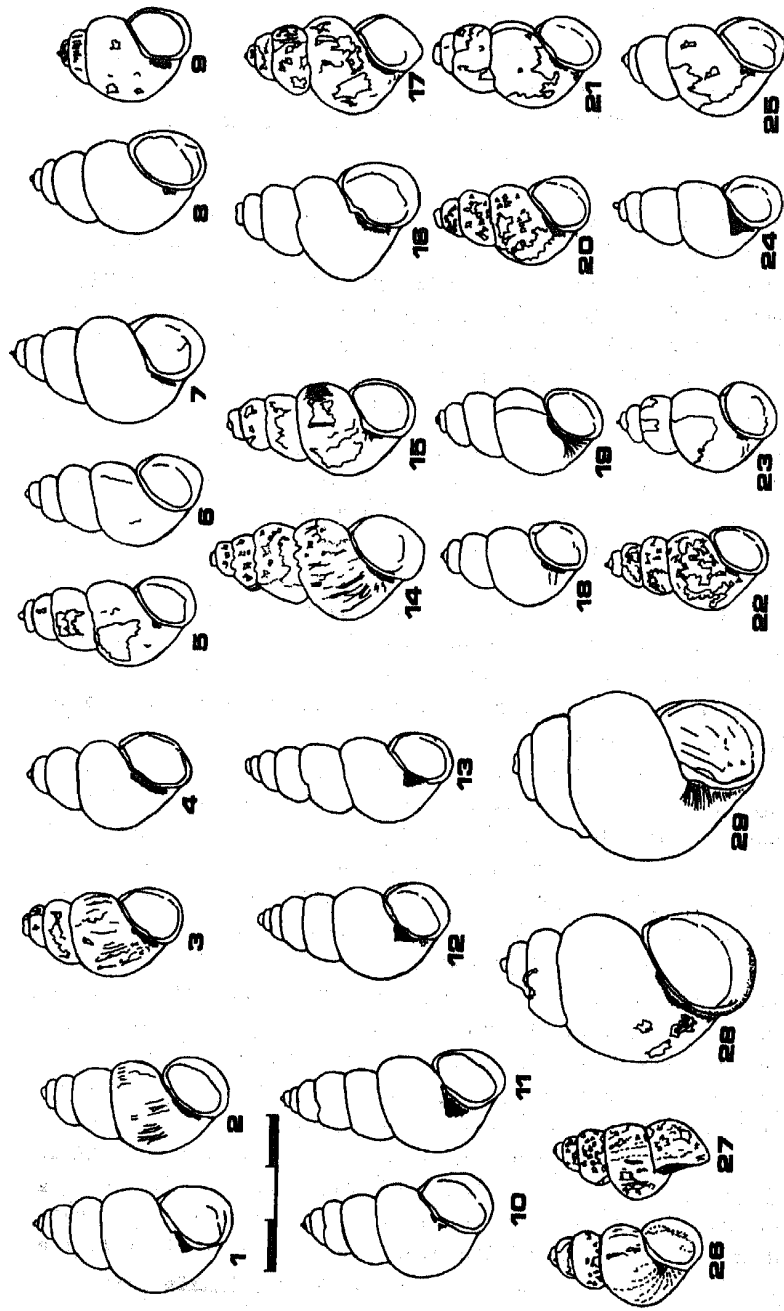


Fig. 4. Shells of *Hydrobia ventrosa*: 1 - 9, 17 and 21 - females; 10 - Kaaskenswater, North of Zierikzee, Island of Schouwen-Duiveland, Prov. of Zeeland; the Netherlands, leg. R.A. Bank, L. Butot; the left - Puck Bay, the Baltic; 10 - 16, 18 - 20; 22 - 25 and 28 - 29 - males; 10 - 13 - Kaaskenswater, the Netherlands, leg. R.A. Bank, L. Butot; the left - Puck Bay, the Baltic; 28 - 29 - young males, on the scale of 2 : 1 compared with the rest; Puck Bay; 26 - 27 - lectotype, Sandwich, Kent, Great Britain, British Museum (Natural History), after Bank, Butot and Gittenberger (1979), the sex unknown, drawn to a scale different from the other drawings

2. *Hydrobia ventrosa* (Montagu, 1803)A - *Turbo ventrosus* Montagu, 1803*Hydrobia pusilla* Eichwald, 1830*Ventrosia stagnorum*: Radoman 1977, non *Helix stagnorum* Gmelin, 1791

This species was often mentioned in the literature as *H. stagnalis* (Baster, 1765) or *H. stagnorum* (Gmelin, 1791). The completely unclear situation in its nomenclature was explained by Bank, Butot and Gittenberger (1979) who identified *Turbo stagnalis* Baster, 1765 with *Helix stagnalis* Linnaeus, 1767 = *Helix stagnorum* Gmelin, 1791, being a separate species rather distantly related with *H. ventrosa* (Montagu, 1803), belonging to the genus *Heleobia* Stimpson, 1865 and recorded scarcely from a few localities (the Netherlands, Italy).

B - The shell (Figs 4, 1 - 4, 29) sharply conical, ovate, sometimes turreted or fusiform, its breadth equals 0.53 - 0.56 of its height, so in comparison with *H. ulvae* it is somewhat less slim and more ovate in outline, however, not always. The whorl number somewhat higher than in *H. ulvae*: 5 - 6, exceptionally 7 - 9, whorls more convex and divided by a deeper suture. This is one of the most striking differences, though the variability ranges are often much overlapping. However, while in *H. ulvae* the whorls are frequently convex and the sutures deep in *H. ventrosa* the whorls are never as flat and the suture as deep as in the typical form of *H. ulvae*.

The whorls grow regularly and slowly, the body whorl proportionally lower than in *H. ulvae* and somewhat more swollen, while the last but one usually proportionally higher than in *H. ulvae*. The apex blunt with the common strong or very strong corrosion, the apex angle slightly more acute than in *H. ulvae* ($30 - 35^\circ$). The mouth closely adhering, parietal lip broad, and the shape of the aperture nearly always different from that of *H. ulvae*: elliptical or ovate, the angle in the upper part absent or poorly marked. Although variable, the shape of the aperture is the best diagnostic character distinguishing *H. ulvae* (acute angle, conspicuous, only in some specimens poorly marked) from *H. ventrosa*. The peristome of *H. ventrosa* always continuous. The outer lip absent, mouth edge thin: thinner than in *H. ulvae*.

The variability range of the umbilicus is the same as in *H. ulvae*, however, in *H. ulvae* it is usually (61%) absent, while in *H. ventrosa* usually (64% of the specimens from Puck Bay) in the form of a very narrow slit, and the other types of the umbilicus are approximately frequent (each of about 9%). The shell smaller than in *H. ulvae*. The di-

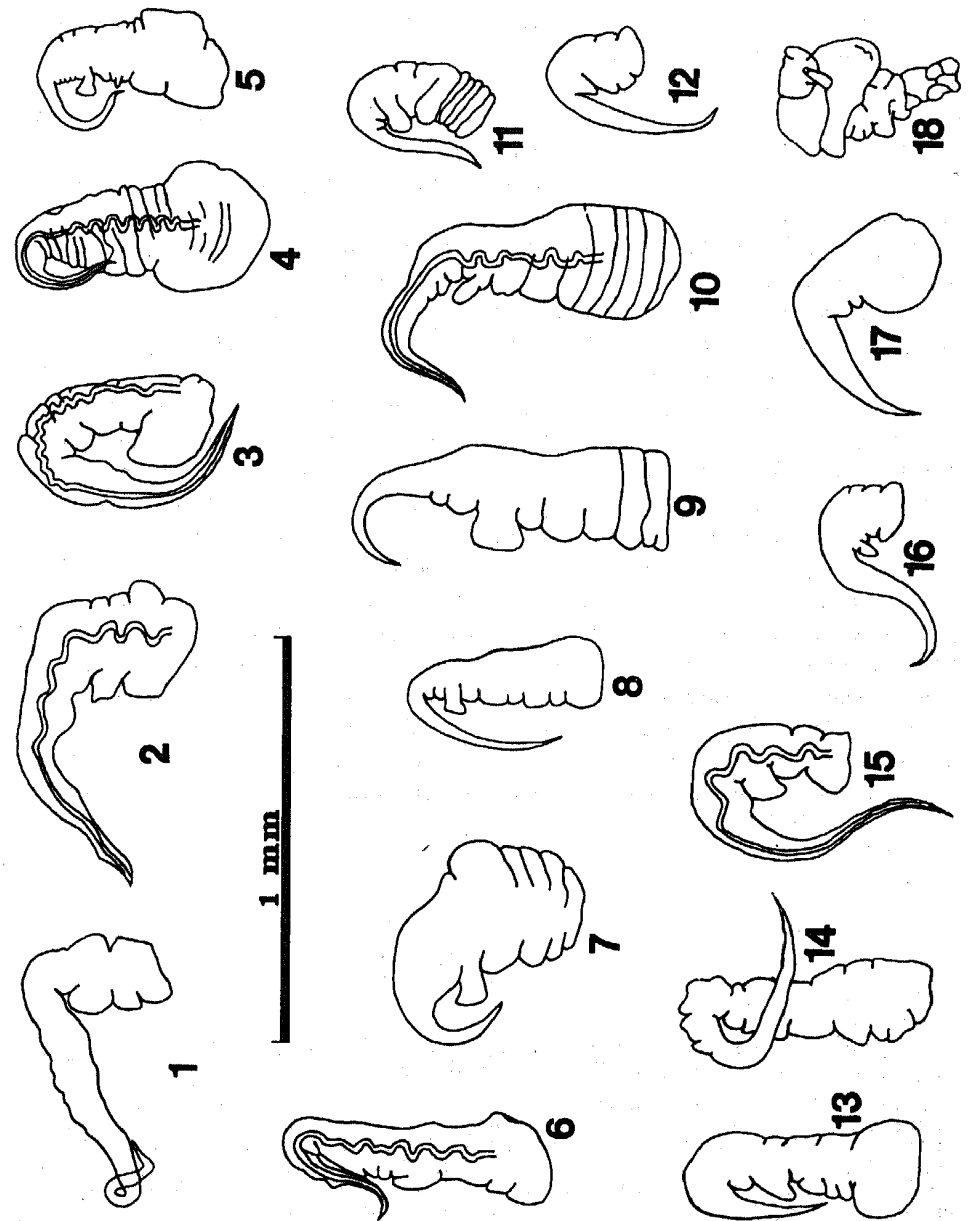


Fig. 5. Penes of *Hydrobia ventrosa*: 1 - 3 - Kaaskenswater, North of Zierikzee, Island of Schouwen-Duiveland, Prov. of Zeeland, the Netherlands, leg. R.A. Bank, L. Butot; 4 - 17 - Puck Bay, the Baltic. 18 - *H. ventrosa*, the prostate, Puck Bay, the Baltic, drawn to another scale

mensions of those from the waters of the salinity higher than that of the Polish Baltic: height: 2.6 - 6.2, exceptionally in giants: up to 8.4; breadth: 1.5 - 3.0, in giants: up to 3.2. The shell height of the Polish specimens: males: 2.145 - 4.0, usually: 2.9 - 3.6; females: 2.7 - 3.7, usually: 3.0 - 3.5. The females need not be bigger than. Moreover, there are reports of somewhat larger dimensions of H. ventrosa from the Polish Baltic: up to 4.5 - 4.8 x 2.0 - 2.5.

The shell usually thin-walled, generally more delicate than in H. ulvae, though sometimes thick-walled specimens can be found. The shell colour from pale yellow to horn or brownish, but it may seem dark as the pigmented mantle is visible through the translucent shell. The surface of the uncorroded shell smooth and glossy.

The shells of the specimens from Puck Bay (Figs 4,2 - 4,9; 4,14 - 4,25 and 4,28 - 4,29) do not differ significantly from either the Dutch specimens (Figs 4,1 and 4,10 - 4,13) or the lectotype (Figs 4,26 - 4,27). Muus (1967) regards the variability range of H. ventrosa as wider than that of H. ulvae, however, this opinion cannot be acknowledged. Actually, H. ventrosa is characterized by a wider variability range of the whorl number along with a greater variation of the habitus and proportions as well as more common occurrence of the turreted forms. Nevertheless, most of the characters as: whorl convexity, suture depth, whorl growth regularity, mouth shape, peristome, shell colour and its wall thickness are far more variable in H. ulvae.

The reduction of shell dimensions is caused not only by lowered salinity, but also by food shortage, lower temperature, shorter vegeta-

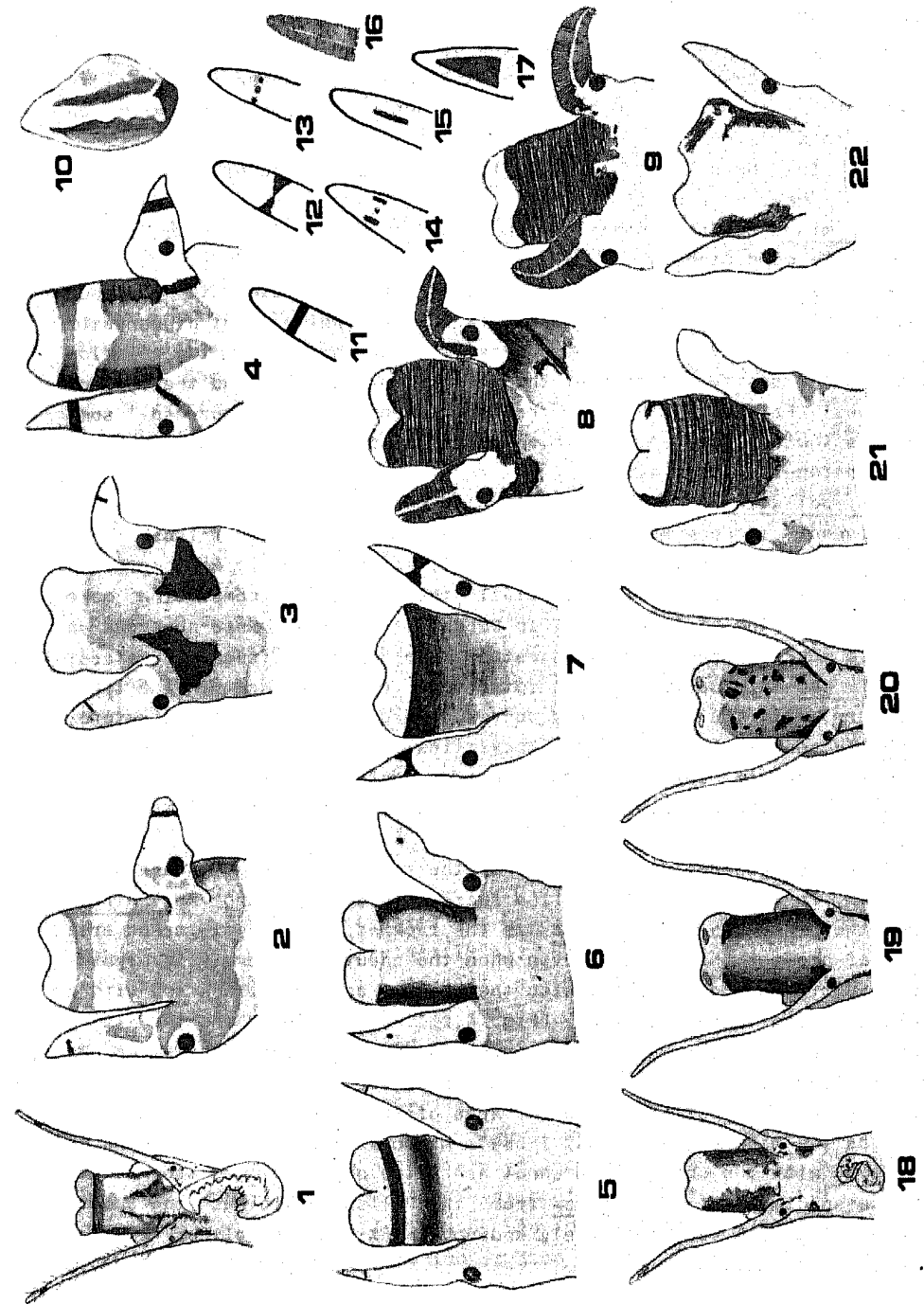


Fig. 6. Pigmentations of Hydrobia ulvae and H. ventrosa: 1 - 17 - H. ulvae: 1 - the head and penis habitus and typical pigmentation pattern of a living Danish specimen (after Muus 1963); 2 - 9 - pigmentation patterns in fixed specimens from Puck Bay; 10 - the opercular lobe pigmentation, Puck Bay; 11 - 17 - tentacle pigmentation patterns: 11 - the typical pattern, Puck Bay; 12 - 16 - specimens from Puck Bay; 17 - an untypical pattern of a Dutch specimen, Ooze of Vianen, Island of Schouwen-Duiveland, Prov. of Zeeland, leg. L. Butot, R.A. Bank; 18 - 22 - H. ventrosa: 18 - 20 - living specimens: 18 - the head and penis habitus and typical pigmentation pattern, Danish coasts (after Muus 1963); 19 - the pigmentation of the typical form (after Seifert 1935); 20 - the pigmentation of f. baltica (after Seifert 1935); 21 - 22 - pigmentation patterns in fixed specimens from Puck Bay. All the figures after Falniowski (1986a)

tion period, deeper location of a habitat, etc., and by the competition with *H. ulvae*. The body whorl of the older specimens is more swollen than that of the younger ones. The shell wall is thinner in chemically unfavourable conditions. Čuchčín (1976b) observed slimmer specimens on deeper localities.

C - In the Polish Baltic the following forms occur out of the numerous ones of the species:

- *f. minor* Jeffreys - small: up to 2.0 - 2.5 x 1.5, stout; in unfavourable conditions;

- *f. baltica* Clessin - a small Baltic form, according to some authors (Seifert (1935) also remarkable for the spotty snout pigmentation pattern (Figs 6,19 - 6,20); my observations do not confirm the relation between the spotty pattern of the snout pigmentation and the form of the shell (Falniowski 1986a); the form is unprecisely described: some authors include all the Baltic specimens into it while the others do not distinguish it at all;

- *f. pellucida* Jeffreys - the shell completely white, glossy and translucent; in Puck Bay relatively more numerous on deeper localities;

- *f. ovata* Jeffreys - the shell small, about 4 whorls more swollen than in the typical form, especially the body whorl comprising more than 1/2 of the shell height; in Puck Bay relatively more numerous on inshore rocks, generally seems rather more common in freshened waters;

- *f. decolata* Jeffreys - the spire more elongate than in the typical form, with the whorls more convex and divided by a deeper suture; probably associated with deeper localities;

- *f. elongata* Jeffreys - the shell elongate, sharply turreted, up to 8 whorls; the extremal form, often an effect of the parasitic infection.

D - The pigmentation patterns of the snout and tentacles are shown in Figs 6,18 - 6,22. The feature distinguishing *H. ventrosa* from the other Baltic *Hydrobia* is the lack of a distinct transverse belt of pigment (Fig. 6,18), even when the snout is intensively pigmented. Sometimes the specimens with the snouts entirely black and with a delicate transverse striation (Fig. 6,21) can be found and then it is impossible to distinguish this specimen from *H. ulvae* basing on the snout pigmentation only. Usually the spots of pigment of various intensity cover a greater or smaller area of the snout laterally, diluted towards the middle (Falniowski 1986a). Moreover, while the specimens of *H. ulvae* with the unpigmented snout are extremely rare, as many as 44% of the specimens of *H. ventrosa* from the Polish Baltic has the snouts unpigmented; 31% very delicately and up to 25% intensively or very intensively pigmented.

Like in *H. ulvae*, the pigmentation of the tentacles is a better diagnostic feature than the pigmentation of the snout. The tentacles of 88% of the specimens of *H. ventrosa* from the Polish Baltic are unpigmented, what is a very exception within the other two *Hydrobia* species. If the pigmentation occurs, frequently only one tentacle is pigmented. The pattern can be in the form of diluted dark brown spots, dottings, diluted terminal longitudinal belt, or resembling that of *H. ulvae* (Figs 6,8 - 6,9 and 6,16) though less intensive.

E - The number of the ctenidium lamellae lower than in *H. ulvae*: 17 - 22: males: 17 - 22, females: 19 - 22 (Puck Bay); in the Dutch specimens considerably higher: 29 - 30 (Bank and Butot 1984: about 28; Giusti and Pezzoli 1984: about 25).

G - The radula was described by: Woodward (1892); Kuhlitz (1898); Krull (1935); Seifert (1935); Muus (1963, 1967); Bishop (1976); Čuchčín (1976b); Falniowski, Dyduch and Smagowicz (1977); Bank and Butot (1984); Giusti and Pezzoli (1984).

H - Unlike in *H. ulvae*, the vas deferens leaves the prostate at its ventral side, far from the distal end (Fig. 8,18).

I - The penes of the Polish specimens (Figs 8,4 - 8,17) do not differ from both those of the Dutch specimens (Figs 8,1 - 8,3) and those described and drawn in the literature. Up to 0.7 - 1.0 long they are quite smaller than those of *H. ulvae*.

The penis slim with a markedly distinguishable, slim and long filament which is absent in the other two *Hydrobia*. A small second arm at the left side of the filament, also absent in the other Polish *Hydrobia*. The gonoporus at the sharp tip of the filament. Like in *H. ulvae* numerous and well marked folds and the vas deferens travelling through the proximal and medial part of the penis easily distinguishable. The accessory duct also lacking.

J - The female reproductive organs described by: Robson (1922); Krull (1935); Fretter and Graham (1962); Čuchčín (1976b); Radoman (1977); Bank and Butot (1984); Giusti and Pezzoli (1984); Falniowski (1986b). Also in respect of the female reproductive organs the Polish specimens (Figs 9,6 and 9,8 - 9,9) not different from the Dutch ones (Fig. 9,7), and also very similar to those described in *H. ulvae* (Falniowski 1986b). The differences concern only the bursa copulatrix which is of a similar shape (straight, not bent) but when compared with both the accessory gland complex and receptaculum seminis the bursa, usually more bulgy, always much bigger than that of *H. ulvae*. The duct of bursa also markedly distinguishable but fairly long; often longer than the bursa itself and, in spite of the great variability, nearly always proportionally longer than in that species. The recepta-

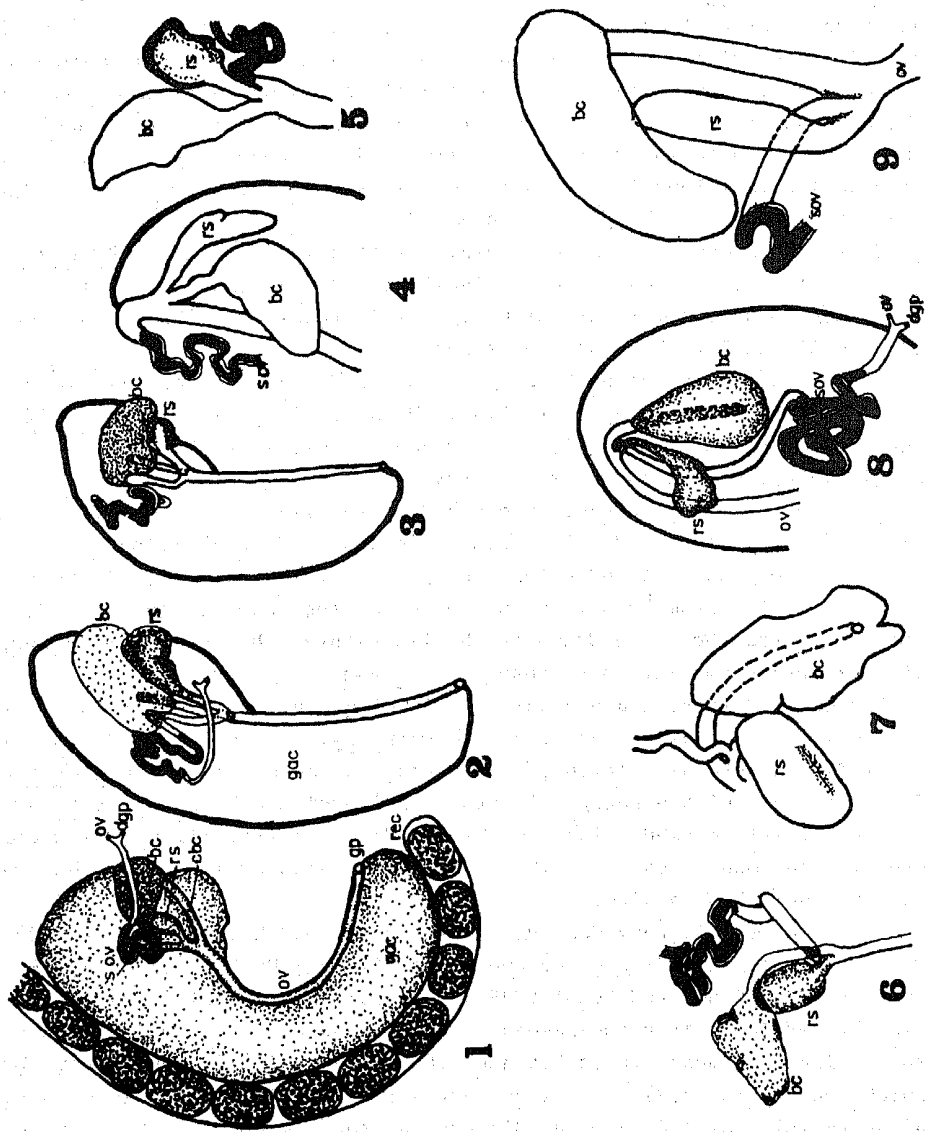


Fig. 7. Female reproductive organs: 1 - 5 - *Hydrobia ulvae*: 1 - 4 - Puck Bay; 5 - Ooze of Vianen, Island of Schouwen-Duiveland, Prov. of Zeeland, the Netherlands, leg. L. Butot, R.A. Bank; 6 - 9 - *H. ventrosa*: 6 and 8 - 9 - Puck Bay; 7 - Kaaskenswater, North of Zierikzee, Island of Schouwen-Duiveland, Prov. of Zeeland, the Netherlands, leg. R.A. Bank, L. Butot. All the figures after Falniowski (1986b)

culum seminis often without a distinguishable duct, or the duct shorter than in *H. ulvae*.

K - *H. ventrosa* inhabits brackish waters in Europe, North Africa and West Asia (Žadin 1952; Ehrmann 1956; Fretter and Graham 1962; Nordsieck 1972). In the Baltic it occurs from the Danish Straits to Suomenlahti and Bottenhavet where it reaches 63°04' N. In the Atlantic: from the White Sea and Norway to Spain. Around the British Isles and Outer Hebrides present, though locally rare. Also in some German brackish lakes (Dodendorf, Artern, Salzige See in Mansfeld) as well as in Zuidersee and its canals (the Netherlands). Its range covers also the Mediterranean, Black Sea, Sea of Azov, Caspian Sea, Sea of Aral and brackish lakes in southern Kazakstan.

It is worth mentioning that Radoman has described *H. ventrosa* from the Black Sea as a distinct species *Ventrosia pontieuxini* Radoman, 1973, but this separateness raises doubts. On the other hand some authors (Bishop 1976) predict that the North American *H. totteni* Morrison, 1954 may be identical with the European *H. ventrosa*: thus the range of *H. ventrosa* would cover also North American shore of the Atlantic.

3. *Hydrobia neglecta* Muus, 1963

A - Nordsieck (1972) erroneously regarded *H. neglecta* as a form of *H. minuta* (Totten, 1834). *Turbo minutus* Totten, 1834, non Brown, 1818 was not fully and clearly described; it was redescribed as *H. totteni* Morrison, 1954 and is obviously different from *H. neglecta*. However, the name *H. minuta* or *H. ventrosa* f. *minuta* has been sometimes used in reference to the European gastropods which may have been *H. neglecta*, as Muus (1963) suggested basing on the drawings from the literature.

B - The shell sharply conical, turreted or ovate, sometimes fusiform, the spire sometimes rather shortened, but often much elongate; the shell habitus between *H. ulvae* and *H. ventrosa*, more often approximate to *H. ventrosa*: especially the turreted forms of both the species are conchologically non-distinguishable, though those from Puck Bay (Figs 8.1 - 8.4) resemble rather *H. ulvae*.

The shell breadth of the typical specimens up to 0.47 - 0.49 of its height, so this is the most slim shell among the three *Hydrobia*. As in the other species the spire elongate or strongly elongate. Whorls 4-6, exceptionally up to 7, usually 5, so it is also between the number in *H. ulvae* and *H. ventrosa*. The whorl convexity and suture depth also intermediate: usually moderate. The body whorl proportionally lower than in

H. ulvae, of similar height as in H. ventrosa and, like in that species, much more swollen than in H. ulvae. The whorl growth regular and slow as in H. ventrosa. The apex somewhat sharper than in the other two species.

The mouth adhering, parietal lip conspicuous, no outer lip, mouth edge not thickened, like in those two species. The shape of the aperture, peristome and umbilicus between H. ulvae and H. ventrosa. The aperture ovate with a conspicuous angle upwards, the peristome usually continuous, but may be almost continuous. The umbilicus always present; usually in the form of a very narrow slit but may be wider to a fairly wide. The smallest among the Baltic Hydrobia. Muus (1963) for Danish specimens gives the height: 2 - 3, exceptionally in giants: up to 4; breadth: 1 - 1.8, in giants: up to 2.1. Bishop (1976) indicates the shell height of British specimens: males: 2.4 - 3.6; females: 2.9 - 3.7. Polish specimens reach up to 2.2 - 3.5, so the "miniaturization" due to lower salinity is practically not observed in this species.

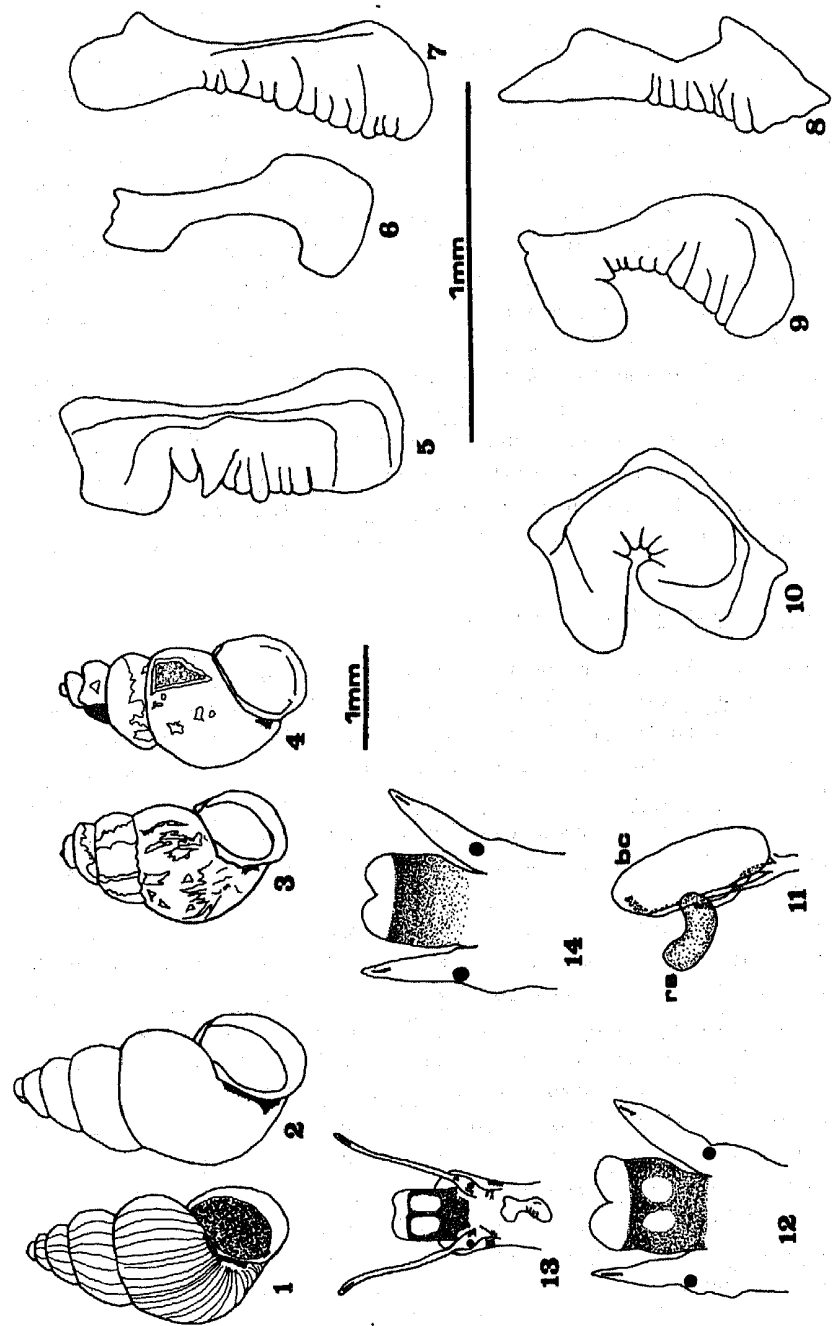
The shell wall translucent and the thinnest among the Hydrobia described, but may be thicker. The shell grey brown, its surface often with delicate spiral striae, or sometimes with very delicate "ribs" of growth lines (Fig. 8,1). The older whorls often corroded, frequently very strongly.

It should be stressed that the Polish specimens (Figs 8,1 - 8,4) resemble more H. ulvae than the typical of H. neglecta. The most approximate to the type is the specimen in Fig. 8,2. In general the shell variability of H. neglecta is considerably smaller than that of H. ulvae or H. ventrosa, but is entirely consisted between the typical forms of those two. Because of the occurrence of the interspecific variability overlap it should be acknowledged that the determination of H. neglecta basing on the conchological features is impossible.

D - The typically pigmented snout with a distinct, transverse belt of pigment (Fig. 8,13) like in H. ulvae but unlike in H. ventrosa. The proximal part of the snout usually more intensively pigmented than in H. ulvae, and between this and the belt two irregular unpigmented spots of various size and outline but symmetrical to each other - absent in H. ulvae. In the Polish specimens (Figs 8,12 and 8,14) these spots not always distinguishable (Fig. 8,14), the proximal part of the snout occasionally appears delicately pigmented, also the pigmentation of the entire snout appears delicate, sometimes very delicate. The variability overlaps that of H. ulvae.

The tentacles always with a dorsal, longitudinal pigmented belt of a greater length than its distance from the tip of the tentacle. This differs H. neglecta from both H. ventrosa lacking this belt, and H. ulvae

Fig. 8. Hydrobia neglecta: 1 - 12 and 14 - Puck Bay, the Baltic; 1 - 4 - shells; 1 - 2 - females, 3 - 4 - males; 5 - 10 - penes; 11 - a fragment of the female reproductive organs; 12 and 14 - head pigmentation in fixed specimens; 13 - the head and penis habitus and typical pigmentation pattern of a living Danish specimen (after Muus 1963)



with the transverse and narrow belt only exceptionally longitudinal (in such case rathermore distant from the tentacle tip than in *H. neglecta*).

G - The radula was described by: Muus (1963, 1967); Bishop (1976); Falniowski, Dyduch and Smagowicz (1977).

I - The penis is the most characteristic feature of *H. neglecta*, in the Polish specimens (Figs 8,5 - 8,10) it looks like those of the figured and described Dutch and British specimens (Muus 1963, 1967; Bishop 1976).

The penis small as in *H. ventrosa*, but stout as in *H. ulvae*. Unlike in *H. ventrosa*, no filament nor the second arm. Unlike in *H. ulvae* the gonoporus lies distally on the right, but not left side, at a broad and poorly distinguishable small lobe, but not a small papilla. The penis of *H. neglecta* differs from the other two Polish *Hydrobia* by the presence of a left, distal, blunt, broad and large lobe and by the accessory duct running along the left side of the vas deferens. The vas deferens poorly distinguishable, running proximally and medially straight, not in zigzag as in the other two species.

J - The female reproductive organs (Fig. 8,11) have not been described yet. The bursa copulatrix big, massive and rather bulgy, with a markedly distinguishable duct. The duct somewhat longer than the bursa itself and markedly thin. The length of the receptaculum seminis equal to about 0.5 of the length of the bursa. The receptaculum bean-shaped, with the duct more markedly distinguishable than that in *H. ulvae* and *H. ventrosa*.

K - *H. neglecta* was described in 1963 from Ajstrup Bay in Mariager Fjord of Eastern shores of Jutland. Soon afterwards it was found along the whole Danish coast. Janssen and Vogel (1965) recorded it in the Netherlands, Kerney (1966) gave the first record from Great Britain, Bishop (1976) reported several localities from England and Scotland. Falniowski, Dyduch and Smagowicz (1977) mentioned the species from the Polish Baltic (Puck Bay) where it is very scarce, however. It is common on hardly any area of the range. Its distribution is not continuous, and still fragmentarically known. It seems that further studies should show the occurrence of *H. neglecta* in the range from the North Sea to the Mediterranean, as Nordsieck (1972) suggests.

GENUS *BYTHINELLA* MOQUIN-TANDON, 1855

The genus *Bythinella* presents the greatest taxonomical difficulties among the Polish prosobranchs, and its systematics causes a greatest deal of controversies. For instance, Radoman (1976) basing on the shell features only describes new and new species from Balkans and Asia Minor. He reckons that there cannot be simply any anatomical differences between closely related species. The contrary opinion is that of Giusti and Pezzoli (1977a,b, 1980, correspondence contact) who have analysed both the conchological and anatomical features of the Italian *Bythinella* species and they have come to the conclusion that indeed several local populations differ between one another, but the differences are insignificant and the entire genus is of a superspecies character and then it should be recognized as such together, under one specific name.

Boeters (1973) has reduced the number of the West European *Bythinella* species basing on the anatomical features and showing conspicuous differences between the species redescribed in this way. The analysis of the features that Boeters has based on seems to point out that he has considered an insufficient material and this has let him regard as certain these features which are highly variable in fact. Considering the shell only and completely neglecting the anatomy, in fact, Jungbluth (1971a,b, 1972) has reduced the number of the species to only a few in the whole Europe. However, this does not fit my observations which point out that the shell as the criterion in the systematics of *Bythinella* is entirely useless.

Among numerous papers discussing only the shell of *Bythinella* there are worth mentioning those of: Frauenfeld (1864); Clessin (1876, 1887); Hazay (1881); Ehrmann (1956); and Jaeckel (1976). *B. austriaca* from Poland is usually recognized as such, but this means that the name is applied to practically all *Bythinella* specimens found in Poland without an appropriate criticism. Some earlier records noted also the occurrence of *B. cylindrica* and *B. hungarica*.

The shell of *Bythinella* is characterized by a great variability along with a simple habitus, the lack of distinct characters and a considerable overlap of the variability ranges of the particular taxons. The features of the shell do not allow to consider it as the basic criterion. On the other hand the descriptions of the shell in the literature, especially those earlier, are vague and ambiguous, and each description could refer to almost all the *Bythinella*. Furthermore, most of the descriptions of locus typicus are not precise enough. As the result, the earlier systematics of *Bythinella*, although still in force accord-

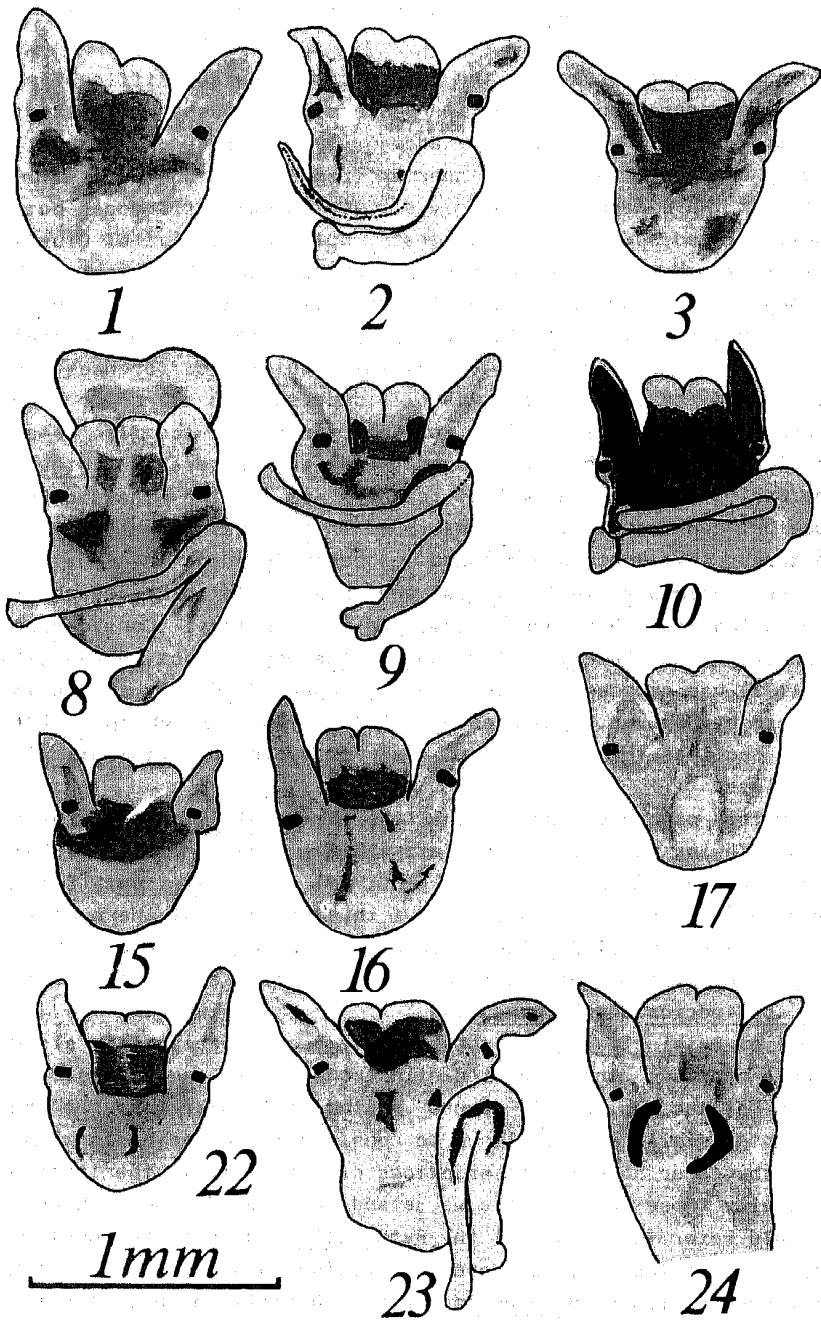
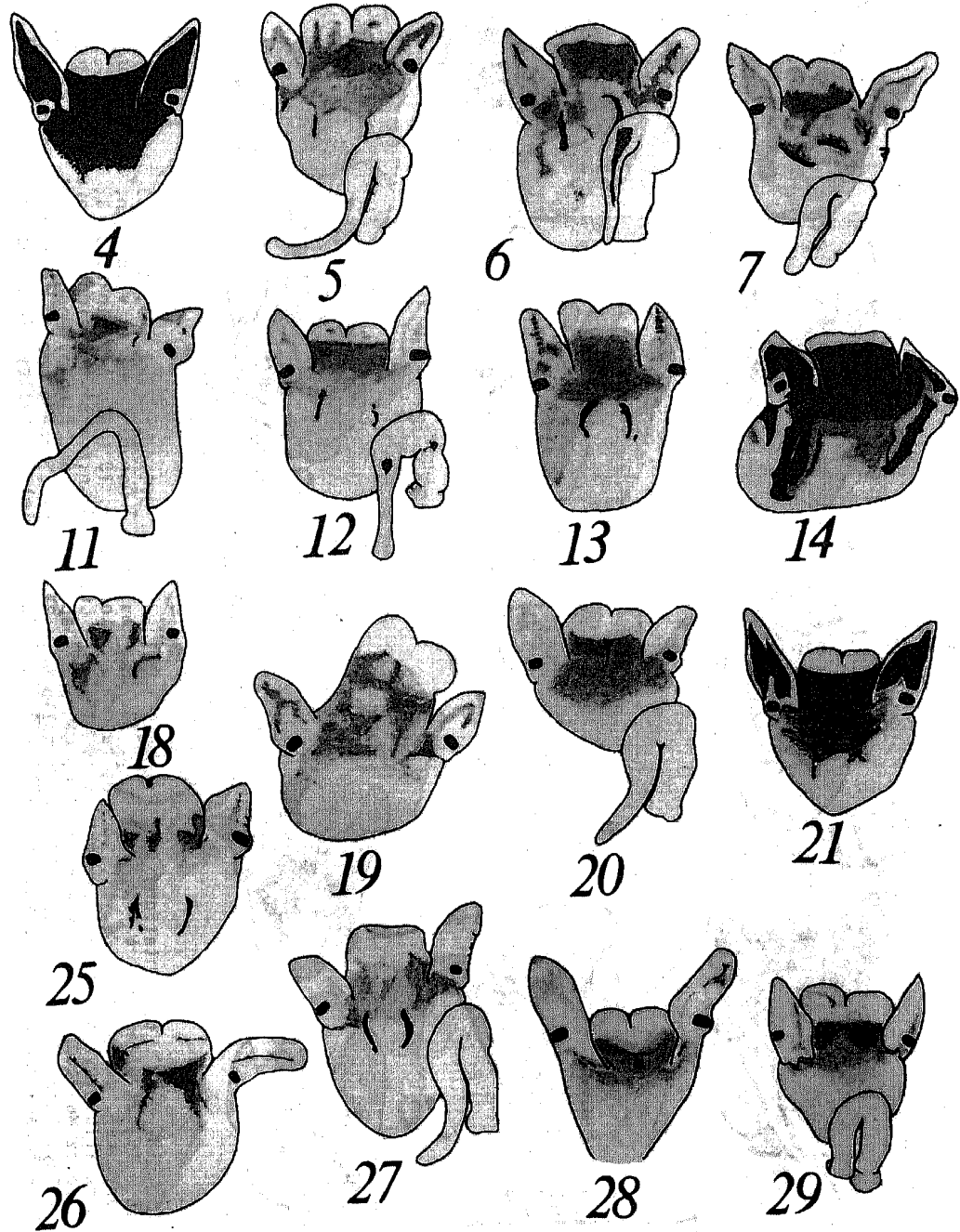


Fig. 9. Head pigmentations in *Bythinella austriaca*: 1, 3 - 4, 13 - 19, 21, 22, 24 - 26 and 28 - females; 2, 5 - 12, 20, 23, 27, 29 - males; 1, 8 - 9, 15, 22 - Kremšdnster, Oberdnsterreich, Austria, leg. L. Butot; 2 - 3, 10, 16, 23 - Zelazno near Kłodzko; 17, 24 - Strážyska Valley, stream, Tatra Mountains; 4, 11, 18 - Przystup Kominiarski, Tatra Mountains; 5, 12, 25 - 26 - Ojcw, Saspowska Valley; 6, 13, 19, 27 - Zygmont Springs by Złoty Potok near Czestochowa; 7, 14, 20 - 21, 28 - 29 - Mników Valley



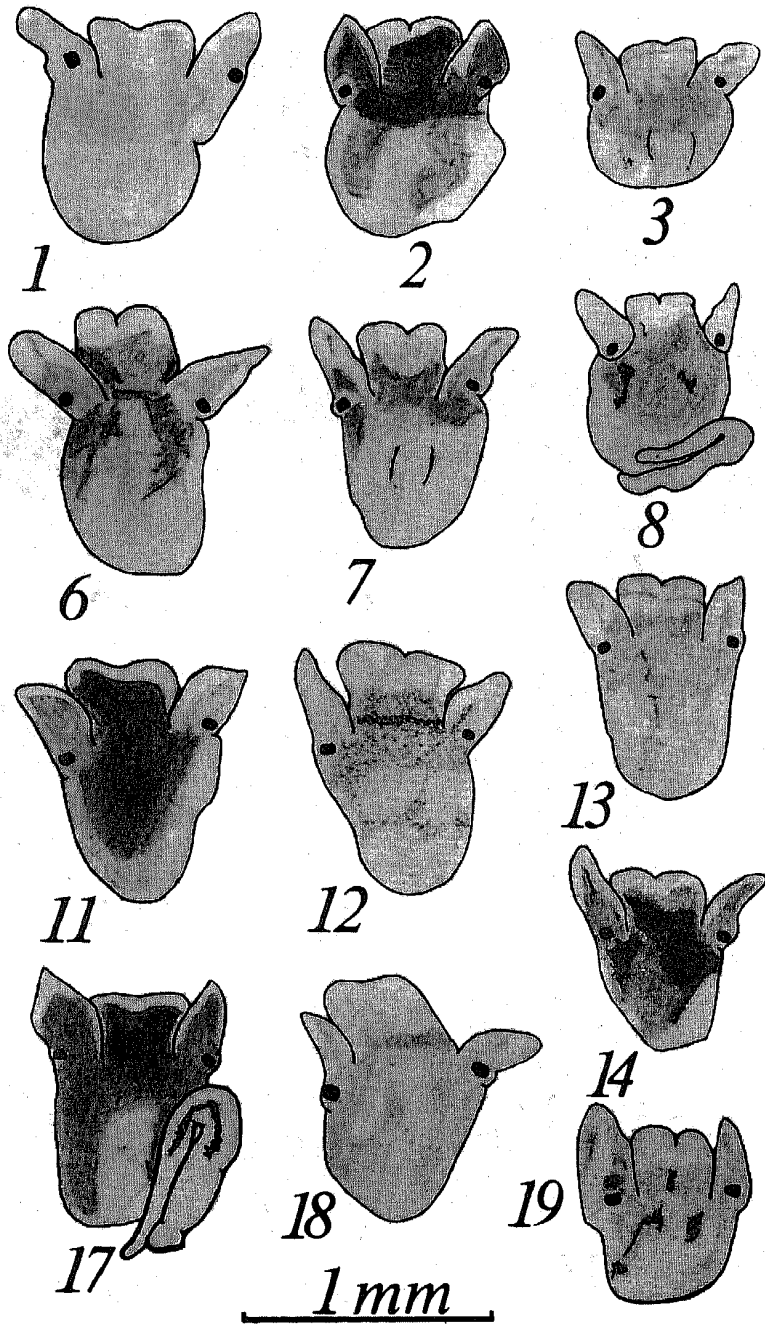
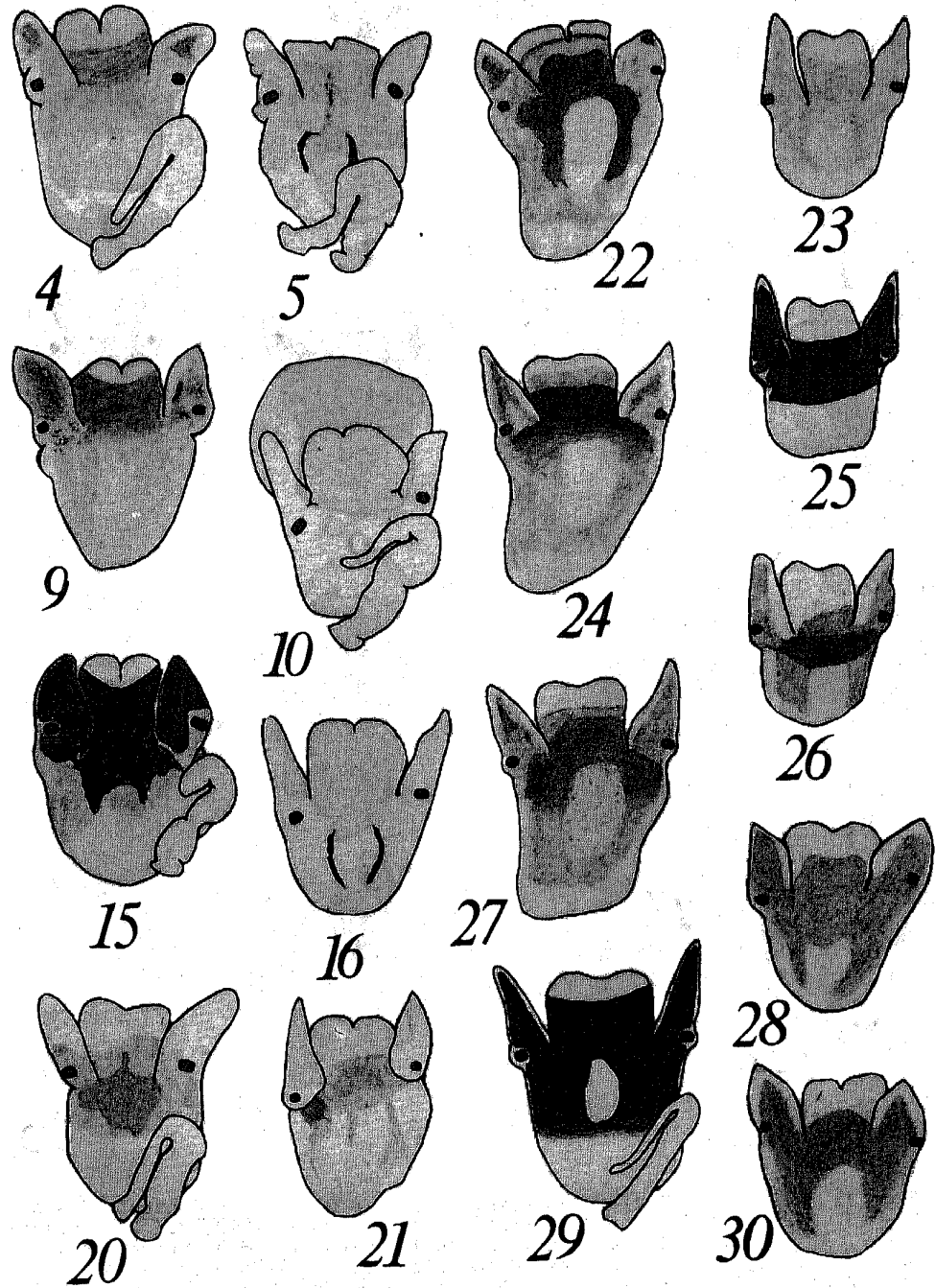


Fig. 10. Head pigmentations in *Bythinella*: 1 - 21 - *B. cylindrica*: 1 - 3, 6 - 7, 9, 11 - 14, 16, 18 - 19, 21 - females; 4 - 5, 8, 10, 15, 17, 20 - males; 1 - Danube River at Vilshofen, Bayern, Germany, Leg. L. Butot; 2, 6, 11, 17 - Ostre near Żywiec; 3, 8, 13 - Żylica tributary spring by Skrzyczne; 4, 9, 15, 19 - Lubomir Mountain at the side of Kobielnik; 5, 20 - Turbacz Mountain at the side of Koninki; 10, 16 - spring, Ociemne, Pieniny Mountains; 21 - Mała Łąka Valley, Tatra Mountains; 22 - 30 - *Bythinella* sp.: 29 - a male, the others - females; 22 - 24, 27, 29 - Poiana Pisana, Tatra Mountains; 25 - 26, 28, 30 - Koscieliska Valley, Tatra Mountains



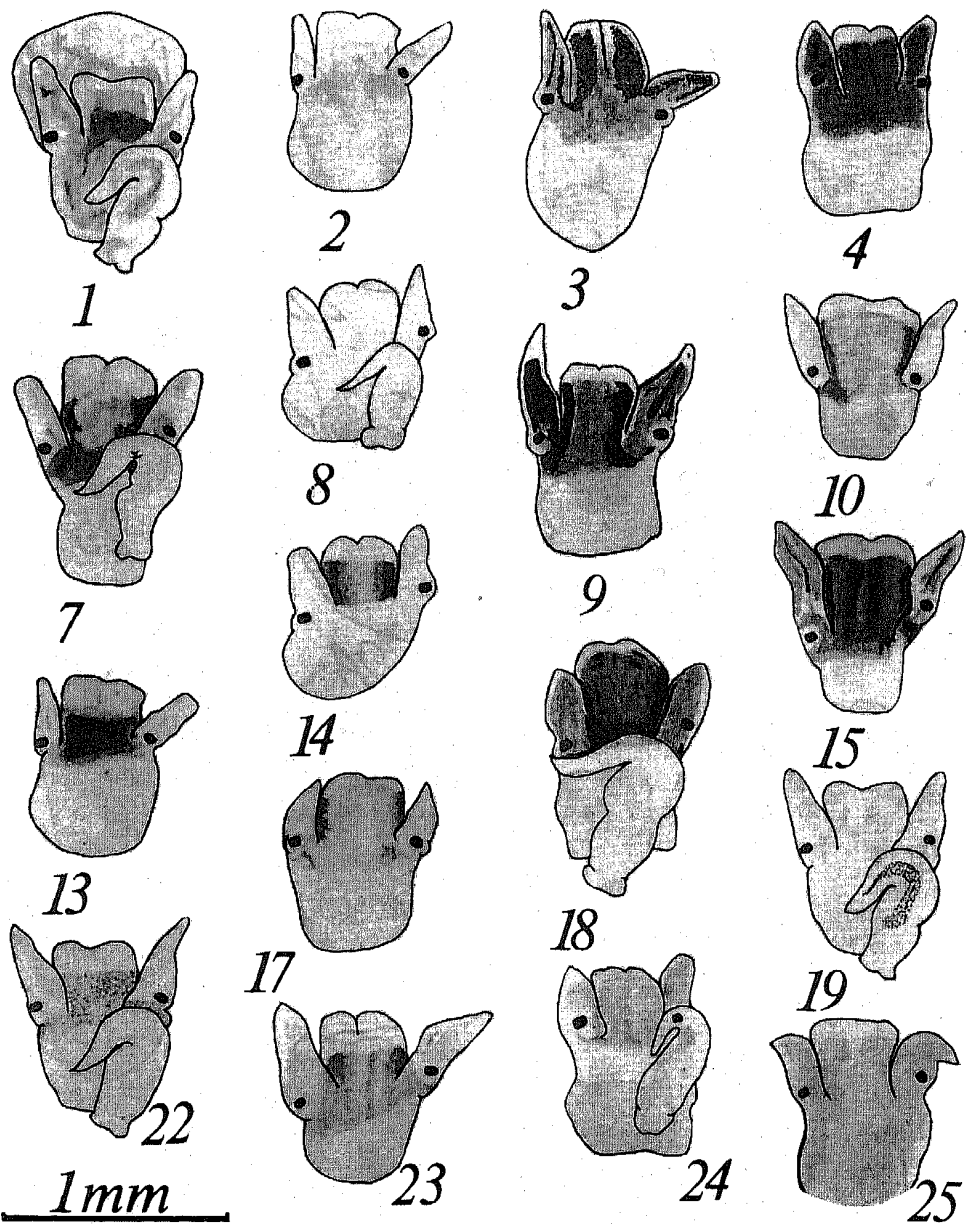
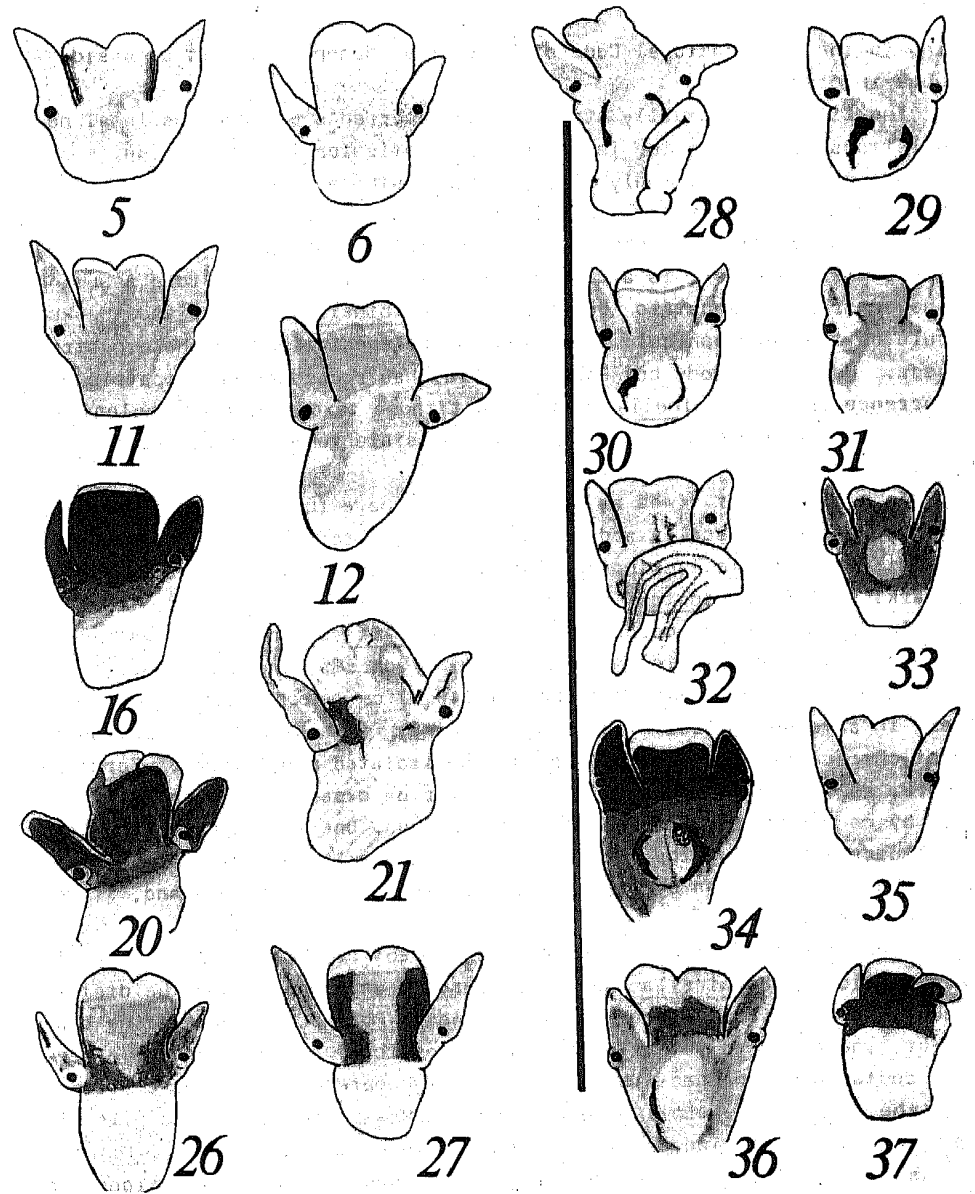


Fig. 11. Head pigmentations in *Bythinella*: 1 - 27 - *B. zyvionteki*: 2 - 6, 9 - 17, 20 - 21, 23, 25 - 27 - females; 1, 7 - 8, 18 - 19, 22, 24 - males; 1 - 2, 7, 13, 22 - Siedem Zródeł, Centuria tributary, Biała Przemsza Tributary; 8, 14, 17, 23 - Kwaśnik-Golczowice; 3, 9 - Mszana Dolna; 4, 10, 18, 24 - Zawoja-Składy, Babia Góra; 15 - Zawoja-Widły, spring, Babia Góra, typical form; 5, 11, 19, 25 - Zawoja-Widły, spring, Babia Góra, minute form;



6, 16, 20, 26 - Zawoja-Widły, spring area, Babia Góra, typical form; 12, 21, 27 - Krowiarki Pass, Babia Góra; 28 - 37 - *B. metarubra*: 28 and 32 - females; the others - females: 28 - 30 - Trzy Korony Mountain, Pieniny Mountains; 31 - 32, 34, 36 - Strążyska Valley, stream - beech forest, Tatra Mountains; 33 - 35 - spring in the middle of Lejowa Valley, Tatra Mountains; 37 - spring in the end of Lejowa Valley

ing to the International Code of Zoological Nomenclature is unconsiderable in practice.

The literature usually stresses the occurrence of numerous local populations as well as the isolation of particular localities (springs). It has not been until only recently that authors seem rather to abandon the concept: "a spring - a distinct group of phenotypes" and, instead, use the concept: "a catchment area - a distinct group of phenotypes": the latter, however, is a merely evolution of the same idea assuming the entirely allopatric occurrence of Bythinella species and the key rule of the geographical isolation in the speciation of these gastropods. Perhaps nobody but Radoman (1976) has recorded the sympatric occurrence of two Bythinella species, but those taxons were conchologically so much conspicuous that it was impossible to miss their differences.

In a couple of times at one station I have found the occurrence of two taxons anatomically and, in some cases, also conchologically markedly different while lacking any intermediate forms. For instance, at Krowiarki Pass B. zyvionteki cooccurs with B. cylindrica and in Strążyska Valley B. metarubra cooccurs with Bythinella sp. Moreover, as it is shown in the description of the following species, the geographic variation of a clinal character (Mayr 1974a,b) can be occasionally observed in some anatomical features; certainly this kind of variation is not characteristic of the group of the isolated populations. Furthermore, as I have mentioned in the chapter on expansion, such isolation is by no means either so complete or obvious. One can suppose, that the molluscs inhabiting the localities as stable in character as springs may be characterized by a very slow evolutionary progress and, then, speciation rate.

Thus, the theoretical bases of the concept of the entirely geographic speciation of Bythinella cannot be approved any longer, and the distribution of particular taxons of the genus in Poland contradicts the concept, and presents rather a complicate mosaic of ranges than the ordered contiguous monospecific ranges. It is remarkable that the character of the Bythinella shell, noted above, makes it impossible to give its objective description distinctive enough to compare with other authors. This, at least in some cases, may be a source of the allegations on conchologically distinct local populations.

Another source of these allegations, still in use, could be the insufficiency of the material. The figures included here (chosen from 426 pictures drawn by myself) show that most of the local populations are conchologically rather hardly distinct. It has to be noted that I



Fig. 12. Ctenidia and osphradia in *Bythinella* (1 - 4, 8 - 11, 14 - 15, 18 - 24, 30, 32, 35 - 36, 39, 43 - 45, 48, 50 - 51, 54 - ctenidium with osphradium; (the others - osphradium alone): 1 - 29 - *B. austriaca*: 1 - 2 - Kremsmünster, Oberösterreich, Austria, leg. L. Butot, females; 3 - 8 - Żelazno near Kłodzko: 3 - 4 and 6 - 7 - females, 5 and 8 - males; 9 - Strażyska Valley, stream, Tatra Mountains, a male; 10 - 14 - Ojców, Saspowska Valley: 10 - 12 and 14 - males, 13 - a female; 15 - 20 - Zygmunt Springs by Złoty Potok near Częstochowa: 15 - 17 and 20 - females, 18 - 19 - males; 21 - 29 - Mników Valley: 21, 24 - 25, 27 and 29 - females; 22 - 23, 26 and 28 - males; 30 - 44 - *B. cylindrica*: 30 - Ostre near Żywiec, a female; 31 - 32 - Żylica tribu-
 tary spring by Skrzyczne, females; 33 - 36 - Wisła-Malinka: 33 - a male, 34 - 36 - females; 37 - 39 - Lubomir Mountain at the side of Kobielnik: 37 - 38 - females, 39 - a male; 40 - 43 - Turbacz Mountain at the side of Koninki: 40 - 41 and 43 - males, 42 - a female; 44 - 45 - Ociemne, Pieniny Mountains, a female; 46 - 54 - *B. zywionteki*: 45 - 51 and 54 - Siedem Źródeł, Centuria tributary, Biała Przemsza tributary: 45, 48, 51 and 54 - males; 46 - 47 and 49 - 50 - females; 52 - 53 - Kwaśnik-Golczowice: 52 - a female, 53 - a male

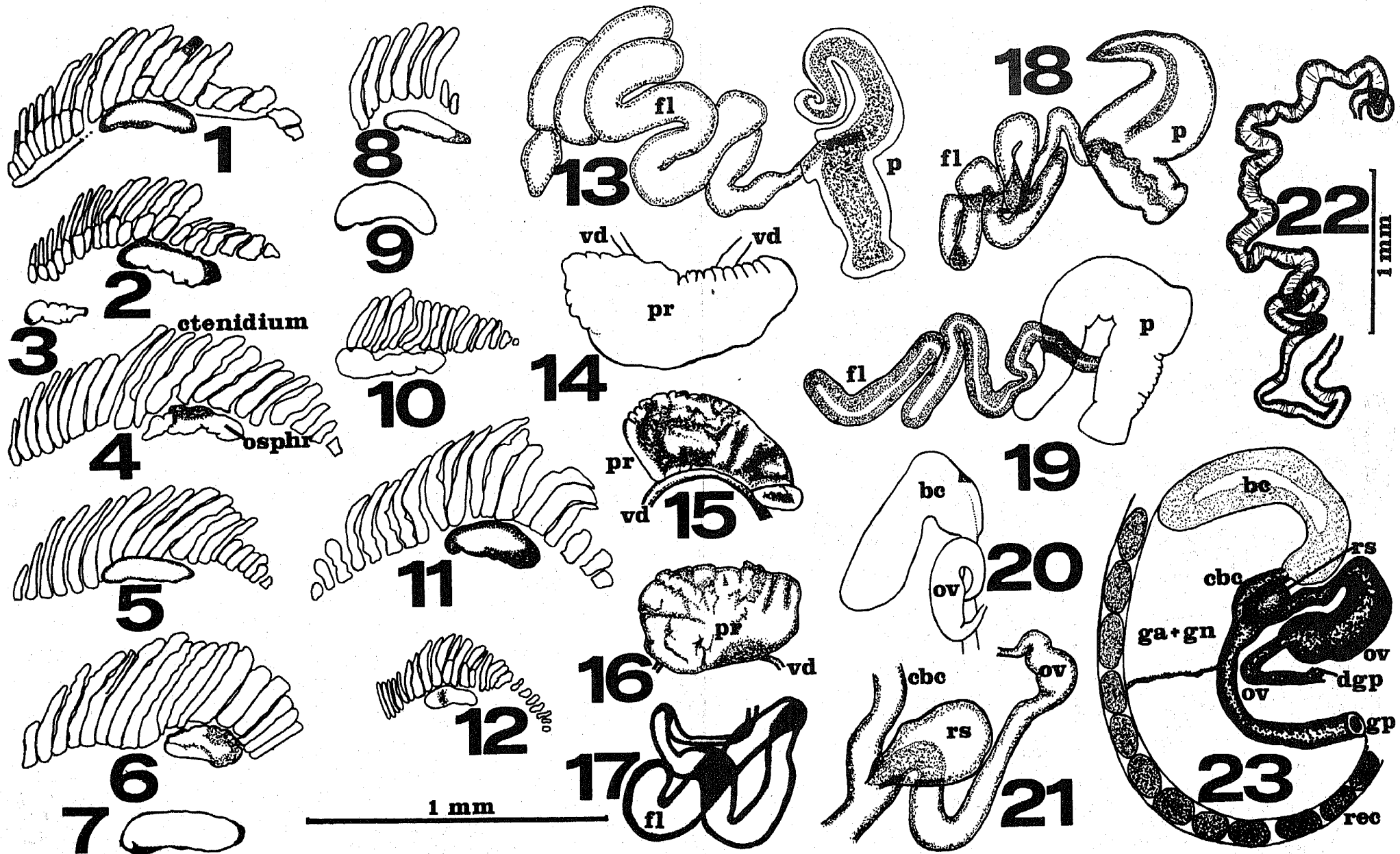


Fig. 13. 1 - 12 - ctenidia and osphradia in *Bythinella* (1 - 2, 4 - 6, 8, 10 - 12 - ctenidium with osphradium; 3, 7, 9 - osphradium alone): 1 - 9 - *B. zvyionteki*: 1 - 2 - Kwaśnik-Golczowice, males; 3 - 4 - Mszana Dolna, males; 5 - 6 - Zawoja-Składy, meadow stream, males; 7 - Zawoja-Widły, spring area, a male; 8 - 9 - Krowiarki Pass, Babia Góra: 8 - a female, 9 - a male; 10 - 11 - *B. metarubra*, Trzy Korony Mountain, Pieniny Mountains, females; 12 - *Bythinella* sp., Polana Pisana, Tatra Mountains, a female, 13 - *Bythinella* sp. penis with flagellum, Polana Pisana, Tatra Mountains; 14 - 18 - *B. zvyion*

teki: 14 - 16 - prostate: 14 - the outline, ventrally, Zawoja-Składy, Babia Góra; 15 - the same as 14, dorsally, another scale; 16 - ventrally, Zawoja-Widły, spring, Babia Góra; 17 - flagellum, Zawoja-Składy; 18 - penis with flagellum, Zawoja-Składy; 19 - 21 - *B. austriaca*: 19 - penis with flagellum, Zygmunt Springs by Żłoty Potok near Częstochowa; 20 - bursa copulatrix and thickened loop of oviduct, natural arrangement, receptaculum seminis covered with the loop, Mników Valley; 21 - loop of oviduct, receptaculum seminis and a fragment of the duct of bursa copulatrix, to show the arrangement, Kremsmünster, Austria; 22 - *B. zvyionteki*, vas deferens, Zawoja-Składy; 23 - the distal section of the female reproductive organs of *B. austriaca*, Zygmunt Springs, to show their structure in *Bythinella*

submit all the conchological types actually found, ignoring their frequencies since this is the only way to describe the whole variability ranges of all the characters. The interspecific differences are poorly marked and of a statistical character.

The wide variability with interspecific range-overlap concerns not only the shell but all the characters of Bythinella practically. Continuous as it is, it is grouped in several intervals for the majority of the features. Furthermore, there is not a single univocally decisive feature. To determine Bythinella means then both to study the anatomy and to consider an abundant material. In many cases it can be impossible to determine a species if a single specimen is concerned. Undoubtedly, such situation though hardly favoured by a zoologist is, unfortunately, a really existing one. In the revision of Polish Bythinella presented below I based throughoutly on the biological concept of species. This has led me to the description of the issue that is far from the Linnean model: "determination = systematics"; the divergence between the biologically existing units of the species level and the well morphologically defined, easily distinguishable groups of specimens is markedly notable in Bythinella.

The complex examination of the female reproductive organs (i.e. bursa copulatrix with its duct and receptaculum seminis), penis, flagellum, pigmentation, and in some cases also some other characters in at least several specimens from a given station would usually enable the certain determination of a species. To determine a species means here, practically, to find the most frequent variability intervals of at least two structures. The variability ranges determined in this manner and, last but not least, their reciprocal coexistence allow to determine a species for certainty.

Such an inconvenient and burdensome procedure is, what I would like to stress again, inevitable. All my studies indicate that this is the actual character of the interspecific differences within the genus Bythinella whose species exist as real biological units, but show very poorly marked morphological distinctness. The above is also confirmed by my studies on the differences in the ultrastructures of the shell and radula in B. micherdzinskii and B. zyvionteki examined so far, showing that these differences are not less significant than those between the species within the other prosobranch genera.

Beside of B. micherdzinskii described earlier (Falniowski 1980) the species distinguished in my studies cannot be related to any of the known from the literature and described only on the basis of shell examination. On the other hand, this has been my aim to produce as little

confusion in the nomenclature as possible. The occurrence of B. austriaca in Kremsmünster, Austria has been recorded in the literature many times. Ehrmann (1956) recorded B. austriaca subsp. ehrmanni from Żelazno in Kłodzko Basin. Thus I regarded as B. austriaca the specimens from Kremsmünster, similar to those from Żelazno and then I included the other similar populations to this species.

The specimens conchologically approximate to B. cylindrica, coming from the Danube at Vilshofen (Germany) then from "terra typica", are regarded here as belonging to this species and grouped together with the other similar populations from Poland under its name. I must point out that I cannot regard B. cylindrica defined in this way as only a geographic race of B. austriaca, what has been often approved by the majority of the authors recently. Here probably belongs (since the material consists of a single dry shell) the specimen from Budapest from Hazay's collection, i.e. from the locus typicus of B. hungarica. This is merely a typical specimen of B. cylindrica. However, at the station on Lubomir Mountain at the side of Kobielnik I have found some dozen of big, cylindrical specimens of Bythinella, closely corresponding to the descriptions of B. hungarica. They show neither anatomical nor pigmentation differences while comparing them with a typical B. cylindrica, so B. hungarica must be acknowledged as a mere conchological form of B. cylindrica.

The other three species cannot be in any possible way related to those described earlier. Two of them were then described as a new (Falniowski 1986c,d). The third one, though not less distinct, has been, in the time being, recorded only in the Tatra Mountains on a couple of localities close to each other, therefore as long as information on its distribution and variability has been completed it will be provisionally defined as: Bythinella sp.

In the time being the distribution of the particular species as partially known is presented in the form of a list of stations. It should be stressed that I mention not all the stations studied, but only those from which the material was both rich and fixed well enough to enable the certain determination of a species.

Another general remark concerns the dimensions of the penis of particular species given in the paper. The shape of the bi-armed penis of Bythinella makes the exact measurement of its entire length impossible. Hence, I acknowledge the length of the penis in its natural position i.e. unstraightened. Of course, such a measurement cannot be absolutely exact (various arrangement and degree of contraction of the arms) and is of a merely estimative quality, but the measurement of the artificially straightened penis would not be more representative.

1. The right arm of the penis (with the outlet of the flagellum) large, massive, very broad and bluntly terminated, while the left arm (with the outlet of the vas deferens) astonishingly short in relation to the right, narrow and sharply terminated one B. zyvionteki
- The right arm of the penis never so massive and always much less broad, terminated sharply or if at all blunted, and the difference between the arms breadth much less conspicuous 2
2. Bursa copulatrix proximally sharpened, distally (frequently considerably) broadened, the very short and narrow duct of bursa poorly distinguishable from the bursa itself, with no sharp demarcation Bythinella sp.
- Bursa copulatrix only exceptionally proximally sharpened, of another shape, the duct of bursa always longer and often broader and markedly distinguishable from the bursa itself, with a sharp demarcation 3
3. Penis moderately slender, the receptaculum seminis of a medium size or big, sac-shaped B. cylindrica
- Penis markedly slender, the receptaculum seminis small or if at all maximally of a medium size, almost spherical 4
4. Bursa copulatrix straight, the duct of bursa very long and narrow; shell minute, slender, columnar, whorls fairly convex and numerous, divided by a shallow suture B. metarubra
- Bursa copulatrix only exceptionally straight, the duct of bursa always less long and broader; the shell usually of another shape, but if similar, then always much bigger 5
5. Penis with the left arm usually longer, while the right thicker (or the arms of similar thickness), the left arm tip often almost spherical, the duct of bursa rather broad, receptaculum seminis small or of a medium size B. austriaca
- Penis with the right arm usually longer, while the left thicker (not markedly), the left arm tip almost always sharp, the duct of bursa less thick, receptaculum seminis may be small or of a medium size but mostly extremely small B. micherdzinskii

Note: this key, due to a great variability and slight interspecific differences within Bythinella, enables to determine no more than the majority of specimens and each time the determination has to be compared thoroughly with the description of a given species.

4. Bythinella austriaca (Frauenfeld, 1856)

A - Paludinella austriaca Frauenfeld, 1856
Bythinella austriaca subsp. ehrmanni Pax, 1938

B - The shell (Figs 14,1 - 14,36 and 15,1 - 15,39) ovate or more or less cylindrically-ovate, rather slender; its slenderness widely variable. Whorls poorly convex, flattened, divided by a moderately deep suture rather sloped to the columella. The whorl number at different stations: maximum: $4 \frac{1}{2}$ - $5 \frac{1}{2}$, usually: 5; mean: $4 \frac{1}{3}$ - 5, usually: $4 \frac{1}{2}$. The greatest variability of the mean whorl number among the Polish Bythinella, while the variability range of the maximum number narrower than in B. cylindrica. The highest whorl number in the specimens from Żelazno.

The apex moderately sharp, sometimes flattened or slantingly truncate. The aperture oval in outline, relatively slightly variable, with a moderately marked angle upward at right, the mouth poorly protruded. The peristome nearly always continuous, parietal lip always present, marked poorly to moderately, only sometimes - strongly. The outer lip absent. The umbilicus in the form of a rather wide and moderately deep gutter along the lower section of the twisted parietal lip.

Shell dimensions at the stations: height: 1.85 - 3.50, mean: 2.3 - 3.1, usually: 2.5 - 2.7; breadth: 1.2 - 2.2, mean: 1.4 - 1.8, usually: about 1.7. The biggest shells were characteristic of the specimens from Żelazno, the smallest from Krzeszowice, though at the both stations the shell proportions were similar to those at the other localities. The shell colour creamy yellow to moderately dark brown, usually yellowishbrown.

C - f. ehmanni Pax - the shell very high, over 3, slender, roller-shaped (Figs 14,10 - 14,23), the apex slantingly truncate (that is neither marked so well nor so much characteristic of this form as the literature suggests); occurred only at one station in Poland, near Żelazno (at the foot of the Krowiarki Chain) near Kłodzko (by the road to Bystrzyca Kłodzka) besides a station in Czechoslovakia (Javornik in Trave Valley), the other stations no longer exist (Wiktor 1964); often regarded as a subspecies and a glacial relict. Thorough analyses of the features of the specimens from Żelazno point out that the specimens are not anatomically distinct and that the actually existing and constant differences are limited only to the larger shell size. The latter does not support the recognition of the subspecies rank of the form and it necessitates the regard of f. ehmanni as a mere local conchological form which may be a result of the geographic isolation, though its size may be related to the habitat fitness, as well.

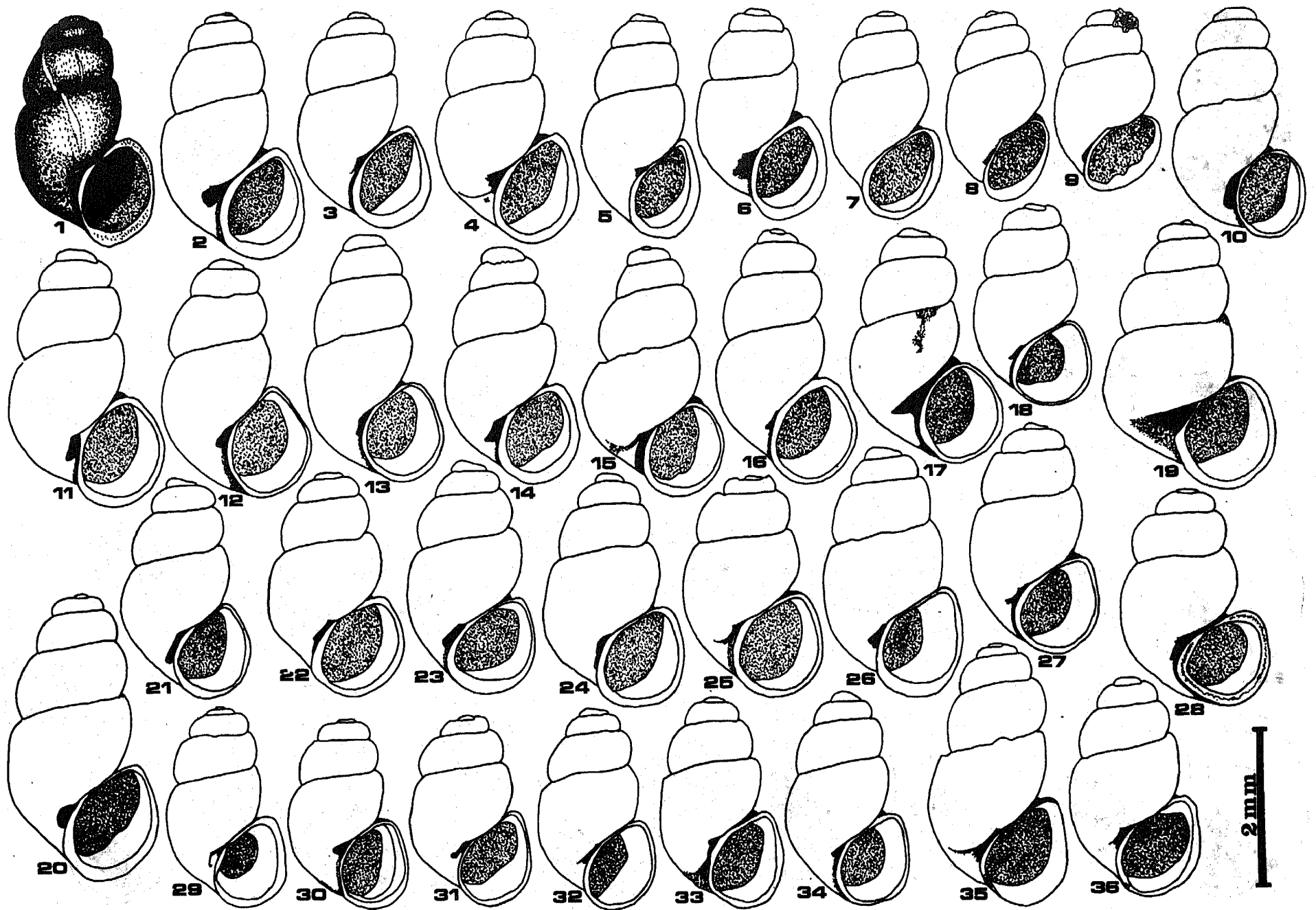


Fig. 14. Shells of *Bythinella austriaca*: 1 - 9 - Kremsmünster, Oberösterreich, Austria, leg. L. Butot (8 - 9 - iuv.); 10 - 23 - Żelazno near Kłodzko (10 and 20 1/2 whorls, 11 - 16 and 19 - over 5 whorls); 24 - 28 - Strážyska Valley, stream, Tatra Mountains (24 - 5 whorls); 29 - 36 - Przysłop Komiński, Tatra Mountains (35 - 5 1/4 whorls)

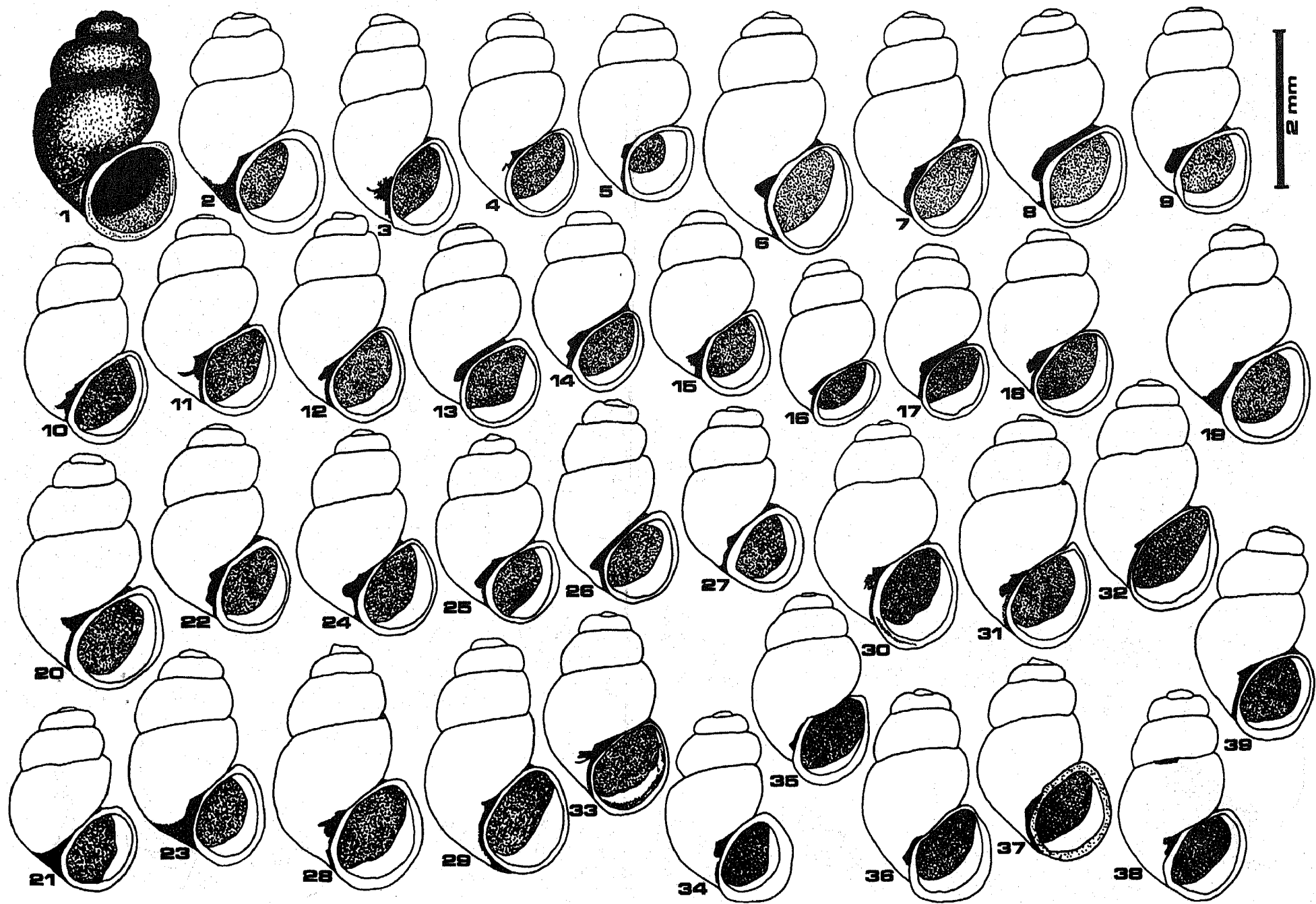


Fig. 15. Shells of *Bythinella austriaca*: 1 - 2 - Strażyska Valley, stream, Tatra Mountains; 3 - Babia Góra; 4 - 5 - Jamki Gorge, Ojców; 6 - 18 - Saszowska Valley, Ojców (6 - the biggest specimen at the station, 4 1/2 whorls); 19 - 27 - Zygmunt

Springs by Żłoty Potok near Częstochowa (20 - the biggest specimen at the station, 4 2/5 whorls, 21 - 4 3/4 whorls); 28 - 39 - Mników Valley (28 - 29 - over 5 whorls)

D - The head pigmentation (Figs 9,1 - 9,29) variable, ranging from the complete lack of pigment, through the pattern of different intensity, to the entire head black. The pigmented belt varying from quite narrow to rather wide or to quite wide occurring rarely (Figs 9,10; 9,14). The "spottiness" (Figs 9,6 - 9,7; 9,9; 9,11; 9,18 - 9,19; 9,25; 9,27), that is the occurrence of irregular, often numerous intensively pigmented spots with the background of a rather delicate pigmentation, common. Posteriorly to the snout there is not an unpigmented spot surrounded by a pigment of various intensity. Frequent (in about 50% of specimens) twin semilunar spots of intensive pigmentation more or less symmetrically arranged posteriorly to the snout (Figs 9,5; 9,12 - 9,13; 9,22 - 9,27).

E - The ctenidium quite variable (Figs 12,1 - 12,4; 12,8 - 12,11; 12,14 - 12,15; 12,18 - 12,24), generally the longest among the Polish Bythinella, elongate, with relatively short and, often, bent lamellae, listed below with the lamellae number:

Station	Males	Females
1. Kremsdünster, Austria	17 - 21 mean 19.0	17 - 19 mean 18.0
2. Żelazno near Kłodzko	23 - 29 mean 25.3	24 - 28 mean 18.0
3. Strążyska Valley, str.	15 - 19 mean 16.7	15 - 18 mean 16.3
4. Przysłop Kominiarski	- mean 21.0	19 - 21 mean 20.0
5. Saspowska Valley	20 - 22 mean 21.3	18 - 23 mean 20.8
6. Zygmunt Springs	21 - 23 mean 22.0	21 - 25 mean 22.5
7. Mnikowska Valley	16 - 23 mean 20.0	19 - 23 mean 20.7

F - The osphradium (Figs 12,1 - 12,29) usually oval, straight or slightly arched, rarely irregular (Figs 12,2 and 12,9). A thinner fold visible as the complete or, less often, partial darker border of a more or less constant width. The variability considerable, though the smallest among the Polish Bythinella.

H - The flagellum (fig. 13,19) of a thickness varying within a wide range, but generally the thickest among the Polish Bythinella; moderately long (about 0.9 - 1.8 of the length of the penis measured along its curvature from tip to tip).

I - The penis (Figs 16,1 - 16,36 and 17,1 - 17,20) usually very slim, with the left arm longer, sometimes considerably, and the right one only slightly thicker than the left one or both of similar thickness. The tip of the left arm almost spherically swollen, in the other Polish Bythinella species it is not so often and distinctly marked. The terminal section of the right arm usually distinguish-

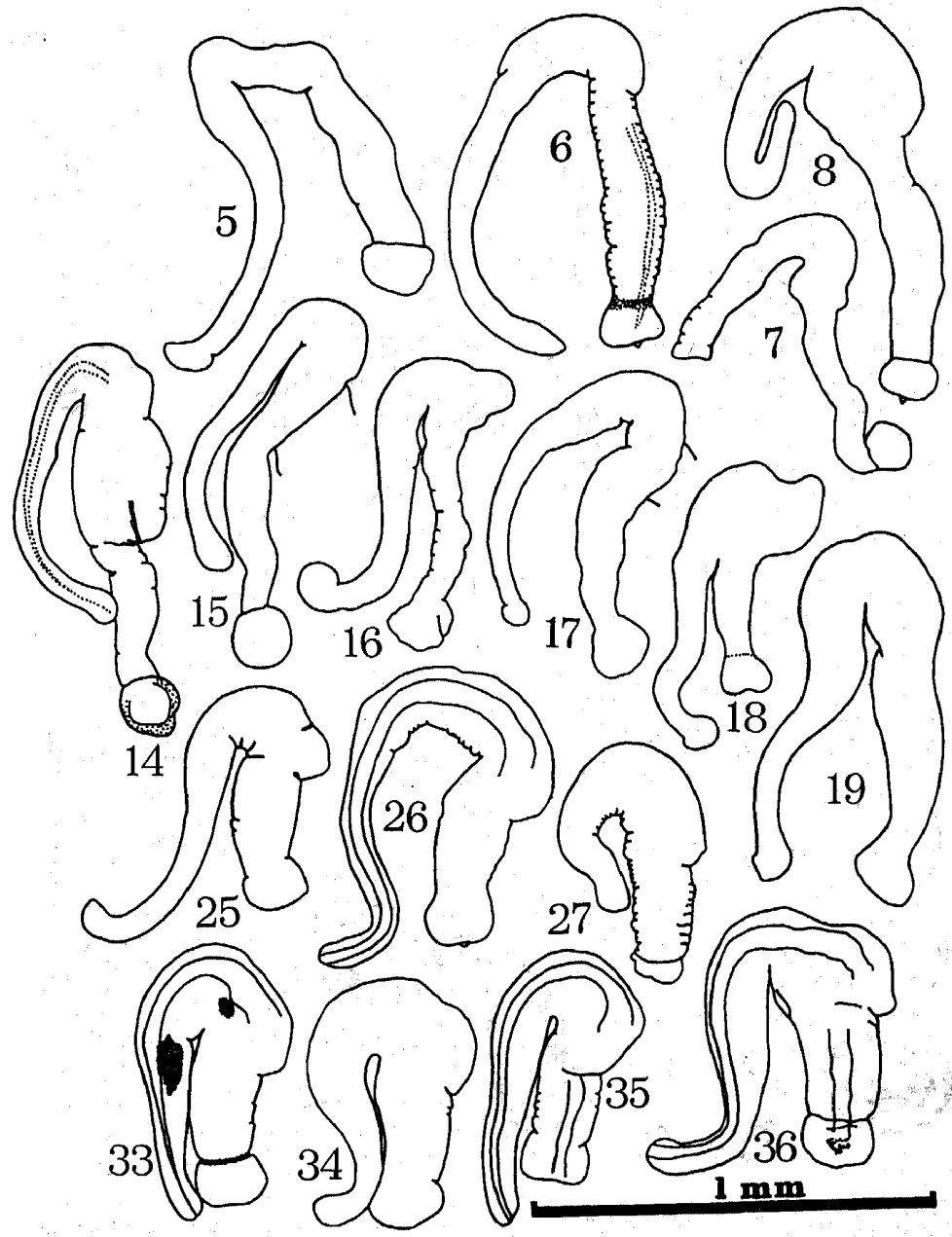
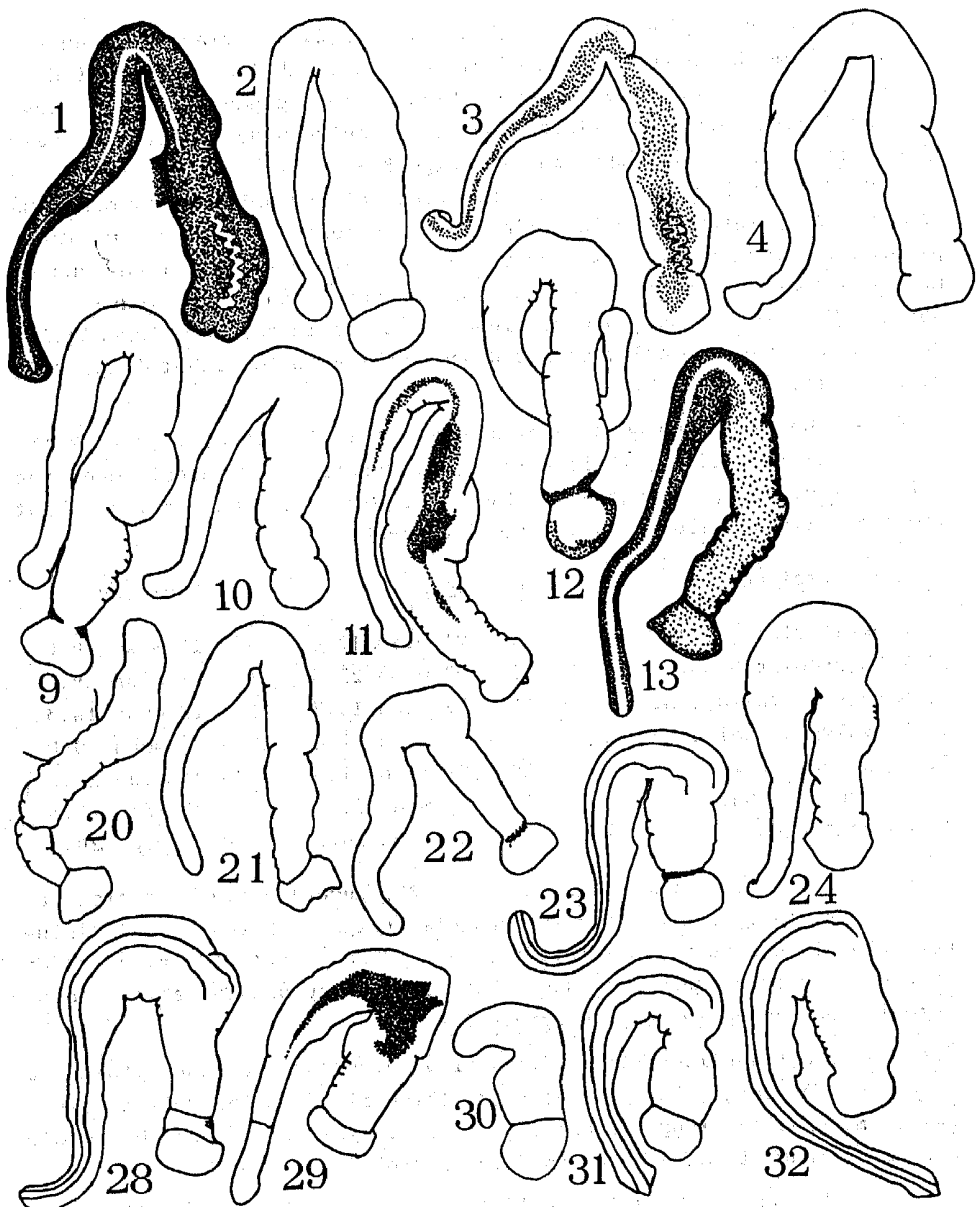


Fig. 16. Penes of *Bythinella austriaca*: 1 - 5 - Kremsmünster, Oberösterreich, Austria, leg. L. Butot; 6 - 15 - Żelazno near Kłodzko; 16 - 19 - Strążyska Valley, stream, Tatra Mountains; 20 - 22 - Przysłop Kominiarski,

Tatra Mountains; 23 - 32 - Sąspowska Valley, Ojców; 33 - 36 - Zygmunt Springs by Złoty Potok near Częstochowa

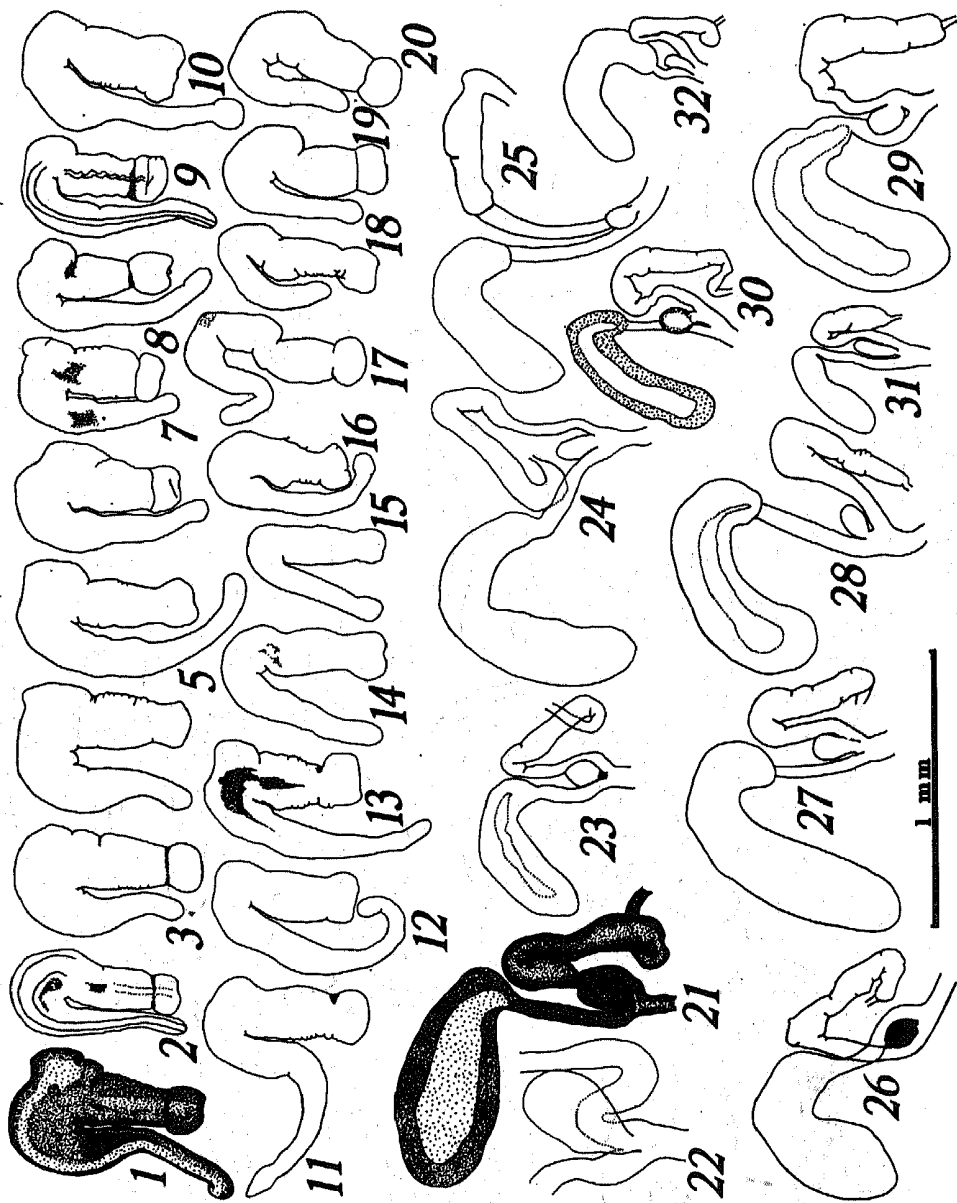


Fig. 17. *Bythinella austriaca*: 1 - 20 - penes: 1 - 5 - Zygmont Springs by Złoty Potok near Częstochowa; 6 - 20 - Mników Valley; 21 - 32 - loop of oviduct, receptaculum seminis and bursa copulatrix; 21 - 23 - Kremsmünster, Oberösterreich, Austria, leg. L. Butot; 24 - 29 - Żelazno near Kłodzko; 30 - 31 - Przysłop Kominiarski, Tatra Mountains; 32 - Sąspowska Valley, Ojców

able. The canals inside the penis (i.e. the terminal sections of the vas deferens and flagellum) best and mostly visible while compared with the other Polish *Bythinella*.

The penis is the biggest among the Polish *Bythinella*. The mean length values: Kremsmünster, Austria: 0.92; Żelazno: 1.01; Strążyska Valley, a stream: 0.86; Przysłop Kominiarski: 0.78; Sąspowska Valley: 0.77; Zygmont Springs: 0.74; Mników Valley: 0.70.

As the pictures show the penes of the specimens from Żelazno and from most of the stations in the Tatra Mountains are, practically, the same as those of the specimens from Austria. However, the penes of the gastropods from Jura (Mników Valley, Sąspowska Valley, Zygmont Springs) are somewhat different: the right arm is broader and in general the penis habitus variability tends, to some extent, towards that of *B. cylindrica*. It seems to result from the location of those stations on the periphery of the genus range, or even within the isolated enclave in fact, far northward from the main part of the range. This kind of geographic isolates are in several cases extremely distinct in respect of some characters, sometimes to the extent that makes the decision on their systematic position considerably difficult.

J - The female reproductive organs (Fig. 13,23) are considerably variable (Figs 17,21 - 17,32 and 18,1 - 18,16). The bursa copulatrix nearly always with a markedly distinguishable duct. Its shape covers the whole variability range: usually U-shaped, less often: J-shaped, rarely: arched or straight. Its proximal end sharpened only exceptionally. The duct of bursa rather broad, similarly broad as the oviduct reaching the receptaculum seminis. The length of the duct variable within a wide range, but generally moderate. The receptaculum almost spherical, small or of a medium size.

Like the penis, also the bursa shows the shape variability of geographic character. The bursa of the specimens from Kremsmünster J-shaped, rarely approximate to U-shaped; in Żelazno the gastropods with the U-shaped bursa rather common; the bursa of the specimens from Jura Krakowsko-Częstochowska usually U-shaped and the other shapes occurring occasionally. As in the respect of the penis, this corresponds probably to the distinctness of the geographic isolates occurring on the range peripheries. Moreover, it should be noted that while the penis of these *B. austriaca* to some extent corresponds to the typical of *B. cylindrica*, the variability of bursa copulatrix on the contrary shows opposite tendencies.

- K - 1. Kremsmünster, Oberösterreich, Austria, leg. L. Butot.
2. Żelazno near Kłodzko, the Sudetes Mountains, a large, troughed

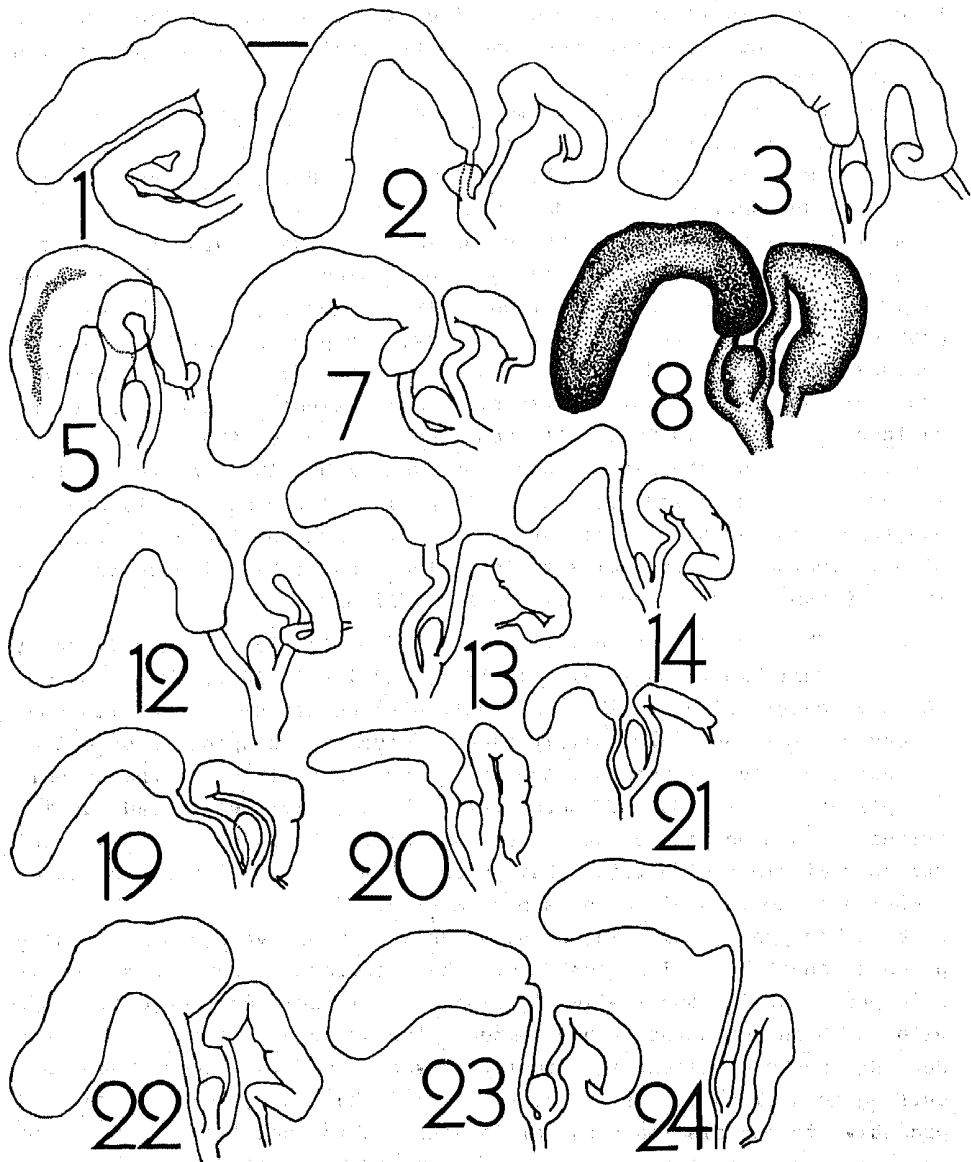
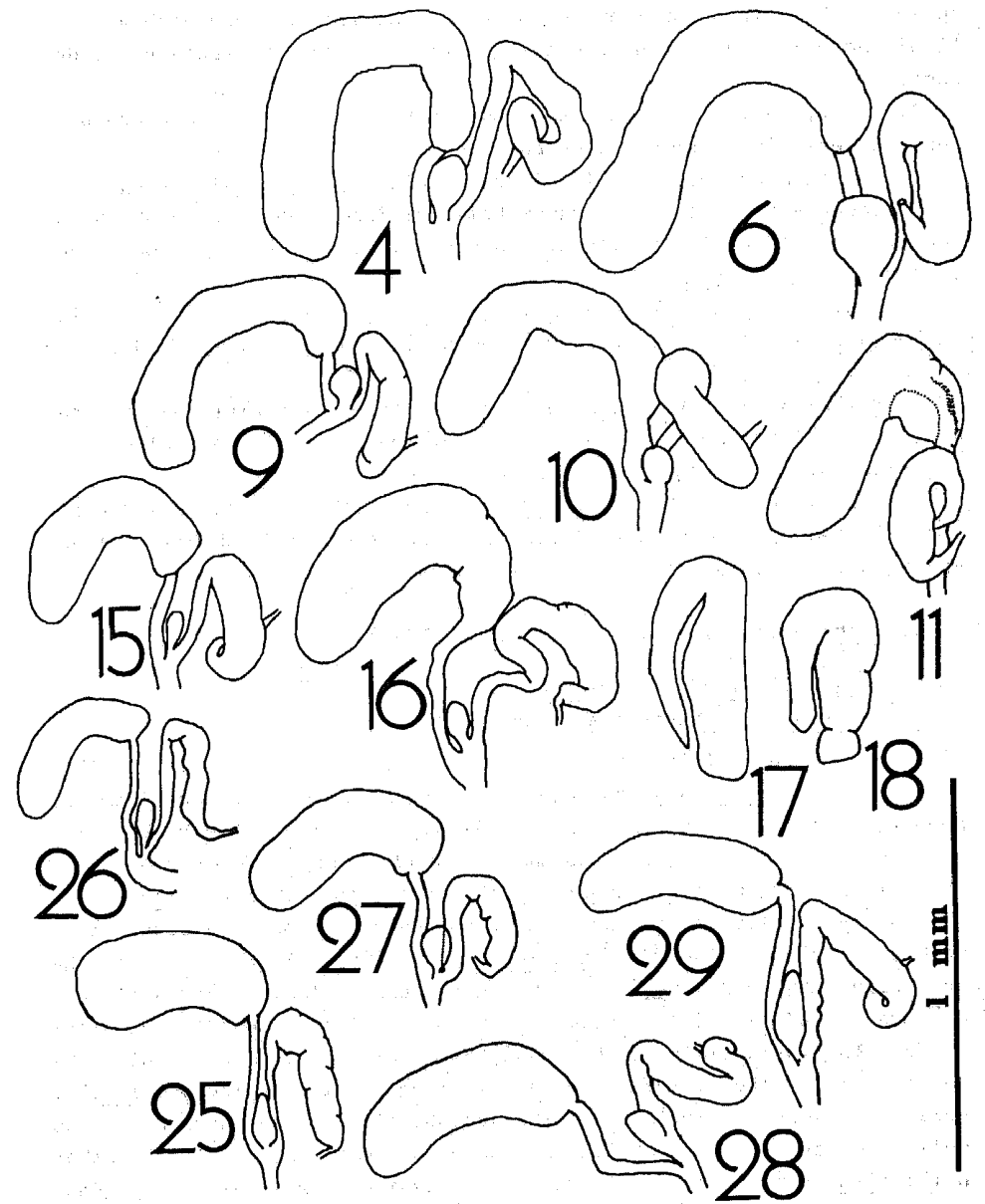


Fig. 18. 1 - 16 - *Bythinella austriaca*, loop of oviduct, receptaculum seminis and bursa copulatrix: 1 - 5 - Saspowska Valley, Ujców (1 - natural arrangement; 2 - the same specimen, arranged to show the structure, like the others); 6 - 10 - Zygmont Springs by Złoty Potok near Częstochowa; 11 - 16 - Mników Valley (11 - natural arrangement); 17 - 29 - *B. cylindrica*: 17 - 18 - penes, Krowiarki Pass, Babia Góra; 19 - 29 - loop of ovi-



duct, receptaculum seminis and bursa copulatrix: 19 - 21 - Żylica tributary spring by Skrzyczne (21 - iuv.); 22 - 25 - Lubomir Mountain at the side of Kobielnik; 26 - Ociemne, Pieniny Mountains; 27 - 29 - Turbacz Mountain at the side of Koninki

spring with a strong outflow of water percolating through rich vegetation: both the submerged and lower parts of stems and roots of meadow weeds.

3. Strążyska Valley, the Tatra Mountains, a stream: the edges of a small stream, in mosses on limestone rocks.

4. Przysłop Kominiarski, the Tatra Mountains, a typical spring.

5. Sąpowska Valley, The Ojców National Park, Jura Krakowsko-Częstochowska Upland, a spring of a medium size, on the limestone substrate.

6. Zygmunt Springs (Źródła Zygmunta), near Złoty Potok near Częstochowa, Jura Krakowsko-Częstochowska Upland, a complex of small Jurassic springs.

7. Mnikowska Valley, Garb Tęczyński Hills, the vicinities of Kraków, a small spring of a poor water outflow and rich vegetation in a limestone area, at the bottom of the valley.

This list suggests that B. austriaca is rather characteristic for typical springs, flowing out from limestone rocks and inhabits neither spring areas nor fallen leaves on the stream edges.

5. Bythinella cylindrica (Frauenfeld, 1856)

A - Paludinella cylindrica Frauenfeld, 1856
Bythinella hungarica Hazay, 1881

B - The shell (Figs 19,1 - 19,42 and 20,1 - 20,39) similar to that of B. austriaca but generally less slim (the exception: f. hungarica from Lubomir Mountain). As well as in B. austriaca the whorl growth rather regular and the body whorl poorly swollen; its height a little less than in B. austriaca (the exception: f. hungarica). The whorls usually less flattened, rather poorly convex but the suture less marked (the exception: f. hungarica) and rather less sloped to the columella than in B. austriaca. The whorl number at different stations: maximum: $4 \frac{1}{3}$ - $5 \frac{2}{3}$, usually: 5; mean: $4 \frac{1}{3}$ - $4 \frac{3}{4}$, usually: $4 \frac{1}{3}$. The variability of the mean whorl number is slight, while the variability of the maximum - the greatest among the Polish Bythinella. However, it is noteworthy that the variability of the whorl number as well as of the other conchological features in comparison to the other Bythinella seems quite low in the common typical form whereas the general variability range is made relatively wider by the uncommon, turreted f. hungarica considerably different from the typical form.

The apex, unlike in B. austriaca, usually flat, the aperture outline more variable: the distinctness of the angle ranging from a better marking to absentness, the mouth usually more protruded and the parietal

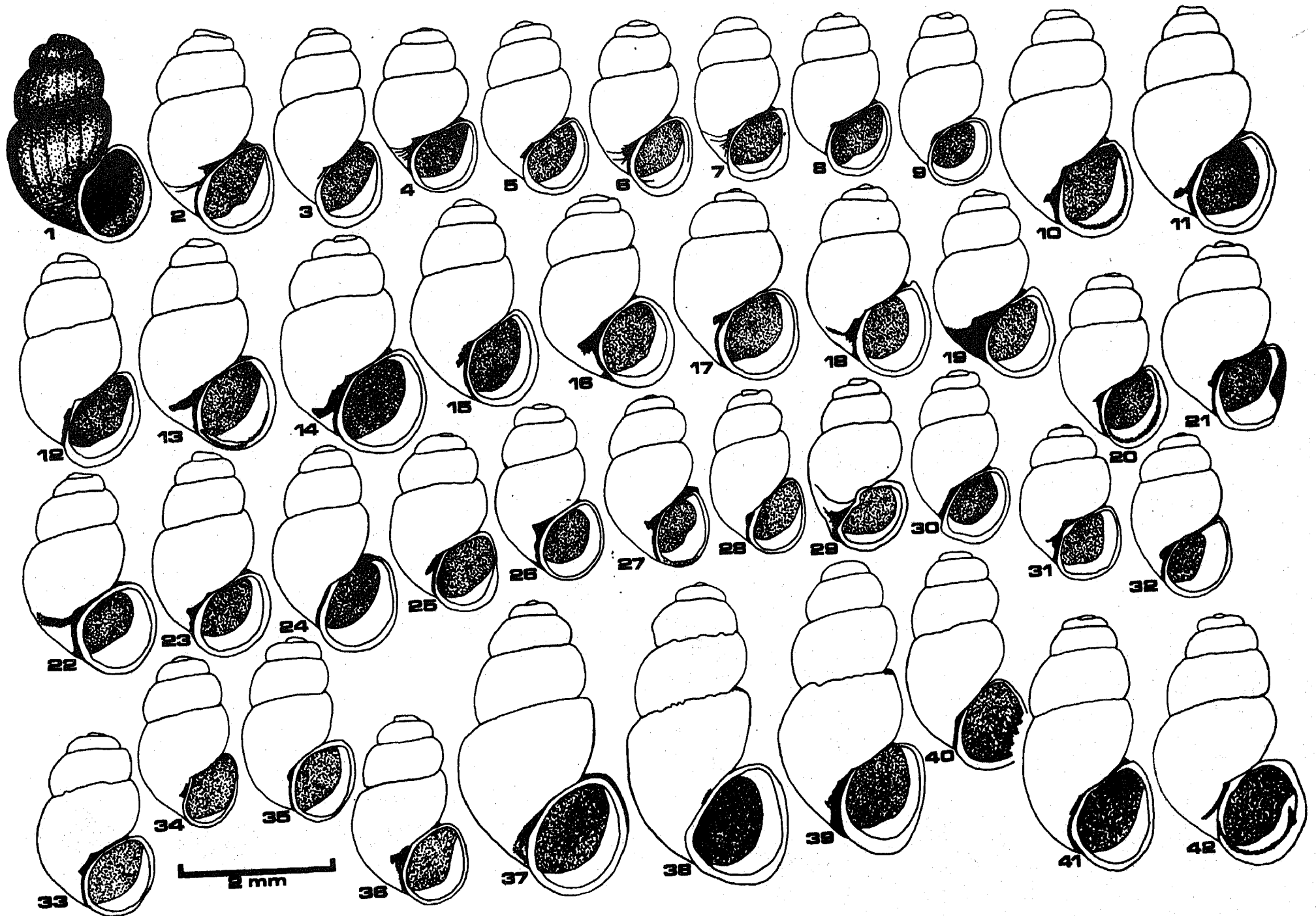


Fig. 19. Shells of *Bythinella cylindrica*: 1 - 8 - Danube River at Vilshofen, Bayern, Germany, leg. L. Butot (1 - 5 whorls, 2 - 5 2/3 whorls); 9 - "*B. hungarica*", Budapest, ex coll. Hazay; 10 - 21 - Ostre near Żywiec (10 - 11 - 4 3/4 whorls; 12 - iuv., 4 1/2 whorls); 22 - 32 - Wisła-Malinka; 33 - 36 - Żylica tributary spring by Skrzysz-
 ne; 37 - 42 - Lubomir Mountain at the side of Kobielnik (37 - 39 - about 5 1/4 whorls)

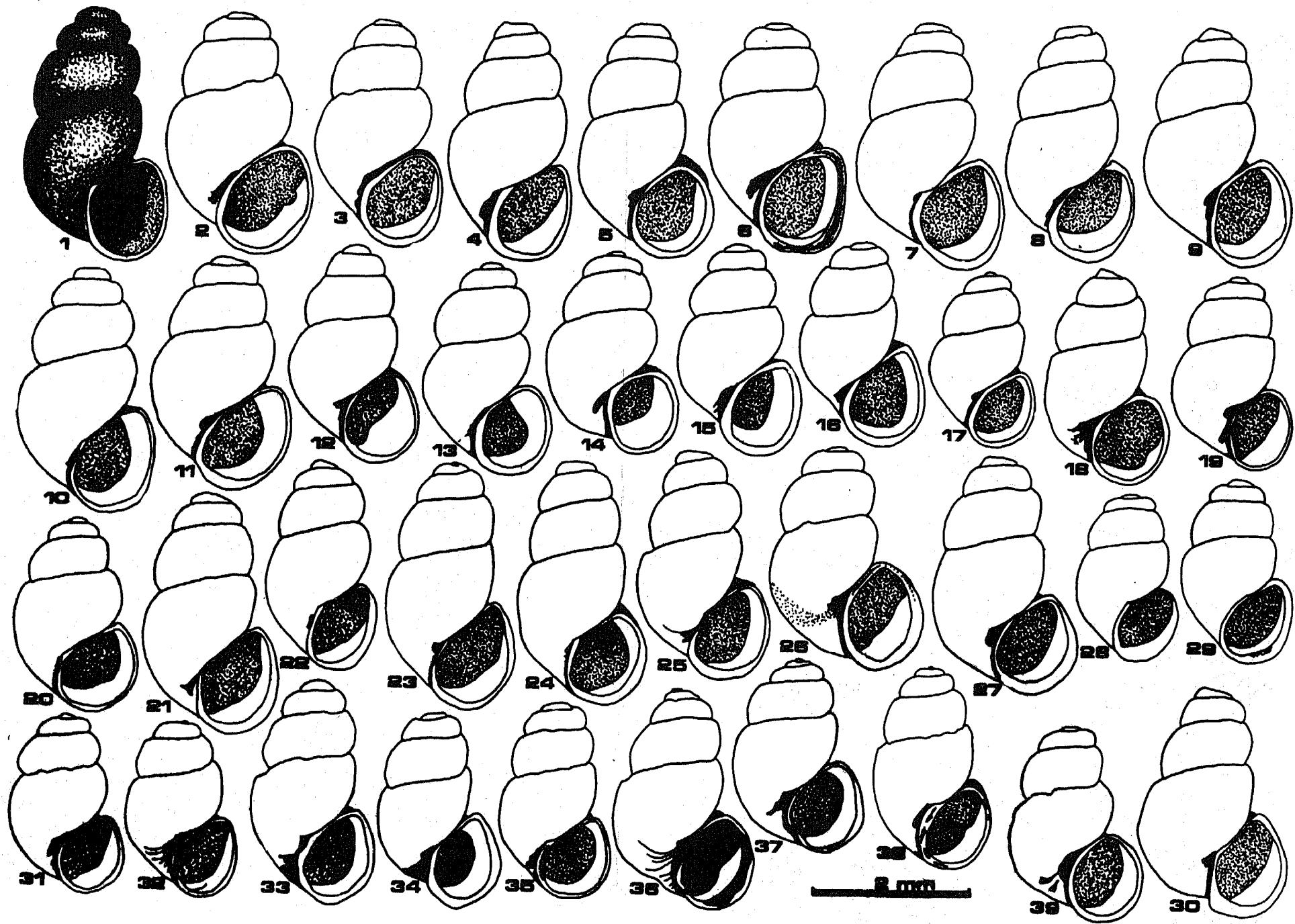


Fig. 20. Shells of *Bythinella cylindrica*: 1 - 6 - Lubomir Mountain at the side of Kobielnik (6 - strongly thickened outer lip); 7 - 20 - Turbacz Mountain at the side of Koninki (7 - 8 - over 5 whorls); 21 - 22 - spring by Irzy Korony Mountain, Sobozański Gorge, Pieniny Mountains; 23 - 30 - Ociemne, Pieniny Mountains; 31 - 39 - Mała Łąka Valley, Tatra Mountains

lip often less marked (not always present). The peristome not always continuous. The umbilicus quite variable, sometimes absent.

The shell dimensions at the stations: height: 2.0 - 3.9, mean: 2.2 - 3.2, usually: 2.4 - 2.7; breadth: 1.25 - 2.15, mean: 1.4 - 1.8, usually: 1.60 - 1.65. The biggest shells, being in general the biggest of Bythinella in my collection, came from the station on Lubomir. The shell colour like in B. austriaca.

C - f. hungarica Hazay - the shell cylindrical and slim, over 3 high, whorls 5 1/2 or more, growing less regularly, the height of the body whorl of about 1/2 of the shell height; some records of its occurrence in Poland, mostly the Tatra Mountains; I found it at only one station on Lubomir Mountain at the side of Kobielnik. It shows distinctness of neither the anatomy nor the morphology of soft parts, therefore it can be regarded as nothing but a conchological form of B. cylindrica occurring possibly in some particular conditions. It is noteworthy that the forms of a similar shell habitus are found also among other Polish Bythinella.

D - The head pigmentation (Figs 10,1 - 10,21) varying from very delicate to entirely black but usually not quite intensive or very delicate, sometimes no pigmentation (more often in males); even with a poor pigmentation the belt of pigment wide: wider than in B. austriaca. The "spottiness" considerably rarer than in that species (Figs 10,6 and 10,19). The borders of areas of various intensity pigmentation often diluted (shaded). Posteriorly to the snout sometimes an unpigmented spot surrounded by pigment (Figs 10,2; 10,17; 10,21) while in B. austriaca it is present very exceptionally and never fully marked. The twin semilunar spots of intensive pigmentation (Figs 10,3; 19,5; 10,7; 10,16) posteriorly to the snout rarer than in B. austriaca.

E - The ctenidium (Figs 12,30; 12,32; 12,35 - 12,36; 12,39 and 12,43 - 12,44) variable like in B. austriaca, usually shorter and less elongate with the lamellae of similar length but less commonly bent, listed below with the lamellae number:

Station	Males	Females
1. Danube at Vilshofen	- mean	- mean 23.0
2. Ostre near Żywiec	- mean 18.0	16 - 24 mean 20.5
3. Wisła-Malinka	12 - 17 mean 15.0	13 - 17 mean 15.4
4. Skrzyczne	14 - 18 mean 16.0	13 - 19 mean 16.7
5. Lubomir	24 - 28 mean 26.0	21 - 28 mean 24.3
6. Turbacz	16 - 22 mean 19.7	15 - 27 mean 23.4

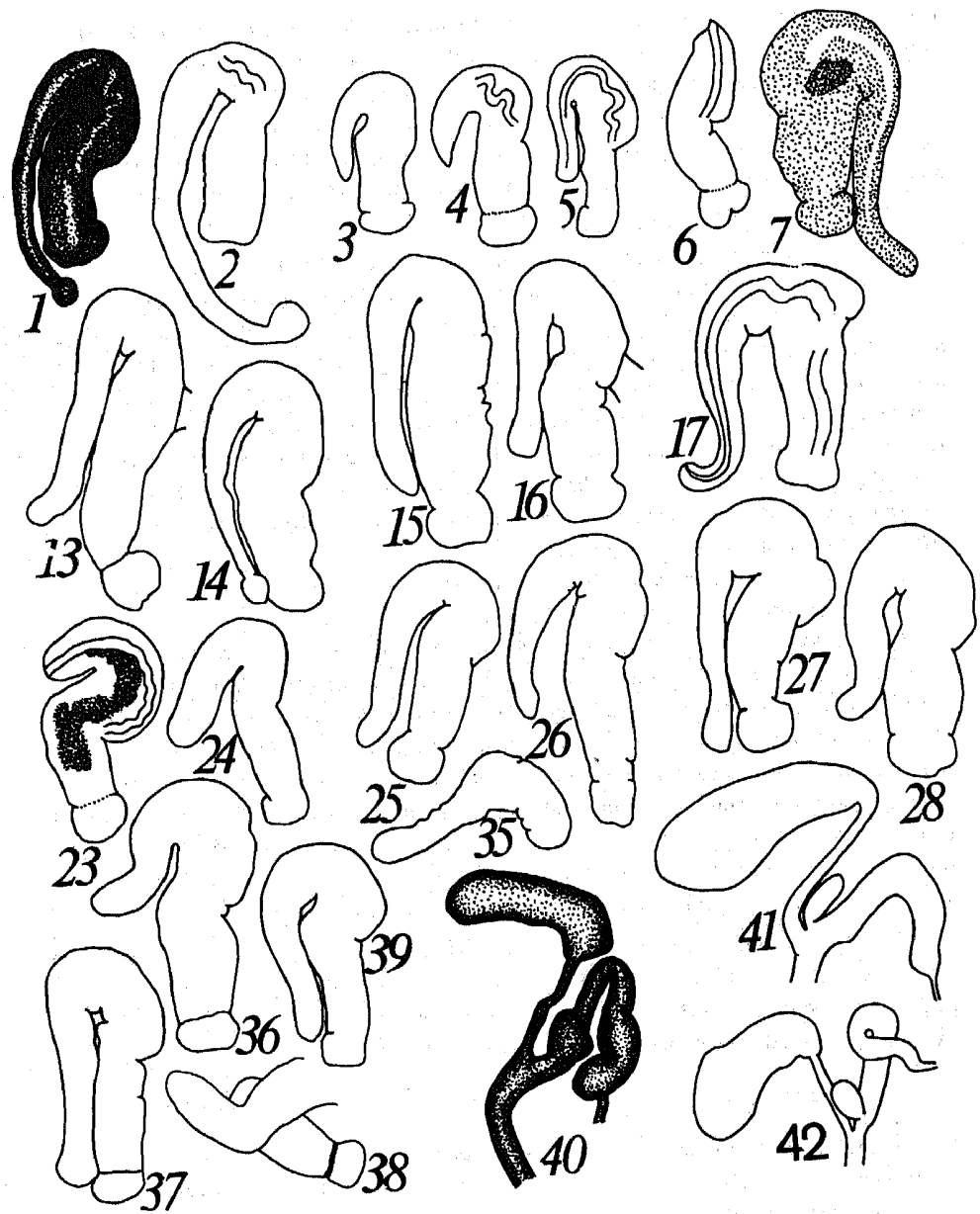
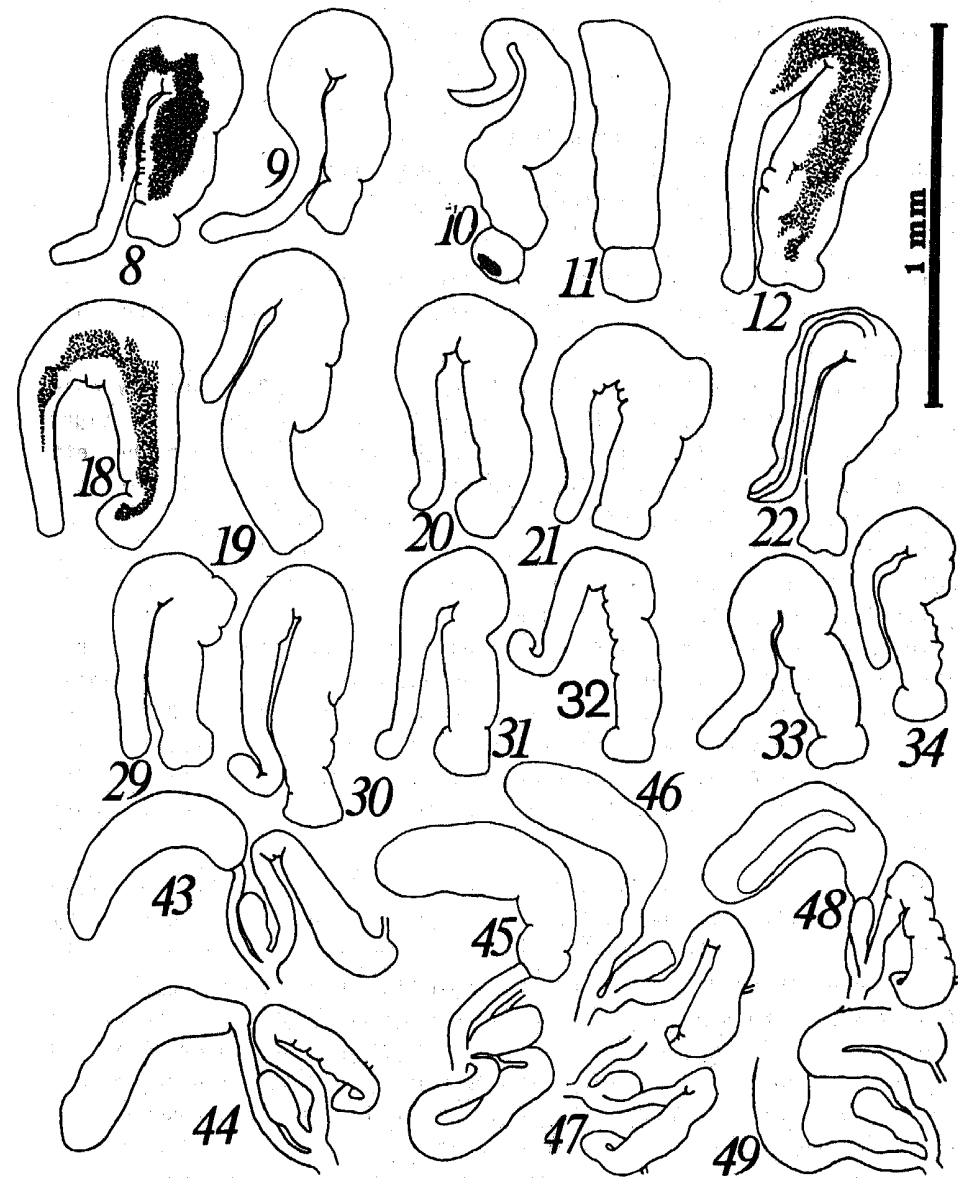


Fig. 21. *Bythinella cylindrica*: 1 - 39 - penes (7 - ventrally, the others - dorsally): 1 - 6 - Danube River at Vilshofen, Bayern, Germany, leg. L. Butot; 7 - 16 - Ostre near Żywiec; 17 - 21 - Wisła-Malinka; 22 - Żylica tributary spring by Skrzyczne; 23 - 27 - Lubomir Mountain at the side of Kobielnik; 28 - 35 - Turbacz Mountain at the side of Koninki (35 - a spe-



cimen very strongly infected with larval trematodes); 36 - Ociemne, Pieńiny Mountains; 37 - 39 - Mała Łąka Valley, Tatra Mountains; 40 - 42 - loop of oviduct, receptaculum seminis and bursa copulatrix; 40 - 42 - Danube River at Vilshofen, Bayern, Germany, leg L. Butot; 43 - 44 - Ostre near Żywiec; 45 - 49 - Wisła-Malinka (47 and 49 - a fragment)

7. Near Ociemne, Pieniny	-	mean 17.0	-	mean 14.0
8. Mała Łąka Valley	14 - 22	mean 17.3	14 - 18	mean 16.0
9. Krowiarki Pass	-	mean 14.0	14 - 17	mean 15.2

F - The osphradium (Figs 12,30 - 12,44) more variable than in B. austriaca, often much irregular in shape, sometimes with large notches, arched less often than in B. austriaca. The darker border rarely present, if so irregular and making the distinct lobes of the osphradium (Figs 12,35 and 12,43).

H - The flagellum thinner (its thickness slightly variable) and generally shorter (0.63 - 1.52 of the penis length) than in B. austriaca.

I - The penis (Figs 18,17 - 18,18 and 21,1 - 21,39) generally considerably not so slim as in B. austriaca, and usually the right but not the left arm is longer. The right arm thicker than the left one; the difference in arms thickness marked much more distinctly than in B. austriaca. The tip of the left arm usually blunt and only exceptionally semispherically swollen. The tip of the right arm usually undistinguishable, the canals inside the penis less visible than in B. austriaca. The penis less variable.

The penis smaller than in B. austriaca, its dimensions little variable; mean length: the Danube at Vilshofen, Germany: 0.63; Ostre near Żywiec: 0.78; Wisła-Malinka: 0.72; Skrzyczne: 0.75; Lubomir: 0.71; Turbacz: 0.67; near Ociemne, the Pieniny: 0.80; Mała Łąka Valley: 0.68; Krowiarki Pass: 0.60. It is noteworthy that the enormous specimens from Lubomir Mountain (f. hungarica) are characterized by a markedly small penis.

J - The female reproductive organs (Figs 18,19 - 18,29 and 21,40 - 21,49) including the bursa copulatrix with the duct nearly always markedly distinguishable like in B. austriaca. The bursa variable within a narrower range: never U-shaped (in B. austriaca the most often case), usually arched (a shape rare in B. austriaca), sometimes J-shaped, exceptionally straight. As in that species the proximal end of the bursa only exceptionally sharpened. The duct of bursa rather narrow, narrower than in B. austriaca (as in that species, however, its breadth approximates to the thickness of the oviduct reaching the receptaculum seminis) and also longer in general. The receptaculum bigger: ranging from medium to big, usually sac-shaped (in B. austriaca usually semispherical).

Different populations of the species when compared in respect of the female reproductive organs show their geographic variation of a clinal character. In a series of stations: Lubomir, Turbacz, the Pieniny, the

Tatra stations, that means in the southward direction the slimness of both the bursa copulatrix and receptaculum seminis increases; the bursa elongates; the length of receptaculum increases proportionally to the length of the bursa. The gradient is rather well recognizable in mean values for different stations.

K - 1. The Danube at Vilshofen, Bayern, Germany, leg. L. Butot.

2. Ostre near Żywiec, the Beskid Żywiecki Mountains, a spring in the form of a small shallow trough, almost entirely filled with fallen beech and hornbeam leaves, the water outflow very poor; situated in a forest; quite numerous inhabited by Bythinella.

3. Wisła-Malinka, the Beskid Śląski Mountains, a very small outflow poor in cold water percolating through leaves, at the edge of a small stream, in a beech forest.

4. A spring of a tributary of the Żylica Stream near Skrzyczne, the Beskid Śląski Mountains, in the form of a trough of about 10 cm in diameter, filled with fallen beech leaves, the water outflow very poor, in a small ravine on the slope overgrown with beeches.

5. Lubomir Mountain, the side of Kobielnik, the Beskid Wyspowy Mountains, a shallow ditch at the edge of a meadow, probably partly supplied with underwater but the water temperature moderate; very muddy; numerous Bythinella on its edges, among roots and lower parts of stems of grasses around the ditch.

6. Turbacz Mountain, the side of Koninki, the Gorce Mountains, the locality identical to that near Skrzyczne.

7. Near Ociemne, the Pieniny Mountains, a small stream among limestone rocks, in a beech forest.

8. The Mała Łąka Valley, the Tatra Mountains, a small spring in a beech forest.

9. Krowiarki Pass, Babia Góra Mountain, the Beskid Wysoki Mountains, on stones and weeds in a small spring of a trough type.

10. Budapest, ex coll. Hazay (? : empty shell).

It seems that the ecological spectrum of B. cylindrica is different from that of B. austriaca; these two species never occur sympatrically at the stations studied. While B. austriaca seems to favour large springs in limestone areas, with the bed overgrown with mosses. B. cylindrica usually inhabits small springs or water outflows in the spring areas on the substratum containing only the intrusions of limestone or calcareous cement; it occurs commonly among fallen leaves, usually beech, less often hornbeam.

6. Bythinella zyvionteki Falniowski, 1986

A - Falniowski (1980) erroneously regards this species as B. austriaca (Frauenfeld, 1856).

B - The shell (Figs 22,1 - 22,12; 22,28 - 22,29; 22,31; 22,34; 22,38; 23,1 - 23,40 and 24,1 - 24,42) ovate or cylindrically-ovate, ovate more often than in B. austriaca or B. cylindrica and generally less slim, more bulgy. Whorl growth rather regular, the body whorl usually poorly but sometimes strongly swollen. The body whorl relatively high, its height not so variable and proportionally never so small as in those two species. Whorls more convex and divided by a deeper suture medially sloped to the columella. For different stations the whorl number: maximum: $4 \frac{2}{3}$ - $5 \frac{1}{8}$, usually: over 5; mean: $4 \frac{1}{3}$ - almost 5, usually: $4 \frac{1}{2}$. The mean number of whorls considerably variable, while the maximum number slightly variable.

The apex broad, often flattened. The aperture oval in outline, the angle upwards usually poorly marked or absent, the mouth often markedly protruded. The peristome not always continuous, parietal lip usually poorly marked, sometimes absent. The outer lip absent. The umbilicus development ranging from lacking to conspicuous, gutter-shaped, very variable.

The shell dimensions at the stations: height: 1.85 - 3.45, mean: 2.2 - 2.9, continuous variability within: 2.65 - 2.9, outside these limits a minute form from Zawoja with its mean: 2.2; breadth: 1.2 - 1.95, mean: 1.3 - 1.7; except for the minute form the variability extremely low. The shell usually of a brighter colour than in B. austriaca and B. cylindrica often seems bluegrey due to the pigmented mantle visible through. The shell corrosion common.

C - minute form - the shell small, usually slim, with the mouth fully developed and a high number of whorls; found at two stations at Zawoja (Zawoja-Składy, a meadow stream, and Zawoja-Wisły, a spring area). Occurred sympatrically with the typical form, showing well marked conchological distinctness: the specimens of the minute form, though often smaller than the young specimens of the typical form, characterized by the shells with numerous whorls typical of adults. The rank of this form is not clear, no anatomical separateness was found, though it needs confirmation.

D - The head pigmentation (Figs 11,1 - 11,27) variable within the whole range from the complete lack of pigment (more common in males also in this species: Fig. 11,8) through a delicate to entirely black pigmentation, an intensive or quite intensive one is common. The "spottiness" occurring in both B. austriaca and B. cylindrica, in this

species is extremely rarely observed. The borders of spots sometimes diluted. The pigmentation pattern differences between B. zyvionteki and the two species are observable in the narrowness of the pigmented belt usually only slightly extending over behind the snout, resulting then in the lack of both the unpigmented spot surrounded by a pigmented area and the semilunar spots of an intensive pigmentation placed posteriorly to the snout.

E - The ctenidium (Figs 12,45; 12,48; 12,50 - 12,51; 12,54; 13,1 - 13,2; 13,4 - 13,6 and 13,8) variable as in B. austriaca and B. cylindrica. Usually not very long and moderately elongate, its lamellae long and almost always straight, listed below with the lamellae number:

Station	Males	Females
1. Siedem Żródeł	16 - 24 mean 20.0	17 - 22 mean 20.0
2. Kwaśnik-Golczowice	14 - 21 mean 16.4	16 - 20 mean 18.0
3. Mszana Dolna	14 - 19 mean 16.8	15 - 23 mean 20.0
4. Zawoja-Składy	14 - 18 mean 15.3	16 - 21 mean 18.5
5. Zawoja-Widły spring	12 - 19 mean 15.7	15 - 21 mean 17.3
6. Zawoja-Widły s. area	16 - 20 mean 18.3	16 - 22 mean 18.4

F - The osphradium (Figs 12,45 - 12,54 and 13,1 - 13,9) very variable in shape and proportions. Often markedly arched or narrow and fairly elongate, may be also quite irregular (Figs 13,3 and 13,4). Its edge may be rather deeply notched, though not to such an extent as in B. cylindrica; as in that species the dark border uncommon, irregular and incomplete, and often marking distinct lobes of the osphradium (Fig. 13,2); shadings (the areas of lower thickness) sometimes also run across the osphradium (Figs 13,4 and 13,6).

G - The radula is described by Falniowski (in press).

H - The prostate (Figs 13,14 - 13,16) rather big, kidney-shaped or irregularly oval. The vas deferens connecting the testis with the prostate (Fig. 13,22) long and strongly twisted. The flagellum (Figs 13,17 - 13,18) with a very conspicuous lumen. Its length variable within a wide range; in general the thinnest one among the Polish Bythinella and a longer one than that in B. austriaca and B. cylindrica (1.13 - 2.09 of the penis length).

I - The penis (Figs 22,13 - 22,22; 22,33; 22,36 - 22,37 and 25,1 - 25,34) smallest among the Polish Bythinella. Unlike in B. austriaca and B. cylindrica, when compared to the left arm, the right one always longer, often considerably, and always fairly thicker: in

its proportions the thickest among the Polish Bythinella. The tip of the left arm always sharp (in B. austriaca usually almost spherically swollen, and in B. cylindrica blunt). The tip of the right arm usually not markedly distinguishable. The terminal section of the vas deferens often well visible, while the terminal section of the flagellum nearly always invisible.

The variability of the penis size rather low; mean lengths: Siedem Źródeł: 0.68; Kwaśnik-Golczowice: 0.65; Mszana Dolna: 0.72; Zawoja-Składy: 0.67; Zawoja-Widły, a spring: 0.72; Zawoja-Widły, a spring area: 0.72; Krowiarki Pass: 0.60.

The penis, markedly different from those of the other Bythinella, is the most characteristic and constant feature. The massiveness of the thick right arm compared with the shortness of the relatively thin and sharply-tipped left arm appears striking. Moreover, the variability is low, quite inconspicuous in the populations from the Biała Przemsza River catchment area, higher in Mszana Dolna and Zawoja where the specimens with penes less typical but undoubtedly belonging to this species can be found. This is, probably, another example of the geographic variation.

J - The duct of bursa copulatrix (Figs 22,23 - 22,27; 22,30; 22,32; 22,35 and 25,35 - 25,46) as in the species described above markedly distinguishable in general, whereas the poorly distinguishable one less rare than in those species. The proximal end of the bursa only exceptionally sharpened. The shape of bursa variable inside the whole range: from U-shaped, through J-shaped and arched, to straight; its variability is the highest among all the Bythinella and it is difficult to indicate the most common and typical shape of it. In general the duct of bursa rather narrow, like in B. cylindrica but unlike in B. austriaca; its diameter, unlike in both those species, usually lower than the diameter of the oviduct reaching the receptaculum seminis. The length of the duct variable inside a wide range, usually medium. The receptaculum ranging from extremely small, found in neither of those species, to small or even medium size. The typical shape of the receptaculum cannot be pointed out either.

The geographic variation seems to manifestate in the species as well. In the populations from the Biała Przemsza River catchment area the bursa is usually U-shaped, less often arched, with the duct always markedly distinguishable. In the populations from the Beskidy the bursa is more variable: it may be arched, J-shaped or straight, and quite rarely U-shaped, the duct not always markedly distinguishable.

B. zyvionteki shows a great variability of the structure of the female reproductive organs, often parallel to the variability character-

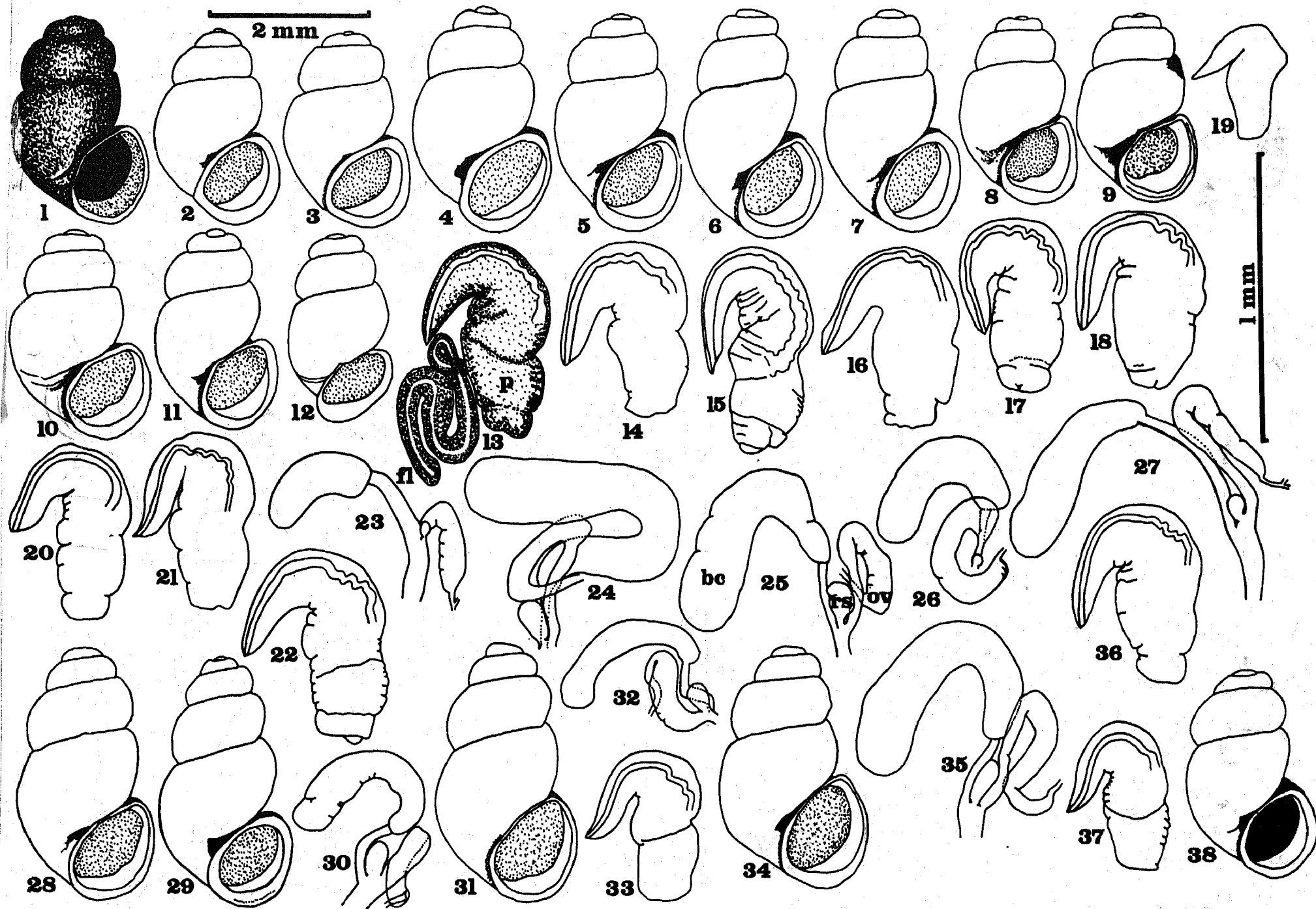


Fig. 22. *Bythinella zyvionteki*: 1 - 27 - Siedem Źródeł, Centuria tributary, Biała Przemsza tributary: 1 - 12 - shells; 13 - 22 - penes; 23 - 27 - loop of oviduct, receptaculum seminis and bursa copulatrix; 28 - 29, 31, 34 and 38 - shells; 30, 32 and 35 - loop of oviduct, receptaculum seminis and bursa copulatrix; 33 and 36 - 37 - penes (after Falniowski 1986c)

31, 34 and 38 - shells; 30, 32 and 35 - loop of oviduct, receptaculum seminis and bursa copulatrix; 33 and 36 - 37 - penes (after Falniowski 1986c)

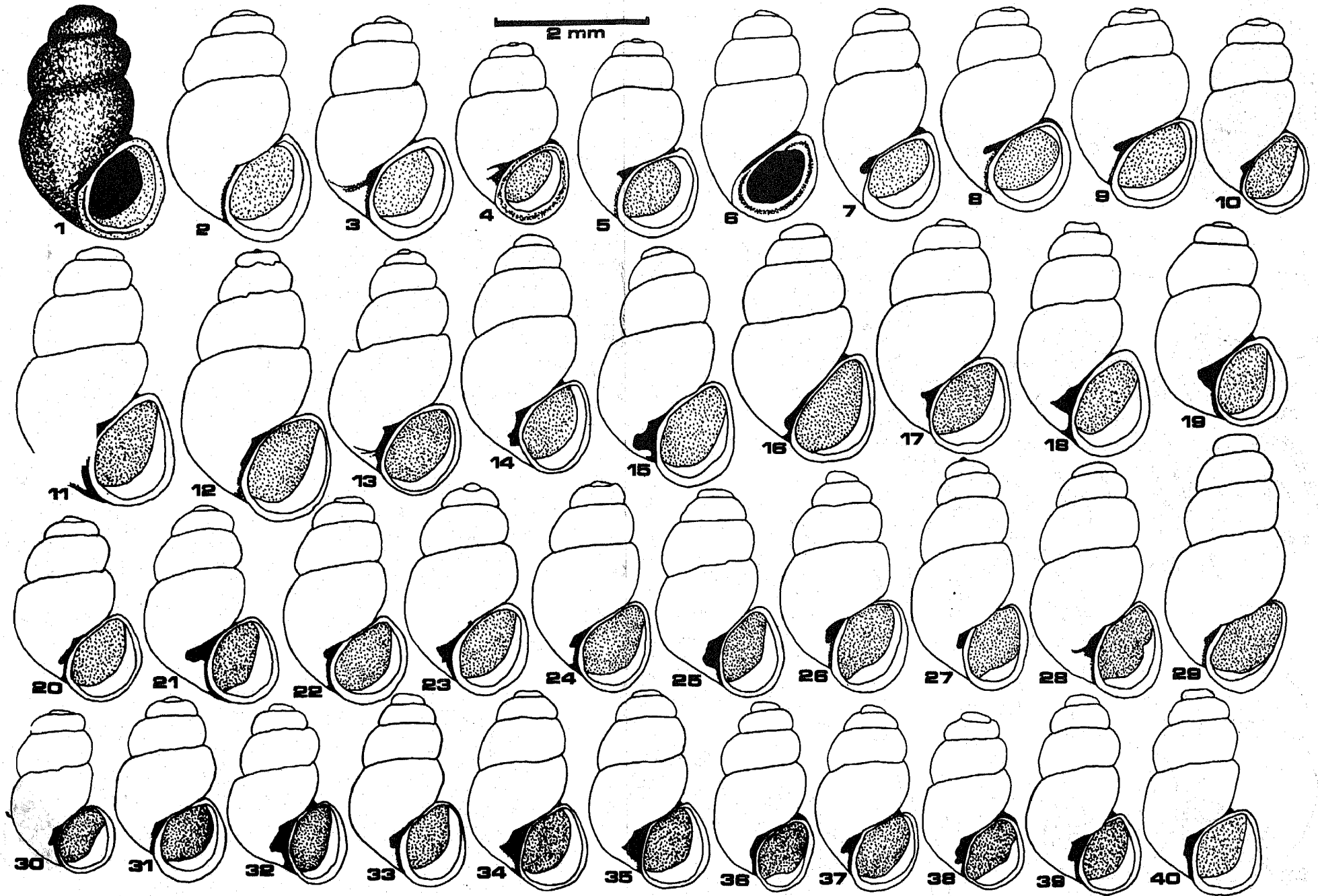


Fig. 23. Shells of *Bythinella zyvionteki*: 1 - 9 Kwaśnik-Golczowice; 10 - 24 - Mszana Dolna; 25 - 40 - Zawoja-Skiady, Babia Góra: 25 - 29 - typical form, 30 - 40 - minute form

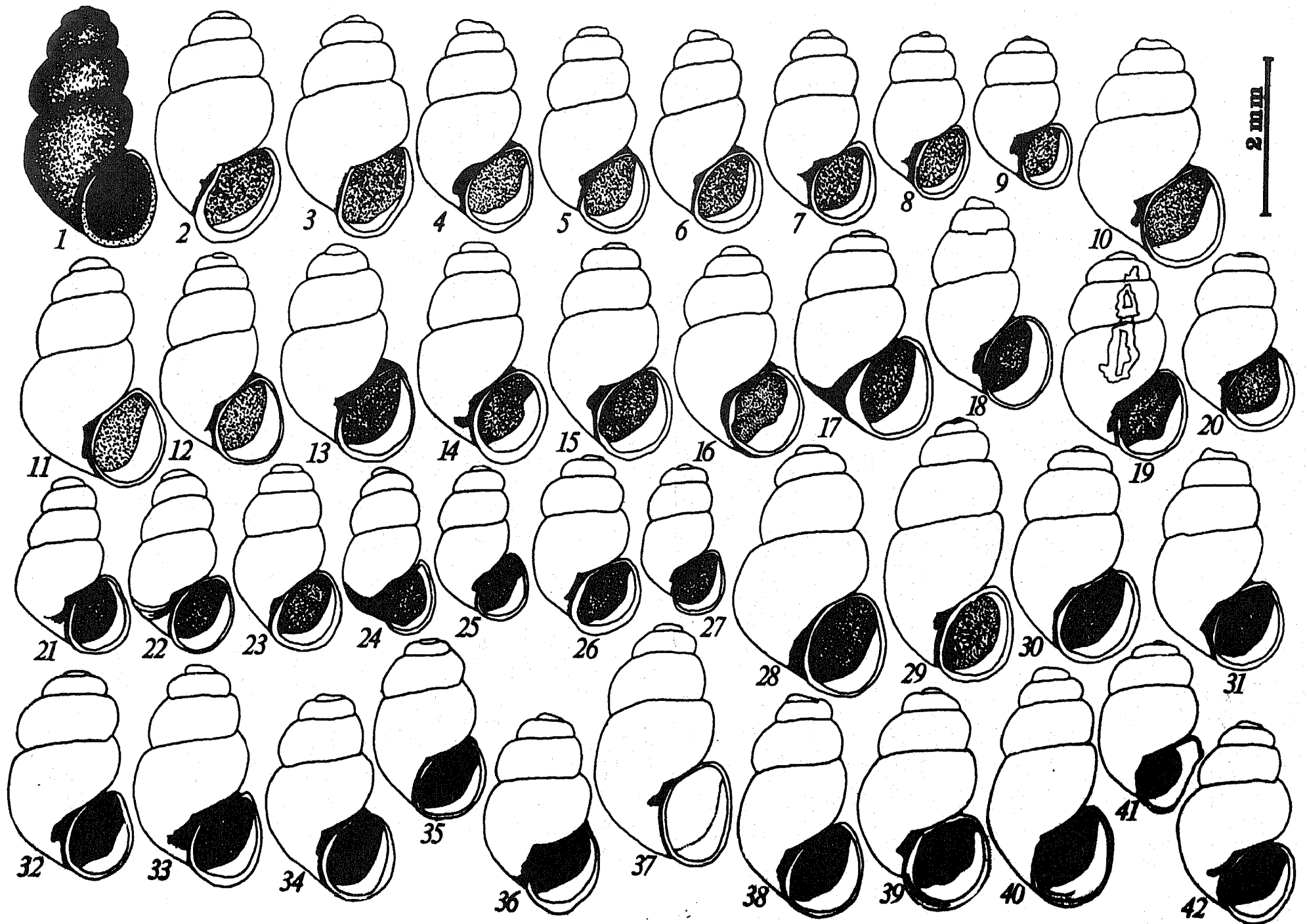


Fig. 24. Shells of *Bythinella zyvionteki*: 1 - 9 - Zawoja-Składy, Babia Góra: 1 - 3 - - over 5 whorls, 12 - almost 5 whorls, 13 - 14 - 4 3/4 whorls, 15 - 19 - 4 1/2 whorls); - typical form: 1 - adult; 2 - 3 - iuv. (2 - 4 2/3, 3 - 4 1/2 whorls); 4 - 9 - minute form (4 - 4 7/8 whorls; 8 - 4 whorls, the mouth not fully developed; 9 - 4 1/8 - 4 1/3 whorls. 27 - 4 1/8 whorls); 28 - 36 - Zawoja-Widły, spring area (28 - over 5 whorls); 10 - 27 - Zawoja-Widły, spring, Babia Góra: 10 - 19 - typical form (10 - 11 - whorls, 29 - 5 1/8 whorls); 37 - 42 - Krowiarki Pass, Babia Góra

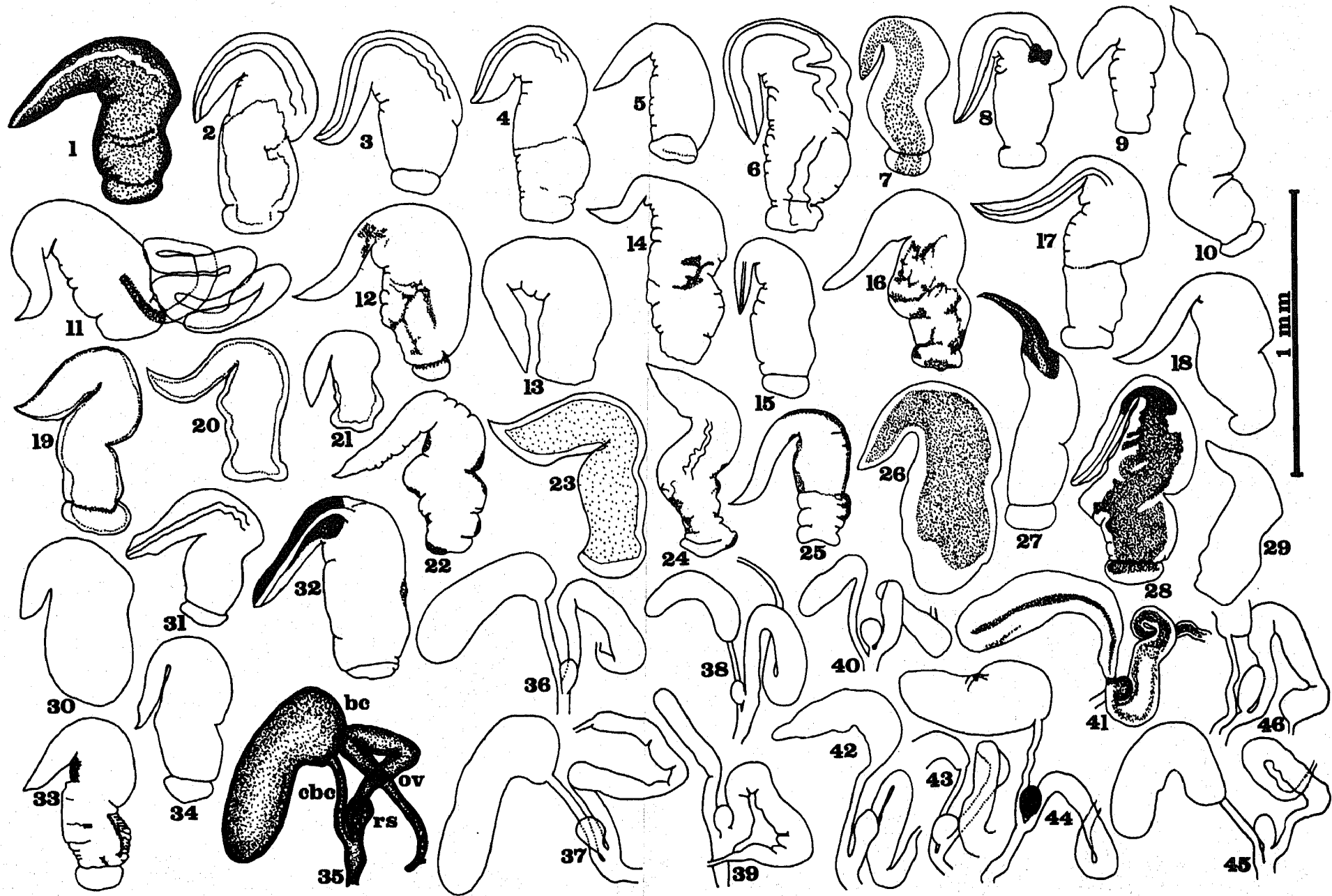


Fig. 25. *Bythinella zyvionteki*: 1 - 34 - penes (11 - with flagellum): 1 - 5 - Kwaśnik-Golczowice; 6 - 10 - Mszana Dolna; 11 - 18 - Zawoja-Składy, Babia Góra; 19 - Zawoja-Widły, spring, typical form; 20 - 25 - Zawoja-Widły, spring, minute form; 26 - 32 - Zawoja-Widły, spring area; 33 - 34 - Krowiarki Pass, Babia Góra; 35 - 46 - loop of oviduct, receptaculum

seminis and bursa copulatrix; 35 - 37 - Mszana Dolna; 38 - 39 - Zawoja-Składy; 40 - 42 - Zawoja-Widły, spring; 40 - 41 - typical form; 42 - minute form; 43 - 45 - Zawoja-Widły, spring area (43 - a fragment); 46 - Krowiarki Pass, Babia Góra, the main part of the bursa not drawn

istic of the other species. Therefore, the anatomy of the female reproductive organs is not a feature enabling the determination of this species easy and certain.

K - 1. Siedem Źródeł springs, a tributary of Centuria stream, a tributary of the Biała Przemsza River, Jura Krakowsko-Częstochowska Upland, numerous Jurassic springs with a very rich water outflow, on the slope of an unwooded hill; the substrate overgrown with mosses and algae.

2. Kwaśnik-Golczowice, the Biała Przemsza catchment basin, Jura Krakowsko-Częstochowska, a small (about 50 x 30 cm) spring in the form of a meadow pit about 10 - 20 cm deep, with a poor water outflow, in the rocky area; the substrate scarcely overgrown with algae.

3. Mszana Dolna, the Beskid Wyspowy Mountains, a small meadow stream with cold water, probably in the spring area.

4. Zawoja-Składy, the Beskid Wysoki Mountains, a small meadow stream similar to that in Mszana Dolna.

5. Zawoja-Widły, the Beskid Wysoki Mountains, a small spring in the form of a small trough, overgrown with macrophytes, situated in a meadow.

6. Zawoja-Widły, the Beskid Wysoki, a spring area in a meadow, temporarily drying out; among numerous hygrophytes.

7. Krowiarki Pass, the massif of the Babia Góra Mountain, the Beskid Wysoki, a small troughed spring; on stones, among plants; sympatric occurrence with B. cylindrica.

The ecological spectrum of B. zyvionteki seems wide: ranging from typical springs to spring areas, or small meadow flows. It has been found neither in forests nor among fallen leaves. On the Babia Góra the vertical vicariontism of B. zyvionteki and B. cylindrica can be observed. They occur together on Krowiarki Pass, while B. cylindrica and B. zyvionteki only at higher and lower altitude respectively. B. zyvionteki seems characteristic of the localities situated at lower altitude.

7. Bythinella metarubra Falniowski, 1986

B - The shell (Figs 26,1 - 26,21) conspicuously constant, its habitus cylindrically-ovate, different from the three species described above, whorl growth less regular. The body whorl poorly or very poorly swollen; its proportional height as well as the shell slimness and the suture slant most distinct among the Polish Bythinella. The whorls poorly but regularly convex, not flattened, the suture deep and regular. The whorl number at the stations: maximum: 4 1/2 - 4 3/4, usually: 4 3/4; mean: 4 1/4 - 4 1/2, usually: 4 1/3. The lowest variability among the Polish Bythinella.

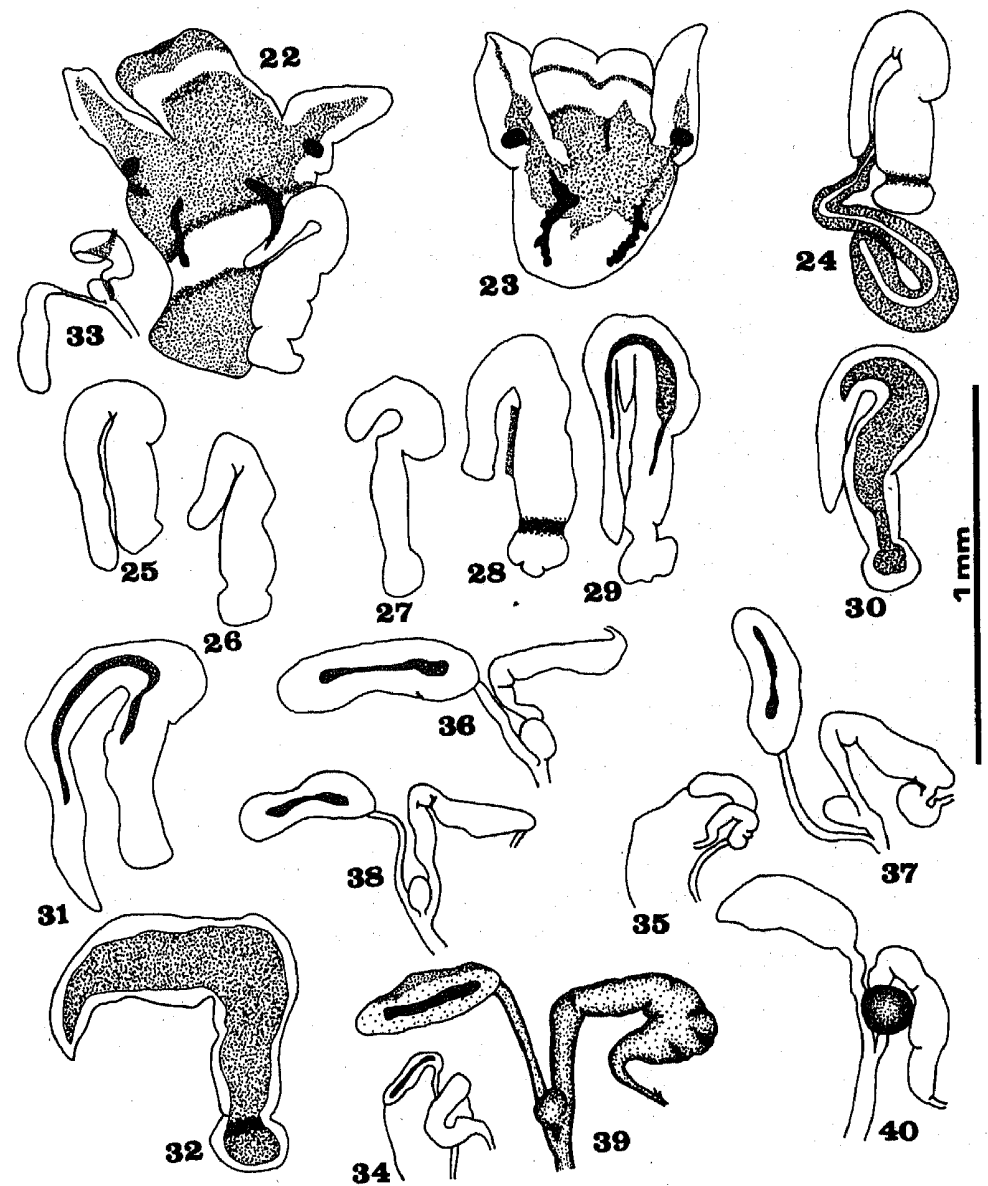
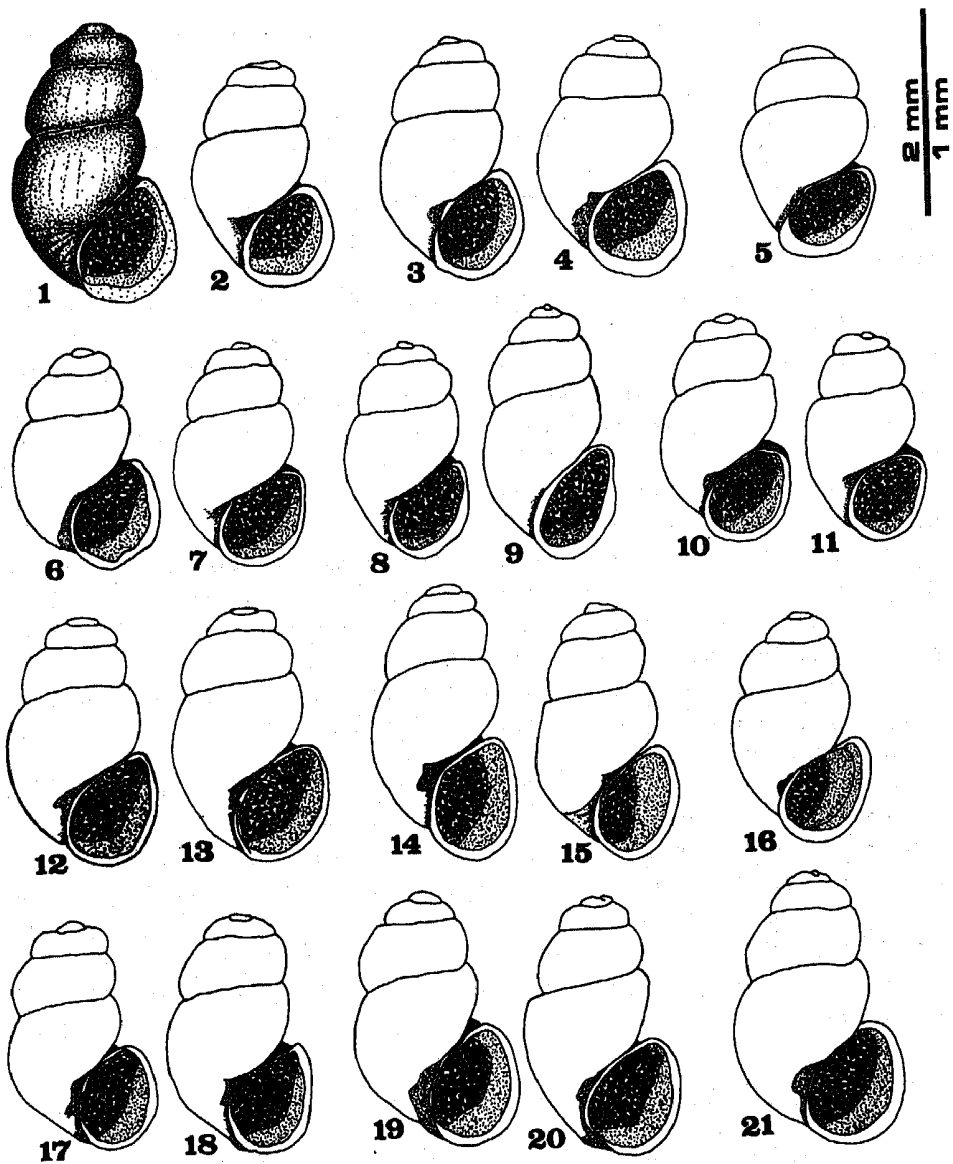


Fig. 26. *Bythinella metarubra*: 1 - 21 - shells: 1 - 5 - Trzy Korony Mountain, Pieniny Mountains; 6 - 11 - Strążyska Valley, stream-beech forest, Tatra Mountains; 12 - 16 - Lejowa Valley, spring in the middle, Tatra Mountains; 17 - 21 - Lejowa Valley, spring in the end; 22 - 23 - head pigmentation, Trzy Korony Mountain, Pieniny Mountains; 22 - a male, 23 - a female; 24 - penis with flagellum, Trzy Korony Mountain; 25 - 32 - penes:

25 - 28 - Trzy Korony Mountain; 29 - 31 - Strążyska Valley, stream-beech forest; 32 - Lejowa Valley, spring in the end; 33 - 40 - loop of oviduct, receptaculum seminis and bursae copulatrix (33, 34 and 35 on the scale 4: 7 to the others): 33 and 35 - Strążyska Valley, stream-beech forest; 34 and 39 - Lejowa Valley, spring in the middle; 36 - 38 - Trzy Korony Mountain; 40 - Lejowa Valley, spring in the end. After Falniowski (1986d)

The apex rounded. The mouth slightly variable, little protruded, narrow, strongly extended upwards, but in general with no angle. The peristome always continuous, though the parietal lip may be very narrow. The umbilicus in the form a narrow slit, slightly variable.

The shell dimensions at the stations: height: 1.65 - 2.85, mean: 2.1 - 2.5; breadth: 1.15 - 1.75, mean: 1.3 - 1.5. The whole variability range at the Trzy Korony Mountain, at the other stations the dimensions less variable. The shell rather brown than yellowish or cream.

The species determinable on the basis of the shell: the smallest among the Polish Bythinella, slim, columnar, with numerous poorly convex whorls divided by a deep suture.

D - The head pigmentation (Figs 11, 28 - 11,37 and 26,22 - 26,23) usually poor or very poor but may be very intensive in females (Figs 11,34 and 11,37), never in males. The pigmented belt wide, "spot-tiness" absent. The spot posterior to the snout common, sometimes quite regular in shape (Fig. 11,33). The most characteristic is the very common occurrence of the intensively pigmented semilunar spots posteriorly to the snout, also in the specimens lacking pigment anywhere else (Fig. 11,28).

E - The ctenidium (Figs 13,10 - 13,11) markedly big, proportionally to the shell height actually biggest within the Polish Bythinella. Elongate only little, with long, straight or slightly arched but not bent lamellae; listed below with the lamellae number:

Station	Males	Females
1. Trzy Korony, Pieniny	15 - 20 mean 17.5	12 - 19 mean 14.8
2. Strążyska Valley s.-b.	15 - 17 mean 16.0	14 - 17 mean 15.0
3. Lejowa Valley, edge	- mean 19.0	- mean 21.0
4. Lejowa Valley, middle	- mean	15 - 18 mean 16.7

F - The osphradium (Figs 13,10 - 13,11), proportionally to the shell size, biggest among the Polish Bythinella, elongate, straight and irregular or oval slightly arched. Darker border absent, or somewhat irregular, tending to form the distinct lobes of the osphradium.

H - The flagellum moderately thick (as in B. cylindrica) and extremely long (up to 2.39 of the penis length).

I - The penis (Figs 26,24 - 26,32) very slim or slim (the exception: the specimen in Fig. 26,32) like in B. austriaca. The right arm longer and thicker: the proportions of the arm length and thickness like in B. cylindrica. The tip of the left arm usually

blunt, of the right one distinguishable, sometimes very markedly. The canals inside the penis always invisible.

The penis not big, but proportionally to the shell size the biggest among the Polish Bythinella; for instance, it is not smaller than the penis of the giant B. cylindrica f. hungarica from Lubomir; mean length: Trzy Korony, Pieniny: 0.62; Strążyska Valley, stream-beech forest: 0.72; Lejowa Valley, edge: 0.75.

J - The duct of the bursa copulatrix (Figs 26,33 - 26,40) always very markedly distinguishable. Only in this species the bursa always straight, its shape showing practically no variation, the proximal end only sharpened in extremely rare cases. The duct of bursa narrowest among the Bythinella described above and always narrower than the oviduct reaching the receptaculum seminis, longest among the Polish Bythinella. The receptaculum small and almost spherical, as in B. austriaca.

The variability of the female reproductive organs low, in general. Their structure is one of the basic diagnostical features of this species.

K - 1. Trzy Korony Mountain, the Pieniny Mountains, a small spring under the top of the mountain, in a beech forest.

2. Strążyska Valley, a stream in a beech forest, the Tatra Mountains, the edges of a small flow; among beech fallen leaves; occurrence sympatric with Bythinella sp.

3. Lejowa Valley, middle part, the Tatra Mountains, a small spring in the form of an outflow among fallen leaves.

4. Lejowa Valley, edge, the Tatra Mountains, a small spring of a similar kind as that in the middle part of the valley.

5. Vicinity of springs of Białka Tatrzańska stream (empty shells only, the material not labelled more precisely).

The species is probably in a relation with rather small springs in quite calcareous and mountain areas, as well as with fallen and decaying beech leaves.

8. Bythinella sp.

B - The shell (Figs 27,1 - 27,22) ovate or cylindrically-ovate (cylindricity usually poorly marked), moderately slim. As in B. metarubra whorl growth rather abrupt and the body whorl high; the above features little variable. The body whorl most strongly swollen among the Polish Bythinella. Whorls slightly stepped, the suture most distinct within the Polish Bythinella, almost as sloped to the columella as in B. metarubra, whorls rather convex. Their maximum number (for

different stations): $4 \frac{3}{4}$ - almost $5 \frac{1}{2}$, usually: 5 - almost $5 \frac{1}{2}$; mean: $4 \frac{2}{5}$ - $4 \frac{3}{4}$, usually: $4 \frac{3}{4}$.

The apex rather sharp. The mouth characteristic: most protruded among the Polish Bythinella, strongly widening downwards and often considerably narrowing upwards but with the angle poorly marked or absent. The peristome always continuous, outer lip absent. The umbilicus: narrow to wide.

The shell dimensions at the stations: height: 2.5 - 3.2, mean: 2.85 - 2.90, usually: 2.85; breadth: 1.45 - 2.0, mean: 1.65 - 1.80. The variability low.

D - The head pigmentation (Figs 10,22 - 10,30) varying from poor to very intensive (black) also in males, often intensive or very intensive. Almost always the belt of pigment very wide and "spot-tiness" absent, shadings very rarely present. Placed posteriorly to the snout, the unpigmented spot almost in each specimen distinct and regular, the semilunar spots of an intensive pigmentation absent.

E - The ctenidium (Fig. 13,12) rather strongly elongate, with relatively short and almost straight lamellae. Its very small size appears striking: proportionally to the shell size it is smallest among the Polish Bythinella, which cannot result from a habitat conditions, since B. metarubra with the proportionally biggest ctenidium occurred sympatrically. The number of lamellae:

Station	Males	Females
1. Polana Pisana	16 - 24 mean 19.8	19 - 24 mean 22.0
2. Kościeliska Valley	18 - 20 mean 18.7	14 - 18 mean 16.3
3. Strążyska Valley s.-b.	16 - 24 mean 20.0	16 - 23 mean 19.7

F - The osphradium (Fig. 13,12) also very small, proportionally to the shell size smallest within the Polish Bythinella. Moderately elongate and poorly arched, of irregular shape, without the darker border but with a darker transverse spot.

H - The flagellum (Fig. 13,13) usually thick (as in B. austriaca) and (besides of B. metarubra) longest among the Polish Bythinella (up to 2.39 of the penis length).

I - The penis (Figs 27,23 - 27,33) slim or very slim, as in B. austriaca and B. metarubra; the right arm always longer, but not considerably and not quite thicker than the left one. The tip of the left arm nearly always blunt. The tip of the right one always distinguishable; the above feature highly invariable: such the invariability of the feature never occurring in the other Polish Bythinella.

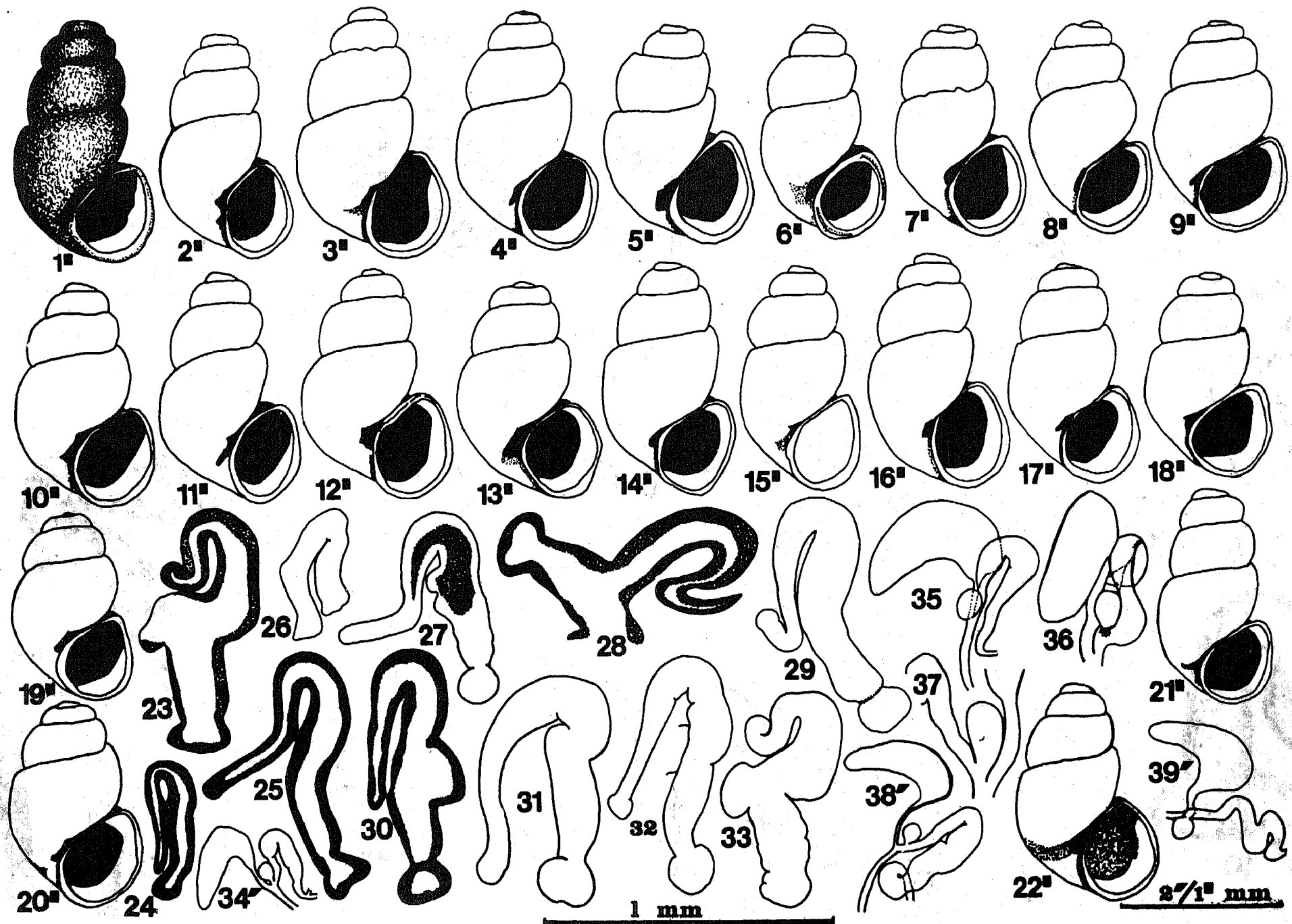


Fig. 27 *Bythinella* sp., Tatra Mountains: 1 - 22 - shells: 1 - 14 - Polana Pisana; 15 - 19 - Strážyska Valley, stream-beech forest; 20 - 22 - Kościeliska Valley; 23 - 33 - penes: 23 - 27 - Polana Pisana; 28 and 30 - Strážyska Valley, stream-beech forest; 29 and 31 - 33 - Kościeliska Valley; 34 - 39 - loop of oviduct, receptaculum

seminis and bursa copulatrix: 34 and 39 - Kościeliska Valley; 35 and - 38 - Polana Pisana; 36 - 37 - Strážyska Valley, stream-beech forest (37 - a fragment). Note: The middle (longer) 1 mm scale is related to the numbers with no marks, the right (shorter) one to the others; 1 mm is related to the numbers with points while 2 mm to the ones with comas

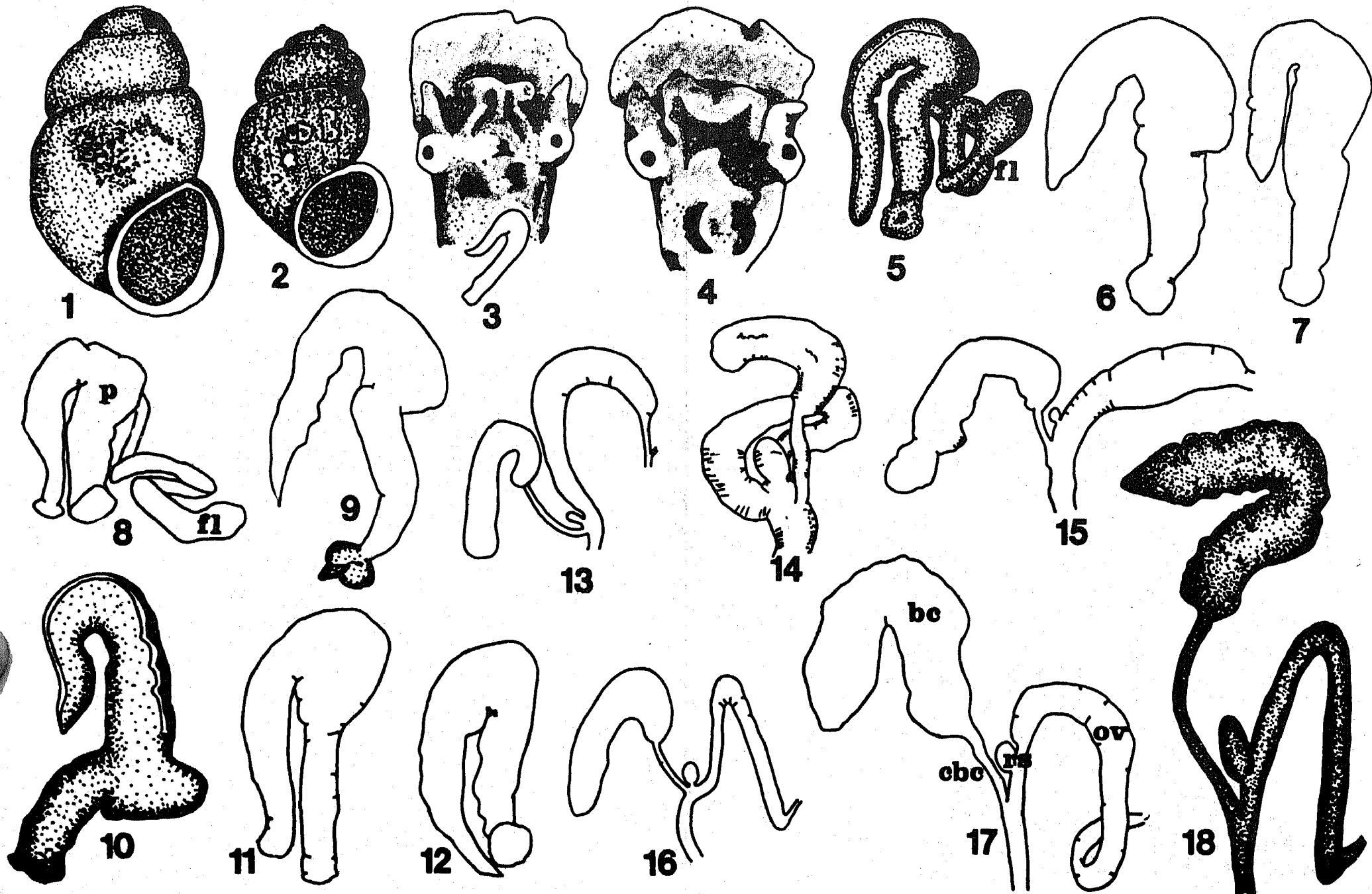


Fig. 28. *Bythinella micherdzinskii*, Bieszczady Mountains: 1 - 2 - shells: 1 - the holotype, probably a female, Rawka massif; 2 - a male, Rawka massif; 3 - 4 - head pigmentations, Rawka massif: 3 - a male, 4 - a female; 5 - 12 - penes (5 and 8 - with flagellum): 5 - 11 - Rawka massif, 12 - vicinity of Ustrzyki Górne; 13 - 18 - loop of oviduct, receptaculum seminis and bursa copulatrix, Rawka massif

The canals inside the penis invisible, as in B. metarubra. At the base of the arms at left, a common, characteristic outgrowth occurs (Figs 27,23; 27,27 and 27,33), while unnoticeable in the other Polish Bythinella. The penis variability low.

The penis rather big. Mean length: Polana Pisana: 0.74; Kościeliska Valley: 0.89; Strążyska Valley, a stream-beech forest: 0.90.

J - Unlike in the other Polish Bythinella, the duct of the bursa copulatrix (Figs 27,34-27,39) never markedly distinguishable, passing slowly into the bursa without a marked demarcation, the bursa itself very characteristic in shape, slightly variable: the bursa arched, at the proximal end always markedly sharpened while distally widened, often strongly. The duct of bursa extremely narrow (as in B. metarubra), always narrower than the oviduct reaching the receptaculum seminis, and extremely short: the shortest among the Polish Bythinella. The receptaculum small to of medium size, rather almost spherical, as in B. austriaca. The variability low.

- K - 1. Polana Pisana, the Tatra Mountains, a small spring in the form of a trough in a rocky area.
2. Kościeliska Valley, the Tatra Mountains, a large spring with an immense water outflow, situated on the bottom of the valley, more or less in its middle part, the bed of limestones quite overgrown, mainly with mosses Fontinalis.
3. Strążyska Valley, the Tatra Mountains, a stream in a beech forest, among fallen decaying beech leaves at the edges of a tiny flow probably supplied with underwater; occurs sympatrically with B. metarubra.

The species seems to avoid neither large springs nor small flows, occurs among mosses as well as fallen beech leaves, only in the limestone part of the Tatra Mountains.

9. Bythinella micherdzinski Falniowski, 1980

B - The shell (Figs 28,1 - 28,2) ovate (barrel-shaped), broad and stout, the whorl growth abrupt but rather regular, the body whorl about 2/3 of the shell height, poorly swollen. The whorls rather flat, the suture deep, slightly sloped to the columella. The whorl number: 4 - 4 3/4, usually: 4 1/2.

The apex rounded. The peristome continuous, without the outer lip, the umbilicus almost completely absent. The mouth showing a well marked sexual dimorphism. In females slightly protruded and narrow, ovate, with a very poorly marked angle. In males quite protruded and wide, almost circular, with no angle. The parietal lip rather broad, in males

developed better. In males the shell also somewhat smaller, slimmer, with the whorls more convex and the suture more distinct.

The shell height: 2.8; breadth: 1.15 (the holotype). The shell horny-yellow with a whitish shade, around the aperture a brown margin common, found also in other Bythinella. The shell translucent, glossy. The variability except for the dimorphism rather little. The specimens with similar shells are found also among the other Polish Bythinella.

D - The head pigmentation pattern (Figs 28,3 - 28,4) with a broad belt of pigment, without shadings, rather intensively spotted. Posterior to the snout the unpigmented spot surrounded by pigment absent, the semilunar spots intensively pigmented occurring, but not always.

E - The number of lamellae of the ctenidium (the station in the Rawka massif): males: 16 - 21, mean: 19; females: 14 - 16, mean: 15.

G - The radula is described by Falniowski (in press).

H - The flagellum rather long and massive, its variability unrecognized.

I - The penis (Figs 28,5 - 28,12) relatively slightly variable, unlike in B. cylindrica and B. zyvionteki slim; the difference between the arms in their length and thickness poorly marked: the right one longer, the left one often thicker that is noticeable only in this species of all the Polish Bythinella. The tip of the left arm almost always sharp, while the tip of the right one usually distinguishable, sometimes very markedly. The canals poorly visible, the vas deferens relatively more distinct.

J - The duct of the bursa copulatrix (Figs 28,13 - 28,18) always markedly distinguishable. The bursa J-shaped, slightly less often U-shaped, with the proximal end only exceptionally sharpened, its narrow variability range corresponding to the most common interval of B. austriaca. The duct narrower than in that species, and narrower than the oviduct reaching the receptaculum seminis; its length very variable, may be much short. The receptaculum semispherical, the size may be either medium or small but usually is extremely small (except for that found only in B. zyvionteki). Despite an unnumerous material collected a considerable variability appeared noticeable.

K - 1. Rawka massif from the side of Wetlina, Bieszczady, tiny flows among fallen beech leaves in the spring area on a slope.
2. Ustrzyki Górne, Bieszczady, at the road Ustrzyki Górne - Pszczeliny, tiny flows on the slopes overgrown with beeches.

The station at the Babia Góra (Falniowski 1980) was given as the effect of an erroneous identification. Occurrence only in noncalcareous areas and in the mountains of a medium height, overgrown with beech forests. In small, cold flows percolating through fallen beech or hornbeam leaves, near springs or in the spring areas, never in rather large springs.

GENUS MARSTONIOPSIS VAN REGTEREN ALTENA, 1936

10. Marstoniopsis scholtzi (A. Schmidt, 1856)

A - Hydrobia scholtzi A. Schmidt, 1856

Hydrobia steinii Martens, 1858

Paludinella armoricana Paladilhe, 1869

Paludestrina taylori E.A. Smith, 1901

Amnicola steinii pallida Krausp, 1936

B - The shell (Figs 30,5 - 30,7) ovoid-cylindrical, rather slim, with the spire about 2 times higher than the mouth and 4 - 5 whorls rather convex, slowly and regularly growing, divided by a relatively deep, fluted suture. The body whorl round, not swollen, slightly surpassing in height the previous whorl. The apex nearly always asymmetrical, truncate (the dislocation in the direction opposite to the mouth). The aperture small, ovate in outline, with the angle slightly marked. The peristome continuous, the outer lip absent, the parietal lip considerably reduced and almost completely covering the umbilicus, which is subsequently deep but narrow, in the form of a slit. The shell dimensions: height: 2 - 3 - 3.5; breadth: 1.5 - 2. The shell thin-walled and translucent, matt, with poorly marked growth lines, greyhorny or light brown of a greenish shade; usually covered with a blackish sediment of the substrate particles.

The variability low and without a significant relation to the environmental conditions, expressed in the mouth shape, more circular or ovate, the wall thickness, shell slimness, whorl convexity and suture depth.

D - The head (van Regteren Altena 1936; Fretter and Graham 1962) with the snout short, broad and intensively pigmented (Fig. 31,27), the tentacles cylindrical, poorly pigmented and the eyes big, imbedded in big, poorly convex and yellowish eye stalks.

E - The number of ctenidium lamellae: males: 16 - 18 (21 according to Boeters 1973), females: 15 - 27 (28: Boeters 1973).

F - Osphradium in the shape of a hen comb.

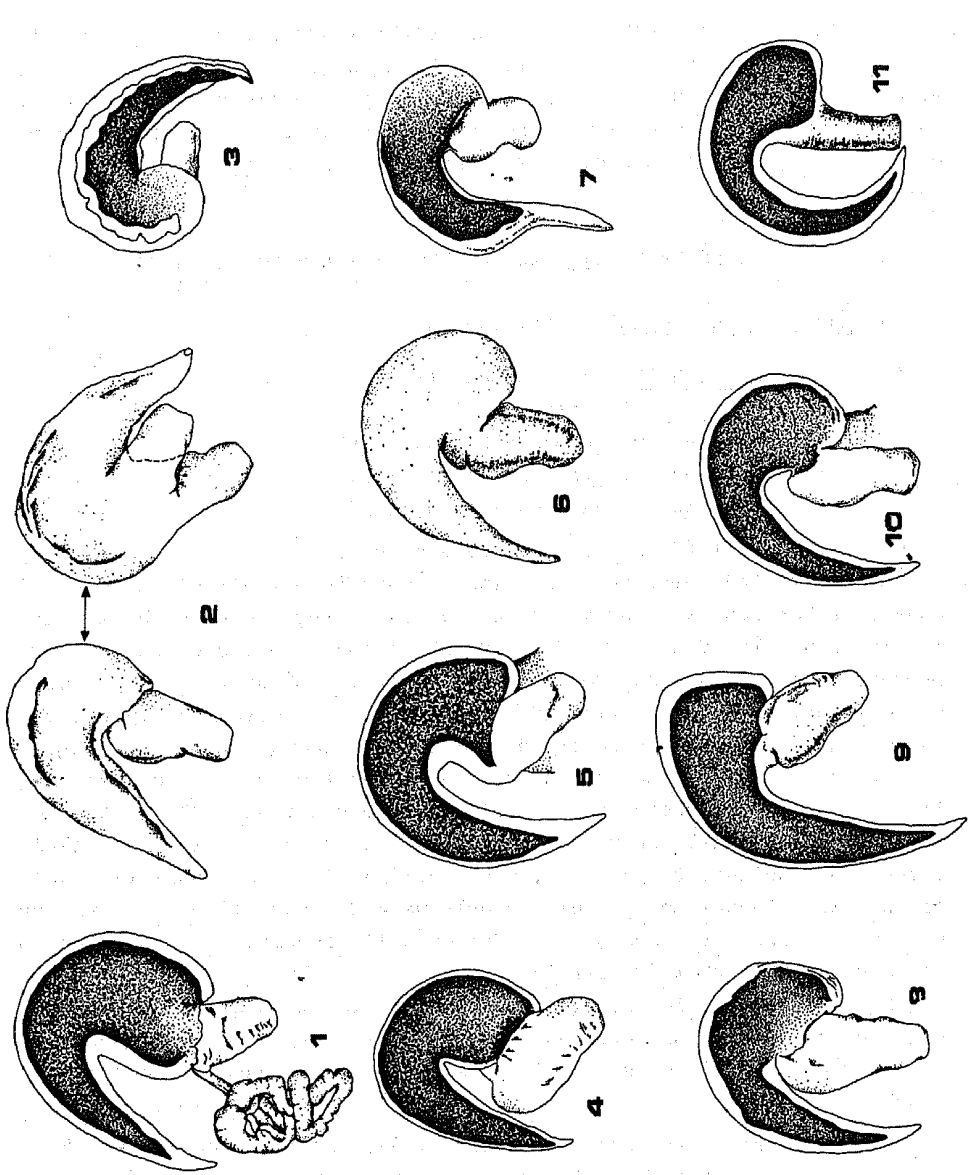


Fig. 29. Penes of *Marstoniopsis scholtzi* (4 - with flagellum, 5 - ventrally and dorsally, the others - dorsally): 1 - 10 - Śniardwy Lake; 11 - Mijntjes, Municipality of Voorst, Prov. Gelderland, the Netherlands, leg. F.F. Repko, After Falniowski 1983)

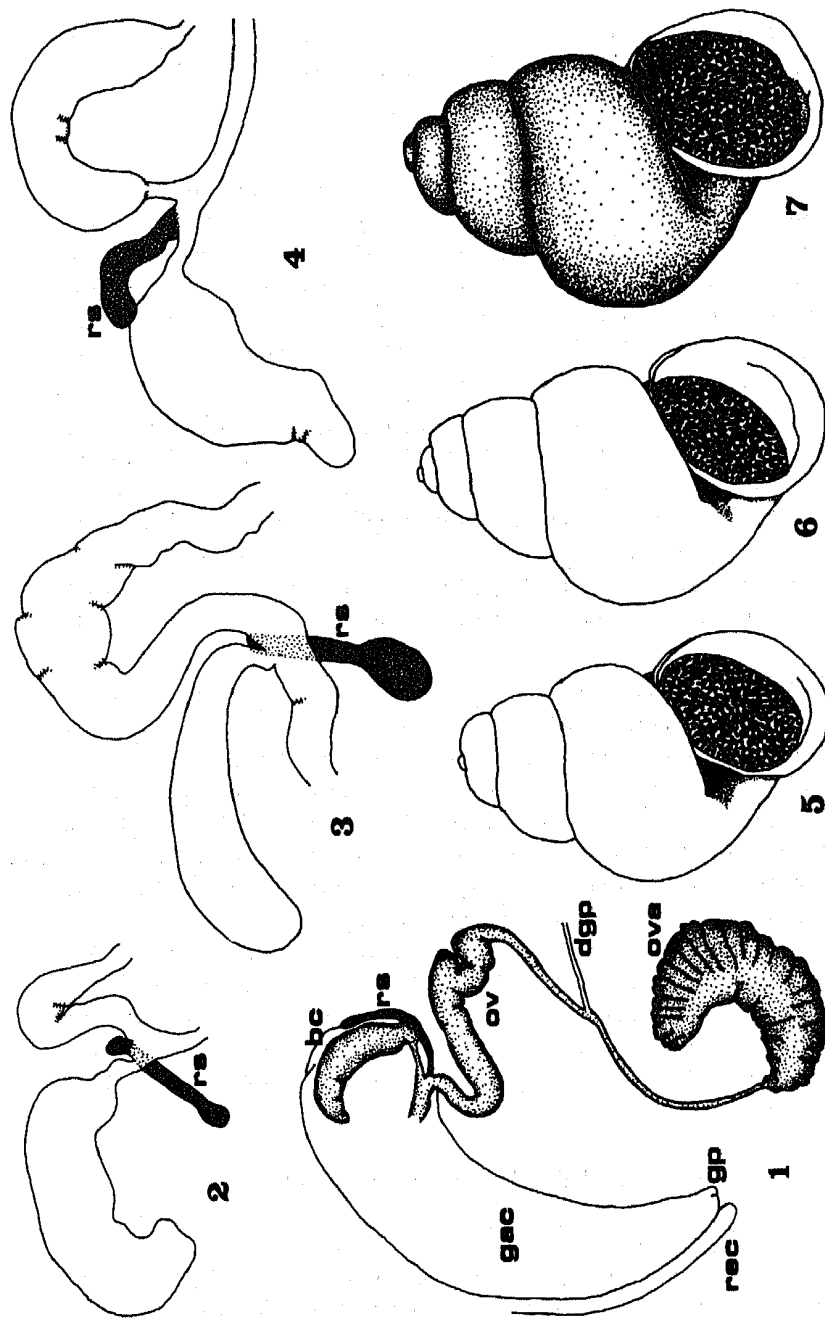


Fig. 30. *Marstoniopsis scholtzi*: 1 - female reproductive organs, Gardno Lake; 2 - 4 - loop of oviduct, receptaculum seminis and bursa copulatrix: 2 - 3 - Gardno Lake; 4 - Śniardwy Lake; 5 - 7 - shells, Śniardwy Lake

- G - The radula descriptions given by: Johansen (1918); Krull (1935); van Regteren Altena (1936) and Falniowski (1983).
- H - The flagellum (Fig. 29,4) short and rather thick.
- I - The penis bi-armed (Figs 29,1 - 29,11), with the arm containing the outlet of the vas deferens usually much longer, slim, slowly narrowing to its tip quite thin, intensively pigmented dark. The arm with the outlet of the flagellum usually considerably shorter, in the shape of a slightly narrowing cylinder, unpigmented. The variability considerable, especially of the arm with the outlet of the flagellum (Johansen 1918; Krull 1935; van Regteren Altena 1936; Boeters 1973; Falniowski 1983).

J - The female reproductive organs (Fig. 30,1) described incompletely and unclearly by Krull (1935) and Boeters (1973), a more detailed description given by Falniowski (1983). The loop of the oviduct (Figs 30,2 - 30,4) strongly thickened. The bursa copulatrix straight, J-shaped, U-shaped, or irregular. In Polish specimens the duct of bursa quite short, while in Dutch specimens longer (Falniowski 1983). The receptaculum seminis long, narrow, sometimes proximally swollen.

K - The distribution range of M. scholtzi covers North Europe, from Great Britain (only a couple of stations in the middle and southern parts: vicinities of Manchester, docks of Grangemouth, Stirling), through the Netherlands, North Germany and Denmark (East Jutland, Fünen, the islands), to the central Sweden (up to 60°40'N: Ehrmann 1956), Finland, and the Baltic republics of USSR (the northern part of the Volga and the Dnieper catchment basins, vicinities of Kaliningrad, Lithuania, Latvia, Estonia to the Ladoga Lake).

In Poland it occurs in the northern and central parts of the country, in the Pomeranian and Masurian Lakes, the Suwałki Lakes, Kujawy, Wielkopolska, Podlasie, Mazowsze regions, Lublin Upland, and the Lower Silesia. The farthest southward stations are near Wrocław (a vicinity of the locus typicus) and near Ispina (the northern part of the Niepołomice Forest nearby Kraków: the author's data).

GENUS LITHOGLYPHUS HARTMANN, 1821

11. Lithoglyphus naticoides C. Pfeiffer, 1828

A - Bole (1981) includes into this species several taxons at the subspecies rank, usually regarded as distinct species, unrecorded from Poland; their names would be then the synonyms of L. naticoides.

B - The shell (Figs 31,1 - 31,12) massive, strong and thick-walled, bulgy, almost spherical, low, with the spire low (up to about 1/3 of the shell height), shortly conical and blunt. The whorls 4 - 4 1/2 - 5 in number, convex, divided by a rather deep suture, growing abruptly. The body whorl large (2/3 - 3/4 of the shell height), very strongly swollen. The apex sharp. The aperture big, considerably widened, ovate or circular with the angle more or less marked. The parietal lip thick, the other edges sharp, the outer lip absent. The umbilicus lacking. The shell dimensions: height: 6 - 9-11, breadth: 5 - 7 - 8. The shell colour greywhite to greenishyellow, commonly with a thick layer of a dark, sometimes black sediment: organic debris or calcareous algae.

The shell shows a conspicuous sexual dimorphism in the outline of the outer edge of the mouth (Figs 31,7 - 31,12). In females (Figs 31,10 - 31,12) the edge straight, while in males (Figs 31,7 - 31,8) protruded forming an obtuse angle in the middle part, less distinctly marked however, than in the figures by Krause (1948), and some protrusion of the edge observable also in females (Fig. 31,9).

The variability rather high, expressed in the size, wall thickness, spire height and mouth shape. Its character, seemingly, partly both ecophenotypical and geographic.

C - The variability range with a complete continuum of forms within the extremal ones given below:

- f. berolinensis Westerlund - the shell thin-walled, the mouth without or almost without the angle, North Germany.

- f. alatus Westerlund - the shell heavily thick-walled, the mouth protruded upwards into the well marked acute angle.

D - The head (Figs 31,13 - 31,17) rather intensively pigmented, with the elongate snout and long tentacles intensively pigmented at the dorsal side. The eyes in the eye stalks, small and often with orange pigmentation.

E - The number of ctenidium lamellae showing relatively little correlation with the gastropod size: males: 27 - 30, females: 32 - 37.

F - The osphradium big, strip-shaped.

G - The radula described by Falniowski (in press).

H - The prostate big, vas deferens leaving the prostate big and almost straight.

I - The penis (Figs 31,18 - 31,22) uni-armed, straight, with no outgrowths, very big and massive, triangular in outline. The

triangle base broad and its proportions variable, probably due to various contraction. Dorsally, along the middle of the penis, a wide belt of dark pigment.

J - The female reproductive organs (Fig. 31,26) described by: Krause (1948); Radoman (1966, 1973); and Bole (1981). The loop of the oviduct poorly thickened and forming a characteristic triangle ventrally adjoining to the oviduct accessory gland complex. Both the big, elongate receptaculum seminis and the big, slightly arched bursa copulatrix with a poorly distinguishable duct, sunk in the tissue of the accessory gland complex. The characteristic are: the arrangement of the oviduct loop, receptaculum and bursa reciprocally positioned (Figs 31,23 - 31,25), particularly the oviduct running seemingly along the extension of the duct of the receptaculum.

K - In Poland this species records from: Pomerania, Masuria, Suwałki Lakes, Wielkopolska, Kujawy, Mazowsze, Podlasie, and Sub-Carpathian Lowlands (Urbański 1947); occurrence in great rivers as the Vistula, Bug, Oder, Warta, Noteć and Obra, also in Zalew Wiślany (Vistula Lagoon) and Zalew Szczeciński (Oder Lagoon). Till now, due to a considerable river pollution, at most of the stations the gastropod has disappeared and become a rare species.

Actually the still existing stations are only: the station in the Drwęca River (Drozdowski 1979), at Lubicz, as well as found by myself: the Bug River at Serpelice and near Siemiatycze, the Wieprz River near Lublin, the Rega River at Trzebiatów and its mouth at Mrzeżyno. *L. naticoides* was also recorded from a large flow lake Jeziorak (Masurian Lakes) but due to my researches in this lake the records may have been a result of an erroneous identification of a specimen of Bithynia tentaculata f. ventricosa Menke with an extremely low spire and swollen mouth.

GENEUS POTAMOPYRGUS STIMPSON, 1865

12. Potamopyrgus jenkinsi (E. A. Smith, 1889) f. A. Warwick, 1952

A - Hydrobia jenkinsi E.A. Smith, 1889

Paludestrina jenkinsi (E.A. Smith, 1889)

Hydrobia ventrosa var. carinata Marshall, 1889

Potamopyrgus crystallinus carinatus Marshall, 1889

Warwick (1952, 1969) described three forms: strains A, B and C, differing in the shell shape, pigmentation pattern, radula, penis and electrophoretic characters (Warwick correspondence contact). While the shell is poorly distinct and the variability continuous (Winterbourn

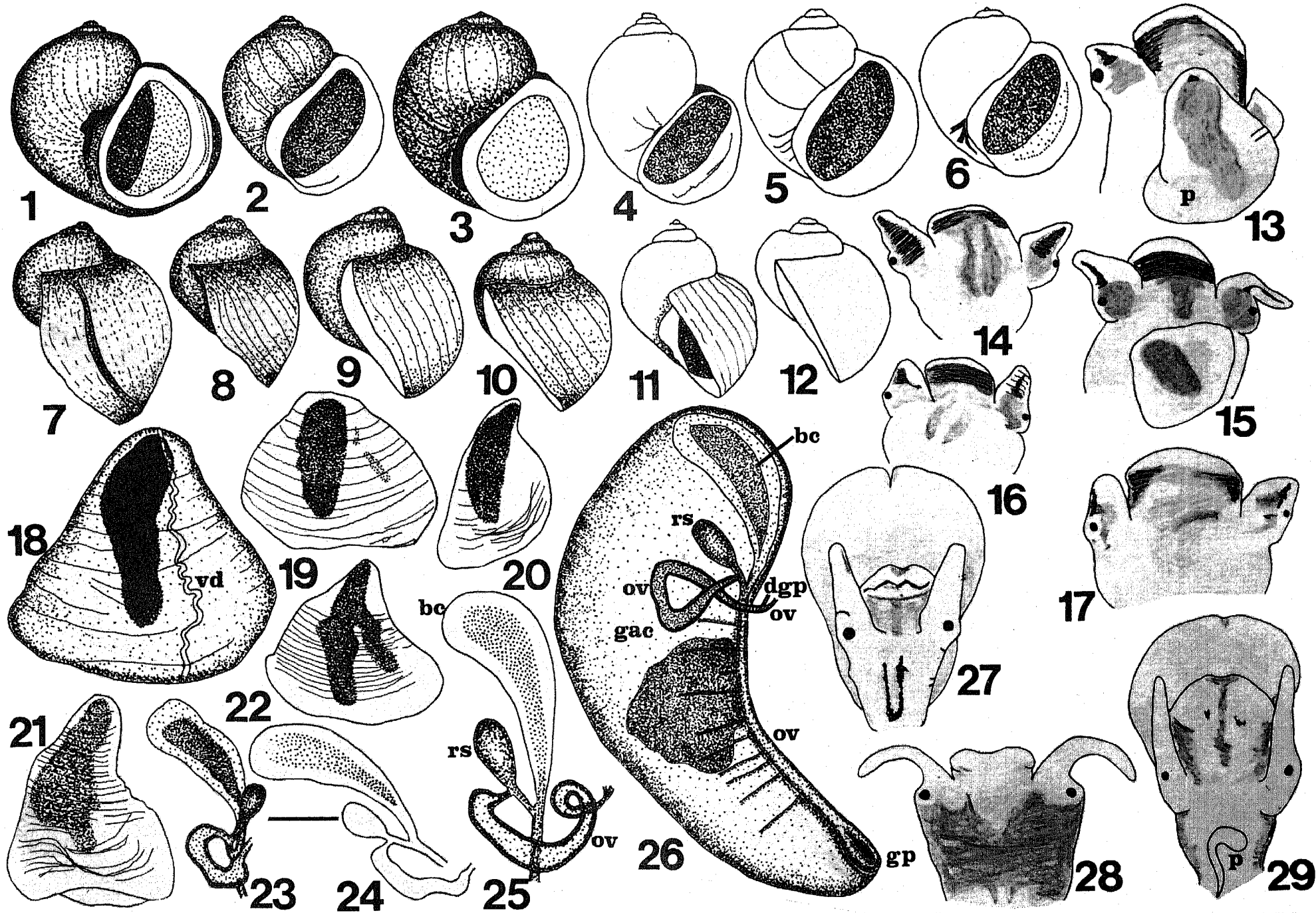


Fig. 31.1 - 26 *Lithoglyphus naticoides*: 1, 6, 7, 12 - 14, 17, 22 - 25 - Bug River at Serpelice; 2 - 4, 8 - 9, 11, 16, 18, 26 - Rega River at Mrzeżyno; 5, 10, 15, 19 - 21 - Bug River at Siemiatycze: 1 - 2 - males, 3 - 6 - females; 7 - 12 - sexual dimorphism of the shell: 7 - 8 - males; 9 - a female with an untypical mouth, resembling a male; 10 - 12 - typical females; 13 - 17 - head pigmentations: 13, 15 - males; 14, 16 - 17 - females; 18 - 22 - penes; 23 - 25 - loop of oviduct, recep-
 tulum seminis and bursa copulatrix (24 - artificially arranged specimen 23 to show the structure); 26 - distal section of female reproductive organs. 27 - *Marstoniopsis scholtzi*, female head pigmentation, Gardno Lake, 28 - 29 - *Potamopyrgus jenkinsi*, head pigmentations: 28 - a typical, parthenogenetical female; 29 - the only Polish male. Sarag Lake, Pasłęka River outflow (after Falniowski 1979)

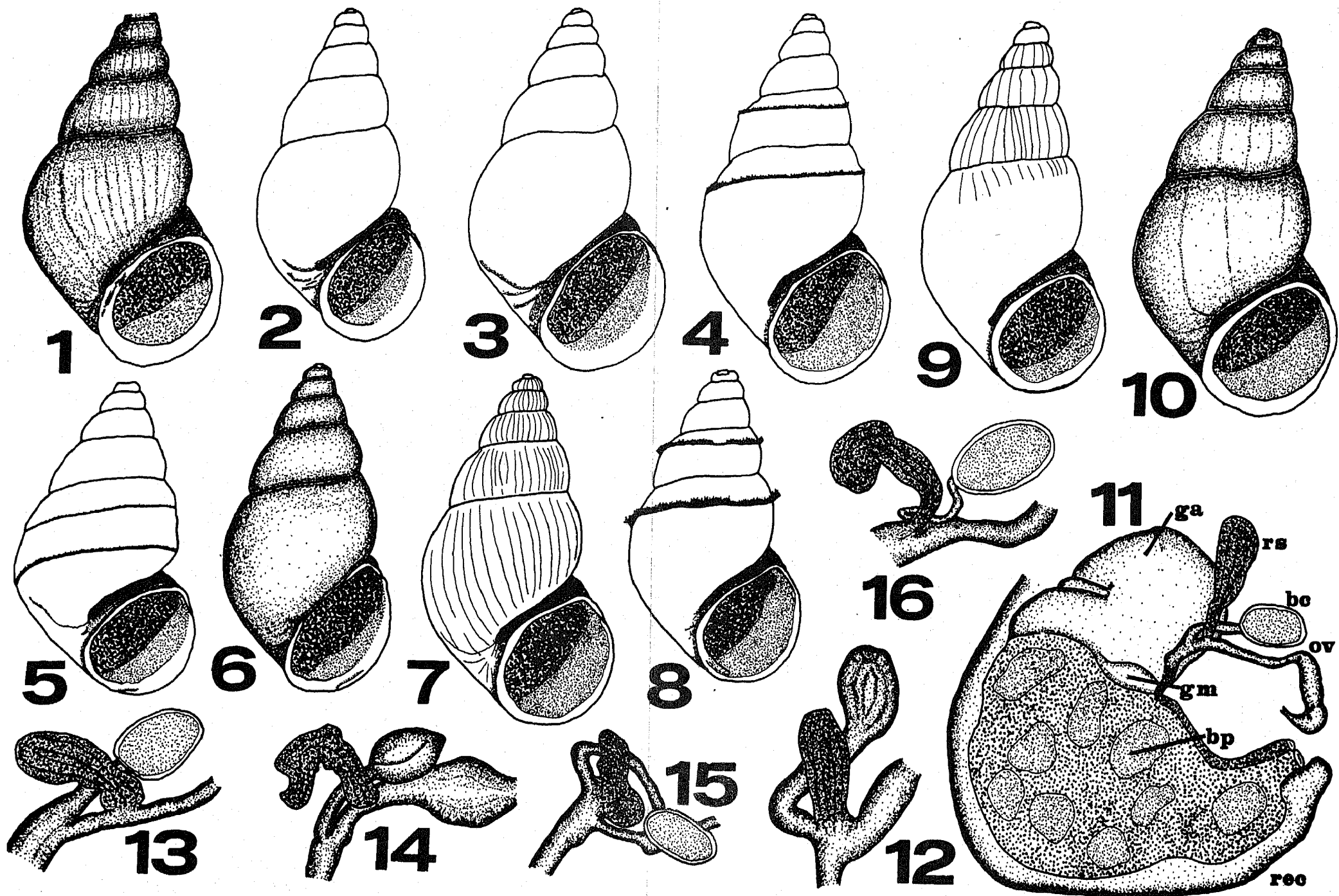


Fig. 32. *Potamopyrgus jenkinsi*: 1 - 10 - shells: 1 - 2 - Sarag Lake; 3 - 5 - Jeziorak Lake; 5 - 8 - Gardno Lake; 9 - 10 - Wielkie Lake near Poznań; 11 - 16 - reproductive organs of parthenogenetical females: 11 - distal section, Gardno Lake; 12 - 16 - loop of oviduct, receptaculum seminis and bursa copulatrix: 12 - 13 - Sarag Lake, 14 - Gardno Lake, 15 - Jeziorak Lake, 16 - Głębokie Lake by Szczecin

1972, Simpson 1976), the other features indicate the specific separate-ness of these forms. In Poland there occurs only the strain A different from P. jenkinsi s. stricto (strain B; all the specimens were examined by dr. T. Warwick). Until it has been described by Warwick as a new species I shall name it P. jenkinsi f. A. The description in this paper covers all the three strains.

B - The shell (Figs 32,1 - 32,10) conical, slim, rather thick-walled and strong, with a high spire. The whorls number 5 1/2 - 6, exceptionally 7, whorls poorly or moderately convex and divided by a moderately deep suture. The whorls growing quickly and regularly, the body whorl high. The apex sharp and symmetrical. The aperture ovate, with an obtuse, moderately marked angle, equals about 2/5 of the shell height. The parietal lip well developed and protruded, usually separated from the body whorl by a marked slit. The outer lip delicate, poorly thickened. The umbilicus covered by the parietal lip. The shell dimensions: height: 4 - 5 - 6, exceptionally: 6.5; breadth: 2.4 - 2.8 - 3, exceptionally: 3.5. The shell cleaned of dark sediment is smooth, glossy and translucent, yellowish- or reddishhornbrown, sometimes creamy or whitish.

The shell variability considerable, covering its dimensions, proportions, whorl convexity and suture depth, as well as the shape and extent of the protrusion of the body whorl; also the occurrence and form of the keel (bristles). The keel, if present, runs from the third whorl parallelly and close to the suture, in the form of a row of tiny bristles fused into a continuous, more or less distinct fold. In some cases instead of or along with the keel there is a row of large, distinct bristles; exceptionally the similar but much less developed structures may occur parallelly to the keel. The entirely conchioline keel (Falniowski in press) is produced by a small, blunt appendix of the mantle edge (Fretter and Graham 1962). There are distinguished 3 forms of various ornamentation:

- f. ecarinata Jenkins - the shell smooth, neither the keel nor bristles present; the form conspicuously most common and numerous in my materials from Poland, at many stations the only present what is confirmed by: Urbański (1938); Réal (1973); Berger and Dzięczkowski (1977) and Wallace (1979);

- f. carinata Marshall - the more or less distinct keel on the younger whorls, no bristles; in Poland on numerous localities, though never as the dominant;

- f. aculeata Overton - on the younger whorls there is a row of individual, well marked, often giant and massive bristles, among which the keel may occur, as well; from Poland only a single, empty shell has

been recorded from Puck Bay (Falniowski, Dyduch and Smagowicz 1977).

The keel determination, although studied for many years, is still unclear. The keeled form was found earlier than the smooth one and all the older records, both from the British Isles and from Belgium (Fretter and Graham 1962), mention the keel among the diagnostic characters. *P. badia* is always keeled (Boettger 1951). Bondesen and Kaiser (1949) suggest that the keel was diminished when the gastropod invaded freshwater. Laboratory studies (Robson 1926; Boycott 1929; Seifert 1935; Warwick 1944, 1952, 1969; Boettger 1949) showed a partial relation between the occurrence of the keel or bristles and the environmental conditions, what is confirmed by the field studies. The relationship between the occurrence of the keel and water salinity or pollution was often stressed. Boettger (1949) regarded the keel as an effect of the influence of the factors such as: food, water oxygen content, temperature, and pH. Warwick (1952) observed a partially genetic background of the keel determination (e.g. various frequency of the keeled or bristled specimens in various strains) and its partial relationship with the occurrence of algae metabolites in water. In his later paper (1969) he concluded that the keel or bristles are formed as soon as the occurrence of humous substances in water or food is sufficient. In natural conditions some source of these materials are fallen leaves of trees as well as dead stalks and leaves of *Carex* spp.

C - All the strains (A, B and C), potentially distinct species, co-occur in the River Tay (Simpson 1976), but usually the differences between their habitats may be pointed out. In Great Britain A and B may coexist in brackishwaters, but usually B dominates and may step by step eliminate form A completely (Warwick correspondence contact).

- *Potamopyrgus jenkinsi* s. *stricto* (strain B Warwick)

The specimens similar to those found in the Thames estuary (locus typicus), with the whorls relatively convex and divided by a rather deep suture, growing rapidly a stout shell. The mantle pigmented intensively dark, the dense patch of pigment near the eye. The penis complex (Warwick correspondence contact). In Western Europe usually limited to brackish water and freshwaters of the coastal zone, rarely found in the inland localities. From Finland to the Mediterranean coast of France (Warwick 1969). In spite of some variation in shell shape, the taxon not polymorphic (Warwick 1969). Populations with well marked keels rare. Usually all specimens in a population smooth or the keel present only as a line in a low proportion. It bears a distinct resemblance to *Potamopyrgus* species from SE Australia, Tasmania and New Zea-

land, however, it differs from those Australian species in some characters.

- *Potamopyrgus jenkinsi* f. A (strain A Warwick)

The shell slimmer and more elongate, with the whorls distinctly less convex, somewhat flat and growing less rapidly; the suture shallower. The mantle colouration and the patch near the eye much paler. The penis simple, with no outgrowths (Falniowski 1979). The shell ornamentation as in strain B. This strain is the most common and widespread form of *P. jenkinsi* in Europe. In Western Europe characteristic mainly of inland waters, where usually the only form. Found also in brackish waters, can withstand up to 19% seawater (Warwick 1969). In Poland the only form of *P. jenkinsi*.

- *Potamopyrgus jenkinsi* f. C (strain C Warwick)

The shell as in f. B or medium, between f. A and f. B. The black pigment patch near the eye as in f. B, though the mantle pigmentation different: the pale ground colour with numerous irregular patches of a darker pigment which develop with age (Simpson 1976). The penis complex (Warwick correspondence contact). The form characteristic of the highest proportion of keeled specimens, with the keel in the form of a row of bristles (*f. aculeata*). It is noteworthy that f. C may be hardly distinguishable from f. B, differing in the mantle pigmentation and the occurrence of bristled specimens; its specific distinctness suggested by Warwick rather doubtful. The rarest form, recorded from coastal streams in Wales, Ireland, Kent and East Anglia, as well as from a couple of localities near Biarritz (Bay of Biscay), France. In Derbyshire occurring inland. The type of distribution like that of *P. jenkinsi* s. *stricto*.

D - The head pigmentation described by: Robson (1920); Fretter and Graham (1962); Muus (1967); Warwick (1969); Graham (1971). In Polish females (Fig. 31,28) the head colouration and pattern rather variable, usually blueishgrey and regular, the head and tentacles commonly unpigmented what contradicts literature data. The head of the only Polish male (Fig. 31,29) poorly pigmented; the snout and tentacles more massive than in females.

E - The ctenidium is considerably elongate; with short and straight lamellae. Robson (1920) recorded 27 - 30 lamellae, Giusti and Pezzoli (1984): 26 - 27. Four selected Polish stations: Głębokie Lake by Szczecin: 22; Jeziorak Lake (Masurian Lakes): 29 - 32; Sarag Lake (Masurian Lakes): 18 - 32; brackish waters: 28 - 36. Mean values: 22.0; 30.5; 24.7; 30.9 for Polish stations respectively. In *f. carina-*

ta, common in Jeziorak Lake and in brackish waters, the mean lamellae number is somewhat higher.

F - The osphradium elongately ovate with a dark border of various width, lacking notches.

G - The radula described by: Muus (1967); Nordsieck (1972); Falniowski, Dyduch and Smagowicz (1977); Giusti and Pezzoli (1984); Falniowski (in press).

H - The first male of this parthenogenetic species was found by Patil (1958) in the Thames at Sonning. The shell of this male was of similar size as those of parthenogenetic females and keeled. The reproductive organs were with a big prostate, but without an extra outlet of the vas deferens to the mantle cavity; they contained regularly developed spermatozoa. For a long time it was the only known male specimen of this species. Wallace (1979) during her studies on *P. jenkinsi* from England, Scotland, Wales and the Netherlands found 101 males of this species, among which 65 with keeled or bristly shells and 36 with smooth shells. 94 of them were from Wales, 6 from the Netherlands and 1 from Scotland. In spite of her thorough researches she did not find any male in England, including the Thames at Sonning. She found a statistically significant difference in shell size between smaller males and bigger females, as well as somewhat different shell proportions.

One male of f. B was found by Butot in the Netherlands; Warwick found 2 males of the same form in small streams in the Isles of Scilly, several miles from Land's End, Cornwall (Warwick correspondence contact). In some populations besides smaller males there also occur ones in size similar to females.

The only Polish male specimen was found in the outflow of the Pasłęka River from Sarąg Lake (Falniowski 1979). It resembled females in size, its shell was smooth, the reproductive organs fully developed, with a big, yellowish prostate, similar to those described by Patil (1958). It belonged to f. A, as those 5 collected by Wallace in a brackish pond near Dunbar, Scotland, East Coast (Warwick correspondence contact).

The data above seem to suggest that sexual breeding may be in some cases not all that rare in this species. This would account for the great variability and adaptive capacity of this eurytopic species, hard to combine with an assumption of the complete lack of recombination in the reproductive process. Under new, difficult conditions males probably begin to occur more frequently, sexual reproduction takes place, and it is only the better adapted form, the result of genetic recombina-

tion, that settles the given area. This opinion is supported by numerous data from the literature on the high mortality of *P. jenkinsi* transferred to other conditions different from those occurring in their original environment, when confronted with a rapid spread in practically any type of habitat.

I - The penis of f. A (Fig. 31,29) small, simple, slim, with no outgrowths (Falniowski 1979), in the form of an elongate and sharpened cone, resembling the penis of *P. antipodarum* (Gray, 1843) from New Zealand (Winterbourn 1970).

J - The female reproductive organs described by: Robson (1920), Fretter and Graham (1962), Giusti and Pezzoli (1984). The albuminoid gland big, beside it a small mucous gland, instead of the nidamental gland a big brood pouch (Fig. 32,11). The loop of the oviduct (Figs 32,12 - 32,16) only slightly thickened; the bursa copulatrix usually with a distinguishable duct, unpigmented and translucent, the receptaculum seminis very large, tube-shaped, usually bent and crossed with the duct of bursa. Both the bursa and the receptaculum developed typically of sexually breeding gastropods, although they usually do not function normally. This also seems to confirm that parthenogenesis is facultative in *P. jenkinsi*. Giusti and Pezzoli (1984) figure the organs of an Italian specimen with the bursa and receptaculum conspicuously different; they do not precise to which form the specimen studied belongs.

K - The present range of the species in Europe covers the area from North-Western Spain and South France to Orkneys, Ireland, Hebrides, North-Western Jutland, the Rhone catchment basin, Finland, Baltic republics of USSR and Western part of the Russian FSSR, North and a part of Central Poland.

In Poland in the brackish water of the Baltic (presently it seems to be rare there), in coastal water bodies along the Baltic coast (except for heavily polluted lagoons: Zalew Wiślany and Zalew Szczeciński), and also in almost the whole Wielkopolska, West Pomerania, Kujawy, Masuria, Suwałki and Augustów Lakes (I collected it, for instance, in Wigry Lake), Ziemia Lubuska.

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Streszczenie

Hydrobioidea Polski (Prosobranchia: Gastropoda)

Praca omawia polskie Hydrobioidea, zarówno słodkowodne jak i morskie. Autor zwraca uwagę na bardzo słaby stopień poznania tych ślimaków w Polsce, pozostających właściwie poza zakresem zainteresowań badaczy. Część ogólną otwiera krótkie omówienie pozycji systematycznej i pokrewieństw w obrębie polskich Hydrobioidea. Autor przedstawia w zarysie systemy różnych badaczy i wskazuje, że zadowalającego, współczesnego systemu tych ślimaków brak. Proponowany przez autora system, ograniczający się do Hydrobioidea Polski przedstawia tabela I.

Autor zamieszcza krótką charakterystykę morfologiczno-anatomiczną przedstawianych ślimaków, zwracając uwagę na cechy przydatne w systematyce na poziomie gatunku. Następny rozdział poświęcony jest rozmnażaniu. Po przedstawieniu historii sporu o występowanie i długość życia larwy veliger u Hydrobia ulvae autor krótko opisuje jaja i kokony, płodność, okres rozrodu, a także długość życia polskich Hydrobioidea. Kolejny rozdział omawia odżywianie. Po ogólnych uwagach dotyczących odżywiania detritusem, autor zamieszcza (zestawioną głównie w oparciu o dane z literatury) listę pokarmu polskich Hydrobioidea, a następnie, na przykładzie bałtyckich Hydrobia, omawia wymijanie się niszy pokarmowych bliskich sobie gatunków, współwystępujących w warunkach naturalnych.

Po przedstawieniu pasożytów i zmian, wywoływanych przez nie u żywicieli, zwłaszcza gigantyzmu, autor omawia kolejne czynniki siedliskowe: zasolenie (wyróżniając ślimaki typowo słodkowodne, słonawowodne, słonawowodno-morskie i słonawowodno-słodkowodne), zawartość tlenu w wodzie, pH, twardość, temperaturę, ruch wody, stabilność siedliska, podłoże i roślinność (wymienia rośliny, których związek z występowaniem poszczególnych gatunków był wskazywany w literaturze). Autor wskazuje, że wszystkie te czynniki niejednokrotnie nie określają w sumie obecności lub braku poszczególnych gatunków na stanowisku i często nie wśród nich szukać trzeba czynników decydujących. Oprócz istotnego znaczenia historii słodkowodnych siedlisk, autor zwraca uwagę na niemałe znaczenie często niedocenianej konkurencji z innymi gatunkami, co omawia na przykładzie bałtyckich Hydrobia. Następnie krótko przedstawiono oddziaływanie antropopresji na ślimaki z nadrodziny Hydrobioidea.

Kolejny rozdział omawia sposoby ekspansji tych drobnych ślimaków, bynajmniej nie tak ograniczone jak mogłoby się to wydawać. Następnie autor wskazuje gatunki rzadkie, gatunki występujące masowo, niezbyt masowo i nielicznie, a także omawia tworzenie agregacji u niektórych polskich przedstawicieli Hydrobioidea. Rozważania o ekologii zamyka zestawienie siedlisk poszczególnych gatunków.

Następny rozdział omawia pochodzenie polskich Hydrobioidea. Hydrobia uznano za element atlantycki, Bythinella za alpejski i relikty epoki lodowcowej. Wskazano trudności ustalenia pochodzenia Bythinella i blis-

kiego im Marstoniopsis scholtzi, Lithoglyphus naticoides, element pontyjski, dokonał ekspansji której historię przedstawiono, podobnie historię ekspansji Potamopyrgus jenkinsi najprawdopodobniej pochodzącego z Nowej Zelandii. Część ogólną zamykają krótkie wskazówki dotyczące metod zbierania, konserwacji i badania przedstawicieli Hydrobioidea oraz klucz do rodzajów i zestawienie skrótów anatomicznych używanych w opisach rycin.

W części systematycznej opisano krótko rodzaje: Hydrobia i Bythinella i zamieszczono w obu przypadkach klucze do gatunków. Opisy pozostałych rodzajów, reprezentowanych w polskiej faunie przez pojedyncze gatunki, pominięto. Dla wszystkich 3 Hydrobia z polskiego Bałtyku (*H. ulvae*, *H. ventrosa* i rzadka *H. Neglecta*) omówiono wielką zmienność muszli niemal wykluczającą tę strukturę jako kryterium taksonomiczne. Opisano pigmentację głowy, budowę prącia i żeńskich narządów rozrodczych. Wskazano na brak istotniejszych różnic w stosunku do opisów z literatury oraz badanych okazów spoza Bałtyku.

Zwrócono uwagę na kontrowersyjność stosunków systematycznych w obrębie rodzaju Bythinella, ogromną zmienność muszli (niemal zupełnie nieprzydatnej dla systematyki), a także innych struktur, wynikającą stąd płynność cech i duże trudności, zarówno taksonomiczne jak i nomenklatoryczne. Za najlepsze cechy uznano wykształcenie torebki kopulacyjnej wraz z przewodem i receptaculum seminis oraz pokrój prącia, za pomocnicze - pigmentację głowy, pokrój osphradium, ktenidium i flagellum, czasem - także muszli. Podkreślono, że oznaczenie gatunku Bythinella = ustalenie najczęstszych przedziałów zmienności co najmniej 2 cech u serii okazów. Zwrócono uwagę na przypadki sympatycznego występowania 2 gatunków Bythinella i zmienność geograficzną o charakterze klinalnym, co przeczy kluczowości izolacji geograficznej jako czynnika specjacji.

Wyróżniono 6 gatunków Bythinella: B. austriaca, B. cylindrica, B. zyvionteki, B. metarubra, Bythinella sp. (określona tak chwilowo do czasu poszerzenia danych o zmienności i zasięgu) oraz B. micherdzinskii. Wszystkie te gatunki omówiono w aspekcie cech charakterystycznych oraz zmienności: muszli oraz morfologii i anatomii części miękkich.

W podobny sposób przedstawiono Marstoniopsis scholtzi, Lithoglyphus naticoides i Potamopyrgus jenkinsi. U tego ostatniego zwrócono uwagę na niejasność stosunków systematycznych w obrębie europejskiego Potamopyrgus, reprezentowanego w Polsce wyłącznie przez P. jenkinsi f. A nieidentyczną z P. jenkinsi s. stricto. Omówiono też występowanie osobników o muszli z kilem i/lub kolcami oraz najnowsze dane o trafiaaniu się niekiedy samców u tego partenogenetycznego gatunku.

